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Multispecies Models Relevant to Management of Living Resources

A Symposium held in The Hague, 2–4 October 1989

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

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Co-edited by N. Daan and M.P. Sissenwine

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MULTISPECIES MODELS RELEVANT TO MANAGEMENT OF LIVING RESOURCES

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Multispecies Models Relevant to Management of Living Resources

Preface

Scientific quality is undoubtedly the most important aspect of a contribution to a symposium, but the value of a contribution is also greatly heightened by a vivid and stirring presentation, and the discussion it stimulates. In order to underline the importance of the latter in communicating scientific results, it was decided to give awards for the "best presentations". On the basis of a plenary vote, the awards were presented to H. Gislason (paper) and to M. Tasker, R. Furness, M. Harris, and R. S. Bailey (poster) for their excellent use of audiovisual aids.

The Co-conveners would like to express their gratitude to J. Harwood (UK), A. Laurec (France), J. G. Pope (UK), and H. Sparholt (Denmark), who put great effort into the organization of the Symposium as members of the Steering Committee. In addition, they would like to thank the referees of the papers selected for publication for their invaluable contribution and expertise in formulating many suggestions for improvement. It seems only appropriate that the names of these scientists be listed here: R. S. Bailey, N. J. Bax, W. Brugge, S. Clark, E. B. Cohen, W. Dekker, W. Gabriel, S. Garcia, H. Gislason, J. Gulland, T. Helgason, J. R. G. Hislop, M. Holden, E. Houde, G. R. Lilly, J. McGlade, G. Magnusson, R. Marasco, B. M. van der Meer, S. Mehl, B. Mesnil, S. A. Murawski, W. J. Overholtz, O. K. Pálsson, D. Pauly, E. K. Pikitch, J. G. Pope, J. E. Powers, J. C. Rice, A. Rosenberg, B. J. Rothschild, K. J. Sainsbury, F. M. Serchuk, T. Smith, H. Sparholt, W. Stobo, K. J. Sullivan, and C. Tucker.

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Dedication to Jenne Johan Zijlstra (11 May 1926 – 2 August 1989)

Jenne Johan Zijlstra was born in Groningen in the Netherlands, where he attended school and spent his entire youth. He was a lively boy and the son of a banker.

His keen interest in the natural environment developed when he became an enthusiastic member, and soon a leader, of the N.J.N. (Netherlands Youth Society for the Study of Nature). Already at this stage he focused on animals living in wet surroundings (amphibians, crustaceans, and fishes) and made frequent trips on board shrimp boats sailing from Noordpolderzijl and fishing the gullies of the Waddensea. His love of fishing lasted throughout his life, and even during his later days he spent many free hours on the waterfront with a fishing rod.

He studied biology at the University of Groningen, where Professor Dr G. P. Baerends and Professor L. Tinbergen were his teachers. After an interruption of several years during which, as a conscientious objector, he served the nation as a nurse in a clinic, he obtained his master's degree with honours in December 1954. At the university, the foundation for his later career was laid with ethological work on cyclid fish, ecological work on the migration of chaffinches, and taxonomic work on herring.

Immediately after his final examination, in January 1955 he joined the Netherlands Institute for Fishery Investigations (RIVO) in IJmuiden, and was charged with conducting research on pelagic fish species, with emphasis on herring. His taxonomic studies were continued by sampling catches of the Dutch herring fleet at the spawning grounds. He made numerous trips on board loggers and trawlers and became a well-known and respected scientist throughout the fleet. A long string of publications originated from this work. One of his major contributions, "On the herring races spawning in the southern North Sea and English Channel" (1958), puts forward the hypothesis that the existence of different races within the North Sea stock is caused by homing to the places where the herring were hatched as larvae.

Jenne Zijlstra's herring research and publications established his reputation within the international community of fishery biologists, in which he took a very active part right from the beginning. Between his first meeting in 1956 and his last in 1988, he attended 23 ICES Statutory Meetings. He was a member of various committees throughout this period and acted as chairman of a large number of working groups, among others the Second Young Herring Tagging Working Group. In 1967 he was elected chairman of the Pelagic Fish Committee, and he served two terms as a member of the Publications Committee in 1978–1980 and 1986–1988. He was also one of the great proponents of monitoring programmes such as the Young Fish, Herring Larvae, and Young Flatfish Surveys in the North Sea, the results of which later proved to be of indispensable value for the assessment tasks of the Advisory Committee on Fishery Management.

After serving for seven years as head of the Marine Department of RIVO, he was offered the job of biological director of the Netherlands Institute for Sea Research (NIOZ) at Texel in 1972. This was a difficult decision to make because he was devoted to the field of fish and fisheries. But since he had always been keen to accept new challenges, particularly if the challenge met his zest for leading others, in the end he accepted. His energy was virtually unlimited, and even during that first year at NIOZ he found the time to bring together his fisheries work by writing his thesis, "Het Rassenonderzoek bij Haring (*Clupea harengus*) en de interpretatie van de veranderingen in de Noordzeeharingvisserij",[1] which earned him his doctor's degree on 18 June 1973.

Jenne Zijlstra's forceful personality and broad interest in fundamental research lent great momentum to the investigations conducted by the Texel Institute in the Waddensea, the North Sea, and later the oceans as well. Using his RIVO experience, the Waddensea research was intensified in order to complement the existing knowledge on phytoplankton and shellfish with data on zooplankton and pelagic and demersal fish species. For many years this research programme, with emphasis on plaice, remained Jenne's personal scientific pet. Meanwhile, he had exchanged the Pelagic Fish Committee for the Biological Oceanography Committee and his intense involvement in ICES matters remained unchanged. In 1982 he took on a major task in convening the ICES Symposium on the Biological Productivity of North Atlantic Shelf Areas, held in Kiel, and subsequently editing the proceedings published in *Rapports et Procès-Verbaux des Réunions*, Volume 183.

From the Waddensea and North Sea, the activities of the Institute and his own activities were gradually redirected to the world oceans. Larger research vessels became available and research topics were selected aimed at a better understanding of the marine ecosystems in very different areas. Among these comparative programmes, he most of all enjoyed leading the Banda Sea survey in the eastern Indonesian Archipelago during the Snellius II expedition in 1984–1985.

In recognition of his success in promoting and spreading the interests of fundamental research, he was elected to the Royal Academy of Sciences in Amsterdam in 1982; and he was appointed part-time professor in Marine Zoology in Groningen in 1986. Both positions gave him the opportunity to exercise direct influence on the organization and planning of the biological sciences in the Netherlands in general and the marine sciences in particular, much to his satisfaction.

His broad knowledge and insights in research planning were also internationally appreciated, and he became a foreign member of Die Arbeitsgruppe für Meeresforschung in the Federal Republic of Germany. Together with the staff of the Alfred Wegener Institute for Polar Research in Bremen, he made extensive plans for expanding the Dutch Antarctic research programme. His desire to participate actively in the investigations in polar waters could not be fulfilled. After a short but severe illness he passed away on 2 August 1989 in Schagen.

With the loss of Jenne Zijlstra, marine science has lost an energetic, inspiring, and gifted scientist with outstanding initiative. Many of us have lost a faithful companion.

K. H. Postuma
Santpoort, The Netherlands

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[1] Racial investigations of herring (*Clupea harengus*) and the interpretation of changes in the North Sea herring fisheries.

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Welcome address

M. Heuver

Director of Agricultural Research
Ministry of Agriculture, Nature Management and Fisheries
The Netherlands

Mr President, distinguished scientists,

The environment and the Living Resources contained within the environment have become central issues in the world politics of the late 1980s. Management is almost axiomatically considered to be the key to profit and welfare. Our generation cherishes a profound belief that Models represent the ultimate gate to our understanding of reality. And Multispecies is more than one species and therefore undoubtedly more sophisticated.

Thus, the topic of this Symposium on "Multispecies Models Relevant to Management of Living Resources" appears to have been very aptly chosen to attract the scientific community of the whole world. Indeed, as the program indicates, many contributors have been prepared to cross oceans in order to discuss multispecies models. There are even some of our antipodes represented in this room. Although the title of the Symposium does not preclude terrestrial and freshwater resources, it appears from the list of contributions that this particular area of research is entirely restricted to the field of marine fisheries. The more likely explanation, however, is presumably that this Symposium is organized by the International Council for the Exploration of the Sea.

Our country has kept very close connections with this renowned organization ever since our first governmentally appointed fisheries biologist Dr P. P. C. Hoek became its first General Secretary. Therefore, I am particularly pleased to welcome such a large and distinguished group of marine scientists in The Hague.

Traditionally, management of living resources in general and fisheries in particular have been largely concerned with sustainable yields in order to maximize or optimize long-term economic returns. This is not to say that in the past our common heritage has been managed very successfully in this respect. Overall, management probably deserves qualifications which range between bad and worse rather than between good and better.

Still, our society remains highly dependent on the world's living resources, both for food and, more so than ever before, for our quality of life. On a world-wide scale, human societies are increasingly faced with the effects of our negligence towards the environment. As a consequence, many of our living resources are threatened. All technological developments contributing to our welfare appear to be equally contributing to our misery, for that matter!

Marine fish stocks appear to provide a special class of problems among the Living Resources. Fishing is one of the oldest forms of utilization of renewable natural resources persisting in modern times and fisheries on a world-wide scale represent an economically viable industry and an important contribution to human welfare.

If we exclude fish farming, fishing is an extraordinary industry in that man is incapable of controlling the production process, only the amount taken, the yield. Therefore, the concept of sustainable yields has been a familiar one for a long time among scientists and managers, but in recent years severe doubts have been cast on the appropriateness of this concept.

It seems that in the past scientists and managers have been concerned too much with economic returns from a particular species and too little with the overall effects on the ecosystems which supported these resources. We have viewed our marine resources as sets of single species which could be managed on an individual basis, whereas they should perhaps be viewed as components of an ecosystem requiring integrated management.

This broader issue of Nature Management and Sustainable Development has been brought up very strongly in the Brundtland Report "Our Common Future", which was presented to the General Assembly of the United Nations by the World Commission on Environment and Development in 1987. Although anyone might agree in principle on this concept, it would seem hard to put it directly into practice.

Proper management should be based on independent science, but it is obviously much more difficult to understand the processes governing an entire ecosystem than those affecting just one species. It seems to me that you are heading for a compromise rather than trying to make the big jump in one leap: multispecies models must be somewhere in between simple single-species models and very elaborate ecosystem models.

Apart from biological interactions between species – one eating the other – I understand that there are also important technological interactions, due to the fact that many species are caught indiscriminately in mixed fisheries. These interactions – biological and technological – introduce two rather different types of problems, which obviously have to be solved before even more elaborate models can be developed.

Solving those problems will undoubtedly improve the basis for fisheries management, and that is of course your main concern. However, it does seem appropriate to draw attention to the fact that, in future, fisheries management probably has to take into account aspects of conservation of the marine environment more explicitly.

Up till now fisheries issues have been largely dealt with separately from other management issues related to the marine environment. However, there can be little doubt that fisheries interfere with other values. The marine ecosystem is an intricate one and the uses and abuses by man are manifold. Most probably, our marine environment will also be at stake, if we are not prepared to integrate various types of management of our seas.

Although fishermen may become worried if criteria other than just long-term yields are also taken into account in regulating their activities, they might actually gain in the long run. Nature Management and Sustainable Development, as defined in the Brundtland Report, do not preclude but encompass fisheries.

Ultimately, one would hope that quantitative ecosystem models would become available to serve as a basis for such an integrated management strategy on behalf of the entire marine environment. However, multispecies models clearly represent one important step forward in this direction. Hopefully this approach will widen the scope for evaluating indirect effects of fishing.

Ladies and Gentlemen,

The primary objective of a scientific symposium is to provide a forum for evaluating the results obtained so far, as well as an opportunity for free exchange of new ideas, in order to set out new buoys for future work. However, I am sure that outside this building there is considerable interest among managers, politicians, users, and environmental pressure groups in the outcome of your discussions.

Particularly in this country, which has been married to the sea for many centuries, we are looking eagerly for ways of restoring the worn liaison to a balanced partnership. The synthesis of your Symposium will help us to solve many practical problems. I wish you an interesting and productive meeting during the forthcoming three days.

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An overview of multispecies models relevant to management of living resources

M. P. Sissenwine and N. Daan

Sissenwine, M. P., and Daan, N. 1991. An overview of multispecies models relevant to management of living resources. – ICES mar. Sci. Symp., 193: 6–11.

Although multispecies models have a long history, they have had little influence on fisheries management. In general, there has been a divergence between the theorists developing the models and the fisheries scientists responsible for most data collection and the provision of fisheries management advice. The development of multispecies virtual population analysis (MSVPA) and its application by ICES scientists has gone a long way toward correcting the situation. MSVPA is an extension of single-species VPA, which treats estimated consumption by fish as part of the virtual population. MSVPA has been extensively evaluated. The method is sensitive to mean recruitment, but long-term results are insensitive to random variations in recruitment. Analyses to date indicate that the suitability coefficients of MSVPA are relatively stable, which is a necessary condition to using the method for forecasting. In addition to MSVPA, there are several other approaches for modeling biological interactions. Some models demonstrate that predator growth rate is affected by prey abundance, which is an effect that is ignored in MSVPA. Models of top predators indicate that fish consumption by marine mammals and seabirds is comparable to the amount taken by the fishery, but that most fish production is consumed by the fish themselves. Technological interaction models have many parallels to biological interaction models. For example, fishermen's preference is analogous to prey suitability. Several case studies further demonstrate the potential of multispecies models, but there are also several unanswered research questions about the models. Nevertheless, the authors believe that these models have a bright future and that it is only a matter of time before widespread multispecies management is a reality.

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Introduction

Mathematical models of multispecies fisheries have a long history. The Italian mathematician, Vito Volterra, was motivated by fish landings from the upper Adriatic to develop one of the first multispecies models. Volterra's model is among the most celebrated contributions from a period known as the "golden age of mathematical ecology". His most frequently cited paper was published by ICES (Volterra, 1928). But interestingly, multispecies models have had little influence on fisheries management. Although the quantitative population dynamics approach has been warmly embraced, attention has primarily focused on interactions between individual stocks and the fisheries that exploit them. Mathematicians and biologists in close cooperation have developed a comprehensive theory on the dynamics of exploited fish populations, culminating in the works of famous fisheries scientists such as Beverton and Holt, and Ricker.

Scientists involved in preparing fisheries management advice were, of course, aware of the interaction between species, but the general belief was that the effects of predation and competition were subordinate to the direct effects of fishing. As a result, theorists continued developing multispecies models which remained of little practical value, because of the divergence between the scientists responsible for data collection and the modelers. Neither the models nor data on species interactions proved particularly useful.

ICES scientists have played a critical role in correcting this situation by bringing multispecies models and data back together. The work of Niels Daan on feeding of North Sea cod and of Erik Ursin and Knut Andersen on a comprehensive North Sea ecosystem model, during the 1970s, set the stage for the required convergence of data and models (Daan, 1973, 1975, and Andersen and Ursin, 1977; respectively).

The comprehensive ecosystems simulation model developed by Andersen and Ursin for the North Sea was the first attempt to quantitatively describe the interactions between fish stocks, both through predation and competition, and to estimate the integrated effects of fisheries on the entire system. Although this approach had great virtues in trying to understand the causes of many changes which had occurred in the North Sea during the 1960s, a general criticism was that the model required too many untestable assumptions to be relied upon for evaluating the effects of possible fisheries management measures. However, elements of the model, such as the concept of predator-specific prey suitability, were an important breakthrough which made it possible to integrate species interaction with traditional stock assessment techniques.

A series of events beginning at the ICES Statutory meeting, in Warsaw, Poland, launched a decade of, in our opinion, unprecedented progress on the extremely complex and important problem of multispecies interactions. In fact, this example of international cooperation under the ICES banner may be a useful model to tackle other complex and important problems.

The key events were:

(1) independent contributions by Pope (1979) and Helgason and Gislason (1979) of two papers which proposed multispecies virtual population analysis (MSVPA);
(2) a meeting in 1980, convened by Niels Daan, to plan "model-driven" collection of stomach contents data;
(3) the international "year of the stomach" in 1981 which produced the data for MSVPA; and
(4) the establishment of the ICES Multispecies Assessment Working Group which developed the computational procedures and computer software necessary for applying MSVPA to the North Sea.

It is interesting that two versions of MSVPA were independently introduced, simultaneously. This truly was convergence of two schools within ICES; the multispecies and single-species schools. John Pope, who is well known for "cohort analysis" (Pope, 1972), one of the cornerstones of single-species assessments, extended his method to multispecies. Helgason and Gislason of the multispecies school simplified Ursin's approach by assuming that weight-at-age is determined exogenously.

Apart from biological interactions, the harvesting technology for many fisheries makes them multispecies. The actual species composition of the catch cannot be controlled. Therefore, the management of a fishery for one species frequently impacts one or more interacting species. Much progress has also been made in modeling these "technological interactions".

Of course, it would be incorrect to think that progress in multispecies modeling has only occurred in the ICES community. In fact, one of the reasons for a Symposium on "Multispecies Models Relevant to Management of Living Resources" was recognition that important progress is being made throughout the world.

The specific goals of the Symposium were to:

(1) encourage quantitative analyses of biological and technological interactions relevant to management of living resources;
(2) provide a forum for comparison of approaches applied both within and beyond the ICES primary area of interest; and
(3) provide a summary of the "state-of-the-art".

The Symposium was held at the Netherlands Congress Centre in The Hague, 2–4 October 1989, with M. P. Sissenwine and N. Daan as co-conveners.

We believe the Symposium was highly successful in highlighting a diverse array of approaches and important results. It also indicated important unanswered questions. The remainder of this paper provides an overview of some of the highlights and it discusses some of the unanswered questions. This overview is based on both the papers presented at the Symposium and the discussions, which were also very informative.

Highlights

Nearly 40 peer-reviewed papers from the Symposium are included in this volume. They address a wide array of topics, such as multispecies virtual population analysis, other models of biological interactions, top predators, technological interactions, and management. There are contributions from five continents, including several countries outside of the ICES community; i.e. Namibia, Senegal, Kuwait, Peru, Australia, and New Zealand.

The first section of the volume, on *multispecies virtual population analysis,* is introduced by Sparre's paper,[1] which gives the basic equations and describes how the method is derived as an extension of single-species virtual population analysis. In effect, the estimated consumption of fish is treated as part of the virtual population. This requires simultaneously solving a modified catch equation for each species within each year. Sparre also describes the strategy for estimating suitability coefficients from stomach contents data.

The most fruitful application of MSVPA, to date, has been by the ICES Multispecies Assessment Working Group (see Pope's paper). The Working Group was

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[1] The paper by Sparre was invited after the Symposium.

extremely successful in developing the computational tools to use the available data to implement MSVPA, and in digesting a tremendous quantity of output from the analysis. The results indicate that predation is a major influence on population dynamics of fish species of the North Sea. The results of MSVPA indicate that traditional single-species methods are adequate for management intended to preserve the status quo, in the short-term, although the status quo may be suboptimal. But, the effects of predation, accounted for by MSVPA (not all predation is accounted for), are important in giving medium- to long-term management advice. In particular, they indicate that for the North Sea there is much less benefit in terms of yield of reducing the fishing mortality or increasing the mesh size for fish predators than is indicated by single-species assessments. In fact, there may even be a disadvantage.

Another important result of the Multispecies Assessment Working Group is that MSVPA is very sensitive to average levels of recruitment. But long-term fisheries management advice, based on MSVPA, should be robust to variability in recruitment, even when there are cross correlations between species (see the paper by Gislason). The effects of autocorrelation in recruitment have not been examined, but one suspects them to be minor for long-term management decisions.

Another conclusion is that the suitability coefficients used in MSVPA appear to be reasonably stable over time, at least according to the available data (see the paper by Rice *et al.*). This is encouraging because if it were not so, MSVPA could not be used for forecasting. It is also intriguing to consider the possibility of taking account of the effects of spatial overlap, between predators and prey, on suitability coefficients. If this were accomplished, suitability coefficients might be more portable (i.e. applicable to other ecosystems).

MSVPA has also been applied to the Baltic Sea (see the paper by Sparholt), which is a simpler system than the North Sea. Nevertheless, the results are even more preliminary because data access has been more difficult. Perhaps the problem of data access further highlights the advantages of a "model-driven" data collection program.

Probably the most important topic considered in the section on *biological interaction* is the estimation of consumption rates which control predation mortality rate estimates from MSVPA. One approach is to use gastric evacuation rates to estimate daily ration from gut contents. Many complications need to be considered including prey size, prey type, the shape of the evacuation rate function, and the condition of experimental animals (see the paper by Bromley). The shape of the evacuation rate function is of particular importance because it influences the design of field data collection.

Several alternative approaches for estimating daily ration were also considered (see the first paper by Jarre *et al.*). For example, for diurnal, nocturnal, or crepuscular feeders, daily ration can be estimated from field data on stomach contents during the course of a 24-hour period. Once daily ration has been reliably estimated, it may be feasible to relate it to environmental factors and body shape parameters of fish.

The section on biological interactions also includes several predator–prey models for cod. The effect of cod predation on prey species is one of the primary biological interactions accounted for by the North Sea MSVPA. In addition to the effects of predation, the cod models in this section consider the "flip side" of MSVPA; i.e. the effect of prey density on cod feeding rate, growth, and production (see the papers by Mehl and Sunnanå, Lilly, and Magnusson and Pálsson). These results indicate that predator weight-at-age is not necessarily determined exogenously, as assumed in MSVPA.

Several other papers on biological interactions introduce interesting approaches. For example, heuristic multispecies models may be fit to the output of MSVPA (see the paper by Sullivan in this section and by Blinov in the section on MSVPA). The heuristic models serve as a vehicle for summarizing the very highly parameterized MSVPA into a model of a few parameters. Another advantage is that the behavior of heuristic models has been studied extensively by mathematical ecologists and heuristic models are used as the basis for bioeconomic models. Fitting heuristic models to MSVPA may help to close the gap between fisheries science, mathematical ecology and resource economics.

Another approach to investigating species interactions is multivariate statistical analysis. For example, principle components analysis was used to describe the evolution of the multispecies demersal finfish community on Georges Bank. In general, the evolution can be explained by three different eras of fishing (see the paper by Rothschild). Multivariate statistical analysis was also used to examine interactions among three pelagic species off the northeastern USA. In this case, some of the inherent difficulties of empirically assessing species interactions from time series data alone are discussed (see the paper by Fogarty *et al.*).

One paper considered the effects of the physical environment on species interactions. The paper by Jarre *et al.* models the effects of water temperature on overlap in predator–prey spatial distributions for the Peruvian upwelling system. Predation mortality is determined by both predator abundance and the degree of overlap.

The third section of the volume addressses biological interactions that involve *top predators*. Fisheries scientists usually think of marine mammals and seabirds as top predators, in addition to mankind. Clearly, there is the potential for marine mammals and seabirds to compete with mankind for fish, since the former consume comparable amounts of fish as the harvest. But the actual effect of marine mammals and seabirds on potential fish yields depends on the degree of species, size and age overlap between fisheries, and consumption by natural top predators.

Some top predators (e.g. some seabirds; see the paper by Bailey *et al.*) may have little impact on their prey, but they may themselves be sensitive to prey abundance. In such cases, top predators may serve as an indication of fish abundance, but non-linearities in the system will make it difficult to interpret the response of indicators quantitatively, relative to the prey.

One paper in this section indicated that some fish species must also be considered to be top predators. The paper by Bax reviewed the partitioning of fish production between predators including fish, marine mammals, seabirds, and mankind. Fish were the most important consumers of fish production for the six ecosystems that were considered. This conclusion also appears to hold for the Peruvian upwelling ecosystem, which was described in Jarre *et al.*'s second paper. The high internal consumption within the fish community has important implications. For example, Sissenwine (1984, 1986) noted that it is analogous to community level cannibalism, which could act to stabilize the overall fish community, but could contribute to variability in recruitment of individual species. In fact, the bioeconomic model described in the paper by Wilson *et al.* (last section of the volume) was motivated by this scenario.

It is tempting to view *technological interactions* (the subject of the fourth section) as easier to model than biological interactions, since fishing activity is easier to observe. That is, if we gather enough data, technological interaction models may be little more than bookkeeping exercises. We believe the Symposium clearly indicated that this view is extremely naive, particularly in the case of making forecasts, which will require improved understanding of fishing behavior.

A general framework for modeling technological interactions is given in the paper by Laurec *et al.* A critical element is the catchability coefficient matrix which relates fishing effort in one fishery to fishing mortality across all fisheries. Another important element is the sub-model for effort allocation within and between fisheries. For forecasting, this sub-model should include feedback between the simulated economic performance of the fishery and future effort allocation. In general, this will require that the coefficients of a "fishing preference matrix" be time invariant, just as it is necessary for suitability coefficients of MSVPA to be time invariant.

There are several papers that model technological interactions. These models capture the effects of competition between user groups. An important element is competition for different sized fish. A bioeconomic model of competition between trawlers and longliners on the Scotian Shelf (see the paper by O'Boyle *et al.*) demonstrates that the longliners are economically more efficient, but that trawlers will displace longliners by catching smaller fish before they are available to longliners. One implication is that even if property rights are assigned (for example, individual transferable quotas; see the paper by Annala *et al.*, in the last section, for a description of the method) to prevent wasteful competition for a limited amount of fish, economic benefits may be reduced as a result of competition for suboptimal sized fish.

The Symposium indicates the need to increase the collection of data to support technological interaction models. A wide variety of economics data is needed, including more disaggregated data (to individual trips or gear sets). It may be necessary, and more efficient, to collect disaggregated data as a sub-sample of data collected by traditional fisheries statistic programs.

Much more data also need to be collected at sea for estimating discard rates and for better understanding fishing operations. It is important to learn why discarding occurs (e.g. improper size, highgrading, regulations such as trip limits).

The last section of the volume addresses the *management* implications of multispecies models. Some of the papers are interesting case studies. For example, the paper by Sainsbury describes the application of adaptive management (Walters, 1986) to a tropical multispecies fishery of Australia. The approach attempts to optimize the economic return from the fishery, taking account of the value of the information gained by using the fishery to experiment with the ecosystem. One advantage of the Australian tropical multispecies fishery for adaptive management is that the fishery can be spatially partitioned into pseudo-replicates. This will be difficult for most fisheries in the ICES area.

The last paper of the volume, by Brugge and Holden, is one of the most telling. The paper considers a fisheries manager's perspective on multispecies models. Brugge and Holden feel that models of multispecies biological interactions are not useful for management because they make management more difficult. This difficulty arises from their complexity, incompleteness, and lack of credibility. In part, Brugge and Holden may be reacting to the problem managers of North Sea fisheries face as a result of MSVPA, which reverses long-standing advice to reduce fishing pressure on cod and increase mesh size. Interestingly, Brugge and Holden are more positive about the potential for technological interaction models, although many Symposium participants felt that models of technological interactions could create analogous difficulties for fisheries managers. Needless to say, Brugge and Holden's views about multispecies models stimulated a lively discussion at the Symposium.

Unanswered questions

The Symposium indicated that there has been a great deal of progress in the development of multispecies models. But, it is also clear that there is no shortage of unanswered questions. Research topics that need more consideration are:

1. Several topics concerning MSVPA, such as:
   a. Feeding sub-models. More complex feeding sub-models, including the possibility of prey density effects on suitability, need to be evaluated. More testing of the assumption of time invariant suitability coefficients is also needed.
   b. Other prey. The assumption about other prey will be more important in future applications of MSVPA, where other prey are a larger proportion of consumption than in the North Sea. At present, the choice between assumptions about other prey (i.e. constant, constant proportion of total diet, total food in the ecosystem constant) is somewhat arbitrary.
   c. Extension of MSVPA to take account of effects of predation on recruitment. MSVPA is very sensitive to mean levels of recruitment. Applications of MSVPA to date have not taken account of the effects of predation on early juveniles, larvae, and eggs on recruitment. It is unclear how far back into the pre-recruit period MSVPA can be extended. If it is extended back into the early life history, it will be necessary to consider the uniqueness of solutions, since predation mortality rates are likely to be too high to meet the condition proven to be sufficient for a unique solution.
   d. Modification of MSVPA for application to areas with limited catch-at-age data. There are some areas that have more limited catch-at-age data than the North Sea, but have extensive resource survey data (e.g. off the northeastern USA). It should be feasible to apply a modified MSVPA to such areas.
2. There is a need to develop more models that take account of the effects of prey abundance on predators. MSVPA only considers the effect of predator/prey interactions in the opposite direction.
3. It is clear that more needs to be known about consumption rates. Is the traditional approach of interpreting gut contents data based on gastric evacuation rates the best way to proceed? Can we introduce new technology for conducting experiments; e.g. marking prey with radioactive isotope tracers, soft-bodied x-rays to measure gut contents without sacrificing fish? It seems that the sophistication of models has advanced more rapidly than our techniques for collecting the data necessary to apply the models.
4. In the case of technological interactions, we need to know more about the socio-economic factors that determine fishing behavior and effort allocation, and how these behaviors relate to regulations. In particular, if we model a system with a specific description of fishing behavior which is affected by regulations, can we forecast for a new set of regulations?
5. More consideration needs to be given to the issue of "simple vs. complex". In almost every case we have to make a decision about how much complexity to introduce in our models. In some cases we may be introducing more complexity than is necessary to serve the purpose of the model, or than is useful when considering constraints on the control variables available to managers. When we introduce unnecessary complexity, we stand the chance of detracting from the usefulness of the model. That is, people may argue about details that don't really matter.

   In this regard, it is noteworthy how much more interest there has been in multispecies models on the part of traditional stock assessment researchers and managers, since the focus has shifted from the complex North Sea model to MSVPA, which is less complex.

The most emotional unanswered question from the Symposium is the usefulness of multispecies models for management, now and in the future. In general, we seem to agree that multispecies models are more realistic than single-species models – they are plausible. It is hard to justify accepting models which we know are wrong (i.e. single-species models when making medium- to long-term management decisions) because we are not sure that the alternative models (i.e. multispecies models) are right.

But it is legitimate for managers to ask if each generation of new models is converging towards the truth, in the sense of a consistent statistic, or are they just giving different answers. This is an issue scientists have to resolve. In part, it means that we need more robust models relative to management options. Maybe adaptive management can help us to determine whether we are converging or just changing.

It should also be recognized that the problem of making multispecies models useful for management is not just the responsibility of scientists. As we advance our understanding of fishery systems, our management institutions will need to evolve to use the new types of information. Bad models will not help managers. Good models are a necessary condition for good management, but they are not a sufficient condition. Management institutions that cannot use the best scientific information available need to change. But these changes will be slow, and at least some degree of inertia is probably a good thing.

In general, we are optimistic about the value of multispecies models for future management decisions. During the 1970s we recall Erik Ursin described the North Sea model to a largely uninterested or skeptical ICES audience. In 1980, when the Working Group met to plan the "year of the stomach", we remember skeptical words from the chairman of the Advisory Committee of Fisheries Management. Now, we all recognize the importance of Ursin's contribution. The point is, multispecies models are now a part of the thinking of the community of scientists that formulate advice to managers. Undoubtedly, some of these scientists will be the managers of the future. It is only a matter of time before multispecies management is reality.

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I. Multispecies virtual population analysis

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Introduction to multispecies virtual population analysis

Per Sparre

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Starting from single-species virtual population analysis, the basic features of multispecies virtual population analysis are introduced, with emphasis on the mathematical description and computational procedures.

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Introduction

Multispecies virtual population analysis (MSVPA) has been developed largely as a joint venture within the ICES Ad hoc Multispecies Working Group (Anon., 1984a, b, 1986, 1987, 1988). The method integrates the suitability concept of Andersen and Ursin (1977) for describing predator–prey relationships with traditional virtual population analysis (VPA) as developed by Fry (1949) and Gulland (1965). The first steps in this direction were taken by Helgason and Gislason (1979), Pope (1979), and Sparre (1980). For a historic review of the development of these methods the reader is referred to Pope (1991).

MSVPA takes into account predation among exploited fish populations. Essentially, it is a number-crunching exercise to estimate fishing and predation mortalities by year and age group simultaneously for a number of species on the basis of catch-at-age data and stomach-content data by age group of predator and prey.

This contribution aims at introducing the basic features of this estimation technique, with particular emphasis on the mathematical description and computational procedures. For more details on VPA, see Beyer and Sparre (1983), Jones (1984), and Sparre *et al.* (1989). Beyer and Sparre (1983) introduce MSVPA in connection with VPA.

Single-species VPA

The single-species VPA is derived from Baranov's catch equation (1918)

$$C = F \times \bar{N}$$

where C is the catch in numbers from a cohort, F is the fishing mortality coefficient, and N is the average number of survivors from the cohort.

The same mathematical expression applies in the case of the number of deaths caused by natural causes (D), i.e. all causes other than fishing (predation, disease, starvation, spawning stress, old age, parasites, etc.)

$$D = M \times \bar{N}$$

where M is the natural mortality coefficient. Figure 1 illustrates the flow of fish (number of fish) as described by Baranov's equation. The N-boxes symbolize the number of survivors on the birthday of the cohort, i.e. the number at the beginning of a period. Boxes C and D symbolize the losses in numbers caused by fishing and

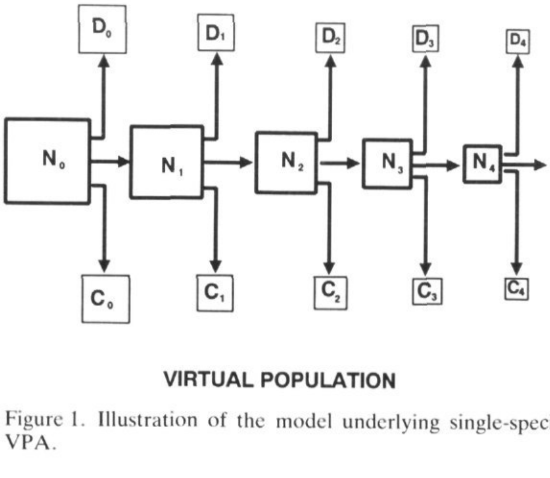

Figure 1. Illustration of the model underlying single-species VPA.

natural mortality, respectively, during each year of life. Boxes D and C are the accumulated numbers of deaths during the year and are conceptually different from the N-boxes. The "virtual population" is the C-boxes in Figure 1, that is, the part of the population one can actually see when visiting the fishing harbours. By estimating the C's from sampling the commercial landings, and assuming that M is known, N, D, and F can be calculated. With this technique, known as VPA (virtual population analysis), it can be calculated how many fish there must have been in the sea to account for the number caught.

Fry (1949) introduced the concept of "virtual population" and derived a method for estimating exploitation rate which is virtually the same as that presented by Gulland (1965) – the method usually referred to as "VPA".

One feature to be noted here is that in single species VPA each cohort can be treated separately. The results of one cohort have no influence on the results of the others. As will be shown later this is not true for MSVPA.

Single species VPA requires the natural mortality coefficient as input. The VPA equations link F and M in a functional relationship, so if M is overestimated the stock numbers (N) will also be overestimated and the fishing mortalities (F) underestimated, and vice versa.

The natural mortality coefficient is difficult to estimate for exploited fish stocks because the number of fish dying from natural causes (D-boxes in Figure 1) is difficult to observe. The traditional approach is to make a "qualified guess" for M.

For a stock assumed to be in an equilibrium situation, the total mortality

$$Z = F + M$$

can be estimated from age-frequency samples. If the stock is unexploited, then $F = 0$ and consequently $M = Z$. Thus, in this case there is a simple way of estimating M.

However, important fish stocks are usually exploited and not in equilibrium. Although we may be able to estimate Z for exploited stocks, there is no reliable way of estimating the split into M and F for individual age groups. Several attempts to devise simple methods of estimating M, based on general knowledge about the physiology and behaviour of a fish species, have been suggested. They are all indirect methods and are based on assumptions which are questionable. For a further discussion of these topics the reader is referred to Chapters 4 and 5 in Sparre *et al.* (1989).

Natural mortality occurs through a variety of causes, e.g. predation, diseases, parasites. In principle, the number of fish dying from predation by fish can be sampled by analysing the contents of stomachs of predatory fish. For young (small) fish the predation mortality is believed to be the dominating source of mortality compared to all other sources, including fishing. This idea was inspired by quantitative findings on the consumption of some predatory fish, notably, North Sea cod (*Gadus morhua*) (Daan, 1973, 1975). It was therefore natural to concentrate on the predation mortality when searching for a solution to the "M problem".

Andersen and Ursin's model

Andersen and Ursin (1977) developed the basic conceptual framework for predation which allowed extension of VPA to MSVPA. This framework was actually embedded in a general and comprehensive model of an exploited marine ecosystem.

Although a valuable model, it was not really "operational" because of the large number of parameters which were difficult to estimate. But, by removing a number of components from their model and by simplifying the remaining part of it, the bases of MSVPA are revealed.

Four alternative reductions of the Andersen and Ursin model (AU model) to an "operational model" have been suggested by Helgason and Gislason (1979), Gislason and Helgason (1985), Pope (1979), Sparre (1980), and Ursin (in Sparre, 1980). The following descriptions of the AU model refer to the predator–prey relationship, which I consider the cornerstone of the Andersen and Ursin (1977) model, and which has served as the basis for the development of the MSVPA version of this model.

The flow of biomass between components of the ecosystem is illustrated in Figure 2. The components of

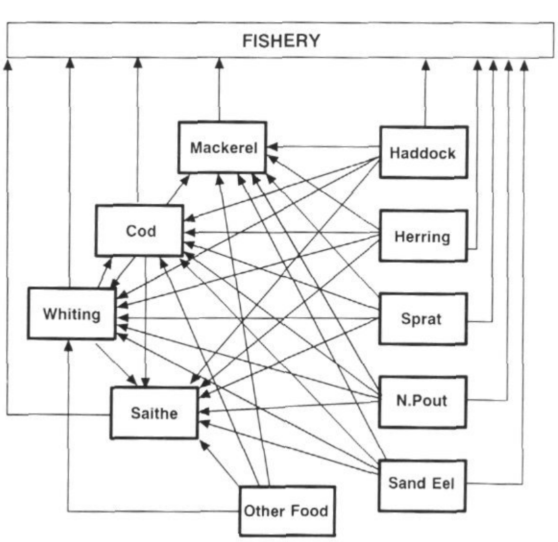

Figure 2. Flow chart of biomass between components in the AU model for the North Sea considered by the ICES multispecies working group.

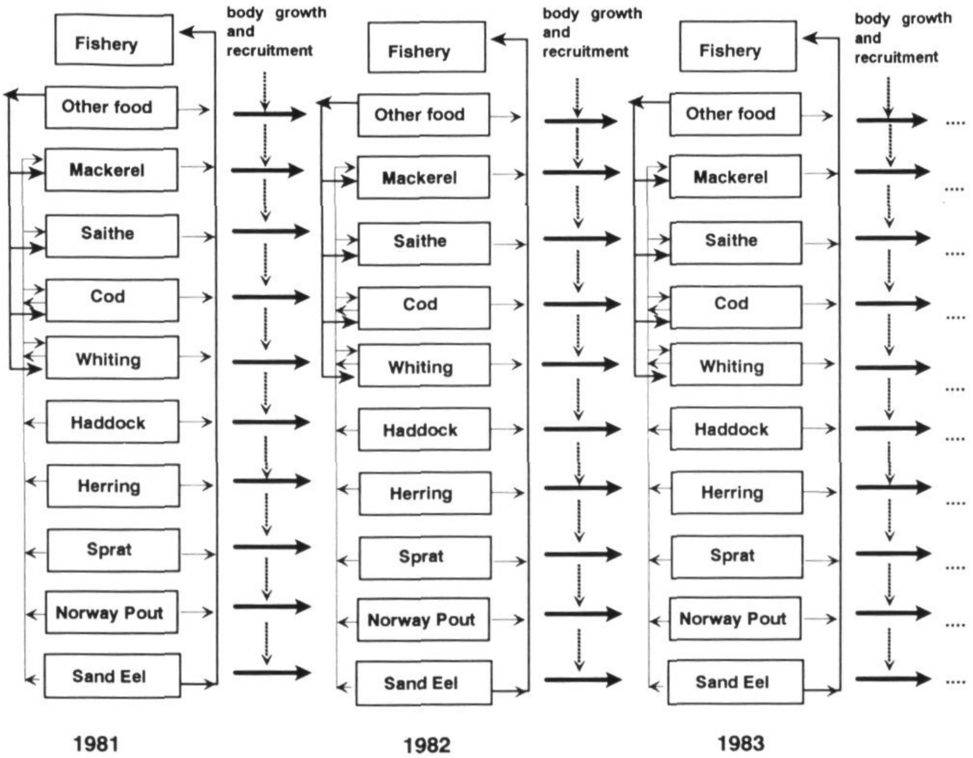

Figure 3. Flow of population numbers along the time axis in the AU model.

the North Sea considered by the ICES Multispecies Working Group (Anon., 1984b, 1986, 1987) are used as an example. Some stocks are predators only, some are prey only, and some are both predators and prey. This classification was based on the results from stomach content examinations (Anon., 1984a). In addition to exploited fish species, a category "other food" is considered, in which all other prey types are lumped together. The AU model also describes the dynamics of the system along the time axis, as illustrated in Figure 3.

The flow of numbers of fish in time is associated with body growth and reproduction (or recruitment). Although the numbers in each cohort are subsequently reduced due to mortality, the corresponding biomass may (or may not) increase due to growth of individuals. This process is linked to the age of the cohort. Thus, flows of both numbers and biomasses between components and along the time axis are described in the AU model. The AU model takes food availability into account when calculating body growth rates, whereas this aspect has been ignored in MSVPA. Irrespective of the biomass of prey the predators are assumed to have a constant growth rate in MSVP. In order to model the flows of biomass between the components, the AU model divides natural mortality into predation mortality (M2) and "other" natural mortality (M1):

$$M = M1 + M2$$

and

$$D = (M1 + M2) \times \bar{N}$$

In MSVPA the predation mortality (M2) is estimated within the model whereas M1 still has to be guessed just as M is in single species VPA. Using index p for prey species by age group the number of deaths (P) caused by predation thus becomes

$$P_p = M2_p \times \bar{N}_p$$

The total number dying from predation is further divided into the numbers eaten by each predator species age group (i):

$$P_p = \sum P_{pi}$$

and the number eaten by predator type i becomes:

$$P_{pi} = M2_{pi} \times \bar{N}_p$$

The AU model is based on the concept of "food suitability" (U_{pi}). U_{pi} is a measure of the suitability of prey p as food for predator i. The Upi's are fractions and add up to one. To define suitability, we introduce the relative stomach content, S_{pi}, which is defined as:

$$S_{pi} = \frac{\text{Weight of prey p in the stomach of predator i}}{\text{Total weight of stomach content of predator i}}.$$

S_{pi} is a measurable quantity given accurate food composition data.

The AU model assumes that the relative stomach content of prey p in the stomach of predator i is given by:

$$S_{pi} = \frac{\text{Suitable biomass of prey p}}{\text{Total suitable biomass available to predator p}}$$

or

$$S_{pi} = \frac{\bar{N}_p \times w_p \times U_{pi}}{\sum \times w_j \times w_j U_{ji}} \tag{2}$$

where w_p is the average body weight of a prey species p. S_{pi} represents a fraction, and the S_{pi}'s summed over prey (index p) add up to 1.0. Thus, U_{pi} reflects the diet composition of the predators relative to the available food.

Manly (1974) introduced a similar concept in a more general ecological context. If R_i is the total annual food consumption of predator i, then the total number of prey p eaten by predator i, P_{pi}, is

$$P_{pi} = \frac{\bar{N}_i \times R_i \times S_{pi}}{w_p} \tag{3}$$

Combining Equations (1), (2), and (3) we get:

$$M2_{pi} = \frac{\bar{N}_i \times R_i \times U_{pi}}{\sum_j N_j \times w_j \times U_{ji}} \tag{4}$$

from which the total predation mortality is obtained by summing over the predator index:

$$M2_p = \sum_j M2_{pi}$$

"Other food"

One problem faced in practice is that the data required for estimating the parameters of the AU model are available only for a limited number of stocks of major commercial interest. Thus the components of the model have to be categorized into stocks for which data are available and a residual group for which limited information is available. In the North Sea, the latter group contains mainly prey species, and was therefore called "other food".

The four alternative simplifications of the AU model mentioned above differ only in the way they treat the "other food" compartment. Pope (1979) assumed that "other food" constituted a fixed proportion of the total consumption, i.e. a fixed proportion of the stomach content stems from "other food".

Helgason and Gislason (1979) and Gislason and Helgason (1985) assumed that the biomass of "other food" in the sea remained constant. The proportion of "other

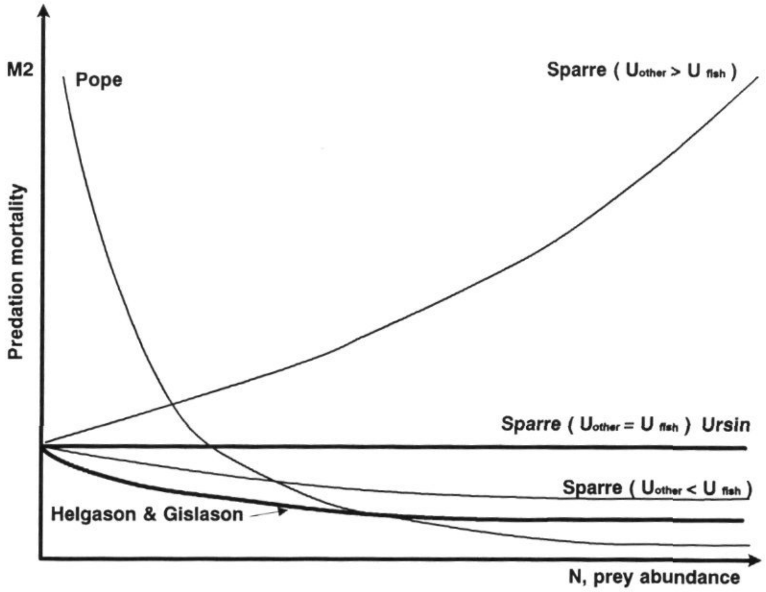

Figure 4. Predation mortality (M2) as a function of prey stock size for the four alternative assumptions on "other food" (redrawn from Sparre, 1980).

food" in the stomach contents was thus allowed to vary in accordance with the availability of the various prey species.

Sparre (1980) assumed that the total biomass of all populations in the sea (including other food) remained constant.

Ursin (quoted in Sparre 1980) suggested that the total biomass of populations weighted by their suitability (including other food) remained constant. This assumption would make MSVPA consistent with the model of food availability dependent growth rate in the AU model.

Figure 4 illustrates the differences in the four alternative assumptions in the case of only one predator and one prey. It shows how the predation mortality changes as a function of the prey abundance under each of the four alternative assumptions. It has not so far been possible to demonstrate that any one model is superior to the others. Three models were tested by the ICES NMVPA Working Group. Because of its computational complexity, Ursin's suggestion was not tested, although from a purely theoretical point of view I feel that it is the most satisfactory one, because it is consistent with the assumption on constant body growth rate in MSVPA.

Multispecies VPA

MSVPA is a computation technique by which we can calculate the amount of fish there must have been in the sea to account for the observed catches in fisheries and the observed stomach contents of predators. A basic assumption is that suitabilities are constant from year to year. Figure 5 summarizes the MSVPA in terms of input and output as explained in the foregoing sections.

One principal difference compared to VPA is, of course, that MSVPA deals with several stocks at a time. MSVPA executes a series of parallel linked VPAs.

In single species VPA each cohort can be treated separately, the results being independent of the results of the other cohorts. The usual procedure is to work backwards in time, starting with the oldest age group and ending with the recruits. For MSVPA this would not work. All cohorts of all species have to be dealt with simultaneously, as the value of the predation mortality depends on the abundances of predators and prey. Thus MSVPA works on a "by-year basis" rather than on a by-cohort basis.

The technical computation problem in MSVPA is that: (1) To calculate the numbers in the sea from the catches and from the stomach contents of predators, fishing mortalities and predation mortalities must be known. (2) To calculate the predation mortalities the number in the sea and the suitability coefficients must be known (cf. Equation (4)). To solve this complex of problems, we start by assuming that the suitability coefficients are known. This implies that if the N's are known we can calculate the M2's using Equation (4). Once the M2's are known the N's and the F's can be calculated using single species VPA techniques. However, since the N's are not known, this problem can only be solved using iterative techniques.

An initial guess on the M2's allows us to make a first estimate of the N's. With these N's and the given suitability coefficients, new values of M2 can be calculated using Equation (4), which in turn can be used to estimate new values of the N's. The process is repeated until two consecutive iterations converge to marginally different M2 values according to predefined criteria.

The iterative procedure illustrated in Figure 6 deals with one year's data at a time only. Thus, the process has to be repeated for each year of the time series considered.

The computation procedure involves in fact two iterations, as illustrated in Figure 7. The "inner" iteration deals with the solution of the catch equation for given M in respect of F, i.e. to solve $C = F \times \bar{N}$ for F. As N is a non-linear function of F (i.e. $\bar{N} = N(1 - \exp(-F - M))/(F + M)$), it can only be derived through iteration.

The second iteration deals with the estimation of the M2's. The procedure is repeated for each data year starting with the most recent data year and proceeding backwards in time, just as in traditional VPA.

Thus, if the suitability coefficients were known the MSVPA could now be run. However, since they are not known an extra iterative procedure on top of the MSVPA iteration is required. To introduce the "suitability iteration", we first show how the suitability coefficients can be derived from the observed stomach content data under the assumption that stock numbers are known. It can be shown algebraically that Equation (2) together with $\Sigma U_{pi} = \Sigma Spi = 1.0$ implies that (Sparre, 1980):

$$U_{pi} = \frac{S_{pi}/\bar{N}_{pi} \times w_p)}{\sum S_{ji}/(N_{ji} \times w_j)} \qquad (5)$$

Thus, if the N's are known the U's can be calculated, as the S's are given by the stomach content data.

Equation (5) is the key formula in MSVPA, which turns the AU model into an estimation technique: It converts stomach contents into suitability coefficients, which in turn may be used to calculate mortalities.

The estimation of suitability coefficients is illustrated by a small hypothetical example in Tables 1A–D. The computation presented in this table corresponds to a single step in the iterative procedure described below. The example deals with three species with 3, 2, and 3 age groups respectively, as shown in Table A. We assume that the values in column N are derived from the MSVPA iteration procedure described above. Weights

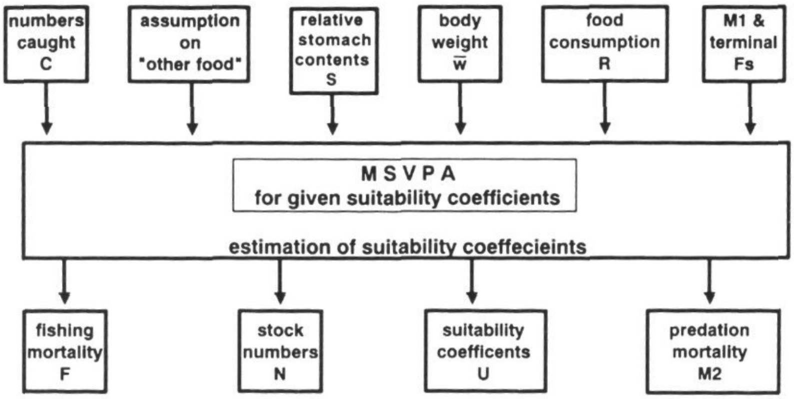

Figure 5. Inputs and outputs to MSVPA.

are inputs from other sources. Table B shows relative stomach contents derived from samples. Thus, Tables A and B represent the input data. Table C is calculated from Tables A and B and represents the fraction of each prey category divided by biomass. The suitabilities are immediately obtained from Table C and they are shown in Table D. The biomass of all stocks is in this case assumed to remain constant.

The iterative process used to estimate the suitability coefficients is shown in Figure 8. Note that the "MSVPA" box contains the iterative process illustrated in Figures 6 and 7.

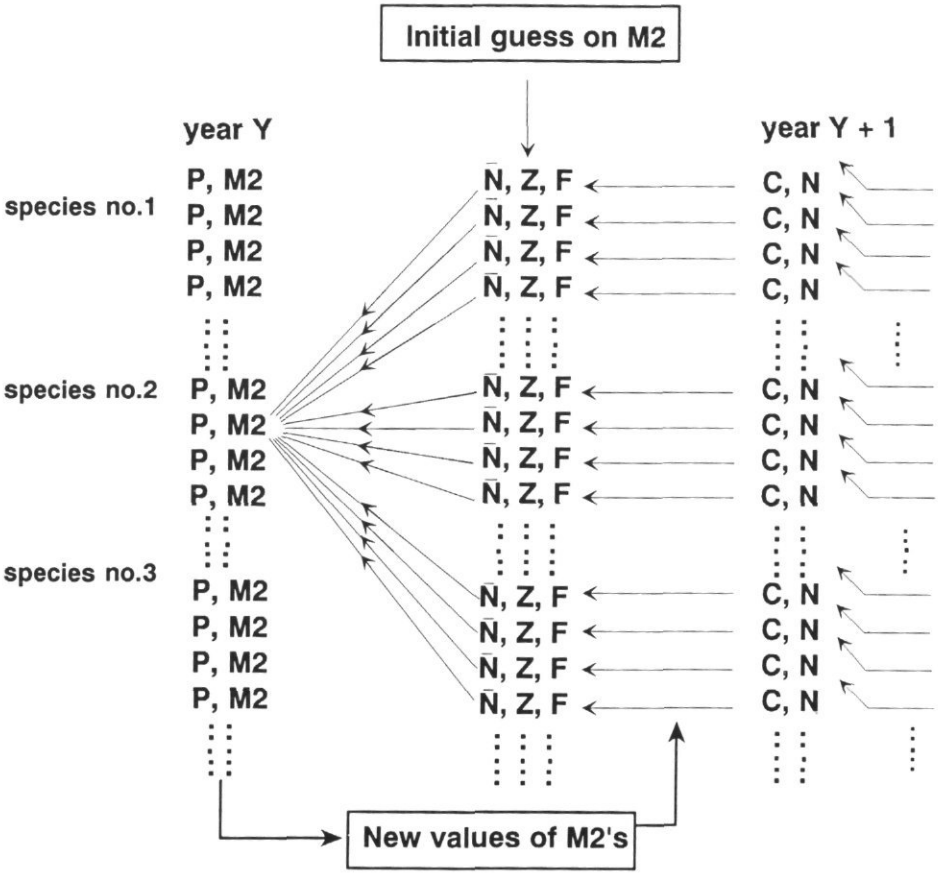

Figure 6. Iterative computational procedure for one year of MSVPA.

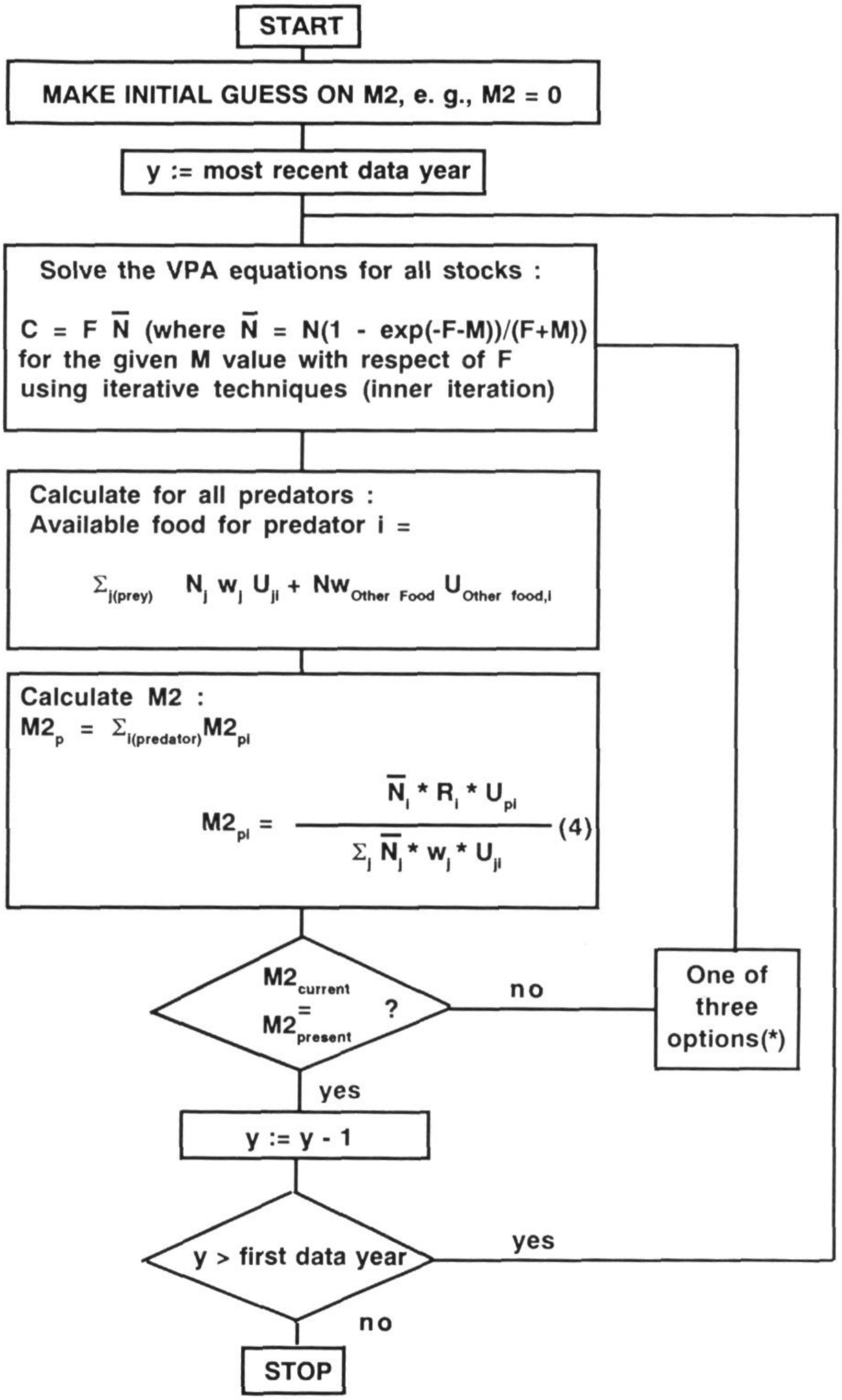

Figure 7. The iterative computation procedure for MSVPA when suitability coefficients are fixed. Options for other food (*) are (1) amount of other food is constant, (2) amount needed to hold total biomass constant, or (3) zero other food.

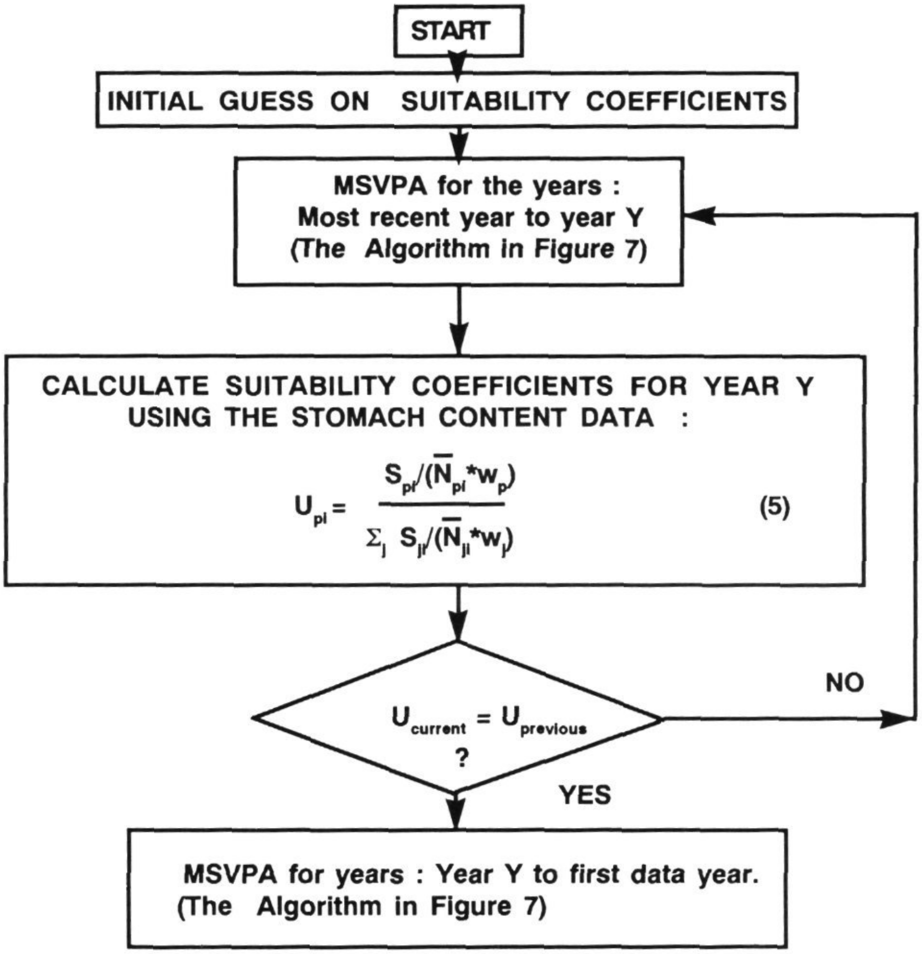

Figure 8. The iterative procedure for estimation of suitability coefficients. Year Y represents the year for which stomach content data are available.

Table 1A. Estimation of suitability coefficients from MSVPA output and relative stomach contents illustrated by a hypothetical example (from Sparre, 1980). Output from MSVPA (N) and body weights (w) necessary for the estimation of suitability coefficients.

Species	Age	$\bar{N}$	$\bar{w}$	$\overline{Nw}$
1	1	200	5	1 000
	2	100	50	5 000
	3	50	80	4 000
2	1	50 000	1	50 000
	2	20 000	5	100 000
3	1	1 000	5	5 000
	2	500	20	10 000
	3	100	30	3 000
Total fish biomass:				178 000
Total ecosystem biomass:				1 000 000
Other food biomass:				822 000

An initial guess on the suitability coefficients allows running the MSVPA back to Y, the year for which stomach content data are available. With the estimated N's for year Y in combination with the stomach content data, new suitability coefficients can be estimated using Equation (5). This procedure is repeated until suitabilities converge according to predefined criteria.

The first MSVPA was carried out by the ICES Multispecies Working Group at its meeting in 1984 (Anon., 1984b). The computations were made with a FORTRAN 77 program prepared for the meeting, and executed on the VAX/11/750 mini-computer at the Danish Institute for Fisheries and Marine Research (Sparre, 1984). The FORTRAN source code makes up some 100 A4 pages, a large part of which comprises the comprehensive comments. A first version of the program was presented in Sparre (1984). One complete run with the MSVPA program took about 5 min of CPA time on the VAX/11/750 mini-computer. The program was ex-

Table 1B. Relative stomach contents (S(a,a,j,b)).

				Predator (j,b)							
	j			1			2		3		
	s	a	b	1	2	3	1	2	1	2	3
Prey	1	1		0	0	0.05	0	0	0	0	0
		2		0	0	0	0	0	0	0	0
		3		0	0	0	0	0	0	0	0
	2	1		0.5	0.5	0.3	0	0.2	0.2	0.2	0.2
		2		0	0.3	0.4	0	0	0	0.1	0.3
	3	1		0	0.1	0.15	0	0	0	0	0.1
		2		0	0	0.05	0	0	0	0	0
(s,a)		3		0	0	0	0	0	0	0	0
Other food				0.5	0.1	0.05	1.0	0.8	0.8	0.7	0.4
Total				1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 1C. Fraction of relative stomach contents over biomass ($\times 10^{+5}$), S(s,a,j,b)/[N(y,s,a)w(s,a)].

				Predator (j,b)								
	j			1			2		3			$\bar{N}\bar{w}$ (from Table A)
	s	a	b	1	2	3	1	2	1	2	3	
Prey	1	1		0	0	5.0	0	0	0	0	0	1 000
		2		0	0	0	0	0	0	0	0	5 000
		3		0	0	0	0	0	0	0	0	4 000
	2	1		1.0	1.0	0.6	0	0.4	0.4	0.4	0.4	50 000
		2		0	0.3	0.4	0	0	0	0.1	0.3	100 000
	3	1		0	2.0	3.0	0	0	0	0	3.0	5 000
		2		0	0	0.5	0	0	0	0	0	10 000
		3		0	0	0	0	0	0	0	0	3 000
Other food				0.061	0.012	0.006	0.122	0.097	0.097	0.085	0.049	822 000
Total ecosystem				1.061	3.312	9.506	0.112	0.497	0.497	0.589	3.749	1 000 000

Table 1D. Food suitability matrix; U(s,a,j,b).

				Predator (j,b)							
	j			1			2		3		
	s	a	b	1	2	3	1	2	1	2	3
Prey	1	1		0	0	0.53	0	0	0	0	0
		2		0	0	0	0	0	0	0	0
		3		0	0	0	0	0	0	0	0
	2	1		0.94	0.30	0.06	0	0.80	0.80	0.68	0.11
		2		0	0.09	0.04	0	0	0	0.18	0.08
	3	1		0	0.60	0.32	0	0	0	0	0.80
		2		0	0	0.05	0	0	0	0	0
(s,a)		3		0	0	0	0	0	0	0	0
Other food				0.06	0.01	0.05	1.00	0.20	0.20	0.14	0.01
Total				1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

tended and modified later (Anon., 1986, 1987; Sparre and Gislason, 1986; Gislason and Sparre, 1987).

Catch prediction

VPA, which deals with the analysis of historical catch data, has a counterpart, the Thompson and Bell model (1934), which deals with predictions or simulations. MSVPA also has a catch prediction counterpart. The first version of the multispecies prediction program was presented in Sparre (1980), whereas a later version included some economic features (Sparre, 1983).

These predictive programs are more straightforward applications because they use the parameter values obtained from MSVPA in the simulation and require only one iterative loop.

Acknowledgments

This description of the MSVPA has concentrated on the mathematical description of the computation procedures, the reason being that I worked mainly in that field. However, I am well aware that without the biological fieldwork carried out by my colleagues and without the input from these field workers there would have been no MSVPA. My task was to translate their observations and ideas into formulas and computer programs. Amongst them I mention the coordinators of the ICES stomach sampling program (1981) and in particular their chairman, who suggested that I took up the task to program the MSVPA, and who had a major influence on the design of the MSVPA program.

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The ICES Multispecies Assessment Working Group: evolution, insights, and future problems

J. G. Pope

Pope, J. G. 1991. The ICES Multispecies Assessment Working Group: evolution, insights, and future problems. – ICES mar. Sci. Symp., 193: 22–33.

An overview of the work of the ICES Multispecies Assessment Working Group is presented. This Working Group has been a powerful engine for developing practical multispecies assessment methods in the ICES area. Methods for multispecies virtual population analysis (MSVPA) have been developed and implemented in such a way as to utilize the available data sets. The results of these analyses have caused a profound rethinking of our picture of the North Sea, with predation mortality emerging as a major factor. Prospective models have also been developed which attempt to predict the future behaviour of the system under changing exploitation patterns. These predictions produce results which contradict single-species assessment and indicate that long-term advice has to be based upon multispecies models. Sensitivity analysis of such models indicates that recruitment is a major determinant of these predictions. This suggests that multispecies effects need to be investigated from early life history stages onwards. MSVPA techniques do not seem appropriate for these investigations and fresh modelling initiatives need to be considered. A further area needing urgent modelling investigations is concerned with the interactions between fisheries. These determine the feasible directions of change in exploitation patterns and thus indicate how and in which directions the exploitation of the system can be modified.

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Introduction

The possibility of multispecies effects on the life history parameters of fish were considered by Beverton and Holt (1957). However, in practice for the next twenty years their models were applied assuming that such effects were constant from year to year. This assumption was questioned by the studies of cod stomachs conducted by Daan (1973) and by the pioneering modelling work of Andersen and Ursin (1977). In particular, they suggested that natural mortality would be influenced by predator stock sizes. Two papers presented to the ICES statutory meeting in 1979 (Helgason and Gislason, 1979; Pope, 1979) and also a paper by Sparre (1980) suggested that the estimation of natural mortality could be achieved by using algorithms for the simultaneous solution of virtual population analysis (VPA) for more than one stock. This led to the setting up of the ICES Ad hoc Working Group on Multispecies Assessment Model Testing in 1980 (Anon., 1980). This WG appointed coordinators for an extensive international stomach sampling programme in 1981 for the predators cod, whiting, saithe, mackerel, and haddock (Daan ed., 1989). The coordinators reported to the 1983 and 1984 ICES statutory meetings (Daan, 1983; Anon., 1984a). This in turn led to the setting up of the Ad hoc Multispecies Assessment Working Group, which first met in 1984 (Anon., 1984b). This paper reviews the progress and the main achievements and insights of this WG and attempts to suggest important areas of work for its future programme.

Progress in multispecies assessment

The WG first met in 1984 with subsequent meetings in 1985, 1986, 1988, and 1989 (Anon., 1984b, 1986a, 1987, 1988a, 1989a). These meetings focussed on applying the multispecies VPA model (MSVPA) to the data collected by the species coordinators of the 1981 stomach sampling programme and on applying the results to provide management advice for the North Sea fish stocks. In addition, the group has tried to keep abreast of multispecies developments in other areas of the North Atlantic, particularly the Barents Sea, Iceland, and Newfoundland where the problems are somewhat different from the North Sea. A parallel working group considered the problems of the Baltic Sea (Anon., 1988b; Sparholt, 1991).

The 1984 meeting

During its first meeting, the WG concentrated on the task of producing the first runs of MSVPA based upon the 1981 feeding data. Suitable computer programs, including a method for tuning suitability estimates to stomach content data, were developed by P. Sparre of the Danish Charlottenlund Laboratory (Sparre, 1984). To run the programs necessarily required the creation of a number of new databases, in particular the stomach content database, estimates of feeding levels, estimates of other natural mortality, and a database of quarterly catch-at-age data. A fundamental problem identified during the meeting was that different ages and species of predators were eating different sizes of particular prey ages. This problem results from the lack of a size within age dimension in the model. For example, the ingestion weights of one-year-old sandeel found in the stomachs of one-year-old cod were 94% of the average weight in the sea, while the ingestion weights of the same prey age group in stomachs of five-year-old cod were 116% of the weight in the sea. For whiting the equivalent change was from 33% to 180%. Clearly, the model had to be modified to take this feature of prey selection into account. This was eventually achieved by using a predator-species and age-specific prey weight in the stomach in the formulation, rather than a general average weight-at-age of prey in the sea. There was heated discussion about the validity of this approach and it took some rather hard thinking and arguing to resolve the approach to everyone's reasonable satisfaction.

In setting up the databases there was still considerable uncertainty about the appropriate food selection model to use, and about the correct levels of some of the inputs, particularly the age-specific feeding levels of predators and the level of other natural mortality (M1) to be used. A first attempt at a sensitivity analysis of the MSVPA results indicated that these were sensitive to these inputs in the ways which might perhaps have been predicted. For example, lower feeding levels reduced predation mortality estimates but not by the full proportional amount. Lower M1 values reduced fishing mortality estimates while having little impact on predation mortality estimates. Table 1 shows the effect of input changes to the estimates of average predation mortality of haddock.

Short-term effects of adopting a multispecies assessment approach were investigated by regressing MSVPA recruitment results against the equivalent results from single species assessments. Although the multispecies recruitment indices were larger, they correlated well with the single species results and thus would probably not affect the calculation of short-term management advice such as Total Allowable Catches (TACs). Figure 1 illustrates the similarity of single and multispecies recruitment estimates using cod data as an example. A regression of this log/log plot gives a highly significant association (r = 0.98; d.f. = 13) with a slope which is near to unity. The single species and multispecies results would thus appear to vary in proportion to one another.

Table 1. A comparison of predation mortality rate (yr^{-1}) on North Sea haddock from the key-run with results from runs with reduced feeding levels and with reduced M1 levels (from Anon., 1984b).

Age	Key-run	Feeding level halved	M1 level halved
0	1.45	1.08	1.50
1	1.04	0.61	1.03
2	0.16	0.08	0.16
3	0.05	0.02	0.05
4	0.04	0.02	0.05
5	0.02	0.01	0.02
6+	–	–	–

Due to pressure of time, it was not possible to quantify the effects of multispecies interactions on long-term yield. However, the quite difficult problem of how to present such results was considered. The approach recommended was to approximate the gradient of the yield surface for each species for each of a number of fishing fleets. This was to be achieved by considering the effects of an increase of 10% in each of the fishing fleets in turn on the yield of each species by each fleet. This might be thought of as akin to the Jacobian matrix (J(f,s,g,)).

$$J(f,s,g,) = \partial Y(f,s)/\partial E(g)$$

where Y(f,s) is the yield of species s obtained by fleet f and E(g) is the effort of fleet g. The resulting matrix of the changes in yield caused by 10% changes in effort of

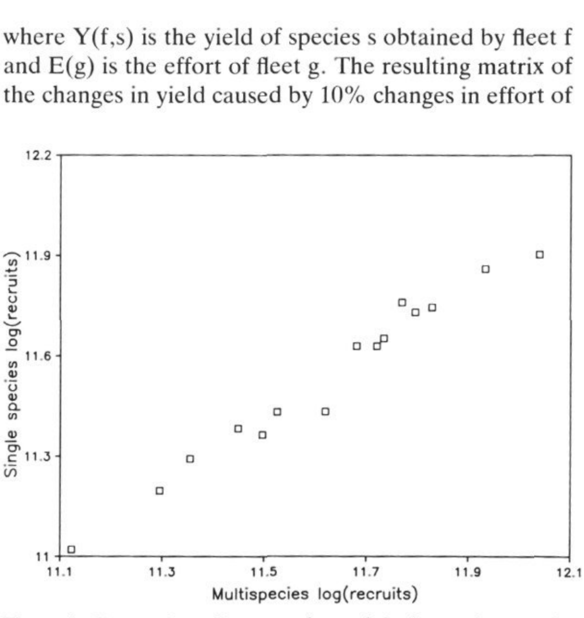

Figure 1. Regression of log-transformed single-species recruitment estimates of cod at age 1 on the equivalent multispecies estimates.

particular fleets is often referred to as the Jacobian matrix, though in fact it is strictly J(f,s,g)/10.

A further problem initially addressed at this meeting was that of the uniqueness of MSVPA. This had been previously subject to investigations by Dekker (1982) and by Magnus and Magnusson (1983). The latter authors provide mathematically "sufficient" conditions for the results of MSVPA to be unique. So far no one has provided the mathematical "necessary" conditions for uniqueness.

The 1985 meeting

The 1985 meeting of the WG saw a number of technical improvements in the MSVPA computer program (Sparre and Gislason, 1985) and a narrowing down of the assumptions made about feeding. Particularly interesting, however, was an investigation started in this WG but continued in the WG on Methods of Fish Stock Assessment (Anon., 1986b). This concerned the question of whether short-term TAC advice was invariant under changes in the average level of natural mortality used in single species VPAs. This was important because there was a fear that the changing estimates of natural mortality obtained from MSVPA, as its use matured, might cause large and systematic variations in TAC estimates. Some theoretical considerations (Pope, 1983) suggested that this would not be the case, but some actual calculations based upon the work of the North Sea Roundfish WG (Anon., 1985) suggested that there could be problems for some stocks. The WG on Methods of Fish Stock Assessment managed to resolve these difficulties by pointing out that the discrepancies occurred because of the way in which estimates of the recruiting age groups were introduced into single species forecasts. This result, coupled with the finding that MSVPA estimates of recruitment were closely correlated with the single-species estimates, led to the more general conclusion that there was no particular need to take multispecies effects into account (except by adjusting average natural mortality rates) when short-term advice was provided. Such advice could therefore continue to be provided by the single-species working groups.

The other main development in 1985 was the first calculation of the Jacobian matrix of long-term yield, indicating that long-term yield estimates calculated by a simple method (Shepherd, 1984) were generally at variance with yield estimated under single-species assumptions. This difference is discussed further in a later section of this paper.

An integral part of the long-term analysis was calculation of smoothed values of predation mortality (M2) per unit biomass and of the suitability coefficient. These smoothed values provided a means of summarizing some of the more detailed internal results of MSVPA and also a quality check on particular input data. The approach of fitting an Ursin (1973) lognormal feeding curve was to become of considerable importance to future meetings. The paper by Rice *et al.* (1991) provides an up-to-date review of this work. The WG summarized the biological results into tables of "who eats who" and also considered the variance of stomach content data.

The 1986 meeting

In 1986, the WG continued to build on the work of previous years. Of particular importance were some fresh insights on the subject of M1 calculations. Previously, values of M1 had been based upon conventional levels suggested by the single species working groups, but a working paper (Sparholt, 1986) suggested how estimates might be improved by considering the predation caused by other predatory fish in the North Sea and by birds and mammals. These latter calculations were assisted by inputs on birds from Bailey (1986) and on seals from Prime and Hammond (1986).

The results on short-term yield effects from the previous meeting were confirmed.

Results on long-term yield were derived from two different model methods, proposed by Shepherd (1984) and Sparre (1986), respectively. The results exhibited similar proportional changes in yield but rather different long-term status quo steady state yields. This difference could not be resolved at the time and was held over for the next meeting.

A major initiative was the consideration of the sensitivity of long-term yield to assumptions about recruitment and ration size. Results are shown in Figure 2a and b. Typically, recruitment of a species emerged as the input to which the long-term yield of that species was most sensitive. This was usually followed by the recruitment of other prey species. Relative sensitivities of species to their own recruitment were less than unity for cod, whiting, and haddock suggesting that cannibalism had a buffering effect. In contrast, sensitivities were greater than unity for the small prey species (sprat, Norway pout, and sandeel), suggesting these species might be able to saturate the predators. The other factors had little effect on any species except herring, but the herring results appear to be anomalous and probably the data have been corrupted. Results for herring should therefore not be taken seriously.

The 1988 meeting

At the 1988 meeting, the additional stomach data collected in the first and third quarters of 1985, 1986, and 1987 for some of the predator species became available. These were incorporated into the database and the program was modified to utilize extra data sets (Gislason and Sparre, 1987). This enabled a study of the extent to which suitability remains constant from year to year. The tentative conclusion reached was that suitability

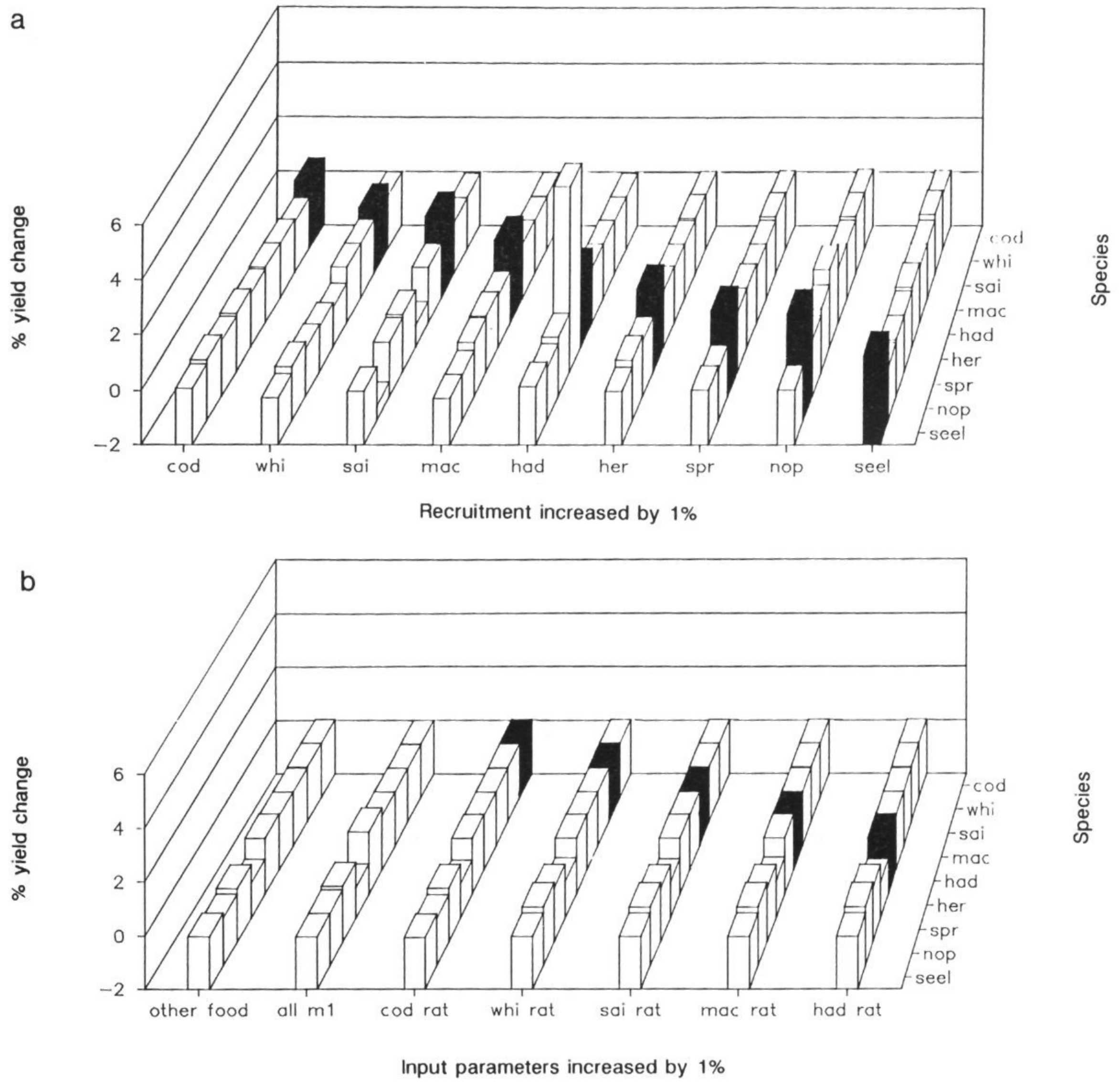

Figure 2. Relative sensitivity of the long-term yield of North Sea species to recruitment and feeding assumptions. (a) Recruitment. (b) Ration size as well as some other parameters (highlighted cells indicate within-species effects).

varied a little from year to year but not by very much. To some extent the changes in suitability could be accounted for by changes in the relative biomass of prey species. The changes identified were consistent with a reaction to the increased abundance of herring in 1985–1987 compared to 1981 when herring was at very low levels. However, a definitive study was hampered by the new stomach data only being available for certain quarters for certain species. With the wisdom of hindsight, a repeat of the complete 1981 study in say 1986 might have been a better choice, since this would have allowed completely independent estimates of suitability for all species and quarters.

On the subject of long-term yield, the difference between the predictions given by the Shepherd model and the Sparre MSFOR model could be resolved by modifying the Shepherd model to take unsmoothed estimates of M2s. This modification gave substantially the same results with both models and indicated that the differences noted in 1986 were due rather to the use of smoothed or unsmoothed M2s than to differences in the feeding models adopted. The problem seems to be that, while the unsmoothed data will undoubtedly contain extra variance due to the sampling error inherent in stomach content investigations, the current methods for smoothing of M2s introduced quite serious biases. In particular, they appeared to spread M2 over more prey ages than had been observed in the predator stomachs.

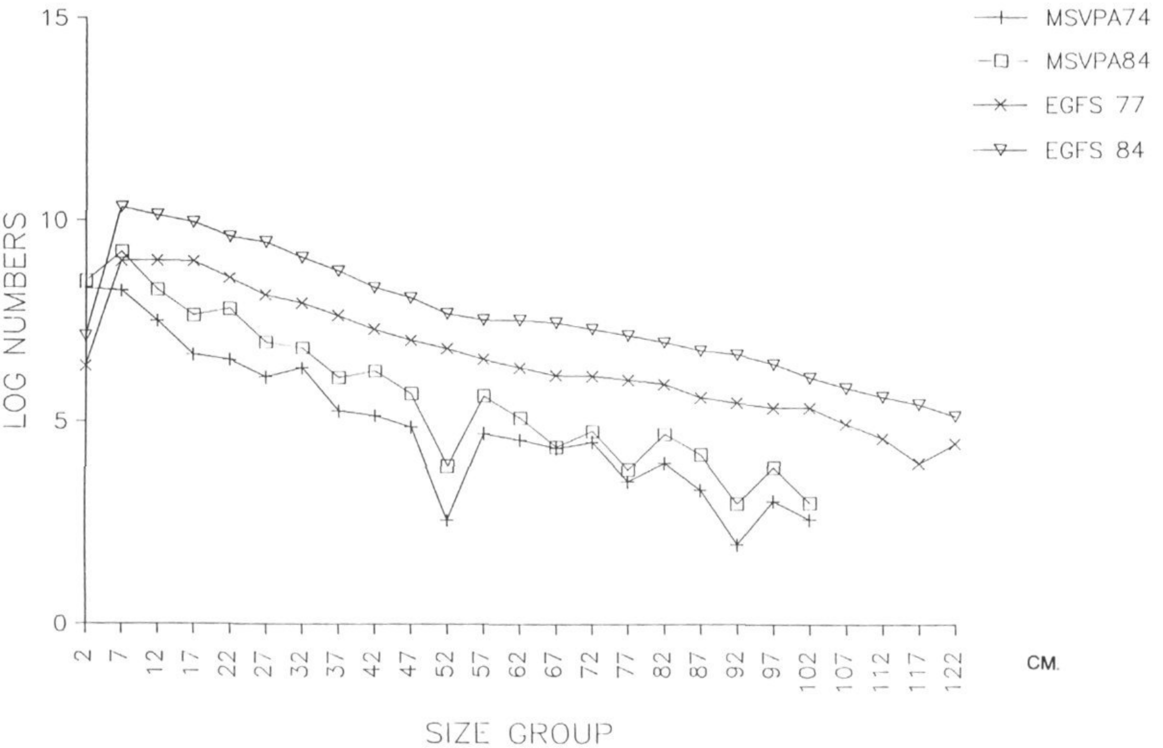

Figure 3. Comparison of the North Sea size composition observed in the English ground fish surveys (EGFS) described by Pope *et al.* (1988) with results from MSVPA for 1974 and 1984.

Both the Sparre MSFOR model and the modified Shepherd model were used to calculate the effect of changing to a 120 mm mesh size in the roundfish fleet and the saithe fleet. The calculations suggested that increasing mesh size would tend to decrease both the yield and the value of the majority of species, a result contrary to the advice given by single-species assessments.

As always, the WG broke some new ground. In order to investigate the fleet structure of the North Sea fisheries, a Principal Component Analysis was run using the partial F structure of the various nations' fisheries. Finally, to encourage the work being conducted on Boreal systems, it was proposed to hold a special meeting of the WG on this topic in 1990.

The 1989 meeting

The 1989 meeting was called with the intention of extending the work on mesh assessments. In particular, the effect of increasing mesh size on only that part of the roundfish fishery dedicated to cod was investigated. The results were less extreme than those obtained in 1988 but showed a similar divergence from the results of single species mesh assessments.

In addition, the work on the comparison of suitabilities begun in 1988 was extended. The conclusion that suitability varied little between years was sustained.

Several new initiatives were taken. One was to try to work the multispecies assessment back before 1974. Estimates of cod, whiting, saithe, haddock, and mackerel year classes were projected back to 1963 (see Pope and Macer, 1991, for detailed results). Attempts to find approximate formulae to fit the yield surfaces were also initiated. The size distribution of the North Sea system was investigated, following Pope *et al.* (1988), who compared the size compositions of the fish in the North Sea and on Georges Bank and showed that these can be considered as conservative properties of the two systems. Figure 3 compares empirical survey data (Pope *et al.*, 1988) with size compositions estimated from MSVPA, indicating that the slopes in both data sets are very similar.

Major insights

The most important insight gained from the work of the Multispecies Assessment WG is that, after accounting for inter- and intraspecific predation mortality, natural mortality rates are much higher than previously estimated and are variable from year to year. Figure 4 shows the average level of predation mortality rate for each of the seven prey species in the model, while Figure 5 illustrates the variability in predation mortality rate for haddock. The higher levels of natural mortality mean that the numbers of juvenile fish in the North Sea had

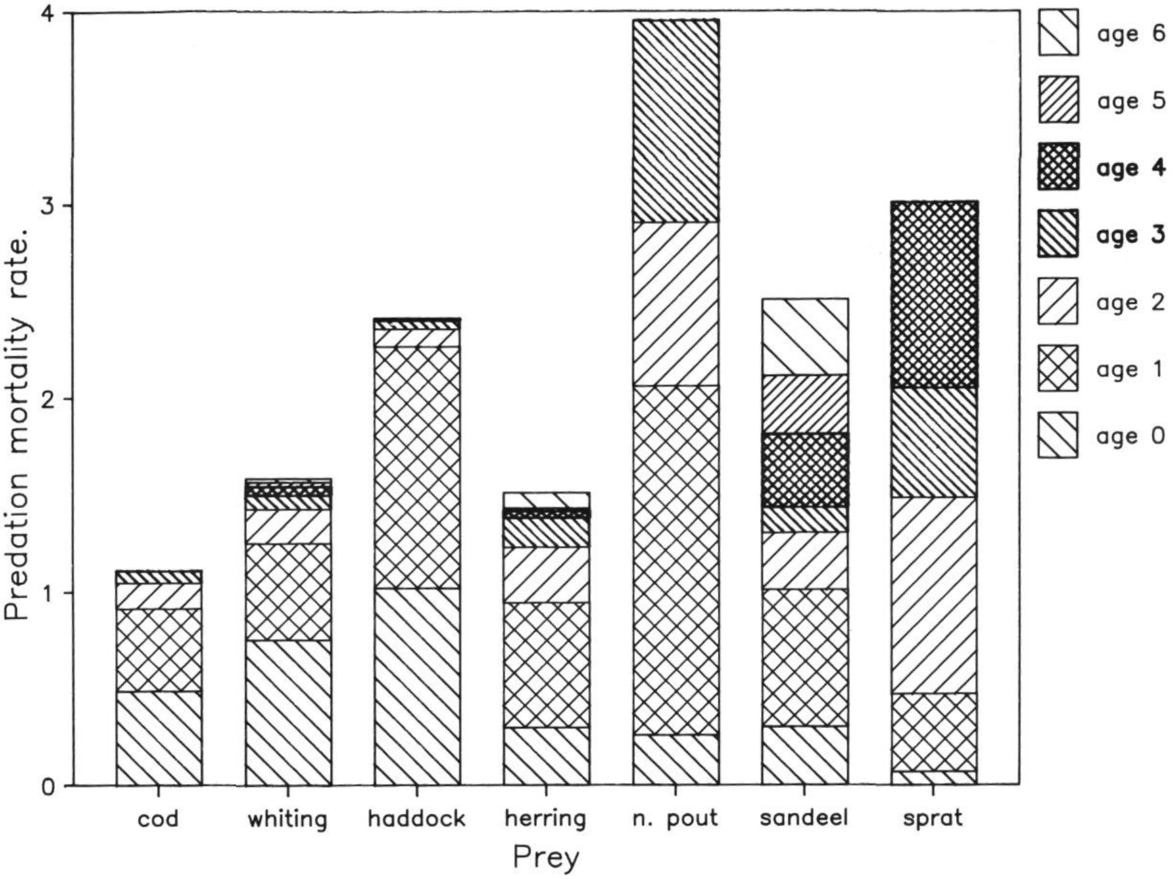

Figure 4. Average levels of predation mortality for each of the seven prey species in the MSVPA model.

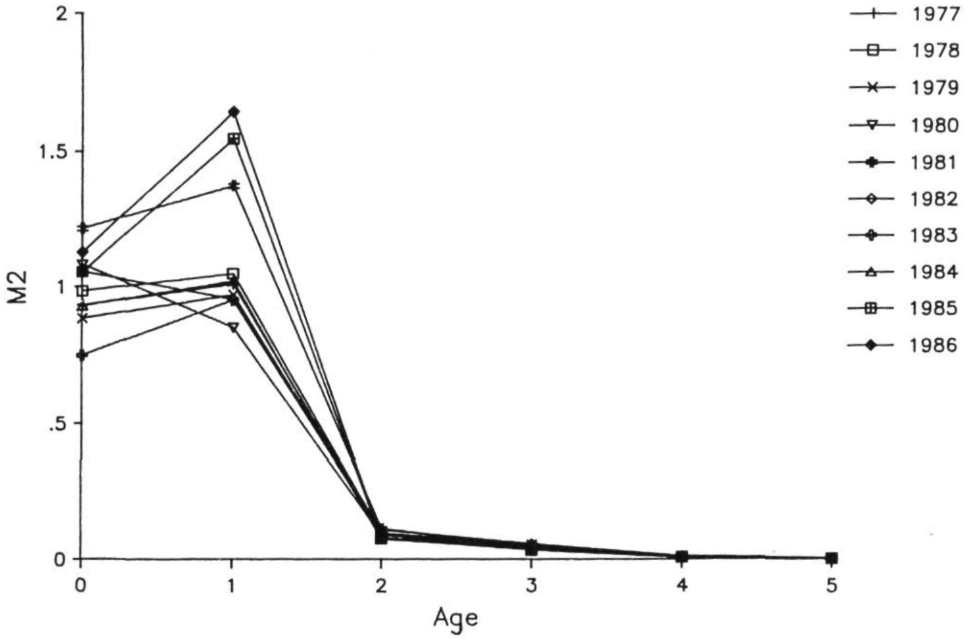

Figure 5. Variability of predation mortality by age and year for haddock as estimated by MSVPA.

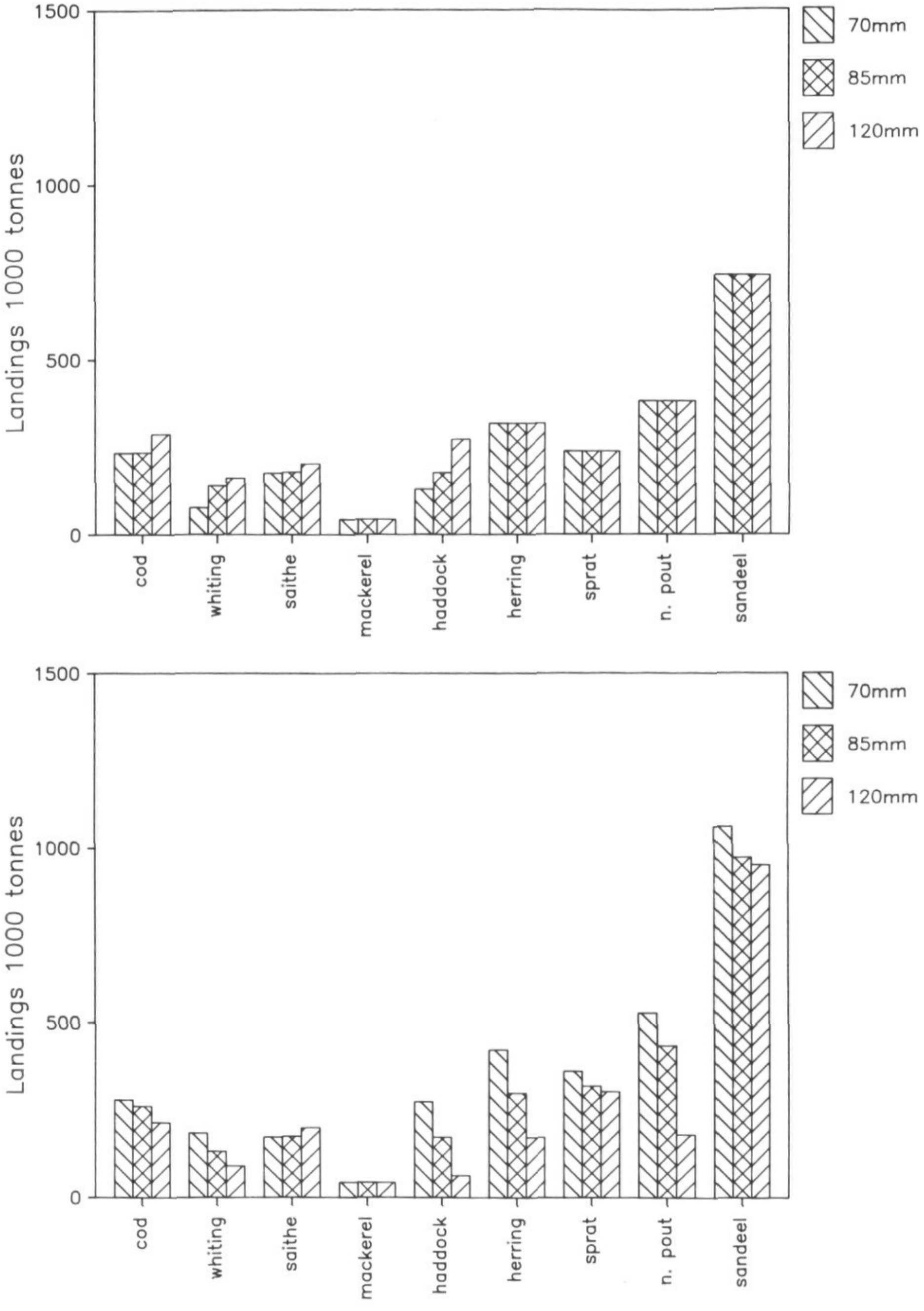

Figure 6. Yield change caused by mesh changes in the roundfish human consumption fishery calculated by single-species models (top) and multispecies models (bottom).

previously been underestimated. The variability implied that single-species and multispecies estimates of recruitment might not correlate very well. However, in practice this does not seem to be the case, at least in the period since 1974 (cf. Fig. 1). It is possible that divergence might be greater before that date if natural mortality rates were systematically higher in the earlier period (Pope and Macer, 1991).

The higher and variable levels of natural mortality have serious implications for the yield of the multispecies system. Single species models predict increases in long-term yield if effort is decreased in the roundfish (cod, haddock, and whiting) and saithe fisheries or if mesh sizes are increased in these fisheries. Multispecies models predict the opposite. Figures 6a and b taken from (Anon., 1988) illustrate these findings for mesh

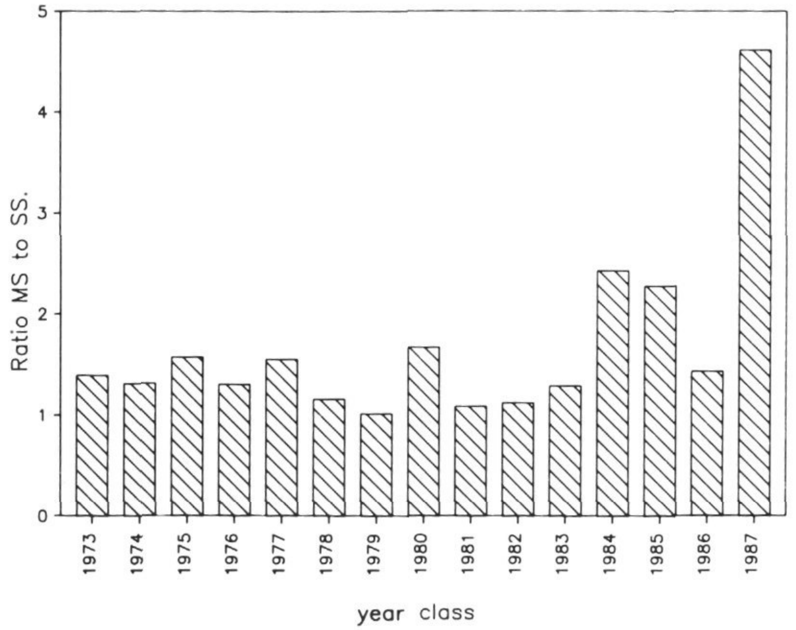

Figure 7. Multispecies estimates of haddock recruitment as a ratio of the single species estimates, by year class.

changes in the roundfish and saithe fleet according to single-species and multispecies predictions, respectively.

It should be carefully noted that these differences come about not because the multispecies natural mortality rates are high but because they vary with predator density and hence increase if management measures generate higher stocks of predators such as cod, whiting, and saithe. In fact, the comparable single-species models were generated using average levels of natural mortality derived from MSVPA. This difference between single and multispecies models is mainly important in the case of long-term yield. In the short term, the yield will be much the same whether calculated on a single or multispecies basis. The reason for this is that in short-term yield calculations natural mortality rate values are used to convert catch estimates into current population sizes using VPA. They are also used for converting the population estimates into future catches using prediction programs. The values of natural mortality rate tend to cancel out in these calculations provided they are approximately constant through time. It is possible, however, that systematic shifts in the level of predation mortality might cause differences, particularly in the estimates of recruitment used.

The North Sea haddock illustrates this problem. Figure 7 shows the ratios of multispecies estimates of recruitment and the equivalent single-species recruitment. Natural mortality rates on one-year-old fish have increased in some recent years and this has caused a change in the relationship between single and multispecies estimates of recruitment, particularly for the 1984, 1985, and possibly the 1987 year classes.

Finally, the multispecies model has given fresh insights into the total fish biomass of the North Sea and how much is taken each year by fishing and how much by predation by fish. The various WG reports describe "who eats who" by predator. Figure 8 shows a composite of these to express how much of the biomass is eaten and how much is caught each year. Clearly, the North Sea is a system with a very high turnover rate and predatory fish are very important as competitors to man.

The future of multispecies models

Within North Sea multispecies modelling studies, there is a continuous tension between the need to increase realism by adding details and the need to increase comprehensibility by using simplifying assumptions. To some extent extended models may need developing even if the result is only to show that their effects are relatively unimportant. Incorporation of additional predators and of an area-based stock option for species such as the sandeel and mackerel would seem desirable and obvious extensions to the existing model. Other complications, such as area and size-based models, may need development in order to answer specific management questions, such as the effect of closed areas. For the North Sea, such models may well be derived from collaboration between the Multispecies Assessment WG and the WG on Technical Measures of the Scientific and Technical Committee for Fisheries (STCF) of the EC (Anon., 1988c). The latter WG is collecting detailed information on the spatial distribution of catch and effort of different national fleets which, combined with results from the multispecies assessments, could lead to

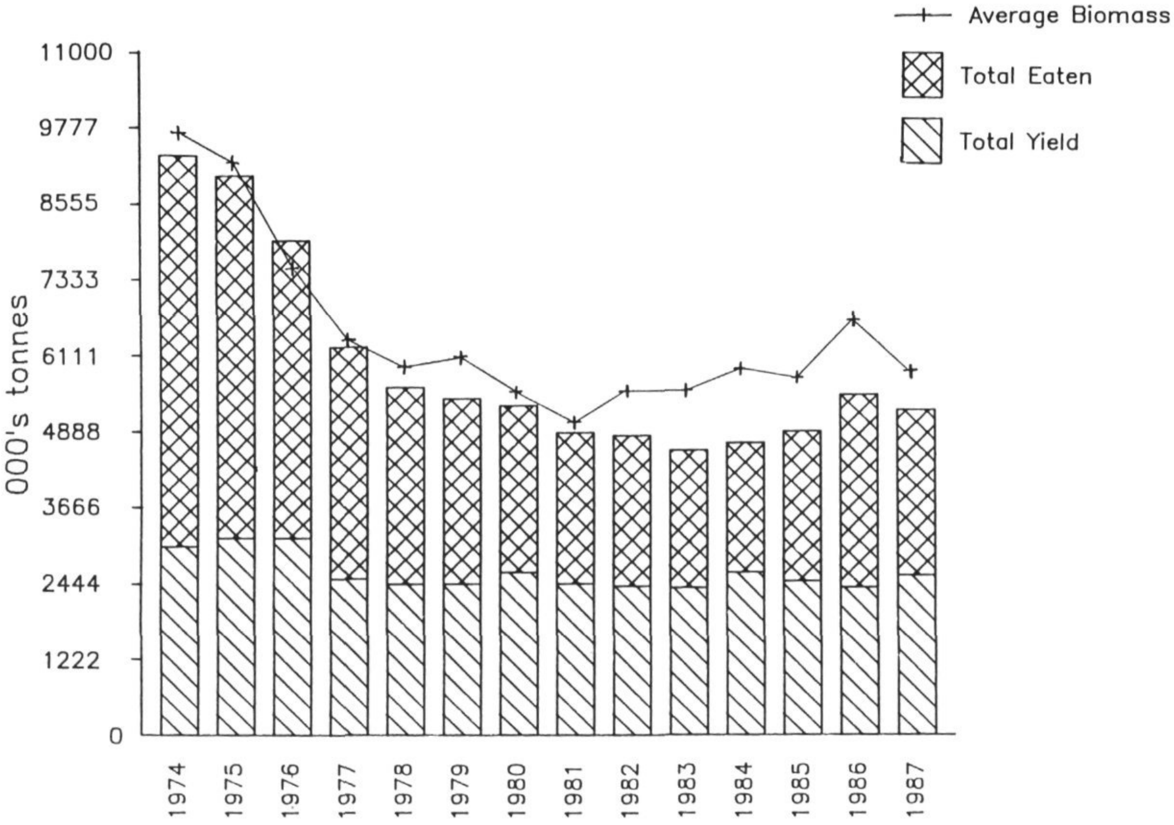

Figure 8. Total biomass of the nine species of fish in the North Sea model together with estimates of consumption and catch given on an annual basis.

an area-based description including predation effects, migration, and fishing. At present this would seem rather a large job but stomach samples were originally collected in an area-specific fashion and the STCF WG is trying to provide similar information for catch-at-age data. If the long-term effects of area closures or any other technical measure are to be correctly estimated, then undoubtedly species interaction effects must be taken into account, because the results obtained so far indicate that omitting these is likely to produce misleading results.

One possible way an area-based multispecies model might be developed would be to revive a proposal of Gislason and Sparre (1967) for including geographical effects in the estimation of suitability (see also section 6.7.2 of Anon., 1986a). This proposal suggested that it should be possible to estimate the consumption by subarea of the North Sea using geographically disaggregated stomach content data and survey based descriptions of the proportion of the stocks of predators and prey species in each subarea. This option is becoming more possible in recent years with the wider availability and standardization of trawl surveys (e.g. Anon., 1989b). There would, however, still be problems with the spatial distribution of some prey species such as sandeels, which are not adequately represented in trawl samples. Ms S. Singh (pers. comm.) suggests a possible way around this by making an analysis of variance of the log stomach content data of all predator species at once. The analysis includes predator × prey interactions and prey × station interactions. These interaction terms correspond to the suitability of prey for individual predators and the local availability of prey, respectively. Such a multiplicative analysis of course contains an unknown aliasing effect between availability of prey and their suitability, which is to say that the same data could support the hypothesis that prey are abundant but unsuitable or vice versa. This aliasing can, however, be corrected for, providing estimates are available of the total North Sea population of the species. This approach could therefore provide a way of obtaining spatial distribution data for prey which are not covered by trawl surveys. The only problem would be that such distributional data would only become available for years in which stomach sampling was carried out and therefore the distribution patterns would have to be assumed constant for other years.

Given the technical possibilities for an area-based description of predation, appropriate models would obviously be valuable in studies of the effects of closed areas in the North Sea. This approach would also be valuable for exporting the North Sea results to other areas, because the estimates of within subarea suitability might be expected to be much less determined by the geographical overlap and far more by just size ratios and ecological characteristics of predators and prey. These latter components of suitability (Andersen and Ursin, 1977) are presumably less North Sea specific and might be exported to other areas where they could be recombined with overlap factors specific to those areas to provide overall suitability indices.

Simplifications

One simplification considered in Anon. (1989a) was fitting simple representations of the yield surface. Pope (1989) suggested that quadratic yield or value surfaces could be fitted using the Jacobian matrix results. Alternatively, surfaces in the form of a multispecies Fox model could be fitted. Fits of such surfaces provide a simple basis for estimating multispecies equivalents to the biological reference points MSY and $F_{0.1}$. In a multispecies context, $F_{0.1}$ can have two meanings. One is the point on the surface where the gradient of the yield of each fleet is 1/10 of that fleet's gradient at the origin. The other concept is where the gradient of the overall yield with respect to each fleet is 1/10 of its value at the origin. Where a quadratic surface is fitted to the yield surface, the calculation of these points can in principle be achieved using simple linear algebra. In practice, however, these often refer either to negative levels of effort for some fleets or alternatively very high levels of effort and associated negative populations of some species. It is thus sometimes necessary to constrain solutions within certain limits to obtain sensible answers. Table 2 shows results from Anon. (1989a) giving the effort changes in each fleet which would lead to the biological reference points, provided the quadratic surface was representative. Perhaps the most informative reference points are the fleet $F_{0.1}$ values, which for both yield and value are close to the status quo. Assuming a linear relationship between cost and effort and zero profit at the present level of effort, the maximum economic yield (MEY) may also be estimated. It suggests a reduction in the effort in the roundfish and industrial fisheries while more or less maintaining effort in the herring, saithe, and mackerel fisheries. Of course, these results are only valid if the quadratic surfaces fit well to the model surface, in this case MSFOR, and if MSFOR is a reasonable representation of the system. Assuming that the predictions of MSFOR are the best currently available, this leaves the fit of the quadratic surface in question. In practice the fit is likely to break down at high values of effort, because eventually the quadratic model must predict negative yields and values. Clearly, this is not compatible with

Table 2. Relative effort changes required for reaching biological reference points and estimated yield, value, and profit according to the quadratic multispecies yield (A) and value (B) surface.

Fleet	MSY	Overall $F_{0.1}$	Fleet $F_{0.1}$	MEY	Status quo
A.					
Roundfish	1.89	1.76	1.04		1.00
Ind. demersal	1.49	1.40	1.11		1.00
Ind. pelagic	1.08	0.97	1.22		1.00
Herring	1.39	1.30	1.10		1.00
Saithe	1.75	1.75*	0.87		1.00
Mackerel	2.00*	2.00*	0.96		1.00
Total yield[a]	3949	3931	2821		2985
Total value[b]	339	377	355		378
Total profit[b]	−314	−240	−37		0
B.					
Roundfish	1.29	1.20	0.92	0.59	1.00
Ind. demersal	0.96	0.92	1.10	0.21	1.00
Ind. pelagic	0.10*	0.10*	1.22	0.10*	1.00
Herring	2.00*	1.97	1.04	0.92	1.00
Saithe	1.75*	1.79	0.84	0.98	1.00
Mackerel	2.00*	2.00*	0.96	0.98	1.00
Total yield[a]	3349	3284	2744	1421	2895
Total value[b]	469	468	349	319	378
Total profit[b]	−28	−10	−13	94	0

[a] Tonnes × 10^{-3}; [b] ECU × 10^{-6}; * Constrained.

MSFOR. The multispecies Fox model (cf. Fox, 1970) also seems to suffer from problems at high effort levels. Therefore, a differently formulated surface needs to be developed which is asymptotically more sensible than either the multispecies quadratic or the Fox surfaces. Such a development would be valuable for presenting the results of multispecies yield calculations, particularly when available in the format of a spreadsheet program which could be interrogated by advisory bodies or by management agencies.

Size compositions of total fish biomass form another possible approach to simplifying the description of multispecies systems (Fig. 3; Pope *et al.*, 1988). Other simplifications worth consideration might include an adequate mathematical description of the suitability coefficients between predators and prey which would enable a less heavily parameterized model to be developed. However, the full advantages would only be gained if the mathematical formulation was unbiased.

Behind any desire to simplify or elaborate the model is the need to both describe and understand the system. Sensitivity analyses of the long-term yield identify recruitment as the most important input for calculating the long-term yield of the North Sea system. We therefore need to know the factors that influence recruitment, particularly those which are related to the abundance of the species in question as well as of other species in the system. For example, if the decline in herring really caused the gadoid outburst, then we must know how, if we are to make predictions for the future. Fortunately, while forward predictions are sensitive to assumptions about recruitment, MSVPA does not require any implicit assumptions and therefore MSVPA, or variants of it, can be used to study actual recruitment levels that occurred in the past. It has proved possible to back track the method further than the previous 1974 time horizon and with some more simplifications and robust assumptions based upon our new knowledge it may be possible to push our multispecies understanding of the North Sea back to the immediate postwar period. To do this, ways have to be found of incorporating rather coarser data than the catch-at-age data currently used. Possible sources might include survey data, total catch data, and catch per unit effort data. Inevitably, the answers will be less accurate but fortunately great precision in recruitment studies is not needed and estimating year-class strength to within a factor of 2 will probably suffice. Coupled with such an approach should be a modelling effort designed to discover what different states of the North Sea could exist given (a) our present knowledge of species interactions and (b) plausible assumptions about how recruitment is affected by spawning-stock size and by as yet unsolved species interactions in the early life phases (e.g. herring predation, Daan *et al.*, 1985).

An alternative approach is to study multispecies interaction effects on the younger ages of fish. The forthcoming 1991 stomach sampling programme includes sampling of pelagic 0-group fish for stomach analysis in its aims and it seems quite probable that this will yield insights into further species interactions. To take advantage of this data source will require new approaches to modelling, since it is unlikely that MSVPA can be profitably extended down to this life stage.

Conclusions

The work in ICES on multispecies assessment conducted first by the ICES Ad hoc Working Group on Multispecies Assessment Model Testing (Anon., 1980) continued by the coordinators of the 1981 stomach sampling programme (Anon., 1984a) and extended by the ICES Multispecies Assessment Working Group (Anon., 1984b, 1986a, 1987, 1988a, 1989a) has changed our perception of how the North Sea should be assessed, how it works, and raises some profound questions about how it should be managed. This paper picks out some of these achievements, but it can only serve as a brief taste of this body of work. It is also very difficult to plot all the directions that such a wide study of the North Sea's fisheries might lead to in the future although some obvious directions have been indicated.

It is imperative to stress the need for multispecies recruitment studies. The great achievement of the WG to date has been to show that interactions that were previously neglected in fish stock assessment were in fact rather more important than some interactions which were considered. We must be very careful to make sure that in the future we consider any other factors that are likely to affect the state of the North Sea system. Of these, multispecies effects on recruitment seem the most probable source of significant interactions which are as yet unquantified.

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The stability of estimates of suitabilities in MSVPA over four years of data from predator stomachs

J. C. Rice, N. Daan, J. G. Pope, and H. Gislason

Rice, J. C., Daan, N., Pope, J. G., and Gislason, H. 1991. The stability of estimates of suitabilities in MSVPA over four years of data from predator stomachs. – ICES mar. Sci. Symp., 193: 34–45.

This work investigates how consistent predator preferences and prey vulnerabilities are over time. The multispecies VPA (MSVPA), as parameterized for the North Sea, provides estimates of suitabilities of each age of each prey for each age of each predator. MSVPA outputs parameterized with four years of stomach data allowed investigation of the stability of these suitabilities over time. The suitabilities were analysed with several linear models. One set of analyses investigated the total variance in suitabilities. The overall variance increased by about 20% when four years of data were included, compared with the variance in suitability based on a single year of data. Root mean square errors differed by less than 2% when the same linear models are fitted to the natural log of suitability from single-year and multi-year parameterizations. Other analyses were done treating each predator–year combination as a level of the factor predator. In most cases parameter estimates of the same predator in different years did not differ significantly. Predator–prey interaction terms showed some changes from year to year, but far fewer than expected by chance. Slopes of predator size preferences also did not change from year to year for cod or saithe, but did for whiting. Together these analyses indicate that predator preferences and prey vulnerabilities are stable over time when the effects of changing abundance and age structure are accounted for. This suggests that good multispecies models, parameterized with good field data, may be used to investigate predator–prey dynamics in multispecies management.

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Introduction

Theorists working on generic models can focus on how processes are represented, and not be greatly concerned about specific parameterizations of the models. However, when actual management advice is to be developed for a specific stock or stocks, useful models must both represent relevant processes well and be correctly parameterized. Selecting the proper functional form and estimating correct parameters is often challenging even for simple models. These problems compound with multispecies models.

Trophic interactions among species are important processes in many multispecies management models. Stomach contents data of predators are often used to parameterize predator–prey relationships. However, stomach contents may reflect predator preferences, prey vulnerabilities, relative and absolute abundances of the predators and prey, overlap of the predators and prey in space and time, and other processes. In the context of development of management advice from multispecies trophic models, it may be correct (and often necessary) to assume that preferences and vulnerabilities remain consistent. However, biomasses, age structures, and overlaps of predator and prey populations will almost certainly have changed from the conditions prevailing at the time when the predator stomachs were collected to the time when the advice is to be provided.

Andersen and Ursin (1977) provided a theoretical foundation for incorporating predator–prey interactions in fisheries management models. Andersen (1982), Helgason and Gislason (1979), and Gislason and Helgason (1985) developed that foundation, focusing on predator–prey interactions in fisheries systems. Among the reasons why these theoretical treatments have been influential in the development of multispecies modelling for fisheries resources is that they allow explicit consideration of the various factors which can influence the representation of food items in predator stomachs. This provides the necessary bridge from observations to predictions.

The MSVPA (Sparre, 1984, 1991; Gislason and Sparre, 1987) implementation of the Anderson and Ursin theoretical work partitions effects of predator preferences and prey vulnerabilities, collectively referred to as suitabilities, from the abundances of the species in the model. This separability of predator and prey density from preference and vulnerability is a critical assumption of MSVPA. This partitioning allowed the ICES Multispecies Assessment Working Group to parameterize MSVPA for the North Sea, using the extensive database on stomach contents of major predators collected in the 1981 "Year of the Stomach" project (Anon., 1984; Pope and Hunton 1985). Pope (1991) and Sparre (1984, 1991) discuss aspects of MSVPA, and how the data from predator stomachs were used quantitatively to estimate age specific suitabilities of each predator–prey combination.

For some of the predators, stomach data were available for the first and third quarters of 1985–1987, as well as from 1981 (Anon., 1988b). These additional data allowed suitabilities to be estimated separately for each year's stomach contents, with the MSVPA calculations taking account of changes in population sizes and age structures of the predators and prey. These estimates allow testing of the stabilities of the suitability estimates over time, and thereby provide insight into the usefulness of trophic-based multispecies models. If parameters are stable, good models may be used to include trophic interactions in the development of management advice. If the parameter estimates vary greatly from year to year, even models which represent underlying processes may well have little value for the management of any specific system.

Additional questions arise if suitabilities change when different years of feeding data are used in MSVPA. They involve apportioning the changes to random variation in feeding from year to year, and to systematic changes in predator–prey interactions. If the random variation in suitabilities from year to year is large, then MSVPA may represent the predator–prey interactions well, but the interactions (and predictions from models of them) are noisy. If there are large systematic changes in suitabilities, then there are influential processes not captured in the MSVPA formulation. Systematic changes could arise from non-linearities in functional feeding responses of predators to prey other than those included in the suitability calculations. Examples of additional non-linearities include prey-switching, predator-swamping, or other behavioral responses. Systematic changes could also result from differences in overlap of predators and prey, or from other factors (Hilden, 1988). Relating changes in suitabilities among years to changes in predator and prey biomasses and overlaps allowed preliminary investigation of these processes.

Methods

MSVPA assumptions

In the context of analyses of suitability, there are several important assumptions. One is that the Anderson–Ursin formulation of predator–prey dynamics does capture the important components of the interactions in its terms for species identity, season, and size preference of predators. Also, when it is used in forecast mode it assumes suitabilities remain constant over time. MSVPA does not include any spatial components nor does it adjust relative suitability for changes in preferences or vulnerabilities as relative predator or prey abundance changes. All these assumptions will be explored directly, in goodness of model fits, examinations of stability of parameter estimates of the model fits, and the ability of biomass and spatial overlaps to account for residuals from the model fit to the empirical suitabilities. MSVPA also requires assumptions about the role and interannual dynamics of other food (prey other than the species specifically modelled in MSVPA). These assumptions cannot be explored directly in these analyses, but stable model parameters would suggest other food is being treated in at least a generally correct way in the MSVPA formulation.

Data sets

Outputs of tuned runs of MSVPA include estimates of suitabilities of each age of each prey to each age of each predator in the model. The suitabilities are based on the stomach data provided to the model, and biomasses of each age of predator and prey. These biomasses were calculated from input age-specific weights and catch-at-age data, which were converted into population sizes using VPA methods. In MSVPA, suitabilities are calculated empirically, in a series of iterative steps. Input data include observed stomach contents of predators, catch-at-age and weight(w)-at-age data for predators and prey. The algorithms are presented in detail in Sparre (1984, 1991) and Gislason and Sparre (1987). Subscripts denote quarter (q), prey species (s), prey age (a), predator species (j), predator age (b), and year (y). Absolute abundance of observed stomach contents is converted into relative abundance (S) by the equation:

$$S(s,a,j,b) = \frac{\text{Weight of prey (s,a) in stomachs of predator (j,b)}}{\sum_{s}\sum_{a} \text{Weight of contents of predator (j,b)}}$$

Then, for each iteration in which MSVPA estimates numbers (N) at age for all species of predator and prey

$$\mathrm{SUIT}(y,s,a,j,b) = \frac{\dfrac{S(s,a,j,b)}{\bar{N}(y,s,a) * W(s,a)}}{\sum_{i}\sum_{d} \dfrac{S(i,d,j,b)}{\bar{N}(y,i,d) * W(i,d)}}$$

where $\bar{N}(y,s,a) * W(s,a)$ is the VPA estimate of biomass of the ath age of the sth prey, and the denominator is the sum of the suitabilities of all prey to the bth age of the jth predator, so suitabilities sum to 1.0 for each age group of each predator.

Different sets of suitabilities were estimated by inputting the same catch-at-age data but different portions of the total stomach contents database. The key data set (referred to as NSALL) used all data available from 1981 to 1987. Partial data sets, referred to as NS81, NS85, NS86, and NS87, included only stomach data for cod, whiting, and saithe from 1981, 1985, 1986, or 1987 for the first and third quarters. Only 1981 data were available for mackerel and haddock, and were used to estimate suitabilities for all sets. No first-quarter data from saithe were available in later years. When some analyses were conducted whiting data were not available for 1987 and saithe data were not available for 1985. For all these data sets, population estimates were developed using catch data available in 1988. Details of these runs are available from ICES Multispecies Assessment Working Group Reports (Anon., 1987, 1988a, 1989). At the meeting in June 1989, the catch data were updated, and suitabilities were calculated using all the stomach data and the updated catch-at-age data (set NSUPDATE). Meeting time did not permit recalculation of the suitabilities based on the updated catch-at-age data with subsets of the stomach data. However, NSUPDATE was useful for checking many NSALL analyses, as the age-structured population estimates were based on an additional year's catch-at-age data, and were more reliable for the period of interest.

Analyses

The total variance in the suitabilities of the various data sets was examined. Contrasting the variances of the individual restricted data sets (NS81 to NS87) with the total variance of NSALL documents how much suitabilities change with additional years of data. Year to year changes in suitabilities would show up as increased variance in NSALL, over the combined variance of the four single-year estimates, which individually contain all within-year variance.

MSVPA produces thousands of suitability estimates; too many to examine individually. Following from the theory of Andersen and Ursin (1977) and Helgason and Gislason (1979), however, the suitabilities should reflect effects of season, predator and prey species, as well as curvilinear size preference functions of predators. As a first step, linear models were fit to the logged empirical suitabilities of NSALL and NSUPDATE. These models contained factors for predator and prey species and quarter, various interactions, and covariates for the species-specific size preferences. Several models with various representations of these terms were explored. The models differed in the numbers of interactions included, and in the level of nesting of the covariates.

For some comparison of suitabilities based on different stomach data sets, the data sets of output suitabilities were restructured. The restructuring consisted of recoding the suitabilities for predators with multiple years of stomach data. Suitabilities were estimated separately with each year's data and then coded as if they were derived from separate predators. These data sets are referred to as restructured.

From the model fits, parameter estimates for the levels of the factors, interactions, and covariates reflected the systematic portion of the variation in suitabilities. For the model which was accepted by the Working Group, these parameter estimates were contrasted within and among the various data sets.

Also, the LS Means procedure of SAS (SAS Institute 1985) was used to calculate appropriately weighted means of the levels of the factors and interactions, and to make pairwise comparisons of these means. Means of the same predator, prey, and predator–prey combinations in different years were contrasted. With many pairwise contrasts, levels of significance were viewed critically, and only overall patterns were considered meaningful.

Individual suitabilities differed among the restricted data sets (NS81–NS87), as did the MSVPA estimates of predator and prey biomasses at age. From the North Sea youngfish surveys (IFYS) for 1981, 1985, 1986, and 1987, overlap indices (Houghton, 1986) of each age of predator and prey were calculated. Changes in suitabilities were regressed on changes in biomasses and overlap indices for all pairwise combinations of NS81, NS85, NS86, and NS87. Again, contrasts were numerous, and not fully independent, so levels of statistical significance should be treated with caution.

Results

The kernel model

The ICES Multispecies Assessment Working Group considered in depth the proper model for fitting suitabilities (Anon., 1986, 1988, 1989). The extremely large data sets (often over 6000 individual suitabilities) gave extremely sensitive statistical tests, so higher-order interaction terms were often highly statistically significant, yet accounted for little variance. The final decision on the structure of the kernel model was based largely on biological considerations, rather than on including all

Table 1. Statistics of fit of kernel model to the major data sets of suitabilities used in subsequent analyses. Differences among data sets are described in text. All model terms are significant at $p < 0.01$.

	NSALL		NSUPDATE		Restructured NSUPDATE	
Source	Sum square	d.f.	Sum square	d.f.	Sum square	d.f.
Model	13 747.8	54	11 779.8	55	11 316	115
Type III terms:						
Quarter	89.7	1	34.3	1	78.2	1
Predator	409.9	4	263.8	4	307.9	11
Prey	273.5	6	232.6	6	309.1	6
Pred. × prey	2 420.2	21	1 295.0	21	1 458.9	63
Quar. × pred.	848.2	4	610.6	4	548.0	9
Quar. × prey	1 206.7	6	1 244.0	6	1 250.2	6
Wt. ratio (pred.)	631.4	4	528.6	4	572.4	11
Wt. ratio (prey)	365.9	6	339.0	6	462.1	6
$(\text{Wt. ratio})^2$	117.8	1	81.0	1	97.8	1
Residual	16 302.8	6 346	12 313.17	5 156	12 120.8	5 095
Total r^2	0.457		0.475		0.483	
Root mean square error	1.603		1.545		1.542	

statistically significant terms. Main effects for season (quarter), predator and prey species, and the three two-way interactions (season by predator, season by prey, predator by prey) were included. For the size preference covariates, slopes of the logged weight ratio of predator to prey were calculated separately for (i.e. nested under) each predator and prey species. The non-linear components of the size preference covariate (the weight ratio term squared) was not nested, but estimated as a single term for all predators and prey. The full model is listed in Table 1. All model terms were highly significant (Table 1). Using Type III sum-squares and allowing for differences in degrees of freedom, interaction terms generally captured as much or more variance than respective main effects, and the linear weight ratio terms accounted for substantially more variance than the squared term. Depending on the individual data set of suitabilities, there were modest differences in apportionment of variance among terms, but total r^2 values were consistently between 0.45 and 0.50. Likewise, various nestings of the size preference function partitioned the variance in different ways, but never led to large changes in the total variance explained.

Variance of suitabilities among years

NS81 contains the large data set from the Year of the Stomach project. NS85 to NS87 add data from sampling in quarters 1 and 3 of 1985–1987. Any increase in variance among suitabilities from the combined NS81 to NS87 compared to NSALL must be due to changes in stomach contents from year to year for the same predator–prey combinations. When the total variances are contrasted, the increase in variance of the suitabilities is about 21% from the restricted to the total stomach data sets (Tables 1 and 2). NS87 appears the most different, but also has the fewest cases (lowest df, Table 2).

The impact of variation in stomach contents among years on suitabilities can also be examined by contrasting the residual variance of a model fit to the complete data set, and to the same data, restructured so each year's stomach data are treated as coming from a different level of the factor predator. The total variance is the same in both sets, but in the restructured data set additional levels of predator capture variation due to changes in stomach contents of the same species in different years. The error mean square decreases by less than 1% with the additional levels of the factor predator (Table 1).

Both of these looks at overall variance suggest that suitabilities are quite consistent over years. Nonetheless, several qualifiers are necessary. Several problems arise because only parts of the stomach data were replicated among years, so the research design is very unbalanced. In every data set except NS81, suitabilities for some predators are calculated using stomachs collected in other years. Which predators fall into this category changes from year to year although only 1981

Table 2. Sum of squares for model and residual, for fits of kernel model to the four individual year data sets (NS81 to NS87).

Data set	SS Model	SS Residual	Total d.f.
NS81	2 363.1	3 560.2	1608
NS85	3 028.7	3 388.6	1 614
NS86	2 564.9	4 363.7	1 609
NS87	1 960.5	3 518.1	1 565
Sum of NS8x	9 917.2	14 830.6	6 396

Table 3. Parameter estimates and standard errors of estimates for the levels of main-effect predator. Estimates taken from the kernel model fit the restructured NSALL and NSUPDATE data sets.

	NSALL		NSUPDATE	
	Parameter est.	s.e.	Parameter est.	s.e.
Cod 1981	−1.493	0.346	−0.649	0.655
Cod 1985	−1.685	0.347	−0.627	0.655
Cod 1986	−1.529	0.373	−0.616	0.656
Cod 1987	−0.219	0.333	−0.509	0.667
Whiting 1981	−0.143	0.343	−1.435	0.700
Whiting 1985	+0.605	0.333	−0.923	0.693
Whiting 1986	***		−0.877	0.698
Saithe 1981	+0.466	0.331	−1.999	0.550
Saithe 1986	−0.602	0.335	−0.521	0.566
Saithe 1987	−0.101	0.340	−1.386	0.561

stomachs were available for estimating mackerel and haddock suitabilities for NS85 to NS87. These partial redundancies among NS81 to NS87 make it challenging to determine the degree to which individual suitabilities are independent among data sets. Moreover, although the total variance changes very little with the additional years of data, there is no assurance that individual suitabilities remain stable. Possibly individual suitabilities vary from year to year, even if the overall distribution of suitabilities remains fairly consistent. The model runs make this unlikely, but the specific parameter estimates and least squares means can be examined to test these points directly.

Parameter estimates

Parameter estimates were taken from model fits to NSALL and NSUPDATE, restructured so that each year's stomach data from a predator were coded as a separate level of the factor predator. For cod as predator, parameter estimates of the main effect are very similar for all years (Table 3, Fig. 1). For whiting, parameter estimates differ somewhat more, and for saithe the estimates differ substantially. The suitabilities of saithe in 1981 appear markedly different from the patterns in later years.

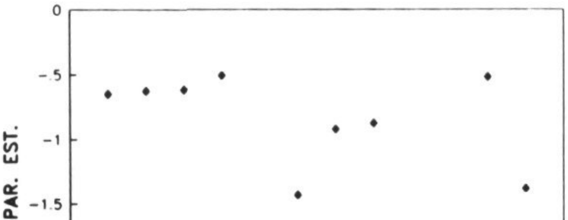

Figure 1. Parameter estimates for levels of predator, from the fit of the kernel model to the suitabilities calculated with restructured NSUPDATE. Error terms in Table 3.

A similar pattern is observed when the parameter estimates for specific predator–prey combinations (i.e. predator main effect + prey main effect + interaction) are examined. Suitabilities of various prey of cod differ somewhat in absolute value from year to year, but only for 1987 could any values be considered outliers (cod and sprat, Fig. 2). The absolute values of parameter estimates of whiting and saithe vary more among years, but order of prey remains consistent generally. The estimates of the suitability of sprat for saithe are particularly irregular. Standard errors for the interaction parameter estimates are generally between 0.310 and 0.350, except for those with cod and sprat as prey, when the standard errors were between 0.390 and 0.420. Hence the parameters rarely showed changes which would be statistically significant, were all cases wholly independent.

The slopes of the size preference terms are highly consistent for cod, and slightly less so for whiting and saithe (Table 4, Fig. 3). Standard errors are consistently between 0.14 and 0.18. Note the slopes are steeper for whiting and saithe than for cod, suggesting that cod prefer larger prey for their size than do the other two species. This also appears in the position of the peak of the size preference functions of Figure 3. The parabolas for cod peak much further to the left, indicating a preference for relatively larger prey than for whiting or saithe.

Least-squares means

The four years of suitability estimates of cod do not differ from each other (Fig. 4) using the LS means from the restructured NSALL. For whiting the differences are larger, but not statistically significant (Table 5). For saithe the 1986 value is atypically low. The whiting and saithe values come from NSUPDATE, where the popu-

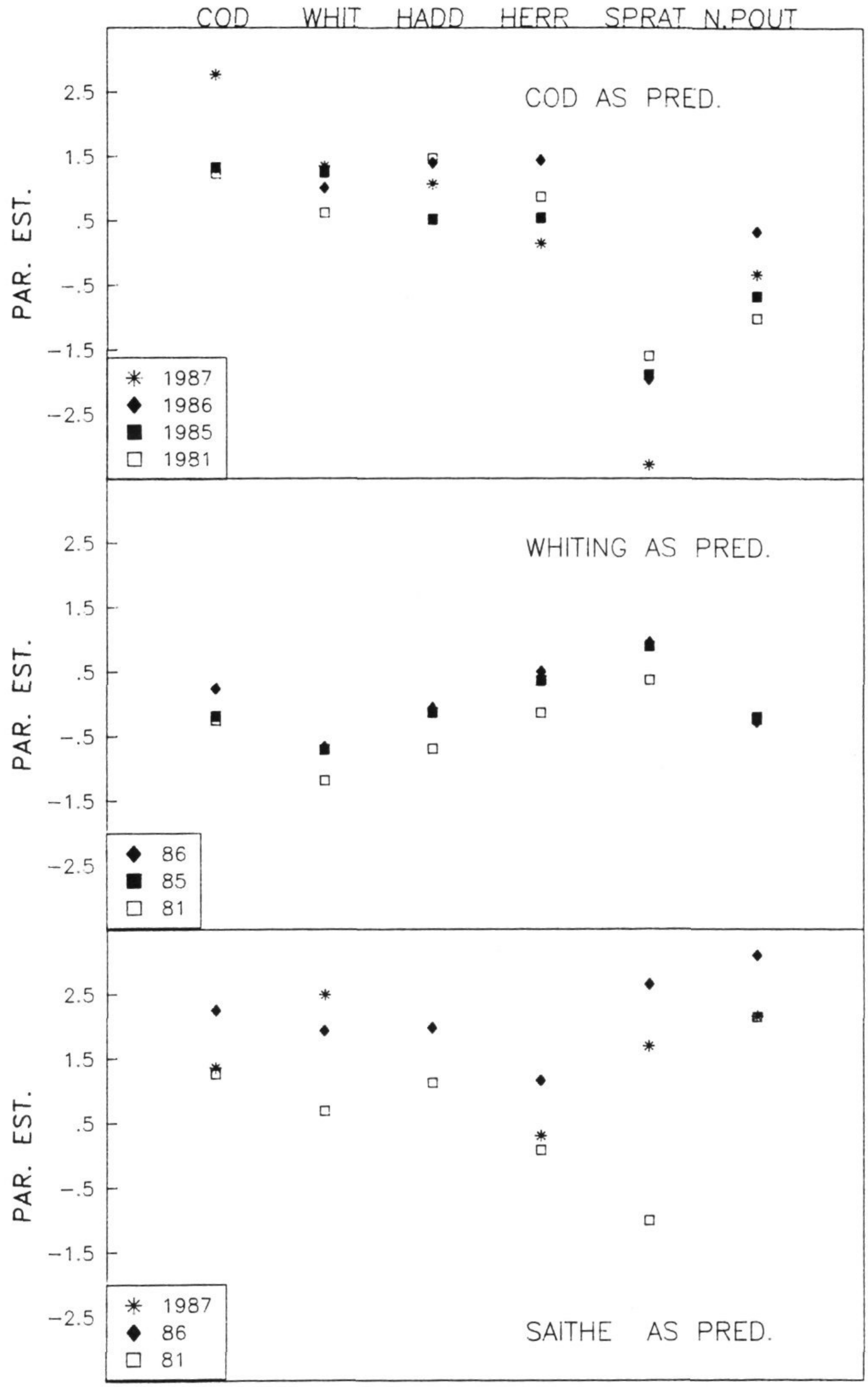

Figure 2. Parameter estimates for unique predator–prey combinations from the same sources as Figure 1.

Table 4. Parameter estimates of slopes of the logged weight ratio terms nested under each level of predator for the restructured NSALL and NSUPDATE data sets.

Predator	Year	Parameter estimates	
		NSALL	NSUPDATE
Cod	1981	0.817	0.120
Cod	1985	0.823	0.123
Cod	1986	0.788	0.120
Cod	1987	0.802	0.119
Whiting	1981	1.433	0.537
Whiting	1985	0.815	0.393
Whiting	1986	–	0.376
Saithe	1981	1.637	0.357
Saithe	1986	0.933	0.256
Saithe	1987	1.230	0.372

lation estimates of several age groups were more reliable.

There are many pairwise interaction means, so it is statistically invalid to compare them all. There are 80 unique pairwise combinations of the 12 "predators" and 7 prey, leading to 6320 contrasts of interaction means. Of these, 2721 were not significant (43.1%) at a Type I error rate of 0.01 (to the extent that levels of significance are meaningful with so many pairwise comparisons). Of the 42 contrasts of cod in one year feeding on a specific prey with cod on other years feeding on the same prey, 29 were not different, i.e. had $p > 0.01$. This is significantly more than expected, given the overall proportion of contrasts with p values greater than 0.01 ($\chi^2 = 11.58$, $p < 0.01$). For whiting, all 21 contrasts matched for predator and prey species were not different ($\chi^2 = 27.42$, $p < 0.01$), and for saithe 16 of 21 were not different ($\chi^2 = 9.53$, $p < 0.01$). On the basis of these least squares means, the actual suitabilities are more similar than expected given the overall data, even with highly inflated initial error rates.

Relationship of suitabilities to biomasses

Because of the ties between MSVPA and the Andersen–Ursin formulation of multispecies trophic associations, models fit to suitabilities contained only terms from their formulation. Associations of suitabilities and biomasses were investigated by regressing residuals of the kernel model on biomass estimates of predator and prey from the same MSVPA run. First the kernel model, including all terms in Table 1, was fitted to the suitabilities estimated with the NSALL data set. The residuals from that model fit were sorted by predator species, and separately by prey species, into 12 subsets. Each individual SUIT (y, s, a, j, b) was included in two subsets; the jth predator and the sth prey. For each subset, a regression was conducted, fitting the model:

$$\text{RESIDUAL} = \log(\text{predator biomass at age}) + \\ + \log(\text{prey biomass at age}) + \text{error}.$$

The predator and prey biomasses were estimated in the MSVPA run which calculated the initial suitabilities.

Regardless of whether the suitabilities are partitioned by predator or by prey, for all species the regressions are highly significant, with r^2 values generally moderate to

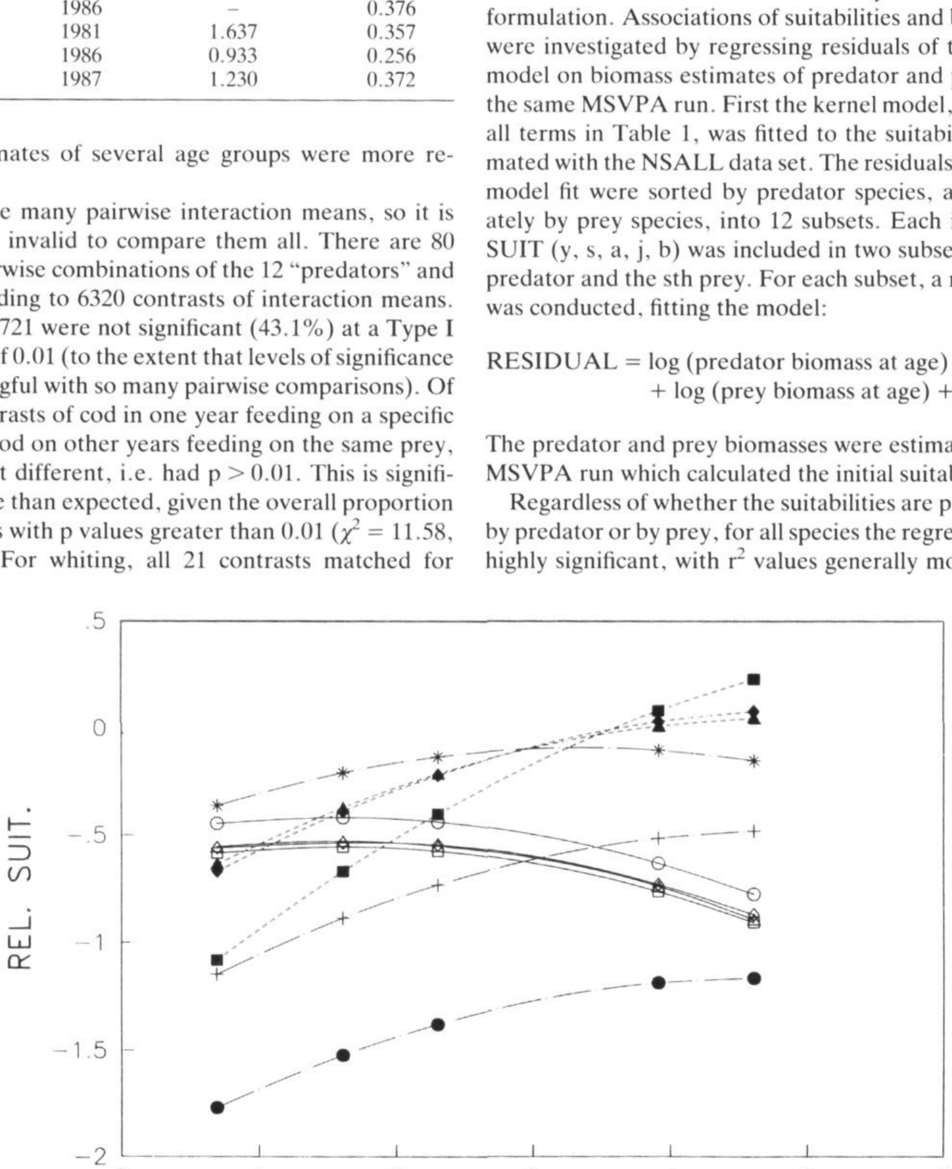

Figure 3. Curves of size preference functions for cod, whiting, and saithe as predators, from species-year specific intercepts and slopes, and global curvature parameters, estimated from the fit of the kernel model to the suitabilities calculated with restructured NSUPDATE. Separate lines for each year; solid lines for cod, dashed line for whiting, dash-dot for saithe.

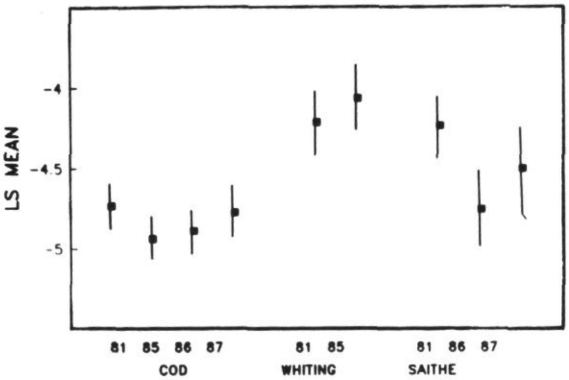

Figure 4. Least-squares means for actual suitabilities from fit of kernel model to suitabilities calculated with restructured NSALL. Bars represent two standard errors.

Table 5. Probabilities that various least-squares means are the same.

Mean 1	Mean 2	Probability
Cod 1981	Cod 1984	0.058
Cod 1981	Cod 1985	0.157
Cod 1981	Cod 1986	0.864
Cod 1984	Cod 1985	0.663
Cod 1984	Cod 1986	0.126
Cod 1985	Cod 1986	0.267
Whiting 1981	Whiting 1984	0.344
Saithe 1981	Saithe 1985	0.001
Saithe 1981	Saithe 1986	0.122
Saithe 1985	Saithe 1986	0.174

large (Table 6). The signs of the regression coefficients for predator biomasses are always positive, for prey biomasses always negative. Interpretation of these results is not straightforward, however, because biomasses of predators and prey change both from age to age and from year to year.

The same analyses were repeated with NS81 to NS87. Partitioned by predator, cod and whiting were the only species with enough different stomachs each year for meaningful tests. Only 1 of 16 possible terms was significant (Table 7a), a result expected by chance if there were no associations (binomial $P = 0.279$ if $p = \alpha = 0.05$).

Many more terms were significant when the NS81–NS87 residuals were examined prey by prey (Table 7b). The predator biomass term was significant in only 2 of 28 cases, again not different from chance (binomial $P = 0.412$). The prey biomass term was significant in 11 of 28 cases, however. It was usually significant for sprat (4 of 4) and Norway pout (3 of 4); rarely for cod (none), haddock (1), and herring (1). Signs of the regression coefficients were evenly split between positive and negative. For sprat and Norway pout the coefficients were usually (5 of 7) negative, suggesting suitabilities declined more slowly than biomass did with age. For whiting and haddock the signs were positive, suggesting suitabilities declined with age faster than biomass did. In all species, biomass at age decreased, as did numbers at age.

Changes in suitability regressions

To the extent that suitabilities did change from set to set among NS81 to NS87, the regressions of the differences in suitabilities among pairs of years on differences in predator and prey biomasses and in their overlaps explored these relationships. Cod and whiting were the only predators with enough replicated stomach data for legitimate comparisons. For whiting, four regressions

Table 6. Regression statistics for relationships of log predator and prey biomasses to residuals of kernel model fit to NSALL suitabilities.

			Slopes of biomass terms	
Species	F of regression	r^2	Predator	Prey
Predator:				
Cod	1554.3	0.602	+0.620	−0.822
Whiting	1716.0	0.715	0.683	−0.664
Saithe	515.8	0.390	0.401	−0.421
Mackerel	2162.4	0.862	0.894	−1.173
Haddock	263.7	0.500	0.439	−0.397
Prey:				
Cod	580.8	0.796	0.820	−1.079
Whiting	1083.1	0.710	0.626	−0.604
Haddock	1043.4	0.750	0.783	−0.768
Herring	1550.1	0.739	0.708	−0.773
Sprat	336.6	0.425	0.463	−0.525
Norway pout	300.8	0.370	0.384	−0.499
Sandeel	724.4	0.492	0.534	−0.564

Table 7. Regression statistics for relationship of log predator and prey biomasses to residuals of kernel model fit to portions of NS81–NS87 data. Only cod and whiting as predator were included, because there were no first quarter data from saithe, and only 1981 data for mackerel and haddock. "*" means the term was not significant at the liberal level of $p \leqslant 0.05$.

				Slopes of biomass terms	
Species	Year	F of regression	r^2	Predator	Prey
(a) Suitabilities sorted by predator					
Cod	1981	4.681	0.050	*	+0.173
Whiting	1981	1.394	0.007	*	*
Cod	1985	0.503	0.007	*	*
Whiting	1985	0.084	0.002	*	*
Cod	1986	1.505	0.008	*	*
Whiting	1986	2.640	0.030	*	*
Cod	1987	0.380	0.007	*	*
Whiting	1987	1.716	0.013	*	*
(b) Suitabilities sorted by prey					
Cod	1981	0.131	0.018	*	*
Whiting	1981	0.971	0.050	*	*
Haddock	1981	1.330	0.023	*	*
Herring	1981	5.063	0.245	*	−2.032
Sprat	1981	23.185	0.497	*	+0.390
Norway pout	1981	6.746	0.271	*	−0.308
Sandeel	1981	0.562	0.019	*	*
Cod	1985	0.377	0.055	*	*
Whiting	1985	36.797	0.117	*	+0.558
Haddock	1985	4.893	0.218	*	+0.539
Herring	1985	2.025	0.049	*	*
Sprat	1985	8.340	0.250	*	−0.376
Norway pout	1985	1.345	0.022	*	*
Sandeel	1985	0.044	0.002	*	*
Cod	1986	0.202	0.028	*	*
Whiting	1986	0.399	0.022	*	*
Haddock	1986	1.458	0.035	*	*
Herring	1986	1.289	0.015	*	*
Sprat	1986	5.612	0.173	+0.625	−0.315
Norway pout	1986	2.848	0.106	*	−0.267
Sandeel	1986	0.023	0.001	*	*
Cod	1987	0.819	0.011	*	*
Whiting	1987	2.105	0.067	*	+0.493
Haddock	1987	2.086	0.072	*	*
Herring	1987	0.121	0.007	*	*
Sprat	1987	15.241	0.463	+0.451	+0.299
Norway pout	1987	14.222	0.460	*	−0.425
Sandeel	1987	1.402	0.017	*	*

accounted for significant variance in the differenced suitabilities; for cod, three were significant, one was marginal (Table 8a). In all significant regressions of changes in suitabilities of prey for cod, the significant term was prey biomass. For whiting, three of four regressions had prey biomass as the only significant term; one had overlap. In six of the seven regressions where change in prey biomass was the significant term, the sign of the parameter was positive. This suggests suitability changed as prey abundance changed; higher suitability when a prey was abundant, and/or lower suitability when a prey was rare, relative to the prey's usual level of abundance.

When changes in suitability are partitioned by prey species, instead of predator species, the pattern is quite different. Significant (or marginal) regressions occur for about half the pairs of years for cod, whiting, haddock, and herring. For sprat and Norway pout, regressions are significant for all pairs of years (Table 8b). When the changes are partitioned by prey species, rather than by predator, significant terms in the regressions show little consistency. For sprat and Norway pout, where all six pairs of years produced significant regressions, all three influences (changes in predator biomass, changes in prey biomasses, changes in overlap) were significant in two or more regressions. Change in overlap was not a significant term for any other prey species, but changes in predator and prey biomasses were both significant in at least one case for each of the other species (although prey biomass changes were only marginal in one regression for cod).

Most regression parameter estimates are positive for the suitability changes partitioned by prey species. These suggest again prey become more suitable as they

Table 8. Regression statistics for relationship of changes in predator and prey biomasses and spatial overlap to changes in suitabilities, from the same data as in Table 7. Due to aliasing in the analyses of suitabilities, changes in suitability of sandeel as prey were not calculated.

				Slopes of terms for change in:		
				Biomasses of		
Species	Years	F of regression	r^2	Predator	Prey	Spatial overlap
(a) Changes in suitabilities sorted by predator						
Cod	81–85	3.535	0.064	*	−0.613	*
Whiting	81–85	0.910	0.039	*	*	*
Cod	81–86	1.985	0.031	*	*	*
Whiting	81–86	847.270	0.972	*	+0.897	*
Cod	81–87	0.261	0.008	*	*	*
Whiting	81–87	314.140	0.926	*	+0.903	*
Cod	85–86	2.759	0.043	*	+0.388	*
Whiting	85–86	6.859	0.201	*	*	+2.232
Cod	85–87	6.176	0.121	*	+0.478	−0.269
Whiting	85–87	1.124	0.005	*	*	*
Cod	86–87	5.302	0.108	*	+0.418	*
Whiting	86–87	446.451	0.983	*	+0.921	*
(b) Changes in suitabilities sorted by prey						
Cod	81–85	1.396	0.073	*	*	*
Whiting	81–85	1.273	0.020	*	*	*
Haddock	81–85	0.757	0.080	*	*	*
Herring	81–85	6.313	0.420	*	−2.865	*
Sprat	81–85	4.487	0.192	*	*	+0.754
Norway pout	81–85	2.847	0.160	*	*	+0.633
Cod	81–86	9.213	0.606	+1.141	*	*
Whiting	81–86	5.936	0.286	*	+1.818	*
Haddock	81–86	9.145	0.505	*	+0.916	*
Herring	81–86	1.804	0.103	*	*	*
Sprat	81–86	8.879	0.350	+1.389	*	+1.263
Norway pout	81–86	17.306	0.620	−0.560	+1.253	*
Cod	81–87	1.370	0.730	*	*	*
Whiting	81–87	1.758	0.059	*	*	*
Haddock	81–87	7.693	0.427	*	+0.688	*
Herring	81–87	3.491	0.237	*	*	*
Sprat	81–87	8.119	0.366	+2.273	*	*
Norway pout	81–87	9.481	0.451	*	+0.728	*
Cod	85–86	6.112	0.505	*	*	*
Whiting	85–86	2.261	0.093	*	*	*
Haddock	85–86	0.866	0.015	*	*	*
Herring	85–86	3.709	0.181	*	*	+2.529
Sprat	85–86	4.281	0.186	*	+0.543	*
Norway pout	85–86	6.047	0.335	*	*	+2.093
Cod	85–87	3.658	0.380	*	−1.113	*
Whiting	85–87	4.030	0.202	+1.069	*	*
Haddock	85–87	2.636	0.149	*	*	−0.326
Herring	85–87	5.753	0.278	+3.366	*	*
Sprat	85–87	4.017	0.201	*	+0.812	*
Norway pout	85–87	3.335	0.195	−1.289	*	*
Cod	86–87	4.609	0.437	+1.879	*	*
Whiting	86–87	7.341	0.346	+1.166	*	*
Haddock	86–87	4.096	0.271	+0.699	*	*
Herring	86–87	8.867	0.389	+1.094	*	*
Sprat	86–87	18.378	0.591	*	+1.084	*
Norway pout	86–87	5.115	0.292	+1.100	*	*

become more abundant. It is worth noting that for Norway pout, in two of the three cases where change in predator biomass is a significant predictor of change in prey suitability from one year to another, the regression coefficient is negative. This suggests predators, when scarce, feed proportionately more on Norway pout, or else they feed less on Norway pout when the predators become common.

Discussion

To summarize the results, only 17% of the total variance in suitabilities was due to interannual effects, including any sampling error among years as well as any systematic changes in preferences and vulnerabilities. Parameter estimates were quite stable over four years, and where changes in absolute values were observed, relative patterns among species persisted. The general stability of parameter estimates was present in terms of predators alone (consistent preferences), prey alone (consistent vulnerabilities), or specific combinations of predators and prey.

The bottom line from these diverse analyses is that the suitabilities are quite consistent over time. This is a reassuring finding, in that it suggests that if a multispecies model represents processes correctly, and if there are adequate data to parameterize the model for a specific system, those parameters may remain stable long enough for the model to be useful in management. The analyses also suggest MSVPA assumptions are generally good ones, although several avenues which may lead to improvements are discussed below.

Any statistically oriented fisheries scientist could point out problems with the suitability data sets. The partial repetition of stomach contents from one year to calculate suitabilities in another year, even for the NS81 to NS87 data set, means the suitabilities are not wholly independent. We must await the results of the major stomach sampling programme which ICES plans for 1991 to provide enough data to parameterize MSVPA completely independently of the 1981 data. If the MSVPA parameterized with 1991 data provides results very similar to the present ones, it will be strong support for using MSVPA in developing long-term management advice.

Unfortunately, many things in the North Sea will have changed in the decade from 1981 to 1991. If suitabilities from the 1991 data do differ greatly from those derived from the 1981 data, it will be difficult to interpret the changes. Possibly the multispecies dynamics of the predators and prey in MSVPA will have remained reasonably consistent, but the environment in which those interactions are played out has altered greatly. A decade is a long time for any parameterized model to describe a system; even an excellent model of a simple system.

If the 1991 results differ greatly from the 1981 results, it will be important to determine why results and suitabilities have changed. If ecosystem dynamics are changing markedly due to environmental degradation, ocean climate change, or any other reason, the changes may make management strategies based on historic data and single-species models at least as inappropriate as management strategies based on multispecies models. What may be shown is that multispecies models are much more sensitive indicators of human impacts (or other influences) on the ecosystem and all its components including important fisheries, than single-species models are.

The results suggest MSVPA is at least a good model of a complex system. The 21% increase in variance of suitabilities from pooling four years of data compared to four single years of data may not be the true upper limit to the variance in suitabilities, as there were only replicated data for 12 of the 20 predator–year combinations. However, even some of this increase may be captured in future multispecies models. From the regression analyses, the changes in suitabilities seem to be affected by changes in prey biomass in several cases. There is already substantial interest in the shape of feeding relationships among predators and prey (Hilden, 1988; Lilly, 1991; Magnusson and Pálsson, 1991). These analyses suggest that it may be useful to explore prey abundance in the context of MSVPA, or to pursue the finding of the multispecies working group that prey biomass could be an important term in models used to smooth suitabilities (Anon., 1988).

The fact that prey biomass influences suitabilities raises an additional possibility. As discussed in Gislason and Sparre (1987), the mean weight of a specific age of prey in the sea may differ markedly from the mean weight of that age of prey in a predator's stomach. The size preference of predators suggests that when predators consume prey which are relatively younger than optimal for a given size (age) of predator they maintain the preferred size ratio by eating the largest prey in the age group. The calculation of suitabilities in MSVPA allows an overall size preference but requires that the age-specific selectivity pattern remain constant. A large change in biomass-at-age of a prey could also change the distribution of weights for that age group. Perhaps more small prey survive in a large year class, so the distribution of weights in the sea shifts to the left, or perhaps prey grow faster and are larger at age, shifting the distribution to the right. If the size preference of the predator did not change, it would harvest different portions of these distributions. With the MSVPA assuming no change in the portion of the size distribution eaten, suitabilities would be different with data from the different prey biomass scenarios. Therefore, it would be worthwhile first examining size distributions at age for prey whose biomasses changed. If the size distributions altered, it would be informative to examine any changes in appropriate suitabilities to see if they reflected feeding on the same sizes of prey drawn from changing distributions of prey available. If that turns out to be an important factor, MSVPA could be modified to incorporate it.

Even without further additions, the degree of stability shown by the suitabilities in MSVPA suggests the model can be used with confidence to provide advice on fish stocks in the North Sea. More generally, these results should encourage those developing multispecies models for provision of advice on other systems, as long as enough work is done to formulate and parameterize them well.

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Multispecies virtual population analysis of North Sea predators for the years 1963–1987

J. G. Pope and C. T. Macer

Pope, J. G., and Macer, C. T. 1991. Multispecies virtual population analysis of North Sea predators for the years 1963–1987. – ICES mar. Sci. Symp., 193: 46–49.

A modified version of MSVPA, based on a simple model for deriving predation mortalities, has been used to estimate population numbers and mortality rates for the main predators in the North Sea for years earlier (1963–1973) than those for which appropriate data are available for use in the full MSVPA. The results suggest that predation mortality was higher in the earlier years. Hence, the resultant estimates of population numbers in the young fish diverge increasingly from those derived from single species VPA, as the time series is extended backwards.

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Introduction

The multispecies virtual population analysis (MSVPA) adopted by the ICES Multispecies Working Group (Anon., 1984) is based on the method of Gislason and Helgason (1988). The method assumes that the various prey items eaten by a predator are taken in proportion to the prey biomass multiplied by a suitability factor. Thus, in a run of MSVPA it is necessary to have catch-at-age data for all prey and predator species included in the analysis for all years. This limits the scope of the analysis to the time series of the shortest data set. For the North Sea, the shortest data set begins in 1974 (Anon., 1984). It would obviously be desirable to run the MSVPA further backwards to include earlier years but this would require either constructing dubious catch-at-age data for some species or including prey species for which only recent data are available in the "other food" compartment of the model.

An alternative to this approach is to develop a retrospective analysis using the simple feeding model proposed by Shepherd (1988). This model assumes that the predation mortality on a prey item, generated by a predator age group, is proportional to the biomass of the predator alone. With this model, there is no need to consider the availability of other prey items and it suffices to have catch-at-age data for the predators only. However, there is an implicit assumption that any changes in the biomass of other prey will not affect the predation generated on the species included. The purpose of this contribution is to develop a simple version of MSVPA based on the Shepherd feeding model and to apply it to the North Sea for as many years as possible.

Theory

The simple model proposed (Shepherd, 1988) for making multispecies predictions can be adapted to yield a MSVPA-like method of retrospective analysis. A modified version of this model assumes that predation mortality (M2) for a given prey (j) of age (b) in a particular year (y) caused by all predators denoted by species (i) of age (a) is given by:

$$\mathrm{M2(j,b,y)} = \sum_{\mathrm{i}} \sum_{\mathrm{a}} \mathrm{UM2(i,a,j,b,@)} * \bar{\mathrm{P}}\mathrm{(i,a,y))} \qquad (1)$$

where UM2 is the average predation mortality generated by one individual of the predator age group for some averaging period (@). The advantage of this formulation is that only the average numbers of predators ($\bar{\mathrm{P}}$) are needed to estimate M2 and thus a form of MSVPA can be extended backwards in time to cover periods when catch-at-age data are available for the predator species but not for all prey species.

The procedure for applying the method was chosen for simplicity rather than strict accuracy. First, the surviving populations are estimated for each cohort to give P(j,b,t + 1) and P(j,g + 1,y), where t and g denote the last year and oldest age of species j, respectively.

Table 1. Average values of fishing mortality (yr^{-1}) per 5-year period.

Species	Age	1963–1967	1968–1972	1973–1977	1978–1982	1983–1987
Cod	0	0.00	0.00	0.00	0.00	0.00
	1	0.03	0.04	0.09	0.11	0.14
	2	0.45	0.63	0.79	0.96	0.85
	3	0.58	0.74	0.76	1.00	0.85
Whiting	0	0.02	0.12	0.03	0.07	0.05
	1	0.24	0.44	0.30	0.16	0.19
	2	0.56	0.67	0.81	0.40	0.41
	3	0.74	0.78	1.16	0.71	0.74
Haddock	0	0.04	0.01	0.01	0.05	0.01
	1	0.61	0.16	0.26	0.21	0.13
	2	0.70	0.71	0.77	0.68	0.75
	3	0.67	1.11	1.02	1.04	1.04

Then $\bar{P}(j,b,t)$ is initially estimated as $P(j,b+1,t+1)$. Note that $P(i,a)$ and $P(j,b)$ may overlap, but UM2 is non-zero only for predator–prey interactions found in MSVPA. Thus, for example, we treat 1-year-old cod as potential predators on 10-year-old cod, but they generate zero predation mortality. Equation (1) is then used to estimate $M2(j,b,t)$, using values of UM2 obtained from the standard MSVPA. A file containing such results is a standard output of the MSVPA. Given estimates of all $M2(j,b,t)$ it is possible to estimate all $P(j,b,t)$, using a simple cohort analysis formulation:

$$P(j,b,t) = \left[C(j,b,t) + \sum_{i}\sum_{b} M2(j,b,y) * \bar{P}(j,b,t)\right] \times \exp(M1/2) + P(j,b+1,t+1)\ \exp(M1) \qquad (2)$$

where M1 is natural mortality other than that due to predation. It is then straightforward to estimate total and fishing mortality and hence acquire a new and better estimate of $\bar{P}(j,b,t)$. The above sequence of steps is repeated until the values of the M2 values stabilize. The equivalent analysis is then continued for year $t-1$ and so on, backwards to the earliest year.

Data

Five species (the predators in standard MSVPA) were included in the analysis: cod, whiting, saithe, mackerel, and haddock. The data input were: catch-at-age for the period 1963 to 1987, mean weight-at-age in the catch and in the stock, the maturity ogive, natural mortality other than that due to predation (M1), the population number at the start of 1988, survivor population size, and M2 per unit predator number. The data sources for catch-at-age and mean weight-at-age were the single species working group files as supplied to the Multispecies Working Group (Anon., 1989), except for pre-1969 mackerel data which were estimated from Postuma (1972) and from Norwegian data kindly provided by D. Skagen (pers. comm.). The other data were the same as those resulting from the current MSVPA run (Anon., 1989), except that survivor population sizes for earlier years

Table 2. Average values of predation mortality (yr^{-1}) per 5-year period.

Species	Age	1963–1967	1968–1972	1973–1977	1978–1982	1983–1987
Cod	0	1.32	1.13	1.00	0.61	0.50
	1	0.53	0.67	0.53	0.50	0.41
	2	0.16	0.22	0.16	0.13	0.11
	3	0.09	0.12	0.09	0.07	0.07
Whiting	0	0.96	1.10	1.16	1.01	0.74
	1	0.53	0.63	0.50	0.57	0.44
	2	0.15	0.21	0.14	0.13	0.11
	3	0.10	0.14	0.10	0.08	0.07
Haddock	0	0.94	1.38	1.22	1.05	0.99
	1	0.78	1.72	1.37	0.99	1.18
	2	0.11	0.16	0.12	0.10	0.08
	3	0.06	0.08	0.06	0.05	0.04

Table 3. Average values of population number (millions) per 5-year period.

Species	Age	1963–1967	1968–1972	1973–1977	1978–1982	1983–1987
Cod	0	3 599	2 869	2 055	1 842	933
	1	533	639	474	633	423
	2	160	230	117	226	173
	3	52	69	51	58	45
Whiting	0	21 949	20 382	25 722	15 645	11 626
	1	4 199	5 723	6 078	4 098	3 122
	2	1 186	1 214	1 663	1 250	747
	3	431	376	383	564	259
Haddock	0	113 312	105 638	73 326	25 686	30 720
	1	5 859	28 025	11 842	4 687	5 888
	2	911	2 628	1 516	635	669
	3	329	787	655	217	219

Table 4. Average values of spawning-stock biomass (000 t) per 5-year period.

Species	1963–1967	1968–1972	1973–1977	1978–1982	1983–1987
Cod	124	175	121	91	78
Whiting	249	219	236	283	167
Haddock	340	740	512	232	214

were based on catch data for the oldest age and assumed values for fishing mortality.

Results

A run was made for the period 1963–1987 and ages 0–10 for the five North Sea predator species. Tables 1–3 present the average levels of fishing mortality, predation mortality, and population numbers for ages 0–3 for cod, whiting, and haddock for each of the five 5-year periods between 1963 and 1987. Table 4 gives the estimates of spawning biomass. Results for saithe and for mackerel are not shown because they do not suffer predation mortality in the model and thus have similar population

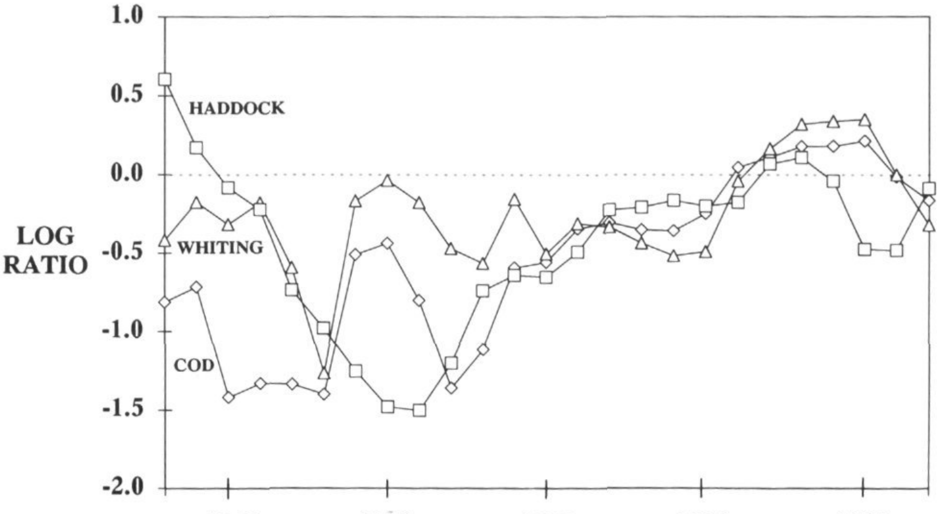

Figure 1. The log ratio of population numbers at age 0 as estimated from single-species VPA to those from multispecies VPA for the period 1963–1987, for cod, haddock, and whiting.

Table 5. Comparison of values of predation mortality (M2). A: present work; B: Multispecies Working Group (Anon. 1989).

		Period 1974–1980		Period 1981–1986	
		Model		Model	
Species	Age	A	B	A	B
Cod	0	0.801	0.775	0.443	0.489
	1	0.507	0.426	0.375	0.427
	2	0.137	0.116	0.108	0.113
	3	0.079	0.071	0.061	0.061
Whiting	0	1.116	0.935	0.656	0.755
	1	0.517	0.441	0.434	0.499
	2	0.129	0.111	0.108	0.117
	3	0.085	0.072	0.066	0.071
Haddock	0	1.144	0.930	0.950	1.022
	1	1.160	1.066	1.095	1.249
	2	0.104	0.094	0.082	0.090
	3	0.049	0.043	0.042	0.043

parameters whether assessed with a single or multispecies analysis.

The results indicate that, after an initial general increase, predation mortality on the younger ages systematically declines through the remainder of the period, in response to reductions in predator biomass. To compare the multispecies results with equivalent single species results, the model was rerun with UM2 set to 0 and the M1 term increased to the average levels of M1 + M2 for 1978–1982 presented in Anon. (1989). The single and multispecies estimates of the populations of 0-group fish indicate that the two models increasingly diverge in the earlier years. Figure 1 shows the difference between the log numbers of 0-group fish estimated for each species by the single species and multispecies models.

Discussion

The present results from the simplified version of MSVPA compare reasonably well with those from the full MSVPA, as shown in Table 5. This table compares values of predation mortality for ages 0–3, as estimated from the present method, with those resulting from the full MSVPA (Anon., 1989) for two different periods (1974–1980 and 1981–1986). Comparisons with single species VPA results over the full period suggest that the latter may contain some systematic biases in recruitment estimates due to changes in natural mortality on some species. This in turn is due to the change in the biomasses of some of the important predators over the time period, particularly the collapse of the mackerel stock.

There is the implicit assumption in the present method that the level of food available to predators has not shifted sufficiently to affect the predation mortality per unit biomass imposed on the species included. However, there have been changes in the abundances of some prey stocks over the time period, with herring for example being at a considerably higher level in the earlier years (Burd, 1978). Such changes could have affected the relative levels of predation on the various prey species and have recruitment estimates.

Improved estimates of recruitment in the earlier years are important because they may, for example, help us to comprehend the "gadoid outburst" (see, e.g. Cushing, 1984). The present work suggests that multispecies models may be necessary to obtain a consistent picture of recruitment to North Sea stocks.

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The influence of variations in recruitment on multispecies yield predictions in the North Sea

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Because of interactions among fish predators and their prey, multispecies predictions of yield are not directly proportional to recruitment as in the single species Y/R model. It is therefore important to examine to what extent changes in recruitment will affect the results. A Monte Carlo simulation technique is used to study the influence of variations in recruitment to the North Sea fish stocks on the yield predictions of the MSFOR model. Recruitment is drawn at random from a lognormal distribution and the average long-term yield is estimated. In an attempt to include interactions not accounted for by the model, a principal components analysis is used to preserve the observed correlation between recruitment to the various stocks in the forecast. The results show that the long-term predictions of yield of the MSFOR model are largely insensitive to random variation in recruitment. They are, however, sensitive to the level around which this variation occurs. Taking the correlation of recruitment into account does not change this conclusion.

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Introduction

In the classical single-species model of Beverton and Holt (1957) the yield is directly proportional to recruitment. This is not the case when species interactions are taken into account. In the multispecies VPA (MSVPA) and corresponding forecast (MSFOR) used by the Multispecies Working Group (Gislason and Sparre, 1987; Anon., 1988) predation mortality is proportional to the number of predators and inversely proportional to the total amount of food available to the predators. This implies that the total natural mortality will change as the stock sizes of predators and prey change. The change in natural mortality with stock size makes long- and medium-term predictions from the MSFOR model dependent on recruitment. As shown in Anon. (1987) the long-term yield is highly sensitive to changes in recruitment. Long-term yield was in fact found to be more sensitive to recruitment than to predator rations, to residual mortality, and to the amount of other food.

This paper is an attempt to study how the level of recruitment and fluctuations around this level affect yield and biomass predictions from the MSFOR model.

The literature on fisheries biology is full of attempts to explain variation in recruitment by the size of the spawning stock, biological interaction, and environmental influences. Instead of constructing a recruitment model based on postulated causal links between recruitment and spawning-stock size, abiotic factors, and biological interactions, recruitment is here assumed to be constant, to be randomly fluctuating around a constant level, or to be fluctuating around a constant level in a way which takes interspecific correlations into account.

The MSVPA and MSFOR models

The MSVPA is used by the ICES Multispecies Assessment Working Group to provide estimates of the stock size, predation mortality, and fishing mortality of commercially exploited fish stocks in the North Sea (Pope, 1991).

The MSVPA model is an extension of the single species VPA (Gulland, 1965). The only difference is that the natural mortality is split into a mortality, M2, due to predation and a constant residual mortality, M1, due to all other natural causes. The predation mortality, M2, is accounted for by adding one more equation to the usual VPA equations:

$$C_{i,t} = F_{i,t} \times N_{i,t+1} \times (e^{Z_{i,t}} - 1)/Z_{i,t}$$

$$N_{i,t} = N_{i,t+1} \times e^{Z_{i,t}}$$

$$M2_{i,t} = \sum_{p} S_{p,i} \times R_p \times \bar{N}_{p,t}/(\bar{N}_{i,t} \times W_i)$$

where the summation runs over all predator species age groups, p, and

$$\bar{N}_{i,t} = N_{i,t+1}(e^{Z_{i,t}} - 1)/Z_{i,t}$$

$$Z_{i,t} = F_{i,t} + M1_i + M2_{i,t}$$

where: $N_{i,t}$ = stock size of prey species age group i at time t; $C_{i,t}$ = catch of i during the time interval from t to t + 1; $Z_{i,t}$ = total mortality; $F_{i,t}$ = fishing mortality; $S_{p,i}$ = fraction of the food of predator species age group p which constitutes prey species age group i; R_p = total food intake (per individual) of p in time interval from t to t + 1; $\bar{N}_{i,t}$ = average stock size of i in time interval from t to t + 1; and W_i = body weight of species age group i.

If estimates of food intake and food composition are available for each time interval these equations can be solved without having to make any more assumptions than required for solving the single species VPA. However, as this is seldom the case additional assumptions are required. The first of these is that the food intake, R_p, is constant over time, the second is that the food composition can be described as a function of the available prey by an equation from Andersen and Ursin (1977):

$$S_{p,i} = \frac{G_{p,i} \times \bar{N}_{i,t} \times W_i}{\sum_j G_{p,j} \times \bar{N}_{j,t} \times W_j + G_{p,o} \times B_o}$$

where the summation runs over all prey species age groups, $G_{p,i}$ is a constant which reflects the suitability of a particular prey species age group, i, to predation by a particular predator species age group, p, and B_o is the biomass of "other food", o, i.e. food consisting of species not included directly in the model. Assuming suitability and other food to be constant over time makes it possible to estimate the suitabilities, $G_{p,i}$, within the model provided food composition data is available for one or several time intervals (Gislason and Sparre, 1987).

Given catch in numbers at age, food composition, food intake, weight-at-age, and fishing mortality for the oldest age group in each cohort the equations are solved simultaneously for all predator and prey stocks within a given time interval. As in the single species VPA the estimated stock numbers are then used as input to the calculations for the preceding time interval. For each cohort the calculations are only carried back to 1 July for the 0-group; therefore MSVPA does not account for predation on eggs, larvae, and small juveniles.

The output from the MSVPA consists of estimates of stock sizes, fishing mortalities, predation mortalities, and suitability coefficients.

The MSFOR model is the predictive counterpart of the MSVPA and is based on the same set of equations. The predation parameters and terminal stock sizes are transferred from the MSVPA, but as the traditional single species forecast, the MSFOR requires estimates of the future recruitment and fishing mortalities.

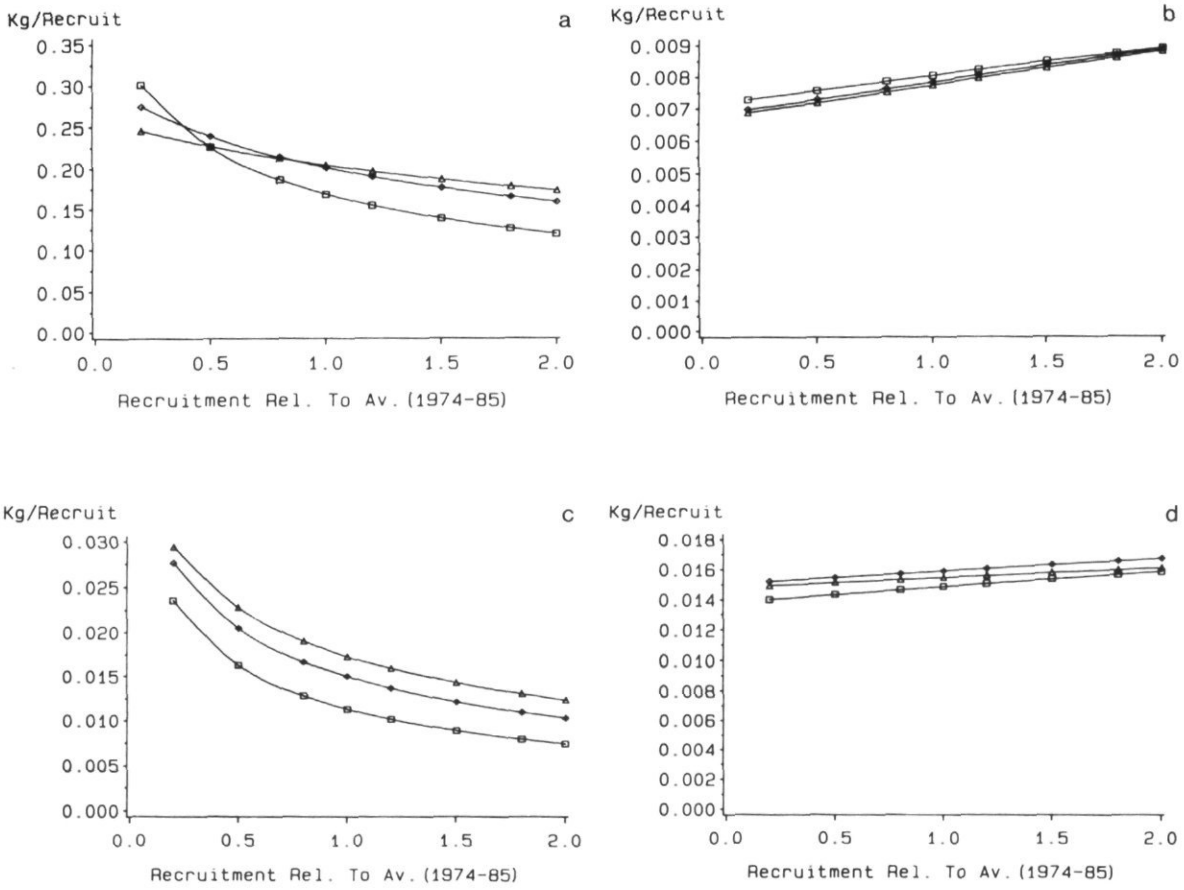
The MSFOR program and database used in this paper is the same as was used at the 1988 meeting of the ICES Multispecies Assessment Working Group (Anon., 1988). The database includes cod, whiting, saithe, mackerel, and haddock as predators and cod, whiting, haddock, herring, sprat, Norway pout, and sandeel as prey. In the predictions the status quo level of fishing mortality is defined as the average (1980–1985) fishing mortality at age estimated from the MSVPA and recruitment as the number of 0-group fish at 1 July from the MSVPA for the period 1974 to 1985 (Table 1).

Changing the level of recruitment

The MSFOR model was run until an equilibrium situation was obtained in which the change in stock size in numbers at age was less than 0.01% over a 9-year period. This usually required predicting approximately 50 years ahead. The predictions were repeated with recruitment changed for one stock at a time from 20% to 200% of the average of the period 1974 to 1985. At each level of recruitment the Y/R was calculated in the equilibrium situation. For each stock the calculations were repeated for three values of average fishing mortality, a 50% reduction, status quo, and a 50% increase. Figure 1 shows Y/R versus recruitment for cod, whiting, haddock, herring, sprat, Norway pout, and sandeel. No results are presented for saithe and mackerel, which are not predated upon and therefore behave in accordance with the traditional single-species model in which Y/R is independent of recruitment.

As seen in Figure 1, Y/R changes in a non-linear way as a function of recruitment. As recruitment increases Y/R declines for cod and whiting and increases for haddock, herring, sprat, Norway pout, and sandeel. The decline for cod and whiting is an effect of cannibalism. When recruitment increases the total stock size will increase. This leads to an increase in the mortality due to cannibalism, to a decrease in the survival of the recruits, and to a subsequent reduction in Y/R. The increase in the Y/R of the prey species is a result of predator satiation. As prey biomass increases the predators will eat a decreasing proportion of the prey biomass, natural mortality will decrease, and Y/R will increase.

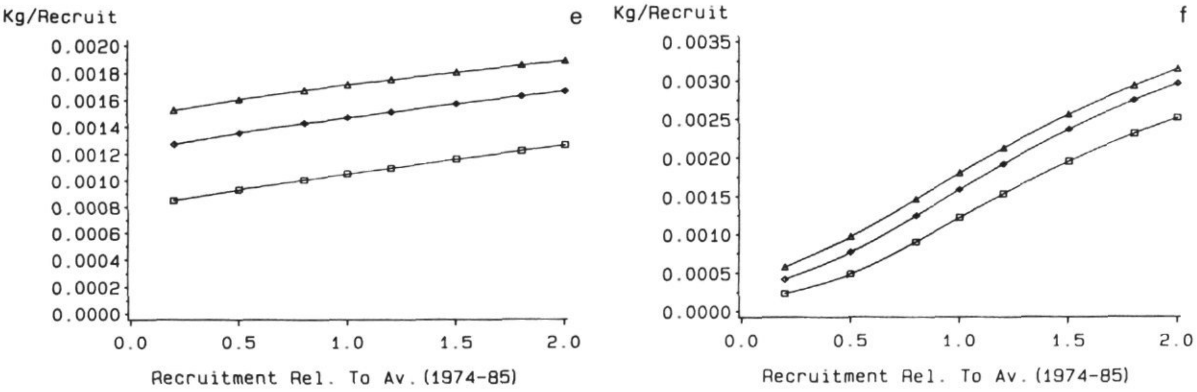
With the exception of cod, the Y/R changes in the same way irrespective of the level of fishing mortality. The curves are close to parallel. This signifies that the shape of the Y/R curve in this range of fishing mortality is unaffected by recruitment to the stock itself. For cod, however, the three curves intersect. At the present level of recruitment a small gain in yield is to be expected by increasing the fishing mortality by 50%, but if the level



of recruitment is reduced to 20% of the present the conclusion is the opposite. The highest Y/R is now obtained when the fishing mortality is reduced. The explanation for this somewhat surprising result is that cannibalism is insignificant when the stock size of cod is low (low recruitment), but increases in significance as the stock size increases (high recruitment). If cannibalism is of minor importance the yield will increase as fishing mortality is reduced and cod is allowed to reach a larger size before it is caught. If cannibalism is important the highest yield is obtained by increasing the fishing mortality in order to reduce the adult stock and protect the juveniles. In terms of the usual Y/R curve this means that the shape of the curve will change and F_{MSY} will shift from the right to the left of the present level.

Remembering that the outcome of Y/R calculations reflects the balance between natural mortality, fishing mortality, and rate of growth it is not surprising that the three curves do not intersect for whiting even though whiting is also a cannibal. The total rate of natural mortality of whiting is at the same level as for cod, but the rate of growth is much lower. For this reason and as shown by Figure 2 the yield curve of whiting does not exhibit a maximum as it does for cod. Decreasing mortality due to cannibalism by reducing recruitment to 20% of the present level does not reduce the total natural mortality sufficiently to produce a Y/R curve with a maximum to the left of the present level of fishing mortality. In terms of Figure 1 this means that the three curves do not intersect when recruitment is reduced.

In the present formulation of the food selection model, i.e. with a constant amount of other food, reducing recruitment for all species at the same time will lower the level of predation mortality. When the stock sizes of prey are low predation mortality will be roughly proportional to the stock size of the predators. As the predator stocks are reduced the Y/R curves will change towards the single species Y/R curves with a constant natural mortality equal to the constant other mortality, M1. This means that the single species Y/R curve will function as an upper limit to the multispecies predictions.



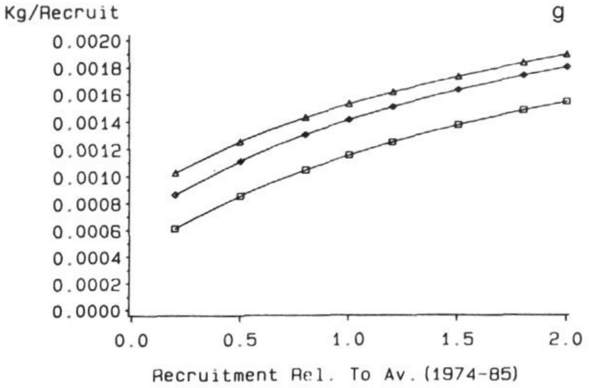


Figure 1. Yield per recruit as a function of recruitment for three levels of fishing mortality. □: 50% reduction, ◇: present level, △: 50% increase. (a) Cod, (b) haddock, (c) whiting, (d) herring, (e) sprat, (f) Norway pout, (g) sandeel.

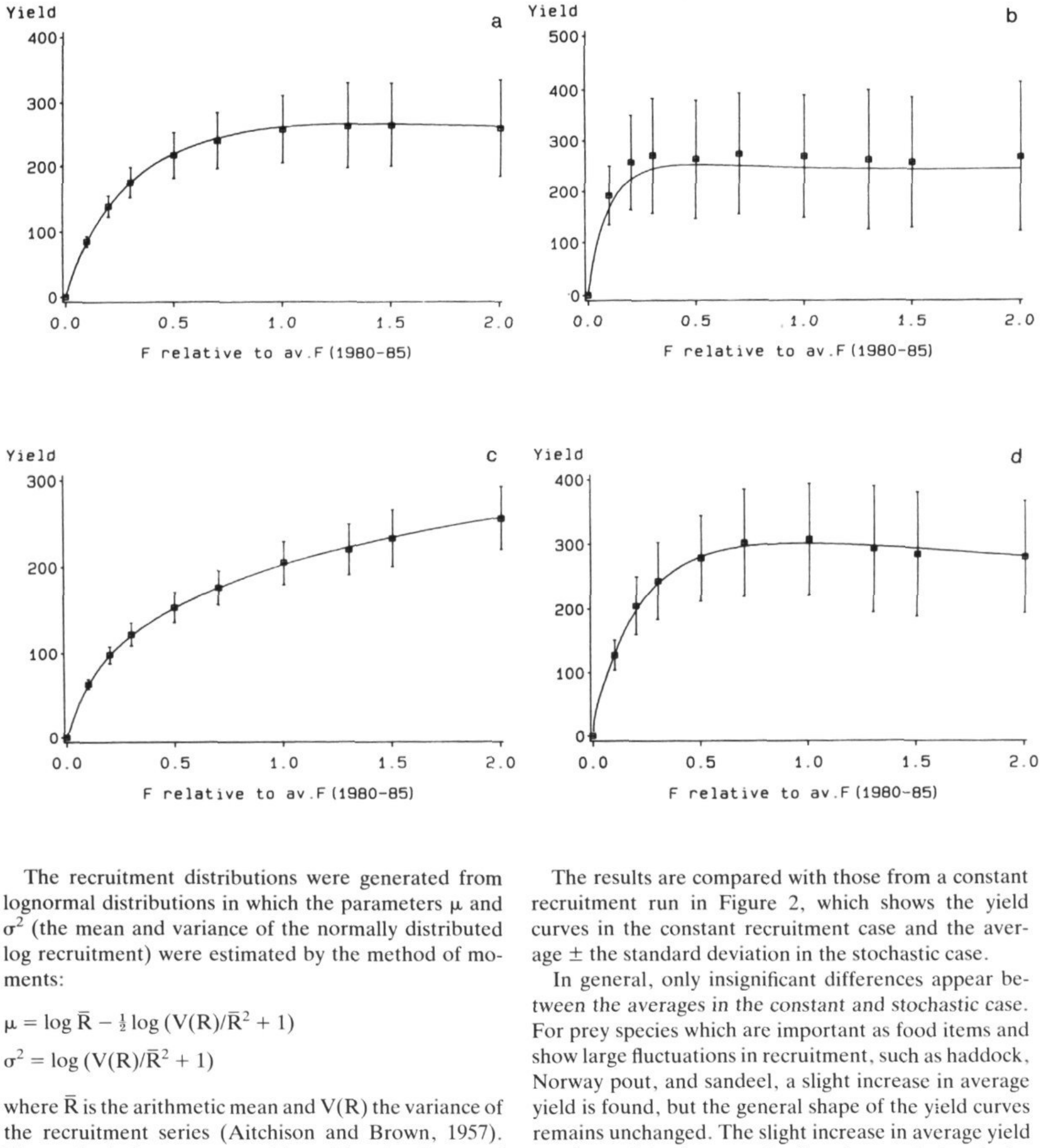
The effect of random fluctuations in recruitment

As shown in Figure 1, yield per recruit is a non-linear function of recruitment. Year-to-year variations in recruitment will thus produce non-linear responses which, if important, may change the average long-term predictions, e.g. by reducing large year classes less than small.

It is generally believed that recruitment fluctuations are lognormally distributed (Hennemuth *et al.*, 1980). Recruitment was therefore modelled as a stochastic process by random selection from a lognormal distribution with a mean and variance equal to the arithmetic mean and variance of the historic recruitment estimates from the MSVPA (0-group, 1 July) in the period 1974–1985 (Table 1).

Table 1. Estimates of recruitment (0-group, 1 July) from MSVPA (in millions). Data from Anon. (1988).

	Species								
Year	Cod	Whiting	Saithe	Mackerel	Haddock	Herring	Sprat	Norway pout	Sandeel
1974	1 479	17 388	210	590	82 749	16 659	386 873	336 486	1 376 701
1975	693	16 124	133	316	10 148	3 355	530 123	466 621	842 078
1976	2 449	15 595	144	190	12 935	3 097	293 887	343 641	825 973
1977	1 306	17 541	130	34	24 893	4 461	276 389	178 131	823 558
1978	1 330	18 589	296	113	28 548	4 681	464 121	231 383	596 900
1979	2 470	19 802	190	160	44 215	12 824	197 196	241 322	674 895
1980	988	14 049	235	238	20 040	18 711	124 377	124 003	345 929
1981	1 534	8 624	386	254	30 690	30 423	60 983	376 187	832 013
1982	732	7 213	571	30	17 876	40 913	31 599	277 541	252 674
1983	1 313	7 913	528	8	46 555	34 054	104 758	220 317	643 445
1984	267	7 579	175	550	25 723	23 301	133 759	222 510	199 935
1985	1 180	11 851	246	118	32 424	34 776	20 659	278 608	885 688



The recruitment distributions were generated from lognormal distributions in which the parameters μ and σ^2 (the mean and variance of the normally distributed log recruitment) were estimated by the method of moments:

$$\mu = \log \bar{R} - \tfrac{1}{2} \log (V(R)/\bar{R}^2 + 1)$$

$$\sigma^2 = \log (V(R)/\bar{R}^2 + 1)$$

where $\bar{R}$ is the arithmetic mean and V(R) the variance of the recruitment series (Aitchison and Brown, 1957). The method of moments provides unbiased estimates of μ and σ^2 which are less efficient than the maximum likelihood estimators. They were nevertheless preferred because they generate simulated values with an arithmetic mean and variance identical to the observations and hence render the stochastic and constant recruitment runs directly comparable.

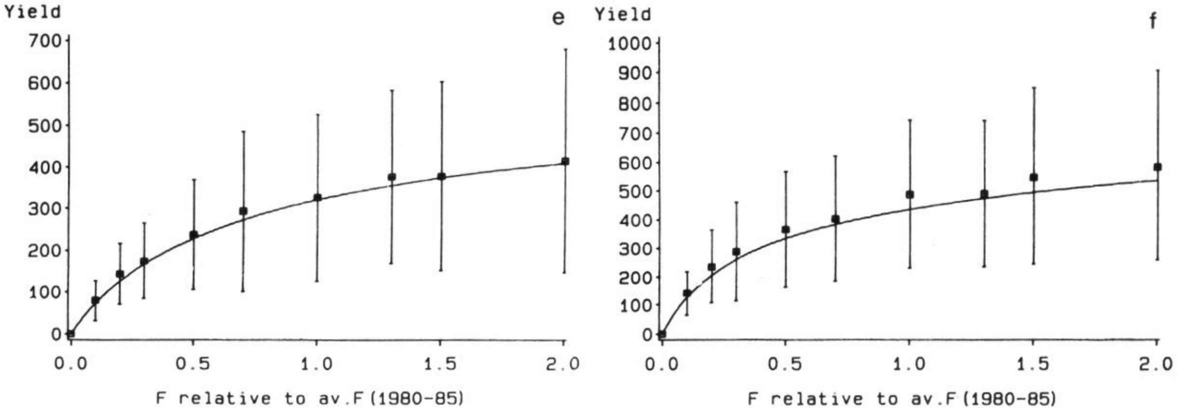
The MSFOR was then run for 1000 years in each of which a new set of recruitment estimates was drawn at random. At the end of the 1000 year period the average and standard deviation of the catch and spawning-stock biomass (SSB) was estimated.

The results are compared with those from a constant recruitment run in Figure 2, which shows the yield curves in the constant recruitment case and the average ± the standard deviation in the stochastic case.

In general, only insignificant differences appear between the averages in the constant and stochastic case. For prey species which are important as food items and show large fluctuations in recruitment, such as haddock, Norway pout, and sandeel, a slight increase in average yield is found, but the general shape of the yield curves remains unchanged. The slight increase in average yield may be explained as a result of predator satiation. In the MSFOR (and MSVPA) the predators have a fixed total ration which sets an upper limit on the amount predated. When a large year class occurs the predation mortality will be reduced and Y/R will increase.

Including interspecific correlations

The above predictions were based on preserving the mean and the variance of the observed recruitment in the period from 1974 to 1985. At best this is an oversimplified representation of the recruitment process. Be-



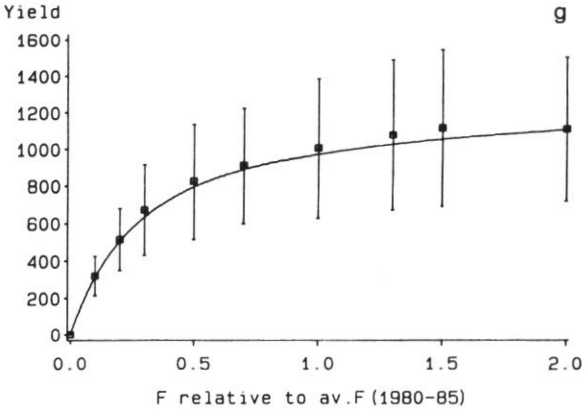


Figure 2. Yield predictions for constant (curve) and stochastic recruitment. ☐: Average yield plus minus standard deviation in stochastic simulation. (a) Cod, (b) haddock, (c) whiting, (d) herring, (e) sprat, (f) Norway pout, (g) sandeel.

cause of interactions among the juveniles and common responses to environmental changes it is likely that recruitment to one stock will be related to recruitment to other stocks. A high recruitment to one stock may thus be more likely if recruitment to another stock is low, etc. This interdependence could change the results. It may therefore be of interest to make predictions in which these between species links are preserved.

The correlation matrix of the logged recruitment estimates from the MSVPA is given in Table 2. Out of 32 correlations seven are significant, i.e. larger than 0.576 ($p = 0.05$ on 10 d.f.). Of these, three are significant at the $p = 0.01$ level. Recruitments of herring and sprat, herring and whiting, and sprat and saithe are negatively correlated, while cod and sandeel, whiting and sprat, whiting and saithe, and herring and saithe are positively correlated.

The correlations were preserved in the predictions by Principal Components Analysis (PCA), which is a technique used for similar problems in models of weather and climate (Preisendorfer, 1988).

A PCA may be considered as a transformation of coordinates. In this case a PCA transforms the nine time series of logged recruitment data into a new coordinate system in which they are represented by nine new uncorrelated time series (the principal components scores). The idea is then to draw values at random from the uncorrelated principal components scores and to back-transform them to correlated estimates of recruitment.

With y years and n species the transformation may be written

$$\underline{\mathrm{PCS}} = \underline{\mathrm{A}}\,\underline{\mathrm{LR}} \quad \text{or} \quad \underline{\mathrm{LR}} = \underline{\mathrm{A}}^{\mathrm{T}}\,\underline{\mathrm{PCS}}$$

where $\underline{\mathrm{LR}}$ is a $(y \times n)$ matrix of log recruitment values, $\underline{\mathrm{A}}$ is the $(n \times n)$ matrix of eigenvectors, $\underline{\mathrm{PCS}}$ is a $(y \times n)$ matrix of uncorrelated principal components scores, and T denotes matrix transpose.

The transformation matrix, $\underline{\mathrm{A}}$, is used to go from one set of coordinates to the other. Given a vector of principal component scores pertaining to a particular year the corresponding log recruitment values can be found by multiplication with $\underline{\mathrm{A}}^{\mathrm{T}}$. If (as assumed) the log recruitment values are normally distributed, the corresponding principal component scores will also be normally distributed.

Table 2. Results of a principal components analysis of logged recruitment data from MSVPA (Anon., 1988). Correlation matrix.

	Cod	Whiting	Saithe	Mackerel	Haddock	Herring	Sprat	Norway pout	Sandeel
Cod	1.00								
Whiting	0.54	1.00							
Saithe	−0.01	−0.66*	1.00						
Mackerel	−0.18	0.30	−0.54	1.00					
Haddock	0.27	0.04	0.29	−0.05	1.00				
Herring	−0.20	−0.74**	0.72**	−0.19	0.47	1.00			
Sprat	0.16	0.69*	−0.60*	0.30	0.07	−0.82**	1.00		
Norway pout	0.11	−0.01	−0.07	0.29	−0.15	−0.17	0.11	1.00	
Sandeel	0.69*	0.57	−0.27	0.08	0.31	−0.35	0.33	0.46	1.00

*Significant at $p = 0.05$ level (10 d.f.).
**Significant at $p = 0.01$ level (10 d.f.).

Principal component	Eigenvalues	Prop. of variance explained
1	2.54	0.485
2	1.39	0.265
3	0.63	0.120
4	0.35	0.067
5	0.16	0.030
6	0.11	0.021
7	0.03	0.005
8	0.02	0.004
9	0.01	0.002

	Eigenvectors								
	1	2	3	4	5	6	7	8	9
Cod	0.05	−0.24	0.54	−0.34	−0.28	0.54	−0.37	−0.14	0.01
Whiting	0.18	−0.11	0.16	−0.05	−0.34	−0.03	0.48	0.32	0.70
Saithe	−0.26	−0.01	0.08	0.14	0.36	0.64	0.54	0.20	−0.21
Mackerel	0.54	0.80	0.12	−0.08	−0.04	0.16	0.06	0.00	−0.11
Haddock	−0.08	0.05	0.56	0.53	−0.11	−0.24	−0.16	0.50	−0.24
Herring	−0.51	0.41	0.24	0.29	0.06	0.02	−0.07	−0.47	0.45
Sprat	0.56	−0.32	−0.02	0.61	0.22	0.19	−0.08	−0.31	0.16
Norway pout	0.06	0.04	0.09	−0.24	0.72	−0.02	−0.36	0.37	0.38
Sandeel	0.13	−0.15	0.53	−0.26	0.32	−0.42	0.40	−0.37	−0.17

The results of a PCA of the nine logged time series of recruitment from the MSVPA are shown in Table 2. The first principal component explains 48% of the total variance, the second an additional 26%. Only the first of these series of principal component scores (the one associated with the highest variance) shows a significant decline with time, the others remain stable (Fig. 3).

In the simple stochastic recruitment case μ and σ^2 were used to create the distributions. This complicates our analysis somewhat. We may, however, use $\underline{A}$ to transform the original vectors μ and σ^2 into the new system of coordinates. Thus:

$$\underline{\mu}' = \underline{A}\underline{\mu} \quad \text{and} \quad \underline{\sigma}'^2 = \underline{B}\underline{\sigma}^2$$

where $\underline{B}$ is a $(n \times n)$ matrix containing the elements of $\underline{A}$ squared. The two formulas are only approximative because the covariances have been ignored in estimating $\underline{\sigma}'^2$ and because $\underline{A}$ has been estimated directly from the log recruitment series and not from the variances, $\underline{\sigma}^2$, and covariances of the normal distributions of log recruitment. In practice, however, the use of $\underline{\mu}'$ and $\underline{\sigma}'^2$ produced only minor differences between the original arithmetic mean and variance and the simulated.

The MSFOR was then used to predict 1000 years ahead. In each of the years the PCA scores were drawn from normal distributions with parameters (μ', σ'^2). The scores were then transformed to estimates of log recruitments by $\underline{A}^T$ and backtransformed to recruitment values. The results in terms of average yield are shown in Figure 4.

As in the simple stochastic case no major difference is seen between the constant recruitment runs and the simulations.

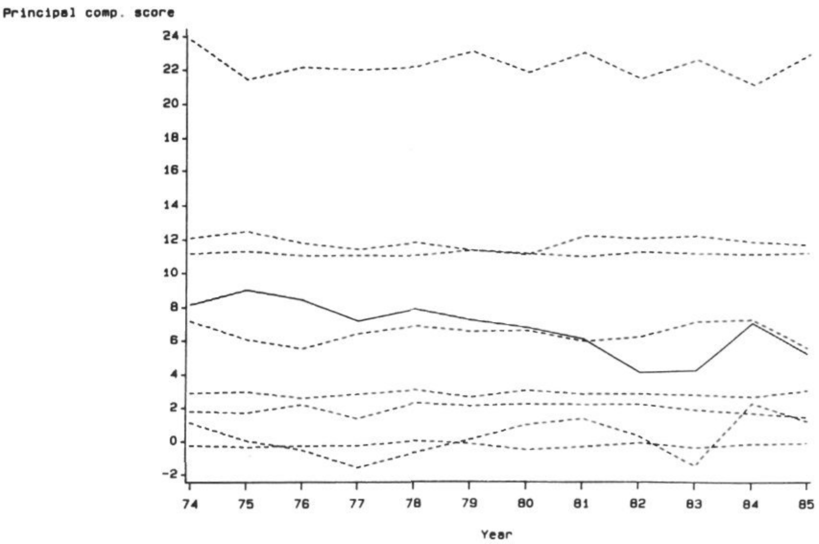


Figure 3. Time series of principal component scores of recruitment. First principal component score shown as unbroken curve.

Discussion

The results show that yield predictions from the MSFOR for the North Sea depend on the level of recruitment in a non-linear way. This dependency is, however, mainly important in a management context if the shape of the Y/R curve changes. With cod as an exception this change does not seem to be of importance if the level of recruitment remains between 20 and 200% of the present level. This signifies that fishing strategies can be defined which will be robust to changes in recruitment provided these changes take place within reasonable limits.

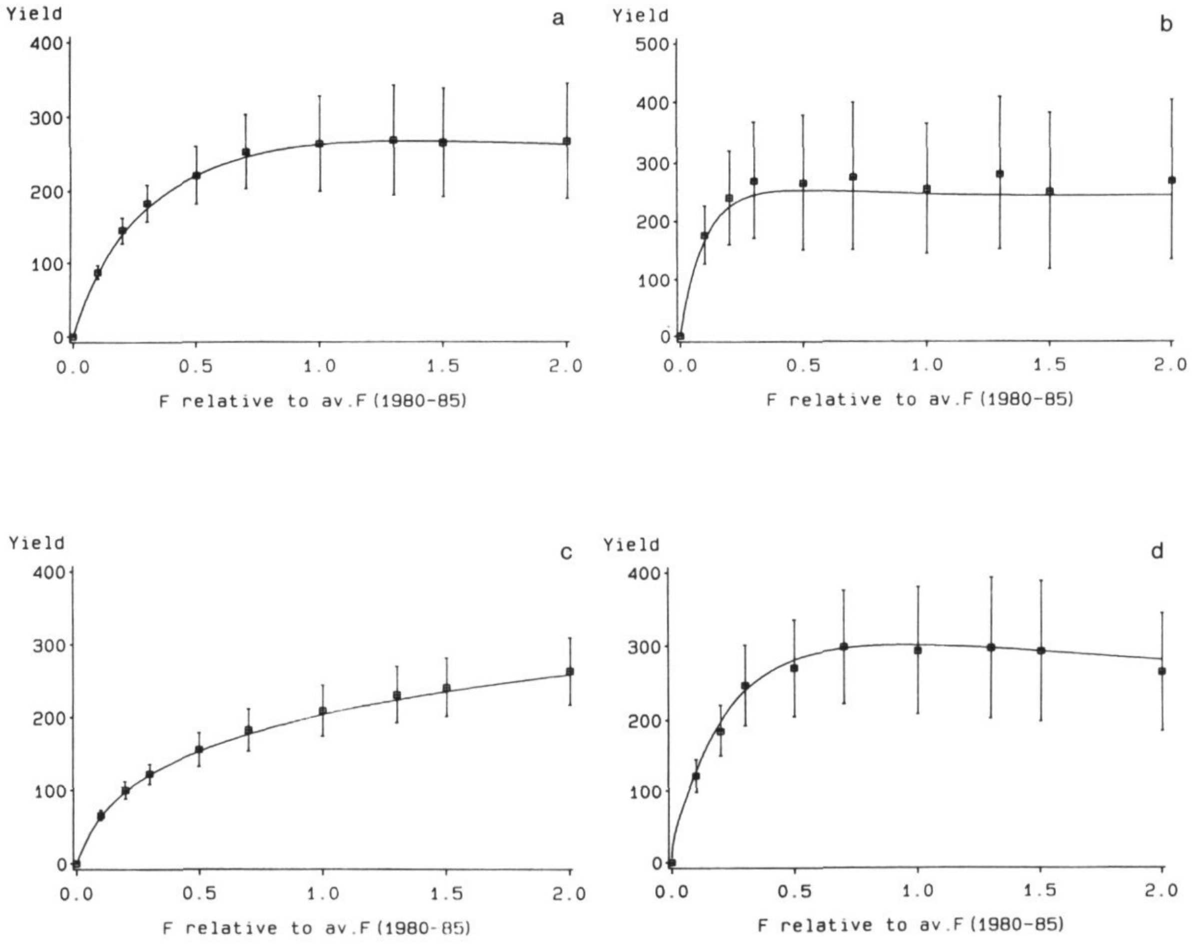
As shown by the change in F_{MSY} of cod, gains and losses of a change in fishing strategy should in practice be evaluated for different levels of recruitment to ensure that gains are not converted to losses if the level of recruitment changes. This evaluation should not (as in this paper) only consider the effect of changing the level of recruitment for a particular species to the yield of the species itself, but should also consider interactions of a higher order, e.g. how changes in the recruitment of whiting affect the Y/R curve of cod at various levels of cod recruitment.

Adding stochastic noise to the recruitment does not significantly change the average long-term yield predicted by the MSFOR, except for species which show large year-to-year fluctuations in recruitment and/or are important prey. For all species the shape of the yield curve remains the same as in the constant recruitment case.

Throughout this exercise it has been assumed (as in the single species Y/R model) that the size of the spawning stock does not influence subsequent recruitment. Several models have been proposed in order to link recruitment to the size of the spawning stock, but usually these models have not explained much of the observed variation. Daan *et al.* (1989) concluded that no correlation could be observed between spawning-stock size and subsequent recruitment for the North Sea stocks, with herring and mackerel as two possible exceptions. As long as the predictions do not fall outside the historic range of spawning-stock biomasses, the stock recruitment relationship may thus be ignored.

Environmental changes and biological interactions have also been used to explain both short- and long-term variations in recruitment. Taking the covariance of the recruitment into account by the use of a principal components analysis is an attempt to include shared responses to these variables in the predictions. The observed correlation is thought to be due to shared interactions between older fish and the 0-groups prior to 1 July, interactions among the 0-groups themselves, shared responses to environmental factors, and of course to chance. Preserving the correlation in the predictions is based on the assumption that these interactions will not change over time, i.e. that the effects will operate in the same way in the future as in the past.

Whether this is a reasonable assumption remains to be seen. Shepherd *et al.* (1984) found that the first principal component of recruitment data for North Sea cod, haddock, saithe, sole, plaice, whiting, and herring correlated significantly with the average March temperature in the central North Sea. Thompson and Hilden (1987) extended their analysis by including more recent data points and found that the correlation became weaker. From 1962 to 1973 temperature seems to have been important, but later on some other factor or combination of factors appears to have taken over. It is



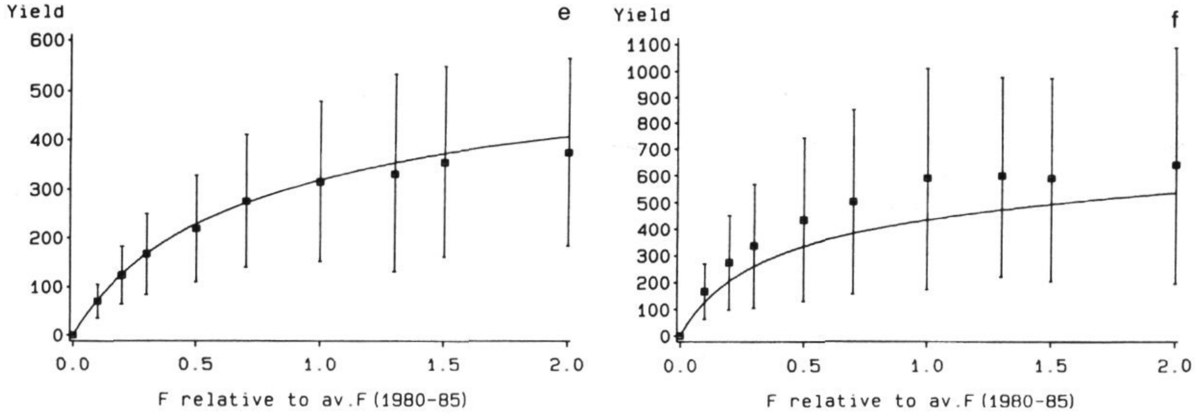
unlikely that there is a simple explanation for the decrease in the first principal component over time in this exercise.

Preserving the correlations in the predictions does not seem to change the shape of the yield curve. This conclusion, however, is based on an approximative formula and should be rechecked when an exact formula which relates the covariances of the recruitment and logged recruitment series has been found.

It has also been observed that recruitment data may show a significant amount of autocorrelation (Cook and Armstrong, 1984; Rothschild, 1986). Preserving the autocorrelations in the predictions would be interesting. Even though the total variance of the simulated recruitment data would be the same, a positive correlation between recruitment in year y and year $y - 1$ would increase the amplitude of the fluctuations in stock size and yield, due to the increased probability of having several large or poor year classes in succession. Most likely this would increase the effects of the non-linear description of predation mortality, leading to a larger discrepancy between the predicted yield in the constant and stochastic recruitment case. A negative autocorrelation would work the other way around, decrease the amplitude and the importance of non-linear interactions, and therefore lead to an even greater correspondence between the constant and stochastic case.

Thus it is difficult to say whether including autocorrelations would change the conclusion that variations in recruitment are of minor importance. It would depend very much on the magnitude of the estimated autocorrelations and on whether they were positive or negative.

With only 12 years of data at hand it seems premature to fit a time-series model including both correlations and autocorrelations. With such a short series, estimates of covariance and autocovariance would be highly correlated, and little confidence could be given to the actual outcome. However, given a longer time series of MSVPA recruitment estimates, such an approach should certainly be pursued.



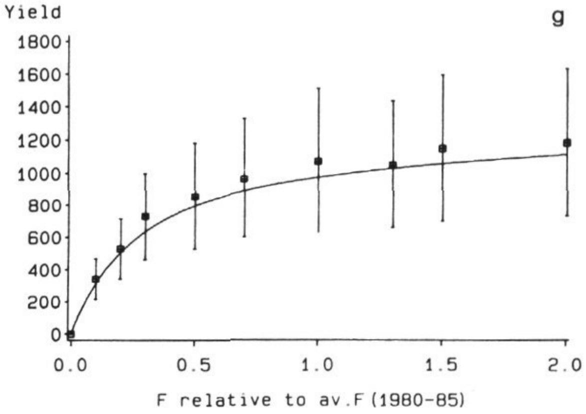


Figure 4. Yield predictions for constant (curve) and stochastic recruitment. □: Average yield plus minus standard deviation in stochastic simulation in which the between-species correlation has been preserved. (a) Cod, (b) haddock, (c) whiting, (d) herring, (e) sprat, (f) Norway pout, (g) sandeel.

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ICES mar. Sci. Symp., 193: 60–63. 1991

Variability in stomach content weights and prey numbers, and the calculation of overlap coefficients in relation to MSVPA

W. P. de Winter

Winter, W. P. de. 1991. Variability in stomach content weights and prey numbers, and the calculation of overlap coefficients in relation to MSVPA. – ICES mar. Sci. Symp., 193: 60–63.

A comparison of the spatial and seasonal coefficients of variation in stomach content weights and in the number of prey organisms in stomachs of cod sampled in the North Sea in 1981 indicates that the variances are in the same order of magnitude. This suggests that the number-based multispecies virtual population analysis (MSVPA) may be a useful alternative to weight-based MSVPA, but additional analyses are needed to confirm this conclusion. The MSVPA concept of constant suitability is incongruent with the observation that distribution patterns of predator and prey vary. In view of further refinements of the model, appropriate overlap coefficients were derived in order to take account of non-linear local differences in abundance between a predator and its prey assortment. Unfortunately, a solution to the equations that were obtained has not yet been found.

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Introduction

The traditional multispecies virtual population analysis (MSVPA), as used in ICES, estimates numbers of prey eaten on the basis of weights consumed and average prey weights (Anon., 1984; Sparre, 1984), assuming that suitability of prey biomass is constant. The calculation procedures could be simplified by direct estimation of numbers of prey eaten from the numbers of prey organisms observed in stomachs (Daan, 1986), which requires that suitability in terms of prey numbers is constant. The implicit assumptions of the two approaches differ to the extent that the weight-based MSVPA (MSVPA-w) requires that both rations in weights and average prey weights for each category are approximately constant from year to year, and the number-based MSVPA that only rations in terms of numbers are constant. The goal of the first part of this investigation was to compare how well the MSVPA-w and MSVPA-n adhered to these assumptions by estimating the associated coefficients of variation in the parameters. Unless the MSVPA-n does significantly poorer in this respect, it would be simpler to use it instead of MSVPA-w.

The second goal was to try to develop an appropriate formulation for the overlap coefficient between predator and prey. The suitability concept of Andersen and Ursin (1977) refers to the composite effect of different aspects of vulnerability, including for instance ecological vulnerability, size preference, and geographical overlap as contributing factors. In order to be able to solve the set of MSVPA equations, the assumption has to be made that suitability is constant from year to year. Although Rice *et al.* (1991) conclude that suitabilities are indeed relatively stable from year to year, it is quite clear from survey data that distribution patterns of both predators and prey change significantly from year to year. This suggests that at least some variations in suitability can be expected. If an appropriate measure of overlap could be derived from survey data, this information might be used in a modified version of MSVPA, where ecological vulnerability and size preference are still assumed to be constant but where overall suitability is allowed to vary according to variations in overlap (Gislason, 1985; Houghton, 1986). However, an unbiased estimator of overlap has not yet been derived.

Coefficients of variation in weights and numbers of prey in cod stomachs

Since at the time of this research stomach content data were only available for one year, it was not possible to test directly the assumptions of constant stomach content weights and numbers of prey in stomachs, and of constant prey weights between years. However, the 1981 cod database (Anon., 1984) allowed a study of the spatial and temporal stability of these parameters by

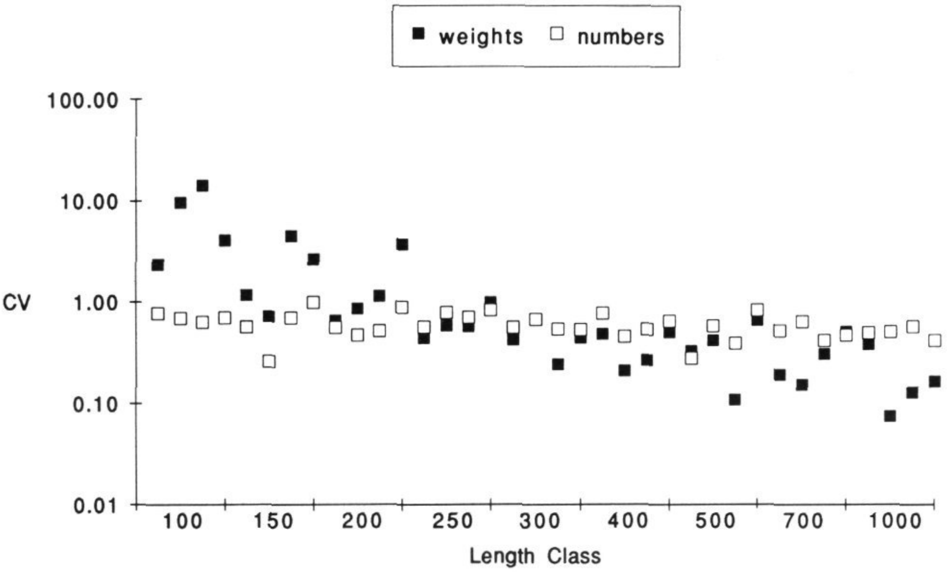

Figure 1. Coefficient of variation (CV) in weights and numbers for different size classes. The four values within a size class refer to consecutive quarters.

working up the data for each quarter and ICES roundfish area separately. The implicit assumption advanced by this approach is that differences in variability within a year can be translated to differences between years.

Since stomach contents of different fish within a sample had been pooled before analysis, a statistical evaluation of the variability per fish is impossible. Therefore, the logarithms of the mean stomach content weights and the mean numbers of prey per stomach per quarter and area were treated as single data from which for each predator size class means and standard deviations were calculated. The relative dispersion (standard deviation/mean) was compared for both weights and numbers.

Prey weights provide a problem, because the information available from stomach analysis refers to the average weight of a prey as recovered in the stomachs rather than fresh weights. Because of large variations in stage of digestion, the associated variances in average recovered weights per prey category probably overestimate variations in fresh weights. In addition, it is obvious that within a year the assumption of a constant prey weight per category is invalid because of growth of fish within a cohort. Therefore, analysis of the variability in prey weights was not conducted.

The results indicate that overall there appears to be little difference between the estimated coefficients of variation (CV) in stomach content weights and prey numbers in stomachs (Fig. 1). However, CV of weights drop markedly from small cod to large cod, whereas CV in numbers are relatively constant over the entire size range. This suggests that the scatter in stomach content weights is less among cod >25 cm than the scatter in numbers, whereas the opposite is true for cod <25 cm. The higher stability in stomach content weights with increasing size may be related to the gradual switch from invertebrate prey to fish prey (Daan, 1973).

Overlap coefficients in relation to the suitability concept

In MSVPA, the predation is estimated as the biomass transferred from prey cohort j to predator cohort i according to

$$N_i \times R_i \times \Phi^i_j \tag{1}$$

where i and j refer to individual age groups, N_i represents the total number of i, R_i the ration of an individual predator i, and Φ^i_j the relative availability of j to i. The availability is a weighing term that compares the biomass (B) and suitability (G) of j to all other preys of i:

$$\Phi^i_j = B_j \times G^i_j \tag{2}$$

If O is a measure of overlap between a predator and prey which varies between years, suitability can be split in

$$G^i_j = O^i_j \times G'^i_j \tag{3}$$

where G′ (referred to as residual suitability) includes all measures of vulnerability which are independent of horizontal distribution. It is assumed to be constant in time. In a homogeneous area, O^i_j equals 1. The total biomass of j that is eaten in subarea q (E_j^{iq}) by predator i is therefore defined by

$$E_j^{iq} = \frac{N_{iq} \times R_i \times N_{jq} \times w_j \times G'^i_j}{\sum_{p=1}^{np} N_{pq} \times w_p \times G'^i_p} \tag{4}$$

and

$$E_j^i = \sum_{q=1}^{nq} E_j^{iq} \tag{5}$$

where np denotes the number of prey categories p, nq the number of subareas, and w the average prey weight. Further, MSVPA defines the total biomass consumed also as:

$$E_j^i = \frac{N_i \times R_i \times N_j \times w_j \times G'^i_j \times O_j^i}{\sum_{p=1}^{np} N_{pq} \times w_p \times G'^i_p \times O_p^i} \tag{6}$$

Putting (6) equal to (5) combined with (4) yields:

$$O_j^i = \sum_{p=1}^{np} (N_p \times w_p \times G'^i_p \times O_p^i) \times \\ \times \sum_{q=1}^{nq} [P_{iq} \times P_{jq}] \Big/ \left[\sum_{p=1}^{np} N_{pq} \times w_p \times G'^i_p\right] \tag{7}$$

where P_{iq} denotes the fraction of the total population occurring in subarea q. The first sum term is constant within a predator category and can therefore be omitted. Thus (8) reduces to

$$O_j^i = \sum_{q=1}^{nq} [P_{iq} \times P_{jq}] \Big/ \left[\sum_{p=1}^{np} N_{pq} \times w_p \times G'^i_p\right] \tag{8}$$

This definition differs from the one proposed by Houghton (1986) by the presence of the denominator term that takes account of the local availability of all other prey species. Since both the overlap (O) and the residual suitability (G′) are unknown, (9) might only be solved iteratively by dividing the suitabilities as calculated from stomach content analyses by the overlap coefficient. So far, this non-linear set of equations could not be solved (de Winter, 1989).

Conclusions

Among the larger size classes of cod, MSVPA-n appears to meet the assumption of a constant ration in numbers somewhat less than MSVPA-w the assumption of constant ration in weights, but in the lower size range the opposite is true. This conclusion is of course only true if stomach weights and numbers reflect the respective rations. However, a constant weight ration coinciding with a variable number ration implies a variable prey weight. Thus, MSVPA-w does not meet its second assumption of constant prey weights. Therefore, these data support the findings by Daan (1986) and suggest there is no significant loss of information when applying MSVPA-n, whereas the gains in terms of analytical labour might be significant.

While these results indicate that number-based MSVPA may be a useful alternative to weight-based MSVPA, comparison of CVs of stomach content weights and prey numbers between years are needed if firm conclusions are to be drawn. The results also indicate considerable areal heterogeneity, which suggests the need for an area-based MSVPA as proposed by Gislason (1985).

As regards the question of the possible use of measures of overlap from trawl surveys in relation to MSVPA with a view to calculating adjusted suitability indices for individual years, the analysis has not been conclusive. It would appear that if an appropriate algorithm could be found for solving the obtained set of equations numerically, there would be no theoretical impediment to improve the MSVPA in this respect. However, it should be noted that in principle quantitative distribution patterns for all possible prey species in all years would be required and this would obviously be highly impractical. Although it might be more appropriate to search for approximate methods, investigations into the possible bias of such methods can probably only be carried out when the results can be checked against the model presented.

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Multispecies assessment of Baltic fish stocks

Henrik Sparholt

Sparholt, H. 1991. Multispecies assessment of Baltic fish stocks. – ICES mar. Sci. Symp., 193: 64–79.

The Working Group on Multispecies Assessment of Baltic Fish was established in 1981 with the aim of developing assessment methods that would take into account species interactions in the Baltic Sea. These were to replace the conventional single-species models used until then in the standard assessment of cod, herring, and sprat stocks. After a short description of the Baltic ecosystem (serving as a background), attempts to quantify species interactions in the area are reviewed and the progress made by the Working Group is described. Some future perspectives are presented.

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1. Introduction

Several multispecies models based on the concept of Andersen and Ursin (1977) have been developed for the Baltic Sea as well as for other areas in the latter half of the 1970s. In 1980 the International Council for the Exploration of the Sea established the Ad hoc Working Group on Multispecies Assessment Model Testing in order to coordinate these efforts (Anon., 1980). Because this Working Group concentrated on North Sea problems, another Ad hoc Working Group on Multispecies Assessment of the Baltic was established in 1981 to deal specifically with multispecies modelling of the Baltic Sea.

The primary reason for this separate Working Group being established was the large fluctuations in the cod, herring, and sprat stocks in the Baltic that had been observed in the past. These were explained by several authors as predator–prey interactions (e.g. Jensen, 1929, 1962, 1966; Lishev and Uzars, 1967). It was felt that particularly in this area multispecies models might elucidate the observed phenomena and be used as a valuable tool in preparing management advice.

The primary aim of the first meeting of this Working Group in 1981 was to discuss the general approach to follow and to advise on data requirements (Anon., 1981). Since then four meetings have been held (Anon., 1982, 1987a, 1988a, 1989a). Although preliminary runs of multispecies virtual population analysis (MSVPA; Gislason and Sparre, 1987) have been obtained, the Working Group is still focusing on the compilation of stomach data from the various countries.

Quantitative models on species interactions require extensive data on the food composition of the dominant predator species and reliable estimates of consumption rates (Anon., 1980). In the Baltic, stomachs have been collected by various countries since the beginning of the 1970s. These investigations have not been properly coordinated and as yet not all samples have been adequately worked up. To speed up this process, a special meeting of a Study Group on Cod Stomach Data for the Baltic was held recently (Anon., 1989d). Although useful data are available at least from 1977 onwards, even more stomach content data are needed and, as suggested by Anon. (1989b), the database should probably be updated every tenth year in order to check whether the interaction parameters have remained constant.

Since 1981 a few experiments on the digestion rates of predators have been carried out and these form the basis for estimating consumption rates. However, according to the results of a recent Workshop reviewing the knowledge on stomach evacuation rates in fish (Anon., 1989c), the results obtained so far are not conclusive and further work is required.

The present paper describes the state of the art and future of the multispecies modelling in the Baltic against the background of our wider knowledge about the biological and physical conditions of this system.

2. The Baltic Sea ecosystem

Historically, the Baltic ecosystem, the largest brackish water area in the world (Jansson, 1972), has undergone profound change and its present state has existed for only about 3000 years (Ignatius *et al.*, 1981). Although exposed to a large runoff of fresh water, the strong marine influence is demonstrated by the fact that three

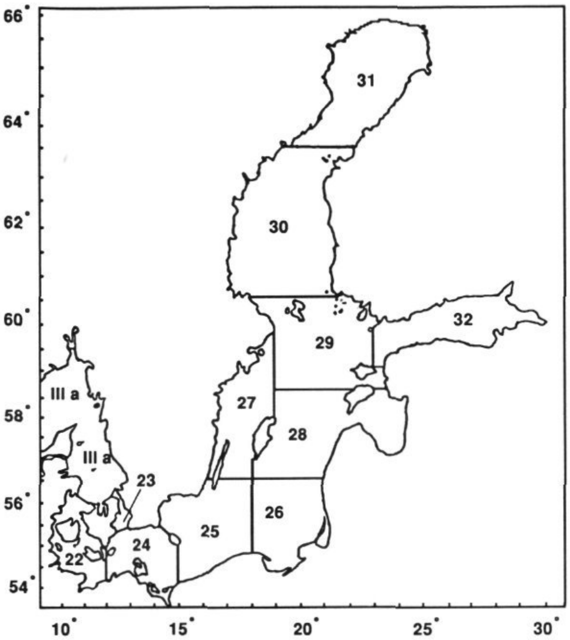

Figure 1. The Baltic Sea with Subdivisions for stock assessment.

typically marine fish species dominate the commercial catch. This influence is characterized by large injections of North Sea water, which may occur at intervals of several years and greatly affect the salinity and oxygen conditions in the deeper basins.

The Baltic Sea (Fig. 1) is a shallow sea with a mean depth of about 60 m and covers an area of 366 000 km^2. The presence of shallow sills at the inlets causes a stable stratification of the water column. The average turnover time is 34 years (Cushing, 1982). An intermittent stream of the North Sea water flows, after mixing with Baltic water in the Belt Sea and the Sound, with a salinity of about 17 into the Baltic. A strong halocline is formed between the deeper water and the out-flowing Baltic water, which has a mean salinity of about 8.

The vertical position of the primary halocline has changed from 80 to 60 m depth since the beginning of the century, which means an increase in the volume of the hypolimnion of 200 km^3 (Jansson, 1972). The vertical mixing is very small because of the halocline and the presence of an additional thermocline at 15–20 m depth during the summer season. Thanks to aeration by wind action, shortage of oxygen above the halocline has only been recorded in polluted bays, but below the halocline anoxic conditions are frequent (Anon., 1987b). The injections of North Sea water are extremely important because they supply oxygen to the stagnant bottom water.

The surface temperature generally varies between 2 and 16°C and the bottom temperature between 3 and 9°C, according to Lenz (1971).

Table 1. The mean annual commercial landings (t) in the Baltic Sea by species (groups) in 1980–1984. (From: Bull. Stat. 65–69.)

Species	*Landings*
Freshwater fish	18 983
Eel	2 404
Salmon	2 783
Smelt	3 803
Trout	774
Various diadromous	3 797
Brill	19
Dab	2 091
Flounder	8 989
Lemon sole	16
Plaice	2 145
Sole	3
Turbot	132
Various pleuronectiformes	3 466
Cod	393 260
Ling	1
Pollack	3
Saithe	2
Tusk	–
Whiting	3 707
Catfish	2
Sandeel	25
Various demersal percomorphs	3 579
Garfish	1 086
Horse mackerel	291
Herring	452 219
Sprat	47 558
Mackerel	24
Unidentified	14 226
Total	965 343

According to Elmgren (1984), the primary production is 156 g C m^{-2} yr^{-1} in the Baltic proper, 110 g C m^{-2} yr^{-1} in the Bothnian Sea, and only 28 g C m^{-2} yr^{-1} in the Bothnian Bay. The biomass and production of macrobenthos in the Baltic proper were estimated by Elmgren (1984) at 3.3 g C m^{-2} and 3.0 g C m^{-2} yr^{-1}, respectively, taking into account that up to about 100 000 km^2 is devoid of macrobenthos because of low oxygen level. Comparable values for the Bothnian Sea were 6.5 g C m^{-2} yr^{-1} and 5.9 g C m^{-2} yr^{-1}, respectively. The zooplankton production in the Baltic proper is given by Jansson (1972) as 4.4 g C m^{-2} yr^{-1} and in Kiel Bay by Arntz (1978) as 3.2 g C m^{-2} yr^{-1}.

The fish fauna is characterized by a relatively small number of species and the occurrence of both marine and freshwater species. Cod (*Gadus morhua*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) constitute about 40%, 50%, and 5% (means for 1980–1984), respectively, of the total commercial catches in the area (Table 1). Other marine species are flounder (*Platichthys flesus*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), whiting (*Merlangius merlangus*),

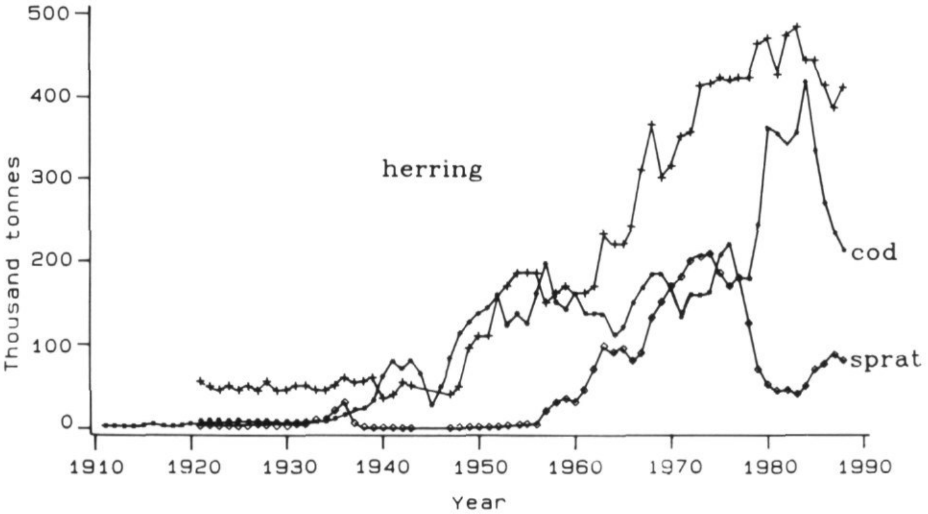

Figure 2. The total catch of cod, herring, and sprat in the Baltic Sea since 1900. (After: Ojaveer, 1981: Anon., 1989e, 1989f).

and garfish (*Belone belone*). Typical freshwater species include bream (*Abramis brama*), pike (*Esox lucius*), perch (*Perca fluviatilis*), pike-perch (*Lucioperca lucioperca*), roach (*Rutilus rutilus*), and burbot (*Lota lota*). Compared to truly marine areas, the contribution of diadromous species is large, consisting mainly of salmon (*Salmo salar*), trout (*Salmo trutta*), eel (*Anguilla anguilla*), and smelt (*Osmerus eperlanus*). In some years sticklebacks (*Gasterosteus aculeatus*) occur in large numbers and occasionally an industrial fishery directed to this species has been established. Generally, more marine species are found in the Western Baltic and more freshwater species in the Northern and Eastern parts due to the salinity conditions.

Commercial catch statistics cannot of course be regarded as an unbiased reflection of the species composition in an area. Some abundant species in the Baltic are never landed by fishermen. As an example, the four-bearded rockling (*Enchelyopus cimbrius*) is often caught in large numbers in trawl surveys and relatively often found in cod stomachs (Fester, 1974).

Thurow (1984) estimated the biomas of species other than cod, herring, and sprat to be 1.1 million tonnes in 1970 and 0.5 million tonnes in 1977. These estimates were based on catch statistics and "guesstimated" unreported and discarded catches, assuming that the yield/biomass ratio for these other species was the same as for cod, herring, and sprat. For comparison, the biomass of cod, herring, and sprat in 1980–1984 has been estimated at 4.1 million tonnes (Anon., 1989e, f).

3. Cod, herring, and sprat

3.1. Commercial catches

The commercial catches of cod, herring, and sprat have fluctuated widely during the past 80 years, but there has been a clear increasing trend from a total of less than 100 000 t in the 1930s to over 900 000 t in 1984. Thereafter, landings decreased again to 730 000 t in 1987 (Fig. 2).

The catch of cod was only about 5000 t per year at the beginning of the century up until 1935. From 1935 to 1950 the catches increased gradually, and from 1950 to 1978 were relatively stable at around 150 000 t per year. From 1979 onwards the cod catches increased sharply, reaching a maximum in 1984 of 414 000 t. Since 1984, a steady decline has been observed to 223 000 t in 1988. In recent years, cod is a heavily over-exploited species in the Baltic, with a fishing mortality coefficient (F) of about $1.0\,\mathrm{yr}^{-1}$ (Anon., 1989e).

Commercial catches of herring have not fluctuated as much as cod catches. During the first half of the century, these were stable at around 50 000 t. From 1945 onwards, catches increased fairly steadily to about 400 000–500 000 t by the beginning of the 1970s. They have remained at this level since then. Herring is heavily exploited in the western parts of the Baltic ($F \approx 0.8\,\mathrm{yr}^{-1}$) but in the eastern parts it is only moderately exploited ($F < 0.4\,\mathrm{yr}^{-1}$; Anon., 1989f).

Several thousand tonnes of sprat were landed per year in the 1930s but catches decreased to virtually zero by the middle of the 1950s. Thereafter, they increased to a maximum of about 200 000 t by the middle of the 1970s, followed by a steep decline to about 50 000–100 000 t since then. Sprat is generally lightly exploited ($F < 0.3\,\mathrm{yr}^{-1}$) in the Baltic (Anon., 1989f).

The catch statistics before 1970 are probably not very reliable. According to Table 2, the exploitation level in the cod stock must have increased after 1929 in all important fishing areas, because the mean age in the catch has decreased. However, this change has not been large enough to explain the enormous increase in the cod catches after the 1940s. According to J. Netzel (pers.

Table 2. Mean age of cod in commercial catches by period and area. (From: Bagge, 1981a.)

Period	Kiel Bay	Bornholm Deep	Gdansk Deep	Gotland Deep
1929–1938	4.77	4.51	4.74	5.95
1939–1944	2.77	4.22	3.48	4.48
1946–1957	2.02	3.58	3.71	4.33
1960–1967	1.59	3.60	3.68	3.78
1965–1977	2.34	3.57	3.94	4.00

comm.), Polish fisherman complained in the 1930s about poor catches compared to the situation in the 1880s and 1890s. So the cod stock has probably been considerably smaller in the first half of this century than previously. The reason is likely to be found in low recruitment. Since cod eggs can survive only at salinities above 10 (Bagge, 1981a), the low level of salinity at that time might give a clue here. According to Anon. (1987b), salinity reached a peak by the end of the 1970s, and this corresponds to a period of sharp increase in the catches between the 1970s and 1980s (Anon., 1989e), indicating the appearance of strong year classes of cod. This hypothesis about a relationship between salinity and cod recruitment should, however, be seen in the light of other changes. One important change during this century is the increased input of nutrients (Anon., 1987b). Eutrophication might have increased the food supply to fish larvae and enhanced survival, although negative effects might be expected from an associated reduction in the oxygen content of the deep parts of the Baltic. From a multispecies modelling point of view, these anthropogenic changes are of great interest because they could have a major impact on the fish community.

The increase in the herring catches since the 1940s appears to be largely due to an increase in effort (Ojaveer, 1981). Up until now, there has been no good explanation for the observed fluctuations in recruitment of herring.

According to Aps (1989), the fluctuations in the sprat catches reflect variations in the stock caused by large year classes in 1955–1957, 1959, 1967, 1969, 1972, and 1975. Aps (1989) investigated a large array of environmental parameters in relation to sprat recruitment but did not find significant correlations.

Because cod preys heavily on both herring and sprat (Anon., 1989a), fluctuations in predation pressure might also explain some of the observed fluctuations in the herring and sprat stocks.

3.2. Stock units

In the Baltic there are two cod stocks which have been shown to differ in morphometric and meristic characters: in haemoglobulin types, in otolith structure, and in allele frequencies. A review of cod stock identifications is given by Bagge and Steffensen (1989). Also the weight-at-age differs between the two stocks (Anon., 1989e). The Western Baltic Sea cod stock is distributed west of Bornholm Island, in the Belt Seas, and the Sound (Subdivisions 22–24) and is connected with cod in the Kattegat and Skagerrak (Division IIIa) as well as with cod in Subdivision 25. The Eastern Baltic Sea cod stock is distributed east of Bornholm up to the northern parts of the Bothnian Sea and to the eastern parts of the Gulf of Finland (Subdivisions 25–32). Although the border between these two main stocks is diffuse and there is evidently some mixing in the Arkona Basin (Subdivision 24) and in the Bornholm Basin (Subdivision 25), tagging experiments indicate that a line from Sweden to Poland/GDR over Bornholm marks an adequate borderline between the two stocks. The migrations of Baltic cod have been reviewed by Aro (1989).

The stock structure of herring in the Baltic is fairly complex, with many stocks and a large degree of overlap between stocks. In routine ICES stock assessment, herring is separated into eight different stock units (Anon., 1989f) differing by morphological, meristic, and biological characters. However, unlike cod, these differences are probably not genetically defined (Ryman *et al.*, 1985), but more a phenotypic reflection of the environmental gradient from the south to the northeast.

The herring in the Western Baltic (Subdivisions 22–24) spawn during spring and migrate to the Kattegat/Skagerrak area to feed during summer. Migration of herring from Subdivision 24 to Subdivision 25 or the other way around is rare (Otterlind, 1984). The borderlines between the stocks east of Bornholm are less well defined or documented and an analysis carried out by Anon. (1989f) indicates that at least some of these stocks might better be lumped together in one common unit.

The stock structure of sprat is not quite as complex as that of herring, and in the routine stock assessment only three separate stock units are used (Anon., 1989f). The boundaries between neighbouring stocks are not quite clear, however, and apparently the stocks mix during feeding and over-wintering (Rechlin, 1967, 1975, 1986). The ranges covered during migration and the rate of mixing are not well known. Some authors appear to be in favour of more localized stocks (Aps and Lotman, 1984; Aps *et al.*, 1987), whereas others suggest that there is considerable migration and mixing between stocks (Grauman, 1976; Khoziosky *et al.*, 1983). An analysis carried out by Anon. (1989f) indicates that all three sprat stocks are interrelated as regards year-class strength and that precision in the assessment appears to be enhanced when they are considered as one stock.

3.3. Growth

Weight-at-age of cod is in general higher in the western part of the Baltic than in the eastern part according to

Table 3. Mean weight-at-age (g) of cod in commercial catches from Subdivisions 25–32. (From Anon., 1989e.)

Age	1981	1982	1983	1984	1985	1986	1987	1988
2	395	356	452	351	465	508	567	557
3	716	622	658	574	729	682	806	725
4	902	937	916	888	1080	994	1175	1103
5	1201	1327	1361	1357	1575	1458	1750	1740
6	2011	1859	1799	1921	2104	1967	2508	2387
7	2460	2664	2410	2558	2426	2325	2972	3251
8	4158	3639	4272	3716	3484	3210	3559	3910
9	5227	5078	5195	4602	5206	5261	4494	4745
10+	7068	6332	6486	7969	6953	7309	6090	6428

data provided by Anon. (1989e). Differences within Subdivisions 25–32 appear to be small. Thurow (1974) found no differences in mean length-at-age for ages 1 to 9 between the Bornholm Deep and the Gotland Deep. Comparison with data from Modin (1987) for the Bothnian Sea (Subdivision 30) revealed no significant differences either. This is in agreement with the observation that the cod east of Bornholm migrate extensively over wide areas (Aro, 1989) and confirms that this part is inhabited by one unit stock.

Several authors have tried to relate changes in growth of cod to annual changes in feeding conditions and stock abundance (Baranov and Uzars, 1986; Baranov, 1989; Horbowy, 1984). However, the observed changes in mean weight-at-age in the commercial catches (Table 3) have been comparatively small and could be biased by changes in selectivity of the fleet, changes from demersal to pelagic trawling, and so on. They may therefore actually largely represent noise in the data. Over the period 1981 to 1988 the cod biomass has changed from over 1.0 to about 0.4 million tonnes and yet the mean weights-at-age have not changed significantly between these years according to an analysis of variance with age and year as class variables ($p = 95\%$ for the year effect). Only age 4 and older cod were used in this analysis because they were considered to be fully recruited to the exploited stock (Anon., 1989e). Furthermore, annual weight increments during the same period showed no correlation with year-class abundance. Also over a longer time span, data on mean length of 3-group cod from Kiel Bay, Bornholm Deep, Gdansk Deep, and Gotland Deep do not indicate significant changes in growth between 1931 and 1977 (Bagge, 1981a).

The growth of herring differs significantly between areas. Generally, the length-at-age decreases from the southwestern to the northeastern parts (Table 4). In addition, the growth within a subdivision may vary substantially over time. According to Ojaveer (1981), there has been a gradual increase in weight-at-age in both the Southern Baltic and the Gulf of Riga from 1960 to 1980, followed by a reduction (Anon., 1989f, g). In some of the major stocks differences between years are in the order of 40%.

There are only minor differences in the weight-at-age of sprat between subdivisions (Table 5), which confirms the observation that this species migrates extensively over the area (Aro, 1989). According to data provided by Anon. (1989f), the annual variations in weight-at-age have been minor between 1970 and 1988. Since especially the 4 years and older sprats are difficult to age in some areas, considerable noise may be expected in the data, and time trends cannot be firmly established. Still, Aps (1989) showed that the weight-at-age in the Northern Baltic increased from the 1950s to the 1980s by about 30%, coinciding with a reduction in sprat biomass suggesting density-dependent growth.

Table 4. Theoretical asymptotic length (L_∞) and mean length of 3-year-old fish (L3) in cm of spring- and autumn-spawning herring and sprat in different areas. (From: Ojaveer, 1981.)

Area	Subdiv.	Spring herring		Autumn herring		Sprat
		L_∞	L3	L_∞	L3	L3
Bothnian Sea	30	20.3	15.9			
Western Gulf of Finland	32	19.1	15.9	18.4	16.2	11.9
Gulf of Riga	28	20.6	15.2	19.8	16.1	
Hiiumaa	29	21.8	16.9	19.7	16.6	11.8
Saaremaa	28	21.8	18.2	21.0	18.4	
Gulf of Gdansk	26	25.2	19.6	24.4	21.6	12.7
Bornholm	25			27.9	23.2	13.3
Rügen	24	28.3	22.0			
Southwestern Baltic	22–24		23.9		24.8	

Table 5. Mean weight-at-age (g) of sprat in October 1987 according to hydroacoustic survey data (Anon., 1989g).

	Subdivision					
Age	24	25	26	27	28	29S
0	3.7	3.0	3.5			
1	10.5	11.2	9.9	10.2	10.0	10.9
2	12.9	12.4	12.4	13.6	12.6	13.6
3	15.6	15.1	14.7	15.2	14.5	15.0
4	16.5	16.9	16.0	16.1	15.8	15.8
5	17.9	17.4	17.1	17.1	15.5	16.4
6	19.3	17.0	17.0	16.2	18.0	19.8
7	18.2	24.0	20.8	17.7		17.2
8		19.0	16.0	19.6	19.1	17.8
9	18.2	16.5		16.0	19.8	17.5
10+						19.0

3.4. Natural mortality

There have been several attempts to estimate the natural mortality of cod, herring, and sprat in the Baltic based on different approaches. Since the estimation of predation mortality is the central point in the MSVPA models, it is important to take a thorough look at the work done hitherto on this subject.

Thurow (1974) estimated the natural mortality coefficient (M) at 0.4 yr^{-1} in the 1930s for age 4 and older cod by plotting total mortality (Z) obtained from catch curves against yield. Strictly speaking, Z is a function of the fishing effort and this method would only hold true when recruitment does not change. Although variations in recruitment have probably occurred, especially since the early 1950s, and therefore the slope of the estimated line might be biased, the intercept at zero yield is mainly determined by the total mortality during the early years when effort was low. However, the method also requires no change in exploitation pattern. Since the fishery was concentrated close to the coast in the 1930s, where small and young cod are particularly abundant, moving gradually to offshore waters, Z and thus also M have probably been overestimated by Thurow.

Kosior (1978) estimated M at 0.18 for ages 3–5 on the basis of catch and effort data for the pre-spawning season in Subdivision 26 from 1965 to 1977, following the method of Paloheimo (1961). Grzebielec and Kosior (1987) obtained values between 0.12 and 0.18 for the cod stock in Subdivisions 25–32 during the period 1973–1985, using the same methods. Paloheimo's method is based on annual changes in F by age group. Since fishing mortalities in this stock have changed only slightly, the precision of these estimates is probably low. Furthermore, the effort series used represents only a minor fraction of the total effort employed in the fishery, so the results might be biased.

Thus, although the available evidence supports an M level in the order of 0.2 for cod in the Baltic as applied in other areas (e.g. Anon., 1988b), the data do not allow a very precise estimate.

From catch curves of herring around Bornholm during 1939–1945 (data from Jensen, 1947), Beverton (1963) estimated Z at 0.45 for age 3 and older. Since the total catch of herring in the Baltic at that time was only about 50 000 t, this value should be approximately equal to M, unless the herring stock was considerably smaller in 1939–1945 than it is now.

Ojaveer (1974) estimated M at 0.26 for ages 3–8 autumn spawners in Subdivisions 28 + 29S in 1963–1964 during a period when this herring stock was virtually unexploited.

Lassen and Sjöstrand (1980) obtained a value of 0.4 in Subdivisions 25–29S for age 3 and older herring based on acoustic estimates of absolute stock number-at-age in 1979 and catch-at-age data.

Sparholt (1989) estimated M at 0.16 with confidence limits of ±0.18 for herring aged 2–6 in the Western Baltic and the Skagerrak/Kattegat area (Subdivisions 22–24 and Division IIIa). These estimates were based on acoustic estimates, young fish survey indices, and catch data for 1981–1986 and a maximum likelihood method was used in a stochastic integrated model. Following the same approach (except that young fish survey indices were not available) a value of 0.18 was obtained for ages 1–9 herring in Subdivisions 25–27 (Sparholt, 1988).

The available evidence suggests that the natural mortality is in the order of 0.2, but no reliable estimates of M on young herring have so far been obtained on the basis of these types of models.

The total mortality of sprat was estimated by Beverton (1963) at 0.8 for age 1 and older based on catch curves for Subdivisions 25–26 in 1954–1959 (Elwertowski, 1957, 1958, 1959, 1960; Elwertowski and Janko, 1961). Since the effort in that period was very low, M constituted the main part of the estimated Z.

Wlodarczyk (1978) obtained M values ranging from 0.45 to 0.61 for 1969–1977 in Subdivision 26 based on regressions of effort data against Z.

According to Anon. (1988c) and Shvetsov and Gradalev (1988), in 1984–1987 M was about 0.5 for age 0 and 1, 0.2–0.3 for ages 3–5, and 0.4 for ages 6–8 in Subdivisions 26 + 28. These estimates were based on acoustic estimates of absolute stock numbers at age and the results agreed very well with c.p.u.e. data.

Shvetsov (1982) estimated M at between 0.40 and 0.51 for mature sprat in Subdivisions 26 + 28 in 1977–1979 based on absolute spawning-stock estimates from egg and larvae surveys.

Lassen (1979) applied an Andersen and Ursin (1977) type model with cod as predator and sprat as prey in Subdivisions 26 + 28 and found M values ranging from 0.5 to 0.7 for 1970–1978.

Hoziosky *et al.* (1989) obtained a value of 0.86 for 1981–1985 in Subdivisions 26 + 28, based on acoustic estimates of absolute stock numbers, catch data from the commercial fishery, and number of sprat eaten by cod.

The total natural mortality was split in a predation mortality (M2) and a residual natural mortality (M1). M1 was taken as 0.22–0.24 as estimated for Subdivision 32 for a time period when cod in that area was virtually absent.

The acoustic estimates of stock numbers of sprat of age 1 and older in Subdivisions 24–29S are about three to five times higher than the annual catch, according to data given by Anon. (1989g). This indicates that F on sprat in this area must be rather small. M should therefore constitute the main component of Z. According to Anon. (1989f), Z is approximately constant from age 4 onwards and varied from year to year between 0.84 and 1.02 (mean over ages 4–7) during 1974–1980 and between 0.52 and 0.66 during 1983–1988.

The data available thus suggest that M has varied over time. Although the estimates cannot be considered very reliable, M appears to have decreased in the 1980s and the northern stocks (Subdivision 28) probably suffer lower natural mortalities than the southern ones (Subdivision 25). The value of 0.4 used by Anon. (1989f) for sprat in all Subdivisions appears to be on the low side, with the possible exception of the later years and the northern areas.

3.5. Feeding rates

Feeding rates of the predators represent crucial parameters in MSVPA models because changes in these rates result in almost proportional changes in estimated mortality rates (Anon., 1986). Even though cod is one of the most studied species (Bagge, 1977; Daan, 1973; Degnbol and Stockholm, in prep.; Dos Santos and Jobling, 1988; Hodal, 1977; Jones, 1974; Lishev and Uzars, 1980), the results from these investigations have not been conclusive and reliable estimates of feeding rates of fish in the sea are extremely difficult to obtain.

No laboratory experiments on feeding rate have been reported for Baltic cod or under salinity conditions comparable to those found in the Baltic. Some *in situ* investigations made by Degnbol and Stockholm (in prep.) indicate that the evacuation time of a 50 cm cod is about 85 h. In contrast, Zalachowski's (1985a) consumption estimates, which are based on extensive stomach content data from the same area investigated by Degnbol and Stockholm, and on stomach evacuation models by Jones (1974) and Bajkov (1935), would suggest an evacuation time of 42 h for the same meal size and cod length. This suggests that the corresponding estimates of daily food intake according to Degnbol and Stockholm could be only half of those by Zalachowski. Lishev and Uzars (1980) estimated the consumption/biomass ratio to be 3.2 for adult cod. A comparable estimate of this ratio based on Zalachowski's data yields a value of 4.4, indicating that the Lishev and Uzars' estimate would be approximately halfway between the two extremes. However, the estimates of Degnbol and Stockholm and of Lishev and Uzars are based on an evaluation of diurnal changes in total stomach content and in the degree of digestion of the food in the stomachs, both of which are associated with large variances.

3.6. Interaction between species

The existence of a predator–prey relationship between cod and herring in Subdivision 22 has already been indicated by Jensen (1929), who discovered a significant negative correlation between the catch of cod and the catch of autumn-spawning herring in pond nets two years later. Using the same procedure, he also found negative correlations between cod and herring in the North Sea, in Subdivisions 24–32, and between cod and sprat in the Skagerrak and in Subdivision 22 (Jensen, 1962, 1966). However, the relationship became less pronounced in the 1960s. Lishev and Uzars (1967) observed a similar negative relationship between the catch of cod in year n and that of sprat in year n + 2, n + 1, n, and n − 1 and of herring in year n − 1 and n − 2 in Subdivisions 26 + 28. These findings have generally been interpreted as indicating that cod have a negative influence on herring and sprat because of predation. However, since cod eggs have been observed in herring stomachs (Fritz Köster, pers. comm.), there is a possibility that large year classes of herring and sprat impose an increased predation mortality on cod eggs and larvae, resulting in reduced recruitment. This would also lead to an inverse relationship.

Table 6 briefly reviews attempts made in the past to quantify the impact of cod predation on herring, sprat, and other food items in the Baltic based on stomach data. Although the results vary greatly the impact is generally estimated to be substantial.

In the Western Baltic (Subdivisions 22–24), the diet of cod is fairly diverse and is dominated by herring, sprat, the mollusk *Cyprina islandica*, various polychaetes, the crustaceans *Diastylis rathkei* and *Mesidothea entemon*, and various teleosts (mainly *Gobiidae*; Arntz, 1978; Bagge, 1981b; Schultz, 1987). In the central and eastern parts of the Baltic (Subdivisions 25–32), the food includes only a few species. Herring, sprat, the crustaceans *Mesidothea entemon*, *Mysis mixta*, and the polychaete *Harmothoae sarsi* provide the bulk of the diet (Uzars, 1985; Zalachowski, 1985b).

Several multispecies models have been developed for the Baltic Sea with the aim of estimating the natural mortality rates and growth of cod, herring, and sprat for potential use in the management of these stocks.

Mandecki (1976) applied an Andersen and Ursin (1977) type model for the entire Baltic Sea in which zooplankton was included as a dynamic component besides the three main fish species. Majkovski (1977) developed a very similar model for cod, herring, and sprat stocks in the Baltic proper (approximately Subdivisions 25–29). Both models were fitted to cod stomach

Table 6. Review of estimates of cod predation in the Baltic (biomass and consumption in thousand tonnes; SB: stock biomass; C: consumption by cod; n: number of cod stomachs examined).

Author(s)	Species	SB	C	C/SB	n	Period	Remarks
Lishev and Uzars (1967)	Cod	30	–	6.0	Unknown	1963–1966	Subdiv. 26 + 28
	Herring		20				
	Sprat		47				
	Others		108				
Uzars (1975)	Cod	233	–	12.9	11 000	1963–1973	Subdiv. not specified
	Herring		276				
	Sprat		408				
	Others		2311				
Zalachowski *et al.* (1976)	Cod	323	47		7 106	1971–1974	Central and Southern Baltic (approx. Subdiv. 25 + 26)
	Herring		315				
	Sprat		266				
	Others		484				
Axell (1982)	Cod	534	–	4.0	406	1976–1977	Only stomachs from Åland Sea; extrapolated to Subdiv. 25–32
	Herring		666				
	Sprat		851				
	Others		617				
Lishev and Uzars (1980)	Cod	324	–	3.3	Unknown	1975–1978	Stomachs from Subdiv. 26 + 28; C based on *in situ* evac. rate
	Herring		141				
	Sprat		156				
	Others		785				
Bagge (1981b)	Cod	221	–	2.7/5.2	2 452	1976–1980	Subdiv. 25; lower C-values: Daan (1973); higher C-values: Jones (1974)
	Herring		265/539				
	Sprat		–				
	Others		239/421				
Schultz (1987)	Cod	79	2 117	3.9	7 179	1978–1984	Subdiv. 22–24
	Herring		26 165				
Anon. (1988a)	Cod	1201		–	11 536	1980–1985	Subdiv. 25–29N
	Herring	1761	681				
	Sprat		953				
Anon. (1989a)	Cod	67	–	–	5 711	1980–1987	Subdiv. 22–24
	Herring	459	63				
	Sprat		9				
Anon. (1989a)	Cod	1038	–	–	11 536	1980–1987	Subdiv. 25–29N
	Herring	2013	573				
	Sprat	972	487				

data of Chrzan (1962) from the Gulf of Gdansk and the predation mortalities obtained were practically identical.

Lassen (1979) developed a modified VPA for sprat in Subdivisions 26 + 28 which takes into account predation by cod. The formulation of the natural mortality was based on Andersen and Ursin (1977). Although this model was simpler than the previous two models, the estimation of natural mortality is still fairly complicated and mathematically not quite satisfying, because the approximation procedure used is sensitive to large changes in the cod stock.

Horbowy and Kuptel (1980) also applied the Andersen and Ursin (1977) model to the Baltic Sea. They included several stocks of cod, herring, and sprat and two stocks of zooplankton and benthos. Horbowy (1989) developed the model further for Subdivisions 25–29S and verified it for internal consistency.

The same criticism that has been applied to Andersen and Ursin's North Sea model can also be applied to all the above models: the models are very complex and a substantial part of the input parameters are unknown and have to be guessed. Table 7 shows the predation mortalities estimated by some of the above

Table 7. Estimated predation mortalities (M2) from some multispecies models.

	Age	Horbowy (in press) Subdivisions 25–29S	Mandecki (1976) Subdivisions 22–32	Lassen (1979) Subdivisions 26 + 28
Sprat	0	0.69	–	
	1	0.71	0.6	
	2	0.52	0.6	0.52–0.59[1]
	3	0.40	0.5	
	4	0.32	0.5	
	5	0.28	0.5	
	6	0.25	0.5	
Herring	0	0.28	–	
	1	0.24	0.5	
	2	0.13	0.4	
	3	0.08	0.3	No estimates
	4	0.06	0.2	
	5	0.04	0.2	
	6	0.04	0.2	
	7	0.04	0.2	
Cod	0	0.18	–	
	1	0.08	0.6	
	2	0.02	0.2	
	3	0	0.1	
	4	0	0.1	
	5+	0		

[1] Values depending on availability index (100 and 25, respectively).

models. These seem to agree about the level of predation mortality on sprat but result in considerable differences for cod and herring.

4. MSVPA

Since the stocks of cod and herring east and west of Bornholm are fairly well isolated from each other, the Working Group on Multispecies Assessment on Baltic Fish decided to consider these two parts of the Baltic Sea as isolated systems and to develop independent databases as input for MSVPA. This separation applies also for sprat, although this species migrates across the border. An alternative might have been to couple the two systems, allowing for migration of sprat, but the databases can easily be merged at some later stage if this is thought appropriate.

The goal of MSVPA models is not to simulate entire ecosystems, but rather to extend the traditional VPA model to incorporate the first-order effect of predators on prey (Anon., 1980), i.e. MSVPA provides estimates of the predation component of natural mortality rates besides the usual VPA parameters, which are fishing mortality rate and stock numbers. Essentially, however, MSVPA exhibits the same tuning problems as VPA, because the number of observations is less than the number of parameters to be estimated. Therefore, some parameters have to be guessed or obtained from external sources. Typically, these parameters are the natural mortality M (VPA) or the residual natural mortality M1 (MSVPA) and the terminal fishing mortalities, i.e. fishing mortality rates at age for the last year and for the last age group in each year. The main input data are catch-at-age in numbers, mean weight-at-age, feeding rations, and food composition. As in the North Sea, the MSVPA for the Baltic stocks is run on a quarterly basis because predation on juvenile fish changes markedly between seasons. For a detailed description of the model and computer program see Gislason and Sparre (1987).

The computer program offers three different options as regards treatment of food other than the fish prey specified in the model. In the results presented here it has been assumed that the biomass of other food is constant over time. Cod is the only predator with herring and sprat as prey.

4.1. Subdivisions 25–32

The stocks included in this model are one cod stock (Subdivisions 25–32), two herring stocks (Subdivisions 25–27 and 28 + 29S), and two sprat stocks (Subdivisions 25 and 26 + 28). Usually, few cod are found in Subdivisions 29N and 30–32 and herring and sprat stocks in these areas are therefore not included. The stock units used are the same as used in routine stock assessment for cod (Anon., 1989e) and herring (Anon., 1989f). For sprat, a separate stock unit is introduced for Subdivision 25 compared to routine assessment (Anon., 1989f).

The geographical segregation of the herring and sprat stocks requires information on the distribution of the cod stock in order to evaluate the actual predation pressure exerted on each prey stock. Based on the distribution of the annual cod catch, it has been tentatively assumed that 80% of the cod stock is present in Subdivisions 25–27 and 20% in Subdivisions 28 + 29S, and that equal amounts of cod are present in Subdivision 25 and Subdivisions 26 + 28.

The stomach content data used so far are still of a preliminary nature. Only data from samples collected by Poland and the USSR from 1982–1984 and Subdivisions 25, 26, and 28 are available. These represent only a small fraction of all stomachs collected (Table 8). The average stomach contents over the three years have been used as a measure of the food composition in 1983. The herring observed in stomachs originating from Subdivisions 25, 26, and 28 were assumed to belong to the corresponding stocks, but the sprat data were pooled and the amount of sprat eaten was equally partitioned over the two stocks.

Consumption rates (C) were based on the mean stomach content in samples from Subdivisions 25–26 and on evacuation rates given by Jones (1974) for North Sea cod. They were calculated according to the following equation derived from Zalachowski (1985a):

$$C_{i,q} = FI_q \times 0.14 \times [w_{i,q}/0.01 \times K_i]^{(2.32/3)}$$

Table 8. Number of cod stomachs sampled by country and Subdivisions. (From: Anon., 1989d.)

	Subdivision							
	22	24	25	26	27	28	29	30 + 32
Denmark	904	647	7 051	586		953	168	
FRG	8 072							
Finland							118	1 500*
GDR	3 511	3 608						
Poland			4 681	7 877				
Sweden		226	738	219	457			112
USSR				14 979		14 734	640	441
Total	12 487	4 481	12 470	23 661	457	15 687	926	2 053
Grand total								72 222

*Including some stomachs from Subdivision 29.

where i is age, q is quarter of the year, w is mean weight of the cod, K is average condition factor, and FI is a feeding index reflecting that consumption varies between seasons. FI represents the relative stomach content by quarter and was estimated as 1.015, 0.915, 1.048, and 1.022 for the first to the fourth quarter, respectively. A temperature effect has not been taken into account.

Input data to the model are given in Anon. (1988a, 1989a). Since specific information on herring and sprat mean weight in the sea and mean weight in the cod stomachs is lacking, mean weight-at-age data for the commercial catch have been applied instead.

4.2. Subdivisions 22–24

The stocks included in this model are one cod stock (Subdivisions 22 + 24), one herring stock (Subdivisions 22–24 and Division IIIa) and one sprat stock (Subdivisions 22 + 24). Unfortunately, it is impossible to separate the herring stock in Subdivisions 22–24 from the stock in Division IIIa (Skagerrak/Kattegat). According to Sparholt (1989), the majority of the herring in Subdivisions 22–24 leave this area each year after spawning in March–May for a feeding migration to the North. Thus, the predation mortality estimated will account for only a fraction of the total predation mortality in this area. Seasonal differences in distribution of the herring are not taken into account.

The stomach data used are also in this case preliminary. Only data collected by the German Democratic Republic in Subdivisions 22–24 for 1980–1985 have been incorporated (Table 8). Consumption rates were calculated using the formula given in section 4.1 and FI was estimated as 0.917, 0.933, 0.836, and 1.314 for the first to the fourth quarter, respectively. Other input data to the model are given in Anon. (1988a, 1989a).

5. Results

It is no trivial problem presenting the results from MSVPA in a comprehensive way, because the bulky output from the program includes multidimensional arrays of fishing mortalities, predation mortalities, stock numbers, etc., for each stock and quarter. Since it is impossible to present here a detailed account of the results for the two areas, the following description is an attempt to condense the most significant results to a tractable size.

Summaries of the total biomass, cod biomass, yields of cod, herring, and sprat, and biomass of herring and sprat eaten by cod in the two areas are given in Table 9 for 1980–1987. In Subdivisions 25–32, the total biomass of these stocks has varied between 2.9 and 4.8 million tonnes. The cod biomass has decreased from 1.31 million tonnes in 1980 to 0.69 million tonnes in 1987. This decrease is largely attributable to fluctuations in recruitment, since fishing mortality in cod has not varied much during the last 20 years (Anon., 1987c, 1989e). The amount of herring and sprat eaten by cod shows large variation: between 1.63 (1982) and 0.33 million tonnes (1987). These fluctuations are much larger than the variations in cod biomass due to changes in the age structure of the cod stock, because during the years with high cod biomass the stock was dominated by juveniles, which are characterized by higher consumption rates relative to their weight than older cod. The total yield of herring and sprat has generally been much less than the amount eaten by cod and the substantial reduction in predation has not led to a corresponding increase in the catches of prey species, although their yields tend to have increased slightly in recent years.

In Subdivisions 22–24 the total biomass has varied between 454 000 and 676 000 t. The cod biomass was stable at about 80 000 t until 1985 and decreased to about 41 000 t in 1987. In this case, too, fishing mortality has not varied much in recent years (Anon., 1987c, 1989e), and fluctuations in recruitment are largely responsible for the changes in biomass and yield. The total yield has varied between 178 000 and 274 000 t. The fluctuations are mainly due to the herring catch, a substantial part of which is taken outside the Baltic in Division IIIa. The amount of herring and sprat eaten by cod dropped from

Table 9. Biomasses, yield, and amount of herring and sprat consumed by cod ('000 tonnes) as estimated by MSVPA.

	Stock biomass		Yield		Consumption of herring and sprat by cod
	Total	Cod	Cod	Herring + sprat	
a. Subdivisions 25–32					
1980	3706	1314	380	181	962
1981	4398	1306	335	199	1520
1982	4677	1270	336	190	1632
1983	4852	1172	337	187	1620
1984	4565	1027	412	190	1245
1985	3830	768	279	240	763
1986	3229	760	252	244	415
1987	2928	688	180	266	327
b. Subdivisions 22–24					
1980	454	77	41	137*	84
1981	508	87	58	169*	78
1982	502	79	48	167*	88
1983	559	80	52	170*	90
1984	644	75	45	191*	85
1985	651	58	38	221*	60
1986	595	40	26	190*	41
1987	676	41	29	245*	48

*Including spring-spawning herring caught in Division IIIa and the eastern part of the North Sea.

80 000–90 000 t in 1980–1985 to 48 000 t in 1987. The total yield of herring and sprat in this area has generally been higher than the amount eaten by cod. Also in this area, the reduction in predation coincides with a slight increase in yield of the prey species.

Figures 3 and 4 show the relationship between estimated predation mortality rates by age and mean weight-at-age for each prey stock in the two areas. Although results obtained for the North Sea indicated a log-linear relationship between these two variables independent of prey species (Anon., 1988e), these data indicate that the predation mortalities are rather more variable in the Baltic in relation to size of prey.

6. Discussion

The central feature in MSVPA models is the estimation of the predation component of the natural mortality rates. The values obtained could be compared with the other estimates of M given in section 3.4. However, the preliminary nature of the feeding data used so far does

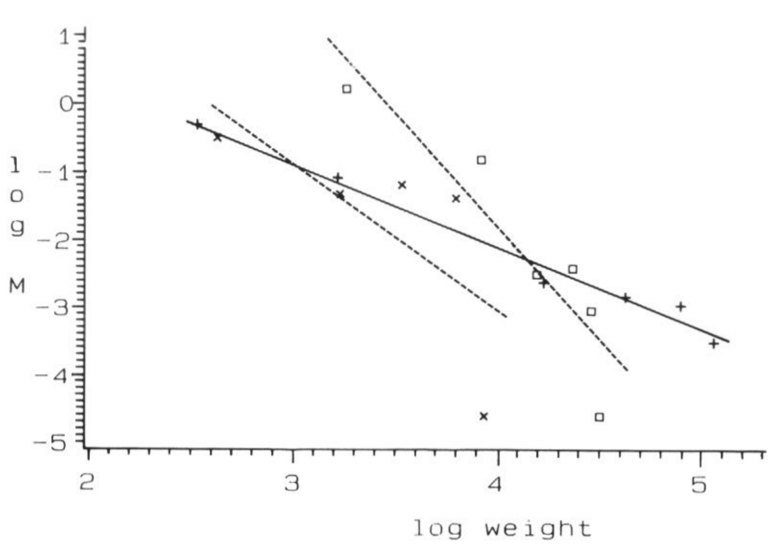

Figure 3. Plots of log M estimated from the MSVPA against log weight for herring stocks. □ Subdivisions 22–24; + Subdivisions 25–27; × Subdivisions 28 + 29S. Regression lines shown.

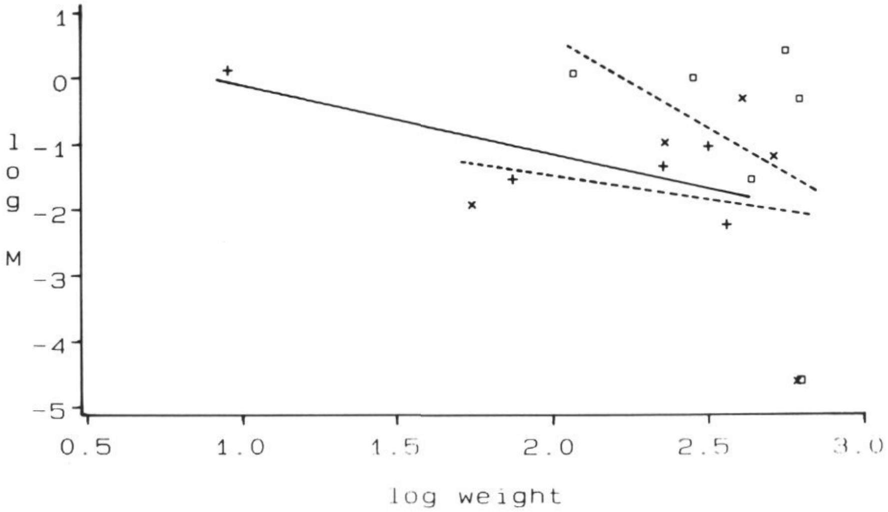

Figure 4. Plots of log M from the MSVPA against log weight for sprat stocks. + Subdivisions 22–24; □ Subdivision 25; × Subdivisions 26 + 28. Regression lines shown.

not allow a proper evaluation of the appropriate level of natural mortality in the Baltic at this stage.

The availability of stomach content data for several individual years for Subdivisions 22–24 provides the opportunity to test one of the basal assumptions of MSVPA, namely that suitabilities are constant from year to year. Another possibility would be that suitabilities vary as a function of prey abundance, for example due to prey switching (Murdoch and Bence, 1986). One way of testing this assumption is to consider the ratio of the difference between estimated and observed food composition over the estimated food composition for individual age groups of cod and prey. These ratios are plotted against prey biomass for some selected predator–prey combinations in Figure 5. The results vary and certainly the assumption that suitabilities are constant is not falsified by this test. However, further analysis is obviously needed when all stomach content data have been worked up.

The appropriate consumption rates for cod are still highly uncertain (Anon., 1989c). The values used in the Baltic (based on Jones, 1974) are between 20% and 60% higher than those applied to equally sized cod in the North Sea (based largely on Daan, 1973). The average weight of the stomach contents of cod of comparable size is similar in the two areas, suggesting that the evacuation time is shorter in Baltic cod than in North Sea cod. However, *in situ* observations indicate that evacuation time is relatively long in the Baltic (Degnbol and Stockholm, in prep.) and that the consumption rates used so far may be about 40% above the actual value (Lishev and Uzars, 1980). Because the environments are different, particularly with respect to salinity and oxygen concentrations, values for North Sea cod cannot *a priori* be regarded as valid for the Baltic; more work is urgently required.

The tuning of terminal F values constitutes a special problem because this has to be done on several stocks simultaneously. Very little attention has hitherto been drawn to this problem. Since cod is not treated as a prey, the procedure for single-species VPA can be adopted for this species, but for herring and sprat new methods have to be developed. The present procedure is based on annual terminal F-values from the single-species VPA's which are not valid in the MSVPA context. In particular, the moderately exploited sprat stocks might be seriously affected if wrong terminal F-values are chosen. Methods using external information, such as acoustic estimates of stock numbers or abundance indices from surveys, would be preferable.

The present MSVPA for Subdivisions 25–32 incorporates geographically separated stocks. Therefore, information on the distribution of the cod stock is required in order to estimate the predation in each area. An alternative to the present pragmatic approach would be to develop an MSVPA with spatial resolution, as suggested by Gislason and Sparre (1987), and to consider migration in the model. However, the migration data required would be difficult to obtain and the likely gains of further model complications would probably be small.

The stock units used for Subdivisions 25–32 can be questioned. There are significant exchanges between the herring stocks in Subdivisions 25–27 and 28 + 29S (Anon. 1989f) and, although there are differences in growth, both recruitment and stock sizes appear to be highly correlated. Sprat seems to be even more migratory than herring and the observed differences in growth rate between different areas are only small. Therefore, combining the two herring and the two sprat stocks in single units should be given serious consideration.

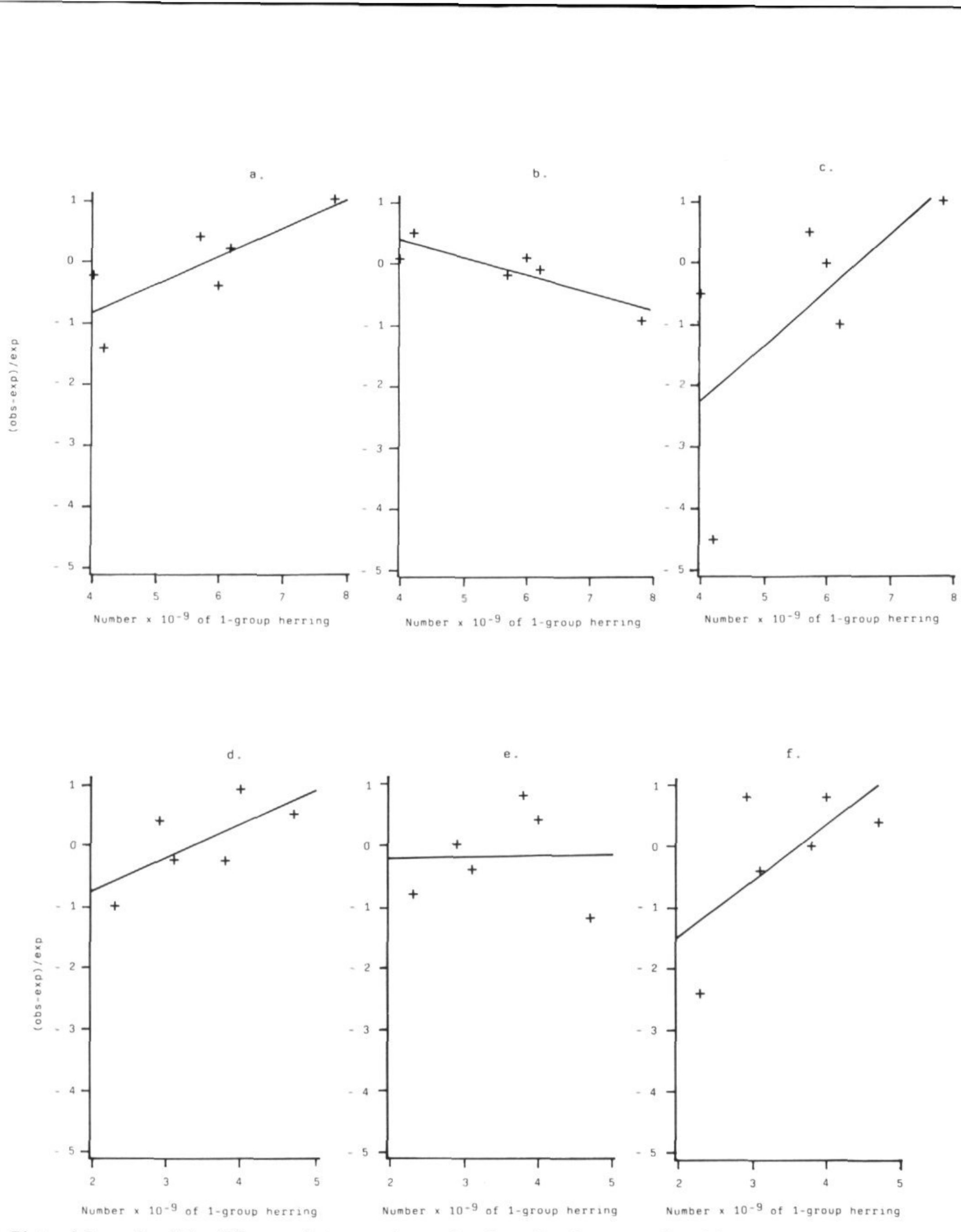

Figure 5. Plots of the ratio of the difference between observed and predicted over predicted fraction of 1-group herring in cod stomachs of different age groups versus stock numbers of 1-group herring in Subdivisions 22–24 in 1980–1985. a, b, c: age groups 2, 3, 4, respectively, during the first quarter. d, e, f: age groups 2, 3, 4, respectively, during the fourth quarter.

During periods of high abundance, cod tend to spread into the northern parts of the Baltic (Subdivisions 29N, 30, and 32). Although spawning aggregations may sometimes be formed in these areas (Modin, 1987), eggs do not hatch because of the low salinity, and a separate stock cannot be established. Since the influence on the herring and sprat stocks in these areas may be significant in those years, inclusion of these stocks would seem appropriate, even when this would have to be done in a special way because of the periodic character of the cod invasions.

Cannibalism in Baltic cod is a relatively rare phenomenon and restricted to years when small cod are abundant (Bagge, 1981b; Uzars, 1985; Zalachowski, 1985b; Schultz, 1987). According to Zalachowski (1985b), small cod represented about 10% of the diet of cod of age 4 and older during the years 1977–1982. During this period, the stock sizes of herring and sprat were large as well and the cannibalism among cod might have been higher if this had not been the case. It would therefore seem worthwhile to include cod as prey in the models.

The other food component in Subdivisions 25–32 consists of only a few species. Including these species in the model would offer possibilities for refining the assumptions about the biomass of other food as well as for studying prey switching.

Table 10. Results of an analysis of covariance of the weight-at-age of herring in Subdivision 25, and in Subdivisions 28 + 29S according to the model: log[weight-at-age/(cod biomass)] = log(year × age).

Source	Sum of squares	d.f.	F	p > F	R^2
Subdivision 25 – acoustic surveys 1982–1988:					
Age	5.16	6	45.62	0.0001	
Cod biomass	0.64	1	33.88	0.0001	
Error	0.77	41			
Total	6.57	48			0.88
Subdivisions 28 + 29S – commercial catches 1978–1988:					
Age	18.53	6	195.28	0.0001	
Cod biomass	0.61	1	38.75	0.0001	
Error	1.09	69			
Total	20.23	76			0.95

The mean weight-at-age of prey found in cod stomachs was copied from the weight-at-age array for the commercial catches. Since cod are likely to select on average smaller individuals within an age class than the commercial vessels, the numbers of young herring and sprat consumed are probably underestimated in the MSVPA. In future, methods estimating prey weights directly should be pursued.

The mean weight-at-age in the catch of herring and sprat has varied by as much as 40% during the last 10–20 years in most areas. This variability has serious implications for catch predictions because, even if numbers of fish can be predicted correctly, the prediction in tonnes may be off by a considerable amount due to the fact that growth variations are largely unpredictable. Changed migration patterns (Anon., 1988f) and bad feeding conditions due to thermal conditions (Wyszynski, 1989) have been suggested as possible causes of these large variations. Fluctuations in predation pressure pose another possibility. Since predation mortality decreases with increasing prey size, a reduction in predation pressure can be expected to lead to a reduction in mean weight-at-age. Table 10 gives the results of an analysis of covariance of the relationship between cod biomass and two sets of weight-at-age data for herring carried out with age as class variable, cod biomass as the continuous independent variable, and weight-at-age as the dependent variable. The cod biomass effect is highly significant for both data sets and explains about half of the residual variation of the weight-at-age data when the age effect is taken out. Although such a causal relationship might be included in the model, the additional and unpredictable effects of severe winters or changed migration patterns might be more important and the associated uncertainty in catch prediction cannot be resolved.

The time period covered so far by MSVPA is 1980–1987. However, a substantial amount of stomach content data is available from earlier years and it might be worthwhile to extend the period backward. This would enhance the possibilities for verifying some of the underlying assumptions of the model and the precision of the suitability estimates, as well as improving our general understanding of the system.

The spatial and temporal distribution of stomach samples is not entirely satisfactory. The northern parts of Subdivisions 25–32 are poorly covered and samples from Subdivisions 22–24 in the second and third quarters are limited. This could result in significant bias and future sampling should be directed to these areas in the appropriate quarters of the year.

The objective of the MSVPA is not to model the entire ecosystem but to improve the basis of management advice by taking interspecific predation into account. At the same time, the dramatic changes in the various fish stocks during the period covered by the analysis offer the possibility to study specific regulatory mechanisms within the system in more detail. However, before these problems can be effectively approached, the main task in the near future will be to extend the stomach content database and to improve the consumption estimates.

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A robust approach to the analysis of feeding data and an attempt to link multispecies virtual population analysis and Volterra predator–prey system analysis

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Blinov, V. V. 1991. A robust approach to the analysis of feeding data and an attempt to link multispecies virtual population analysis and Volterra predator–prey system analysis. – ICES mar. Sci. Symp., 193: 80–85.

A robust approach to the analysis of Cape hake feeding data is briefly described in relation to the application of multispecies virtual population analysis (MSVPA). A mean feeding intensity by age group was calculated based on a probabilistic function of the frequency distribution of stomach fullness values in the samples. The MSVPA results suggest a major change in the feeding behaviour of the hake: the level of cannibalism was high during 1971–1979 but decreased sharply in 1980–1984, when young hake in the food were replaced by horse mackerel. The results are presented as phase diagrams of the abundances of the two species as well as of young and old hake. A first attempt is presented to link MSVPA to a Volterra predator–prey system analysis, which opens perspectives for improved understanding of multispecies systems. As an example, the predation function of Cape hake on horse mackerel was assessed for a simple Volterra system based on MSVPA data. The results of this work are discussed in light of recent developments in North Sea multispecies assessment.

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Introduction

The appropriate treatment of stomach content data with regard to feeding periods, stomach evacuation rates, and empty stomachs is still under discussion (e.g. Jobling, 1986; Olson and Mullen, 1986; Persson, 1986; Blinov, 1989a). This contribution continues the development of a robust approach (Blinov, 1988a) to feeding data of Cape hake from ICSEAF region 1.3–1.5 as an alternative to costly annual, large-scale research programmes establishing the spatial and temporal feeding relationships between predators and prey in the region. This approach is related to the development of a multispecies virtual population analysis (MSVPA) for the area and of a simple beta method based on results of MSVPA which predicts the catch of horse mackerel (Blinov, 1988b). The present paper also includes an attempt to link MSVPA to a Volterra predator–prey system analysis (VPPSA), which was formulated as the inverse mode of a discrete Volterra system. The approach is discussed in relation to recent developments within the ICES Multispecies Assessment Working Group (Anon., 1989a). Compared to the original Symposium contributions (Blinov, 1989a, b), the present text is greatly condensed and the interested reader is referred to these papers for details.

Analysis of feeding data

The strategies most commonly followed in studies of fish feeding are discussed by Blinov (1989a). The strategy adopted here in analysing the Cape hake feeding data was to: (1) group scattered stomach samples and smooth the results, because the available data were of rather diverse quality; (2) put reasonable restrictions on the number of different food categories distinguished in order to reduce variability and keep computing time low; (3) make a rational hypothesis about the "other food" component; (4) extrapolate feeding data for as large a time period as possible; and (5) develop an algorithm that allowed comparison of the results with those obtained from single-species VPA.

The core of the approach is to find an expression for the mean feeding intensity ($\bar{I}$) of predator cohort b in the survey area when the total number of samples is n:

$$\bar{I}^b = \sum_{i=1}^{n} X_i^b \times P(X_i^b) \qquad (1)$$

where $P(X_i^b)$ is the probability of finding a stomach fullness index X_i in a stomach sample of a predator of age b. Here i is a subscript for a sample irrespective of the station grid or of the number of stomachs collected at a station, i.e. i is related to a coarse, 'unstructured' sampling strategy, unlike a strategy aimed for instance at collecting individual stomachs (cf. Anon., 1989a, b). The probability $P(X_i^b)$ is assessed from the frequency $n_i(X_i)/n$, where $n_i(X_i)$ is the number of stomachs with fullness index X_i.

Equation (1) provides the mean feeding intensity for an age group. Although further averaging over age groups is trivial, there is no need to do this, because input data for MSVPA are structured by age group. Unfortunately, this point has not been made clear by Blinov (1989a). The approach presented here might be useful when a sampling strategy aimed at collecting individual stomachs is adopted for the North Sea Stomach Sampling Programme in 1991 (Anon., 1989b). Empty stomachs were considered to be valid samples with $X = 0$ having a finite probability of occurrence (Zweifel and Smith, 1981). In addition, it was assumed that an extended spatial survey should, as in statistical mechanics, yield the same probabilities of occurrence as a prolonged survey in a restricted area (as long as it is completed within the same time frame of course).

Available qualitative feeding data (e.g. stomach fullness indices) were calibrated against quantitative weight determinations. Diurnally collected stomach content data have been used to estimate mean quarterly estimates of feeding intensity. These quarterly values are rather lower than those of Feldman (1991), since empty stomachs were included in this study, but they appear to be more realistic.

The quarterly food consumption was based on the maximum daily ration estimated by Preński (1980), adjusted by a correction factor for mean feeding intensity. The quarterly estimates of the "other food" component, obtained by subtracting the quantities of Cape hake and horse mackerel in the food from the total, appeared to support the hypothesis of Pope (1979) that the contribution of "other food" in absolute weight is constant. Therefore, the function for the suitability (SUIT) was taken as:

$$\mathrm{SUIT}_{(q,s,a,b)} = (\zeta_{(q,s,b)}/\bar{w}_{(q,s,a)}) \Big/ \sum_{s}\sum_{q} \zeta_{(q,s,b)}/\bar{w}_{(q,s,a)} \qquad (2)$$

where s is prey species index, a is prey age index, $\bar{w}$ is mean prey weight, q is quarter, and ζ represents the weight fraction of a particular prey in the stomach of a particular predator.

Through an iterative procedure the values of residual mortality (M1) and predation mortality (M2) were obtained according to:

$$M1 = M - M2 \quad (\text{conditional on } M1 > 0) \qquad (3)$$

where the natural mortality coefficient (M) was assumed to be 0.3 and 0.4 for Cape hake and horse mackerel, respectively. This procedure is analogous to two single-species VPAs solved simultaneously, since cohort size at age is not affected by predation.

The MSVPA results for Cape hake and horse mackerel in ICSEAF region 1.3–1.5 for the period 1971–1984 are shown in Figure 1. The annual biomasses of the two species vary apparently in antiphase and the time span studied can be split into two periods: the annual consumption by large hake of its own young ones decreases during the years 1971–1979, while stabilizing during the period 1980–1984; the amount of horse mackerel also decreases in the first period, but increases sharply during the second one. The increase in the Cape hake stock after 1979 may be explained by the decrease in the rate of cannibalism.

The amount of horse mackerel consumed by hake after 1979 increased by 60–70%, i.e. by an amount which approximately equals the weight difference between individuals of the two species of the same length. Thus, during the period 1971–1984, a reorientation occurred in the food preference of hake from juvenile hake to horse mackerel.

A comparison of the biomasses of the two stocks leads to a phase diagram of the predator–prey system (Fig. 2; see also Blinov, 1988a, 1989a) and the line representing the functional relationship appears to exhibit a clear saddle point or minimum, which supports the idea of a change in the interactions between the two species. This line may be seen as a trajectory of a Volterra system, the form of which has to be reconstructed (Blinov, 1988b).

The fish fraction in the stomach contents of hake increases sharply when the fish become older than 5 years, largely due to higher rates of cannibalism in the older fish (Fig. 3). Thus, the Cape hake population may be viewed as composed of two interrelated subpopulations: young hake between 1 and 5 years old, and cannibals between 6 and 10 years old. The phase diagram for such a system shows two sharply distinct succession stages in the development of the system (Fig. 4), emphasizing once more the changes that have taken place in the intra-specific relations.

Volterra predator–prey system analysis (VPPSA)

A Volterra predator–prey system of equations has to contain terms that reflect the following processes: repro-

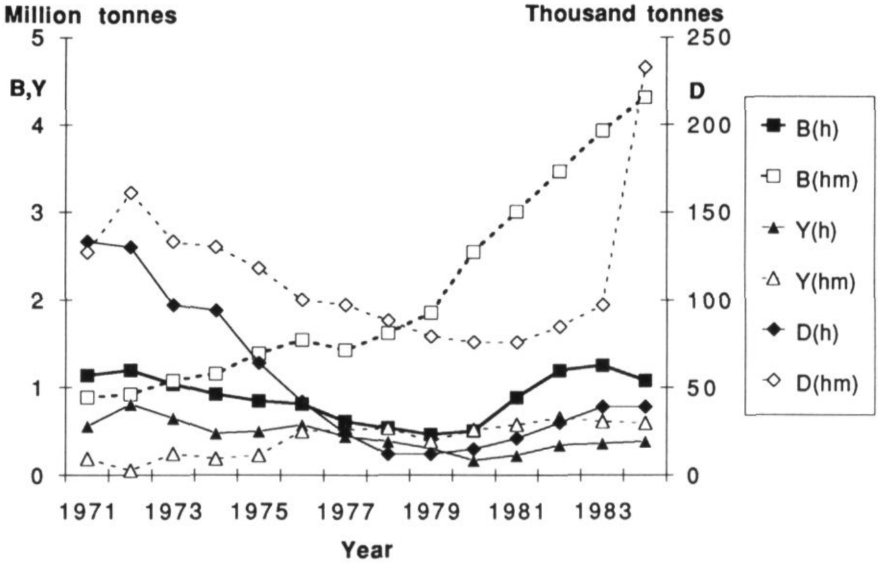

Figure 1. Stock biomasses (B), yields (Y), and number of deaths due to predation by hake (D) of Cape hake (h) and horse mackerel (hm) according to MSVPA.

duction, intra- and interspecific predation, compensation due to competition for food, fishing mortality, and natural losses due to causes other than predation. In a simplified system (Volterra, 1931; Blinov, 1988b) reproduction is assumed to be evenly spread through time and is represented by a constant ϵ. For a more realistic description of the reproduction dynamics within a year, the spawning process must be represented by a pulse type function, as for example by Dirac's ∂ function multiplied by some function of time:

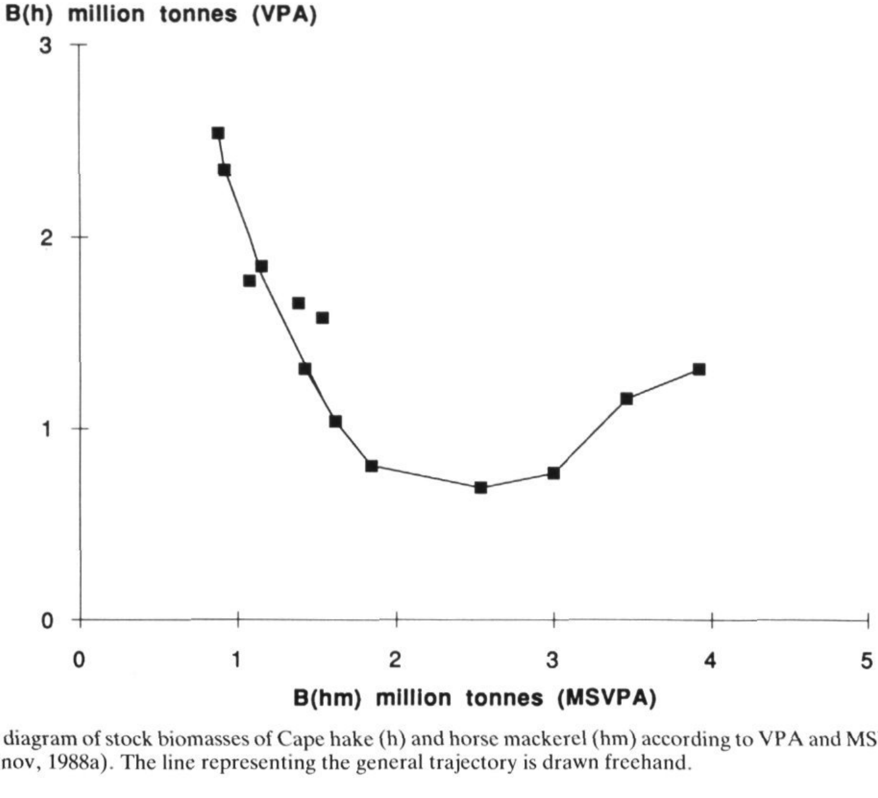

Figure 2. Phase diagram of stock biomasses of Cape hake (h) and horse mackerel (hm) according to VPA and MSVPA estimates, respectively (Blinov, 1988a). The line representing the general trajectory is drawn freehand.

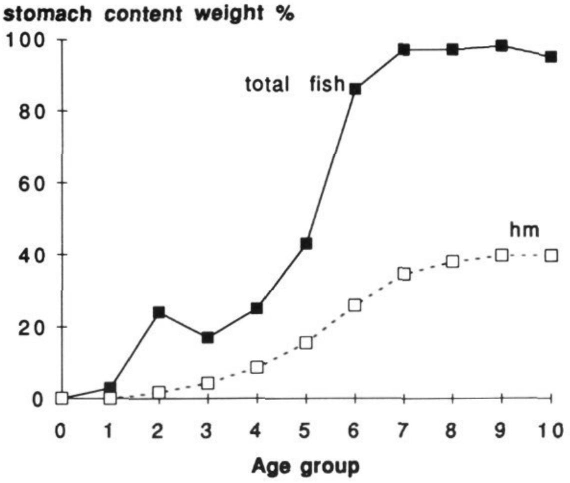

Figure 3. Weight percentages of fish prey (drawn line) and horse mackerel (dashed line) in the stomach contents of Cape hake by age group.

$$\epsilon(t) \times \partial(t - t_s) \tag{4}$$

Here t_s represents a characteristic spawning time within a year and $\epsilon(t)$ is most often given a bell type function but not necessarily a periodic one. Quasi-periodicity of (4) is obtained by switching on the ∂ function at successive time intervals $t_s, t_{s+1}, \ldots$ The reproduction, or rather recruitment, function (R) can be verified by checking against the pattern of abundance indices (A) of juvenile fish from surveys:

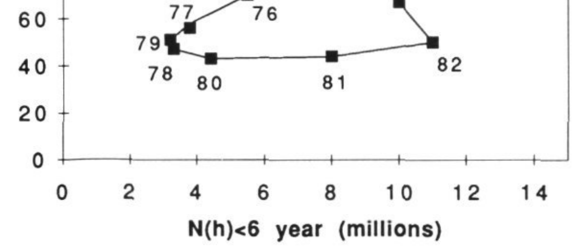

Figure 4. Phase diagram of the stock numbers according to MSVPA of adult (>6 years) and of juvenile hake (<6 years) serving as food for the older hake. The years of observation are indicated. The line representing the general trajectory is drawn freehand.

$$R = \int \epsilon(t) \times \partial(t - t_s) \times dt \approx R_{obs}(A) \tag{5}$$

in order to check the realism of the numerical analysis. In the present case, such reproduction functions must be formulated for Cape hake and horse mackerel separately. Blinov (1989b) provides one of many possible forms of an extended Volterra system, and gives an expression for the annual consumption of the predator in terms of a predation function.

If two structurally different approaches, MSVPA and VPPSA, are carried out in a multispecies analysis of the same system, it is appropriate to try to find the boundary conditions on the dynamics through which the two systems can be linked. This can be realized by using the output from MSVPA as input to the Volterra system. Hence, VPPSA can be seen as the solution of the inverse problem of a Volterra system, i.e. it is aimed at a formulation of the equations so that the system dynamics would satisfy the boundary conditions set by the results from MSVPA according to a predefined degree of accuracy.

There is reason to believe that the MSVPA results are characterized by a higher degree of accuracy than a traditional Volterra system could ever produce, given the imperfections and oversimplifications in the formulation of the basic functions, and the inaccuracies involved in estimating parameter values for a highly complex system from aggregated data. Thus, the primary problem is to develop a Volterra system model, which is functionally as complete as possible but is also directly related to the processes as they are formulated and structured in MSVPA, so that the output of the two become mutually exchangeable. If successful, such a Volterra system might be used to analyse particular properties of MSVPA and could also provide important additional information on the dynamics of the natural system.

A hypothetical example of the kind of procedures that would be involved in finding a solution for a Volterra system is shown in Figure 5. The starting-point is given by the quarterly estimates of abundance of a population provided by MSVPA. The first step is then to define all necessary terms on the right-hand side of the Volterra system equations. During this process, one may observe that some possible solutions to the problem lead to developments which deviate significantly from the observations according to MSVPA as indicated by the arrows. The criteria for acceptance may also be defined quantitatively, so that any formulation that does not meet the criteria can be rejected. In this way one may end up with a formulation which gives reasonable answers, as for instance indicated by lines a and b. When satisfied with the results, the final set of equations may still give an infinite number of solutions. The unique solution for the appropriate parameter values of the system may then be found by an iterative procedure

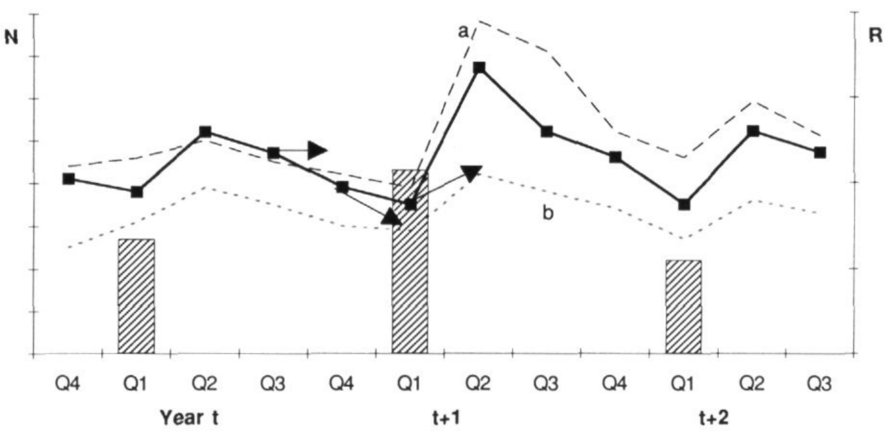

Figure 5. Schematic representation of the procedures involved in finding a solution for a Volterra system (hypothetical example; only one species shown). Dots represent available MSVPA abundance estimates (N) by quarter and bars recruitment estimates (R). Arrows indicate the directions of the predicted changes in each time step according to an initial formulation of the Volterra system. Lines a and b represent examples of different "acceptable" solutions. See also text.

using the MSVPA output figures as boundary conditions.

A simple example of the kind of problem faced in VPPSA is given in Figure 6. The function for predation by Cape hake on horse mackerel during 1976–1980 increased sharply, whereas the predation function on Cape hake decreased for no obvious reason. Such an inadequacy points to an oversimplification of the predation equation for hake in the system.

Discussion

The approach to MSVPA presented here is based on a simple interpretation of feeding data and a robust probabilistic treatment of the stomachs collected in sampling schemes to evaluate the seasonal feeding intensity of Cape hake by age group. The results indicate that the quantities consumed are far below the maximum rations of individuals observed both in the field and in the laboratory.

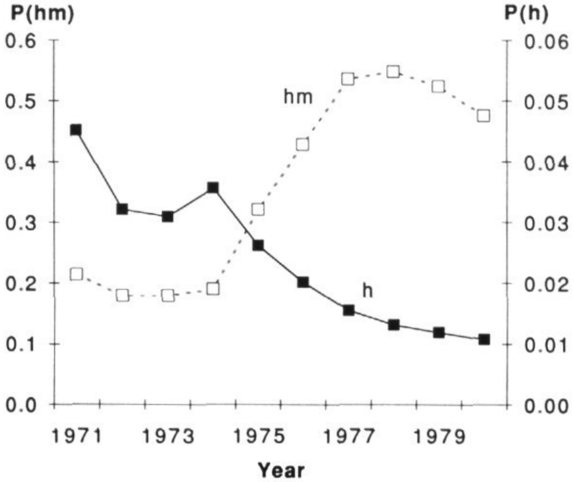

Figure 6. Estimated values of the predation function (P) of Cape hake (cf. Blinov, 1989b) on juvenile hake (h) and horse mackerel (hm) according to a simplified Volterra predator–prey system of the two species.

Our approach assumes that the feeding habits of a predator are relatively stable and we have extrapolated the information based on limited feeding data to apply to the entire period. Such a procedure was recently questioned by Daan (1987). The ICES Multispecies Assessment Working Group, however, concluded that the predatory fish investigated in the North Sea exhibit feeding habits which are sufficiently stable for constant vulnerability of the prey to be assumed (Anon., 1989a). This supports our approach in respect of smoothing the available data and extracting general feeding relationships for Cape hake for the purpose of extrapolation within reasonable limits.

Considerable progress has been made in studies of fish feeding in relation to MSVPA during the last few years (Anon., 1989a). Also, multispecies analysis has geographically expanded and now includes, apart from the Northeast Atlantic, the Bering Sea (Laevastu and Bax, 1991), the Peruvian upwelling area (Jarre *et al.*, 1991), and the Southeast Atlantic (Blinov, 1989a, b). In particular, the ICES Multispecies Assessment Working Group has successfully developed new methods of smoothing feeding data, analysing prey preferences, and predicting multispecies effects of management measures (Anon., 1989a).

Still, there may be scope for further analysis of the North Sea data. From Daan's (1987) table 2 it would appear to be possible to obtain a more detailed relationship between weight and number fractions of prey observed in stomachs as affected by the factors quarter, species, age, environment, and sampling limitations. According to Daan's table 4, the variability in predation is highly skewed and low predation rates are more common than high predation rates. It would be interesting to explore the impact of the highest predation rates on the fish community. If possible, predation levels should be studied in relation to the density distribution of predator and prey, including major categories of zooplankton and benthos that compose 30–90% of the "other food" (Anon., 1989a). Special models could be constructed for areas with large overlap in the distribution of predators and their prey.

Daan (1987) correctly concluded that long-term gains due to increased mesh sizes were generally overestimated. Blinov (1986a, b, 1989b) indicated also that the expected effects were usually too optimistic, even without accounting for injured fish, which become an easy prey for predators after they have escaped through the meshes.

Daan (1987) indicates that many biologically sensible management options might be chosen. Anon. (1989a) stresses the need for a thorough study of a vast number of possible options, but it will be difficult to make an appropriate selection. A compromise might possibly be found by choosing a small number of "normative" levels of exploitation for multispecies stocks (Blinov, 1989b), based on firm ecological evidence.

The issue of linking MSVPA and VPPSA is quite new in stock assessment practice and population modelling and it would be worthwhile to develop this approach further in the future.

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Multispecies interactions on Georges Bank

B. J. Rothschild

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The interactions among sixteen Georges Bank stocks of fish were studied. A traditional approach to the study of such interactions involves examining the correlations among the time series of species abundance. However, in considering the variability of biomass on Georges Bank, many interactions among important food fish play a relatively minor role. A study of the eigenstructure of the variance–covariance matrix of the temporal abundance of the sixteen species revealed that the dominant variation was attributable to three species: spiny dogfish, winter skate, and haddock. The methodology enabled tracking the eigenassemblages of these fish over time. The temporal variability of these assemblages was affected by fishing.

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Introduction

The interactions among species are scientifically and practically important. From a scientific point of view, an understanding of species interactions is required to understand ecosystem dynamics. Attempting to understand the interactions is particularly complex because they are imbedded in a system of seemingly infinite dimensionalities. Mathematical theory can only accommodate several populations at most (Nisbet and Gurney, 1982) and empirical studies suggest that in some instances population interactions may not even be discernible (cf. Sissenwine *et al.*, 1982). From a practical point of view, an imperfect understanding of species interactions constrains answering fishery management questions such as whether regulating fishing mortality of a particular population affects other populations; whether collapsed stocks are "replaced" (raising the question of whether manipulating "replacing" stocks will result in the recovery of the original stock, see Daan, 1980); and whether so-called anthropogenic activity, fishing or otherwise, affects only the small subset of directly influenced populations, or, on the other hand, whether the effects cascade to affect other populations as well. If consistent linkages among particular populations occur, then the complex of populations can be managed on an ecosystem basis. If such linkages do not exist, then emphasis on the "single species approaches" needs to be reconsidered.

Despite the theoretical difficulties and the weak linkages between theory and observations, interactions among species must exist because ecosystem biomass varies less than the sum of the variations in the biomass of each individual population that comprises the ecosystem. To deduce that the abundances of some of the species are correlated is then an elementary statistical proposition.

Since populations must interact, it would seem to be a simple matter to estimate the correlations, determine which are important, and then draw conclusions with regard to fishery management and ecosystem energetics. However, the problem is not that simple. Of the trajectories of a large number of populations, some will always be correlated owing only to chance alone. Even if populations are not correlated in a statistical sense, the abundance of one may control the abundance of the other. Populations may strongly interact for only one or two years, the temporary effects may be quite important and may last several years, yet the abundance of the populations may not be correlated in the Pearson correlation-coefficient sense. In other words, strong interactions among populations may not be detectable if they are measured by use of the Pearson correlation coefficient. Thus, it is impossible to ascertain from data alone whether or not populations that have correlated or uncorrelated abundances interact. Additional information must be supplied in the form of theory. Paradoxically, the development of a theoretical framework often depends upon observation.

In this paper, we intend to show how fishing has affected the multispecies interactions, and the predator–prey balance on Georges Bank resulting in a significant change in the metabolism of the Georges Bank ecosystem. We use data from the National Marine Fishing Service Trawl Survey conducted since 1963 in the western North Atlantic off the US Coast (see Clark and Brown, 1977). In the early years, these surveys have only been conducted in the fall. Subsequent to 1967, they were conducted in the spring as well. Our analysis concerns only the fall data from Georges Bank. The basic abundance indices are numbers of fish per tow and kg per tow. Estimates of these indices are made using the delta estimator. The data are taken (with appropriate caveats on constant catchability, etc.) to be fairly representative of the abundance of the sixteen major Georges Bank species (Stephen Clark, pers. comm.) caught with a bottom trawl.

Our approach involves considering the correlations among the abundance trajectories of the sixteen species. We next sorted out the major sources of variability in biomass by studying the eigenstructure of the variance of the kg-per-tow data, using techniques of principal component analyses (PCA).

Table 1. Mean abundance in kg per tow of the 16 most abundant species on Georges Bank for the years 1963 to 1988 and the 22 positive and negative pairs of "significant" correlations among these species. Also included are abbreviations for each species which are used subsequently.

Species	kg per tow	Correlated species
Spiny dogfish (SD)	29.0	WS+ SS+AP−YF−
Winter skate (WS)	23.4	SD+ TS− AP− G− YF− LON+
Haddock (HA)	17.1	G+ YF+
Little skate (LS)	7.1	AC+
Atlantic cod (AC)	6.2	WH+ SS+ LS+ TS+
Yellowtail flounder (YF)	4.0	HA+ SD− WS− LON−
Red hake (RH)	2.7	
Long-fin squid (LON)	2.5	WS+ YF− AP−
Winter flounder (WF)	2.2	WH+
Silver hake (SH)	2.1	
Short-fin squid (SS)	2.1	SD+ AC+
Goosefish (G)	1.6	HA+ WS− AP+
Thorny skate (TS)	1.4	AC+ AP+ WS− WH+
Pollack (PO)	0.9	
White hake (WH)	0.8	AP+ WF+ TS+ AC+
American plaice (AP)	0.3	TS+ WH+ G+ SD− WS− LON−

Results

The relative mean catch rates of the sixteen species are presented in Table 1. Over the 26-year period, the spiny dogfish has been the species with the greatest mean abundance, followed by winter skate, haddock, little skate, Atlantic cod, and yellowtail flounder, etc. The two or three most abundant species are in the order of perhaps 10–30 times more abundant than most of the other species. Though not shown, the variability in abundance was roughly proportional to the mean abundance.

One index of interspecific interaction is the correlation among the species over time. Data were first standardized by computing deviations from the mean for each species and then correlations among all standardized time series were computed. "Significant" correlations at the 5% level are also displayed in Table 1. Of the 120 possible correlations 22 are "significant". Obviously, we would expect to find several significant correlations owing to chance alone. Therefore, we computed Bonferroni-adjusted probabilities for the correlation coefficients and found that none were significant. Owing to the fact that assumptions underlying the tests of significance are not completely fulfilled, the "truth" regarding the correlations must be somewhere in the middle, i.e. some of the correlations may be "meaningful".

Our interest is not so much in the average mean abundance or in the correlations among the populations, but in the magnitude, form, and dynamics of the variability in multidimensional space. This information is contained in the eigenstructure of the variance–covariance matrix of the kg-per-tow time series for each population. The eigenstructure of this matrix can be represented by its eigenvalues, eigenvectors, and its time-dependent amplitude or factor scores (Priesendorfer, 1988).

The first five eigenvalues of the variance–covariance matrix are shown in Table 2. The dominant component of the variance is represented by the first three eigenvalues, because these account for nearly 98% of the variance. We use these three eigenvectors to represent variability in the ecosystem biomass (i.e. the sixteen species). Each eigenvector represents the "direction" of the eigenvalue variation. The magnitude of each element in the three eigenvectors is plotted in Figure 1. The figure shows that (1) the first eigenvector is positioned to reflect a positive dominance of spiny dogfish and winter skate and a negative dominance of haddock; (2) the

Table 2. Eigenvalue and percentage of total variance explained by each component for first five eigenvalues. (The eigenvalues of the remaining 11 eigenvectors are much smaller than the first five and are not included.)

Eigenvalue number	1	2	3	4	5
Eigenvalue	1319.6	528.1	249.9	16.2	9.6
% variance	61.6	24.6	11.7	0.7	0.4

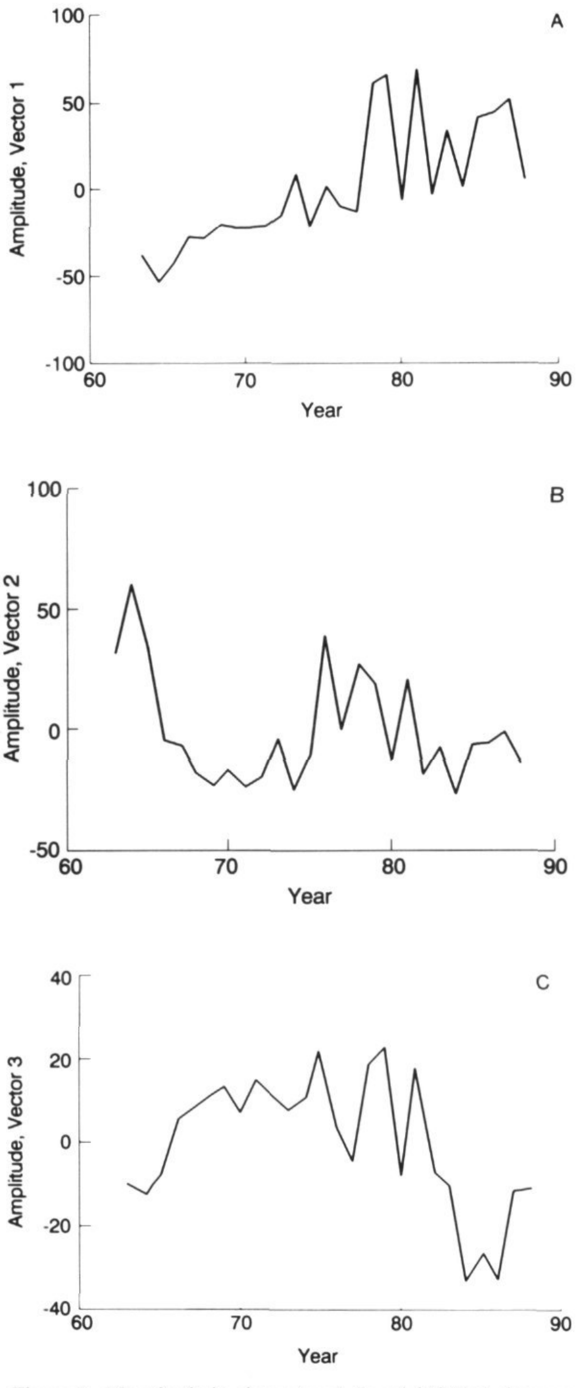

Figure 1. Magnitude in elements of, Panel (A) first eigenvector; Panel (B) second eigenvector; and Panel (C) third eigenvector, corresponding to each of the sixteen species (abbreviations in Table 1).

second eigenvector is positioned to reflect a dominance of haddock and spiny dogfish; and (3) the third eigenvector is positioned to reflect a negative dominance of winter skate.

The three dominant eigenvectors can be thought of as representing three "eigenassemblages". In any year, each eigenassemblage makes a variable contribution to the total biomass. Put another way, the biomass in each year can be represented as a mixture of three eigenassemblages. The proportion of each eigenassemblage present in each year is given by the three mutually orthogonal time series of amplitudes, each of which modulates its corresponding eigenvector.

The time series of amplitudes associated with each eigenvector are displayed in Figure 2. The first eigenvector time-series amplitude (dominant spiny dogfish and winter skate) increases steadily from the early 1960s to the present. The increase, however, only became substantial in the mid-1970s and is paralleled by an increase in variability. The second eigenvector time-series amplitude (dominant haddock and spiny dogfish) decreases during the early 1970s; then in the mid-1970s we see a sharp increase followed by increased variability and a declining trend. The third eigenvector time-series amplitude (lack of winter skate) increases in the early 1960s; we see an increase in variability in the mid-1970s followed by a decline.

In sum, then, the analysis of the eigenstructure of the variance shows that on Georges Bank the biomass variability is dominated by three species: the spiny dogfish, the winter skate, and the haddock. Each eigenvector or eigenassemblage of species carries information on the correlation among the species, while the three mutually orthogonal time-series amplitudes give an annual measure of the strength of each eigenassemblage.

Discussion

The data are typical of those from multiple-species fisheries in that numerous qualifications underlie the use of the data. These involve the use of simple indices that do not account for age distribution, or for the distribution of fish relative to sampling stations, for example. In this analysis, we consider that the data give a fair representation of the temporal abundance of fish on Georges Bank during the fall of the year. This assumption is particularly reasonable because we are concentrating on the variance-dominant species. We have not considered the time series for the spring, nor have we considered the catch in numbers per tow. With regard to the former, the spring and fall series must be correlated but there are undoubtedly factors that cause them to diverge, the discussion of which is beyond the scope of the paper. Likewise, a similar analysis of numbers per tow could have been made. Such an analysis would contain information on recruitment, as tempered by mortality rate. Since recruitment of the various stocks on Georges Bank has been the focus of a number of studies, we have circumscribed our work by focusing on

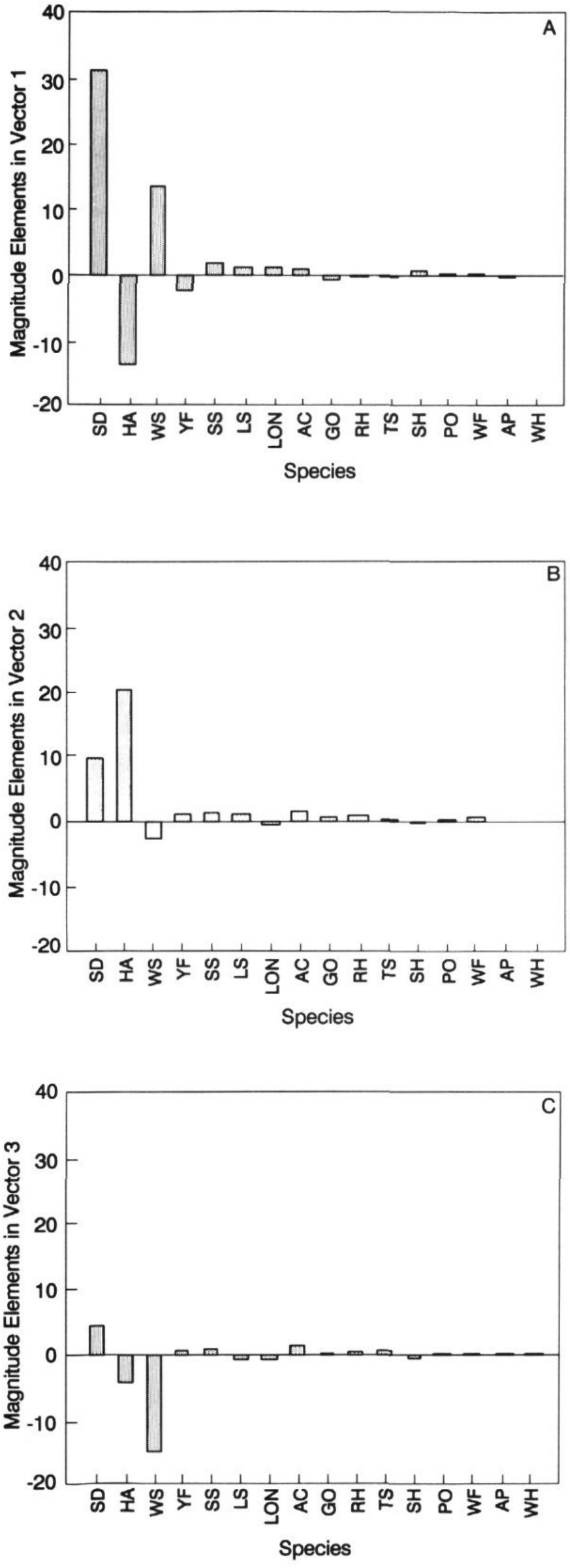

Figure 2. Time series of amplitudes associated with the, Panel (A) first, Panel (B) second, and Panel (C) third eigenvectors.

biomass, which is arguably more important than recruitment, as biomass directs the flow of ecological energy and ultimately constrains the level of recruitment.

Even restricting the analysis to fall kg per tow data, alternative modes of analysis would have been possible using the PCA technique. For example, the decomposition of the kg per tow variance–covariance matrix could have been accomplished in sample space rather than in state space. We chose to examine the problem in state space because we were interested in the temporal modulation of the state of the biomass, which is, by assumption, proportional to the kg per tow for each species.

The problem could have also been addressed from the point of view of decomposing matrices based on data which have been standardized with respect to their standard deviation. Our choice, to analyze the data in a time-centered but otherwise unstandardized form, was made in order to emphasize the actual variations in biomass among the species. If the data were weighted by standard deviations, we would be comparing the variations among species as if each species was of equivalent magnitude in abundance. Pollock for example would in this case be as variable as spiny dogfish. The decomposition of the standardized matrix would certainly be interesting, but we reserve its implementation for future study.

Our approach differs from approaches that define clusters or assemblages of fish in the sense that such approaches take into account certain similarities or dissimilarities among species over the entire data set and therefore they may "average out" time-series changes. In the PCA we have essentially defined not a single assemblage – that is, an assemblage that is fixed and constant over the entire time period represented by the data set – but rather three eigenassemblages that are present in varying components over time (cf. Overholtz and Tyler, 1985, 1986). By doing so, we have essentially defined two clusters: a variance-dominant cluster containing spiny dogfish, haddock, and winter skate; and a noise dominated cluster containing all of the other species. This does not mean that the correlation between the thorny skate and the pollock, for example, is in itself unimportant, but rather that such correlations are of minor statistical importance relative to the total biomass flux among the fish of Georges Bank.

If there are multiple-species interactions, then it seems reasonable that they should occur among the three dominant species. In considering the interactions among the dogfish, the winter skate, and the haddock, it is interesting to observe that the spiny dogfish and the winter skate are not always included in analyses of Georges Bank biomass (evidently because they are not an important species in the normal commercial landings). Yet these two species must be, in addition to haddock, of considerable ecological importance. The dogfish is evidently an important predator on small and juvenile fish. Its large variability in biomass is trans-

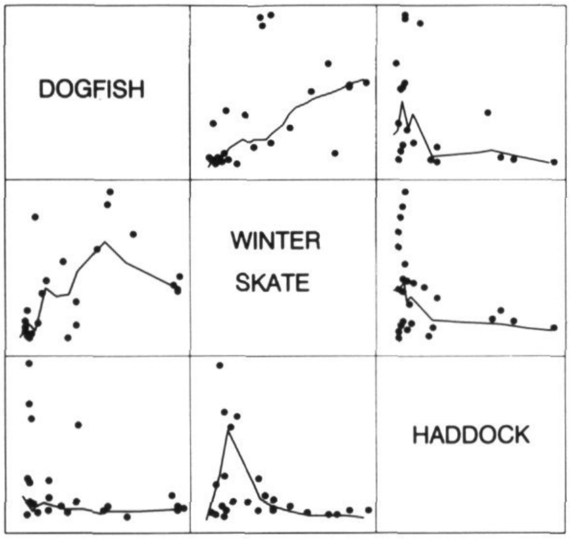

Figure 3. The LOWESS smoother applied to the kg-per-tow time series of dogfish, winter skate, and haddock.

latable into generating a large variability in predation mortality on a variety of juvenile fish species. This predation could very well produce a greater variance in mortality of small fish than that due to fishing, particularly considering that the variation in mortality in juvenile fish can be amplified in terms of adult fish biomass, owing to yield per recruit considerations. At the same time the winter skate and the haddock both feed on benthic invertebrates. Although they have been reported to feed on a different mix of invertebrates, it seems likely that there is an overlap in their food resources.

Are the increases and decreases among the spiny dogfish, the haddock, and the winter skate related, and if they are, are they causal in nature? As implied earlier, the relation between correlations and interactions can be deceptive. The Pearson correlation coefficient is only a measure of linear correlation. The magnitude of a computed correlation coefficient might not reflect the nature of relationships between variables that were not linearly related. At first thought, it would be surprising indeed if linear correlations did exist, since we would expect *a priori* that relationships would tend to be curvilinear because of density dependence. In order to study this in more detail, we examine the relationships among the correlated species.

To examine this problem, we have used the LOWESS Smoother to smooth Y values conditioned on ordered X values (Fig. 3). First consider the relations among the variance-dominant species. The smoothed data show the temporal increase in dogfish and winter skate, while haddock declines (Fig. 2a, b, and c), and the interpretation thus parallels the analysis of eigenvector amplitudes. The smoothed data suggest that in many instances the linear correlation coefficient might not be the best way of assessing whether or not a relationship exists among species, as in some instances the relationship appears to be curvilinear. For example, the dogfish/winter skate interaction (Fig. 3) implies that the dogfish and winter skate both increase concomitantly to an intermediate level of dogfish and winter skate abundance; at the intermediate level, however, the winter skate declines in abundance while the dogfish continues to increase. Even though dogfish and winter skate appear under one statistical technique to increase together, under another there appears to be a density-dependent effect of dogfish on winter skate. In a second example, dogfish and haddock are not correlated. This is confirmed by the smoothed data since haddock have an almost constant abundance as the dogfish population increases. On the other hand, the smoothed values of dogfish reflect a peak when the haddock population is at a low level. Considering the relation between winter skate and haddock, the correlation measure shows no relationship yet under the smoothing method, as winter skate increases in abundance, we find haddock increases and then decreases in abundance. Conversely, winter skate appears to be at its highest level of abundance when the haddock population is at its lowest levels.

In a way, these results are both consistent and inconsistent with the PCA. The consistency is evident in the relationship among the three eigenvectors and the corresponding amplitudes – the way that they vary over time – imply a change in the weighting associated with each eigenassemblage which parallels the non-linear relationship. The inconsistency arises because the most comfortable interpretation of the relation among the eigenassemblages occurs when the relationship among the species is linear. The main points are (a) that the time era represented by the data reflects that the biomass of the dogfish and the winter skate has tended to increase at the "expense" of the haddock and (b) that the plots of the smoothed data reflect curvilinearity, suggesting that correlation coefficients might not be efficient for detecting relationships. On the one hand this challenges the utility of the PCA, but on the other hand the statistical adequacy of the smoothing technique can also be challenged. Still, the magnitude of the PCA results is striking.

Speculations

To draw conclusions on multiple-species interactions from these analyses is difficult for several reasons. These involve (a) the complexities associated with the calibration of the raw data and (b) a lack of information on the life history and on the influence of fishing on two of the three critical species (i.e. the dogfish and the winter skate). The lack of life-history information makes it difficult to assess age structure and hence the magnitude

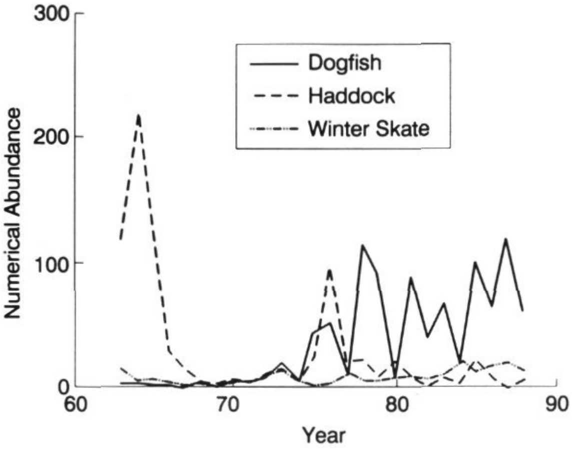

Figure 4. Time series in numbers per tow of spiny dogfish (solid line), haddock (dotted line), and winter skate (dashed line).

of recruitment. We can, however, develop a speculative scenario on the factors affecting the changes in abundance of the three dominant species.

With respect to recruitment, we know that recruitment to the haddock population was very large in the early 1960s and in the mid-1970s. For the dogfish and the winter skate, the catch in number per tow can be used as an index of recruitment. We can see (Fig. 4) that in terms of number per tow index, the recruitment to the spiny dogfish population increased sharply and sporadically in the mid-1970s. In contrast, the recruitment to the winter skate population increased only to the slightest extent. In contrasting changes in number with the observed changes in weight, which were quite large and steady in the winter skate (Fig. 5), we can attribute the variability in the three variance-dominant species to various modalities of population change.

Variability in the dogfish is a recruitment process and as recruitment increased it became especially variable. Part of the variability is probably due to the fact that dogfish bear their young alive and that the gestation period is longer than one year. The variability in the winter skate is due not so much to increased recruitment as to increased production of biomass. This could occur as a result of higher fishing mortality on competing species generating increased food for skate, and thus higher growth rate and possibly lower natural mortality. In the case of haddock, the major changes in biomass appear to owe to a few large year classes. The large year classes in the mid-1970s are probably due to a relaxation in fishing, an increase in haddock spawning-stock biomass, and then a cessation in future large year classes because of heavy fishing on the haddock stock.

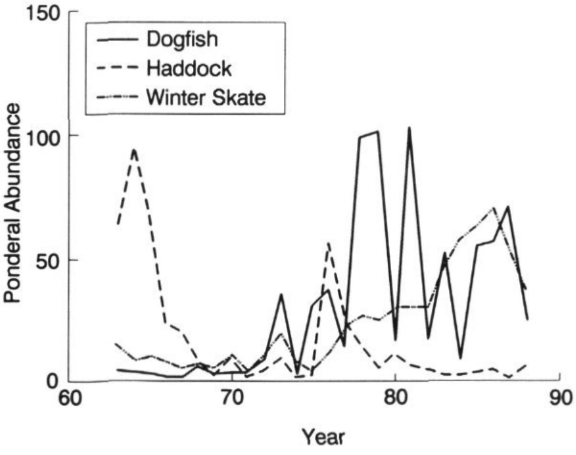

Figure 5. Time series in kg per tow of spiny dogfish (solid line), haddock (dotted line), and winter skate (dashed line).

The additional point needs to be made that prior to the mid-1970s Georges Bank was subject to ever-increasing fishing effort. By the mid-1970s catches began to drop precipitously, signifying that the heavily fished species were at all-time low levels of abundance. This was not only true for groundfish but also for heavily exploited pelagic species such as herring. In the mid-1970s, there was a considerable although temporary decline in fishing effort because of extended jurisdiction. Related to these dynamics are not only the rapid changes noted in the mid-1970s in the variance-dominant fish, but also in the mid-1970s an "explosion" in the sandeel and in the short-fin squid populations and then, more contemporaneously, in the mackerel and the herring. These observations lend to a scenario for the dynamics of the major fish of the variance-dominant demersal stocks.

In the 1960s and early 1970s, Georges Bank was subjected to intense fishing by distant-water fleets. These fleets were evidently indiscriminate in the species that they landed, as species that would ordinarily be of low value in North America at that time were important food fish in Europe or were used for fish meal by these factory-vessel fleets. As an example, Brown (1987) reports on high catch of dogfish prior to 1975.

By the mid-1970s the intense fishing had evidently depleted the stocks on Georges Bank and nominal fishing effort had evidently declined. This set the stage for the production of large year classes in haddock and increased abundance of spiny dogfish and sandeels.

The extension of jurisdiction in 1976 excluded the distant water fisheries from Georges Bank and set the stage for expansion of the domestic or coastal-state fleets along with the existence of large year classes of some species. We surmise that the coastal-state fleets were more selective, targeting on valuable food fish such as the haddock, while ignoring the spiny dogfish and the winter skate.

This created complex interactions. The fact that the haddock have not produced large year classes since the mid-1970s is the result of heavy fishing since that time. In addition, the heavy fishing is likely to be compounded by what must be close to a thirty-fold increase in biomass of the spiny dogfish (cf. Table 1 and Fig. 2a) as the dogfish is known to be a predator on small fish and probably affected the recruitment to the haddock and other populations (note, however, that negative correlations only occur between dogfish and plaice and yellowtail flounder). Perhaps more importantly, the variations in the abundance of the dogfish are so large that it is likely the dogfish contributes to a significant degree to the variability in recruitment of other species. To be sure, it might be argued that the large short-term variability of this species owes to sampling problems associated with the simple fact that the variance is often proportional to mean abundance in trawl catches. The apparent periodicity may also be due to the low fecundity and long gestation period, which could generate population oscillations.

The increase in the winter skate is attributable to reduction in fishing mortality, increased growth and possibly decreased natural mortality. It is tempting to further speculate that the increased growth owes in part to more food being available as a result of a reduced haddock population. The alternative speculation is that a large winter skate population contributes, through competition for food, to keeping the haddock population at a low level. It must be mentioned that, while both the haddock and the winter skate feed on benthic invertebrates, it is not exactly clear that they always eat the same food items.

As the spawning-stock biomass of the demersal stocks on Georges Bank declines, the mortality on food for larval and juvenile demersals must be reduced. This could release food for pelagics such as the mackerel and herring populations which have been subject to recent increases in abundance.

The only other major predators on Georges Bank are seabirds and mammals. The impact of these predators on the variance of the major fish species would need to be through variability in the seabird and mammal stocks, a subject beyond the scope of this paper.

It seems then that there is evidence that multiple-species interactions do occur on Georges Bank, but they are complex and often not correlative in the Pearson correlation coefficient sense. While we can identify causal mechanisms, data that ensure the complete veracity of our speculative scenario are lacking.

Nevertheless, it seems safe to say that the changes in the variance dominant species were at least triggered by fishing, that the variability in major predators almost certainly contributes to variability in recruitment, mortality, and growth among associated species; and that a targeted reduction in the stocks of dogfish and winter skate would be an experiment that, if successful, would result in an increase in more valuable biomass of groundfish on Georges Bank, given of course that overall fishing mortality could be controlled.

Acknowledgements

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Gastric evacuation in cod (*Gadus morhua* L.)

P. J. Bromley

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This paper describes an investigation of the shape of the gastric evacuation curve of cod feeding on whole natural prey. Linear gastric evacuation models fitted the results for the evacuation of sprats (*Sprattus sprattus*) and Norway lobsters (*Nephrops norvegicus*). Single and multiple meals of sprat were evacuated from the stomach at similar rates but these tended to be slightly higher than the average feeding rates sustained by cod in longer term feeding trials. It was found that sprats were evacuated at a much faster rate than *Nephrops*, which if translated generally would appear to put cod feeding on Crustacea at a disadvantage.

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Introduction

An ICES workshop was held in Lowestoft during 2–5 April 1989 (Anon., 1989a) to evaluate the significance of gastric evacuation experiments in estimating feeding rates of fish populations. This area of work is central to the success of multispecies virtual population analysis (MSVPA) as a management tool, since the credibility of MSVPA relies in large measure on the validity of the predation rate estimates used in the model (Anon., 1988). Concern in this field is also topical in view of the proposed ICES 1991 "Return of the year of the stomach" programme (Anon., 1989b). The concept behind this programme is that feeding rates can be estimated by applying information on the gastric evacuation rates of prey derived from tank experiments to data on the stomach contents of fish sampled in the field. However, this apparently simple procedure is fraught with difficulties and uncertainties, some of which are addressed here.

There is considerable controversy over which gastric evacuation curve best describes the emptying of the stomach after a meal. This has variously been described as linear, rectilinear, exponential, square root, and surface area dependent (Bajkov, 1935; Kitchell and Windell, 1968; Brett and Higgs, 1979; Tyler, 1970; Elliot, 1972; Jobling, 1980, 1986; Bromley, 1987, 1988). This paper includes investigations on the shape of the evacuation curve of cod feeding on intact natural prey.

In addition, a comparison was made of single and multiple meal experimental designs; some authors have reported that food is evacuated at a faster rate when fish are fed multiple meals as opposed to a single meal fed in isolation (Talbot, 1985; Jones, 1974), whereas others have found single and multiple meals to be evacuated at similar rates (Bromley, 1987).

Implications of the shape of the evacuation curve on the models for predicting feeding rate are also considered. Comparisons were made between the results of evacuation and feeding experiments to see what part experimental feeding studies can play in elucidating the feeding rates of natural fish populations.

Materials and methods

North Sea cod were acclimated to tank conditions for at least two months prior to use. During this time they were fed two or three times a week on prey similar to that used in the experiments. This included assorted small whole frozen sandeels, gadoids, and sprat (*Sprattus sprattus*), and occasionally *Nephrops norvegicus*, along with biweekly feeds of fresh lugworm (*Arenicola marina*). The rostra were removed from the Nephrops prior to feeding.

The experimental tanks were constructed of plastic or fibre glass and ranged in capacity from 225 to 12500 l and were supplied with a through flow of filtered sea water (Scholes, 1980). The water was aerated using airstones. Illuminations was by fluorescent tubes on a 12-h light, 12-h dark cycle. Fish were fed by hand to satiation over a 15–20 min period and uneaten food was

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Table 1. Details of the gastric evacuation experiments.

Treatment	Number of fish	Mean weight (g)	Weight range (g)	Mean temperature (°C ± s.d.)
1. Single meal of *Nephrops*	33	790	187–3375	8.8 ± 0.7
2. Single meal of sprat	55	787	357–1637	12.9 ± 0.7
3. Multiple meals of sprat	78	737–2134	480–3213	12.1 ± 0.1

removed and weighed to determine the amount consumed.

The conditions and methodologies used in the gastric evacuation experiments were based on those developed for whiting (Bromley, 1988). The cod were not fed for four days before each experiment to give time for the stomachs to empty. At intervals after feeding the stomach contents were sampled by gastric lavage and the cod were also weighed and measured.

The stomach contents were collected in a 50-meshes cm^{-1} net and drained of excess water. Normally, in fish sampled up to 48 h after feeding, it was possible to separate and weigh the prey items individually, but thereafter it was generally only feasible to weigh total stomach contents. The weight of food evacuated from the stomach was calculated as the difference between the weight eaten and the weight of stomach contents recovered. After drying in an oven at 80°C, the stomach contents were re-weighed, homogenized, and aliquots from each sampling time were pelleted and their calorific values ($kJ\,g^{-1}$) determined by bomb calorimetry. Food samples were also analysed for calorific value.

Statistical techniques used to analyse the data included analysis of variance and multiple linear regression. The gastric evacuation curve was also analysed by the method developed by Bromley (1988), which takes account of censoring of the data due to an increase in the number of empty stomachs during the latter stages of evacuation experiments.

Gastric evacuation experiments were conducted on cod using single meals of *Nephrops* or sprat and, for comparison, multiple meals of sprat. Details of the individual experiments are given in Table 1. In the single meal *Nephrops* experiment two or three fish at a time were fed on pre-weighed *Nephrops* and the amount eaten by individual fish was observed and recorded. The stomach contents were sampled at intervals ranging from 2 to 48 h after feeding. In the single meal sprat experiment a total of 55 cod were fed communally to satiation on sprats with a mean weight of 18.0 g (s.d. ± 0.7 g). Batches of five fish were taken from the tank and their stomachs pumped. This was done immediately after feeding, at intervals of 3, 6, 9, 12, 24 h and thereafter twice daily until all the stomachs were empty. The weights eaten (F) and evacuated (WE) for individual fish over the first 48 h were calculated using the equations

$$F = N_t \times W_0 \text{ g}$$

$$WE = F - (N_t \times W_t) \text{ g}$$

where N_t is the number of sprat observed in the stomach, W_0 is the average weight of sprat fed, and W_t is the average weight of sprat recovered at time of sampling.

In the multiple meal sprat experiment six batches of from 3 to 37 cod were fed communally to satiation on sprats and for the next four or six days they were topped up with more sprats each morning. Finally, food was withheld for two days, after which the stomachs were pumped and the total amount of food evacuated by the fish in each tank was calculated.

Experiments were also undertaken to determine the average daily feeding rates of cod (average temperature 13.2°C ± 2.27) for comparison with the gastric evacuation rates. Batches of 11–85 cod of mean weight 6.7–3595 g were fed to satiation for periods of 14–36 days on either assorted frozen fish or a semi-moist pellet comprising 60% commercial trout starter diet, 37% mixed gadoids, and 1.5% each of cod liver oil and vitamin mix (Castell and Tiews, 1980). Feeding frequency ranged from twice a day for small cod to once daily for the larger ones. The cod were measured and weighed at the start and finish of each trial.

Results

Evacuation of a single meal of *Nephrops*

Meal size was variable, with individuals eating between one and seven *Nephrops*. Larger fish tended to eat larger total amounts of food, although relative to body weight there was a slight but significant decline in percentage meal size in larger fish ($R = -0.365$, $p < 0.05$). Average meal size was 18.2 g (s.d. = 15.9), equivalent to 2.3% of body weight (s.d. = 1.79%). The weight of material evacuated by individual fish varied (Fig. 1a) and a multiple regression model was fitted to the data (Table 2). The amount of food evacuated from the stomach depended mainly on body size and time after feeding, but there was a slight tendency for large meals to be evacuated at a faster rate than small meals. In the model, the depletion of stomach contents was linearly related to time after feeding. On average, the evacuation rate was $0.29\,g\,h^{-1}$, or $1.59\%\,h^{-1}$ of the initial meal size, which if extrapolated beyond 48 h predicts that on average it

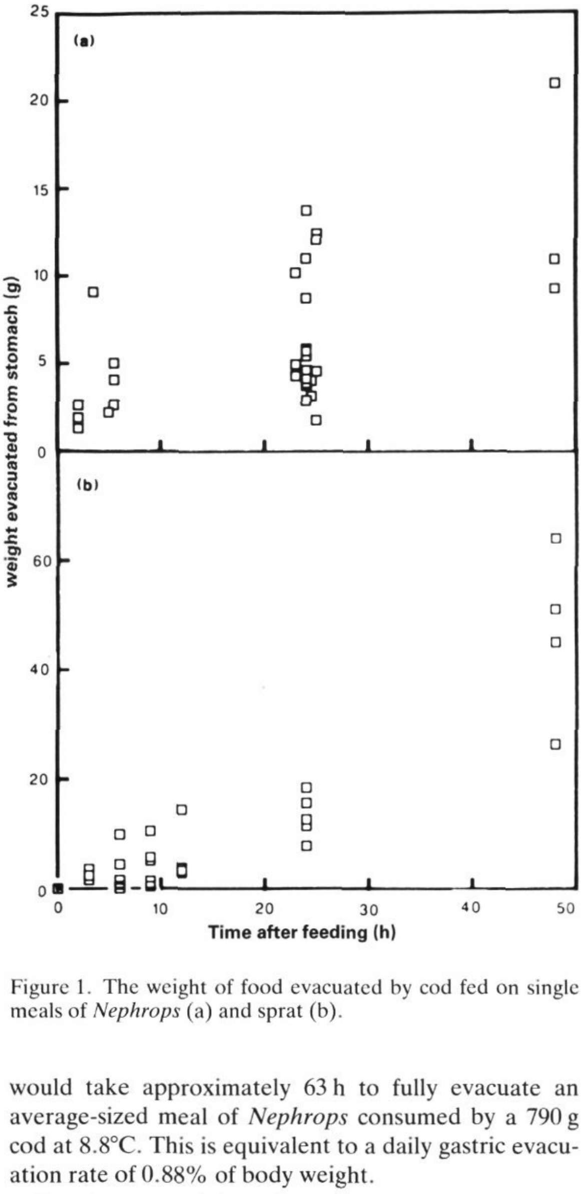

Figure 1. The weight of food evacuated by cod fed on single meals of *Nephrops* (a) and sprat (b).

would take approximately 63 h to fully evacuate an average-sized meal of *Nephrops* consumed by a 790 g cod at 8.8°C. This is equivalent to a daily gastric evacuation rate of 0.88% of body weight.

The dry : wet weight ratio and the energy content per gram wet weight of stomach contents declined during the experiment (Fig. 2), although the energy content per gram dry weight was fairly stable. The depletion in energy per gram wet weight of *Nephrops* was particularly rapid over the first 24 h. The model is given in Table 2. This implies that energy evacuation was faster during the early stages and slowed down during the latter stages of digestion as stomach fullness declined. Figure 3 shows the energy evacuation curve predicted for cod under average conditions.

Evacuation of a single meal of sprat

The cod sampled over the first 48 h consumed on average 2.6 sprats (range 1–5), weighing on average a total of 46.8 g (s.d. = 20.9 g), which was 5.9% of body weight. The weight of food evacuated by individual fish over the first 48 h is shown in Figure 1b.

A multiple regression model similar to that used on the *Nephrops* data was fitted to the gastric evacuation data for sprat over the first 48 h (Table 2). Unlike the *Nephrops* model, body size and percentage meal size did not significantly influence ($p > 0.05$) the weight of food evacuated and a simple regression of weight evacuated on time, fitted through the origin, proved to be an adequate model of the results. This implies a stable rate of evacuation during the first 48 h averaging 0.83 g h^{-1} for the size range of fish in this experiment. On a percentage basis, this is equivalent to an average evacuation rate of $1.76\% \text{ h}^{-1}$ of the original meal size, giving a projected time of 57 h to fully evacuate an averaged size meal at 12.9°C.

The plot of mean stomach content on time (Fig. 4) appears to contradict this conclusion since it shows a curved relationship with an apparent slowing down in the evacuation rate at low level of stomach fullness during the later stages of digestion, indicating an evacuation time of about 100 h to empty the stomach. However, Bromley (1988) pointed out that in single meal experiments the pattern of evacuation exhibited by individual fish, which can be regarded as the functional relationship, is unlikely to be the same as the pattern exhibited by a plot of mean stomach content on time after feeding. This is due to the constraint that stomach

Table 2. Parameter values of gastric evacuation models derived from the experimental results: Model 1 (single meals of *Nephrops*): $WE = \alpha + \beta \log_e W + \gamma H + \partial PM$; Model 2 (energy depletion in *Nephrops*): $dE = \alpha + \gamma \log_e H$; Model 3 (single meals of sprats): $WE = \alpha + \beta \log_e W + \gamma H + \partial PM$ (where WE = weight of food evacuated in g, W = weight of cod in g, H = hours after feeding, PM = meal size as a percentage of body weight, dE = depletion in energy content of tissue in kJ g^{-1}).

Model	R^2	α	β	γ	∂
1	0.86	−33.81	4.87	0.29	1.02
SE		3.66	0.47	0.03	0.02
2	0.99	4.8		−0.65	
SE		0.01		0.35	
3	0.84	−33.1	4.1	0.91	0.5
SE		17.2	2.5	0.08	0.4

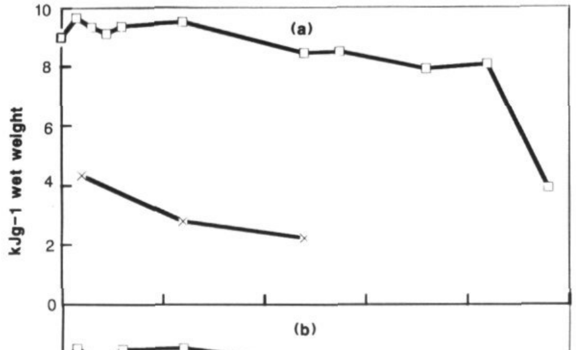

Figure 2. Changes in the energy content per g wet weight (a) and dry weight (b), and the dry: wet weight ratio (c) of sprat (□) and *Nephrops* (×) in the single meal experiments.

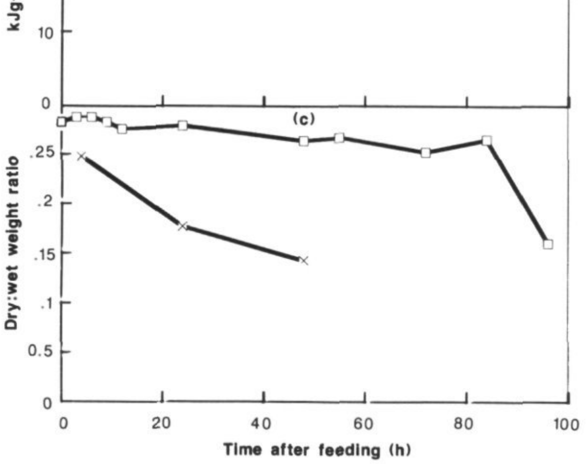

Figure 3. The energy gastric evacuation curve for a 790 g cod fed an averaged-sized meal of *Nephrops*.

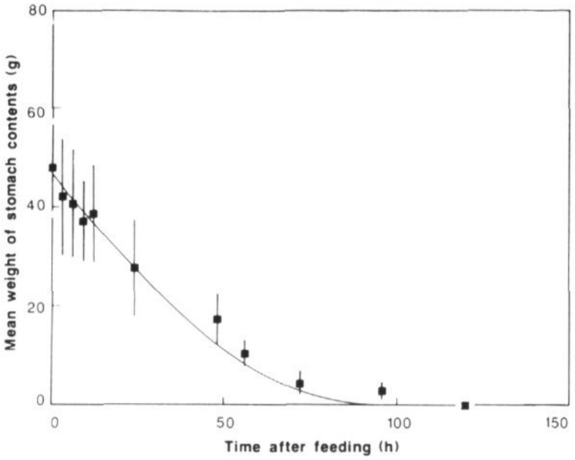

Figure 4. The relationship between mean stomach content (±s.d.) and time after feeding for cod fed to satiation on sprat. The fitted curve was generated from a linear evacuation model which accounted for censoring of the data.

content cannot fall below zero, so that the data from the later stages of the experiment become censored due to an increase in the proportion of empty stomachs in the samples. This will tend to produce a curved relationship which exaggerates any decline in the evacuation rate during the later stages of digestion. The magnitude of the discrepancy between the two patterns of evacuation is largely dependent on the variation in meal size and evacuation rates between individuals.

The sprat data were fitted to a corrected version of Bromley's (1988) model* to predict the curve of mean stomach content on time, based on the assumption that evacuation in g h^{-1} remained constant and was the same in the later stages of digestion as in the first 48 h, when censoring was negligible. The curvature in the relationship in Figure 4 was generated entirely as a result of censoring and the impression of a slowing down of the evacuation rate is an artefact. The goodness-of-fit of the model supports the conclusion that for most practical purposes gastric evacuation can be regarded as a constant amount per unit time during digestion of a meal. However, slight underestimation of mean stomach content in the later stages is consistent with a slight decline in evacuation rate when skeletal remains predominate.

The dry: wet weight ratio and calorific value of the stomach contents are shown in Figure 2. There was no significant ($p > 0.05$) drop in the energy content per

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*Corrected version of Bromley model:

$$E[y_t] = \mu_t[1 - F(-\mu_t/\theta)] + \theta f(-\mu_t/\theta)$$

where $E[y_t]$ = mean stomach content, μ_t = functional linear evacuation model, θ = standard deviation of meal size, F = standardized cumulative normal probability distribution, f = standardized normal probability density function.

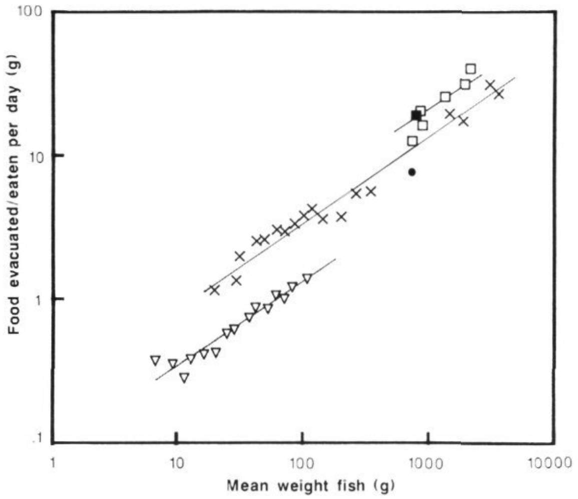

Figure 5. The daily evacuation rates of cod fed single (■) and multiple meals (□) of sprat and single meals of *Nephrops* (●), and the mean daily feeding rates of cod fed on assorted fish (×) or a semi-moist diet (△).

gram wet and dry weight during the early stages of digestion and only later, when digestion was nearing completion and skeletal remains predominated, did energy levels fall to any great extent. Evacuation rate was stable throughout the larger part of the process in energy terms, as well as in wet weight terms.

Evacuation of multiple meals of sprat and comparison with feeding experiments

The results of the single and the multiple meal evacuation experiments are shown in Figure 5 along with the results of the feeding experiments. Temperature was not significantly different and analysis of covariance showed that the slopes were not significantly different between treatments. Therefore, a linear model with a common slope was fitted to the data for the evacuation of sprat and the data for feeding on fish and artificial food (Fig. 5). This showed strong correlation between food evacuation (i.e. consumption) and body weight, with a common slope of 0.59 (s.e. ± 0.02) for $\log_e$ body weight and significantly different ($p < 0.05$) intercepts. Cod feeding on frozen fish ate a greater total weight of food compared to the semi-moist diet. However, the latter was more concentrated nutritionally due to its reduced water content and on a dry weight basis consumption was similar.

Discussion

There were considerable differences between the results for sprat and *Nephrops* which affected meal size, evacuation rate, and energy availability, which would appear to put cod feeding predominantly on foods such as *Nephrops* at a disadvantage.

In the single meal experiments, on average twice as much sprat as *Nephrops* was eaten. This may have been a problem of palatability since the cod were not used to feeding on *Nephrops* and many would not swallow these prey unless the rostra had been removed first. In addition, the rigid exoskeleton, awkward shape, and numerous appendages probably made it impossible for cod to pack their stomachs as tightly as with the more streamlined and pliable sprat.

Evacuation of *Nephrops* was essentially linear in wet weight terms but in energy terms the rate of evacuation slowed down during the later stages of evacuation, so that in effect energy evacuation rate was related to stomach fullness. *Nephrops* had only half the calorific value of sprat and this value was halved again by 48 h after feeding. There was no such early decline in the energy content per gram wet weight of sprat and the evacuation curve was linear in both weight and energy terms. These differences in the pattern of digestion might be a more general feature of preys with endo- and exoskeletons.

Digestion of the flexible membranes at the joints between exoskeletal plates occurs at an early stage and they soon rupture, enabling the energy-rich internal organs to be digested. Digestion of the bulky and presumably energy-poor exoskeleton is more protracted and skeletal remains tended to be the last component to be emptied from the stomach. The *Nephrops* used here had been stored frozen and were obviously more fragile than live ones, which are likely to exhibit more of a lag during the initial stages of digestion because of the longer time needed to rupture the membranes covering the joints. Sprats, by contrast, have relatively less skeletal material and will be digested from the outside inwards with no marked change in the energy levels of the stomach contents until the stage when mainly bones are left.

The evacuation rate of a single meal of sprat fell within the range exhibited by the fish fed on multiple meals. However, the gastric evacuation rates were slightly higher than the mean feeding rates of cod in the longer-term feeding experiments, indicating that gastric evacuation rate did not limit feeding rate. Perhaps withholding food for four days prior to the start of the evacuation experiments led to a temporary speeding up of the evacuation rate when the cod were fed. This mechanism would allow fish to make up for periods without food in situations where food availability is erratic. It would also explain why the evacuation rate (15.3 d^{-1} for sprats) found by Daan (1973) for cod (mean weight 1241 g at 11.9°C) which had not previously been starved was almost identical to the feeding rate found here (15.0 $\mathrm{g\,d}^{-1}$) for cod of the same size.

The apparent slowing down of the evacuation rate as the level of stomach fullness declined during the evacuation of single meals of sprat (Fig. 4) could largely be explained as an artefact due to censoring caused by an increasing proportion of empty or near empty stomachs during the later stages of the experiment. The results for cod appear to be in line with the findings for turbot (Bromley, 1987) and whiting (Bromley, 1988) fed on whole fish. For most practical purposes, therefore, the results were consistent with the fish exhibiting a constant rate of evacuation in $\mathrm{g\,h^{-1}}$ throughout digestion of a meal of sprat. However, there was evidence of a slight decline in evacuation rate during the late stages of digestion, when skeletal material predominated in the stomach. Tyler (1970) found a slowing down in evacuation rate at very low levels of stomach fullness, but it is not clear how much of this could be the result of censoring.

In the sprat single meal experiment, body size did not significantly influence evacuation rate. This might be due to the narrower size range of fish used compared with the other experiments where there was high correlation between evacuation/feeding rates and body weight.

Comparison of the wet weight evacuation rates of sprat and *Nephrops* showed that the former were evacuated at a rate three times faster. Even after a temperature correction using data provided by Jobling (1988), which indicates that approximately a 30% difference in evacuation rate might be due to differences in temperature between the two experiments, sprats would be evacuated twice as fast in wet weight terms. In energy terms the difference was even more marked, since on a wet weight basis *Nephrops* contained only half the energy content of sprat (4.49 and 9.33 $\mathrm{kJ\,g^{-1}}$, respectively). Evacuation of sprat by 787 g cod was estimated to be 7.75 $\mathrm{kJ\,h^{-1}}$ at 12.9°C compared with a maximum evacuation rate of *Nephrops* of 1.25 $\mathrm{kJ\,h^{-1}}$ over the first 24 h at 8.8°C. After correction for temperature, the evacuation rate for *Nephrops* is 1.7 $\mathrm{kJ\,h^{-1}}$, which is over four times slower than for sprats.

The results suggest that feeding on *Crustacea* rather than on fish could restrict energy intake and growth rate. The optimum strategy when feeding on these prey items would be to consume the largest meals possible, since large meals tended to be evacuated at a faster rate than small meals, but considerable benefits would be gained by switching to a fish diet when it is available, provided that the cost of foraging for fish was not excessive.

Overall, the results lead to the conclusion that the level of stomach fullness is of little value as an indicator of evacuation rate. For most practical purposes, evacuation could be considered linear, and, even if evacuation rate was related to the level of stomach fullness, the effect is likely to be insignificant compared to the large differences in evacuation rates between prey types. It would also appear that feeding experiments offer a simple way of estimating the evacuation rates of different prey types.

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Some new analytical and comparative methods for estimating the food consumption of fish[1]

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Methods of obtaining estimates of daily ration (R_d) and population-weighted food consumption (Q/B) are presented. These include (a) a method for estimating R_d from changes in stomach contents in the course of a 24-h period, which allows either one of two feeding periods per day (i.e. for diurnal, nocturnal, or crepuscular feeders); (b) a method for estimating R_d and Q/B from estimates of gross food conversion efficiency, and growth and mortality parameters of the population; and (c) multiple regression models for predicting Q/B from temperature, asymptotic size, food type, and morphometric attributes of the fish in the population studied, based on species ranging from guppy to tuna, and from temperate to tropical habitats.

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Introduction

Most tropical and subtropical fisheries are based on multispecies resources. Hence, management oriented modelling studies which take multispecies aspects into account require the estimation of vital statistics for a large number of species, often without access to a historic database (Pauly, 1982). For statistics such as growth and mortality, this problem can largely be resolved by giving emphasis to the analysis of easily obtainable length-frequency data (Pauly and Morgan, 1987) and estimates derived from comparative studies of mortality and growth rates (Pauly, 1980; Munro and Pauly, 1983; Pauly and Munro, 1984; Moreau *et al.*, 1986.

A further basic requirement encountered in constructing a multispecies model is knowledge about food requirements of the constituent organisms. Such knowledge is often hard to obtain for individual species and therefore one may be tempted to transfer estimates from one species to the other. However, in order to ensure that the values thus transferred are realistic, it is appropriate to devise general relationships between metabolic expenditure of populations and their ecological or morphological characteristics (Pauly, 1989).

In this paper, we present (1) an analytical method for estimating relative food consumption by individual fish from diurnal stomach sampling investigations; (2) a model for estimating food consumption in relation to biomass for a fish population; and (3) how some attributes of fishes which are easy to quantify can be used to predict their food consumption.

Estimation of daily ration from the dynamics of stomach contents

Starting with Bajkov (1935), numerous methods have been proposed for estimating the daily ration (R_d) of fish in nature, based on quantitative analyses of their stomach contents (Daan, 1973; Elliott and Persson, 1978; Olson, 1981; Durbin *et al.*, 1983; Gorelova, 1984; Pennington, 1985). Methods which are widely applied emphasize the estimation of stomach evacuation rate, and this had led to a lively discussion as to its proper parameterization (e.g. Jobling, 1981, 1986; Mullen, 1986; Temming, 1986).

Sainsbury (1986) proposed an alternative approach, wherein the estimation of R_d from stomach content data, sampled over a single cycle of arbitrary duration, is

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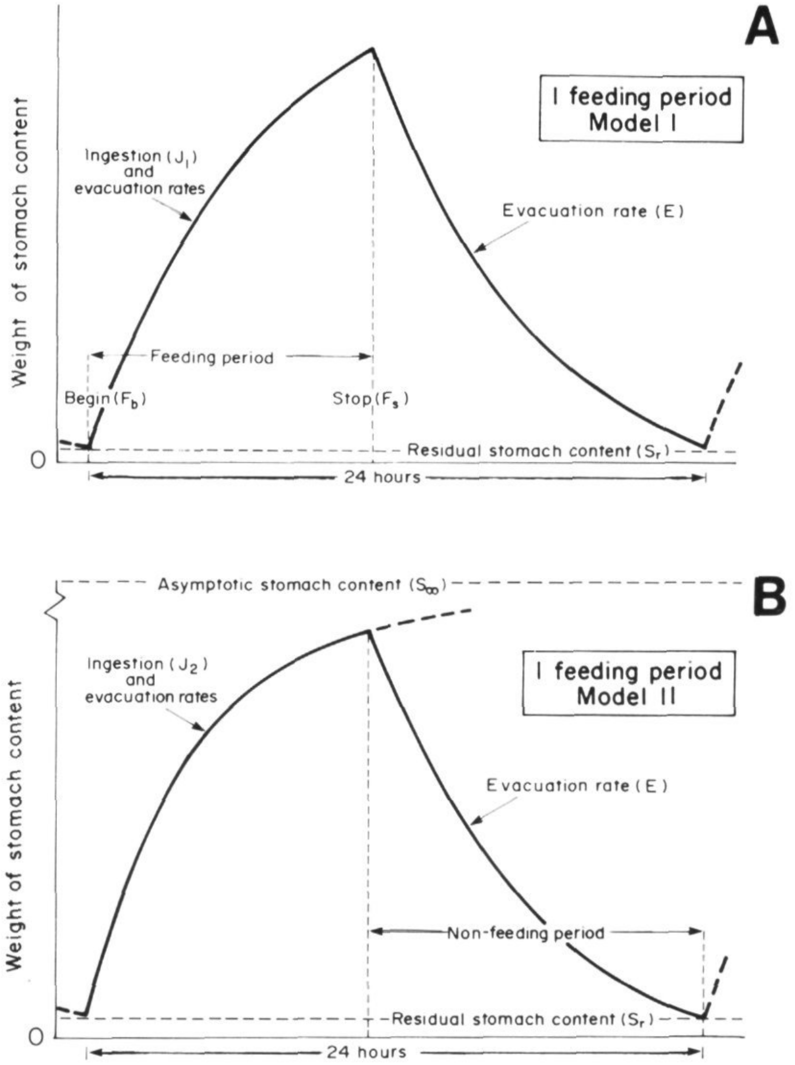

Figure 1. Schematic representation of different models of stomach content dynamics: A. One feeding period per day, feeding rate constant; B. One feeding period per day, feeding rate proportional to stomach content; C. Two feeding periods per day, feeding rate constant; D. Two feeding periods per day, feeding rate proportional to stomach content.

part of an integrated estimation process which also involves other parameters, particularly feeding and evacuation rates, duration of the feeding period, and asymptotic stomach contents. He developed two models, one ("Model I") assuming a constant feeding rate and another ("Model II") assuming a feeding rate inversely proportional to stomach contents. Both models assume a simple exponential evacuation rate. Slightly modified, the time trajectories and the computations are given in the Appendix. A schematic representation of the trajectories is provided in Figure 1.

The two models fit the same type of curve, but differ in the parameters involved in the computation of the slope of the trajectory and the asymptotic stomach content weight, as explained in the Appendix. Assuming steady-state conditions, the residual stomach content before the beginning of the feeding period can be directly calculated from the other parameters. The stomach content at the end of the feeding period is readily computed from the time trajectory. Finally, the daily ration R_d is integrated from the food ingestion over the duration of the feeding period.

Sainsbury's (1986) approach allows for the estimation of either parameter set for a feeding period covering a cycle of 24 h, or the estimation of several sets of parameters (one for each of the feeding cycles within a day).

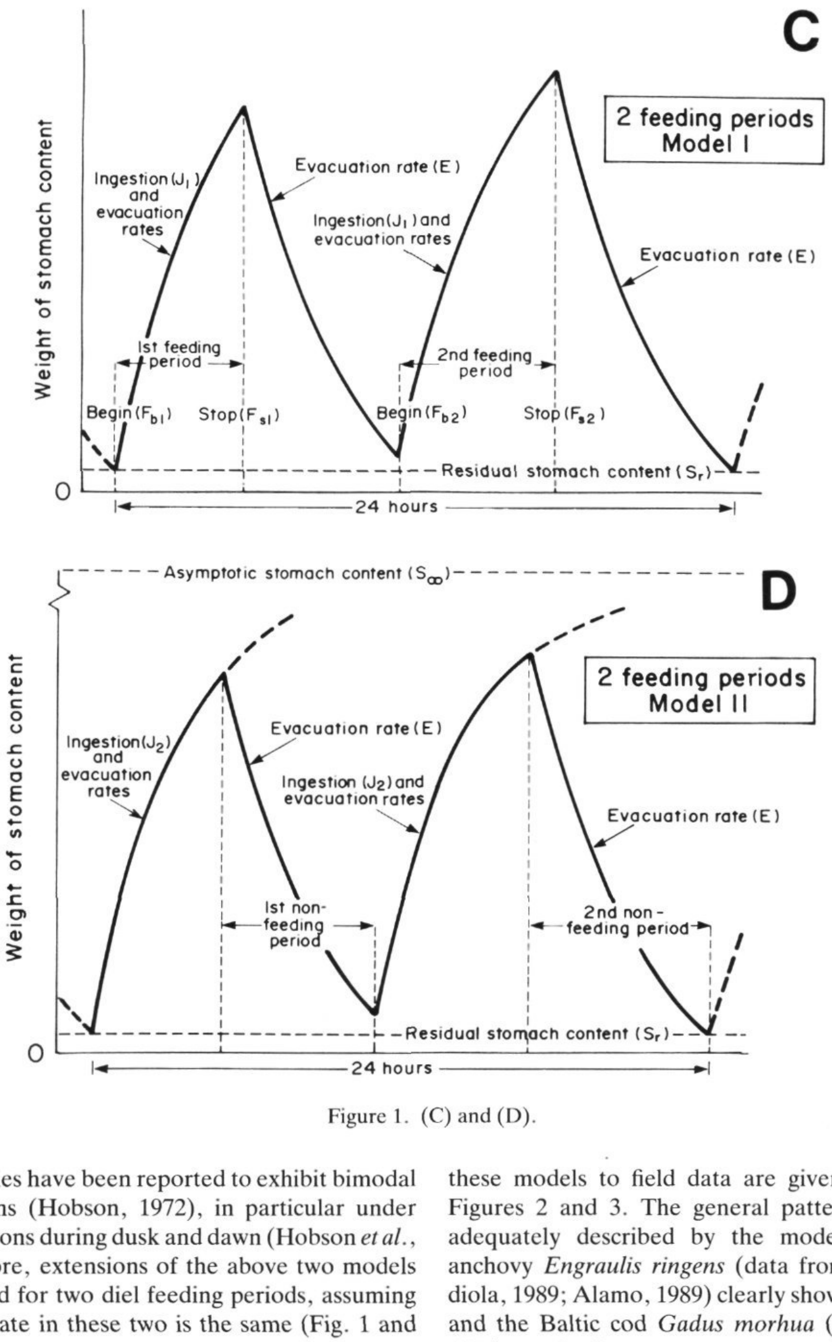

Figure 1. (C) and (D).

Some fish species have been reported to exhibit bimodal activity patterns (Hobson, 1972), in particular under twilight conditions during dusk and dawn (Hobson *et al.*, 1981). Therefore, extensions of the above two models were developed for two diel feeding periods, assuming the ingestion rate in these two is the same (Fig. 1 and Appendix).

In this extension, both feeding periods can be treated separately, with an adjustment for the feeding and non-feeding times. The integration to compute R_d is in principle the same as before, with an adjustment for two ascending branches and the appropriate times for the integral limits[1] (Appendix). Examples of application of these models to field data are given in Table 1 and Figures 2 and 3. The general pattern appears to be adequately described by the models, the Peruvian anchovy *Engraulis ringens* (data from Rojas de Mendiola, 1989; Alamo, 1989) clearly showing one diel cycle and the Baltic cod *Gadus morhua* (data from Arntz, 1974) two feeding cycles.

Relating size-specific estimates of daily ration to consumption by an entire fish population

Other methods for estimating daily ration (e.g. Mann, 1978; Olson and Boggs, 1986) share with those presented above the feature that the results are size-specific, i.e. they pertain to the size of the fish sampled in the field or used in the experiments. Box models, how-

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[1] A user-friendly program for IBM and compatible personal computers implementing this approach and the Q/B model presented below is available upon request.

Table 1. Parameter estimates for the models of stomach content dynamics for *Engraulis ringens* (data from Rojas de Mendiola, 1989, and Alamo, 1989), and *Gadus morhua* (length class 26–30 cm; data from Arntz, 1974).

	Model I	Model II	Unit
Engraulis ringens			
Beginning of feeding period	12:50	13:15	h
End of feeding period	1:50	1:40	h
Evacuation rate	0.16	0.13	h^{-1}
Ingestion rate	0.04	0.05	*
Asymptotic stomach content	–	0.27	g
Sum of squared residuals	0.01	0.01	g^2
Daily ration	0.57	0.50	gd^{-1}
Gadus morhua			
Beginning of 1st feeding period	5:20	5:30	h
End of 1st feeding period	8:05	8:00	h
Beginning of 2nd feeding period	13:50	14:05	h
End of 2nd feeding period	18:35	18:35	h
Evacuation rate	0.25	0.25	h^{-1}
Ingestion rate	0.67	0.14	*
Asymptotic stomach content	–	2.22	g
Sum of squared residuals	0.08	0.08	g^2
Daily ration	5.02	4.92	gd^{-1}

*Model I: unit gh^{-1}; Model II: unit h^{-1}.

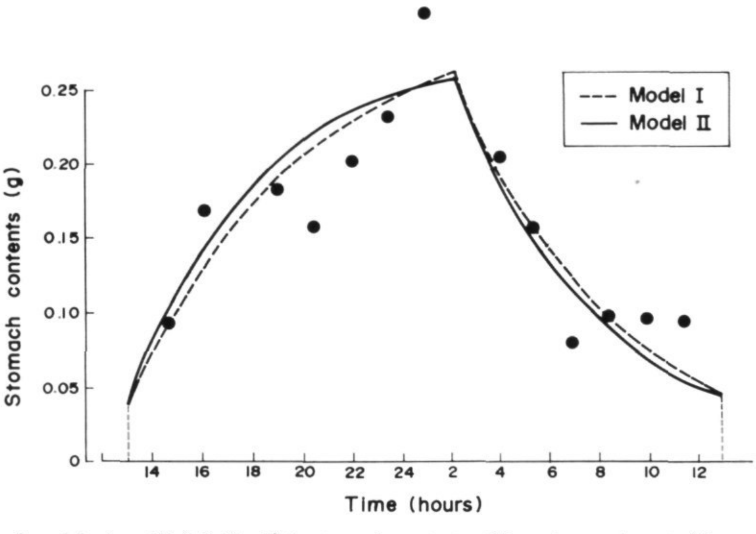

Figure 2. Application of models A and B (cf. Fig. 1) to stomach contents of Peruvian anchoveta (*Engraulis ringens*) (mean live weight = 19.7 g; data from Rojas de Mendiola, 1989 and Alamo, 1989).

ever, usually deal with entire populations and not with cohorts characterized by a limited size range. Since small fish consume relatively more food than big fish of the same species (Pauly, 1986), and are also more abundant, estimates of R_d pertaining to a specific size have to be converted into estimates of food consumption (Q) per unit biomass (B) and per unit time of an age-structured population. This requires estimates of the individual growth of the fish in the population, as well as estimates of the instantaneous rate of total mortality prevailing in this population. Pauly (1986) derived a comprehensive model for the estimation of Q/B from growth parameters of the von Bertalanffy growth equation (von Bertalanffy, 1938; Beverton and Holt, 1957), total mortality (Z), and gross food conversion efficiency K_1 (Ivlev, 1945). A slightly simplified version (Palomares and Pauly, 1989) reads

$$Q/B = \int_{t_r}^{t_{max}} \frac{[dw/dt] \times N_t}{K_{1[t]}}\, dt \bigg/ \int_{t_r}^{t_{max}} W_t \times N_t \, dt \qquad (1)$$

In a sensitivity analysis of this model, Pauly (1986) shows that the output is largely insensitive to changes in age of recruitment (t_r) and age of exit (t_{max}) from the exploited stock. Therefore, these two parameters can be replaced in the integration by 0 and ∞, respectively.

The number of animals of age t in the population (N_t) is obtained from the mortality equation

$$N_t = N_0 \times \exp(-Z \times (t - t_0)) \qquad (2)$$

Assuming constant recruitment, N_0 cancels out in the integration of Q/B, and therefore does not appear as a parameter in the equation set.

The actual weight-at-age (W_t) is given by the von Bertalanffy growth equation and the weight increment (dw/dt) is computed from its first derivative. Conversion efficiency (K_1) is obtained according to its definition from the daily weight increment divided by the daily ration. Pauly (1986) provided a method for computing the conversion efficiency at age ($K_{1[t]}$). Palomares and Pauly (1989) give details of a least squares approach of Q/B for cases when several R_d values, pertaining to different fish sizes, are available. It should be observed that the value of Q/B is very sensitive to the parameters which relate body weight to size and conversion efficiency to age. It should further be noted that the assumptions for this model include a steady-state population under constant recruitment.

The model has been applied to the Peruvian anchoveta data shown in Table 1 and Figure 2. The ration estimated from "Model I" is $0.57\ g \times d^{-1}$ for specimens with a mean weight of 19.7 g. On the basis of the growth parameters given by Palomares *et al.* (1987), the conversion efficiency is estimated at 0.091. If the total mortality rate is taken as $2.5\ yr^{-1}$, the integration of Equation (1) then yields $Q/B = 14.0\ yr^{-1}$. From this, the gross efficiency of Peruvian anchovy can be calculated as the ratio of production and consumption: $GE = 2.5/14.0 = 0.18$.

Estimating Q/B through empirical equations derived from comparative studies

The methods proposed above for estimating R_d and Q/B are associated with data requirements which will often not be met. Empirical models for the prediction of Q/B from easily quantifiable morphometric characteristics of fish, which take the very different metabolic levels of different types of fish into account, might help to overcome this problem (Pauly, 1989). In this contribution, we briefly follow up on three aspects of models recently presented for this purpose by Palomares and Pauly (1989) and Pauly (1989), by (a) relating the aspect ratio of the caudal fin of a fish to its level of activity, (b) accounting for the body depth ratio in the model, and (c) adjusting the linearizing transformation function of temperature.

The models of these authors used the aspect ratio (A) of the caudal fin of fishes as key variable. Figure 4 provides two examples of fish belonging to the "sluggish" and "active" type, both of which types appear to be well characterized by their respective values of A. As shown in Palomares and Pauly (1989) and Pauly (1989), A correlates rather well with Q/B. We show here on the basis of a documented data set (Table 2; Gray, 1954) that, according to physiological expectations, A is also correlated with gill area. Since the available data refer to fish of different weights, we accounted for size by regressing relative gill area (G, in cm^2/g) vs. weight (W, in g). Only species recognized as "intermediate" as regards activity level by Ursin (1967) were included (Table 2). This led to

$$\ln G = 2.632 - 0.180 \times \ln W \qquad (3)$$

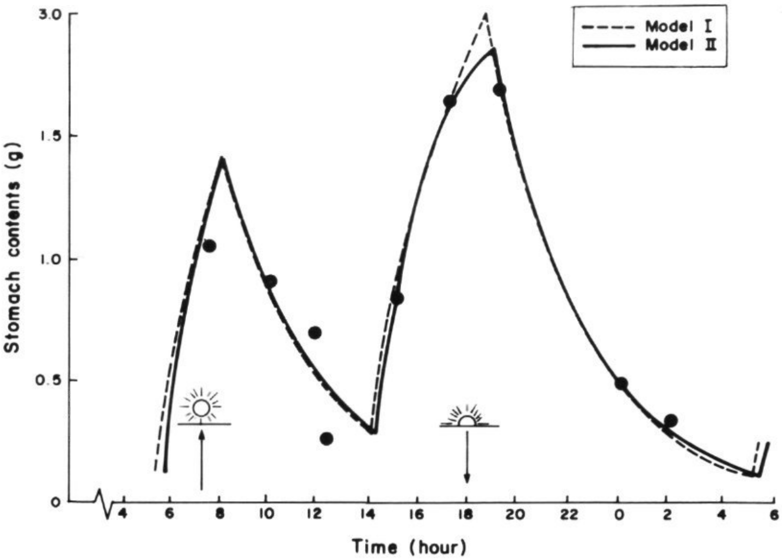

Figure 3. Application of models C and D (cf. Fig. 1) to stomach contents of Baltic cod (length class 26–30 cm; data from Arntz, 1974).

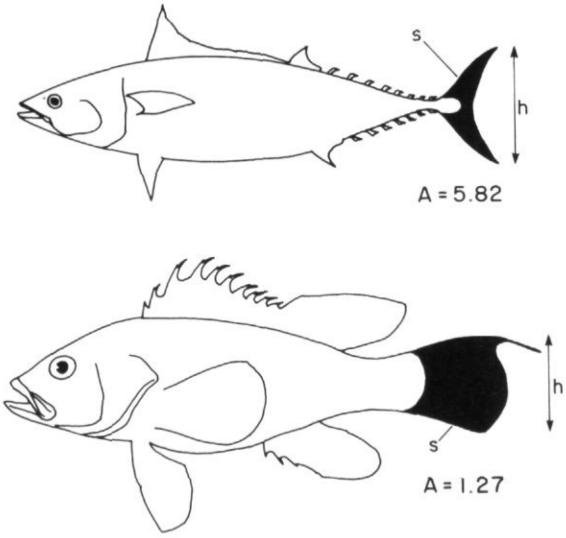

Figure 4. Examples of the variation in the aspect ratio ($A = h^2 s^{-1}$) of the caudal fin: top *Euthynnus alletteratus*, an "active" species; bottom *Centropristis striatus*, an "intermediate" species (see text).

Applying this equation (r = 0.547; d.f. = 17) to all fish of Table 2 for which A could be computed yielded predicted values of G. These were subtracted from the observed values and the residuals (Res) when plotted vs. A led to the significant (r = 0.627; d.f. = 26; $\alpha = 0.01$) relationship.

$$\text{Res} = -1.749 + 5.337 \times \ln A \qquad (4)$$

Aleev (1969) noted that high values of A occur both among streamlined, active fishes and among less active fishes when they are deep-bodied. In the latter case, the reason is that the propulsive effect of the caudal fin is strongest for those parts of the fin which are outside the zone of vortices in the wake of the swimming fish (shaded areas in Fig. 5). Therefore, deep-bodied fish tend to have caudal fin lobes that are spread wide apart, and hence high values of A even if they are not particularly active (Aleev, 1969). The empirical model of Palomares and Pauly (1989) did not account for this effect; the model of Pauly (1989) does include depth ratio (D, standard length/maximal body depth) as a variable, but the rationale given here was not stated.

The empirical models of Palomares and Pauly (1989)

Table 2. Mean body weight, relative gill area, aspect ratio of the caudal fin, and Ursin's activity code for various species. (Mean weights and gill area from Table 1 in Gray, 1954; activity codes from Ursin, 1967; A ≈ "active", S ≈ "sluggish", U ≈ "intermediate".)

Species	Mean weight (g)	Gill area (cm^2)	Aspect ratio	Ursin's code
Gymnosarda alleterata	5216	19.39	5.82	A
Brevoortia tyrannus	613	17.73	2.65	A
Coryphaena hippurus	4015	7.10	2.42	A
Sarda sarda	2192	5.95	4.28	A
Pomatomus saltatrix	1035	6.52	2.12	U
Scomber scombrus	182	11.58	2.65	A
Scomberomorus maculatus	478	7.69	3.38	A
Mugil cephalus	166	9.54	1.44	A
Caranx crysos	129	9.82	4.11	U
Roccus lineatus	3059	3.02	1.99	U
Archosargus probatocephalus	2366	3.28	2.29	U
Chilomycterus schoepfi	316	4.37	0.94	U
Stenotomus chrysops	395	5.06	2.25	U
Tautoga onitus	580	3.92	1.95	U
Prionotus strigatus	460	4.83	1.48	U
Poronotus triacanthus	199	5.98	2.28	U
Cynoscion regalis	807	3.73	1.30	U
Palinurichthyes perciformis	199	5.06	1.57	U
Echeneis naucrates	393	5.49	0.77	U
Spheroides maculatus	250	4.70	1.35	U
Centropristis striatus	244	4.58	1.27	U
Lophius piscatorius	6392	1.96	0.85	S
Peprilus alepidatus	71	5.05	2.58	U
Leptocephalus conger	2560	1.35	–	S
Prionotus carolinus	213	3.60	1.48	U
Trichiurus lepturus	116	5.36	–	U
Anguilla rostrata	428	3.02	–	S
Paralichthys dentatus	766	2.42	0.79	U
Pseudopleuronectes americanus	734	2.00	1.56	S
Opsanus tau	233	1.97	1.81	S
Lophopsetta maculata	411	1.88	0.86	S

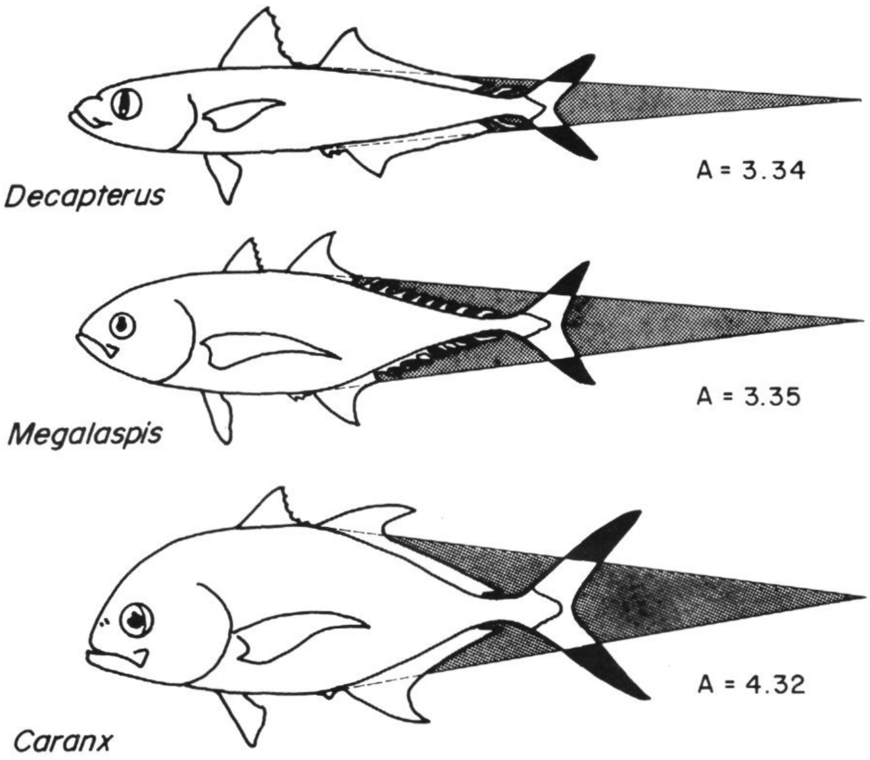

Figure 5. Schematic representation of the turbulent wake (shaded) caused by swimming fish of different shape to show that high-bodied fishes must have a higher aspect ratio of their caudal fin if the lobes are to reach outside the wake (adapted from Figures 80 and 83 in Aleev, 1969; see text).

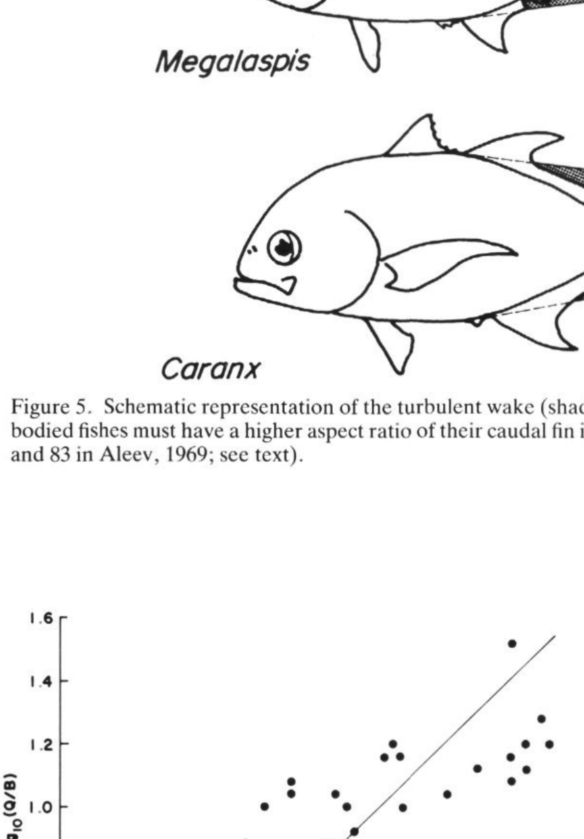

Figure 6. Predicted vs. observed food consumption per unit biomass using the data from Table II in Pauly (1989) and Equation (5) in this paper.

and Pauly (1989) include temperature as a predictor variable. Recently, Regier *et al.* (1990) suggested that it would be physiologically more appropriate to use a transformation of temperature in biological models by 1/T, where T is the temperature in Kelvin, rather than using °C or its logarithmic transformation. With this transformation, the slopes of the regression lines obtained can be compared across a wide range of biological parameters (Regier *et al.*, 1990). Using the data in Table II of Pauly (1989), we have therefore derived the model ($R = 0.743$, d.f. $= 69$):

$$\begin{aligned}\log_{10} Q/B &= \\ &= 4.885 - 1309.139 \times (1/T) + 0.423 \times \log_{10} A + \\ &\quad + 0.285 \times \log_{10} D - 0.111 \times \log_{10} W_\infty - \\ &\quad - 0.445 \times \log_{10} P \end{aligned} \qquad (5)$$

where P is the relative height of the caudal peduncle (i.e. caudal peduncle depth/maximum body depth), which distinguishes "burst" swimmers from continuous swimmers (Pauly, 1989). All other parameters are as introduced above. The partial slopes are all significant ($\alpha = 0.01$). Hence, the model appears to be marginally better, both on biological and statistical grounds, than the model of Pauly (1989). A plot of predicted vs.

observed values of food consumption is shown in Figure 6.

Discussion

The examples of estimates of daily ration show that the two feeding models yield very similar results in both cases. Field observations usually do not allow for a precise assessment of feeding periodicity. On the other hand, behavioural changes of captive fishes may bias experimental results on feeding periodicity and associated estimates of ingestion and evacuation rates. Parameterizing the feeding times of fish in nature in addition to the feeding rates may therefore yield more realistic estimates of daily rations than the computation of daily rations from the difference in weight of the stomach contents before and after an arbitrarily defined feeding period. Arntz (1974) used the latter approach, which gives a minimum estimate of $4.4\ \text{g} \times \text{d}^{-1}$. As the models presented here account for evacuation during the feeding period, it is not surprising that the results obtained are slightly higher. With respect to the Peruvian anchovy, Pauly *et al.* (1989) showed that the estimate obtained by applying the method presented here is similar to an earlier, independent estimate by Cushing (1978).

With regard to the empirical models for predicting Q/B, the results suggest that the biological basis for predicting food consumption from shape-related parameters and temperature is sound. However, the model derived by Pauly (1989) as well as the new model presented here (Equation 5) do not lead to very precise estimates. Also, as Figure 6 suggests, predicted values of Q/B tend to be biased upward in the lower range, and downward in the upper range. We attribute this bias to a failure of the logarithmic transformation to linearize the models satisfactorily, a theme that is presently being explored.

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Appendix

1. Introduction

Let t be the time (in h) and S the stomach contents (in g). For feeding period F let index b mark the beginning and s the end (F_b and F_s for one feeding period per day). If there are two periods per day, index 1 marks the first and index 2 the second (F_{b1}, F_{s1}, F_{b2}, and F_{s2}). In addition, let: E = instantaneous rate of gastric evacuation (in h^{-1}); J1 = ingestion rate (in $g \times h^{-1}$); J2 = instantaneous rate of ingestion (in h^{-1}); S_t = stomach contents at time t; S_r = residual stomach contents; S_f = stomach contents after the feeding period; S_∞ = the asymptotic stomach contents.

Regardless of the number of feeding periods per day, let the gastric evacuation be described by the differential equation

$$dS/dt = -E \times S$$

We consider two models of ingestion, Model I assuming a constant ingestion over time, and Model II assuming that the ingestion declines with increasing stomach contents:

Model I: $dS/dt = J1 - E \times S$

Model II: $dS/dt = J2 \times (S_m - S) - E \times S$

where S_m is the stomach content at which the ingestion becomes zero, and which is related to S_∞ through

$$S_\infty = J2 \times S_m/(J2 + E).$$

2. Time trajectories[1]

The solutions to the differential equations lead to the time trajectories of stomach contents for feeding and non-feeding periods. For each feeding period we get:

$$S_t = S_r \times \exp(A \times (t - F_b)) + B \times \\ \times (1 - \exp(A \times (t - F_b))$$

where

for Model I: $A = -E$ and $B = J1/E$

for Model II: $A = -(E + J2)$ and $B = S_\infty$

We further get for each non-feeding period

$$S_t = S_f \times \exp(-E \times (t - F_s))$$

For the models pertaining to two feeding periods, simple adjustments have to be made by replacing (F_b, F_s, S_r, S_f) by (F_{b1}, F_{s1}, S_{r1}, S_{f1}) and (F_{b2}, F_{s2}, S_{r2}, S_{f2}), respectively.

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[1] The special case of one feeding period per day is presented in Sainsbury (1986) in a slightly modified version.

3. Computation of S_r

Assuming steady-state conditions, the residual stomach contents can be computed from the other parameters, and hence have not to be estimated independently.

3.1. One feeding period

$$S_r = B \times D \times X_1 \times (1 - X_2)$$

where

for Model I: $D = 1/(1 - \exp(-24 \times E))$

for Model II:
$D = 1/(1 - \exp(-24 \times E - J2 \times (F_s - F_b)))$

and

$$X_1 = \exp(-E \times 24 - (F_s - F_b))$$

$$X_2 = \exp(A \times (F_s - F_b))$$

3.2. Two feeding periods

The residual stomach contents before the second feeding period are directly computed from the time trajectory of the first feeding period. For the residual stomach contents before the first feeding period, we obtain

$$S_r = B \times D \times X_1 \times (1 - X_2 \times (1 - X_3 \times (1 - X_4)))$$

where D is defined as above (3.1), and

$$X_1 = \exp(-E \times (24h + F_{b1} - F_{s2}))$$

$$X_2 = \exp(A \times (F_{s2} - F_{b2}))$$

$$X_3 = \exp(-E \times (F_{b2} - F_{s1}))$$

$$X_4 = \exp(A \times (F_{s1} - F_{b1}))$$

4. Computation of daily ration R_d

4.1. Model I, one feeding period

$$R_d = \int_{F_b}^{F_s} J1\,dt = J1 \times (F_s - F_b)$$

4.2. Model I, two feeding periods

$$R_d = \int_{F_{b1}}^{F_{s1}} J1\,dt + \int_{F_{b2}}^{F_{s2}} J1\,dt$$

$$= J1 \times (F_{s1} - F_{b1} + F_{s2} - F_{b2})$$

4.3. Model II, one feeding period

$$R_d = \int_{F_{b1}}^{F_{s1}} [S_\infty \times (E + J2) - J2 \times S_t]\,dt$$

$$= E \times S_\infty \times (F_s - F_b) +$$

$$+ (S_\infty - S_r)/(1 + E/J2) \times$$

$$\times (1 - \exp(-(E + J2) \times (F_s - F_b)))$$

4.4. Model II, two feeding periods

$$R_d = \int_{F_{b1}}^{F_{s1}} [S_\infty \times (E + J2) - J2 \times S_t]\,dt +$$

$$+ \int_{F_{b2}}^{F_{s2}} [S_\infty \times (E + J2) - J2 \times S_t]\,dt$$

$$= E \times S_\infty \times (F_{s1} - F_{b1} + F_{s2} - F_{b1}) +$$

$$+ (S_\infty - S_{r1})/(1 + E/J2) \times$$

$$\times (1 - \exp(-(E + J2) \times (F_{s1} - F_{b1}))) +$$

$$+ (S_\infty - S_{r2})/(1 + E/J2) \times$$

$$\times (1 - \exp(-(E + J2) \times (F_{s2} - F_{b2})))$$

ICES mar. Sci. Symp., 193: 109–112. 1991

Changes in growth of Northeast Arctic cod in relation to food consumption in 1984–1988

Sigbjørn Mehl and Knut Sunnanå

Mehl, S., and Sunnanå, K. 1991. Changes in growth of Northeast Arctic cod in relation to food consumption in 1984–1988. – ICES mar. Sci. Symp., 193: 109–112.

From 1984 to 1988 the average weight of cod (*Gadus morhua*) by age group in the Northeast Arctic stock was reduced by about 60% in most age groups. During the same period, the estimated individual food consumption by age group has decreased by 40–70%. It is concluded that these two features are closely correlated and that the decimation of the stock of one of the major prey species, the capelin (*Mallotus villosus*), is ultimately largely responsible.

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Introduction

During the first half of the 1980s average weight-at-age in the Northeast Arctic cod (*Gadus morhua*) stock increased to peak values in 1984–1985 (Anon., 1989), then rapidly declined. During the period 1984–1986 the cod stock increased from about 1 million tonnes to 1.5 million tonnes, mainly due to improved recruitment from the 1982 and particularly the 1983 year classes.

The two main prey species during this period (Mehl, 1989) were capelin (*Mallotus villosus*) and deep-sea shrimp (*Pandalus borealis*). However, at the end of 1986 the capelin stock became seriously depleted (Anon., 1987) and Hylen and Øynes (1986) showed that from 1984 to 1986 the shrimp stock was reduced by more than half (Fig. 1). The increased consumption by the cod stock was probably one of the reasons for the decline in the prey stocks (Mehl, 1989).

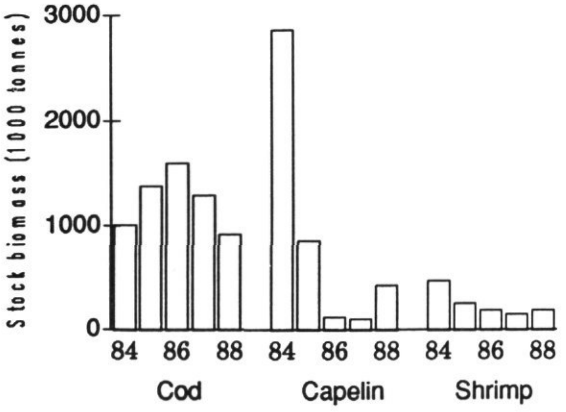

Figure 1. Stock biomass in 1000 t of cod, capelin, and shrimp in the Barents Sea and Svalbard area in 1984–1988.

Lilly (1987, 1991) has shown that cod in eastern Canadian waters did not prey more intensively on other prey at times of low capelin abundance. And Magnusson and Palsson (1989) observed that cod in Icelandic waters had lower stomach contents, a reduced feeding level, and a smaller growth rate when the capelin stock declined to low levels. In this paper we estimate the total annual consumption of individual cod by age group during the period 1984–1988 and compare the results with changes in average weight over the same period.

Materials and methods

The primary data used in the calculations are annually collected stomach content data for cod by age group, area, and season from the Barents Sea (Mehl, 1989). Distribution of the trawl stations where stomachs have been collected is shown in Figure 2. In addition, acoustic survey data for determining the geographical distribution of the different cod age groups (Hylen *et al.*, 1989; Jakobsen *et al.*, 1989; and unpubl. data) have been used. The temperature-corrected evacuation rates from the North Sea, which had been applied earlier, were substituted by new gastric evacuation rates from Northern Norway (J. Santos, pers. comm.; Mehl, 1989), because the latter are based on prey species and temperatures which are typical for the Barents Sea. The annual consumption of individual cod was estimated using essentially the same approach as Mehl (1989), where total consumption by the cod stock has been estimated by multiplying the mean stomach weight by

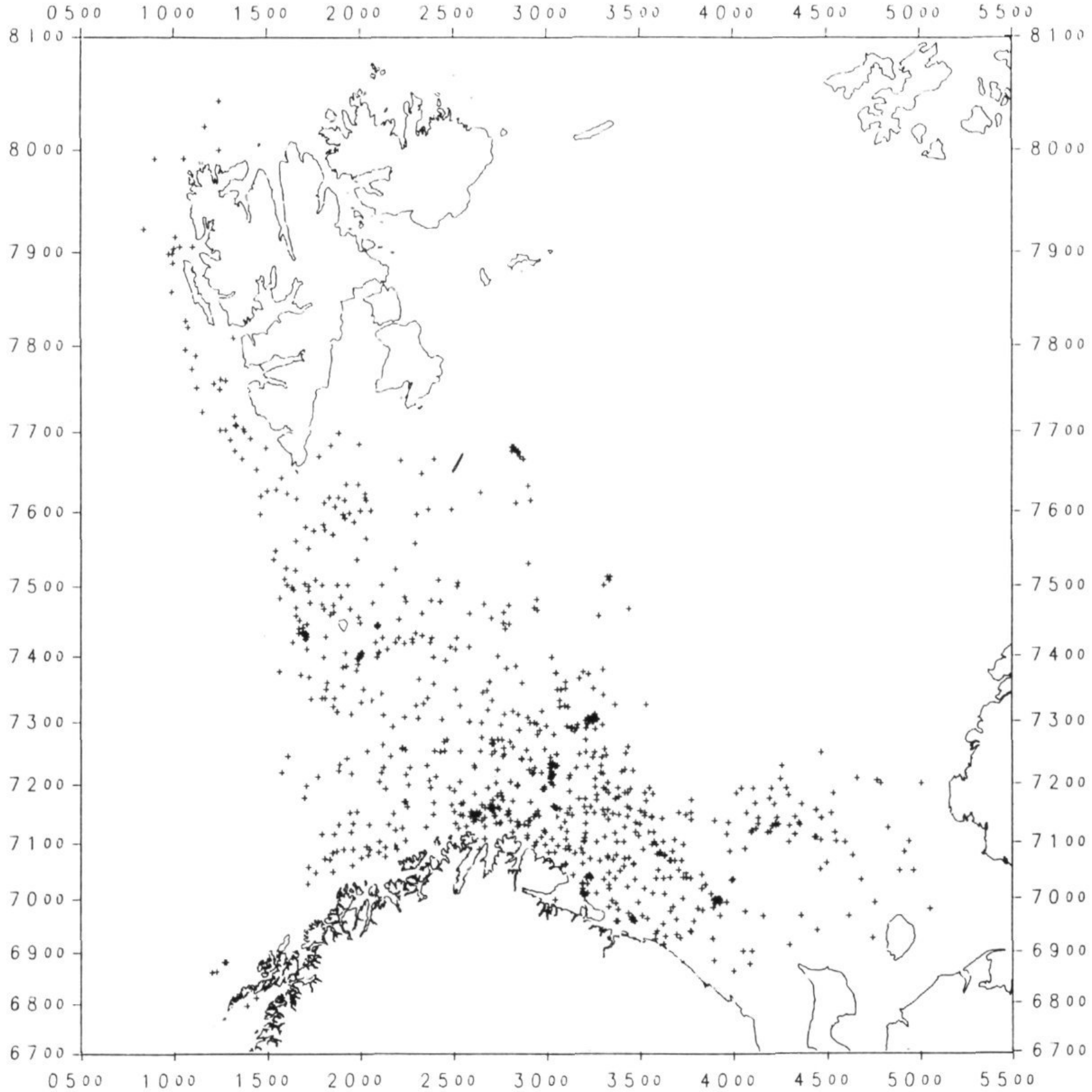

Figure 2. Geographical distribution of trawl stations in the Barents Sea and Svalbard area with sampling of cod stomachs in 1984–1988.

the rate of gastric evacuation and the number of cod in each age group, area, and season. Here, the number of cod were excluded from the calculations.

Weights-at-age in the cod stock are averages of values derived from Norwegian surveys in January–February and USSR surveys in November–December. They are assumed to be representative of the weights in the stock at 1 January (Anon., 1990).

Results and discussion

Figure 3 presents the estimated annual consumption of capelin and other prey by age group of individual cod in 1984–1988. Because of the way consumption is calculated, the figures are directly proportional to the weight of the stomach content. Although J. Santos (pers. comm.) observed slower evacuation rates at large meal sizes, meal size effects have not been taken into account so far. The stomach content weights are generally highest during the winter season, when cod feed intensively on capelin during the spawning migration of the latter (Mehl, 1986, 1989). A very high content of capelin was observed in most age groups particularly during the winter survey in 1985. This may reflect a larger degree of overlap between cod and capelin during the survey in 1985 compared to the survey in 1984. Since unpublished

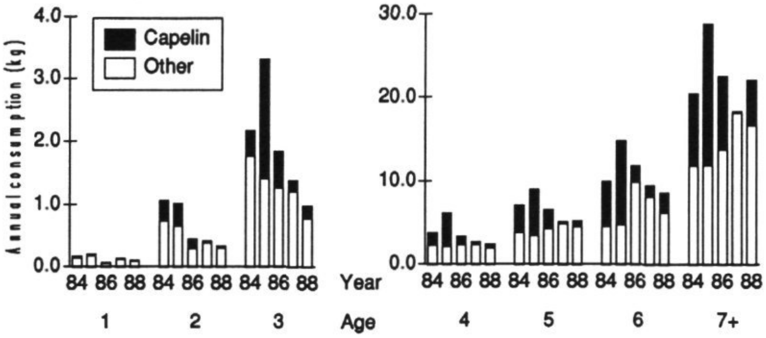

Figure 3. Annual consumption of capelin and other prey per cod by age group in 1984–1988.

data indicate that the overlap during the 1985 survey was higher than during other parts of the season when cod prey upon capelin, the consumption in 1985 is probably overestimated.

From 1985 onwards, the estimated total consumption declines rapidly in most age groups mainly due to the large reduction in consumption of capelin (Fig. 3). Apparently, the reduced contribution of capelin was only partly compensated by a higher consumption of other prey species. The reduction in annual consumption from 1985 to 1988 is largest in age groups 2–4 (60–70%), while in the older age groups the reduction is about 40–50%.

Figure 4 presents the mean weights by age group in the cod stock during the same years. The general trend is very similar to the one in total annual consumption: a large reduction from 1984–1985 to 1988. For age groups 2, 3, 4, and 5 the reduction in mean weight starts as early as 1985, while the older age groups show the first signs of a reduction in average weight in 1986. One explanation might be that at first the older age groups managed to compensate for a reduced intake of capelin by preying more intensively on larger fish prey, e.g. herring (*Clupea harengus*), haddock (*Melanogrammus aeglefinus*), and young cod. Overall, the reduction in weight-at-age from 1984 to 1988 varied between 20 and 70%.

The reduction in both consumption and mean weight is largest for medium-sized fish (age groups 2–5). The stomach content data show (Fig. 3) that the food of these age groups contains the highest percentages of capelin, and obviously they have been least successful in replacing this main prey item. Age group 1 is less dependent on capelin and continued to feed more upon smaller crustaceans. Older cod have managed to find other suitable prey species to a larger extent.

It seems questionable whether the weight reduction is caused entirely by a reduction in total food intake. The quality of the food may have changed when the cod had to replace capelin by food containing less energy. This is indicated by the fact that fishes of different ages but of the same weight do not show weight increments proportional to the annual consumption (Figs. 3 and 4).

Other factors may be related to fishing or to the hydrographic conditions. Since the decline in mean weight in age groups not yet or only partly recruited to the fishery is similar to the one in fully recruited age groups, fishing can hardly be considered an important factor.

The temperatures during the winter surveys in 1984–1985 were close to the 30-year mean. However, they were about 0.5°C lower in 1986 (Hylen *et al.*, 1986) and also in 1987 (Godø *et al.*, 1987). In 1988, they had increased slightly again but were still below the long-term mean (Hylen *et al.*, 1988). It seems doubtful whether a decrease by half a degree could have any significant effect on growth. The rate of gastric evacu-

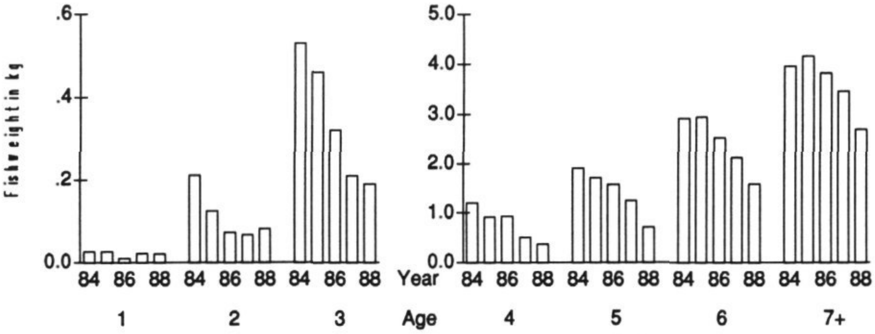

Figure 4. Mean weight of cod by age group in 1984–1988.

ation will obviously decline slightly, but so will the maintenance ration. At the beginning of the 1980s, the winter temperatures in the Barents Sea were more than 2°C lower (Dalen *et al.*, 1983), but, even though, the annual length increments were higher than in 1985–1988 (Anon., 1985). Daan (1974) observed a higher growth rate in cod during winter than during summer in the southern North Sea, indicating that lower temperatures can be more than compensated for by better feeding conditions. Also cod in the Barents Sea usually have the highest stomach content during the first part of the year when temperatures are relatively low (Mehl, 1986).

We therefore conclude that the reduced total annual consumption following the depletion of the capelin stock is closely correlated with the large reduction in mean weight-at-age in the cod stock. The latter has caused severe management problems. Because of lower individual weights, more fish than expected have been caught for the TAC set and, in addition, discards have increased. Also, natural mortality has probably increased during the period because cannibalism was raised by a factor of 3 (Mehl, 1989). These factors have caused several downward amendments in the prognosis on stock biomass and catch. In order to overcome the associated management problems of revisions in stock assessment, it is extremely important that multispecies considerations are included in the assessment and management of the main predator and prey stocks in the Barents Sea.

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A simulation model of two interacting exploited fish populations through competition in the early phases of life

A. F. Sharov and E. A. Kriksunov

Sharov, A. F., and Kriksunov, E. A. 1991. A simulation model of two interacting exploited fish populations through competition in the early phases of life. – ICES mar. Sci. Symp., 193: 113–116.

A model is presented of two fish populations, in which an age-structured competition model for the juvenile phase is combined with a traditional dynamic pool model for the adult phase. The main characteristic is a common food resource parameter for the juvenile populations when competition is assumed to operate. This affects the growth rate during this phase of life, which subsequently influences the spawning-stock biomass and thus numbers of eggs produced in the next years. The model is applied to vendace (*Coregonus albula* L.) and lake smelt (*Osmerus eperlanus* L.) in Pskov-Chud lake. The results show that lake smelt is more sensitive to changes in environmental conditions, but the resultant change in food utilization may induce secondary changes in the vendace population. At sufficiently high levels of exploitation of the vendace population, the yield of this fishery is significantly affected by the level of exploitation of the lake smelt.

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Introduction

Antagonistic fluctuations in the abundance and yield of different fish populations from a particular system are usually considered as reflecting some kind of interaction between the species. Essentially, two types of species interactions can be distinguished: predator–prey relationships and competition for a common food resource. Although the dynamics of interspecific predation have been subject to extensive modelling studies, the effects of food competition appear to have been neglected.

One way of studying the influence of interspecific relationships among fish is by creating trophodynamic models with a complex internal structure (e.g. Menshutkin, 1971; Andersen and Ursin, 1977; Laevastu and Larkin, 1981). However, such simulation models have generally been developed for specific systems and cannot be applied to solve more universal problems in practical fisheries management. A more prospective way might be to develop multispecies models on the basis of conventional fish stock assessment approaches.

In earlier studies of the stocks of vendace (*Coregonus albula* L.) and lake smelt (*Osmerus eperlanus* L.) of Pskov-Chud lake (Kriksunov and Sharov, 1987), we developed single-species models based on survey data and 30 years of catch statistics. In this paper, we attempt to construct a stock recruitment model for two populations consuming a common food resource during their early life history. This model is then applied to the vendace and lake smelt stocks with a view to evaluating the effect of competition in the recruitment phase on the yield surface as influenced by modifying the exploitation rate on the individual stocks.

The model

Kriksunov and Snetkov (1985) proposed an age-discrete model for a cohort of species s, with state variables N_t being the number of juveniles and W_t their average weight during the period of density-dependent growth and mortality (T), in the form of the following set of equations:

$$dN_t^s/dt = (\alpha^s N_t^s + \beta^s) \times N_t^s \quad (1)$$

$$dW_t^s/dt = \gamma/(1/\partial^s + \gamma/N_t^s) \quad (2)$$

where α and β are the density-dependent and independent mortality coefficients, respectively, γ is the amount of food available for growth and ∂ is the maximum growth rate. Competition for food was introduced in the model by have a common food parameter γ for the two species. Other parameters are species specific.

The later phases of life are described by a traditional dynamic pool model based on Baranov's equation:

$$N_{i+1} = N_i \times \exp(-M + F) \tag{3}$$

where N represents the abundance of a cohort at age i for the lifespan after the age of recruitment. Growth of the vendace is well approximated by the von Bertalanffy equation and biomasses were calculated based on estimated weights-at-age, accordingly. Growth of lake smelt, however, has been modelled in accordance with Equation (2), using a separate set of parameters ∂' and γ'. If it is assumed that fish mature after achieving some minimum weight (W_m), and that their weights in each cohort are normally distributed with mean W_a and variance σ, the number of mature fish (X) in each age group (a) can be defined as:

$$X_a = N_a \times \frac{1}{\sigma\sqrt{2\pi}} \times \\ \times \int_{w=W_m}^{\infty} W_a \exp\left(-\frac{(W_a - W_m)^2}{2\sigma^2}\right) dw \tag{4}$$

or

$$X_a = N_a \times \Phi_a(1/\sigma(W_a - W_m) \tag{5}$$

where Φ represents a normalized distribution function of weight-at-age to calculate the proportion of mature fish in the age group. The spawning-stock biomass (B) in year k is then obtained from

$$B^k = \sum_{a=i}^{\infty} X_a^k \times W_a^k \tag{6}$$

The number of eggs (N_0), which represents the initial abundance of the new year class, is calculated as the product of spawning-stock biomass, relative fecundity (f) and sex ratio (ρ):

$$N_0 = B \times f \times \rho \tag{7}$$

A flowchart of the model is given in Figure 1.

Results

The values of the various parameters for the early life history model for lake smelt and vendace, based on an application of the single-species counterpart of the model (Kriksunov and Sharov, 1967) described in the former section, are given in Table 1.

Table 1. Parameter values used in the simulations.

Parameter	Lake smelt	Vendace	Dimension
α	2.8×10^{-14}	1.0×10^{-12}	day^{-1} $number^{-1}$
β	0.034	0.026	day^{-1}
γ	2.62	2.02	g
∂	4.27×10^{-2}	4.42×10^{-2}	day^{-1}
T	180	180	days
σ	1.46		
W_m	1.5	13.0	g
M	0.7	0.34	$year^{-1}$
ρ	1010	168	eggs/g
Bertalanffy growth parameters			
W_∞		173.3	g
k		0.158	
t_0		0.28	year

The ultimate value of the common food resource parameter used in the simulations was obtained from simple addition of the values estimated for species individually. On the basis of experimental evidence that consumption of the common food resource was approximately proportional to the biomass of both species, this resource was allocated proportionally to the ratio of the biomasses of the juveniles during each time step. Initial runs indicated that under constant conditions (i.e. constant parameter values) biomasses of both species

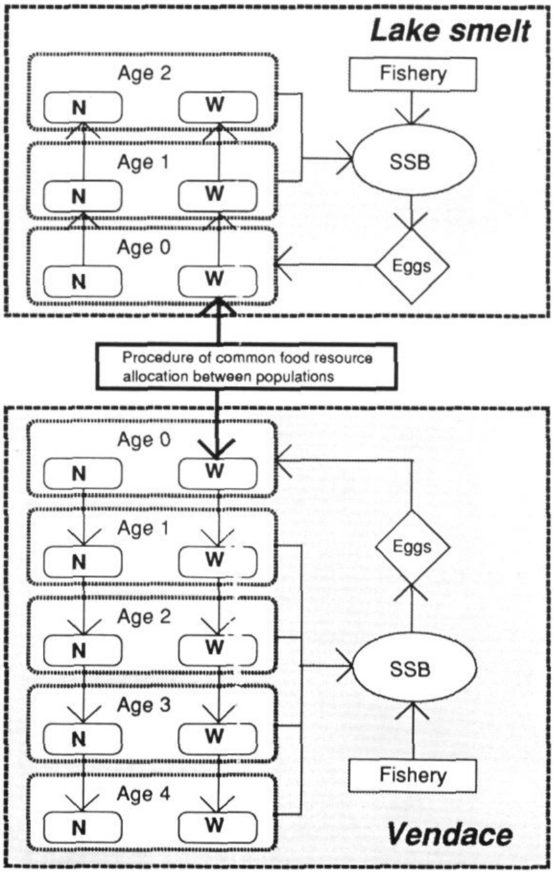

Figure 1. Flow chart of the model for lake smelt and vendace populations.

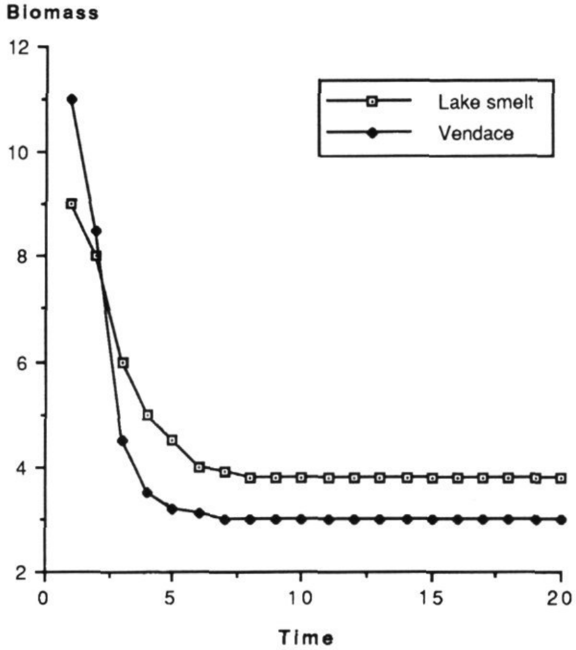

Figure 2. Development of steady-state spawning-stock biomasses (tonnes × 10^{-3}) when starting off with arbitrary population sizes.

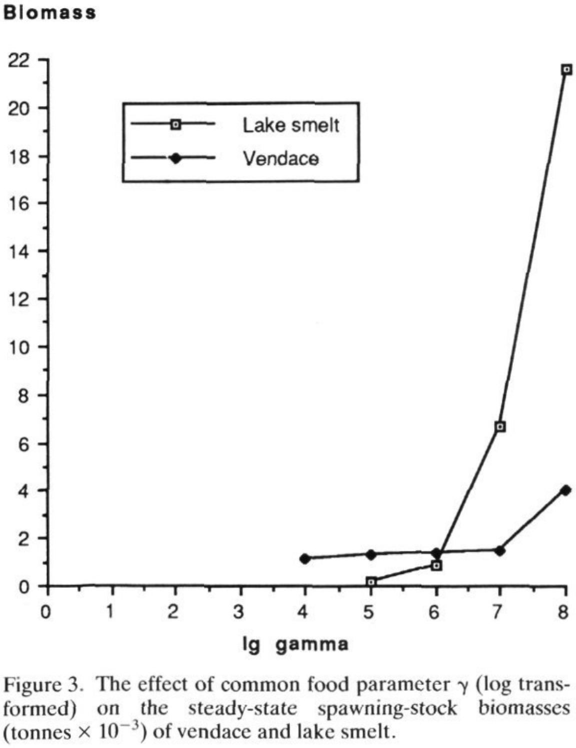

Figure 3. The effect of common food parameter γ (log transformed) on the steady-state spawning-stock biomasses (tonnes × 10^{-3}) of vendace and lake smelt.

approached stable equilibria (Fig. 2). However, their relative positions depended strongly on the food parameter γ (Fig. 3). Particularly noteworthy is the high sensitivity of lake smelt to changes in food abundance for juveniles. This can be partly explained by the low density dependent mortality coefficient. However, because the life cycle is shorter, the relative duration of the juvenile phase is much larger and the conditions for juvenile growth influence the process of maturation significantly. At very low food levels, growth was strongly reduced and the lake smelt did not reach the required minimum weight for becoming mature. As a consequence, the population died out.

An interesting feature of the model is that changes in the density independent mortality in one species can have a marked effect on the abundance of the other. An example is shown in Figure 4, where, keeping all other parameters constant, a sinusoid change in β of lake smelt

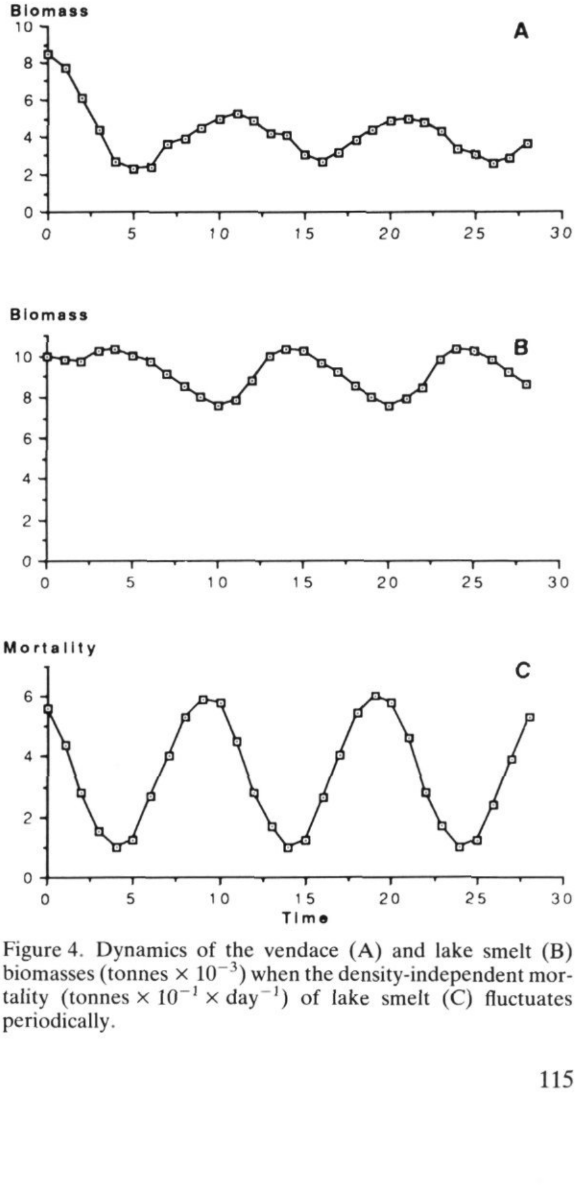

Figure 4. Dynamics of the vendace (A) and lake smelt (B) biomasses (tonnes × 10^{-3}) when the density-independent mortality (tonnes × 10^{-1} × day^{-1}) of lake smelt (C) fluctuates periodically.

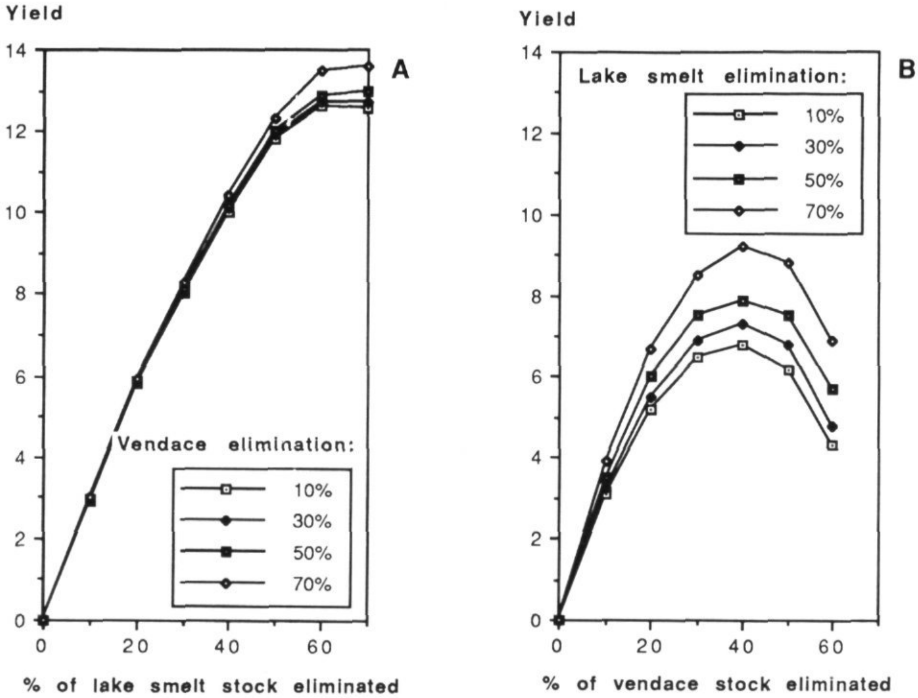

Figure 5. Sustainable yields (tonnes × 10^{-2}) of lake smelt (A) and vendace (B) in relation to percentage removals per year by each fishery.

has been introduced. This has a marked effect on the dynamics of the lake smelt population, which induces a secondary and opposite response in the vendace population.

In Figure 5, the combined effect of exploitation of the mature components of the two stocks on their respective sustainable yields is shown. Obviously, the sustainable yields of vendace are much more affected by the fishery on lake smelt than the other way around. However, these effects only become apparent at relatively high values of fishing mortality on the vendace.

Discussion

In general, the lake smelt population appears to be much more sensitive to changes in the environment as exemplified by variations in food conditions of larval fish and by variations in density independent mortality. Nevertheless, lake smelt is the dominant species in Pskov-Chud lake. The observed negative correlations between the biomasses of the two species could be induced by interannual fluctuations in the survival conditions for juvenile lake smelt, but also by differential exploitation through the fisheries.

This exercise shows that a simple model may help considerably in trying to understand the dynamics of a multispecies system. However, in view of the sensitivity of the model results to various parameter values, research should be directed towards the estimation of interannual changes in food conditions and mortality factors of juvenile fish in order to strengthen the basis of this simulation study for future management advice.

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Is the whole always less than the sum of the parts?

K. M. Brander and R. K. Mohn

Brander, K. M., and Mohn, R. K. 1991. Is the whole always less than the sum of the parts? – ICES mar. Sci. Symp., 193: 117–119.

We question the view that the total yield from a multispecies fishery must necessarily be less than the sum of the maximum yields of the component species, if each were optimized separately. A predator–prey model is used to show that this view depends on the assumptions which are made about predation mortality.

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Introduction

Several papers comparing the use of single-species and multispecies models (e.g. Pope, 1976; Steel *et al.*, 1980; Pikitch, 1988) state that the total yield from a multispecies fishery can never exceed and will generally be much less than the sum of the maximum yields from individual species, if each were optimized separately. This can be shown for models which include only technical interactions between fisheries (e.g. Paulik *et al.*, 1967) and a standard argument is that it is unlikely the conditions for optimizing the yield of each individual species can be maintained simultaneously in a mixed fishery.

If there are biological interactions (e.g. predation, competition), then the maximum yield for each species can only be defined for given levels of abundance of the other species (Anderson, 1975). Unless these population levels are specified, then it is not clear what is meant by "optimizing each species separately". In practice, single species assessments implicitly assume that biological interactions are fixed and are incorporated in the estimates of natural mortality and growth. Andersen and Ursin (1977) subdivided natural mortality into predation, poisonous pollutants, disease, old age, spawning strain, physical conditions, and larval mortality due to starvation. In a single species model these factors are fixed constraints on the yield, but in a multispecies model some of the constraints, in particular predation, may vary. Therefore it is not obvious that the total optimum yield is always less than the sum of the optimum yields of the individual species. The paper addresses this question by means of a simple predator–prey model.

Schaeffer type predator–prey model

Figure 1 shows a predator–prey model in which both are caught in the same fishery. The biomass of both predator and prey is inversely proportional to fishing effort (i.e. Schaeffer type), but the catchability of the predator is greater, so that it is fished out first. The predator eats three times its biomass per time period (say 1 year). The equations for biomass as a function of fishing effort are:

$$\text{Predator} = \text{Predmax} \times (1 - \text{effort} \times q_{\text{pred}})$$

$$\text{Prey} = \text{Preymax} \times (1 - \text{effort} \times q_{\text{prey}}) - \text{Predator} \times 3$$

where Predmax is the maximum predator biomass in the absence of fishing and Preymax is the maximum prey

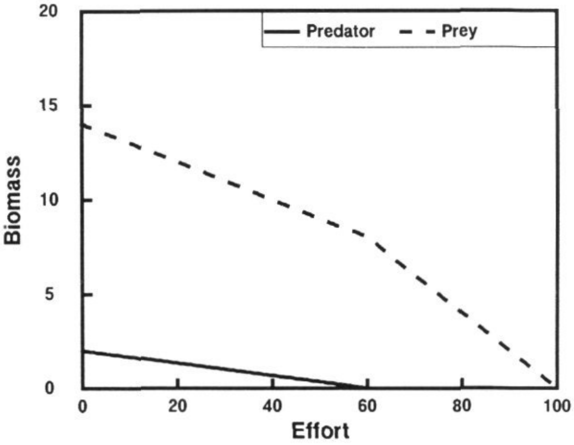

Figure 1. Predator and prey biomass as a function of fishing effort.

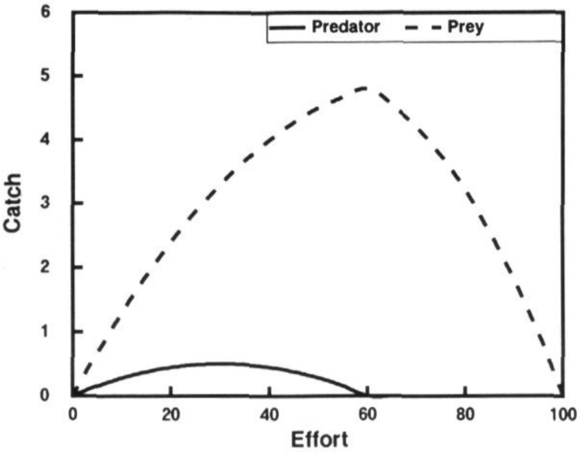

Figure 2. Predator and prey catch as a function of fishing effort.

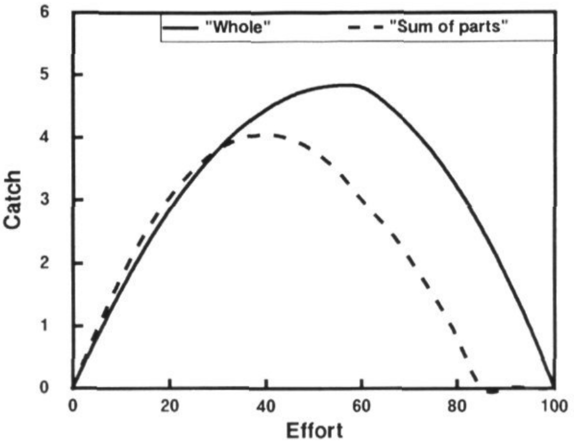

Figure 4. Total catch of predator plus prey as a function of fishing effort, using Schaeffer type predator–prey model. For explanation see text.

biomass in the absence of fishing and of predator. q_{pred} and q_{prey} are the catchability coefficients for predator and prey, respectively. The values used to construct Figure 1 were Predmax = 2, Preymax = 20, $q_{pred} = 1/60$, $q_{prey} = 1/100$.

Figure 2 shows the predator and prey catch as a function of fishing effort, where catch = biomass × effort × q. The sum of the predator and prey catch (i.e. the yield of the "whole" two species system) is shown as "whole" in Figure 4.

Turning now to the single species assessments, the predator yield is exactly the same as before, because the biological interaction does not affect predator biomass. For the prey species we have to make arbitrary assumptions about predator biomass in order to calculate yield. Three possible assumptions, whose consequences for prey biomass are shown in Figure 3, are that: (1) predator biomass = 0; (2) predator biomass = Predmax/2; (3) predator biomass = Predmax.

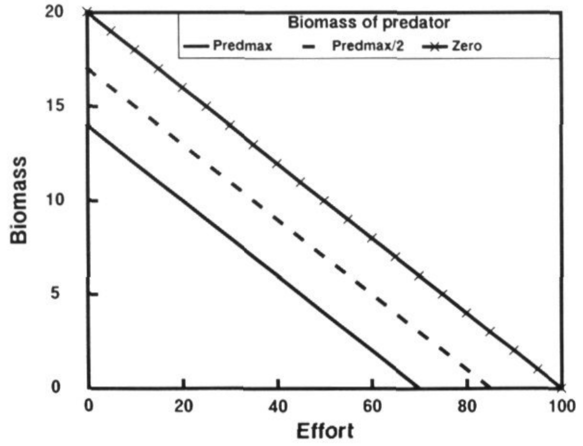

Figure 3. Prey biomass as a function of fishing effort, for three different assumptions about the predator biomass.

The yield of prey under the second of these assumptions has been added to the predator yield and is shown as "sum of parts" in Figure 4, where it can be compared with the yield calculated for the "whole" two species system. In this case the yield from the multispecies model is greater than the sum of the individual yields of the two species. If the first assumption (predator biomass = 0) had been used then the "sum of parts" would be greater than the "whole". Thus the maximum yield from the predator prey model with biological interactions may exceed the sum of the maxima of single species assessments of predator and prey, but this depends on what assumptions are made about predation mortality.

Age structured predator–prey model

More realistic models are required to explore whether the differences in yield calculated using single species and multispecies methods are likely to be of practical significance. As an example, an age-structured model was developed with a prey having three age classes and a predator having four. The underlying model for the two populations is the same as in our non-age-structured models above. Recruitment in the two populations is controlled by a linear density dependent term, as in the Schaeffer production model. The ratio of the predator to prey carrying capacities is 3:1. The predator preferentially removes smaller prey at a rate proportional to the predator's biomass.

The curve labelled "Sum of parts" in Figure 5 was derived with an average predation mortality of 0.2. The "Whole" curve results when the predator–prey interaction is operant; the predation mortality ranges from

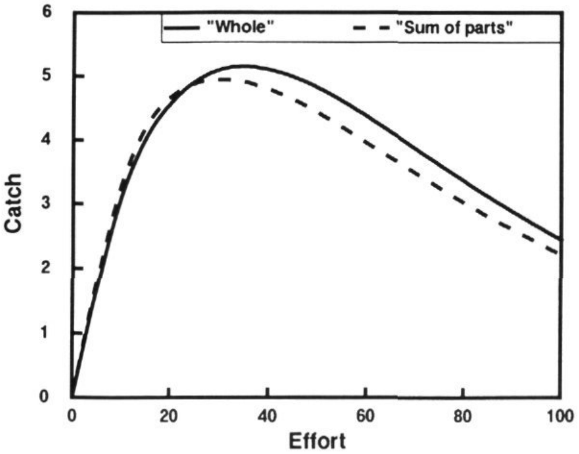

Figure 5. Total catch of predator plus prey as a function of fishing effort, using an age-structured predator–prey model. For explanation see text.

0.5 to less than 0.1 over the range of effort used. The two curves resemble patterns frequently seen for yield per recruit curves, displaying a rapid rise in yield at low effort levels and a gradual decline at higher effort levels. The difference between the two curves is not large and would probably be undetectable given the uncertainty in most fisheries data. Of course, this is just one realization of the model and more work is called for, including sensitivity analysis and stochastic modelling, before the importance of biological interactions can be assessed.

Discussion

If biological interactions significantly affect yield estimates then models which do not include them (e.g. single-species models) are incomplete (Silvert, 1981). Since single species and multispecies models require different kinds of assumptions they may even be regarded as incommensurable, as the arbitrary choice of a level of predator biomass in the single-species models above shows. The models shown in Figures 1–4 are trivial; their only purpose is to question the common view that single-species assessments will always overestimate the potential yield of a multispecies system.

It is very difficult to tell what kind of assumptions might be made in practice by someone assessing a real predator–prey relationship by fitting Schaeffer curves for each species. In his model of a mixed fishery for pilchard and anchovy with and without interactions, Pope (1976) looked at the hypothetical effect of introducing a predation term and compared this with the maximum yields if each species were present on its own. He comments, however, that "in practice, these yields would probably be assessed in the presence of the other species and not when it is extinct". It does indeed seem odd to calculate maximum yields for each species as though the other were absent and then add the two together to give a joint maximum.

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Predation and the regulation of sand lance populations: an exploratory analysis

Michael J. Fogarty, Edward B. Cohen, William L. Michaels, and Wallace W. Morse

Fogarty, M. J., Cohen, E. B., Michaels, W. L., and Morse, W. W. 1991. Predation and the regulation of sand lance populations: an exploratory analysis. – ICES mar. Sci. Symp., 193: 120–124.

Large-scale shifts in abundance and relative species composition have been observed in the pelagic fish community on the continental shelf off the northeastern United States. Here, we examine empirical evidence for regulation of sand lance populations (*Ammodytes* spp.) by Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus*) populations in an exploratory analysis. Changes in the abundance of sand lance are consistent with the hypothesis of predatory control by herring and mackerel. A significant negative interaction between sand lance recruitment and an integrated measure of herring and mackerel biomass was indicated. Direct evidence for predation by herring and mackerel is available to support these results.

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Introduction

The pelagic fish community off the northeastern United States has undergone dramatic shifts in biomass and relative species composition during the last two decades (Fig. 1). Population levels of Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) substantially declined during the 1970s in response to intensive fishing pressure (Grosslein *et al.*, 1980). A concomitant increase in American sand lance (*Ammodytes* spp.)[1] abundance was noted based on research vessel surveys conducted on the northeast continental shelf (Smith *et al.*, 1978; Meyer *et al.*, 1979; Sherman *et al.*, 1981) and in coastal waters (Monteleone *et al.*, 1987). Sherman *et al.* (1981) suggested that this apparent switch in species dominance was mediated by trophic interactions. Here, we evaluate empirical evidence for control of sand lance populations by herring and mackerel off the northeastern United States as a guide to formulating more detailed mechanistic models.

Trophic studies in the Northwest Atlantic indicated that both herring and mackerel prey on sand lance (Maurer, 1976; Grosslein *et al.*, 1980; Warzocha 1988; Michaels *et al.*, in prep.). Predator–prey interactions between herring and mackerel have also been demonstrated (Grosslein *et al.*, 1980). Further, overlap in diet composition of all three species is high, indicating the possibility of competitive interactions under limiting resource conditions (Maurer, 1976; Bowman *et al.*, 1984; Meyer *et al.*, 1979). It is assumed here that the dominant interaction is predation, based on direct evidence from diet composition studies and the lack of clear evidence of food limitation.

Herring, mackerel, and sand lance also comprise an important forage base for piscivorous fish, marine mammals, and seabirds (Grosslein *et al.*, 1980; Overholtz and Nicholas, 1979; Overholtz *et al.*, 1991; Powers and Backus, 1987). Although predation pressure by other piscivores clearly has important effects on the dynamics of sand lance populations in this region, we chose to focus initially on the potential role of predation by herring and mackerel populations because (1) direct sampling of diet composition indicates potentially important interactions among these species, (2) population levels for each of these species have undergone large-scale changes during the last two decades, providing sufficient contrast to detect possible interactions, and (3)

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[1] Sand lance taxonomy in this region has recently been reexamined (Nizinski *et al.*, 1990). Our samples are assumed to be predominantly the offshore species *A. dubius*; however, it is possible that the inshore species *A. americanus* is also represented.

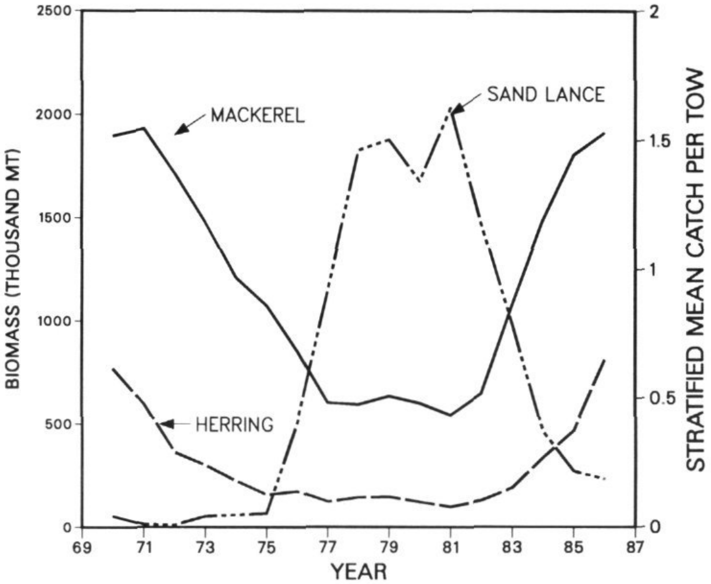

Figure 1. Trends in biomass of mackerel (age 1+) and herring (age 3+) derived from virtual population analysis and trends in relative abundance (stratified mean catch per tow; kg) of sand lance (age 2+) based on research vessel surveys.

similar changes in system structure are evident in the North Sea (Andersen and Ursin, 1977; Daan, 1980; Cushing, 1980; Sherman *et al.*, 1981; Jones, 1983), allowing regional comparisons. Overholtz *et al.* (1991) provide an analysis of predation on herring, mackerel, and sand lance by marine mammals, sea birds, and three species of piscivorous fish off the northeastern United States.

Data sources

Abundance estimates for herring and mackerel populations for this region were derived from virtual population analyses (VPA). Biomass estimates for the mackerel stock off the northeastern United States (Overholtz and Parry, 1985; W. J. Overholtz, pers. comm.) were used in these analyses. We combined abundance estimates for the Georges Bank and Gulf of Maine herring stocks (Anthony and Waring, 1980; Fogarty *et al.*, 1989) to provide an estimate of total herring biomass in this region. Both stocks overwinter in the southern New England-Mid Atlantic region and can potentially affect sand lance populations in this area during the winter–spring period. Estimates based on VPA for the Georges Bank herring stock were not available following the collapse of the fishery in 1977. Accordingly, abundance was estimated for the post-1977 period based on an empirical relationship between biomass and research vessel trawl survey indices.

Predation by herring on sand lance off the northeastern United States is primarily by larger herring (Michaels, pers. obs.). We used herring biomass estimates for ages 3 and older as a measure of the herring predator field in our analyses. A broader size spectrum of mackerel prey on sand lance (Michaels, pers. obs.). Mackerel biomass for ages 1 and older was therefore used in all subsequent analyses.

Sand lance are not commercially harvested in this area. We therefore used relative biomass indices derived from offshore (>27 m depth) trawl surveys conducted during spring as a measure of abundance. The region from Georges Bank to the Middle Atlantic region was considered in these analyses. The efficiency of the sampling gear for sand lance is not known. The dramatic increase in abundance of sand lance during the mid-1970s is, however, reflected in both the trawl survey index and ichthyoplankton surveys (Smith *et al.*, 1978; Sherman *et al.*, 1981; Morse, 1982).

Spring surveys during 1968–1972 and from 1982 to the present were conducted using a standard Yankee 36 trawl; surveys carried out during 1973–1981 utilized a high-opening Yankee 41 trawl (Azarovitz, 1981). We developed gear conversion coefficients for sand lance based on fishing power experiments conducted during 1975 (Sissenwine and Bowman, 1978). Sand lance data from these experiments had not been previously analyzed. Conversion coefficients were derived using the general linear model approach described by Sissenwine and Bowman (1978). The multiplier for conversion from the Yankee 36 to 41 trawls was 2.82.

Relative recruitment estimates (age 2) for sand lance were derived from survey data and age-length keys (Nelson, 1990). Similarly, estimates of spawning biomass were based on size-maturity relations and age-specific abundance estimates (Nelson, 1990). We applied the time-series methods described by Pennington

(1985) in an attempt to separate sampling error from process error in the sand lance survey estimates. The method involves fitting an autoregressive-integrated-moving-average model (Box and Jenkins, 1976) to the $\log_e$ transformed survey estimates.

Population estimates for each of the species from the years 1972–1986 were included in these analyses. This range spanned the period from immediately prior to the increase in sand lance abundance through the subsequent decline. Population estimates for herring and mackerel after 1986 were sensitive to the terminal fishing mortality rates assumed in the virtual population analyses and were not used.

Analysis

Changes in population biomass levels can be used to test directly for evidence of interactions among species (e.g. Sissenwine *et al.*, 1982; Beverton, 1984; Walters *et al.*, 1986). We used a multispecies extension of the Ricker model (Murphy, 1986) to test for potentially important interactions. The model can be written:

$$R_t = \alpha S_{t-r} \exp\left[-\beta S_{t-r} - \Sigma\,\Sigma\, \partial_{ij} P_{j,t-k}\right]$$

where R_t is sand lance recruitment in year t, S_{t-r} is the spawning biomass of sand lance at time $t - r$ (r is the time delay between spawning and recruitment; $r = 2$ in this analysis), $P_{j,t-k}$ is the biomass of predator species j (herring or mackerel) at time $t - k$ (k reflects the timing of predation events during the pre-recruit phase; $k \leq r$), α and β are coefficients of density-independent and compensatory mortality respectively for sand lance, and ∂_{ij} is the effect of predator species j on age i sand lance ($i = r - k$). We tested for possible species interactions using a linearized form of this model (Murphy, 1968; Beverton, 1984; Walters *et al.*, 1986):

$$\log_e (R_t/S_{t-r}) = \log_e \alpha - \beta S_{t-r} - \Sigma\,\Sigma\, \partial_{ij} P_{t-k}.$$

The linearized form of the model does incur some disadvantage because of the confounding of the dependent variable with the spawning biomass estimates. Further, the spawning biomass estimates and the predator biomass estimates are measured with error and application of ordinary least squares (OLS) methods may result in an overestimate of the compensatory coefficient and an underestimate of the predation coefficients (Walters *et al.*, 1986). Our interest was primarily in the species interaction terms and therefore we assumed that our analysis would result in a conservative assessment of possible interactions.

Preliminary analyses indicated significant ($p < 0.05$) interaction coefficients for herring and mackerel abundance at lags of 1 and 2 years in four separate analyses incorporating each predation term individually. However, models with multiple predation terms demonstrated high levels of intercorrelation among the independent variables. This collinearity among the regressor variables resulted in unstable parameter estimates. This difficulty stems from high levels of autocorrelation in both the herring and mackerel series and from significant cross-correlations between herring and mackerel biomass. The first-order correlation coefficient was 0.80 and 0.57 (both significant at the 0.05 level) for mackerel and herring respectively. The correlation between mackerel and herring was 0.90 ($p < 0.05$). It is therefore effectively impossible to distinguish the relative roles of herring and mackerel and the timing of predation events from the time-series data alone. We therefore developed an integrated index of herring and mackerel abundance at lags of 1 and 2 years (relative to sand lance recruitment) using principle component analysis. An overview of the general approach and rationale for regression on principle components is provided by Draper and Smith (1981).

Results

Principle components analysis indicated that the first two eigenvalues accounted for 96.7% of the standardized variance in the biomass index. Examination of the eigenvectors showed that the first principle component, which accounted for 81% of the standardized variance, represented approximately equal contributions by mackerel and herring biomass at both lag periods. Initial stepwise regression analyses for the linearized recruitment model indicated that the coefficient for the second principle component was not statistically significant ($p > 0.05$). The final regression model therefore included only the first principle component as an index of biomass of these predators.

The final regression model including a compensatory coefficient and the predator index was highly significant ($F = 10.58$; d.f. $= 2, 12$; $p = 0.002$; $r = 0.80$). Estimates of the regression coefficients and associated statistics are provided in Table 1. The estimates of the compensatory and predation coefficient were highly correlated ($r = 0.77$), again indicating difficulties in separating the relative influences of the regressor variables. A Durbin–Watson test indicated no evidence of first-order autocorrelation in the residuals ($D = 2.007$; $p > 0.05$).

Discussion

Several lines of evidence indicate potentially important effects of mackerel and herring predation on sand lance populations. Warzocha (1988) reported that sand lance comprised up to 40% of the stomach contents by weight of mackerel in the Southern New England region during the winter/spring period of 1984. The diet of herring for this area and time period consisted of nearly 10% sand

Table 1. Results of regression analysis for multispecies recruitment model incorporating an index of predator biomass derived from a principle components analysis. Parameter estimates (α' is the natural logarithm of the density-independent parameter, β is the coefficient of compensation, and ∂ is the interaction term) and associated standard errors are provided with the *t*-statistic and significance levels. The signs of the coefficients are taken directly from the multiple linear regression analysis.

Parameter	Estimate	s.e.	T	P
α'	−0.503	0.346	−1.450	0.020
β	−0.0022	0.00062	−3.526	0.012
∂	−0.957	0.208	−4.589	0.001

lance by weight (Warzocha, 1988). Michaels *et al.* (in prep.) reported similar results and noted that at some locations, mackerel fed exclusively on sand lance and that mean stomach content weight was markedly higher at these locations than at other locations where zooplankton comprised most of the diet.

Monteleone *et al.* (1987) indicated two periods (1962–1966 and 1977–1982) of peak sand lance abundance in Long Island Sound during the last three decades based on an analysis of ichthyoplankton samples. Mackerel biomass was low during 1962–1966 but rapidly increased to peak levels in 1970–1971 (Overholtz and Parry, 1985). Both periods of high sand lance abundance identified by Monteleone *et al.* (1987) coincided with low mackerel population levels. In contrast, herring populations were at relatively high levels during the earlier period (Anthony and Waring, 1980). Direct observations of predation by mackerel on sand lance in Long Island Sound are available (Monteleone *et al.*, 1987). These results suggest that, for sand lance in Long Island Sound, predation by mackerel may be a dominant regulatory factor.

In the North Sea, Jones (1983) noted an inverse relationship between mackerel and sand lance abundance and reported that spatial overlap was high between mackerel and sand lance populations. Juvenile herring and sand lance co-occur in the North Sea (Jones, 1983), although predation by juvenile herring on sand lance is assumed to be low. Competitive interactions could occur between juvenile herring and sand lance if food resources were limiting. Cushing (1980) questioned the accuracy of available sand lance population estimates for the North Sea but did note the potential role of predation by herring and mackerel on sand lance. Direct evidence of predation by herring and mackerel is available (Cushing, 1980). Several gadoid species (including established predators of sand lance) increased in abundance concurrently with sand lance in the North Sea following declines in the herring and mackerel populations, suggesting that predation by these gadoids did not regulate sand lance populations in the North Sea.

Results of the exploratory analysis described above are consistent with the hypothesis that predation by pelagic predators has played an important role in regulating sand lance populations on the northeast continental shelf of the United States. However, problems in estimating the relative importance of predation by herring and mackerel and the timing of predation events highlight the difficulty of empirically assessing species interactions using time-series data alone. Further, analysis of relative changes in abundance levels of potentially interacting species cannot determine causal relationships but can only point to possible interactions. In the present case, direct evidence of predation by mackerel and herring is available to support the inference of interactions between sand lance and pelagic predators.

Alternative hypotheses that must be considered in any explanation of the apparent population explosion of sand lance off the northeastern United States include the role of other predators (piscivorous fish, marine mammals, and sea birds). Overholtz *et al.* (1991) examine the question of predation on small pelagic fish by these components of the system. Clearly, it is possible that synergistic effects by a suite of predators has dominated sand lance biomass in this region. Smith *et al.* (1978) also cite physical transport mechanisms as potential factors underlying fluctuations in sand lance abundance.

Deliberate manipulation of the abundance levels of the presumed dominant predators would provide the most effective method of further testing the effects of predation on sand lance populations. In particular, controlled reduction of mackerel biomass in an adaptive management experiment (Walters, 1987) could help distinguish the impact of mackerel predation on sand lance populations from other sources of predation mortality. A combined strategy of direct assessment of predation mortality through diet composition studies, experimental manipulation of predator biomass, and continued monitoring of changes in population levels will afford the best opportunity to understand the interactions in this system.

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Transparent multispecies analysis: an exploration of fisheries and survey data off the Norwegian coast and Barents Sea

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Bax, N. J., Mehl, S., Godø, O. R., and Sunnanå, K. 1991. Transparent multispecies analysis: an exploration of fisheries and survey data off the Norwegian coast and Barents Sea. – ICES mar. Sci. Symp., 193: 125–132.

An integrated spreadsheet system was designed to combine biomass estimates for species including commercial fish species, mammals, and various other groups off the Norwegian coast and in the Barents Sea with catch data and feeding data in order to evaluate annual changes in the stocks. A time interval of two weeks was used in the simulation. No attempt was made to balance the spreadsheet; it was left transparent, with few assumptions and with results directly attributable to the data input. Eventually, the output can be used to track down important multispecies interactions and ecosystem functions. More importantly, however, the model highlights obvious gaps and deficiencies in our data and knowledge of the ecosystem, which will help to focus subsequent research.

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Introduction

There is no lack of models in fisheries science to study the population dynamics of exploited species, all of which need adequate data to give sensible results. However, it is often the case that data from commercial catches and scientific surveys suffer from both bias and imprecision (Byrne *et al.*, 1981; Nilssen *et al.*, 1986; Engås and Godø, 1989a, b). Such data inadequacy becomes easily masked when only one species is considered at a time, as though the species existed in a vacuum; additional insights from multispecies analysis would provide a check for internal consistency of data from interacting species. The educational qualities of an ecosystem approach in that respect are well exemplified by the work of Andersen and Ursin (1977).

The principal objections often raised against multispecies models is that they require inordinate amounts of data, that their internal structure is complicated, and that the results are difficult to comprehend (Gulland, 1979, 1982). There are only a few areas where there are sufficient data, and personnel, to apply elaborate multispecies assessment models such as multispecies virtual population analysis (Anon., 1989a, b). We present here a multispecies analysis of the Norwegian coast and Barents Sea ecosystem (NORFISK) that is easy to apply and has a transparent internal structure. The analysis is based on commercial spreadsheet software, and directly manipulates data tables through a minimum of simple equations, to provide the trophic relationships between the different species. The spreadsheet format ensures that all data and equations are readily accessible to the user.

We attempt to make optimum use of the available data and to restrict the necessary assumptions. The main objective at this stage concentrates on two questions: "Are the available data for the different species consistent and do these lead to a coherent picture of the community processes?", and "If not, where do the inconsistencies lie?"

Outline of NORFISK

General features

The aim of the NORFISK spreadsheet model is to simulate the changes in total biomass of species, or groups of species, off the Norwegian coast and in the Barents Sea over the course of a year. It is our expectation that over this period biomass growth will be approximately equal to biomass losses resulting from fishing, predation, and other natural mortality.

Therefore we assume that biomass will not change over the one year modelled. Biomass losses and gains are computed and recorded for each time step in the model but are not subtracted from, or added to, the biomass in each time step. The losses and gains in each time step are summed, and the total is compared with

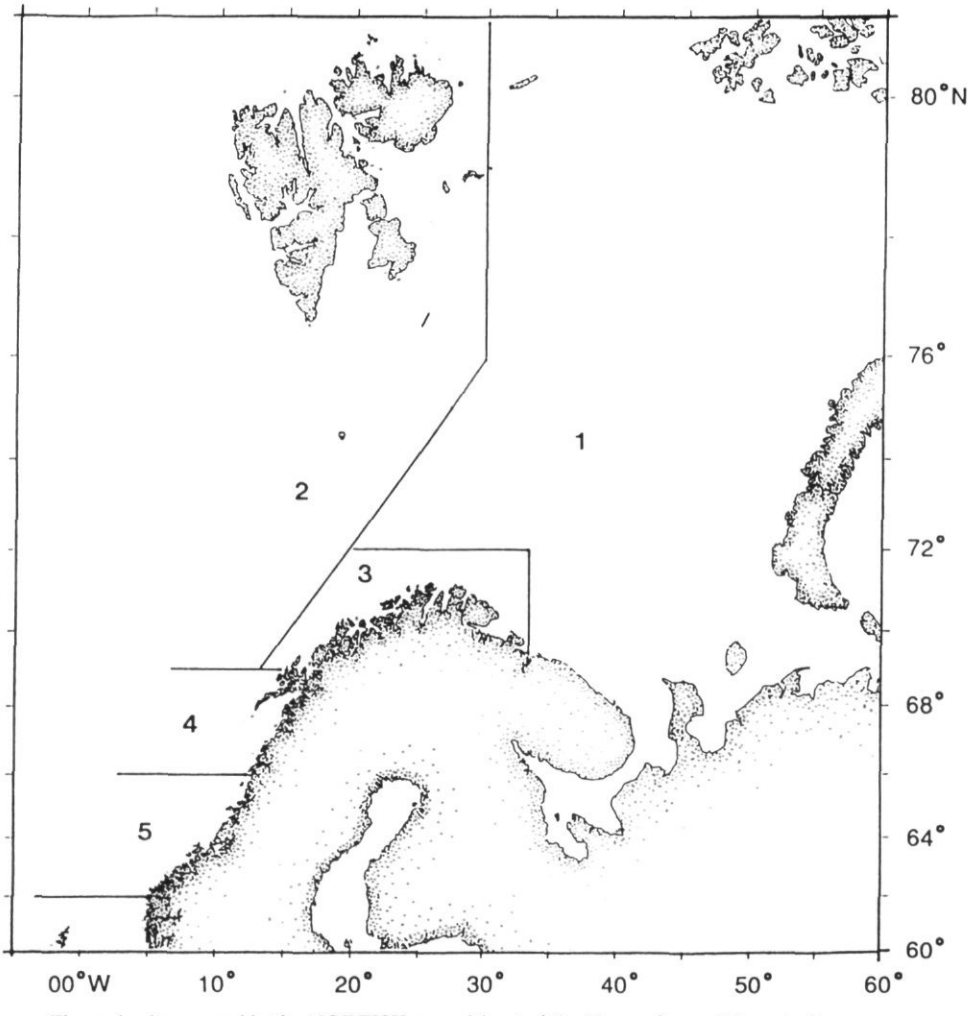

Figure 1. Areas used in the NORFISK spreadsheet of the Norwegian and Barents Seas.

the input (constant) biomass at the end of the simulation.

Species included

Capelin and herring are the major pelagic species, and cod and haddock the major demersal ones in the area of study. A total of nineteen groups are included in NORFISK. Nine species of fish (herring, capelin, blue whiting, polar cod, redfish, Greenland halibut, cod, haddock, and saithe) form individual groups, and three further groups consist of the flatfish, other predators, and other prey, respectively. Shrimp are included as one group, squids as another, seals as a third, and whales as a fourth. The last two groups are zooplankton and benthos. No data were included for birds.

Spatial resolution

The region considered has been split into five contiguous areas around the Norwegian coast extending from 62°N along the western and northern coasts of Norway, including the Barents Sea (Fig. 1). The study area is 1 500 000 km^2.

Temporal resolution

For the present purpose data have been compiled for a single year running from May 1984 to April 1985. This represents a time when both capelin and herring were abundant, and when the cod stock in the Barents Sea was growing. The model has a two-week time step.

Migration

Many of the species considered are highly migratory, and are present in different quantities in each area in different seasons. This greatly affects the predation pressure that they exert in the different areas. The proportions of the stocks in each area by two-week period are not known quantitatively. However, the start- and end-points of the annual migration periods are known. On the basis of data from surveys and commercial catches, the relative distribution of the biomass during the spawning and feeding season was estimated. Using these pieces of information, the biomass by two-week period was redistributed by linear interpolation. Finally, point estimates of the total biomass present in the system at the beginning of the year are available from routine fish stock assessment.

The migrations of herring, capelin, cod, haddock, saithe, seals, and whales are modelled in NORFISK. For other species there are insufficient data available on the seasonal distribution to model their migration. Whales are treated differently, because they are considered not to be inside the model area for the whole year. They are present only from May to August (unpubl. data, Institute Marine Research, Bergen).

Input data

Catch data for fishing areas off the Norwegian coast are available at different levels of spatial and temporal resolution. Domestic catches are provided for Norwegian and ICES statistical areas by month. Foreign catches are only available as annual totals by ICES area. The correspondence between Norwegian, ICES, and model areas is as follows:

Model area	ICES area	Norwegian area
1	I	1, 2, 10, 11, 13–19, 24
2	IIb	12, 20–23
3		3, 4, half of 5
4	IIa	0, half of 5
5		6, 7

The following assumptions were made to apportion the catches into two-week periods. It was assumed that Norwegian monthly catches were spread evenly over the entire month. Foreign catches, which were reported as an annual total, were split by assuming that foreign catches of cod, haddock, saithe, redfish, and Greenland halibut had the same distribution over time as Norwegian trawl catches. The catch of shrimp was considered equally distributed from March to December, while catches of flatfish were considered equally distributed over the whole year. In the case of herring, 60% of the catch was assumed to be taken from January to April, and 40% from August to November. International capelin catches were assumed to follow the same distribution as Norwegian capelin catches. Catches of polar cod were considered equally distributed from June to December. There was no foreign catch of blue whiting.

Biomass estimates of the commercial fish stocks, seals, and whales at the beginning of 1985 by Norwegian statistical area were taken, or interpolated, from published and unpublished data reports. Biomass estimates of non-commercial species represent the best guesses of the authors, based on survey experience, and published data from other areas.

Further data were required for species whose migration is modelled. These data, taken from survey reports of the Institute of Marine Research, were the distribution of the biomass during spawning and/or the most southerly distribution of the species, and the time that the southerly spawning migration began, peaked, and ended. The January biomasses provide the northernmost distribution of biomass.

Whales are modelled as being inside the area only from May to August, and thus they exert no predation pressure during eight months of the year.

Diet composition data were taken from published stomach content analyses (Mehl, 1986; Burgos and Mehl, 1987), from unpublished records (including those of PINRO, Murmansk), and from published reports for other areas. Two separate sets were prepared for the period January to April, and the rest of the year on the basis of stomach collections in 1984 and 1985. Diet composition data were specific to each area in the model. Diets for some species were derived from the literature or even from comparison of similar species.

Several biomass parameters are needed to initiate the model. One important parameter is that determining food requirements. These are divided into the food required for maintenance and food required for growth. Equations estimating these parameters as a function of body weight (W) and temperature were fitted to values reported in the literature (Sunnanå, unpubl. manus.). An approximate value for maintenance ration (MR) at 5°C for individual fish is:

$$MR = 2.0 \times W^{0.67}$$

This formula was applied to the average weight-at-age composition of the population to arrive at a maintenance ration for the biomass of the population per unit biomass per two-week period.

A different equation was used for marine mammals:

$$MR = 1.5 \times W^{0.75}$$

Food requirements for growth were calculated from realized growth rate. The following formula for individual growth in weight (W) has been applied:

$$W = a \times t_b$$

$$dW/dt = b/t \times W$$

where t is age and a and b are parameters.

These equations have been fitted to weight-at-age for the population and the resulting values averaged over all

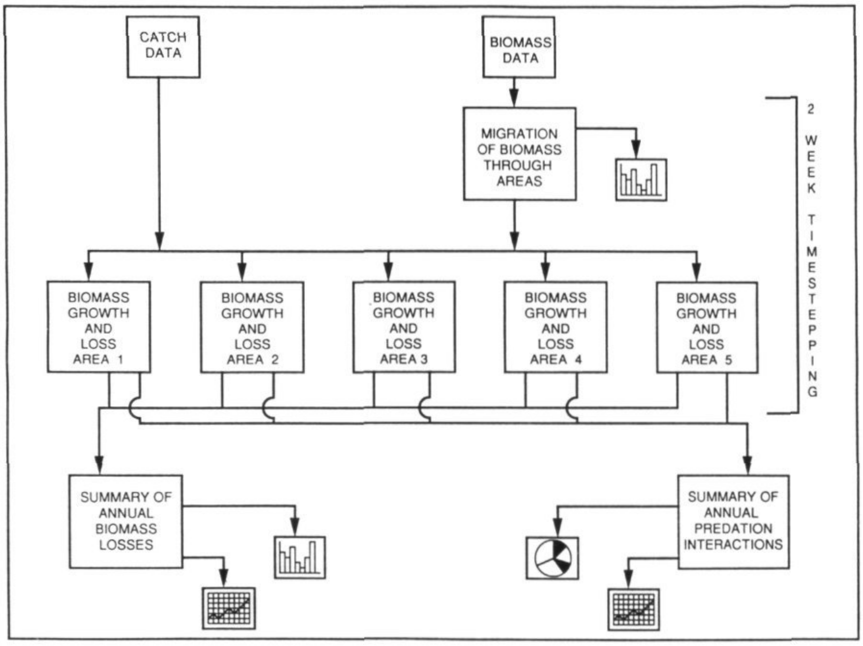

Figure 2. Schematic of the NORFISK spreadsheet showing data inputs, processing, and outputs.

ages in the population to estimate relative maximum growth in biomass per time unit.

The food requirement for growth was set at 1.7 times biomass growth. This value, together with the food requirements for maintenance, produces daily food requirements in accord with published values.

A last parameter is the non-predation natural mortality. Since all major species, including mammals, are included in the model this value represents largely disease, senescent mortalities, and emigration from the entire region. It has been set at the nominal value of 0.001 for each two-week period.

Spreadsheet overview

There are three stages in the analysis (Fig. 2). First, catch data and biomass data are prepared for each area by two-week interval. In the second stage, these catch and biomass data are added to the main spreadsheet by area, which computes food requirements, food composition, mortalities, and change in biomass over each two-week period (Table 1). Finally, the results from the five areas are combined to provide an overall picture of biomass flows, and the overall change in biomass over the year for each ecological entity.

Calculations are performed for each two-week period independently. First, the food requirements of each species in each area are calculated and the biomass removed by each predator is computed using the food composition tables. Then on the basis of the growth parameters, the catch data, and the losses due to predation, the change in biomass is obtained for each species in each two-week period. Any gains or losses to the biomass in one period are not transferred to the subsequent period. Thus biomass gains and losses for each period are computed from constant (input) biomass values, subject only to migration within the total modelled area.

Apart from these major computations, additional tables are produced to show the amount of each species consumed by each species during the summer and winter season, and over the entire year (Table 2). Summary statistics show for each species the mean biomass, the food intake, the biomass production, and the losses to mammals, birds, fish, non-predation mortality, and fishing, all over the entire year (Table 3). Finally, ratios of biomass production to intake, and the ratio of biomass loss to intake are calculated.

Results

For most species, the simulated annual percentage change in biomass is within the likely order of magnitude (Fig. 3). However, several groups stand out as having implausible losses in total biomass over the course of one year. Shrimps and "other prey" disappear and also polar cod and redfish show very large losses. On the other hand zooplankton exhibits an increase of 300%. Evidently, some important inputs for these groups are incorrect. In Figure 4 the causes of the biomass loss are shown, again for the five areas combined. In the case of shrimp and other prey, the major loss is due to fish, whereas polar cod and redfish suffer major predation by mammals. Figure 5 delineates the loss in shrimp further

Table 1. Example of input data for main spreadsheet of Area 1 (habitat not currently used).

	Herring	Capelin	Blue whiting	Polar cod
Biweekly growth	0.0162	0.0403	0.019	0.02
Biweekly M1	0.001	0.001	0.001	0.001
Annual catch	*820*	*491 538*	*0*	5227
Habitat (0 = S; 1 = B)	0	0	0	0
DFR maintenance	0.6	0.8	0.9	0.9
Ration food growth	1.7	1.7	1.7	1.7

Diet composition January to April 1985

		Species as prey			
		Herring	Capelin	Blue whiting	Polar cod
	Herring	0.0	0.0	0.0	0.0
	Capelin	0.0	0.0	0.0	0.0
P	Blue whiting	0.0	0.0	0.0	0.0
R	Polar cod	0.0	0.0	0.0	0.0
E	Redfish	0.0	0.0	0.0	0.0
D	G. halibut	0.0	0.0	0.0	0.0
A	Cod	13.4	71.7	0.0	0.0
T	Haddock	0.0	47.0	0.0	0.0
O	Saithe	0.0	0.0	0.0	0.0
R	Flatfish	0.0	0.0	0.0	0.0
S	Shrimps	0.0	0.0	0.0	0.0
	Other predators	0.0	0.0	0.0	0.0
	Other prey	0.0	0.0	0.0	0.0
	Squids	0.0	0.0	0.0	0.0
	Seals	10.0	20.0	0.0	20.0
	Whales	10.0	20.0	0.0	7.0
	Birds	0.0	0.0	0.0	0.0
	Benthos	0.0	0.0	0.0	0.0
	Zooplankton	0.0	0.0	0.0	0.0

Table 2. Example of total predation by species for the combined areas over one year.

		Species as prey			
		Herring	Capelin	Blue whiting	Polar cod
	Herring	0	0	0	0
	Capelin	0	0	0	0
P	Blue whiting	0	0	0	0
R	Polar cod	0	0	0	0
E	Redfish	0	0	0	0
D	G. halibut	0	0	0	0
A	Cod	409	1044	5	0
T	Haddock	166	118	0	0
O	Saithe	96	0	0	0
R	Flatfish	0	0	0	0
S	Shrimps	0	0	0	0
	Other predators	0	0	0	0
	Other prey	0	0	0	0
	Squids	85	0	0	0
	Seals	256	509	0	509
	Whales	1816	1374	0	481
	Birds	0	0	0	0
	Benthos	0	0	0	0
	Zooplankton	0	0	0	0
	Total loss	2827	3045	5	990

Table 3. Example of summary statistics for the combined areas over one year.

	Herring	Capelin	Blue whiting	Polar cod
Biomass	2370	2257	120	122
Intake	6974	10878	495	521
% Body weight/day	0.8	1.3	1.1	1.2
Growth	1356	3994	75	84
Losses				
Mammals	2072	1883	0	990
Birds	0	0	0	0
Fish	671	1162	5	0
Other	85	0	0	0
Fishing	59	1498	1	6
Total	2886	4543	6	996
Loss/biomass	1.2	2.0	0.0	8.1
Loss/intake	0.4	0.4	0.0	1.9
Growth/intake	0.2	0.4	0.2	0.2

as being attributable to cod, and the loss in "other prey" to cod, saithe, and other predators.

Discussion

The NORFISK model is only a crude representation of the system in the area studied. Many input data are not specific to the area, and temperature effects have not been included. However, the model does suggest the major biomass flows within the area, and, as importantly, indicates where the available data are implausible. The advantage of the model is its simplicity (or transparency), which enables initial evaluations and recommendations to be made from data which often fit the modelled biomass dynamics poorly.

It is apparent from the results that the role of both shrimp and other prey in the diet of fish in this region requires better data, or that the abundance and growth dynamics of these species are poorly understood. Observations on the biomass dynamics of Balsfjorden (Bax and Eliassen, 1990) and the German Wattenmeer (Bax and Weber, unpublished data) have indicated that survey data frequently fail to account for a sufficient abundance of shrimp to satisfy the estimated predation pressure.

The "other prey" category is always difficult to estimate, being composed of a diverse assortment of species, most of them of no commercial value. The biomass of these poorly sampled species necessary to satisfy the feeding requirements of the predator species may provide a more precise estimate than traditional survey techniques.

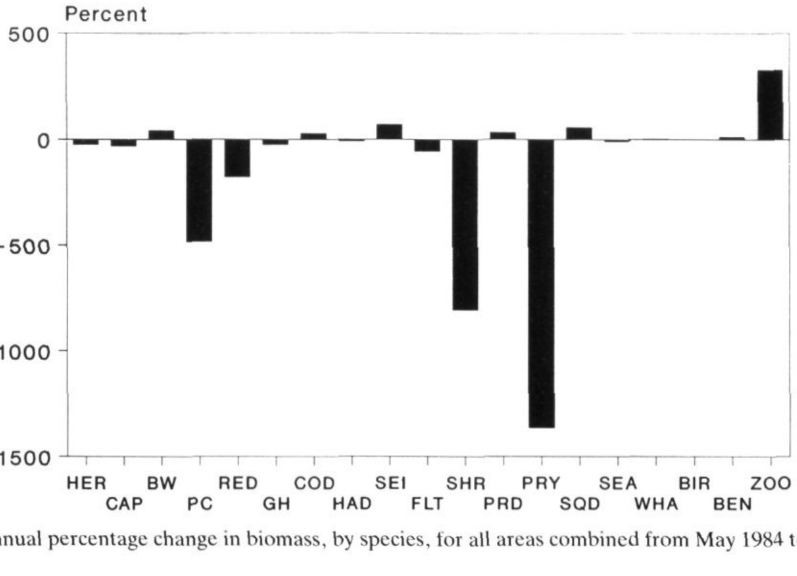

Figure 3. Annual percentage change in biomass, by species, for all areas combined from May 1984 to April 1985.

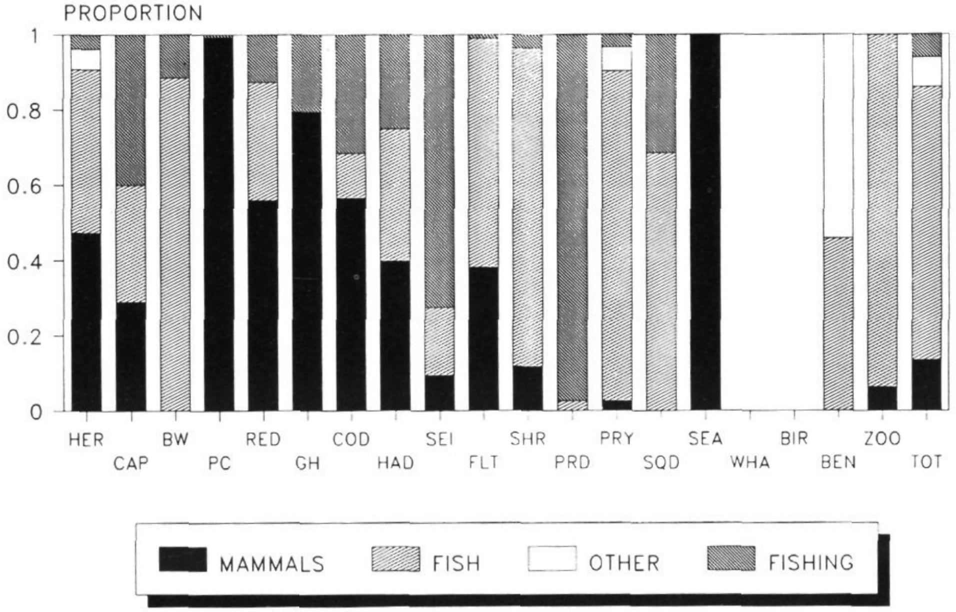

Figure 4. Proportion of the total biomass lost from May 1984 to April 1985 to mammals, fish, other species, and fishing.

The large proportion of biomass loss of polar cod and redfish going to marine mammals (Fig. 4), which of necessity occurs only in areas 1 and 2, again indicates an imbalance in the data. Either the biomasses of polar cod and redfish are underestimated, or the predation by marine mammals is overestimated. The latter could arise through incorrect estimates of the biomass of marine mammals, incorrect assessment of their migration patterns, incorrect food composition data, or through inflated estimates of their food requirements.

It is still premature to lend much credence to the results derived from this analysis; however, some general observations can be made. Disposition of biomass from the combined species is given in the final column of Figure 4. Most of the biomass in the system appears to end up as food for fish, followed by mammals, other

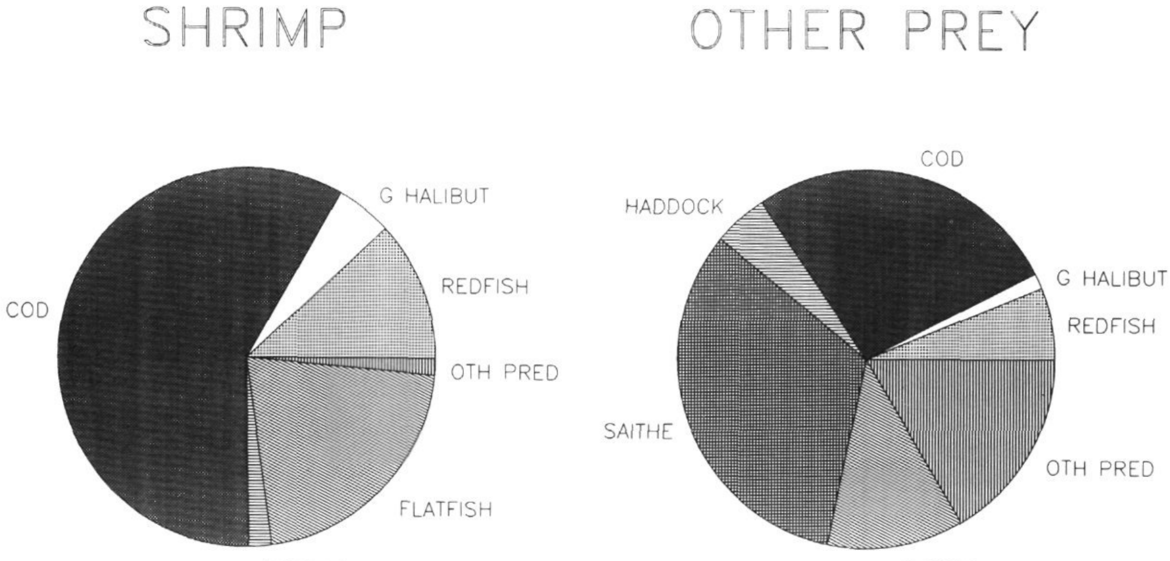

Figure 5. Disposition of shrimp and other prey biomass lost to fish predators. All time periods and areas combined (cf. Figure 4 for total fractions lost to fish predators).

species (squids, shrimp, benthos), and lastly fishing. The percentages obtained are 64, 24, 7, and 5 respectively. This result is due largely to the zooplankton, benthos, and squid groups.

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ICES mar. Sci. Symp., 193: 133–146. 1991

Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland

G. R. Lilly

Lilly, G. R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. – ICES mar. Sci. Symp., 193: 133–146.

The influence of changes in the abundance of capelin (*Mallotus villosus*) on the feeding of cod (*Gadus morhua*) was investigated on the southern Labrador Shelf and the northeast Newfoundland Shelf (NAFO Div. 2J3K) in the Northwest Atlantic. Examination of the stomachs of cod caught during bottom-trawl surveys in the autumns of 1978 and 1980–1986 revealed that capelin was the major prey in most years. The average quantity of capelin in stomachs of medium-sized cod (36–71 cm) varied with capelin abundance, which increased from very low in the late 1970s to high in the mid-1980s. Capelin distribution varied among years. The combination of variable abundance and changing distribution resulted in high among-year variability in the quantity of capelin in cod stomachs in specific regions within the study area and enhanced examination of the role of alternate prey. The most important alternate prey were hyperiid amphipods, Arctic cod (*Boreogadus saida*), shrimp (primarily *Pandalus borealis*), and crabs (primarily small *Chionoecetes opilio*). The quantities of benthic prey in cod stomachs remained relatively small in all years. The quantities of alternate pelagic prey were more variable, but appeared to vary independently of capelin. If stomach fullness is an index of feeding rate, then for the 2J3K area as a whole, and for five smaller regions, there was no evidence that cod compensated during years of low capelin abundance by feeding more intensively on other prey.

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Introduction

Capelin (*Mallotus villosus*) is an important trophic link between zooplankters and a variety of fish, birds, and mammals in northern regions of the Atlantic Ocean (Jangaard, 1974). It is one of the major prey of cod (*Gadus morhua*) toward the northern limit of cod distribution from eastern Newfoundland and Labrador (Popova, 1962; Lilly, 1987) to West Greenland (Hansen, 1949), Iceland (Palsson, 1983), and the Barents Sea (Grinkevich, 1957; Mehl, 1989). A small inshore fishery for capelin existed in Newfoundland for many years (Carscadden, 1984) and, although there were occasional complaints about the effect of such landings (Akenhead *et al.*, 1982), the small catches were seldom considered a threat to the well-being of the economically and socially vital cod fishery. However, the initiation of an offshore capelin fishery in the early 1970s (Carscadden, 1984) created concern that the production and migrations of the cod might be adversely affected (Anon., 1975; Akenhead *et al.*, 1982; Lear *et al.*, 1986). Capelin catches were relatively large until five consecutive weak year classes caused a dramatic decline in capelin abundance in the late 1970s. Since 1979, the exploitation rates have been set no higher than the conservative level of 10% of spawning biomass, partly in recognition of the importance of capelin to cod as well as to other predators (Anon., 1982).

The influence of capelin abundance on cod growth was examined by Akenhead *et al.* (1982), who found no relationship between annual growth increments in cod and biomass of capelin. Although the authors expressed serious reservations concerning the appropriateness of the data available for addressing this question, they also noted that cod might not be strongly linked to capelin and that other prey might provide adequate forage during periods of low capelin abundance.

The rate of feeding on capelin by a cod population depends on the degree to which cod overlap with capelin and aggregate in areas of high capelin density (aggregative numerical response), and on the rate of cod feeding at each point in horizontal space as a function of capelin density and availability (functional feeding response; e.g. Valiela, 1984). The rate of feeding on a particular prey will increase with prey density and may reach a limit at some prey density below maximum. Thus, as capelin density declines from maximum, we expect, at some density, a decline in capelin consumption by cod. The decrease in capelin consumption might result in a proportional decrease in total consumption by cod, or might be compensated for, at least partly, by predation on other prey. These other prey could be organisms which vary independently of capelin abundance or organisms which increased in abundance because they are either competitors or prey of capelin.

This paper will examine the functional feeding response in a coarse way and will test whether cod feed more intensively on other prey during times of low capelin abundance.

Materials and methods

Cod were caught during random depth-stratified bottom-trawl surveys during the autumns of 1978–1986 on the continental shelf and upper slope (<1000 m) off southern Labrador and northeastern Newfoundland (Fig. 1). The locations and sizes of the 58 strata surveyed in recent years are provided by Doubleday (1981). The continental shelf in this area is broad and deep; 80% of the 189 508 km^2 surveyed in recent years is deeper than 200 m, and 24% is within 301–400 m. Temperatures are low. For example, the average bottom temperature at trawling sites was 1.31°C (s.d. = 1.59; n = 306) in 1985, a cold year, and 2.35°C (s.d. = 1.01; n = 210) in 1986, a warm year. The cold intermediate layer of the Labrador Current is deepest and coldest toward the coast, and temperatures below 0°C are found to depths of about 200 m in many years (Petrie *et al.*, 1988). Maximum bottom temperatures in the survey area are usually about 4°C and occur on the upper slope.

The survey pattern changed several times. In 1978, a single trip surveyed depths from 100 to 400 m in Division 2J and 200 to 400 m in Division 3K. In both 1979 and 1980, the area was surveyed twice, the first trip fishing depths 200–1500 m and the second fishing 100–400 m in Division 2J and 200–400 m in Division 3K. The first trip in each of these years was earlier than trips in other years and is not included in the present study. The fishing pattern became more standardized in 1981, with two or three consecutive non-overlapping trips fishing depths of 100–1000 m in Division 2J and 200–1000 m in Division 3K. Depths between 100 and 200 m in northwestern Division 3K (St. Anthony Shelf and Grey Islands Shelf) were added in 1984 and subsequent years, but this depth range has not been surveyed in southern Division 3K (Baie Verte Shelf and Fogo Shelf). In all years, fishing was conducted on a 24-h basis.

Stomachs were collected from cod caught in all trips except the second one in 1979. The present analysis, therefore, lacks samples from 1979. In 1978, a stratified-random sample of up to 5 cod per 10-cm length group was taken from the catch of every set. The sample size was reduced to 3 per 10-cm length group for 1979–1982, and changed to 3 per 9-cm length group in 1983–1986. Stomachs from 25 fishing sets in northern Division 3K in 1981 were lost. The sampling protocol ensured that sampling was well distributed with respect to cod size and geographic distribution.

Cod stomachs were individually tagged, and fixed and preserved in 4% formaldehyde solution in sea water prior to examination in the laboratory. Examination involved separation of food items into taxonomic categories. Fish and decapod crustaceans were identified to species, but many other groups were combined into higher order taxa. Items in each taxon were placed briefly on absorbent paper to remove excess liquid, and then counted and weighed to the nearest 0.1 g. The relative importance of individual prey taxa was assessed with indices of occurrence, number and weight (Clark, 1985), and a stomach fullness index. The mean partial fullness index of prey i was calculated as:

$$\mathrm{PFI_i} = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{ij}}{L_j^3}\times 10^4$$

where W_{ij} is the weight of prey i in fish j, Lj is the length of fish j, and n is the number of fish in the sample. Mean total fullness index was calculated as:

$$\mathrm{TFI} = \sum_{i=1}^{m}\mathrm{PFI_i}$$

where m is the number of prey categories.

Each index has its advantages and limitations, depending on the question addressed (Hyslop, 1980). I shall use the partial fullness index to examine variability related to cod size, trawling site, and year of sampling, because it emphasizes the weight of specific prey in relation to predator size.

Results

Prey spectrum

The prey spectrum in 1986 (Table 1) may be taken as representative of other years as well. Fish were dominant by weight (80%) and crustaceans were dominant by number (91%). The most important fish was capelin, but Arctic cod (*Boreogadus saida*) and flatfish (Pleuronectidae, especially *Reinhardtius hippoglossoides*) contributed more than 1% by weight. Cannibalism was noted very infrequently. Some of the prey identified as Gadidae may have been cod, but most unidentified gadids

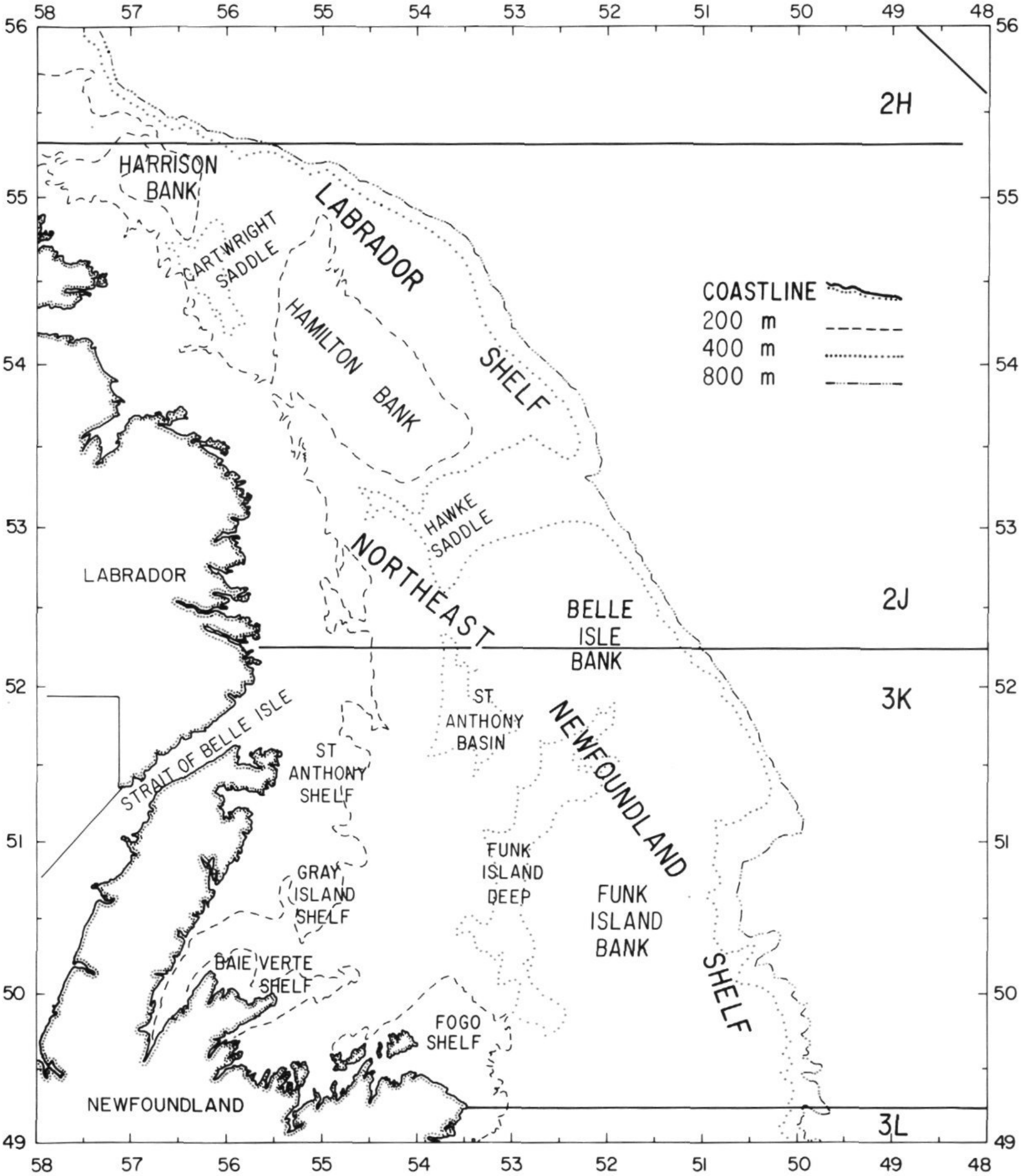

Figure 1. Map of study area showing major physiographic features and NAFO Divisions.

were of the same size as the Arctic cod found in the stomachs and caught by the trawl. Since very few cod of similar size were taken by the trawl, I assume that most prey identified as Gadidae were Arctic cod. Unidentified fish was a large portion (by weight) of the stomach contents. The major crustacea in terms of weight were hyperiid amphipods, shrimp (mainly *Pandalus borealis*), and crabs (mainly *Chionoecetes opilio*). Several invertebrate groups, such as polychaetes, gammarid amphipods, mysids, and euphausiids, occurred frequently but were not important in terms of weight.

The relative importance of the various prey in 1986 varied with cod length, although changes tended to be gradual (Fig. 2). Capelin were important for all but the

Table 1. Percentages of occurrence (O), numbers (N), and weights (W) and mean partial fullness indices (PFI) in different (groups of) species in the stomach contents of cod from the southern Labrador Shelf and northeast Newfoundland Shelf (NAFO Div. 2J, 3K) in the autumn of 1986.

	O (%)	N (%)[a]	W (%)[a]	PFI[a]
Invertebrata (misc.)	8.2	0.3	0.3	0.01
Anthozoa	0.5	+	0.1	+
Ctenophora	0.3	+	+	+
Gastropoda	1.5	0.1	0.1	+
Cephalopoda	4.3	0.1	0.5	0.01
Polychaeta	17.4	0.7	0.3	0.01
Ophiuroidea	0.7	+	+	+
Crustacea (total)	90.7	90.6	16.7	0.47
Hyperiidae	52.7	71.1	3.8	0.13
Gammaridea	34.1	6.9	0.4	0.02
Mysidacea	20.9	3.5	0.1	0.01
Euphausiacea	8.0	1.4	0.1	0.01
Natantia				
Pandalus borealis	19.7	1.3	2.4	0.07
Pandalus montagui	7.3	0.4	0.8	0.03
Others and unid.[b]	40.3	4.5	3.9	0.13
Reptantia				
Chionoecetes opilio	8.7	0.5	3.8	0.05
Hyas coarctatus	2.3	0.1	0.4	0.01
Others and unid.	7.6	0.3	0.6	0.01
Others and unid.	12.4	0.5	0.3	0.01
Pisces (total)	55.9	8.2	80.0	1.73
Mallotus villosus	18.7	3.4	40.2	0.87
Gadidae (unid.)	1.2	0.1	1.5	0.02
Boreogadus saida	2.5	0.2	2.6	0.08
Gadus morhua	0.1	+	0.9	0.01
Zoarcidae	0.2	+	0.6	0.01
Sebastes sp.	0.1	+	0.1	+
Pleuronectidae	2.6	0.1	1.3	0.03
Others	5.1	0.2	3.9	0.06
Unidentified	45.3	4.2	28.7	0.65
Unidentified and misc.	31.5		2.3	0.06
Total				2.30
No. of stomachs		2125		
Percent empty		1.3		
Length: mean		50.9		
minimum		16		
maximum		93		

[a] + indicates percentage < 0.05 or mean PFI < 0.005.

[b] Other shrimp occurring in more than 1% of the stomachs were: *Eualus macilentus*, *E. gaimardii*, *Spirontocaris spinus*, *Lebbeus polaris*, and *Sabinea septemcarinata*.

small cod. Groundfish and crabs were found primarily in large cod (>71 cm). Hyperiids and shrimp were found in a wide size range of cod, with a tendency to be less important in large cod. Not shown here is the tendency for the median prey size within a taxonomic category to increase with predator size (Lilly, 1984, 1987).

The cod which are likely to be most affected by changes in capelin abundance are those within the length range for which this species is the most important prey. Cod start to prey intensively on capelin when they reach about 30–35 cm, and cod larger than about 70 cm tend to feed to an increasing extent on groundfish and crabs (Fig. 2; Lilly and Fleming, 1981). Subsequent analysis of spatial and annual variability is restricted to cod within the 36–71 cm length-range.

Capelin distribution

In 1985, capelin were found in stomachs of cod from almost all fishing sets on Hamilton Bank and the coastal

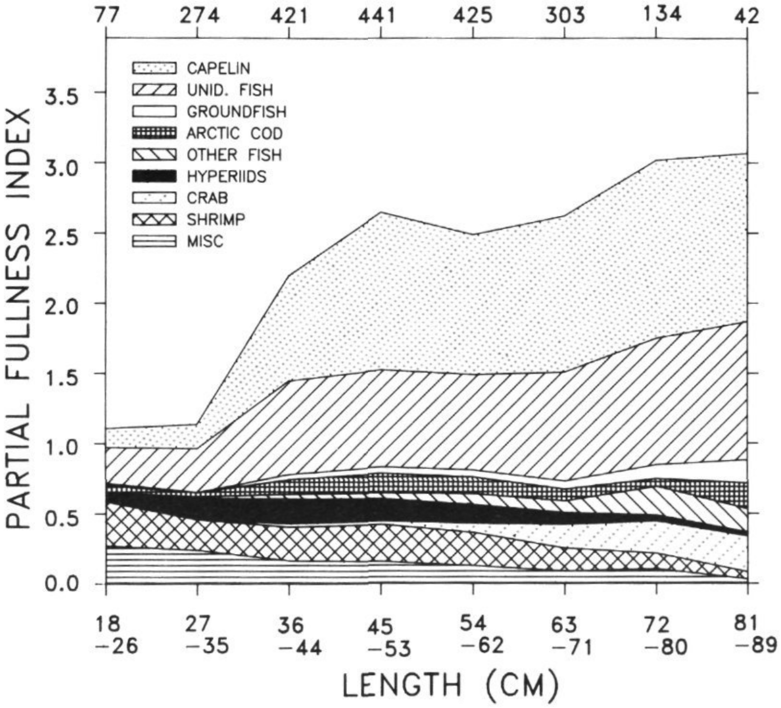

Figure 2. Stomach contents (expressed as partial fullness indices) in relation to predator length (9-cm length groups) for cod from Division 2J3K in 1986. Arctic cod includes *Gadidae*. Groundfish are cod, grenadiers (*Macrouridae*), wolffish (*Anarhichadidae*), eelpouts (*Zoarcidae*), redfish (*Sebastes* spp.), and flatfish (*Pleuronectidae*). Sample sizes are given at the top.

shelf off southern Labrador (Fig. 3). Capelin were also found in stomachs in Division 3K, particularly toward the west. In contrast, in 1986 there was almost a complete absence of capelin in cod from Hamilton Bank and the coastal shelf off southern Labrador, but very frequent occurrence, often in large quantities, on Belle Isle Bank and central and western Division 3K (Fig. 4). The concentration of capelin in the central and southwestern part of the survey area, with almost complete absence from Hamilton Bank, was not seen in any other year in the series.

Annual variability

For cod in the length-range 36–71 cm, the total fullness index varied from 0.94 in 1978 to 2.58 in 1985 (Fig. 5). Most of the variability was due to capelin, which rose from a very low level in 1978 to a peak in 1981, declined in 1982 and 1983, and then increased again to a high level in 1985 and 1986. A large proportion of the fish was unidentified, and much of this was probably capelin. Arctic cod (including Gadidae) was more important than capelin in 1980, and reached another peak in 1985 when capelin was dominant. Other fish prey combined were relatively unimportant and did not vary greatly. All shrimp combined and all crabs combined remained fairly constant throughout the period. The only taxon other than capelin to vary considerably was hyperiid amphipods, which declined from 0.32 in 1978 to 0.05 in 1982, increased each succeeding year to 0.38 in 1985, and declined to 0.14 in 1986.

Functional feeding response

Although capelin were caught in the bottom-trawl surveys, the catches were usually small. They give some indication of distribution and perhaps relative abundance (Carscadden *et al.*, 1989), but cannot be used to provide estimates of capelin density at each trawling site. Therefore, they cannot be used in examination of the functional feeding response of cod.

To obtain some indication of the functional response, I shall use the mean partial fullness index of capelin in each year as an index of the rate of feeding by cod on capelin, and shall compare these values with estimates of abundance of the whole 2 + 3K capelin stock. To reduce the influence of between-year variability in cod distribution, the fullness indices are not weighed by catch.

Partial fullness indices of capelin (PFI_c) from stomachs of cod (36–71 cm only) in the survey area as a whole varied from <0.001 to 1.024 (Table 2). Much of the fish in the stomachs was unidentified, and a portion of this would have been highly digested capelin. A second estimate of PFI for capelin (PFI'_c) was obtained by assuming that the ratio of capelin to other fish was the same in the unidentified fish as it is in the identified fish.

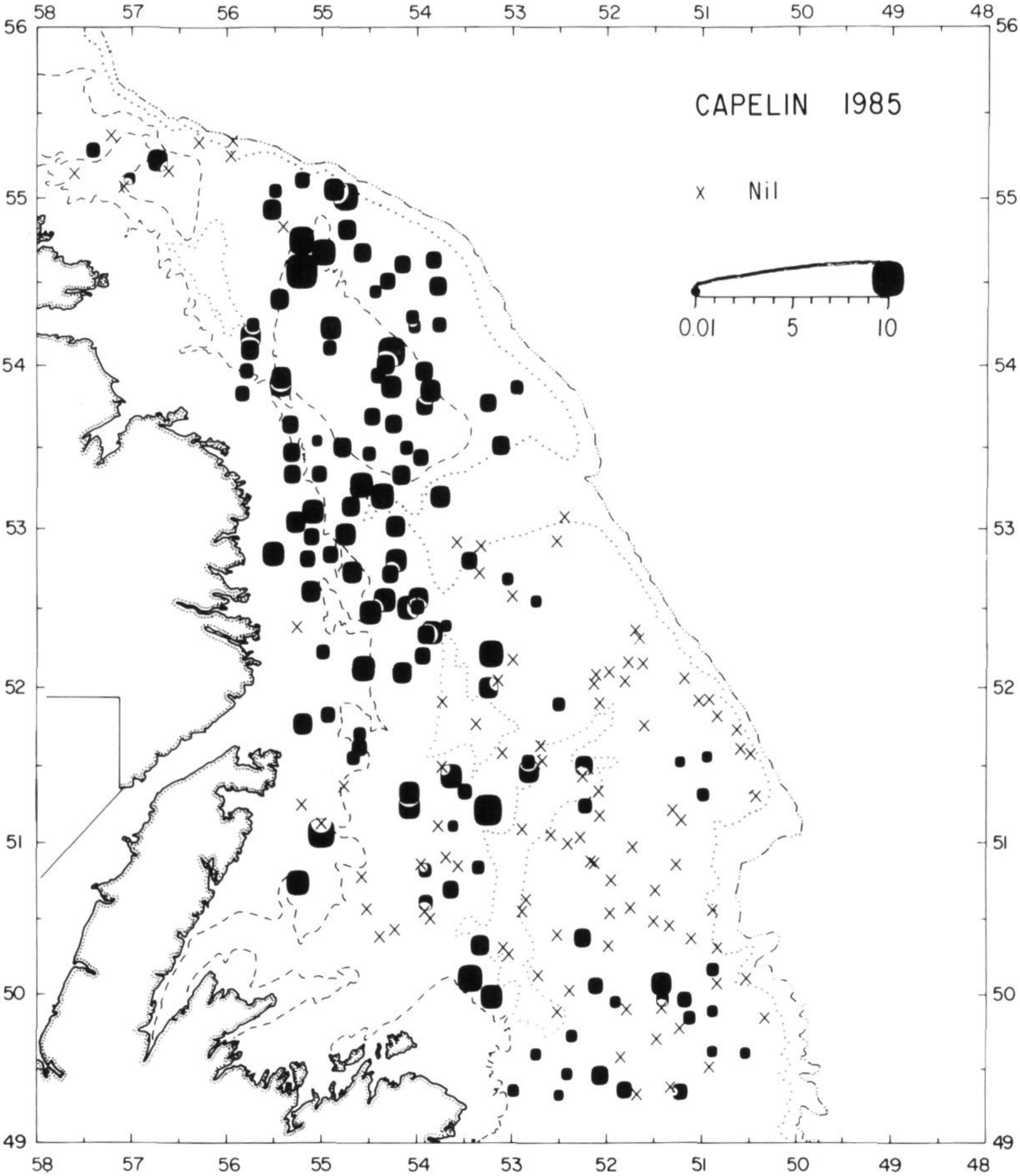

Figure 3. Mean partial fullness index of capelin in stomachs of cod (36–71 cm only) by set in 1985.

This procedure reverses the rank order of 1985 and 1986, which are the years of highest PFI (Table 2).

Estimates of abundance for the 2 + 3K capelin stock have been derived from a variety of sources, including catch per unit effort in the offshore commercial fishery, a sequential population abundance model, Soviet hydroacoustic surveys and Canadian hydroacoustic surveys. There are various problems with each series (see Carscadden, 1984 and Lear *et al.*, 1986, for reviews). However, the four series are in agreement on broad trends: high biomass in the mid-1970s, low biomass in the late 1970s and early 1980s, and an increase in biomass in the mid-1980s (Carscadden *et al.*, 1988). The mean partial fullness indices (Table 2) are in agreement with this broad trend.

There is less agreement, however, when fullness indi-

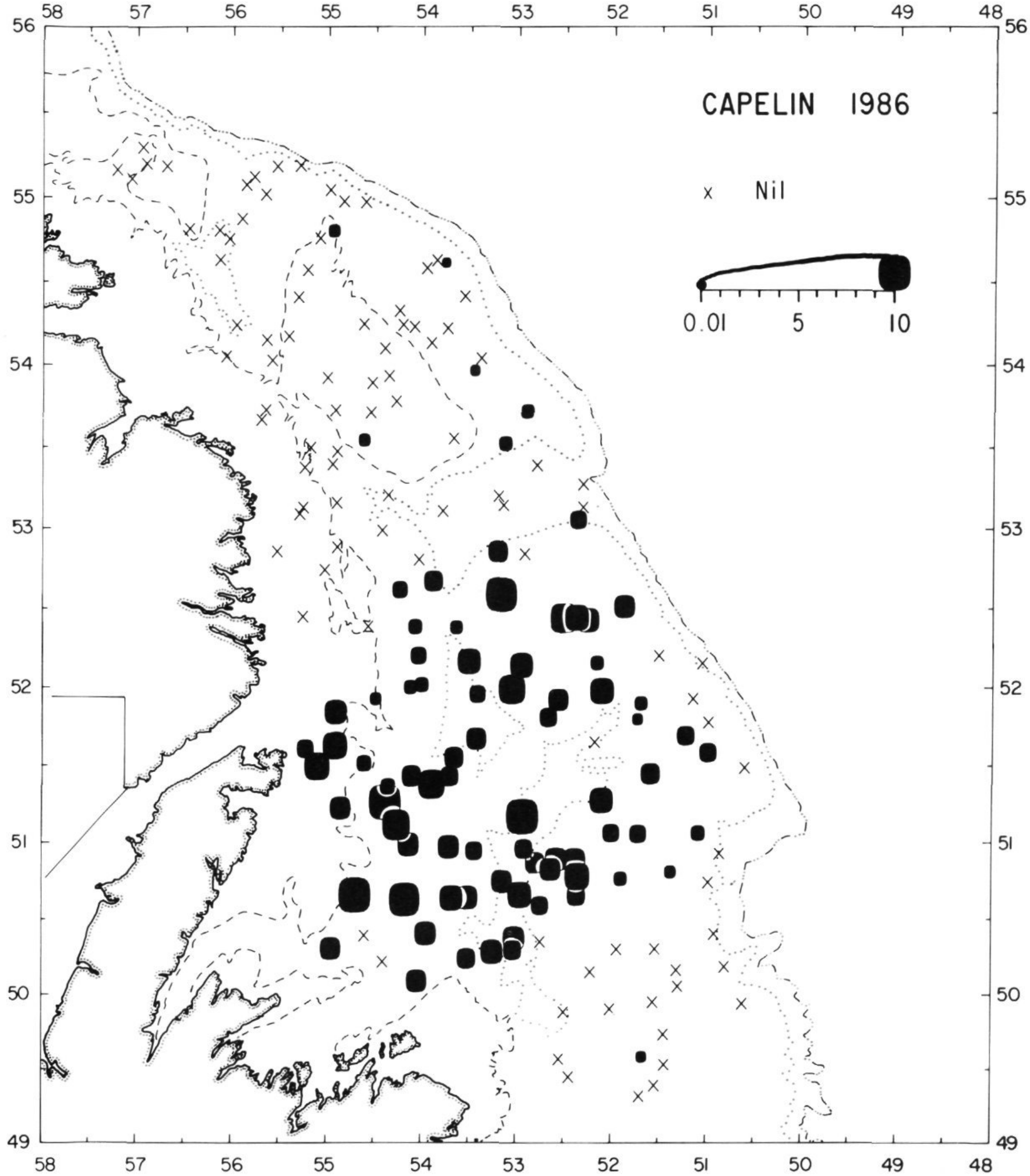

Figure 4. Mean partial fullness index of capelin in stomachs of cod (36–71 cm only) by set in 1986. Fullness indices greater than 10 were set to 10.

ces are compared with the acoustic estimates on a yearly basis. The USSR did not conduct a survey in 1981, and the Canadian series started in 1981 and excluded 1982 (Table 2). The two series are not correlated ($r = -0.004$; $p = 0.995$; $n = 5$). Reasons for differences between the two series are not clear, but could include differences in equipment, survey design, geographic coverage, and timing. The fullness indices (PFI'_c) are correlated with the USSR estimates ($r = 0.93$; $p < 0.01$; $n = 7$), but not with the Canadian estimates ($r = 0.22$;

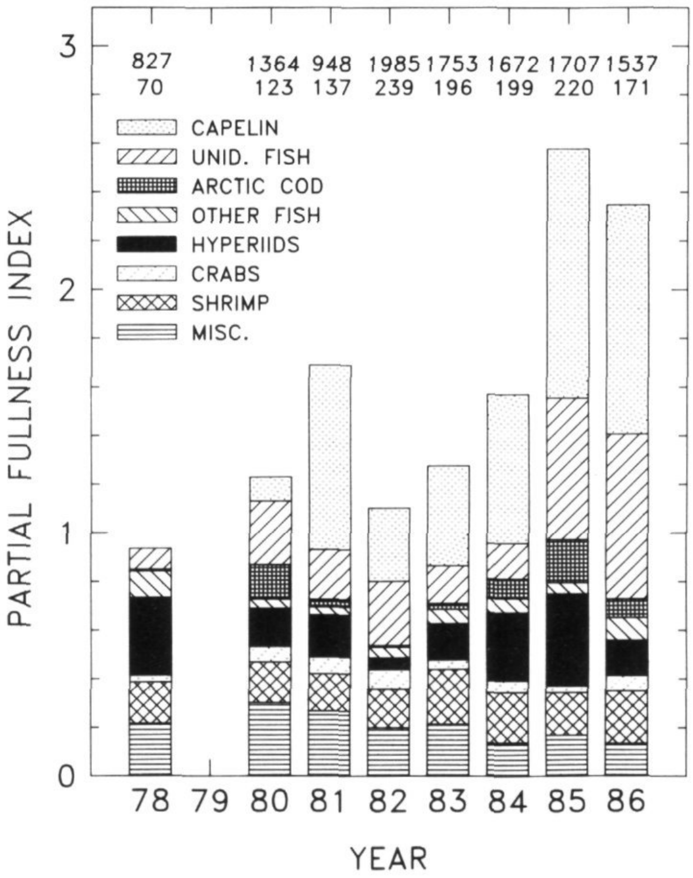

Figure 5. Annual variation in mean partial fullness indices of cod (36–71 cm only) from NAFO Division 2J3K in autumn. Arctic cod includes *Gadidae*. Stomachs collected in Division 3K from less than 200 m are not included. The number of stomachs examined each year, and the number of sets from which at least one stomach was collected, are given at the top (upper and lower rows respectively).

$p = 0.72$; $n = 5$) (Fig. 6). Comparison with the Canadian series suffers from the lack of acoustic estimates during the years of very low capelin abundance (1978–1980).

Role of alternate prey

In years when predation on capelin was low, cod did not compensate by feeding more intensively on other prey. A negative correlation was not found between the partial fullness index for capelin (PFI'_c) and the PFI for all other prey combined, nor was a negative correlation found between PFI'_c and PFI for four selected taxonomic groupings: Arctic cod (including *Gadidae*), hyperiid amphipods, shrimp, and crabs (Table 3).

To investigate the role of alternate prey in more detail, I defined five regions within the study area (Fig. 7). These regions are large enough to be represented by large sample sizes in most years, but small enough to be influenced strongly by annual variability in capelin distribution (Figs. 3, 4). The between-year variability in total fullness index and PFI'_c is much higher within regions (Fig. 8) than in the study area as a whole (Fig. 5). In none of these regions was the partial fullness index of capelin (PFI'_c) negatively correlated with the partial fullness index of combined alternate prey, and in only one case (crabs in region 3) was a significant negative correlation found between PFI'_c and PFI of the four selected taxonomic categories (Table 3).

Discussion

Capelin was the major component of the stomach contents of cod from the southern Labrador Shelf and the northeast Newfoundland Shelf during autumn in most years from 1978 to 1986. The quantity of capelin in the stomachs varied among years and mirrored the broad changes in capelin abundance from low in the late 1970s and early 1980s to relatively high by the mid-1980s. However, the relationship between stomach fullness and capelin abundance is not well described, and a continuation of monitoring is required. In particular, information at even higher levels of capelin abundance,

Table 2. Partial fullness indices for capelin in stomachs of cod (36–71 cm), and abundance estimates for capelin, for Divisions 2J, 3K in the autumns of 1978–1987.

	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Cod stomach fullness										
PFI$_c$	*<0.001*		*0.099*	*0.757*	*0.300*	*0.410*	*0.612*	*1.024*	*0.942*	
PFI$'_c$[a]	<0.001		0.192	0.946	0.526	0.540	0.731	1.501	1.516	
Acoustic abundance estimates ($\times 10^{-3}$ t)										
USSR[b]	59	14	20	–	611	852	263[c]	1514	1535	1164
Canada[d]	–	–	–	1494	–	94	826	1035	431	134

[a] $PFI'_c = PFI_c + ((PFI_c/(PFI_c + PFI_{of})) \times PFI_{uf})$, where of refers to other fish and uf refers to unidentified fish.

[b] Bakanev (1983), Mamylov and Bakanev (1984), Bakanev and Mamylov (1988).

[c] Considered an underestimate relative to the rest of the series (Bakanev and Gorchinsky, 1985).

[d] Carscadden *et al.* (1988).

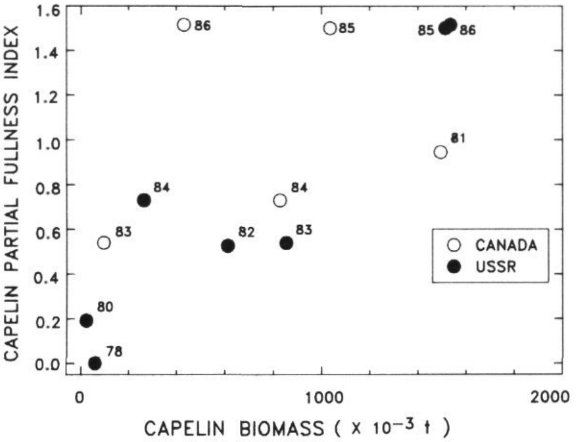

Figure 6. Relationship between the partial fullness index for capelin (PFI$'_c$) in stomachs of cod (36–71 cm only) and estimates of capelin abundance from Canadian and Soviet acoustic surveys.

if such are possible, would be interesting because as yet there is no evidence of a plateau in the relationship. Additional data are also required at very low levels of capelin abundance, because sample sizes were relatively small in the early part of the series when capelin abundance was low. A major problem in trying to describe a functional feeding response is obtaining reliable measures of capelin abundance, because there are recognized problems with all methods presently used.

I have assumed that the average stomach fullness in a fish population is an index of the feeding rate of that population. This is in line with the conclusions from many laboratory studies, which indicate that the rate of stomach evacuation (g h^{-1}) decreases as the quantity of food in the stomach decreases (e.g. reviews by Jobling, 1986; Persson, 1986). However, Bromley (1987, 1988) argued that the apparent curvature in evacuation rate in experimental studies is an artifact of inappropriate treatment of data. He concluded that evacuation rate (g h^{-1}) is constant and independent of the level of stomach fullness. Under such circumstances, the rate of feeding by a population would be proportional to the percentage of fish with food in their stomachs.

This uncertainty regarding the influence of stomach fullness on the rate of stomach evacuation is critical to the interpretation of the role of alternative prey. If the rate of feeding by the cod population is proportional to average stomach fullness, then the cod did not compensate during periods of low capelin abundance by feeding more intensively on alternative prey. If, however, there is no relationship between feeding rate and stomach fullness, then the low percentage of empty stomachs in all years (5% in 1983; <3% in all other years) indicates that feeding rate did not vary between years, and compensation did occur. It is possible that the percentage of empty stomachs would have been higher and more variable if stomachs containing only relatively indigestible remains were also classed as empty, as proposed by Bromley (1988), but this has not yet been investigated.

Table 3. Correlations between partial fullness indices for capelin (PFI$'_c$) and partial fullness indices for other prey groupings (*$p < 0.05$ in one-tailed test).

	All alternative prey combined	Arctic cod + Gadidae	Hyperiid amphipods	Shrimp	Crabs
Total area	0.08	0.30	0.15	0.28	−0.01
Region 1	0.51	0.25	0.35	−0.28	0.23
Region 2	0.10	0.09	0.90	0.02	−0.80*
Region 3	−0.02	−0.03	0.65	0.19	−0.23
Region 4	−0.33	−0.11	−0.21	0.13	0.06
Region 5	−0.39	−0.35	−0.56	0.31	0.76

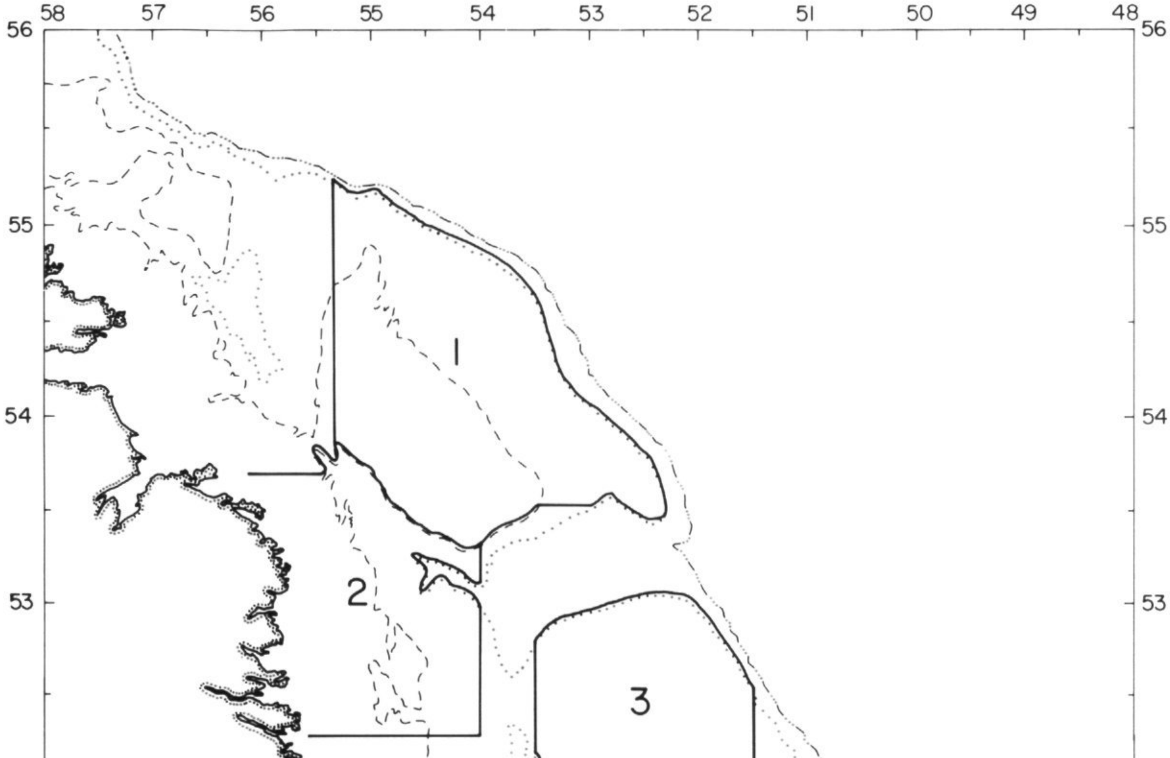

Figure 7. Five regions selected for investigation of between-year variability in feeding by cod on capelin and other prey.

Another factor which may affect the degree of compensation is prey type. Soft-bodied prey such as polychaetes are digested and evacuated more quickly than hard-bodied prey (Macdonald *et al.*, 1982). Therefore, even if evacuation rate is independent of stomach fullness, feeding rate may have been slower in years when the diet was primarily crustacean (e.g. 1978) than in years when a high proportion of the diet was fish (e.g. 1985, 1986). That is, the cod may have eaten more shrimp and crabs in years of low capelin abundance, but slower digestion rates may have resulted in less than complete compensation.

The influence of stomach fullness and prey type on stomach evacuation must be thoroughly understood

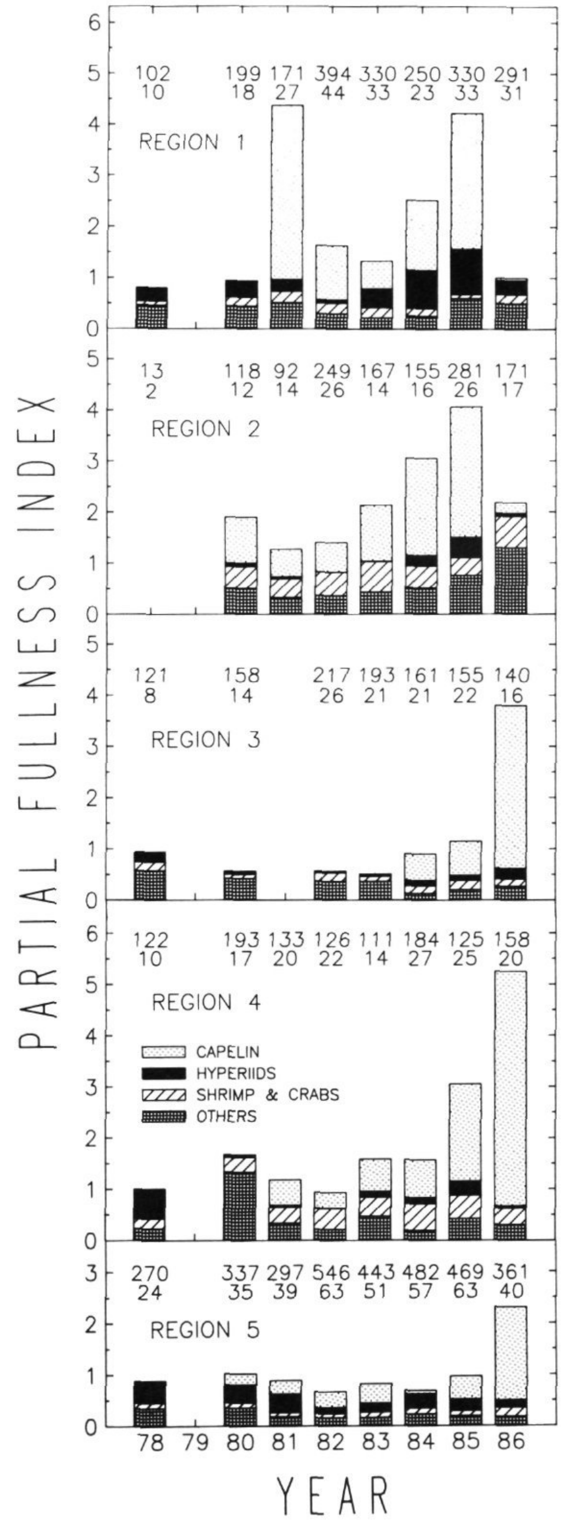

Figure 8. Annual variation in partial fullness indices of cod (36–71 cm only) from five regions within NAFO Division 2J3K.

before we can use stomach contents to investigate questions of functional feeding response and the role of alternative prey.

The observations in this study are relevant to how one treats "other food" in multispecies virtual population analysis. As reviewed by Ursin (1982) and Daan (1987), the options suggested are to assume that other prey is a constant fraction of total consumption, that the biomass of other prey is constant, or that biomass of total available prey is constant. As discussed above, the quantity of food other than capelin in the stomachs of cod on the southern Labrador Shelf and northeast Newfoundland Shelf did not vary greatly among years. Factors affecting digestion and gastric evacuation must be better understood before it can be determined whether the consumption of these prey varied among years.

However, one can use the fullness indices to investigate changes in the biomass of other prey, if one assumes that the extent to which a cod fills its stomach with a specific prey depends on the availability of that prey. I have not tested this assumption directly, but it is clear that stomach fullness indices vary greatly in space and time. Total fullness indices greater than 20 have been recorded in individual cod from Newfoundland waters, and sample means between 10 and 15 have been found for cod caught in inshore waters where capelin are concentrated prior to spawning (Lilly and Botta, 1984; Lilly and Osborne, 1984). In the present study, partial fullness indices of all other prey combined (Table 4) were small compared to the cod's stomach capacity, even in years of low capelin abundance (Fig. 5). I tentatively conclude that alternative prey did not become more available when capelin abundance declined.

This conclusion is not in agreement with the scenario postulated by Vesin *et al.* (1981). They stated that the large reduction in capelin biomass in the late 1970s should have released large quantities of zooplankton to other predators, and could have improved the growth and/or recruitment of these species.

The only zooplankton taxon whose abundance can be tracked with cod stomachs is the family Hyperiidae. The partial fullness index for hyperiids was indeed high in 1978 when capelin abundance was low, and declined in the early 1980s as capelin biomass started to recover. However, the hyperiids reached another peak in 1985 when capelin was very abundant (Fig. 5). There is thus no clear evidence of a reciprocal relationship between capelin abundance and hyperiid abundance.

The major planktivorous fish species which might benefit from a capelin decline is Arctic cod which, like the capelin, feeds largely on calanoid copepods and hyperiids in this area (Chan and Carscadden, 1976; Lilly, 1980). As Vesin *et al.* (1981) pointed out, Arctic cod were prominent in this area in the late 1970s and early 1980s. They were relatively important in the pelagic biomass according to acoustic surveys conducted by Canada in 1978–1980 (Miller, 1979; Carscadden and

Table 4. Partial fullness indices of all prey other than capelin. N = number of years.

Region	Mean	s.d.	Min	Max	N
Total 2J3K	0.85	0.17	0.58	1.08	8
Region 1	0.96	0.30	0.57	1.57	8
Region 2	1.18	0.43	0.73	1.97	7
Region 3	0.58	0.17	0.39	0.94	7
Region 4	0.95	0.34	0.62	1.67	8
Region 5	0.59	0.18	0.36	0.88	8

Miller, 1980; Miller and Carscadden, 1981) and by the USSR in 1978 and 1980 (Seliverstov and Serebrov, 1979; Bakanev, 1981). Additional evidence for a high relative abundance of Arctic cod was the high by-catch of this species in the Romanian capelin fishery in 1979 (Maxim, 1980). However, a high relative abundance of Arctic cod could have resulted from the severe reduction in capelin abundance, with no absolute increase in Arctic cod abundance. This latter possibility is supported by catches of Arctic cod during bottom-trawl surveys (Lear and Baird, 1985), although it is recognized that a bottom-trawl may not be a good sampling tool for a semi-pelagic species. The estimates of Arctic cod biomass from these surveys fluctuated from year to year, with no indication that biomass was higher in 1978–1980 than in 1981–1983. The partial fullness index of Arctic cod in cod stomachs declined to a very low level by 1982–1983, but peaked in 1985 when capelin also peaked. As with hyperiids, there is no clear evidence of a reciprocal relationship between Arctic cod abundance and capelin abundance.

These conclusions regarding the response of alternative prey should be considered preliminary. The time series is still short. There has been only one period of low capelin abundance, and sampling during that period was less intensive than in more recent years. A longer time series would also aid the search for time lags in the interactions. In addition, although using a predator as a sampling tool is an effective and relatively inexpensive way to obtain information on prey species, direct estimates of the abundance of Arctic cod, hyperiids, and other prey would add confidence to the conclusions.

The response of zooplankters and planktivores to declines in capelin abundance is important, because capelin is a major component of the diet of many fish, birds, and mammals; and there appears to be no planktivore which might replace capelin over much of its range. Capelin is often considered a boreo-arctic species, with its centre of distribution between Arctic cod, an arctic species, and Atlantic herring (*Clupea harengus*), a boreal species (Nikolsky and Radakov, 1968; Prokhorov, 1968). Capelin is the dominant planktivore on the southern Labrador Shelf and northeast Newfoundland Shelf. Large schools of Arctic cod have been detected far to the north on the northern Labrador Shelf (Lear, 1979), but in Division 2J3K the schools tend to be much smaller. They are found primarily on Hamilton Bank and the coastal shelves (Lear, 1979), where the cold core of the Labrador Current is most intense and often impinges on the bottom. Sand lance (*Ammodytes dubius*) is abundant to the south on Grand Bank (Winters, 1983), where it is an important prey of cod (Lilly and Rice, 1983; Lilly and Meron, 1986), but the two species of sand lance found in Division 2J3K are restricted to inshore waters (Pinhorn, 1976; Winters and Dalley, 1988). Herring also are found only in coastal waters (Templeman, 1966). No sand lance or herring were caught during the surveys reported here and none were identified in cod stomachs, even in the early years (1978–1980) when capelin abundance was low. These observations support the hypothesis that the relative distributions and abundances of planktivorous fish off Labrador and northeastern Newfoundland are not strongly influenced by competitive interactions, and lend support to the concern that a sustained large reduction in capelin biomass might cause a decrease in productivity of predator stocks.

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Predation-controlled recruitment in the Bering Sea fish ecosystem

T. Laevastu and N. Bax

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Factors controlling recruitment to the exploitable stock, quantitative knowledge of them, and their relative magnitudes, are briefly reviewed. This review indicates that predation on eggs, larvae, and pre-fishery juveniles may be a major recruitment-controlling process in mid-latitude fish ecosystems. Predation in the Bering Sea fish ecosystem is evaluated numerically. This evaluation shows that predation on larvae and juveniles is the principal cause of fish mortality in the eastern Bering Sea. If this predation is prey-density dependent within the ecosystem, it can act to stabilize recruitment from year to year. Cod recruitment from 1978 to 1987 in the Bering Sea is given as an example. Changes in fishing patterns are suggested to affect the observed age composition of catches and thus apparent recruitment. The numerical methods of computation of recruitment and predation in biomass-based fish ecosystem simulations are briefly described, their interactions explained, and the advantages and shortcomings of recruitment forecasts explored.

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Processes controlling recruitment

Recruitment to the exploitable part of a stock is defined as the numbers of young fish surviving to recruit to the fishery. In this paper we review the processes which may affect the survival of young fish. Some of the processes and factors affecting recruitment are listed in Table 1. Each factor affects recruitment to various degrees depending on species, region, and year. Quantitative evaluation of these effects is difficult, especially determination of the effect of the environment on early life history stages (Laevastu *et al.*, 1988), which has frequently been considered the main cause of recruitment variation. Several environmental effects on recruitment could be mediated via predation, such as the effect of temperature on growth and food requirements. Some of the environmental effects influencing advection and migration also relate to predation because of their impact on the joint distribution of predator and prey.

Some causes of mortalities in fish and their relative magnitudes are presented in Table 2. Quantitative knowledge on mortalities is quite incomplete. However, recent stomach analyses and ecosystem simulations suggest that predation might be one of the main processes controlling juvenile abundance and thus recruitment (e.g. Sissenwine *et al.*, 1984; Gislason and Helgason, 1985).

The effects and importance of predation on fish mortalities and on fish ecosystem dynamics in general can be evaluated with numerical ecosystem simulation. Among the essential basic input data to these simulations are food composition data (from stomach content analyses),

Table 1. Determinants of recruitment (a general summary).

Process/condition	State of knowledge
Spawning	
Size of spawning stock	Great variability in S/R relation
Egg survival and hatching Turbulence (e.g. by storms) Temperature anomalies	Effects known, little quantified, but usually small.
Larvae (survival)	
Starvation	Might occur, but not a major factor.
Predation	Evidence indicates that it might be major factor in larval mortality.
Transport	Little quantified, variable in space and time.
Prefishery juveniles	
Predation	Recent analyses and multispecies research show predation to be main process controlling juvenile abundance.
Other mortalities	Less quantified than predation (see Table 2).
Emigration/immigration	Magnitude and variability little known.

Table 2. Mortalities in fish stocks (Laevastu and Favorite, 1988, modified).

Mortalities	Relative magnitude
Natural mortalities	
Predation	In most cases the largest component of natural mortality
Senescent or spawning stress	May be largest component of mortality in older age classes
Diseases	Little known, assumed small
Starvation	Increases susceptibility to predation
Morphologically malformed larvae	Probably minor, although see Kaufman (1966), Blaxter (1968), Vladimirov (1975)
Environmental extremes	
Cold	Occurs seldom
Oxygen (lack of)	Rare local occurrence
Pollution	Small, local (e.g. estuaries)
Fishing (mortality)	None to very large, depends on intensity of fishing

Table 3. Standing stocks and annual consumption in the eastern Bering Sea and Aleutian Region.

	Annual mean			
	Standing stock		Consumption	
Ecological group	t (mill.)	%	t (mill.)	%
Fish[1]	33.2	32.8	21.4	21.8
Zooplankton	53.3	52.6	62.4	63.5
Epifauna	8.5	8.4	8.0	8.2
Infauna	6.3	6.2	6.0	6.5

[1] Including squids, 0.53 million tonnes and crab, 1.35 million tonnes.

food requirements, growth rates, and the total species composition of the ecosystem (which is one of the determinants of the availability and relative density of food items). The PROBUB ecosystem simulation for the eastern Bering Sea (Laevastu and Larkins, 1981), pertaining to the year 1980, was used in this study. The model was modified to allow substitution of "basic food" (zooplankton and benthos) for preferred prey items if the seasonal abundance of "basic food" permitted this and preferred prey items were unavailable. Otherwise partial starvation was permitted to occur and to affect growth rates. The simulation was run in seasonal time steps to an internally consistent equilibrium, which was reached when the removal of biomasses by predation, other mortalities, and fishing equaled biomass production.

Some of the results from ecosystem simulation for the eastern Bering Sea pertaining to predation are shown in Tables 3 to 5 and Figure 1. The standing stocks and annual consumption of marine ecological groups (fish, zooplankton, and macrobenthos) in the eastern Bering Sea and Aleutians are shown in Table 3. Fish are further divided into three additional ecological groups in Table 4. Annual predation rate, or predation to biomass ratio, is computed as total annual predation divided by the annual mean standing stock. More detailed data on annual production, mortalities, food composition, and predation on cod are given in Table 5.

The predominance of predation over other mortalities is indicated by the observation that of the annual growth of biomass (or biomass production) of cod, 74% is removed by fish predation, the main predator being pollock which is the most abundant species in the Bering Sea. Mammals eat 9% of the annual production of cod. Cod is one of the major piscivores in the eastern Bering Sea, with fish constituting 35% of its food.

Considering that predation is by far the greatest component of mortality of fish and that it operates mainly on larvae and juveniles, it becomes obvious that predation will materially affect the recruitment in most species in the eastern and central Bering Sea. Predation rate depends on the relative sizes of predator and prey, their relative (size specific) abundance, and the availability of alternative prey; thus predation is dependent on the relative density of prey items. Consequently, if recruitment were mainly affected by predation, it would vary relatively little from year to year; long-term trends would be evident when the ecosystems composition changes. To test this hypothesis, the variation in recruitment of cod in the eastern Bering Sea is considered in the next section.

Fish constitutes about 22% of the food of the fish in the eastern Bering Sea ecosystem (Fig. 1). Consequently the carrying capacity of a given ocean region with a high standing stock of fish depends not only on the pro-

Table 4. Standing stocks, annual growth rate (production to biomass ratio), and predation rate (predation to biomass ratio) of fish ecosystem components in the eastern Bering Sea and Aleutian Region (area 900 000 km^2).

	Annual mean		
Fish ecosystem component	Standing stock t (mill.)	Growth rate (per unit biomass)	Predation rate (per unit biomass)
Pelagic fish and squids	4.8	1.07	0.84
Semipelagic fish	17.6	0.84	0.68
Demersal fish and crabs	10.9	0.60	0.50

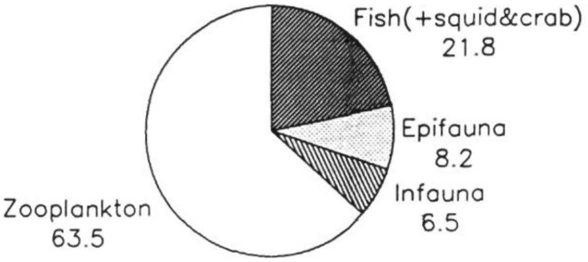

Figure 1. Annual mean food composition of the fish component of the eastern Bering Sea ecosystem.

duction of basic food (zooplankton and benthos), but also on the availability and production of fish as food for other fish, i.e. the species composition and general trophic status of the fish ecosystem as well. Vanni *et al.* (1990) document an interesting example of a change in phytoplankton biomass in Lake Mendota following a marine fish kill. Returning to marine systems, if the level of a prey species such as capelin or herring in a given ecosystem is low, the predator species might suffer partial starvation and the predation pressure on their larvae and juveniles would increase through cannibalism. Recruitment of a predominantly predator species (e.g. cod) would be reduced. This seems to be the case at present in the Barents Sea (Hamre, 1988; C. C. E. Hopkins, pers. comm.). The recovery of piscivorous and other species in such a "depressed" fish ecosystem might be slow due to the increased predation pressure on the larvae and juveniles of these fish. Growth rates of the piscivorous fish might also be affected.

Table 5. Pacific cod biomass, its production and utilization in the eastern Bering Sea and Aleutian Region (area 900 000 km^2).

	1000 t	%[a]
Total annual mean biomass (0.5 years to maximum age)	1470	
Exploitable biomass	956	65
Annual production	1352	92
Disease mortality	90	6.7
Catch (including discards)	150	11.1
Apex predation (mammals and birds)	115	8.5
Predation by fish	997	73.7
Predation on cod		
Pelagic fish	98	9.8
Semipelagic fish (pollock)	770	77.2
Demersal fish	130	13.0
Consumption by cod		
Zooplankton	1964	43.1
Fish	1577	34.6
Benthos	1016	22.3

[a] Percentage of exploitable biomass and annual production refers to annual mean biomass; percentages of mortality, predation, and consumption refer to the totals of these processes, respectively.

Age composition of catches and recruitment of cod in the eastern Bering Sea from 1978 to 1987

US fishery observers on board fishing vessels in the eastern Bering Sea have obtained a great number of length measurements from commercial catches. The extensive observer coverage of the catches (in later years greater than 95% of foreign vessels, which comprised the majority of the fleet until recent years) allows us to assume that these data are representative of all catches from the eastern and central Bering Sea. The age compositions (derived, using age-length key) of catches of cod from 1978 to 1987 from the eastern and central Bering Sea are given in Figure 2.

Figure 2B shows that the age composition of catches of cod have changed little during the last five years (1983 to 1987 inclusive), and age-class strength at full recruitment (4 years for cod) has also fluctuated little. However, using all available corresponding data in earlier years (1978 to 1982) considerable fluctuations in age-class strengths are indicated (see Fig. 2A). The age of full recruitment in these earlier years seems to be one year (in some cases even two years) earlier than at present. Attempts to explain these differences by the occurrence of stronger age classes reflecting years of better than average recruitment show considerable inconsistencies and suggest that changes of age in the full recruitment and apparent age-class strength of catches in these earlier years might have been caused by changes in fishing patterns (changes of types of gear, fishing areas, and depths) rather than by changes in year-class strength. Some of the changes of age-class strength in these data might also be an artifact due to incomplete sampling caused by less observer coverage in the early years (see Fig. 3A). These possible causes of changes in age composition of catches were further investigated to discriminate real changes in year-class strength from artifacts due to changes in fishery and sampling patterns.

In the early 1980s changes occurred with the use of different gear (see example of the effect of different gear on age composition of catches in Fig. 4) and with changes in fishing grounds (area and depths) (see Fig. 3B) some of which were dictated by management. Different age groups of fish tend to be found in different temperature and depth regimes, with older fish usually in northern (colder) areas and in deeper water (for example, cod caught by long lines from the continental slope, Fig. 4). Consequently the change in age composition of catches of cod in the early years (Fig. 2A) might be largely explained by changes in fishing patterns with respect to area and depth (Fig. 3B). Effects of changes in fishing patterns on the age composition of catches and on stock assessment have been pointed out earlier (e.g. Shepherd, 1988).

With the possible effects of changes in fishing patterns on the age composition of catches of cod taken into account, there appears to be little year-to-year variation in age composition of the stocks of cod in the eastern Bering Sea in the decade 1978 to 1988. This suggests that mechanisms such as predation, which can act to reduce changes in the relative abundance of different resources, might control recruitment as discussed in the previous section.

Recruitment in holistic ecosystem simulation

If recruitment would be prescribed explicitly in any prognostic population dynamics model, the results of prognoses with the model are determined to an overwhelming degree by the form of this prescribed recruitment. In reality, a simple stock/recruitment relationship does not exist in most species and thus cannot be used for meaningful prognostic ecosystem simulation, as recruitment is influenced by many other processes and factors (see Table 1).

In ecosystem simulations such as DYNUMES and PROBUB no explicit prescription of recruitment is necessary. Stock size fluctuations in these simulations are largely determined by predation and by environmental effects on it (e.g. effects of temperature on growth and food requirement). At present it is unrealistic to attempt to capture the variability in larval and early juvenile life history stages, thus possible variability in survival in these life stages is not explicitly computed in these biomass based simulations. Predation on the juveniles before full recruitment controls most of the fluctuations of biomasses in these models.

Predation in these ecosystem simulations is dependent on the availability (depicted with relative density) of potential prey and its changes over space and time. Starvation is also possible and allowed in the simulations, affecting biomass growth. Simulations with high spatial resolution (such as DYNUMES) allow the computation of food availability and density-dependent predation at each grid point, thus the effects of seasonal migrations (and those caused by environmental anomal-

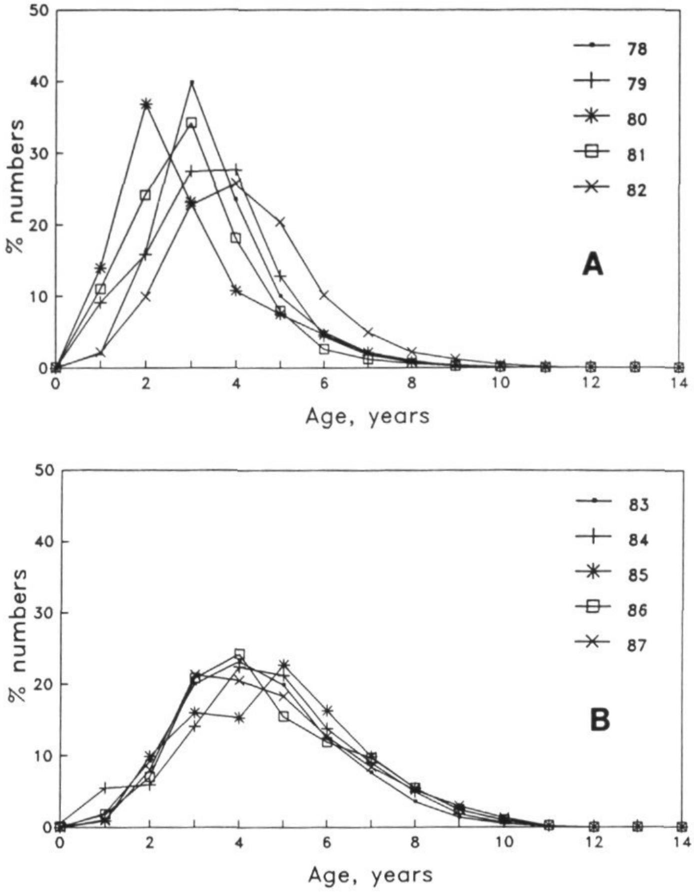

Figure 2. Age composition of catches of Pacific cod from the eastern Bering Sea. A. Age distribution of catches from 1978 to 1982. B. Age distribution of catches from 1983 to 1987.

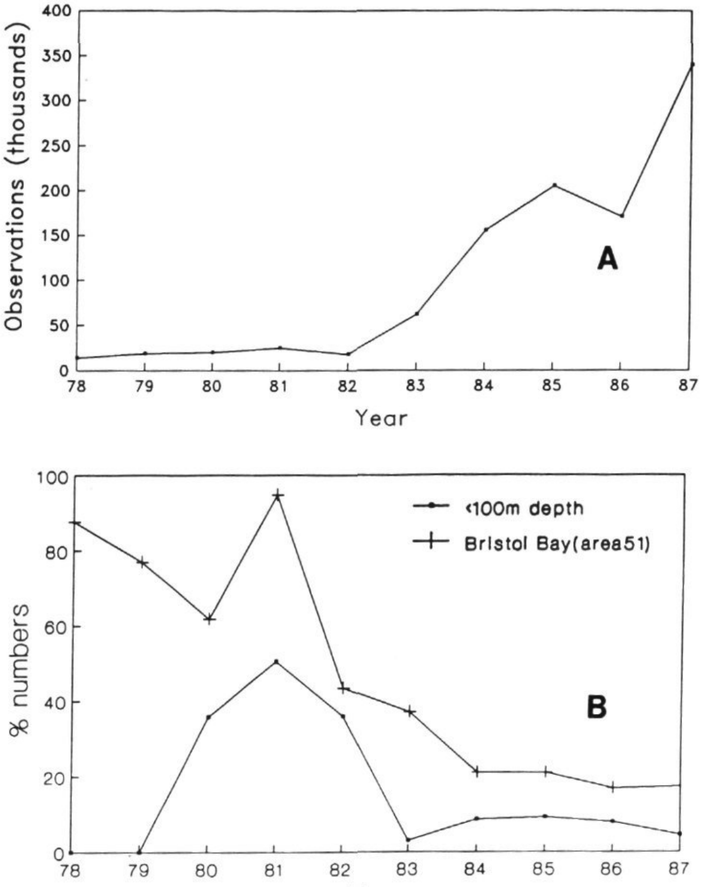

Figure 3 A. Number of observations of cod lengths per year from the eastern Bering Sea, 1978 to 1987. B. Percentual distribution of length observations of cod in areas shallower than 100 m and from statistical area 51 (Bristol Bay).

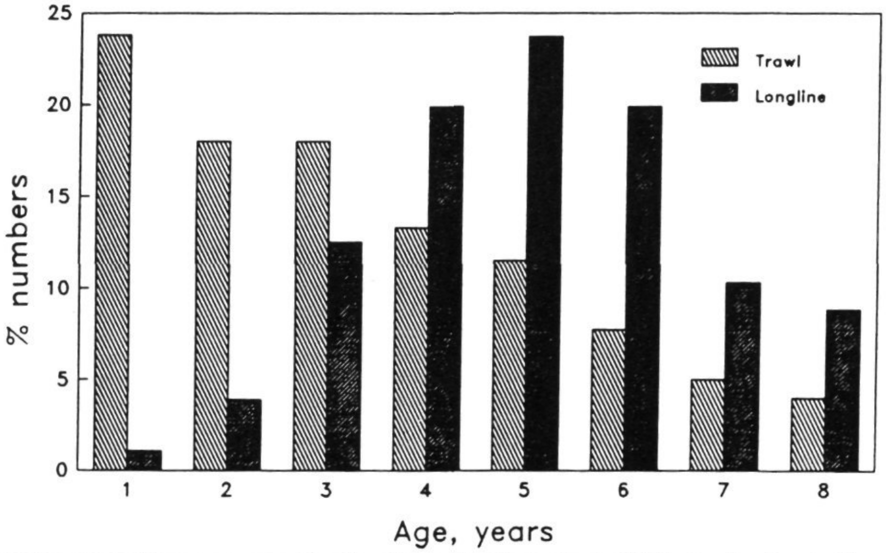

Figure 4. Age composition of Japanese cod catches from the eastern Bering Sea in 1984 by trawlers (on shelf) and by longliners (on continental slope).

ies) causing changes in spatial predator–prey overlap, can be accounted for.

These holistic ecosystem simulations are large and complex and fisheries biologists and managers often do not have the time or resources to evaluate these simulations. However, the natural world is complex and simpler models and approaches do not simulate a complex system correctly, but instead produce a caricature of some recently observed events, often with unrealistic estimates of precision. Although larger ecosystem models do not reproduce the full complexity and dynamism of the natural world, they do more realistically represent the state of uncertainty that is associated with any attempt to model and forecast events in fisheries.

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Predator–prey interactions of cod and capelin in Icelandic waters

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Magnússon, K. G., and Pálsson, Ó. K. 1991. Predator–prey interactions of cod and capelin in Icelandic waters. – ICES mar. Sci. Symp., 193: 153–170.

Detailed stomach content data for Icelandic cod are available for the period 1980–1988. These data are used to calculate the total consumption by age and also consumption of different age groups of capelin by cod. Acoustic abundance estimates for 2- and 3-year-old capelin in November and 3- and 4-year-old capelin in February are available for most years. These data are used to estimate the following for each age group of cod: (a) The relationship between the prey abundance (i.e. capelin) and predation per unit predator weight. It is found that this functional relationship is of type III, i.e. has a sigmoid shape. (b) The relationship between consumption of capelin and total consumption per unit predator weight. It is found that the cod can only partly compensate for the loss of capelin by switching to other food. This holds true for all age groups of cod between 3 and 8 years old. These relationships are then used in a simulation model predicting growth rates and biomass of cod on the basis of capelin abundance – which is determined by the recruitment of capelin – and on the size of the cod stock. The growth rates of the different age groups of cod are determined by the total consumption, which is determined by the consumption of capelin, which again is determined by capelin abundance. Thus the dependence of the biomass and yield of cod (by weight) on capelin biomass for a given stock size (in numbers) of cod and prescribed fishing mortality rates can be calculated. The results indicate that cod growth, biomass, and yield are not greatly affected as long as capelin biomass is above approximately 2 million tonnes. When capelin biomass is further reduced a more rapid decline in cod growth, biomass, and yield is observed.

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1. Introduction

The trophic ecology of Icelandic cod (*Gadus morhua* (L.)) was discussed in Magnússon and Pálsson (1989). Stomach content data were used to calculate the monthly consumption in early and late winter (March and October/November respectively) of various prey species by the cod stock. By far the most important prey item was capelin (*Mallotus villosus* (Mull.)). In early winter, between 22% and 77% of the total food consumed was capelin and 50–85% in late winter. It was indicated that the consumption of capelin depends strongly on the stock size of capelin and also that total consumption decreases with decreasing capelin consumption, i.e. the cod is not fully able to compensate for the loss of capelin by increasing its consumption of other types of food. In this paper we will consider in greater detail the relationship between these two species. In particular we will consider how the consumption of capelin by cod depends on the stock size of capelin and how total food intake of cod depends on consumption of capelin. This is done separately for each age class of cod.

In view of the fact that food intake of cod depends on the availability of capelin it might thus be expected that the dynamics of the cod stock are affected by the size of the capelin stock. In fact, all of the following three parameters might be affected: Natural mortality rate, recruitment, and growth rate. In view of the lack of information about the first two parameters, we will ignore any possible effects on natural mortality rates and recruitment and concentrate on the growth rate. We will present a simulation model which predicts growth rates and biomass of cod – and hence yield in tonnes for fixed fishing mortality rates – on the basis of availability of capelin. Other food is assumed constant; thus variability in consumption comes only from variability in the capelin stock.

2. Material

The following data have been used:

1. Cod stomach content data by length groups in March 1980–1988 and in October/November 1980–1983, 1985, and 1988. We use both average total amount in the stomach and the fraction of the various age groups of capelin of the total food. For details concerning stomach sampling, length segregation, area sampled, numbers of stomachs sampled, average contents, etc., see Pálsson (1983) and Magnússon and Pálsson (1989).
2. Average near-bottom temperatures north and east of Iceland in March and October/November.
3. Length distribution of cod for each age group. This together with the empirical length–weight relationship – $W = 0.0046L^{3.16}$ (Pálsson *et al.*, 1988) – was used to calculate the average weight of each age group by

   $$\bar{W} = 0.0046(\bar{L})^{3.16} + 0.016s^2(\bar{L})^{1.16}$$

   where $\bar{L}$ is the average length in the age group and s is the standard deviation.
4. Abundance estimates of capelin, age 2 years and older (2^+) in October/November and 3 years and older (3^+) in January/February, obtained by acoustic methods (Table 1).

Items 1 and 2 are used to calculate the average daily consumption of a fish in a certain length group i, at a temperature T (°C), by

$$R_i = 2.60(L_i/40)^{1.15}\,1.09^{T-6}\,\sqrt{S_i}\ \text{g/day}$$

where L_i is the average length (cm) in length group i and S_i is the average stomach content (g) of fish in this length group (Magnússon and Pálsson, 1989). This relationship was obtained by using the data from Jones (1974).

Our simulation model will be age specific rather than length-specific and thus we require consumption by age groups rather than by length groups.

Table 1. Acoustic abundance estimate of the stock of 3+ capelin in January and the 2+ stock in October (thousand tonnes) (H. Vilhjálmsson, pers. comm.).

Year	January	October
1980	755.8	506.0
1981	322.0	342.2
1982	182.5	300.1
1983	311.7	1269.5
1984	1044.7	814.0
1985	914.9	1097.0
1986	–	1093.9
1987	1146.2	1299.0
1988	–	1278.6
1989	947.8	–

Let $f_{a,i}$ be the relative frequency of length group i for cod of age a (note that $\Sigma_i f_{a,i} = 1$). The average daily consumption for cod of age a will then be

$$R_a = \sum_i f_{ai}R_i$$

If h_{ij} is the fraction of prey type j in the stomach content in length group i, then

$$R_{aj} = \sum_i f_{ai}h_{ij}R_i$$

is the amount of prey type j (e.g. 2^+ or 3^+ capelin) consumed by a cod of age a.

3. Predator–prey relationships

Our ultimate goal is to find how the abundance of capelin determines the growth of cod. This relationship consists of three steps.

Capelin abundance → Consumption of capelin
→ Total consumption → Growth

3.1. Relationship between capelin abundance and consumption of capelin

The first thing of interest is to find out the relationship between capelin abundance and consumption of capelin by cod. The percentage of capelin in the diet of cod is highest for cod aged 4–6 (Magnússon and Pálsson, 1989). It is thus likely that there are differences between the age groups of cod as regards how important capelin is as food. This may be caused by factors such as cod size, differences in spatial overlap between predator and prey age groups, and the distribution of other suitable prey. For this reason we look at the relationship between prey abundance and consumption separately for each age group from 2 years to 8 years.

As mentioned above the acoustic surveys for capelin are undertaken in October/November and in January/February. These surveys only estimate the abundance of capelin at age 2 and 3 years and age 3 and 4 years respectively. We therefore have to relate the abundance of 2+ capelin in October/November and 3+ in January/February, to the consumption of these particular age groups by cod in the respective months. Usually, the major part of the capelin consumed is from these age groups (Magnússon and Pálsson, 1989).

As pointed out in Magnússon and Pálsson (1989) a complication arises because the combined catch and consumption over winter is not compatible with the abundance estimates obtained by acoustic methods, since the change in biomass from October/November to January/February, as obtained from acoustic methods, is too small compared with the total catch and consumption by cod in the intervening period. However, if the acoustic abundance estimate is treated as an index of abundance rather than as an absolute abundance estimate, then we can obtain a scaling factor as follows.

From the acoustic estimates in October and in January/February, we can obtain the total mortality rate from October to March inclusive, by

$$z = -k \ln [n(3+)/n(2+)]$$

where k is a scaling factor used to scale z to a period of six months, which is the unit of time in these calculations. The numbers n(2+) and n(3+) are the stock estimates in numbers in early and mid-winter respectively.

The predation in numbers of this particular age group of capelin over the six-month period, can be calculated by

$$E = 3(E_1 + E_2)/w$$

where E_1 and E_2 are the calculated monthly predation by weight in October and the following March respectively, and w is the average of the weights over the six-month period, weighted by the population numbers of the two age groups (i.e. 2- and 3-year-olds in October). We can then calculate the stock size at the beginning of October

$$n_c(0) = (c + E)\frac{z}{z - m} \quad \frac{1}{1 - \exp(-z)}$$

where c is the catch in numbers over the six months and m is the mortality rate from other causes than predation by cod and fishing. For a given value of m, we can calculate the ratio of calculated stock size at the beginning of October $n_c(0)$, to "acoustic" stock size at the same time $n_a(0)$. Data only exist for the winters 1980–1981, 1981–1982, 1982–1983, and 1983–1984. The value of m which minimizes the standard deviation of the scaling factor between $n_c(0)$ and $n_a(0)$ is 0.01 (per six months). This gives a scaling factor of 1.9 which is not very sensitive to the value of m up to $m = 0.05$. Thus we transform the measured biomass into the assumed true biomass by $b_{true} = 1.9b_{obs}$. The possibility of overestimation of consumption should be considered in the context of the daily food ratio of 0.5 to 1.5% of bodyweight per day (Magnússon and Pálsson, 1989). This ratio does not appear high compared to other results (e.g. Daan, 1973; Mehl, 1989).

The stomach measurements are taken in March, whereas the acoustic abundance estimate is taken in January or February. Thus, as a measure of prey abundance in March we use the January/February acoustic biomass estimate of the 3+ group, times 1.9, less the February catch and half the March catch of the same age groups, i.e.

$$b_{true}(\text{March}) = 1.9b_{obs}(\text{Jan.}) - C(\text{Feb.}) - C(\text{March})/2$$

It could be argued that the consumption in February and half of March should also be subtracted as well as the catch. This has not been done here since we do not have stomach measurements in February and therefore no direct estimate of the consumption. Natural mortality other than predation and growth of capelin is not taken into account in this equation, since the effect of these parameters on the stock size of the capelin must be regarded as negligible during this short period of time.

In the case of early winter measurements, the acoustic abundance estimate and the calculated consumption refer to approximately the same period, i.e. October/November. Thus the measure of prey abundance in October will be the result of the October survey times 1.9.

This measure of prey abundance is then related to the consumption of the respective age groups per unit of weight of predator for cod age $2, 3, \ldots, 8$, that is, grammes of 2+ (or 3+) capelin consumed per kg of cod weight per day (i.e. ‰ of weight per day). The consumption was normalized to a temperature of 2°C in March and 4°C in October/November. The corrected stock size and the consumption of capelin are given in Tables 2 and 3.

Clearly, the total abundance of the prey is not available to the predator in the same amount at any given time or location. The actual amount of prey available to the predator will primarily be determined by the spatial overlap in the distribution of predator and prey. However, this is difficult to deal with quantitatively and has not been taken into account in this paper.

Let us denote the prey abundance by x and the consumption by y. Then the functional form relating x and y which we will consider is

$$y = \frac{rx^n}{s^n + x^n} \tag{1}$$

The graphs of these functions all have $y = r$ as a horizontal asymptote. For $n \leq 1$, the graph is everywhere concave, i.e. the second derivative y'' is negative everywhere, i.e. a type II functional relationship. For $n > 1$, the graph has a sigmoid shape, with the steepness of the graph increasing with increasing n, i.e. type III functional relationship. Equation (1) can be rewritten as $1/y = 1/r + s^n/r(1/x^n)$ and hence the coefficients r and s can be estimated by linear regression. The GLIM statist-

Table 2. Stock size (thousand tonnes) and consumption by cod (g of capelin/kg of cod/day) of 3+ capelin in March.

Year	Stock	Age of cod						
		2	3	4	5	6	7	8
1980	1257.1	0.59	3.23	4.30	4.14	6.06	6.34	5.43
1981	549.6	0.14	0.95	2.55	2.53	1.64	1.64	1.43
1982	348.6	0.00	0.66	0.87	0.80	0.91	0.54	0.21
1983	595.3	0.10	1.23	2.11	2.00	1.52	1.26	1.19
1984	1656.2	0.75	5.80	8.69	9.23	9.42	8.79	8.41
1985	1548.2	1.91	4.54	7.76	9.29	8.94	8.30	7.30
1986	–	4.28	9.69	8.40	7.15	6.07	5.07	4.30
1987	1912.5	0.42	4.73	4.69	5.62	4.84	4.06	2.93
1988	–	2.61	13.38	10.74	8.03	7.35	6.00	5.00

Table 3. Stock size (thousand tonnes) and consumption by cod (g of capelin/kg of cod/day) of 2+ capelin in October/November.

Year	Stock	Age of cod						
		2	3	4	5	6	7	8
1980	966.5	0.00	0.00	0.06	0.75	1.39	1.04	0.27
1981	653.6	0.00	0.00	0.80	3.05	4.32	4.10	2.96
1982	573.2	0.00	0.09	0.91	1.12	1.39	0.97	0.45
1983	2424.7	4.01	6.65	8.28	8.31	6.98	5.10	3.10
1985	2095.3	5.63	4.97	4.10	4.24	4.30	3.39	1.62
1988	2442.1	1.64	7.73	8.26	8.32	6.94	4.01	1.94

ical package from the Royal Statistical Society was used with a reciprocal link function.

It should be noted that with a sigmoid relationship (type III), consumption (and hence growth) changes more sharply with changes in prey stock around the middle of the range of the prey stock size than with a concave (type II) relationship. In other words, consumption falls more sharply with decreasing prey stock size.

For late winter (i.e. March), data on both capelin stock size and on consumption are available for the years 1980–1985 and 1987. Curves with n-values of 1, 2, and 3 were tried. The best fit was for $n = 3$. The data points, together with the curve for $n = 3$, for cod age groups 3 . . . 8 are shown in Figure 1. It is clear that a type III curve fits the data better than a type II curve. All the data fit such a sigmoid curve fairly well with the exception of the 1987 point where the capelin stock was at its highest, but consumption was only moderate. The values of r and s for $n = 3$ are given in Table 4.

The relationship between capelin stock size and capelin consumption by cod in March is significant at the 5% level for all age groups except 2- and 8-year-olds. The correlation between the coefficients r and s in Equation (1) is fairly high, between -0.3 and -0.4. However, we are mainly interested in determining a function which approximates the data reasonably well and can be used for the purpose of simulation. The values of r – which is the horizontal asymptote – show that the older fish have a greater appetite for capelin (higher r values) than the younger ones. The values for 2-year-old fish are of little interest, since the 3+ capelin consumption by this age group is less than 20% of its total consumption in all cases, and usually much less.

For early winter (i.e. October/November) both types of data are available for 1980–1983, 1985, and 1988. Here there were problems in fitting a sigmoid curve in the case of 2-year-olds and 3-year-olds. This was overcome by fixing the value of r and estimating s. The value of r was set at 20.0. The data points and the curves are shown in Figure 2 and the values of r and s are given in Table 5. It should be noted here that age 2 is not included in the simulations described below.

The relationship between stock size and consumption in October/November is significant at the 5% level for age groups 3, 4, 5, and 6. For age 7 and over, there is no relationship between consumption and stock size.

3.2. Relationship between consumption of capelin and total consumption

The next question which has to be answered is: What is the relationship between capelin consumption and total consumption? It is obviously of interest to see if total consumption declines with declining capelin consumption as a result of a reduction in the stock size of capelin. Total consumption for the different age groups of cod is given in Tables 6 and 7.

Let us denote the total consumption per unit predator weight by h and the consumption of the relevant age groups of capelin per unit predator weight by e. Then we assume a relationship of the form

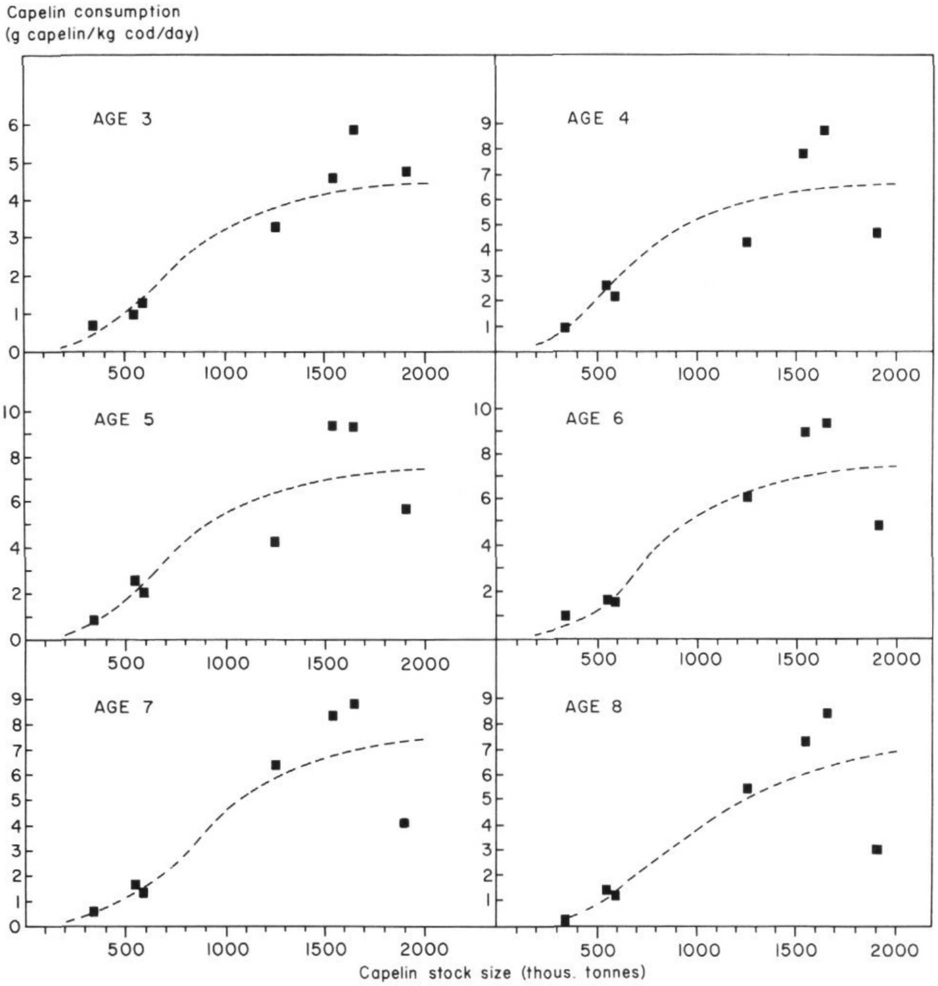

Figure 1. Capelin stock size and capelin consumption by cod age groups 3–8 in late winter (March).

$$h = ue + v \quad (2)$$

for March and October/November and for cod age groups 2, 3, . . ., 8.

Figures 3 and 4 show plots of capelin consumption and total consumption per unit predator weight together with the regression line through the points for March and October/November respectively, for cod aged 2, . . ., 7 years old. For March, data are available for the periods 1980–1988 and 1980–1983, 1985, and 1988 for October/November. The regression coefficients are given in Tables 4 and 5, where u is the slope and v the intercept.

For the March data, the slope is significant at the 5% level for all age groups except the 3-year-olds, but for the October/November data it is only significant (at the 10%

Table 4. March. Parameters in Equations (1) and (2) and calculated maximum consumption of 3+ capelin (e_{max}) and maximum total consumption (h_{max}). Stock in million tonnes and consumption in g/kg/day.

Age	r	s	u	v	e_{max}	h_{max}	e_{max}/h_{max} (%)
2	1.59	1.41	2.11	10.60			
3	4.91	0.75	0.42	10.51	4.91	12.56	39.09
4	6.84	0.69	0.38	8.76	6.84	11.33	60.38
5	7.80	0.74	0.42	7.17	7.80	10.43	74.79
6	8.00	0.79	0.50	6.06	8.00	10.07	79.44
7	8.06	0.89	0.53	5.79	8.06	10.05	80.21
8	7.79	1.02	0.54	5.51	7.79	9.67	80.52

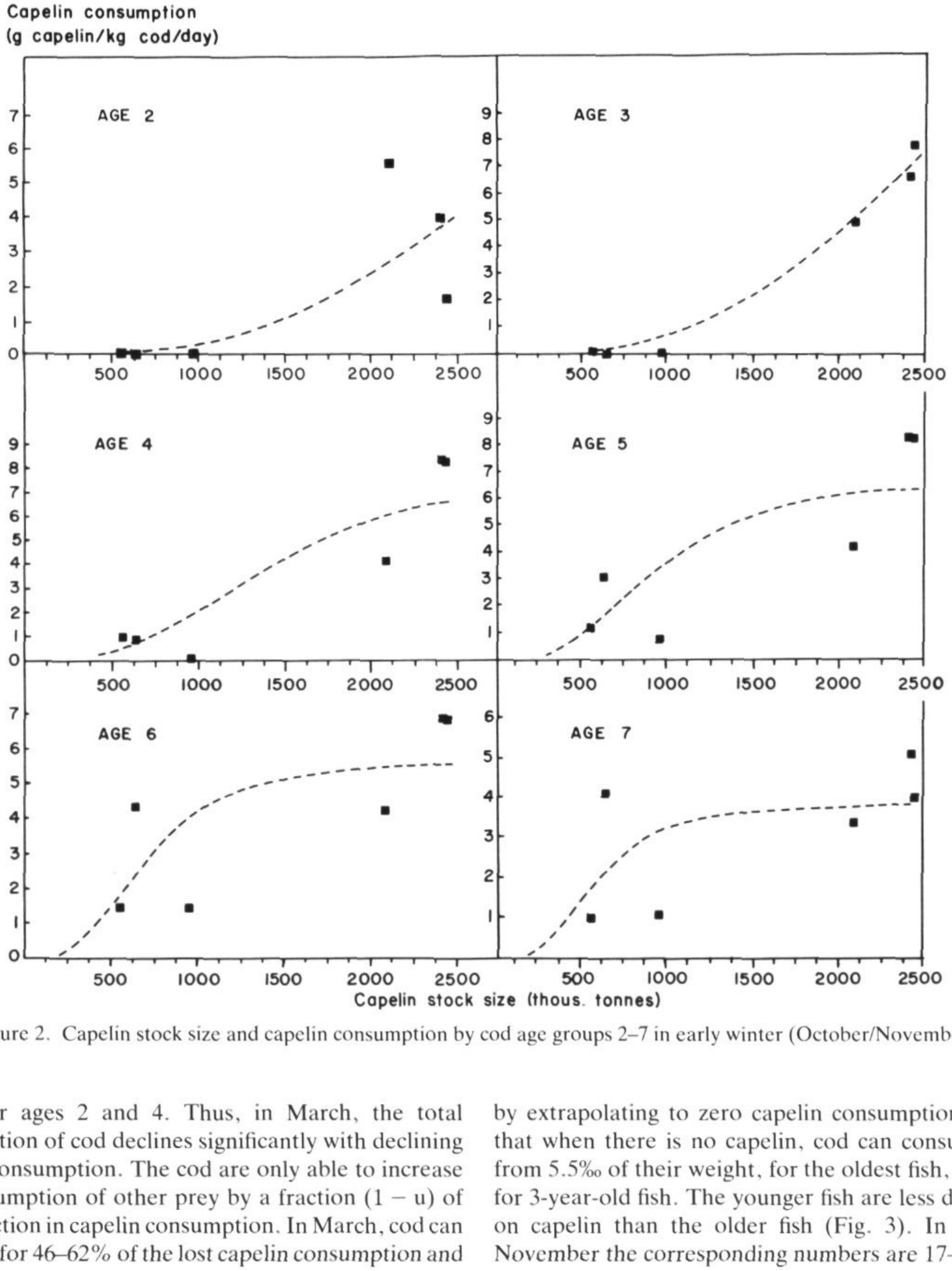

Figure 2. Capelin stock size and capelin consumption by cod age groups 2–7 in early winter (October/November).

level) for ages 2 and 4. Thus, in March, the total consumption of cod declines significantly with declining capelin consumption. The cod are only able to increase the consumption of other prey by a fraction (1 − u) of the reduction in capelin consumption. In March, cod can make up for 46–62% of the lost capelin consumption and by extrapolating to zero capelin consumption, we see that when there is no capelin, cod can consume daily from 5.5‰ of their weight, for the oldest fish, to 10.5‰ for 3-year-old fish. The younger fish are less dependent on capelin than the older fish (Fig. 3). In October/November the corresponding numbers are 17–63% and

Table 5. October/November. Parameters in Equations (1) and (2) and calculated maximum consumption of 2+ capelin (e_{max}) and maximum total consumption (h_{max}). Stock in million tonnes and consumption in g/kg/day.

Age	r	s	u	v	e_{max}	h_{max}	e_{max}/h_{max} (%)
2	20.00	3.91	0.80	10.43			
3	20.00	2.98	0.46	9.69			
4	7.69	1.36	0.48	8.27	7.69	11.98	64.21
5	6.71	0.92	0.47	7.67	6.71	10.83	61.95
6	5.70	0.70	0.37	7.75	5.70	9.86	57.80
7	3.88	0.60	0.40	7.24	3.88	8.78	44.19
8	2.01	0.51	0.83	6.21	2.01	7.88	25.52

Table 6. Total consumption (g/kg of cod/day) of cod in March.

Year	Age of cod						
	2	3	4	5	6	7	8
1980	12.81	10.47	10.36	8.08	8.72	7.92	6.54
1981	9.52	9.14	10.30	9.43	7.42	7.28	6.66
1982	13.74	11.06	8.29	7.39	6.81	6.28	6.04
1983	14.96	13.26	10.66	8.49	7.18	6.19	5.88
1984	9.08	14.16	13.20	12.89	12.50	11.69	11.24
1985	12.80	16.72	13.74	11.72	10.75	10.12	9.16
1986	21.26	11.79	10.34	9.02	8.13	7.44	6.71
1987	8.08	8.82	8.65	8.92	7.88	8.65	7.65
1988	15.89	17.64	12.12	8.99	8.56	8.75	9.06

6.2–10.4‰. There is no clear relationship between capelin consumption and total consumption for older cod. In fact total consumption is independent of capelin consumption for these age groups in this period (Fig. 4).

The value of the slope can be thought of as a measure of the importance of the prey to the predator, since it gives a measure of by how many units (i.e. g kg^{-1} d^{-1}) total consumption goes down when the consumption of the particular prey species goes down by one unit. Obviously, $0 \leq u \leq 1$ should hold. However, this is not the case for age group 2 in March (Table 4), for which capelin is of limited importance as food. In fact this age group is not treated in the simulations. If $u = 0$ then total consumption is independent of the consumption of the particular prey, since the predator can fully make up for the loss in the consumption of the prey by increasing its consumption of other prey. On the other hand if $u = 1$, all the marginal consumption of the predator consists exclusively of the prey in question and the predator does not increase its consumption of other prey types as the abundance of the favoured prey decreases.

An obvious constraint is $e \leq h$ and thus the intersection of the line $h = ue + v$ with the line $h = e$ is the upper bound on e and h. This upper bound – call it M – can be regarded as the maximum consumption and is given by

$$M = v/(1 - u).$$

It turns out that $M > r$ in all cases, where r is the limit of the capelin consumption as the stock of capelin increases. There are two possible explanations for this. Firstly, it is possible that r is underestimated due to lack of observations at high stock levels of capelin, i.e. at the upper end of the curve, where it is close to being horizontal. The other explanation is that r refers only to maximum consumption of capelin, not to the maximum total consumption. In other words, there is always some consumption of other prey, irrespective of the size of the capelin stock. The fraction of capelin in the diet increases with increasing stock size of capelin, but reaches a maximum which is lower than 100%. This maximum fraction is e_{max}/h_{max} where $e_{max} = r$ and $h_{max} = ue_{max} + v$. This maximum fraction is given in Table 4 for cod aged 3–8 for the March data. As expected, the fraction is higher for older cod. Table 5 gives the same fraction for the October/November data. Here the fraction is lower for the older cod. From Tables 4 and 5 it seems that in late winter all cod 3 years and older are heavily dependent on capelin, the older age groups more so. In October/November the situation is the reverse, the older groups are not greatly dependent on capelin, but the 4 and 5 groups are. The data for 2- and 3-year-olds are too poor to allow any conclusions to be drawn. These differences between early and late winter in the feeding relationships reflect the differences in the trophic ecology of the capelin stock in these periods; in early winter the stock is turning from extensive feeding migrations into spawning migration mode, whereas in late winter the stock is approaching spawning and migrating in concentrated schools, and the fish are heavily loaded with spawning products.

Table 7. Total consumption (g/kg of cod/day) of cod in October/November.

Year	Age of cod						
	2	3	4	5	6	7	8
1980	9.08	10.16	8.03	6.52	7.06	6.71	5.60
1981	11.90	8.15	7.45	8.11	8.45	8.18	7.97
1982	11.53	9.81	8.62	9.23	9.62	8.73	6.26
1983	14.47	13.67	12.68	12.20	10.99	9.82	8.06
1985	14.90	14.40	13.10	11.90	9.93	8.54	8.56
1988	9.68	10.96	10.55	10.20	9.82	8.85	9.37

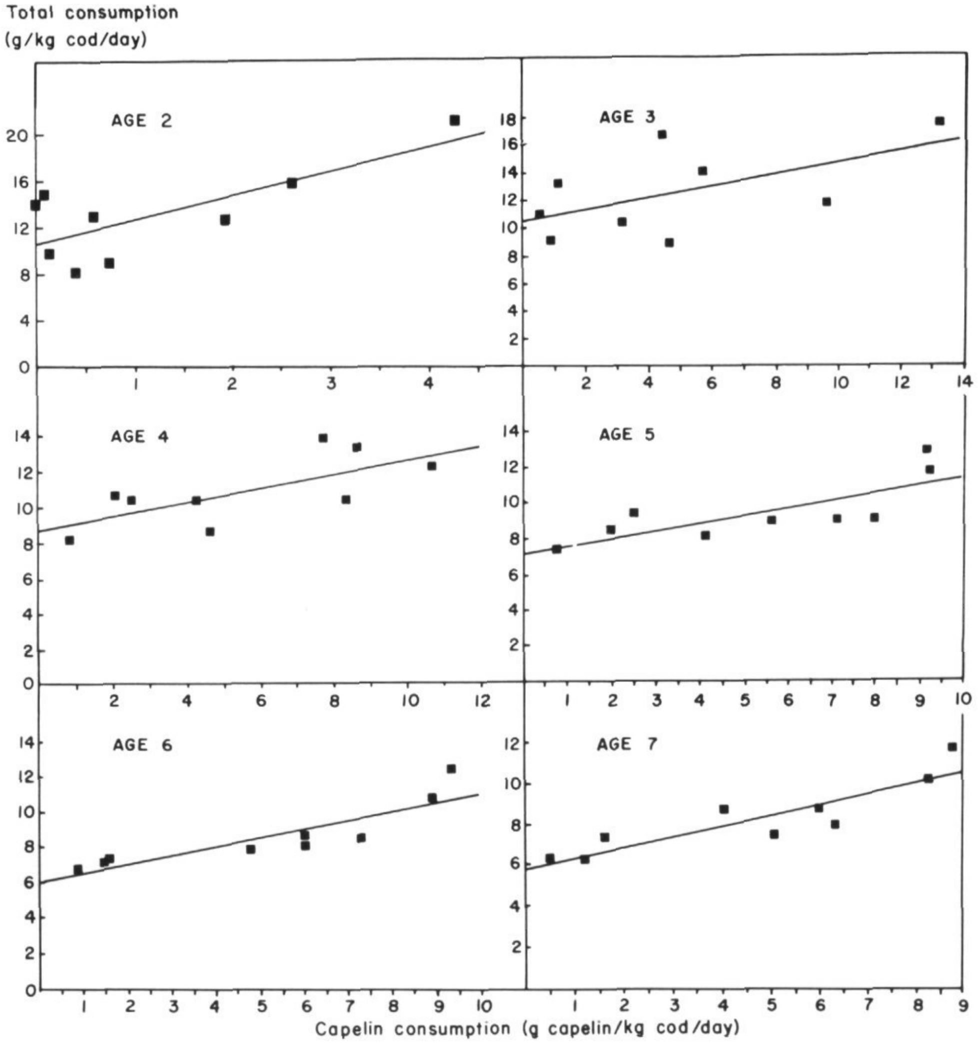

Figure 3. Capelin consumption and total consumption by cod per unit predator weight with regression line through the points for March for cod aged 2–7 years old.

3.3. Relationship between consumption and growth

The third problem is to relate growth increments to food consumption. Here we will use the relationship

$$\Delta W = \alpha(A - \beta W^{m}) \qquad (3)$$

(Jones, 1976) where A is the food consumption over the relevant period and the second term in the parentheses is the amount of food which is required for maintenance. The values of the parameters α, β, and m given by Jones (1976) are as follows: $m = 0.8$, $\alpha = 0.2$–0.4, and $\beta = 0.24 \exp(0.081T + 0.76V)$ g/month, where T is the temperature and V is the swimming speed in body-lengths per second.

4. Description of the simulation model

This simulation model has been made as simple as possible so that values of the relevant parameters can be obtained. The purpose of the model is to predict growth rates of cod for different capelin abundance and hence different availability of capelin as food for cod. In other words, we want to see what effect different abundances of capelin might have on the growth rates of cod and hence on the total harvest of cod under a harvesting regime of constant fishing mortality. The unit of time is one month, i.e. the relevant variables of the model are calculated from one month to the next. An illustration of the main components of the model and how they connect together is given as Figure 5.

The variables referring to capelin are denoted by

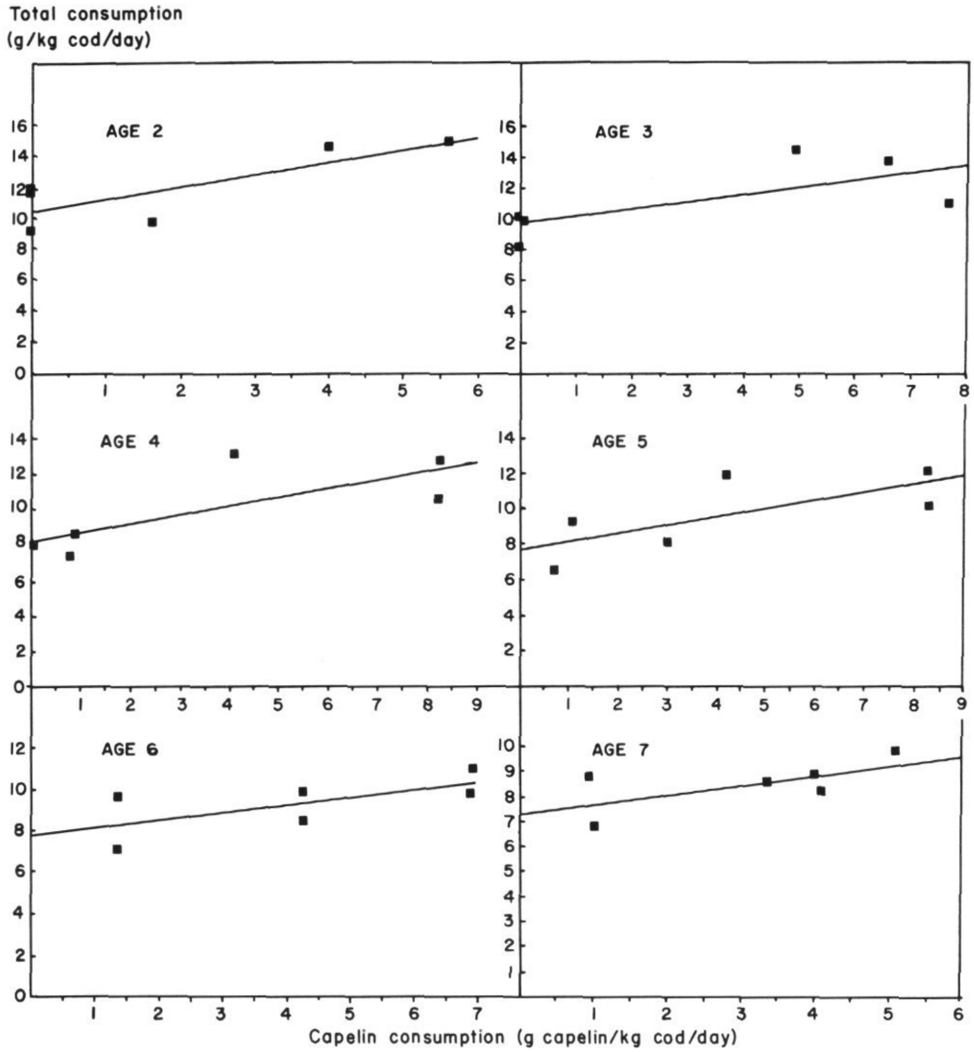

Figure 4. Capelin consumption and total consumption by cod per unit predator weight with regression line through the points for October/November for cod aged 2–7 years old.

lower case letters and those referring to cod by capital letters. The indices used are: i – month ($i = 1, 2, \ldots, 12$); t – year ($t = 1, 2, \ldots$); a – age of capelin ($a = 0, 1, 2, 3$, i.e. four age classes); b – age of cod ($b = 3, 4, 5, 6, 7, 8, 9, 10$, i.e. eight age classes). For the sake of convenience we have taken the first month of the year to be May, the first month after spawning takes place.

4.1 Capelin

List of variables and parameters

$b_{a,t,i}$ – biomass of a year old capelin at the beginning of month i in year t.

bs_t – biomass of the spawning stock of capelin at the end of year t.

$w_{a,t,i}$ – average weight of a year old capelin in month i, year t.

$c_{a,t,i}$ – catch (by weight) of a year old capelin in month i, year t.

$E_{a,t,i}$ – total amount of a year old capelin eaten by cod in month i, year t.

$m_{a,i}$ – fraction of a year old capelin that dies from natural causes other than predation by cod in month i.

x_t – fraction of 2-year-old capelin which is mature at the end of year t.

h_i – fraction of the yearly catch taken in month i.

Change in biomass from month i to month i + 1

$$b_{a,t,i+1} = (1 + \Delta w_{a,t,i}/w_{a,t,i}) \times [(1 - m_{a,i})b_{a,t,i} - (c_{a,t,i} + E_{a,t,i})] \tag{4}$$

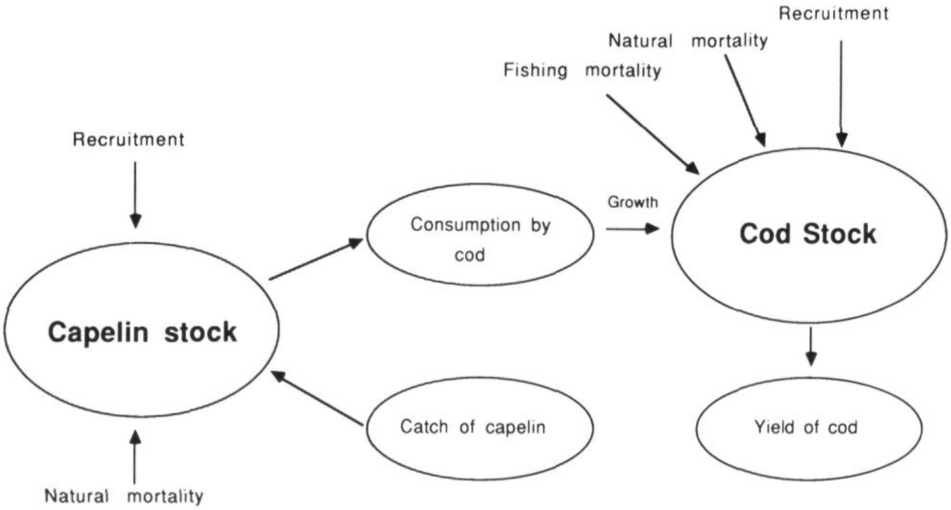

Figure 5. Simulation model predicting growth rates of cod for different capelin abundance.

This equation is based on the assumption that the growth and death processes take place in the following sequence: b is the biomass at the beginning of the month, then a fraction m dies from natural causes other than predation by cod, followed by the removal of the catch c and the consumption E. Growth is the last process.

The weights are given by

$$w_{a,t,i} = w_{a,t,i-1} + \Delta w_{a,t,i-1} \qquad (5)$$

The weight increment Δw is taken to be constant which is a fair approximation to the existing data.

There is no information on the natural mortality fraction m. However, on the basis of the discussion in section 3.1, we will consider m independent of age and month and equal to $0.01/6 \cong 0.002$. This value is probably too low, particularly if there are marine mammal predators.

A part of the 2-year-old capelin spawns in April, the last month of the simulation year. After spawning the capelin subsequently die. Thus Equation (4) is not valid when $a = 2$ and $i = 12$. Instead we will use

$$\begin{aligned} b_{3,t+1,1} = {} & (1 - x_t)(1 + \Delta w_{2,t,12}/w_{2,t,12}) \\ & \times [(1 - m_{2,12})b_{2,t,12} - (c_{2,t,12} + E_{2,t,12})] \qquad (6) \end{aligned}$$

The parameter x_t is approximately 0.7.

Recruitment

Little or no information on the stock recruitment relationship of capelin is available. The function we use here is

$$b_{o,t+1,1} = \begin{cases} a \times bs_t & \text{if} \quad bs_t < bs_{crit} \\ a \times bs_{crit} & \text{if} \quad bs_t > bs_{crit} \end{cases} \qquad (7)$$

where $bs_t = x_t b_{2,t,12} + b_{3,t,12}$ is the spawning stock at the time of spawning in year t. Note that this gives a linear relationship between spawning stock and recruitment for spawning stocks less than the critical value bs_{crit} and constant recruitment if the spawning stock is above the critical value. No information on this critical value exists, and in the simulations described below it is taken to be virtually zero, so in effect recruitment is constant.

Catch

The capelin season starts in August/September and lasts until March the following year. The catch consists primarily of the cohorts which are 2 or 3 years old at the beginning of the season. In these simulations we will assume that there is no catch of younger capelin.

We will take the total capelin catch quota over the entire season – i.e. the yearly quota – as input into the model. This catch is denoted by c_t^*. The yearly catch is split up into monthly catches according to a predetermined pattern. Thus

$$c_{t,i} = h_i c_t^* \qquad i = 1, 2, 3, \ldots, 12 \qquad (8)$$

where the h_i are given inputs, $\Sigma_{i=1}^{12} h_i = 1$. In the simulations described below we have taken $\bar{h} = (0, 0, 0, 0, 0, 0.1, 0.15, 0.15, 0.2, 0.25, 0.15, 0)$. This is approximately the pattern for the two seasons 1987–1988 and 1988–1989. Note that May is the first month of the year.

The catch in each month is divided into the two age groups involved according to their relative biomass

$$c_{a,t,i} = c_{t,i} b_{a,t,i}/(b_{2,t,i} + b_{3,t,i}); \qquad a = 2, 3 \qquad (9)$$

4.2. Cod

List of variables and parameters

$B_{b,t,i}$ – biomass of b-year-old cod at the beginning of month i in year t. The biomass of the oldest age group, i.e. b = 10 is not taken to be the accumulated biomass.

Bs_t – biomass of the spawning stock of cod at the end of year t.

$W_{b,t,i}$ – weight of a b-year-old cod at the beginning of month i, year t.

$C_{b,t,i}$ – catch (by weight) of b-year-old cod in month i, year t.

$M_{b,t,i}$ – fraction of b-year-old cod that die from natural causes in month i, year t ($0 \leq M_{b,t,i} \leq 1$).

$F_{b,t,i}$ – fraction of b-year-old cod that die from fishing in month i, year t ($0 \leq F_{b,t,i} \leq 1$).

$A_{b,t,i}$ – average total monthly consumption by one b-year-old cod in month i, year t.

Change in biomass from month i to month i + 1

$$B_{b,t,i+1} = (1 + \Delta W_{b,t,i}/W_{b,t,i})(1 - F_{b,t,i} - M_{b,t,i})B_{b,t,i} \quad (10)$$

The value of M is taken to be constant, $M = 0.2/12$. The fishing mortality fractions F are inputs into the model and separated into age effects (S_b), month effects (E_i), and year effects ($\hat{E}_t$)

$$F_{b,t,i} = S_b \times E_i \times \hat{E}_t \quad (11)$$

Here S_b is the selection pattern according to age. It would be more realistic to let the selection be dependent on the size of the fish and thus vary from year to year for each age group as the growth rate varies. However, for simplicity we will assume to begin with, that the selection depends only on the age of the fish. Alternatively the values of the fishing mortality fractions $F_{b,t,i}$ can be taken directly as inputs.

We note that when the unit of time is one month there is little difference over a whole year between using yearly mortality rates and monthly mortality fractions. Let the yearly mortality rate be Z and the monthly mortality fraction Z/12. In the former case the relationship between the stock size in numbers from one year to the next is $N(1) = \exp(-Z)N(0)$ and in the latter case $N(1) = (1 - Z/12)^{12}N(0)$. The difference between these two expressions is small as long as Z is not unduly large. Similarly, in the expression for the yearly catch we will have $(F/Z)(1 - \exp(-Z))N(0)$ and $(F/Z)(1 - (1 - Z/12)^{12})N(0)$ respectively. Thus it is a fair approximation to use yearly mortality rates as obtained from VPA divided by 12 as the monthly mortality fraction.

Recruitment

Let q_b be the fraction of b-year-old cod which is mature. Then the spawning stock at the end of year t is

$$Bs_t = \sum_{b=3}^{10} q_b B_{b,t,12} \quad (12)$$

Again it would be more reasonable to assume that the q's are dependent on size and thus the fraction of b-year-old cod which is mature might vary between years depending on the growth rates and hence the size of the fish.

The recruitment will be given by a piecewise linear function R of the same shape as the function in Equation (7). Thus:

$$B_{3,t+1,1} = R(Bs_{t-3}) \quad (13)$$

We assume that recruitment takes place three years after hatching. As with capelin, we will take the critical spawning stock to be virtually zero, so recruitment is constant and independent of the spawning stock.

Catch

The catch of b-year-old cod in month i year t is given by

$$C_{b,t,i} = F_{b,t,i}B_{b,t,i} \quad (14)$$

Growth

The weight increment in g/month of b-year-old cod in month i, year t is

$$\Delta W_{b,t,i} = 0.29W^{-0.25}[A_{b,t,i} \exp(0.081(T - T_{o,i})) - 0.24(W_{b,t,i})^{0.8} \exp(0.081T + 0.76V)] \quad (15)$$

(see section 3.3). The consumption is assumed to increase with increasing temperature, $T_{o,i}$ is the standard temperature used to normalize consumption in estimating the constants in Equation (1). $T_{o,i}$ is 2°C for those months in which the March relationship is used, and 4°C for those months when the October relationship is used. If there were no such temperature term multiplying the consumption, then with a constant food supply the growth would decline with increasing temperature because the maintenance term increases with increasing temperature. This is contrary to most observations. Jones (1976) gives the range 0.2–0.4 for the net efficiency. With a constant value of the net efficiency and using observed values of consumption per unit weight, the calculated growth rates tend to be too low for small fish or too high for large fish. Thus we have taken the net efficiency to be dependent on the weight of the fish, i.e. $0.29W^{-0.25}$. This gives a value of 0.36 for a 400 g fish, which is the observed average weight of a 3-year-old cod as it is recruited to the fishery and 0.19 for a 5-kg cod. This *ad hoc* relationship between weight and net efficiency has been chosen so as to give growth rates which are similar to those observed. Blaxter (1969) gives the cruising speed for gadoid species of two to three bodylengths per second. Here we are concerned with an average speed over 24 h. This average speed will definitely be lower than the cruising speed and has been set at one bodylength per second.

In some cases the above growth equation gives growth rates for the largest fish which are unnaturally high. Thus a maximum weight limit has been imposed on cod aged 8, 9, and 10 of 7.7, 9.0, and 11.0 kg respectively. This maximum is 10% above the highest historical value. At present the model does not take into consideration the weight loss due to spawning. This might be one reason why the largest fish grow too fast. In fact only the 9- and 10-year-old fish attain the imposed upper weight limit. Their biomass is small and they form only a very small part of the total yield of the cod stock.

4.3. Interaction

List of variables and parameters (as before, the index t refers to the year)

$e_{a,b,t,i}$ – biomass of a year old capelin consumed by one unit of weight of b-year-old cod in month i.

$E_{a,b,t,i}$ – biomass of a year old capelin consumed by the stock of b-year-old cod in month i.

$h_{b,t,i}$ – total monthly consumption by one unit of weight of b-year-old cod in month i.

$H_{b,t,i}$ – total monthly consumption by the stock of b-year-old cod.

$e_{x,b,t,i}$ – biomass of food other than capelin consumed by one unit of weight of b-year-old cod in month i.

$g_{a,b,i}$ – suitability coefficient of a year old capelin (a = 0, 1) for b-year-old cod relative to "other food".

$\Phi_{b,i}$ – the suitable biomass of "other food" available to b-year-old cod in month i.

Consumption by cod of the 2+ group of capelin

The relationship between the consumption by cod and 2+ capelin in October/November and biomass of 3+ capelin in March was given in section 3.1. We had

$$e_{2+,b,t,i} = r_{b,i}\frac{(b_{2+,t,i})^3}{(s_{b,i})^3 + (b_{2+,t,i})^3} \qquad (16)$$

Note that since we let the year start in May, the 2+ capelin in October/November and the 3+ capelin in March is 2+ in both cases. Here "b" denotes capelin biomass as before.

The coefficients r and s are dependent on the time of the year. They have been estimated for b = 2,3, . . ., 8 and i = 6 (October) and i = 11 (March). We use the i = 6 estimates for i = 6, 7, 8 (October–December) and the i = 11 estimate for i = 9, 10, 11, 12 (January–April). As for summer, as a first approximation we assume that there is no predation by cod on adult capelin, i.e. 2 years and older. This is not quite true since there is some predation on capelin in limited areas (Pálsson, 1985). However, in summer most of the 2-year-old and older capelin have migrated far to the north, out of reach of the cod stock (Vilhjálmsson, 1983).

Hence we put $r_{b,i} = 0$ for i = 1, 2, 3, 4, 5. The value of s is then immaterial.

For ages 9 and 10 we use the same values of r and s as for age 8.

To find the respective consumption of the two groups comprising the 2+ capelin group, i.e. 2- and 3-year-olds, we separate the consumption of the 2+ group according to their respective biomasses, i.e.

$$e_{a,b,t,i} = e_{2+,b,t,i}b_{a,t,i}/(b_{2,t,i} + b_{3,t,i}) \quad a = 2, 3. \qquad (17)$$

It is not as simple to find the consumption of young capelin, i.e. 0- and 1-year-old. The consumption per unit weight of predator of young capelin and all other food is $h_{b,t,i} - e_{2+,b,t,i}$. Then we will assume that the consumption of capelin and of other food is

$$e_{a,b,t,i} = (h_{b,t,i} - e_{2+,b,t,i}) \times \frac{(g_{a,b,i}b_{a,t,i})}{(\Phi_{b,i} + g_{0,b,i}b_{0,t,i} + g_{1,b,i}b_{1,t,i})} \quad a = 0, 1 \qquad (18)$$

$$e_{x,b,t,i} = (h_{b,t,i} - e_{2+,b,t,i}) \times \frac{(\Phi_{b,i})}{(\Phi_{b,i} + g_{0,b,i}b_{0,t,i} + g_{1,b,i}b_{1,t,i})} \qquad (19)$$

Here $\Phi_{b,i}$ is the biomass of "other food", available to b-year-old cod and $g_{a,b,i}$ is a measure of how "suitable and available" capelin of age a is to b-year-old cod, relative to other food. The values of the g's and Φ can only be guessed. However, they are chosen so as to make the consumption of young capelin similar to what has been observed in the past, which is usually only a small fraction of the total capelin consumption (Magnússon and Pálsson, 1989).

Finally, we calculate the total consumption of a year old capelin by the cod stock

$$E_{a,t,i} = \sum_{b=3}^{10} E_{a,b,t,i} = \sum_{b=3}^{10} e_{a,b,t,i}B_{b,t,i} \qquad (20)$$

Relationship between 2+ capelin consumption and total consumption

As explained in section 3.2 an empirical linear relationship has been derived for b = 2, 3, . . ., 8 (age of cod) and i = 6 (October) and i = 11 (March)

$$h_{b,t,i} = u_{b,i}e_{2+,b,t,i} + v_{b,i} \qquad (21)$$

We will let the October relationship hold for October–December (i = 6, 7, 8) and the March relationship for January–April (i = 9–12). Furthermore, we will assume that for $b \geq 5$ the available food is the same in summer as in early winter, and thus use the October relationship for May–September. Since we have assumed that there is no consumption of 2+ capelin during the summer months, this means that the total consumption per unit weight is always $v_{b,i}$. If the v as observed in October is used in summer, for cod aged 3 and 4, it turns out that the growth is too slow. Thus, for age groups 3 and 4 we will assume that the food supply is greater in summer than in winter. Thus we put $v_{b,i} = 15$ for i = 1–5 and b = 3 and 4. This is in accordance with the small amount of data that exist on consumption during the summer months. These data give consumption of between 1% and 1.5% of body weight per day for small fish. The results available on stomach content weights (Pálsson, 1983) indicate similar stomach content weights in late winter and summer, although slightly higher for the smallest cod, whereas smaller stomach weights were observed in October–December.

Hence, the total consumption by all b-year-old cod is

$$H_{b,t,i} = h_{b,t,i}B_{b,t,i} \qquad (22)$$

and the consumption by the entire cod stock is

$$H_{t,i} = \sum_{b=3}^{10} h_{b,t,i}B_{b,t,i} \qquad (23)$$

The average total consumption by one b-year-old cod is

$$A_{b,t,i} = W_{b,t,i}h_{b,t,i} \qquad (24)$$

and the fraction of a year old capelin in the diet of cod aged b is

$$p_{a,b,t,i} = e_{a,b,t,i}/h_{b,t,i} \qquad (25)$$

4.4. General

Initial conditions are required for some of the variables, i.e. the cod weights and the biomass vectors of cod and capelin. We take the monthly weight increment of capelin to be constant, thus the weights are fixed for each age and month. The inputs (or the control variables) and the outputs are the following:

Input

c_t^* – the total catch of capelin in season (year) t.

h_i – the distribution of the capelin catch over the year, $i = 1, 2, 3, \ldots, 12$ (the previous two parameters give the monthly catch of capelin in year t).

$F_{b,t,i} = S_b \times E_i \times \hat{E}_t$ – the fishing mortality fraction; the actual inputs are S_b, E_i, and $\hat{E}_t$. Alternatively, values of $F_{b,t,i}$ can be used directly as inputs.

T_i – temperature in month i

The recruitment of capelin is also an input into the model.

Output

$\sum_{b=3}^{10} C_{b,t,i}$ – total yield of cod (in tonnes) in year t.

Additional output can also be considered, e.g. weights and biomass of cod, amount of capelin consumed, predation and fishing mortality fractions for capelin.

Note that when the initial stock of cod, recruitment, and the fishing mortality fractions are given the catch in numbers for the next years is then determined. However, different growth rates due to different amounts of capelin available as food for cod will lead to different average weights and hence different yields (in tonnes) in spite of the numbers caught being fixed.

5. Results and discussion

In order to illustrate the possible effects of different stock sizes of capelin on growth and biomass, and hence yield, of cod, we have conducted some deterministic simulations for different capelin recruitment values. These simulations are preliminary and the outcome should only be taken as an indication of the possible effects. What is mainly of interest here is the relative change in growth and biomass of cod with changing capelin abundance caused by changes in capelin recruitment.

The model requires initial values for cod biomass and cod weights as well as capelin biomass. The initial weights of cod were calculated from the observed length distribution at age in March–April 1988 by the length–weight relationship given in Pálsson *et al.* (1988) for ages 3–8, and from observed values in the catch for ages 9 and 10. The initial biomass was then calculated by using these weights together with stock in numbers at age for 1988 obtained from VPA (Anon., 1989). The initial biomass values for capelin aged 0–3 were 100 000, 1 000 000, 1 500 000, and 500 000 t respectively at the beginning of the "year", i.e. beginning of May. In fact, these initial values have no effect on the results, since here we present only long-term values of the relevant variables.

The fishing mortalities for cod F were in all cases constant in time and were set as the 1988 values.

Table 8. Simulated long-term weights-at-age of cod (kg) and total biomass of cod (thousand tonnes) with varying capelin stock size (thousand tonnes).

Capelin stock	Weight-at-age 3	4	5	6	7	8	9	10	Cod biomass
0	0.49	0.95	1.65	2.08	2.62	3.19	3.72	4.07	544
323	0.49	0.97	1.69	2.16	2.74	3.37	3.96	4.78	558
613	0.50	1.01	1.81	2.39	3.14	3.94	4.71	5.78	598
893	0.51	1.05	1.94	2.66	3.60	4.59	5.60	6.93	643
1175	0.52	1.09	2.06	2.91	4.03	5.22	6.46	8.06	684
1467	0.52	1.12	2.17	3.13	4.40	5.78	7.23	9.08	720
1769	0.52	1.15	2.26	3.31	4.70	6.22	7.77	9.18	750
2080	0.53	1.18	2.34	3.45	4.94	6.57	7.77	9.91	774
2398	0.53	1.21	2.41	3.57	5.13	6.84	7.86	9.02	795
2720	0.53	1.23	2.48	3.67	5.28	7.06	7.75	9.17	814
3046	0.53	1.26	2.56	3.75	5.41	7.24	7.77	9.19	830
3376	0.53	1.28	2.58	3.83	5.52	7.40	7.80	9.13	844
3707	0.53	1.30	2.62	3.89	5.61	7.52	7.72	9.14	855
4043	0.53	1.32	2.65	3.94	5.69	7.53	7.73	9.15	865
4380	0.53	1.33	2.68	3.98	5.75	7.61	7.71	9.13	873
4721	0.53	1.34	2.70	4.02	5.79	7.67	7.78	9.21	880

We do not want to consider the possibilities of recruitment failure, so the critical spawning biomass for both capelin and cod was set very low. This is virtually equivalent to assuming constant recruitment. The recruitment for cod was taken as the average over 1980–1988, i.e. 196 million 3-year-old fish and the weight of a 3-year-old fish in January as it enters the fishery is 400 g, which is approximately the average over the past years. Thus recruitment is 78.4 thousand tonnes. This recruitment refers to 1 January.

The capelin biomass was changed by means of variable recruitment so as to give a wide range of biomass of recruited capelin (age 2+) on 1 October, i.e. from 0 to 4.7 million tonnes (Tables 8 and 9). This was done by varying a × bs_{crit} in Equation (7). The recruitment was constant from year to year in each simulation.

The yearly temperature profile was assumed the same for all years, with the temperature in each month being set as the 1980–1989 average north and east of Iceland.

When the fishing mortalities and recruitment are kept constant throughout, the system settles down to an equilibrium after 10 years and the initial conditions have no influence. Here we present only these long-term values of the variables of interest, since the short-term values will be heavily influenced by the initial values.

The results of these simulations in the case when there is no capelin harvest are presented in Tables 8 and 9, which give cod weights-at-age, total biomass of cod,

Table 9. Simulated long-term annual capelin consumption by cod (thousand tonnes) and annual yield of cod (thousand tonnes) with varying capelin stock size (thousand tonnes).

Capelin stock	Consumption by cod by prey age (years) 1	2	3	4	Total	Cod yield
0	0	0	0	0	0	198
323	5	13	38	13	69	205
613	10	26	104	45	184	226
893	14	39	319	75	447	249
1175	18	51	471	103	643	271
1467	21	62	602	129	814	290
1769	25	74	706	155	960	305
2080	29	85	785	179	1078	318
2398	32	97	847	201	1177	328
2720	36	109	896	221	1262	336
3046	39	120	937	240	1336	344
3376	43	132	970	257	1402	350
3707	47	143	996	271	1457	355
4043	50	154	1017	285	1506	359
4380	53	165	1034	296	1548	363
4721	57	176	1047	307	1587	366

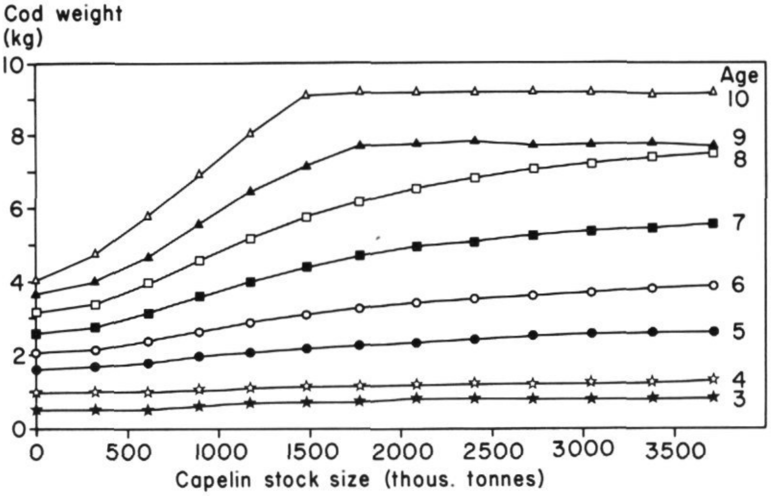

Figure 6. Long-term cod weights for ages 3–10 for different values of recruited capelin stock size.

consumption of capelin by age and total yield of cod after 10 years, for the different values of recruited capelin biomass on 1 October.

Figure 6 shows long-term cod weights for ages 3 to 10 years for different values of recruited capelin stock size (0 to 3.7 million tonnes). It can be seen from the figure and Table 8 that the effect of decreasing capelin stock increases with cod age and reaches a maximum for 8-year-old cod. This is due to the fact that older age groups have been subject to the trophic conditions for a longer period of time, i.e. over more ages. The reason that 9- and 10-year-old fish are less affected is that for a high capelin stock the maximum weight is reached and growth of these age groups is artificially constrained within the model (see section 4.2 "Growth").

Figure 7 shows the long-term biomass of cod as a function of the stock size of recruited capelin. The biomass of cod decreases from 880 000 down to 774 000 t as the capelin biomass decreases from 4.7 to 2.1 million tonnes. When capelin biomass is reduced further cod biomass decreases more rapidly, especially when capelin biomass has been reduced below approximately 1.5 million tonnes. When the capelin stock has been "exterminated" the biomass of cod is down to 544 000 t.

Figure 8 shows the yield of cod as a function of capelin biomass, which reflects the pattern seen in Figure 7, as would be expected. When the biomass of capelin is reduced from 4.7 to 2.1 million tonnes the yield of cod is reduced from 366 000 to 318 000 t, or by 13%. By further reduction of capelin biomass, cod yield is reduced more rapidly and is down to 198 000 t for an "exterminated" capelin stock.

These results indicate that growth and biomass of cod and hence the yield is not too greatly affected as long as capelin biomass is more than approximately 2 million

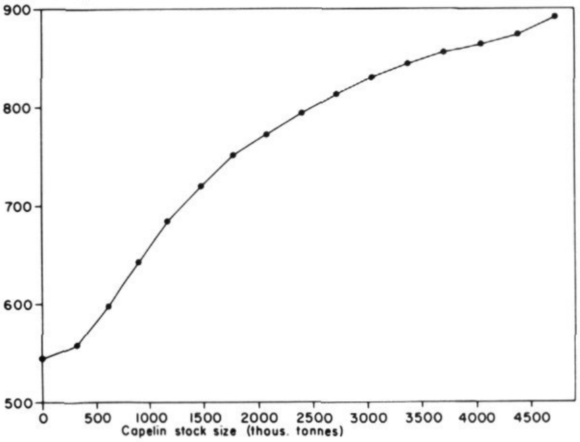

Figure 7. Long-term biomass of cod as a function of the stock size of recruited capelin.

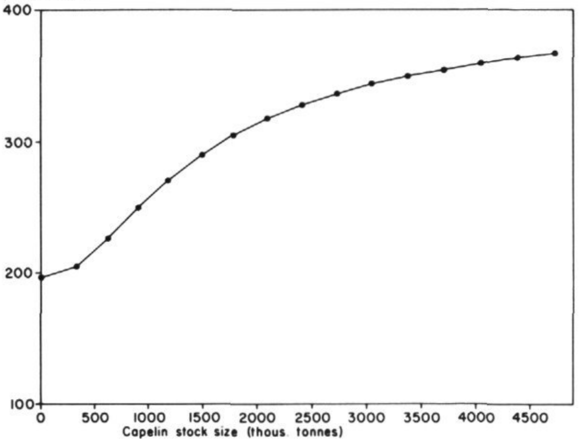

Figure 8. Yield of cod as a function of capelin biomass.

Table 10. Catch of capelin and yield of cod (thousand tonnes) for low (A) and average (B) capelin biomass and capelin catches taken in early winter (h1), throughout winter (h2), and late winter (h3).

	Yield of cod					
	A			B		
Catch of capelin	h1	h2	h3	h1	h2	h3
0	305	305	305	344	344	344
200	295	298	299	340	341	342
400	282	288	290	336	339	340
600	267	276	280	331	336	337
800	249	263	268	325	331	334
1000	231	250	258	316	326	330
1200	216	239	–	305	319	323
1400	–	–	–	291	308	314
1600	–	–	–	274	–	–
1800	–	–	–	255	–	–

tonnes. When capelin biomass is reduced further, a more pronounced effect is observed especially when capelin biomass is less than approximately 1.5 million tonnes.

The amount of capelin available to the cod over the year depends not just on the size of the recruited capelin stock on 1 October. The capelin stock is harvested, which of course affects the amount available to the cod stock. If we assume a fixed pattern in the distribution of the catch over the year, i.e. a fixed $\bar{h}$, the yield of cod is a function of both capelin stock size on 1 October and of the catch of capelin over the year. The yield is then represented by a two-dimensional surface in (b, c, C) space (recruited capelin biomass on 1 October, capelin catch, and cod yield respectively). Figure 8 is thus the vertical cross-section for $c = 0$.

In order to see the effect of different capelin catches on the cod yield we take two vertical cross-sections of the yield surface for fixed capelin biomass on 1 October. That is, we fix the recruitment to give a recruited capelin biomass on 1 October of 3 046 000 t, which can be regarded as an average value, and 1 769 000 t, which is a low value, and look at the effect on cod yield of different capelin catches. In order to examine the sensitivity of the yield with respect to the pattern in the distribution of the catch over the season, we consider three different patterns: (1) All the catch is taken in early winter, i.e. $h = 0.4,\ 0.4,\ 0.2$ for October, November, and December, respectively. (2) The pattern based on the 1987–1989 catches (see section 4.1 "Catch"). (3) All the catch is taken in late winter ($h = 0.4, 0.4, 0.2$ for January, February, March, respectively).

The results are shown in Table 10 and the corresponding curves in Figure 9. As expected, cod yield is most affected when all the capelin catch is taken early in the season, because then the food availability for cod will be lower for the major part of the year. Higher capelin catches can also be sustained in this case since they are taken before the cod stock has had a chance to make a significant indentation in the capelin stock. It is also clear from the figures that cod yield decreases much more sharply with increasing capelin catch at low capelin recruitment values. In fact, for the 1987–1989 catch

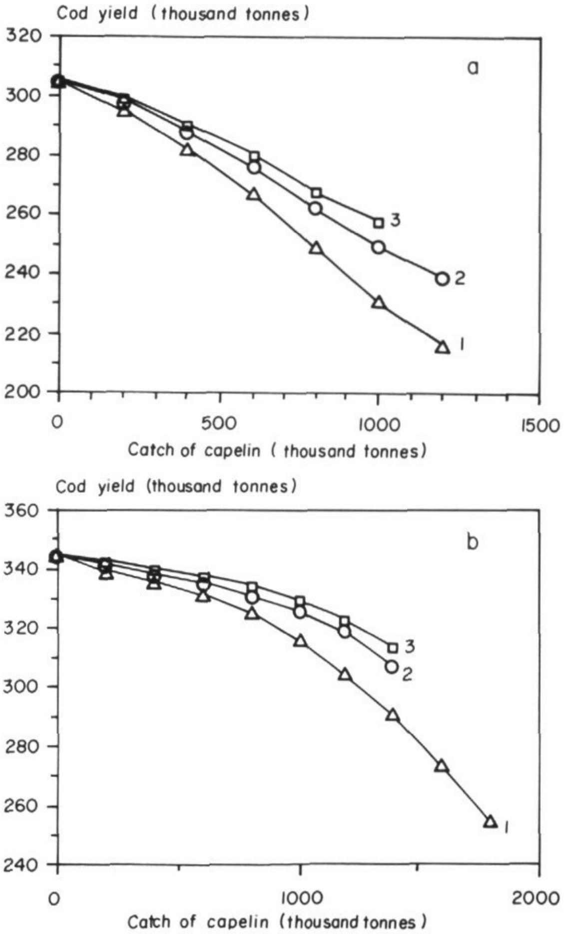

Figure 9. Catch of capelin and yield of cod for low (a) and average (b) capelin biomass and capelin catches taken in early winter (1), throughout winter (2), and late winter (3).

pattern for capelin, cod yield decreases by 55 000 t (18%) as capelin catch increases from zero to one million tonnes, but only by 18 000 t (5.2%) for the higher recruitment value, since in the latter case it is the flat upper part of the predation function (cf. Figs. 1 and 2) which is relevant. Indeed, it can be argued that capelin catches up to one million tonnes do not significantly affect the cod yield as long as the long-term recruitment of capelin is not greatly below the average over the last decade, and that the catch is not taken too early in the season.

During the last three or four years the size of the capelin stock (age 2 and older, 1 August) has been approximately 2 million tonnes, based on acoustic estimates (Anon., 1989), which corresponds to about 3.8 million tonnes of corrected biomass. This is well above the average for the period since 1978 (Anon., 1989). During this period the catch of capelin was 1.1 million tonnes annually on the average. In the early 1980s, however, the (acoustic) capelin biomass was reduced to 600 000 t (Anon., 1989). According to the present results this would lead to a significant decrease in cod growth and biomass and hence in cod yield, which was the case during this period. It should be noted that in some years substantial catches of capelin have been taken in August and September. Thus, the numbers from the simulation model for recruited capelin stock on 1 October are not really comparable to the acoustic estimates in October given in Table 1, since in the model no catches are taken prior to October. The model numbers are more comparable to stock sizes on 1 August, as back calculated from the October acoustic estimates (Anon., 1989).

A few simulations were also carried out with different parameters (e.g. different net efficiency in the growth equation, different natural mortality for capelin, etc.). The outcomes in absolute terms were of course different, but the relative changes in cod biomass and yield with changing capelin biomass/quota were similar. For example, if the monthly natural mortality fraction (from other causes than predation by cod, see section 4.1 "Change in biomass . . .") is 0.01 instead of 0.002, then cod yield decreases by 5–10%. It should be noted that the increased natural mortality affects all age groups of capelin, also the younger groups. Thus, the effect is not just increased natural mortality for the recruited capelin, but also lower recruitment to the 2^+ age class. The change in the cod yield as natural mortality is increased should be viewed with this in mind.

It should be stressed that in these simulations the loss in cod yield with decreasing capelin biomass is only due to slower growth rates and hence lower average weights. No account is taken of possible recruitment failure for either cod or capelin, but the possibility of a lower than average recruitment due to a smaller spawning-stock biomass should not be ruled out.

A number of further simulations and modifications are required. First, it is desirable to "tune" the model by using actual historical data on recruitment, fishing mortalities, etc., for both stocks and compare the output to observations of say, growth rates, consumption of capelin, and capelin stock sizes. Second, some tests should be done on the effects of changes in the stock size and age composition of the cod stock, e.g. effect of conservation measures for young cod. Third, the effect of temperature changes should be investigated and, finally, using the known variability in recruitment of both species, stochastic simulations should be carried out, giving the average and the standard deviation of the cod yield.

Some modifications to the model might be for example:

1. The model does not take into consideration the energy requirements due to spawning. Incorporating this might go some way towards slowing down the growth of the largest fish, which is occasionally too fast.
2. No data on summer consumption have been used here. Some such data already exist and more will be collected in the future. Thus, information on the value of the coefficients in the key relationships in Equations (1) and (2) for the summer months will be obtained.
3. Take into account the difference between food types for growth, e.g. transform "other food" into the "capelin equivalent" for the purpose of growth. Or, preferably, the estimates of daily consumption and growth rates should be based on experiments with Icelandic cod fed whole capelin and other natural prey at the actual temperatures in Icelandic waters.

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Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem[1]

Astrid Jarre, Peter Muck, and Daniel Pauly

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The major interactions between fish stocks of the Peruvian upwelling ecosystem are predation of anchoveta (Engraulis ringens) by the teleosts Trachurus murphyi, Scomber japonicus, Sarda chiliensis, and Merluccius gayi, by three species of guano birds, and by two pinniped species. Their distributions are mediated mainly by sea surface temperature. Predation levels are determined by relative population sizes and the temporal and spatial overlap of the distribution of these species. Balanced "box" models which quantify these, and other trophic interactions for the periods 1953–1959, 1960–1969, and 1973–1979 are presented, along with the basic structure of a spatial simulation model incorporating dynamic versions of these interactions. The interrelationships of the steady-state box models, and of the simulation models are outlined, as are their potential uses for research management.

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Introduction

The Peruvian upwelling ecosystem is a typical eastern boundary current area (Parrish *et al.*, 1983). During the 1960s and the early 1970s, it supported the largest single-species fishery in the world, that for the anchoveta (*Engraulis ringens*) (Cushing, 1969; Ryther, 1969; Pauly and Tsukayama, 1987). As defined here, this system has an alongshore extension of 2100 km, from 3.5°S to 18.5°S, and an offshore extension of 200 nautical miles (nm) or about 370 km, with a total area of about 780 000 km^2 (Fig. 1). The shelf is wider in the north than in the south; its mean width is 60 nm. This paper is based predominantly on data pertaining to the northern and central region of the system, i.e. from 4°S to 14°S, corresponding to a total area of approximately 82 000 km^2, which covers the main distribution area of anchoveta.

In the late 1970s, a cooperative fisheries research project was initiated between Peru and the Federal Republic of Germany, the Programa Cooperativo Peruano-Aléman de Investigacion Pesquera (PROCOPA), based at the Instituto del Mar del Perú (IMARPE), Callao, Peru, to construct a model of the pelagic fisheries of the Peruvian ecosystem. It was anticipated that this model would be used either for real time fishery management, i.e. for fleet deployment and the identification of optimum responses to complex occurrences such as El Niño events, or at least to help sensitize managers to environmental effects and their management implications.

Major results of the analyses of field data from the project are contained in two books, one edited by Pauly and Tsukayama (1987), the other by Pauly *et al.* (1989). The contributions in these books present numerous time series of oceanographic and climatic data, covering the period from 1953 to the mid-1980s on a monthly basis, as well as time series of primary production (Chavez *et al.*, 1989; Mendo *et al.*, 1989), and zooplankton and fish biomass (Fig. 2). Also included are documentations of the dynamics of various anchoveta predators and models of their anchoveta consumption. The species (groups) covered are: bonito (*Sarda chiliensis*) (Pauly *et al.*, 1987); mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) (Muck and Sanchez, 1987); hake (*Merluccius gayi*) (Espino and Wosnitza-Mendo, 1989; Muck, 1989a); guano birds (cormorant (*Phalacrocorax bougainvillii*), booby (*Sula variegata*) and pelican (*Pelecanus thagus*)) (Muck and Pauly, 1987); pinnipeds (fur seal (*Arctocephalus australis*) and sea lion (*Otaria byronia*)) (Muck and Fuentes, 1987).

The estimates of predation on anchoveta, computed

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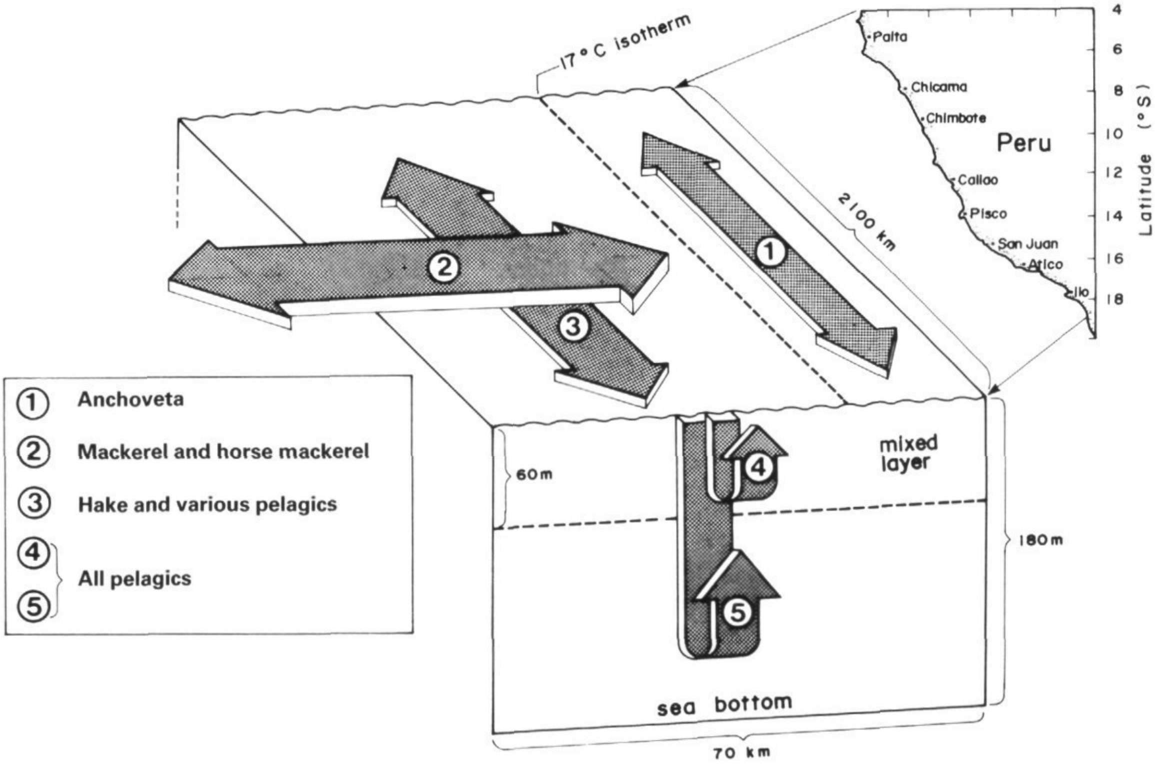

Figure 1. Schematic representation of the Peruvian upwelling system, showing axes of seasonal migration and/or diurnal movements of major resource species (see text).

on a monthly basis from 1953 to 1982 (and beyond), combined with fishery catch data, were used to reconstruct monthly anchoveta biomass and a number of derived variables, e.g. estimates of the part of natural mortality caused by the various predators (Fig. 3). These results have made it possible to model the Peruvian upwelling ecosystem as a whole. This paper briefly documents what has been achieved to date.

Steady-state modelling

Steady-state trophic models are commonly used to integrate biomass and rate estimates, to identify major energy pathways and gaps in one's knowledge of an ecosystem (see, e.g., Steele, 1974; Silvert, 1982). In view of the known variability of the Peruvian upwelling ecosystem (see, e.g., Bohle-Carbonell, 1989; Muck, 1989b), we have opted for constructing several models describing distinct periods during which the biomass of major species (groups) or "boxes" did not fluctuate so much as to render meaningless the estimation of mean values. Pending analyses on a shorter time scale, we present here results for three periods: (i) 1953–1959, during which anchoveta was moderately abundant and the fishery was limited; (ii) 1960–1969, during which anchoveta biomass and fishery efforts and catches were high, and (iii) 1973–1979, i.e., the period following the 1972/73 collapse of the fishery (Fig. 3, Table 1).

The basic concept of the ECOPATH model of J. J. Polovina and associates (Polovina, 1984a, b, 1985; Polovina and Ow, 1983; Grigg *et al.*, 1984) as further developed by Pauly *et al.* (1987), was used for model constructions.

In this formulation, for any species (group) (i) in a system, the rate of change of biomass $dB/dt = 0$, i.e.

Production by (i) = all predation on (i) + non-predatory biomass losses of (i) + fishery catches of (i) + other exports of (i) (1)

For each of the species (groups), its energy balance is given by

Consumption + import = predation mortality + export + contributions to detritus + respiration (2)

Equation (1), applied to all components of the model, leads to a system of linear equations which can be solved for a given set of unknowns. Polovina and Ow (1983) provide a computer program which implements this

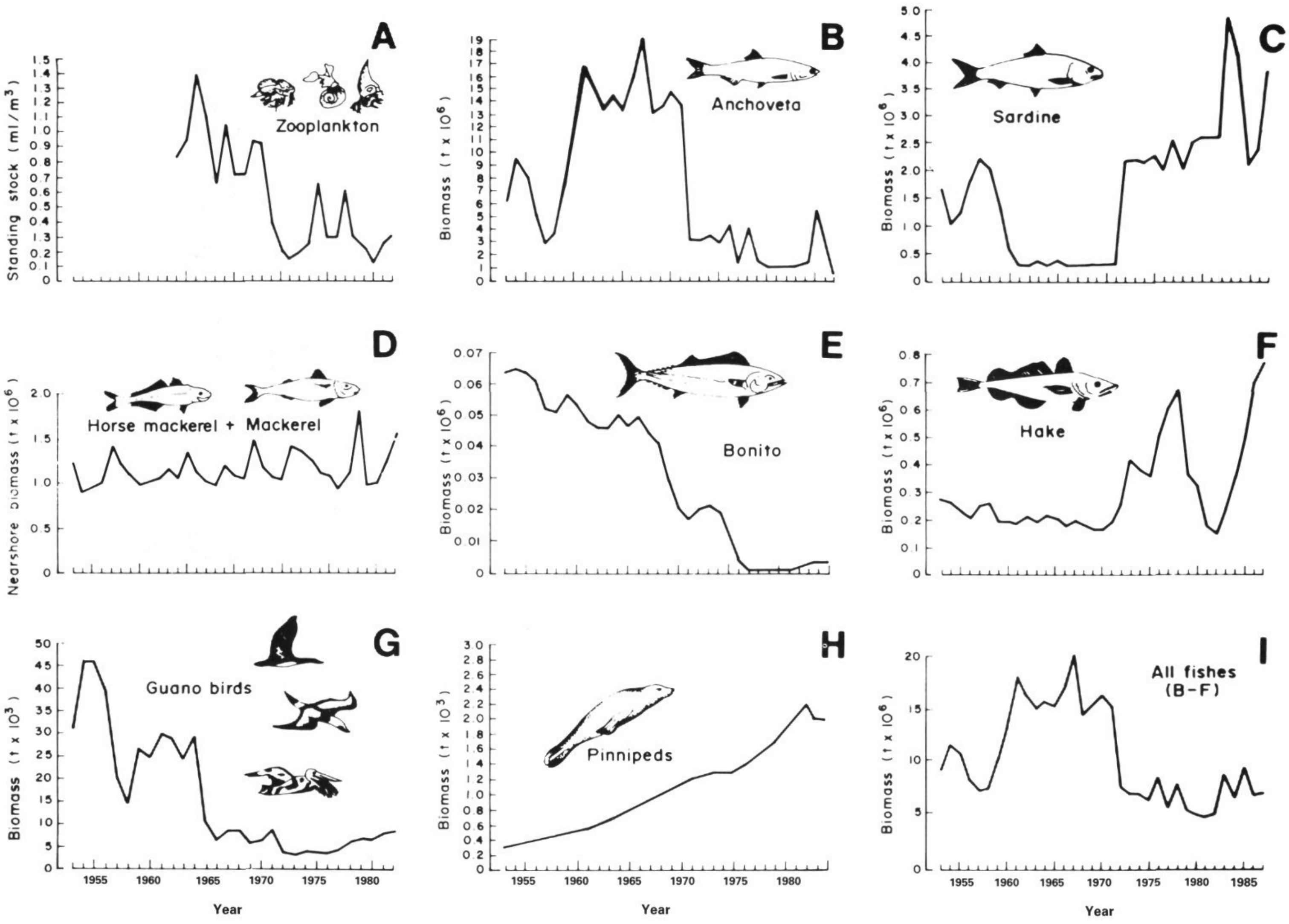

Figure 2. Biomass of major species of the Peruvian upwelling system, as estimated using approaches documented in Pauly and Tsukayama (1987) and in Pauly *et al.* (1989). Note different Y-scales.

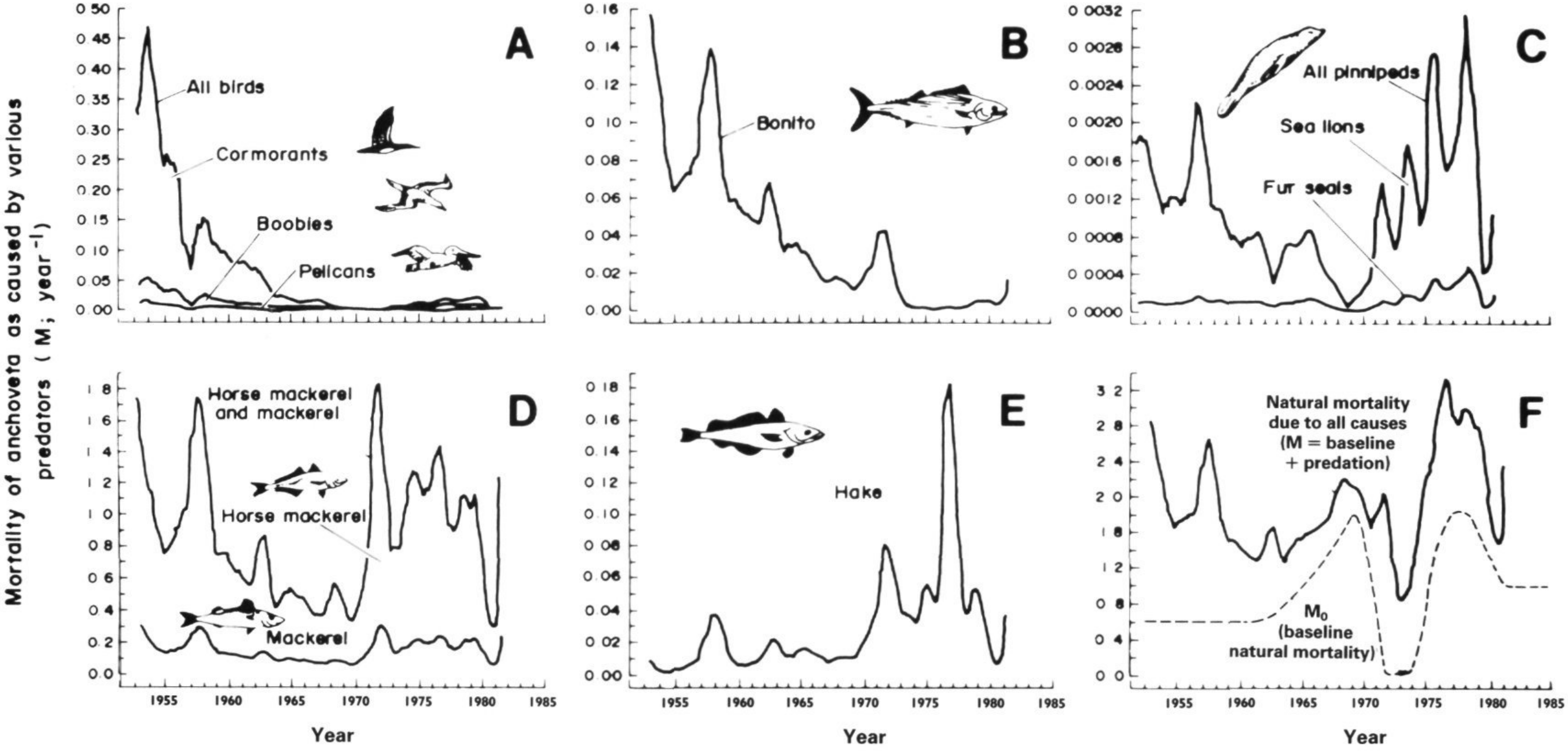

Figure 3. Estimates of natural mortality (M) of anchoveta (*Engraulis ringens*) as caused by its various predators. M is decomposed into its various components using estimates of predator-specific predation and a length-structured VPA technique. This was calibrated using acoustic estimates of biomass and allowed for estimation of baseline natural mortality (M_o) (adapted from Pauly and Palomares, 1989). Note relative constancy of overall M due to complementarity of some predators (A vs. D).

Table 1. Fishery catches ($t \times km^{-2}$) used for construction of box models of the Peruvian upwelling ecosystem in Figures 4–6. Data from IMARPE (1987), contributions in Pauly and Tsukayama (1987) or Pauly *et al.* (1989).

Group	1953–1959	1960–1969	1973–1979
Macrobenthos	0.010	0.090	0.190
Anchoveta	6.820	110.240	32.150
Sardine	0.010	0.040	7.490
Mackerel	0.070	0.100	0.800
Horse mackerel	0.030	0.030	2.280
Bonito	0.060	0.050	0.060
Hake	0.070	0.070	1.610
Other pelagics	0.230	0.240	0.290
Other demersals	0.180	0.300	0.600
Other mammals	0.001	0.001	0.002

approach for the estimation of biomasses. The data requirements are:

- estimates of mean total mortality (Z, per year) for each box
- estimates of mean annual Q/B, the food consumption (Q) per unit biomass (B) for each box
- estimates of ecotrophic efficiency for each box (the fraction of the total production of a box that is consumed by predators included in the model)
- an estimate of catch or of biomass for the top predator(s), as needed to solve the system of equations from the "top down"
- a "diet-consumption matrix", in which the fraction (in weight) of each box in the diet of each other box is indicated and in which the rows must add up to unity.

Pauly *et al.* (1987) modified the program of Polovina and Ow (1983). Major changes are:

(i) The system of equations can be solved for unknowns other than the biomasses. Also, the routine used for matrix inversion (Mackay, 1981) computes least-squares estimates of the unknowns when the system is overdetermined, and provides (non-unique) solutions when the system is slightly underdetermined.
(ii) A number of physiological and ecological attributes of the species (groups) included in each box are automatically computed after their biomass, food consumption, and production have been estimated.
(iii) The computed flows between "boxes" are used to compute statistics relevant to Ulanowicz's (1986) theory of ecosystem phenomenology.

In this study, the biomasses were known (Fig. 2), or could be straightforwardly approximated, as were the mortalities and the food consumption estimates. Because of limited information on excretion and egestion values of most boxes, default values of 5% for excretion and 15% for egestion (Winberg, 1956) were accepted.

We used some of the attributes in (ii) above to assess the mutual compatibility of our inputs. These attributes were:

(a) Ecotrophic efficiency (see above), where $0 \leq EE < 1$ serves as constraint.
(b) Gross transfer efficiency (all production from a box/all inputs into that box); the range of which is usually between 0 and 0.3.
(c) Ivlev's electivity index, defined by:

$$I = (r_i - p_i)/(r_i + p_i) \tag{3}$$

where r_i is the relative count or biomass of a species i in the diet of a particular predator, and p_i is its relative count or biomass in the ecosystem (i.e. included in the model) (Ivlev, 1961; Parsons and LeBrasseur, 1970). This index can range from −1 (prey is not consumed at all) to near +1 (prey is consumed exclusively).

The construction of the model involved: (1) preparation of an initial set of biomass and rate inputs and of an initial diet-composition matrix; (2) estimation of model parameters, and of the physiological and ecological attributes listed above; (3) performing small changes in the initial values and returning to item (2) until all attributes examined took values within a range considered acceptable. (The initial and modified values for each of the periods considered here are given in Jarre *et al.*, 1989.)

Figures 4, 5, and 6 give the results obtained. These three graphs and their associated parameters indicate that our quantifications of the biomasses and our concepts of the interactions between various species (groups) of the Peruvian ecosystem are mutually compatible within a factor of about two with their published value. Major changes had to be made only (i) in the initial estimate of the zooplankton biomass (by a factor of three) for the 1950s and 1960s, probably due to our limited knowledge on the actual mortality and consumption rates of this species group; (ii) the biomasses of the heterogeneous groups of "other pelagics" and "other demersals", for which the official catch statistics might not be the adequate basis for estimation of biomass; and (iii) the mortality of the sardine, which had to be raised from a published value that was very low to a value close to that of anchoveta.

An interesting aspect of Figures 4, 5, and 6 is their immediate visual impact, i.e. the strong difference in ecosystem structure which they indicate. This impact was achieved by two techniques, apparently not used previously for the graphical representation of box models, i.e.: (1) making the area of each box proportional to the logarithm of the biomass it represents, and (2) using the trophic level[1] of each box to arrange the boxes vertically.

The graphs thus allow a direct assessment of the

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[1] The trophic level of a species (group) is defined as one plus the mean of the tropic levels of its prey items, weighted by their fraction in the total diet.

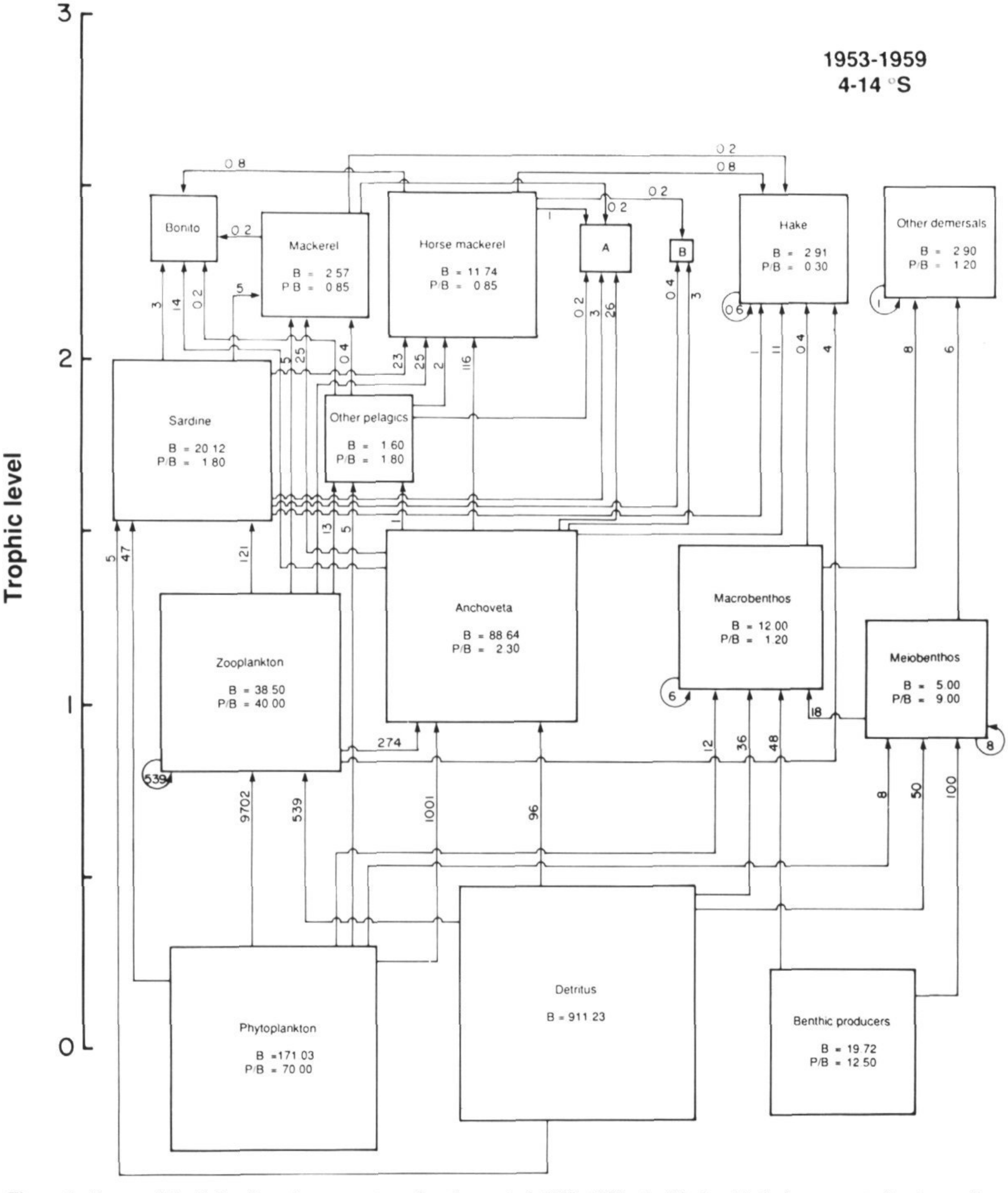

Figure 4. Box model of the Peruvian ecosystem for the period 1953–1959. A. Marine birds (cormorant, booby, pelican; $B = 0.40\,t \times km^{-2}$, $P/B = 0.04\,yr^{-1}$). B. Sea mammals (sea lion, fur seal, and others: $B = 0.07\,t \times km^{-2}$, $P/B = 0.09\,yr^{-1}$). Bonito: $B = 0.72\,t \times km^{-2}$, $P/B = 0.91\,yr^{-1}$. Flows greater than $1\,t \times km^{-2} \times yr^{-1}$ are rounded to integer numbers; those between 0.1 and $0.9\,t \times km^{-2}\,yr^{-1}$ are rounded to one digit. Flows of less than $0.1\,t \times km^{-2} \times yr^{-1}$, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

differences between the three periods considered here, e.g. anchoveta is more important in the 1960–1969 period than in the earlier and later periods; and sardine is more important in the 1973–1979 period than in the two earlier periods. The trophic level of the top predators is increased as a consequence of increased consumption of sardine instead of anchoveta as well as increased consumption of mackerel and horse mackerel.

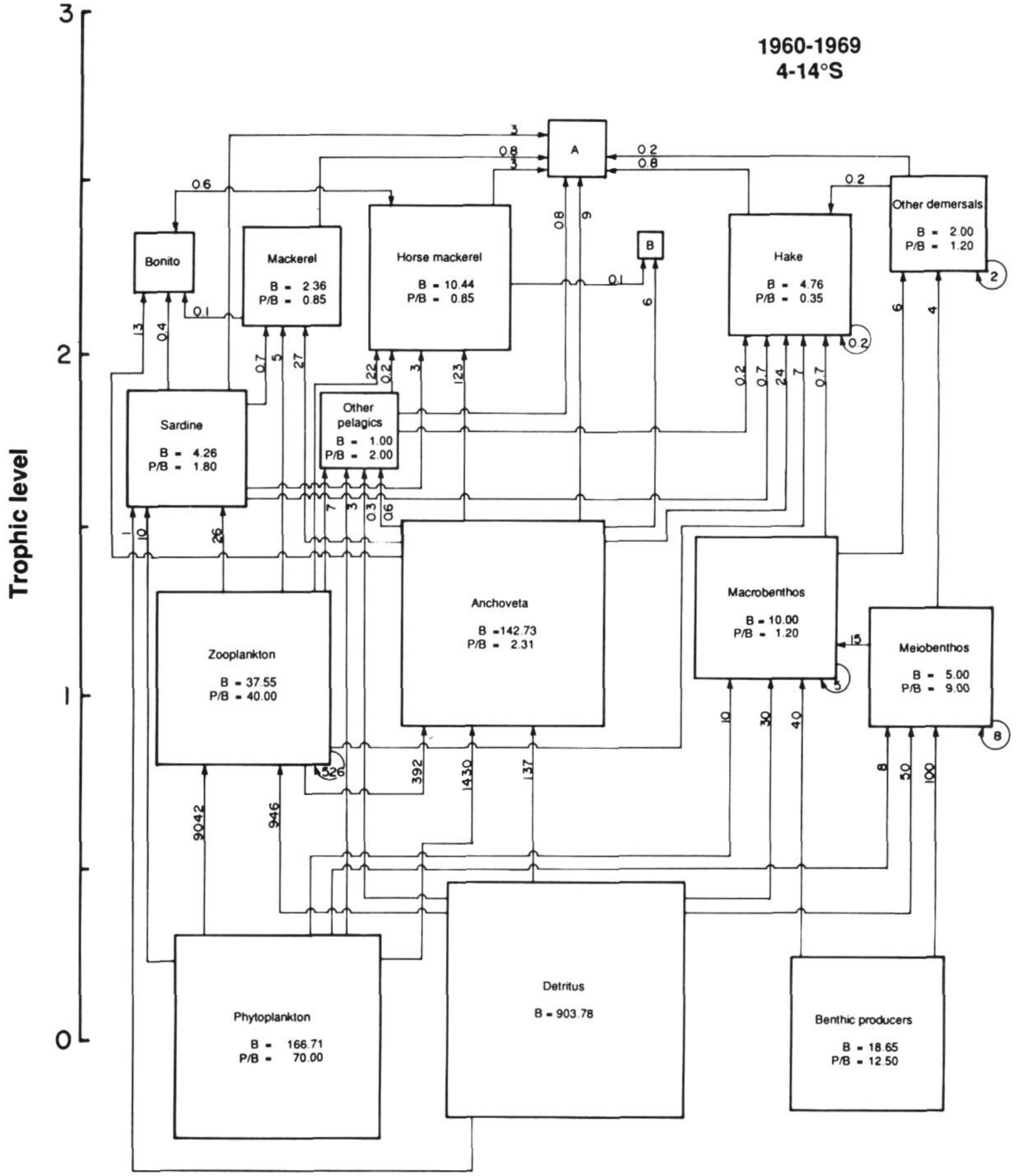

Figure 5. Box model of the Peruvian ecosystem for the period 1960–1969. A. Marine birds (cormorant, booby, pelican; $B = 0.21\,t \times km^{-2}$, $P/B = 0.04\,yr^{-1}$). B. Sea mammals (sea lion, fur seal, and others: $B = 0.07\,t \times km^{-2}$, $P/B = 0.09\,yr^{-1}$). Bonito: $B = 0.55\,t \times km^{-2}$, $P/B = 0.93\,yr^{-1}$. Flows greater than $1\,t \times km^{-2} \times yr^{-1}$ are rounded to integer numbers; those between 0.1 and $0.9\,t \times km^{-2} \times yr^{-1}$ are rounded to one digit. Flows of less than $0.1\,t \times km^{-2} \times yr^{-1}$, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

Another approach for the interpretation of the "weighted graphs" in Figures 4–6 is via the theory of Ulanowicz (1986), who introduced a set of single-number characteristics of ecosystems. The "ascendancy" of an ecosystem is defined as the product of the total system throughput (sum of all flows within the system) and the "average mutual information"; the latter index is computed from the network structure, and

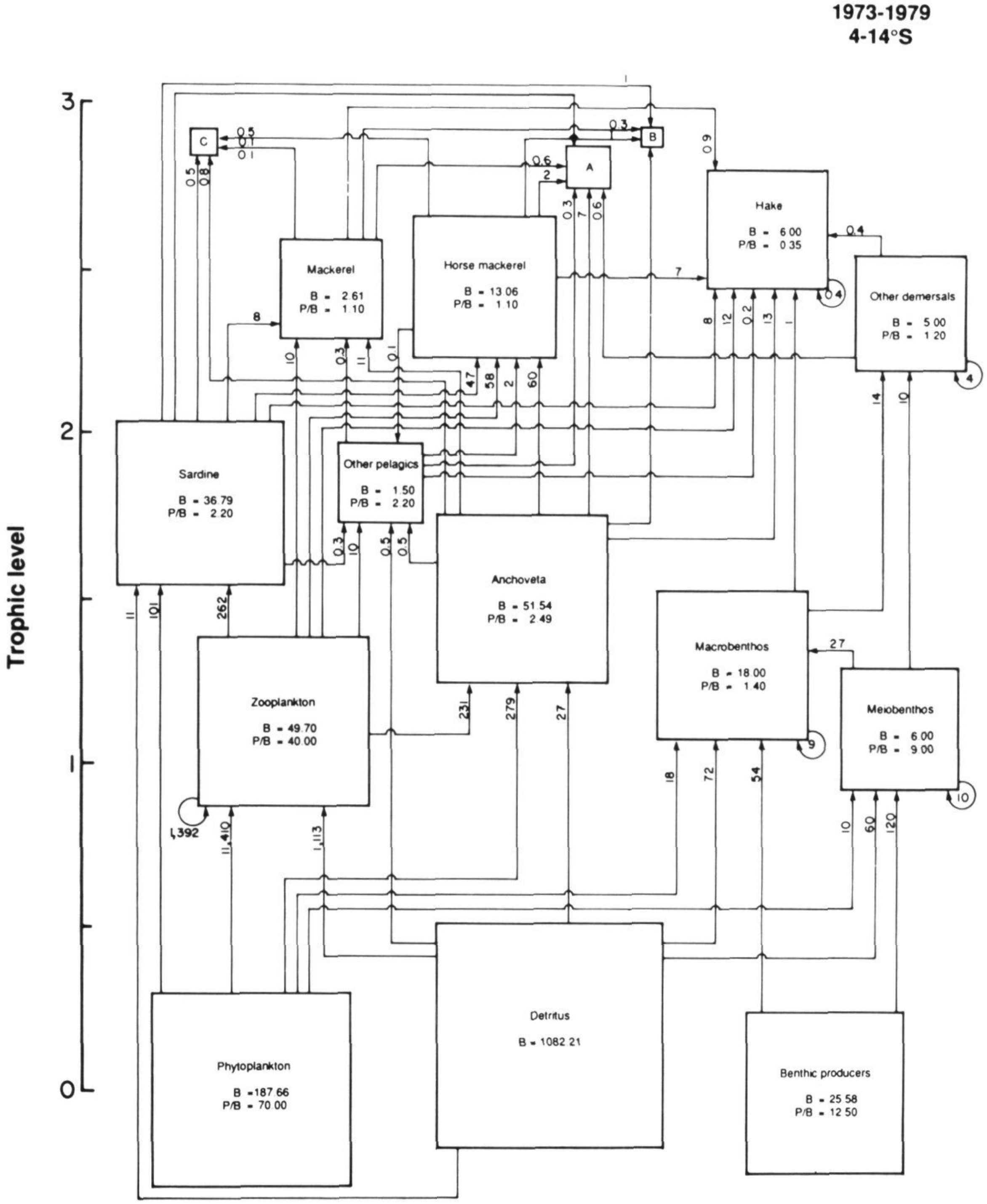

Figure 6. Box model of the Peruvian ecosystem for the period 1973–1979. A. Marine birds (cormorant, booby, pelican; $B = 0.28\,t \times km^{-2}$, $P/B = 0.04\,yr^{-1}$). B. Sea mammals (sea lion, fur seal, and others; $B = 0.09\,t \times km^{-2}$, $P/B = 0.09\,yr^{-1}$). C. Bonito ($B = 0.09\,t \times km^{-2}$, $P/B = 0.93\,yr^{-1}$). Flows greater than $1\,t \times km^{-2} \times yr^{-1}$ are rounded to integer numbers; those between 0.1 and $0.9\,t \times km^{-2} \times yr^{-1}$ are rounded to one digit. Flows of less than $0.1\,t \times km^{-2} \times yr^{-1}$, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

Table 2. Whole-system indices of the box models in Figures 4–6, and indices computed by Pauly (1987) from the models in Walsh (1981).

Index	This study 1953–1959	This study 1963–1969	This study 1973–1979	Walsh's model before 1972	Walsh's model after 1972
Number of boxes[a]	19	19	19	12	12
Total system throughput (t wet weight × km^{-2})	29 600	29 382	33 539	37 027[b]	34 591[b]
Full development capacity (t wet weight × km^{-2})	57 521	57 358	61 905	81 529[b]	73 484[b]
Full ascendency (%)	39.4	37.4	36.4	64.6	61.6
System redundancy (%)	27.5	30.6	34.4	12.8	15.1
Fishery "trophic level"	2.4	2.2	2.7	–	–
Fishery gross efficiency	0.0006	0.0093	0.0034	–	–

[a] Excluding fishery.

[b] The estimates of Walsh (1981) were converted from carbon to wet weight using 1 gC = 13.93 g wet weight (average of Cushing (1971) and Ryther (1969)).

is maximized if (i) flows are equally distributed among the boxes and (ii) each box has only one input and one output (i.e. origin and destination of any flowbit are determined). The "system redundancy" describes the loss of information due to multiple flows between the boxes of the ecosystem (i.e. the existence of multiple ways of connecting any two boxes).

These summary statistics, computed for the three models presented here, are given in Table 2. The throughput of the system was similar during the 1950s and 1960s, and increased in the 1970s, partly due to an increase in primary production in the upwelling system (Mendo *et al.*, 1989). The ascendency decreased, which in this case means a loss in "mutual information", also shown in the decrease of 12% of the corresponding index from the 1950s to the 1970s. The increase in redundancy is due to the fact that the anchoveta, previously of overwhelming importance to piscivores, was in part replaced by other components of the system, including anchoveta predators. This led to an increase in parallel energy transfer, as mentioned above. Our preliminary conclusion, based on the three periods considered here, is that the Peruvian ecosystem is less mature (*sensu* Odum, 1969, see Ulanowicz, 1986, p. 122) after the decline of the anchoveta than it was before.

The fishery fits in the model as an almost pure "anchoveta predator" in the 1950s and 1960s. Its "trophic level" increased in the 1970s, after the anchoveta collapse, due to the increased catch of anchoveta predators mackerel, horse mackerel, and hake. The increase in fishing effort from the 1950s to the 1960s is clearly reflected in the 15-fold increase of the fishery's gross efficiency (total catch/primary production), and the collapse of the fishery after 1972 in the decline of its efficiency to only 36% of the high value of the 1960s. It should be noted, however, that the fishery still retained an efficiency which is more than five times higher than the value from the 1950s. The partitioning of the total fish predation among fishes, birds, mammals, and the fishery (Fig. 7) shows the same pattern, albeit less pronounced.

Pauly *et al.* (1987) computed the above summary statistics from the model of the Peruvian upwelling ecosystem presented by Walsh (1981). Since Walsh's models set focus on different parts of the ecosystem, and hence had a different basic structure than the models in the present study, it is difficult to directly compare the values of ascendency and redundancy obtained. The changes in the system, i.e. the decrease of mutual information, the decline of ascendency and the increase in redundancy, however, are apparent from Walsh's (1981) approach as well (Table 2).

Simulation modelling

Our simulation model of the fish resources and fisheries of the Peruvian upwelling ecosystem is not complete. However, its basic structure with regard to spatial resolution and the role of sea surface temperature (SST) as driving factor is established. SST is used as a key factor because it has been shown by various authors to determine the distribution, hence the overlap and potential for trophic interactions, of the various pelagic species of the Peruvian upwelling ecosystem as follows:

1. When coastal SSTs are low, i.e. when the upwelling is strong, anchoveta occur near the surface on the shelf along the coast of Peru. Hake stay in the north because the bottom O_2 concentration in the upwelling area is low. Mackerel and horse mackerel stay offshore as they are oceanic species requiring temperatures of at least 20°C.
2. When coastal SSTs are high, anchoveta tend to crowd within a few remaining pockets of cold water and/or

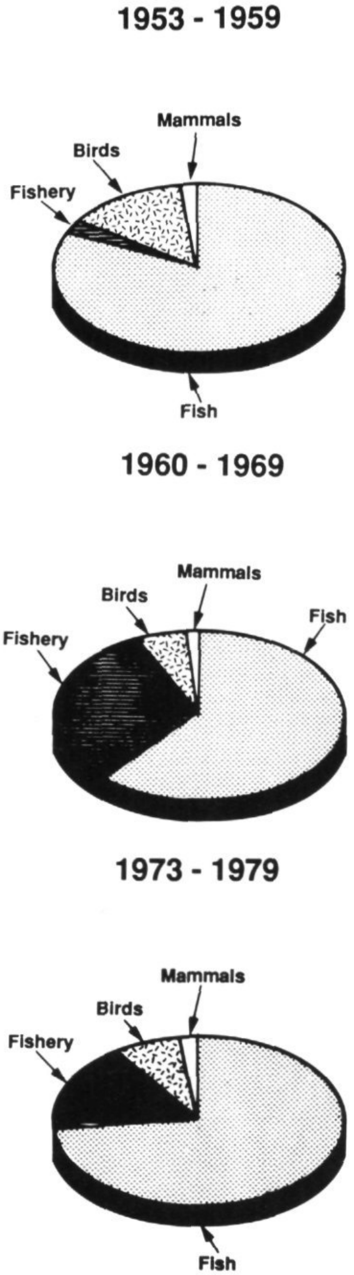

Figure 7. Partitioning of total fish production among fishes, birds, mammals, and the fishery, from the models in Figures 4–6. Contributions to detritus are disregarded.

to escape to greater depths, hence out of reach of guano birds and purse seiners. Hake migrate southward and feed on anchoveta, and mackerel and horse mackerel move inshore and consume large quantities of anchoveta.

The situation in (1) is typical of (austral) winter conditions; that in (2) is typical of summer conditions, and particularly of El Niño events, during which the crowding of anchoveta and their consumption by hake, mackerel, and especially by horse mackerel, become extremely pronounced. A brief account is given below of a simulation model which incorporates these features.

The large area of the Peruvian upwelling ecosystem was divided into manageable units by grouping administrative "fishing areas" (*areas de pesca*) as defined by IMARPE. This resulted in a total of 150 approximately rectangular "local areas", each of which extend one degree latitude southwards (covering the range from 3.5°S to 18.5°S) and 20 nm offshore, parallel to an idealized coastline (Fig. 8A). To estimate the size of the fish stock in each subarea at a particular time (month), a "local potential distribution volume" has been defined. Its size is assumed to depend on (i) the physical properties of this subarea; and (ii) the specific physiological requirements of each species with respect to temperature and oxygen content of the water column (Fig. 8B, C, D). We assume that the fish are homogeneously distributed inside this volume. Species-specific "local shelf preference indices" are introduced to account for the depth preference of coastal and demersal species, food related preferences and other factors. The size of a population in a given subarea is proportional to the local potential distribution volume divided by the total distribution volume of the ecosystem.

For the calculation of the local potential distribution volume, temperature tolerance limits were obtained from field observations (Jordan, 1971; Zuta *et al.*, 1983; Espino *et al.*, 1985; Serra and Tsukayama, 1988); they are 14–21°C for anchoveta, 16–23°C for sardine, 15–25°C for mackerel, 16–26°C for horse mackerel, and 14–22°C for hake. Oxygen tolerance limits were taken as 1.8 ml O_2/l for anchoveta, mackerel, and horse mackerel (Villavicencio and Muck, 1985; Mathisen, 1989), 2 ml O_2/l for sardine (Serra and Tsukayama 1988), and 0.4 ml O_2/l for hake (see Fig. 1 in Espino and Wosnitza-Mendo, 1988).

Temperature and oxygen concentration vertical profiles were computed from SST based on relationships given in Espino *et al.* (1985). SSTs were estimated from the data from nine Peruvian shore stations (Muck *et al.*, 1989) and the offshore temperature series in Bakun (1987), yielding a regression which was used to estimate local SST within 70 nm from the coast. Coastal SSTs are linearly interpolated between shore stations. For distances of more than 70 nm, SST is assumed constant along offshore transects.

In any given subarea, the vulnerability of a particular fish species to its predators (i.e. the degree of overlap of water volume inhabited by predator and prey) and to the fishery is determined by their distribution within the entire water column (Fig. 8E). The amount actually consumed is determined by the biomass of the predators, their temperature-mediated food requirements, and the biomass and vulnerability of the prey, following

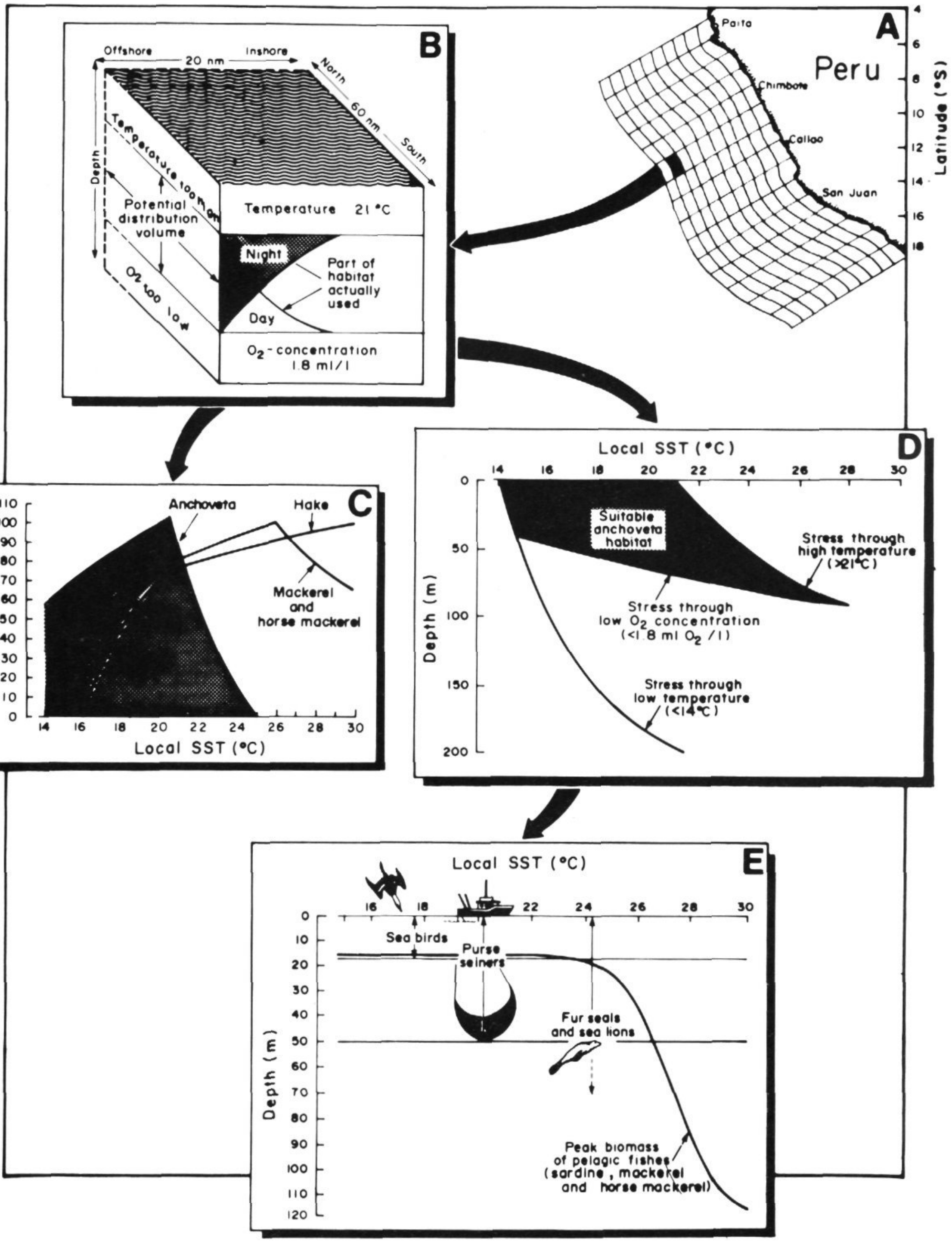

Figure 8. Schematic representation of submodels incorporated in large simulation model of the Peruvian upwelling ecosystem. A. Definition of the 15×10 subareas used for spatial modelling. B. The volume potentially inhabited by a given species within each subarea is a function of SST, O_2 concentration, and time of the day; C. Each species has different physiological requirements which, given changing SST, result in different fractions of a subarea's water column being occupied by that species. D. The effects in (C) cause vertical changes in distribution, all of which occur within a narrow range of temperature and above a critical O_2 concentration. E. Combined, these effects determine whether the fish will be high enough in the water column to be caught by guano birds, marine mammals, or purse seiners.

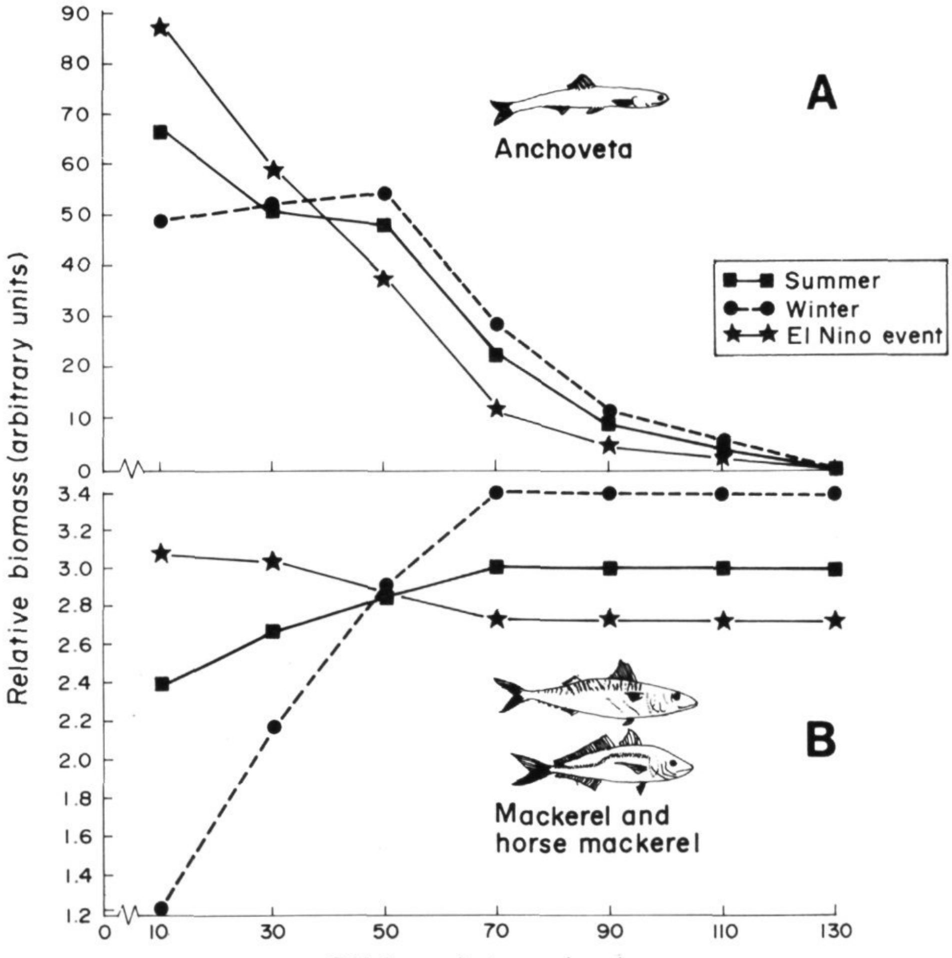

Figure 9. Relative biomass of anchoveta, mackerel, and horse mackerel off Peru as a function of distance offshore and SST regime, as estimated from the simulation model presented in the text.

Ursin (1967) and Andersen and Ursin (1977). The fishery catches are modelled for any given subarea as a function of (i) the biomass of the fish species; (ii) their depth distribution, i.e. their vulnerability to purse seines (Fig. 8E); and (iii) the fishing effort, i.e. the deployment of purse seiners and trawlers in that area.

Figure 9 gives, as some preliminary results, the offshore distribution of anchoveta and mackerels for different SST regimes. The model will eventually be parameterized using spatial distribution data based on fisheries operation in the 1960s and 1970s, and it is ntended to be interfaced with an economic submodel, based on Agüero (1987).

Discussion

The usefulness of top-down steady-state models of the type described above lies particularly in the identification of knowledge gaps, and of states or rate estimates that are mutually consistent (Silvert, 1981, 1982). In the case of the three models derived here, no major inconsistencies with previously published biomass estimates were noted except for zooplankton. Also, most of the available published estimates of key rates (food consumption, total mortality, etc.) for the groups included in the models did not have to be altered significantly to balance the model (except for sardine, see above). Hence, these models show the consistency of the concepts and estimates used for their construction. Future emphasis will be put on a more detailed representation of the planktonic and benthic groups in the model, and use of a shorter time interval.

The approach used to construct a spatially structured simulation model of the fish and fisheries of the Peruvian upwelling system may be as robust as our top-down model. Temperature is a variable which has, off Peru, an extremely strong impact on the distribution of major groups of organisms. Thus any model which uses SST as forcing variable is likely to be able to reproduce the key features of the distribution of the biota and the fishery, and the overlap of major predator and prey species.

Note that the model described here is still overly simplistic, and it will be refined after testing. For example, temperature distribution may need to be modified to take account of seasonal oscillations, and the offshore distribution of the major fish species may need to be related to plankton occurrence.

A similar approach in which SST and parameters directly dependent on SST were used to identify areas of potential availability of tuna to purse seiners and other gears has been presented by Sharp (1979) for the Indian Ocean. The concept of the simulation model presented here also corresponds, albeit indirectly, to the ideas of McCall (1984) concerning the tendency of a fish population to concentrate itself where conditions are optimal, such that, overall, conditions for individual fishes are similar over the whole area of distribution of that population.

One potential use of the simulation model is to optimize spatial deployment of the Peruvian purse seiner fleet, based on SST data from coastal stations. Even if the model is not used for real time management, it may lead to an improved understanding by Peruvian fishing managers and administrators of the factors that determine fishing success, and the consequences of fleet deployment strategies particularly during El Niño events, when anchoveta tend to become highly vulnerable.

Both models will allow us to follow up on some implications of Ulanowicz's theory. We will use the simulation model to generate the biomasses within boxes and some flows between boxes for various "steady-states" representing various environmental and fishing regimes. This will allow us to identify how Ulanowicz's indices (see Table 2) actually track environmental stress, or stress due to overexploitation.

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The estimation of parameters of the multispecies production model

Kevin J. Sullivan

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In this study the parameters of the multispecies Schaefer model are interpreted in terms of their biological significance. For any particular fishery the parameters in the model are the intrinsic rate of increase for each species, the intraspecific density-dependence terms and the interspecific interaction terms between each pair of species. In a fishery for n species there are n(n+1) parameters to be estimated. The Baltic multispecies fish assemblage of cod, herring, and sprat was modelled using a multispecies length cohort analysis in which predator/prey interactions occurred. A range of equilibrium states was found for predator and prey biomass and these were then fitted with a Schaefer multispecies production model by multiple linear regression. The results showed that significant interactions occurred between the prey species which were not the result of any direct interaction but were caused indirectly by the feeding behaviour of the predator in the model. The presence of these indirect interactions between species suggests that the only way to fit the Schaefer multispecies model may be empirically. A long data series would be needed to fit even the simplest multispecies system. One approach to improve the parameter estimation would be to predict some of the values outside the model. For the intrinsic rate of increase, predictive relationships were investigated using data from single-species assessments of exploited populations. Such relationships may allow wider use of multispecies production models but also may be useful to predict the potential yield from developing fisheries.

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Introduction

The use of single-species models is generally limited to short-term management objectives as they fail to account for interactions between fisheries and between fish species. In recent years the multispecies or ecosystem approach to modelling of fish stocks has received more attention (Hobson and Lenarz, 1977; FAO, 1978; Mercer, 1982). One difficulty with multispecies studies is the number of species for which data are required. This often means that multispecies models will need to be simple models. One of the simplest formulations which includes interactions is the multispecies Schaefer model (Larkin, 1966; Walter and Hogman, 1971; Pope, 1976). The yield of species 1 in a three-species multispecies production model has the form

$$Y_1/P_1 = A_1 - B_1P_1 + C_1P_2 + D_1P_3$$

where P is the biomass and Y the equilibrium yield of species 1, 2, and 3. A represents the intrinsic rate of increase, at which the biomass of a species would grow if resources were unlimited. B represents the limitation on population growth by environmental factors and intraspecific density dependence. It may be regarded as a scalar for each stock in any given situation. C and D are interspecific interaction terms, representing competition and predation. In a fishery for n species there are n(n+1) parameters to be estimated.

To examine the relationship between the interaction terms in the multispecies Schaefer model and observed biological processes, a theoretical model was applied to the multispecies fish complex in the Baltic. Mandecki (1976) suggested that fish stocks in the Baltic form a simple food chain of a peak predator (cod) which feeds on smaller cod, herring, and sprat, which in turn feed on the zooplankton. The small number of species involved and the strong predator/prey interaction makes this an ideal system to study the parameters of the multispecies production model. This fishery has also been studied by Majkowski (1977), Horbowy (1982), and by an ICES multispecies assessment working group (Anon., 1982a). The rates of growth, feeding, and natural mortality were available from these other studies.

Simulation model

The behaviour of the Baltic fish complex was modelled using the multispecies length cohort analysis of Pope (1980). This model uses catch-at-length data and assumes the data apply to a steady-state condition. In other respects the model is equivalent to the multispecies virtual population analysis. A full description of the model and the input parameters may be found in Sullivan (1983); only the major features and assumptions of the model are described here.

The steady state which results in the model depends on the catch data input to the model and the feeding relationships between the species. In the Baltic system the feeding of cod is the main determinant of the stock sizes of herring and sprat. Therefore the model was initialized such that the biomass of cod at equilibrium matched the average biomass of cod from 1970–1974, as estimated by the working group on demersal stock assessments in the Baltic (Anon., 1982m). No attempt was made to match the biomass estimates of herring and sprat stocks, as reported by the working groups.

Cod is the only fish which feeds in the model, and predation by cod largely determines the size of the herring and sprat stocks, as increased levels of predation result in greater biomass estimates of the prey species. The model assumes that the cod ration is fixed and that a constant proportion of the diet is fish, which is taken from the smaller fish in the model. The feeding level and the distribution of predation mortality between the fish stocks are therefore determined by the annual ration of food (based on Daan, 1973), the proportion of fish in the diet (based on the working group report Anon., 1982a), and the size and species preference of the cod. A lognormal distribution of prey size preference was used (Ursin, 1973), while food preference of the predator for each species was set equal to one. This made the distribution of predation a function of size only.

The model of Pope (1980) was extended to include stock-recruitment relationships (SRR) for each species, and the rate of fishing was varied for predator and prey separately. An asymptotic SRR was used, based on the steady state used to initialize the model. As predation effects are considered explicitly in the feeding model, the form of SRR is not important in determining the equilibrium point found at each level of fishing. However, the values of the parameters used in the SRR and the feeding level of cod are important in scaling the relative sizes of the stocks.

Two fisheries were considered to operate, one for herring and sprat and the other for cod. A range of fishing strategies was simulated to find equilibrium conditions over a wide range of biomass levels of predator and prey species. The exploitation pattern is assumed constant and changes in the rate of fishing are simulated as multiples of the fishing mortality rates estimated in the preliminary analysis. The model was then iterated to find the new equilibrium state for the new fishing levels. A number of processes operated concurrently in the iterations: (i) The new rates of fishing mortality changed the yield and biomass of each species. (ii) The level of predation and the effects on young cod, herring, and sprat changed with the relative size and length distribution of the cod stock. (iii) The SRR for each species determined the number of fish in the smallest length group. Generally, convergence was achieved fairly rapidly if a new equilibrium point existed. When the cod stock was larger than the initial steady state, feeding by the cod tended to cause the collapse of the herring stock and no new equilibrium point was found.

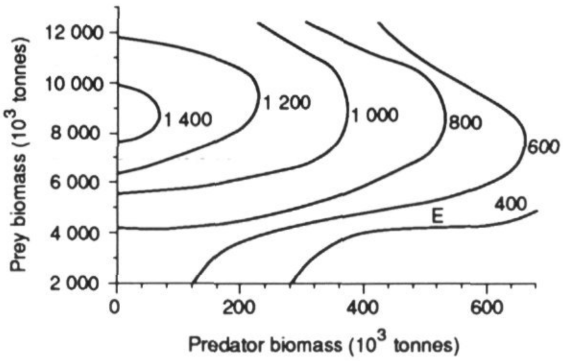

Figure 1. Contours of equal total yield (1000 t) from the simulation data of the Baltic multispecies fishery. The point E represents the equilibrium state at which the model was initialized.

In Figure 1 contours of equal total yield for all species are plotted against the biomass of predator and prey. The plot shows the expected result from a predator/prey model and the maximum total yield occurs at very low biomass levels of cod. The point E represents the point where fishing intensity equals one for all species (i.e. the original steady state used to initialize the model).

Fitting the multispecies Schaefer model

The estimates of equilibrium catch and biomass of each species from the simulation model were fitted by multiple linear regression to determine the parameters of the multispecies Schaefer model. The catch/biomass ratios of each species in turn were regressed against the biomass estimates of cod (P_C), herring (P_H), and sprat (P_S). The regression for each species explained over 90% of the total sum of squares, and all the variables were highly significant. For the cod stock the regression equation is

$$Y_C/P_C = 0.354 - 0.148P_C + 0.05P_H - 0.125P_S$$

where biomass units are million tonnes. The main feature of the regression is the size of the interaction terms for herring and sprat. In practice, these terms cancel each other out as the average biomass of herring was 2.5 times the average biomass of sprat. The cod stock follows a single species Schaefer model fairly closely.

The regression equations for the prey species are

Sprat

$$Y_S/P_S = 0.339 - 0.294P_C + 0.014P_H - 0.085P_S$$

Herring

$$Y_H/P_H = 0.191 - 0.145P_C + 0.019P_H - 0.085P_S$$

These equations are quite different from those of single-species Schaefer models. There are strong interactions both from the feeding of the predator and between the prey species. In the equation for the herring stock the interaction coefficient of cod biomass is about half that seen in the equation for sprat (0.145 compared with 0.294). It appears that sprat are a more suitable size than herring for the cod. Although the level of predation by cod is similar on the two stocks, the herring biomass is much larger than the sprat biomass indicating greater preference (size-related) for sprat. The coefficient of sprat biomass represents an indirect interaction between herring and sprat, caused by the feeding of cod in the model. As the stock of cod is fished more heavily, the average size of fish decreases; the sprat stock becomes more suited by size to be eaten by cod and the feeding on herring is reduced. When the fishing on cod is reduced the average size increases and more herring are eaten; this also causes the herring stock to collapse at high cod biomass. This behaviour would be accentuated at higher feeding levels of cod.

The results indicate that the multispecies production model is a good representation of the simulation model and may be useful for summarizing the more complex workings of the feeding model. The multiple regression produced coefficients of the interaction terms caused by predation by cod on herring and sprat similar to the average of the simulation runs (for herring predation 0.145 predicted against 0.1 average, for sprat predation 0.294 predicted against 0.22 average).

However, the model also showed that there are significant interactions between the sprat and herring stocks (which are not feeding on each other). There appears no way to quantify these other terms except by fitting the model as they represent indirect effects between the species involved. If this result is generally true, then the only way to capture some behaviour of multispecies systems may be empirically.

In practice, there is likely to be a limit to the number of terms which can be fitted by regression methods. This effectively restricts the fitting of the model to only a few species in an ecosystem. In addition the measures of population abundance and fishing intensity have been found to be highly correlated, preventing the estimation of the parameters even in the simplest two-species interacting system (Pope and Harris, 1975). Some improvement would be expected if some or all of the parameters could be estimated outside the regression. In the following section predictive relationships for the intrinsic rate of increase are investigated.

Predicting the intrinsic rate of increase from biological characteristics of fish stocks

The intrinsic rate of increase represents the turnover rate of a species. It has been interpreted as the productivity of an exponentially growing population (Fenchel, 1974), or a potential rate which in nature is tempered by environmental and biological factors. It is considered to reflect the strategy a species adopts in order to survive (Pianka, 1970), those species with high rates of increase are regarded as opportunists, and those with low values as specialists.

Empirical relationships between life history parameters have been used by many authors to predict parameters of interest from other data which are more easily measured. Beverton and Holt (1959) and Cushing (1968) used values of K to predict natural mortality. Pauly (1980) extended this analysis to include temperature and body size. Other workers have shown significant relationships between body weight and various ecological and physiological characteristics of animal groups (Blueweiss *et al.*, 1978 gives a review). Of particular interest is the result that the intrinsic rate of increase, for a range of species varying in size from bacteria to whales, decreases with increasing body size (Smith, 1974; Fenchel, 1974). On the basis of these observed relationships, the intrinsic rate of increase would be expected to be directly related to M and K, and inversely related to body size and age of first maturity.

For a range of fish stocks the intrinsic rate of increase was estimated from a single species Schaefer model of population growth. Biomass estimates were taken from virtual population analyses of these stocks. The mean biomass in each year was plotted against the catch/biomass ratio in the previous year. As an example, Figure 2 shows the fit of the model to the Pacific halibut fishery from 1951–1973. A regression was fitted to estimate the intercept which represents the intrinsic rate of increase of the Schaefer model (Pope, 1979).

From a total of over 100 stocks for which VPA results were available, 44 stocks were found to meet the criteria for estimating the value of the intrinsic rate of increase. These stocks were found to give a satisfactory fit to the Schaefer model for a series of years. Those stocks which were excluded did not generally show enough contrast in the size of the population over the years studied, and the regression was considered to be extrapolated too far beyond the range of data points to accurately estimate the intercept. The 44 stocks which were accepted are listed in Table 1, with references to the original VPA results.

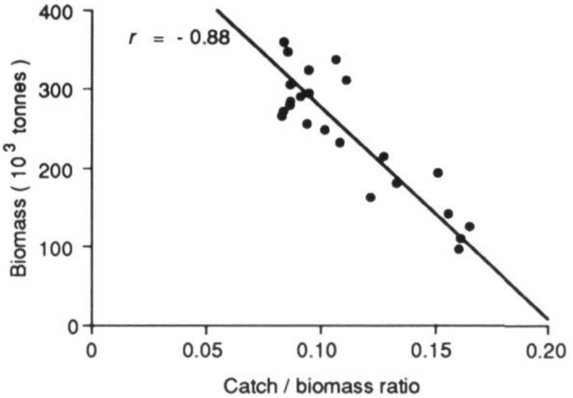

Figure 2. Fit of the Schaefer single-species model to the Pacific halibut fishery. The biomass in each year is plotted against the catch/biomass ratio in the previous year.

This method of estimating the intrinsic rate of increase assumes that the Schaefer single species model represents the growth of the population. Equilibrium conditions are assumed at each point and fishing is considered to be the cause of the observed decline in stock biomass. The fit of the model in any fish stock may be influenced by: (a) the effect of strong year classes; (b) the environment; (c) the exploitation pattern throughout the period; (d) non-equilibrium conditions; and (e) whether the stock is a predator or a prey species. Although these factors are likely to be important in the application of the single species model, no stocks were excluded for any of the above reasons.

Biological parameters were selected for each stock to represent differences in size, growth rate, and reproductive strategy. The parameters for each stock are listed in Table 2: (i) Age at first maturity is taken as the age when 50% of the female fish in the stock are mature (most recent year). (ii) Size at first maturity was the weight in grams of the female fish at this age. (iii) Von Bertalanffy parameters of K, W_∞, and L_∞ were taken from the sources listed in Table 1. (iv) Natural mortality was assumed constant for all ages and the value taken from the original VPA.

Figure 3 shows the values of the other variables plotted against the intrinsic rate of increase. Examination of these plots suggested that there were some differences between the distribution of points representing the gadoid stocks and those of the other stocks. Therefore the data were split into these two groups for further analysis.

Correlation analysis showed that most of the parameters were significantly correlated with the intrinsic rate of increase (Table 3). The values of K and M were positively correlated with the intrinsic rate of increase (A) while age at first maturity and the size parameters were inversely related to A. Multiple linear regressions (MLR) were fitted to the intrinsic rate of increase and the independent variables using a stepwise procedure as follows. The independent variable which explained the most variance in the linear regression was retained in the model. Further variables were added until the addition of further variables failed to reduce the deviance of the model by a significant amount, as tested by the ratio of the mean squares.

For the gadoid stocks, all the variables except K were highly correlated with the intrinsic rate of increase. The plots were essentially linear except for temperature; these values were therefore squared to linearize the relationship. In the MLR the first variable temperature squared (TS) explained 59% of the total sum of squares and the addition of the natural logarithm of weight at first maturity (ln C) increased this to 73%. The addition of other variables was not significant; the predictive equation is

$$A = 1.335 + 0.0049TS - 0.1124 \ln (C)$$

and the standard deviation around the regression line is 0.152.

For the non-gadoid stocks the rate of natural mortality was also considered in the analysis (Table 3). The growth constant K gave the highest value of the correlation coefficient, and in the MLR explained 67% of the sum of squares. The addition of the natural logarithm of W_∞ ($\ln W_\infty$) was significant at the 5% level and the two variables explained 73% of the total sum of squares. The predictive equation is

$$A = 0.947 + 1.189K - 0.095 \ln (W_\infty)$$

and the standard deviation around the regression line is 0.174.

The gadoid stocks are closely related, and all the stocks came from the North Atlantic. These fish are the dominant demersal fish fauna in the area and represent a highly successful group. Most of the stocks had been overexploited in the past and the fit of the Schaefer model gave good estimates of the intrinsic rate of increase. The use of mean surface temperature in the predictive relationship probably reflects the differences between water temperatures in areas inhabited by these stocks. Taylor (1958) found a significant relationship between temperature and the value of K for North Atlantic cod stocks. The use of weight at first maturity as a second parameter scales the stocks by relative size, such that smaller fish at the same temperature are expected to have higher values of the intrinsic rate of increase.

The other group was more diverse, mainly comprising the small pelagic schooling fish but also including the Pacific halibut and other flatfish. The use of K and W_∞ in the predictive equation scales the predicted values in a similar way to the relationship for the cod stocks; faster

Table 1. List of stocks studied for intrinsic rate of increase and references for virtual population analyses and biological data.

No.	Species	Stock	VPA reference	References to biological data
1	Cod	North Sea	Anon. (1982g)	Garrod (1977)
2		Arcto–Norwegian	Anon. (1982b)	Garrod (1977)
3		Iceland	Anon. (1976)	Garrod (1977)
4		S Gulf of St Lawrence	Maguire and Waiwood (1982)	Pauly (1980)
5		West Greenland	Horsted (1981)	Garrod (1977)
6		Grand Bank	Bishop and Gavaris (1981)	Garrod (1977)
7		Labrador–E Newfoundland	Wells (1981)	May *et al.* (1975)
8		Irish Sea	Anon. (1982k)	Garrod (1977)
9		St Pierre Bank	Bishop and Gavaris (1982)	Garrod (1977)
10		Banquereau	Maguire *et al.* (1982)	Garrod (1977)
11		East Greenland	Anon. (1982d)	Anon. (1982d)
12	Haddock	Brown's Bank	O'Boyle and White (1982)	Beverton (1965)
13		Georges Bank	Clark *et al.* (1982)	Clark *et al.* (1982)
14		North Sea	Anon. (1982g)	Beverton and Holt (1959)
15		Arctic	Anon. (1982b)	Anon. (1982b)
16		West Scotland	Anon. (1982g)	Anon. (1982g)
17	Saithe	North Sea	Anon. (1982h)	Anon (1982h)
18		Arctic	Anon. (1982h)	Beverton and Holt (1959)
19		Iceland	Anon. (1982h)	Pauly (1980)
20	Whiting	North Sea	Anon. (1982g)	Anon. (1982g)
21		West Scotland	Anon. (1982g)	Anon. (1982g)
22	Herring	North Sea	Anon. (1982f)	Pauly (1980)
23		Celtic Sea	Anon. (1982f)	Anthony and Waring (1980)
24		Norwegian	Dragesund and Ulltang (1978)	Beverton (1963)
25		West Scotland	Anon. (1982f)	Anthony and Waring (1980)
26		SW Nova Scotia (4WX)	Sinclair *et al.* (1982)	Anthony and Waring (1980)
27		Georges Bank	Anthony and Waring (1980)	Anthony and Waring (1980)
28		Iceland – Summer-spawning	Jakobsson (1980)	Anthony and Waring (1980)
29		Iceland – Spring-spawning	Anon. (1982j)	Anthony and Waring (1980)
30		West Ireland (VII BC)	Anon. (1982f)	Anon. (1982f)
31		Baltic (22 + 24)	Anon. (1982l)	Pauly (1980)
32		S Gulf of St Lawrence	Cleary (1982)	Anthony and Waring (1980)
33	Mackerel	NW Atlantic	Maguire (1981)	Anderson and Paciorkowski (1980)
34		North Sea	Anon. (1982i)	Dr S. Lockwood (pers. comm.)
35		Pacific	Parrish and MacCall (1978)	Parrish and MacCall (1978)
36	Sole	North Sea	Anon. (1982c)	de Veen (1978)
37	Halibut	Pacific	Hoag and McNaughton (1978)	Southward and Chapman (1965)
38	American plaice	3LNO	Brodie and Pitt (1982a)	Pauly (1980)
39	Yellowtail flounder	3LNO	Brodie and Pitt (1982b)	Pauly (1980)
40	Sardine	Pacific	Murphy (1966)	Pauly (1980)
41	Pilchard	S Africa (1.6)	Davies *et al.* (1981)	Davies *et al.* (1981)
42		SW Africa (1.4–1.5)	Le Clus and Thomas (1982)	Davies *et al.* (1981)
43	Redfish	3LN	Nikolskaya *et al.* (1980)	Beverton (1965)
44	Sprat	North Sea	Anon. (1982e)	Beverton (1963)

growth and smaller body size result in higher intrinsic rates of increase.

These results suggest that it may be possible to predict the intrinsic rate of increase from other biological characteristics of fish stocks. The number of stocks used in this study was limited by the available stock assessment data using VPA and the fit of the single species Schaefer model. In the future, as more stocks are assessed using VPA methods, this analysis may be extended to cover a wider database.

For the Baltic cod stock the predictive relationship given here suggests an intrinsic rate of increase of 0.85. This is much higher than the value estimated from the simulation results of the multispecies model. It indicates that the values used in the stock recruitment relationship for cod in the model may be inappropriate and the stock sizes of each species may not be well represented by the simulation model. However, using values of the intrinsic rate of increase predicted for each species in the Baltic multispecies fish complex may allow the parameters of the Schaefer multispecies model to be fitted to actual estimates of catch and biomass observed in the fishery. The number of parameters to be fitted by multiple regression would be reduced and an improvement in the fit of the model would be expected.

Discussion

The results of this study indicate that using a multispecies production model may not always be the simplest

Table 2. Values of the intrinsic rate of increase, biological parameters, and temperature for the stocks listed in Table 1. A = intrinsic rate of increase; B = Age of first maturity (50%); C = Weight at first maturity (gm); W_∞ = Maximum theoretical weight from the von Bertalanffy equation (gm); L_∞ = Maximum theoretical length from the von Bertalanffy equation (cm); K = Growth parameter; T = Temperature (mean annual surface temperature °C); M = Natural mortality used in VPA.

Stock	A	B	C	W	L	K	T	M
1	1.14	3	2134	16000	115	0.3	10	0.2
2	0.87	8	4700	17000	130	0.12	7	0.2
3	0.55	7	4650	15000	118	0.16	7	0.2
4	0.58	6	1660	15000	115	0.1	6	0.2
5	0.51	6	3000	8000	100	0.2	2	0.2
6	0.81	7	3000	12000	114	0.11	7	0.2
7	0.6	6	1720	8000	102	0.16	3	0.2
8	1.01	3	3330	12000	101	0.33	11	0.2
9	0.68	7	2300	18000	137	0.1	7	0.2
10	0.76	7	1200	11000	105	0.14	8	0.2
11	0.47	7	3210	16000	120	0.1	1	0.2
12	0.54	6	2220	4300	70	0.22	8	0.2
13	0.71	2.5	1000	4374	74	0.38	8	0.2
14	1.2	2	256	3000	53	0.2	10	0.2
15	0.79	6	2380	10000	70	0.15	7	0.2
16	0.86	2	356	3000	65	0.2	9	0.2
17	0.87	5	2360	15000	110	0.1	10	0.2
18	0.72	6	2760	12000	107	0.19	7	0.2
19	0.55	6	3670	18000	124	0.14	7	0.2
20	1.58	2	177	1200	45	0.1	10	0.2
21	1.11	2	177	1200	45	0.1	9	0.2
22	1.16	4	211	200	30	0.38	10	0.1
23	0.83	2	162	200	30	0.39	11	0.1
24	0.5	4	248	350	36	0.21	8	0.16
25	1.0	2	121	200	30	0.35	9	0.2
26	0.67	4	172	450	39	0.18	8	0.2
27	0.77	4	180	355	34	0.38	11	0.2
28	0.91	3	210	400	36	0.25	7	0.1
29	0.92	4	250	400	36	0.25	7	0.1
30	0.68	2	130	200	31	0.35	11	0.2
31	0.93	3	91	160	28	0.48	9	0.3
32	0.67	4	240	399	36	0.25	6	0.2
33	0.44	3	306	735	41	0.25	8	0.3
34	0.33	3	325	500	39	0.19	9	0.15
35	0.56	2	320	1000	44	0.24	15	0.4
36	0.58	3	256	800	40	0.39	10	0.1
37	0.2	12	12800	31000	160	0.05	5	0.2
38	0.43	13	989	3500	60	0.1	5	0.23
39	0.69	6	493	1183	50	0.34	3	0.3
40	0.71	2	93	337	30	0.45	15	0.4
41	0.74	2	55	250	31	0.23	15	0.5
42	0.71	2	55	250	31	0.23	15	0.5
43	0.23	14	600	1200	40	0.11	5	0.1
44	1.7	2	16	25	14	0.7	10	0.8

means for assessing the potential yield from multispecies fisheries. Model results suggest that significant interactions occurred between species which could not be inferred from first principles. This effectively limits the use of such models to those fisheries where long time series of data are available. Prediction of one or more of the parameters from ancillary information may improve the fit of the model and help in the choice between alternative interpretations.

Significant relationships were found between the intrinsic rate of increase and other biological parameters. These could be used to predict the potential productivity of fish stocks (single species), and also to interpret alternative results from multiple regression analyses of the multispecies Schaefer production model, as found by Sissenwine *et al.* (1982).

In assessing the potential yield from developing fisheries, predictive models using the value of the intrinsic rate of increase may be all that is possible. These will by necessity be single-species models. Pope (1979) suggested that multispecies management should aim to exploit each species at half the rate of the intrinsic rate of increase, which would achieve the maximum yield of a system if no species interactions occurred. When there are strong species interactions and few stocks, this may not be appropriate. However, it is apparent that the

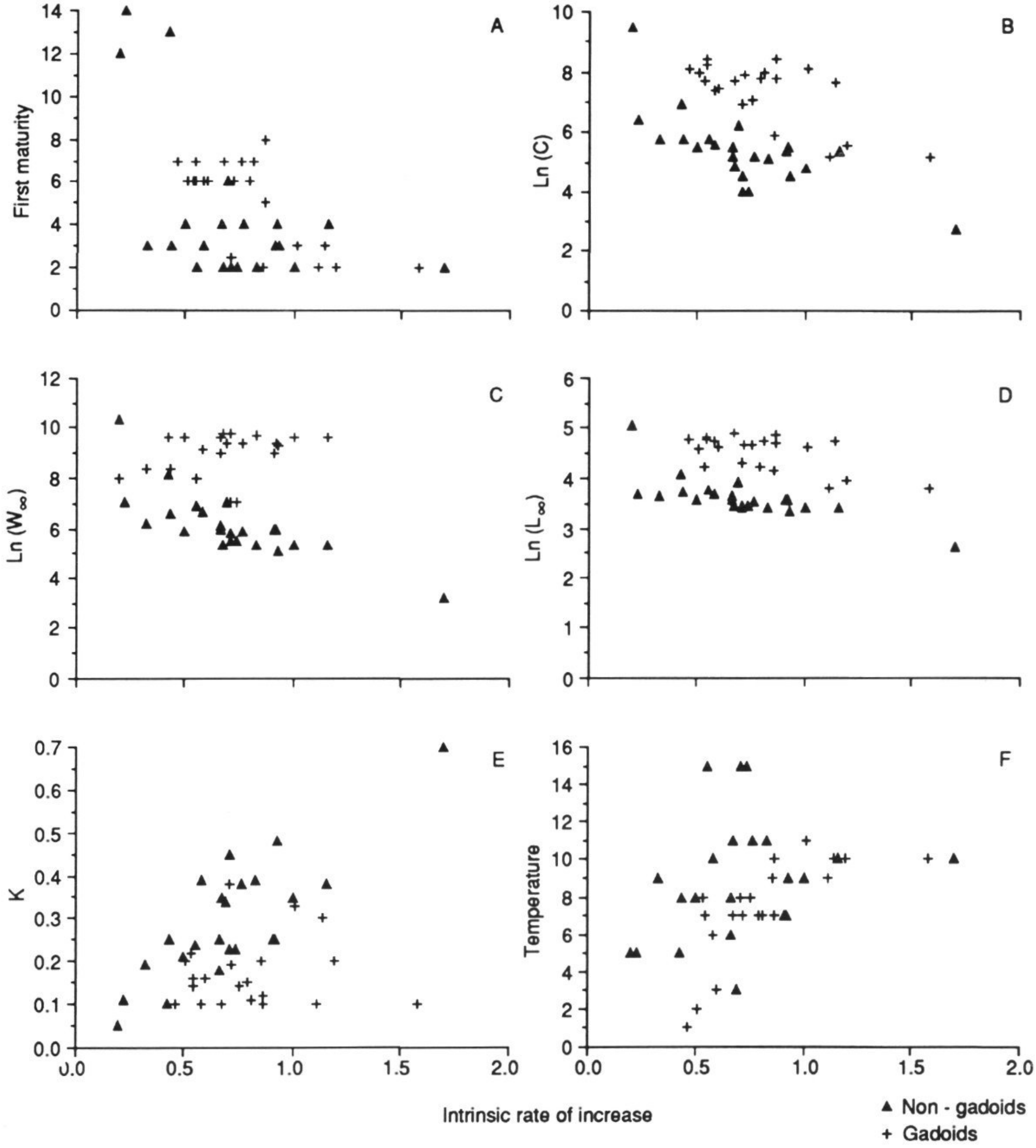

Figure 3. Plots of the intrinsic rate of increase (A) and the other parameters used in the regression analysis for all stocks listed in Table 1: a. Age of first maturity; b. Ln (C) weight at first maturity; c. Ln (W_∞); d. Ln (L_∞); e. K (growth constant); f. Mean water temperature (°C).

direction to change fishing intensities would be to increase the effort directed at a predator stock in order to increase total yield from a fishery. Such an objective would be appropriate where species of equal value are taken or fishing is not targeted. In practice, the biological models require input of relevant economic and social factors before optimal multispecies management is possible.

Table 3. Correlation of the intrinsic rates of increase with other parameters listed in Table 2.

	B	ln (C)	ln (W_∞)	ln (L_∞)	K	T	M
All stocks	-0.55^{**}	-0.42^{**}	-0.30^{*}	-0.32^{*}	0.43^{**}	–	0.31^{*}
Gadoids	-0.70^{**}	-0.68^{**}	-0.58^{**}	-0.61^{**}	-0.05 n.s.	0.71^{**}	–
Non-gadoids	-0.53^{**}	-0.72^{**}	-0.79^{**}	-0.72^{**}	0.82^{**}	–	0.45^{*}

$^{**}p < 0.01$; $^{*}p < 0.05$; n.s. not significant.

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Multispecies fisheries in the Gulf of Mexico

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Browder, J., Brown, B., Nelson, W., and Bane, A. 1991. Multispecies fisheries in the Gulf of Mexico. – ICES mar. Sci. Symp., 193: 194–197.

This paper reviews the recent rapid evolution of fisheries of the Gulf of Mexico. It emphasizes mechanisms that are likely to make biological and technological species interactions important. An integrated approach of simple models, experimental management, and follow-up monitoring of indicators is proposed.

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Introduction

The Gulf of Mexico is one of the United States' most productive fishery regions. US fisheries in the Gulf of Mexico were characterized by rapid growth from the 1950s through the 1980s. Fishery expansion slowed in the 1980s; and fishery management, prompted by concern for stocks, user conflicts, and public awareness, began increasing. Fishery management in the Gulf of Mexico is complicated by the ecological interactions among species and by the multispecies harvests. Here we provide an overview of major fisheries and their problems and propose an integrated management approach that is appropriate to the interconnected nature of the fisheries.

Evolution of the fishery

Fisheries in the US Gulf of Mexico have changed dramatically over the past 10 to 15 years. The traditional fishery species – shrimp (*Penaeus* spp.) and menhaden (*Brevoortia* spp.) – are now fully exploited. In fact, shrimping effort exceeds that which would result in maximum economic yield. Many new target species have become important; and, on some, the intensity of recreational fishing meets or overshadows that of commercial fishing. Concerns for the resource have led to restrictions on fishing for several species or species groups. Fishery management in the Gulf of Mexico is much more comprehensive than 20 years ago, when, essentially, there was no management of US flag vessels.

Fishing by US vessels in the Gulf of Mexico has changed from emphasis on only a few species to the exploitation of many. At least 97 species in 33 families currently are caught, although not all are retained or marketed. Current fishery species fall into four main ecological groups: large oceanic species such as tunas (Thunnidae), coastal pelagic species such as king and Spanish mackerel (*Scomberomorus cavalla* and *maculatus*), reef species such as snapper (*Lutjanidae*) and grouper (*Serranidae*), and estuarine species such as sea trout (*Cynoscion* spp.), red drum (*Sciaenops ocellata*), Gulf menhaden, and the penaeid shrimps.

Certain species in all these ecological groups are reaching exploitation levels at which concern for the resource has led to management controls. Figure 1 shows the increasing pressure on certain oceanic pelagic species in the Gulf of Mexico. Figure 2 shows the decline in stocks of bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*). To prevent further decline, no directed fishing for bluefin tuna is allowed in the Gulf of Mexico. Management plans restricting swordfish and shark (mainly Carcharhinidae) catches are in the latter stages of preparation.

Heavy commercial and recreational fishing for coastal pelagics has resulted in strict regulations on king and Spanish mackerel (*Scomberomorus cavalla* and *maculatus*). Stock sizes for both species, particularly king mackerel, are lower than in past years (Fig. 3).

Intense fishing activity has led to stringent fishing restrictions on estuarine species. For example, capital-intensive commercial fishing for red drum (*Sciaenops ocellata*) is now prohibited throughout the Gulf, and inshore fishing for red drum is restricted in some states.

The reef-fish complex has experienced ever-increasing recreational and commercial fishing pressure and is depressed (Goodyear and Phares, 1990) (Fig. 4). Severe restrictions are proposed that may affect the

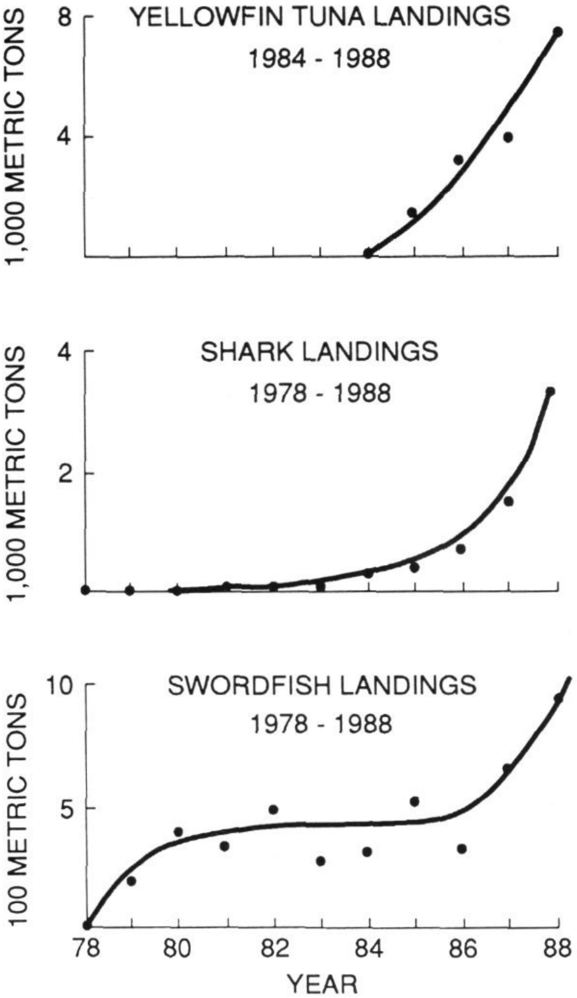

Figure 1. Annual landings of three oceanic pelagic species in the Gulf of Mexico, 1978 to 1988 (data are from unpublished landings statistics of the Southeast Fisheries Center, NOAA/NMFM, Miami).

shrimp fishery, which catches young red snapper incidentally.

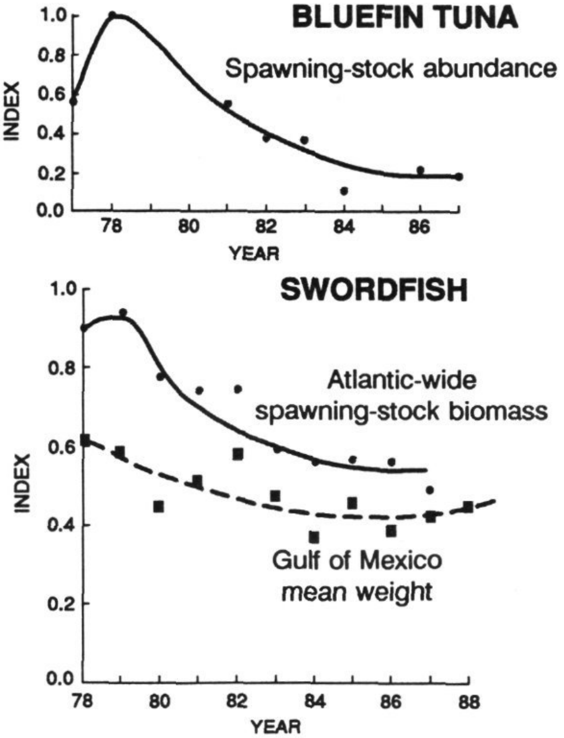

Figure 2. Indicators of annual condition of bluefin tuna and swordfish stocks (data are from ICCAT, 1989a and 1989b).

Shrimp trawling results in an extensive by-catch of bottomfish species such as Atlantic croaker (*Micropogonius undulatus*) and spot (*Leiostomus xanthurus*), most of which are killed and discarded. The increased intensity of shrimp trawling in the northern Gulf of Mexico may be responsible for the decline in bottomfish biomass observed in resource surveys (Fig. 5). The increased economic importance of other species relative to shrimp has brought the discarded shrimp by-catch, once ignored, into the forefront of public consciousness. The percentage occurrence of certain valuable species such as red snapper (*Lutjanus campechanus*) in the by-catch is small, but the total population impact is large (Goodyear and Phares, 1990). A decline in Atlantic croaker stocks, which may have been caused by increased pressure from shrimp trawls, prevented the development of a croaker-based surimi industry on the Gulf coast. Demands for restrictions to reduce the shrimp by-catch are increasing.

Possibly the fastest growing Gulf of Mexico fishery has been that for yellowfin tuna (Fig. 1), which was first documented by fishery port agents in 1984. The US yellowfin tuna fishery in the Gulf of Mexico started as an outgrowth of the swordfish long-line fishery, where yellowfin tuna initially were taken as by-catch. Perceiving a strengthening market for tuna, long-line operators

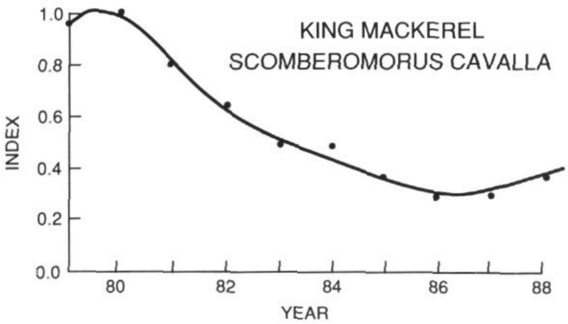

Figure 3. Index of abundance of king mackerel, 1979 to 1988 (data are from SEFC, 1990).

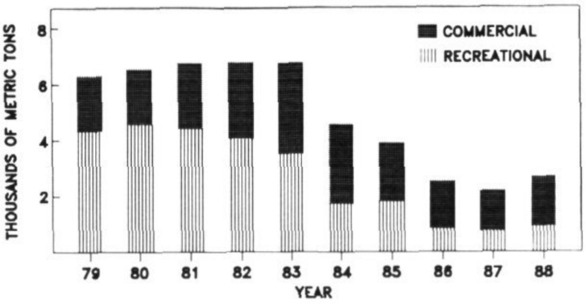

Figure 4. Annual recreational and commercial landings of red snapper in the Gulf of Mexico, 1979 to 1988 (Goodyear and Phares, 1990).

learned how to target this species. A major advance came in 1988 with the introduction of live bait. The departure of the Japanese fleet in the early 1980s undoubtedly contributed to the success of the US fishery. Annual yellowfin tuna landings increased from 352 metric tonnes in 1984 to over 7000 metric tonnes in 1988 – exceeding the highest estimated annual landings of this species in the Gulf of Mexico by the Japanese (Browder *et al.*, in press). At present the only regulation imposed on the US yellowfin tuna fishery is a minimum size; however, 1989 landings were lower than those for 1988, raising some concern for the resource.

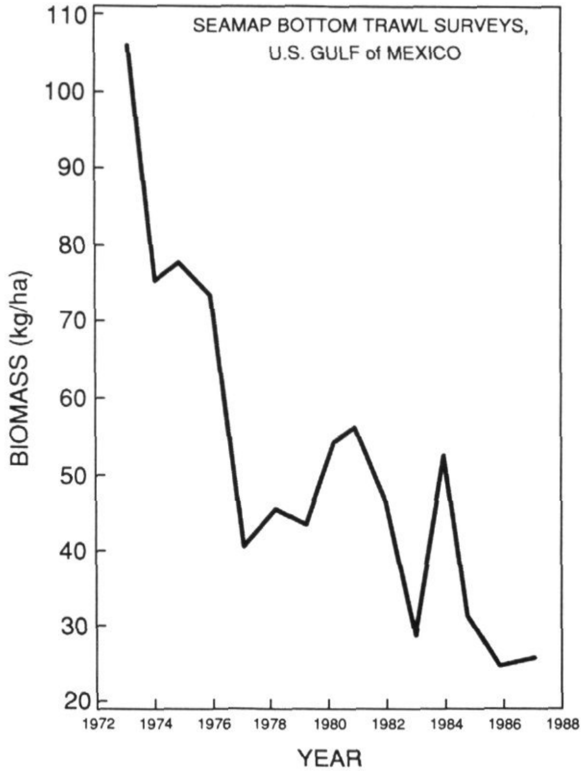

Figure 5. Relative biomass of shrimp by-catch species in the Gulf of Mexico, 1973 to 1987 (Pellegrin, 1982).

Future developments

The Gulf has long been thought to have abundant, unexploited offshore resources of small coastal pelagic species such as jacks (Carangidae), butterfish (*Peprilus* spp.), and herring (Clupeidae); and fisheries for these species currently are developing. Butterfish landings increased from less than one metric tonne in 1986 to several thousand tonnes in 1988. These small pelagic fish are major components of the diets of important fishery species such as the mackerel (Browder *et al.*, in press). Fishery managers, therefore, need to know how the increasing exploitation of prey species may affect stocks and future harvests of their predators. First approximations suggest that a very high proportion of total potential prey biomass is used by recreationally and commercially important predatory fish. Brown *et al.* (in press) calculated that annual prey consumption by current fishery species may be as great as 78% of the total biomass of small coastal pelagic and demersal prey species. Approximately 15% of estimated total prey biomass is now harvested. This includes menhaden and shrimp landings and the by-catch of the shrimp fishery. In view of the ecological relationships between present fishery species and new fishery targets, predator needs should be considered in management planning for exploitation of new resources.

Management models should be developed specifically for Gulf of Mexico fisheries that are appropriate to the limited availability of input data. Little historical fisheries or ecological data are available for the Gulf of Mexico, compared with areas such as the North Sea and the western North Atlantic. Useful ecological models related to Gulf fisheries management can be developed from basic food web information and first-cut estimates of the energetics requirements of predators. We suggest an integrated approach of simple models, experimental management, and follow-up monitoring of indicators. For instance, Sheridan *et al.* (1984) used two types of computer models – a simple energy-flow ecosystem model and a coupled multispecies logistic growth and surplus production model – to evaluate the effect on both shrimp landings and bottomfish landings of alternative harvesting strategies in the shrimp fishery. Results of these analyses potentially could be applied in experimental management, much as Collie *et al.* (1990) applied the results of their computer tests of alternative harvesting strategies in the Fraser River salmon fishery. First, management alternatives are tested with models. Then, on the basis of the modeling results, certain alternatives are selected for application to the real world. Alternatives can be selected with a variety of constructive objectives: to maximize yields, to minimize risks, or simply to reduce the uncertainty regarding model parameters that have the greatest influence on modeling results. The procedure should be iterative and progressive, with modeling, management, and monitoring followed by more modeling based on improved information, which will then be followed by more enlightened management.

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Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA

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An age-structured simulation model was constructed to investigate the impacts of major predators on the pelagic fish community off the northeastern USA. The objective of the study was to improve understanding of the magnitude and distribution of natural mortality attributable to various predators. Preliminary results indicate that predation mortality rates on the youngest age groups of fish (approximately ages 1–3) are much higher than previously assumed. Consumption accounts for far more biomass than present harvests (about 2.0 times). Predatory fish, primarily spiny dogfish, account for most of the mortality in this system, followed by marine mammals and seabirds. Individual species of marine mammals, with the exception of fin whales, do not consume a very large quantity of fish, but cumulative consumption by all marine mammals amounts to 120 ktonnes. Model results suggest that some fishery management actions, when evaluated in a multispecies context, do not always give results consistent with current single-species philosophies. Choice of functional feeding model heavily influences predicted predation mortality rates.

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Introduction

Much progress has been made in the field of multispecies fishery assessment and modeling since the pioneering work of Andersen and Ursin (1977). Powerful analytical methods such as multispecies virtual population analysis (MSVPA) have become useful in providing advice to managers on complex fisheries management problems (Anon., 1986, 1987, 1988). Biological interactions play a significant role in many marine ecosystems and in some cases they represent the dominant factor influencing system dynamics (Walters *et al.*, 1986; Overholtz and Tyler, 1986; Sherman and Alexander, 1986; Sissenwine, 1986; Gislason and Sparre, 1987). Many studies centered on the topic of biological interactions have shown that predation mortality rates on the youngest age groups of fish are dramatically higher than previously assumed (Anon., 1987, 1988; Overholtz *et al.*, 1988). This finding alone is a significant departure from the single-species philosophy of constant natural mortality over all age groups and in some cases the impact of this factor may influence short-term forecasts of yield (Overholtz *et al.*, 1988).

The diverse fishery ecosystem on the continental shelf off the northeastern USA changed profoundly under the pressure of intensive exploitation by foreign distant water fleets in the 1970s (Clark and Brown, 1977). More recently, a rapid build-up of the domestic fleet and ensuing overexploitation of demersal resources is again threatening the ecosystem (NEFC, 1988). Although the region (Fig. 1) is heavily influenced by fishing at present, biological interactions play an important role in shaping the dynamics of this system, especially in the pelagic sector (Sherman and Alexander, 1986).

The Atlantic mackerel stock has been rebuilding in the 1980s and herring stocks have also increased both in the Gulf of Maine and on Georges Bank (NEFC, 1988). In addition, a large shelf-wide stock of sandeels has been present in the region during the 1970s and 1980s (Sherman *et al.*, 1981). Thus a large forage base exists for the many predators that inhabit the area and these prey species as well as others are being heavily utilized. Piscivorous species such as Atlantic cod, silver hake and spiny dogfish are predators of these fishes (Bowman and Michaels, 1984). Large numbers of marine mammals and birds utilize the pelagic resources also (Overholtz

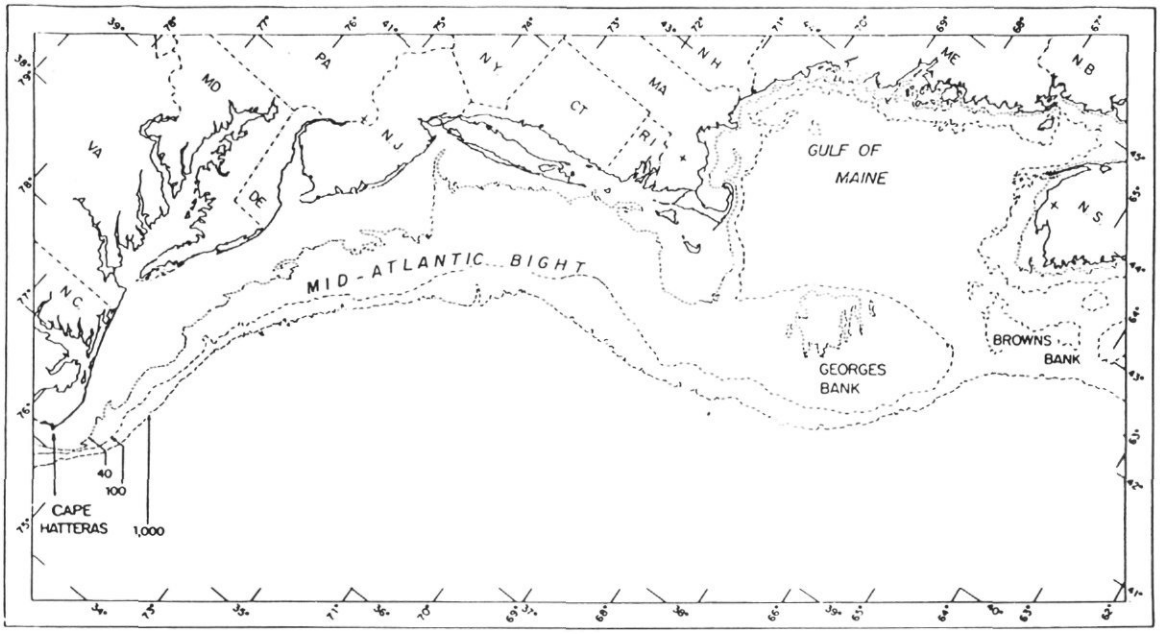

Figure 1. Region from Cape Hatteras to the Gulf of Maine that is inhabited by the species in the pelagic fish ecosystem.

and Nicolas, 1979; Kenny *et al.*, 1983; Payne *et al.*, 1984). Although the energy budget of part of the region has been explored (Cohen *et al.*, 1982) and overall food consumption by several piscivores has been investigated (Cohen and Grosslein, 1981), the impact of predatory fish, marine mammals, and seabirds on specific fish prey has not been systematically quantified.

The aim of the present study is to assess and quantify species-specific consumption of important pelagic resources based on repeated observations of the contribution of these prey in the diets of fish, mammals, and birds in this region. The goals of the study were to investigate the magnitude of the predation mortality caused by the different predators, to examine various alternative hypotheses about harvesting strategies from a regional perspective, and to evaluate the effect of the type of functional feeding response assumed on the results obtained from the model.

Model description

A dynamic simulation model was constructed to investigate the impacts of major predators on the pelagic fish community off the northeast coast of the USA. Ten species of marine mammals (three *Mysticetes* including humpback, finback, and minke whales, six species of *Odontocetes* including grey grampus, pilot whales, white sided, common and bottlenose dolphins, and harbor porpoises, and harbor seals) were included in the model (Fig. 2). Three piscivorous fishes (spiny dogfish, Atlantic cod, and silver hake) were included along with three species of marine birds (Northern gannet, shearwater, and black-legged kittiwake). Pelagic prey fishes included Atlantic mackerel, Atlantic herring, and sandeels, and also the younger age groups of silver hake.

The simulation model was based on available data on food habits, predator abundance, seasonal spatial overlap of predators and prey, prey abundance, current

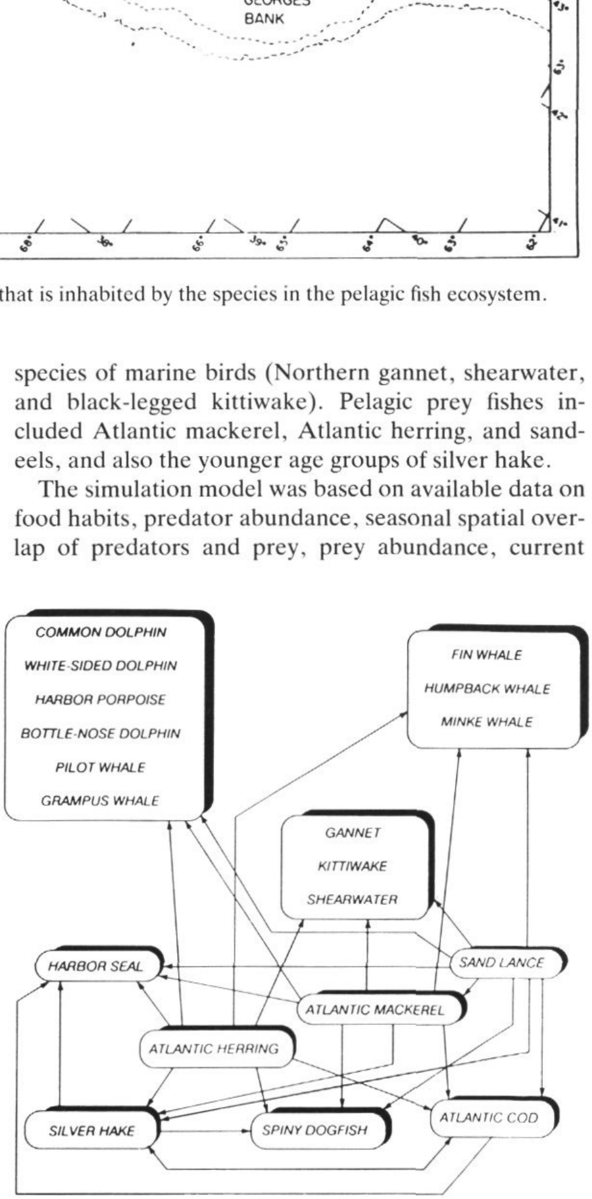

Figure 2. Species of marine mammals, seabirds, and fish that are included in the pelagic fish ecosystem model for the northeastern USA.

species-specific fishing mortality rates, and stock recruitment. The model is age structured for the fish component, maintains a quarterly resolution, utilizes stochastic recruitment functions to update annual fish numbers, and provides short-term forecasts of system variables. Model outputs were based on Monte Carlo simulation runs that included 100 5-year model cycles, chosen for convenience and because of computer time limitations. These model outputs were summarized to produce an average expected response for each variable.

Marine mammals

Aerial surveys to quantify the abundance and distribution of marine mammal species have been conducted by the University of Rhode Island from 1979 to 1981 and shipboard surveys from 1980 to 1983 by Manomet Bird Observatory aboard research vessels (Kenny *et al.*, 1983; Payne *et al.*, 1984). This information was used to estimate relative and absolute seasonal abundance of the ten marine mammal species. Seasonal data on the distribution of each species were used along with information on distribution of potential fish prey to determine whether feeding by mammals on particular prey species/ages was feasible on a time/space basis. This information was used in conjunction with food habits data to construct quarterly diet compositions for the marine mammals by assuming that if predator and prey distribution overlapped in a given quarter the predator diet composition would be similar to that suggested by the available marine mammal food habits literature.

The food habits literature for marine mammals was evaluated to determine the extent of interactions between the species of interest. Most of the information available from the Northwest Atlantic is from strandings, animals taken incidentally in fishing operations, or animals killed in the 1950s in commercial whaling operations off Canada. Information for white-sided dolphins and harbor porpoise indicates that herring, silver hake, mackerel, and sandeels are probably major prey items in the diets of these predators (Smith and Gaskin, 1974; Katona *et al.*, 1978; Sergeant *et al.*, 1980). Recent data from incidental takes of common dolphins (1987–1989) indicate feeding on mackerel and long-finned squid (*Loligo pealei*; Waring *et al.*, in review; Overholtz and Waring, in review). Pilot whales were thought to feed almost exclusively on short-finned squid (*Illex illecebrosus*; Sergeant, 1962), but more recently have been shown to feed on mackerel and long-finned squid (Overholtz and Waring, in review). We assumed on the basis of observations and available literature that marine mammals do not feed on age 1 sand eels or herring because of the small size of these fish.

Larger whales in the Northwestern Atlantic feed mainly on fish (Sergeant, 1963; Mitchell, 1974). In the Gulf of Maine region, there are numerous reports of humpback whales feeding on herring, mackerel, and sandeels (Payne *et al.*, 1986) and observations of feeding behavior by humpback and finback whales in areas with herring and sandeels concentrations are common (Overholtz and Nicholas, 1979; Mayo *et al.*, 1988).

Stomach contents from harbor seals in Southern New England (1977–1983) indicate that herring, silver hake, and sandeels represent important components in the diet (Seltzer *et al.*, 1986). An analysis of scats showed that sandeels were dominant and herring and mackerel were also present in the diet (Payne *et al.*, 1983).

A simple energetics approach was used to calculate consumption by marine mammals (Hinga, 1979; Kenny *et al.*, 1983). Gross basal ration for each species was estimated from average body sizes, estimated assimilation rates, activity coefficients, and energy equivalents methods (Hinga, 1979; Lockyer, 1981; Kenny *et al.*, 1983; Steimle and Terranova, 1985). Consumption of prey species j by predator i in quarter k (C) was then calculated by using quarterly estimates of abundance (N), stomach content fractions (S), and daily ration (DR) assuming that the animals obtained their full daily ration during each day of the quarter (91.25) :

$$C_{ijk} = DR_i \times N_{ik} \times S_{ijk} \times 91.25$$

The consumption estimates were based on the point estimates of population abundance from the aerial and shipboard surveys, an activity coefficient of 1.5, and a set of diet composition values based on the available data.

Seabirds

Seasonal estimates of abundance were derived from shipboard surveys conducted from 1980 to 1983 by research vessels (Payne *et al.*, 1984). Daily consumption rates were taken from Powers and Backus (1987), which was based on an energetics approach. The diet of Northern gannet, black-legged kittiwake, and shearwaters contains a large percentage of fish (Powers and Backus, 1987), most of which belong to pelagic species (Powers, pers. comm.). Although three species of shearwater are found in the region (Powers and Backus, 1987), they were lumped and considered as a single unit. Black-backed and herring gulls eat fish, but they obtain much of their annual ration from terrestrial sources and fishery discards. These gulls were not included in the analysis. Other seabirds are abundant in the region, but fish appear to comprise only a small proportion of their diets, and thus they were also excluded.

Piscivorous fish

Consumption of fish by spiny dogfish, Atlantic cod, and silver hake was estimated from food habits data collected during 1981–1986. Our method of computing consumption (C) by predator i of prey j was based on quarterly estimates of percentage weight of each prey in the predator diet (%R), seasonal estimates of daily ration for the predator (%BW), and predator biomass (B) calculated as:

$$C_{ijk} = B_{ik} \times \%BW_{ik} \times \%R_{ijk} \times 91.25$$

where k is an index of quarter. The estimated consumption in weight was then converted to numbers eaten by age group on the basis of information on the abundance of prey in the sea and the quarterly mean weights of the prey.

Daily ration estimates for each predator were derived from the literature. Silver hake and cod were estimated to consume 1.007 and 0.930% of their body weight (%BW) d^{-1} in spring and 0.607 and 0.837 %BW in autumn, respectively (Durbin *et al.*, 1983). Seasonal consumption was calculated by applying spring estimates to the winter quarter and autumn estimates were used for summer for these species. Since no seasonal estimates of daily ration were available for spiny dogfish, an annual estimate of 0.810 %BW d^{-1} was used in the model (Bowman *et al.*, 1984).

Food habits data from 1981–1986, that include detailed information on the size of fish prey, were examined to determine the diet composition of each predator and seasonal mean values were calculated. Previous studies indicated that cod and silver hake begin to feed on fish at about age 3, and spiny dogfish at age 5 (Bowman and Michaels, 1984; Bowman *et al.*, 1984; Overholtz *et al.*, 1988). This information was used to calculate the proportion of the predator biomass that would feed on fish on an annual basis. Prey size data were used to determine the age groups vulnerable to fish predation as: sandeels ages 1–4; mackerel ages 1–3; herring ages 1–6; silver hake ages 1–3.

Predation mortality rates (M2s) were calculated on a quarterly basis from the number dying (D) and the number alive at the beginning (N) from:

$$D_{jk}/N_{jk} = M2_{jk} \times (1 - e^{-Z_{jk}})/Z_{jk}$$

where the total instantaneous mortality rate (Z) equals the sum of the predation mortality rate (M2), the fishing mortality rate (F), and all other sources of mortality (M1) for each prey j in each quarter k. The values of M1 were assumed equal to 0.2 for all the prey species in the model. Quarterly values of F were input and the relationship was solved iteratively using a binary search algorithm (Press *et al.*, 1986).

Stochastic recruitment functions were parameterized for sandeels, mackerel, herring, silver hake, and cod. Stock-recruit data from virtual population analysis were used for all species except sandeel and spiny dogfish. A linear stock-recruit function was used for spiny dogfish (Overholtz and Tyler, 1986). A relationship for sandeels was developed using estimates of spawning-stock size and larval production from egg and larval surveys (Morse, 1982). A three parameter (a, b, k) model (Shepherd, 1982) with a lognormal white-noise multiplier (LM) was used to generate annual recruitment (R) as a function of spawning-stock biomass (SSB) :

$$R_j = (a \times SSB_j)/[1 + (SSB_j/k)b] \times LM$$

Recruitment estimates were scaled upward by a factor of 1.5 for mackerel, herring, and the two silver hake stocks to account for the fact that in the original virtual population analysis predation mortality rates are not accounted for (Overholtz *et al.*, 1988). Recruitment estimates for cod, spiny dogfish, and sandeels were not scaled in this manner since predation mortality was not modeled for cod and dogfish, and the sandeel stock-recruit relationship was based on larval data with a constant mortality applied to produce age 1 recruits.

Results

Consumption

Total consumption by the three categories of predators was estimated to be about 476 ktonnes per year (Fig. 3). Piscivorous fish, particularly spiny dogfish, account for most of the consumption in the pelagic system, followed by marine mammals and seabirds. Consumption of harvested species is about two times the present levels of landings for herring and silver hake and 2.4 for mackerel. Most of this predation is concentrated on younger age groups that are not normally landed.

Five species of marine mammals accounted for most of the total consumption (120 ktonnes) of pelagic fish by all mammals (Fig. 3, Table 1). Finback whales account for almost half of total consumption, followed by pilot and humpback whales. Common dolphins and harbor seals are also important. Finback and humpback whales account for most of the marine mammal predation on sandeels, although they are also eaten by pilot whales and harbor seals. Mackerel are eaten by every marine mammal in the region, but most of the consumption is by pilot, and finback whales, common dolphins, and humpback whales. Although herring from the Gulf of Maine stock are less abundant than mackerel or sandeels, they are still eaten in quantity by several species. The only significant mammalian predators on silver hake are pilot whales and white-sided and common dolphins.

Of the three predator categories, the annual consumption by seabirds is the smallest (Fig. 3, Table 2). The annual estimate of 19 ktonnes is probably in the right order of magnitude, but precision of this estimate cannot currently be verified because abundance and diet composition data are scarce. Northern gannet accounts for the largest proportion of fish consumption. The most

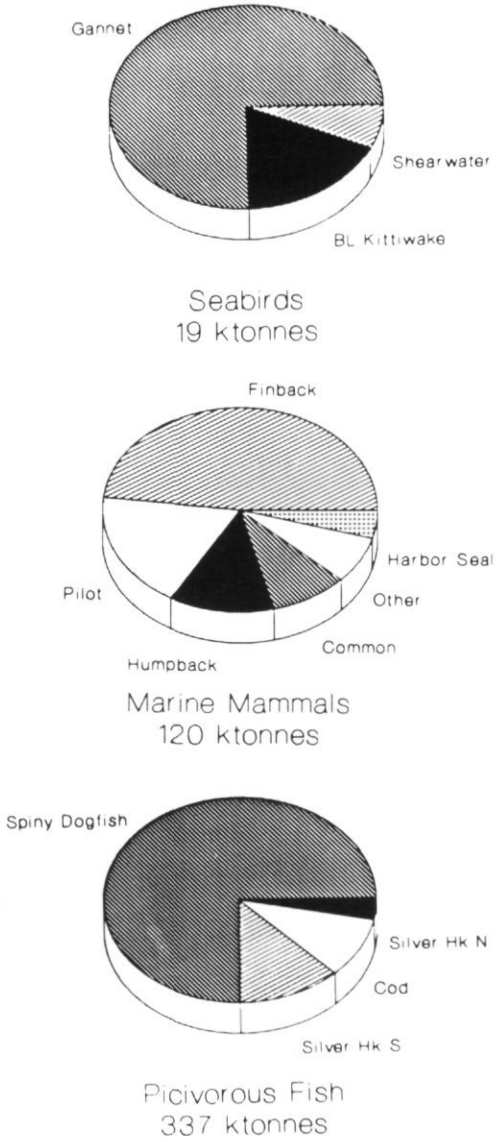

Figure 3. Total consumption and proportion consumed by individual species of seabirds, marine mammals, and piscivorous fish.

significant predator of sandeels appears to be black-legged kittiwakes.

Piscivorous fish consume the largest share of the total pelagic biomass eaten by the three predator groups (Fig. 3, Table 3). Annual consumption by predatory fish was estimated to be about 337 ktonnes. Mackerel account for about 50% and sandeel about 30% of the total. Spiny dogfish, because of their large biomass, account for the largest proportion (75%) of consumption by piscivorous fish. Of the 179 ktonnes of mackerel consumed, about 93% is eaten by the spiny dogfish stock. Dogfish are the largest consumer of sandeels, but cod and the southern silver hake stock also consume significant quantities of this species. The northern stock of silver hake apparently does not overlap with sandeels to any great degree in a particular season, hence consumption is low. Cod and dogfish consume about 18 ktonnes of silver hake from the northern stock and cannibalism accounts for another 5 ktonnes.

Predation mortality

Predation mortality rates (Table 4) for the five species of fish in the pelagic system are generally much higher than the values of natural mortality generally assumed in single species stock assessments. This applies particularly to mackerel (Anderson, 1985) and both silver hake stocks (Almeida, 1987). Still, these rates represent only the predation mortality generated within the model system. Natural mortality on age 1 herring is probably much higher, but the important predators of this age group have not been accounted for in this exercise. The high M2s on the northern silver hake stock are due to cannibalism and heavy consumption by cod and spiny dogfish, especially on age 1 and 2 fish.

Regional ecosystem issues

One advantage of an ecosystem perspective for managing fishery resources is that proposed management strategies can be viewed against the response of all the

Table 1. Average consumption (tonnes) by marine mammals on the five prey species in the pelagic ecosystem for 1988–1992.

	Predator										
Prey	Hump-back	Finback	Minke	Pilot	Grampus	Bottle-nose dolphin	White-sided dolphin	Harbor porpoise	Common dolphin	Harbor seal	Total
Sandeel	9907	37932	607	2834	0	0	428	470	633	2952	55763
Mackerel	2423	9995	110	13413	311	336	560	111	8855	450	36264
Herring	2586	9959	366	2803	0	0	1487	684	0	1433	19318
Silver hake, N	0	0	0	0	0	0	1984	954	0	449	3387
Silver hake, S	0	0	0	3130	333	190	0	0	1798	0	5451
Total cons.	14915	57886	1082	22180	644	527	4459	2218	10986	5284	120182
% Total cons.	12.4	48.2	0.9	18.5	0.5	0.4	3.7	1.8	9.1	4.4	100

Table 2. Average consumption (tonnes) by seabirds on the five prey species in the pelagic ecosystem for 1988–1992.

Prey	Predator			Total
	Northern gannet	Shearwater	Black-legged kittiwake	
Sandeel	0	992	3 332	4 324
Mackerel	10 328	90	26	10 443
Herring	2 827	247	0	3 074
Silver hake, N	0	0	83	83
Silver hake, S	1 443	0	0	1 443
Total consumption	14 597	1 329	3 439	19 365
% Total consumption	75.4	6.9	17.8	100

Table 3. Average consumption (tonnes) by piscivorous fish on the five prey species in the pelagic ecosystem for 1988–1992.

Prey	Predator				Total
	Silver hake, N	Silver hake, S	Cod	Spiny dogfish	
Sandeel	5 798	22 000	18 307	64 962	111 067
Mackerel	338	7 541	3 692	167 463	179 024
Herring	457	1 013	173	4 255	5 898
Silver hake, N	5 275	0	6 046	11 995	23 316
Silver hake, S	0	10 137	3 879	3 353	17 369
Total consumption	11 869	40 690	32 096	252 018	336 673
% Total consumption	3.5	12.1	9.5	74.9	100

interacting species. Simulations can thus provide a general idea of the impact of measures on the fish community as a whole (Anon., 1986, 1987, 1988). For the purpose of simple comparison, several different scenarios were simulated with the pelagic system model. Results are contrasted with present conditions.

If the current fishing mortality regime remains in effect the species in the pelagic ecosystem should maintain a total biomass (1989–1992 mean) of about 3100 ktonnes over the 4-year period (Fig. 4A). The mackerel stock is predicted to stabilize after an initial decline, whereas the sandeel stock markedly increases up to 1991, and then declines. The southern silver hake stock will also gradually increase and the herring and northern silver hake stocks remain virtually unchanged.

To simulate the effect of managing the exploited fish species of the system at $F_{0.1}$, the fishing mortality rates on all species, excluding spiny dogfish and sandeels, were changed. Under these conditions the average total biomass of the system would decline to 2566 ktonnes (Fig. 4B). In particular, the mackerel stock would drop considerably. The response by the other species is similar to runs in which initial conditions are maintained (Fig. 4A), although sand eels would be somewhat reduced and herring biomass might actually increase. Much of the change in the mackerel stock would be due to the increased fishing mortality rate. The changes in the sandeel and silver hake stocks reflect a substantial increase (+81%) in the cod stock accompanying a major decrease in F.

If fishing mortality rates on the silver hake stocks were reduced to about half of their $F_{0.1}$ values, cod F reduced to $F_{0.1}$, and dogfish F remaining the same, the total system biomass would not change significantly from present conditions (Fig. 4C). Mackerel biomass would remain about the same, but sandeel biomass would decline considerably because of the substantial increase in biomass of the two important predators.

Spiny dogfish biomass is at record highs in the region at this time (Pope *et al.*, 1987), prompting some speculation as to the effects of a reduction in the biomass of this species on the abundance of other species. To simulate a major dogfish reduction, the fishing mortality rate on this species was increased to 0.60. Total system biomass would increase to an average of 3356 ktonnes, 10% above present conditions (Fig. 4D). All species would increase compared to runs where initial conditions were maintained, but the overall effects are apparently small.

Alternative feeding models

A critical component of recent efforts to model biological interactions in large marine ecosystems is the re-

Table 4. Age-specific predation mortality rates for the five prey species in the pelagic ecosystem for 1988–1992.

	Age					
Year	1	2	3	4	5	6+
1988						
Sandeel	0.46	0.65	0.32	0.17	0.00	0.00
Mackerel	0.54	0.29	0.20	0.02	0.02	0.01
Herring	0.12	0.27	0.13	0.09	0.07	0.06
Silver hake, N	0.43	0.40	0.30	0.03	0.03	0.00
Silver hake, S	0.30	0.23	0.17	0.05	0.03	0.00
1989						
Sandeel	0.77	0.28	0.14	0.08	0.00	0.00
Mackerel	0.85	0.43	0.30	0.03	0.03	0.02
Herring	0.16	0.28	0.13	0.09	0.07	0.06
Silver hake, N	1.02	0.93	0.68	0.06	0.05	0.00
Silver hake, S	0.34	0.26	0.19	0.45	0.30	0.00
1990						
Sandeel	0.72	0.31	0.15	0.08	0.00	0.00
Mackerel	1.07	0.71	0.60	0.03	0.03	0.02
Herring	0.18	0.34	0.16	0.10	0.09	0.07
Silver hake, N	0.70	0.65	0.50	0.04	0.03	0.00
Silver hake, S	0.24	0.19	0.14	0.03	0.02	0.00
1991						
Sandeel	0.69	0.28	0.14	0.75	0.00	0.00
Mackerel	1.06	0.71	0.53	0.04	0.03	0.02
Herring	0.18	0.36	0.17	0.11	0.09	0.07
Silver hake, N	0.67	0.62	0.48	0.05	0.04	0.00
Silver hake, S	0.20	0.16	0.11	0.02	0.02	0.00
1992						
Sandeel	1.07	0.44	0.21	0.11	0.00	0.00
Mackerel	1.09	0.78	0.60	0.04	0.04	0.03
Herring	0.21	0.40	0.19	0.12	0.10	0.09
Silver hake, N	0.96	0.90	0.73	0.09	0.07	0.00
Silver hake, S	0.22	0.17	0.12	0.02	0.01	0.00

sponse of predators to changes in prey abundance. A generalization from these analyses is that aggregate predation on fish can be thought of as a scaling factor on recruitment; recruitment estimates from single species and multispecies virtual population analysis are highly correlated (Gislason and Sparre, 1987; Anon., 1986, 1987, 1988). This suggests that predation may not be a determinant of year-class strength in marine fishes, at least not after the first year of life.

These models are based on the assumption of constant suitability, which implies that predation mortality is a curvilinear function of the relative abundance of the various prey species. They correspond to a "type 2" functional feeding response (Fig. 5; Holling, 1965). Alternatively, if predators respond differentially to changes in prey density, and for instance exhibited a "type 3" response (Fig. 5; Holling, 1965), then predation might indeed be a source of significant variation in cohort strength for marine fish populations (Hildén, 1988). At present there is a lack of empirical data to support or reject hypotheses about functional feeding responses in marine fish, but some studies suggest that predation may be an important contributing factor in determining year-class strength (Walters *et al.*, 1986; Hildén, 1988).

To study the possible differences that would emerge from alternative types 2 and 3 feeding hypotheses, the model was reprogrammed to allow predatory fish to feed accordingly. The "type 2" response was modeled with a negative exponential relationship, while the "type 3" response was modeled with a function similar to the Shepherd (1982) approach. Both models were parameterized over the same range of prey density and predation mortality for each age group. Predation mortality from marine mammals and seabirds was set to zero, since only a relative comparison between the two models was required.

Results are shown in Figures 6 and 7. Under a "type 2" model, sandeel and herring biomass would be slightly larger than under the type 3 response, but the biomass of mackerel and both silver hake stocks would be smaller. Aggregate biomass would be virtually the same in both cases. Age-specific mortalities, however, would be quite different under the two feeding regimes. Mortalities at

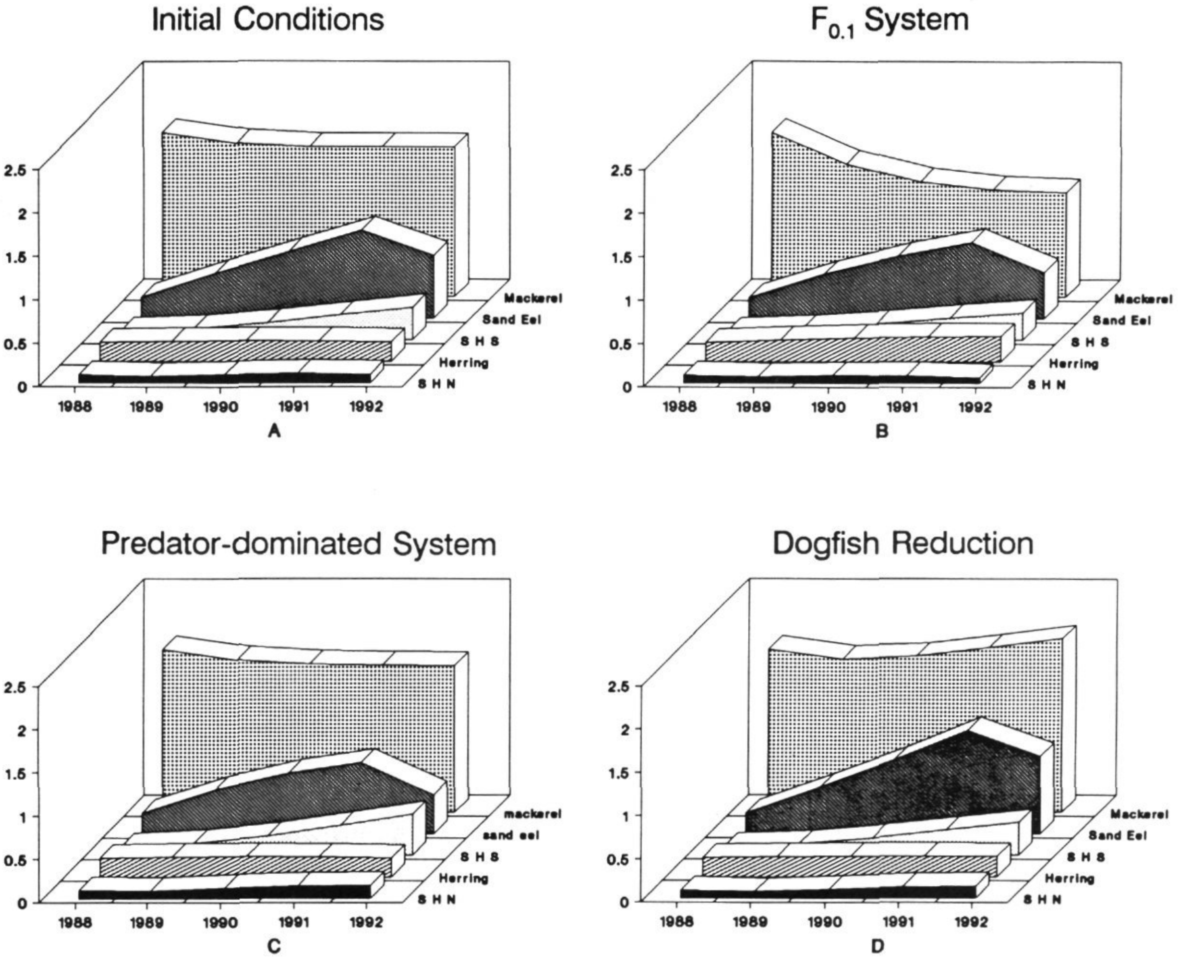

Figure 4. Biomass responses (millions of tonnes) of the pelagic ecosystem model to different management strategies. A: maintaining the initial conditions from the baseline model; B: fishing mortality managed at $F_{0.1}$ level for all species except dogfish and sandeels; C: fishing mortality on silver hake reduced to half the $F_{0.1}$ level, in cod to $F_{0.1}$; other species unchanged; D: fishing mortality on spiny dogfish increased to 0.6; other species unchanged.

age 1 for all species except herring were substantially larger for the type 2 model (Fig. 7).

Discussion

Biological interactions play an important role in the dynamics of the pelagic fish community found off the Northeastern USA. The impact of predation on this system is significant; an estimated 500 ktonnes of biomass is consumed annually by predatory fish, marine mammals, and seabirds. This study is a first attempt to quantify this predatory impact and provide an estimate of the magnitude of predation mortality rates in this system and their specific sources. Results suggest it is important to consider biological interactions in the process of determining management objectives because fishery management plans (FMP) have regional implications and their success is linked to the trophic interactions that occur in the ecosystem. Specifically, our analysis emphasizes that there may be conflict between FMPs intended to conserve and rebuild prey populations, while at the same time the USA Marine Mammal Protection Act prescribes increases in these predators to "optimal sustainable populations". A modeling exercise of this type not only results in a gain in knowledge and perspective about the ecosystem and its functioning parts, but many limitations of present data as well as our understanding become apparent. For example, the importance of seasonal diet composition data, of obtaining large numbers of fish stomachs, and of specific data on the lengths of prey, in resolving the actual magnitude of predation in this system becomes apparent.

Marine mammals are relatively abundant and appear to be important in the dynamics of the pelagic fish community in the Northeastern USA because they con-

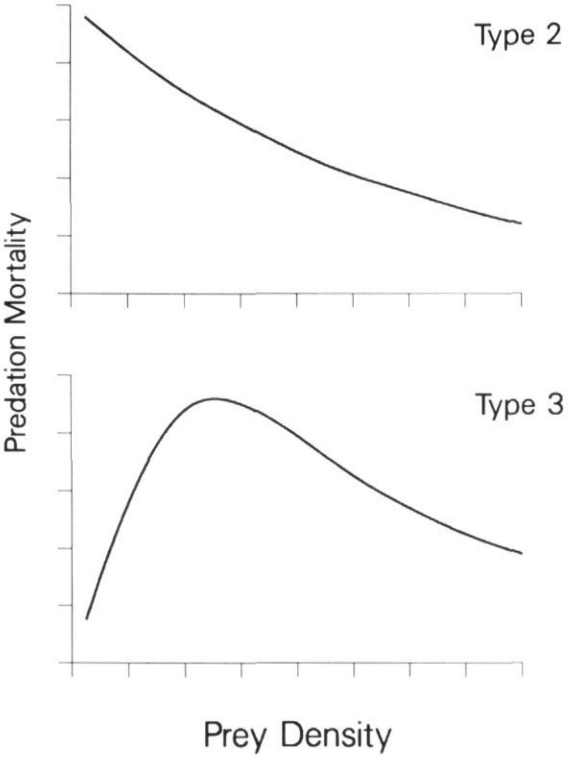

Figure 5. Stylized mortality curves representing the classical "type 2" and "type 3" (Holling, 1965) functional feeding response of predators to changing densities of prey.

sume a relatively large amount of fish prey. This is in contrast to the North Sea and the Baltic, where marine mammals have a very minor influence on the system (Anon., 1987, 1988). Mammals feed intensively during their seasonal excursions to the area, and daily rations are large; humpback and finback whales for example may consume up to 1 tonne per day. The key to an accurate assessment of the total consumption by marine mammals in the region is reliable abundance estimates for the five most important species. The estimate of 120 ktonnes of total consumption is likely in the right order of magnitude, but an estimate of precision cannot be included at the present time. Diet composition for the larger whales will have to be determined by direct observation, which can be accomplished by skilled observers, at least for species like humpbacks (Mayo *et al.*, 1988). The tendency of whales to be very species-specific in their diet composition helps to narrow the number of likely prey (Smith and Gaskin, 1974; Sergeant, 1963). Recent efforts to autopsy the smaller *Odontocetes* that are taken incidentally in fishing operations will also prove very useful (Overholtz and Waring, in review).

Predation mortality rates for juvenile fish excluding 0-group were shown to be higher for most species than previously assumed in single-species analyses (Fogarty and Clark, 1983; Anderson, 1985; Almeida, 1987). This result is not too surprising, but it follows that estimates of recruitment at age 1 for most of these species have likely been too low (Anon., 1988; Overholtz *et al.*, 1988). For most of the species this result will not have a dramatic impact on current single-species analyses since the age at recruitment to the fisheries for these species is usually in the order of 3 years old. Atlantic mackerel, however, suffers significant natural mortality at ages 2 and 3, and this may well invalidate current assessments for this stock (Overholtz *et al.*, 1988).

The estimated predation mortalities from this analysis are preliminary and reflect only the mortality that is accounted for by the predators in the model system. For mackerel, the values may reflect a significant amount of the natural mortality that actually occurs, while for herring much of the mortality is probably generated outside the model system, particularly at age 1. The model of consumption uses average seasonal diet compositions for the 1981–1986 period and therefore the projections must reflect these diet percentages. If other traditional prey resources such as the Georges Bank herring stock become available and if they were, as in the past, eaten by predators, the model at present cannot reflect such changes. The model, however, will

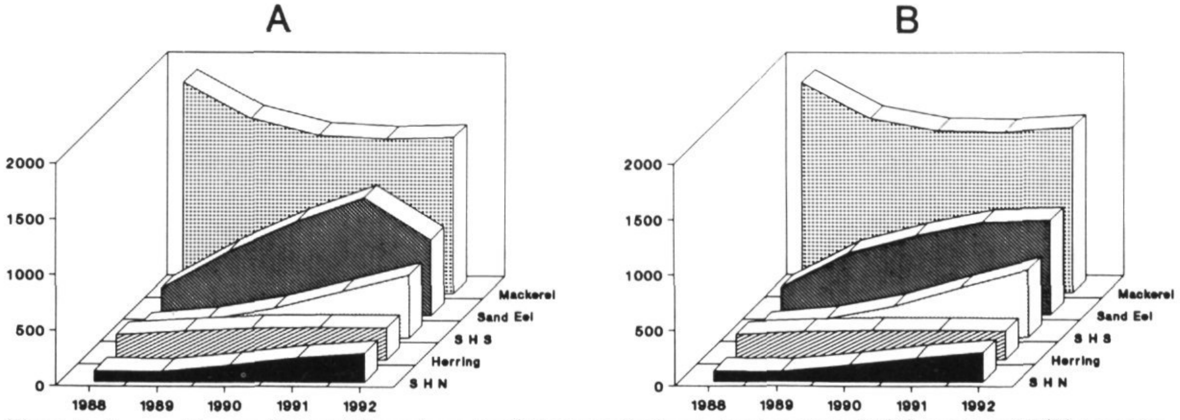

Figure 6. Average biomass (ktonnes) for each species if piscivores feed according to a "type 2" (A) and "type 3" (B) response.

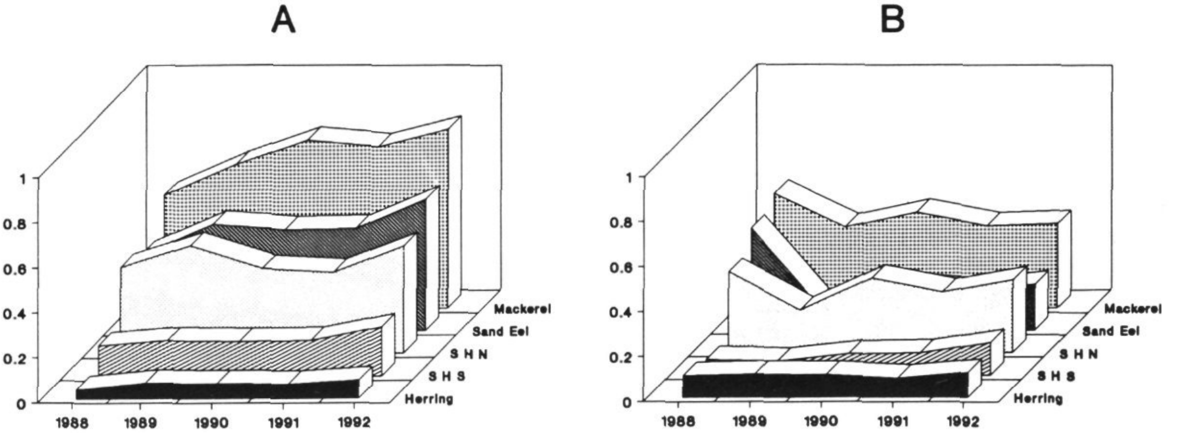

Figure 7. Predation mortality rates on one-year-old fish for each species if piscivores feed according to a "type 2" (A) and "type 3" (B) response.

track any fluctuations that may occur in the five prey species that are currently in the model because the age specific component of the diet does depend on abundance.

The results of the simulations with different feeding responses show that predation mortalities are highly dependent on how the predators respond to prey abundance. For short-term projections this is not a serious issue as long as recruitment does not change dramatically, because annual species-specific consumption will not change much over such a short period of time. In longer-term predictions, however, the choice of feeding model becomes critical when diet compositions change dramatically. A great deal of theoretical, simulation, and fieldwork still needs to be accomplished before we can utilize simple generalizations to accurately predict long-term changes in consumption. Resolving the feeding model question for all categories of predators including fish, marine mammals, and birds will be very important.

This study has dealt with the implications of developing an ecosystem perspective for a large marine system where trophic interactions are important. The insight that has been gained should be useful for policy-makers who need to make complex decisions, usually on a species by species basis, on fishery management strategies (including resource protection strategies for some components such as marine mammals) for large regions. Although not definitive, this study can serve as a guide for posing management related questions for interacting resources. For instance, is it important to determine how extensively mackerel are utilized as prey or whether a dogfish removal fishery would accomplish much relative to the pelagic fish ecosystem and in respect of the amount of effort and capital expended. Future research on biological interactions will remain of considerable practical importance in developing integrated management strategies for regional fishery ecosystems.

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Recent changes in the population of the sandeel (*Ammodytes marinus* Raitt) at Shetland in relation to estimates of seabird predation

R. S. Bailey, R. W. Furness, J. A. Gauld, and P. A. Kunzlik

Bailey, R. S., Furness, R. W., Gauld, J. A. and Kunzlik, P. A. 1991. Recent changes in the population of the sandeel (*Ammodytes marinus* Raitt) at Shetland in relation to estimates of seabird predation. – ICES mar. Sci. Symp., 193: 209–216.

Recent changes in the Shetland population of the lesser sandeel (*Ammodytes marinus* Raitt) have been investigated using data from commercial catches and research-vessel surveys using small-mesh midwater trawls. Both recruitment and total stock size have decreased since the early 1980s. Over the period 1981–1988 there has also been a decrease in consumption of sandeels by seabirds. On the assumption that the natural mortality rate has not changed, the predation mortality caused by seabirds (i.e. the fraction of the population taken) has not decreased significantly. These findings indicate that the switching of seabirds from sandeels to other prey is in approximate proportion to the abundance of sandeels, and that there is no evidence of a non-linear functional response. The estimates on which this analysis is based are subject to considerable uncertainty, however, and annual data on the consumption of sandeels and other prey (in terms of numbers at age) by each of the main groups of predators would be needed to refine the analysis significantly. The importance of incorporating consumption by seabirds and other predators in future assessments of this stock is stressed.

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Introduction

Sandeels (Ammodytidae) are numerically among the most abundant fish in the North Sea (Yang, 1982). As well as supporting large fisheries, they are important in food chain dynamics, and many predators (fish, seabirds, and marine mammals) prey heavily upon them (Harwood and Croxall, 1988; Daan, 1989; Furness, 1990). Since 1974 there has been a sandeel fishery in inshore waters around Shetland which takes almost exclusively the lesser sandeel (*Ammodytes marinus* Raitt). Landings rose to a peak of 52 000 t in 1982 and have subsequently decreased to a much lower level (Anon., 1989).

Sandeels form one of the most important items of the food of many species of seabirds at Shetland, especially during the breeding season (Heubeck, 1989). The estimated quantity of sandeels consumed by seabirds at Shetland in 1981–1983 was about 49 000 t yr^{-1} (Furness, 1990), that is approximately the same as that taken by the fishery. Thus the potential interactions between seabirds, fisheries, and sandeel stocks in this area are of considerable interest to both fisheries scientists and ornithologists (Heubeck, 1989).

In recent years, there has been a decrease in the breeding success of several species of seabirds at Shetland which has been attributed to a shortage or non-availability of sandeels (Heubeck, 1989). In addition, while historical data indicate large increases in several seabird species to unprecedented numbers in the late 1970s (Thom, 1986), the numbers of breeding pairs have recently decreased in some species (Furness, 1989). These findings imply that the quantity of sandeels taken annually by seabirds may vary. Correspondingly, it is also possible that the fraction of the sandeel population taken by seabirds varies as stock size changes. In the absence of prey-switching, seabirds might be expected to show increased predation rates (i.e. take a greater percentage of the available prey) as stock declines owing to their rather stable food requirements. Alternatively, if seabirds switch diet as the sandeel stock declines then the predation rate by seabirds might fall or remain the same. At present, there is no recorded information about the functional response of seabirds to changes in sandeel abundance.

The purpose of this paper is to summarize the evidence for the recent changes in Shetland sandeel population size and to examine the influence of these changes upon the predation rate by seabirds, with particular regard to the implications for the value of natural mortality rate used in fish stock assessment. Since the relevant data on seabird food consumption are not available for all years, the approach taken has been to compare the data from 1981 and 1988, years contrasting in the stock size of sandeels and in the quantity of sandeels consumed by seabirds.

Methods

For assessment purposes the Shetland sandeel population is treated as a separate stock (Anon., 1989). This is justified on the grounds that the fishing areas around Shetland are close inshore (Fig. 1) and therefore isolated from sandeel fishing grounds in other parts of the North Sea, and that growth rates at Shetland are much lower than in other areas of the northern North Sea where sandeel fisheries take place (Anon., 1979). While this does not necessarily mean that the Shetland population is totally isolated from other populations, it is likely that sandeel population dynamics at Shetland are governed principally by local events rather than by immigration or emigration, at least after the juveniles have recruited to the population at around six months of age. The boundaries of the Shetland area used for stock assessment purposes and the fishing grounds at Shetland are shown in Figure 1.

Throughout the sandeel fishing season at Shetland, which usually lasts from April to September, samples of sandeels were taken every month from a random sample of vessels landing at the fishmeal plant on Bressay and at Scalloway. From half-yearly landings in numbers at age (Anon., 1989), estimates of stock size were made by virtual population analysis (VPA; Gulland, 1983). To allow for fish dying from natural causes, estimates of the instantaneous natural mortality coefficient (M) were derived from a multispecies model for the whole North Sea (Anon., 1988). Values of M were based on estimates of the numbers of sandeels eaten by the main fish predators and rough estimates of quantities eaten by other predators and of quantities that die from other causes. The estimates of consumption by other fish were based on extensive stomach sampling in 1981 (Daan, 1989) and on a multispecies virtual population analysis in which it was assumed that the suitability of different prey organisms remained the same over the period 1981–1988 (Anon., 1988). The values of M ($yr^{-0.5}$) obtained were

January–June:
1.0 and 0.4 for 1-group and older fish, respectively;
July–December:
0.8 and 0.2 for 0-group and older fish, respectively.

It is now known whether these values based on the entire North Sea are appropriate for the local Shetland stock, although values of total mortality calculated from catch per unit effort data obtained during the first few years of the Shetland fishery indicate that M cannot be appreciably higher than the values given above (Anon., 1982). Values of M are assumed to be constant from year to year.

Additional data on the abundance of 0-group sandeels in the Shetland area have been obtained from an annual midwater trawling survey of the northwestern North Sea carried out from 1969 to 1988. During these surveys, a pelagic trawl especially designed to catch small gadoid fish and fitted with a knotless codend of 11 mm stretched mesh was towed in a series of stepped hauls fishing close to the bottom, roughly in the middle of the water column and within about 10–15 m of the sea surface (Holden, 1981), and provided samples of sandeels as well as other small fish.

Numbers of breeding pairs of seabirds in Shetland over the years 1981–1983 and in 1988 have been taken from compilations of census data (Tasker *et al.*, 1987; Heubeck, 1989). Decreases in numbers of each species from 1981–1988 have been estimated to the nearest 10% as census data and variations between colonies within Shetland do not allow a more precise treatment. The breeding success of seabirds in 1981 and 1988 was recorded in colonies at Foula as well as in several other colonies in Shetland (Heubeck, 1989).

Seabird feeding data are available from various colonies for the period 1975–1983 and for 1988. For some species, dietary data have been collected by independent studies at two or more colonies. Thus, puffins *Fratercula arctica* have been studied at Unst (Martin, 1989), at Foula (Furness, 1990), at Fetlar (Harris and Hislop, 1978), and at Fair Isle (Harris and Riddiford, 1989). In general, dietary variation between Shetland colonies has been found to be small and so studies at a single colony are taken to represent Shetland as a whole. Over the period 1975–1983, there were no clear changes between years in breeding success or diets except for a declining prevalence of sandeels in gannet *Sula bassana* diet as herring *Clupea harengus* increased (Martin, 1989) and a declining frequency of sandeels in the diet of non-breeding great skuas *Catharacta skua* (Furness, 1987). Thus, dietary data for all the years 1975–1983 have been pooled (except for gannet) to represent diets of breeding seabirds and chicks in 1981. Further information on this compilation of dietary data is given in Furness (1990).

Daily consumption of sandeels by each seabird species was estimated by multiplying breeding numbers by their

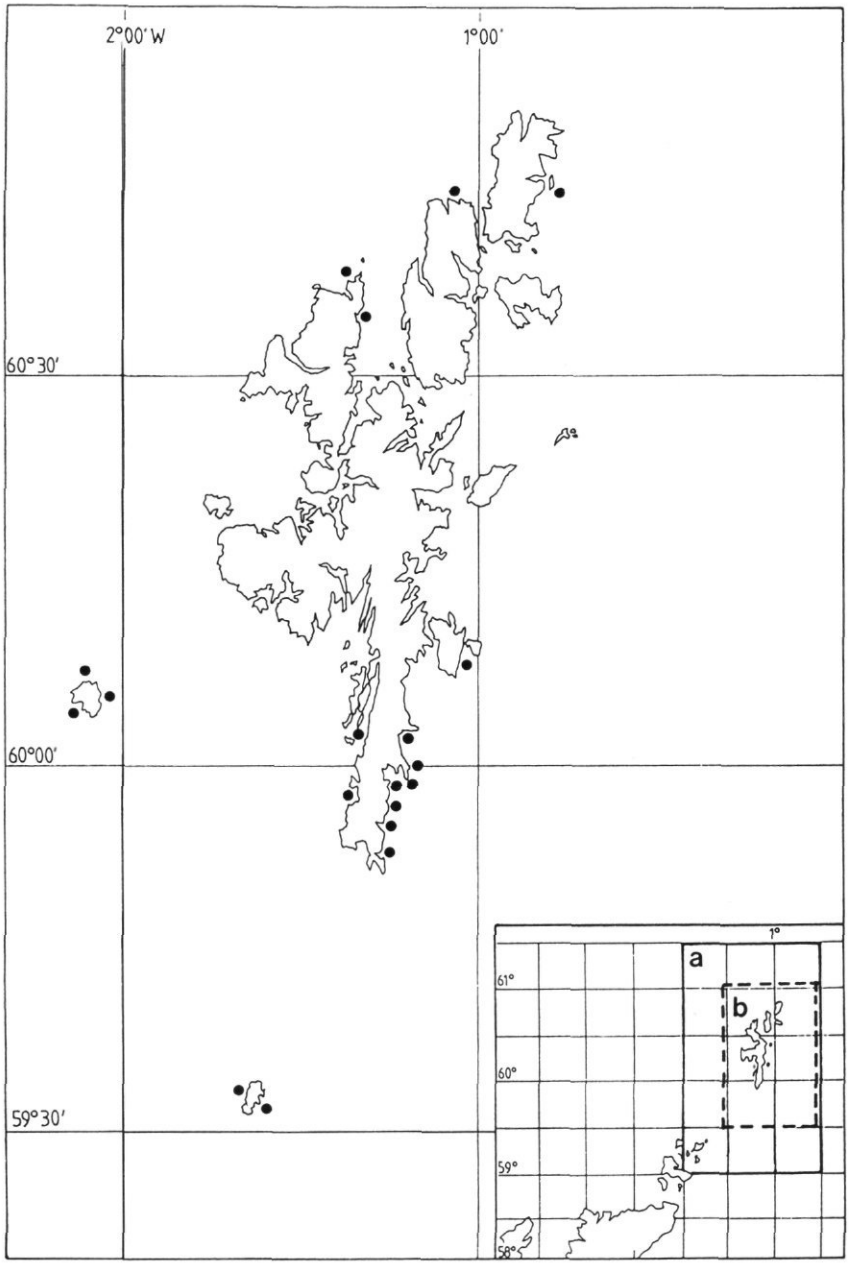

Figure 1. Map showing the position of the Shetland sandeel fishing grounds (filled circles). The inset shows: (a) the Shetland sandeel assessment area used by ICES (Anon., 1989); and (b) the survey area referred to in Table 2.

estimated daily food requirement during chick-rearing and by the proportion of sandeels in their diet. The daily energy requirement was taken as 3.5 times the basal metabolic rate (BMR) with a 30% increase for food requirements of chicks (Furness, 1978). The factor of 3.5 represents the mean of some 20 studies of daily energy budgets of seabirds measured using labelled water (Furness, 1990). No allowance was made for food requirements of non-breeders, as these have previously been shown to contribute little to the total population budget (Furness, 1978) and diets of non-breeders tend to differ from, and contain less sandeels than, diets of breeders or chicks (Hudson, 1986; Furness, 1987).

Results

The numbers at age and biomass of the sandeel population as estimated by the ICES Industrial Fisheries

Table 1. Estimated numbers of sandeels at age (millions) in the Shetland assessment area (Fig. 1) at 1 July and total stock biomass (tonnes) at 1 January (TBM) from 1974 to 1988 (from Anon., 1989).

	1974	1975	1976	1977	1978
0	13 898	32 076	41 765	48 257	36 663
1	4 015	1 973	3 459	4 186	4 372
2	451	1 242	866	1 085	1 119
3	136	126	600	339	452
≥4	167	97	82	282	275
TBM	41 770	34 566	50 640	66 954	78 845
	1979	1980	1981	1982	1983
0	30 605	42 783	76 083	81 180	74 926
1	3 528	4 426	4 264	6 240	8 090
2	1 794	1 363	1 405	1 147	2 626
3	538	653	397	428	402
≥4	373	274	311	193	194
TBM	65 389	68 725	77 152	102 117	109 895
	1984	1985	1986	1987	1988
0	29 188	21 343	19 451	2 208	20 750
1	10 144	3 067	2 742	2 398	253
2	3 088	5 022	1 247	1 405	1 126
3	1 066	1 467	2 396	641	674
≥4	147	566	868	1 721	1 205
TBM	138 177	99 893	86 755	72 421	47 315

Working Group using VPA are shown in Table 1 (Anon., 1989). This analysis indicates that the total stock biomass at 1 January increased over the period 1974–1984. Subsequently, recruitment has been below average and stock biomass has fallen.

Densities of sandeels expressed as the number caught per unit time in ICES statistical rectangles adjacent to Shetland (Fig. 1) are given in Table 2. A high proportion of these fish were 0-group, so this provides an indication of the abundance of each year's recruiting age group in offshore waters. A marked decrease in the abundance of 0-group sandeels is indicated after 1982.

The estimated total biomass of sandeels on 1 July, commercial catch, and total production of the stock, defined as biomass dying plus change in biomass, are given for each year 1974–1988 in Table 3. These data indicate a pronounced decrease in total production from 1983 to 1987. In fact, production in 1987 is estimated to have been less than the 49 000 t of sandeels estimated to have been taken by seabirds in the years 1981–1983 (Furness, 1990).

Most breeding seabirds in Shetland fed themselves and their chicks predominantly on sandeels in June–July 1975–1983, but several species had changed diet in 1988 (Table 4). Populations of several species declined between 1981 and 1988 and several (an overlapping subset) suffered breeding failures in 1988 (Table 4). There is, however, no direct correlation between these two effects.

Combining estimates of BMR (Table 5) with the population and dietary data in Table 4 yields daily consumption of sandeels during the chick-rearing period in 1981–1983 and 1988 as shown in Table 5. Sandeel

Table 2. Geometric mean numbers of sandeels (all age groups) caught in small mesh midwater trawls around Shetland (cf. Fig. 1.).

Year	Mid-date of survey	No. of hauls	Geometric mean
1969	8 July	23	12.20
1970	27 June	3	279.00
1971	24 July	17	5.80
1972	27 July	14	0.93
1973	20 July	4	242.00
1974	18 June	6	25.80
1975	1 July	6	1301.00
1976	23 June	3	744.00
1977	26 June	9	208.00
1978	1 July	7	1368.00
1979	16 June	7	115.00
1980	21 June	6	6.40
1981	14 June	5	75.80
1982	28 June	6	14.90
1983	27 June	4	0.41
1984	No survey	–	–
1985	22 June	5	0.43
1986	5 July	5	0.00
1987	17 June	4	0.50
1988	15 June	6	0.86

Table 3. Estimated total biomass at 1 July, annual change in biomass, biomass dying by all causes, commercial catch, and total production of *A. marinus* in the Shetland assessment area (Fig. 1) for each calendar year from 1974 to 1988 (data from Anon., 1989). All figures in tonnes.

Year	Total biomass	Change in biomass	Biomass dying	Commercial catch[1]	Total production
1974	49 900	−7 200	48 100	8 540	40 900
1975	75 400	+16 100	68 400	13 500	84 500
1976	100 600	+16 300	83 400	17 800	99 700
1977	116 600	+11 900	103 900	25 100	115 800
1978	99 400	−13 400	104 500	32 400	91 100
1979	92 100	+3 300	77 800	13 700	81 100
1980	113 600	+8 400	97 000	22 100	105 400
1981	167 400	+25 000	147 100	44 500	172 100
1982	182 600	+7 800	177 100	57 500	184 900
1983	191 500	+28 300	159 500	27 900	187 800
1984	133 300	−38 300	134 500	28 700	96 200
1985	108 600	−13 100	84 800	14 100	71 700
1986	89 500	−14 300	73 000	12 000	58 700
1987	54 100	−25 100	45 400	5 300	20 300
1988	68 400	+7 100	45 300	3 900	52 400

[1] For comparability, these are estimated by multiplying the numbers caught at each age by mean weights-at-age in the catches. They may not therefore equate exactly to the reported annual catches.

Table 4. Average number of breeding pairs in 1981–1983 (N), percentage decrease in 1988 compared to 1981–1983, breeding success and percentage of sandeels in the diets of breeding adult seabirds and their chicks in June–July for study periods 1981–1983 and 1988 in Shetland.

	Breeding pairs		Chicks per pair[1]		% sandeels[2]	
Species	N 1981–1983	% decrease 1988	1981–1983	1988	1975–1983	1988
Red-throated diver	700	10	0.6	0.3	95	17
Gavia stellata					(62)	(41)
Fulmar	200 000	0	0.6	0.3	70	5
Fulmarus glacialis					(177)	(28)
Gannet	20 000	0	0.6	0.6	80	5
Sula bassana					(137)	(111)
Shag	8 300	30	1.4	1.4	100	100
Phalacrocorax aristotelis					(500)	(35)
Arctic skua	1 900	40	1.1	<0.1	100	100
Stercorarius parasiticus					(200)	(20)
Great skua	5 600	10	1.2	0.0	70	5
Catharacta skua					(>900)	(322)
Herring gull	4 500	20	0.5	nd	20	0
Larus argentatus					(50)	(10)
Great black-backed gull	2 800	0	2.1	2.2	45	0
Larus marinus					(100)	(20)
Kittiwake	54 500	10	1.3	0.0	100	65
Rissa tridactyla					(106)	(6)
Arctic tern	32 000	70	0.5	0.0	100	20
Sterna paradisaea					(>500)	(42)
Guillemot	110 000	30	(0.7)	(0.7)	100	95
Uria aalge					(230)	(91)
Razorbill	12 000	30	(0.7)	(0.6)	100	45
Alca torda					(128)	(7)
Black guillemot	6 000	10	0.9	(0.7)	60	5
Cepphus grylle					(164)	(31)
Puffin	125 000	30	0.7	0.1	95	40
Fratercula arctica					(315)	(121)

[1] Values in parentheses indicate only very approximate estimates; n.d. = no data available.

[2] Dietary data from Furness (unpubl.), Hudson (1986), and Martin (1989); sample sizes are given in parentheses.

Table 5. Estimates of basal metabolic rate (BMR) from allometric equations of Lasiewski and Dawson corrected to 60° latitude (Ellis, 1984) or, where available, from direct measurements for the species (see Furness, 1990); estimates of sandeel consumption per day by the Shetland breeding population during chick-rearing in 1981–1983 and 1988. In the status columns species showing a marked decline in breeding population between 1981 and 1988 (D) and/or a pronounced breeding failure in 1988 (F) are indicated.

Species	BMR (kj day^{-1})	Sandeels consumed (tonnes day^{-1}) 1981–1983	1988	Status	
Red-throated diver	850	0.9	0.2		
Fulmar	330	77.6	5.5		
Gannet	1 230	33.1	2.1		
Shag	855	11.9	8.3	D	
Arctic skua	220	0.7	0.4	D	F
Great skua	710	4.7	0.3		F
Herring gull	390	0.6	0.0		
Great black-backed gull	780	1.7	0.0		
Kittiwake	285	26.1	15.3		F
Arctic tern	105	5.6	0.3	D	F
Guillemot	550	101.6	67.6	D	
Razorbill	395	8.0	2.5	D	
Black guillemot	295	1.8	0.1		
Puffin	280	55.5	15.4	D	F
All seabirds		330	118		

consumption in 1988 was less for all species studied, and varied from 0–70% of the 1981–1983 level.

The consumption of sandeels by seabirds is expressed in terms of weight and data are not available to convert this to numbers of each age group. Comparisons with sandeel stock size and production have therefore been made using the biomasses directly, making the assumption that the mean weights of sandeels taken by seabirds were the same as those in the commercial catch.

The daily rates of consumption can be totalled over the breeding season (see Furness, 1990) to give estimates that can be expressed as a proportion of sandeel stock size. However, the stock size at the beginning of the year in question is not the appropriate value for comparison because 0-group sandeels recruit to the stock in the summer. Instead, from VPA estimates of the numbers and biomass of sandeels dying during the year, the estimated biomass of sandeels eaten by seabirds has been converted to approximate estimates of predation mortality rate. The text table here shows the results for 1981 and 1988 based on the assumption that natural mortality due to all causes did not differ between years, even though the component due to seabird predation may have done. Estimated fishing mortality rates calculated in the same way are also given for comparison. These estimates suggest that seabirds may have exerted a slightly greater mortality on sandeels in 1981 than they did on the reduced stock in 1988. The estimated difference is not great, however, and may well be within the confidence limits of the data. There is no firm evidence that the consumption of sandeels as a proportion of sandeel production changed over the same period.

	1981	1988
Number (10^9) dying due to all causes[a]	66.10	14.80
Biomass (t) dying due to all causes	147 100	45 300
Equivalent total mortality rate[b]	2.16	1.28
Biomass (t) eaten by seabirds	49 000	17 500
Equivalent seabird predation mortality rate	0.72	0.50
Biomass (t) taken in fishery	44 500	3 900
Equivalent value of fishing mortality rate	0.65	0.11
Estimated production of sandeels (t)	172 100	52 400
Seabird consumption: production ratio	0.28	0.33

[a] Assuming that the mortality of 0-group sandeel begins on 1 July.

[b] From VPA; Anon., 1989.

The interpretation of the above results in terms of prey switching is more difficult, largely because the analysis is constrained by the assumption that natural mortality from all causes remains constant from year to year. Ideally, one would wish to incorporate changes in M in the VPA using estimates of the annual consumption in terms of numbers at age by each of the main predator groups. Annual series of appropriate data, however, are available for neither seabirds nor other groups of predators. To explore the possibility of prey switching, it has therefore been assumed that compensatory changes in consumption take place within the community of predators such that the annual rate of natural mortality remains constant. This does not of course mean that the total quantity of sandeels consumed remains constant, only that the proportion of the available stock consumed by predators does so.

Under this assumption, the extent of prey switching can be evaluated by comparing the effectiveness of seabirds in generating mortality on sandeels in 1981 and 1988. Just as in the case of fishing, a measure of effectiveness is given by the catchability coefficient q, i.e. the mortality rate generated by a unit of fishing effort, in this case a pair of seabirds. Taking all species of seabirds together the relevant estimates are given in the accompanying text table. These figures indicate no significant change in catchability even though the stock of sandeels decreased. Seabirds as a group consist of diverse species, however, which may have changed their feeding preferences differentially. A full analysis of this is not possible because different species specialize on different size groups of sandeels. Making the broad assumption that all seabirds take the same sizes, there are indications using the data in Tables 4 and 5 that, among the commonest birds, fulmars, gannets, the two gulls and arctic terns may have actively switched away from sandeels between 1981 and 1988. Shags, and guillemots, on the other hand, may have created a higher proportional mortality by retaining a high proportion of sandeels in their diet even though the sandeel stock had decreased. For kittiwakes, razorbills, and puffins there is no indication of a change in catchability. Even though the proportion of sandeels in their diet diminished, this was in proportion to the change in sandeel stock size, indicating that these species had not actively switched from sandeels to another prey.

Year	Predation mortality	No. of pairs	Catchability coefficient
1981	0.72	583 000	0.00123
1988	0.50	476 000	0.00105

The above findings suggest that seabirds treated together reduced their intake of sandeels but that this was roughly in proportion to the decrease in stock size. The data do not reveal any non-linearities in the response of seabirds to a decrease in the abundance of sandeels.

Changes in catchabilities strictly show the change in efficiency with which seabirds create predation mortality. To evaluate switching as such, one also needs information on compensatory changes in predation mortality on alternative prey. While some seabird species may actively have switched their preference, it is also possible that a decrease in catchability simply represents the extent to which that species failed to catch enough food to meet its full requirements.

Discussion

Two independent sets of data indicate a substantial decrease in sandeel abundance in the Shetland area during the last few years. Using the VPA estimates, total biomass decreased from 77 000 t in 1981 to 47 000 t in 1988 after rising to a peak of 138 000 t in 1984. Over the same period, estimated recruitment of 0-group sandeels to the Shetland stock dropped from 76 billion in 1981 to 2 billion in 1987 and 21 billion in 1988 with a peak of 81 billion in 1982. From the midwater trawling survey, the ratio of 0-group sandeel abundance in waters adjacent to Shetland between 1981 and 1988 was 90:1. There is thus a considerable difference in the timing and magnitude of events in the two data sets. Peak abundance of 0-group in the research vessel surveys occurred in the mid-1970s, whereas VPA results suggest an increase in recruitment up to 1982 and then a decline. The difference could be due to a change in the distribution of the 0-group, since the research vessel hauls at Shetland were made further offshore than the areas trawled by the commercial trawlers.

The validity of the VPA results depends *inter alia* on the applicability of the values of M, which have been derived from studies of the total North Sea sandeel stock including Shetland and which are assumed to remain constant. The VPA estimates for 1988 are further dependent on the validity of the estimates of fishing mortality rate (F) which are based on a regression of F against nominal fishing effort (Anon., 1989). Both M and F are undoubtedly subject to considerable imprecision, which adds to the imprecision of the seabird data. Nevertheless, both sets of data indicate a pronounced decrease in sandeel recruitment in recent years. Predation rates on sandeels by seabirds in Shetland are high, accounting for 30–40% of total mortality. The estimated 49 000 t of sandeels consumed annually in 1981–1983 is almost the same as the industrial fishery catch in the years of peak landings. Seabird consumption represents 27% of the estimated production of sandeels in the years 1981–1983 (Table 3). Since the present VPA analysis of the Shetland sandeel stock uses natural mortality rates based on those estimated from studies of the combined North Sea sandeel stocks and ignores the high concentration of non-fish predators at Shetland, the possibility cannot be excluded that M is different in this area. In this case stock biomass and production may not have been estimated accurately. The high mortality due to seabirds, and possible variation at different stock densities due to ecological responses of seabirds, should be taken into account in the assessment of this stock.

The analyses contained in this paper are subject to considerable uncertainty largely because the natural mortality rate cannot at present be quantified in terms of the different age groups of sandeels consumed by different groups of predators. The exercise should therefore be considered as an exploration of the possible effects of changing prey abundance on a predator community. To investigate if prey switching occurs, better estimates would be needed of the local consumption of sandeels and of other prey, broken down by age group, by all their main predators over a period of years in which stock size changed. Furness (1990) has made provisional estimates of sandeel consumption by seabirds, sea mammals, and other fish for the years 1981–1983, but these are expressed in terms of biomass rather than numbers at age. The additional data requirements for such an analysis are clearly formidable.

With the recent decline in stock size, fishing for sandeels at Shetland has decreased to a low level. Assessment of future changes in stock based on VPA will become increasingly difficult because mortality due to fishing is only a small component of total mortality. Ecological responses of seabirds may provide a crude but simple fishery-independent indication of stock dynamics. For example, it is clear that different seabirds respond differently to changes in stock. Arctic terns *Sterna paradisaea* feed largely on 1-group sandeels early in the year and on 0-group in July (Monaghan *et al.*, 1989). Because they are surface feeders that must forage close to the colony and make many fishing trips per day, they are especially sensitive to reductions in food availability. This is in agreement with the evidence that they have shown the earliest and most severe breeding failures at Shetland (Heubeck, 1989). By contrast, some of the larger seabirds with generalist feeding abilities took sandeels when these were abundantly available but switched diet as the sandeel stock declined. A further possibility is that the availability of sandeels may have changed independently of stock abundance. Any change in vertical distribution, for example, would lead to changes in availability to seabirds, especially surface feeding species. This would complicate attempts to assess changes in fish stock abundance from seabird ecology.

Although similar seabird–fish stock interactions in other parts of the world have recently been documented and discussed (Springer *et al.*, 1986; Cairns, 1987; Montevecchi *et al.*, 1988; Berruti *et al.*, 1989), the reliability of predictions of fish stock abundance from seabird food consumption remains to be tested.

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A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems

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Bax, N. J. 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. – ICES mar. Sci. Symp., 193: 217–224.

Various data sources are used to derive the biomass flow from fish to the fish themselves, to fisheries, and to marine mammals in six ecosystems: Eastern Bering Sea, Norwegian coast and Barents Sea, North Sea, Benguela current, Georges Bank, and Balsfjorden. The largest proportion of fish biomass provides food for the fish themselves in all areas. The North Sea has the highest loss of fish biomass to fishing. Possible reasons for this are discussed.

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Introduction

A concept of ecosystem, and biomass estimation

A marine ecosystem represents an assemblage of organisms or communities within defined physical and physico-chemical boundaries. It is a loose construct, difficult to define in terms of the organisms themselves, which may move into, out of, or through the physical area. In any quantitative consideration of the dynamics of biomasses within a given marine ecosystem, we must know and/or estimate the flow of these biomasses through the boundaries, or we must assume that the given system is closed. The latter assumption is often the easiest to make, but in the presence of highly migratory animals (e.g. marine mammals, birds, migratory fish such as salmon), would engender considerable error in any analysis.

Having defined an ecosystem of interest it is necessary to know the magnitude and type of biota within it. It is rarely possible to use abundance estimates derived from scientific surveys and catch analyses directly in investigating species interactions. There is simply too much error in those estimates for rational interpretation in a multispecies context.

Biomass estimates for the different species within an ecosystem must be mutually consistent as indicated by their interactions through predation. For example, there must be sufficient pollock in the Eastern Bering Sea to sustain predation by marine mammals (1.1 million tonnes), predation by other fish (2.7 million tonnes), and cannibalism (7.4 million tonnes) in addition to an annual loss to the fishery of 1.1 million tonnes (Laevastu *et al.*, 1982). Traditionally, in single species virtual population analyses, only the loss to the fishery is included explicitly, the remaining mortalities often being lumped together and assumed constant over both age and time. Multispecies virtual population analyses (summarized by Gislason and Sparre, 1987) use interspecific predation in the ecosystem to improve estimates of biomass by providing for a time and age variable mortality.

When all major sources of mortality in the ecosystem are known it is theoretically possible to estimate the species production, and hence abundance, independently of resource survey abundance estimates (Laevastu and Larkins, 1981; Laevastu *et al.*, 1982; Polovina and Ow, 1985; Polovina, 1984). Each species (or trophodynamic group) forms one biomass equation, which includes the sources of growth and those of mortality (including interspecific predation). The biomass equations form a simultaneous set, which can be solved for biomass in the standard manner. For the solution to be non-trivial it is necessary that catch (or another variable) be non-zero for at least some species, and that catch (or the other variable) be expressed as an absolute amount rather than as a rate. Species abundance itself does not need to be specified, although a solution to the biomass equations is found more quickly when one or more species biomass is (are) predefined.

It is often the case that the major sources of mortality (for example, the predation matrix) are biased or imprecise, and the abundance estimates from solving the biomass equations will also be in error. In these instances a method is required which uses information contained in both survey abundance estimates and independent mortality estimates (including fishing and predation pressure) to provide new estimates of species abundance and predation interactions satisfying both data sets (Bax and Eliassen, 1990). The solution is no longer unique because more variables are estimated than there are equations. Bax and Eliassen (1990) suggest a method based on the joint minimization of the sum of the squared differences of survey abundance and predation data from estimated abundance and predation data to provide a possible solution.

Methods which include the additional information from predation data improve the historically poor estimates of species abundance in marine ecosystems. Without this important first step ecosystem dynamics cannot be sensibly investigated. Biomass estimates derived from multispecies investigations are used here to determine the fates of finfish biomass in the ecosystem.

Fates of finfish biomass in the ecosystem

A feature common to the multispecies analyses of different ecosystems is the "discovery" that there are more fish out there, particularly juvenile and small fish, than was previously thought (e.g. Cohen and Grosslein, 1982, Laevastu *et al.*, 1982; Gislason and Helgason, 1985; Daan, 1987). Multispecies analyses have highlighted the importance and variation in mortality other than that due to fisheries. Much of the earlier biological advice on mesh selectivity or yield per recruit based on constant natural mortality for all ages has been wrong (Gislason and Helgason, 1985).

There is nothing inherently wrong in analyzing the ecosystem one species at a time, provided that the biology of the species, including potential interactions, is considered. Much of the erroneous information generated by single-species analyses has resulted from undue emphasis on effects of fishing, while ignoring, or assuming constant, all other sources of biomass loss. This simply makes no sense in most ecosystems where fishing mortalities form only a small fraction of the total mortalities over the life time of a species. In this paper I describe annual biomass losses for the combined fish components from six marine ecosystems. There is unresolved error associated with these analyses, and they can only be regarded as gross caricatures of complex natural systems. The analyses will portray the major trends in disposition of fish mortalities in marine ecosystems and highlight differences between the areas.

Data sources

Benguela Current

The Benguela Current area comprises a 185 km wide swathe of the coastal ocean from 15°S to 35°S (Hart and Currie, 1960; Shannon *et al.*, 1983), for a total area of 412 000 km^2. Data for the Benguela Current area were provided by Crawford (pers. comm. R. Crawford, Dept. Environ. Affairs, Cape Town, S.A.). Original data are in thousands of tonnes for five fish groups – epipelagic, mesopelagic, predatory, juvenile hake, and adult hake – together with birds and mammals. Squids are included with predatory fish (Table 1). Estimated daily rations and percentage of diet derived from fish are given.

Table 1. Source data for the Benguela Current ecosystem. (R. Crawford, Dept. Environ. Affairs, Cape Town, S.A.)

Group	Biomass ('000 t)	Ratio (% BWD)	% of diet from fish
Epipelagic fish	2 000	7.0	0.0
Mesopelagic fish	1 500	9.5	0.0
Predatory fish	350	9.5	74.0
Juvenile hake	500	9.5	66.0
Adult hake	200	4.0	97.0
Birds	3	13.0	98.0
Seals	37	8.0	99.5
Catch	655		

Georges Bank

There are many sources of data pertaining to the Georges Bank ecosystem. Sissenwine (1986) had the estimates needed in this comparison. Original units are kcal/m^2, but since the conversion of 1 kcal/g wet weight was used, the same numbers apply to units of mt/km^2. Average values from the two time periods, 1964–1966 and 1973–1975, were used for this comparison (Table 2). Estimates of abundance are based on single-species virtual population analyses. The area is 60 000 km^2. Consumption of fish by large pelagics was included in fish consumption. Consumption of fish by humans (catch) is the average catch 1968–1982.

Balsfjorden

Balsfjorden is a semi-enclosed fjord in northern Norway. It has been extensively studied by researchers from the University of Tromso. Bax and Eliassen (1990)

Table 2. Source data for the Georges Bank ecosystem (Sissenwine, 1986).

Group	Consumption of fish (kcal m^2 yr^{-1})
Fish	39–42[a]
Birds	2.0
Mammals	5.4
Large pelagics	2.0
Catch	6.1

[a] The range refers to the two time periods 1964–1966 and 1973–1975.

Table 3. Source data for the Balsfjorden ecosystem (Bax and Eliassen, 1990).

Group	Annual loss to predation (kg km^2)	Annual loss to fishing (kg km^2)
YOY cod	2 899	23
1 cod	725	157
2+ cod	662	883
Herring	2 879	73
Capelin	2 226	11
Flatfish	337	60
Other fish	3 546	12
Prawn	840	286

provide a description of the Balsfjorden ecosystem for the 1975 to 1976 time period. At that time marine mammals were not considered to be significant predators in Balsfjorden. With the recent influx of seals to this fjord marine mammal predation has increased. The area of Balsfjorden is 240 km^2. Fish are divided into eight categories (Table 3). Biomass values result from multispecies analysis of the fjord, which suggested higher biomasses than had been estimated by standard resource surveys.

Eastern Bering Sea

Laevastu and Larkins (1981) and Laevastu *et al.* (1982) provide descriptions and quantification of the Eastern Bering Sea ecosystem. All major fish species are represented. They have been summarized in Table 4. Biomass estimates tend to be higher than those provided by surveys or virtual population analyses. Data pertain to the late 1970s. The area of the Eastern Bering Sea is 1 169 000 km^2.

North Sea

Multispecies virtual population analyses (MSVPA) for the North Sea provide a good summary of fish mortality. Sparhold (1987) provides an overview of these mortalities and estimates mortalities due to fish not included in the MSVPA (28% of the fish biomass) and for mammals and birds. Fish predation included in these analyses is an underestimate of ecosystem mortalities because it does not include predation by fish included in the MSVPA on other fish, nor predation of other fish on themselves. For my purposes I increased predation by the reciprocal of 0.72 to account for predation on the 28% of fish biomass not included in the MSVPA (Table 5). Jones (1982) gives the area of the North Sea as 570 00 km^2.

Table 4. Source of data for the Eastern Bering Sea ecosystem (Laevastu and Larkins, 1981; Laevastu *et al.*, 1982).

Group	Consumption of fish: Tonnes	Consumption of fish: Tonnes/km^2
Birds	189 415	0.162
Mammals	1 772 800	1.517
Fish	12 840 000	10.988
Catch[a]	1 634 537	1.399

[a] 1985 catch.

Table 5. Source data for the North Sea ecosystem (Sparholt, 1987).

Group	Original fish consumption: Tonnes	Original fish consumption: Tonnes/km^2	Adjusted consumption[a] Tonnes/km^2
MSVPA fish[b]	2 152 972	3.778	5.246
Other fish[c]	746 143	1.309	1.818
Birds	230 000	0.404	0.561
Mammals	57 284	0.100	0.139
Catch	2 500 000	4.386	4.386

[a] Predation values increased to account for predation on the 28% of fish biomass not included in MSVPA.

[b] Predation by fish included in the MSVPA on themselves.

[c] Predation by other fish on fish in the MSVPA.

Norwegian and Barents Sea

Survey and virtual population estimates of biomass for 14 fish groups (including squid and shrimp), and their interactions through predation (from stomach content analyses), have been provided by researchers from the Institute of Marine Research in Bergen and summarized in Bax *et al.* (1991) (Table 6). The analysis accounted for biomass migration through the area comprising the Barents Sea and the Norwegian coast to 62°N, an area of 1 500 000 km^2. Data apply to the period April 1984 to April 1985, when capelin, herring, and a growing cod stock were present in the Barents Sea. Predation by birds was not considered to be significant in terms of biomass, although in terms of numbers the impact would be greater.

Results

Losses of fish in each ecosystem

Disposition of fish in the ecosystems is given in Figure 1. Units are in kg/km^2 and the area of each pie is pro-

Table 6. Source data for the Barents and Norwegian Sea ecosystem (Bax *et al.*, 1991).

Group	Consumption of fish: Tonnes	Consumption of fish: Tonnes/km^2
Fish[a]	7 686 000	5.124
Birds	–	–
Mammals	4 430 000	2.953
Catch	2 650 000	1.767

[a] Includes shrimp and squid.

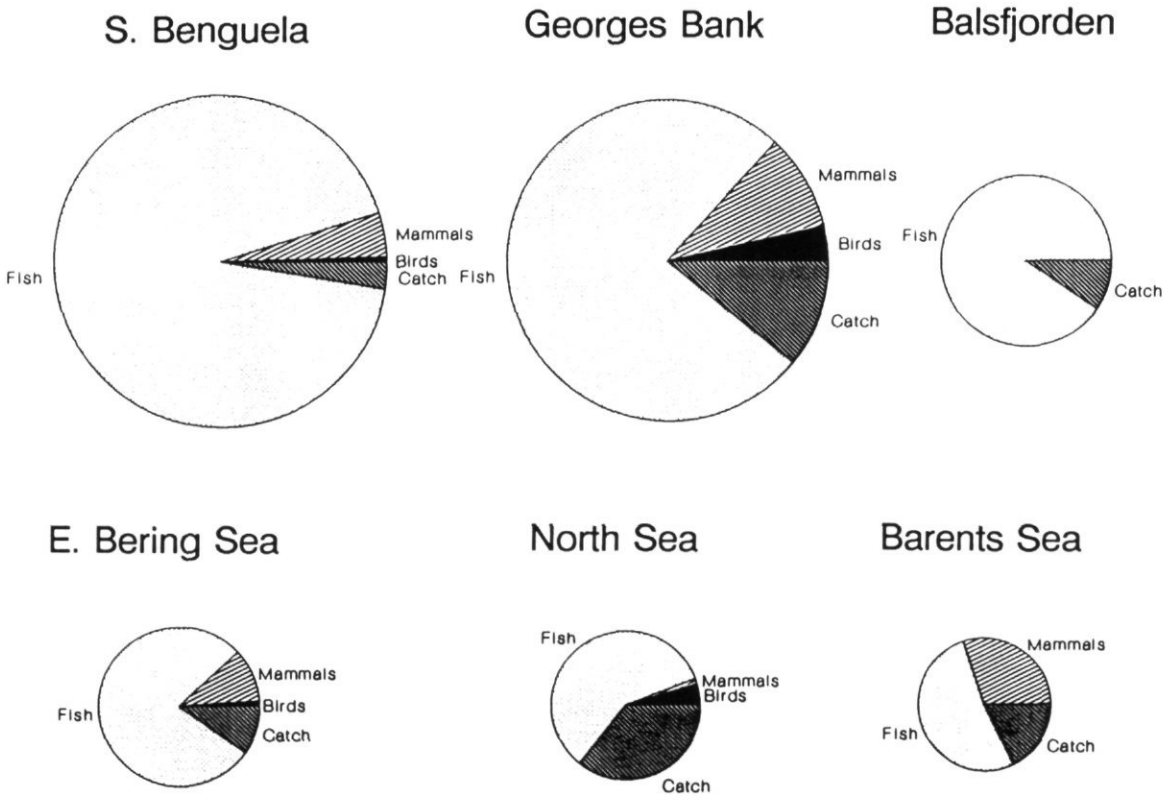

Figure 1. Annual flow of biomass from fish to marine mammals, birds, fish, and to human catch. The area of the pie is proportional to absolute biomass transfer. Data sources are provided in the text.

portional to the annual removals of fish in each ecosystem. No allowance was made for removals due to disease, senescent or spawning stress mortality (Beverton and Holt, 1959), or apparent mortality due to emigration.

The striking feature is the much higher annual fish removals from Georges Bank and the Benguela Current than for the other four areas. Higher fish mortality in the Benguela Current ecosystem is due to the higher consumption of fish by fish themselves; other losses are comparable with other areas. Input data for the Benguela Current ecosystem provide for daily rations for fish of 4.0 to 9.5% bw d^{-1} (Table 1). This ration is much higher than that estimated in the northern ecosystems, where ration is commonly estimated at close to 1.0% bw d^{-1}, and would indicate a more dynamic ecosystem with rapid metabolism, mortalities, and growth. Further studies are required before any definitive conclusions can be drawn.

Georges Bank has the second highest estimated fish loss of the six ecosystems (Fig. 1, Table 7). It has the highest annual loss to birds, mammals, humans, and the

Table 7. Summary of losses of fish in six marine ecosystems.

	Benguela Current	Georges Bank	Balsfjord	E. Bering Sea	North Sea	Barents Sea
			Fish loss (tonnes/km^2)			
Birds	0.3	2.0	0.0	0.2	0.6	0.0
Mammals	2.6	5.4	0.0	1.5	0.1	3.0
Fish	56.5	42.5	14.1	11.0	7.0	5.1
Catch	1.6	6.1	1.5	1.4	4.4	1.8
Total	61.0	56.0	15.6	14.1	12.1	9.9

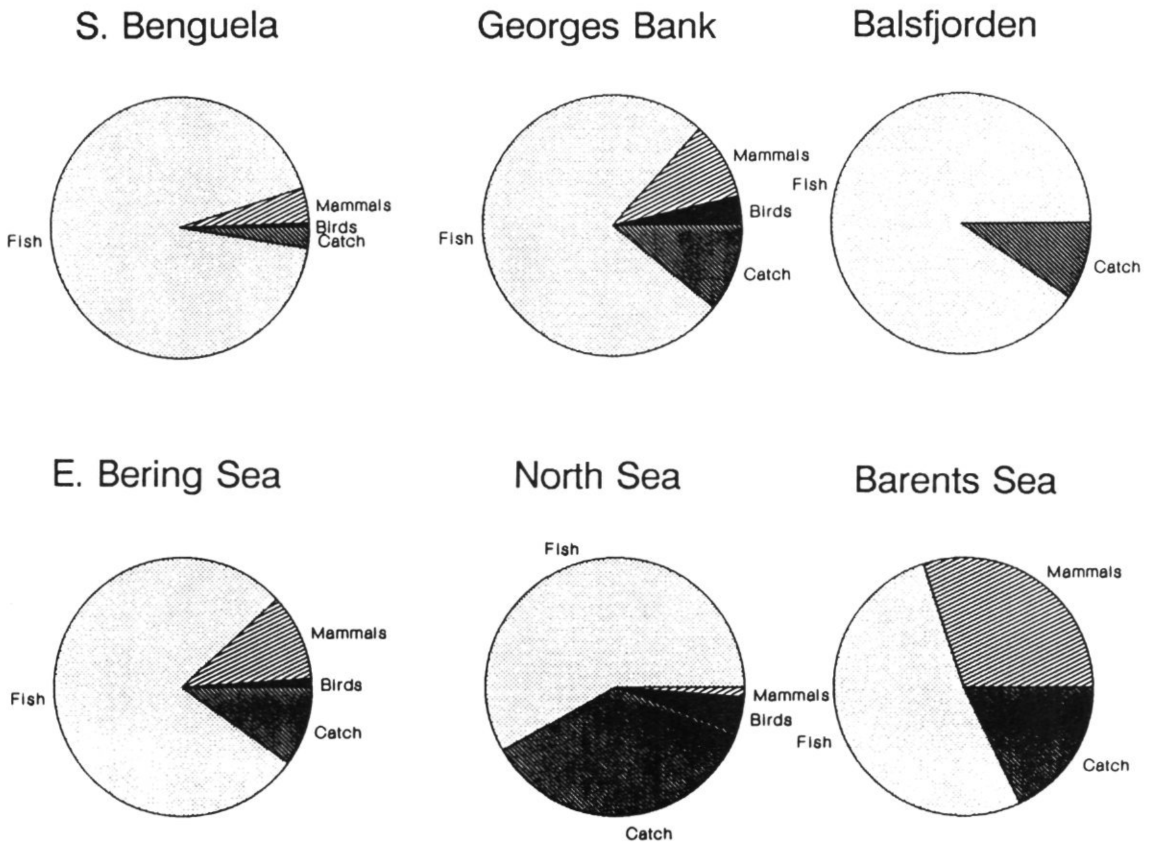

Figure 2. Relative loss of biomass from fish to birds, marine mammals, fish, and to human catch. Data sources are provided in the text.

second highest loss to fish. The reasons for this are not clear; Sissenwine *et al.* (1984) give the mean consumption to biomass ratio of the six major fish species on Georges Bank as 4.1. This translates to a mean ration of 1.1% bw d^{-1}, which is not materially different from the values used for the other four northern ecosystems. Also the loss of fish, and hence production of fish, is high for every category in Table 7, indicating a generally higher productivity. Primary production cannot account for this difference, since estimated primary production for Georges Bank is only half again as high as that for the North Sea (Cohen and Grosslein, 1987), yet total fish loss is almost five times as much.

Another possibility for the higher production rates on Georges Bank is that the data for this area include all life history stages of the fish from egg through to adult. In some of the other areas, especially where the data are taken from MSVPA analyses, the earliest life stages are not included. In the Eastern Bering Sea all life history stages were included in the ecosystem models (T. Laevastu, pers. comm., Alaska Fisheries Science Center, Seattle, WA, USA). In Balsfjorden, growth and consumption of fish larvae were not included explicitly in the analysis. While the growth rates and numbers of fish larvae are exceedingly high their biomass is very low (total pre-exploitable fish biomass on Georges Bank estimated at 10% of exploitable biomass [Sissenwine, 1986]), and cannot fully account for the observed differences.

Cohen and Grosslein (1987) discuss Georges Bank as an "enigma" amongst the six northern ecosystems that they compare because of its "unusually high transfer efficiency from secondary production to fish, but no obvious mechanism to explain it". The enigma status of Georges Bank is even more apparent in this analysis, where total fish production is estimated at five times that for the North Sea, instead of the threefold difference suggested by Cohen and Grosslein (1987). Part of the explanation may come from fish that migrate onto Georges Bank from outside areas (Sissenwine *et al.*, 1984), but this cannot be resolved at present.

Total fish removals from the other four ecosystems are quite comparable (Table 7), ranging from 15.6 mt/km^2 for Balsfjorden down to 9.9 mt/km^2 for the Norwegian and Barents Seas. The latter value is probably low, since abundance estimates are taken from surveys and VPAs which usually underestimate the numbers of young, and highly productive fish. Bax *et al.* (1991) find that this ecosystem representation as currently configured is not stable with shrimp and other prey being likely candidates for underrepresentation in the surveys.

Relative losses of fish in each ecosystem

Relative losses of fish biomass are provided in Figure 2. In all instances the majority of fish biomass lost is consumed by the fish themselves. This seems especially so in the case of the Benguela Current ecosystem, where fish rations are estimated at comparatively high levels. For three of the ecosystems, marine mammals take the second largest component of fish production with catch coming third. The situation for Balsfjorden changed with the seal invasion of 1987 when marine mammal predation would have increased substantially. Marine mammal predation appears especially significant for the Barents and Norwegian Seas; 45% is due to whales and 55% to fish (Bax *et al.*, 1991).

Human utilization of fish is high in the North Sea compared to other areas. Human utilization is also high for the Norwegian and Barents Sea, although it is possible that fish consumption by fish themselves is underestimated since survey estimates may not fully include the young fish. Conversely, the importance of fish predation may be overestimated for the Benguela Current, where fish ration may be set too high. Even without these provisos it is apparent that a substantially higher proportion of fish losses is due to human utilization in the North Sea than in the other five ecosystems.

Discussion

In this paper I stressed the dominant role of fish predation in the marine ecosystem (Figs. 1 and 2). Changes in abundance of major piscivorous fish species will cause a cascading of impacts on the remainder of the ecosystem. Thus empirical observations, summarized by Torsvik (1987), demonstrate the increased consumption by cod in the Barents Sea following their increase in abund-

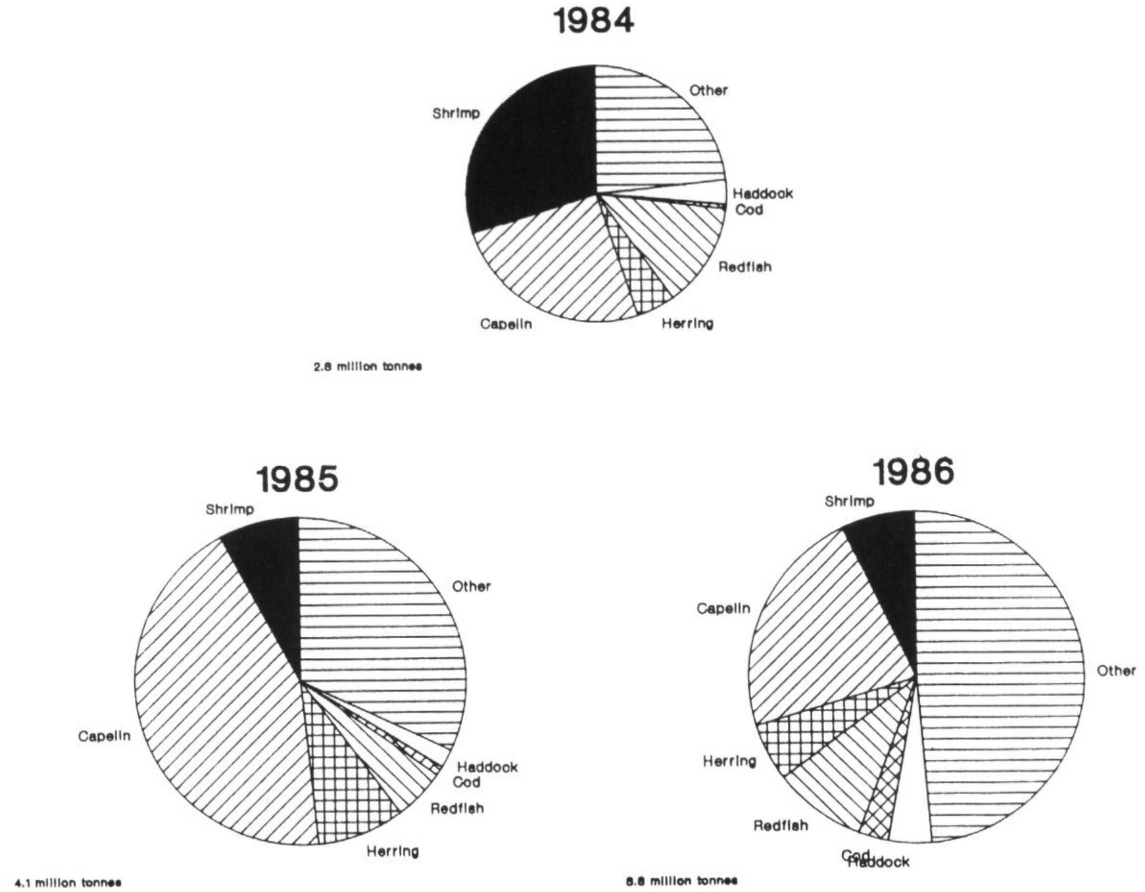

Figure 3. Consumption by Atlantic cod in the Barents Sea from 1984 to 1986. (Reported by Torsvik, 1987.)

ance. These data further illustrate the concurrent changes to other species in the ecosystem as revealed by the contribution of these other species to the diet of cod (Fig. 3), which changed from being dominated by shrimp in 1984 to one dominated by other fish (non-commercial fish, benthos, and squid) in 1986. Cod in the Barents Sea occupies a comparable role in the ecosystem as walleye pollock in the Eastern Bering Sea and cod in the North Sea or Balsfjord or as silver hake did on Georges Bank – they are (or were) all the keystone predators in their system displaying varying levels of cannibalism. Dogfish have now replaced silver hake as dominant fish predator on Georges Bank (Sissenwine, pers. comm.).

Bax (1985) used Monte Carlo error analysis to investigate a model characterizing the Georges Bank ecosystem in the mid-1960s. Predation was shown to be a more important controlling mechanism than food limitation in this area. In accordance with earlier studies by several researchers, silver hake was identified as a keystone predator. Thus food requirements of silver hake were identified as having the most impact on variability in the Georges Bank ecosystem as described by the first two principal components of system variability.

Once species interactions of this magnitude have been recorded for an ecosystem we can begin to consider the potential effects of the selective removal or enhancement of predators. Sissenwine (1986) describes the fish community of Georges Bank as being cannibalistic at the community level, and suggests that this moderated the effects of overfishing in the late 1960s and early 1970s. The potential consequences of increased fishing pressure on pollock, cod, and yellowfin sole in the Eastern Bering Sea were decreases in the biomasses of the target species, but these were compensated by increases in the biomasses of non-target species (Laevastu and Marasco, 1984). Potential long-term effects of changing the fishing patterns in the North Sea would be an increase in the value of the total catch by 50% or more (Gulland, 1982). This potential increase would result primarily from the reduction in abundance of predators of the higher-valued fish.

It is apparent that we have available to us now much of the information that we require to experimentally manage fisheries in a multispecies context, although we are sure to be surprised at some of the outcomes. Our appreciation of the marine environment as an integrated system may well prove to be the easier stage of our education. The second stage will require us to proceed from a divisive to an integrated system of management.

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Modelling technical interactions

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Laurec, A., Biseau, A., and Charuau, A. 1991. Modelling technical interactions. – ICES mar. Sci. Symp., 193: 225–236.

Les interactions techniques sont aisément prises en compte lorsque les mortalités par pêche restent en rapport constant d'un stock à l'autre et pour chaque stock sur les différents groupes d'âge. La réalité étant généralement plus complexe, il est nécessaire de distinguer dans les activités de pêche des activités type, baptisées métiers, telles qu'à l'intérieur d'un métier la règle d'homothétie des mortalités soit vraie. Sur ce principe, des procédures de modélisation sont discutées, pour calculer á partir des efforts par métier les captures et l'évolution des stocks, mais aussi pour prévoir la ventilation des afforts selon l'attractivité économique des différents métiers et donc entre autres selon l'état des diverses ressources. Ces principes ayant été appliqués à la pêcherie de Mer Celtique (Charuau, 1986), des simulations relatives à cette pêcherie sont présentées comme illustration.

The assessment of technical interactions is relatively straightforward when partial fishing mortalities are constant among stocks, ages, and fleets. This implies a constant multispecies fishing pattern, which is generally not the case, however. The definition of fishing practices, or "métiers", by gear, target species, and fishing ground, is suggested. Within each "ḿetier" the multispecies fishing pattern can be considered as constant. Dynamic modelling of multispecies fleet interactions is based on classical population dynamics models, considering as inputs fishing effort by "métiers", and describing changes in the various stocks and catches by species and fleet. The model also includes a feedback effect relating the fishing efforts by "métier" to the benefits they generate, which in turn depend on economic factors and the relative status of the stocks. Simulations based on Celtic Sea fisheries are given as an illustration.

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Introduction

Fisheries management tends to address removals of fish by species. Population dynamics considers assessments by stocks. The importance of predator–prey interactions makes it necessary to include biological interactions within multispecies models, at least for ecosystems such as the North Sea. In addition, the existence of "by-catch problems" has drawn attention to so-called technical interactions. If by-catch is modelled such that the fishing mortalities directed towards target species create proportionally constant mortalities on by-catch species, the implications of by-catch are relatively easy to understand (Mesnil, 1986; Shepherd, 1988). However, the situation is generally much more complex (Anon., 1987a), as illustrated by the by-catch problem in the Celtic Sea *Nephrops* fishery. So-called "Nephrops trawlers" would not survive economically without by-catches of finfish. Some even tend to shift targets within a trip, if not within a day. Thus, there is a first-order effect of technical interaction between *Nephrops* and finfish at the level of any single trawl haul. A second-order effect appears when the trawlers shift targets. A third-order effect arises when trawlers exit or enter the *Nephrops* fishery. This paper addresses economic and biological implications of technical interactions at all three levels.

Models of technical interactions, which are the subject of this paper, and models of biological interactions, which were considered extensively during this symposium, have some interesting similarities. In fact, when a fishery system is treated as a whole, the concept of prey preference and suitability indices (Sparre, 1991) apply to fishermen as predators just as much as to fish as predators.

We propose to treat mixed-species fleets by establishing a typology of fishing activities, leading to types called "métiers" (Anon., 1987a). For a specific distribution of the effort of each fleet to the various métier, the situation is equivalent to the simple case of by-catch fishing mortality as a constant proportion of fishing mortality on the target species. The effort allocation must then be modelled for a system where the inputs correspond to fishing capacities for a limited number of fleets which allocate their efforts to various métiers. Classical populations dynamics models complete the mathematical descriptions of the fishery system.

Instead of reviewing common aspects of the technical problems, covered inter alios by Anon. (1987a), this paper focuses on the critically important effort allocation problem, which is rarely addressed. The Celtic Sea groundfish fishery, which was intensively studied (Charuau, 1986), is used as an illustration.

In this document we: (1) introduce the Celtic Sea issue; (2) define a relatively parsimonious set of mixed-species métiers; (3) outline a modelling scheme for dynamic analyses of such complex systems; (4) discuss the mathematical formalization of such models; and (5) illustrate the dynamic model of technical interactions for the Celtic Sea Fishery System.

The Celtic Sea groundfish fisheries

The Celtic Sea covers approximately ICES Subdivision VIIf, g, h, j (Fig. 1). It is rich in benthic species but also includes many demersal species. Its "moderate" complexity of species and fisheries makes it a desirable candidate system for modelling. Since biological interactions do not seem to play a major part (DuBuit, 1982), it is reasonable to deal only with technical interactions.

The primary fleet fishing this area is the French one, but fishermen from other countries also participate: the UK, Ireland, Belgium, and Spain. Some vessels flying British or Irish flags are operated by Spanish crews, whose fishing pattern is typical of the Spanish fleet and who sell their catches on the Spanish market. The French fleet is made up of trawlers only, in the size range 16 to 33 m. The larger vessels tend to operate in the Celtic Sea part-time, and in other areas (West of Ireland and Scotland) for the rest of the year. Most vessels in fact can operate outside the Celtic Sea, although they concentrate their effort in this area. The pelagic stocks are the targets of distinct (non-interacting) fisheries which are not considered here.

The prominent demersal resource comprises eight species which account for more than 80% of the value of the French landings from the area: Norway lobster (*Nephrops norvegicus*), hake (*Merluccius merluccius*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), megrim (*Lepidorhombus whiffiagonis*), monkfish (*Lophius piscatorius* and *Lophius budegassa*), and rays (*Raja naevus*). Other species appearing in the catches are skate, ling, plaice, sole, lemon sole, and pollack.

Some fleets can be isolated, since they are strictly directed towards one species. The Belgian fleet targets specifically on sole, and has little interaction with other species or fleets. Many Spanish or Spanish-like vessels tend to operate in deep waters, where generally old fish are found. In terms of yield per recruit, they do not directly affect the biomass available to the fleets fishing on the inner shelf.

Initially, the main concern was the interaction between *Nephrops* and finfish fisheries, and more precisely the by-catch in the *Nephrops* trawl fishery. It now appears that this issue is a minor one in a more complex system. Technical interactions also occur within the set of groundfish species, where several (perhaps many) species are caught in a given haul. This is especially the case with benthic species (i.e. fish lying directly on the bottom, such as flounders, but not gadoids which are demersal).

The overall problem cannot be comprehended without consideration of the spatial distribution of the resources, since the species composition is quite different in the various subareas. It is generally considered that the stocks in the Celtic Sea are separate entities, independent of those in adjacent areas. One major exception is hake, the Celtic Sea component being part of the widely distributed Northern stock. Other exceptions are the ling and pollack, which are of little economic importance for the fleets in this area. Because of their movements throughout the Celtic Sea, it can be considered that each demersal species is a single stock. This is not the case for *Nephrops*, which is a sedentary species. *Nephrops* may mix as pre-recruits, but beyond that stage each spot behaves as a stock-let. Other benthic species have restricted migration ranges, too, and are similar to *Nephrops* in this regard.

Finally, it appears that the various stocks are presently confronted with quite different exploitation rates. The *Nephrops* stocks are moderately or under-exploited; *Lophius budegassa* is moderately to fully exploited; *Lophius piscatorius* is moderately over-exploited; megrim does not face an immediate problem, but there is concern for the future of rays because of their biological features (low fecundity); gadoids are fully exploited or over-exploited depending on the species. However, fishing for gadoids is the most economically attractive activity.

The main challenge is to find a management strategy which fully exploits most of the resources without economically overfishing the gadoids or biologically overfishing vulnerable species such as rays.

Basic concepts

Métiers and fleets

Most mixed-species catch models forecast catches for various species and fleets assuming that a fixed catcha-

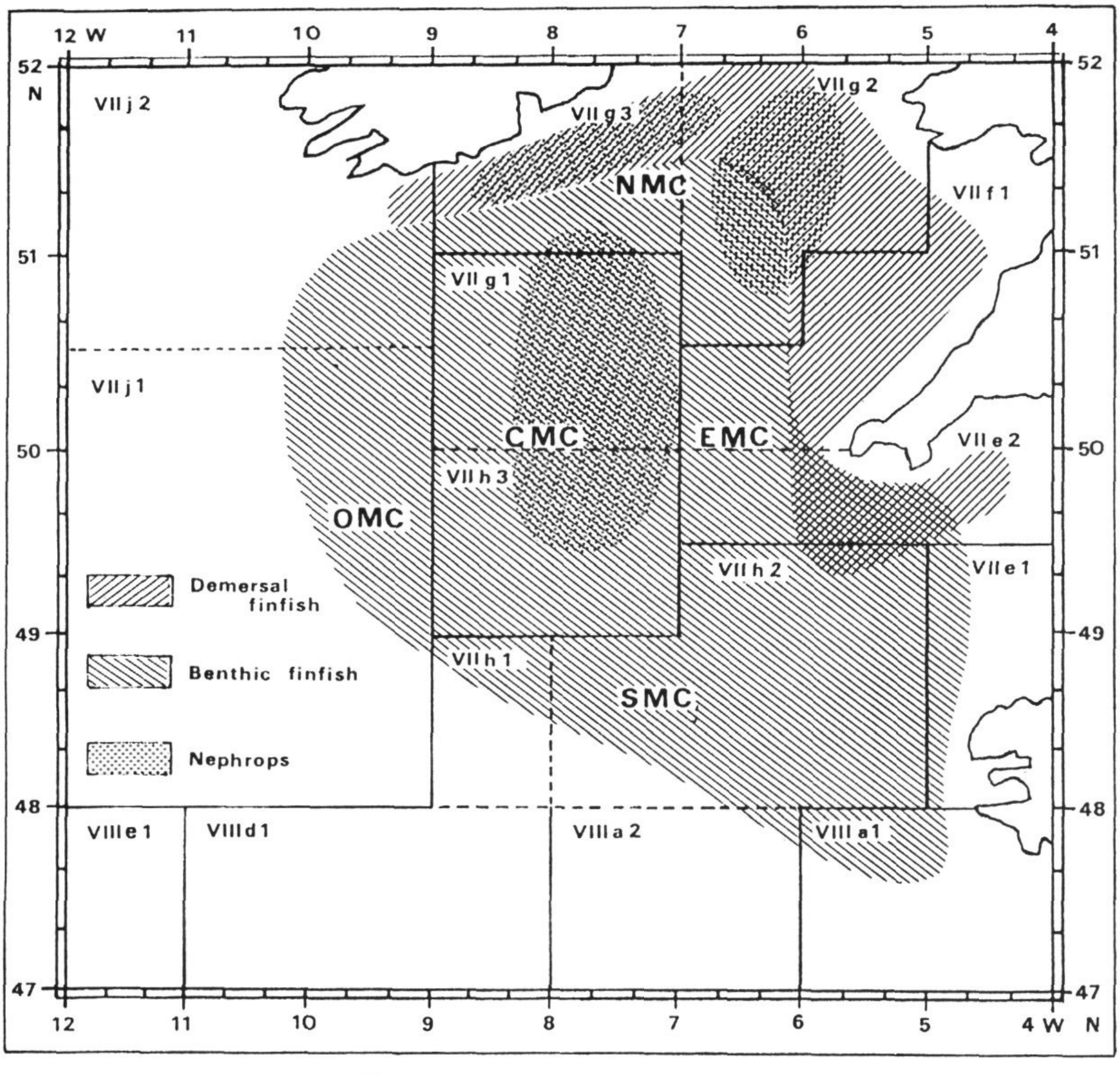

Figure 1. Location of the Celtic Sea fisheries.

bility matrix (age/species) is associated with each fleet. This implies that all fleets keep constant fishing practices from year to year. In other words, they have to stick to the same métiers (gear/target species/fishing grounds). This philosophy has been largely developed by the "VII and VIII ICES Working Group" (Anon., 1987b). Various métiers are considered within this group, corresponding to gears (lines, gillnets, trawls), target species (*Nephrops* and finfishes), and depth range. A whole set of species present in areas VII and VIII are considered. A length-based VPA is performed for each one (Jones, 1974), leading to reference fishing mortality vectors which are partitioned into partial Fs over the various fleets. This approach makes it possible to consider the consequences of changes in the fishing intensities for the various métiers, even in non-equilibrium situations (Mesnil and Shepherd, in press). The forcing variables are the fishing intensities by métier or equivalently (if the constant catchabilities hypothesis holds) the partial fishing mortalities by métier.

This procedure allows possible economic transformations for obtaining the value of the landings instead of catches in weight. But it is impossible to study a vessel's profitability if it switches between métiers. This approach does not allow for specific analysis of the economic consequences of various possible fishing pat-

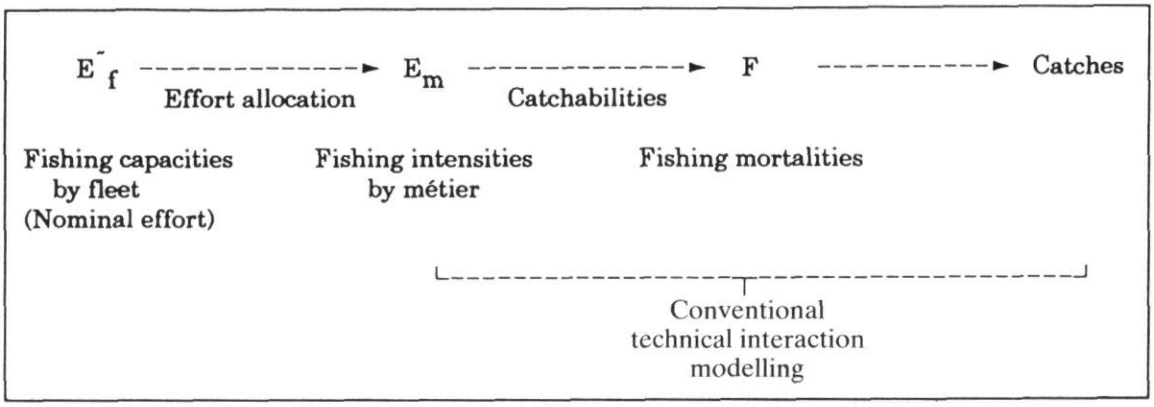

Figure 2. Conventional and extended technical interaction models.

terns, associated to different metiers, with different profitabilities. It is similarly impossible to evaluate the comparative merits of the different management methods, i.e. to assess the impact of TACs, the reaction of fishermen to the exhaustion of a quota must be anticipated. To study such economic consequences it is essential to model the system in a broader context and to use the potential efforts of the various fleets as forcing variables (Charuau, 1986). The difference between most technical interaction models and our more comprehensive approach is summarized in Figure 2. The approach is based on an efficient definition of métiers, as discussed by Laurec *et al.* (1990). It also requires an appropriate model of the effort allocation from the various fleets over the different métiers, which has both a habitual and a profit maximization component.

Choice of time steps

It is first necessary to determine a time scale to define the métiers. In the example we present for the Celtic Sea, a *Nephrops* métier is defined. In fact, depending on whether the ships fish during the day or night, the real targets are either *Nephrops* or finfish. It would be conceivable to recognize two métiers for the same vessels, one of which is practised during the day, the other at night. During a 24-h cycle, the share of the effort devoted to the two activities is largely constant, and, because of this, it is not necessary to create two métiers, although it would have been had the fishing time devoted to *Nephrops* or finfish been highly variable. More generally, it is difficult to use a very detailed definition of métiers related to fishing operations, such as individual hauls. Conversely, grouping various fishing trips can make it difficult to identify functional fishing patterns. An appropriate level of resolution is somewhere between the fishing trip and the fishing day, and will be largely governed by the detail of the information available.

Beyond the time scale used for the definition of métiers, it is not practicable for models to use very small time steps. Thus, as a practical matter, the choice of time interval will be no finer than a month, and probably calendar quarter (this assumes that a vessel can switch between métiers within that model time scale). This choice is dictated by the availability of requisite data, and the necessity of defining time scales in relation to disaggregation processes being studied.

Spatial resolution

The spatial resolution covered by the model will refer to sectors, with each one selected as uniform as possible in terms of distribution and vulnerability of species and ages. This could lead to numerous, small sized, sectors. But computational and data demands imply that sectors must correspond to statistical rectangles, grouped together if possible. This results in a limited number of sectors. Beyond classical multivariate analyses (Murawski *et al.*, 1983), constrained clustering techniques can be useful (Legendre, 1987) for defining sectors.

Fleets

Although it is conceptually feasible to treat individual vessels as unique entities, from a computational and data perspective this is not practicable. The model assumes that the vessels are grouped into fleets. Within a fleet, the various vessels must have similar tactics, comparable efficiencies, and homogeneous cost functions (ownership, wages rules . . .). Relative uniformity of fishing powers among vessels within fleets is necessary for the uniformity of the biological impacts and economic performance. It assumes that the vessels have similar physical characteristics (size, power) and equipment, and employ the same fishing tactics. Group memberships can be associated with the geographic region or home port from which the vessels fish.

General scheme for a model

Allocation of effort

Apart from conventional population dynamic models, effort allocation to the various métiers has to be modelled. Given the abundance of the different stocks, the fishing powers for each fleet and each métier, and the behavioural rules governing the fishing tactics, a matrix, B, is constructed. Each row of the matrix corresponds to a component fleet, and each column to a métier. Each term, $b_{f,m}$, denotes the fraction of the fishing effort of fleet f directed to métier m.

If the fishing power for the standard vessel from fleet f and for métier m is $P_{f,m}$, the effective resulting fishing effort for the métier m, E_m, is equal to:

$$E_m = \sum_f E_f b_{f,m} P_{f,m} \tag{1}$$

where E_f is the total potential fishing effort by fleet.

The catchabilities by métiers allow derivation of the partial fishing mortalities and the application of catch and survival equations. The catches are calculated for each fleet. The transformation of catches in numbers or weights to values can be performed by varying the ex-vessel prices according to the stocks and ages (corresponding to the appropriate market categories), and possibly by including the effect of price elasticity. Thus, it is possible to compute the total value of landings by fleet, and the associated catches per unit of fishing effort (c.p.u.e.). The c.p.u.e. is expressed in catches per day at sea, which may be different from catches per fishing day because of various route times, or inactivity within a trip. Correction factors between days at sea and fishing days, which may be métier-specific, are taken into account.

Consideration is also given to costs, which are partitioned between fixed costs per year, independent of the métiers; operational costs per day, associated with the métier; and costs related to catches (landing costs, share payment, etc. . . .). Modelling the effort allocation among métiers is a significant issue, and has been addressed by various authors (Allen and McGlade, 1986; Murawski and Finn, 1986; Hilborn and Walters, 1987). The mode used here is taken from Charuau (1986) and considers the difference between the ex-vessel value of catches and the operational costs per day at sea. These differences for each métier are the first set of explanatory variables. The effort allocations for the same period and for the previous year are the second set.

Limits of the basic model

Spatial limits of the model

A known area must be circumscribed in space and the fleets concerned delimited. The stocks present in the selected area may have a geographic distribution beyond the area of consideration. The fleets fishing in the area covered by the model may also at times fish in other areas, and to cope with these problems external variables are used. For example, for stock which migrates into and out of the area modelled, with a significant exchange rate, the fishing mortality outside the zone is treated as an external variable. Fleets which are not explicitly considered in the model are also addressed through external variables which correspond to the fishing mortalities they create.

The existence of fishing opportunities outside the area modelled is also addressed by external variables corresponding to the potential c.p.u.e., and to the operational costs, for external métiers.

Economic and administrative external factors

The costs of production can be influenced by events outside the control of fishermen, such as the cost of oil or credit, or the awarding of subsidies. These factors are considered as external variables in the cost functions. Ex-vessel prices may also be partially determined by external factors such as imports (frozen), inventories, or catches outside the modelled area.

Management constraints such as quotas are modelled by giving a nil value to catch from a stock for a fleet (or a set of fleets) when the corresponding quotas have been exhausted and the catch is discarded. It is also possible to model licence schemes for a given métier, which result in effort thresholds, or closure of a zone on a temporary or permanent basis.

Self-regenerating models

For the stocks described by analytical models, the choice must be made between recruitment determined by external variables (e.g. probability distribution), as in this model, or recruitment resulting from a stock-recruitment relationship. Then the major difficulty would be to supply pertinent stock-recruitment parameters.

The fishing capacity per fleet is treated as an external variable. It should be possible to include entry into the fleet as a dynamic. Entry must take account of economic performance over several years. A self-regenerating model of fishing capacities could be developed following the approach used by Lane (1988).

Stochastic models

It is possible to envisage the construction of a stochastic model dealing with the vessels individually (Allen and McGlade, 1986). The calculation times, however, are considerably lengthened. Moreover, a global law for allocation of effort is easier to handle than a set of rules for individual vessels.

Various random factors affecting catchabilities and the spatial distribution of fish could be integrated in the model. As noted above, a stochastic model would also be useful for recruitments, but the current version of the model is deterministic.

Mathematical formalization

Population dynamics

Analytical models

The key element of the model is fishing mortality. The model does not consider variations in natural mortality and a quarter-year time interval is used.

The basic relationship between fishing mortalities and potential fishing efforts is:

$$F_{y,s,a,i} = \sum_{m} \left(\sum_{f} E^{p}_{y,f,i} b_{y,f,m,i} P_{f,m} \right) Q_{m,s,a,i} = \sum_{m} E^{e}_{y,m,i} Q_{m,s,a,i} \qquad (2)$$

where y is the year, f the fleet, s the stock, a the age of the fish, i the quarter, and m the métier; and

$F_{y,s,a,i}$	is the fishing mortality,
$E^{p}_{y,f,i}$	is the potential fishing capacity *for a fleet*,
$E^{e}_{y,m,i}$	is the effective fishing intensity *for a métier*,
$P_{f,m}$	is a fishing power,
$b_{y,f,m,i}$	gives the share of effort dedicated to métier by a fleet,
$Q_{m,s,a,i}$	is the catchability, proportionality constant between F and E.

$E^{p}_{y,f,i}$, $P_{f,m}$, and $Q_{m,s,a,i}$ are inputs to the model. The $b_{y,f,m,i}$ are calculated as indicated.

The catchability parameters deserve particular attention. It is possible to consider phenomena such as saturation, competition, etc. More important is a possible simplification allowing the reduction of the number of parameters. One could for instance write:

$$Q_{m,s,a,i} = Q^{*}_{m,s,a} Q^{**}_{s,a,i} \qquad (3)$$

This is equivalent to neglecting fourth-order interactions between métier, stock, age, and quarter.

Surplus production model

For some important stocks contributing to the multispecies catch, there may not be sufficient data with which to conduct analytical assessments. In these cases we use yield/effort relations in the form of surplus production models which can be applied to the individual stocks for which the available data are inadequate for analytical modelling, although intermediate solutions (Deriso, 1980; Schnute, 1985) are also conceivable.

All the species landed must be considered. It is not generally possible to cover each stock with a model and it is necessary to apply pluri-specific surplus production models. The simplest procedure is to group within a single residual model all the species not covered by a mono-specific model. Several composite models can be used, incorporating species with common characteristics in each one (e.g. by genus, etc.).

The biggest theoretical difficulty when several métiers are defined is the concept of exploited biomass, considered implicitly in surplus production models (Laurec and Le Guen, 1981). This exploited biomass is an average of different age groups and species weighted by fishing mortalities, which can vary from one métier to another. This difficulty will be ignored, however.

The Pella and Tomlinson (1969) model can be written:

$$\frac{dB}{dt} = HB^{m'} - KB - FB \qquad (4)$$

by adopting the notation of Laurec and Le Guen (1981), in which m′ is substituted for the usual m to avoid any confusion with the métier index. To use this model, the relationship between F and the fishing capacities of the various métiers must be specified. Accordingly:

$$F_{y,s,i} = \sum_{f} \sum_{m} E^{p}_{y,f,i} b_{y,f,m,i} P_{f,m} Q_{m,s,i} \qquad (5)$$

for year y, stock s (possibly pluri-specific), and quarter i. This equation is analogous to Equation (2).

Spatial structure of stocks

When division into spatial blocks has been performed, two extremes appear:

(1) immobile or slightly mobile species (at least after recruitment) that allow modelling of the various sectors as separate stocks;
(2) highly mobile species, for which all sectors are treated as a whole (a mixing pool), which implies that the catches made locally immediately affect the entire area.

In the example we present, benthic species (e.g. *Nephrops*) are regarded as "immobile", while the demersal species (cod, whiting) come from a single stock on the scale of the Celtic Sea. This is an approximation. One could question the assumption of unit stocks within a sector. There can also be exchanges between adjacent sectors, sufficiently strong to be non-negligible, and too low for the mixing pool hypothesis to be legitimate.

An efficient solution, much simpler than the approach suggested by Beverton and Holt (1957), is illustrated by Fonteneau (1981). For each sector, an individual stock is considered, with exchange rates between sectors included in the scheme. Application of this approach of course requires information on migration rates.

Economic and effort allocation modelling

Costs and values

Each cost item must be assigned to one of the categories discussed above: (1) fixed costs, (2) operational costs, or (3) costs that depend on catches. In the Celtic Sea example, operational costs are fixed per day at sea, in a given métier, for a given fleet. Catch-related costs are also assumed to be proportional to the value of the catch.

With regard to ex-vessel fish prices, three types of explanatory variables are considered: the distribution of individual sizes or weights in the catches, the time of the year, and the size (quantity) of the landings. In the case of stocks dealt with in production models price differentials by size are, of course, disregarded.

It is not difficult to simultaneously handle the price effects of size and seasonality. Age/commercial category conversions and prices for each category can vary within a year. The introduction of price elasticity is possible through the usual procedures (see Gilly, in Charuau, 1986). However, the simultaneous handling of commercial categories and price elasticity is not simple. This is why, in our Celtic Sea example, a linear relationship is introduced between the logarithm of prices of *Nephrops*, total landings within a month, and the percentage of landings in each of the two commercial sized categories.

Modelling the effort allocation

As previously mentioned, the shares of effort $b_{f,m}$ will be determined to a greater or lesser extent by the relative potential profitabilities among the various métiers, and the corresponding proportions for the previous year, denoted $b^0_{f,m}$.

$S_{f,m}$ is the difference between the (potential) values of catches per day at sea and the corresponding operational costs (i.e. profits). Métiers giving rise to negative profits are excluded. The fraction of effort that would be devoted to métier m_0 in the absence of any influence of past habits, $b^1_{f,m}$ is given by:

$$b^1_{f,m_0} = \frac{(S^+_{f,m_0})^\partial}{\sum_m (S^+_{f,m})^\partial} \qquad (6)$$

where $S^+_{f,m} = S_{f,m}$ or 0, whichever is larger, and ∂ is the so-called preference coefficient. Necessarily positive, it is higher when the fleet concentrates on the métiers offering the greatest profit.

After potential effort shifts are determined based strictly on relative profitability among métiers, a second evaluation is conducted to evaluate the final proportions with respect to the degree of historical adherence to a certain effort pattern. Finally:

$$b_{f,m} = \mu b^0_{f,m} + (1 - \mu) b^1_{f,m}$$

where μ is the co-called adherence parameter, varying from 0 to 1, increasing with the tendency for adherence. Other formulations can be considered (Laloe and Samba, 1989), but the basic framework is robust. The final effort allocation is given by a combination of the previous year situation (b^0) and the preliminary profit based on (b^1). Parameters ∂ and μ may be fleet dependent.

Apart from the adherence, effort allocation is similar to the prey selection in biological interactions models. Any change in suitability indices in response to prey abundance, as discussed by Rice *et al.* (1991), will modify the dynamics of the system. Modelling such changes is a major issue for biological interactions (Hildén, 1988), and the same is true here for technical interactions.

The Celtic Sea application

The details of the Celtic Sea model, and its parameterization, are in Charuau (1986) and Biseau and Charuau (1989). Since 1986, some conceptual clarifications have been made, but the illustration remains pertinent.

Adaptation of the conceptual framework

Sectors

Grouping ICES subdivisions led to the definition of live geographic sectors (see Fig. 1): North (VIIg1 + VIIg2), East (VIIe2 + VIIf1), South (VIIh1 + VIIh2 + VIIIa2), West (VIIj1 + VIIj2), and Center (VIIg1 + VIIh3). These sectors are based on available ecological knowledge.

A basic multivariate analysis

The use of multivariate analysis to define métiers and fleet is discussed by Laurec *et al.* (1990). For the Celtic Sea fisheries, Principal Components Analysis (PCA) has been applied as an ordination technique using covariance matrices of the 1985 data (Biseau et Gondeaux, 1988). The analyses have been summarized in Anon. (1987a). Each individual vessel is considered as an observation (a row in the matrix), and two types of variates have been considered:

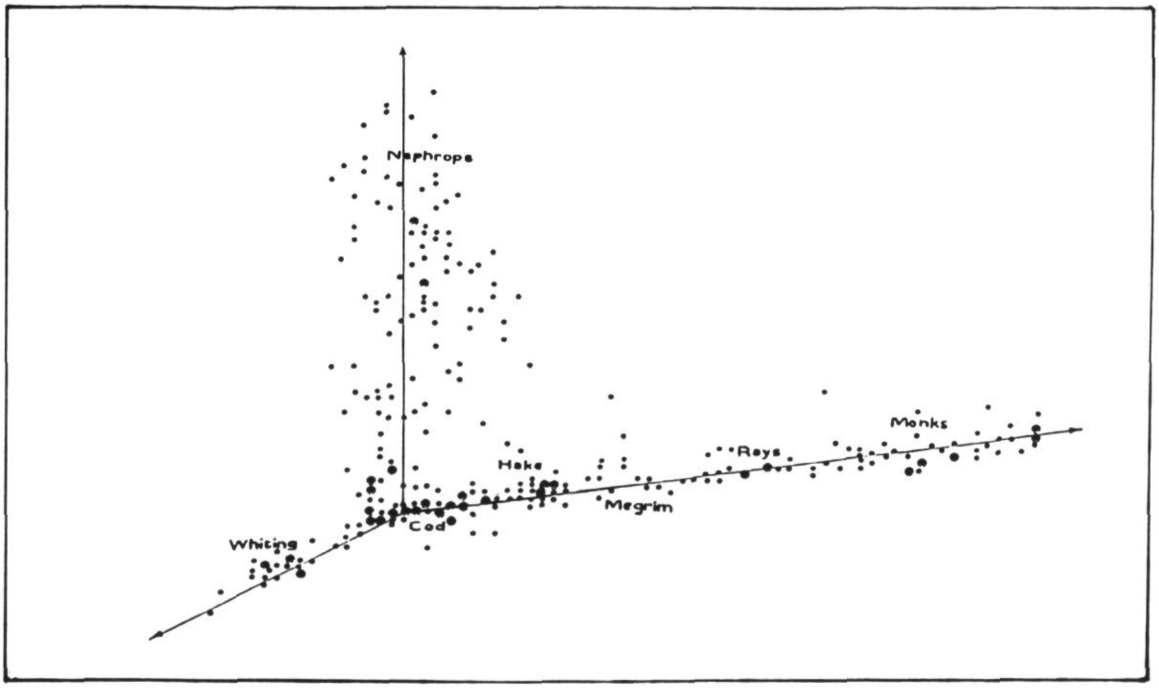

Figure 3. Simultaneous projections after a principal components analysis of the vessels and the species.

1. In analysis 1, the time spent during each month in each area, including outside the Celtic Sea, resulting in 6 × 12 = 72 variables.
2. In analysis 2, the proportion of each of the major species (both species of monkfish being pooled) observed in each month in the landings of each vessel, yielding 7 × 12 = 84 variables.

Both analyses reveal clear structures, especially the second one based on catch compositions (illustrated in Fig. 3). The variables have been plotted making use of the duality properties of PCA (Laurec *et al.*, 1979). With these duality properties in the simultaneous projection of observations (vessels) and variables (species × month) a vessel will be close to a variable when the corresponding species, for the corresponding month, is high in its landings.

The variables associated with the same species, but in different months, are close together, and thus only their centroids appear. A clear-cut structure is revealed in which *Nephrops* (and the vessels specializing on it) is isolated from other species, while another axis discriminates gadoids from the benthic finfishes. Hake occurs in the catches of practically all the vessels. It must be noted that there are virtually no vessels shifting from benthic to *Nephrops* fisheries within the year. The overall structure is summarized by axes corresponding to departure from a kernel. Regrettably it has not been possible to indicate the home ports of the vessels although this factor is very important in determining the structure, i.e. vessels from neighbouring harbours reflect systematically different behaviour.

Species

Eight species are evaluated by analytical models. The five benthic species are: Norway lobster (*Nephrops norvegicus*), megrim (*Lepidorhombus whiffiagonis*), two species of monkfish (*Lophius piscatorius* and *L. budegassa*), a ray (*Raja naevus*). The demersal species are hake (*Merluccius merluccius*), whiting (*Merlangius merlangus*), and cod (*Gadus morhua*).

Benthic species are treated as separate stocks from one sector to another. Demersal species correspond to a single stock. The hake stock has a much wider distribution than the Celtic Sea. Fishing mortality for hake outside the Celtic Sea has been included as an external variable. Sexes may or may not be dealt with separately. Residual catches (catches of species in addition to the eight given above) are attributed to surplus production models of stocks.

Table 1 summarizes the final definition of stocks.

Métiers

Three sets of target species are defined: *Nephrops*, the benthic species (monkfish and ray), and demersal species (cod and whiting). A fourth group could have taken account of all the rest, leading to an "undirected" fishery, but this was not done. For the three possible

Table 1. List of stocks and the numbering of stock units considered in the Celtic Sea technical interaction model. A "×" indicates the absence of a stock in a given sector.

	Geographic sectors of the Celtic Sea				
Species	North	East	South	West	Center
Nephrops (Male)	1	×	×	×	3
Nephrops (Female)	2	×	×	×	4
Megrim (Male)	5	×	7	×	9
Megrim (Female)	6	×	8	×	10
L. piscatorius	11	12	13	×	14
L. budegassa	15	16	17	×	18
Raja naevus (Male)	×	×	19	×	×
Raja naevus (Female)	×	×	20	×	×
Hake*			21		
Whiting			22		
Cod			23		
Benthic/residuals	24	25	26	27	28
Demersal/residual			29		

*? Footnote missing? (See hake).

targets and the five sectors, 10 métiers are considered (certain target species are not considered in some sectors).

Fleets

All vessels considered in the model are trawlers, the specific design and the rigging of the trawls is uniquely adapted in the métiers to the target species group. A Celtic Sea métier is defined by a simple target species and a sector (e.g. Benthic/South). Since the fleets also operate outside the Celtic Sea, five external métiers are considered for a total of 15 métiers.

The total fleet comprises vessels of widely differing physical characteristics. So-called "artisanal" vessels are owned by the skippers, which is not so in the case of "semi-industrial" vessels. Three fleet categories are considered in the model: semi-industrial vessels (22 to 34 m), large artisanal vessels (19 to 21 m), and small artisanal vessels (16 to 18 m). Vessels are also grouped according to home port, so a total of 19 fleets are considered in the model. The validity of these groupings is demonstrated by the previously mentioned ordination and the duality scheme.

Influence of the parameters governing the fleet tactics/simulations

In order to estimate μ and ∂ statistically, a minimum of two years of data would be required. Unfortunately, our intensive study of the fleets was conducted for one year only, so we have conducted a systematic exploration of the ranges of possible values for the two parameters. Simulations have been performed over ten-year periods, starting from a reference year (year 0), for preference coefficients (∂) ranging from 0 to 10 and adherence coefficients (μ) from 0.01 to 1.

Profits in the final year

The profits, summed over all the fleets and Celtic Sea métiers, appear in Table 2. When calculating profits per fleet and métier, which required a Celtic Sea total cost per fleet, fixed costs have been allocated proportionally to the days at sea inside and outside the Celtic Sea. Apart from the cases in which adherence is strong (μ equal to 1. or 0.95), the profits for the 10th year seem to be determined by the opportunism, measured by ∂. Only simulations with ∂ equal to 5 or 10 have a positive profit. For a given value of ∂, non-monotonic variations of the total profits with μ appear. When ∂ is low, the best situation – the only one which generates some profit – is that of total stability in the effort allocation.

Yearly changes

The convergence towards the final level (10 years) occurs faster when the adherence is low (Fig. 4). A high

Table 2. Financial profits (revenues–costs) summed over all fleets and Celtic Sea métiers for the 10th year (in millions of French francs).

		Preference (∂)				
		0.0	1.0	2.0	5.0	10.0
Adherence (μ)	0.01	−61	−31	−10	37	70
	0.1	−61	−31	−10	37	70
	0.5	−62	−30	−9	37	71
	0.8	−52	−31	−11	30	60
	0.95	−5	−2	0	5	12
	1.00	24	24	24	24	24

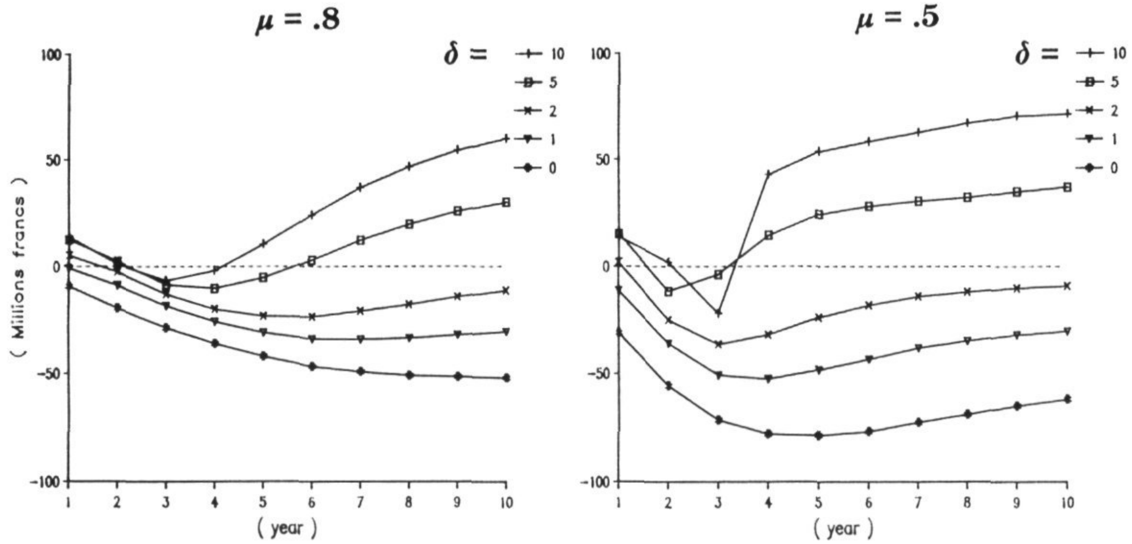

Figure 4. Yearly changes in overall profit for the Celtic Sea fisheries.

value for μ causes delays: effort shifts are very slow and the opportunities may disappear before they are taken up.

High capacities for opportunistic operations may be misleading insofar as the profits actually obtained can differ greatly from the projected profits. This is the case when large concentrations of effort occur on sensitive stocks.

Effort allocation

Table 3 shows the influence of μ and ∂ in the allocation of effort on métiers 1 (Benthic/South) and 2 (Demersal/East). In the reference situation (year 0) for the first quarter, métier 1 accounted for 33% of the total effort. But the anticipated profit for this métier is relatively low in year 1, which, as ∂ increases and/or μ decreases, leads to movement of effort from this métier. Conversely, métier 2 offers a much more attractive potential profit for the same period, and the effort assigned to it rises when ∂ increases or μ decreases.

Figure 5 shows the distribution of efforts summed over all fleets during the second quarter of the 10 years of the simulation for an assumption of very high opportunism ($\partial = 10$, $\mu = 0.1$). In this case the effort distribution stabilizes relatively rapidly. The first year sees a transfer of effort from the external and the South/Benthic to the East/Demersal in the Celtic Sea. The *Nephrops* métiers exhibit globally higher effort although in line with asynchronous oscillations; the movement of effort occurs more slowly than for the other métiers.

Table 3. Percentages of fishing effort during the first quarter of the first year, for métiers 1 (left of the slash) and 2 (right), within various effort allocation rules.

		Preference (∂)				
		0.0	1.0	2.0	5.0	10.0
	0.01	12/8				2/63
	0.1	14/7	12/13	10/20	7/40	4/58
Adherence	0.5	22/5	21/8	20/12	18/23	17/33
(μ)	0.8	29/3	28/4	28/6	27/10	26/14
	0.95	32/2	32/2	32/3	31/4	31/5
	1.00	33/2	33/2	33/2	33/2	33/2

The benthic métiers, especially in the South, are abandoned during the first year, but re-acquire effort when other demersal métiers lose their attraction, which occurs as soon as the consequences of overexploitation are exhibited.

Conclusion

Modelling technical interactions appears to be a tractable problem which may have significant influence on how we assess and manage fisheries. It requires the cooperation of population dynamicists, economists, and the classical disciplines if difficult problems, such as the effort allocation question, are to be resolved. In one regard, modelling preference decisions of fishermen is much more tractable than the corresponding biological question, since fishermen can be surveyed concerning their decisions before, during, and after effort is allocated. Our modelling procedure is based on the concept of métier, which groups the vessels targeting consistent species, mixed into homogeneous fleets, and over a space/time cell. Not enough emphasis can be placed on the importance of analysis for defining consistent métiers which retain their identity over the simulation interval.

The second critical need is adequate data. It is essen-

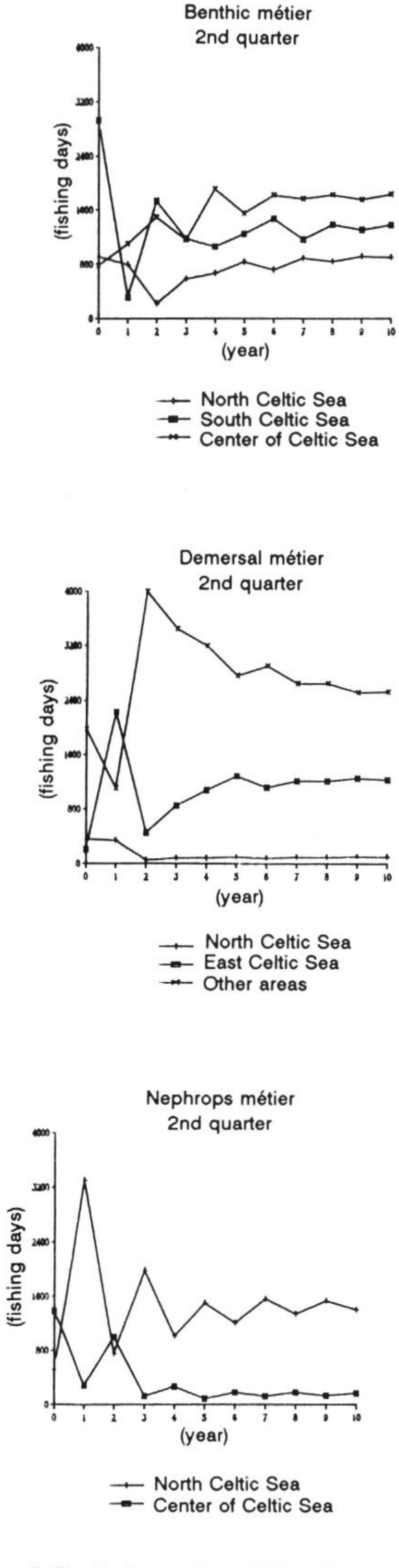

Figure 5. Yearly changes in the fishing effort per métier.

tial to obtain catch data disaggregated in space, and if possible by age. This may require detailed catch/effort data, a logbook system, and the definition of suitable biological and economic sampling schemes. Studying the relationships between c.p.u.e. and abundance, and therefore catchabilities, and analysing and estimating fishing power is also very important. This may require processing techniques adapted to disaggregated data (Laurec and Perodou, 1987; Perodou, 1988). Biological and economic data will be required over several years to fit and validate the model.

The modelling framework presented in this paper has been developed for the Celtic Sea situation, but it can be generalized to other situations (Anon., 1987a; Murawski *et al.*, 1991). Applications of the model to other fishery systems could lead to fruitful comparisons, which may serve to validate the basic mechanisms of effort allocation among fleet target activities.

Technical, economical, and biological interactions should be simultaneously studied. As a first step, some situations offer a better opportunity to study a single issue, but a complete understanding, and if possible a modelling of the overall fishery systems, should be pursued.

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An analysis of technological interactions among Gulf of Maine mixed-species fisheries

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Murawski, S. A., Lange, A. M., and Idoine, J. S. 1991. An analysis of technological interactions among Gulf of Maine mixed-species fisheries. – ICES mar. Sci. Symp., 193: 237–252.

Demersal resources of the Gulf of Maine (Northeast USA) are exploited by a system of technologically interdependent fisheries. Interactions among these fisheries occur when: (1) small-mesh fisheries discard undersized individuals of target species for large-mesh fisheries, (2) large-mesh fisheries discard animals below minimum landing sizes, and (3) fisheries operating simultaneously or sequentially compete for the same species/age groups. This study explores equilibrium mixed-species/multi-fishery interactions for the system of Gulf of Maine demersal resources and fisheries, contingent upon: (1) the amount and distribution of standardized fishing effort among the competing fisheries, (2) selection and discarding characteristics of gears, (3) the elasticity of ex-vessel prices in relation to supply, and (4) alternative stock-recruitment relationships for the species simulated. The equilibrium model is appropriate for analyzing long-term effects of alternative effort allocation and gear selection schemes among the fisheries because biological reference points for management are the percentage of maximum spawning-stock biomass per recruit (SSB/R) targets. Simulations for the 15-species, 6-fishery system emphasize the dependency of aggregate yields on current high discard rates in both small- and large-mesh trawl fisheries. Although total system yields are somewhat insensitive to modest effort changes, levels of groundfish percentage maximum SSB/R levels may be altered significantly with modest changes of effort in particular fisheries. Highly elastic prices (as seen during the 1980s) tend to stabilize the aggregate value surface, even when the biomass of some species is depleted. Evaluation of the transitory effects of biological conditions and management will require the development of dynamic models of fleet behavior, which may be particularly appropriate for these open-access fisheries.

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Introduction

Technological interactions are an increasingly important theme in fishery management arenas throughout the world. Emphasis on fishery interactions has been heightened by the trend to more complete utilization of mixed resources, and the incompatibility of that trend with traditional single-species biological reference points and related management measures. Technological interactions research has concentrated on extensions of analytic and simulation methods to examine management strategies as they affect the balance of species yields accruing to interacting fisheries (Pope, 1979; Sparre, 1980; Murawski, 1984; Sainsbury, 1984; Anon., 1987a; Shepherd, 1988). Programs to assess technical interactions have entered the mainstream of stock assessment advice in a number of regions (Brander and Bennett, 1986; Pikitch, 1987; Anon., 1987a, 1988a, b, 1989a). Use of these methods in a fishery management context, particularly including economic aspects, has in turn stimulated the development of increasingly sophisticated techniques for mixed-species, multi-fishery evaluation (e.g. Charuau and Biseau, 1989; Mesnil and Shepherd, 1990; Laurec *et al.*, 1991).

In this study we elaborate on existing mixed-species, multi-fishery yield models, and apply the methods to a system of interacting mixed-species fisheries in the Gulf of Maine region, off the northeast USA (Fig. 1). Our model integrates various features of previous techniques (Anon., 1987a), and additionally: (1) accounts for discards by fishery, (2) incorporates optional price/volume relationships to simulate price elasticities in relation to supply, (3) includes a surplus production module to evaluate yields of species or species groups for which

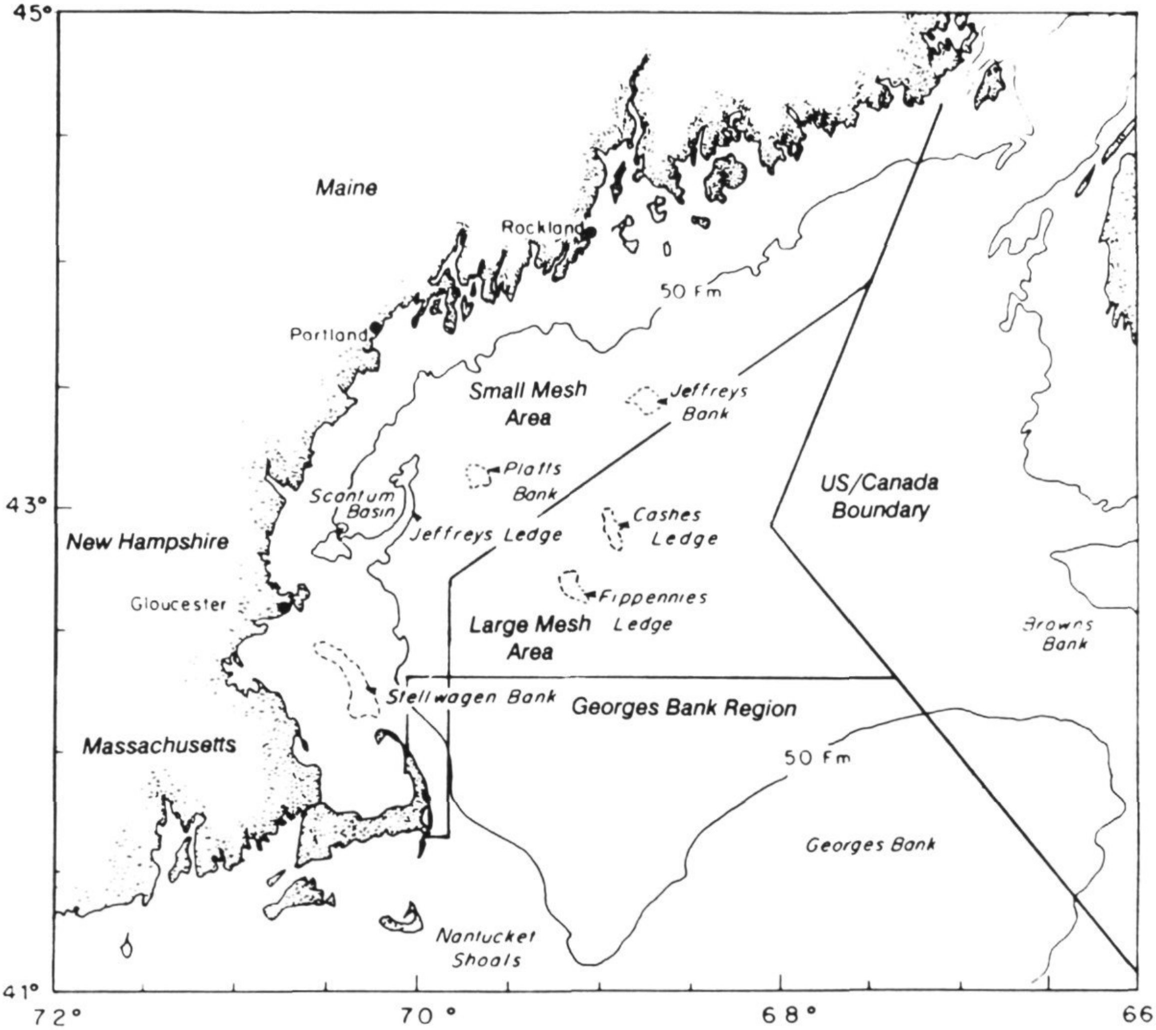

Figure 1. The Gulf of Maine region off the Northeast USA and Southeastern Canada. Geographic boundaries of the regulated large-mesh-only fishing area (>140 mm mesh size), and the exempted small-mesh fishing area in nearshore waters are illustrated. Modeling of technological interactions pertains to the area bounded by the USA/Canada maritime boundary, the USA coastline, and the Georges Bank region.

age-based population dynamics data are not available, and (4) incorporates the effects of fishing on the stocks when they are taken outside the region being modeled.

Gulf of Maine demersal resources (finfish and pandalid shrimp) are exploited by a number of technologically interdependent fisheries which are distinguished by gear type, target species composition, and differing management regulations (e.g. regulated mesh areas). The main source of interaction occurs between small- and large-mesh fleets. In particular, discarding in both small- and large-mesh fisheries is considered problematic to the attainment of management targets for important species. Demersal fisheries in USA waters of the Gulf of Maine (Fig. 1) are not quota regulated, nor is access to these fisheries regulated. Thus, the nature of technological interactions is not the incompatibility of single-species quotas with mixed species fisheries, but rather the effects of the various fisheries on attainment of equilibrium reference points (such as percentage maximum spawning-stock biomass/recruit in the case of most important groundfish). Regulation of the various fisheries (shrimp, groundfish, hakes) is conducted by several independent management entities, but there is currently no overall evaluation of the aggregate fishery and species impacts of the individual management programs. We explore the mixed-species, multi-fishery yield surface for the system of Gulf of Maine demersal resources, dependent upon: (1) the amount and distribution of standardized fishing effort among the fisheries, (2) selection and discarding characteristics of gears used

Table 1. Common and scientific names of species considered in analyzing Gulf of Maine demersal fisheries. Number of ages, instantaneous natural mortality rate (M), and literature citations for population dynamics data are also given.

Common name	Scientific name	Number of age groups	M	Sources of data[1]
Silver hake	*Merluccius bilinearis*	9+	0.4	Almeida (1978), Almeida (1987)
Atlantic cod	*Gadus morhua*	18+	0.2	Penttila and Gifford (1976), Serchuk (1988)
Haddock	*Melanogrammus aeglefinus*	17+	0.2	Clark *et al*. (1982)
Pollock	*Pollachius virens*	15+	0.2	Clark *et al*. (1977), Annand *et al*. (1987)
Redfish	*Sebastes fasciatus*	20+	0.05	Mayo (1980)
Witch flounder	*Glyptocephalus cynoglossus*	20+	0.15	Burnett (1987)
Red hake	*Urophycis chuss*	9+	0.4	NEFC File Data
White hake	*Urophycis tenuis*	20+	0.2	Hunt (1982), Burnett *et al*. (1984)
American plaice	*Hippoglossoides platessoides*	17+	0.2	Sullivan (1982)
Winter flounder	*Pseudopleuronectes americanus*	12+	0.2	Berry *et al*. (1965), Howe and Coates (1975)
Goosefish	*Lophius americanus*	11+	0.1	Armstrong (1987)
Yellowtail flounder	*Limanda ferruginea*	8+	0.2	Libey (1973)
Northern shrimp	*Pandalus borealis*	6+	0.5	Haynes and Wigley (1969)
Spiny dogfish	*Squalus acanthias*	20+	0.05	Nammack *et al*. (1985)

[1] Maturity data for most fish are from Morse (1979). Spawning times are from Colton *et al*. (1979).

in the various fisheries, (3) the elasticity of ex-vessel prices in relation to supply, and (4) potential stock-recruitment relationships for the species simulated.

An important goal of this modeling program is to evaluate changes in long-term yields and stock abundance to be expected from different effort levels in one or more of the competing fisheries. Management reference points for most of the important groundfish resources of the Gulf of Maine are percentage maximum spawning-stock biomass/recruit values. A deterministic modeling approach to evaluate this and other equilibrium stock attributes is thus consistent with current management. An analysis of scenarios involving modest effort changes in each of the fisheries individually provides managers with an assessment of the relative magnitude and sign of yield and stock changes to be expected from alternative effort management policies. Our primary intent is to develop the framework for such overall evaluations, and to assess the availability and adequacy of requisite data. Current ongoing data collection programs, particularly emphasizing at-sea discard sampling, will provide critical but heretofore imprecise information. Accordingly, specific results must be preliminary, pending more complete population dynamics data for some species. Finally, we evaluate the limits of an equilibrium approach to modeling systems such as the Gulf of Maine demersal fisheries and comment on the utility of dynamic models of stock abundance and fleet effort allocation, such as those proposed by Laurec *et al.* (1991).

System description

Fishery ecology

The Gulf of Maine region (Fig. 1) is a varied ecological setting, inhabited by a diverse fisheries fauna (Murawski *et al.*, 1983). Shallow waters of the western Gulf serve as nursery areas for a variety of flounders and gadoids (Hacunda, 1981; Wigley and Gabriel, 1991). The demersal fishery community changes considerably with depth: shallow waters are characterized by a high proportion of flounders, hakes, northern shrimp, and roundfishes (Table 1). Deeper waters account primarily for redfish, haddock, white hake, and deep-water flounders. About 25 species are routinely landed by the demersal fisheries of the region (Murawski *et al.*, 1983; Anon., 1987b). Predominant gears landing demersal species include large mesh (>140 mm) and small mesh (<140 mm) otter trawls and gill nets. Small quantities of landings are also derived with set line, by recreational fisheries and as by-catch in other miscellaneous gears. Species listed in Table 1 generally account for 90–95% of the annual landings by gears targeted to demersal resources.

Fisheries for demersal species in the Gulf of Maine are characterized by a distinct seasonality, reflecting the spatial-temporal aggregation patterns of the resources. Pollock migrate to the western Gulf in winter months to spawn. Gillnet and large-mesh trawl fisheries derive most of the annual pollock landings during this season. Similarly, northern shrimp aggregate nearshore in winter, and are available to an intensive small-mesh trawl fishery during several months. Silver hake are fished with small-mesh trawl gear primarily in summer and autumn. Spiny dogfish are fished during summer and autumn in a directed small-mesh trawl fishery and in gillnets. This migratory stock is virtually absent from the Gulf in winter. The demersal resources are generally highly mixed, reflecting overlapping environmental preferences of the various species (Murawski and Finn, 1988; Wigley and Gabriel, 1991).

Important fish prey of the demersal fishes of the region are primarily pelagic species (Langton and Bow-

Table 2. Regulated minimum landing sizes, lengths at 50% maturity (M_{50}, for females), and lengths at 50% retention (L_{50}) for fish species considered in the Gulf of Maine Region. Data are in cm.

Species	Minimum landing length (cm)	M_{50}	50% retention length for mesh size			
			44 mm	57 mm	114 mm	140 mm
Atlantic cod[1]	48	50	16	21	41	50
Haddock[1]	48	43	15	20	40	49
Pollock[1]	48	48	14	19	37	46
Witch flounder[1]	36	35	12	14	26	32
American plaice[1]	36	34	10	13	26	32
Yellowtail flounder[1]	33	28	10	13	25	31
Winter flounder[1]	28	26	10	13	25	31
Redfish[2]	23	24	6	10	30	40
Silver hake[2]	–	27	15	20	43	54
Red hake[2]	–	28	17	22	44	55
White hake	–	48	17	22	44	55
Goosefish	–	49	11	14	29	35
Spiny dogfish	–	78	17	22	43	53

[1] Selectivity data based on Smolowitz (1983).
[2] Selectivity data based on Clay (1979).

man, 1980, 1981). Hacunda (1981) noted little interspecies predation among demersal fishes in nearshore Gulf of Maine areas. There are some data indicating fish predation on northern shrimp (Langton and Bowman, 1980). However, in no case did shrimp comprise more than 20% (by weight) of the diet of demersal fish species. Our evaluation of Gulf of Maine demersal resources focuses on technological interactions among the various mixed-species fisheries. Potential biological interactions among these demersal species are beyond the scope of this study.

Current management

Demersal fisheries of the Gulf of Maine region are managed through a complex set of regulations, promulgated by several independent management jurisdictions. In USA waters there are separate management programs for northern shrimp, groundfish, and silver and red hakes. Northern shrimp are regulated under an inter-state management plan promulgated by the Atlantic States Marine Fisheries Commission. Current regulations pertaining to shrimp fishing include a 6-month fishing season (December–May), an areal restriction of shrimping to the exempted small-mesh fishing area (Fig. 1), and a by-catch limit on regulated demersal fish species, as a percentage of the total landings of shrimp fishing trips. Important demersal finfish species (i.e. cod, haddock, pollock, witch flounder, American plaice, yellowtail flounder, winter flounder, redfish, white hake, and windowpane flounder, *Scopthalmus aquosus*) are regulated under the Northeast Multispecies Fishery Management Plan (FMP) of the New England Fishery Management Council (Technical Monitoring Group 1988). Provisions of this plan include minimum landed sizes for eight species (Table 2), and a minimum mesh size for large-mesh trawl and gillnet fisheries of 140 mm (5.5 inches). Silver and red hakes are regulated under a fishery management plan administered by the National Marine Fisheries Service (although silver hake may be regulated under the Northeast Multispecies FMP in the future). Small-mesh fisheries for hakes, spiny dogfish, shrimp, and other species are restricted to the exempted small-mesh fishing area (Fig. 1). There are no direct controls on total or species catches or on fishing effort in these fisheries.

Management targets for the species managed under the Northeast Multispecies FMP are levels of percentage maximum spawning-stock biomass per recruit (generally ranging from 20 to 30% of the unfished biomass levels). Mesh-size restrictions are intended to modify the selection patterns of these stocks to achieve the target levels of percentage maximum SSB/R.

A recent evaluation of the effectiveness of the Northeast Multispecies FMP has concluded that while the compliance with minimum size restrictions on landings is high (Table 2), compliance with minimum mesh-size regulations is not (Technical Monitoring Group 1988). It was estimated that the effective mesh size is approximately one inch smaller than the 140 mm mesh regulation (114 mm or 4.5 inches; Anon., 1987b). Thus, in order to meet the minimum landed size requirements, there are likely significant discards of regulated species in nominal large-mesh fisheries (Table 2). Significant discards of regulated finfish species also occur in small-mesh fisheries targeted at shrimp, hakes, and other species (Howell and Langan, 1987).

Given the reported high discard rates in both small and nominal large-mesh fisheries, a program to evaluate at-sea catch and discard patterns was initiated in January 1989 and will intensively sample a number of trawl and gillnet fisheries to evaluate gear selection and discarding practices. These data, when fully available, will be critical in evaluating interaction effects among the various fisheries of the region.

Fishery definition

A typology of the Gulf of Maine demersal fisheries is a necessary requisite for modeling studies of fishery interaction. The relatively large number of vessels and gear types must be aggregated into a few distinct operational fisheries (Anon., 1987a; Laurec *et al.*, 1991). The basis of this typology is a combination of attributes including: (1) co-occurrence patterns of mixed catches in time and space, (2) the operational characteristics of fishing gears used (e.g. gear type and mesh size), and (3) regulatory schemes that impose structure to the fisheries (e.g. the regulated mesh areas). Such a typology is necessarily a compromise between the need to define sufficient fishery units to capture the diversity of fishing patterns in use, and the necessity of defining relatively few operational fisheries that retain their functional identity over time (Murawski *et al.*, 1983). A significant consideration in this regard is the availability of fishery population dynamics data, disaggregated to the level of fishery definition. Accordingly, the following six fisheries are defined as exploiting demersal resources in the Gulf of Maine region:

1. Large-mesh trawl in the large-mesh area (LM/LMA)
2. Large-mesh trawl in the small-mesh area (LM/SMA)
3. Gillnet (GN)
4. Small-mesh trawl targeted at northern shrimp (SHRIMP)
5. Small-mesh trawl targeted at silver hake (SHAKE)
6. Small-mesh trawl targeted at other species (OSM)

It is recognized that to the extent that there is a diversity of species targeting within any one of the defined fisheries, partial fishing mortality rates generated within that fishery will not be a simple multiple of the total amount of fishing effort. However, given the quarterly time-step used in our modeling studies, seasonal patterns of species targeting within the various fisheries can be taken into account to some degree if this time-step is fine enough.

Catches of demersal species by other gear types operating in the Gulf of Maine are considered as fishing mortalities generated external to the six-fishery system considered. Additionally, some of the stocks evaluated (Table 1) have geographical ranges beyond the Gulf of Maine region. Catches of these stocks outside the Gulf of Maine are similarly treated as external fishing mortality rates. The following is a brief summary of fishery performance and species catches in the defined fisheries for the period 1982–1988.

Fishery performance

Landings, value, and nominal fishing effort data for 1982–1988 were aggregated by fishery unit, based on the typology of fisheries given above (Tables 3 and 4; Figs. 2 and 3). Mixed-species fishing effort was standardized to account for the differing sizes of vessels predominant in various fisheries, and the two gear types used (trawl and gillnet). Mixed-species landings per unit of effort (l.p.u.e.) was used as the dependent variable. Fishing power coefficients by vessel size class and gear type were estimated with a general linear model (Anon., 1987b). Fishing power coefficients so derived were used to standardize nominal fishing effort data by vessel size class, gear type, and fishery (Table 3).

Total mixed-species landings by the six fisheries were relatively stable during 1982–1985, but have since declined by 35% from a maximum of 70.6 thousand t in 1983 to 46.1 thousand t in 1988 (Table 3). Mixed-species l.p.u.e. for all fisheries declined from 4.6 to 2.5 $\mathrm{t\,d^{-1}}$ fished (−46%) during 1982–1988. Standardized trawl effort doubled from 1976 to 1987 (Anon., 1987b), and gillnet effort increased substantially from 1982 to 1987 (+62%). Total standardized effort increased 37% during 1982–1987, but declined by 10% from 1987 to 1988. Some of the effort was shifted to the Georges Bank region in 1988 (Fig. 1), primarily by the large-mesh trawl fishery operating in the large-mesh area. During the period 1982–1988 effort increased substantially in the large-mesh trawl fishery in the exempted small-mesh area, the gillnet fishery, and the shrimp fishery. Other fisheries exhibited stable or declining effort trends (Table 3). In 1988 the small-mesh fisheries accounted for 23% of mixed-species landings, 22% of the landed value, and 19% of total fishing effort among the six demersal fisheries.

Species compositions of aggregate landings in weight and value are given in Figure 2. Predominant species have changed somewhat during the period, reflecting declines in the abundance of haddock, flounders, and cod, and more recently pollock and other species. Most species have exhibited declining landings over the period. Currently landings are dominated by pollock, cod, hakes, and shrimp. Most of the landed value is accounted for by cod, witch flounder, pollock, and shrimp. Species composition of the various fisheries in 1987 is given in Table 4. The large-mesh trawl fishery in the large-mesh area lands primarily pollock, white hake, cod, and witch. Large-mesh trawling in the small-mesh area is dominated by pollock, cod, plaice, witch, and goosefish. Gillnet fishing targets three main species: pollock, cod, and spiny dogfish. Small-mesh fisheries land mostly shrimp, hakes, spiny dogfish, and other species, particularly ocean pout (*Macrozoarces americanus*).

The aggregate value of landings peaked in 1987 at USD 74.5 million, and declined by 28% during 1988.

Table 3. Aggregate mixed-species landings (t), ex-vessel value ($s), and standardized fishing effort (days fished) in six demersal fisheries operating in the Gulf of Maine, 1982–1988.

Fishery	1982	1983	1984	1985	1986	1987	1988
				Landings			
Large mesh/LMA	13 778	15 473	13 884	14 781	12 019	10 212	5 095
Large mesh/SMA	24 689	24 335	21 712	22 613	20 649	16 674	16 640
Gillnet	11 456	11 029	12 805	11 268	13 361	13 358	13 691
Shrimp	2544	2 831	4 043	5 498	6 731	6 118	3 828
Silver hake	4 145	5 886	8 293	8 177	7 919	4 557	3 880
Other small mesh	13 713	11 053	7 290	6 550	5 144	4 236	3 009
	70 325	70 607	68 027	68 887	65 823	55 155	46 143
				Ex-vessel value (000's $)			
Large mesh/LMA	10 979	12 370	12 514	14 553	15 346	16 072	8 062
Large mesh/SMA	20 206	20 510	20 861	23 360	25 499	27 438	23 644
Gillnet	5 420	5 235	5 830	5 865	9 918	13 344	10 296
Shrimp	2 891	3 280	4 085	4 999	8 331	13 300	8 051
Silver hake	2 206	2 303	2 501	3 713	3 597	2 736	2 306
Other small mesh	8 553	6 796	3 532	3 364	3 188	1 667	1 251
	50 255	50 494	49 323	55 854	65 879	74 557	53 610
				Standardized days fished			
Large mesh/LMA	2 793	3 345	3 743	4 722	4 902	4 600	2 766
Large mesh/SMA	6 069	5 874	6 255	7 134	7 187	7 457	7 927
Gillnet	2 821	3 128	3 345	3 331	3 915	4 562	4 516
Shrimp	773	955	1 366	1 683	2 555	2 867	2 209
Silver hake	566	654	708	788	953	804	880
Other small mesh	2 146	1 728	927	892	763	416	391
	15 168	15 684	16 344	18 550	20 275	20 706	18 689

Table 4. Landings (t) of Gulf of Maine demersal species in six defined fisheries during 1987. Proportion of species yields by fishery are given in parentheses. Abbreviations of fishery units are: LM/LMA = large mesh trawling in the large mesh area, LM/SMA = large mesh trawling in the small mesh area, GN = gillnet, SHRIMP = shrimp trawl, SHAKE = silver hake trawl fishery, OSM = other small mesh.

	Fishery						
Species	LM/LMA	LM/SMA	GN	Shrimp	Shake	OSM	Total
Silver hake	29 (0.01)	131 (0.03)	56 (0.01)	411 (0.10)	3 434 (0.80)	250 (0.06)	4 311
Cod	1 244 (0.17)	2 736 (0.37)	3 001 (0.41)	237 (0.03)	87 (0.01)	50 (0.01)	7 355
Haddock	366 (0.45)	275 (0.34)	159 (0.20)	6 (0.01)	4 (0.01)	2 (0.01)	812
Pollock	3 575 (0.24)	3 720 (0.25)	7 440 (0.50)	44 (0.01)	26 (0.01)	15 (0.01)	14 819
Redfish	621 (0.55)	373 (0.33)	37 (0.03)	76 (0.07)	13 (0.01)	9 (0.01)	1 129
Witch	827 (0.32)	1 634 (0.63)	31 (0.01)	40 (0.02)	24 (0.01)	21 (0.01)	2 577
Red hake	8 (0.01)	61 (0.08)	2 (0.01)	168 (0.21)	414 (0.53)	130 (0.17)	783
White hake	1 544 (0.39)	1 532 (0.39)	769 (0.20)	35 (0.01)	29 (0.01)	13 (0.01)	3 922
Plaice	660 (0.25)	1 792 (0.67)	30 (0.01)	127 (0.05)	59 (0.02)	24 (0.01)	2 693
Winter flounder	20 (0.02)	718 (0.65)	162 (0.15)	97 (0.09)	14 (0.01)	97 (0.09)	1 106
Goosefish	750 (0.27)	1 609 (0.57)	225 (0.08)	70 (0.02)	94 (0.03)	54 (0.02)	2 803
Yellowtail	1 (0.01)	736 (0.80)	96 (0.10)	18 (0.02)	15 (0.02)	49 (0.05)	916
Shrimp	0 (0.00)	3 (0.01)	0 (0.00)	4 603 (0.99)	9 (0.01)	40 (0.01)	4 655
Spiny dogfish	0 (0.00)	31 (0.01)	801 (0.32)	0 (0.00)	52 (0.02)	1 655 (0.65)	2 539
Other species	565 (0.12)	1 324 (0.28)	548 (0.12)	187 (0.04)	284 (0.06)	1 826 (0.39)	4 734

The decline in landed value is in part due to overall reductions in landed weight, combined with lower ex-vessel unit values for several of the important species (Table 3, Figure 3). Annual ex-vessel unit values, as a function of landings, are plotted for seven of the species in Figure 4. Significant negative relationships are apparent between deflated unit values and total species landings. These relationships are confounded by the increasing demand for fish during the period and by the fact that ex-vessel values for the Gulf of Maine region are

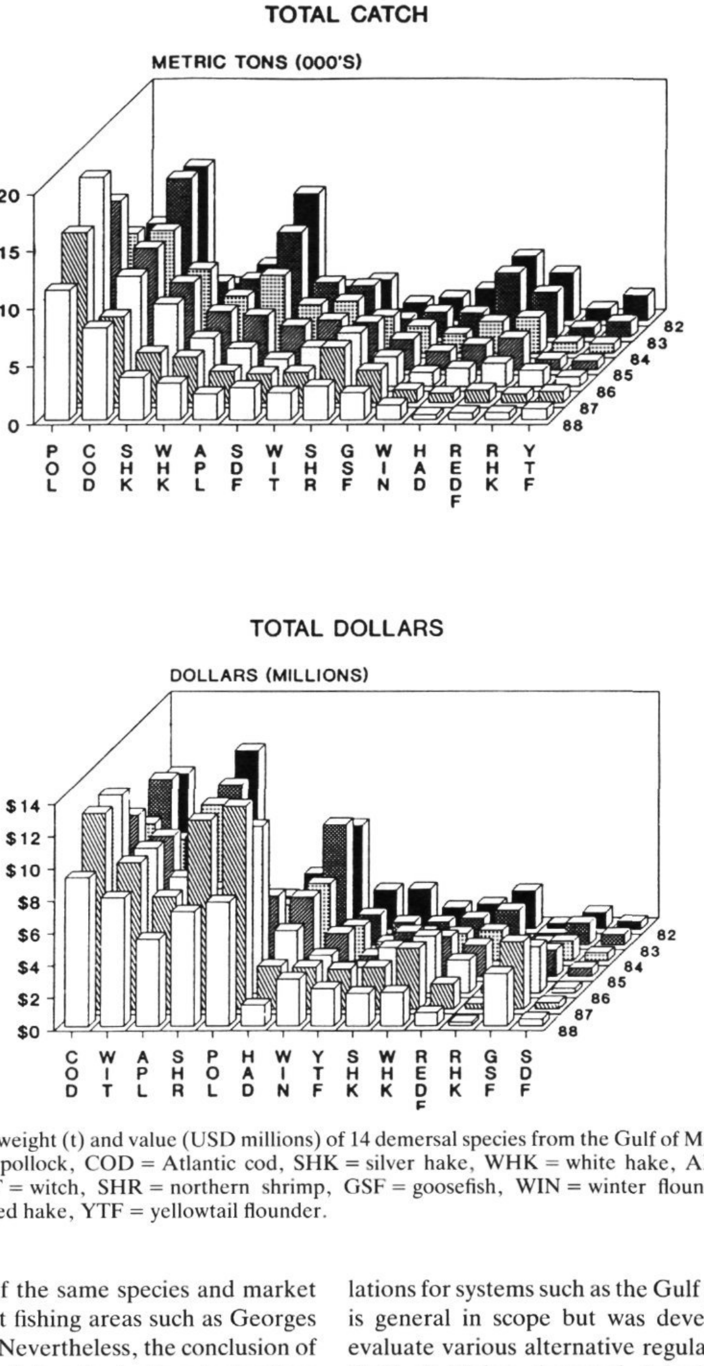

Figure 2. Total landings in weight (t) and value (USD millions) of 14 demersal species from the Gulf of Maine region, 1982–1988. Species codes are: POL = pollock, COD = Atlantic cod, SHK = silver hake, WHK = white hake, APL = American Plaice, SDF = spiny dogfish, WIT = witch, SHR = northern shrimp, GSF = goosefish, WIN = winter flounder, HAD = haddock, REDF = redfish, RHK = red hake, YTF = yellowtail flounder.

influenced by landings of the same species and market substitutes from adjacent fishing areas such as Georges Bank and from imports. Nevertheless, the conclusion of increased unit value in relation to declines in landings has important implications for evaluating global management strategies for these resources. Thus, we simulated such relationships in the context of mixed-species, multi-fishery analyses.

Model description

An equilibrium, mixed-species/multi-fishery model has been developed to allow evaluation of harvest regulations for systems such as the Gulf of Maine. The model is general in scope but was developed specifically to evaluate various alternative regulation schemes for the Gulf of Maine demersal fisheries. An equilibrium modeling approach is deemed appropriate for this analysis, since management targets for important groundfish species are percentages of equilibrium spawning-stock biomass per recruit values. The structure of the model is similar to that outlined in Murawski (1984). The most important modifications allow for: (1) explicit accounting of discards in numbers and weights by fishery unit, (2) a more realistic economic sub-model to compute variable prices as a function of volume of species land-

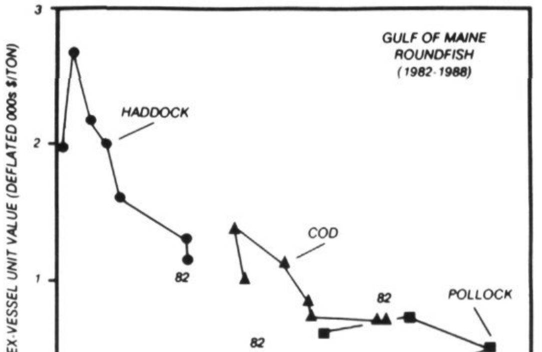

Figure 3. Ex-vessel unit value (USD/t) for seven demersal species landed from the Gulf of Maine region, 1982–1988. Data are deflated to 1982 standard USD by the consumer price indices.

ings, (3) a surplus production subroutine (SPROD) that allows for catch/effort relationships of species or species groups for which adequate age-based information is not available, and (4) inclusion of "external" fishing mortalities on the stocks when they are fished outside the region, or they are fished by gears not included in the overall analysis.

A FORTRAN computer program (MSMF.FOR) was developed to evaluate mixed-species, multi-fleet fisheries as a function of (1) the amount and distribution of standardized fishing effort among competing fisheries, (2) selection and discarding characteristics of the gear used in the various fisheries, (3) the elasticity of ex-vessel prices in relation to landings, and (4) potential stock-recruitment relationships for the species simulated. The model currently allows for up to 15 species, 20 age groups per species (the last a plus-group), and 10 fisheries to be analyzed. Following is a brief description of the program subroutines, internal calculations, and input data output options:

Subroutine YPR: Total fishing mortality rate, F, by species (s), age (a), and quarter (q), attributable to fishery (f) is computed as:

$$F_{s,a,q,f} = PR_{s,a,q,f} \times \\ \times [Q_{s,q,f} \times (PE_{q,f} \times \text{Total annual effort})] \qquad (1)$$

where PR = the partial recruitment factor, Q = the catchability coefficient, and PE = the proportion of total standardized effort. Landings per recruit (L/R) is derived by:

$$L/R_{s,a,q,f} = F_{s,a,q,f} \times \bar{W}_{s,a,q,f} \times \bar{N}_{s,a,q} \times PL_{s,a,q,f} \qquad (2)$$

where $\bar{W}$ = mean weight-at-age in landings, $\bar{N}$ = average numbers of animals alive during the time period (quarter), and PL = proportion of catch that is landed. Similarly, discards per recruit (D/R) are calculated as:

$$D/R_{s,a,q,f} = F_{s,a,q,f} \times \overline{WD}_{s,a,q,f} \times \bar{N}_{s,a,q} \times PD_{s,a,q,f} \qquad (3)$$

where $\overline{WD}$ = mean weight-at-age in discards, and PD = proportion of catch that is discarded. Spawning-stock biomass per recruit is computed only for quarters in which the particular species spawns:

$$SSB/R_{s,a,q} = PM_{s,a} \times \overline{WS}_{s,a,q} \times \bar{N}_{s,a,q} \quad | \\ \text{if } q = \text{quarter of spawning} \qquad (4)$$

where PM = proportion-at-age that is sexually mature, and $\overline{WS}$ = mean weight-at-age in the spawning stock.

Numbers per recruit carried from one quarter to the next are decremented by total Fs for the six fisheries, external fishing mortality rates, and natural mortality rates. Quarterly estimates of the above quantities are summed for all ages to estimate total species and fishery yields, etc.

Subroutine RECRUIT: Recruitment (R) is determined based on the three parameter relation of Shepherd (1982):

$$R = \alpha \times SSB/[1 + (SSB/\kappa)^{\beta}] \qquad (5)$$

where SSB is spawning-stock biomass and α, κ and β are parameters of the model. Total SSB is determined by algebraic manipulation of (5), in combination with SSB/R as computed in (4):

$$SSB = \kappa(\alpha \times SSB/R - 1)^{1/\beta} \qquad (6)$$

Recruitment is then derived from:

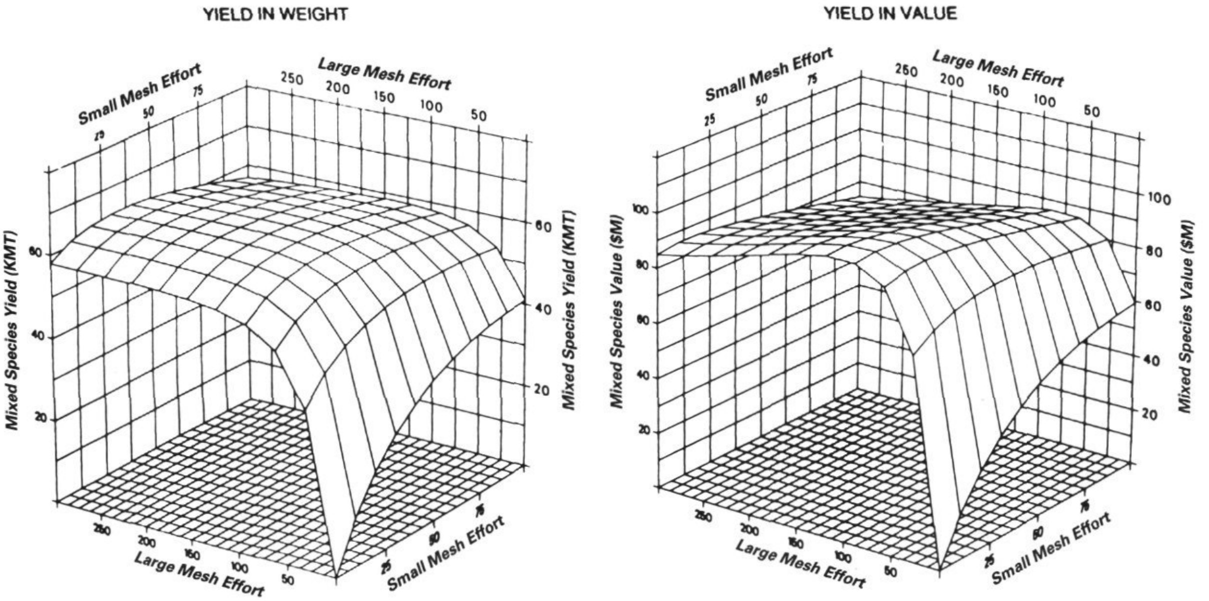

Figure 4. Aggregate mixed-species yield (in thousands of tonnes and millions of USD) of 15 species or groups, from the Gulf of Maine region, based on mixed-species, multi-fishery equilibrium analyses. Yields are simulated based on differing levels of effort in small- and large-mesh fisheries (standardized days fished, in hundreds). Analyses assume 114-mm mesh in large-mesh trawl fisheries, constant recruitment of each species at all effort levels, and constant USD/t (value) relationships.

$$R = SSB/(SSB/R) \tag{7}$$

Total landings and discards are determined by multiplying L/R and D/R by recruitment estimated from (7).

Subroutine SPROD: A quadratic yield/effort relationship is incorporated into subroutine SPROD to allow estimation of landings for species or groups for which age-based data are not available. Yield by species (Y_s) is estimated by an overall quadratic equation:

$$Y_s = \gamma_s \times spf_{s**} - \phi_s \times spf^2_{s**} \tag{8}$$

where γ and ϕ are species-specific parameters and spf_{s**} is total surplus production effort on species (or group) s, expended in all quarters and fisheries. Surplus production effort is defined as:

$$spf_{s,q,f} = PEq,f \times [Q_{s,q,f} \times \text{Total annual effort}] \tag{9}$$

where PE and Q are defined as in Equation (1). Surplus production yield by species and fishery is computed by dividing the aggregate species yield by the weighted proportion of surplus production effort exerted by each fishery:

$$Y_{s,f} = Y_s \times (spf_{s*f}/spf_{s**}) \tag{10}$$

Subroutine PRICE: Total price per tonne (ppt) by species and fishery is determined by a three-parameter model similar in structure to the stock-recruitment relation:

$$ppt_{s,f} = \theta_{s,f} \times L_s/[1 + (L_s/\partial_{s,f})^{\psi}s,f] \tag{11}$$

where L_s is the total landings of species s over all fisheries, and θ, ∂, and ψ are parameters of the relationship. This functional form can be used to simulate constant or variable prices per tonne as a function of total landings by species. Total value of landings (V) by species and fishery is determined by multiplying the price per tonne by the landings in weight in each fishery:

$$V_{s,f} = ppt_{s,f} \times L_{s,f} \tag{12}$$

Because of the highly seasonal nature of fisheries defined in the Gulf of Maine, our simulations were conducted with a quarterly time-step. Rather than estimating all quarterly mean fishery and discard weights and discard and partial recruitment rates at age, we input these data only for the first calendar quarter. The program computes values of these parameters for the second, third, and fourth quarters, based on a linear interpolation algorithm. This procedure obviates considerable data estimation and entry, and probably does not significantly bias overall results.

A second FORTRAN program was written to conduct a systematic evaluation of a number of combinations of effort in small- and large-mesh fisheries (Figs. 4 and 5).

This program (MSMF3D.FOR) allows the user to specify the grid of effort combinations to be simulated, with the output limited to aggregate mixed-species, multi-fishery landings in weight and value. The program computes values of PE by fishery, based on the specified level of total effort in large- vs. small-mesh fisheries, assuming a constant ratio of effort among the fisheries in each category (Table 3).

Fishery analysis

Simulation parameters

A series of model runs was made to evaluate yields, discards, and spawning-stock biomasses as a function of total fishing effort, gear selectivity characteristics, price/landings, and stock-recruitment relationships. These analyses explore the yield surfaces in weight and value in relation to the above variables, but are not intended to be definitive in their conclusions or exhaustive in their evaluation of management alternatives.

We included 14 aged species in the analyses (Table 1), as well as a 15th category of aggregated "other species". The latter category was assessed using the surplus production module (SPROD) of the computer model. Catchability coefficients (Q) by species, quarter and fishery were estimated based on the 1987 distribution of species landings among the fisheries (Table 4), as well as 1987 fishing mortality rates, and proportions of landings generated external to the six-fishery system (proportional to the fishing mortality rate external to the system). The following total and external Fs were assumed for 1987:

Species	Total F	F (External)
Silver hake	0.46	0.11
Cod	1.00	0.08
Haddock	0.80	0.09
Pollock	0.54	0.43
Redfish	0.08	0.03
Witch	0.80	0.20
Red hake	0.30	0.07
White hake	0.50	0.16
Plaice	0.80	0.24
Winter flounder	0.80	0.02
Goosefish	0.60	0.01
Yellowtail flounder	1.00	0.32
Northern shrimp	0.40	0.04
Spiny dogfish	0.004	0.002

In some cases these estimates are from analytical assessments or research vessel catch-at-age data. Where F estimates were not available we assumed total Fs based on information for similar species. Most of the large-mesh target species are considered to be substantially growth-overfished, and some exhibit apparent recruitment overfishing. Small-mesh targets are generally fished at moderate rates (Anon., 1987b). Catchability coefficients were estimated by dividing partial Fs attributable to each fishery by the total standardized effort in that fishery (Table 3).

Some of the population dynamics data for the various stocks are given in Tables 1 and 2. The complete listing of all such biological and fishery data is too voluminous to be presented here. Initial simulations assumed the following effective mesh sizes in each fishery:

Large-mesh trawl/LMA:	114 mm (4.5 inches)
Large-mesh trawl/SMA:	114 mm (4.5 inches)
Gillnet:	140 mm (5.5 inches)
Shrimp trawl:	44 mm (1.75 inches)
Silver hake trawl:	57 mm (2.25 inches)
Other small-mesh trawl:	57 mm (2.25 inches)

Partial recruitment factors (PR) by species, age, and fishery were estimated considering the mesh selection factors, mesh sizes, and distributions of lengths-at-age by species. Discard rates (PD) by species, age, and fishery were based on the limited data available (e.g. Howell and Langan, 1987), and the selection characteristics of the gear in relation to regulated minimum landing sizes (Table 2).

Simulations assuming constant unit values by species and fishery used 1987 value per tonne data (Tables 5–7, Fig. 4). Constant recruitment simulations (Tables 5–7, Fig. 4) were based on iterating the yield simulations with various recruitment values for each of the species to achieve the observed average species composition of landings in 1982–1988. Variable price per tonne relationships were simulated for 8 of the 14 species (Fig. 5). Constant prices were assumed for pollock, red hake, white hake, goosefish, shrimp, and dogfish in all model runs. Parameters for the variable price per tonne relationships (Equation (11)) were estimated from data given in Figure 3 and similar information for the remaining species. Variable recruitment simulations (Fig. 5) assumed moderate reductions in recruitment with declining SSB (Equation (5)). Because of the relatively high fishing mortality rates for most species, these stock-recruitment relationships have no super-compensation in recruitment at high SSB/R levels.

Preliminary results

Because of the quantity and complexity of model results generated, we review only selected output from the runs conducted. Aggregate mixed-species yields by fishery (in weight and value) are presented in Table 5. Maximum yield in weight increased only modestly (+11%) when the larger mesh size (140 mm) was assumed for the large-mesh trawl fisheries. Maximum value of landings (assuming constant price/landings relationships) increased 13% with the larger assumed mesh. Both small- and large-mesh fisheries exhibited rather flat-topped yield curves as a function of total fishing effort.

Table 5. Aggregate mixed-species yield (weight in tonnes, ex-vessel value in USD) for six demersal fisheries operating in the Gulf of Maine region, in relation to total fishing effort and the assumed effective mesh size used in large-mesh trawl fisheries.

		Fishing effort (thousands of days fished)									
Fishery	Mesh size	1	4	7	10	13	16	19	21	24	28
						Yield in tonnes					
LM/LMA	114	3 615	9 251	11 434	12 317	12 656	12 753	12 740	12 676	12 586	12 482
	140	3 525	9 285	11 736	12 855	13 368	13 583	13 644	13 620	13 548	13 446
LM/SMA	114	7 467	18 300	21 712	22 475	22 214	21 564	20 785	19 988	19 213	18 474
	140	7 355	18 676	22 823	24 200	24 385	24 030	23 433	22 733	21 995	21 250
Gillnet	114	3 851	9 272	11 282	12 222	12 778	13 171	13 479	13 733	13 946	14 123
	140	3 917	9 872	12 394	13 765	14 658	15 313	15 827	16 245	16 590	16 875
Shrimp	114	901	2 677	3 775	4 546	5 124	5 569	5 914	6 183	6 388	6 541
	140	910	2 767	3 956	4 810	5 457	5 960	6 355	6 665	6 907	7 091
S. hake	114	914	2 791	3 968	4 759	5 305	5 685	5 947	6 122	6 232	6 292
	140	920	2 837	4 058	4 885	5 459	5 861	6 140	6 328	6 448	6 515
Other Sm.	114	583	1 847	2 732	3 402	3 919	4 312	4 598	4 787	4 886	4 901
	140	587	1 887	2 811	3 515	4 059	4 474	4 777	4 980	5 091	5 117
Total	114	17 333	44 158	54 903	59 721	61 996	63 053	63 463	63 488	63 252	62 814
	140	17 215	45 324	57 778	64 030	67 386	69 221	70 176	70 571	70 579	70 294
						Yield in value (0000's of USD)					
LM/LMA	114	778	1 964	2 368	2 474	2 459	2 397	2 318	2 236	2 157	2 083
	140	768	2 012	2 503	2 683	2 724	2 698	2 642	2 573	2 499	2 424
LM/SMA	114	1 526	3 750	4 405	4 483	4 339	4 115	3 871	3 634	3 411	3 208
	140	1 513	3 873	4 716	4 951	4 922	4 774	4 577	4 364	4 149	3 942
Gillnet	114	576	1 321	1 515	1 550	1 535	1 505	1 473	1 442	1 414	1 389
	140	587	1 417	1 699	1 805	1 844	1 856	1 855	1 848	1 838	1 826
Shrimp	114	189	567	801	965	1 087	1 181	1 254	1 311	1 354	1 387
	140	191	586	841	1 024	1 162	1 269	1 352	1 418	1 470	1 509
S. hake	114	78	214	284	323	347	362	370	375	376	376
	140	79	222	299	344	373	391	402	408	411	412
Other Sm.	114	51	133	169	187	197	202	204	204	202	199
	140	52	142	186	212	228	238	244	247	248	247
Total	114	3 198	7 950	9 541	9 982	9 964	9 762	9 491	9 202	8 916	8 642
	140	3 189	8 252	10 244	11 019	11 252	11 226	11 073	10 859	10 616	10 360

Table 6. Percentage change in yield in weight (W) and value (V), contingent on a 10% reduction in fishing effort in each Gulf of Maine fishery, individually. Analyses assume constant recruitment, constant value, and a 114 mm effective mesh size for large-mesh fisheries.

		10% reduction in effort by fishery					
Fishery		LM/LMA	LM/SMA	Gillnet	Shrimp	S. Hake	OSM
LM/LMA	W	−7.29	4.67	1.60	1.02	0.18	0.24
	V	−6.68	5.94	1.46	1.50	0.21	0.23
LM/SMA	W	2.85	−4.40	1.63	1.67	0.34	0.52
	V	3.27	−3.29	1.40	2.11	0.33	0.46
Gillnet	W	1.95	3.36	−7.75	0.37	0.17	0.68
	V	2.79	4.80	−7.26	0.59	0.19	0.37
Shrimp	W	0.56	1.42	0.35	−6.60	0.76	0.26
	V	0.56	1.50	0.29	−6.13	0.37	0.18
S. hake	W	0.38	0.76	0.28	0.86	−5.00	0.61
	V	0.87	1.90	0.48	1.07	−5.58	0.45
OSM	W	0.28	1.61	0.72	0.78	0.49	−7.23
	V	0.81	4.66	0.67	1.70	0.70	−8.57
Total	W	−0.01	0.58	−0.70	0.33	−0.19	−0.09
	V	0.25	1.27	−0.14	0.54	0.06	0.15

Table 7. Percentage change in yield (weight, W) and percentage maximum spawning-stock biomass per recruit (%SSB), by species, contingent on a 10% reduction in fishing effort in each Gulf of Maine fishery, individually. Analyses assume constant recruitment, constant value, and a 114 mm effective mesh size for large-mesh fisheries.

		10% reduction in effort by fishery					
Species		LM/LMA	LM/SMA	Gillnet	Shrimp	S. Hake	OSM
Silver hake	W	0.00	0.00	0.00	0.05	−2.15	−0.18
	%SSB	0.00	0.00	0.00	1.43	8.93	0.71
Cod	W	1.39	3.06	1.37	0.68	0.21	0.12
	%SSB	2.08	6.25	4.17	0.00	0.00	0.00
Haddock	W	1.84	1.39	0.11	0.08	0.08	0.04
	%SSB	5.33	3.55	1.18	0.00	0.00	0.00
Pollock	W	−1.69	−1.67	−3.75	−0.04	−0.02	0.00
	%SSB	0.68	0.68	1.36	0.00	0.00	0.00
Redfish	W	−3.83	−2.53	−0.15	−0.67	−0.11	0.00
	%SSB	1.96	1.31	0.00	0.65	0.00	0.00
Witch	W	1.86	3.70	0.03	0.73	0.14	0.14
	%SSB	4.90	9.80	0.98	0.98	0.98	0.98
Red hake	W	0.00	−0.10	0.00	−1.12	−2.97	−0.92
	%SSB	0.00	0.21	0.00	1.87	3.53	1.25
White hake	W	−0.18	−0.18	−0.25	0.00	0.02	0.00
	%SSB	3.91	3.91	1.78	0.36	0.36	0.00
Plaice	W	0.43	1.09	0.00	5.41	0.19	0.13
	%SSB	3.85	10.26	1.28	7.69	1.28	1.28
Winter flounder	W	0.06	1.98	0.06	1.15	0.13	0.82
	%SSB	0.00	8.99	1.12	2.25	0.00	2.25
Goosefish	W	2.71	5.93	0.60	0.46	0.46	0.28
	%SSB	5.56	11.11	0.00	0.00	0.00	0.00
Yellowtail	W	0.00	0.00	0.00	0.00	0.00	0.37
	%SSB	0.00	8.40	0.42	0.42	0.42	1.26
Shrimp	W	0.00	0.03	0.00	−5.23	0.00	−0.03
	%SSB	0.00	0.00	0.00	8.07	0.00	0.00
Spiny dogfish	W	0.00	−0.09	−2.38	0.00	−0.17	−2.18
	%SSB	0.49	0.24	2.43	0.00	0.49	5.58
Others	W	−0.25	−0.56	−0.34	−0.02	−0.25	−0.15
Total	W	−0.01	0.58	−0.70	0.33	−0.19	−0.09

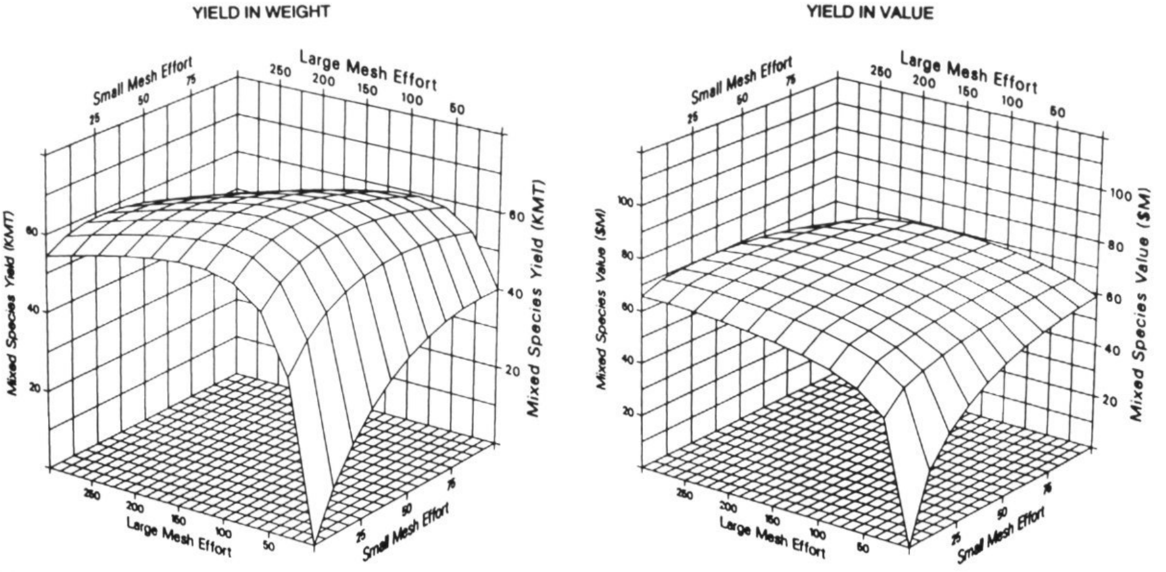

Figure 5. Aggregate mixed-species yield (in thousands of tonnes and millions of USD) of 15 species or groups, from the Gulf of Maine region, based on mixed-species, multi-fishery equilibrium analyses. Yields are simulated based on differing levels of effort in small- and large-mesh fisheries (standardized days fished, in hundreds). Analyses assume 114-mm mesh in large-mesh trawl fisheries, variable recruitment and variable USD/t (value) relationships.

In the case of the small-mesh fisheries, this reflects the generally high natural mortality rates of the main target species (hakes, shrimp, etc.) as well as the current moderate fishing mortality rates for most of the small-mesh target stocks. Large-mesh trawl fisheries did exhibit yield maxima at intermediate effort levels, but the reduction in yield at high effort values was generally small. Yield in weight in the gillnet fishery did not decline over the range of fishing effort simulated (Tables 5 and 6). This was primarily due to the fact that two of the three main species landed by gillnet fisheries (pollock and spiny dogfish) were not significantly growth overfished (Table 7).

Yield of the large-mesh trawl fisheries in value, as a function of effort, was much more peaked than the corresponding yield function in weight (Table 5). This was due to the relative degree of growth overfishing at high effort levels on valuable flounders, haddock, and cod (Fig. 3). The value function for the gillnet fishery did exhibit a maximum at intermediate effort levels, primarily due to the influence of cod (Table 4).

Model results also evaluated the relative influence of changing the distribution and magnitude of fishing effort among the small- vs. large-mesh fisheries (Figs. 4 and 5). Effort in the small-mesh fisheries was varied from 0 to 10 000 standardized days fished. Effort in large-mesh fisheries was simulated at 0 to 30 000 days. These simulations assume a constant ratio of effort distribution among the three small-mesh and three large-mesh fisheries, at all effort combinations. The maximum effort levels simulated for the two categories of fisheries are roughly double the maximum observed in recent years (Table 3). The mixed-species yield (weight) surface, assuming 114 mm mesh in large-mesh trawl fisheries, was very flat-topped over a wide range of effort combinations in large- and small-mesh fisheries (Fig. 4). When the 140 mm mesh was assumed for the large-mesh trawl fisheries the level of the surface increased significantly, but again was rather insensitive to a wide-range of effort combinations. Value surfaces were more peaked, reflecting the importance of high-valued and potentially long-lived species (especially the flounders). Significant increases in the level of the value surfaces occurred when the larger mesh size was assumed.

The rather flat-topped yield surfaces, particularly under conditions of high effort in small-mesh fisheries, were somewhat surprising, considering the low natural mortality rates and high relative values of some large-mesh target species that are discarded in quantity in small-mesh fisheries. We had anticipated that the combination of high effort in the small-mesh fisheries and particularly the use of 140-mm mesh in the large-mesh fisheries would produce steeply sloped yield surfaces emphasizing the negative effects to cumulative yields of high-effort levels in small-mesh fisheries. The lack of a definitive point of diminishing returns to increased effort in large- and small-mesh fisheries was due to two factors: (1) some of the important large-mesh target species (e.g. pollock, white hake, redfish) are growth-underfished, thus declines in their yields counteract increases in other large-mesh targets (including cod, haddock, and flounders) when effort is reduced, and (2) even when full compliance with the 140-mm mesh is assumed for all large-mesh fisheries, the cumulative discard rates of some flounders and gadoids in these fisheries remain high. In some cases over 50% of the large-mesh catches will be discarded as not meeting the minimum landed sizes (Table 2). Even at low levels of effort in small-mesh fisheries, the assumed discard rates on the large-mesh target species are functionally equivalent to higher natural mortality rates, resulting in a large number of fish deaths that accumulate no landings. Thus, the L/R surface appears asymptotic to increasing total effort.

Simulations assuming variable recruitment as a function of SSB, and variable price/landings relationships (Fig. 5) exhibited some significant differences with the previous results. When the 114-mm mesh was simulated, yield in weight was maximized at between 3000 and 4000 days fished in small-mesh fisheries, and 12 000–15 000 days fished in large-mesh fisheries. The use of a 140-mm mesh under these conditions significantly increases yield in weight as compared to the smaller mesh. Maximum yield in weight increases from 67.6 to 76.4 thousand tonnes (+13%) when the larger mesh is simulated. However, because of the elasticity of ex-vessel prices, maximum value increases only 5%, from USD71.8 million for the 114-mm mesh to USD75.5 million for the 140-mm mesh. The mixed-species value surfaces were, for both mesh sizes, much more flat-topped than corresponding yield in weight surfaces. The elasticity of ex-vessel prices thus de-emphasizes declines in yields due to both growth and recruitment overfishing at relatively high effort levels.

The relative impact on fishery and species yields of modest reductions in effort in each fishery individually is evaluated in Tables 6 and 7. These analyses essentially estimate the matrix of partial derivatives (Jacobian matrix) of yields, contingent on effort change in the various fisheries (Anon., 1989b). In all cases, effort reductions by fishery result in declining yields to that fishery, but have variable feed-back with respect to global yields (Table 6). Effort reductions in the large-mesh trawl fishery operating in the small-mesh area, and the shrimp fishery elicit higher overall landings and ex-vessel value. For the other four fisheries, however, overall changes in yields are negative or negligible. The balances of species gains and losses contributing to overall fishery yields are evaluated in Table 7. Effort reductions in all fisheries result in gains in yield for growth-overfished stocks including cod, haddock, flounders, and goosefish. These increases are countered by reduced yields of growth-underfished stocks including pollock, silver hake, red hake, white hake, shrimp, and spiny dogfish. Because of the rather substantial differences in yield response to effort change among the species, aggregate species yields to the various fisheries is obviously sensitive to the average recruitment values assumed. Our simulations were tuned to average recruitment levels for the recent (1982–1988) period, but a longer-term perspective would result in a different emphasis in importance of the various species comprising the fisheries (Murawski *et al.*, 1983).

The effects of modest effort reductions on percentage maximum SSB/R for the various species is summarized in Table 7. These results provide an evaluation of the relative leverage on the percentage maximum SSB/R reference points of 10% reductions in effort for the six Gulf of Maine fisheries. In the case of American plaice, the relative impacts of effort reductions in the shrimp and the large-mesh trawl fishery in the small-mesh area are about equal. For roundfish (cod, haddock, pollock) there is little benefit to percentage maximum SSB/R for these species of reducing small-mesh effort. Although these analyses are based on preliminary discarding data, they indicate the importance of such analyses in developing management measures to achieve reference points such as percentage maximum SSB/R.

Discussion

These analyses are intended to define the system of interacting demersal fisheries in the Gulf of Maine region and to present an integrated approach for evaluating global effects of various fishery management options. Because of the preliminary nature of critical input data, conclusions to date must be regarded with caution and are subject to change with the inclusion of refined data. Nevertheless, several important conclusions regarding the system of interacting fisheries of the Gulf of Maine emerge from the results that are likely to be robust to the preliminary nature of discard and in some cases fishing mortality rate estimates. Significant discards of important large-mesh target species occur not only in small-mesh fisheries, but in nominal large-mesh fisheries as well. Even if full compliance with the 140-mm mesh was assumed, there will likely be significant discards of flounders and some gadoids from the large-mesh fisheries. This is due to the incompatibility of current minimum landing sizes with the lengths at selection by the gear for some species (Table 2). Thus, even if small-mesh fishing is significantly curtailed, the benefits to aggregate yields of the long-lived species are marginal. This occurs essentially because animals that are not discarded in small-mesh fisheries are then discarded in quantity by the large-mesh fisheries. In this regard it would be enlightening to simulate the effects of alternative mesh and minimum landings sizes that may be more compatible. For example, what would be the effects of a 152-mm (6 inch) mesh size for large-mesh trawl fisheries, combined with setting minimum landings sizes for the species to the L_{25} values for that mesh? Such a strategy would likely produce a more highly peaked yield surface as compared to those presented.

The assumption of highly elastic prices in relation to the volume of landings resulted in significantly more stable value surfaces as compared with yield in weight. This behavior occurred in model runs wherein both growth and recruitment overfishing were simulated. Such mechanisms may explain why effort persists in heavily exploited fishery systems in spite of significant declines in the resource populations and landings. It is obvious that considerably more study of this phenomenon is justified, particularly in the context of mixed-species, multi-fishery systems.

Models developed herein can be used to evaluate a much wider range of options than the few considered. For example, in Figures 4 and 5 we varied fishing effort in large- vs. small-mesh fisheries, but assumed that the relative distributions of effort remained constant among the three fisheries within the large- and small-mesh categories. Modest effort changes in each fishery were evaluated in Tables 6 and 7. The model could be used to evaluate the system-wide impacts of specific management proposals for individual fisheries or combinations. Such proposals might include, for example, the use of gear that reduces finfish discards in the shrimp fishery. An interesting simulation would be to evaluate the combined use of shrimp separator trawls to reduce finfish discards in that fishery, and simultaneous changes in the minimum mesh and landings sizes in the large-mesh fisheries. What would be the effects on yields and values derived from these individual fisheries, and the aggregate from the system? The relative effects of various strategies and their combinations on biological reference points such as percentage maximum SSB/R are particularly important, given the current depressed condition of Gulf of Maine groundfish stocks.

As the nature of fishery management questions becomes more complex, the challenge will be to develop increasingly sophisticated analytical tools and requisite data bases to address the needs of managers. Such is the current situation with technical interactions research. In particular, the development of models to explicitly account for spatial effects in both the fish populations and the fleets will be required to answer questions such as the mixed-species impacts of fishery closure areas (Anon., 1989a). Equally important is the development and validation of dynamic models of interacting fisheries, such as those proposed by Laurec *et al.* (1991). In the case of the Gulf of Maine fisheries, there have been complex interactions among the mixed-species demersal fisheries, and substantial effort has switched among them (Table 3). Understanding the factors controlling dynamic effort allocation among alternative fishing activities, particularly in open-access fisheries such as in the Gulf of Maine, will require more elaborate models of the species, economic, and behavioral aspects contributing to fishermen's decisions of where and when to fish. In this regard, technological interactions' research seems to be converging with models of biological interactions in trying to understand complex interactions involving preference decisions.

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Technological interactions in the US West Coast groundfish trawl fishery and their implications for management

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Pikitch, E. K. 1991. Technological interactions in the US West Coast groundfish trawl fishery and their implications for management. – ICES mar. Sci. Symp., 193: 253–263.

The US West Coast groundfish fishery off California, Oregon, and Washington is a mixed-species fishery, with landings obtained primarily by trawl gear. To date, both the objectives and strategies of management have been largely single-species in nature. A voluntary domestic observer program was conducted from 1985 to 1987 to describe species assemblages caught by the major fishing strategies in the fishery and to evaluate the effectiveness of the current management regime. Results demonstrated that significant quantities of marketable fish were discarded during the three-year period as a direct consequence of regulations in force. While annual landings were generally close to annual harvest goals, total catch (landings plus discards) exceeded these goals for several key species – in some cases by as much as 28%. Landings data have been heavily relied upon in stock-assessment work. Thus, the discards represent a loss of information, as well as a potentially significant economic loss. Current research, which includes both field and simulation modelling approaches, is focusing on an exploration of alternative methods for managing the multispecies trawl fishery. A mixed-species fishery model which incorporates both yield-per-recruit and spawner-recruit analyses has been developed to facilitate assessment of the consequences of alternative management objectives and strategies in a manner which accounts for technological interactions within the fishery. Simulation results indicate that a change in gear selectivity patterns may enhance long-term yields, reduce discards, and lead to less sensitivity of yield to effort. The major objectives of the field research component are to estimate the short-term consequences of changes in regulated codend mesh size and to provide data needed to improve estimates of gear selectivity coefficients. Analyses of data collected during the 1988 field season show that revenues per trawling hour generally decrease as diamond mesh size increases. The largest difference in revenues observed was that between the 76-mm and 114-mm mesh codends for rockfish, with gross revenues per trawling hour for the 114-mm mesh averaging approximately one-third of the revenues generated by the 76-mm codend.

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Introduction

The US West Coast groundfish fishery off California, Oregon and Washington is a mixed-species fishery, with landings obtained primarily by trawl gear. The fishery expanded greatly during the late 1970s following enactment of the Magnuson Fishery Conservation and Management Act. To date, the number of vessels that can participate in the fishery has not been restricted. In recognition of the increasing pressure on the multispecies resources a stringent management regime was put into effect during the early 1980s which included the institution of annual and trip quotas for individual species. There were two major objectives of this new regime. The purpose of the annual quotas was to control fishing mortality rates and thus prevent overharvest of individual species, whereas trip quotas were employed to meet the objective of maintaining a year-round fishery. The number of species managed in this way has steadily increased, and in many cases the magnitudes of the quotas have decreased over time. This is in contrast to the New England groundfish fishery where mesh size restrictions have replaced quotas as the primary management tools (New England Fishery Management Council, 1985; Hanna, 1988). Thus, while the original intent of the West Coast groundfish fishery management plan (PFMC, 1982) was to manage the multispecies resources as a group, actual practices in recent years have been largely single species in nature (Huppert, 1985; Pikitch, 1987a).

A number of concerns have been raised about the complex regime developed to manage West Coast groundfish. Trip quotas were perceived as regulating inefficiency in a fleet in which many vessels were capable of harvesting much greater quantities of fish than allowed under new limits. The institution of trip quotas was also perceived by some as inequitable, as larger capacity vessels were impacted more than smaller vessels. There were also concerns that the single-species nature of the trip quotas would limit the flexibility of vessel operators and force changes in fishing patterns.

Because quota regulations applied only to landings (i.e. not catch), it was feared that trip limits could promote at-sea discards. In the short term, discards of marketable fish were viewed as wasteful of resources, and a potentially significant economic loss. In addition, if discards were large, fishing mortality rates could greatly exceed target levels and ultimately diminish resource productivity. Due to the lack of an observer program, there were no effective means of monitoring discard levels. Thus, the accuracy of stock assessments, which had presumed that landing statistics corresponded to the total fishery removals, could also be compromised. These concerns have spawned an interest in field and analytical research designed to obtain a better understanding of the nature of the fishery, the impact of existing management measures, and the bioeconomic consequences of alternative management tools.

In this paper I first briefly review the results of studies in the mid-1980s, their implications for management of the West Coast groundfish fishery, and their impacts on further research directions. I then present preliminary results of an ongoing study containing both field and modeling components that is primarily aimed at assessing the potential for gear restrictions to improve management of the fishery. Finally, I describe future work planned, and some general challenges faced by those involved in research and management of mixed-species fisheries.

The 1985–1987 observer study

The first major field study to examine the impacts of current US West Coast groundfish management practices was a voluntary at-sea sampling observer program conducted aboard commercial fishing vessels operating primarily out of Oregon ports (Pikitch *et al.*, 1985; Pikitch *et al.*, 1987). Species regulated by trip quotas comprised approximately 50% of the total catch sampled (Pikitch, 1987a; Pikitch *et al.*, 1988). Whereas market forces (minimum acceptable size limits and species preferences) were the major factor causing discards of non-quota species, Pikitch *et al.* (1988) found that the major reason given by fishermen for discarding species regulated by trip quotas was the trip quota restrictions themselves (Fig. 1). Some discards were observed for each of the species regulated by trip limits, and the rate of discard increased as the trip regulations became more restrictive. Because the majority of the fish discarded were of marketable quality, and because few fish discarded in temperate water trawl fisheries can be expected to survive (Saila, 1983), these discards represented a potentially significant economic loss. For example, the ex-vessel value of widow rockfish (*Sebastes entomelas*) discarded during 1985–1987 was estimated to be approximately one million dollars per year, while that of sablefish (*Anoplopoma fimbria*) averaged USD 800 000 per year (Pikitch *et al.*, 1988). Given the observed pattern of increased discard rates resulting from declining trip quotas, such losses would be expected to increase were trip quotas to continue to decrease over time.

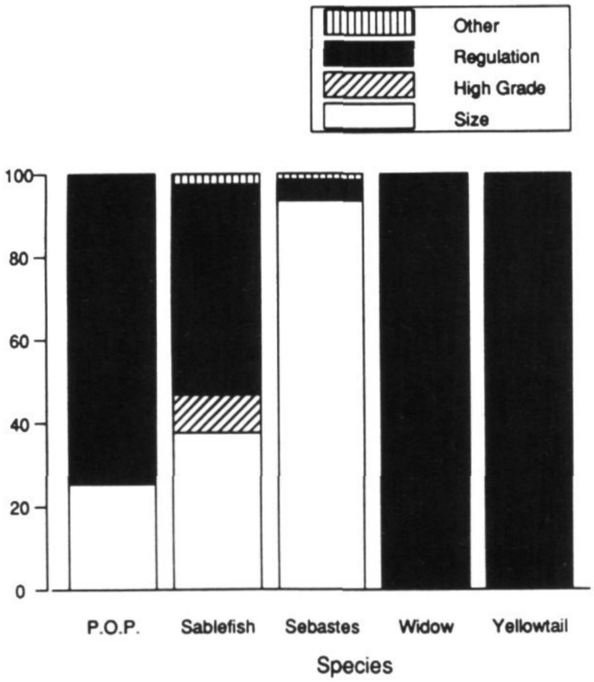

Figure 1. Percentage of the discarded catch (by weight) of species regulated by trip quotas attributed to various causes by fishermen (Reasons: regulation = trip limit for species previously reached; high grade = fish have lesser value per unit weight than other individuals, but are marketable; size = fish are below the minimum acceptable market size; other = other reasons for discard. Species: P.O.P. = Pacific ocean perch (*Sebastes alutus*), Sablefish = *Anoplopoma fimbria*, Sebastes = Sebastes complex; Widow = widow rockfish (*Sebastes entomelas*), Yellowtail = yellowtail rockfish (*Sebastes flavidus*). From Pikitch *et al.* (1988).

While annual landings were generally close to harvest goals during the course of the study, total catches (landings plus discards) were estimated to exceed annual quotas for several key species (Pikitch *et al.*, 1988). For sablefish, the estimated ratio of total catch to landed catch ranged from 1.11 to 1.20, and the estimated ratio of total catch to annual quota was 1.24, 1.07, and 1.28 in 1985, 1986, and 1987, respectively (Fig. 2). Because

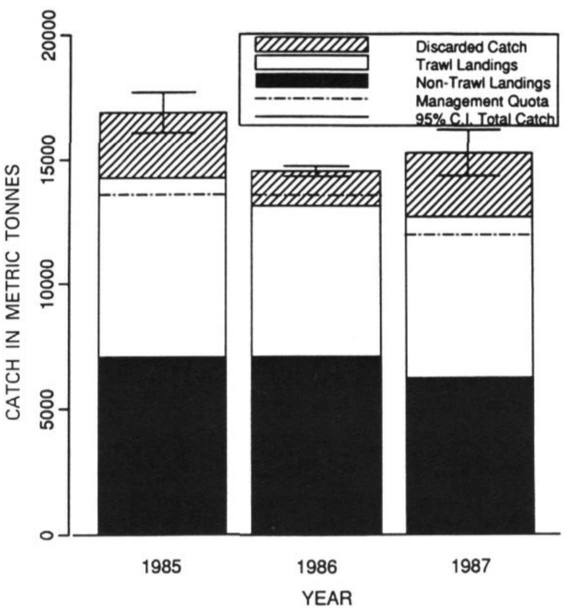

Figure 2. Estimated coastwide catch (non-trawl catch = black, trawl landings = white, trawl discard catch = hatched) of sablefish and annual management quota (OY, dashed line), for each of the years 1985 through 1987. Landings data are from the PacFIN database; discarded catch was estimated for the trawl fishery based on data from the observer study and the PacFIN database. No information on non-trawl discard was available, thus the above figures do not reflect any discard that may occur in this portion of the fishery. From Pikitch *et al.* (1988).

landings data are heavily relied upon in stock assessment work, the discards also represent a significant loss of information, hindering the ability to monitor the effectiveness of such regulations in the future.

For these reasons one of the major conclusions of the observer study (Pikitch *et al.*, 1988) was that it would be worthwhile to consider alternative forms of management that are easier to monitor and evaluate, improve utilization of the resource, and better account for the multispecies nature of the fishery. Some of the alternatives suggested included modification of the trip quota system, limitations on fishing effort, modification of the objectives of management, and greater reliance on gear regulations as a management tool. Much of the ensuing research has focused on evaluating the last alternative, and in particular on examining the expected effects of changes in trawl codend mesh size and shape on the bioeconomic condition of the fishery.

The focus on gear research was largely motivated by industry preferences. Traditionally, gear regulations have been employed to reduce discards of undersized fish and to enhance yield-per-recruit. There was clearly interest in determining whether a change in regulated codend mesh size could enhance yields of both quota and non-quota components of the West Coast groundfish trawl fishery. An increase in yields could subsequently result in reduction of the severity of other management measures such as trip and annual quotas. (However, such benefits could be short-lived if fleet size were to increase in response to such changes.) There was also interest in exploring the potential of gear regulations to reduce catch rates, and thus serve as an alternative or complement to trip quota restrictions, regardless of whether or not yields would increase. This perhaps less traditional use of gear restrictions would not alleviate concerns about regulated inefficiency that accompanied the institution of trip quotas. However, many in the industry preferred gear restrictions over trip quotas, as the former was perceived as being a more equitable form of management that would also permit greater operating flexibility. The widespread nature of the preference for gear restrictions is evidenced by the statement "Gear restrictions to minimize the necessity for other management measures will be used whenever practicable", which is listed as one of the objectives of the Pacific Coast Fishery Management Plan (PFMC, 1989).

The Pikitch (1987b) mixed-species yield-per-recruit model

The first effort to address the effects of changing mesh size restrictions on the fishery was a modeling exercise which analyzed optimal mesh size for a segment of the fishery under various management policies. Given the disparate life history characteristics of species in the West Coast groundfish fishery, it was expected that the optimal mesh size would differ among species. The fact that it is not possible to maximize the yield of each species when biological or technological interrelationships exist is a general constraint on management objectives for multispecies fisheries (Paulik *et al.*, 1967; Anderson, 1975; Mitchell, 1982; Brander and Bennett, 1986; Pikitch, 1988). However, maximum yield for a multispecies complex as a whole can be examined given an appropriate framework.

Beverton and Holt (1957, p. 422) provided an early example of how single-species yield models could be combined via the fishing mortality rate term to derive aggregate yield estimates for mixed-species fisheries with technological interactions. During the 1980s several mixed-species models were developed which extended Beverton and Holt's approach (e.g. Murawski, 1984; Sainsbury, 1984; Pikitch, 1987b; Shepherd, 1988; Silvestre and Soriano, 1988) Murawski's (1984) model examined multiple-fleet in addition to mixed-species interactions in the Georges Bank otter trawl fishery. Sainsbury (1984) applied a mixed-species yield model to a tropical multispecies trawl fishery and provides an excellent discussion of data requirements and parameter estimation methods for such models. Silvestre and Soriano (1988) compared results of simulations of a mixed-species model assuming knife-edged selection with results obtained when a selectivity ogive was used. Shepherd's (1988) model contains several extensions of the linked-single-species approach, including the addition of stock-recruitment relationships and predator–prey interactions.

The Pikitch (1987b) mixed-species yield-per-recruit model examined a segment of the fishery consisting of three flatfish species of major commercial importance caught in an area off the Oregon coast. The overall model consisted of a series of linked single-species yield-per-recruit models. The single-species models assumed constant recruitment over time, but accounted for differences among sexes in growth, mortality, and susceptibility to capture. The model also accounted for discards of fish at-sea and onshore due to processor restrictions on landing fish below market size.

The single-species models were linked via the fishing mortality rate term, that is: $F_i = q_i \times f$, where F_i represents the instantaneous fishing mortality rate for fully vulnerable fish of species i, f is total fishing effort (in trawling hours) for all species combined, and q_i represents the catchability coefficient for fully vulnerable fish of species i (derived by dividing an estimate of F_i by f for the years 1971–1974. Note that this approach assumes that q_i values are constant over time). Fishing mortality rates for incompletely recruited age classes were estimated as the product of F_i and PR_{ti} where PR_{ti} = fraction of age t fish, species i, retained by the mesh sized being considered. Estimates of PR_{ti} were computed from data presented in Best (1961).

A number of simulations were performed to determine the sensitivity of equilibrium fishery yields and optimal mesh sizes for alternative management objectives. The management policies examined were maximization of aggregate yield (in weight), maximization of gross revenues, maximization of net revenues, and a "mesh size only" policy for which it was assumed that effort would stabilize at a level where no net revenues are generated by the fishery (see e.g. Gordon, 1953, 1954). For the mesh size only policy, mesh sizes which produced maximum yields and maximum gross revenues at the level of effort corresponding to zero net revenues were computed.

Results of the modeling exercise indicated that optimal mesh size was sensitive to the management policy selected, but robust to fluctuations in recruitment and operating costs. To illustrate the latter point, Figure 3 presents the relationship between optimal mesh size and operating costs for a policy that seeks to maximize net revenues generated by the fishery. As costs increase above levels estimated for the mid-1980s optimal mesh size remains stable at 114 mm. At very low cost levels, there would be a slight increase in equilibrium net revenues were mesh size increased to 127 mm. In contrast, the estimated optimal mesh size under a mixed-species MSY policy was higher than the present regulatory minimum mesh size of 4.5″ (114 mm) for flatfish trawls (Pikitch, 1987b).

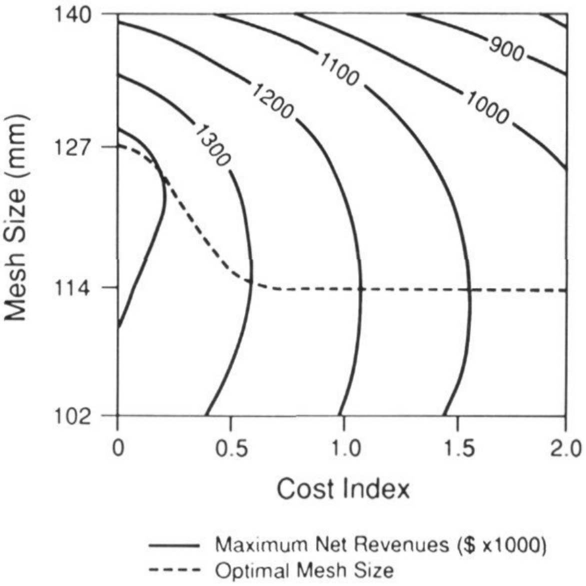

Figure 3. Maximum net revenues (in thousand dollars; solid curves) as a function of operating costs and effort. For the operating cost index, a value of 1.0 represents the current estimate of operating costs (USD 36.42 per trawling hour), a value of 2.0 represents twice the current estimate, and so on. The optimal mesh curve represents the mesh size that yields the greatest maximum net revenues for each level of cost and is indicated by the broken curve. Simulation results were obtained using the mixed-species yield-per-recruit model developed by Pikitch (1987b).

The West Coast groundfish mesh size study

The general sense of unease about the quota management system, coupled with the results of early studies, stimulated interest in further research on codend mesh size effects. Results of the Pikitch (1987b) model indicated that an increase in regulated minimum mesh size could increase MSY (a primary management objective) for the three species flatfish complex. The model provided an example of an approach that could be used to examine potential yields for other segments of the mixed-species trawl fishery. However, the data available to parameterize an expanded modeling effort were limited. Thus, estimation of gear selectivity coefficients for other species would require either field research (the preferred, but costly approach), or extrapolation of the results of other studies. A task force was established to discuss research needs and priorities. The task force concluded that further modeling work which would make use of existing information should be the next step in such efforts. If this work indicated that mesh size changes were likely to produce substantial benefits for the fishery-at-large, experimental field trials would then be conducted under commercial production conditions. A four-phase research plan was developed as follows.

Phase I: Expand the Pikitch (1987b) model to include stock-recruitment relationships and a greater number of species, and, using existing data, apply the model to estimate the magnitude of benefits that could be realized through gear regulations.

Phase II: Design and conduct a pilot field study to obtain a preliminary assessment of the effects of various trawl codend mesh sizes and configurations on catch amount, composition, value and sorting time, and to provide data needed to plan Phase III.

Phase III: Conduct a comprehensive field study under commercial fishing conditions to obtain a more complete assessment of the effects of gear changes on fishery parameters. Concurrently, refine the model to permit examination of short-term and dynamic effects, and to incorporate variability and uncertainty of model parameters.

Phase IV: Combine and apply the results of Phases I–III to predict the short- and long-term consequences of changes in codend regulations on the bioeconomic condition of the fishery. Present results to the PFMC.

The research plan was thus designed to obtain estimates of both the long- and short-term effects of changes in regulated codend mesh size and shape. Estimates of long-term effects are expected to be less certain than short-term predictions, because the former are dependent on the accuracy of a number of assumptions about population dynamics and the response of the fishing fleet to a change in regulations. In contrast, many of the short-term consequences of a change in mesh size can be measured directly in the field. It was reasoned that information on both types of effects is needed to formulate changes in management policy, because if short-term losses are severe, the fishing industry could face financial disaster, and not survive to experience the increased sustainable yields forecast by scientists.

Results of Phase I

The mixed-species yield-per-recruit model developed during Phase I (Vaga and Pikitch, 1988) was an expanded version of the Pikitch (1987b) model. In contrast to the three species of flatfish considered by Pikitch, the expanded model incorporated information on ten species including rockfish (*Sebastes* spp.), roundfish, and flatfish. The ten species were selected based on their current or potential commercial importance, and to a lesser degree, the availability of data necessary to parameterize the model. Another major difference was the inclusion of Beverton–Holt stock-recruitment relationships for most species, rather than assuming constant recruitment, as was done in the initial modeling exercise. The parameters of the stock-recruitment curves were generally derived based on the assumption that recruitment at 50% of virgin stock biomass would equal 90% of virgin recruitment. Estimates of virgin recruitment and other life history and fishery parameters needed to parameterize the model were taken from Rogers and Pikitch (1989).

Because few gear studies focused on West Coast groundfish species had been conducted, it was necessary to make a number of assumptions and extrapolations in order to estimate species and age-specific gear selectivity coefficients. The key assumption made was that girth and body morphology were the most important factors influencing retention of a given fish in the codend. Girth–length relationships were established for each species and sex based on data obtained from the NMFS West Coast roundfish survey conducted in 1986. Estimates of length at 50% selection were extracted from the literature for a number of species and mesh sizes and converted to girth at 50% selection (g_{50}) based on the girth–length regressions. Data were then pooled into three groups corresponding to body morphology categories: rockfish, flatfish, and roundfish. Finally, for each category, a regression of g_{50} versus mesh size was performed, and the resulting equations were applied to obtain estimates of g_{50} for species for which no gear selectivity data were available.

The standard two-parameter cumulative normal distribution equation was used to derive selectivity ogives, with one parameter representing the g_{50} and the other determining the steepness of the ogive. Far fewer data were available on the steepness parameter than for the g_{50} parameter. Thus, for species for which data were lacking the value of this parameter was set equal to the mean value for those species for which estimates were available.

A number of model runs were also made assuming knife-edged selection at the point of 50% selection. The effects of knife-edged selectivity were examined because of interest in exploring the effects of square and other mesh types that have been shown to be more selective than conventional, diamond-shaped meshes (Robertson, 1982; Robertson, 1983; Robertson and Polanski, 1984; Robertson, 1986). More recently, square mesh has been shown to reduce the escape time of fish initially captured by trawls (DeAlteris and Reifsteck, 1988), and to improve survival of escapees (Main, 1988; DeAlteris and Reifsteck, 1988).

The economic component of the Vaga and Pikitch model was simplistic. Ex-vessel price per unit weight was set equal to 1985 estimates for each species. Thus, equilibrium gross revenue estimates are in 1985 dollars, and implicitly assume that relative values among species are insensitive to changes in their relative availability. Model outputs were limited to equilibrium yield (in weight) and equilibrium gross revenues. No attempt was made to estimate net revenues.

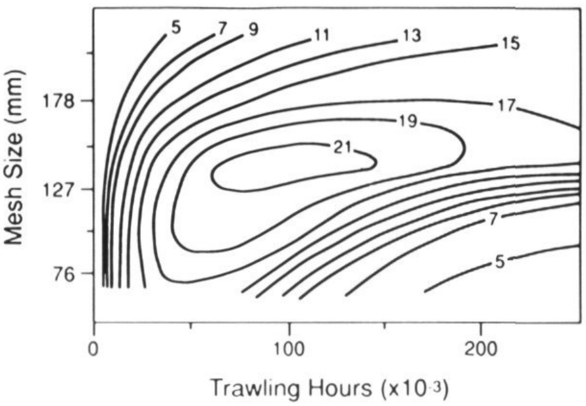

Figure 4. Yield surface for a multispecies fishery consisting of ten species of commercial importance as a function of codend mesh size and fishing effort (in trawling hours). Contours are gross revenues in two million dollar increments. Simulation results were obtained using the mixed-species yield-per-recruit model developed by Vaga and Pikitch (1988).

A major result of Phase I was that an increase in mesh size would increase fishery yields and revenues and reduce the sensitivity of fishery output to effort changes. To illustrate, the yield-isopleth diagram for gross revenues as a function of mesh size and fishing effort is shown in Figure 4. Maximum gross revenues were predicted to occur at a mesh size of approximately 140 mm, which represents an increase of 15% compared with 1985 gross revenues. In addition, at the 1985 level of fishing effort (75 000 trawling hours per annum), an increase in mesh size would be expected to have a much greater impact on equilibrium revenues than a decrease in effort. Perhaps, most importantly, given the current minimum mesh regulations of 76 mm for rockfish gear and 114 mm for flatfish gear, further increases in fishing effort would result in dramatic declines in equilibrium revenue (Fig. 4). The results for yield in weight were similar to those for gross revenues, and indicated that an increase in mesh size could enhance equilibrium yields by 22%. However, sensitivity analyses indicated that the results were highly dependent on the g_{50} estimates, but rather insensitive to the steepness parameter.

Thus, Phase I results indicated that the potential benefits of changes in mesh size regulations were large, but that field and further analytical research were needed to accurately determine selectivity ogive parameters and optimal mesh sizes for management purposes, and to determine the short-term consequences of mesh-size changes. The Pacific Fishery Management Council urged that remaining phases of the study be conducted.

Results of Phase II

Data obtained from the observer study described above were analyzed to assess the statistical efficiency of alternative study designs for Phase II. The analysis focused on two key mesh size responses: the mean length captured for selected fish species, and the gross value (in dollars-per-trawling hour) of all species in the catch. This choice of response variables was motivated by the desire to focus on estimation of short-term effects in the initial phase of fieldwork. A randomized complete block design in which all codend types were fished in randomized order on all trips (as opposed to a design where each vessel carries a single codend type) was selected (see Bergh *et al.* (1990) for further discussion and justification of this choice of experimental design).

The 1988 fieldwork examined four codend treatment types (three diamond mesh codends: 76 mm, 114 mm, and 127 mm; and one square-mesh codend: 127 mm). Codends were constructed to standardized specifications and differed only in mesh size and/or shape. Detachable codends were used to minimize lost fishing time due to the frequent codend changes imposed by the experimental design.

Two fishing strategies; one aimed primarily at a deepwater assemblage consisting largely of Dover sole (*Microstomus pacificus*), sablefish, and shortspine thornyhead (*Sebastolobus alascanus*); and the other directed at a variety of rockfish species using roller gear on the ocean bottom, were examined during the 1988 field trials. These strategies were selected because they are both heavily impacted by trip quotas (Pikitch, 1987a; Pikitch *et al.*, 1988), and because preliminary analyses indicated that they represent the extremes in the fishery in terms of variability in catch composition and amount. Catches in the rockfish fishery are highly variable in species composition and volume, whereas catch composition and amount for the deepwater fishery are quite stable.

All fieldwork performed during Phase II was conducted under commercial production conditions (i.e. tows of normal duration conducted by commercial vessels fishing in customary locations) with vessel time donated by the fishing industry. An experimental fishing permit was obtained which waived trip limit restrictions for cooperating vessels. The geographic extent of the study ranged from approximately San Francisco, California to Blaine, Washington. Twenty-six sampling trips were conducted. During those trips 345 successful tows were sampled, and 65 tows were aborted. For the deepwater Dover sole strategy, 35 complete blocks of three experimental codend tows (76 mm, 114 mm, and 127 mm diamond) and 23 complete blocks of four experimental codend tows (127 mm square in addition to the three diamond mesh codends) were obtained. For the bottom rockfish strategy, 45 complete blocks of three codends and 24 blocks of four codends were completed.

Analysis of Phase II data focused on the measurement of short-term effects of a change in mesh size. A detailed description of these results is presented in Pikitch *et al.*

Table 1. ANOVA results for dollars-per-trawling hour for (a) rockfish, 3-codend data set, (b) flatfish, 3-codend data set, (c) rockfish, 4-codend data set, and (d) flatfish, 4-codend data set.

Component	SS	df	MS	F	p (F)
(a)					
Overall mesh effect	21.56	2	10.78	7.70	0.001
Block	1.22	44	2.07	1.48	0.061
Covariates	5.04	2	2.52	1.80	0.172
Residual	120.44	86	1.40		
Total	238.26	134			
(b)					
Overall mesh effect	8.06	2	4.03	8.90	<0.0005
Block	32.73	34	0.96	2.13	0.004
Covariates	1.61	2	0.81	1.78	0.177
Residual	29.87	66	0.45		
Total	72.27	104			
(c)					
Overall mesh effect	19.02	3	6.34	5.97	0.001
Block	33.47	23	1.46	1.37	0.161
Covariates	4.07	2	2.04	1.91	0.155
Residual	71.21	67	1.06		
Total	127.77	95			
(d)					
Overall mesh effect	13.33	3	4.44	11.82	<0.0005
Block	19.61	22	0.89	2.37	0.004
Covariates	1.06	2	0.53	1.41	0.253
Residual	24.05	64	0.38		
Total	58.05	91			

Table 2. Mean dollars-per-trawling hour (in 1988 USD), by fishing strategy, codend configuration, and mesh size.

	Rockfish		Flatfish	
Mesh size (mm)	3-codend	4-codend	3-codend	4-codend
76 diamond	1 789	2 289	311	276
114 diamond	698	830	246	204
127 diamond	795	806	155	109
127 square	–	737	–	115

(1990). Here I describe the methods and results of analyses performed for the response variable dollars-per-trawling-hour (DPH). For each tow, DPH was estimated by summing the product of marketable catch weight and ex-vessel price per unit weight for all species and dividing the resultant sum by tow duration. The logarithmic transformation was then used to achieve normality and equal variances prior to performing analysis of variance (ANOVA). The model for the ANOVA was that for a randomized complete block design including average tow depth and tow duration as covariates. ANOVAs were performed separately for the 3- and 4-codend data sets and for each fishing strategy, resulting in a total of four ANOVAs. A summary of ANOVA results is presented in Table 1, and the mean responses by codend type are given in Table 2. P-values from *t*-tests for all pairwise comparisons among codend types are reported in Table 4. Finally, estimates of the number of blocks needed to reject the null hypothesis of no treatment effect for all pairwise comparisons, which were calculated using the method detailed in Bergh *et al.* (1990), are presented in Table 5.

For all four cases examined (rockfish and flatfish, 3- and 4-codend data sets), the overall mesh effect is highly significant ($p(F_{mesh} < 0.001)$), confirming the expectation that mesh size has a significant effect on gross revenues per trawl hour (Table 1).

For the rockfish sub-study, all pairwise comparisons involving the 76 mm diamond mesh codend were statistically significant (Table 4). The increase in gross revenue

Table 3. Total catch weight sampled (in metric tonnes), by fishing strategy, codend configuration, and mesh size.

	Rockfish		Flatfish	
Mesh size (mm)	3-codend	4-codend	3-codend	4-codend
76 diamond	121.5	62.4	85.0	55.7
114 diamond	65.5	36.5	58.3	36.6
127 diamond	58.1	23.2	58.1	24.1
127 square	–	21.3	–	28.3

Table 4. P-values from *t*-tests for all possible pairwise comparisons among codend types for the response variable dollars-per-trawl-hour by fishing strategy and codend configuration. D denotes diamond and S denotes square mesh.

Codend pairs	Rockfish		Flatfish	
Mesh size (mm)	3-codend	4-codend	3-codend	4-codend
76D–114D	<0.0005	0.001	0.076	0.053
76D–127D	0.001	0.001	<0.0005	<0.0005
114D–127D	0.303	0.462	0.003	0.001
76D–127S	–	<0.0005	–	<0.0005
114D–127S	–	0.348	–	0.002
127D–127S	–	0.384	–	0.370

Table 5. Estimate of the number of blocks needed to reject the null hypotheses of no difference among codend types in dollars-per-trawling-hour by fishing strategy and codend configuration. D denotes diamond and S denotes square mesh.

Codend pairs	Rockfish		Flatfish	
Mesh size (mm)	3-codend	4-codend	3-codend	4-codend
76D–114D	21	14	102	51
76D–127D	27	14	13	7
114D–127D	1 038	15 837	26	14
76D–127S	–	12	–	8
114D–127S	–	956	–	15
127D–127S	–	1 681	–	1 271

obtained with the 76-mm net compared with the 114-mm net is about threefold (the 95% confidence interval for that ratio R is $2.08 < R < 3.80$), and is the largest relative effect between two consecutive treatment types observed for this response variable (Figs. 5 and 6, Table 2). Differences between the 114 mm, 127 mm diamond, and 127 mm square nets were not statistically significant. Moreover, there were inconsistencies in the results of the 3- and 4-codend data set. For example, for the 3-codend data set, mean gross revenues were higher for the 127 mm diamond codend than for the 114 mm diamond codend (contrary to expectation), whereas the reverse was the case for the 4-codend data set (Table 2). Estimates of the number of blocks needed to detect significant differences in DPH among pairs of codends involving the 114 mm diamond, 127 mm diamond, and 127 mm square codends ranged from 956 to 15 837 blocks (Table 5). The costs of obtaining sample sizes of this magnitude are impractical. Taken together, these results indicate that differences in DPH among the three large codends are probably small for rockfish tows, and that additional research (within the scope of expected and anticipated funding levels) is unlikely to improve estimates of differences that may exist. The results clearly document, however, that an increase in mesh size from 76 mm to mesh sizes of 114 mm and greater would result in large declines in gross revenues of rockfish tows (on a unit time basis) in the short term.

For flatfish tows, DPH declined as diamond mesh size increased, with consistent trends seen for both 3- and 4-codend data sets (Fig. 6, Table 2). Interestingly, DPH was greater for the 127-mm square codend than for the 127-mm diamond codend, although this result was not statistically significant. All pairwise comparisons among diamond mesh sizes were statistically significant for the 3-codend data set (Table 4). For the 4-codend data set, which included the 127-mm square codend in addition to the three diamond mesh sizes, a reasonable amount of additional sampling effort would help to clarify the magnitude of difference in DPH for certain pairwise comparisons (Table 5).

Comparing the results with respect to DPH of the two sub-studies, we see that on average rockfish fishing generates at least four times more revenue than flatfish

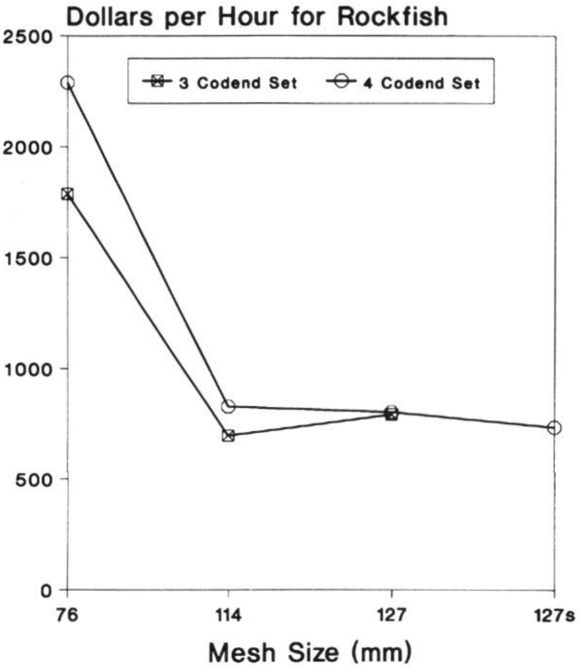

Figure 5. Estimated mean gross revenues (in 1988 USD) per trawling hour as a function of codend mesh type for rockfish tows. Results for the 3-codend data set are indicated by open squares, whereas results for the 4-codend data set are indicated by open circles. Results are from the 1988 field study described in the text and in Pikitch *et al.* 1990.

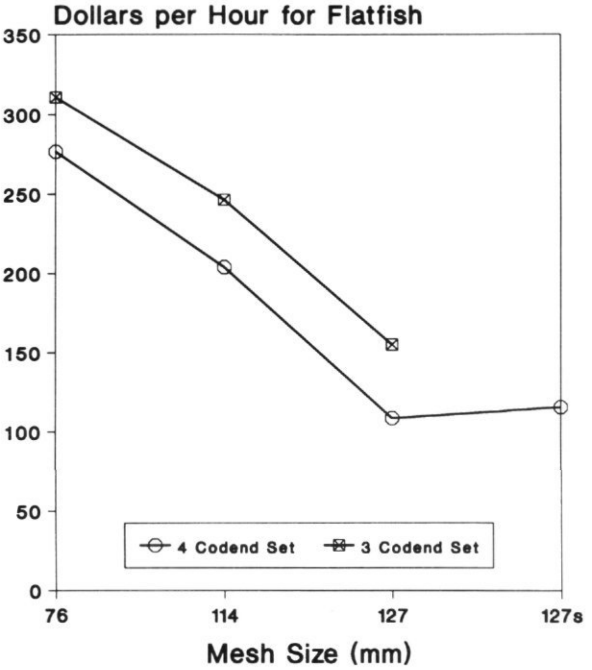

Figure 6. Estimated mean gross revenues (in 1988 USD) per trawling hour as a function of codend mesh type for flatfish tows. Results for the 3-codend data set are indicated by open squares, whereas results for the 4-codend data set are indicated by open circles. Results are from the 1988 field study described in the text and in Pikitch *et al.* 1990.

fishing. For both rockfish and flatfish, declines were seen in DPH with increasing mesh size. However, for rockfish, the only significant declines were between the 76-mm diamond mesh codends and codends of larger mesh size. For flatfish, trends in DPH with increasing mesh size were more consistent, and differences in the magnitude of response tended to be smaller than those for rockfish.

Total catches (in mt) obtained by codend type and fishing strategy are reported in Table 3. Comparison of these values with those presented for DPH in Table 2 provides some information on the differences in responses for these two variables. For rockfish, declines in total catch levels with increasing diamond mesh sizes tended to be smaller than those seen for DPH. For example, the ratios of mean responses for the 76-mm and 114-mm mesh sizes were 2.76 for DPH and 1.71 for total catch for the 4-codend data set. This indicates that the catch of relatively more valuable species may be reduced to a greater degree than that of lesser-valued species as mesh size increases. The opposite tendency is seen for flatfish, although the differences are not as great as those observed for rockfish.

Results of the 1988 field study clearly demonstrate that codend mesh size and type have important impacts on fishery responses of key importance when fishing occurs under commercial production conditions. Specifically, it was shown that increases in diamond mesh size generally result in significant decreases in DPH. Declines in catch rates (as reflected by DPH), observed to occur with mesh size increases, indicate that codend regulations could be used as an alternative, or complement, to trip limits as a means of maintaining a year-round fishing season and conserving fish stocks. The dramatic decline in DPH seen for rockfish as mesh size increased from 76 to 114 mm, suggests that if such a change were desirable from a long-term standpoint, then a gradual phase-in of such a change over some period of time would warrant serious consideration.

Phase III and beyond

A more comprehensive field study was conducted during 1989, and further fieldwork is planned for 1990. The basic experimental design used in 1989 was the same as that used in 1988, but two additional codends were included (140-mm diamond mesh and 114 mm square). In addition, the geographic scope and the number of fishing strategies examined were expanded for 1989 and 1990 fieldwork. Data analyses to be conducted in Phases III and IV will include estimation of gear selectivity coefficients in addition to measurement of short-term effects. The design of the field study was a variant of the alternate-haul technique and length frequency measurements were recorded for each tow conducted. Thus standard methodologies for estimating gear selectivity coefficients for alternate-haul studies (e.g. Pope *et al.* 1975) can be applied, with the 76-mm mesh codend serving as the "small-mesh" net in this case. Alternative approaches which combine field data and results of stock assessments will also be considered. Further modeling work will provide revised equilibrium yield predictions, and yield trajectories over time that would result from various mesh size regulations and phase-in periods. Model modifications in progress include restructuring the model to better represent assemblages of fish caught together by particular fishing strategies.

Perhaps the biggest challenge facing modelers of multispecies systems is the ability to predict the dynamics of the fleet in response to changes in gear regulations. The previous modeling work performed for this fishery, as well as much of the technological modeling work performed for other fisheries (see e.g., Murawski, 1984; Sainsbury, 1984; Shepherd, 1988; Silvestre and Soriano, 1988), assumed that no change in relative catchabilities of fully vulnerable fish would occur among species under a wide range of mesh size regulations and effort levels. This assumption is undoubtedly incorrect, and in fact some evidence for this has already been seen in the preliminary results of the 1988 effort (pers. obs.). The West Coast groundfish study will enable a comparison of the strategies employed and catches obtained from vessels under current trip restrictions, and vessels free of such restrictions, operating in similar locations and times. This will allow some testing of alternative hypotheses on fleet responses to regulation changes to be performed. Later modeling work will incorporate a fleet behavior component based on such analyses.

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A bioeconomic model of an age-structured groundfish resource exploited by a multi-gear fishing fleet

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A bioeconomic model of the Scotian Shelf groundfish fishery involving otter trawler and longliner fleets was constructed to examine the biological, economic, and regulatory consequences of the interaction of these two fleets. Otter trawlers catch younger fish than longliners and the revenue-cost pictures are very different. The model allowed examination of the long-term equilibrium levels and short-term transitory paths. The results of simulation indicated that both yield and employment were superior for longliners. However, otter trawlers, although experiencing higher operating costs, could "out-compete" longliners owing to higher sustained catch rates and thus revenue per unit cost. From a regulatory point of view, it was determined that, under the assumptions of this study, the fishery could be managed by regulating only trawler activity. The longliner fleet could be left essentially unregulated since it is not economical for it to overfish the stock. The results of this study have significant implications for the management of multispecies, multigear fisheries in which differential age effects of exploitation are present.

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Introduction

The Scotian Shelf groundfish fishery is dominated by two gear types – otter trawlers and longliners. Since 1970, this fishery has been regulated by quota management. In recent years, there has been a tendency for otter trawlers to catch their annual allocation or share of the quota before the longliners, and has led to calls from the industry for a redistribution of quota shares between the two fleets. Transfers between fleets have usually been one way – longliners to trawlers – and have caused concern that one fleet has a competitive advantage over the other. At the heart of this interaction is the difference in age-specific exploitation of the groundfish resource by the two fleets.

Two processes affect the age groups of the fish populations available to exploitation by the two fleets. The first is the biological availability of the fish. Sinclair and Smith (1987) have shown that young cod on the Scotian Shelf occur at a higher relative abundance than old cod in shallow water. Otter trawlers traditionally operate on the smooth bottoms which tend to be found in relatively shallow water. Since otter trawls are towed on the bottom and longlines are anchored, the two gears cannot be deployed in the same areas. Consequently, longlines have been set in the deeper water areas which usually have a rougher bottom. These effects imply a higher availability of young cod to otter trawl than to longline gear.

The second influential factor is the selectivity of the gear. In the few cases where the selectivity of otter trawl and longline gear has been compared, the latter has tended to catch larger, older fish. Thus, as a consequence of availability and selectivity factors, otter trawls currently catch smaller fish than longlines (O'Boyle *et al.*, 1983; Sinclair, 1986). Clearly this would give an advantage to vessels using otter trawls if their fishing mortality substantially reduces abundance before cod reach the size at age vulnerable to longlines.

This study used a bioeconomic model to examine the interactions of two fleets exploiting the same resource. The Scotian Shelf cod management unit is used as a case study. This is the largest groundfish resource exploited by Canadians on the Scotian Shelf. Data specific to the biological, economic, and operational aspects of this fishery were used to develop a realistic picture of the fishery. Nevertheless, the model was kept purposely simple to facilitate both the understanding of the main forcing factors and to identify model and data deficiencies which will require further research. The dynamics of the fishery under various limited entry conditions were examined. Conclusions relevant to possible future management of the fishery are presented.

Description of the model

The model simulates the interaction between a single fish population and two competing fishing fleets. Conceptually it is composed of two interlinked components, one describing the biology of the resource including its harvesting, and the other describing the economics of the two fleets. In reality, one fish stock is rarely harvested by two fleets in isolation of other resources. For instance, the Scotian Shelf cod fishery is exploited by several fleets. In addition, there are other stocks and species which are also simultaneously harvested (Sinclair, 1985). Ideally, one would want to model the dynamics of the Scotian Shelf fisheries as a whole to adequately describe how resource size in one fishing period influences profitability and thus investment decisions for the next. Such a model is, however, not possible at the moment due to data limitations. Nevertheless, the first step in developing such a model would be to consider the key elements of the system. This is what is done here.

Given that only a part of the system is being modelled, the concept of participation in the fishery, as opposed to existence of a vessel, was developed. When modelling the entire Shelf, the success/failure of vessels participating in the various fisheries will determine their overall future existence, i.e. the vessel may be retired from the fishery due to business failure. When modelling a part of the whole, this feature cannot be captured. Consequently, the dynamics of the vessels moving in and out of a single fishery were studied, assuming a constant overall vessel pool size.

The time frame for decisions on participation is influenced by the speed at which information on profitability flows through the fleets. The experience of the authors is that this occurs over the period of weeks rather than days. In other words, fishing success in the first half of March will affect participation rates in the latter half of that month. Consequently, the model used semi-monthly time-steps for the fishing process and decision-making. The following sections describe the equations and parameters (Table 1) used in the biological and economic components of the model along with derivations of equation coefficients.

The biological component

Table 1. Parameter descriptions and abbreviations used in this paper.

Parameter	Description
a	age, in years after birth
m	semi-monthly period of year
t	time, in years
a_0	hypothetical age of individual at which the fish would have been zero length if it had always grown according to the von Bertalanffy equation
g	fleet (either otter trawl or longliner)
l	number of gears in fishery
n	maximum number of age groups in population
$N_{a,m,t}$	beginning of time period, m, t, numbers (10^3) at age a
$\bar{W}_{a,m}$	mean weight (kg) of age a individual in period m
L_∞	mean asymptotic length (cm) of individual
K	Brody Growth Coefficient
α	slope of Shepherd stock-recruitment relationship at origin
SSB_{max}	threshold biomass (t) of Shepherd stock-recruitment relationship
β	"density-dependence" coefficient of Shepherd stock-recruitment relationship
$Z_{a,m,t}$	instantaneous total mortality rate of age a, year t population during period m
M	instantanteous natural mortality rate of population
$F_{a,m,t,g}$	instantaneous fishing mortality rate of age a, year t population during period m due to fleet g
$Y_{a,m,t,g}$	yield (t) taken from the age a, period m population in year t by fleet g
$q_{a,m,g}$	catchability coefficient of fleet g for age a fish in period m
$f_{m,t,g}$	effort in days fishing expended by fleet g in period m of year t
$\bar{D}_{m,t}$	average number of days fished per vessel of fleet g in period m
$V_{m,t,g}$	number of vessels in fleet g in period m of year t
$C_{a,t,g}$	catch numbers (10^3) at age a, in year t for gear g
r	coefficient of response of fleet to profitability of fishery
$TR_{m,t,g}$	total revenue of fleet g in period m of year t
P_g	price (dollars/tonne) of fish landed by fleet g
$TC_{m,t,g}$	total cost of fleet g in period m of year t
$FC_{m,t,g}$ $VC_{m,t,g}$ $L_{m,t,g}$	fixed, variable and labour costs of fleet g in period m of year t
$FCPV_g$	fixed cost per vessel of fleet g
$VCPDF_g$	variable cost per day fished of vessel in fleet g

The Shepherd (1982) stock-recruitment model was used to describe recruitment of age one cod as a function of the previous year's spawning-stock biomass. To parameterize this model, estimates of age one recruitment for 1958–1985 were obtained from Gagné *et al.* (1984) and Sinclair and Annand (1986). These sources were also used to provide estimates of mid-year total population biomass for ages 1 to 15, and with estimates of female maturity-at-age (Beacham, 1983) were used to estimate female spawning-stock biomass. Preliminary examination of these data indicated that a Ricker stock-recruitment relationship was appropriate for this resource. The coefficients ($a = 3.33$, $\beta = 2.5$, and $SSB_{max} = 70\,000$) of the relationship were determined

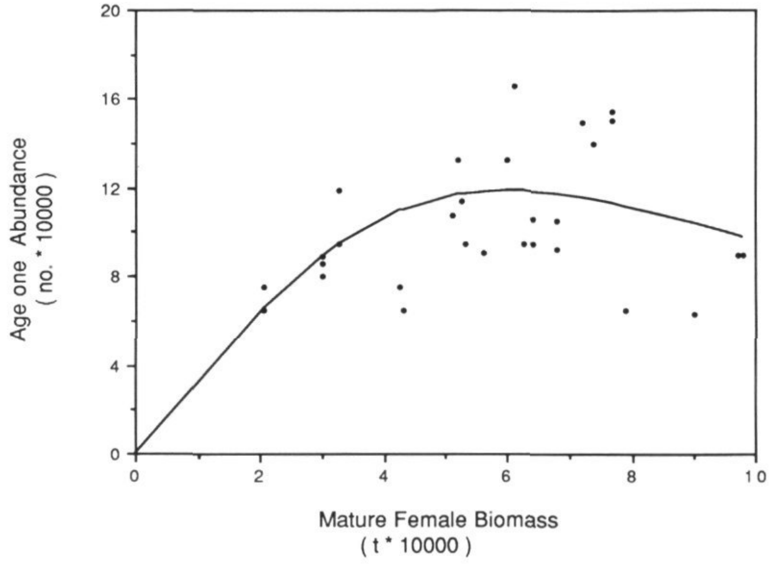

Figure 1. Relationship between age one recruitment numbers in year t + 1 and mature female population biomass in year t for Scotian Shelf cod.

using the approach of Shepherd (1982) (Fig. 1). Gagné and O'Boyle (1984) determined that peak spawning of cod on the Scotian Shelf occurs about the end of March. Consequently, in the model the end of March spawning-stock biomass was used to calculate age one recruitment for the coming year.

Annual mean lengths-(cm)-at-age were derived from weights-(kg)-at-age and length–weight coefficients ($w = 0.00001 \times L^{3.0}$) (Gagné *et al.*, 1984; Sinclair and Annand, 1986). A von Bertalanffy growth curve was fitted to these data to provide estimates of length-at-age for each time step used in the model. The equation constants were $L_\infty = 127.396$, $K = 0.092$, and $a_0 = 0.385$. Natural mortality by age, season, and year was set at 0.2 annually or 0.0083 per time-step (Sinclair and Annand, 1986).

In the simulations, total population mortality, gear-specific yield, and the change in the population-at-age between time-steps were calculated as per Equations (1), (2), and (3).

$$N_{a,m+1,t} = N_{a,m,t} \times e^{-Za,m,t} \quad (1)$$

$$Y_{a,m,t,g} = F_{a,m,t,g} \times \bar{W}_{a,m} \times N_{a,m,t} \times \frac{(1 - e^{-Za,m,t})}{Z_{a,m,t}} \quad (2)$$

$$Z_{a,m,t} = M + \sum_{g-1}^{1} F_{a,m,t,g} \quad (3)$$

$$F_{a,m,t,g} = q_{a,m,g} \times f_{m,t,g} \quad (4)$$

These equations require estimates of fishing mortality (Equation (4)) which in turn requires estimates of q, the age-specific catchability coefficient, and effort, in days fished. Effort is derived from the economic submodel described in the next section. Age- and gear-specific catchability coefficients for the two gears were estimated from 1977–1985 data (Sinclair and Annand, 1986) as follows. First, age-specific fishing mortality matrices were calculated as

$$F_{a,t,g} = F_{a,t} \times \frac{C_{a,t,g}}{\sum_{g=1}^{1} C_{a,t,g}} \quad (5)$$

for the two gears. Annual estimates of gear-specific catch rates for cod directed trips were obtained from data in NAFO Statistical Bulletins. Annual effort for each gear was estimated by the ratio of that gear's cod catch to the cod-directed catch rate. Catchabilities ($q_{a,t,g}$) were then derived by dividing $F_{a,t,g}$ by annual effort.

These estimates represented the 1977–1985 period. Average age- and gear-specific catchabilities were derived by applying the above matrices to an age-gear separable analysis. This involved the use of a multiple regression using dummy variables (Draper and Smith, 1966) to represent the age and gear effects. The gear effects were not significant ($p > 0.05$), showing that the catchability coefficients were time invariant. Age effects were significant ($p < 0.01$) and provided age-specific catchability coefficients ($q_{a,g}$) for the two gears (Fig. 2).

Recruitment of cod to otter trawl gear occurs at a younger age than to longline gear. As well, recruitment for the latter is asymptotic, whereas that for the former falls off in the older age groups.

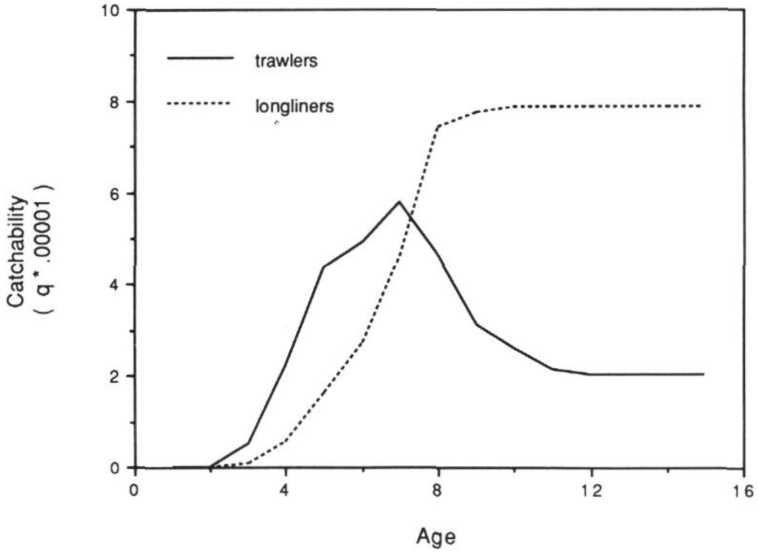

Figure 2. Trend in catchability coefficient with age for otter trawlers and longliners participating in the Scotian Shelf cod fishery.

The estimates of the catchability coefficients ($q_{a,g}$) are for the mid-year only. The model required catchability for each monthly time-step ($q_{a,m,g}$). To adjust the annual estimates to the time-step, catchability was assumed to be a function of fish length, the latter being obtained from the von Bertalanffy curve described above. The annual estimates $q_{a,g}$ were plotted against mid-year length for that age, and a linear interpolation used to provide estimates of $q_{a,m,g}$ for the appropriate time-step, m.

The economic component

The fishing effort (Equation (6)) expended by the two fleets was represented as the average number of days that a vessel can fish ($D_{m,g}$) multiplied by the total number of vessels participating in the fishery ($V_{m,t,g}$).

$$f_{m,t,g} = \bar{D}_{m,g} \times V_{m,t,g} \tag{6}$$

Monthly estimates of $\bar{D}_{m,g}$ were obtained for directed groundfish trips during 1977–1985 from the commercial database (McMillan and O'Boyle, 1986). These estimates were divided by two to provide the model with semi-monthly values of days fished per vessel.

Allen and McGlade (1986) described the change in fleet size between time steps as a function of the ratio of net earnings (revenue-cost) to the total revenue in the previous time period. In their formulation changes in fleet size could vary between $-\infty$ and $+1$ times the existing fleet size. Thus, fleet sizes could become negative. We considered that it would be more reasonable for the fleet to vary according to the ratio of net earnings to total cost, and that negative fleet sizes should not be allowed. In the formulation we used (Equation (7)), fleet size could vary between -1 and $+\infty$ times the existing fleet size.

$$V_{m+1,t,g} = rV_{m,t,g} \frac{TR_{m,t,g} - TC_{m,t,g}}{TC_{m,t,g}} + V_{m,t,g} \tag{7}$$

The coefficient, r, in Equation (7) is the rate of response of the fleet to the profit/cost ratio. Data from the commercial fishery (McMillan and O'Boyle, 1986) were used to investigate how monthly changes in fleet size related to the profit/cost ratio and thus allow the calculation of estimates of r. A wide range of estimates was observed with 80% of these being between −0.5 and +0.5. Given the range of values and the presence of negative estimates, the empirical data could not be used to derive estimates of r.

Preliminary model runs, with r set to one, were conducted to observe model behaviour. The model output never reached an equilibrium state. When r was set to 0.5, the model reached an equilibrium. For the purpose of this exercise, r was set to 0.5. It is recognized that short-term transitory states will be affected by this, but the long-term equilibrium conditions are not likely to be. This part of the model does, however, require further examination.

Total revenue was calculated using Equation (8). The yield was provided by the biological submodel.

$$TR_{m,t,g} = P_g \times \sum_{a=1}^{n} Y_{a,m,t,g} \tag{8}$$

Price information was obtained from the commercial database (McMillan and O'Boyle, 1986). Monthly average cod prices for otter trawlers and longliners during

Table 2. Fixed and variable cost information used in the simulation (from Anon., 1985).

Fleet	Fixed costs per vessel per year ($FCPV_g$)	Variable costs per vessel per year	Days fishing per year	Variable cost per day fishing per vessel per year ($VCPDF_g$)
Otter trawl	24 142	61 486	77.8	790.69
Longliner	10 130	59 499	72.3	822.56

1980–1985 were compiled. No seasonal trends in either were identified, although there were significant seasonal trends in landings. It is evident that these fleets are "price takers" in the market place. Without knowing what the external influences determining price were, it was decided to set the otter trawler and longliner prices at the 1980–1985 averages of \$437 and \$568 per metric tonne, respectively. Thus, this is a fixed price model.

Total cost was calculated as the sum of fixed costs, variable costs, and labour (Equation (9)). Information pertaining to these costs was obtained from Anon. (1985) and is summarized in Table 2. The estimates of $FCPV_g$ were divided by 24 to reflect semi-monthly expenditures. This assumes that, when not in the cod fishery, fixed costs will be accrued against revenue earned in those other fisheries. The fixed costs per time-step were calculated as $FCPV_g$ times the number of participants (Equation (10)). Variable costs per time-step were calculated as per Equation (11). Labour (Equation (12)) was assessed at 40% of the total revenue (Anon., 1985).

$$TC_{m,t,g} = FC_{m,t,g} + VC_{m,t,g} + L_{m,t,g} \tag{9}$$

$$FC_{m,t,g} = V_{m,t,g} \times FCPV_g \tag{10}$$

$$VC_{m,t,g} = V_{m,t,g} \times \bar{D}_{m,g} \times VCPDF_g \tag{11}$$

$$L_{m,t,g} = TR_{m,t,g} \times 0.4 \tag{12}$$

Program flow

The model was written in APL on a CDC Cyber 840 facility. A listing is available upon request from the authors, and a flow chart of the model is presented in Figure 3.

The first step is programme initialization, which sets the number of years of the simulation, zeros out all the relevant arrays, and sets up the initial population conditions, including starting fleet sizes. Following this, the population is harvested in the biological submodel. The yield is passed on to the economic submodel where it is used to calculate the fleet revenues, costs, and size for the next time-step. At this point, the model either loops back to the biological submodel to conduct the calculations for the next two-week time interval (if the end of the year has not been reached) or calculates age one recruitment using the Shepherd stock-recruitment model, prior to conducting the biological calculations. Once the simulation reaches the user defined maximum number of years, tabular and graphical output of the results is generated and the run terminated.

Results

Fishery dynamics and the effects of limited entry

In 1985, about 379 otter trawler and 1801 longliner licences were available to the fishery. Many of these were inactive. Indeed, only about 137 otter trawlers and 85 longliners contributed 80% of the inshore fleet catch on the Scotian Shelf. In an initial set of simulations, starting fleet size for otter trawlers and longliners was set at 137 and 85, respectively. Next, a series of runs was conducted with different otter trawler and longliner licensing restrictions. The first (status quo) run set the licence limit at 379 otter trawlers and 1801 longliners. Next, the longliner limit and then the otter trawler limit were reduced to evaluate their respective impacts.

Under the status quo licensing restrictions, both fleets undergo large variations in size for the first 10 years. After 15 years the longliner fleet decreases in size, by 20 years it has been completely displaced by the otter trawl fleet, which has grown to a maximum size of about 300 vessels.

When the longliner licence limit is reduced, the net result is the same as for the status quo license restrictions – phase out of the longliner fleet. Fleet composition is thus insensitive to restriction of longliner entry.

This is not the case with otter trawler restrictions. When the number of otter trawler licenses is systematically reduced, the longliner fleet grows in size (Fig. 4).

The socio-economics of the various otter trawler license limits are summarized in Table 3. Because of the assumption of the model, they are illustrative of trends and should not be taken as absolute values. The total revenue gained from the fishery ranges between \$32 and 43×10^6. Net earnings are maximal at a trawler limit of 150. As longliner participation increases, so do revenues and costs. As otter trawler participation decreases, net earnings first increase and then decrease.

The employment profile for the fishery closely follows that of the fleet-specific participation rates. This is because employment was calculated based on fleet-specific crew levels – 3.1 for trawlers and 4.3 for long-

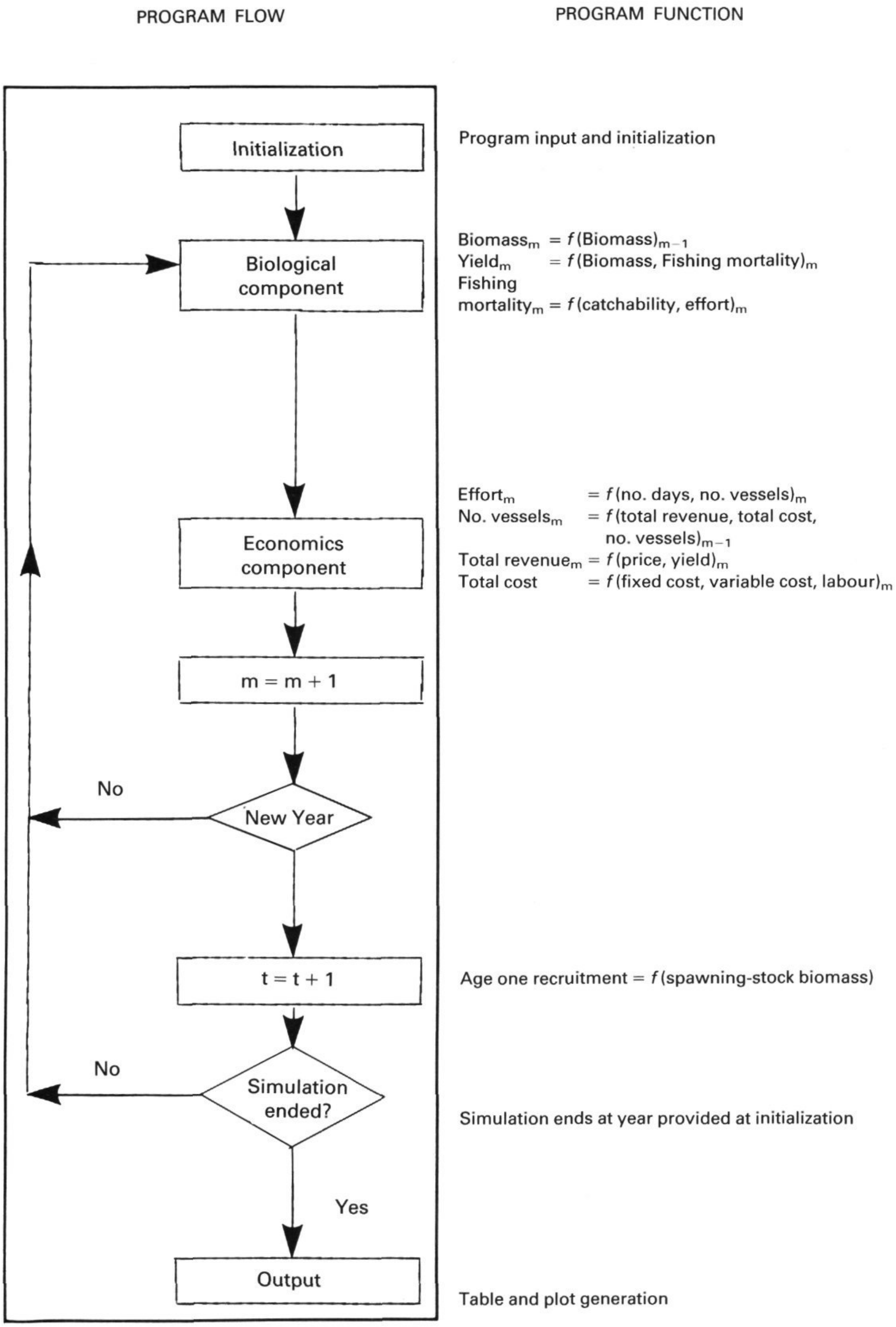

Figure 3. Program flow and function of bioeconomic model of the Scotian Shelf cod fishery.

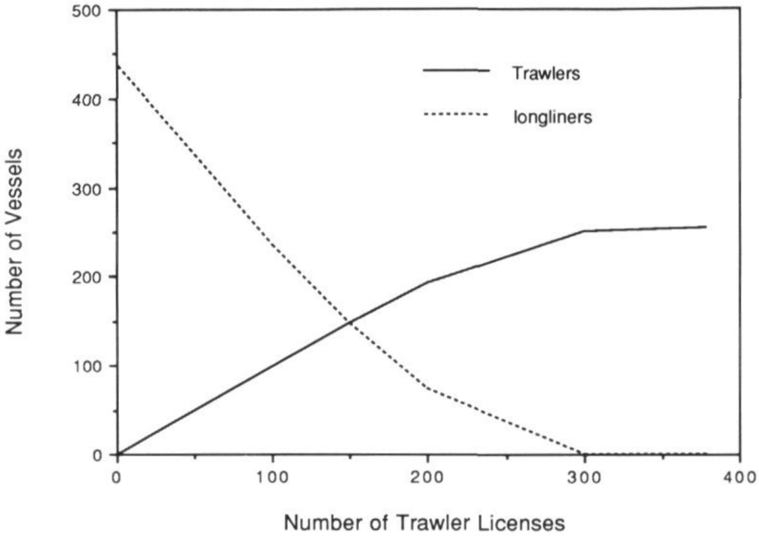

Figure 4. Relationship between long-term otter trawler and longliner fleet size and the number of otter trawler licenses available.

liners. Employment is highest in a purely longline fishery (2043) and lowest (935) at a restricted trawler fleet size of 300 vessels. When the two fleets are equivalent in size, employment is about 1147.

Salaries were calculated by dividing the annual crew share (0.4 × total revenue) by the vessel crew size plus 1 (to account for the captain's double share). There is a significant difference between the two fleets in the salaries earned by participants. Longliner salaries at all trawler license levels do not significantly change, being around $8400 annually. Trawler salaries on the other hand range from $13 000 to $21 000 and rise gradually as participation in the fishery is restricted.

In summary, then, it appears that the size of the longliner fleet can be influenced indirectly through control of the otter trawler fleet. When the size of the trawler fleet is reduced through limited entry, the longline fleet is able to grow. Also, the trawler fleet generates significant net revenues when their numbers are limited. This net revenue represents resource rent and could be recovered by taxation or royalty schemes.

These simulations do not explore the full range of fleet

Table 3. The response of various model output parameters to licence limitation of the otter trawler fleet.

		Licence limit for otter trawlers					
Parameter (in equilibrium)	Fleet	379	300	200	150	100	1
Fleet size (nos.)	OT	254	250	192	148	99	1
	LL	1	1	73	148	236	437
	Total	255	251	265	296	335	438
Fleet revenue ($\$ \times 10^{-6}$)	OT	31.50	30.90	26.30	21.08	14.70	0.16
	LL	0.095	0.095	7.11	14.43	23.10	42.90
	Total	31.60	31.00	33.41	35.51	37.80	43.06
Fleet net earnings ($\$ \times 10^{-6}$)	OT	0.710	0.670	2.00	2.09	1.76	0.03
	LL	−0.001	−0.002	0.07	0.12	0.22	0.47
	Total	0.709	0.668	2.07	2.21	1.98	0.50
Fleet employment	OT	976	930	620	465	310	3
	LL	5	5	336	682	1091	2040
	Total	981	935	956	1147	1401	2043
Average crew salary 10^{-3}	OT	12.9	13.3	17.0	18.1	19.0	20.3
	LL	8.3	8.3	8.5	8.5	8.5	8.4

Table 4. Yield and economic results of simulations of exclusive trawler (a) and exclusive longliner (b) fisheries at different fleet sizes. MEY is the maximum economic yield, MSY is the maximum sustainable yield, and OAE is the open access equilibrium.

	No. of vessels	Long-term yield ($t \times 10^{-3}$)	Total revenue ($\$ \times 10^{-6}$)	Fixed cost ($\$ \times 10^{-6}$)	Variable cost ($\$ \times 10^{-6}$)	Labour cost ($\$ \times 10^{-6}$)	Total cost ($\$ \times 10^{-6}$)	Net earnings per vessel ($\$ \times 10^{-3}$)	Number employed	Crew share ($\$ \times 10^{-3}$)	Net earnings ($\$ \times 10^{-6}$)
(a)											
MEY	139	64.1	28.0	3.4	6.5	11.2	21.1	49.8	431	26.0	6.9
MSY	237	77.5	33.9	5.7	11.1	13.5	30.4	14.6	735	18.4	3.5
OAE	277	75.3	32.9	6.7	13.0	13.2	32.9	0	859	15.3	0
(b)											
MEY	113	61.7	35.0	1.1	5.3	14.0	20.5	128.5	486	28.8	14.5
MSY	460	76.2	43.3	4.7	21.8	17.3	43.8	−1.0	1978	8.8	−0.5
OAE	452	76.2	43.3	4.6	21.4	17.3	43.3	0	1944	8.9	0

interactions and thus do not allow estimation of joint Maximum Economic Yield (MEY) conditions. The following section describes simulation results under a full range of joint fleet sizes to allow description of fishery surplus production dynamics.

Estimation of optimal yield conditions

Long-term yield conditions for exclusive trawl and longline fisheries were examined. For each gear, a series of model runs was made in which the number of vessels active in the fishery was fixed and the model run until a stable level of yield was reached. This normally took about 20 years. The level of effort was varied over a range sufficient to characterize the surplus production curve for that fishery. Surplus production models were fitted to these data to determine optimal yield and effort levels using a linear regression of catch rate on effort (Ricker, 1975). Yield and effort values were converted to cost and revenue curves for each fishery to estimate open access equilibrium and MEY conditions (Table 4).

Open access equilibrium, where total revenue equals total cost in an exclusive trawler fishery, occurred at an effort level of 277 vessels, producing an equilibrium yield of 75 290 t which generated a total revenue of $\$32.90 \times 10^6$. Total employment in the fishery was 859 with crew shares of $15 326. Maximum sustainable yield was 77 480 t with 237 vessels, an increase of 3% in yield for a 14% decrease in effort. Net earnings per vessel were $14 566 and crew shares had risen to $18 434; however, employment had dropped 14% (proportional to effort) to 735. Maximum economic yield occurred at an effort level of 139 vessels (50% of open access effort), producing a yield of 64 140 t. Total net revenue rose to $\$6.9 \times 10^6$, giving $49 837 per vessel, and crew shares rose to $26 019. Employment in the fishery dropped to 431.

Open access equilibrium in an exclusive long-line fishery occurred with 452 vessels, producing an equilibrium yield of 76 240 t, slightly larger than that produced at open access equilibrium by the trawl fishery. Total revenues generated were $\$43.3 \times 10^6$ reflecting the higher price paid for longline-caught fish; however, these revenues are offset by higher variable costs for longliners and the larger number of vessels producing costs required to generate these revenues. Employment at open access equilibrium was 1944 due to the high effort and the larger crew size for longliners; however, crew shares were only $8 757. Maximum sustainable yield for this fishery occurred at an effort level slightly greater than that of open access equilibrium. This implies that under the assumptions of this model, an exclusive longliner fishery would be unable to harvest this stock above MSY and thus be unable to overexploit the resource. Maximum economic yield occurred at a level of effort of 113 vessels, producing 61 668 t of yield, slightly lower than that for the trawler fishery. Greater total revenue due to higher prices and lower costs results in a total net revenue of $\$14.5 \times 10^6$, giving net earnings of $128 518 per vessel and crew shares of $28 835. Employment was 486, 13% greater than at MEY in the trawler fishery. In both the otter trawler and longliner scenarios, the cost lines (Fig. 5) were curved, contrary to most theoretical formulations. This is a result of labour costs being a function of the revenue.

In summary, longliners alone are unlikely to overexploit the stock under the catchability-at-age conditions described in this paper. At MEY, longliners will produce a slightly lower yield than trawlers, but will employ more people, and higher prices will result in higher net earnings and crew shares. However, when effort expands beyond a fleet size of about 300 vessels, crew shares drop below $12 000. Trawlers, on the other hand, are more effective at harvesting and employing smaller crews, and can produce crew shares above $15 000 right up to open access equilibrium.

Single fleet surplus production calculations indicated MEY effort levels of between 100 and 150 vessels. In order to investigate the joint fleet MEY effort conditions, several additional runs of the model were performed at fixed effort levels of between 0 and 500 vessels of each type. However, the highest net revenue is taken at the MEY point in an exclusive longline fishery. The addition of trawler effort, except at very low longline

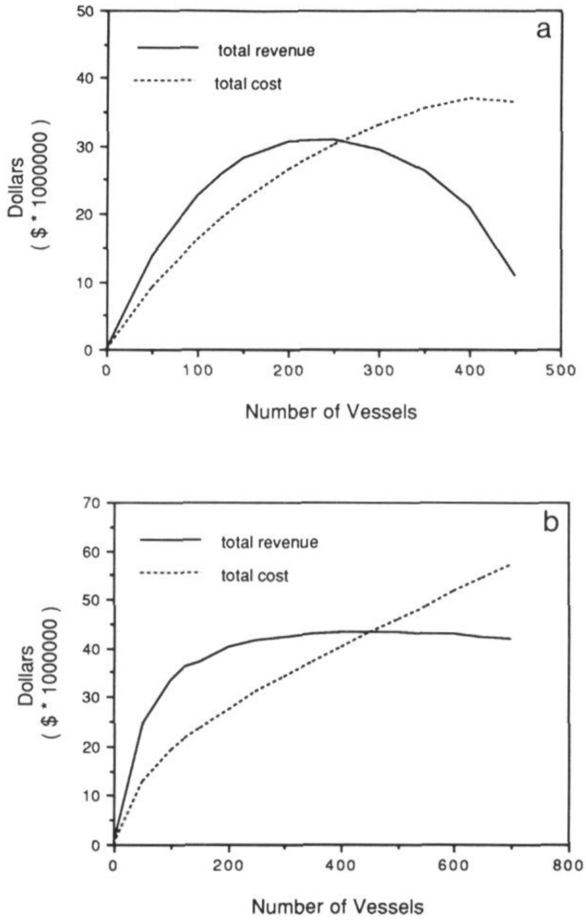

Figure 5. Relationship at equilibrium between total revenue, total cost, and size of the fleet for exclusive (a) otter trawler and (b) longliner fisheries.

effort (less than 50 vessels) has the effect of reducing the total net revenue.

Discussion

The results of this study indicate three main features of the Scotian Shelf cod fishery; (1) that without constraints the trawlers will out-compete the longliners, (2) that longliners are unlikely to over-exploit the resource if they maintain the same age-specific catchabilities and costs, and (3) that effort regulation is only necessary for otter trawlers to protect the cod resource.

These conclusions are dependent on the degree to which the model was able to describe the essential features of the interaction between the fish stock and the two fleets. We follow with a review of the model, its assumptions and limitations and discuss in general terms the sensitivity of these results to the key model parameters.

A major feature of the model is its treatment of vessel participation rates. The current model is of the malleable capital type (Charles, 1983). It is assumed that if the Scotian Shelf cod fishery is unprofitable, participation in the directed cod fishery will fall, while that in other fisheries will increase. Overall capital investment is assumed to be constant. It is recognized that the modelling of long-term capital investment decisions along with short-term changes in participation is a desirable feature of any model. In a multispecies, multi-fleet fishery such as occurs on the Scotian Shelf, all aspects of the system must be modelled simultaneously. This is beyond the scope of the present work. It is worth mentioning, however, that the fishery described here has relatively low by-catch (less than 15%) of other species (Sinclair, 1985). Thus, participants in the Scotian Shelf cod fishery earn the majority of their revenue from cod and relatively little from by-catch.

The way in which participation in the fishery has been treated is considered to be over-simplified. It has been calculated based on the profitability of fishing in the immediately previous time-step. In reality, participation would be determined by complex human behaviour, depending in part on the historical experience of the fishermen, the proximity to fishing grounds, and the success of alternative fisheries. This inadequacy in the model is likely to have important effects on the estimated short-term dynamics; however, we consider that the long-term results will not be seriously affected.

Economic factors considered influential on the model results involve revenue, driven mainly by price, and costs. The model was deliberately established as one of fixed price. Given the empirical data, it was not considered realistic to assume that one fleet component can significantly influence price trends. Pricing is more appropriately considered in a global marketing submodel than directly influenced by harvesting success in one fleet sector.

It was noted that the fixed price of fish to longliners was higher than that to trawlers, but this was not enough to offset the competitive advantage that the latter had in the combined fleet situation. It is evident that the results of this study would remain unaltered except where the price to longliners for their fish was dramatically higher than that to trawlers.

The cost side of the issue also favours the longliners. Here we are referring to the cost per day of fishing, not the cost per unit of production. Longliners are generally operated at lower cost than the trawlers. As with price, this differential is not enough to provide the longliner fleet with a competitive advantage. Thus from this point of view, the cost differential would have to increase before the results of this study would be altered.

From an economic perspective then, the longliner fleet had a clear advantage over the trawlers. Thus, the reason why the trawlers were more successful in our model must be sought in the biology – recruitment to the population and to the fishery.

Recruitment in the model is considered to be a deterministic function of spawning-stock biomass. There are several ways of incorporating uncertainty into the formulation (Getz and Swartzman, 1981) that could be investigated in other models. However, deterministic solutions are useful in defining broad system behaviour (Clark *et al.*, 1985), which is the goal here. Thus, this should not detract from the usefulness of the exercise.

Regarding the form of the relationship, given the variability in the empirical data set, other models could legitimately be used to describe recruitment as a function of spawning-stock biomass. It is felt that use of a different model, i.e. Beverton–Holt versus Ricker would only increase the frequency of entry of large year classes into the population and thus provide more yield to the otter trawl fishery. As a consequence, the results of this study would be essentially the same.

At the heart of the competition between the two fleets is the difference in the age-specific catchability coefficients. Without conducting a formal sensitivity analysis, it is evident that the dramatic difference in the age-specific recruitment to the fishery causes the trawlers to intercept the cod before they enter the longline fishery. As the difference in age-specific recruitment decreases, competition between the two fleets decreases. Nevertheless, if both fleets had the same age-specific catchabilities, it is likely that the longliners would out-compete the trawlers owing to a better revenue-cost picture.

On balance then, it is felt that the results of the study are relatively insensitive to most key parameters other than for the catchability coefficients. Interestingly, although longliners currently catch larger fish than trawlers, there is little evidence to suggest that this will always be the case. If there are strong relationships between hook and fish size, the fleet-specific catchability coefficients by age could change dramatically and thus put the longline fleet at a competitive advantage, although catching smaller fish might reduce their price advantage. Field studies are required to examine critically the selectivity characteristics of longline gear. Given the sensitivity of the model to this parameter, more study would have to be undertaken before the results of this paper are applied to management.

Given the many assumptions of the model, it is comforting to note that output revenue, cost, and salaries are close to those observed. For instance, trawler revenue per vessel generated by the model varied around \$150 000 annually, comparable to the \$157 000 quoted in the literature (Anon., 1985). Costs are also comparable. Revenue and costs for longliners in the simulation (approx. \$100 000) are, however, well below empirical estimates of \$180 000. This may be due to the observed high profitability of the longline fishery in 1984, rather than to deficiencies in the model. Crew salaries are also comparable to empirical data sets (Kirby, 1982), in the order of \$10 000–20 000 annually. Thus, the model provides results that are comparable to those seen in the real world and provides confidence for the conclusions being drawn.

If the assumptions of this exercise are valid, our results indicate that without constraints being placed upon the system the trawlers will out-compete the longliners. By gaining access first, otter trawler effort will reduce the yield potentially available to longliners. This advantage occurs despite the higher annual operating costs (\$71 152 for draggers vs. \$57 468 for longliners) and the lower price available (\$437 t^{-1} for trawlers vs. \$568 t^{-1} for longliners) to trawlers. From the aspect of maximizing net revenue, employment, and salaries, however, there are advantages to a pure longline fishery. In addition, longliners generally provide a high quality, large fish for the fresh fish market (Kirby, 1982), while otter trawler landings can vary in quality and size of fish caught. Maintenance of market niches, if important to the objectives of management, would then require some presence of both types of gear. Finally, although longliners were outfished by trawlers, the longliner fleet would not likely by itself critically deplete the resource.

These results have implications for quota management systems currently in use in Atlantic Canada, as they apply to both fleets and individual vessels. Quota systems require some sharing of the Total Allowable Catch (TAC) among participants. If account is not taken of the competitive advantages due to differences in catchability by age, the system may drive some participants out of the fishery. Individual transferable quota (ITQ) systems have been established to prevent a "race for the fish", which results in dissipation of rent. But the model results indicate that there may still be a race for the fish at a smaller size, which may eliminate longliners even though a longline fishery could produce greater net revenues. Measures such as gear size and area closures may be useful to moderate the effects of age-specific exploitation patterns of the various fleets. Indeed, the results of this study tend to indicate that, if the assumptions are correct, the overall exploitation of the resource by both fleets can be controlled by only regulating that fleet which captures the small, younger fish. This has substantial implications for enforcement agencies.

This study shows that given two fleets of markedly different age-specific exploitation rates jointly harvesting one stock, the one catching the younger fish will likely, over time, displace the one catching older fish. This occurs even though the latter fleet has a slightly better economic performance than the former. This observation has implications for the appropriate regulatory measures that give all participants equal access to the resource. Size composition, in addition to quantity of fish caught, must be considered.

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By-catch: a bioeconomic assessment of North Pacific groundfish fisheries

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In its early years, the North Pacific Fishery Management Council spent considerable time setting catch quotas and dividing them between foreign, joint venture, and domestic fisheries. Conservation of stocks and the development of a United States groundfish fishery were the main concerns during this period. Expansion of United States groundfish fisheries has increased the controversy surrounding allocation decisions. One of the most politically volatile issues is the catch of non-target species (by-catch) in the groundfish fishery, particularly by trawlers. Mathematical programming techniques are used to explore this issue. Models constructed contain both biological and economic components. Costs and benefits of controlling by-catch in both target and non-target fisheries are examined.

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Introduction

The broad shelf areas of Alaska, especially of the Bering Sea (Fig. 1), support a large groundfish resource. Principal species are pollock (*Theragra chalcogramma*), yellowfin sole (*Limanda aspera*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and several other species of flounders including flathead sole (*Hippoglossoides elassodon*), rock sole (*Lepidopsetta bilineata*), Alaska plaice (*Pleuronectes quadrituberculatus*), arrowtooth flounder (*Atheresthes stomias*), and Greenland turbot (*Reinhardtius hippoglossoides).* Rockfishes (*Sebastes* and *Sebastolobus* spp.), sablefish (*Anopolopoma fimbria*), and Atka mackerel (*Pleurogrammus monopterygius*) are other important species.

Both Japan and the Soviet Union began exploratory fishing operations off Alaska before World War II. Large-scale foreign fisheries in the Bering Sea (Fig. 1) began in the middle and late 1950s, and expanded into the Gulf of Alaska in the early 1960s. Effort grew until 1972, when the catch reached 2.6 million tonnes of fish. The rapid growth in foreign fishing effort coupled with declines in the abundance of key fishery resources sparked concern over the welfare of the stocks. Bilateral agreements were reached with Japan and the Soviet Union in 1973 and 1974 that imposed catch quotas and time/area restrictions on their groundfish fisheries.

Concern over the impact of foreign fisheries on fish populations, here and elsewhere, sparked interest in extending management jurisdiction by the United States. This led to passage of the Magnuson Fishery Conservation and Management Act of 1976 (MFCMA).

The MFCMA, a radical departure from the legal and philosophical foundations of past United States fishery management, extended jurisdiction over fishery resources out to 200 miles. Responsibility for developing management regimes fell on eight regional fishery management councils.[1] The Act also specified that fishery management plans must be consistent with a set of national conservation and management standards.

In its early years, the North Pacific Fishery Management Council (NPFMC) spent considerable time setting catch quotas and dividing them among foreign, joint venture, and domestic fisheries.[2] Conservation of stocks and the development of a United States groundfish fishery were the main concern during this period.

Expansion of United States groundfish fisheries (Fig. 2) has increased the controversy surrounding allocation

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[1] The North Pacific Fishery Management Council is one of eight regional fishery management councils created by the MFCMA. It is made up of individuals from state and federal agencies, as well as the private sector. It is charged with the responsibility of managing fisheries that occur in the Exclusive Economic Zone (EEZ) off Alaska.

[2] A joint venture fishery is one where fish caught by domestic vessels are transferred at sea to foreign processing vessels.

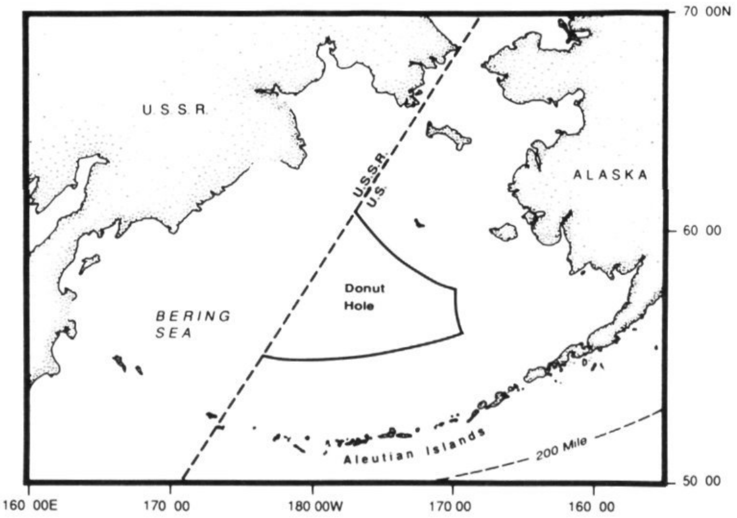

Figure 1. The Bering Sea showing the US and USSR boundary and the US 200-mile exclusive economic zone. The "Donut Hole" is an area in the Bering Sea formed by the surrounding exclusive economic zones of the US and USSR.

decisions. A very serious allocation issue concerns the catch of non-target species (by-catch) in the groundfish fishery, particularly by trawlers.

Information on the amount of by-catch taken by foreign fisheries became available with the implementation of a comprehensive observer program.[1] Data obtained from these fisheries confirmed prior information collected during joint United States industry–government trawl surveys that showed a high by-catch of crab and halibut (prohibited species)[2] in trawl fisheries. The almost total dependence of historical domestic fisheries on species prohibited to trawl gear led the NPFMC in 1983 to adopt stringent management measures to restrict the by-catch of prohibited species in foreign fisheries.

Data collected by observers in the joint venture fishery for yellowfin sole in the Bering Sea showed that this fishery also involved by-catch of prohibited species. The large by-catch of king crab in 1985 (more than 1 million animals), at a time when crab fisheries were severely restricted because of the critical state of the resource, led crab fishermen to persuade the NPFMC to adopt management measures intended to limit by-catch and close an area with high densities of female king crab to trawling.

Comprehensive by-catch data for domestic fisheries are lacking. Observer coverage of domestic fishery operations has been limited to date. Data available, however, indicate that by-catch rates for these fisheries are as high and possibly higher than those found in foreign and joint venture fisheries. In the face of growing concern over the size of the by-catch in these fisheries, the inability to avoid completely the harvesting of prohibited species in trawl fisheries, and the controversial nature of the act making retention politically impossible, the NPFMC formed a committee made up of various segments of the fishing industry to develop a set of management options for its consideration. This effort culminated in the NPFMC adopting by-catch quotas for red king crab, *Paralithodes camtschatica*, Tanner crab, *Chionoecetes bairdi*, and Pacific halibut.

During the course of the debate, considerable interest was expressed in how prohibited species populations would be affected by either increased or decreased removals of groundfish species. Some participants in the debate expressed the opinion that prohibited species would benefit from reductions in the size of groundfish stocks, since groundfish such as Pacific cod prey on crab and Pacific halibut. It was suggested that this complementary relationship between groundfish removals and the biomass of prohibited species justified relaxation of by-catch restrictions. This paper reports initial results of an analysis examining this relationship.

The model

Biological submodel

A numerical simulation model of the ecosystem of the eastern Bering Sea was constructed as a basis for the

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[1] The MFCMA requires that a US observer be stationed aboard each foreign fishing vessel while that vessel is engaged in fishing within the EEZ. Since 1984, observer coverage has exceeded 80%.

[2] Prohibited species are defined in the North Pacific Fishery Management Council's Gulf of Alaska and Bering Sea/Aleutian Groundfish Management Plans as, "those species and species groups the catching of which must be avoided while fishing for groundfish and which must be immediately returned to the sea with a minimum of injury when caught and brought aboard except when their retention is authorized by other applicable law".

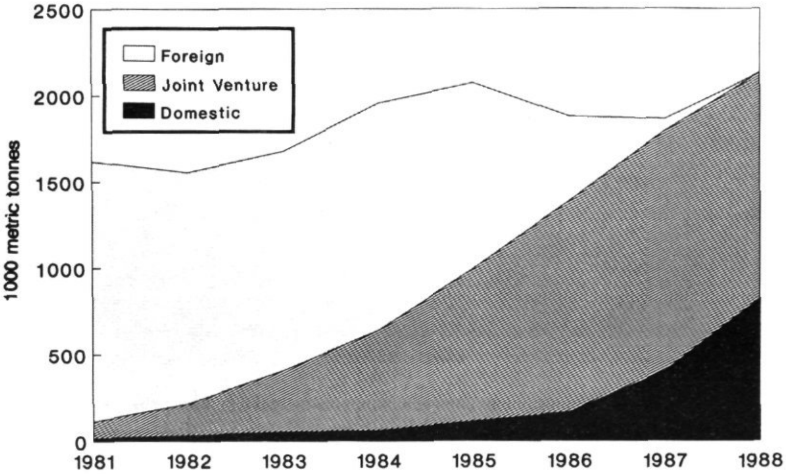

Figure 2. Alaska groundfish catch by fleet, 1981–1988.

analyses. The simulation model is similar to PROBUB, described by Laevastu and Larkins (1981). Seventeen ecological groups and/or species were included in the model. The most abundant fish species, such as pollock, yellowfin sole, and Pacific cod, were included as separate species. An initial simulation was used to determine an internally consistent solution of biomasses and food composition under current fishing conditions, since considerable uncertainty is associated with the empirical data.

Once consistent biomasses and predation interactions were determined, the model was run at quarterly time-steps for 15 years. At each time-step, the biomass of individual groups was increased by the mean biomass growth rate determined from weight-at-age data. Biomass was simultaneously decreased by catch, predation mortalities from all other fish groups, birds and mammals, and by senescent mortalities. Predation is computed in each time-step and is dependent on the availability, suitability, and density of food. Recruitment to the exploitable stock was assumed to be constant and equal to the long-term mean.

Four density-dependent processes were included in the simulations. The degree of density dependence was kept at a low level to ensure that the model dynamics were determined primarily through predation interactions. These processes were:

1. Food density-dependent feeding. If the biomass of a food item changed, its fraction in the food composition of the predator species changed inversely.
2. Growth rate of the total biomass. The growth rate was made to increase as catch increased, representing the removal of older and slower growing fish from the population.
3. Senescent and fishing mortality interaction. Senescent mortality was assumed to decrease as fishing mortality increases, because fishing would remove individuals which would otherwise succumb to senescence.
4. Susceptibility of the fish to predation. When the growth rate of the biomass of the species increases and percentage of juveniles increases, the availability of the juvenile biomass to predation will also increase.

The biological model used is one of several available. Because of the complexity of the system and data limitations, there is no single model that has been validated. The purpose here is not to argue the merits of a specific biological model, but to use one as a caricature of the system to serve as a basis for a bioeconomic model in order to explore the implications of management.

Fishery submodel

A standard linear programming (LP) framework was selected for the fishery submodel. The objective function was structured to maximize economic returns (total product value minus fishing and processing costs less the value of the prohibited species caught) from the groundfish fisheries subject to a series of constraints on the total amount of each species available for harvest.[1]

The primary data requirements for the series of runs were (1) estimates of the annual catch per unit effort (c.p.u.e.) for the different target fisheries; (2) vessel operating and fixed costs; (3) distribution of species by

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[1] The value of prohibited species caught in groundfish fisheries was estimated by determining the number of years between when they are taken as by-catch and when they would enter the directed fishery, adjusting for growth and natural mortality, and applying the wholesale price to the estimated yield loss.

target fishery and product form; (4) product prices and recovery rates (i.e. conversion ratio from round weight to product form); and (5) values of the prohibited species (i.e. halibut, king crab, and Tanner crab) that must be discarded.

Six groups of groundfish were used: walleye pollock, Pacific cod, Greenland turbot/arrowtooth flounder, yellowfin sole/rock sole/other flatfish, Pacific ocean perch/rockfish, and sablefish. While operating in five different target fisheries, vessels harvest these groundfish stocks in addition to having by-catch including three prohibited species: Pacific halibut, red king crab, and Tanner crab. A target fishery was defined by the proportion of a given species in the total catch, using the proportions derived from data collected by Alaska Fisheries Science Center's Observer Program. The five target fisheries used in the model were midwater pollock fishery, a bottom pollock fishery, a flatfish fishery, a rock sole fishery, and a non-specific bottom fishery.

Initial c.p.u.e.s, in metric tonnes per hour, were estimated from observer data for vessels operating in these target fisheries in the eastern Bering Sea. As the projected total biomass of the species fluctuates over the 15-year time frame, the c.p.u.e. estimates change proportionally.[1]

The representative vessel used to model the fishing fleet was a medium-sized factory trawler. A vessel of this size can fish in a variety of fisheries and process a mix of product forms. Factory trawlers currently operating in the eastern Bering sea range in length from 40 to 108 m, with a median length of 68 m. The vessel was assumed to fish/process 240 days of the year and have a total crew of 30. Costs of operating a vessel were divided into fixed and variable components. Variable costs were further divided into harvesting costs that are dependent on c.p.u.e. and those that are not.

Fixed costs per vessel were those that occur irrespective of any fishing or processing activity, and include annual loan payments, insurance, overhead, and a reasonable return on investment. Changes in c.p.u.e.s would change the number of vessels projected in the fleet and thus the total amount of fixed costs for the industry.

Finished product prices and recovery rates were combined to provide estimated product prices per metric tonne of round weight. These estimates were derived from a variety of published and unpublished reports and tend to represent 1988 prices for various products.

Product forms for a given species were based upon the same source as the cost information. Pollock can be used in the production of fillets, surimi, and roe. Pacific cod is either processed into fillets or a head-and-gutted (H&G) product. The remainder of the groundfish species was assumed to be primarily an H&G product, although some of the rockfish can also be processed into fillets. Product prices by species were assumed to be the same regardless of the target fishery responsible for the harvest. The proportion and mix of species by target fishery were derived from data provided by the Observer Program for the 1988 eastern Bering Sea fisheries.

The groundfish trawl fleet is not permitted to retain its incidental harvest of halibut or crab, and thus harvest of these species was presumed discarded and not processed into any product form. The value of by-catch of these species was calculated with 1988 wholesale prices and subtracted from the revenue generated by the groundfish fleet.

Given a series of constraints on the total amount of each species available for harvest across all fisheries, the associated costs and the proportion of products and species for individual target fisheries, the LP locates the combination of catch levels for individual species within target fisheries that generates the highest annual economic return for a given year.

Experimental cases

Simulation experiments were conducted under the following sets of conditions:

Case 1. Groundfish catches by species constrained to be less than or equal to the $F_{0.1}$ exploitation rate times the biomass determined, with by-catches of Pacific halibut, red king crab, and Tanner crab unrestricted.[2]

Case 2. Groundfish catches by species constrained to be less than or equal to the $F_{0.1}$ exploitation rate times the biomass determined, with by-catches of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4 400 t, 158.8 t, and 624 t, respectively.

Case 3. Groundfish catches constrained to be less than or equal to the 1989 Total Allowable Catches, with by-catches of Pacific halibut, red king crab, and Tanner crab unrestricted.[3]

Case 4. Groundfish catches constrained to be less than or equal to the 1989 Total Allowable Catches, with by-catches of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4 400 t, 158.8 t, and 624 t, respectively.

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[1] The limiting nature of this adjustment was recognized. Future versions of the model will contain more realistic functional forms.

[2] $F_{0.1}$ is the fishing mortality rate that reduces catch per unit effort to one-tenth of the value that would be observed if stock biomass were at its pristine level.

[3] Total Allowable Catches (TACs) in 1989 for the eastern Bering Sea by species are: pollock (1 340 000 t), Pacific cod (230 681 t), yellowfin sole (182 675 t), Greenland turbot (8 000 t), arrowtooth flounder (6 000 t), rock sole (90 762 t), other flatfish (75 183 t), sablefish (2 800 t), Pacific ocean perch (5 000 t), and other rockfish (400 t).

Table 1. Comparison of biomass trends for major species categories, in 1000 tonnes.

	Case 1		Case 2	
Species	Year 1	Year 15	Year 1	Year 15
Pollock	12 284	12 611	12 282	12 613
Cod	959	1 021	989	1 023
Flatfish	1 548	1 555	1 606	1 632
Halibut	73	74	74	75
King crab	59	59	59	59
Tanner crab	118	118	118	118

Year 1 represents end-of-year projection. Flatfish: yellowfin sole, rock sole, and other flatfish.
Case 1: Groundfish catches constrained to be less than or equal to the $F_{0.1}$ exploitation rate times the biomass, with no by-catch restrictions on Pacific halibut, red king crab, or Tanner crab. Case 2: Same exploitation rate as in Case 1 but with the additional constraints on by-catch, with the catch of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4400 t, 159 t, and 624 t, respectively.

Results

Biological results

Biomass estimates for the three prohibited species at the end of the 15-year projections were either unchanged or slightly higher than the initial biomass estimates for all four cases (Tables 1 and 2). Imposition of the by-catch constraints in Cases 2 and 4 did cause a slight increase in the Pacific halibut biomass over the unconstrained Cases 1 and 3, but red king crab and Tanner crab biomasses were virtually unchanged.

Catch levels of both groundfish and prohibited species increased over the 15-year time period in Case 1 (Table 3). In Case 2, although catch levels for groundfish stocks did increase in year 15 over year 1, Pacific cod and flatfish harvest levels were lower than in Case 1.

Table 2. Comparison of biomass trends for major species categories, in 1000 tonnes.

	Case 3		Case 4	
Species	Year 1	Year 15	Year 1	Year 15
Pollock	13 690	13 696	13 689	13 694
Cod	1 010	1 039	1 010	1 039
Flatfish	1 506	1 490	1 600	1 623
Halibut	74	75	74	75
King crab	59	59	59	59
Tanner crab	117	118	117	118

Year 1 represents end-of-year projection. Flatfish: yellowfin sole, rock sole and other flatfish.
Case 3: Groundfish catches constrained to be less than or equal to the 1989 total allowable catches with no by-catch restrictions on Pacific halibut, red king crab, or Tanner crab. Case 4: Same groundfish catch constraints as in Case 3; but with the additional constraints on by-catch, with the catch of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4400 t, 159 t, and 624 t, respectively.

Table 3. Comparison of catch trends for major species categories, in tonnes.

	Case 1		Case 2	
Species	Year 1	Year 15	Year 1	Year 15
Pollock	3 107 859	3 190 613	3 107 394	3 191 215
Cod	297 444	316 492	275 720	276 046
Flatfish	244 551	245 755	117 897	117 935
Halibut	5 006	5 304	4 400	4 400
King crab	263	269	159	159
Tanner crab	789	820	579	579

Year 1 represents end-of-year projection. Flatfish: yellowfin sole, rock sole, and other flatfish.
Case 1: Groundfish catches constrained to be less than or equal to the $F_{0.1}$ exploitation rate times the biomass, with no by-catch restrictions on Pacific halibut, red king crab, or Tanner crab. Case 2: Same exploitation rate as in Case 1 but with the additional constraints on by-catch, with the catch of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4400 t, 159 t, and 624 t, respectively.

In Cases 3 and 4, the 1989 TAC catch levels for groundfish stocks acted as a binding constraint for the major species and thus harvest remained constant over the 15-year horizon (Table 4). In Case 4, the binding nature of the red king crab by-catch restriction caused a further reduction in the flatfish catch.

Fishery impacts

By-catch constraints reduced economic returns when groundfish catches were restricted to both $F_{0.1}$ and TAC levels, i.e. Cases 2 and 4, respectively. In the initial year of the simulation, the reduction was larger for the former case. The reduction in economic returns was

Table 4. Comparison of catch trends for major species categories, in tonnes.

	Case 3		Case 4	
Species	Year 1	Year 15	Year 1	Year 15
Pollock	1 340 000	1 340 000	1 340 000	1 340 000
Cod	230 681	230 681	230 681	230 681
Flatfish	348 620	348 620	129 656	129 656
Halibut	4 280	4 280	3 824	3 824
King crab	330	330	159	159
Tanner crab	839	839	537	537

Year 1 represents end-of-year projection. Flatfish: yellowfin sole, rock sole, and other flatfish.
Case 3: Groundfish catches constrained to be less than or equal to the 1989 total allowable catches with no by-catch restrictions on Pacific halibut, red king crab, or Tanner crab. Case 4: Same groundfish catch constraints as in Case 3; but with the additional constraints on by-catch, with the catch of Pacific halibut, red king crab, and Tanner crab restricted to be less than or equal to 4400 t, 159 t, and 624 t, respectively.
With the relatively low catch restrictions in these cases, the catch constraints on the major species were all binding, and thus catch was identical in all years of the model run.

fairly constant over the 15-year time horizon when groundfish catches were constrained to 1989 TAC levels (Case 3 minus Case 4). Differences between economic returns for Cases 1 and 2, while fluctuating over the 15 years, exhibited a downward trend. The difference for the first year of the simulation when contrasted with that for the last year of the simulation was found to be 21% less. When the average difference in economic returns between Cases 1 and 2 was compared with those for Cases 3 and 4, the former was 11% higher than the latter.

Sensitivity analysis

A basic assumption of LP models is that the parameters are known with certainty. Since the actual values used are estimates, a standard procedure is to use the fundamental relationships from the simplex method to analyse whether the optimal solutions are sensitive to changes in the original data. Sensitivity analysis was conducted for independent changes in some of the parameters of the objective function and for the right-hand side values of the constraints (on the amount of each species or species group that can be caught).

Although the objective function value changed, the optimal solution, in terms of target fisheries and species mix, was not very sensitive to changes in either of the constraints. Changes of 100% in either direction still resulted in all fishing activity being concentrated in the midwater pollock, flatfish, and non-specific bottom fisheries, with their constant proportion of species mix.

The optimal solution was also tested for changes in the prices of primary products and for changes in the relative c.p.u.e.s among fisheries. Prices for pollock fillets and surimi had to drop 47% before the catch became concentrated primarily in the yellowfin sole and non-specific bottom fisheries, with cod becoming the most valuable species. For decreases of less than 30% in the cod and yellowfin H&G products, the optimal mix remained the same. Further drops forced even more of the catch into the midwater pollock fishery.

The model appeared most sensitive to changes in the relative rankings of the c.p.u.e.s. A 10% drop in the initial c.p.u.e. for the yellowfin sole fishery resulted in fishing activity occurring in only the midwater pollock and non-specific bottom fisheries. A 28% drop in midwater pollock fishery allowed for harvesting to occur in the bottom fishery in addition to yellowfin sole and non-specific bottom fisheries.

A more complete sensitivity analysis of all parameters will be done after further refinement of the model's structures has taken place.

Discussion and conclusions

Before attempting to discuss the results outlined above, it is necessary to note that this study represents a first attempt at modeling a complex system with sparse data and limited knowledge of important processes. As previously indicated, the biological model is one of several that could have been used; and because of the complexity of the system and data limitations, there is no single model that has been validated. Considerable refinement of the model is required before it can be used for policy decision making purposes. The sensitivity of the results to relaxation of the constant recruitment assumption must be explored. Data currently are being collected that will allow modification of the objective function to include target Pacific halibut and crab fisheries.

Biomasses for each of the prohibited species were either unchanged or slightly higher with the imposition of by-catch restrictions in this analysis. This behavior was considered due to the level of exploitation allowed on groundfish stocks. It is possible that more intense harvesting of groundfish species would be required to impact the prohibited species biomasses.

The behavior of the annual difference in economic returns for Cases 1 and 2 stems from increases in the biomass of some groundfish stocks when by-catch constraints were imposed. The binding nature of groundfish catches constraints coupled with those placed on prohibited species is responsible for the lack of variation in the annual difference in economic returns for Cases 3 and 4.

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A simulation model of artisanal fisheries of Senegal

Francis Laloë and Alassane Samba

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A simulation model was designed to correspond to a Senegalese artisanal fishery. Each fishing unit has a strategy, and at a given time chooses a tactic from a set of available tactics, according to a decision rule taking into account expected "revenues". The multispecies resource is modelled with simple stock production models, assuming quantities of biomass are inaccessible, depending on the resource component, season, and tactic. We compare the results of two simulations with the same number of fishing units, the same gears, and the same resource, but with different strategies. One set of strategies has smaller sets of tactics available than the other. Results indicate the importance of flexibility of the fishermen, which must be taken into account in management studies.

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Introduction

Artisanal fishing is of major social and economic interest in Senegal. A yearly catch of about 200 000 tonnes is made by about 4000 fishing units.

Exploitation patterns of several species show marked changes during the last 20 years, which, in some cases, cannot be explained within the classical population dynamics paradigm, which assumes that fishing mortality changes are due to changes in overall fishing activity. The number of fishing units remained quite stable and, with the exception of the purse seines, there was little technological innovation as a result of fisheries "development programmes".

Analysis of data collected by CRODT since 1974 (field investigation of more than 100 000 "one-day fishing trips" and daily fishing effort data) indicates that changes in exploitation pattern between species may have resulted from tactical choices of fishermen. These changes may sometimes be related to modifications in socio-economic or environmental conditions (Laloë and Samba, 1989). In other words, in a context of stable potential fishing effort, fishermen have changed the distribution of fishing mortality among exploitable stocks. This problem was identified by Garrod (1973). In this paper, we give a description of a multispecies–multigear system which may be subject to changes in the multispecies pattern of fishing mortality due to environmental effects on the resource and the fishery. In such a fishery, it is not valid to assume a long-term state of equilibrium that could *a fortiori* be seen as an "optimum", because fishermen have their own strategy, a consequence of which is variations in the fishing mortality applied to each exploitable stock. The ability of fishermen to adapt is probably necessary to success in this type of fishery and needs to be taken into account in fishery management (Laloë *et al.*, 1989).

We present the simulation model that was designed to correspond to a Senegalese artisanal fishery; that is, the model simulates activity and behaves analogously to the Senegalese artisanal fishery, and it reproduces the evolution of the fishery (Laloë and Samba, 1989). The model takes into account fleet dynamics characteristics, a need identified by Hilborn and Ledbetter (1979) and Hilborn (1985); it is also a useful tool for exploring the behaviour of fisheries as dynamic systems (Allen and McGlade, 1986; Hilborn and Walters, 1987; Charuau and Biseau, 1989).

The model

The activity of each fishing unit produces fishing mortality (which may be nil) on each exploitable component of the resource. That mortality depends on the tactic used, which is chosen from a set of available tactics. A "strategy" is a set of available tactics and the "decision rule" which leads to the adoption of one of them at a given time.

Description of fishing tactics

Two fishing trips are considered to have adopted the same tactic if they generate impacts on resource com-

Table 1. Definition of strategies related to available tactics.

Tactic	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	Number of units
Strategy																			
Gillnets	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	100
Hand lines (Kayar)	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	150
Hand lines (Saint-Louis)	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1000
Hand lines (south)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1800
Glacières	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	0	0	150
Glacières-seines	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	100
Seines	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	80
Seines (south)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	250
Industry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100

ponents which can be simply added (impact of tactic (j) during month (m) will be for example computed from the number of daily fishing trips using that tactic during that month; the fishing units which make those trips do not necessarily have the same strategy).

In our example we distinguish 18 fishing tactics, each of them corresponding to a combination of gear, target species, and geographical location. The first six tactics (a–f) correspond to hand lines. As an example, tactic (a) is fishing with hand lines on rocky bottoms along the northern coast of Senegal; the target species are mostly members of the serranidae family ("tiofs"), even if catches are possible on some other components of the resource. Tactics (g) and (h) correspond to hand lines with ice on board ("glacières") along the northern or southern coasts of Senegal. Tactics (i), (j), and (k) correspond to different uses of purse seines, and tactics (l) and (m) to different uses of gillnets. Tactic (n) means "agriculture" and tactics (o), (p), and (q) correspond to "no fishing". These latter tactics are introduced because fishing units may sometimes choose to do something other than fishing. The last tactic, r, "industry", is introduced to take into account catches made by industrial fisheries. Daily cost of fishing (Cj) or "non-fishing revenue" (NFR_j, to take into account opportunity costs) are given with each fishing or non-fishing tactic; they are used to estimate "net revenues" from the use of each tactic.

Description of fishing units by strategies

Two fishing units have the same strategy if, at a given time, they have the same probability of choosing each of the possible tactics (two fishing units with the same strategy do not necessarily use the same tactic at a given time).

Table 1 describes nine strategies with sets of available tactics. As an example, it can be seen that hand liners from Kayar may practise agriculture while hand liners from Saint-Louis cannot, but the latter have a wider choice of fishing tactics. The last column of Table 1 shows the number of fishing units with the corresponding strategy (as an example 1000 fishing units have the "hand lines from Saint-Louis" strategy). Some fishing units may use more than one gear, such as gillnets or hand lines, with or without ice (strategy "glacière").

Description of the resource

A component of the resource is a set of one or more populations. The state of that set is specified by one quantity ("biomass"), with a simple stock production model used to describe its dynamics. We used stock production models because of their low parameter requirements and the nature of our available information (in another context, a simulation model with analytical description of stocks dynamics was built by Charuau and Biseau (1989)).

Table 2 describes 11 resource components, or target groups, of one or more species. These descriptions were made using qualitative and quantitative information on artisanal and industrial fisheries in Senegal and Mauritania.

The principle of the simulation

Each month, fishing activity is distributed among the different tactics. The number of trips using tactic j during a month m ($f_{j,m}$) may be computed from the proportions $p_{kj,m}$ of units of k^{th} strategy using tactic j during month m, the number of units of each strategy and the number of workable days in a month.

Knowing $f_{j,m}$ values and the state $B_{i,m-1}$ of each resource component at the beginning of month m, we model B_i and estimate its mean biomass values ($Bm_{i,m}$) during that month from:

$$dB_{it}/dt = H_i \times B_{it} \times (B_{it} - Bv_i) - \\ - \sum_{j=1}^{18} q_{ij} \times f_{j,m} \times (B_{it} - \alpha_{ij,m} \times Bv_i)$$

where the H_i's are functions ($H_i = -4 \times MSY_i/Bv_i^2$) of the unfished biomass and potential yields (Table 2). This equation differs from the Graham–Schaefer model by assuming the existence of an inaccessible quantity of

Table 2. Characteristics of the 11 resource components.

Stock	Observed yields (t)	Natural mortality	Virgin biomass (t)	Potential yield (t)	Price/kg (F.CFA)
Tiofs	4 000	0.3	33 333	5 000	400
Pageots	9 000	0.5	40 000	10 000	220
Chinchards	50 000	0.5	200 000	50 000	100
Dentés	2 500	0.4	20 000	4 000	200
Tassergal	7 000	0.3	66 666	10 000	220
Sardinelles	70 000	1.0	150 000	75 000	70
Sole	1 000	0.5	5 000	1 250	400
Gillnet fishes	3 000	0.4	20 000	4 000	150
South demersals	50 000	0.4	300 000	60 000	250
South pelagics	140 000	0.8	375 000	150 000	50
Out south Senegal	14 000	0.4	100 000	20 000	100

Table 3. Catchability coefficients (10^6) for the 18 tactics with the 11 components of the resource.

	Stock										
Tactic	1	2	3	4	5	6	7	8	9	10	11
a	3	1	1	0	1	0	0	0	0	0	0
b	1	3	1	0	1	0	0	0	0	0	0
c	1	1	1	2	0	0	0	0	0	0	0
d	1	1	1	0	3	0	0	0	0	0	0
e	0	0	0	0	0	0	0	0	0.5	0	0
f	0	0	0	0	0	0	0	0	0	0	4
g	5	1	1	1	1	0	0	0	0	0	0
h	0	0	0	0	0	0	0	0	1	0	0
i	0	0	0	0	40	0	0	0	0	0	0
j	0	0	30	0	0	25	0	0	0	0	0
k	0	0	0	0	0	0	0	0	0	10	0
l	0	0	0	0	0	0	1	5	0	0	0
m	0	0	0	0	0	0	30	1	0	0	0
n	0	0	0	0	0	0	0	0	0	0	0
o	0	0	0	0	0	0	0	0	0	0	0
p	0	0	0	0	0	0	0	0	0	0	0
q	0	0	0	0	0	0	0	0	0	0	0
r	5	20	20	10	6	30	0	0	5	3	15

Table 4. Monthly proportion (α) of the unfished biomass of the tiof resource component inaccessible to tactics (those values only concern tactics which permit catches of tiof).

Tactic	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Glacières (g)	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Others (a–d)	0.1	0.1	0.1	0.1	0.1	0.2	0.4	0.4	0.4	0.2	0.1	0.1
Industry (r)	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

biomass ($\alpha_{ij,m} \times Bv_i$) that can be expressed as a proportion $\alpha_{ij,m}$ of the unfished biomass. We used this equation because it allows for "local over-exploitation" which may be important within the short range of the canoe fishery (Fréon, 1986), and because the catch-effort equilibrium curves are analogous to Pella and Tomlinson curves with exponents lower than 2 if α is greater than 0. This would not be the case if inaccessible biomass was a proportion of "current" biomass. This model is described in more detail by Laloë (1988).

In a given month m, we assume that quantity $\alpha_{ij,m} \times Bv_i$ depends on the resource component i, the tactic j, and the season. Each q_{ij} value is the "catchability" of the available biomass of the i^{th} resource component with tactic j (Table 3).

Values of $\alpha_{ij,m}$ were chosen in order to reproduce observed catches per trips and their seasonalities. As an example, inaccessible proportions of the "tiof" unfished biomass are given in Table 4. Lower accessibility (higher α values) for the "tiof" from June to October is assumed to affect only hand liners that have a shorter operating range than "glacières" or industrial vessels.

Table 5. Definition of strategies related to available tactics (second simulation).

Tactic	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	Number of units
Strategy																			
Gillnets	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	100
Hand lines (Kayar)	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	150
Hand lines (Saint-Louis)	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1000
Hand lines (south)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1800
Glacières	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	150
Glacières-seines	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	100
Seines	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	80
Seines (south)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	250
Industry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100

At a "high frequency level" (from one month to another) changes in effort distribution may come from changes in $p_{kj,m}$ values. Values of p_{kj} at month m+1 are computed from p_{kj} at month m and "net revenues" ($\mathcal{R}_{j,m+1}$) expected from available information by fishermen for each tactic j. Those expected revenues are computed from observed "net revenues" during months m and m−11 (one year earlier):

$$\mathcal{R}_{j,m+1} = (R_{j,m} + R_{j,m-11})/2$$

with

$$R_{j,m} = \sum_{i=1}^{11} P_i \times q_{ij} \times (Bm_{i,m} - \alpha_{ij,m} \times Bv_i) - C_j$$

for fishing tactics and $R_{j,m} = NFR_j$ for non-fishing tactics. Results from former years are used to take into account the fishermen's knowledge of global annual periodicity of stock availability.

$p_{kj,m}$ values may then be computed from:

$$p_{kj,m+1} = p_{kj,m} + \lambda \times (\mathcal{R}_{j,m+1} - \bar{\mathcal{R}}_{k,m+1})/\bar{\mathcal{R}}_{k,m+1}$$

where $\bar{\mathcal{R}}_{k,m+1}$ is the mean of expected revenue calculated with the set of tactics available to units having strategy k. If necessary, some transformations are made in order to ensure that $0 \leq p_{kj,m} \leq 1$ and $\Sigma_j\, p_{kj,m} = 1$. The parameter λ is a flexibility parameter whose value must be chosen in relation to the time-step used (a month in our example). We took a value $\lambda = 1.5$ from very simple considerations: if there are only two available tactics, one of which gives an expected revenue twice that of the other, the increase in the proportion of units which will choose the "best" tactic will be 0.5.

At lower frequency levels, changes in effort may come from changes in number of units, strategy definitions, or in parameter values (e.g. prices, costs, availabilities, etc.).

We made a 13-year simulation with the following initialization: all biomass initial values ($B_{i,o}$) were half of the unfished values and, for each strategy, all $p_{kj,o}$ values were assumed to be equals. At certain times during the 13-year period we changed some parameter values in order to introduce observed or assumed changes in general fishermen and resource environment. These changes are discussed below.

Until the beginning of the sixth year, catchabilities of tactics (f), (g), (i), and (j) are nil; use of these tactics occurred at that time. At the beginning of the seventh year, catchability of tactic (d) decreases from 3×10^{-6} to 2×10^{-6}; this corresponds to the collaboration between hand liners and seiners (i) which search for "tassergal" (bluefish) along the northern coast of Senegal.

At the beginning of the ninth year, catchability of industrials (r) on "chinchard" (horse mackerel) is multiplied by 2 in order to reproduce the corresponding increase in effort of industrial fishery on that particular target group.

At the beginning of the tenth year, the price of "dentés" increases from 200 to 400 F.CFA/kg. The prohibitive cost (60 000 F.CFA) of tactic (m) (gillnets searching for sole) decreases to the "normal" cost of 4000 F.CFA. This could simulate an authorization of the use of that prohibited tactic in the town of Kayar. Availability of tassergal for all concerned artisanal tactics decreases to take into account an empirically observed relation with upwelling intensity in Senegal and Mauritania. Values of α lower than 0.6 were arbitrarily increased to this value.

Results

Throughout the simulation, we tried to reproduce the observations we had made (catches per trip, number of trips, and their time paths). We did not use any quantitative fitting methods, but instead looked for a resemblance to the observed situations.

The simulation gave quite acceptable results in the sense that we could find what we were looking for, with little tuning of parameters. Some aspects could have been improved, especially regarding the number of

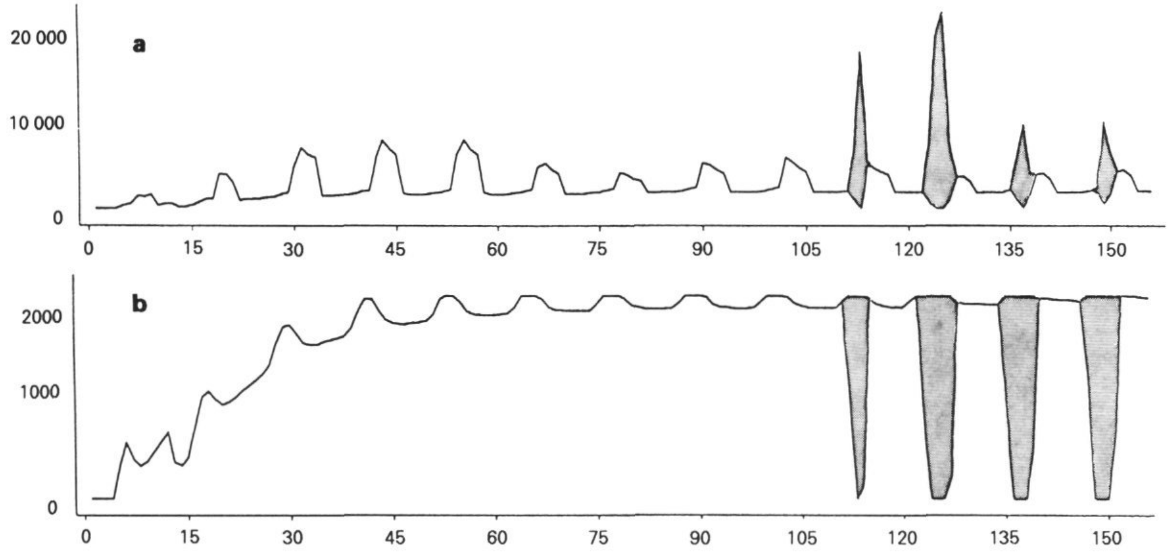

Figure 1. Monthly number of daily trips with tactic (m) (gillnets targeting sole, shaded) and (1) (gillnets targeting other fishes). a: first simulation; b: second simulation.

trips, which appear to have been higher than we know from the real situation. The problem may perhaps be in the excessive versatility of this kind of simulation model: in order to obtain a more satisfying result, the user of the model may choose between many solutions, and it is difficult to say which of them is the best one (if any). Such a model must therefore be used with caution and with the help of biologists, economists, environmentalists, and sociologists with a good knowledge of the fishery being simulated.

We also found some unexpected results, which are perhaps the most interesting. As an example, the hand line c.p.u.e. with the "dentés" target group showed a seasonal pattern which gave higher values when its accessibility was at a low level! This effect results because the seasonal patterns in accessibility of other target groups are more contrasted.

We made a second simulation of another fishery, using the same resource components, the same types of gear and the same number of fishing units. The difference was in strategies; there were fewer choices between tactics (Table 5). Tactics which do not appear in this

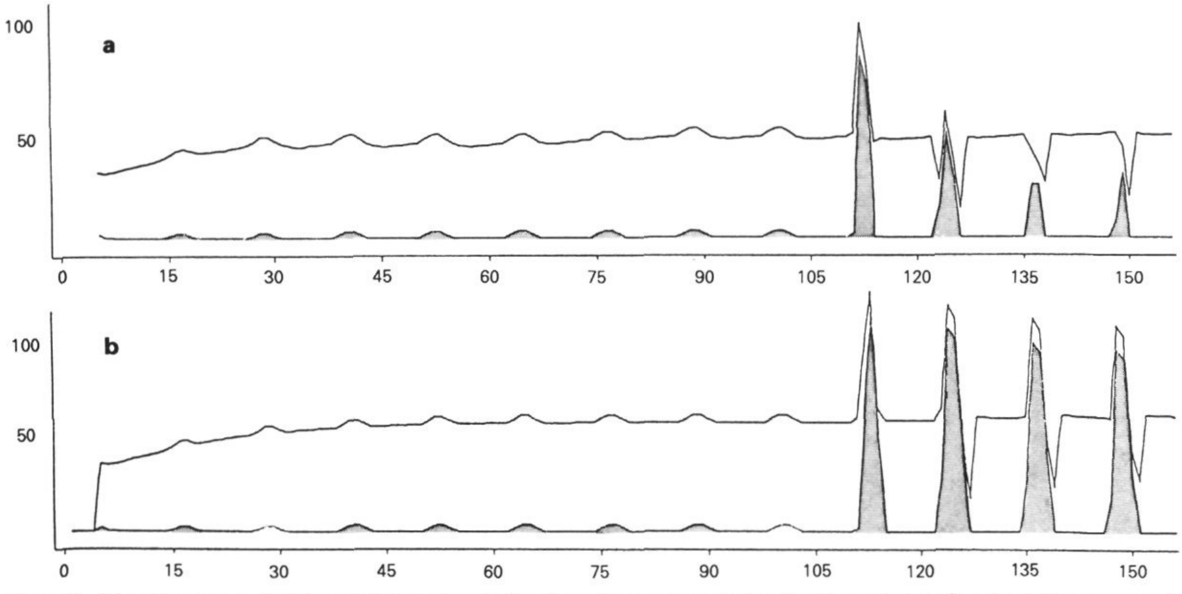

Figure 2. Monthly c.p.u.e. (kg) for sole (shaded) and other fishes from aggregated tactics (l) and (m). a: first simulation; b: second simulation.

second simulation are some of those which were not introduced through "Fisheries development programmes", or promoted by scientific studies.

Results indicate that this second fishery does not work as well as the first one; number of days at sea is lower, as well as total yield and aggregated revenues.

We show in Figure 1 the monthly number of trips with tactics (l) and (m) (gillnets targeting gillnet fishes or sole). In Figure 2 we show the evolution of the c.p.u.e. (kg) in the sole and gillnet fishes from these two aggregated tactics. One can see different possible impacts caused by the authorization of tactic m.

In the first simulation, effort becomes considerable (up to 20 000 trips per month) during the tenth and eleventh years, which leads to an over-exploitation phenomenon and low c.p.u.e. During the last two years, we observe a strong decrease in effort on sole.

In the second simulation, use of tactic (m) is much lower, because only 100 fishing units (see Table 5) can use this tactic. The consequence is an under-exploitation rate which is stable during the last four years of the simulation. This example highlights the consequence in terms of "autoregulation capacity" of flexibility.

Conclusion

While our model must be improved in order to reliably describe the behaviour of a flexible multispecies, multigear fishery, the results demonstrate that stock assessment and *a fortiori* management are not adequate if we neglect the flexibility of fishermen.

In our study, we had a considerable amount of data that provided evidence of flexibility and gave good information on spatial-temporal catches and efforts. We tried to offer a descriptive framework which takes into account characteristics of fleet dynamics and interactions between components of the fishery system. We hope to have been at least partly successful, but we also found a need for more satisfactory descriptions and classifications. As an example, definition of our "flexibility parameter" λ is perhaps too simplistic and its value too arbitrarily fixed. Research effort must be maintained to improve the description of that part of the system in order to enhance the global framework which is necessary to a better use and understanding of the available information.

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Management of multispecies fisheries with chaotic population dynamics

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The economic and management implications of chaotic population dynamics are explored in a multispecies fishery model with community predation. The model includes an explicit constraint on the total carrying capacity, which is enforced by reducing the young populations of all species. Simulations show that this constraint can yield a chaotic state, exhibiting characteristic attributes of many real multispecies ecosystems. In particular, within the chaotic state, compensation occurs, with growth in one or more species balanced by declines in others. Such correlated population patterns, combined with long-term variability in individual species population, are not generated by stochastic models. Here we emphasize the consequences of both biological and economic effects, including the impact of increased fishing effort, opportunistic fishing, restricting age of first capture, and altering consumer preferences. Our results suggest the potential utility of market-oriented policies and the possible pitfalls of strategies based upon population predictions in managing chaotic systems.

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1. Introduction

Unpredictable recruitment poses a major challenge to effective fisheries management. In this paper we examine a bioeconomic model that reproduces this observed variability, as well as other major attributes of multispecies systems. The model is a dynamic simulator based on a set of difference equations which exhibit deterministic chaos, periodicity, and steady-state solutions.

In Section 2, we outline the biological components of the model: spawning, growth, and mortality for each species combined with a total carrying capacity limit. This limit explicitly restricts the size of the fishery, linking the age classes of all species and creating an intricate system-wide density dependence. In our simulations, the mechanism used to maintain the carrying capacity limit is intended to mimic community predation of pre-recruits of all species (Sissenwine, 1986). The dynamics of the biological sector of this model show that, in the chaotic regime only, three observed tendencies of multispecies systems are replicated. It exhibits relative stability of the total biomass with highly variable species populations; it is energy efficient, and it exhibits interspecies compensation. Thus, the general characteristics of this deterministic chaotic population dynamics produce a multispecies picture consistent with the dynamic attributes of real systems.

The presence of chaos raises fundamental questions about fisheries management. If fisheries populations are indeed chaotic, then the problem of prediction and control of fisheries may be qualitatively similar to the problem of predicting the weather, for example. A chaotic environment implies limited predictability and requires extremely demanding measurement capabilities for effective manipulative control. Therefore, as a practical matter, a chaotic ecosystem would appear to require reliance on management that is beneficially adaptive rather than manipulative. Further, the most complete knowledge of the system that is practically obtainable may well be its broad or typical ecological patterns with the possibility of detailed predictions being effectively ruled out.

The third section, consequently, reports on certain kinds of patterns that occur in a simulated chaotic

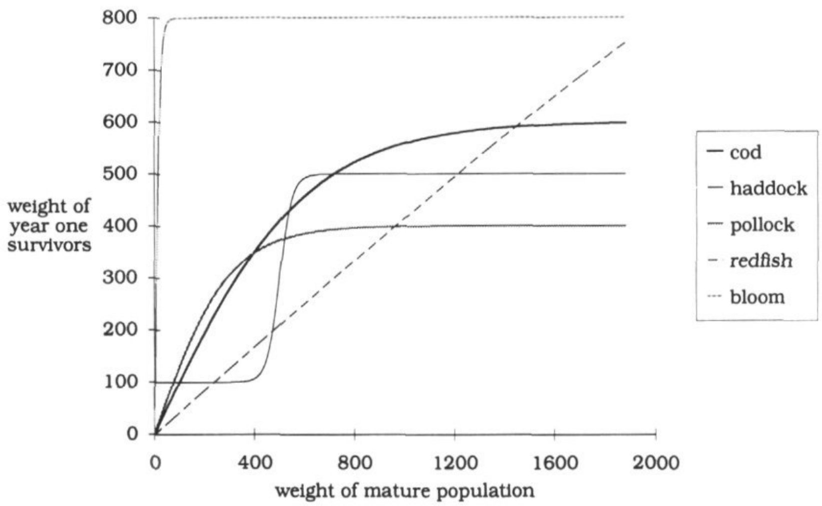

Figure 1. Spawning-survivor curves determine initial age zero numbers for each species.

fisheries system. To demonstrate this, we describe a multispecies population simulator that includes an economic component (Wilson *et al.*, 1990) and then illustrate the simulator's reaction to exploitation under a variety of conditions. Economic elements in the model calculations described in Section 3 include a five-dimensional production possibilities simulation. On the basis of each year's relative abundance and consumer preferences (the elasticity of substitution), the production possibilities simulator determines the allocation of fishing effort, consumption by species, and relative species prices.

Within this biological and economic framework, we test various management schemes. The results are presented in Section 4. The biological and economic sectors of the simulator can interact in non-linear ways to produce behavior quite different from that predicted by models emphasizing equilibrium concepts.

2. The biological simulator

Our initial research efforts sought to investigate appropriate management measures given unpredictable recruitment to fisheries populations. We had no theories about the source of unpredictability, but simply wished to take unpredictability as a biological given and then address what we saw as essentially an economic question. Consequently, we set about creating a plausible but unpredictable biological environment in which we intended to explore the economic questions of interest. From Hennemuth (1979), Sissenwine (1986), Bax and Laevastu (1990), Laurence (in press) studies of multispecies fisheries we extracted a set of dynamic attributes that appear to be typical of these systems. Such systems tend to:

(1) show relative stability of the overall biomass in the presence of unpredictable, highly variable component species populations;
(2) be energy efficient, i.e. food limited or "tight"; and
(3) reflect a high degree of internal consumption of fish by the fish community, or community predation, that should cause negative feed-back leading to interspecific compensation.

Our objective was to produce a simulator with plausible biological mechanisms that qualitatively replicated these dynamic attributes. We were not interested in developing a simulator that replicates the data of an actual fishery. We were simply looking for a typical, or generic, system.

On the basis of the same literature we constructed a conventional age-structured multispecies simulator and added a total biomass, or carrying capacity, constraint (Hennemuth, 1979), that is enforced via a process of community predation, described below. Without the addition of any randomness and for a wide range of parameter values, the simulator generates population time paths that are deterministically chaotic. It is only in the chaotic state that the simulator is capable of fulfilling the dynamic attributes, or criteria, listed above, for a multispecies system. Consequently, to the extent that the mechanisms and parameter values used are considered plausible, the simulator suggests the potential for chaotic behavior in real fisheries systems.

The simulator is constructed as follows: There are five age-structured populations. For each population there is a spawning-survivor curve that determines the number of fish that spawn and survive the first year in the absence of community predation (Fig. 1). The size of each successive year class of a species is equal to the number of fish in that year class from the preceding year, reduced

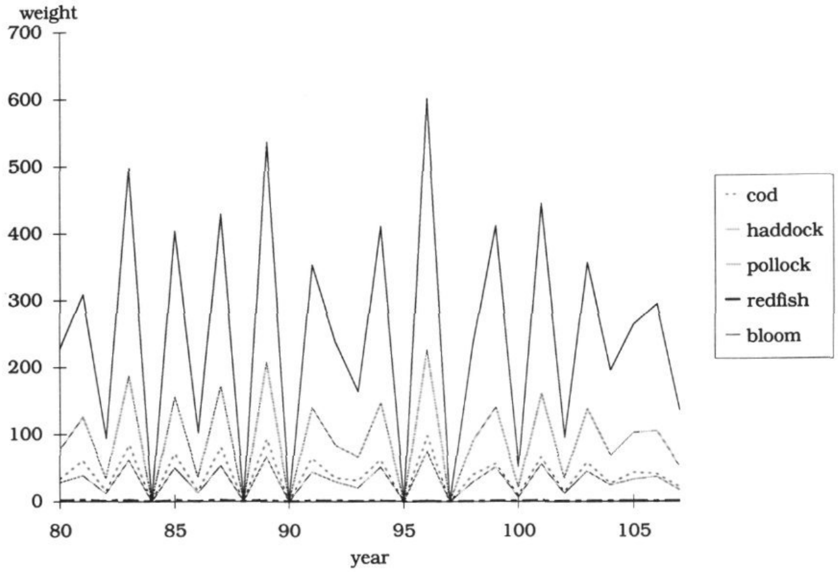

Figure 2. Age zero survivors with community predation proportional to age zero class strength.

by natural mortality (taken to be a constant after age one) and fishing mortality (if present). The weight of each year class is determined by a von Bertalanffy growth equation. The growth, mortality, and spawning parameters of four of the five species are chosen to approximate a typical groundfish aggregation. For convenience only we named the first four species cod, haddock, pollock, and redfish. The fifth species, "bloom", is a very fast-growing fish with a high rate of natural mortality. In the combined bioeconomic simulator, "bloom" is used to represent the unexploited part of the biomass.

The only interaction among the five species occurs through effects on recruitment which might be caused by community predation. We define community predation as a system-wide density-dependent factor influencing the mortality of age zero fish of all species. In other words, when resources become scarce, mortality through predation increases among young fish exclusively. The rate of community predation for all age zero fish as a group (but not the allocation of mortality among species) is determined by the relationship of total system weight and the limiting weight associated with the system's carrying capacity. There are a number of ways the rate of total community predation can be formulated. In the simplest formulation we use, the rate is determined in three discrete steps: (1) If in any year the weight of all year classes of all species is less than the carrying capacity constraint, the constraint has no effect on the system. (2) If total weight exceeds the carrying capacity, the numbers of fish progressing from age zero (determined by the spawning-survivor functions) to age one is reduced until the weight of the newly determined number of age one fish plus all other fish together satisfies the carrying capacity. (3) If all age one fish of all species are eliminated and the constraint is still not satisfied, the weight of the system is allowed to temporarily exceed the carrying capacity. Alternative formulations of the rate of community predation that treat community predation as (1) an exponentially or (2) a linearly increasing function of system weight produce qualitatively similar dynamic patterns.

The rule for allocating community predation among species is very important to the characteristic behavior of the system. For example, when a simple rule that allocates mortality in proportion to each species' age zero class strength is used, the year classes of all species tend to vary in phase, as does total system weight (Fig. 2). Under this allocation rule the dynamic behavior of the system can be chaotic, but nevertheless exhibits none of the attributes typical of a multispecies system. On the other hand, an allocation rule that (1) treats the age zero fish of each species as differently susceptible to community predation and (2) treats the species-specific rate of mortality as a function of the state of the entire system (rather than the relevant population) can generate dynamic behavior consistent with multispecies system attributes.[1] When these two general aspects are incorporated in the rule governing the allocation of mortality due to community predation (and given other parameter values described below), community predation has a stabilizing effect on the entire system, but from year to year produces highly variable age zero

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[1] In addition, to avoid or to minimize the possibility of extinction, susceptibility to community predation must be roughly correlated with spawning potential.

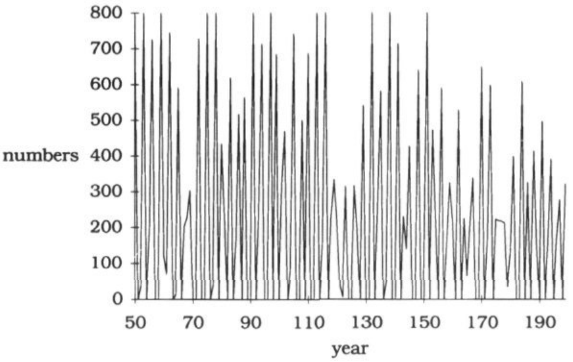

Figure 3. Number of age one, "bloom" species with carrying capacity 8000.

mortality and year class strengths among individual populations. Figure 3 shows a typical time series of survivors to age one for the "bloom" species; Figure 4 gives similar information for cod in the form of a spawning stock/recruitment graph. Associated with species variability is interspecies compensation (Fig. 5). This occurs because of the system-wide negative feed-back created by community predation which also tends to keep total system weight close to the carrying capacity of the system (Fig. 6). In short, the simulator generates behavior consistent with the real world attributes of at least some multispecies systems.

Any number of specific mechanisms for the allocation of age zero mortality, for example, a rule based on data from stomach content analysis, could satisfy these conditions. Additionally, mortality due to community predation need not be limited to age zero fish so long as these conditions are met. For the results reported here, however, we have used a very simple algorithm in order to keep the analysis of simulator output tractable.[1]

Depending on parameter values for the remainder of the system, the simulator produces a wide range of dynamic patterns. These patterns or solutions can be steady state, periodic, quasi-periodic, chaotic, or a mixture of the above where, for example, some populations are in a steady state and others show periodic and/or chaotic attributes. In general, the nature of the dynamic solution depends upon the relationship between the maximum attainable weight of all species together and the system limiting weight associated with the system's carrying capacity. When the parameters of the system are chosen so that the maximum attainable weight of the system is less than the carrying capacity, community predation does not occur and the system exhibits steady-state behavior. When the maximum attainable weight of the system is in the vicinity of the carrying capacity, periodic or quasi-periodic behavior is observed; and when the carrying capacity is well below the maximum attainable weight of the system, chaotic behavior occurs.[2] It is only in the chaotic state that the

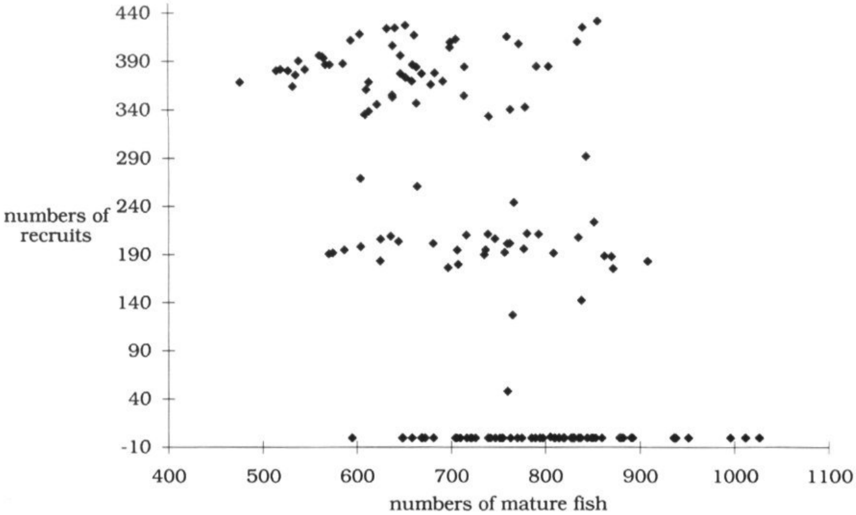

Figure 4. Cod recruitment. The grouping of recruitment into ranges is due to the characteristics of the community predation (age zero mortality) algorithm (cf. footnote 2).

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[1] The specific algorithm is as follows: whenever the system's total weight exceeds the carrying capacity, up to 75% of the spawning-survivors from the "bloom" species are reduced first. If the resulting weight of all species is still larger than the carrying capacity, then up to 50% of the spawning-survivors from first cod, then pollock and finally haddock are eliminated. Then 25% of the slow-growing redfish spawning-survivors are reduced. This sequence is followed repetitiously until the carrying capacity constraint is met or until there are no age zero fish remaining. In the latter case, the total weight of the system is allowed to temporarily exceed the carrying capacity.

[2] When linear or exponential carrying capacity functions are used, community predation occurs continuously and generates chaotic behavior.

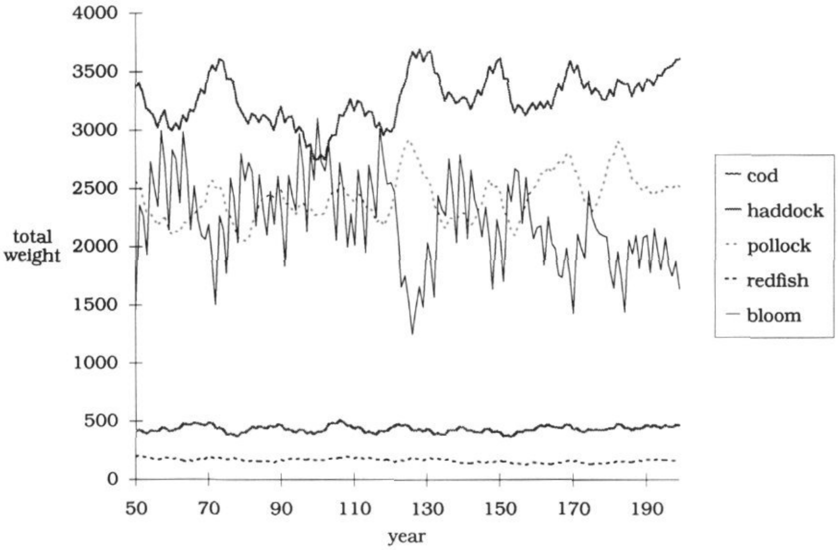

Figure 5. Chaotic regime. No fishing is included.

simulator fulfils the dynamic attributes of real world multispecies systems.

The dynamic process that generates this chaotic behavior is rather straightforward. For example, in any given year, the distribution of fish among the age classes of the five species will lead to a particular net growth in the total weight of the system. If this growth is slow (e.g. a preponderance of older, slower-growing fish), the total system weight may not reach (or may exceed only slightly) the carrying capacity. As a result, mortality due to community predation will be zero (or low). If on the other hand, the age class distribution leads to rapid growth, total system weight may greatly exceed the carrying capacity and the subsequent amount of community predation among young fish may be very high. This process leads to continually changing year-class strengths and, of course, variable populations.

In summary, our explorations of the biological simulator have attempted to determine the minimum conditions necessary to replicate qualitatively the dynamic attributes of a typical multispecies system. We find that these conditions can be met by a simulator that:

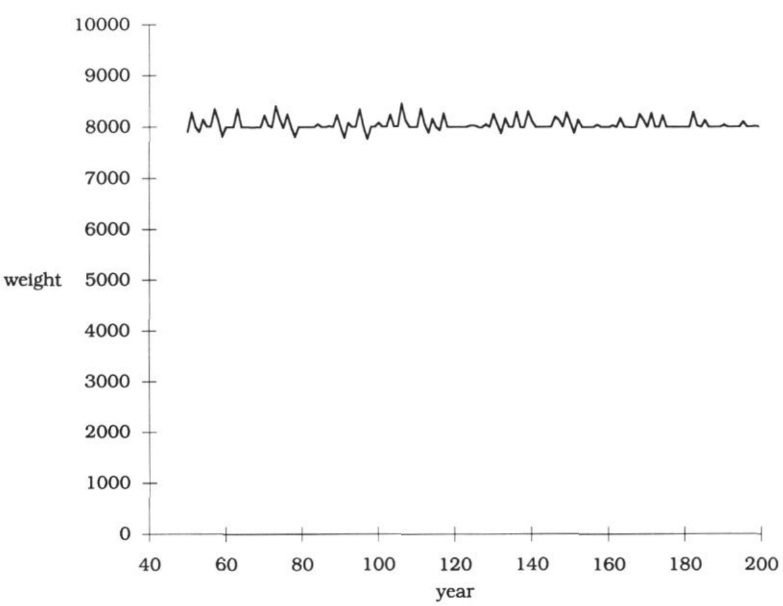

Figure 6. Total biomass for the five species shown in Figure 5.

(1) incorporates conventional spawning, growth, and post-recruit mortality functions for each (differentiated) species,
(2) includes a system-carrying capacity constraint,
(3) includes a community predation mechanism in which the total rate of pre-recruit mortality is determined by the relationship of total system weight and system-carrying capacity,
(4) allocates mortality due to community predation in a way that results in different pre-recruit mortality rates by species, and
(5) employs parameters (for spawning, growth, and mortality) whose values cause the maximum weight attainable by the system to exceed its carrying capacity.

The process of community predation is central to the dynamic behavior of the system. For the system as a whole community predation has the effect of a density-dependent stabilizer. For individual populations, however, community predation tends to be destabilizing because it increases or decreases the pre-recruit mortality of a population according to factors unrelated to the state or condition of the individual population. As a result, strong or weak year classes can appear at almost any time and, although there is a clear relationship between the size of the spawning population and initial numbers of age zero fish, there is no clear relationship that develops between spawners and recruits. Year-class strength is established as a result of community predation. The chaotic properties of the model are quite robust and persist over a wide range of parameter values and alternative specifications so long as the minimal conditions listed above are met.

3. The bioeconomic simulator

The bioeconomic simulator consists of the biological simulator just described with an economic component included. The latter assumes fishermen are profit maximizers who are free to allocate their effort according to the price and abundance of each species. Each year fisherman's decisions impact the biological component of the simulator by changing the allocation of fishing effort and, consequently, fishing mortality by species.

The economic component is implemented as a five-dimensional, elliptical version of production possibilities theory (Fig. 7). In any given year the allocation of fishing effort is determined by the relative prices of species (shown constant in Fig. 7), and the production possibilities curve. The shape of the production possibilities curve is determined by the abundance of each species in a given year. The ellipse shape shows the diminishing returns fishermen experience in a single year when more effort is directed at a single stock. The optimal economic allocation of effort occurs when the returns to harvesting each species are proportional to the relative prices of the species. This is shown as points E1 (for one year) and E2 (for some other year in which the abundance of the two stocks is different) in the diagram. In year 1 harvests of A1 of stock A and B1 of stock B occur. In the other year harvests of A2 and B2 occur.

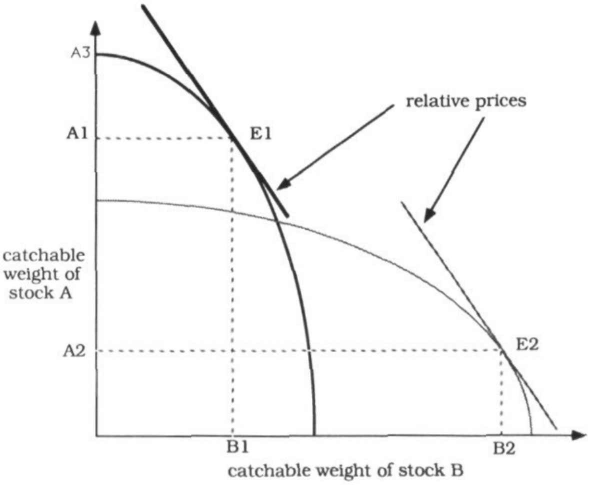

Figure 7. The economic submodel.

Prices are determined endogenously as the result of the simultaneous interplay of supply (harvest) and demand (consumption). Just as fishermen use prices to determine their allocation of fishing effort given relative abundance, consumers use prices to determine the allocation of their expenditures by species given their preferences. Preferences determine consumers' willingness to substitute one species for another in the market. If the price of a species rises, consumers switch from this species to others. The rate of switching in response to price changes is termed the elasticity of substitution.

The economic component can be modified to simulate a number of different conditions or policies in the fishery. For example, different consumer habits can be simulated by changing the elasticity of substitution. Mesh-size policies can be simulated by changing the age at first capture. Quotas can be implemented by limiting the catch of one or more species according to a particular rule, and so on.

Fishing effort is also adjustable. The simulator defines effort as the percentage of the catchable population of a particular species that would be caught if all fishing were directed at that species. Effort is indexed so that one unit of effort results in a 10% fishing mortality on one species if all effort were directed at that species, 20% equals two units, etc. In other words, at effort level two, if all boats in the fleet directed all their activity at one species, 20% of that species and nothing of other species would be caught in one year. If that same fishing effort were spread among all four exploited species it would reduce the effect of the diminishing returns. Consequently, rather than 5% of each of the four species being caught anywhere from 6 to 10% might be landed, depending on relative prices. For example, in Figure 7, A3 corresponds to the allocation of all effort to one species, E1 to an (optimal) allocation spread among the two species. Our definitions of effort can be roughly translated into catch rates: when effort is set at 10 (the maximum required to completely reduce a single population), catch rates for the four exploited species are typically in the range of 60% to 70%, of the post-recruit population. At effort levels of 2, as mentioned, catch rates are in the range of 6% to 10%.

This definition of effort departs from the usual formulation in fisheries models in which fishing effort and instantaneous fishing mortality are proportional. The conceptual advantage of our approach is that it allows for diminishing returns in the harvesting process for economic (i.e. market or price-related) as well as stock-related reasons. Consequently, it permits the endogenous determination of the allocation of effort in response to changes in both relative prices and species abundance.

4. Results

By varying parameters in the biological and economic sectors, an extremely wide range of different conditions and/or policies can be simulated. We report here only the results of simulations that we feel are relatively general in their applicability. That is, we believe that these results are not limited to particular states of consumer preferences or particular population parameters. Four general cases are considered. The results discussed below report data from the last 150 years of a 200-year simulation; data from the first 50 years are discarded to eliminate the effects of initial conditions.

4.1. The effects of increasing effort with different carrying capacities

Increased fishing is generally thought to increase the variability of fished populations. On the other hand (in our simulator), fishing increases total mortality and, to a certain extent, replaces mortality from community predation. This reduces the maximum attainable weight of the system. Consequently, heavy fishing could cause the system to slip out of the chaotic state and into a stable, steady-state system not typical of a multispecies fishery. For these reasons we wanted to look at the effects of varying fishing and carrying capacity. The runs reported included randomness in the spawning functions in order to avoid steady-state behavior with heavy fishing.

Figures 8 to 10 summarize the consequences of changing fishing effort under different carrying capacity conditions, with limits of 3000, 8000, and 20 000 weight units, respectively. The three sets of graphs represent situations in which chaotic effects persist over all levels of effort (3000 weight units); chaotic effects diminish as effort is increased (8000 weight units); and chaotic effects are only present at low levels of effort (20 000 weight units).[1] The age of first capture (cf. below) is set at the age of reproductive maturity for each species.

In an unfished system, the maximum attainable weight of all species occurs in the neighborhood of 24 000 weight units. If the carrying capacity constraint is set at a level above 24 000 weight units, the constraint is never activated. When the constraint is set at levels below 24 000 units, the total weight of the system grows to a level sufficient to activate the constraint. The lower the constraint, the more frequently the system weight exceeds the constraint. Fishing increases mortality and reduces the rate of growth of the weight of the system, so that any given carrying capacity constraint is less frequently activated.

Figures 8, 9, and 10 present average catches of each species at various effort levels for each carrying capacity constraint. Additionally, they show the coefficient of variation (i.e. the ratio of the standard deviation to the mean) for each species at various effort levels for each carrying capacity constraint. These three figures also present the frequency with which the carrying capacity constraint is activated for each effort level. In all three cases, higher levels of fishing effort lead to a moderate decline in average catch, and, more noticeably, an increase in the variability of the catch. In the runs with carrying capacities of 8000 and 20 000 (Figs. 9 and 10) variability increases with increases in fishing effort as expected. In both cases the range of variability (with heavy fishing) is approximately the same. When the carrying capacity is set at 3000, however, the same patterns are observed except that the magnitude of the variability is 50–100% greater (Fig. 8). The difference is attributable solely to the fact that at a carrying capacity of 3000 the system remains chaotic and conforms to all the dynamic criteria for a multispecies system. At 8000 and 20 000 heavy fishing causes chaotic effects to diminish and disappear; the principal source of variance that remains is from the randomness introduced in the spawning functions and that is the same at all carrying capacities. We conclude from this that fishing creates much greater variability when the system is still capable of attaining its carrying capacity. Under these circumstances system-wide density-dependent effects still occur and destabilize individual populations.

4.2. The effects of allowing opportunistic fishing

The income of multispecies fishermen in real fisheries rarely fluctuates as much as the catch of any given

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[1] Note that the units of weight here are arbitrary and have meaning only in terms of the potential weight attainable by the entire system.

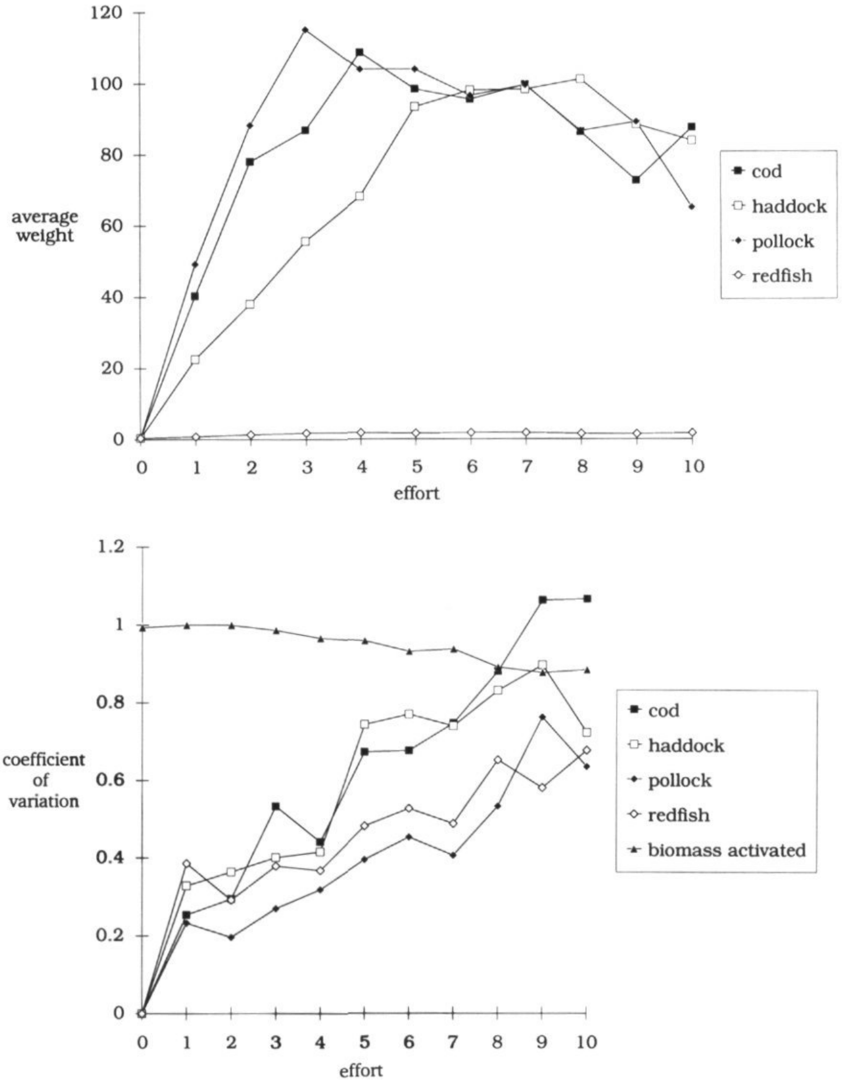

Figure 8. (a) Catch vs. effort and (b) variability of catch vs. effort, with carrying capacity 3000. "Biomass activated" refers to the percentage of time the total biomass of all species reaches the carrying capacity of the system and activates the community predation process.

species (J. A. Wilson *et al.*, in press). Two reasons can be offered for this: First, there are compensating price changes; when catch is low price is often high (and vice versa). Second, fishermen respond to changes in the availability of different species from year to year and season to season by altering the mix of their catch (i.e. opportunistically switching from species to species) (Acheson, 1988). Both of these effects contribute to greater stability of income. In our simulator, the total weight of the system is more stable than the weight of any single species, as observed in real fisheries (Hennemuth, 1979). It is natural to hypothesize that fishermen's switching is an adaptive response to interspecies compensation effects. If the cod population, for instance, is declining, one or more of the other species must be increasing according to the simulator. To help determine whether this behavior (1) is rational and (2) has positive or negative biological effects, at least in the confines of our simulator, we compared simulations in which fishermen were free to switch from species to species with simulations in which fishing effort on each species is set at a fixed level. In both sets of simulations a substantial change was made in the economic component of the simulator. Relative prices were held constant in order to isolate the allocative effects of changing abundance. This corresponds with a situation in which prices are established in a large market, of which the simulated fishery is a small part. Additionally, to facilitate comparisons average catch rates for the switching and non-switching cases were set equal. The

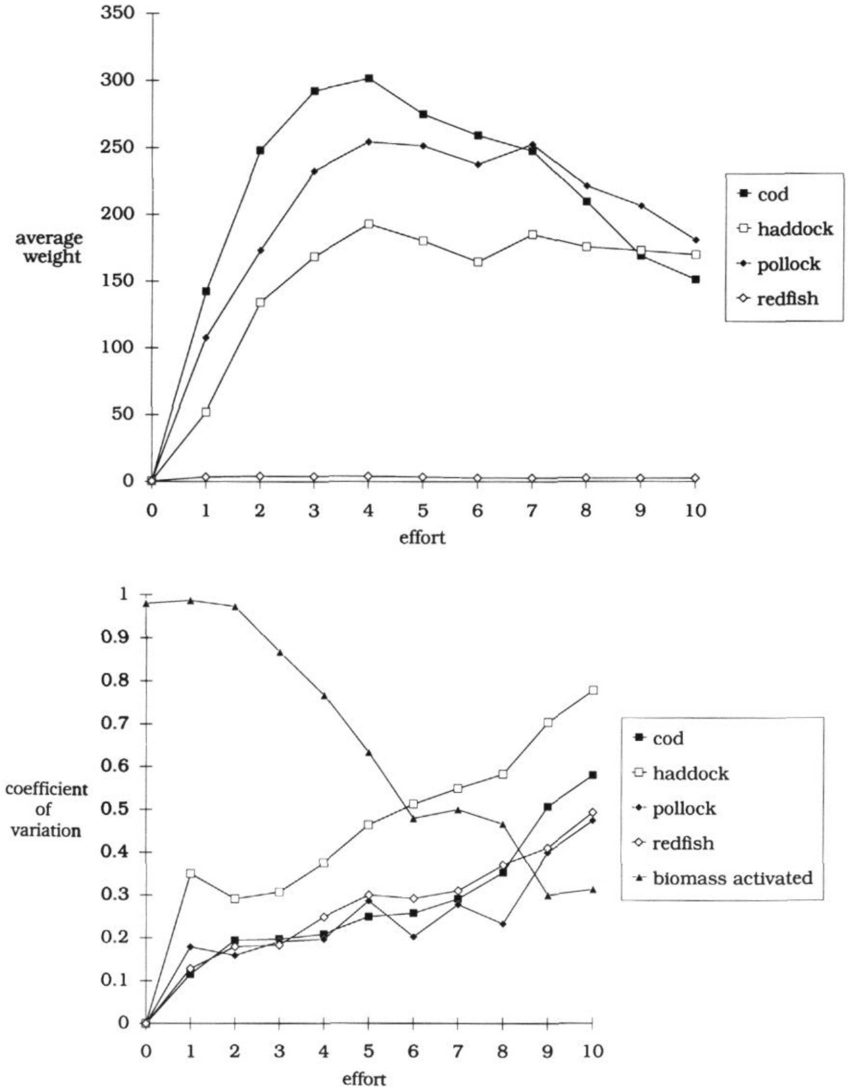

Figure 9. (a) Catch vs. effort and (b) variability of catch vs. effort, with carrying capacity 8000. "Biomass activated" refers to the percentage of time the total biomass of all species reaches the carrying capacity of the system and activates the community predation process.

behavioral difference between these two cases is that with switching allowed, profit maximizing causes fishermen to reallocate effort toward the more abundant species in each year. In the non-switching case, effort is constant for each species over all the years (150) of each simulation.

Comparison of the two cases for a range of fishing efforts indicates that both biological and economic benefits accrue from switching behavior. At low levels of effort, average catch and income are roughly comparable in the two cases. (Since prices were held constant, catch and income are proportional.) However, the variability of the non-switching fishermen's income is 5–20% (of average income) higher. Individual species populations are comparable in size, but the variability of populations in the non-switching case is about one-third larger than with switching. In other words, although fishing increases population variability (as in result one reported above), with switching the increase in variability is much less. At very high levels of effort, these differences become more pronounced. Switching fishermen enjoy about 10% more income and the variability of that income is 35–45% lower than the income earned by non-switching fishermen (depending on which species they fish). The populations of each exploited species also benefit. The higher catch and income of switching fishermen, in spite of identical catch rates, derives from the fact that with switching the population of each species is higher than without. This occurs because switching leads to very selective harvesting patterns: basically, when a

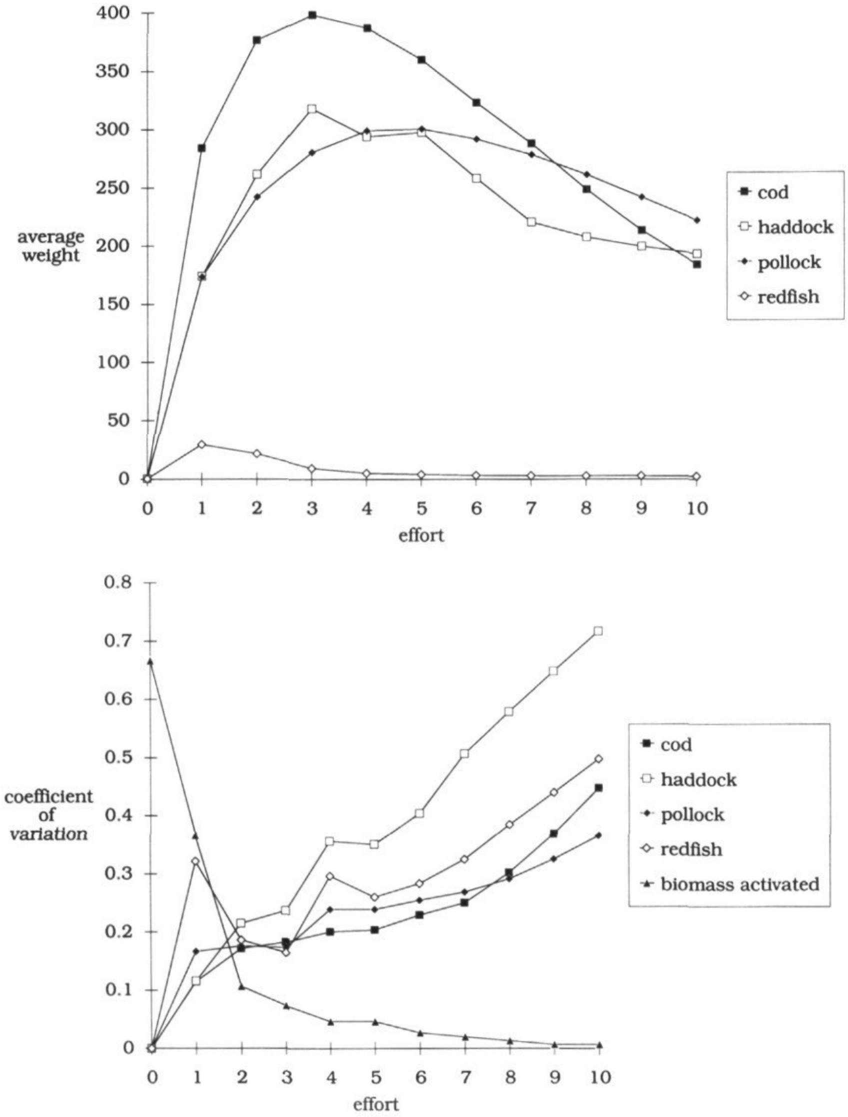

Figure 10. (a) Catch vs. effort and (b) variability of catch vs. effort, with carrying capacity 20 000. "Biomass activated" refers to the percentage of time the total biomass of all species reaches the carrying capacity of the system and activates the community predation process.

species is depressed, profitability declines and fishermen have an incentive to reallocate effort towards more abundant species. This, of course, has favorable biological effects. Note that with constant prices, shortages of a species in the market do not push up prices to encourage greater effort on the stock. Such price effects are examined in the next section.

4.3. The effects of market substitutability

Consumer response to changes in the market supplies of particular species (the elasticity of substitution) can also have strong effects on the allocation of fishing effort and on the outcomes in multispecies fisheries. If consumers are very responsive to price changes (i.e. easily change the kinds of fish they purchase), a drop in the supply of a given species will cause its price to rise but this rise will be tempered by the tendency of consumers to reallocate their expenditure to other, now less expensive, species. In this case, the elasticity of substitution is greater than one. On the other hand, if consumers are very habit bound and do not change their purchases easily in response to supply changes, a decline in the supply of a given species will be accompanied by a large (more than proportionate) increase in the price of the species. Here, the elasticity of substitution is less than one. These differing price effects impact on the profitability of fishing for one or another species and, as a result, the

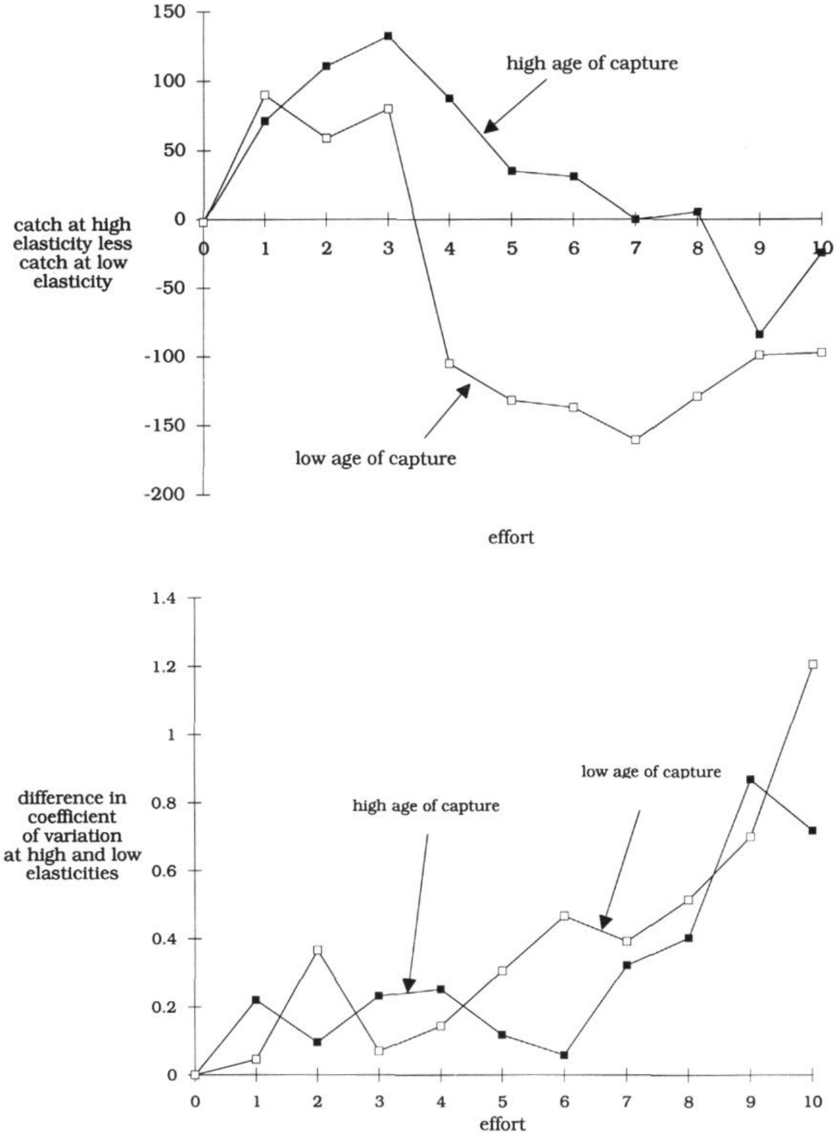

Figure 11. Differences in (a) total catch and (b) variance of total catch at high and low elasticities for two ages of capture.

allocation of fishing effort by species. From economic theory one would expect that when elasticity of substitution is high, declines in the supply of a species would lead to declines in profitability, a shift of effort away from that species and a tendency for the species to recover. Exactly the opposite would be expected to occur at low elasticities.

We tested this theoretical expectation by comparing runs of the simulator at differing values of the elasticity for a range of effort levels. The carrying capacity constraint was set at 3000 weight units so that chaos occurred at all levels of effort and age of first capture was set at one year below maturity. We found that at low and moderate levels of fishing, higher elasticities tend to result in larger populations and larger total catches, as expected. As effort increases, however, the favorable effects of high elasticities tend to disappear. This effect is apparently connected to the increasing variability of each species as effort increases (as noted above, see Figs. 8, 9, and 10). Because of the large differences in relative supplies of each species, at high effort levels, relative prices and, consequently, profitability result in high fishing mortality for less abundant species. Thus, the opportunities for recovery are limited. At low elasticities and high levels of effort, however, the catch rate of declining species remains very high (allowing little recovery), but the catch rate of relatively abundant species declines (allowing some recovery). Consequently, the

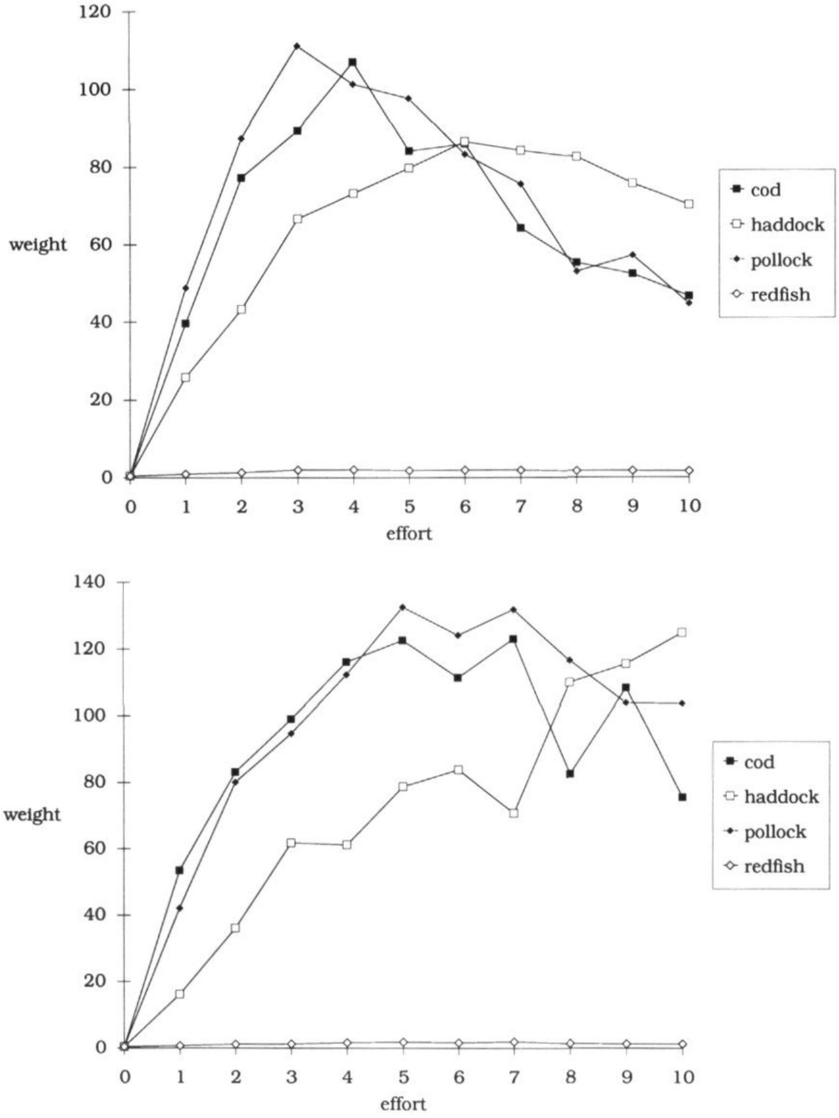

Figure 12. Catch vs. effort with age of capture (a) decreased and (b) increased.

long-term effects of low elasticity are more positive at high levels of effort (generally higher populations and catches).

To investigate these supply/price effects further, we re-ran the simulator, as above, but at an age of first capture one year above maturity. The effect of the increase in the age of first capture is to produce consistently higher supplies of all species at all levels of effort (cf. below). As expected, these larger supplies have the effect of extending the positive effects of high elasticities to higher levels of effort. Figures 11a and 11b summarize these results for both minimum age of capture at maturity ("low age of capture") and minimum age of capture one year above maturity ("high age of capture"). These figures show the differences between catch at high elasticity and catch at low elasticity. For example, at effort level two and with a high age of capture, total catch is about 65 weight units higher with high elasticities (Fig. 11a) and the coefficient of variation is about 0.1 units higher (Fig. 11b).

The anomalous behavior of the simulator at high levels of effort occurs because prices are allowed to range between zero and infinity. It is unlikely that real world markets would see the wide fluctuations in price produced by the simulator; imports or consumer behavioral changes would always temper extreme price fluctuations. With less extreme price fluctuations the benefits of high elasticities would be greater at high levels of fishing effort and more consistent with the theoretical expectation. In summary, the simulator indicates the

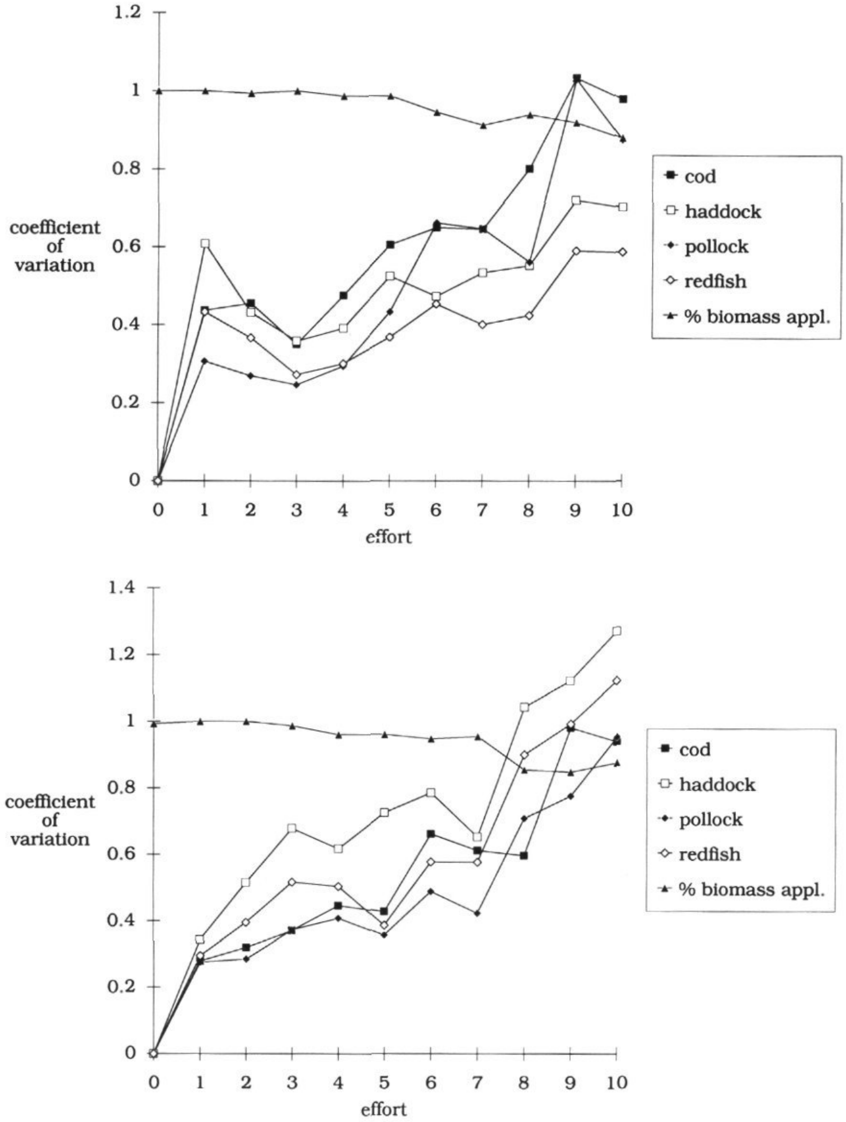

Figure 13. Variability in total weight with age of capture (a) decreased and (b) increased.

biological and economic importance of market conditions and the potential for market directed policies that might improve the harvesting environment of multi-species fisheries.

4.4. The effects of changes in age of first capture

Switching and consumer substitution are interesting phenomena because they cause a selective, and automatic, reallocation of effort as biological conditions change. Age of first capture or mesh-size rules produce similar automatic reallocations of fishing effort. Given the highly variable year-class strengths produced by the simulator, the effect of mesh rules is to create an annual, automatic reallocation of effort among year classes and species. In the literature, larger mesh sizes are invariably seen as efficacious. In our simulator, however, the process of community predation raises the possibility that more older and larger fish may raise the rate of community predation and lead to a reduction in recruitment. In order to test the effects of different mesh-size regulations, we ran the simulator allowing catch to be made on fish one year below maturity and older and, then, on fish one year above maturity and older.

Figures 12a and 12b summarize the results of typical runs. The minimum age of capture is one year below maturity in Figure 12a and one year above maturity in Figure 12b. The carrying-capacity constraint is 3000 weight units in both cases. Increasing the age of first capture by two years has strong positive effects on the abundance and catch of all the exploited species. Basically, abundance is higher at all levels of effort and especially so at high levels of effort. Because of interspecies compensation effects, the gains in total weight that are seen in the exploited populations arise at the expense of the unexploited species (so long as the system remains in a chaotic state). Interestingly, there are no significant effects upon the variability of catch, but increasing the age of capture does tend to reduce the variability in the total weight of each species. These trends are typical for a wide range of parameter values.

5. Implications of a chaotic system

The problem of prediction has been a theoretical and practical concern in fisheries science for a number of years. The possibility of chaotic behavior is therefore of interest for three principal reasons:

1. The limited predictive capability and the near absence of the ability to manipulate or control in a chaotic system has serious biological, social, and economic consequences for the practical management of fisheries. For example, any policy to avoid recruitment failure is usually based on the assumption of a known relationship between spawning biomass and recruitment. Policies such as quotas, effort limitations, and other measures designed to affect spawning biomass and ultimately recruitment are not costless social or economic policies. If, because of the predictability and control problem, the outcomes of such policies are unknown, then there is reason to question the imposition of the required social and economic costs of this kind of management. There may be alternative policies that produce automatic adaptive responses to changes in the system that work better in this kind of environment.
2. Unlike randomness, chaos is deterministic and, although not subject to prediction in the traditional use of the word, it does generate patterns. These patterns reflect the underlying ecological conditions in the system and impart a limited predictive potential. If a system is chaotic, then there is reason to attempt to discern its patterns. Furthermore, because such complex systems can generate a very large variety of behaviors, the search for patterns must be driven by knowledge of the probable mechanisms – both biological and socio-economic – operating in the system. Put differently, if the source of unpredictability is thought to be chaos (as opposed to randomness), then a research agenda emphasizing the ecological-economic interactions of the system is implied.
3. The behavior of chaotic systems may be suggestive of new policies for the management of fisheries systems. For example, one of the "patterns" reported above concerns the response of the system to changes in consumer substitutability. Since this response includes feed-back into the biological component of the system, there is the broad suggestion that biological management problems might be approached, at least in part, through economic- or market-oriented policies that would normally be considered totally removed from the biological component of the fishery.

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Application of an experimental approach to management of a tropical multispecies fishery with highly uncertain dynamics

K. J. Sainsbury

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In most multispecies fisheries there is considerable uncertainty in selection of an appropriate model to represent the dynamics of the resource. Many model structures and/or parameterizations may be consistent with ecological principles and the available data. These models may have very different management implications, but may be impossible to distinguish by process-oriented research at reasonable cost and on a time frame of relevance to management. In some circumstances an adaptive experimental management regime can be economically beneficial by allowing empirical learning about resource dynamics and discrimination between alternative models. However, in any particular situation it must be determined whether an experimental regime is economically viable, and which management actions and research observations should be included in the regime. The development and application of an experimental management regime for the fisheries operating on a tropical fish community in northwestern Australia are described. The history of exploitation is summarized and a number of simple models are suggested which can mimic past changes observed in fish community composition. These models include interspecific, intraspecific, and habitat modification mechanisms. Possible socio-economic responses of the fishing industry to changes in the resource state are important to evaluation of a prospective fishing regime, and these are also modelled. The models are used to evaluate options for management of competing trap and trawl fisheries on the Northwest Shelf. It was found that if an experimental management regime were adopted for about 5–15 years (during which time key uncertainties in the resource dynamics and socio-economic responses could be resolved) a larger expected value could be obtained from the resource than if the existing management regime were continued. Some experimental management regimes also provided a greater expected value than would be obtained from immediate application of the management regime that is optimal for any of the individual resource models. Experimental management periods of less than about 5 y did not allow sufficient resolution of uncertainties to be worthwhile, and periods of longer than about 15 y often resulted in the costs of obtaining the additional resolution exceeding the value of the expected improvement in returns from the resource.

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Managing the species composition of a fish community is fundamental to management of a multispecies fishery because species composition broadly determines the types of fishing industry that are possible and usually determines the gross economic value of the catch. However, the dynamics of marine communities are very poorly understood. There is little agreement even about the general class of mechanisms that drives community dynamics (e.g. Diamond and Case, 1986; Sainsbury, 1988), and in the available data mean it is often impossible to assess the validity of inferences drawn about these mechanisms (Schaffer, 1981; Gardner *et al.*, 1982; Sugihara *et al.*, 1984). Typically, ecological theory can be used to derive a number of different hypotheses about mechanisms and dynamics that are all consistent with the observations of an exploited community. The available data usually cannot support objective discrimination between the competing hypotheses because of confounding among supposed control variables (e.g. fishing patterns, technological developments, species abundances, and environmental variables), the aggregation of space, time, and species in most fisheries data, and the absence of some species from the observations. These problems occur in most fisheries but are particularly severe in tropical regions, where the harvested communities are very diverse and fishery data sets are often incomplete and contain highly aggregated data. Indeed, the profound lack of scientific understanding of the mechanisms controlling community structure and dynamics is perhaps best illustrated by the absence of a widely accepted explanation for one of the most obvious ecological features on earth: the latitudinal gradient in species diversity (see Stevens, 1989, for a recent review), of which the high species diversity of tropical fish communities is a part.

The lack of a widely accepted scientific theory of community dynamics and structure has two important implications for fishery management aimed at controlling the species composition of a harvested community:

(i) *A priori* it is not at all clear to what extent the species composition of a harvested community can be controlled by fishery management. Assumptions about "controllability" are obviously the basis for any management action (or lack thereof), but the value of resolving uncertainty in these assumptions is little considered.

(ii) Management decisions concerning community structure will be, and have been, made on the basis of assumptions that would not be widely accepted by the scientific community of ecologists because there is no widely accepted scientific theory of community dynamics. This weak scientific basis for management decision-making provides ample opportunities for criticism of any decision by opponents of that decision. Furthermore, it is very unlikely that process-oriented scientific research will provide clear answers to the questions of community dynamics on a time frame that is relevant to most management decisions and at reasonable cost (if at all). This is a serious dilemma for management agencies whose decisions are open to public scrutiny, and is probably a major reason why management of the species composition of exploited communities is usually not made an explicit management aim. Instead, management objectives are usually focused primarily on single species and the economic performance of individual fisheries, and community composition is left to emerge "naturally" from the decisions based on these reasonably tractable considerations.

A notable exception to this focus of management is provided by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which has among its aims the "maintenance of the ecological relationships between harvested, dependent and related populations" and "prevention of changes in the marine ecosystem which are not potentially reversible". However, these objectives have not resulted in management actions aimed at achieving a specified ecological community or a specified aspect of community dynamics. Rather, management actions have been based on single-species considerations and the few discussions of possible actions to meet the community level aims have simply highlighted the difficulties of reaching defensible management decisions when there is a high level of uncertainty in scientific understanding of resource dynamics (e.g. see CCAMLR 1989, pp. 41–45).

This paper describes an attempt to manage the species composition of an exploited fish community on the Northwest Shelf of tropical Australia, and particularly the way in which uncertainty was incorporated into the scientific evaluation of prospective management actions. The fish community has highly uncertain dynamics, and the socio-economic response of the fishing industry to changes in the fish community composition is also very uncertain. This paper provides the basis for scientific management advice given for the Northwest Shelf fisheries in 1985 and describes some of the subsequent management changes. Scientific advice to management was based on an experimental or actively adaptive approach (e.g. Bar-Shalom and Tse, 1976; Walters and Hilborn, 1976; Walters, 1986). In this approach, management actions are explicitly regarded as having dual aims: to provide an economic yield and to allow empirical learning about aspects of the dynamics of the resources that will lead to improved achievement of management aims. Prospective management actions are evaluated across alternative hypotheses about resource dynamics and monitoring schedules. The evaluations consider economic benefits, the value of distinguishing between the alternative hypotheses in leading to improved management decisions, the ability to distinguish between the alternative hypotheses on the basis of observations made under the proposed management action, and the cost of observations.

The paper is in three main sections: the first describes the ecological and fishery background to the Northwest Shelf resource and the management question that emerged; the second outlines the method used to evaluate management options; and the third identifies alternative models of resource dynamics, details the evaluation of some management options and describes the management actions taken. A simplification of the methodology is briefly described in Sainsbury (1988), but here the original calculations are described. In particular, the full set of models is described, details of model parameter estimation are provided, transient yields following experimental manipulation are included in the evaluations, and the economic uncertainties are treated more fully.

1. The Northwest Shelf and its fisheries

1.1. The Northwest Shelf

The continental shelf of northwestern Australia (between longitudes 114°E and 123°E to a depth of 200 m, Fig. 1) has a substrate consisting mostly of calcareous

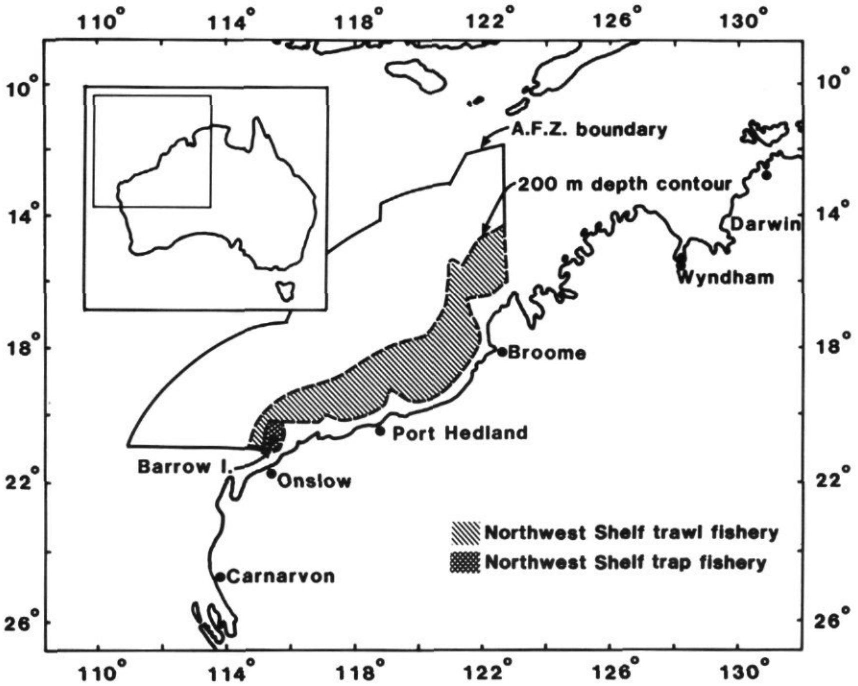

Figure 1. The 200-nmi Australian Fishing Zone, the 200-m depth contour and the Northwest Shelf. The Northwest Shelf region was defined by cluster analysis of the fish species composition recorded during research-vessel cruises in 1978–1980. The areas exploited by trap and trawl fisheries are also shown.

sands (Jones, 1973; McLoughlin and Young, 1985) with calcareous coral reef occurring only in restricted patches in depths less than about 30 m. The hydrographic regime is tropical (Wyrtki, 1961) and highly dynamic. Strong semidiurnal tides and internal tide waves cause high current speeds (Holloway, 1983a, b) and the vertical movement of isotherms through 50 m within some days (Holloway, 1987). The water column is well mixed between about May and October each year, and the annual temperature range is 21–26°C near the seabed at about mid-shelf (e.g. Holloway and Nye, 1985). Interannual variability of water temperature and sea-level height is strongly influenced by the El Nino–Southern Oscillation (Bye and Gordon, 1982; Pariwono *et al.*, 1986). Biological productivity is high (Tranter, 1962; Kabanova, 1968), and the diverse demersal fish community, comprising over 600 species, has strong Indo-West Pacific affinities (Sainsbury *et al.*, 1985). The Northwest Shelf supports a characteristic fish fauna that is clearly distinguishable from the tropical fauna to the east of 123°E by cluster analysis of the species composition of research vessel catches, and obviously different from the more temperate fauna of the west coast of Australia.

1.2. The fisheries of the Northwest Shelf

The histories of the fisheries on the Northwest Shelf are described in Sainsbury (1987). Briefly, they are:

(i) A Japanese trawl fishery from 1959 to 1963 targeted on fish of the genus *Lethrinus* (tropical emperor) and mostly operated between 116°E and 117°30′E (Fig. 2). *Lethrinus* comprised about half of the catch weight, and the catch rate did not decline during the period of the fishery (Suzuki *et al.*, 1964; Robins, 1969). However, there was a considerable change in the size composition of *Lethrinus*, with animals heavier than 0.6 kg disappearing from the catch after eight months of fishing (Suzuki *et al.*, 1964). This may have been due to the loss of *L. nebulosus* from the catch (Sainsbury, 1987). A total of about 7 600 h of trawling was exerted during the about 3-year duration of the fishery, for a total catch of about 16 700 t.

(ii) A Taiwanese trawl fishery from 1972 to the present takes a wide range of species. The retained catch mostly comprises the genera *Nemipterus* (threadfin bream), *Saurida* (lizard fish), *Lutjanus* (tropical snapper), and *Lethrinus* (Liu *et al.*, 1978). The fishery began in international waters and came under Australian jurisdiction in 1979 with declaration of the 200 nmi Australian Fishing Zone. The fishery has operated throughout the Northwest Shelf between depths of about 30 and 120 m, but effort has been particularly concentrated between 115°E and 120°E (Liu *et al.*, 1978). All fishing vessels are pair trawlers of 200–500 gross tons and have similar fishing power (Yeh and Chin, 1982); typically a pair of vessels 0.5 km apart tow a 30 m headline net on 850 m of wire cable. Codend mesh sizes of about 45 mm

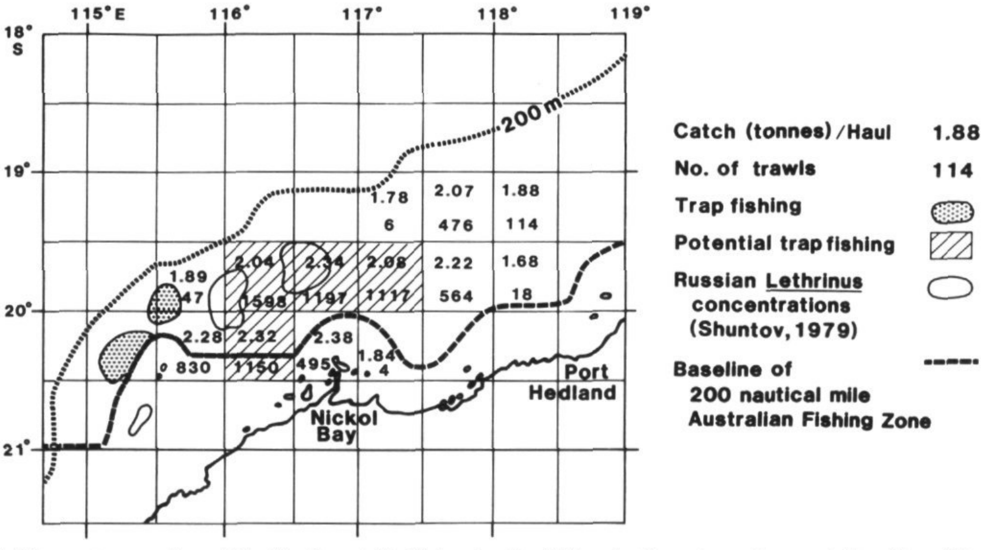

Figure 2. The western portion of the Northwest Shelf showing the 200-m depth contour, the coastal baseline of the Australian fishing zone, and fishery information from Japanese commercial fishing and Russian surveys. For each 30′ square the catch rate (upper figure) and number of trawls (lower figure) obtained by the Japanese fishery in 1959–1963 are given (after Robins, 1969); about half of all catches were of *Lethrinus*. The areas of high *Lethrinus* concentration identified during Russian research surveys in 1962–1973 (Shuntov, 1979) are also indicated.

were common until the introduction of a 60-mm minimum mesh size in 1981 (Sainsbury, 1984). A log-book programme to record fishing effort and retained catch by broad commercial category (generally at the generic level of taxon) was initiated by the National Taiwan University in 1974, and similar records have been collected by the Australian Federal Department of Primary Industry since 1979. There is no information on discards. Estimates of the catch and effort for 1972 and 1973 were compiled retrospectively by the National Taiwan University from the available fishing company log-books, but these data are not considered as reliable as those for later years (H. C. Liu, National Taiwan University, pers. comm.). Fishing effort increased rapidly to a peak of about 80 000 h of trawling in 1974, and subsequently declined to less than half this value (Table 1). Management of the pair trawl fishery since 1979 has been by total retained catch quota and minimum mesh size regulation. Both were calculated from combined analysis of a non-interacting, dynamic pool model for each of 10 major species groups (Sainsbury, 1984, 1987).

(iii) A domestic Australian trap fishery began in 1984, which targets fishes of the genera *Lethrinus* (mainly *L. nebulosus* and occasionally *L. choerorynchus*), *Lutjanus* (mainly *L. sebae*), together with the

Table 1. Fishing effort and retained catch (total and for four important genera, in tonnes) for the Taiwanese pairtrawl fishery on the Northwest Shelf. Data for 1972–1979 were obtained from annual reports of the National Taiwan University (Anon., 1972–1979) and for 1980–1985 from the Australian Department of Primary Industries and Energy database of fishing operations in the Australian Fishing Zone.

Year	Effort (h)	Total catch (T)	*Nemipterus*	*Saurida*	*Lethrinus*	*Lutjanus*
1972	500	272.0	39.2	16.1	29.9	33.5
1973	64 545	37 143.0	8 377.3	2 711.4	4 076.4	3 944.1
1974	79 860	31 256.3	7 934.7	4 276.4	2 653.3	2 784.8
1975	57 767	21 288.6	5 033.5	3 355.7	2 865.7	2 255.0
1976	46 592	18 929.2	4 530.9	3 061.9	1 840.7	805.3
1977	56 413	19 080.0	4 517.9	3 199.4	2 000.0	1 333.3
1978	40 998	14 488.3	3 431.5	1 951.9	1 701.2	1 351.3
1979	33 500	10 764.0	2 168.5	1 937.2	753.6	707.7
1980	36 173	12 512.6	3 663.6	886.3	1 707.1	1 332.1
1981	30 652	10 929.2	4 007.9	733.6	1 162.0	1 057.8
1982	38 991	13 418.1	3 884.4	558.4	1 855.1	1 886.6
1983	29 890	9 745.4	3 634.4	386.5	1 113.8	1 137.5
1984	32 743	8 899.7	3 286.5	525.1	791.9	1 372.4
1985	27 974	7 237.2	2 370.8	532.1	725.5	1 025.5

Table 2. The year, mean total catch rate ($\mathrm{kg\,h^{-1}}$), mean catch rate for the main taxa, number of trawls (N), and net headline length (m) for nine research surveys of the central Northwest Shelf (116–119°E). for each of four taxa the mean catch rate ($\mathrm{kg\,h^{-1}}$) is reported and the relative abundance (percentage of the total mean catch rate) is given in parentheses.

Vessel and source	Year	Total catch rate	*Nemipteridae*	*Saurida*	*Lethrinidae*	*Lutjanidae*	N	Headline
RV "Oshoro Maru" Anon. (1964) Masuda *et al.* (1964)	1962	206	2.3 (1.1)	11.3 (5.5)	42.6 (20.7)	73.3 (35.6)	15	38.2
RV "Oshoro Maru" Anon. (1965) Masuda *et al.* (1964) Suzuki *et al.* (1964)	1963	564	36.6 (6.5)	14.6 (2.6)	91.3 (16.2)	111.7 (19.8)	20	38.2
RV "Nagasaki Maru" Abe *et al.* (1967)	1966	316	23.7 (7.5)	31.6 (10.0)	88.1 (27.9)	69.2 (21.9)	14	33.6
RV "Hai Ching" Shu *et al.* (1972)	1972	134	9.9 (7.4)	7.5 (5.6)	33.1 (24.7)	40.6 (30.3)	54	34
RV "Hai Ching" Shu *et al.* (1973)	1973	92	5.8 (6.3)	7.2 (7.8)	21.7 (23.6)	29.1 (31.6)	73	34
RV "Oh Dae San Ho" Anon. (1980)	1979	235	62.0 (26.4)	19.3 (8.2)	24.6 (10.5)	14.6 (6.2)	24	38.5
RV "Hai-Kung" Chen *et al.* (1979)	1979	359	45.6 (12.7)	128.9 (35.9)	24.7 (6.9)	64.3 (17.9)	12	27.5
RV "Soela" 1/83 CSIRO unpubl. data	1983	327	40.8 (12.5)	30.1 (9.2)	22.2 (6.8)	37.9 (11.6)	62	25.9
RV "Soela" 4/83 CSIRO unpubl. data	1983	250	30.0 (12.0)	34.2 (13.7)	13.5 (5.4)	20.2 (8.1)	70	25.9

serranids *Plectropomus maculatus* (coral trout) and *Epinephelus multinotatus* (tropical cod). The traps are baited and operated to depths of about 80 m and in areas that have been subjected to little trawling (Fig. 1). There is no by-catch of *Saurida* and an extremely small by-catch of *Nemipterus* (M. Moran, Department of Fisheries and Wildlife, Western Australia, pers. comm.). There is interest in expanding this fishery, but to date fishing effort has been low and the total annual catch is about 300–500 t.

1.3. Changes in the resource community

The composition of the Northwest Shelf fish community since 1960 can be broadly determined from the results of various research vessel trawl surveys (Sainsbury, 1987). Nine surveys were conducted and reported in a manner that provides reasonably consistent information and survey coverage of the central part of the Northwest Shelf (116–119°E). All surveys were conducted by similar-sized stern trawlers using similar-sized nets, and compatible catch records are available at the generic level of taxon for *Saurida* and at the familial level for Lutjanidae, Lethrinidae, and Nemipteridae (Table 2).

Total fish catch rate showed no significant correlation with year of survey (Table 3). However, both the Lethrinidae and Lutjanidae significantly decreased in both relative and absolute abundance with time. Conversely, both Nemipteridae and *Saurida* show a significant increase in relative abundance during the same time. The

Table 3. Spearman's rank correlation coefficients (r_s) for the correlation between year of observation and the research vessel catch data give in Table 2. The relative catch rate is the catch rate for that taxon divided by the total catch rate. The probability (p) that $r_s = 0$ is given, and values statistically significant at $\alpha = 0.05$ are marked with an asterisk.

Variable	r_s	p
Total catch rate	0.1	0.14
Nemipteridae		
Catch rate	0.55	0.15
Relative catch rate	0.73*	0.04
Saurida		
Catch rate	0.55	0.15
Relative catch rate	0.75*	0.03
Lethrinidae		
Catch rate	−0.83*	0.01
Relative catch rate	−0.75*	0.03
Lutjanidae		
Catch rate	−0.75*	0.04
Relative catch rate	−0.73*	0.04

nemipterid and saurid data are quite variable and, while suggestive of an increase, neither show a significant increase in absolute abundance. However, more detailed data on the relative abundance of *Saurida* since 1978 shows that between 1978 and 1983 a small-bodied species (*Saurida* sp2 of Sainsbury *et al.*, 1985) has increased in numbers by about two orders of magnitude and a larger bodied species (*Saurida undosquamis*) has increased by about an order of magnitude (Thresher *et al.*, 1986). These changes in the community are also supported by information from research surveys conducted by the USSR between 1962 and 1973. While the available description of these surveys is insufficiently detailed to allow their inclusion in the above analysis, catches were reported to comprise 47% Lethrinidae, 12% Lutjanidae, and 3% *Saurida*, with no data being available for Nemipteridae (Anon., 1978). Overall, then, the fish community has maintained about the same biomass between 1962 and 1983, but its composition has altered from initially comprising 40–60% by weight of *Lethrinus* and *Lutjanus* combined and about 10% *Nemipterus* and *Saurida* combined, to comprising about 10% *Lethrinus* and *Lutjanus* and about 25% *Nemipterus* and *Saurida*.

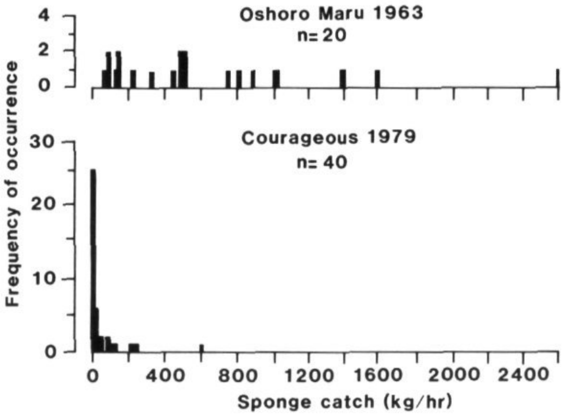

Figure 3. Sponge catch rates on the Northwest Shelf in 1963 (Anon., 1965) and 1979 (Sainsbury, 1987). Catch rates differ significantly (Mann-Whitney U = 763, $p < 0.01$).

The demersal habitat on the Northwest Shelf also changed in the period between these research surveys. Most of the pre-1972 research surveys reported large catches of large epibenthic fauna (mostly sponges, alcyonarians, and gorgonians), particularly from the area between 115°E and 120°E (Anon., 1965; Shu *et al.*, 1972; Shu *et al.*, 1973), and fishery inspectors observed large sponge catches in the early years of the pair trawl fishery (C. Ossel, Department of Fisheries and Wildlife, Western Australia, pers. comm.). Comparison of the sponge catches from 20 trawl hauls in 1963 (Anon., 1965) with those from 40 hauls in 1979 (Sainsbury, 1987) shows a significant reduction in sponge catch rates (Fig. 3). It is presumed that the reduction in epibenthos is due to its incidental removal by trawls. A crude measure of the use fish make of the habitat provided by the large epibenthos compared with the open sand habitat was obtained by mounting a 35 mm camera on the headline of the research trawl and taking photographs of the demersal habitat and fish in the path of each trawl. About 80 equally spaced photographs were taken on each of 108 randomly located trawls in the central part of the Northwest Shelf (116°E–119°E) in 1983. The photographs were scored for the presence and absence of large epibenthos (>25 cm along the longest axis) and the main genera of fish. From these data the probability of finding each fish genus in the presence and in the absence of the large epibenthos habitat was calculated (Table 4). This is a conservative method for detecting the pattern of habitat usage, because herding of fish by the trawl will result in any natural pattern being disturbed so that fish are likely to be observed in habitats where they would not naturally occur. This conservative bias is expected to be particularly severe in detecting usage of small, relatively isolated patches of habitat such as patches of large epibenthos. Despite this, however, the observations showed that *Lethrinus* and *Lutjanus* have a higher probability of occurring in the demersal habitat containing

Table 4. Frequency of occurrence and probability of occurrence of each of four fish genera in the presence and absence of large (25 cm) epibenthic organisms. The standard error of each probability of occurrence is given in parentheses. Estimates are based on photographs taken at regular intervals from the trawl headline during 108 randomly located research trawl hauls between 116°E and 119°E in 1983. Each photograph includes about 4 m^2 of sea floor. Standard errors were calculated assuming each photograph provides an independent observation of a binomial process, and so may be underestimated.

	Large benthos present		Large benthos absent	
Fish genus	Number of frames with this genus	Probability	Number of frames with this genus	Probability
Nemipterus	26	0.022 (0.004)	340	0.047 (0.002)
Saurida	110	0.092 (0.008)	999	0.138 (0.004)
Lethrinus	25	0.021 (0.004)	21	0.003 (0.001)
Lutjanus	9	0.008 (0.006)	22	0.003 (0.001)
	Total frames 1199		Total frames 7229	

large epibenthos than in the habitat without large epibenthos, while *Nemipterus* and *Saurida* have a higher probability of occurring in the open sand habitat (Table 4). If this habitat usage pattern remains constant it is clear that alteration in the proportion of the sea floor occupied by large epibenthos would cause an alteration in the composition of the fish community.

1.4. The management issue

In the decade following declaration of the Australian Fishing Zone management of the pair trawl fishery utilized a minimum mesh size and a total catch quota to maximize the yield of the species groups commonly retained by the pair trawl fleet (Sainsbury, 1984). Obtaining the maximum total catch in a mixed species trawl fishery will almost always result in overfishing the less productive species groups (in this case *Lutjanus* and *Lethrinus*) to obtain good yields of the more productive species groups (in this case *Nemipterus* and *Saurida*). This strategy reduces the proportionate abundance of the less productive species groups. Changes in relative abundance among the groups *Lutjanus*, *Lethrinus*, and *Nemipterus* are of little consequence to the pair trawl fishery, because all have similar values on the Taiwanese market (Liu and Lai, 1980). However, changes in the abundance of these fish groups are very important when development of the Australian trap fishery is considered.

The domestic fishery relies heavily on *Lethrinus* and *Lutjanus*, because *Nemipterus* has no net value in the Australian fishery. Consequently the trap fishery is restricted to the small areas where trawling has been light and the desired fish groups are still abundant. The historical fish community on the Northwest Shelf would have provided a suitable and large resource for the domestic fishery, but this fish community no longer exists. There is little prospect of significant development of the trap fishery with the present fish community composition. Furthermore, it is not certain that social and economic conditions in this remote part of Australia would allow expansion of the domestic fishery even if the resource had its historical composition, whereas it is known that the pair trawl fishery can generate income to Australia from the existing resource community.

The aims of management include maximizing the benefit to Australia from the resource, preferably by maximizing the involvement of the domestic fishing industry (Anon., 1985). The available data suggest that achieving these aims may require recovery of the species composition to its former dominance by *Lethrinus* and *Lutjanus*. However, the poor state of knowledge about the ecology and dynamics of the resource make prediction of the resource's response to major alterations in the management regime highly uncertain. In addition, there are substantial uncertainties associated with the social and economic factors that determine the response of the fishing industry to any recovery the resource may show. Questions relating to the management of the competing trap and trawl fisheries are:

- Can the historical composition be recovered?
- Is it worth trying to recover the historical composition (i.e. do the rewards justify the risks and costs)?
- If recovery is attempted what is an appropriate strategy to follow?

2. Evaluation of management options

2.1. The general approach

Scientific management advice in fisheries usually has an implicit assumption of "certainty equivalence" (e.g. Bar-Shalom and Tse, 1976). A scientific group reviews the data and somehow selects one model structure and one parameterization of that model that is thought to be scientifically "best". The implications of this one "best" model/parameterization are then examined with respect to the management aims, strategies, and tactics determined by the resource managers. The management actions considered feasible and desirable are then selected by the managers and applied to the whole of the resource as though this "best" model/parameterization were true. The selection of the best scientific model is often accompanied by lengthy discussion of uncertainty and confidence bounds, but this rarely influences the management decision-making process or the final management decision. In addition to being "certainly equivalent", this approach to management is also usually "passively adaptive". It relies upon errors in the management process or unplanned external events to provide the contrasts in the control variables that are necessary to identify the important processes and allow precise estimation of model parameters (Walters and Hilborn, 1978). Good examples of this passive adaptation occurred when fishing effort was reduced in the North Sea during the two World Wars. The reduction in fishing effort during World War I demonstrated the reality of overfishing, and changes in the yield after the reduction of effort during World War II provided empirical support for the method of yield per recruit analysis of growth overfishing (e.g. Beverton and Holt, 1957; Smith, 1988).

Under some circumstances an approach based on passive adaptation and certainty equivalence may provide close to optimal policies (e.g. Walters and Hilborn, 1978), but it appears unlikely that this is generally the case for resources with highly non-linear dynamics or when there is considerable uncertainty about the basic structure of the appropriate model of resource dynamics. Furthermore, such an approach usually treats the whole resource as one unit, so that all of the resource is at risk if an error is made. Possible control variables (e.g. population sizes, temporally varying environmental variables) are also confounded under this approach. Consequently, future observations of the resource have little power to discriminate hypotheses or allow recognition of suboptimal situations.

The prospect of avoiding the uncertainties in resource management by identifying the key features of the existing dynamics of a complex biological community through a process-oriented research programme seems remote. Even if achieved, it would not be certain that the identified features would remain the key factors under the novel perturbations provided by a changed fishing regime.

From these considerations it is concluded that community level management is largely empirical, even if this is not explicitly recognized, and that there is possible benefit in trying to increase the efficiency of that empiricism while maintaining revenue from the resource (Sainsbury, 1982, 1988). In particular there is a need to develop a reasoned empiricism, and avoid blind trial and error, by formally evaluating the performance of prospective management actions across alternative models while taking explicit account of future learning and the identification of policy improvements. This approach is sometimes called "actively adaptive" (e.g. Bar-Shalom and Tse, 1976; Walters and Hilborn, 1978; Walters, 1986) because it includes the possibility of taking management action that intentionally increases the contrast between key variables, so as to permit identification of important processes and therey increase the precision of model parameter estimates.

2.2. Assessment of Northwest Shelf

2.2.1. Assessment method

A framework for evaluating actively adaptive management is provided by Walters and Hilborn (1980) and Walters (1986), and a simple version of this methodology is applied to the Northwest Shelf. This evaluation examines a limited number of long-term management regimes (U_k, $k = 1$ to m) that are regarded as feasible, across a series of alternative models of the resource (M_j, $j = 1$ to n). At present time, T, models of resource dynamics that are consistent with the historical data are identified. The U_k examined here are the fixed harvesting regimes that are close to optimal for each of the M_j.

The expected economic value obtained from immediate application of one of the U_k regimes is compared to the expected value of first attempting to learn more about the relative credibility of the alternative hypotheses and then selecting the long-term management regime. It is of interest to determine whether or not additional learning is of economic value, and if so what combined harvesting and observation regime gives the greatest economic return. In the evaluations performed here, learning is considered to occur only during a "learning period" of duration t (i.e. the interval $T, T + t$) during which some trial fishing regime W is applied and various observations of the system are made. After the learning period, at time $T + t$, the observations are used to update the relative credibility of each of the alternative models, and the long-term regime that now appears most appropriate is selected and applied to the resource. The annual revenue during the learning period, including costs of the observations, and under the chosen U_k is calculated. This revenue flow is expressed as a present value by applying an economic discount rate to future revenues (e.g. Clark, 1976). The expected present value from the resource, under both the learning period regime W and the U_k chosen at time $T + t$, is calculated across all the models using the relative probability placed on each model at time T. These values are used to find a combination of W and t that results in selection of the most appropriate U_k at $T + t$ while also providing an acceptable overall economic return from the resource.

An ideal W regime would allow correct identification of each model if that model were true, would provide high revenues during the learning period, would not compromise the revenue from any of the regimes that might be selected at the end of the learning period, and would not involve expensive observations. The expected economic return from actively adaptive management in this context is the result of "trade-offs" between the revenue generated during the learning period, the costs of observations made during the learning period, the discrimination between models achieved from the observations, and the long-term economic value resulting from the achieved model discrimination.

The first step is to assign relative probabilities to each of the proposed models of resource dynamics. At time T all models are consistent with historical observations and can be reasonably parameterized with the historical data set, and so all models are assumed to have equal probability at time T (i.e. $P_T(M_i) = 1/n$).

The next step is to determine the relative probabilities placed on each model after application of the trial policy W for the learning period t. The probabilities placed on each model are updated on the basis of the observations made during this period. For trial regime W and model M_j, data sets $O_{j,W}$ are generated by Monte-Carlo simulation of the observation process (i.e. sampling) and the behaviour of model M_j under policy W during the interval $(T, T + t)$. The $O_{j,W}$ are examples of the data that might be available at time $T + t$ if model j is true. For each data set, the likelihood that it was generated by each of the models is calculated (i.e. the likelihood, $L(O_{j,W}|M_i)$, when model M_i is fitted to observations $O_{j,W}$). The probability placed at the end of the learning period on model M_i when model M_j is true is then calculated from Bayes' theorem.

As used here Bayes' theorem provides a method of calculating the conditional probability placed on a hypothesis from an initial statement of the probability of that hypothesis and some observed outcomes of trials (see Hays and Winkler, 1971). For example, Bayes' rule could be used to calculate how the probability placed on alternative hypotheses about the bias in a coin would change as a result of observing a number of throws. Two hypotheses are formulated about the probability of a coin returning a head on being thrown: H_1 being that the probability of a head is 0.5 and H_2 being that the probability of a head is 0.8. Because most coins are fair, it is initially thought that H_1 has probability 0.75 of being correct and that H_2 has probability 0.25. These are known as the prior probabilities placed on the hypotheses. If three throws all return heads, then Bayes' theorem allows calculation of the probability placed on each hypothesis conditional on the observed outcome of the throws. The updated probability on H_1 is

$$\begin{aligned}
&P(H_1\ \text{true}|\text{observations}) = \\
&\quad = \frac{P(H_1)P(\text{observations}|H_1\ \text{true})}{P(H_1)P(\text{observations}|H_1\ \text{true}) + \\ + P(H_2)P(\text{observations}|H_2\ \text{true})} \\
&\quad = 0.75 \times 0.5^3/(0.75 \times 0.5^3 + 0.25 \times 0.8^3) \\
&\quad = 0.423
\end{aligned}$$

and similarly the updated probability on H_2 is 0.577.

A slightly different application of Bayes' theorem can be used to calculate the probability placed on the alternative models of resource dynamics at time T + t, given the observations made during the learning period t, under each possible model and treatment of the resource during T. In this application

$$P_{T+t}(M_i|W,M_j) = \frac{P_T(M_i)L(O_{j,W}|M_i)}{\sum_{k=1}^{k=n} P_T(M_k)L(O_{j,W}|M_k)}$$

If W is perfectly informative then $P_{T+t}(M_i|W,M_j) = 1$ for i = j and zero otherwise, while if W is totally uninformative then $P_{T+t}(M_i|W,M_j) = P_T(M_i)$.

For each model the present economic value from the resource under each combination of learning period policy and subsequent long-term policy can be calculated. For model M_j, the present value of applying policy W during (T,T + t) and then applying policy U_k is

$$V(U_k|W,M_j) = \sum_{v=0}^{v=t} R_{T+v}(W|M_j)\Phi^V + \\ + \sum_{V=t+1}^{V=\infty} R_{T+v}(U_k|M_j)\Phi^v$$

where $R_{T+v}(W|M_j)$ is the annual net economic return (including observation costs) from policy W applied to model M_j in year T + v, and Φ is a discount rate factor.

If at time T + t the decision to follow a particular U_k is made, then the data available from true model M_j will be interpreted as being due to model M_i with probability $P_{T+t}\ (M_i|W,M_j)$. This probability will then be erroneously associated with the annual value from the resource under U_k when model M_i is true. At T + t, perceptions of the value of the resource under the alternative long-term management regimes will be influenced by such errors, and selection of a management regime at T + t will be based on an "apparent value" made up of the revenue expected from each management regime when applied to each model and the relative probability placed on each model at that time. Here it is assumed that the resource manager is risk neutral (e.g. Lewis, 1982, p. 19) and will choose the U_k with the greatest expected value. For model M_j true the chosen U_k will maximize the "apparent value"

$$AV_{T+t}(U_k|W,M_j) = \sum_{i=1}^{i=n} P_{T+t}(M_i|W,M_j) \times \\ \times \sum_{v=t+1}^{v=\infty} R_{T+v}(U_k|M_i)\Phi^{v-t-1}.$$

The $P_{T+t}(M_i|W,M_j)$ are random variables because $O_{j,W}$ is influenced by random processes such as sampling. A matrix of probabilities, $Q_{T+t}(U_k|W,M_j)$, can then be defined with elements giving the probability of selecting each of the U_k at time T + t when W is applied and model M_j is true. $Q_{T+t}(U_k|W,M_j)$ is calculated by using repeated simulations of the observation process to give data sets $O_{j,W}$, calculation of $AV_{T+t}(U_k|W,M_j)$ for each data set, and simulation of the decision process. The expected value from the policy with regime W for period t across all models is then

$$E[V(W,t)] = \sum_{j=1}^{j=n} P_T(M_j) \sum_{k=1}^{k=m} Q_{T+t}(U_k|W,M_j) \times \\ \times V(U_k|W,t,M_j).$$

To this stage in the analysis it is assumed that any W or U_k can be successfully applied. In the case of the Northwest Shelf it is not at all clear that fisheries and management regimes other than the existing one are viable. The Australian fishing industry never attempted to establish fishing operations in the region prior to development of the foreign trawl fishery, presumably for socio-economic reasons; feasibility trials of Australian fish trawling soon after declaration of the 200 nmi fishing zone proved to be uneconomic (Anon., 1980); and the trap fishery is very small and would require a major increase in infrastructure to handle the ten-fold increases in catches implied by some of the U_k. Indeed, a major reason for licensing operation of a foreign fishery on the Northwest Shelf was the perception that the

Australian fishing industry could not economically harvest and market the available yield in this remote and sparsely populated part of Australia.

Consequently assessment of the fishery options for the Northwest Shelf resource needs to recognize that attempts to apply W and U_k may not be successful. In particular, social and unknown economic constraints may prevent the domestic trap fishery from expanding even if the historical species composition of the resource were restored. Failure of the trap fishery to expand was thought to be the most likely cause of failure to achieve a stated W or U_k. Other causes of failure to achieve a stated W or U_k are conceivable, such as the inability to enforce a trawl closure, but in this analysis only fishing regimes that attempt expansion of the trap fishery were considered to involve the possibility of failing. If expansion of the trap fishery is successful then the target fishing mortality specified by the W or U_k is achieved, and if unsuccessful the catch does not increase above the presently observed annual catch of 300 t.

Observation of the success or failure of the domestic fishery to expand during the learning period will alter perceptions of the possibility that the trap fishery will ever develop. These altered perceptions affect the "apparent value" of each U_k, and so will influence how long the opportunity to expand is made available to a fishery that shows no sign of expansion. If foreign access fees are foregone in providing the opportunity for the trap fishery to expand, then the success or failure of the trap fishery to expand will also affect the economic return from the resource. While the course of development of the trap fishery could be examined using a detailed economic model of fishery development, a simple *ad hoc* method was adopted here. The economic values obtained from success or failure of the regimes attempted are represented by the subscripts + for success and − for failure. So if both U_k and W fail, then the economic value obtained is represented by $V({}_{-}U_k|{}_{-}W,M_j)$, while the value of successful application of both U_k and W is represented by $V({}_{+}U_k|{}_{+}W,M_j)$.

Three probabilities must be specified to allow incorporation of this *ad hoc* treatment of the socio-economic responses into the assessment of (W,t).

(i) S_T, the probability that the trap fishery can expand.
(ii) S'_t, the probability that a trap fishery will have shown evidence of expansion by t years, given that expansion is possible.
(iii) S''_t, the probability that a manager who observes t years of non-expansion of the trap fishery places on that fishery ever expanding.

S_T and S'_t determine the probabilities of the various outcomes of applying W then applying U_k; the probability of ${}_{+}W$ followed by ${}_{+}U_k$ is $S_TS'_t$; the probability of ${}_{-}W$ followed by ${}_{+}U_k$ is $S_T(1-S'_t)$; and the probability of ${}_{-}W$ followed by ${}_{-}U_k$ is $(1-S_T)$. It is considered that ${}_{+}W$ followed by ${}_{-}U_k$ (which corresponds to successful expansion during the learning period then failure to expand after the learning period) cannot happen. Guidance on appropriate values for S_T and S'_t could perhaps be obtained from detailed economic analysis of the fishing industry. However, these probabilities are the result of numerous micro-economic and social decisions by companies and individuals, and it is notoriously difficult to determine such quantities. Here it is assumed that $S_T = 0.5$, giving development and failure an equal chance, and $S'_t = 1 - \psi^t$ with $\psi = 0.7$, because it seems reasonable to assume that signs of expansion would be about 80% probable to occur after 5 years if they are ever to occur. There is no necessary connection between S''_t and the real chance of ultimate expansion of the trap fishery, because S'' relates to management perceptions rather than fact. However, it is assumed here that the manager has knowledge that is consistent with the processes actually occurring, so that S''_t is the conditional probability that expansion will ultimately occur given that t years of non-expansion have been observed, i.e. $S''_t = S_T(1-S'_t)/(1-S_TS'_t)$. Even in the highly simplified decision-making process considered here, the manager's perceptions have a major influence on the decisions made, and it is interesting to note that irrational perceptions (i.e. those that are not based on evidence and that favour or discount certain outcomes) can give greater value from the resource than rationally based perceptions if the irrational perceptions are correct but can give a much lower value if wrong. It is difficult to improve on a lucky guess based on a correct but irrational bias.

With these additional considerations, the "apparent value" of applying U_k at time T + t, on which the manager bases policy selection, is

$$AV_{T+t}(U_k|{}_{+}W,M_j) = \sum_{i=1}^{i=n} P_{T+t}(M_i|{}_{+}W,M_j)V({}_{+}U_k|{}_{+}W,M_i)$$

for calculation of $Q_{T+t}(U_k|{}_{+}W,M_j)$ after observation of successful expansion of the trap fishery during the learning period, and

$$AV_{T+t}(U_k|{}_{-}W,M_j) = \sum_{i=1}^{i=n} P_{T+t}(M_i|{}_{-}W,M_j)\,[S''_tV({}_{+}U_k|{}_{-}W,M_i) + (1-S''_t)V({}_{-}U_k|{}_{-}W,M_i)]$$

for calculation of $Q_{T+t}(U_k|{}_{-}W,M_j)$ after observation of no expansion of the trap fishery during the learning period. Consequently, the overall expected value of W for time t is

$$\mathrm{E[V(W,t)]} = \sum_{j=1}^{j=n} \mathrm{P_T(M_j)} \times$$

$$\times \left\{ \mathrm{S_T} \left[\sum_{k=1}^{k=m} \mathrm{S'_t Q_{T+t}(U_k|_+W,M_j) V(_+U_k|_+W,M_j)} + \right.\right.$$

$$\left. + \mathrm{(1-S'_t) Q_{T+t}(U_k|_-W,M_j) V(_+U_k|_-W,M_j)} \right] +$$

$$\left. + \mathrm{(1-S_T)} \sum_{k=1}^{k=m} \mathrm{Q_{T+t}(U_k|_-W,M_j) V(_-U_k|_-W,M_j)} \right]\Bigg\}.$$

It is often useful to calculate the expected value of perfect information (EVPI, see Hays and Winkler, 1971; Walters, 1986) to indicate the upper bound on the management value of distinguishing the alternative resource models and to gauge the absolute performance of a particular learning period regime. The expected value of perfect resource information from W applied for time t is

$$\mathrm{EVPI} = \sum_{j=1}^{j=n} \mathrm{P_T(M_j)} \{ \mathrm{S_T S'_t V(_+U^{*}_{k,j}|_+W,M_j)} +$$

$$+ \mathrm{S_T(1-S'_t) V(_+U^{**}_{k,j}|_-W,M_j)} +$$

$$+ \mathrm{(1-S_T) V(_-U^{**}_{k,j}|_-W,M_j)} \}$$

where $\mathrm{U^{*}_{k,j}}$ is the $\mathrm{U_k}$ that gives maximum $\mathrm{V(_+U_k|_+W,M_j)}$ and $\mathrm{U^{**}_{k,j}}$ is the $\mathrm{U_k}$ that gives maximum $\mathrm{S''_t V(_+U_k|_-W,M_j) + (1-S''_t) V(_-U_k|_-W,M_j)}$. This is the expected value if W perfectly discriminated the resource models after t years. The EVPI from resolution of the uncertainties in both the resource dynamics and the expansion of the trap fishery is given by the above expression evaluated with $\mathrm{S'_t} = 1.0$ and $\mathrm{S''_t} = 0.0$.

2.2.2. Models of the Northwest Shelf fish resource

Four models of the dynamics of the four main species groups comprising the Northwest Shelf resource were examined, each model reflecting a different interpretation of the available data. The models are very simple because the data do not permit estimation of many parameters. Model parameters were obtained for each model by separately examining the likelihood surface for the two sets of data available, the research vessel catch rates and the commercial catch and effort (Tables 1 and 2). Each model was expressed in difference equation form for biomass ($\mathrm{B_T}$) and fishing effort ($\mathrm{E_T}$) at time T,

$$\mathrm{B_{T+1} = B_T(f(B_T) - q_f E_T)},$$

with the predicted commercial catch ($\mathrm{C_T}$) being

$$\mathrm{C_T = q_f E_T B_T} \epsilon$$

where $\mathrm{q_f}$ is the catchability coefficient for commercial vessels and ϵ is an error term such that $\log_e \epsilon$ has a normal distribution with mean zero and standard deviation 0.4. No allowance for discarding was made and the commercial effort data were regarded as being reliable. The predicted research vessel catch rate is given by

$$\mu_\mathrm{T} = \mathrm{q_r B_T} \gamma$$

where $\mathrm{q_r}$ is a research vessel catchability and $\log_e \gamma$ has a normal distribution with mean zero and standard deviation 0.34. The standard deviations for the error distributions were chosen in the belief that each research catch rate observation was probably within half to double the value implied by the true biomass, and that the recorded commercial catch observations were probably somewhat worse than this.

The likelihood of each model was calculated by fitting data to the non-equilibrium form of the model directly, beginning in 1960 and assuming that the populations were initially at equilibrium under no fishing effort. The models were fitted to the research survey and commercial data sets separately, with the log likelihoods for n observations being calculated from

$$-0.5\mathrm{n} \log(2\pi\sigma_\epsilon^2) - (2\sigma_\epsilon^2)^{-1} \sum_{\mathrm{T}=1}^{\mathrm{T}=\mathrm{n}} \log(\mathrm{C_T/qfE_TB_T})$$

for the commercial data set and

$$-0.5\mathrm{n} \log(2\pi\sigma_\gamma^2) - (2\sigma_\gamma^2)^{-1} \sum_{\mathrm{T}=1}^{\mathrm{T}=\mathrm{n}} \log(\mu_\mathrm{T}/\mathrm{q_r B_T})$$

for the research vessel data set.

In most cases a single set of parameter values corresponding to the maximum of both surfaces could be found; in other cases the parameter set corresponded to the maximum if each surface was accepted so that two parameter sets were considered for some models. Each parameter set/model combination was treated as a different model in the evaluation of management options. The commercial catch data beyond 1979 for *Saurida* were not included in the analysis because of changes in commercial retention practices (see Thresher *et al.*, 1986).

Model 1

All species groups are controlled by "intraspecific" processes. This model represents the multiple single species approach to assessment.

Lethrinus and *Lutjanus* follow the difference equation for logistic population growth,

$$\mathrm{B_{T+1} = B_T[1 + r - (rB_T/K) - q_f E_T]}$$

where r is the intrinsic population growth rate and K is the carrying capacity. Best estimates of the three parameters of this model are given in Table 5.

Nemipterus and *Saurida* increased in abundance with fishing, which, assuming only intraspecific population processes, suggests that the population growth rate depends upon population age structure. This might be due to high levels of cannibalism by old individuals which are subsequently removed by the fishery, or a highly domed relation between population egg production and recruitment combined with strongly age-dependent individual fecundities. A simple model of this is

$$B_{T+1} = B_T[1 + r - (a_T r B_T/K) - ((1 - a_T) r B_T/\partial K) - q_f E_T]$$

where a_T is the proportion of the population biomass at time T made up of animals younger than some critical age (T_{crit}) at which they strongly retard population growth and ∂ determines the strength of this retardation. Inclusion of a_T and ∂ is a crude method of allowing a production model to exhibit some age structure behaviour. From a simple age structured population model

$$a_T = \sum_{t=0}^{t=T_{crit}} \left[\exp\left(-Mt - q_f \sum_{i=T-t}^{i=T} E_i\right)(1 - \exp(-kt))^3\right] \div \sum_{t=0}^{t=\infty} \left[\exp\left(-Mt - q_f \sum_{\substack{i=T-t \\ i>1971}}^{i=T} E_i\right)(1 - \exp(-kt))^3\right]$$

with the values for the rate of natural mortality (M) and the von Bertalanffy growth coefficient (k) taken from Sainsbury (1984). The best estimates of the five parameters of this model (r, q_f, K, T_{crit}, and ∂) are given in Table 5. The model parameter values suggested by the commercial catch data were substantially different from those suggested by the research survey data, so each was used to give two different parameterizations of the model. Parameter set 1a of Table 5 provides the best fit of the model for *Nemipterus* and *Saurida* to the commercial data, and set 1b provides the best fit to the research survey data.

Model 2

Lethrinus and *Lutjanus* have intraspecifically controlled population growth, as in model 1, while the population growth of *Nemipterus* and *Saurida* is also negatively influenced by the combined biomass of *Lethrinus* and *Lutjanus*. Population growth for *Lethrinus* and *Lutjanus* is given by model 1, and for *Nemipterus* and *Saurida* is

$$B_{T+1} = B_T[1 + r - (rB_T/K) - (\alpha r W_T/K) - q_f E_T]$$

where α is an interaction coefficient and W_T is the combined abundance of *Lethrinus* and *Lutjanus* at time T. Parameter estimates for r, q_f, K, and α are given in Table 5. Parameter set 2a in Table 5 provides the best fit of the model for *Nemipterus* and *Saurida* to the commercial data, while 2b provides the best fit to the research survey data.

Model 3

Nemipterus and *Saurida* have intraspecifically controlled population growth, while the population growth of *Lethrinus* and *Lutjanus* is also negatively influenced by the combined biomass of *Nemipterus* and *Saurida*. Population growth for *Nemipterus* and *Saurida* is as in model 1, and for *Lethrinus* and *Lutjanus* is

$$B_{T+1} = B_T[1 + r - (rB_T/K) - (\alpha r W_T/K) - q_f E_T]$$

where W_T is the combined abundance of *Nemipterus* and *Saurida*. Parameter estimates are given in Table 5. The parameter set 3a in Table 5 follows from *Nemipterus* and *Saurida* having parameters 1a, while parameter set 3b follows from *Nemipterus* and *Saurida* having parameters 1b.

Model 4

The carrying capacity of all groups is determined by the amount of suitable habitat, and habitat abundance is altered by the physical effects of trawling. For all fish groups population growth is

$$B_{T+1} = B_T\left[1 + r - \left(rB_T \middle/ \left(\Delta \sum_{i=1}^{i=2} h_{T,i}\lambda_i\right)\right) - q_f E_T\right]$$

where $h_{T,i}$ is the proportion of the area occupied by habitat i at time t, λ_i is the relative density of the species group in habitat i, and Δ is a constant. Only two demersal habitats were considered, the first containing large (>25 cm) epibenthic organisms and the second not containing these organisms. The estimated probabilities of observing a fish in each habitat type (obtained from the photographic survey data in Table 4) were taken to be estimates of the λ_i. The $h_{T,i}$ were obtained from a simple model of the benthos in which the sea floor is considered to comprise a number of small, independent patches of size equal to the area covered by each survey photograph (about 4 m^2). In this model each patch has a fixed probability (s) of receiving a recruit each year and each benthic organism has a fixed probability (d) of dying each year. If it takes T_{25} years for the organisms to grow to 25 cm then the proportion of patches with one or more individuals of large benthos is

$$1 - \prod_{\phi = T_{25}}^{\phi = \infty} [1 - s \exp(-\phi d)].$$

If each trawl sweeps proportion p of the fished area and an individual aged ϕ is removed with probability r_ϕ on encounter, then the probability of an individual not being removed by trawling that year is approximately $\exp(-pr_\phi E_T)$. Assuming r_ϕ can be written as

$$r_\phi = r_{max}(1 - \exp(-c\phi)),$$

but restricting $r_{T_{25}}$ to be 0.95 of r_{max}, so that c can be expressed solely in terms of T_{25} and r_{max}, gives the proportion of patches with one or more individuals of large benthos at time T (i.e. $h_{T,1}$ in the difference equation for model 4) as approximately

$$h_{T,1} = 1 - \prod_{\phi = T_{25}}^{\phi = \infty} [1 - s \exp(-D_\phi)]$$

where

$$D_\phi = \phi d + p \sum_{k=1}^{k=\phi} r_{\phi - k} E_{T-k}$$

and

$$h_{T,2} = 1 - h_{T,1}.$$

A similar equation can be obtained for the proportion of patches with small benthos, and since both proportions were measured in 1983 this gives two equations in four unknowns, s, d, T_{25}, and r_{max}. The proportion of the area swept by one Taiwanese trawl, p, was $0.84/8 \times 10^4 = 1.05 \times 10^{-5}$. A value of $r_{max} = 0.5$ was considered reasonable from scuba and video observations of trawls in progress, and two values for T_{25} were taken from the literature (Harrison and Cowden, 1976), 6 years and 10 years. These data were used to estimate two parameter sets (s,d), each set corresponding to the growth rate implied by the one of the two T_{25} values. A separate set of parameters for the fish dynamics model (r, Δ, q_f) was then obtained for each (s,d) pair. The estimates of the five parameters of this model are given in Table 5. Parameter set 4a of Table 5 is for $T_{25} = 6$ years and set 4b is for $T_{25} = 10$ years.

2.2.3. *Assessment of management regimes for the Northwest Shelf*

Table 5 defines eight different model/parameter value combinations resulting from two parameterizations of each of four models. Models 1 and 2 imply a low yield to a trap fishery, because the historical decline of *Lethrinus* and *Lutjanus* is interpreted as indicating that these stocks have low productivity. Models 3 and 4 give a high yield to the trap fishery because trapping removes no benthos (which under model 4 allows return of high carrying capacities for *Lethrinus* and *Lutjanus*) and catches few *Nemipterus* and *Saurida* (which under some parameterizations of model 3 allows the *Nemipterus* and *Saurida* populations to decrease to their unfished levels, with consequent reduction in the negative influence they exert on *Lethrinus* and *Lutjanus* population growth).

Assessment of management regimes for the Northwest Shelf examined four different regimes during the learning period (i.e. the W in section 2.2.1), learning periods of up to 20 years, and four different long-term regimes (i.e. the U_k in section 2.2.1).

The long-term fishing regimes considered for possible implementation after the learning period were: U_1 a trap fishery for *Lethrinus* and *Lutjanus* with a fishing mortality of 0.1 (close to maximum sustainable yield for models 1 and 2), U_2 a trap fishery with fishing mortality of 0.2 (close to maximum sustainable yield for model 3), U_3 a trap fishery with fishing mortality of 0.6 (close to maximum sustainable yield for model 4), and U_4 continuation of trawling at the present trawling effort and no further development of the trap fishery.

The yield to the pair trawl fishery is about the same under all models and so the annual return to Australia from this fishery is taken to be the 1985 annual licensing and access fee of AUS\$ 0.5×10^6. Vessels in the trap fishery obtain an after-costs value of about AUS\$ 1142 per tonne of retained catch (M. Moran, Western Australian Department of Fisheries, pers. comm.), and this was used to calculate the annual value of the trap fishery catch from the resource under each model and fishing regime. Failure of the trap fishery to expand is taken to result in the present level of catch to the trap fishery, 300 t per year, irrespective of the resource model. The discount rate factor was assumed to be 0.95 throughout the analysis.

The learning period regimes examined were: W_A indefinite continuation of U_4 (i.e. no learning period, so $t = 0$, and continuation of the *status quo*); W_B immediate application of the U_k giving greatest expected value (i.e. $t = 0$ and application of the regime presently considered best); W_C continued trawling during a learning period of t years, then after the learning period the U_k giving greatest expected value is selected and applied (i.e. learning does not disrupt revenue flow or empirically explore trap fishery expansion); W_D a learning period of t years during which trawling is stopped for a number of years and trap fishing with $F = 0.2$ is attempted, then after the learning period the U_k giving greatest expected value is selected and applied (i.e. learning disrupts revenue flow but empirically explores trap fishery expansion); and W_E a learning period of t years in which half of the area is treated as for W_D and foreign access trawling is continued in the other half

Table 5. Parameter values for each of the four resource dynamics models used in assessment of management regimes. Different parameterizations of each model that were regarded as being equally acceptable for the available data are indicated by letters. The maximum equilibrium sustainable yield (MSY) is given for each species group (i.e. single-species maximum) for each model, and for models 3 and 4 the directed MSY is also given. MSY (directed) is the yield that would be available from *Lethrinus* and *Lutjanus* if they alone were subject to fishing mortality and harvesting did not modify the habitat, and is the yield available from a trap fishery. The units for K and MSY are tonnes, and for T_{crit} are years.

Parameter	*Nemipterus*	*Saurida*	*Lethrinus*	*Lutjanus*
Model 1a				
r	1.1	1.3	0.25	0.35
q_f	0.3×10^{-5}	0.4×10^{-5}	0.4×10^{-5}	0.5×10^{-5}
K	45 000	35 000	20 000	15 000
T_{crit}	5	5		
∂	0.1	0.05		
MSY	12 000	10 200	1 250	1 312
Model 1b				
r	1.5	1.4	0.25	0.35
q_f	0.7×10^{-5}	0.8×10^{-5}	0.4×10^{-5}	0.5×10^{-5}
K	300 000	60 000	20 000	15 000
T_{crit}	5	5		
∂	0.001	0.01		
MSY	70 000	15 700	1 250	1 312
Model 2a				
r	1.4	1.5	0.25	0.35
q_f	0.5×10^{-5}	0.4×10^{-5}	0.4×10^{-5}	0.5×10^{-5}
K	35 000	45 000	20 000	15 000
α	0.5	1.0		
MSY	12 300	16 900	1 250	1 312
Model 2b				
r	1.5	1.5	0.25	0.35
q_f	0.4×10^{-5}	0.4×10^{-5}	0.4×10^{-5}	0.5×10^{-5}
K	45 000	45 000	20 000	15 000
α	1.0	1.0		
MSY	16 900	16 900	1 250	1 312
Model 3a				
r	1.1	1.3	0.4	0.5
q_f	0.3×10^{-5}	0.4×10^{-5}	0.3×10^{-5}	0.4×10^{-5}
K	45 000	35 000	45 000	25 000
T_{crit}	5	5		
∂	0.1	0.05		
α			0.5	0.2
MSY	12 000	10 200	945	1 150
MSY (directed)			1040	1220
Model 3b				
r	1.5	1.4	0.45	0.5
q_f	0.7×10^{-5}	0.8×10^{-5}	0.3×10^{-5}	0.4×10^{-5}
K	300 000	60 000	25 000	20 000
T_{crit}	5	5		
∂	0.001	0.01		
α			0.3	0.2
MSY	70 000	15 700	1 070	1 180
MST (directed)			1 940	1 840
Model 4a				
r	1.2	1.2	1.6	1.2
q_f	0.5×10^{-5}	0.2×10^{-5}	0.7×10^{-5}	0.8×10^{-5}
Δ	550 000	250 000	900 000	1 400 000
MSY	7 730	10 300	1 130	1 320
MSY (directed)			5 890	2 820
Epibenthic organisms				
r_{max}	0.5			
T_{25}	6			
s	0.1332			
d	0.0655			

(*continued*)

Table 5. *Continued.*

Parameter	*Nemipterus*	*Saurida*	*Lethrinus*	*Lutjanus*
Model 4b				
r	1.1	1.1	1.4	1.2
q_f	0.5×10^{-5}	0.2×10^{-5}	0.6×10^{-5}	0.8×10^{-5}
Δ	750 000	250 000	950 000	1 400 000
MSY	9 690	9 490	1 000	1 280
MSY (directed)			6 220	3 090
Epibenthic organisms				
r_{max}	0.5			
T_{25}	10			
s	0.0906			
d	0.0320			

Table 6. The present value (millions of Australian dollars) obtained from each model (M) by immediately applying each of four possible long-term fishing regimes (U). $V({}_{+}U_k|M_j)$ gives the value of successful application of U_k to a resource obeying model M_j, and $V({}_{-}U_k|M_j)$ gives the value of a failed application. U_1 is a trap fishery with $F = 0.1$, U_2 is a trap fishery with $F = 0.2$, U_3 is a trap fishery with $F = 0.6$, and U_4 is continuation of the licensed trawl fishery. A failed trap fishing regime occurs if the fishery fails to expand to provide the target F, and in this event a constant annual catch of 300 t per year is assumed. A discount rate of 0.05 was used throughout.

	$V({}_{+}U_k\|M_j)$				$V({}_{-}U_k\|M_j)$			
M_j	U_1	U_2	U_3	U_4	U_1	U_2	U_3	U_4
1a	48.2	57.3	26.7	9.96	6.85	6.85	6.85	9.96
1b	48.2	57.3	26.7	9.96	6.85	6.85	6.85	9.96
2a	48.2	57.3	26.7	9.96	6.85	6.85	6.85	9.96
2b	48.2	57.3	26.7	9.96	6.85	6.85	6.85	9.96
3a	49.6	54.1	29.1	9.96	6.85	6.85	6.85	9.96
3b	60.1	84.6	32.9	9.96	6.85	6.85	6.85	9.96
4a	39.9	73.8	148.7	9.96	6.85	6.85	6.85	9.96
4b	38.7	71.2	137.1	9.96	6.85	6.85	6.85	9.96

(both halves are assumed to be isolated and have identical dynamics). W_A and W_B are degenerate cases ($t = 0$) and do not involve consideration of further learning, while for W_C, W_D, and W_E the learning period duration giving the greatest economic benefit is of management interest. During all learning periods, observations of the status of the resource are made by an annual research trawl survey. The survey is assumed to cost AUS\$ 0.3×10^6 (based on CSIRO survey costs) and to provide a relative index of the abundance of each of the four fish groups according to

$$\mu_T = q_r B_T \gamma$$

where, as before, B_T is the true abundance, q_r is the research vessel catchability as estimated from the historical data and $\log_e \gamma$ has a normal distribution with mean zero and standard deviation 0.34. Recent surveys appear much more precise than this, but the early surveys of the Northwest Shelf appear to contain variability of this magnitude and it is prudent to take a conservative view of sampling capabilities.

The present values associated with each of the U_k applied immediately to each model (i.e. at time T with no further learning) are given in Table 6. If it were known that the trap fishery could not expand, then the existing trawl fishery gives a higher present value from the resource than a trap fishery irrespective of which of the resource models is true. If trap fishery expansion is possible, then a trap fishery with $F = 0.2$ gives the greatest present value when models 1–3 are true, while a trawl fishery with $F = 0.6$ gives the greatest present value when model 4 is true. Distinguishing between models 1 through 3 has no management value, because they all imply the same management action, but there is considerable benefit from distinguishing model 4 from models 1–3.

The expected present values from each of the W examined are given in Table 7. For W_B, immediate application of a trap fishery with $F = 0.2$ (i.e. U_2) gives highest expected present value from the resource (AUS\$ 35.4×10^6). Immediate application of U_2 gives a larger expected present value than immediate application of U_3 if the probability of model 4 being true (i.e. $P_T(M_{4a}) + P_T(M_{4b})$) is less than about 0.33. The expected value of perfect information (EVPI) for instant resolution of the alternative resource models in 1985 is AUS\$ 45.8×10^6. The best expected value obtainable

Table 7. The expected present value (millions of Australian dollars) of different management strategies (W) for the Northwest Shelf fishery. Policy W_A is continuation of the existing licensed trawl fishery; W_B is to immediately apply one of four possible long-term regimes (U_1 to U_4 as described in the caption to Table 6); W_C is continued trawling for a period t, conducting annual resource surveys during t and using these data to select the best U_k at the end of the period; W_D is conducting annual resource surveys for period t, during which time all fishing is stopped for t_c years and a trap fishery with $F = 0.2$ is applied for the remaining $t - t_c$ years, and then using these data to select the best U_k at the end of the period; W_E is the same as W_D except that the learning period regime is applied to only half the area and the trawl fishery is continued in the other half. The expected value of perfect information (EVPI), with respect to distinguishing the alternative resource dynamics models, is also given for each strategy.

Strategy W_A			9.96	
Strategy W_B				
	U_k		$E[V(U_k)]$	
	U_1		27.2	
	U_2		35.4	
	U_3		31.8	
	U_4		9.96	
	EVPI		45.8	
Strategy W_C				
	t		$E[V(W_C,t)]$	EVPI
	0		35.4	45.8
	5		35.6	36.7
	10		29.7	30.7
	15		25.1	25.8
	20		21.2	21.7
Strategy W_D				
	t	t_c	$E[V(W_D,t)]$	EVPI
	0	0	35.4	45.8
	2	1	35.8	42.0
	5	1	36.8	40.9
	5	2	37.4	40.5
	10	2	37.2	38.7
	10	4	36.8	37.4
	15	2	37.1	37.2
	15	4	35.6	35.6
	20	2	36.3	36.3
	20	4	33.9	33.9
Strategy W_E				
	t	t_c	$E[V(W_D,t)]$	EVPI
	0	0	35.4	45.8
	2	1	35.9	43.1
	5	1	40.5	42.0
	5	2	40.6	41.6
	10	2	40.5	40.7
	10	4	38.9	39.2
	15	2	39.8	39.8
	15	4	38.4	38.7
	20	2	38.6	38.6
	20	4	37.2	37.2

under the present uncertainty is AUS$ 35.4×10^6 (Table 7), and in principle the difference (AUS$ 10.4×10^6) is the amount it would be worth paying to obtain instant resolution of the specified uncertainties in resource dynamics. W_C (continued trawling at the 1985 effort level throughout the learning period) is a very uninformative strategy. Further observations of the community under continued trawling provide little opportunity to recognize model 4 when it is true, and there is no opportunity to test empirically the expansion of the trap fishery. Strategy W_D, a mixture of closing trawling and attempting to expand the trap fishery, can give expected values that are greater than W_B for learning periods less than 15–20 years. Of the strategies examined, a short (about 2 years) closure of the trawl fishery followed by 3–13 years of attempted expansion of the trap fishery, provides close to the maximum expected value from the resource. Maintaining the trawl fishery on half of the Northwest Shelf while examining the trapping option on the other half during the learning period provides a higher expected value than treating the whole shelf as one unit. Longer learning periods, and in particular longer periods of trawl closure, provide greater resolution between the alternative models but the costs of obtaining this additional resolution exceed its value to management. Very short learning periods provide highly variable outcomes because of frequent misidentification of models, and so give relatively low expected values.

The analysis outlined here was provided to the State and Federal Fisheries management authorities. The State authorities saw merit in the suggested management actions, but the Federal authorities initially regarded the *status quo* as acceptable. Both authorities agreed on the goals of management of fisheries in the Australian Fishing Zone (Anon., 1985) – to obtain the greatest benefit from the resource and support domestic fishing industries – but differed in their assessment of how these goals should be achieved. Regional, organizational, political, and individual differences in emphasis on the inevitably multifaceted consequences of a management action are to be expected, and illustrate the difficulty in specifying an objective criterion for decision-making in fisheries management. However, partly for the reasons outlined here and partly for other reasons, the Federal and State fishery managers cooperated to close a portion of the Northwest Shelf to foreign trawling from 1985 (Fig. 4). They similarly cooperated to close an additional area to foreign trawling from 1987 (Fig. 4), thereby providing three areas with contrasting fishing regimes.

Annual surveys of the fish community and epibenthos on the Northwest Shelf west of 119°E have been conducted by CSIRO since 1985. The abundance of fish in the areas closed to trawling increased in the years following the closures, and in 1988 domestic trawlers began to operate in these areas. This development was not anticipated in the 1985 assessment of options for the Northwest Shelf. Domestic trawling has subsequently been restricted to east of 116°45′E so as to maintain non-trawled areas for resource recovery and development of the trap fishery. It is anticipated that the western boundary of the foreign access zone will be further moved eastward to 120°E from 1990 to reduce interaction between the foreign and domestic trawl fisheries. Increase in the domestic trawling effort in the area

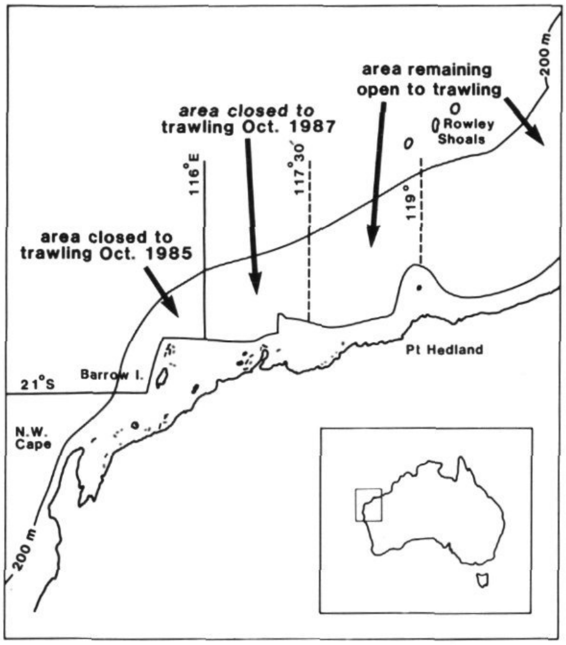

Figure 4. The zones subjected to different fishery management regimes on the Northwest Shelf.

116°45′E–120°E is expected to slow, so that 117°30′E–120°E will probably be trawled only lightly during the next few years.

In practical application, adaptive management was not formally used as the management policy for the resource. However, the adaptive management analysis strongly influenced the management regimes that were adopted. The management regime in place in 1987 was very similar to a regime that performed well in the analysis, although it did not eventuate solely for the reasons used in the analysis. Similarly, the recent development of the domestic trawl fishery was not part of any regime examined in the original analysis, but the benefit demonstrated by that analysis of separating trap and trawl fisheries was used in formulating the management response to development of the domestic trawl fishery.

The principles underlying adaptive management are the credibility placed on different hypotheses of resource dynamics, the economic return from the resource thought to be possible under each hypothesis, and the way that present management actions affect the ability to distinguish between hypotheses with different economic consequences. Practical application of adaptive management involved the application of these principles both to anticipated management options and to management issues and options as they arose.

3. Discussion

The dynamics of the Northwest Shelf fisheries are complex and highly uncertain, and by necessity the assessment of prospective management actions contained many simplifying assumptions. The resource models used were all very simplistic and could be expected to mimic only gross aspects of the dynamics of the real fish community, such as whether a popultion would increase or decrease, quickly or slowly, and with long or short time lags. None of the models used could exhibit behaviour such as multiple stable states, non-stationarity or external forcing, although such behaviour is to be expected in the dynamics of real communities. Furthermore, the complex non-linear interactions between economic investment and resource state were almost totally ignored, and the analysis used a very simple treatment of learning and the use of information by managers. The inclusion of model process error, to allow for stochastic change in the resource models and decision parameters, would be a useful improvement to the analysis. Its inclusion is likely to decrease the estimated ability to distinguish the alternative models.

The experimental designs provided under the various learning period regimes (W) examined were all very simple. More complex designs would be required for resolution of resource models involving spatially and temporally specific influences, but tractable models of these influences could not be constructed with the data available and so were not considered. Also more complex learning period regimes and designs were not considered feasible on the Northwest Shelf.

If the Northwest Shelf community is really driven by highly non-linear interactions, then the implications to parameter estimation, prediction, and the interpretation of any experiment are daunting and well expressed by Neill (1974): "the ecologist is therefore in a difficult position: on the one hand he cannot hope to measure the dynamics of the interactions between pairs of species without perturbing them, and on the other, results of the perturbation depend upon the effects of other species on the competing pair. Properly done the experiment becomes hopelessly difficult."

The approach taken on the Northwest Shelf assumed that it was possible to approximate the important features of the dynamics of the community and its fisheries by simple models. Despite the simplifications the analysis provided a very useful framework for encompassing many processes and uncertainties involved in assessing prospective management actions. It was instrumental in leading to positive management actions despite the initially bewildering level of uncertainty, and proved useful in helping management decisions involving both foreign/domestic and domestic/domestic fishery interactions on the Northwest Shelf.

More generally, there appear to be many underutilized opportunities for fisheries research and management to make active use of the feed-back between management action and empirical learning about resource dynamics. Such opportunities occur almost every time a new management measure is introduced or an old one modified, and yet it is very rare for any consideration to be given to how that measure could be introduced so as to provide the greatest benefit to long-term management (and in particular to learning about the resource's response to the measure). It is quite possible that much research expenditure is currently being devoted to questions that could have been answered more directly and cheaply (or at least posed more sharply) following direct trials using a fishery.

The Northwest Shelf provided a rather unusual situation with many features that favoured an actively adaptive management approach: there were major uncertainties in the dynamics of an extremely complex fish community which made it difficult to select a management regime that could confidently be expected to achieve the management objectives; few scientists were studying the resource so that resolution of the uncertainties by process-oriented research was highly unlikely; the fish had relatively short life spans and hence were expected to respond quickly to changes in the fishing regime; close management control was possible; the existing fishery had relatively low value; the existing fleet had alternative fishing options; and an alternative fishery had relatively high value. The large areas closed to trawling on the Northwest Shelf would not be feasible or justifiable in many fisheries, and even for the Northwest Shelf closures of more than a few years may not be justifiable.

More usually, opportunities for actively adaptive management would be expected to arise from changes in the usual fishery controls such as mesh sizes, catch quotas, and seasonal closures. For example, it may be possible to implement changes in mesh-size regulations in such a way as to maintain revenues and empirically test whether the changes bring about the expected improvements in the fishery. Very little attention has been given to this question, despite the widespread use of mesh regulations, and recent research findings of high mortality among fish that have passed through trawl meshes (e.g. Main, 1988; DeAlteris and Reifstech, 1988) suggest that there would have been considerable value in obtaining empirical support for the use of mesh regulations. Similarly, the difference in yield predictions between single-species models and multispecies models in the North Sea (see Pope, 1991) suggests that it may be possible to devise an experimental management policy that could empirically determine which of these two modelling approaches provides the most reliable management advice. Examination of this possibility appears worthwhile.

While the presented method of analysis can help expose the basic issues and alternative hypotheses for examination and review, this in itself of course does not overcome the uncertainties. Management of marine communities remains fundamentally empirical, and the analysis simply helps guide the choice of which available management actions are worth taking. However, in dealing with difficult community level management problems, where several different views of community dynamics are unresolvable at the time of decision-making, such guidance is perhaps the most constructive outcome possible. The analysis is "scientific", in that the consequences logically follow from stated assumptions, there is emphasis on testing predictions, and it focuses attention on assumptions, their consequences, and their empirical resolution. However, the analysis is not totally objective. Rather it is conditional upon the "state of the world" statements, such as the models to be included and the probabilities initially placed upon them, which cannot be determined with total objectivity. This is a fundamental difficulty with the methodology. Different people with different backgrounds and goals may choose quite different models to include in the set of alternatives, and may choose to assign different prior probability distributions even to the same models. Either of these differences could alter the outcome of the analysis. Furthermore, it is not possible to examine all possible models and prior distributions, and at best the sensitivity to some variation in prior distributions and models could be examined. However, this apparent weakness in the methodology is simply the result of making explicit the process of model selection that occurs in all fishery assessment and management. All assessments involve selection of a general approach, the models to use, and the management implications to examine. But usually it is not obvious that subjective inputs are involved and there is no clear framework for quantitatively specifying or evaluating these inputs. Methodology of the type employed here has the advantage of explicitly examining the value of distinguishing some of these subjective inputs, and determining the ability to do so under various management actions. The widespread use of such methods would perhaps encourage more frequent and rigorous tests of prediction against reality in fisheries management. In this way it may be possible to examine the limits of empiricism and the question of just how predictable and manageable fish communities are.

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Management of multispecies fisheries in New Zealand by individual transferable quotas

John H. Annala, Kevin J. Sullivan, and Arthur J. Hore

Annala, J. H., Sullivan, K. J., and Hore, A. J. 1991. Management of multispecies fisheries in New Zealand by individual transferable quotas. – ICES mar. Sci. Symp., 193: 321–329.

A quota management system (QMS) using individual transferable quotas (ITQs) was introduced into New Zealand's fisheries on 1 October 1986. Most of the 29 species in the system are taken in trawl fisheries which are multi-species in nature. By-catch problems have been experienced because species total allowable catches (TACs) have not been set in proportion to pre-QMS landing levels and because of natural variations in stock size. Management by a QMS system rather than fishing for a total competitive TAC has brought these problems down to the level of the individual fisher rather than the entire fleet. The two major by-catch problems experienced thus far include: (1) TAC over-runs; and (2) TAC under-runs. Current attempts to resolve these problems include: (1) trading of ITQ between individual fishers; (2) fishing on behalf of another ITQ holder; (3) allowance for fishers to overcatch their ITQ by up to 10% in a given fishing year or carry over up to 10% of their ITQ to the next fishing year; (4) surrender of the port price value of over-caught fish to the Crown; and (5) exchange of uncaught ITQ of a certain species for catch of another, over-caught species. These problems and attempts to resolve them are detailed for three different fisheries: the deepwater hoki fishery, the transitional alfonsino/bluenose fishery, and a mixed species inshore fishery. The use of other methods to resolve by-catch problems (basket and sacrificial TACs) is discussed.

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Introduction

A quota management system (QMS) using individual transferable quotas (ITQs) was introduced into New Zealand's fisheries on 1 October 1986. As of 1 October 1989, there were 29 species in the QMS (Appendix A). The fishery for each species is divided into a number of different management units (defined as "fishstocks"), ranging from 2 to 8 for any given species, with a total of 169 fishstocks in the system. Each fishstock is composed of one or more quota management areas (QMAs) (Fig. 1) and may or may not have a biological basis. Details of the QMS are provided in Clark *et al.* (1988).

Most of these species are taken in trawl fisheries which are multispecies in nature. Before the introduction of the QMS, total allowable catches (TACs) were estimated for each of the species to be included in the scheme. By-catch problems have been experienced (mainly in the inshore fisheries) because TACs were not set in proportion to pre-QMS landing levels and because of natural variations in stock size. TACs for the over-exploited inshore species were set at levels from 25% to 75% of the pre-QMS catch levels, depending on the biological status and management objectives for each fishstock. TACs for under- and fully-exploited species taken in the same mixed fisheries were set at levels equal to or greater than the pre-QMS levels. This has resulted in an imbalance in the catch mix relative to the available quota.

Under New Zealand legislation TACs are based on the amount of fish that will produce the maximum sustainable yield (MSY) as qualified by other factors, e.g. economic, environmental, and social. However, only limited data are available for stock assessment for most species in the system. As of May 1988 there were little or no biological data to support stock assessments for 16 of the 29 species (Annala, 1989). For the 1988–1989 fishing year (1 October to 30 September) TACs for 18 species were based mainly on past landings data only. This limited basis for stock assessments has been due mainly to the rapid development of the QMS and has increased the risk of experiencing by-catch problems.

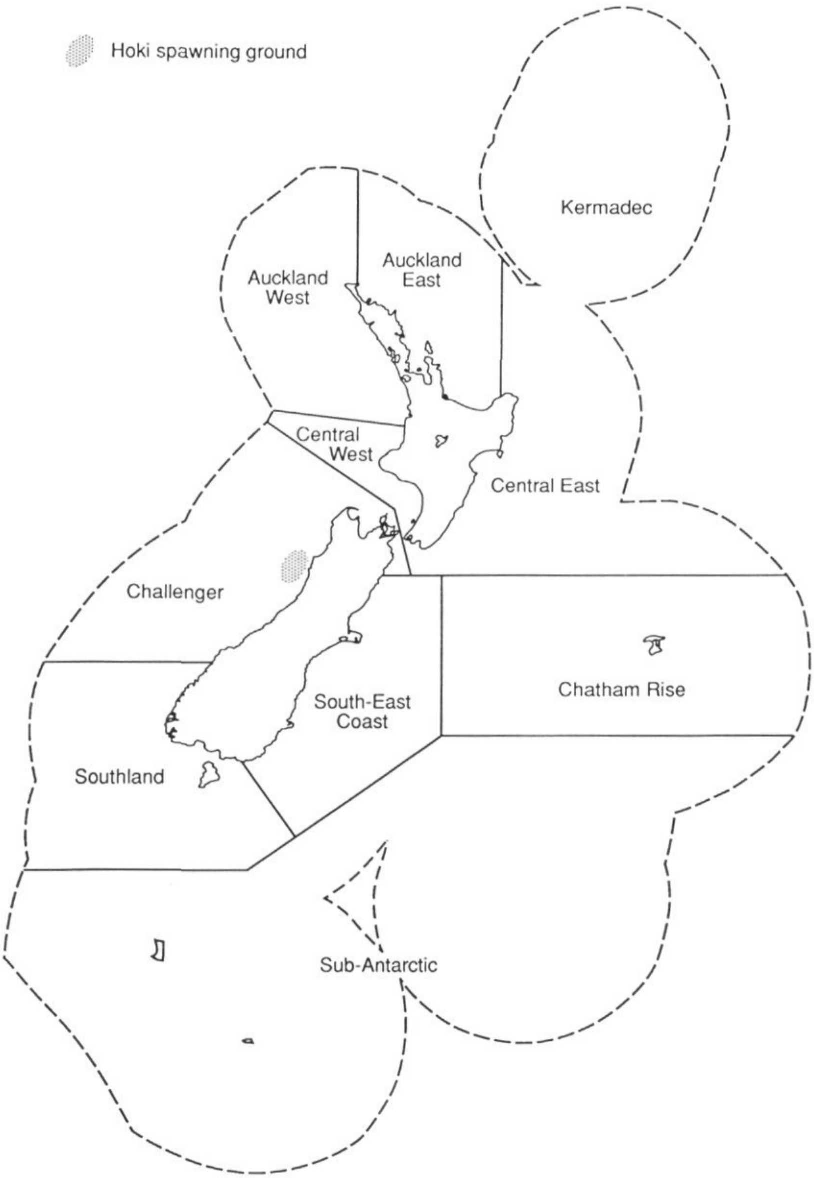

Figure 1. Location of the ten quota management areas in the quota management system and the main hoki spawning ground.

Management by an ITQ system rather than by fishing for a total competitive TAC has brought these problems down to the level of the individual fisher rather than the entire fleet. As a result, individual fishers often do not have the mix of quotas that match their catch.

The main aims of this paper are to describe and discuss (1) the major by-catch problems experienced in the QMS, (2) current attempts to resolve these problems, and (3) other methods to resolve these problems. These points are illustrated by case studies for three different fisheries – the deepwater hoki fishery, the transitional alfonsino/bluenose fishery, and a mixed species inshore fishery.

By-catch problems

Two major by-catch problems have been experienced thus far in New Zealand's QMS. These are: (1) TAC over-runs, and (2) TAC under-runs.

TAC over-runs

Under the QMS, TACs of non-target species are being exceeded because of illegal actions by fishers (i.e. discarding of unwanted species and highgrading) and because of legal mechanisms (allowance for ITQs to be overcaught by up to 10% in a given year, the surrender of overcaught species to the Crown, and the catch/quota trade-off mechanism). There are no constraints in the system which require fishers to stop fishing in multispecies fisheries once quota (either ITQ or TAC) of a particular species has been filled if quota of other associated species has not been caught.

The discarding or "dumping" of unwanted fish of quota species is illegal, except in very limited circumstances. Dumping is known to occur in both the inshore and deepwater fisheries. In the multispecies inshore trawl fisheries, fishers are known to dump quantities of non-target ITQ species for which they have filled their quota while trying to catch uncaught quota of other species rather than using one of the mechanisms described below for dealing with by-catch. In the deepwater trawl fisheries, vessels carrying observers report significantly larger quantities of non-target ITQ species than vessels fishing the same area which do not carry observers, indicating that discarding has taken place.

Highgrading is the discarding of lower quality fish of a given species and is another form of "dumping". Highgrading is known to exist in both the inshore and deepwater trawl fisheries and occurs when a premium price is paid for fish of a certain size, when small fish are discarded because of their unsuitability for processing, etc. The incidence of highgrading increases as ITQs of non-target species are being approached and is most prevalent amongst fishers with small quota holdings.

TACs are also being exceeded by other illegal actions such as mis-reporting and non-reporting. However, these factors do not pertain specifically to the by-catch problems experienced in the QMS, where fishers are attempting to match their catch to their quota portfolios; therefore they will not be discussed here.

The legal mechanisms leading to TAC over-runs are described in the section "Attempts to resolve by-catch problems".

TAC under-runs

Under the QMS, TACs have been undercaught when fishers have stopped fishing when their ITQs of associated non-target species have become filled. A positive aspect of undercatching the TAC is that it helps to conserve the stock and possibly provides for some rebuilding. A negative aspect is that it decreases the gross economic returns from the fishery.

Attempts to resolve by-catch problems

The method preferred by the Ministry of Agriculture and Fisheries (MAF) for dealing with by-catch problems is for fishers to develop innovative methods to match their catches to their quota allocations. Fishers may need to make changes in fishing methods and the setting of fishing gear, as well as adjustments to fishing seasons and areas fished, to ensure catches and quotas are matched. Where these attempts are not successful, the following mechanisms to resolve by-catch problems may be used:

1. Fishers may either lease or purchase quota from other ITQ holders to reflect their catch mix.
2. Fishers can fish on behalf of another ITQ holder or have someone fish on their behalf.
3. Fishers are allowed to catch up to 10% in excess of their ITQ for a given species for a given year or carry over up to 10% of their ITQ to the following year.
4. Fishers surrender the port price value of overcaught fish to the Crown.
5. Where a fisher catches in excess of his ITQ and cannot cover it using one of the mechanisms described above, the fisher can lease to the Crown for that fishing year an equivalent value of unfished ITQ of another species which has been approved by MAF for that QMA (the catch/quota trade-off mechanism). The scheme operates only for selected inshore species and is not permitted in the deepwater fisheries.

Problems experienced during the first two years of the QMS

Overview

The total TAC, total reported catch, quantity of legal over-catch of the TAC, and the quantity of quota traded for all fishstocks combined for each of the 29 species in the QMS during 1986–1987 and 1987–1988 are shown in Table 1. Also shown in Table 1 are the amount and percentage of over-runs or under-runs of the TACs and the major cause of the TAC over-runs attributable to the legal mechanisms described above. It is not always possible to quantify the tonnages for each of the causes separately, so this assessment is qualitative rather than quantitative. The extent of TAC over-runs caused by discarding and highgrading cannot be estimated. However, anecdotal information suggests that the occurrence of highgrading in some fisheries has decreased with the adjustment of quota holdings of individual fishers.

During the 1986–1987 fishing year TACs were reported to be exceeded in only 15 of the 169 fishstocks (Table 1). The over-runs ranged from a low of 1.7% in one of the blue cod stocks to a high of 80.5% in one of the elephant fishstocks. The total of the over-runs for all fishstocks combined equalled 1587 t, 0.3% of the total TAC for all fishstocks combined of 616 679 t. The major causes of TAC over-runs were: 10% ITQ over-runs (10 fishstocks) and surrenders and catch/quota trade-offs (5 fishstocks). Seven of the 15 over-runs were due to over-catching of non-target species in multispecies trawl fisheries.

Surrenders and trade-offs occurred in 93 fishstocks and totalled 1273 t. A total of 122 t of quota was traded in exchange for landed catch in 23 fishstocks. The largest amount of quota traded for a single fishstock was 29 t of blue warehou.

During the 1987–1988 fishing year the number of fish stocks in which TACs were over-run increased to 33. The over-runs ranged from a low of 0.1% in one of the ling stocks to a high of 74.4% in one of the elephant fish stocks. The total of the over-runs for all fishstocks combined equalled 5512 t, 0.9% of the total TAC for all fishstocks combined of 622 465 t. The major causes of TAC over-runs were: 10% ITQ over-runs (9 stocks) and surrenders and catch/quota trade-offs (24 stocks). Seventeen of the 33 over-runs were due to over-catching of non-target species in multispecies trawl fisheries.

The decrease in the use of the 10% ITQ over-run provision during this fishing year was countered by increases in surrenders to the Crown and the amount of fish landed under the catch/quota trade-off system. The catch/quota trade-off system was introduced during the 1986–1987 fishing year on a relatively limited basis in terms of the number of species and areas included in the system. The increase in usage during 1987–1988 was due to a combination of an increase in the number of species and areas in the system and fishers becoming more familiar with its operation. Surrenders and trade-offs occurred in 108 fishstocks and totalled 6242 t. The amount of quota traded increased by more than 14 times and totalled 1735 t in 39 fishstocks. The largest amount of quota traded for a single fishstock was 438 t of blue warehou.

Hoki fishery

Hoki (*Macruronus novaezelandiae*) is a long-tailed hake of the Merluccidae family, found around New Zealand and Australia. The fish is widely distributed in depths of 200–800 m, and is the dominant deepwater demersal species south of 40°S. The fish aggregate during winter

Table 1. Total TAC, total reported catch, quantity of overcatch either surrendered to the Crown or traded-off against other quota holdings, quota exchanged for traded-off overcatch, amount and percentage of over-runs and under-runs of TACs, and the major cause of TAC over-runs for the 29 species in the quota management system.

Species	No. of fish stocks	Total TAC (t)	Total reported catch (t)	Surrender/ by-catch trade-off (t)	Quota traded (t)	Over-run (+)* or under-run of total TAC (t)	Over-run (†) or under-run of total TAC (%)	No. of fishstocks in which TAC was over-run (% over-run)	Major cause† of TAC over-run
					1986–1987				
Hoki	2	250 039	158 165	6	0	91 868	37%	0	–
Arrow squid	4	121 010	74 040	0	0	46 970	39%	0	–
Orange roughy	8	58 920	50 599	0	0	8 321	14%	2 (6%, 9%)	2I
Barracouta	5	31 158	27 405	255	0	3 498	11%	2 (2%, 3%)	2I
Jack mackerels	4	28 180	23 873	0	0	4 306	15%	0	–
Oreos	5	24 010	14 999	128	0	8 883	37%	0	–
Ling	8	18 734	11 678	37	7	7 019	37%	0	–
Red cod	5	15 300	3 943	26	0	11 331	74%	0	–
Silver warehou	4	8 010	6 014	32	0	1 964	25%	0	–
Snapper	6	6 546	5 292	4	2	1 250	19%	0	–
Hake	4	6 510	4 197	34	0	2 279	35%	0	–
Flatfish	5	6 055	2 727	11	5	3 317	55%	0	–
Gemfish	5	5 760	4 601	182	9	977	17%	2 (4%, 40%)	I, S
Tarakihi	8	5 299	4 384	62	8	853	16%	0	–
Blue warehou	6	4 899	2 334	5	29	2 560	52%	0	–
Red gurnard	6	4 267	2 362	12	26	1 889	44%	0	–
Stargazer	8	4 161	1 938	52	<1	2 171	52%	2 (7%, 14%)	2I
Trevally	5	3 260	2 829	16	1	415	13%	1 (8%)	S
School shark	8	2 512	1 852	51	24	609	24%	1 (5%)	S
Blue cod	8	1 940	1 417	5	0	518	27%	1 (2%)	I
Groper	8	1 833	1 026	10	5	797	43%	0	–
Alfonsino	6	1 800	1 432	38	0	330	18%	0	–
Rig	6	1 425	1 507	34	6	334	23%	0	–
Bluenose	6	1 350	1 206	204	<1	+60	+4%	2 (18%, 44%)	2S
Paua	8	1 116	1 078	1	0	35	3%	1 (2%)	I
Grey mullet	5	990	598	<1	<1	392	40%	0	–
John dory	5	862	662	17	0	221	26%	0	–
Elephant fish	6	471	544	41	<1	+115	+25%	1 (80%)	I
Blue moki	5	262	155	9	0	98	37%	0	–

(*continued*)

Table 1. *Continued.*

Species	No. of fish stocks	Total TAC (t)	Total reported catch (t)	Surrender/ by-catch trade-off (t)	Quota traded (t)	Over-run (+)* or under-run of total TAC (t)	Over-run (†) or under-run of total TAC (%)	No. of fishstocks in which TAC was over-run (% over-run)	Major cause† of TAC over-run
1987–1988									
Hoki	2	250 072	218 998	7	0	31 067	12%	0	–
Arrow squid	4	121 010	69 254	65	0	51 691	43%	0	–
Orange roughy	8	61 220	45 746	73	0	15 401	25%	1 (11%)	I
Barracouta	5	31 467	25 790	895	0	4 782	15%	1 (5%)	S
Jack mackerels	4	28 180	22 728	0	0	5 242	19%	0	–
Oreos	5	24 010	18 418	17	0	5 592	23%	1 (13%)	I
Ling	8	18 928	6 658	189	91	12 081	64%	2 (<1%, 5%)	2S
Red cod	5	15 549	4 501	75	56	10 973	71%	0	–
Silver warehou	4	8 025	7 582	1 776	0	+1 333	+17%	2 (46%, 62%)	2S
Snapper	6	6 962	6 817	60	13	85	1%	2 (<1%, 2%)	I, S
Hake	4	6 513	4 565	90	0	1 858	29%	0	–
Flatfish	5	6 249	4 074	3	415	2 172	35%	0	–
Gemfish	5	5 986	4 043	484	213	1 459	24%	2 (11%, 15%)	2S
Tarakihi	8	5 588	4 348	421	189	819	15%	1 (<1%)	S
Blue warehou	6	5 014	1 856	64	438	3 094	62%	0	–
Red gurnard	6	4 370	2 824	303	124	1 243	28%	1 (28%)	S
Stargazer	8	4 306	1 879	460	23	1 967	46%	3 (2%, 35%, 39%)	3S
Trevally	5	3 435	3 037	95	4	303	9%	1 (17%)	S
School shark	8	2 719	2 034	378	48	307	11%	3 (3%, 8%, 12%)	3S
Blue cod	8	2 312	1 380	40	14	892	39%	1 (17%)	S
Groper	8	1 913	1 029	47	61	837	44%	0	–
Alfonsino	6	1 818	1 344	20	0	454	25%	0	–
Rig	6	1 547	1 256	140	28	151	10%	0	–
Bluenose	6	1 430	1 185	90	3	155	11%	2 (10%, 68%)	I, S
Paua	8	1 139	1 180	3	0	+44	+4%	5 (1%, 4%, 4%, 5%, 10%)	5I
Grey mullet	5	1 020	752	3	0	265	26%	0	–
John dory	5	901	690	68	5	143	16%	1 (14%)	S
Elephant fish	6	481	448	164	10	+131	+27%	2 (4%, 74%)	2S
Blue moki	5	301	159	114	<1	28	9%	2 (29%, 40%)	2S

* (Total reported catch + surrender/by-catch trade-off) − Total TAC.

† I = 10% ITQ over-run provision; S = surrender/by-catch trade-off provision.

(July–August) on spawning grounds associated mainly with submarine canyon features.

The hoki fishery was developed by foreign fishing vessels in the early 1970s. Catches increased to almost 98 000 t in 1977, but were subsequently reduced in 1978 following the declaration of the Exclusive Economic Zone (EEZ). Since 1978 the fishery has mainly been operated by foreign chartered vessels fishing for New Zealand companies. The size of the fishery was restricted from 1978 to 1985 by a quota of 20 000 t on the spawning grounds on the west coast of the South Island (Fig. 1). Based on preliminary analyses of biomass estimates from trawl surveys, the TAC was increased to 250 000 t in 1986, which resulted in the rapid development of the fishery.

The total catch of hoki was about 175 000 t in 1986–1987 and 255 000 t in 1987–1988. About 60% of the hoki catch was used for production of surimi. The remainder was mainly exported as frozen fillets or frozen fish which had been headed and gutted.

Midwater and bottom trawl gear are used in the fishery. With the increase in hoki catches in recent years, the by-catch of other non-target species (particularly hake, ling, and silver warehou) on the hoki spawning grounds has become a problem. Although the proportion of by-catch species is usually less than 5% of the total catch in the hoki fishery, of particular concern to quota holders is the ability to catch hoki allocations without exceeding their allocation of the by-catch species.

The by-catch of hake (*Merluccius australis*) has been measured by scientific observers aboard trawlers during the hoki spawning season. The rate of by-catch varies, highest when hoki catches are low, but averaged 2–3% over the whole season.

To ease the administrative problems of hake by-catch in this fishery, the TAC for hake in this area was increased to 3000 t in 1987. The increased quota was leased to hoki quota holders in proportion to the amount of hoki quota held. It was considered undesirable to constrain the development of the hoki fishery by the level of by-catch of hake. The available data suggest that the hake population can sustain the increase in catch at least in the short term. Hoki quota holders have been given a realistic quantity of hake quota to cover genuine by-catch. A certain amount of target fishing for hake is still likely to occur as this is a preferred high-value species.

Although reported catches of ling (*Genypterus blacodes*) did not exceed the TAC in this area, it appears that misreporting of by-catch occurs when vessels are not carrying observers. The rate of by-catch of ling has decreased in the last two years with the change from bottom to midwater trawling by many vessels. Current reported catches are at the level of the TAC but may underestimate true catch levels.

In 1987–1988 the silver warehou (*Seriolella punctata*) TAC for this area was exceeded by 62%. Vessels reported catches and paid forfeiture prices for the excess catch over quota allocations. The rate of by-catch on observed vessels increased from 0.4% in 1986–1987 to 0.75% in 1987–1988. It appears that more fishing effort in 1987–1988 was carried out in the northern fishing grounds, which are shallower and also have greater abundance of silver warehou. Some variation in by-catch rates may be expected from year to year depending on the distribution of the hoki and the deployment of the fishing fleet. The surrender provisions have allowed hoki allocations to be fully caught without any constraint from the level of by-catch of silver warehou. This strategy, however, will not guarantee the sustainability of the silver warehou stock, if recommended catch levels are exceeded every year.

Alfonsino/bluenose fishery

Alfonsino (*Beryx splendens* and *B. decadactylus*) is the target species for a regionally important trawl fishery at depths between 300 and 500 m along the southeast coast of the North Island. Alfonsino appear to form mixed schools with bluenose (*Hyperoglyphe antarctica*), and as a result, bluenose has become a major by-catch of the alfonsino trawl fishery.

The domestic fishery for alfonsino in this area first developed in 1983. Effort increased rapidly early in 1984 with the introduction of new semi-pelagic trawl gear. This gear permitted fishing over foul ground, where most of the fish appear to be aggregated.

Reported landings of alfonsino and bluenose from the 1983–1984 fishing year (1 October to 30 September) through the end of the 1987–1988 fishing year are shown in Table 2. Landings of alfonsino peaked at 1785 t in 1984–1985 and have declined since. During this fishing year alfonsino catches were subject to a total competitive quota of 1500 t, which was exceeded by 285 t. For the 1985–1986 fishing year individual quotas (non-transferable) were introduced as an interim measure leading up to the introduction of the QMS. These individual quotas summed to 1500 t. A TAC of 1510 t has been in place since the start of the QMS during the 1986–1987 fishing year.

Bluenose landings increased steadily during the first four years of the fishery and reached a peak of 953 t in 1986–1987. A TAC of 660 t has been in place since the start of the QMS. This was substantially exceeded (by 44%) during the 1986–1987 fishing year.

In an attempt to reduce the by-catch problems leading to the large TAC over-run for bluenose during the 1986–1987 fishing year, alfonsino and bluenose were included as a two-way catch/quota trade-off beginning in July 1987. However, industry has not utilized these trade-off provisions. Apparently, it is financially lucrative for some quota holders to continue to surrender bluenose to the Crown. The financial gain is made by adding value during the downstream processing of bluenose, and there is little incentive to trade bluenose overcatch for alfonsino quota. However, despite the reluctance of industry to take up the trade-off provisions, the bluenose TAC in this QMA was not exceeded during 1987–1988.

Flatfish fisheries

Flatfish are managed in the QMS as a multispecies assemblage of eight species of flounders, sole, brill, and turbot. Many are shallow water species which grow rapidly and have a short lifespan. The fishable stock generally consists of one- or two-year classes, and recruitment to this stock is highly variable. Maximum yield per recruit is achieved at high levels of fishing mortality.

Flatfish were included in the QMS primarily to put a ceiling on fishing effort in these fisheries and minimize

Table 2. Reported landings (t) of alfonsino and bluenose from the southeast coast of the North Island from the 1983–1984 to the 1987–1988 fishing years (1 October–30 September).

	Reported landings				
	1983–1984	1984–1985	1985–1986	1986–1987	1987–1988
Alfonsino	1533	1785	1454	1387	1252
Bluenose	520	635	742	953	653

conflict between fishing units. However, in order to provide flexibility to fishers in these highly variable fisheries, TACs were set at the sum of the catch histories, which were greater than the highest recorded flatfish catch. In years of high flatfish abundance, TACs were not intended to constrain catches. Thus, the current TACs provide only a limited degree of control on the amount of effort in these fisheries.

In northern New Zealand flatfish are primarily taken by set-net, and a limited range of by-catch species are taken. However, in southern New Zealand flatfish are target species in the mixed species inshore trawl fishery. By-catch species vary by area and include red gurnard (*Chelidonichthys kumu*), rig (*Mustelus lenticulatus*), stargazer (*Kathetostoma giganteum*), and school shark (*Galeorhinus australis*), all of which are included in the QMS. The management strategy of setting flatfish TACs above maximum historic catch levels has caused by-catch problems in trawl fisheries on the northwest coast of the South Island. TACs for by-catch species, such as red gurnard and rig, in this area are lower than pre-QMS catch levels, and ITQs of individual quota holders have been exceeded as fishers attempt to fill their flatfish quotas. Thus far, sufficient economic returns have been realized from the target flatfish species alone, and there have been no incentives to cease fishing once by-catch quotas are filled.

During 1986–1987 flatfish were not included in the catch/quota trade-off system because of the high flatfish TACs. In that year only 552 t of the TAC of 1840 t was taken. During 1987–1988 many fishers continued to trawl for flatfish, despite reaching their quota for by-catch species. This resulted in the surrender of significant quantities of by-catch species to the Crown and the likely discarding of additional quantities at sea. To address this problem trades for specific by-catch species were introduced during 1987–1988 to ensure that by-catch was retained and landed, and 58 t of flatfish were traded. The total catch of flatfish also increased to 1002 t.

Despite the increase in fishing effort for flatfish and the use of the catch/quota trade-off system, TACs for by-catch species in the flatfish trawl fisheries were not exceeded in 1987–1988. There is the potential for this fishery to expand still further, and the inclusion of flatfish in the catch/quota trade-off system may result in TAC over-runs in the future. A management strategy is now required to ensure that TACs for all species (target and by-catch) are not exceeded.

Other methods to resolve by-catch problems

Other methods to resolve by-catch problems include greater use of basket and sacrificial TACs.

Basket TACs are ones in which the quotas for a number of species are amalgamated into one TAC instead of having separate TACs for each species. This approach is already used in the QMS, e.g. the flatfish TAC incorporates eight separate species and the groper TAC two separate species. In practice, the catch/quota trade-off system is a form of a basket TAC because the over-catch of one species can be traded-off against the undercaught quota of another species. The greater use of basket TACs (e.g. by combining all the species taken in a fishery into a single TAC based on multispecies considerations) should be investigated to help with the resolution of by-catch problems. This approach may help to solve administrative by-catch problems for species that are consistently caught together in proportions that are variable through time, especially where species abundance may be negatively correlated with each other, but it may not help to conserve stocks.

Sacrificial TACs are ones in which TACs of a by-catch species are deliberately set at high levels so that the TAC of this species does not constrain the fishery for the target species. However, the legality of this approach is uncertain under New Zealand legislation, which specifies that TACs be set at a level that will produce from that fishery the maximum sustainable yield, as qualified by other relevant factors and allowing for a number of non-commercial interests. In any case, TACs can be exceeded by the legal provisions described above, and sacrificial TACs may not be necessary.

Discussion and conclusions

The largest fisheries (especially the three largest deep-water fisheries for hoki, arrow squid, and orange roughy) included in the QMS have experienced relatively few by-catch problems when compared with the inshore fisheries. The largest fishery, for hoki, takes place mainly on aggregations of spawning fish on the west coast of the South Island. Reported by-catch species (primarily hake, ling, and silver warehou) generally comprise less than 5% of the total hoki catch by weight. TACs for hake and ling in the area of the main hoki fishery have not been reached. However, the TAC for silver warehou in this area was exceeded by 62% during 1987–1988. The effects of continued TAC over-runs on silver warehou stocks in this area are unknown.

Most of the by-catch problems experienced thus far have been in the localized, inshore mixed species trawl fisheries. The main species involved include blue cod, blue moki, elephant fish, flatfish, john dory, red cod, red gurnard, rig, school shark, snapper, stargazer, and tarakihi. These problems have arisen mostly in fisheries where TACs were not set in proportion to the catch levels experienced in the fisheries before the introduction of the QMS. TACs for some over-exploited species were set at levels from 25% to 75% of pre-QMS levels to allow for stock rebuilding, while TACs for other, less fully exploited species were set at pre-QMS levels. Where these species co-occur and are caught in the same trawl fisheries, these over-exploited species have largely become by-catch species, and problems have occurred because of the imbalance in the catch mix relative to the available quota. Fishers still catch the over-exploited species in approximately the same proportion as they had in the past, and over-run their ITQ while trying to fill their quota of the target species.

The use of the surrender and catch/quota trade-off provisions in the inshore fisheries increased substantially in 1987–1988. The increased use of these provisions was the main reason that the number of fishstocks in which TACs were exceeded increased from 15 in 1986–1987 to 33 in 1987–1988.

There are very real dangers in setting TACs too high if the species is included in the catch/quota trade-off system and a large amount of quota remains uncaught. These species then become "quota banks" which may be used for the over-fishing of other species. This provides a mechanism to over-fish species for which no quota is held and has resulted in the over-run of some TACs. For example, the TAC for blue warehou along the east coast of the South Island was 70% undercaught during 1987–1988. A total of 438 t of blue warehou quota was traded-off for over-catch of other species (primarily ling, red gurnard, and tarakihi), which resulted in a TAC over-run for tarakihi.

Under New Zealand legislation TACs are based on single-species considerations only, and do not take into account the multispecies nature of most fisheries. TACs for a given species are based on the amount of fish that will produce the MSY for that species only. Under this management regime by-catch issues are likely to result in conservation problems when one or more of three conditions exist: (1) when by-catch species have a lower production rate than target species; (2) when the catchability coefficient of the by-catch species is greater than the target species; and (3) when by-catch loopholes are used to carry out a directed fishery.

The first condition occurs in some of the inshore trawl fisheries, where the production rates of some by-catch species are much lower than the target species. The third condition also occurs in some inshore trawl fisheries; however, it is illegal to use the surrender and catch/quota trade-off provisions to carry out a directed fishery. The importance of the second condition is unknown.

By-catch is likely to become a conservation problem when it results in TACs being exceeded by significant amounts for sustained periods. What is significant will depend on the level of the TAC in relation to the sustainable yield, which in turn depends upon the population dynamics of the stock. There is a degree of uncertainty in the estimates of sustainable yield and the TACs based on them. This level of uncertainty is greater for less well studied stocks for which there is limited information. If TACs have been set high relative to the "true" sustainable yield, then any catch greater than the TAC could result in stock declines. However, in general high productivity stocks will probably be more resilient to TAC over-runs than low productivity stocks.

One possible option for addressing by-catch problems is to take account of by-catch when setting ITQs for individual fishers. An approach that could be adopted is the use of linear programming (e.g. Brown *et al.*, 1978) to determine the effects of by-catch on total catch levels of a species. This approach could be used to set ITQs for individual fishers based on recent catch ratios or multispecies catchability coefficients. However, this would be a complex task because of the multispecies, multigear nature of most New Zealand inshore fisheries and the large number of quota holders involved (hundreds) in any given fishstock. Moreover, the New Zealand inshore fishery has been very dynamic, especially in the years since the QMS began. Fishers have adjusted their fishing patterns and methods considerably to increase efficiency and decrease costs, and their catch mix has often changed dramatically. Because of this dynamic situation, the use of past data is probably not appropriate. Furthermore, this approach would require adjusting the quotas of individual fishers rather than the TAC of the entire fleet. This would be much more complex than the current situation where TACs are adjusted rather than ITQs.

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Appendix A – Species included in the Quota Management System

Common name	Scientific name
Alfonsino	*Beryx splendens*, *B. decadactylus*
Arrow squid	*Nototodarus gouldi*, *N. sloanii*
Barracouta	*Thyrsites atun*
Blue cod	*Parapercis colias*
Blue moki	*Latridopsis ciliaris*
Bluenose	*Hyperoglyphe antarctica*
Blue warehou	*Seriolella brama*
Elephant fish	*Callorhinchus milii*

Common name	Scientific name
Flatfish	*Colistium guntheri*; *C. nudipinnis*; *Pelotretis flavilatus*; *Peltorhamphus novaezeelandiae*; *Rhombosolea leporina*; *R. plebeia*; *R. retiara*; *R. tapirina*
Gemfish	*Rexea solandri*
Grey mullet	*Mugil cephalus*
Groper	*Polyprion oxygeneios*; *P. moeone*
Hake	*Merluccius australis*
Hoki	*Macruronus novaezelandiae*
Jack mackerels	*Trachus declivis*; *T. murphyi*; *T. novaezelandiae*
John dory	*Zeus faber*
Ling	*Genypterus blacodes*
Orange roughy	*Hoplostethus atlanticus*
Oreos	*Allocyttus* sp.; *Neocyttus rhomboidalis*; *Pseudocyttus maculatus*
Paua	*Haliotis australis*; *H. iris*
Red cod	*Pseudophycis bachus*
Red gurnard	*Chelidonichthys kumu*
Rig	*Mustelus lenticulatus*
School shark	*Galeorhinus australis*
Silver warehou	*Seriolella punctata*
Snapper	*Chrysophrys auratus*
Stargazer	*Kathetostoma giganteum*
Tarakihi	*Nemadactylus macropterus*
Trevally	*Caranx georgianus*

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Management and research strategies in Kuwait's trawl fishery

C. P. Mathews and M. Samuel

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Multispecies dynamic pool modelling was carried out on Kuwait's trawl fishery targeted on penaeid shrimp. Dynamic pool models were applied to seven fish species (based on samples of up to 7500 fish per species per year and up to 12 monthly samples per year). The species included in the study account for 40% of the fish catch by volume (mostly discarded at sea), the remaining 60% of the catch consisting of about 20 much less abundant species. Results of dynamic pool modelling of shrimp were also available. Surplus production modelling was carried out using catch and effort data from twenty finfish stocks and from shrimp stocks. Dynamic pool and surplus production modelling of finfish showed general agreement: for most finfish stocks MSY occurred at levels of 10 000–12 000 days' fishing per year, which was the level in 1986–1987. For shrimp, both types of assessment suggested that MSY was achieved earlier, in 1982–1983, and at effort levels of ~6000 days per year. A simple bioeconomic model showed that the optimization of total value of trawl catches occurred at intermediate levels between those needed to harvest shrimp and finfish. Maximum net profit was obtained at a much lower effort level than needed to maximize total value landed.

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Introduction

Penaeid trawl fisheries are generally targeted on shrimp; some fish are landed on an opportunistic basis, but the vast majority of the fish by-catch is discarded. This paper summarizes work carried out on Kuwait's trawl fishery, where large amounts of fish (×20 times or more the weight of shrimp) are being discarded at sea. If these fish could be successfully marketed, they could add considerably to the value of the fishery. Management of trawl fisheries should take into account the potential to utilize by-catch. In addition, there is the potential for biological (i.e. predator–prey) interactions between fish and shrimp which should be considered in management. A strategy to carry out such assessments is identified. Results reported here include a brief summary of available assessments of shrimp stocks so that all trawlable stocks may be assessed simultaneously, and so that their relative biological and economic importance may be ascertained.

Methods

A multispecies dynamic pool model of the fishery was constructed, using estimates of growth (L_∞, K, t_0, from the von Bertalanffy growth equation) and total mortality (Z) based on samples of fish of known length-at-age for seven by-catch species. The catches of these species include about 40% of the by-catch by volume. Aging techniques included traditional methods applied to temperate and tropical fish (Williams, 1986; Samuel *et al.*, 1987) and otolith microstructural studies ("daily marks", Brothers and Mathews, 1987). Total mortality (Z) was estimated from the lengths-at-age of samples of up to 600 specimens for each species.

Independent estimates of growth parameters (L_∞, K), including parameters for seasonal growth oscillation (WP, C; Pauly and David, 1980; Pauly, 1982) were also obtained, based on up to 7500 measurements per species per year and up to 12 monthly samples per year for seven finfish species, using the Compleat ELEFAN package (Gayanilo *et al.*, 1988). Estimates of natural mortality were obtained by using estimates of L_∞, K, mean annual water temperature and the empirical equation of Pauly (1980). Where estimates of natural mortality were obtained in this way, they are denoted Mp, to distinguish them from estimates obtained through more traditional methods, denoted M.

For shrimp, estimates of growth parameters were obtained by ELEFAN analyses (Mathews *et al.*, 1987), by modal progression from length-converted catch curves (Pauly, 1982); from $Z = K(L_\infty - \bar{L})/\bar{L} - L'$ (Beverton and Holt, 1957), where $\bar{L}$ is the mean length in the catch above the length of full selection (L'); (Mathews, 1984; Mathews *et al.*, 1987).

Estimates of total mortality (Z) for shrimp were obtained as follows:

1. For data from 1978–1980, catch curves were constructed, based on monthly C/E of males and females (Mathews, 1984; Mathews *et al.*, 1987a).
2. Z was estimated from 1979–1984 by applying ELEFAN to size-frequency distributions. These were taken from monthly samples of the artisanal fishery, which provided a full size range and which provided up to 12 monthly samples per year (i.e. in 1979) and never less than 7 samples per year (i.e. in 1984 when samples were not available during the closed season). The method of Pauly and Munro (1984), as applied by Mathews and Samuel (unpublished), was used to ensure that all assessments were carried out using mutually compatible growth parameters: i.e. values of $0'$, the growth performance index, were shown to vary by less than 2% during the study period, indicating that the growth parameters obtained for the population studied were stable. Mathews *et al.* (1987) describe this work in detail.
3. Tagging with streamer tags was also carried out on a total of over 14 000 shrimp, with over 3000 tagged shrimp returns. Total mortality and fishing mortality were estimated.

The results of all of these methods were reviewed by Mathews *et al.* (1987), who concluded that, except for streamer tagging (which provided very high values of Z, probably owing to tag related mortality) the results obtained were comparable, and that results obtained using ELEFAN were probably the most reliable. The time series of results based on ELEFAN was the longest (1979–1984).

Natural mortality for shrimp was estimated in two ways. M was calculated from the difference between F (fishing mortality estimated from tag returns; Mathews and Al-Ghafar, 1986) and Z, estimated from ELEFAN. Mp was also estimated from Pauly's (1980) empirical equation (Mathews *et al.*, 1987). Results obtained were compared by Mathews *et al.* (1988a).

Surplus production modelling was carried out using data on catch rates, effort, and landings for shrimp ("mixed shrimp"), sea catfish, (*Arius* spp.) and the stock of "mixed fish", (i.e. by-catch excluding elasmobranchs, species larger than 45 cm (e.g. *Arius* spp.) and commercially important species, e.g. groupers, snappers, *Pampus argenteus, Otolithes argenteus*, and *Pomadasys argenteus*). The mixed fish unit was also separated into 15 components, each subjected to production modelling. The species covered by surplus production modelling included 80% of by-catch by volume and over 95% of shrimp catches by volume.

The procedures used to estimate catch and effort varied for the different stocks and fisheries. For the artisanal fleet (consisting of wooden hulled, traditional "dhow" boats, operated as side or stern trawlers, usually the latter), interviews were held at the landing place every 3–4 days. Landings occurred only at high tide and were usually timed to allow sales directly into the market which was situated by the landing place. Visits were carried out at appropriate intervals during a 24-h cycle, so that the total number of boats landing shrimp was obtained and their landings sampled. Skippers were interviewed and provided data on the volume of shrimp landed, the number of trawls carried out, and the number of hours fishing during each trawl. Using these data, total effort (hours trawled) and catch rates (kg of whole shrimp per hour's trawling) were obtained. Data were then adjusted to cover the days for which samples were unavailable.

For the industrial fleet (consisting of twin-rigged, steel-hulled, mechanized trawlers), data on total shrimp landings (tails) and total effort per month (days fishing) were provided by the owners from their internal accountancy and fleet control procedures. Catch per unit effort was then calculated (adjusted to catch rate of whole shrimp, kg day^{-1}).

Effort was standardized by dividing total monthly catch for the fishery by mean monthly catch rate for the industrial fishery (which landed up to 60–70% of the shrimp). Mathews and Al-Ghafar (1986) and Mathews (1986) describe the procedures used in detail.

Trawl effort is applied simultaneously to shrimp and fish, with the latter taken as by-catch. Therefore the estimates of total trawl effort for the shrimp stocks were also applicable to the by-catch stocks. The by-catch stocks, however (unlike the shrimp) are seriously under-reported: over 90% of the fish caught at sea were discarded (Mathews and Samuel, 1984). Research vessel data, which include the total catch rate of fish and shrimp, were used to correct for the under-reporting of the former. A surplus production model (Mathews and Samuel, 1990a) was fitted to total catch and effort data, assuming the data represent an equilibrium situation. The method assumes that the research vessel catch rates are representative of the fish catch rate by the shrimp fishery, which covers 70% of the trawlable fishing grounds. Mathews and Samuel (1990a, b) describe the methodology in detail.

It is clear that the surplus production model obtained by this procedure is less than ideal. The simple procedure used provides estimates of total catch which may not be completely independent of effort; Sissenwine (1978) draws attention to this problem. Nevertheless, the procedure used here was the only one available for estimating total catch for the rather short time series available (only 10 years), and it was therefore applied in spite of its shortcomings.

For shrimp, Schaefer (1957) and Fox (1970) models were fitted to the data on total catch and total effort (both obtained from interviews).

Finally, results of production modelling were combined with retail prices to estimate the value of catches and landings that might be obtained at different effort levels. This procedure estimates likely changes in species composition (and value) with changes in effort, but ignores the possibility of any interspecific interactions. In particular, it ignores the possibility that changing effort may vary the amount of shrimp removed by predators, and so affect the amount of shrimp available for harvesting by the fishery.

The procedure used also ignores the effects of price elasticity on potential total value of the finfish catches. No price data are available on by-catch species. Data on the export of by-catch species are unavailable, but it is known that significant amounts of low-value species are exported in return for the importation of more valuable species. Significant amounts of by-catch species are now sold in the market, whereas 10 years ago sales were virtually negligible. Until research is conducted on the price elasticity of by-catch species it will be prudent to assume that the results provided here will tend to represent the upper limit of the total value of the catches of finfish made by trawlers.

The economic model used assumed that open access equilibrium occurs in the fishery. This was probably true during the study period when there was little control of effort expended in the fishery. In 1987, just after the end of the study period, a policy of effort limitation was introduced.

Dietary studies (Euzen, 1987), were used to estimate the importance of predation on shrimp (Pauly and Mathews, 1986; Pauly and Palomares, 1987). The fish studied included all of the more abundant species caught together with shrimp in trawls. During the dietary studies, shrimp were generally identified as "shrimp" and were only occasionally identified to the species (usually *Penaeus semisulcatus*). The significance of this omission is discussed below.

Results

The database

Results include data from 890 trawls carried out from July 1978 to June 1987. Catch rates were recorded for mixed shrimp, mixed fish, and *Arius* spp. in all trawls; species composition of mixed fish was identified initially in representative trawls, eventually in all trawls. Samples including stomach contents, hard parts, and gonads were obtained for over 3000 specimens of the by-catch species studied.

Dynamic pool assessments

Growth and mortality estimates of finfish based on aging

Growth parameters and total mortality were obtained by fitting growth curves to data on age-at-length for five species. Pauly's (1980) method was used to estimate natural mortality. Samuel (in press) provides similar data for *Nemipterus japonicus* and *N. tolu* (n = 600/ species). Results for three species were dubious; suspiciously high values of to were obtained for two species; Mp estimates for three species were suspiciously near Z (*Platycephalus indicus*), or exceeded Z (*Helotes sexlineatus, Saurida undosquamis*). Inconsistencies between ages determined by annual and daily marks (Brothers, unpublished manuscript) also occurred. Therefore results obtained by aging by-catch species are thought to be less reliable than those obtained from size-based analyses, and were not used for assessing by-catch stocks.

Size-based assessments of finfish using the Compleat ELEFAN

Assessments of the seven species covering all years were carried out (Table 1). Values of E_{act} (the exploitation rate estimated to occur in the fishery) and E_{max} (the exploitation rate at which MSY is expected to occur, assuming constant recruitment) show that *S. tumbil, S. undosquamis, N. tolu*, and *N. japonicus* were exploited near MSY, while *Mulloidicthys auriflamma, H. sexlineatus*, and *C. macrolepidotus* were exploited just in excess of MSY. Nevertheless, the yield curves all showed a flat section near the exploitation rate needed to obtain MSY. Observed yield per recruit was near the maximum. Overall, dynamic pool analyses show that the seven species studied (and *P. indicus*, Mathews and Samuel, 1990b) are probably harvested near the effort level expected to provide MSY. Marked increases or reductions in effort would cause corresponding changes in F and would both lead to decreases in yield per recruit, and so in total catches.

Dynamic pool assessment for shrimp

Mathews and Al-Ghafar (1986) produced a model (Fig. 1), for Kuwait's shrimp stock, using the population parameters for *Penaeus semisulcatus* (which provided over 70% of the landings). They showed that MSY occurred at F = 3.0 at 6000 days fishing per year, which was the effort level in 1983–1984. They also suggested that marked increases in effort would not affect landings. Mathews (1986) showed that no marked change in the general level of landings occurred by the end of the 1986–1987 biological year, in spite of a two-fold increase in effort. This observation is consistent with the dynamic pool model (Fig. 1).

Table 1. Results of ELEFAN analysis for combined years.

Species	*Saurida tumbil*	*S. undosquamis*	*N. tolu*	*N. japonicus*	*M. auriflamma*	*H. sexlineatus*
Year	1979–1988	1979–1986	1979–1985	1978–1979	1984–1986	1978–1986
L_∞	39.5	33.0	32.0	33.6	24.5	26.5
K	0.28	0.55	0.42	0.51	0.39	0.46
C	1.00	0.91	0.81	0.90	0.31	0.97
WP	0.84	1.00	0.20	1.00	0.90	0.90
Z	1.228	2.253	2.136	1.756	2.443	3.021
M_p	0.654	1.069	0.904	1.013	0.928	1.011
F	0.575	1.184	1.232	0.744	1.515	2.009
E_{actual}	0.468	0.525	0.577	0.423	0.620	0.665
E_{max}	0.489	0.533	0.556	0.558	0.529	0.514
No. of samples	40	36	36	12	21	46
No. of fish	11 168	12 126	8 665	11 574	7 535	25 080

L_∞: asymptotic length; K: growth parameter in the von Bertalanffy equation; C: amplitude of seasonal growth oscillation; WP: winter point; Z: total mortality; M_p: natural mortality estimated from the equation of Pauly (1980); F: fishing mortality; E_{actual}: exploitation ratio at observed Z, F, M; E_{max}: exploitation ratio which maximizes yield per recruit.

Surplus production models

Models for fish and shrimp stocks based on research vessel catch rates and total effort

Models were fitted to data for the following stocks: (1) mixed shrimp, (2) *Arius* sp., (3) mixed fish, (4) fifteen separate unit stocks which, when combined, form the mixed fish stock. Figure 2 shows the least squares regression lines for mixed fish, mixed shrimp and *Arius* spp.; all three lines show a significant ($p < 0.05$) fall in catch rates during the study period. The results are summarized in Table 2, which indicates the maximum catch and the corresponding effort level for mixed fish combined (21 000 t at 12 000 d yr^{-1}, *Arius* spp. (3800 t at 9000 d yr^{-1}) and shrimp (2100 t at 6000 d yr^{-1}). Actual landings of by-catch species were very much lower (<500 t yr^{-1}, Mathews and Samuel 1984) than estimated catches. Effort levels at the end of the study period were about 12 000 d yr^{-1}. Therefore, the difference between the estimated catches and the actual landings indicates that there is a substantial amount of underutilized fish which is harvested but not landed (Mathews *et al.*, 1988b).

Analyses for the 16 different finfish stocks gave similar results (Fig. 3 is typical) but none of the regression lines were statistically significant over the study period

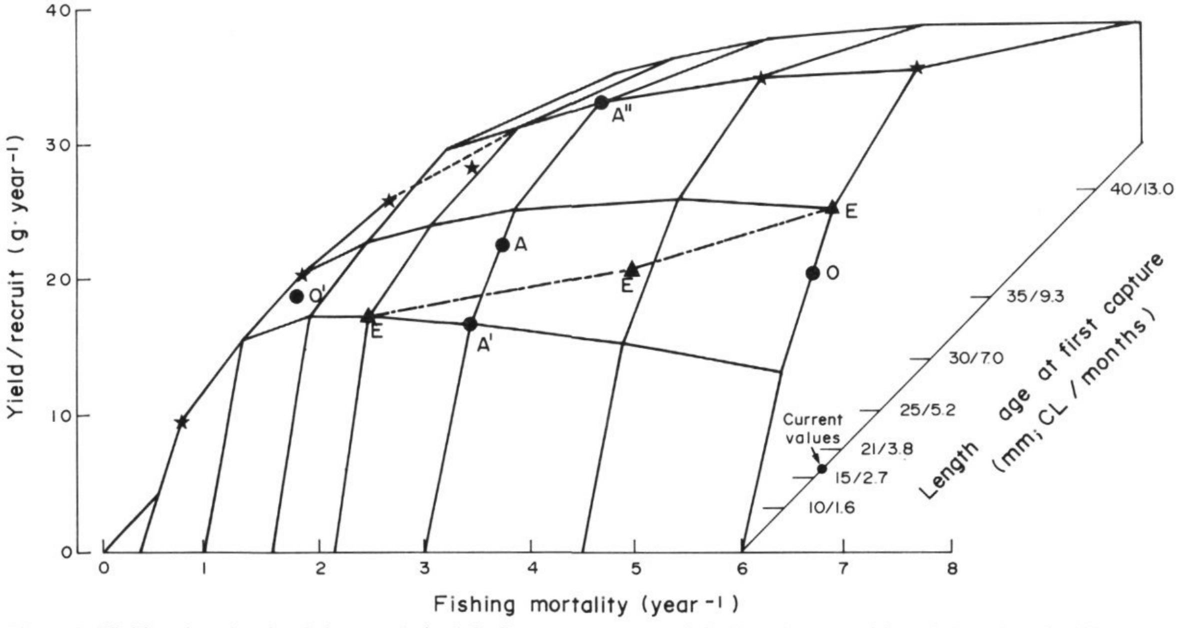

Figure 1. Yield surface for the shrimp stock (mainly *Penaeus semisulcatus*) in Kuwait. A. position of the fishery in 1983–1984. A′. 1983–1984 effort level, lower size at entry. A″. 1983–1984 effort level, higher size at entry. O. 1983–1984 size at entry, higher effort level. O′. 1983–1984 size at entry, lower effort level. E. Points on the eumetric curve, i.e. points at which Y′/R is highest for a particular size at entry. Points at which Y′/R is highest for a particular effort level (A″ is also one of these points).

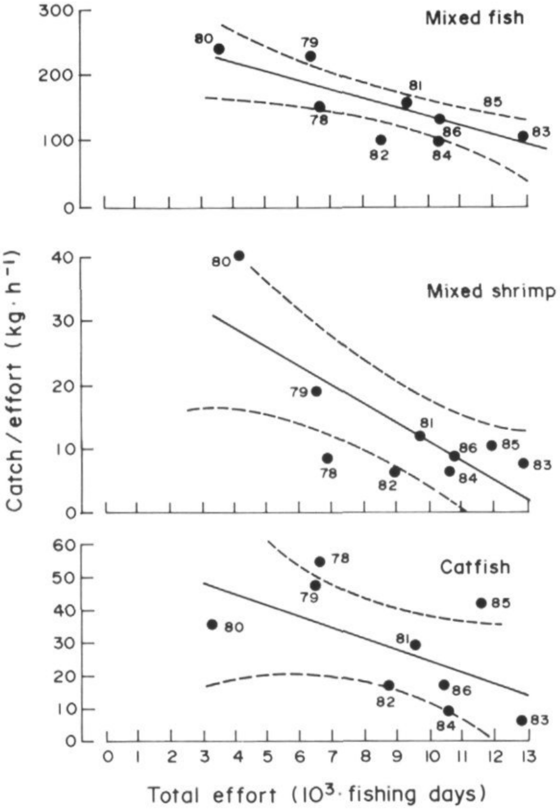

Figure 2. Relationship between catch per unit effort (kg h^{-1} fishing) and total effort (fishing days per year). The dashed lines show the 95% confidence belt around the regression line.

($p > 0.05$), probably because of sampling problems. For most stocks there was a decline in the catch per unit effort over the study period with MSY occurring at effort levels from ~6000 to 12 000 d yr^{-1}.

Surplus production models of shrimp using data on total catch and total effort from interviews

Mathews *et al*. (1987), Mathews and Al-Ghafar (1986), and Mathews and Samuel (1990a), give surplus production models of shrimp obtained by fitting Schaefer and Fox models to data on total catch and effort; Figure 4 shows the best fit obtained to data from 1970–1986; MSY occurs at ~6500 d yr^{-1} and peaks at 1720 t yr^{-1}. Other fits produced slightly higher values of MSY (~1850–2000 t yr^{-1}) at about the same effort level. All models showed that no noticeable increase in yield would be obtained above ~7000 d yr^{-1} (i.e. the level of effort at which MSY occurred), while only a slight fall in landings (<15%) would occur down to ~3000 d yr^{-1}. Results of this surplus production model agreed closely with results of the dynamic pool model (Fig. 1) in suggesting that major increases in effort observed after 1983–1984 would be unlikely to increase landings. The relative stability of the landings during the study period indicates that recruitment was also relatively stable, although landings varied considerably in the late 1960s, prior to the study period (Mathews and Al-Ghafar, 1986).

Bioeconomic modelling

Because of the assumptions made in carrying out this part of the study (including no interactions between species, no allowance for price elasticity: see methods) the calculations are likely to be unrealistic under conditions current in Kuwait's fishery. The calculations have been carried out so as to estimate what might happen if problems of handling and marketing the bycatch could be solved. Table 3 provides the estimated values of the catches of 15 different individual fish stocks (rows 1–15), for the sum of these stocks (row 16), shrimp and *Arius* spp. The total value of the finfish stocks peaks at 12 000 d yr^{-1} and of shrimp at 6000 d yr^{-1}.

The potential value of the finfish approximately equals that of shrimp at low and intermediate levels of effort, but exceeds that of shrimp at high levels. If the data used in Figure 4 are substituted for those in Table 3 the estimated shrimp catches fall much more slowly, so that Table 3 may exaggerate the relative value of finfish at high effort levels.

The effects on total value (row 19) of varying effort level in the trawl fishery are unimportant at intermediate levels (6000–12 000 d yr^{-1}) but are probably economically important at lower and higher levels (<5000 and >12 000 d yr^{-1}).

Discussion

The effects of predator–prey interaction

When this study was started in 1978 little attention was given to the possible biological interactions between the

Table 2. Sustainable yield of mixed fish, mixed shrimp, and *Arius* spp. from Kuwait's trawl fishery (t live weight at different effort levels, in standard days fishing).

Total effort (standard days)	3000	6000	9000	12 000	15 000
Mixed fish	10 800	15 800	19 100	20 700	15 100
Mixed shrimp	1 450	2 075	1 910	890	860
Arius spp.	2 200	3 450	3 800	3 200	1 750

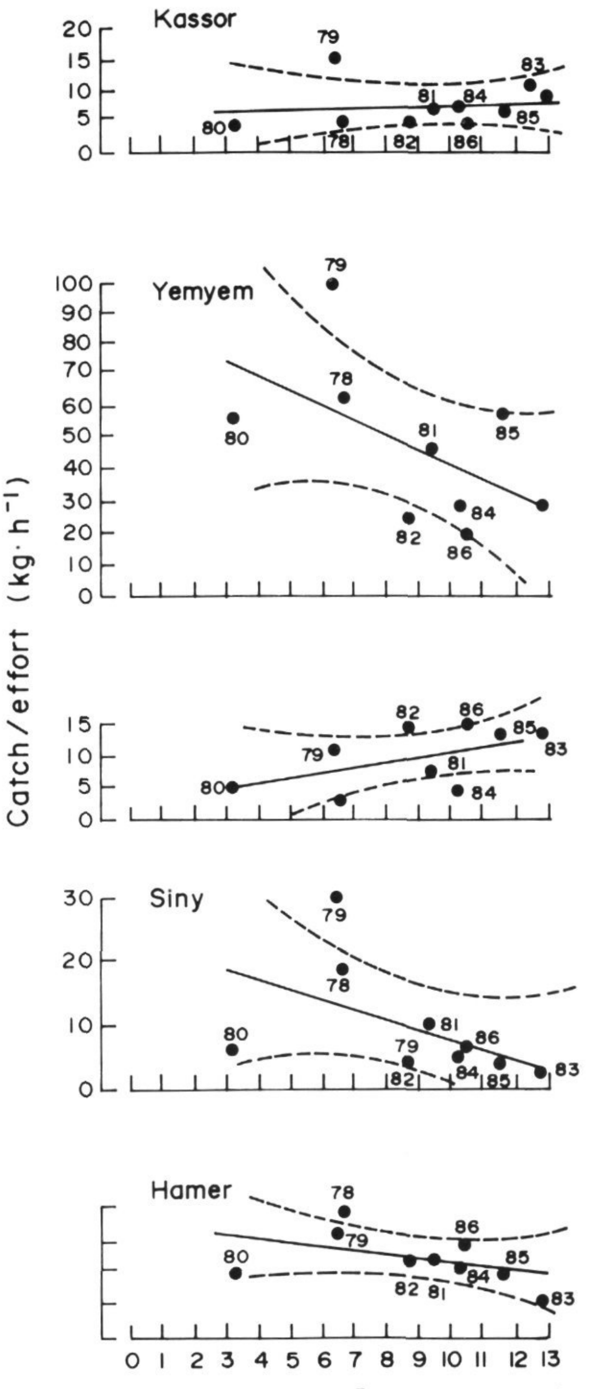

Figure 3. Relationship between catch per unit effort (kg h^{-1} fishing) and total effort (fishing days per year). The dashed lines show the 95% confidence belt around the regression line.

species fished. Nevertheless, as work progressed this question became more important. Pauly and Mathews (1986) and Pauly and Palomares (1987), using data from Mathews and Samuel (1984) and Euzen (1987), estimated shrimp consumption for Kuwait's finfish stocks (Table 4). They found that finfish consumed ~6000 t yr^{-1} of shrimp compared to landings of only ~2000 t yr^{-1}. However, the shrimp consumed by fish were not identified to species in most of the samples. The most important consumer of shrimp was *P. arsius*, a minor by-catch component (~100 t landed per year, Bawazeer, 1987a). Other important shrimp-consuming species are *Charcharinus* spp., *L. coccineus*, *Arius* spp., *C. griseum*, and *P. indicus*. Mixed-fish catch rates fell by from ~250 kg d^{-1} to ~100 kg d^{-1} (Fig. 2) during the study period. This fall probably reflects a significant decrease in fish biomass and probably a consequent decrease in shrimp removal by predators, which would increase the amount of shrimp available for harvesting, depending on the extent to which fish and man harvest the same species (see below).

Mathews (1981) showed that M probably declined as F increased during a 10-year study period in the Gulf of California stock of *P. vannamei*. Pauly (1984) presented data suggesting that M for juvenile and larval shrimp in the Gulf of Thailand decreased as total effort increased and as finfish biomass decreased. Mathews (1986) and Mathews *et al.* (1987a) showed that Z remained approximately constant as effort increased (Fig. 5). Assuming that catchability was approximately constant, there must have been a dramatic fall in M; they suggested that this could be caused by removal of finfish which consume shrimp, so that shrimp natural mortality would decline as F increases. Mathews (in press) explores this rather speculative idea further and examines the possible consequences for management of tropical trawl fisheries.

Pauly and Palomares (1987) also showed that shrimp consumed by finfish in Kuwait were much smaller than those landed (0.5 g and 11.5 g respectively) and that many more were eaten than caught (×60). They suggested that deliberate, possibly subsidized, removal of low-value finfish which consume shrimp might stabilize shrimp recruitment.

The whole line of argument presented here is weakened by a failure to identify the species of shrimp in fish stomachs. If small *P. semisulcatus* dominate, the mechanism proposed here would probably be in operation. If other, smaller species landed commercially (*Metapenaeus affinis* and *Parapenaeopsis stylifera*) dominate, the mechanism proposed is unlikely to operate. The failure to identify the species of shrimp in fish stomachs occurred for two reasons. It is technically difficult to identify small shrimp when partly digested. Furthermore, the result actually obtained (that fish consumed unexpectedly large amounts of shrimp) was not anticipated. The research programme was not designed to study the interactions of man, fish predating on shrimp, and the shrimp regulations. Future work should sample fish stomachs in areas where shrimp recruit to the fishable population, and include identification of the

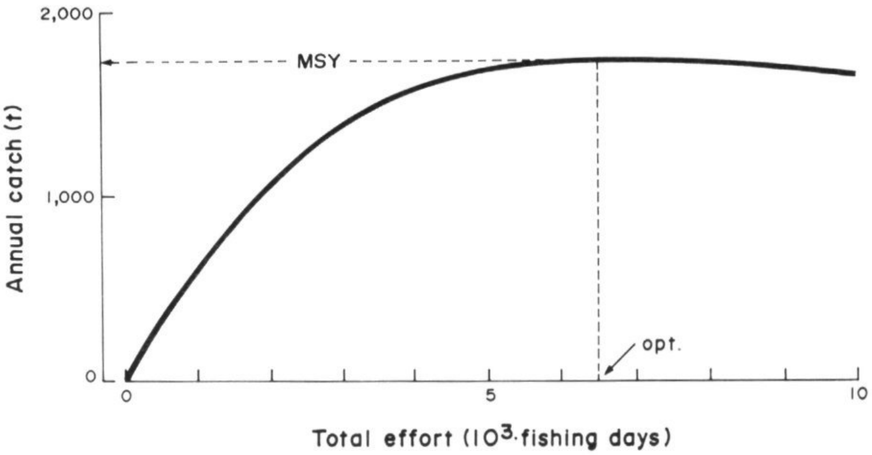

Figure 4. Surplus production model of Kuwait's shrimp fishery (MSY: estimated maximum sustainable yield). opt: effort level at which MSY is estimated to occur.

Table 3. Sustainable yield (t fresh weight) and value (KD) of by-catch at various levels of fishing effort for Kuwait's trawl fishery. Only readily available species are included.

Effort (standard days fishing per year)		3000		6000		9000		12 000		15 000	
Species/stock	Price fils/kg	t	KD	t	KD	t	KD	t	KD	t	KD
1. *Saurida* spp. Kasoor	500	281	140 500	550	27 500	860	430 000	1 500	750 000	1 190	595 000
2. *Helotes sexlineatus* Yem-yam	100	3 190	310 000	4 690	469 000	5 860	568 000	5 960	596 000	5 350	535 000
3. *Caranx* spp. Hamam	100	205	20 000	580	58 000	1 230	123 000	2 220	222 000	2 055	205 000
4. *Therapon puta* Theeb	100	230	23 000	300	30 000	280	28 000	175	17 500	–	–
5. *Leiognathus* spp. Siny	100	830	83 000	1 150	115 000	1 320	132 000	1 130	113 000	1 075	107 500
6. *Nemipterus* spp. Bassi	750	190	142 500	340	255 000	530	397 500	785	588 750	690	517 500
7. *Johnius* spp. Jelayjlee	200	1 060	212 000	1 360	272 000	1 240	248 000	690	120 000	–	–
8. *Mulloidichthys auriflamma* Hamer	200	680	136 000	1 090	218 000	1 480	296 000	1 975	395 000	1 385	277 000
9. *Cynoglossus macrolepidotus* Lessan Althoor	300	540	162 000	800	240 000	945	283 000	1 000	300 000	480	144 000
10. *Nematolosus nasus* Yuwaf	100	490	49 000	515	51 500	215	21 500	–	–	–	–
11. *Ilisha* spp. Sawayah	100	465	46 500	580	58 000	215	215 000	–	–	–	–
12. *Patycephalus* spp. Wahar	–	25	–	50	–	75	–	110	–	450	–
13. *Gerres* spp. Badah	100	30	3 000	80	8 000	165	16 500	300	30 000	315	31 500
14. *Diplodus* noct Mochwa	100	55	5 500	95	9 500	190	19 000	300	30 000	280	28 000
15. Others	–	1 090	–	1 515	–	1 670	–	460	–	375	–
16. Sum of 1–15 (Mixed fish)	–	9 361	1 342 000	13 695	1 811 500	16 460	2 621 000	17 730	3 183 750	13 290	2 441 000
17. Mixed shrimp	1 250	1 450	1 812 500	2 075	2 593 750	1 910	2 387 000	890	1 112 500	860	1 075 000
18. *Arius* spp., Chim	150	2 200	330 000	3 450	517 500	3 800	570 000	3 200	480 000	1 750	262 500
19. Grand total (Sum of 16, 17 and 18)	–	13 011	3 485 000	19 220	4 922 750	22 170	5 578 000	21 820	4 776 256	15 900	3 778 500

NB: 1.000 KD = 1000 fils; 1.000 KD = USD 3.50 (prior to 2 August 1990).

Table 4. Preliminary estimates of annual penaeid shrimp consumption by fish in Kuwait (after Pauly and Palomares 1987).

Taxonomic group	Biomass on shrimp grounds	Annual food consumption per unit biomass	Percentage of penaeid shrimps in diet	Shrimp consumed annually (t)	Mean length of shrimp in stomachs (cm TL)	Mean weight of shrimp in stomachs (g)	Mean number of shrimp eaten (millions)
Miscellaneous guitar fish	360	6.08	10.9	239	5.6	1.4	171
Carcharhinus spp.	660	9.50	14.9	909	5.5	1.3	699
Chiloscylium griseum	1 500	6.08	5.4	492	3.6	0.37	133
Miscellaneous rays	3 960	6.08	0.5	120	3.6	0.37	324
Saurida spp.	1 600	2.67	1.4	60	5.7	1.50	40
Arius spp.	3 300	2.67	6.8	599	3.8	0.44	1 362
Otilithes argenteus	350	2.67	20.2	189	3.3	0.29	652
Epinephelus tauvina	2 130	2.14	5.9	294	4.1	0.55	535
Plectorhynchus spp.	568	2.67	5.9	89	4.1	0.55	162
Pomadasys argenteus	578	2.67	5.9	91	4.1	0.55	165
Acanthopagrus spp.	969	2.78	5.9	159	4.1	0.55	289
Nemipterus spp.	860	2.67	7.9	181	3.4	0.31	584
Platycephalus spp.	2 100	2.67	5.9	331	4.1	0.55	602
Lutjanus coccineus	4 769	2.67	5.9	751	4.1	0.55	1 365
Pseudorhombus arsius	700	8.34	23.8	1 389	4.1	0.55	2 525
Other species	740	2.67	5.9	117	4.1	0.55	213
Total	25 144	–	–	6 010			11 017
Weighted means	–	–	5.9	–	4.1	0.55	–

species consumed. (In Kuwait, stomachs were mostly taken offshore, not on the recruitment grounds, where similar fish species also occur.)

Bioeconomic analyses of trawl fisheries

Figure 6 shows that maximum value of the shrimp landings in Kuwait occurs at ~6500 d yr^{-1} while maximum net profit occurs at ~3000 d yr^{-1}. In 1981–1982 the fishery was already unprofitable when total value of shrimp only was taken into account; the fishery made a small profit when the value of the small amounts of fish landed was included. Hopkins *et al.* (1984) and El-Musa (in press) confirmed this. These results show how important finfish may be in a penaeid trawl fishery. The more detailed data available for shrimp (Mathews, 1984; Mathews *et al.*, 1987) allowed distinctions to be drawn between management objectives such as maximum net profit, total value (MEY and MSY in Figure 6) and total employment (the intercept between TVs + f and TC in Figure 6 at ~10 000 days fishing for the shrimp fishery). The analysis shown in Figure 6 was eventually used to justify a policy aimed at reducing markedly the effort expended in the fishery in spite of the inadequate economic data for fish which precluded presentation of a similar analysis for the whole fishery.

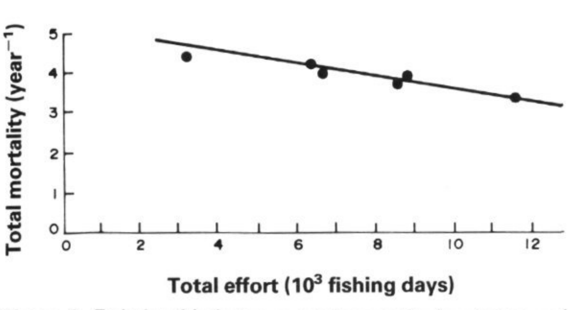

Figure 5. Relationship between total mortality for shrimp and total effort in Kuwait's trawl fishery.

Research priorities for trawl fisheries

Dietary studies

Elasmobranchs, *Arius* spp., *P. arsius*, and *P. indicus* were excluded from detailed assessment work at the beginning of the study in 1978 because of their low value and the low volumes of landings. *L. coccineus* and *E. tauvina* (Table 4) are taken in traps with only small numbers being trawled; predation by non-trawlable species was discounted. *Arius* spp. was eventually assessed because of locally high catches, while *P. arsius* and *P. indicus* were assessed only at the end of the study period. Dietary studies were not included in studies of the trawl fishery because no practically useful results were anticipated. This is now known to have been an important omission.

Bioeconomic analyses

The bioeconomic model used here indicates that the maximum total value of the finfish, when fully exploited, may approximately equal that of the shrimp. This total

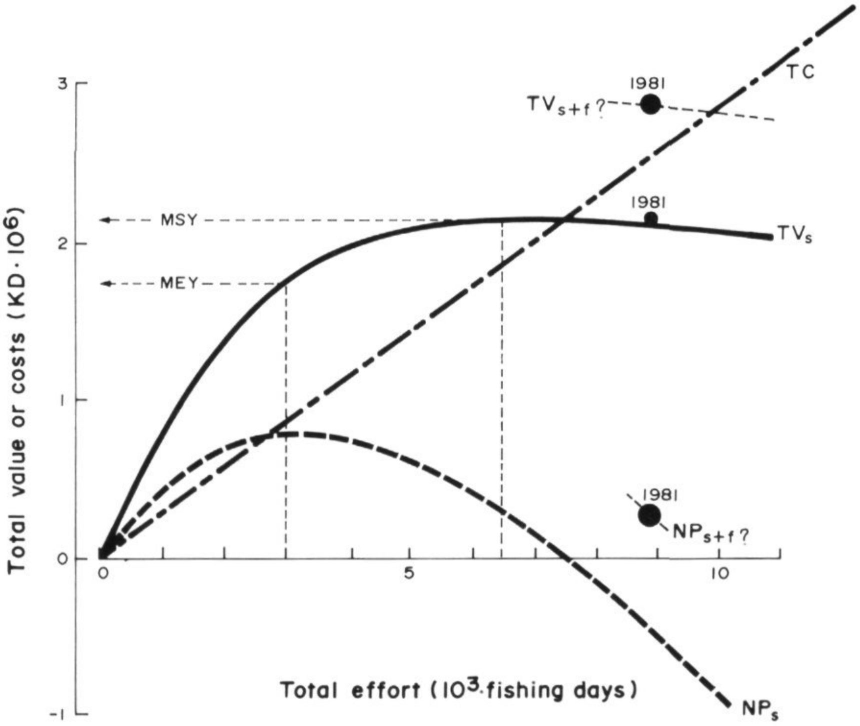

Figure 6. Relationship between revenues and costs of trawling in Kuwait, and the effort level in the trawl fishery. TC: total costs of trawling. TV: total value of the catch. NP: net profit (NP = TV − TC). s: shrimp; s + f: shrimp and fish combined. 1981: estimated datum for 1981.

value cannot currently be harvested in Kuwait because of handling and marketing problems; but these problems are not insoluble. The first author has observed penaeid trawl fisheries in both Cuba and Malaysia, where all of the by-catch is utilized: 30–40% as fish for human consumption and the remainder as raw material for conversion to fish meal and as a source of food for culturing fish. In Cuba, fish prices may be artificially manipulated so as to stimulate landing of high volume, low-value fish. In Malaysia, however a market-driven price mechanism operates. In both countries the problems of fish-landing and marketing have been addressed successfully. Data for Cuba are unavailable, but in Malaysia published statistics suggest that the value of all sorts of finfish landed with shrimp may be about 25% of the value of the shrimp.

The data presented here show that bioeconomic analyses including low-value fish as well as high value shrimp will eventually be a very important factor in managing trawlable fish stocks. This was not understood at the beginning of the study. Future studies of tropical trawl fisheries should include regular collection of retail and wholesale prices in the fishery together with data on sales volumes. Price elasticity should be included in the bioeconomic analyses; management recommendations may identify marketing strategies as well as fishing strategies.

Sampling problems

Variances obtained around catch rates were high in this study. Mathews and Samuel (1990a) describe problems which led to pooling of samples for the whole of Kuwait by year regardless of season. Kuwait's fisheries are adjacent to waters controlled by Iran and Iraq. Difficulties encountered included, in addition to the usual logistic problems associated with establishment of a sea-going sampling system, the loss of the Decca navigation system in the Gulf in 1980, frequent closure of fishing areas due to hostilities, and the effects of security on sampling and research procedures.

Assessment methodology for by-catch species

Mathews (1987b) and Mathews and Samuel (1990b) compared the ELEFAN and age-based approaches to stock assessment and concluded that ELEFAN is particularly suited to the assessment of stocks containing large numbers of species; it is a useful, cost-effective approach to the study of many by-catch species (but has the drawback that confidence limits for growth and mortality parameters cannot be obtained). Nevertheless, aging should always be carried out (Mathews, 1987b), at the very least to identify species to which ELEFAN cannot be applied (e.g. *Arius* spp., which reach up to 20 years of age, Bawazeer, 1987b), unless age data are included.

Implications for multispecies, ecological assessment, and management of trawl fisheries

Currently, penaeid fisheries are usually fished at high effort and low shrimp catch rates; a policy of reducing effort would often increase shrimp catch rates, and so increase profitability of remaining fishing units.

Implementation of an effort reduction policy assumes that no biological interaction exists between shrimp and underutilized fish stocks. Where significant amounts of shrimp are consumed by predatory fish, the situation may be more complex. In Kuwait, a policy of reducing trawl effort by ~50% was adopted (Mathews, 1987a). Yet preliminary dietary studies indicate that several underutilized by-catch species consume shrimp of unknown species in significant amounts, and that for some of these by-catch species high effort levels may lead to reductions in abundance. A reduction in effort could, therefore, lead to an eventual increase in abundance of predatory fish and so to an increase in shrimp consumption by predators competing with the fishery. Increases in shrimp catch rates expected from effort reduction could be offset by decreases in catch rate due to increased natural mortality, as effort falls.

The choice of harvest policy in a multispecies managed trawl fishery will, as in any other, depend on social priorities, e.g. with respect to choice between maximizing effort (and so employment), landings, and profits. But for a multispecies fishery targeted towards full exploitation of the trawlable stocks the ability to realize these different objectives may be limited or facilitated by food web interactions, especially by those between fish predators and prey. Construction and quantitative testing of models based on food web analyses, especially of the effects of predation on shrimp, may facilitate the management of trawl fisheries and could lead to the optimization of total trawlable catch. Mathews (in press) provides research protocols for tackling this question in detail.

Acknowledgements

The work described here is the result of ten years' research by members of the Fisheries Management Projects at KISR. We are grateful to all of them, especially to J. Dashti, M. K. Baddar, and A.S. Bawazeer who have worked with the Project for many years, and to J. U. Lee. We are grateful to Mr N. Hussein and Dr M. Seif of KISR (where data collection and much of the analysis occurred) and to Dr A. Jones of the Zoology Department, Reading, where the work was completed.

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Addendum

On 2 August 1990 Iraq invaded and conquered Kuwait. Shortly afterwards, the Kuwait Insitute for Scientific Research (KISR) was destroyed by the invading troops: the buildings were gutted, equipment was stolen, and all records were systematically destroyed in a deliberate effort to obliterate any signs of the existence of the State of Kuwait. A restored State of Kuwait may eventually address the rebuilding of KISR: but it cannot recreate the database that I established in 1978 and that was continuously enriched from then until my departure in 1988 and which Mathen Samuel maintained and extended from my departure until the Iraqi invasion.

The destruction of KISR in August 1990 was a significant event: the Mariculture and Fisheries Department was the most advanced fisheries research institution in the Gulf, and arguably in the Arab world. Scientists working there had begun to tackle successfully many problems of crucial importance to tropical fisheries science: the successful aging of tropical fish by means of otoliths (some species reach up to 45 years); single and multispecies modelling; selectivity of gillnets and of fish traps, and many other challenging problems. The *Kuwait Bulletin of Marine Science* was publishing each year many useful and innovative papers. Now, all this has gone: this paper, instead of being the first of many papers in the international press by friends and colleagues, will be the last.

Facile comparisons between Saddam Hussein's Iraq, Hitler's Germany, and Stalin's Soviet Union abound. The interested reader should consult Al-Khalil (1989) for a well-presented and accurate analysis of the history of Iraq during the last 20 years, so that he or she may judge the degree to which these comparisons are reasonable, or fall short of the real facts.

At a more personal level, the tragedy is that, in spite of all efforts, I have been unable to contact my coauthor, Mathen Samuel, since August 2. Either he is still imprisoned in Kuwait, or he and his family are refugees and have not yet reached their home, Or, simply, they are not.

I dedicate this paper to all of my friends and colleagues in Kuwait.

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Multispecies models and chaotic dynamics

Joseph E. Powers

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An ideal multispecies model captures the interactions of each of n species with each other and with the physical environment. However, the parameterization of n × n interactions defies most data collection programs for even moderately dimensioned systems. Additionally, the magnification of small errors in estimation of parameters and initial states as the system evolves in time limits the deterministic predictive capability of such an approach. Moreover, even though each species may have a complex interaction matrix, the dynamics of that species are often revealed by a dimension lower than n. The reduced dimension (fractal dimension) of the dynamics of a species may be approximated from time series of data. The chaotic behavior implied by the fractal dimensions of the species of importance to the fishery are described by simple models and interpolation functions. Realizations of the models yield conditional probabilities of relative abundance distributions. An example is given using times series of abundance indices of moderate duration.

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Introduction

Models of multispecies fisheries serve two basic purposes: (1) to describe and understand changes and patterns of changes that have occurred in the past; and (2) to predict patterns in the future. One analytical approach with these data is to attempt to model the interaction of each of a set of n stocks of fish with itself, with the other n − 1 stocks and, perhaps, with the physical environment. Quantitative parameters may be hypothesized. However, estimation of n × n interaction terms becomes problematical for even modestly dimensioned systems (Sissenwine *et al.*, 1982). Commonly, not all of the relevant data are collected nor are they represented in the proper contrasts for estimation. Alternatively, the data may be statistically described with linear models fitted with a few parameters. But, often this will not allow description of the complexity of behavior that occurs in the real system, which is important in extrapolation and prediction. In this paper another modeling alternative is suggested based upon the fractal dimension of the data and the implied chaotic dynamics. This approach can provide useful information for predictions and, thus, for decision-making in fisheries management. The first section of this paper will provide a brief (non-technical) introduction to chaotic dynamics and provide arguments for why an examination of the dimensionality of the data ought to be useful. The second section will be an introduction to fractal dimensions and their estimation. The last section will introduce simple approximation functions based upon the estimated dimension and give examples of conditional probabilities of relative stock size that can ensue from these analyses.

Chaos and dimension

Chaotic systems are, perhaps, best described as nonlinear processes which are sensitive to initial conditions measured with finite precision (Ruelle, 1979). The system is deterministic, but exhibits behavior which may be indistinguishable from purely stochastic systems. The long-term outcome is virtually unpredictable. The state of a system in a future time cannot be known with certainty even though the transition model is deterministic. Yet there are boundaries within which the system persists. Probability statements about future states can *still* be made. These processes were first explored in a population context by May (1976), who examined the one-dimensional quadratic map $x_{t+1} = \mathbf{a}x_t(1 - x_t)$ for increasing values of the parameter **a** and found that the long-term behavior progressed from a stable equilibrium to bifurcations into two-period stable limit cycles, to four-period, to eight and so on, to infinite period behavior which has since become known as chaos. Larger values of the parameter result in windows of periodic behavior and chaos before the mapping begins escaping to infinity. Feigenbaum (1983) showed that with few exceptions this period doubling behavior is universal and that the rate of doubling relative to the parameter change is constant. Mandelbrot (1982) examined the related quadratic map of a complex variable and discovered the set (which now bears his name) of parameter values which were non-escaping. To characterize his results in terms of population models, he showed the circumstances of chaotic behavior of a "population" interacting with its "environment" via a quadratic model.

Fish populations which might exhibit lack of predictive discrimination are those in which growth rates are large, the duration of time of the prediction is long or the fish's external environment is highly variable. Disagreement on the existence of chaotic processes in nature still exists, but to many it is only a question of degree (Schaffer and Kot, 1985). The implications of chaotic behavior to multispecies fisheries are pervasive. If, indeed, the processes are chaotic, then there is no better way to predict stock levels than to watch the stocks evolve over time and measure those levels. Even if measurements were extremely accurate, one could not be absolutely sure of long-term projections with even the most sophisticated of models. However, despite sensitivity to initial conditions, there is stochastic pattern in the dynamics which can be useful for management. Statistical properties of the dynamics can often be ascertained (Jensen and Oberman, 1982). Therefore, probability statements about future conditions of the fishery can still be made. Examination of the dynamics, even when they are deterministically chaotic, will guide the construction of those probability statements.

A feature of dynamical systems is the property of imbedding, i.e. that the dynamics of high-order systems are revealed in fewer dimensions, often *many* fewer dimensions (Schaffer and Kot, 1985). Takens (1981) showed that for an n dimensional system, one can examine almost any one of those state variables x(t) for almost all time-lags T through m-dimensional phase space reconstruction by plotting x(t) vs. x(t + T) vs. x(t + 2T) vs. . . . vs. x[t + $(m - 1)$T]. The phase space reconstruction will have the same dynamical properties as the portrait constructed from the n original independent variables (Schaffer and Kot, 1985). One will need an m no larger than $2n + 1$ and often much smaller (Takens, 1981). Hence, the dynamics of multiple dimensions can be imbedded in a single dimension. Indeed, unidimensional properties have often been seen in population biology (Schaffer, 1984); witness the proliferation of the one-dimensional quadratic map (also referred to as the logistic production function) used in fisheries assessment. Imbedding of dynamics holds promise for multispecies analysis. While we may not be able to measure population levels of each species in the ecosystem, we may be able to describe the dynamics based upon a smaller dimensional model.

Phase space reconstruction is the principal method to examine time series of seemingly noisy, random data. Reconstruction allows structure to be shown in the data and can be used for short-term predictions. Poincaré sections (intersections of a plane with a multidimensional trajectory) often show where areas of determinism exist, as well (Schaffer and Kot, 1985).

Reduced dimensional dynamics may be a result of the signal processing of the fish, themselves. Individual fish and fish populations may integrate and filter their environmental signals into a reduced set upon which they will react. Thus, the population will interpret several external variables as being equivalent, resulting in equivalent responses. In anthropomorphic terms, a harsh, seemingly random, environmental signal is interpreted and filtered into a message. Simple responses (models) are taken based upon the message received. Since additional energy costs are required for further filtering to produce stable or low periodic behavior, seemingly random (but actually deterministic chaotic) behavior may be the norm rather than the exception.

The implications of the above for multispecies analysis are (1) examination of selected species or segments of the system, chosen for anthropic (including economic) reasons, should be the first thrust of the analysis, since it is the dynamics of these segments that are important to the investigation; (2) the analysis should address the dynamic behavior of a multispecies system as revealed through the behavior of the few selected species; and (3) the dimension of the reduced systems should be characterized. One method to do this is through the fractal dimension.

Fractal dimension

Fractal analysis arose in the work of Mandelbrot (1982) and others to quantify the degree of "irregularity or roughness" in the surface of sets such as chaotic time series, perimeters of coastlines and other phenomena (Jones *et al.*, 1989). True fractal surfaces are self-similar in that the amplitude of the fluctuations on the surface of scale hs are proportional to h^{-b}; where h is a non-dimensional factor, s is the distance measure and b is the similarity parameter (Mandelbrot 1982). Increasing or decreasing the resolution (s) of the image will show the same relative fluctuations. For one-dimensional surfaces the fractal dimension is $D = 2 - b$ with $1 \leq D < 2$. A fractal dimension of 1 implies a truly one-dimensional surface (a curve or line), whereas $D = 2$ implies "space filling" of the plane and a completely random surface.

There are a variety of methods to quantify the scale dependent fluctuations (hs). The box counting method (Barnsley, 1988) uses the number of rectangles (h) of side length s needed to cover a graph. A range of values of s are used and the parameter b is chosen by inspection of the log-log plot or regression. Another method by Burrough (1984) uses the variance of the average vertical distance between any two points separated by a given horizontal distance (s). This is repeated for all points and all alternatives for s. In this method (the semivariance method)

$$D = 2 - \{[\text{slope of } \log(\text{variance}) \text{ vs. } \log(s)] \times 0.5\}.$$

The log-log plot is known as a semivariogram in other applications (kriging). Jones *et al.* (1989) suggest some local smoothing and thinning operations before taking differences at larger scales.

In practice, self-similarity is not valid over all scales for real-world phenomena. For that reason the surfaces are often called pseudofractals and the estimated D is reported with reference to the scales measured and the scales over which proportionality is maintained. Additionally, precise estimates of D require many data points, i.e. in the order of 100 or more (Burrough, 1984). Commonly, time series of fisheries indices do not exceed 10 to 30 years in duration. Perhaps all that can be expected in these instances is approximations of D to the first decimal. The limitations of time series data (Burrough, 1984) may not allow the identification of deterministic chaos versus random behavior. However, examination of the dimension of the data can still be helpful in characterizing the variability of the process over the range of observed data. Subsequently, this can be incorporated into stochastic decision analyses. Interpolation functions provide a mechanism to do this.

Interpolation functions

The observed data and the measured fractal dimension can be exploited through what Barnsley (1988) has termed fractal interpolation functions. The data points are a first approximation to the dynamics and the fractal dimension provides information on the degree of attraction to those data points. Fractal dimensions are the philosophical equivalent of variances in stochastic processes; the precision of predictions is dependent upon them. A model which incorporates this information follows.

A process F(x) of independent variables (x) may be approximated by a piece-wise linear function of data points $[(x_i,F_i); i = 0, \ldots, N]$, where the x_i's are ordered, i.e. $x_i < x_{i+1}$ for all i. Barnsley (1988) showed that this can be modeled by N affine transformations ($w_n(\ )$; $n = 1, \ldots, N$) which linearly maps a couplet of vertical (y) and horizontal (x) points into a new couplet:

$$\begin{vmatrix} x \\ y \end{vmatrix} = w_n \begin{vmatrix} x \\ y \end{vmatrix}; \quad w_n \begin{vmatrix} x \\ y \end{vmatrix} = \begin{vmatrix} a_n & 0 \\ c_n & d_n \end{vmatrix} \begin{vmatrix} x \\ y \end{vmatrix} + \begin{vmatrix} e_n \\ f_n \end{vmatrix} \tag{1}$$

and which are constrained by the data such that

$$w_n \begin{vmatrix} x_0 \\ F_0 \end{vmatrix} = \begin{vmatrix} x_{n-1} \\ F_{n-1} \end{vmatrix} \quad \text{and} \quad w_n \begin{vmatrix} x_N \\ F_N \end{vmatrix} = \begin{vmatrix} x_n \\ F_n \end{vmatrix} \tag{2}$$

where the a's, c's, d's, e's, and f's are parameters. A description of affine transformations is those which when inverted and mapped onto themselves become "attractors" to the underlying function (see Barnsley for a rigorous definition). The parameters a_n and e_n can be obtained from the solution of (1) and (2) as functions of the data points:

$$a_n = (x_n - x_{n-1})/(x_N - x_0)$$
$$e_n = (x_N x_{n-1} - x_0 x_n)/(x_N - x_0).$$

Parameters c_n and f_n are functions of both the data points and the free parameters d_n ($n = 1, \ldots, N$):

$$c_n = [(F_n - F_{n-1}) - d_n(F_N - F_0)]/(x_N - x_0)$$
$$f_n = [(x_N F_{n-1} - x_0 F_n) - d_n(x_N F_0 - x_0 F_N)]/(x_N - x_0)$$

The d_n are vertical scaling parameters which are constrained such that

$$\sum_n [|d_n| a_n^{D-1}] = 1, \tag{3}$$

where D is the fractal dimension of the piece-wise linear interpolation function ($1 \leq D < 2$). Iterative realizations of the affine transformations (1) with specified values of d_n are obtained by selecting an initial x and y, randomly selecting an interval (n), generating new couplets (x,y) with (1), plotting or saving the new points, then randomly selecting a new interval and repeating the process a large number of times. As the absolute values of the d_n are reduced (the fractal dimension becomes small), then the realizations are attracted closer and closer to the piece-wise linear function. When $D = 1$, then it is exact. The fractal dimension D provides information about the "irregularity" of the data points and the underlying process. If the process is stationary over the range of x, then the absolute values of d_n can be expected to be equal ($|d_n| = |d|$) which can be obtained from (3). This can be incorporated into the above simulation by solving for c_n and f_n within each iteration and randomly selecting the sign of d, assuming positive and negative values of d are equally likely. Additional information on relative magnitudes of the d_n and their signs can also be exploited using (3) and implemented into the simulations.

Example and discussion

Indices of juvenile (age 1) abundance of two snapper (*Lutjanus*) species in the Gulf of Mexico from a system-

Table 1. Indices of juvenile snapper abundance in number per trawl hour.

Year	Red snapper	Lane snapper
1972	40.69	3.14
1973	11.05	0.47
1974	8.00	0.63
1975	10.60	1.83
1976	8.49	1.09
1977	10.11	2.41
1978	22.13	0.57
1979	7.84	0.21
1980	18.04	1.28
1981	20.17	1.44
1982	19.08	0.60
1983	7.19	0.35
1984	3.55	0.25
1985	5.45	0.62
1986	5.23	1.74
1987	1.87	0.63
1988	7.25	1.32

Source: S. Nichols, 1989. Patterns of variation for red snapper, wenchman, lane snapper, and vermilion snapper catch rates in the Gulf of Mexico fall groundfish survey. NMFS. Miss. Labs., Pascaoula, MS, USA. 56 pp.

atic trawl survey (Table 1) were examined. The dynamics of the abundance of the juveniles of these two species as they change over time and in relation to each other were of particular interest. Are there quantifiable relationships between the juvenile abundances or are they independent of one another? Can the time series of indices be useful in prediction of relative abundances of juveniles of the two species in the future? How far into the future? Predictions would be useful in forecasting fisheries production for the two stocks.

Exploratory analyses were conducted comparing (among other relationships) the log of the ratio of red snapper to lane snapper with the same log ratio m years prior [$\log(rs_{t+m}/ls_{t+m})$ versus $\log(rs_t/ls_t)$], where m is the prediction horizon. The hypothesis is that the dynamics of the two species during the prediction period are similar and that the species composition (as measured by relative abundance) can be predicted from previous values. If so, then management regulation of the multispecies fishery may be adjusted, based upon the relative strength of the juvenile year classes of these two species.

Fractal dimensions were calculated using the semivariance method in which the data were smoothed by linear interpolation in fifty increments of the x range. Prediction horizons (m) of up to 7 years were evaluated. When $m = 3$ (prediction of 3 years), a fractal dimension of 1.5 was obtained. Longer predictions ($m > 3$) resulted in fractal dimensions approaching 2.0, which implies little or no prediction power for these longer periods. If a three-year time horizon for biological prediction is common in fisheries, then this, itself, would be extremely useful for management. However, it would be premature to generalize from these data.

The transformed data for $m = 3$ (Fig. 1) were fitted by an interpolation function in which the absolute vertical scaling parameters, $|d_n|$, were assumed to be equal for all intervals n of the data series with signs of d_n equally likely to be positive or negative, i.e. the fractal properties were assumed to be constant over all intervals of the data. The d_n was determined from Equation (3) with $D = 1.5$. A total of 20 000 realization points (x,y) were generated from an initial (x,y) couplet, random selections of an interval (n), solutions of a_n, e_n, c_n, and f_n and application of the affine transformation to obtain a new (x,y) point (Fig. 2).

Conditional probability density and cumulative distributions were constructed for a selected interval of the initial log ratio (initial log ratio (x): $2.1 \leq x < 3.0$). The fractal properties of the predictions are shown by the "irregularity" in the probability density surface (Fig. 3). Approximate 80% confidence for the conditional prediction (F) of the log ratio is 1.5 to 3.0 (Fig. 4). In this example the interval of x (2.1 to 3.0) results in wide variation in the prediction of F (Figs. 1 and 2). Therefore, the cumulative conditional probability of the prediction is approximately uniform (Fig. 4). If the initial log ratio is measured with more precision (the conditional interval for x is narrower), then the resulting prediction (F) will also be more precise. It is interesting that when the log ratio is low (less than 2; i.e. a lower abundance of red snapper relative to lane snapper), then there is a high probability that the relative abundance of red snapper will respond in three years (Fig. 2). Whereas, at intermediate levels (Fig. 3), there is a tendency for red snapper relative to lane snapper to remain depressed. The usefulness of forecasts with these levels of precision will of course depend upon the management questions being asked and the planning horizon being considered.

An alternative, more traditional form of analysis might be to fit a transfer function to the time-series data. While such a model might be equally as useful in describing central tendency, conditional probability statements could not be made without strong assumptions about the shape of the underlying distributions. Fractal interpolation functions use the observed data to define the probability structure.

Additional examinations of the data would be required for application of these methods to a fisheries assessment and management situation. Model dependent analyses might include estimation of the fractal dimension over a subset of intervals to examine the assumption of equal $|d_n|$; evaluating the validity of equal probability of the signs of the d_n; and evaluate the assumption of equal probability of x-axis interval selection in the simulation. The primary assumption of the model (that the data represent an attractor for a chaotic process which can be approximated by a piece-wise linear function) is to some degree corroborated by the measurement of the fractal dimension of less than 2. If

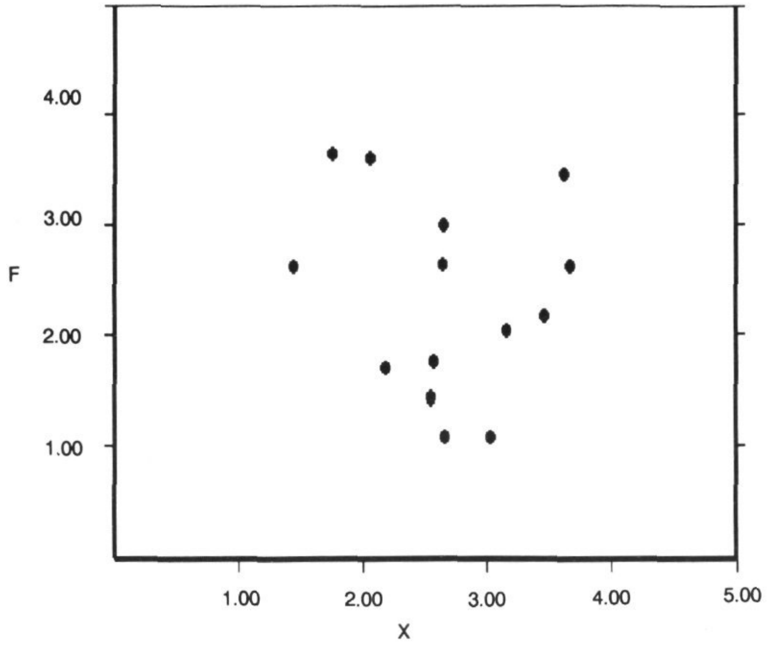

Figure 1. Logarithm of the ratio of abundance indices of red snapper to lane snapper in year t (denoted by x) versus the same log ratio in year t + 3 (denoted by F). From data in Table 1.

this were not the case, then other methods would have had to be explored. However, fractal analysis appears to be a useful tool to have available.

Additionally, a large effort in fractal analysis (indeed in *any* multivariable analysis) should be data-related: exploring the data for other explanatory variables such as adjustments for spawning-stock size, fishing, and other variables which have affected the indices over the

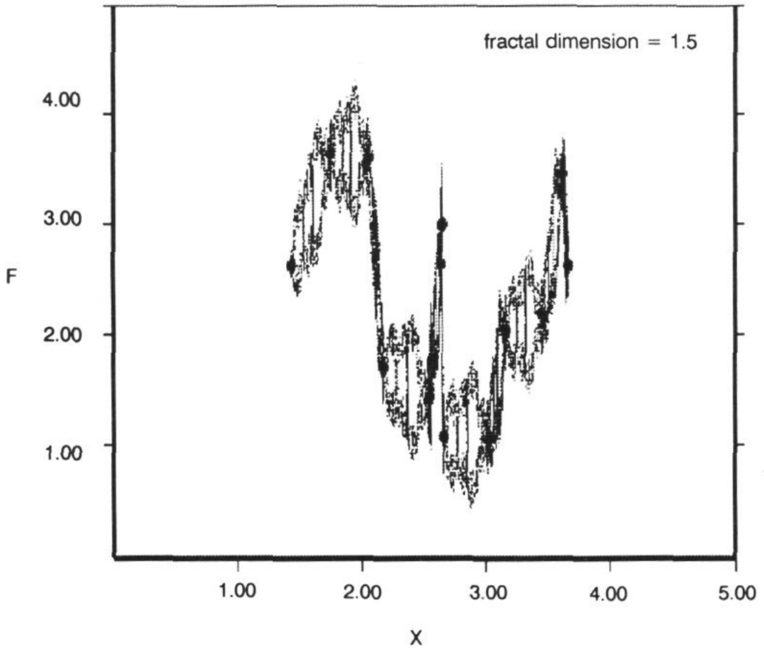

Figure 2. Logarithm of the ratio of abundance indices of red snapper to lane snapper in year t (denoted by x) versus the same log ratio in year t + 3 (denoted by F: see Fig. 1) with 20 000 realizations of the fractal interpolation function. Interpolation function constructed such that $|d_n|$ equal over all intervals (n) and the signs of d_n equally likely to be positive or negative.

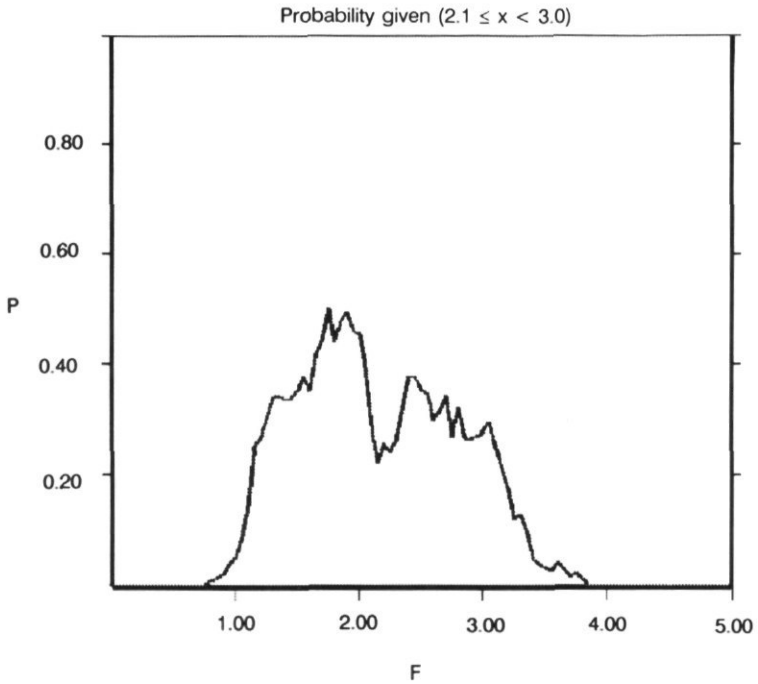

Figure 3. Conditional probability density (P) for the fractal interpolation function in Figure 2 given that x is in the interval $2.1 \leqslant x < 3.0$.

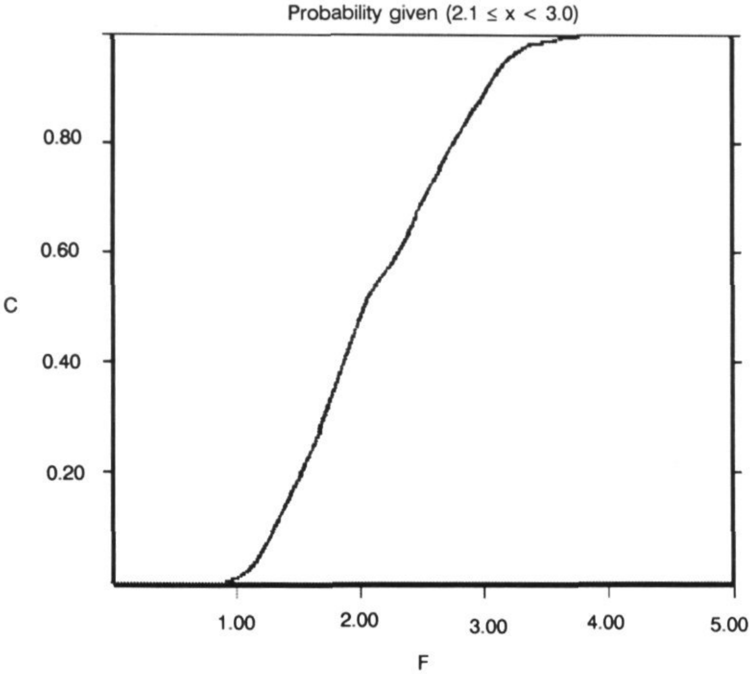

Figure 4. Conditional cumulative probability (C) for the fractal interpolation function in Figure 2 given that x is in the interval $2.1 \leqslant x < 3.0$.

time series. Applications to management prediction problems should include these analyses when appropriate.

Multispecies forecasting models will have to be probabilistic in their predictions if they are to be useful for management. Past dynamics of the species should be explored to determine underlying relationships, to partition chaotic dynamics versus purely random outcomes and to define the limits to the time period of forecasting. In either case of random or deterministic chaotic dynamics, the prediction will be probabilistic. In many instances we may not be able to distinguish between the two. But where deterministic chaos *is* evident, then the probability density functions of predictions can be improved by the incorporation of these aspects.

However, as suggested by Schaffer and Kot (1985), whether we can detect it or not, deterministic chaotic dynamics may be pervasive in biological systems. Thus, multispecies management models used in forecasting should address the possibility of this characteristic.

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Under what conditions will multispecies models lead to better fisheries management?

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The development of multispecies models of exploited fish populations is an important scientific challenge which will lead to better insight into the dynamics of fisheries resources. However, there is a great deal more required for management than scientific results. Resource managers will use multispecies models only when certain criteria are met. The models must be transparent to non-specialists for the results to be acceptable to managers and industry. Model results must be uncontroversial in the sense that they cannot easily be disputed, and the uncertainty must be quantified and explored as far as possible. Policies implied by multispecies models cannot be biased in favor of one interest group at the expense of another, and the benefits of a change in policy direction must be quantified. These criteria are true for the acceptability of most scientific advice, but are particularly important for incorporating multispecies analyses into management. This is because these analyses often imply a major change in direction from past policy and from the conventional wisdom. Such a departure can erode the credibility of scientific advice if managers and industry are not kept informed about research progress, and without strenuous efforts to explain new results clearly. Several examples are given of the interaction between scientific advice and management policy to illustrate these points.

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Introduction

The biological objectives for fisheries management are usually defined on the basis of single-species models, such as a simple yield per recruit analysis. It is widely accepted that these models only roughly approximate biological processes in the ocean. In particular, a vast variety of interactions that can occur between different species are not explicitly accounted for in a single-species context. It is, thus, widely believed that if scientists could devise models that describe adequately multispecies interactions and modify their advice accordingly, this would be welcomed by managers as being a noticeable advance towards the Holy Grail of perfect fishery management.

It is the thesis of this paper that this belief is largely misplaced, that scientists should recognize that multispecies advice will not necessarily be accepted by managers for a variety of reasons. Because of this, scientists must be aware of the difficulties managers will face in applying advice based on multispecies models, and make every effort to direct their research along the most fruitful lines and to explain the results as clearly and straightforwardly as possible. This paper will look at the criteria under which a change in advice is most likely to lead to better management; it examines the extent to which multispecies models are likely to satisfy these criteria and discusses the implications of the conclusions for multispecies approaches to fisheries management.

In what follows, I define a manager to be anyone whose decisions are likely to affect the amount or pattern of fishing. This is a wider definition than the commonly used one, which tends to be limited to senior officials in government departments responsible for framing regulations, e.g. annual catch limits. It is worth remembering that not only are the decisions of these officials likely to be constrained by the views of influential people in industry, but the latter are also likely to take decisions, for example choosing to invest in a new vessel, which can greatly affect the level of fishing in the future. In this sense, they too are managers and have similar requirements for good scientific advice.

A distinction needs to be made between the effect on management in the long term (a couple of decades or

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†Deceased 24 June 1990.

more) of a better understanding of the dynamics of exploited fish populations that should come from the development and use of multispecies models, and the ability of managers to put advice based on these new results into effect in the short to medium term. I do not want to challenge the scientists' natural faith that, in the long run, a better understanding of how multispecies systems work will lead to better management. My concern in this paper is with the ability to translate new, potentially very different, scientific advice into short- and medium-term management actions.

Conditions for better management

Several conditions can be identified which make scientific advice acceptable to managers as a basis for new decisions. It should be clear to scientists that there is a lot more to the management of fisheries resources than the scientific advice itself. New advice is most likely to be used if:

(1) it implies changes in current management practice that are straightforward and preferably minor;
(2) the science involved is transparent to a non-specialist such that the inclusion of new information clearly suggests changes in the advice on management of the resource;
(3) the new results are scientifically uncontroversial, i.e. the provision of the new advice will not be accompanied by substantial debate over the science itself;
(4) suggested new measures will reduce or at least not increase conflicts between different interest groups;
(5) there will be no clear losers that cannot easily be justified and dealt with.

Any scientific advice on resource management will be potentially most useful if it implies changes in management practices that in turn result in substantial benefits, such as greater or more valuable catches or lower harvesting costs. However, unless at least some of the criteria listed above are satisfied such advice will not necessarily be welcomed by resource managers. This is not through cynicism on the part of the managers but is due to the practicality of putting new management measures into effect.

Multispecies fishery models are often divided into those which account explicitly for biological interactions between species and models of technological interactions, for example gear selectivity patterns which harvest several species together under certain conditions. With respect to the criteria listed above for the acceptability of new scientific advice, multispecies analyses of technological interactions are likely to imply more easily implemented management measures than biological interaction models. This is because the science is usually transparent and the results are often uncontroversial and clear. For example, the benefits for spawning-stock size or yield per recruit of reducing the by-catch of young fish by area closures, gear regulations, or adjustments of total allowable catch levels to account for by-catch mortality can often be clearly seen by non-scientists.

The magnitude of the effects of such measures is still subject to substantial uncertainty, of course, due to doubts about the natural mortality rate of young versus older fish for example. Nevertheless, the benefits to be gained by taking account of technological interactions in management policies are often relatively small. There are notable exceptions, such as the potentially great effect of reducing by-catch of finfish in some shrimp fisheries, particularly in the tropics where fish are a very high proportion of the catch, but a small proportion of the landings from shrimping vessels is fish.

For reasons of space, advice from technological interaction models is not discussed further here. It should be noted, however, that while such models are fully reliable at explaining past events, there are doubts about the accuracy of forecasts based on technological interaction models, particularly because of the difficulty of accounting for changing behavior of fishermen in response to new regulations.

One of the major focuses of research on multispecies fisheries models is the work of the ICES Multispecies Working Group (Anon., 1989) which has incorporated predation interactions among the major species in the North Sea into assessment and forecasting models. To some extent, the same comments made with respect to technological interaction models apply to these predation models. The scientific principle used is straightforward; the mortality caused by predators is treated in the same way as that caused by a component of the fishing fleet. Most of the research effort is related to determining the selection pattern for each predator species on each prey species, i.e. the diet composition in terms of species and sizes of prey. This is scientifically demanding but the underlying concept is easily understood by the layman.

As regards the effects of different patterns of fishing on fish that are not major predators, the results of the multispecies models, as expected, do not suggest substantially different management policies than the single-species models. However, scientific advice on the effect of the pattern of fishing on several important resources, notably cod, whiting, and saithe, in a multispecies context indicates a substantial departure from predictions from single-species models. In particular, there may be losses, rather than benefits, from increasing the minimum mesh size or reducing effort in the cod fishery, where conventional single species yield per recruit models indicate increases in yield accompanying decreasing the rate of fishing mortality and increasing the age at recruitment to the fishery for cod.

As Brugge and Holden (1991) point out, this result is not welcomed by managers for two reasons. First, the results may still be considered controversial because there is no clear determination that the new results are nearer the truth than the advice resulting from single-species analyses. This is because there is still a large amount of uncertainty in the estimates obtained from the multispecies models. While there is no doubt that species interactions occur and are important in the sea, estimating the magnitude of the effect on fishery yield is another matter, and the prediction limits for such an estimate are likely to be wide. Second, by casting doubt on the accepted scientific view on how to manage cod for nearly half a century, the new analyses can make it more difficult to persuade the fishing industry to accept management decisions.

The predator–prey interactions between marine mammals and fisheries (see Beddington *et al.* 1985 for a recent review) raise a different set of management problems. In this case, the interactions are often very obvious and striking. A salmon fisherman is much more disturbed by the sight of a seal with a salmon in its mouth next to his net than is a haddock fisherman upon reading scientific reports that predation by whiting may be reducing haddock recruitment. While the principle underlying the science and the likely effect of different policies is relatively simple to understand when only one species of marine mammal, one species of fish and the fishermen are involved, consideration of the case where the fish species eaten by marine mammals is itself a predator on another commercially valuable stock quickly clouds the issue. Furthermore, there is a considerable amount of doubt in the estimates of many of the basic quantities needed for any multispecies analysis. For example, estimates of marine mammal diets are weak and are likely to be biased in favor of concluding that the impact on fish species of interest is greater than it really is simply because only a small number of samples of mammal stomach contents are available and a substantial number of these come from animals killed in or near the fishing nets.

An additional major issue with respect to managing marine mammal-fishery interactions involves the political or philosophical question of what constitutes a proper use of the marine environment and the living resources of the ocean. Managers will find it difficult to accept at face value advice which is likely to substantially increase the conflict between fishermen and conservationists. If an analysis could clearly demonstrate that claims by fishermen of damage to the fish stocks by seal predation were exaggerated and, therefore, politically unpopular culling programs were unwarranted, managers may be expected to welcome such advice because it would provide a basis for satisfying the demands of one interest group without substantial losses to another.

On the other hand, advice indicating that culling seals would give a substantial benefit to commercial and/or recreational fisheries may be more problematic because it would exacerbate conflicts over use of the resources. A case in point is the result of the Canadian Royal Commission on Seals and Sealing which calculated that the benefit to fisheries from culling grey seals, taking into account gear damage and transmission of parasites, as well as competition for fish, was several thousand dollars per seal killed (Anon., 1986), assuming reasonable population parameters for the seals. Management initiatives to undertake a cull can be expected to meet with strong public opposition and the uncertainty of the estimates of benefits make undertaking any such policy problematic.

If a major fishery for krill develops in the Antarctic, interactions with marine mammal populations may be of major concern for managers. The Convention setting up the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) explicitly refers to an ecosystem approach to management. Article II of the Convention provides for "the prevention of decrease of . . . any population . . . below the level close to that which ensures the greatest net annual increment" and the "maintenance of ecological relationships". The wording of this Article was determined by the need to reach agreement between those countries primarily interested in harvesting the resources and those primarily interested in conservation. A key issue for CCAMLR is the possible impact of large-scale krill harvesting on the predators of krill, particularly the large baleen whales.

To date, a major problem has not materialized because the present krill harvest of around half a million metric tonnes per year is not thought to be large enough to have any impact on the standing stock of krill or, therefore, the ability of their predators to find food. Modeling efforts to date have illustrated the basic population dynamics involved (Beddington and May, 1980), but more detailed models will be required to predict how a particular level of krill harvest will impact on the population growth rates of protected stocks of, for example, blue whales. Managers will need this sort of information if a major market for krill develops, which can happen rapidly for fishery products.

A major difficulty which will be faced by managers if the krill fishery develops rapidly will be the uncertainty in any model predictions. At present, it is not certain that blue whale stocks, for example, are increasing at all. On the one hand, those harvesting several million tonnes of krill will not readily accept that the industry should be restricted on uncertain scientific grounds. On the other hand, once conservation groups consider that whales, seals, and penguins, some of the chief symbols of the environmental movement, are potentially being threatened, at least in terms of slowing the recovery of their populations, they will make a strong call for action. Managers are, therefore, unlikely to welcome advice that such a threat is present unless the proof is strong enough to overcome the opposition of the harvesters. Such proof will be difficult to obtain for the Antarctic ecosystem and the manager's position will undoubtedly be awkward.

So far, the mechanisms of species interactions are clear, even if the resulting management problem is formidable. In other cases, an interaction can be suspected which potentially could have a large impact on fisheries, but the mechanism is unclear. The obvious example is in the North Sea. Since the turn of the century, when reliable statistics became available, until 1960, catches of cod and plaice from the North Sea remained very stable. Haddock catches were decreasing regularly before the Second World War and were more variable than the other two species. Beginning in 1963, the catches of these major species increased dramatically to two to five times their previous levels. Much of the increase was due to very large haddock catches in the 1960s and 1970s. The immediate cause of this increase in catch was an increase in average year-class strength (Holden, 1978), but why the increase occurred is unknown. One obvious change in the North Sea around 1960 was the collapse of the herring and mackerel stocks. It is possible to postulate a mechanism linking the decline in herring and mackerel to the increase in recruitment of demersal species, such as reduced predation by adult pelagic fish on larval demersal fish. If this hypothesis could be substantiated then a sensible management policy would be to keep the herring stocks at a level no higher than needed to supply the relatively small human consumption market. The declared policy of fully rebuilding the pelagic stocks could lead to an appreciable fall in the overall value of the North Sea landings (Gulland, 1981). However, managers have found it difficult to act because the prediction of a decline in demersal fish landings following pelagic stock increases is highly uncertain and the actions required would have a major impact on the industry. If, on the other hand, the scientific evidence was clear and pelagic stocks are likely to suppress demersal fish recruitment, then managers would still be faced with the dilemma of favoring one sector of the industry, the demersal fishermen, over another, the pelagic fishermen.

Resource instability or uncertainty can have different implications for the manager when viewed in multispecies versus single-species context. Stocks of pelagic species such as herring, sardines and anchovies often exhibit considerable instability worldwide (Saville, 1980; Sharp and Csirke, 1983). For any one species there have been periods, typically of the order of a few decades, of high abundance which have been separated by other periods of low abundance. Often the shift from high to low has come after a period of heavy fishing (instantaneous fishing mortality rates of 0.5 or more). The standard single-species advice has, therefore, been to avoid such intense fishing rates. Against this, it has often happened that, at about the same time as one species (e.g. anchovy) collapses, another (e.g. sardine) increases. It is tempting to believe that these are examples of substitution, in which case the manager can watch with equanimity the collapse of one species, safe in the knowledge that another species will increase to fill the gap. In these fisheries the manager may welcome the multispecies advice because it can justify his taking no action, though the scientific case for direct substitution is weak.

Discussion

At face value, the examples and conclusions reached so far may seem discouraging for research effort directed towards building better multispecies models in order to improve fisheries management. However, the main point is that management decisions are difficult and, therefore, the scientific results must be convincing enough to warrant a change in policy.

Where the results are of a kind that managers are prepared to welcome and act on them, the actual impact on the fisheries is likely to be small, as is the case with many regulations designed to address technological interaction problems. Where the results bear directly on the main management problem (e.g. krill and whales in the Antarctic), or could have very appreciable impacts on the amount caught (e.g. North Sea demersal fish or pelagic fish in many large upwelling areas) the scientific model projections are often too uncertain for managers to act. I do not believe that the solution to the problem of uncertainty in the results precluding decisive management action is to abandon multispecies modeling efforts altogether or to withdraw from offering advice until perfect models are available. To do either of these things is to ignore the reality of scientific investigation.

The correct approach must be to take the conditions under which managers have to operate more fully into account in the analysis and the presentation of results. Some form of experimental management can be helpful where such an approach is practical, as on the northwest shelf of Australia (Sainsbury, 1991). For the Antarctic, scientists in CCAMLR are considering management policies that concentrate fishing in one or two areas in which any impact of krill fishing on the consumers of krill may be more easily demonstrated.

More generally, more attention needs to be paid to the expression of risk along with the results of scientific analyses. Though fishermen themselves are probably not risk averse, that is, can accept a run of poor catches in the hope of one outstanding trip, this is probably not true of the industry as a whole. The processing and marketing side would probably accept some reduction in expected mean annual catch if this reduced the probability of a very bad year.

Where uncertainties are inevitable, more can be done to explain them and their implications, i.e. express the risk involved in making certain assumptions or adopting a particular policy. In many cases this amounts to including confidence limits or, preferably, some probability measure associated with a particular prediction along with appropriate sensitivity analyses for the results and the advice. This also means expanding advice to make clearer the implications of the alternatives that reflect uncertainty. This should make it easier to act even when the scientific evidence does not point unequivocally in one direction. Thus, it is not enough to say that it is possible that allowing the herring stocks to rebuild fully may result in reduced cod recruitment. If at all possible, some sort of probability should be ascribed to this result. Even if this is not possible, the implications of the alternatives should be fully spelled out in a two by two table, for example, whether the hypothesized effect is true or not true: whether management action is taken on the basis of this hypothesis or not. Then it may be seen, for example, that keeping herring at a low level risks losing X million dollars in herring catches, but failing to do so risks losing Y million dollars in falling cod and haddock recruitment, where Y is much greater than X.

Where possible, advice should look ahead so as to facilitate predictive (or pre-emptive) rather than reactive management. If quantitative krill/whale models can be developed early, then harvesting countries can be warned that possibly undesirable levels of krill harvesting were being approached. The impact of any necessary management measures on the industry may be substantially less with such early warning. Similarly, if investment decisions are made with scientific predictions and likely management scenarios in mind, then it may be easier for harvesters to agree to regulations when they do come.

In summary, I do believe that multispecies models will lead to better management, but the process will not be automatic. It will require further improvements in the communications between biologists and managers – and of course the fishermen themselves.

Managers have a legitimate cause for complaint if they are provided with only "official" advice, and this is suddenly switched from a single-species model basis which calls for increases in mesh size to a multispecies basis which points out the benefits of maintaining a smaller mesh. There will be much less confusion and complaint if additional avenues of information are opened with managers and industry which keep them up to date on the progress of scientific studies on multispecies interactions. If the industry, especially the trade press, were made aware of new studies which were beginning to show that predation interactions play a much greater role in the dynamics of fisheries than previously known, then a change in the "official" view regarding mesh-size requirements can be made without such a major shock to the system and without casting doubt on the reliability of scientific analyses.

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Symposium Editor's note

John Gulland died 24 June 1990 after a long illness. In spite of his illness, he was an enthusiastic participant throughout the Symposium. Final revisions of this paper were prepared by Dr Andrew Rosenberg after John's death. John will be sorely missed.

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Multispecies management: a manager's point of view[1]

W. J. Brugge and M. J. Holden

Brugge, W. J., and Holden, M. J. 1991. Multispecies management: a manager's point of view. – ICES mar. Sci. Symp., 193: 353–358.

Fisheries conservation measures are implemented to obtain the economic benefits which will result from efficient management of the fish stocks. These benefits are inevitably long term and the scientific advice on which they are based invariably predicts that there will be short-term losses. Neither the long-term gains nor the short-term losses may be equally allocated between the different sectors which comprise the fishing industry. In this situation, proposals for legislation in the field of fisheries conservation are inevitably opposed by one or more sectors. In addition, in the present adverse economic situation of the European fisheries, fishermen claim that they will be unable to survive the period of short-term losses until the long-term benefits accrue. Because conservation measures are based on scientific advice, the best strategy for the industry to prevent the adoption of proposed legislation is adversely to criticize that advice. This management problem is examined in respect of two types of multispecies model, the species-interaction model and the fleet-interaction model. The usefulness of both types of model is examined by addressing three questions to each: how credible are the models, what new problems do they present, and what solutions do they provide to present problems? The species-interaction models are very complex and incomplete because they model only a part of the fisheries ecosystem and produce results which do not provide a politically acceptable basis for management measures. In contrast, the fleet-interaction models provide a potentially powerful management decision-making tool. However, the present models are derived from single-species models, which means that management based thereon is subject to the same criticisms as that based on single-species models. It is concluded that two types of model should be merged but that this will not make it easier to introduce management measures based on the results because opposition to them essentially results from the immediate negative impact on profitability.

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Introduction

One of the responsibilities of fisheries managers[2] is to advise whether and to what extent the scientific advice received on the management of fishery resources should be enacted in legislation. In giving this advice he will attempt, within the limits of the information available to him, to evaluate the social, economic, and political advantages and disadvantages of following the advice. His decision-making process will be influenced by how he foresees that fishermen will react to the proposed legislation.

He will be acutely aware that, although fishermen may subscribe to the general principle of fisheries conservation, they generally oppose proposals to introduce specific conservation measures. The reason for this is that the analyses on which fisheries management measures are based predict that, in most cases, short-term losses will occur. They are always ready to accept that these will occur but not that they will experience the long-term gains.

It is a natural reaction for anyone faced with the possible introduction of legislation which will adversely affect his income to try to prevent that legislation from being adopted. Within the fishing industry this general factor is supplemented by two specific factors.

First the fishing industry consists of many sectors, each with its own pattern of fishing and target species.

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[1] The views expressed in this paper are those of the authors and do not necessarily represent those of the Commission of the European Communities.

[2] The term "fisheries manager" is used in this paper in the sense in which it is habitually used in fisheries to mean the national and international civil servants who are responsible for developing fisheries policy and legislation.

Although substantial long-term gains from the introduction of a certain measure may be predicted for the fishing industry as a whole, these may accrue to a limited number of sectors with other sectors experiencing little or no long-term gains or even long-term losses. Thus, the fisheries manager can always expect opposition to his proposals.

In the decision-making process of the European Communities, in which decisions are taken by a system of weighted majority voting, a relatively unimportant sector on the European scale may be able to exert a large influence if it is an important sector in its Member State which is in turn one of the larger Member States having 10 votes.[1]

Second, as a result of fleet overcapacity, the economic situation in many sectors of the European fisheries is critical and fishermen consider that they may be unable to survive the period during which the short-term losses occur until the long-term benefits are obtained.

As fisheries conservation measures are based upon scientific advice, the fishing industry is very aware that the best method by which to prevent proposals for legislation being adopted is to discredit or, at minimum, question the credibility of the scientific advice on which the proposals are based. In a democracy, legislation must be politically acceptable and ministers responsible for fisheries will rarely take action if proposals are vigorously opposed. One of the responsibilities of the fisheries managers to their ministers is, therefore, to assess the science and to evaluate the short- and long-term social and economic consequences which will result from implementing the scientific advice.

There is, in fact, no difference in principle between the decision-making process of fisheries managers examining advice about the level of total allowable catches or minimum mesh sizes based on single-species or multispecies models. The problems are essentially the same: how good is the science and how far are the recommendations politically acceptable? Any difference stems from the fact that the recommendations based upon multispecies species, especially the species-interaction models, are often at total variance from those based on single-species models. The fisheries manager will thus have to defend why his proposals are radically different and possibly totally contradictory to those which he was proposing in the immediate past.

The paper does not attempt to make a formal, scientific evaluation of multispecies management models or to evaluate whether they are better than single-species models. There is no question that they represent an advance but, from a manager's point of view, will they make it easier or more difficult to get fisheries management measures adopted; what are their strengths and weaknesses in the context of the process of translating scientific advice into fisheries legislation?

The managers' approach to advice based upon multispecies models will be to query to what extent the models are more realistic and less sensitive to adverse criticism than the single-species models on which present management is based. The manager will ask three questions: (1) How credible are the models? (2) What new problems do they present? (3) What solutions do they provide to present problems? As there are essentially two types of multispecies models available today, the species-interaction and the fleet-interaction models, and as they are dissimilar in approach, these questions need to be addressed to both of them.

Species-interaction models

The species-interaction models are those which model inter- and intra-specific predation, the "who eats whom?" models.

How credible are these models?

Management measures based on single-species models are criticized because it is recognized that they do not correspond with reality: fish species do interact. Species-interaction models respond to this criticism and they are, therefore, more convincing than single-species models. However, what they gain in credibility on this point they more than lose on others. As with all models, the results obtained depend upon the assumptions made, the quality of the available data, and the complexity of the models, in terms of number of species and the interactions between those species.

Although species-interaction models are inherently more realistic than single-species models, they are much more complex and the results which they produce often deviate considerably from those which might be expected on the basis of intuition and those based on single-species models as, for example, is the case with the model for the North Sea (Anon., 1988). Additionally, because the number of variables is large, it is difficult to demonstrate to what extent the results obtained are dependent upon the assumptions made, especially those about the initial data set. The more complex the model, the more important, in terms of chaos theory, becomes the "butterfly effect". If the reasons for the deviations and differences cannot be convincingly explained, the results will not be acceptable to the industry and politicians will not be prepared to accept management proposals based upon them.

Another argument which can be made is that the

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[1] Each Member State of the European Communities has a number of votes weighted approximately in accordance with its population (France, Germany, Italy, and the UK have 10 votes each, Spain 8 votes, Belgium, The Netherlands, Portugal, and Greece 5 votes each, Denmark and Ireland 3 votes each, and Luxembourg 2 votes, making a total of 76 votes. When voting on a proposal from the Commission, a total of 54 votes must be obtained to obtain a qualified majority.

models, as a consequence of a lack of data, may not represent realistically the ecosystem being analysed: for example, the North Sea species-interaction model considers only nine species and then only from the post-larval stage and treats the North Sea as a single box. This argument can be used to question whether the results obtained from such models are any more realistic than those obtained from single-species models.

From the manager's point of view, there would be considerable difficulty in getting the fishing industry to accept that the results from these models were sufficiently convincing to form a sound basis for management.

What new problems do they present?

One of the major problems which these models present for fisheries managers is that the results which they predict are, in some cases, contrary to the perceived wisdom based on more than half a century of single-species models. It will be all too easy for the industry to query whether the scientists can be sure that the predictions from the species-interaction model are reliable if the basis of management for half a century has been wrong. This represents a fundamental problem which can be very easily used as an argument against legislative proposals based upon the results from these models.

For example, the single-species model predicts long-term gains in the order of 24% in catches of cod in the North Sea if the minimum mesh size were increased to 120 mm, whereas the results from the species-interaction model indicate an 18% fall. For haddock, the results are even more dramatic, the single-species model predicting a 13% increase in catches and the species-interaction model a 73% fall.

A second problem is related to the present method of management of fish stocks under which the catch possibilities available each year for most stocks are divided between different countries, either between different parties as, for example, between the European Economic Community (EEC) and Norway or, internally within the EEC, its Member States.

In consultations between countries which are joint managers of stocks and which have "balanced fish agreements", that is, each party allocates to the other the equivalent amount of tonnes of fish, using a system of "cod equivalent weights", the abundance of the different jointly managed stocks plays a significant role in the consultations. If one of the parties has sufficient catch possibilities for those species in which it is most interested to satisfy its requirements, it has no need to "buy" fish from the other party. On the other hand, if it has insufficient, it must try to "buy" fish, which puts the "selling" party in an advantageous position.

The EEC faces an additional complication. It manages its catch possibilities by dividing up its share of the TAC for each stock on the basis of a fixed key. If one stock becomes depleted, the Member States which have allocations in that stock are not compensated by increased allocations in another stock.

At present the relative abundance of the different stocks cannot be managed by man. The situation has to be accepted as it exists. However, one of the potential uses to which the species-interaction models could be put is to use them to try to manage the relative abundance of the stocks. This would cause major problems. Not only does each country have different species preferences but these may also differ between fleets within the same country. Managers would, therefore, be faced with conflicting demands from the different parties as to how the relative abundance of the stocks should be changed.

To consider a specific example, the North Sea species-interaction model has identified whiting as probably the major predator of other species and indicates that overall gains in catches would be achieved if the stock of whiting was reduced. The UK is allocated 53% of the EEC share of this stock and whiting is of major importance to the Scottish fleet. It is doubtful if the UK authorities would have sufficient confidence in the model to accept that the North Sea stock of whiting should be reduced, even if the predicted gains in other stocks for the UK would compensate its losses in whiting.

Even if it were decided to attempt to reduce the stock of whiting, the question arises as to how it should be done. One possible option which has been put forward is selectively to fish whiting. However, the distribution of whiting in the North Sea overlaps that of haddock. Therefore, in the present state of gear technology, fishing effort on whiting cannot be increased without also increasing it on haddock, which is already heavily over-fished. This option is based on the paradoxical wish to obtain the predicted benefits of reducing the stock of whiting while maintaining catches of whiting for human consumption. It is doubtful if this paradox can be resolved in practice.

If it were accepted that predation by whiting should be reduced, it would seem logical to assume that the earlier in its life history that this were accomplished the greater the benefits. This suggests that the present restrictions on the by-catch limits for whiting in the Norway pout fishery should be abolished. As these limits have been the cause of considerable controversy over many years and a temporary derogation under EEC law in respect of whiting (EEC, 1984) was bitterly criticized by UK fishermen, it can be foreseen that a proposal to manage the whiting stock in this manner would probably not be found acceptable to those fishermen who take the largest share of the catches.

These by-catch limits are based upon one of the most fundamental principles of present management, which is that catches of small fish of all human consumption species should be minimized in order to maximize total catches. Even though fishermen discard very large quantities of fish for various reasons, most fishermen strongly object in principle to catching large quantities of small fish, especially if such catches are used for reduction to meal and oil.[1]

Another problem which the models present is the quantity of data required to run them. Management is hampered at present because insufficient and unreliable data are collected for many stocks with the consequence that either single-species assessments cannot be run or, if they are, the confidence which can be attached to the results is very limited. In the case of the species-interaction model, not only would it be essential to have all the necessary data for all the species involved before reliable results could be produced for all the species treated by the model but, if part of the data set were missing, instead of having no advice for say two out of nine species, there would be no advice for any of the nine species.

Management by single-species models is essentially an annual system, with the possibility of making adjustments during the year in the light of new data. Management using species interaction models would be essentially long term. It would probably take three to five years to determine whether the results being obtained conformed with the predictions from the model. Changes in management strategy could not be made during this period without invalidating what would in effect be a large-scale experiment. Yet experience to date suggests that if the initial changes in the fish stocks did not conform with the predictions there would be enormous pressure from the industry to change the management policy.

What solutions do they provide to present problems?

In their present state of development, the species-interaction models do not provide any specific solutions to the problems facing management. As discussed in the previous section, they present problems rather than providing solutions.

The main contribution which the models make to management at present is to indicate where the predictions based on single-species models may not be realized as, for example, the differences between the predicted results from the single-species and species-interaction models for North Sea cod and haddock described in the previous section.

The high levels of natural mortality for juvenile fish, especially 0-groups and to a lesser extent 1-groups, which were determined in the course of developing the species-interaction models, have also led to a re-assessment of the probable impact of the catches of such individuals on the catches of older fish (CEC, 1989). More directly, the CEC has just adopted a proposal for legislation (CEC, 1990) which has the objective of reducing the stocks of whiting.

The results from the multispecies models also indicate the type of questions which should be directed to the scientists; in this case, what would happen if the change in mesh size could be more directly related to the species being fished rather than being applied to the whole North Sea.

Fleet-interaction models

Fleet-interaction models are those which investigate the consequences of changing the fishing pattern of one or several separate fleet components ("métiers"), all of which are fishing the same complex of stocks. The changes in fishing pattern may be the result of changes in fishing effort or in the exploitation pattern resulting, for example, from changes in minimum mesh sizes or seasonal or area limitations on fishing. It is multispecies in the sense that these models take account of how the losses experienced by one métier from such changes will be distributed as gains amongst the other métiers and vice versa.

How credible are the models?

The results from these models are inherently credible because the manner in which they operate is transparent and can be easily explained. It is obvious that if the activities of one métier are curtailed, then benefits should accrue to other métiers.

What new problems do they present?

Because the models are transparent, they do not pose any new problems. Those available at present are essentially derived from single-species models, which means that they do not represent a major departure from the models on which management is now based. This can be held to be a criticism because single-species models are criticized as being unrealistic. The extent to which this is a serious criticism will depend largely on the magnitude of the proposed changes. However, fleet-interaction models which take into account the findings of multispecies models are now being developed.

What solutions do they provide to present problems?

Fleet-interaction models do not represent a scientific breakthrough in the understanding of fisheries ecosystems. However, they represent a major advance in providing managers with a decision-making tool which

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[1] Since the Symposium was held, the Commission of the European Communities has published a proposal for a Council Regulation (EEC) which contains two measures having the objective of allowing fishing effort on whiting to be increased (CEC, 1990). The industry has been making almost identical comments about this proposal as those predicted in this paper.

should enable them to respond to an increasing requirement of management, which is to quantify the predicted gains and losses resulting from proposed conservation measures in monetary as well as weight terms.

However, the extent to which the output from such models can be used under the present system is questionable because it is unusual for losses arising from the introduction of conservation measures to be compensated. It is usually argued that such losses are compensated by the long-term benefits which accrue to the same group of fishermen.

However, this argument has its basis in the results from single-species models which show only the overall losses and gains whereas, in fact, the losses and gains may be divided very differently between all the métiers fishing the stock, as stated previously.

The results of the ICES Working Group on Fisheries Units in Subareas VII and VIII (Anon., 1989) demonstrate how unequally short-term losses may be divided between métiers. Sixty percent of the cumulative short-term losses by value arising from a change to a uniform 65-mm mesh size in Subarea VIII would be experienced by one métier, "trawling for *Nephrops* in shallow and medium depths in the Bay of Biscay". The results also show that within two years the earnings of two of the three métiers concerned would have returned to their original level, whereas this would take five years for the métier "trawling in deep water".

This example illustrates the potential usefulness of fleet-interaction models in assisting the managers to take management measures. The costs can be determined and the consequences of making the changes greater or smaller can be evaluated. On the basis of such information, a policy can be formulated and defended. Informed decisions, such as the extent of the change to be introduced and the amount of compensation, if any, to be offered, can be taken.

Conclusions

In 1866, Messrs James Caird, Thomas Henry Huxley, and George Shaw Lefevre, Commissioners appointed to enquire into the Sea Fisheries of the United Kingdom, wrote:

> *"But fishermen, as a class, are exceedingly unobservant of anything about fish which is not absolutely forced upon them by their daily vocations; and they are, consequently, not only prone to adopt every belief, however ill founded, which seems to tell in their favour, but they are disposed to depreciate the present in comparison with the past. Nor, in certain localities, do they lack additional temptations to make the worst of the present, offered by the hope that strong statements may lead the State to interfere, in their favour, with dangerous competitors."*

The general thrust of this comment remains as valid now as in 1866. However, certain fishermen are exceedingly observant of developments in fisheries science but this does not necessarily lead them readily to accept proposed management measures. They are still prone to use every argument which seems to tell in their favour and it is often the situation that different sectors use the same scientific advice to support opposing arguments. Before the fisheries manager decides to advise his minister to propose a measure, which he will not do unless he is convinced of the validity of the scientific advice, he has to evaluate how he will obtain the acceptance by the fishing industry of the proposals.

Fleet-interaction models provide managers with a powerful decision-making tool even though they can be criticized for being single-species based. If proposals were based upon them, it is almost certain that this criticism would be used by those sectors of the industry who would potentially be disadvantaged by them even though criticism of single-species models may not originate essentially from the fact that these models are unrealistic but from the fact that such criticism can be used to undermine the results from these models and thereby prevent the implementation of management measures based thereon.

The advantage of fleet-interaction models, from the managers' point of view, is that, because they permit the gains and losses to be quantified and allocated by sector, they provide a means whereby the losing sectors could be compensated. In this situation, it might be expected that such criticism would be muted or disappear.

Whereas fleet-interaction models represent a progressive step in the evolution of fisheries management and provide results which have the potential to be utilized in the existing framework of management, species-interaction models represent an evolutionary jump. Although they are more realistic and, therefore, intellectually more satisfying for the scientist, they do not provide a satisfactory basis for management in their present state of development and the present state of dialogue, or lack of it, between managers and fishermen.

As has been noted, the models are incomplete and are likely to remain so. It is unrealistic to expect that the data will ever become available to enable the interactions in the pelagic larval phase to be modelled, which makes long-term predictions of trends in recruitment impossible. As has been noted, those sectors which might certainly be expected to lose from the introduction of management measures based on species-interaction models will oppose them because of these uncertainties. Additionally, these models do not permit the gains and losses to be quantified by sector so that the manager is prevented from elaborating appropriate compensation schemes.

In addition, the results imply that changes to patterns of exploitation of fish stocks which are at present considered contrary to conservation might have to be introduced. Given the uncertainty of achieving the results predicted from species-interaction models and the changes in fishing patterns that would be needed, it is doubtful if the fishing industry would accept them as a basis for management decision.

Are species-interaction models therefore useless? Almost certainly not. They provide the basis for debate with the fishing industry as to what management action should or might be taken because the industry, managers, and most fishermen agree that single-species models are unrealistic. However, agreeing that single-species models are unrealistic does not make the results from species-interaction models immediately acceptable to the industry, for the reasons given. They represent a qualitative approach compared with the quantitative approach of fleet-interaction models.

Fleet-interaction models which take into account the findings of multispecies models are now being developed. The future of multispecies management must lie in a synthesis of the two types of model, even though this would introduce the uncertainties of the species-interaction models into the fleet-interaction models. However, it would still not resolve the problems of introducing management measures which are essentially related to the natural opposition of any fisherman to changes in his pattern of fishing which might reduce the profitability of his activities in the short term, even if there is a high probability that it will increase in the long term.

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