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STUDY GROUP ON SPATIAL AND TEMPORAL INTEGRATION

University of Strathclyde, Glasgow, Scotland

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INTRODUCTION

The ICES study group on Spatial and Temporal Integration was convened at the request of the working group on Recruitment processes. The study group met over the period 14th-18th June 1993, at the University of Strathclyde, Glasgow Scotland.

The terms of reference, passed to the study group by its parent working group, were:

- (1) to consider methods of statistically characterising the temporal and spatial variability in populations of larval fish and their predators.
- (2) to consider and report on the feasibility of integrating temporally and spatially variable abundance and vital rates over population time and space scales.
- (3) to consider how sub-grid-scale temporal and spatial variability in abundance and rates may be represented at the grid scale in marine ecosystem models.
- (4) to consider methods of determining the most appropriate temporal and spatial grid resolution for models of fish recruitment.

The full membership of the study group, together with affiliations, postal addresses, phone & fax numbers, and e-mail addresses is set out in Appendix M. Those present at the meeting were:

J. Bartsh	- IfM, Hamburg
J.E. Beyer	- DIFMR, Charlottenlund
C.J. Fox	- MAFF, Lowestoft
F. Gauthiez	- IFREMER, Nantes
W. Gurney	- University of Strathclyde (CONVENOR)
M Heath	- SOAFD, Aberdeen
C. Koutsikopoulos	- IFREMER, Nantes
P. Margonski	- SFI, Gdynia
D. Pelletier	- IFREMER, Nantes
P. Pepin	- DFO, St John's
J. Simmonds	- SOAFD, Aberdeen
B. Stensholt	- IMR, Bergen
A. Taylor	- PML, Plymouth
J. Webb	- MAFF, Lowestoft

The structure of this report is as follows:

Introduction
Overview
Conclusions
Session Reports
Scales & Processes
Primary and Secondary Production
Tertiary Production (a super-grid-scale process ?)
Model Inputs and Outputs
Appendices.

OVERVIEW

Terms of Reference 1

Data on the spatial and temporal distribution of larval fish and their prey and predators are too sparse for standard statistical methods of pattern analysis to be usefully employed. We conclude that the most useful approach to this problem is to formulate mechanistic models of the processes underlying these distributions and design studies to test them against data.

Terms of Reference 2

The working group concludes that there is no universal prescription for self-consistent aggregation and smoothing of temporally and spatially diverse data. In general, the spatial and temporal resolution of raw data seem likely to be set by logistical considerations rather than theoretical requirements. However, we believe that determination of the uncertainty of individual measurements should be a high priority.

Terms of Reference 3 & 4

The choice of appropriate spatial, temporal and trophic scales is the central problem in the construction of most marine process and ecosystem models. The range and variability of scales present in different problems precludes universally prescriptive solutions. However we consider that determination of the appropriate scale in any given case will be facilitated if it is recognised that a single model should only be expected to answer a very restricted range of questions.

Restricting the questions asked of a model allows us to optimise our description of the key processes and components while maintaining structural complexity, parameter count and input data requirements at acceptable levels. Where the questions being asked focus on a single trophic level or a small group of related processes (for example the growth and survival of fish larvae) a good rule of thumb seems to be to focus primarily upon that trophic level, to include caricatures of the adjacent levels above and below, and to regard all else in the system as "environment". Where the question being asked relates to broad-scale system properties (e.g. shelf-sea carbon or nitrogen budgets) the trophic focus is necessarily wider. In such cases, a greater degree of spatial aggregation is required if an acceptably simple model is to result.

A central consideration when choosing the spatial, temporal and trophic scale on which a given question can be asked must be the resolution of the data which will be used to parameterize, drive, and test the model. We believe that testing a finely resolved model against coarse-grained or partial data presents no insuperable problems (cf Appendix B). However, where driving data are only determined at a coarse resolution, there is a strong case for arguing that questions cannot usefully be formulated at a finer scale, and the corresponding models will only include more finely grained phenomena for technical or mathematical reasons.

Where scale disparity in a model representation requires us to provide input at a finer resolution than that of the data from which this input is to be determined an interpolation scheme must be devised. Standard statistical interpolation techniques are often based on assumptions of continuity and stationarity which may not be justified for the kinds of data

normally available for ecological problems. Notwithstanding the possibility of employing more esoteric statistical methods, we recommend that priority be given to acquiring localised, fine-grained data from which the detailed structure of the variability at, and below, the model scale can be determined. Where this is not possible, or where the processes which determine the fine-scale distribution are well understood, a preferable approach may be to use a mechanistic model of these processes for the interpolation procedure.

Where model complexity or data availability considerations imply modelling at a trophic or spatial scale larger than that at which key processes occur, a compact caricature of the sub-grid scale effects must be developed. Where the processes concerned form part of the environment of the process of central interest (for example in the transport of larval fish by complex flow fields) standard statistical techniques exist for developing such characterisations. However, where the sub-grid-scale processes form part of a feedback network, and the caricature must counterfeit the dynamic, as well as the static, characteristics of its parent system, we know of few successful examples. We recommend that a programme of research be established in which fine-scale models of local areas known to contain mesoscale features (ocean eddies, fronts, coastal currents, species variation within trophic groups) are compared with field data at an appropriate scale. The behaviour of these detailed models can be used to develop dynamic caricatures valid at coarser scales, which can then be evaluated in the context of wider-ranging models.

In the process of caricature development, as in all other modelling, we believe that the close coupling of modelling, data collection and experimentation is essential. A vital logical and practical element in model testing is selection of comparisons which compare like with like; for example, predictions of spatially average values should be compared with equivalently averaged data not with point measurements. We expect this requirement to be facilitated by close propinquity of modellers and experimentalists.

Finally, we believe that it is vital to appreciate that comparison of model output with observation is a process of model falsification, not validation. Our accumulated experience is that failure to match observation and prediction can tell us about structural inadequacies in our model and/or in our understanding of process. By contrast, coincidence between observation and prediction to within the uncertainty in both tells us only that better data is needed before our model can be further improved.

CONCLUSIONS

- Larval fish distributions observed at currently practicable resolutions cannot be satisfactorily characterised by presently available statistical techniques.
- No universal prescription exists for integrating either abundances or vital rates over diverse space, time or trophic scales.
- To be effective, models must be targeted at specific questions and tied closely to available data.
- The optimal choice of model scales is largely determined by the question being asked, the processes being described, and the resolution of the available input data.
- A suitable choice of scale is one at which sub-grid-scale processes assume second order importance.
- Theoretical work is needed to develop improved techniques for caricaturing the dynamics of sub-grid-scale processes.
- Where model input at a fine scale must be derived from data at a coarser scale, the interpolation scheme used should be based on a knowledge of the statistical structure of, and/or the mechanisms generating, the model-scale variability.
- Model studies should be used to help define optimal sampling schemes at both grid and sub-grid resolutions.
- Model testing is a process of falsification.

SESSION REPORTS

Theme 1 - Scales and Processes

As marine ecologists or modellers of marine systems, we may be called upon to address questions involving almost any biological or physical process or group of organisms occurring in the sea. However, no one model should be expected to cope with answering all questions posed. The best model in each case is the simplest which will serve the purpose. As a rule of thumb, the detail of representation of a process or organism should decrease with trophic distance from the focus of attention. We believe that the focus +/- one trophic level should be modelled in some detail. In general we may think of processes as predator-prey interactions, whether they involve a phytoplankton and nutrients, or a seal and a fish. The outcome of these predator-prey interaction is growth, mortality or reproduction.

The questions which are asked usually concern variations in the abundance and distribution of biota or nutrients, for example, in connection with recruitment or eutrophication. The precision required of the answer is a key consideration when designing a model or sampling programme and has a role in setting the 'grid scale' for measurements or modelling.

There may be a number of potential constraints on the practicable grid scale for modelling or measurement. In particular, there are constraints due to:

- the processes being studied
- computational limitations set by the size and complexity of the system
- availability of forcing data
- availability of validation data

Constraints due to present day computation dictate that typical spatial resolutions in models are at best of the order of 50km in ocean systems, 5km in shelf systems, and 0.5km in coastal regions, but these may be regarded as operational practicalities. Constraints due to the system and the processes involve the inherent characteristics of physical and biological interactions. The relationship between scale and process may be regarded as a fundamental characteristic.

First, as a basic sampling rule, the maximum permissible sampling or grid spacing in time or space should be no more than half the shortest wavelength to be resolved. The problem facing us is that variability occurs on all spatial and temporal scales imaginable. The task is to determine the minimum spatial or temporal scale below which the variation can be regarded as noise. A first definition of this might be -

"the scale at which non-linear responses in a process cause the estimate of the average flux over a time or space interval to fall outside set limits of precision".

The term 'flux' in this context refers to the product of numbers and average individual rates. For operational purposes this minimum scale may be regarded as the limit below which, as the grid scale is reduced, one is not able to resolve differences in the statistical characteristics of a distribution in the field.

Grid scale results should logically be compared with field data averaged over the spatial volume represented by individual grid points. However, computational and other constraints will almost always mean that we cannot model at the scale demanded by the assumption of grid scale homogeneity inherent in most modelling approaches. The sub-grid scale processes and features which are present in the sea will in themselves cause spatially averaged field data to differ from model results. One conceptual way in which this may occur is if sub-grid scale locations all follow the same trajectory through time, but with varying degrees of lag. The effect at the grid scale is to produce a smoothed or smeared version of the sub-grid trajectories. The divergence between grid and sub-grid dynamics is likely to increase as the area or spatial heterogeneity represented by a single grid point increases.

One may ask whether models with a spatial resolution which is so low that sub-grid scale effects are a serious problem, are in any way useful. The answer depends on the application. Clearly, such models are not likely to be helpful in explaining variations if the region of interest is only represented by one grid-point. However, the reason for having low spatial definition may be that one wishes to devote more attention to biological resolution. In that case, gross mean fluxes in the system as a whole, over time periods equivalent to the generation times of organisms, may be effectively modelled by such an arrangement. Results from a low spatial resolution - high biological resolution model might form a useful 'backdrop' for a more detailed spatial representation of a more restricted biological question.

One possible way of addressing the effect of sub-grid scale processes in models where the grid resolution is, for practical reasons, too coarse for the situation being considered, is to caricature the processes implicitly either as environmental forcing of parameter values, or by supplying modifying dynamics. Examination of field data from the North Atlantic and the

North Sea (Appendices A and B) leads one to the conclusion that the interaction of spatial and temporal variability at the sub-grid scale leads to the generation of characteristic frequency distributions of variables. For example, the data on chlorophyll values in a delineated area of the northern North Sea are highly skewed during the spring bloom and becomes more symmetrica[as the season progresses, suggesting that the initial bloom is composed of a small number of intense patches, but as the season develops the patches merge to form a more continuous distribution. Similar examination of temperature and stratification data indicates that this pattern can be explained in terms of the development of stratification in the northern North Sea. The outcome is that at any particular point an observer may experience a bloom event at some time during the spring, but that this is almost completely lost in the time series of spatial averages over the entire region. However, knowledge of the variance and skewness or other distributional characteristics of the phytoplankton population may help one to estimate the area average time series from a point observation or modelled time series.

The sort of sub-grid scale features which one might wish to caricature at the grid scale might include:

- eddy and frontal motions
- stratification
- turbulence and diffusion
- abiotic conditions (temperature, salinity, turbidity, irradiance)
- micropatchiness and cross-spectra between physics and biology
- species composition of functional groups of organisms
- physiology of organisms
- histories of individual organisms resident at a grid point

The major problem in constructing such caricatures is to determine which features will not change the functional form of a biological response, and could therefore be represented as driven parameters, and which will have a dynamic effect on functional responses and therefore require a more sophisticated approach.

Theme 2 - Primary and Secondary Production

Two case studies. In order to focus thoughts the group felt it useful to consider two real-life case studies which embody the problems of spatial-temporal resolution. The case studies, both involving fish populations, were larval cod on George's Bank and North Sea herring larvae.

Larval cod on George's Bank. This area is currently the focus of a major research initiative (U.S. GLOBEC). The area covers approx. 40,000 sq. km with a water depth of <300 m. The central region, water depth <100 m, is vertically mixed while a front approximately over the 300 m isobath separates water which is vertically stratified. During spring, cod spawn in the vicinity of this front. The larvae stay in this area until metamorphosing after 90 - 120 days. Metamorphosed cod are only found in a restricted rocky region on the northern edge of the Bank. During the larval stage they are subjected to losses from:

- Transport away from the area
- Starvation
- Predation
- Disease and parasitism
- Genetically influenced mortality

This system has been studied every year since 1980 using a 20 km grid sampled each month over a 2 week period with a view to assessing larval mortality and growth.

The major problem that modelling would hope to address in this system is that of growth and especially mortality of the larvae. Total losses have been estimated to be 10 - 15% per day. This implies that sampling the population accurately will become increasingly difficult even over a single sampling period. In order to model these losses one needs to understand the processes contributing to them. However these processes operate at significantly smaller time scales than are currently sampled in the field.

Modelling transport of the larvae within and from the Bank must be based on an understanding of the circulation and vertical migration. However, this is hindered by the difficulties of determining cross-isobath flows in this dynamic region.

The potential for larval starvation is probably affected by such factors as local patchiness and turbulence. At present the spatial and temporal scaling of these factors is poorly understood and is clearly not resolved at the current sampling scales. The importance of these sub-grid factors in determining mean measured values is also unclear.

Predation by mackerel may be a potentially important source of mortality. The process can be considered as epidodic, taking place during the northerly migration of the local mackerel population. Because of variations in the timing of the migration and in the distribution of fish during their movement, there may be variations in the interaction between predator and prey on a sub-grid scale relative to that observed using a monthly collection scheme.

Very little is currently known about the influences of disease, parasitism and genetics on fish larval mortality. Because of this these factors have rarely been incorporated into models. This is an example in which biological knowledge is required to stimulate modelling efforts.

North Sea herring larvae. Different groups of herring spawn benthic eggs at various restricted locations around the British Isles. Spawning sites are determined by the presence of appropriate substrate and water conditions. The larvae are released over periods of 2-3 weeks. They are then transported across the North Sea or down the east coast of Britain. In the course of this movement larvae from different locations are dispersed to varying degrees. Depending on the time of spawning, the larvae take from 100 days (spring spawned) to 6 months (autumn, winter spawned) to reach metamorphosis. However, over the whole North Sea, most larvae metamorphose at the same time of year (March - May). During the larval period, they are subjected to mortality due to starvation, predation, disease and genetic abnormality.

Transport of herring larvae in the North Sea has been modelled using a particle tracking approach driven by output from a general circulation model (GCM). The results have been evaluated by direct comparison with field survey data collected at approximately monthly intervals over a 6 month period. The distribution of early larvae (first 2 months) in the

spawning regions was sampled at a spatial resolution equivalent to that of the GCM (20 km). In later surveys a wider area was covered at a lower resolution. Vertical migration was represented in the model on the basis of field observations but little information was available on horizontal variability in this behaviour. In the absence of firm data on this, the sensitivity of dispersal predictions to changes in vertical migration behaviour were tested within the model. The basin-wide dispersal of larvae was adequately accounted for by this general circulation but local retention by sub-grid scale topographic and oceanographic features, which have been observed by targeted field programs, were not resolved by the model.

Criteria for selecting suitable grid-scales. Sampling attempts to produce a synopsis of a dynamic system. Trade-offs inevitably occur between the detail which can be obtained and the area which can be covered. Grid scales for sampling need not necessarily be finer than that used in modelling the system but it is desirable that it is.

The practical limitations on field sampling programs are often the result of resource limitations. These include:

- The speed at which a vessel can reach a sampling station
- The rate at which the data or samples can be gathered
- The rate at which the data or samples can be processed

It was felt that current methods are inadequate for gathering data and samples from the field with a resolution required to parametrize and validate models at scales below currently used grid-scales. Resources expended on generating technical advances in data collection would be more effective if directed towards the requirements of modelling.

Predation on fish larvae. Another model factor which must be considered is that of the degree of biological aggregation within the food web. This aggregation can be visualised as another grid with its associated sub-grid-scale effects. For example, the preference of whiting in the southern North Sea for sandeels over other similarly sized prey items such as chaetognaths. A second sub-grid scale effect which can arise is the possibility that, as fish larvae grow, they may pass through a predation window targetted primarily at other similar sized organisms. The spatial distributions of prey and predators may become important if one wishes to model losses of fish larvae due to predation. To effectively model encounter rates it may be necessary to take account of sub-grid scale spatial and temporal heterogeneity.

Dealing with fine-scale structures in secondary and primary production. Often a substantial proportion of productivity is concentrated in relatively small areas. These areas of high local activity sit within larger areas with lower activity. The hot-spot areas may be geographically fixed (e.g. the Orkneys Shetland gap), mobile (e.g. ocean eddies) or transient (e.g. seasonal fronts). These regions are often characterized by strong gradients in the physical environment. The scales on which large ecosystem models are currently based are incapable of resolving such features. The strong gradients associated with these features need to be accommodated in any model which does not resolve them. One potential way of achieving this may be to employ detailed models of these features to generate descriptions which can be parameterised into coarser models. This may overcome computational limits in embedding fine-scale models into coarse scale large area models.

Fine scale temporal features may also need to be incorporated. An example would be the effect of short lived storm events as observed in Conception Bay during the summer. Phytoplankton responds with bursts of growth which in turn triggers bursts of secondary productivity. The degree to which the secondary producer population can respond will depend on initial seeding conditions and the life strategy of the animals. Microzooplankton have higher growth potential and can respond rapidly to increases in primary production. Egg production by larger zooplankton shows a slower response and so the zooplankton need to be exposed to frequent storm events for successful reproduction. Although it may be easier to resolve temporal events of this type in models, they can easily be overlooked in field data collection. Systems of continuous environmental logging can overcome this.

The response of different groups of organisms to phenomena will vary. This leads to successions of groups whose timing can vary spatially. Thus within a grid-box the populations may be at different stages of the succession.

Running models with time averaged meteorological data can provide significantly different results to forcing the model with more realistic data, this is particularly striking for the spring bloom.

Weather events will be widespread and are often linked to large scale climatic phenomena spanning the North Atlantic. Consequently storm events are unlikely to be a source of spatial sub-grid scale effects. However, it is usually impossible to collect weather data at sufficient spatial resolution. The meteorological forcing data frequently used to drive models is itself derived from other models based on coarse grid-scales. This must be borne in mind.

What level should we model at?

Large ecosystem models - These have extensive spatial and trophic coverage and tend to be generated by the need to answer broad questions. However, the level of detail which can be included is usually low. The resolution of the data is also low. This leads to high uncertainty in model outputs and thus low predictive ability at fine trophic, spatial and temporal scales.

Restricted models - These have limited spatial coverage and are generated by the need to answer specific questions. The level of detail which can be incorporated is medium to high. The resolution of the data is also high and may not be attainable. However, the uncertainties will be generally lower and predictive power at fine trophic, spatial and temporal scales higher.

- To be effective, models must be targetted at specific questions and must be as closely tied to data as possible. The quality of the data used must be viewed critically.
- A suitable scale for a model will be one in which sub-grid scale processes assume second order importance. However, this may not always be possible. There is therefore a need for theoretical work on methods for handling sub-grid scale effects.

Theme 3 - Tertiary Production (a super-grid-scale process?)

Introduction. Tertiary production is defined as the elements of the ecosystem at higher trophic levels than primary and secondary production, including for example; fish, marine mammals, birds, and human interactions. In general tertiary processes operate at a large temporal and spatial scale relative to the physical and lower trophic processes.

Questions Involving Tertiary Processes. In order to illustrate the range and complexity of tertiary modelling problems the following questions which require tertiary process models were discussed briefly:

Intraspecific: What factors control the mean and annual variability of rate of recruitment?
Does fish movement and migration effect fish population estimation?
Is the growth rate of adult and juvenile herring density dependant?
Does the spatial behaviour of fish populations effect their dynamics?

Interspecific: What impact do marine mammals have on exploitable fish stocks?
Does sandeel biomass affect the reproductive success of seabird populations ?
What is the effect of fish predation on benthic communities?
Is fish production in different eco-systems related to primary production.
What is the impact of man on exploitable fish populations?

Modelling Scales. For tertiary processes the range of sizes for a single species is much greater than for primary or secondary processes. Between egg, larval and adult stages there may be five orders of magnitude in scale. Similarly the range of important timescales changes with trophic level. For example larval development occurs more rapidly than development in adult fish.

Each of the studies listed above will require a different scale for a model. For example studies of global carbon budget would be done at a larger scale than studies of sandeel and seabird interaction. The scale selected will also depend upon the question that is addressed.

Modelling Methods. Within a model it may be necessary to describe processes or trophic levels at different scales. This must be compatible both with the intrinsic scale of the process and the purpose of the model. There are a number of approaches to this problem;

- Stacked models, where higher trophic levels are described with lower spatial resolution and their interaction with these lower levels is distributed with time dependent proportions between the lower trophic level spatial blocks.
- A detailed sub-model at each trophic level, combined without feedback between trophic levels.
- Individual based models. However, it is often difficult to provide realistic feedback using this approach and it is thus less suited to problems where feedback effects are central to the dynamics.
- A high trophic level model underpinned by lower level boundary conditions provided by data or a synthetic caricature.

Summary.

- Models without feedback may give poor representation because they ignore multiple interactions between trophic levels.
- In studies of recruitment multiple models are required at different scales in order to study the different stages; egg, larval, juvenile and adult fish. It may be that for studies of recruitment it would be better to concentrate on the special characteristics which describe the individuals that survive rather than on the typical individual within whole population. For this purpose it may be interesting to investigate the individual based modelling methods.
- Models of fish populations must be constructed to include both numbers of individuals and weight as mortality is applied to individuals but growth rates are related to size.
- Models should be used to help define the scale for data sampling.

Theme 4 - Model Inputs and Outputs

Disparity in grid scale between models and data. There is often a disparity between the level of our knowledge for different elements of a model and the level of precision required for these different elements. For example, an intrinsic problem is the representation of different trophic levels in that the range of body sizes within the life cycle increases by many orders of magnitude as one moves from primary producers to higher organisms. For example, algal cells vary in weight by only a factor of 2 over their generation cycle, but fish may vary by a factor of 100,000. Coupling of biological and physical models also provides a good illustration of this type of disparity. Sometimes the problem of scale disparity may be resolvable by representing species as mega-organisms. For example, krill may be represented at the swarm level when considering interactions with whales. In physical sciences, there are well recognized laws and principles which provide the building stones for model definition. Unfortunately, we do not have such well defined principles in the biological sciences, particularly because we know little about the behavioural response of organisms to changes in their environment.

The operating scale of a model is partly determined by the availability of information on the focus organism(s). Representation of the processes impinging on the focus may require that we produce models where the focus reacts with caricatures of lower trophic processes or smaller scales whilst reactions with higher processes are achieved through aggregation.

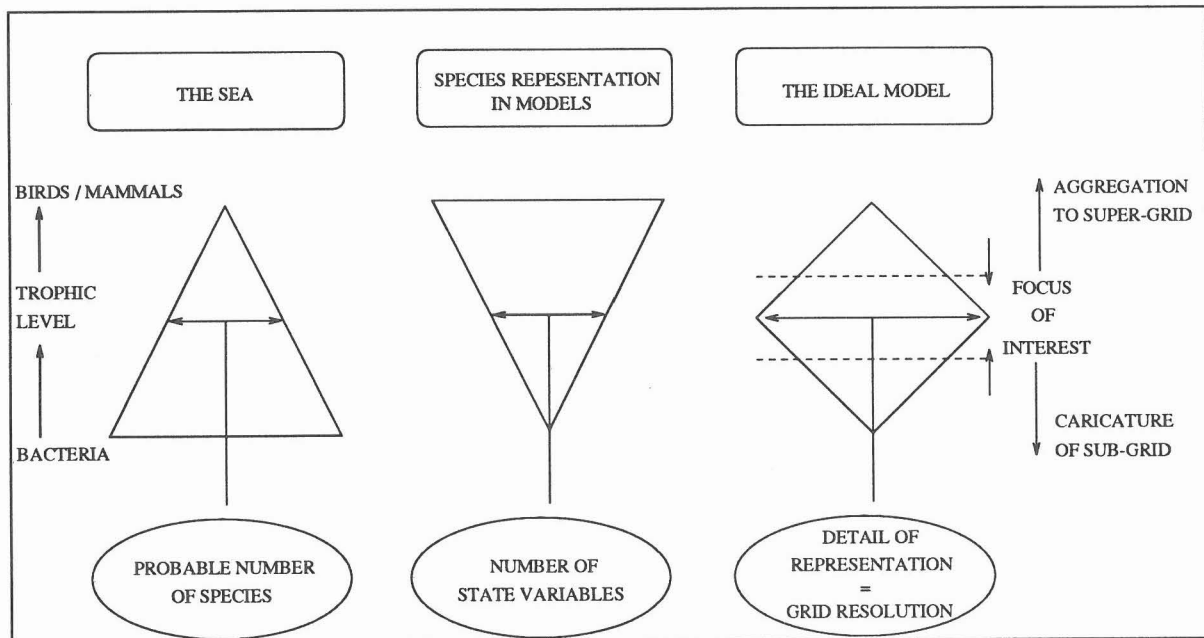
Caricaturing Process Dynamics. A caricature is a way of summarizing processes which occur at a smaller scale than the model grid but which nevertheless have a significant role in determining the dynamics of the focus. This can be achieved by:

- introduction of forcing data and fitting parameters in instances where there is no feedback between the grid and subgrid scales
- introduction of transfer functions where there is dynamic feedback

The first of these approaches has the advantage of reducing the overall number of parameters compared to implementing a detailed representation on a finer grid.

Aggregation. In contrast to a caricature of lower level processes, aggregation consists of summarizing or condensing of relationships from one level in a model (as opposed to data) for introduction at another level. Theory for producing such summaries exists in chemical engineering but has yet to be applied in addressing ecological issues. The form of aggregation should be set by the nature of the question and the level of interest and may involve spatial, temporal, or biological (eg. species resolution within a trophic level) dimensions.

Methods of characterizing and incorporating sub-grid variability. There are a variety of statistical and analytical techniques to characterize sub-grid variability and covariability in a compact way such that it can be used or incorporated into models. Spectral and cross-spectral techniques, geostatistics, transition matrices, and other methods used to describe spatial and temporal autocorrelation are among some of the methods that should be explored. Such methods can be used to characterize patchiness and regenerate synthetic spatial and temporal distributions that can be used as forcing data, including the cross-correlation terms into the flux equations (Appendix F), or additional parameterization of standard functional relationships.



Data interpolation (input and output). Any model requires provision of data on initial conditions at the same resolution as the model grid. Sometimes, these have to be generated from sampling schemes conducted at a coarser resolution. For example, densities of sprat larvae at 2.5km grid points at the start of a particle tracking model run must be interpolated from a coarser sampling grid (Appendix C). In other cases, eg. large box ecosystem models, the problem is different in that data have to be averaged over a wide area and time period with scant knowledge of the spatial and temporal variability. In both cases, attention needs to be given to estimating the variance at the grid scale in the field, for example, replication at sampling grid points, targeted variance study at scales below that of the main sampling grid.

Practical methods of integrating sparse information. Often we are faced with problems which require an estimate of the magnitude of a flux over a wide range of time or space. Usually, such measurements are extremely sparse in the field, representing a small number of values bulked over a trophic level and spanning a wide time interval. For example, primary production measurements in the field can often only be collected at the rate of 1 per day, and carried out on the bulk phytoplankton population or on coarse size categories. One method of expanding the density of data is interpolation of rate measurements from simpler environmental observations using a correlative model calibrated from a small number of in situ data. For example, Joint and Pomeroy (1997) have expanded in situ primary production observations of the southern North Sea. They used a regression of depth integrated carbon fixation against chlorophyll concentration integrated to the base of the euphotic zone. Similarly, one may estimate zooplankton population ingestion rate using a measured relationship between ingestion rate and body size based on a small number of stations and more widespread observations of zooplankton size distributions. These methods, which are attempts at remedying a serious shortage of data, involve a number of bold assumptions. Essentially, they assume that biomass is equivalent to production, ie. they smooth out all the spatial variability in physiological rates over the survey area. Whether the precision of the area average derived from such an approach is more or less precise than that obtained from a simple average of the sparse in-situ data has not been investigated in most cases.

Accounting for estimatable processes. In some circumstances, we may be able to develop relatively accurate models of processes which are governed by well established principles. Such models may provide a framework which can be used to predict the development or trajectory of a population. Projections can be contrasted with data to study potential discrepancies that may be indicative of model inadequacies or spatial or temporal variations in the processes which are unaccounted for in the initial model. An example would involve the use of a particle tracking model to predict the dispersal of a population of larval fish. The model may be used to factor out the dispersal effect on decreasing numbers at known locations, leaving behind the mortality component. Comparison of observations with model predictions can thus be used to assess the potential importance of spatial or temporal variations in mortality rates in the study area. Another example would be to factor out the temperature dependence of growth rates of microzooplankton to reveal the underlying food dependency (Kiorboe 1993).

Model testing -- what sort of data do we need? The procedure of testing is concerned not only with the model's ability to predict mean levels of biomass but also with the structural dynamics of the system that can be detected in the data (eg. temperature and salinity properties, predator-prey trajectories). In order to address the issue it is essential that the model output be presented in the same manner as the data. There is a link between the spatial scale over which the data are representative and the temporal scale over which to average the model output.

Model development and testing clearly requires that the precision of the data can be quantified in order to assess the coincidence with the model results. If a model successfully explains a data set this does not necessarily imply that all the controlling processes have been included. Conversely, if the model fails to explain the data, then important processes have either been

misrepresented or not included. Model falsification rather than validation is the only appropriate philosophical perspective to adopt.

The comparison of model predictions with data is not only one of correlation. There is a need to develop techniques and principles for addressing model robustness by formalizing methods for comparing patterns in model results and data.

Appendix A

Distributional characteristics of parameters in sub-regions of the North Sea

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A database of hydrographic, nutrient and chlorophyll data measurements collected by the Marine Laboratory Aberdeen between 1960 and 1990, has been used to investigate the characteristics of the distributions of values within geographically defined sub-areas on the North Sea. Each data point represented an individual water bottle sample, except for the stratification parameter values (log-phi, the integrated density anomaly down the water column) which were derived from vertical profiles of temperature and salinity. The sub-areas (Figure *) were based on the ICES Flushing Times Working Group boxes (Reference). Data values located within each box were accumulated according to julian day (1-365), irrespective of the year of sampling, to form a composite annual cycle for the 30 year period.

The stratification parameter data (Figure A2) show the basic characteristics of each for the 3 area for which data were available. Values of log-phi >1 are generally taken to indicate that the water column is stratified. Box 1 is almost uniformly stratified in the summer, whilst the degree of heterogeneity increases dramatically as one progresses to Boxes 2 and 6. In the spring, box 1 shows similar heterogeneity to that found in box 2 in the summer. On average, box 6 could probably be regarded as being vertically mixed. Chlorophyll concentration data in the upper 30m of the water column in box 1 (Figure A3) (1400 values) have been grouped into 10 day time intervals. As a first order presentation of the data, the mean and standard deviations of log-transformed values in each 10d interval were calculated (Figure A5). However, closer examination of the data shows that during the spring period (days 100 - 140), the data are very much more skewed than log-normal. The impression is of a large number of low values, and a small number of bloom values (maximum 27mg-chl/m³).

However, later in the year (days 190-250) the distribution of log-transformed values is almost symmetrical (Figure A5). Similar treatment of the temperature data from the same box (3940 values) shows the same type of seasonal trend in skewness. An analysis of the co-variation of temperature and chlorophyll has not yet been carried out on the data set.

A conclusion of the analysis is that in the northern North Sea, sub-box patchiness in the development of stratification in the spring generates inhomogeneities in the distribution of chlorophyll. As the season progresses, and the area becomes more uniformly stratified, so the distribution of chlorophyll values becomes less severely skewed.

The role of interannual variation in the analysis and interpretation has not been addressed. There are no individual years in which sufficient data have been collected to address the questions on a strict within year basis. Even grouping data into decadal period does not retain sufficient seasonal coverage in box 1. Other areas with more data values, may be more amenable to this approach.

Without going into details, there are clear differences in the variance and skewness of chlorophyll distributions for any 10 day interval between boxes 1 and 6 (Figure A6). Box 6 is very much more heterogeneous in terms of water masses and stratification, and covers a larger latitudinal range than box 1. It may therefore be surprising that the variance normalised to the mean of log-transformed chlorophyll values during the spring bloom period is lower in box 6 than in box 1. One might infer that the processes driving the onset of the spring bloom are different in the two areas.

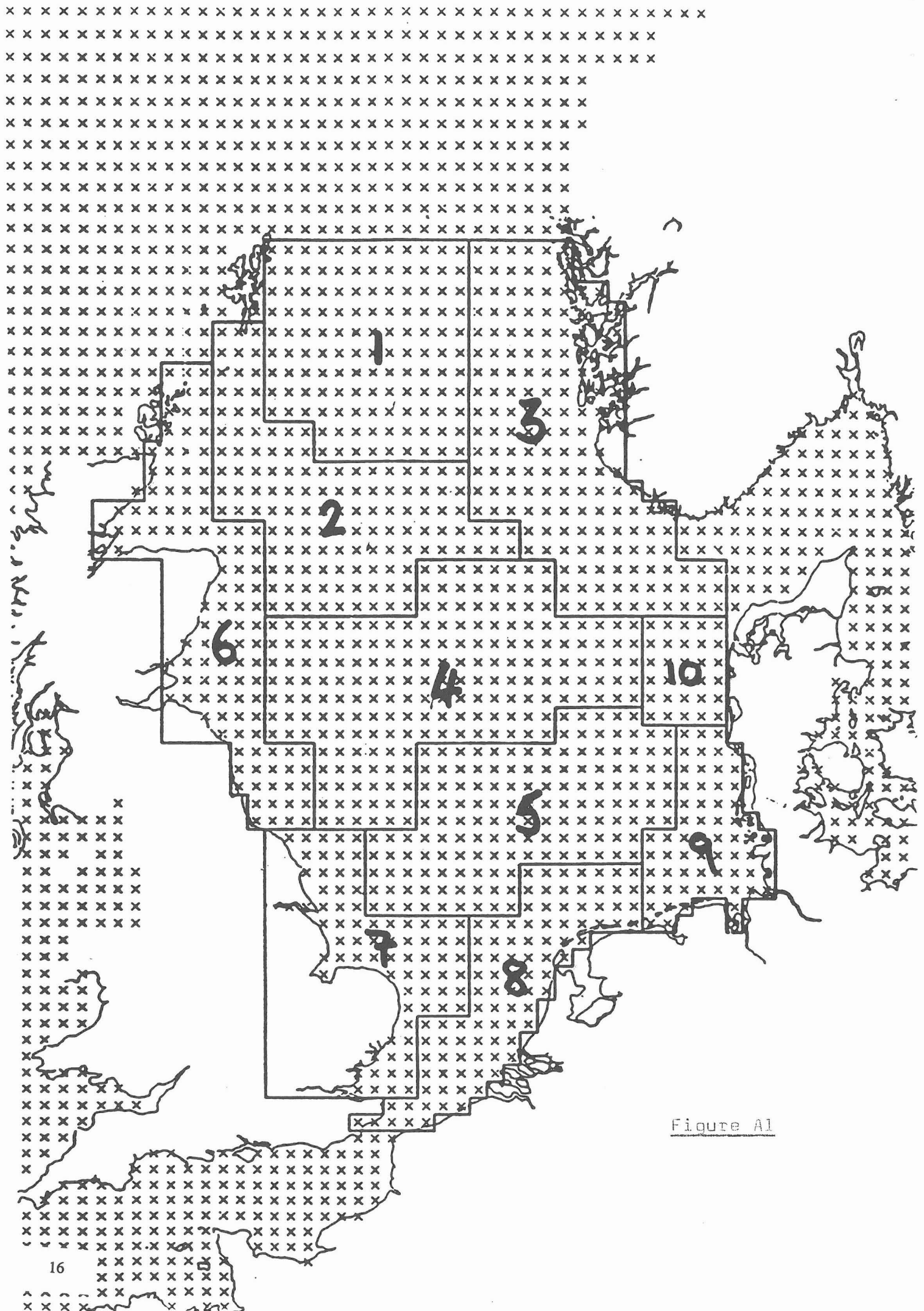


Figure A1

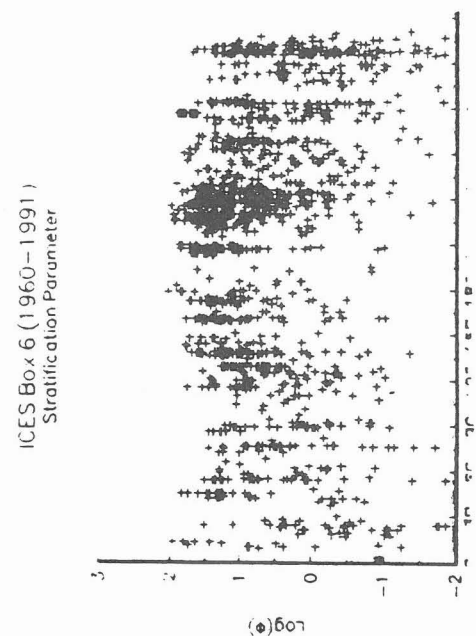
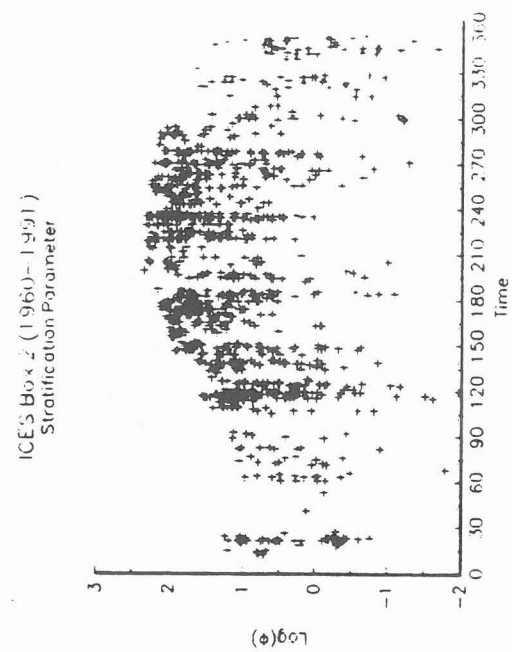
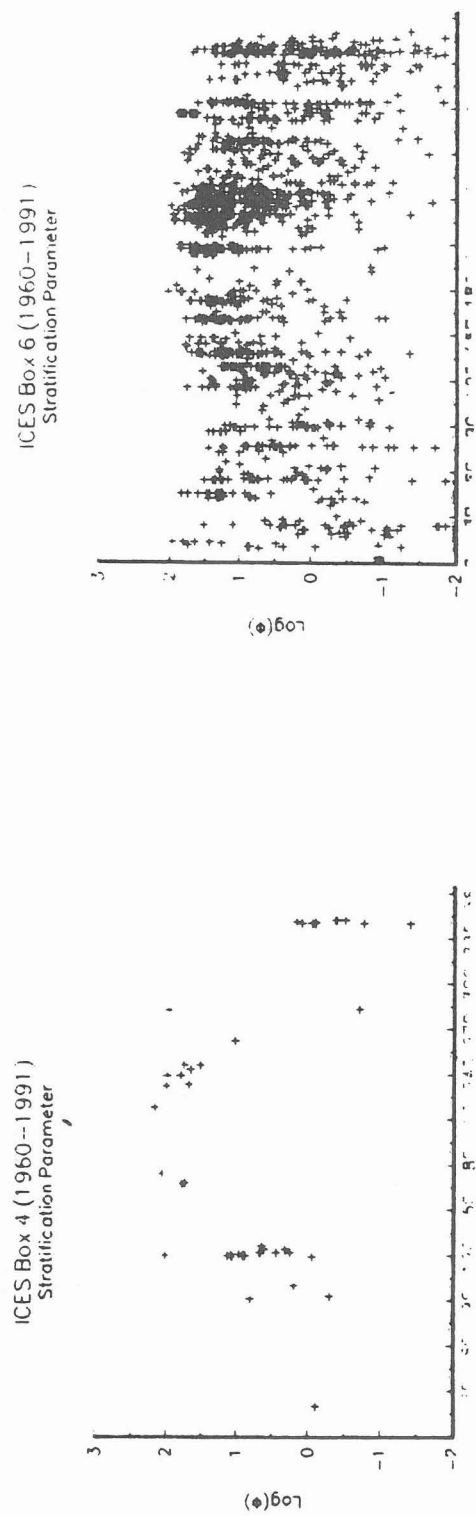
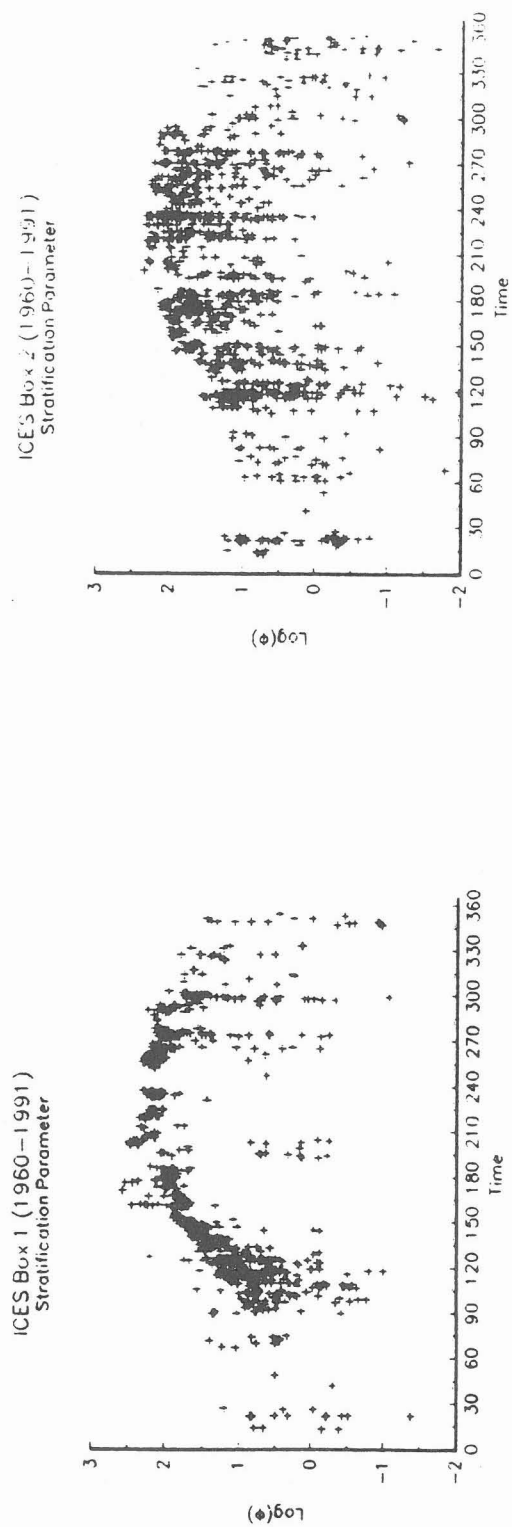


Figure A2

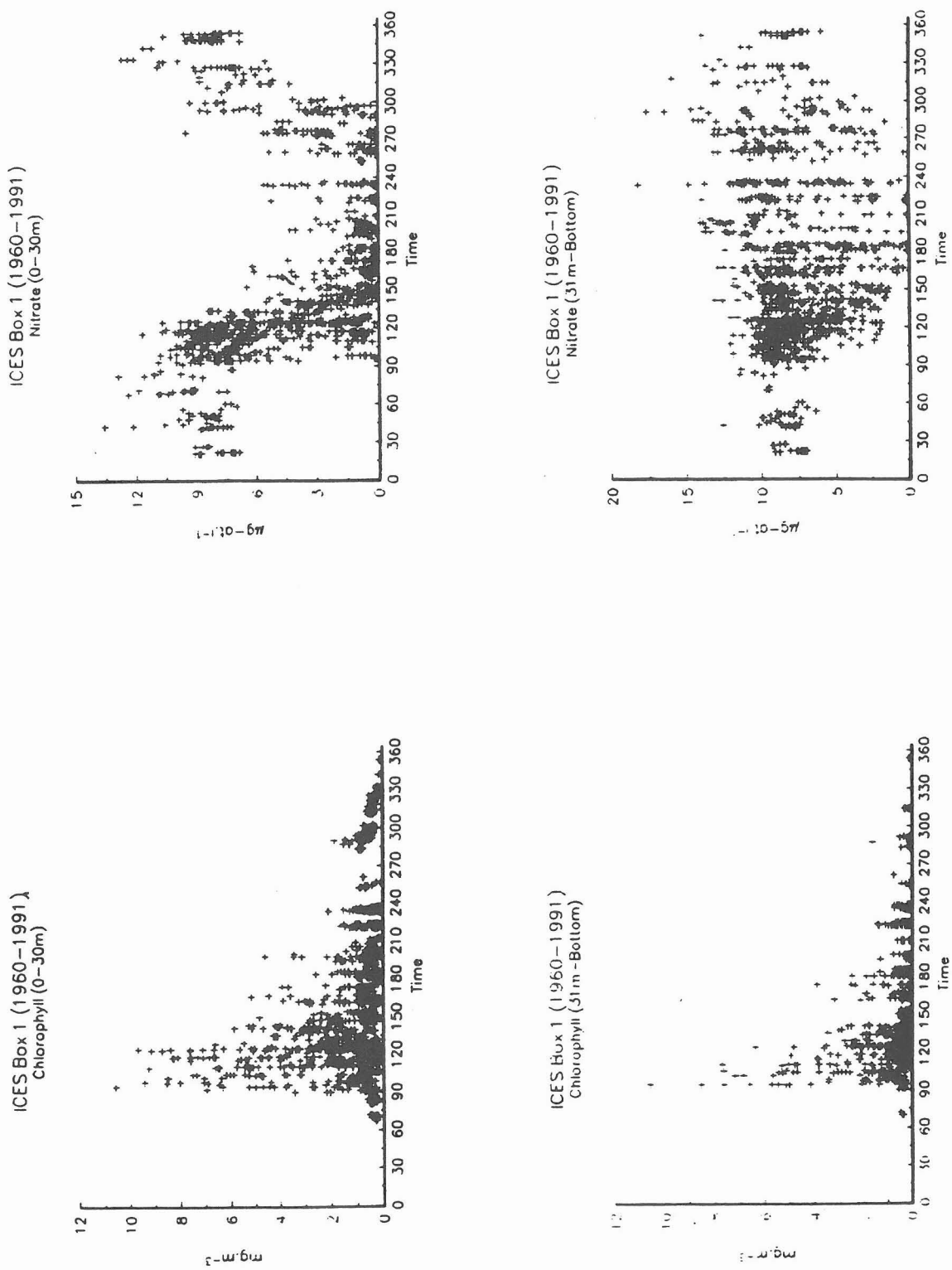


Figure A3

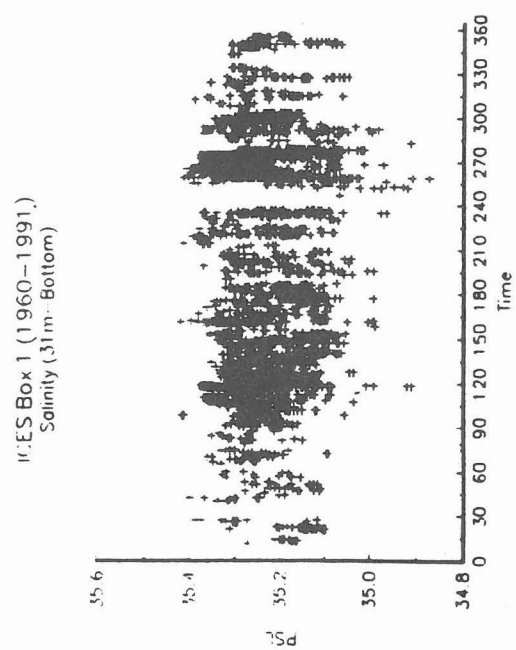
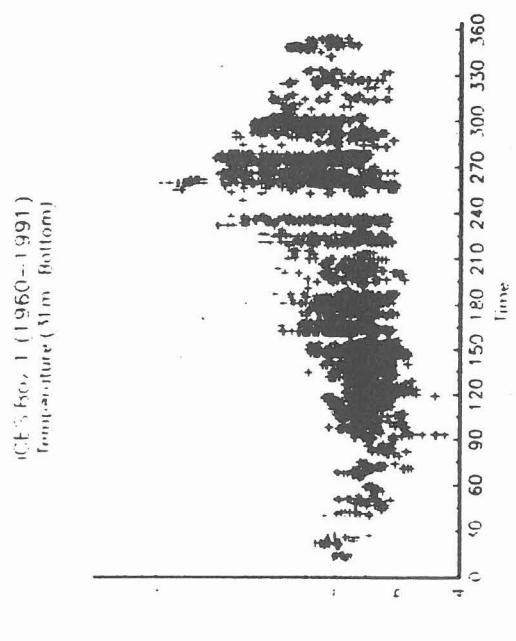
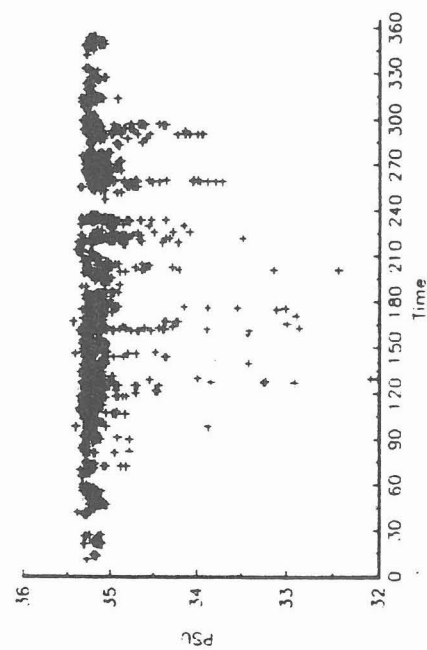
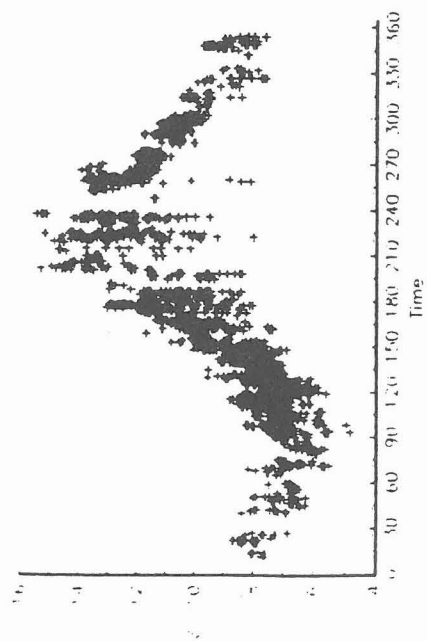


Figure A4

Figure A5

ERSEM box 1, 1960-1990

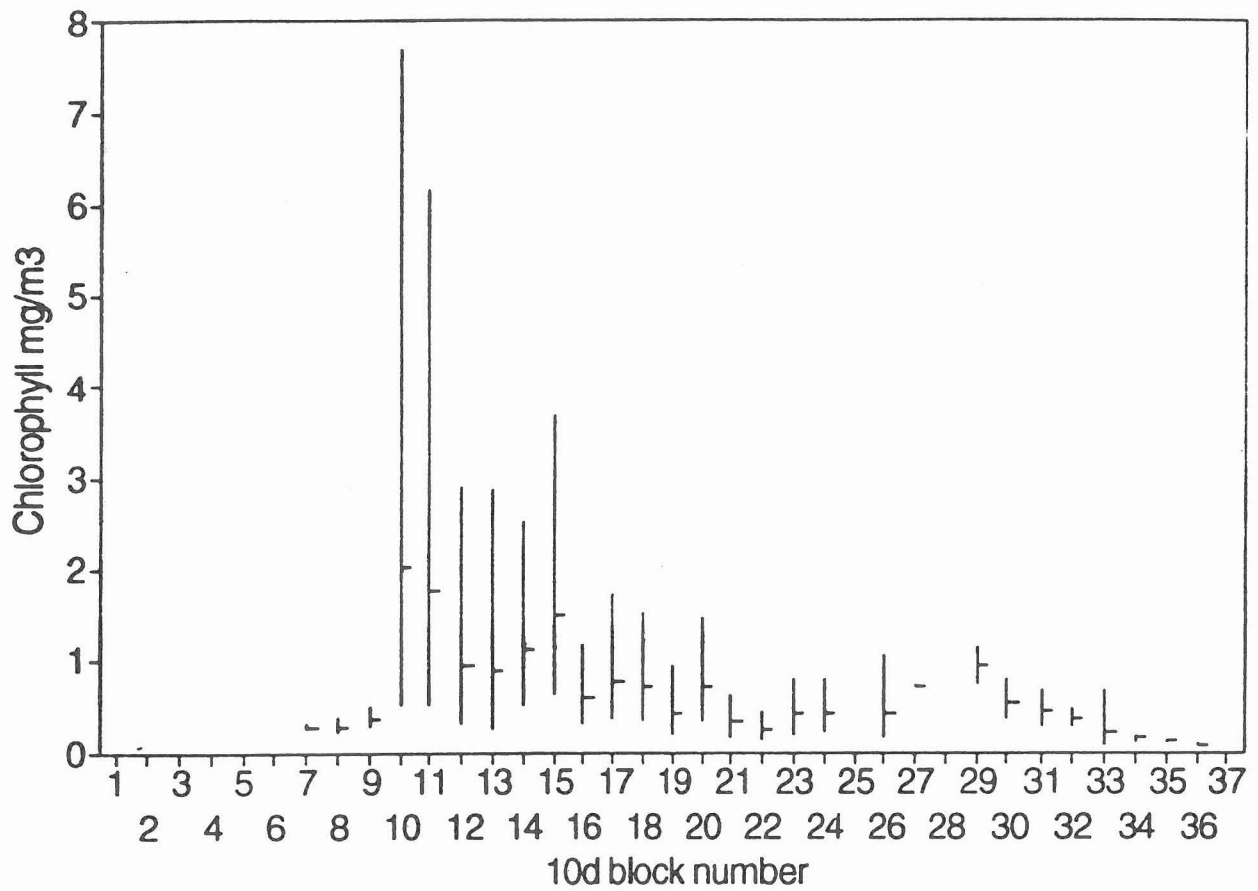
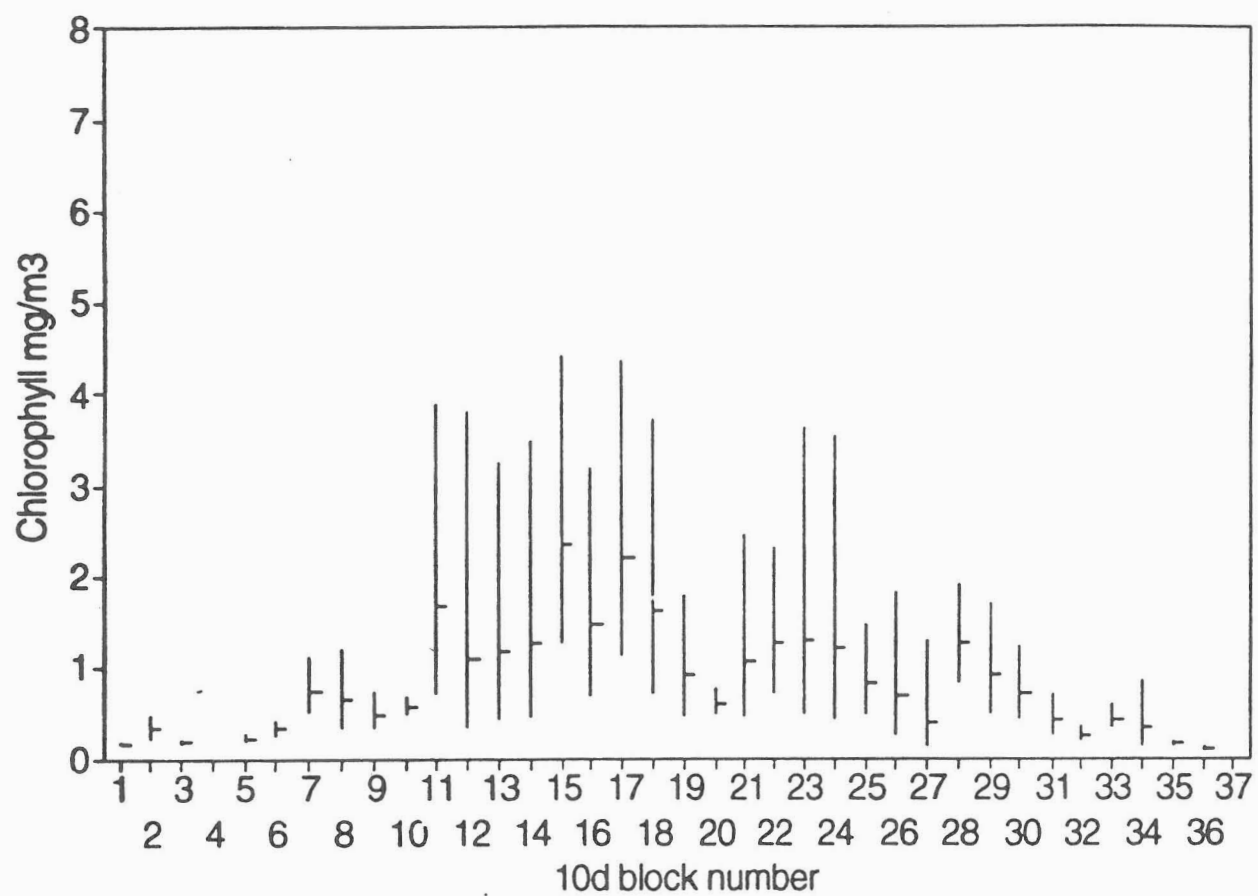


Figure A6

ERSEM box 6, 1960-1990



Appendix C

Transport of Fish Larvae in the North Sea

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A model system consisting of a three-dimensional circulation and transport model was used to simulate the dispersal of sprat larvae in the German Bight. The circulation model has a horizontal grid resolution of 2.5 km and a vertical resolution of 5 m except for the bottom layer. The driving forces of the circulation model are the M_2 -tide, six-hourly time dependent wind stress and air pressure fields, as well as monthly climatological density fields.

The model area, grid size and the vertical resolution of the transport model are in accordance with the circulation model. Using a tracer method the transport model simulates advection, diffusion and incorporates a simulation of active vertical movement of the larvae. This vertical migration is dependent on the time of day and size of the larvae and is based on field data from the German Bight.

Five field surveys were carried out at three week intervals in the German Bight during spring and summer 1991. On these cruises larval distribution, prey abundance and hydrography was investigated. The data was collected on a grid having a resolution of 7.5' (approx. 13.9 km) in the N-S direction and of 15' (approx. 16.3 km) in the E-W direction (Fig. 1). The horizontal larvae distribution data, which was collected on a much coarser grid than that of the model, was interpolated onto the model grid so that it could be used as the initial tracer distribution in the simulations using the transport model.

Tracer dispersal was simulated for a duration of approximately three weeks and the resulting distribution was compared to the interpolated larvae distribution observed during a cruise which took place about three weeks after the time of the cruise yielding the initial distribution (Figs. 2 - 4).

Similarities and discrepancies were observed when comparing model results and field observations. Discrepancies may result from the fact that the transport model does not account for influx of larvae into the area or spawning in the area between cruises. However, model results indicated that the main drawback of the current model is that mortality was neglected.

The simulations focussed attention on problem areas of the model system and indicated means of how it could be improved. These improvements will be implemented in coming investigations.

Fig. 1 - Area of model grid and survey area in the German Bight

Fig. 2 - Observed sprat larvae distributions on the survey grid in the German Bight between 16. 6. - 23. 6. 1991.

Fig. 3 - Observed sprat larvae distributions on the survey grid in the German Bight between 11. 7. - 16. 7. 1991.

Fig. 4 - Tracer distributions on 14. 7. 1991 after 25 days of simulation using initial sprat larvae distributions from the cruise between 16. 6. - 23. 6. 1991.

Figure C1

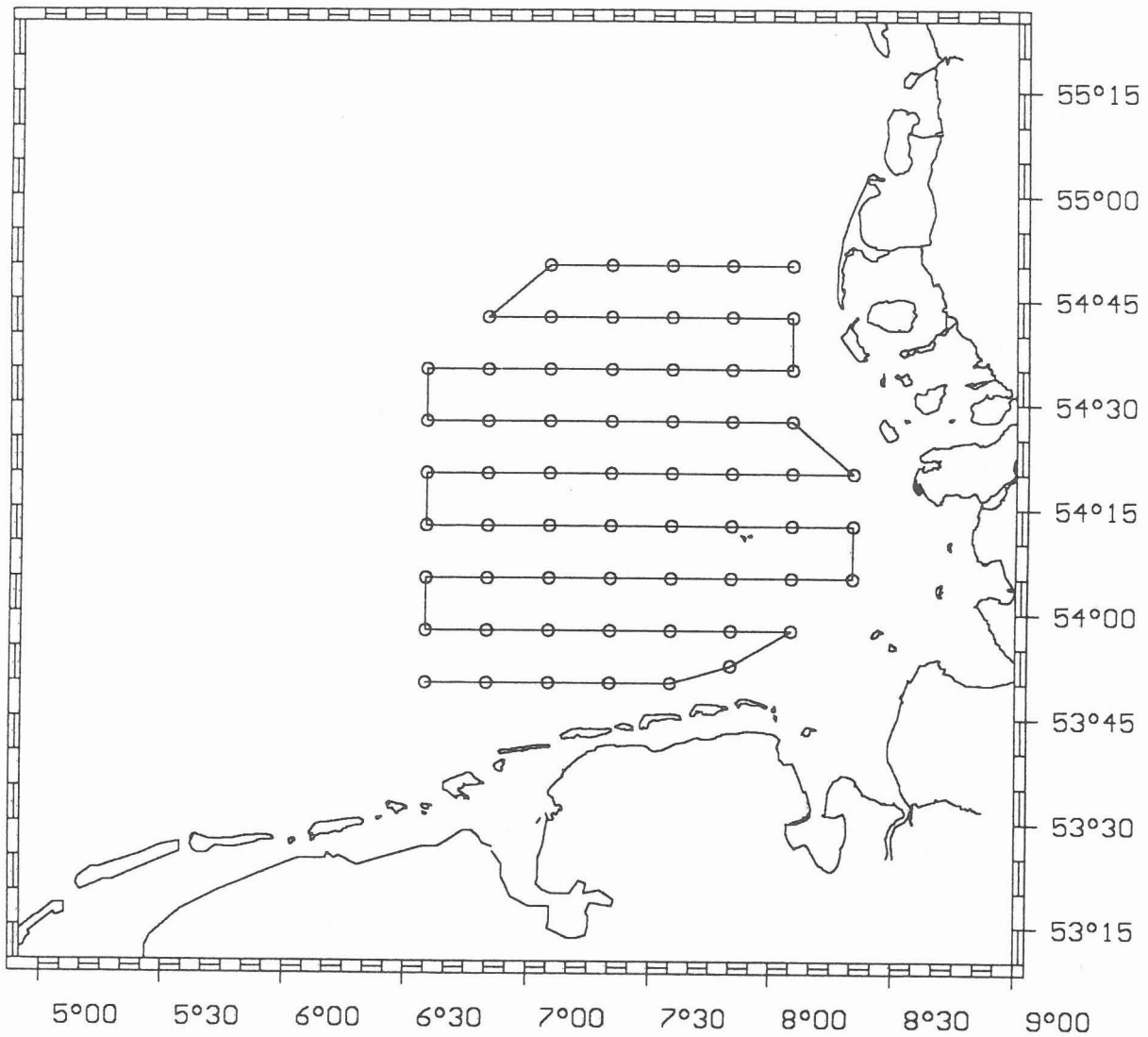


Figure C2

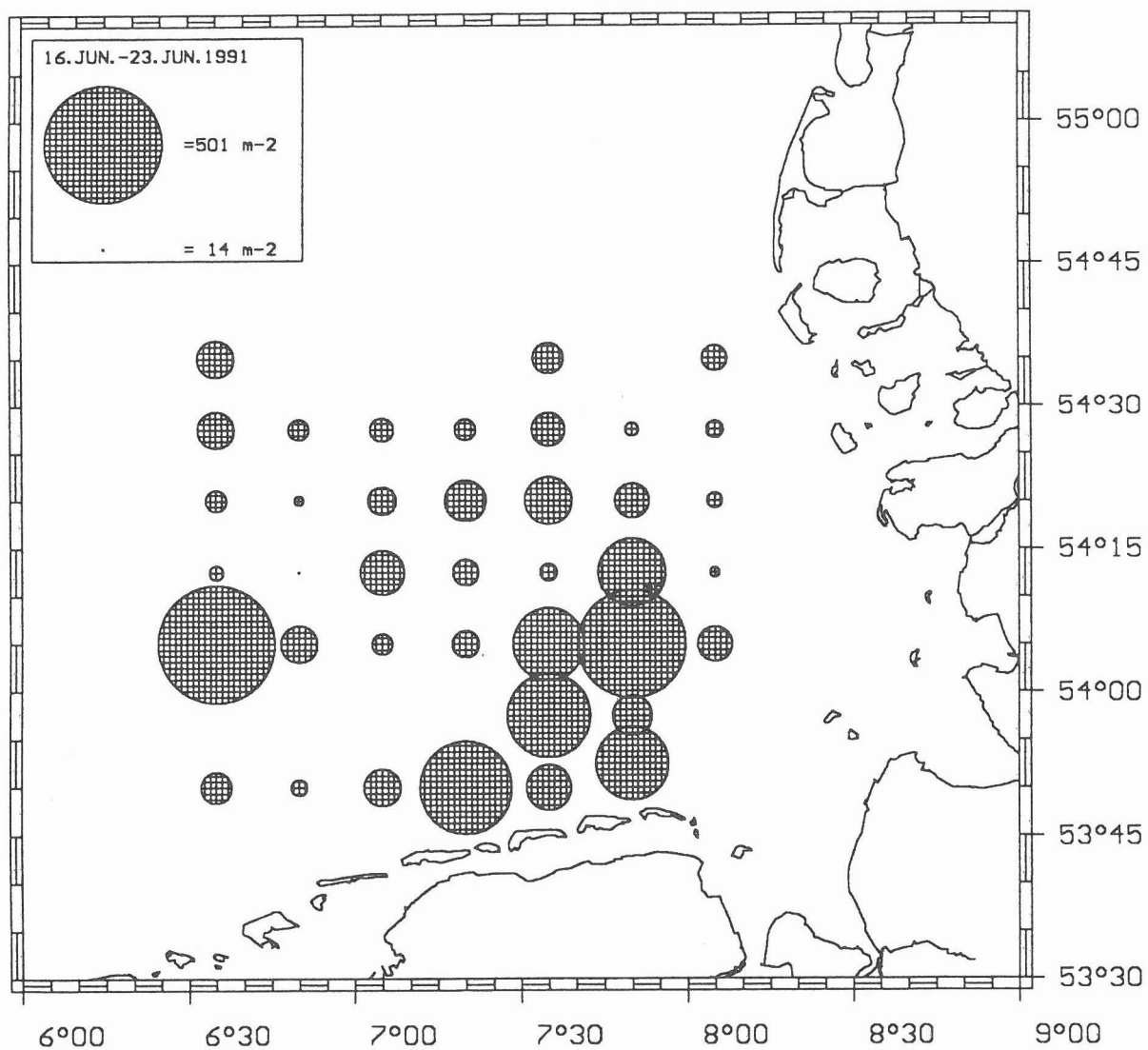


Figure C3

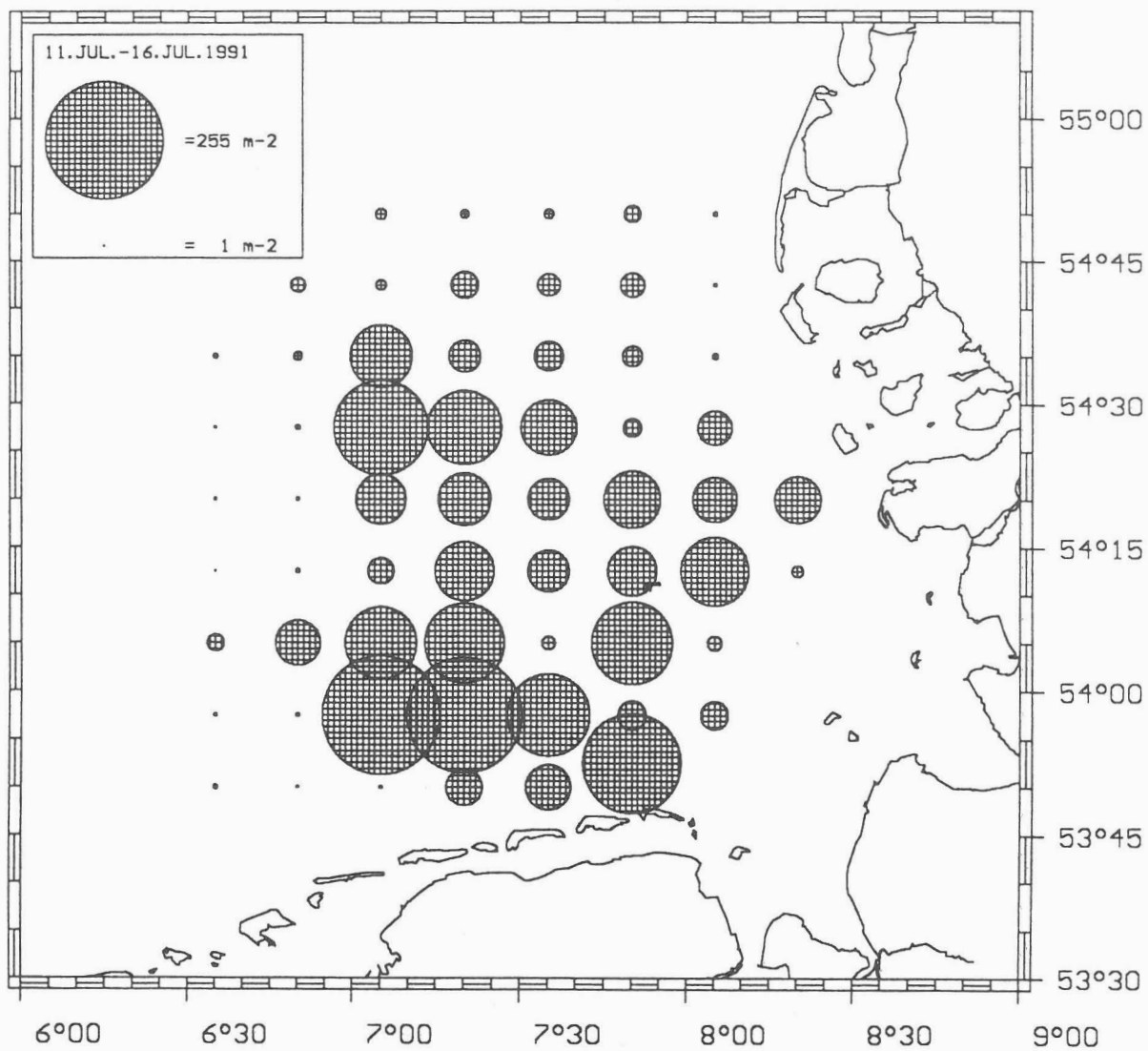
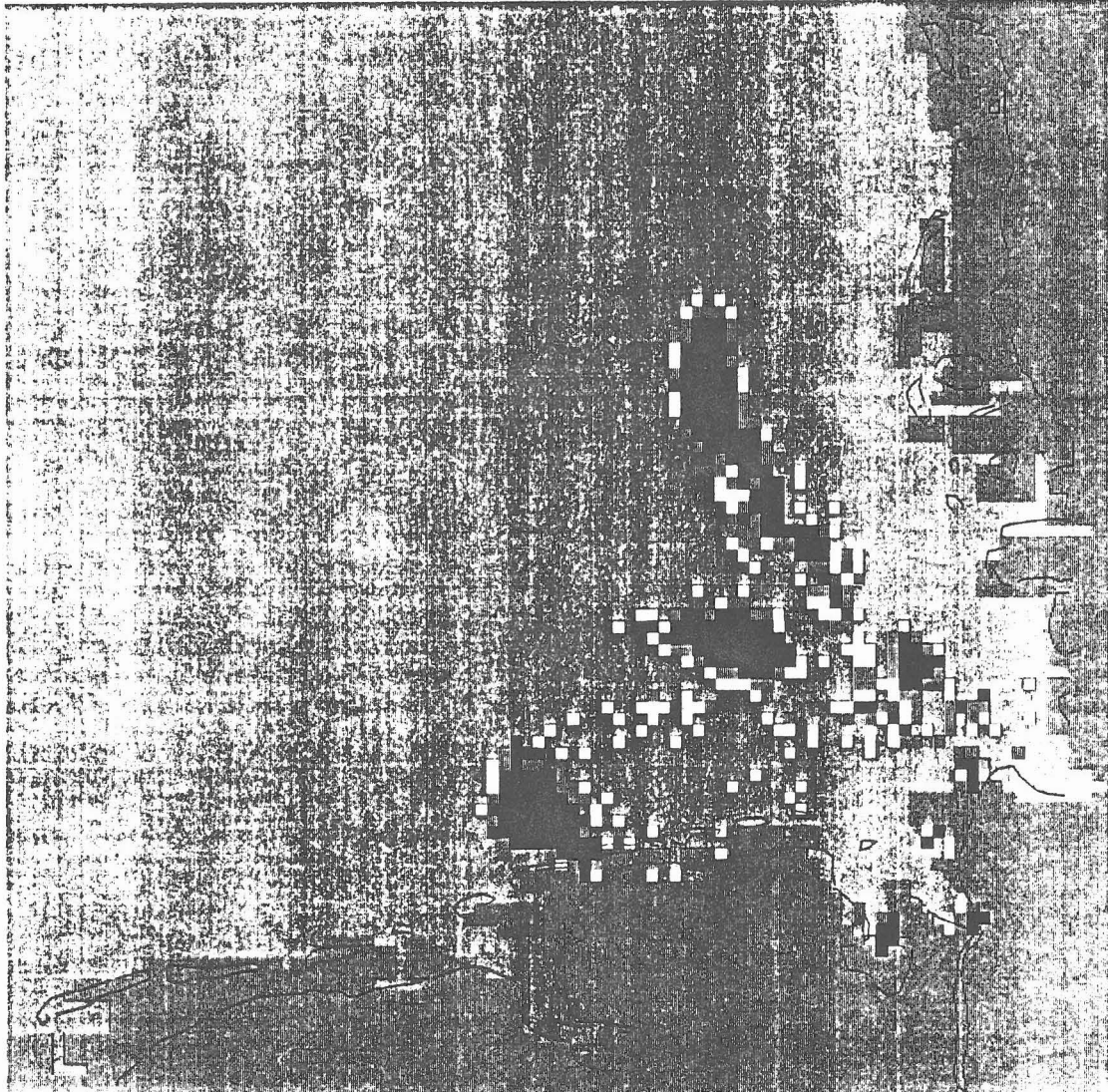


Figure C4

TRACER DISTRIBUTIONS ON 14. 7. 1991 25 DAYS AFTER BEGIN OF SIMULATION



CONCENTRATION OF SPRAT LARVAE
IN THE GERMAN BIGHT
14. 7. 1991

INSTITUT FUER MEERESKUNDE
UNIVERSITAET HAMBURG
10-LAYER GERMAN BIGHT MODEL

Appendix D

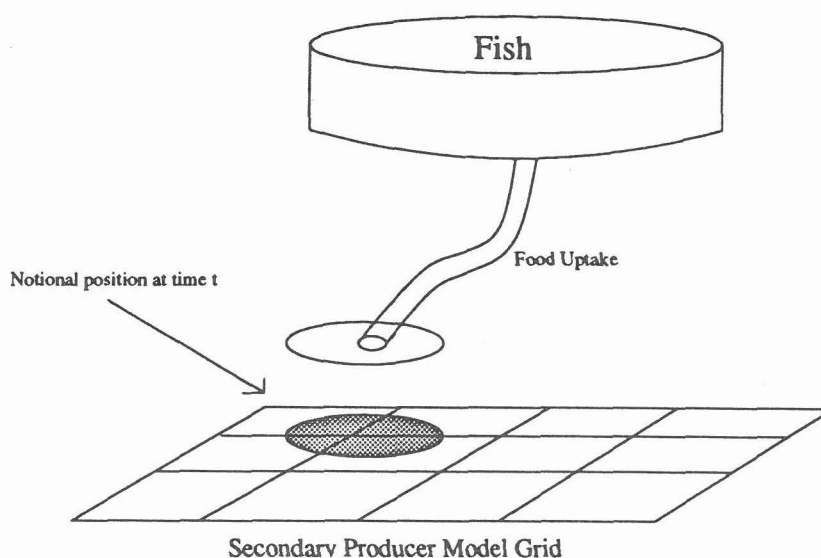
An Aggregated Description of a Fish Population in the ERSEM Model

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Marine ecosystems contain organisms ranging in size from microns (bacteria) to metres (sea mammals). In consequence, when formulating models of such systems it is common to find that no choice of grid size is uniformly satisfactory. The most widely appreciated difficulty is that processes which affect dynamics at the grid-scale can take place at a smaller scale which it is not technically, or conceptually, possible to represent explicitly. For example, an ocean model may well only just resolve (and hence distort) major eddies which influence primary production both by changing the depth of the mixed layer, and by altering horizontal transport effects. However, a parallel problem of scale disparity appears when considering large organisms such as fish or sea-mammals, whose foraging range is very large compared to the grid scale on which the dynamics of their prey would naturally be represented.

A partial solution to the general problem of scale disparity is to adhere to the "trophic level of interest ± 1 " principal advocated in the main body of this report. However, this generally provides only a partial solution, since the scale disparity between (for example) a planktivorous fish, and its prey is still considerable. In many cases, the actual scale disparity to be overcome is much worse than this minimal value because a model originally formulated to represent primary and secondary production (e.g. the ERSEM model) is being modified to include higher trophic levels.

An Aggregated Description of a Fish Population



The ERSEM model is highly spatially aggregated, and represents the entire North Sea by only 11 spatial boxes. However, when modelling a pelagic fish, such as herring, it unclear that a representation in terms of local densities in each box, although entirely feasible, is either realistic or helpful. Even when dealing with such large boxes, a representation in terms of local density implies a necessity to represent transport (or coupling) between the populations of different boxes. It is clear that passive physical transport is irrelevant, and that the organisms own motion is the determining factor. None of the key features of the dynamic rules governing these movements are well known, and it is consequently difficult to see how to model them well.

Two features come to our aid. The first is that to a large extent the changes in local density represent not a minor interchange between more or less separate populations, but wholesale migrations of whole groups of individuals. Moreover,, for commercial species, catch records give us quite good information about where the fish of a given size are at any given time of year.

The strategy adopted by the ERSEM project was thus to regard the population of a given species of pelagic fish as a global object (see figure), characterised by a central position and extent which change systematically with time, in a manner determined from catch records. Within its current extent, the population is regarded as being uniformly distributed. Thus if the total fish population at time t is N , the fraction of that population regarded as being in box i at time t is $X_i(t)$, and the food species density in box i is $F_i(t)$ then the total uptake rate of carbon by the fish population is

$$U = \sum_i N X_i \frac{F_i}{F_i + F_0}.$$

Appendix E

ICES/GLOBEC Working Group on Cod & Climate Change

Lowestoft 7-11 June 1993

Mathematical modelling of physical, chemical or biological systems is not concerned with replicating reality - rather about caricaturing reality. Just as in a caricature of a personality one should be able to recognise the subject, so in a mathematical model the aim is to caricature essential features of the system such that the result provide an explanation of recognisable distinguishing features of that system. If the model cannot be falsified with available data, then it may have some predictive capability given different external forcing scenarios.

Model construction may be considered to have at least three core activities: a) statement of the question(s) to be addressed, b) simplification and formulation of processes, c) provision of boundary/driving conditions. Simplification is a necessary component of modelling, designed to make the system numerically and analytically tractable and is the essence of the caricaturing process. Increasing complexity in a model may lead to decreased comprehension of the results. A major skill in modelling activity involves devising novel numerical methods of implicitly representing or caricaturing important sub-grid scale processes in the model. The term grid-scale in this context refers to the basic temporal, spatial or biological structural units of the model (eg. distance between spatial grid points) In the context of marine ecological models the main processes to be dealt with are dispersal and predator-prey interactions of the constituent biota. The term of reference is concerned with striking the balance between the necessary simplification of processes and structure, whilst retaining sufficient detail to address questions concerning the population dynamics of particular species. The underlying assumption is that the two conditions may not necessarily be compatible.

Simplification of structure and processes may take place at spatial, temporal and biological levels, to varying degrees, dependent upon the content of the question being addressed. In the following section the constraints on these three levels of simplification are briefly described in the context of shelf scale (eg. North Sea, Georges Bank/Gulf of Maine) ecosystem models, since this is the underlying intent of the term of reference. The discussion of constraints is not intended to be read as a raft of obstacles to progress - more a reminder of the need for careful consideration during model construction, to be aware of the consequences of decisions, and the need for compromise.

Temporal simplification. The biological components of most ecosystem models ignore processes occurring at time scales less than 1 day, due partly to computational constraints but also to lack of understanding of sub-daily biological processes, and the perception that the diurnal light cycle is a primary forcing function on the biology and therefore a logical time unit. Immediately, this means that biological processes on the time scale of the semi-diurnal tidal cycle are not considered explicitly but must be caricatured implicitly if it is considered that they are an essential aspect of the system in question. Clearly, the physical components of ecosystem models are very much concerned with shorter time scale processes and hence, the provision of physical forcing data to the biological component of such ecosystem models must involve schemes for temporal integration.

Spatial simplification. The spatial resolution of ecosystem models is limited in the first instance by that of the underlying physical component, but also by computational constraints. Clearly, there must be a trade off between the biological and spatial complexity of the model. Setting the spatial resolution of an ecosystem model is a clear area with scope for clever mathematical caricaturing of the effects of sub-grid scale features (eg. fronts, vertical stratification, particle contact scale turbulence) without recourse to complicated explicit representation. One can argue here, that there is a need to carry out explicit

modelling of the sub-grid scale features in isolation in order to understand their function, before attempting to condense their effect into a larger scale construct.

Biological simplification. The major limitation to representing biological components in an ecosystem is the lack of basic understanding of physiology and behaviour at the species and individual level. Species differentiation is especially problematic among the lower organisms, whilst lack of understanding of the role of individual behavioural variability is prevalent among higher organisms. The typical consequence of these constraints is that the structural complexity of model food webs may be the inverse of that in reality. For example, there are probably a very large number of marine bacteria species, but these are typically represented by a single state variable, whilst the (probably) smaller number of fish species tend to be represented by several variables since, it is argued, the known feeding habits of fish are very diverse. This has certain consequences for the representation of prey preference dynamics in a model.

Functional grouping of organisms in ecosystem models into aggregate state variables is clearly a necessary action if one is concerned to capture the effects of the entire predation pressure at a particular trophic level. However, biological aggregation carries several penalties:

- creation of artificial omnivores
- need for artificial stabilisation
- mechanisms to damp predator-prey oscillations
- parameterisation problems (should one use an archetype species or an unrecognisable 'functional average')

Predation closure at the top of the food web is held by some to be a problem in ecological modelling. Basically, the mortality rate of the highest trophic level in a model food web needs to be imposed as (essentially) a driving function. Often, this is achieved by inflicting a static mortality rate on the top modelled predator to represent the rate of removal by unmodelled, unseen, even-higher predators. However this carries the penalty that the unseen predator does not react to declines in the modelled predator and continues to remove animals even at vanishingly small densities.

There is a fundamental difference, in modelling terms, between unicellular binary fission organisms and metazoans. Binary organisms are amenable to biomass-only based representation, since the biomass per individual of a species varies only marginally. For higher organisms, biomass per individual can vary considerably over the life cycle (eg. copepod eggs - adults; fish larvae - adults). This carries potential problems since mortality is essentially a numbers based rate, not a biomass based rate. Thus, in a long-lived organisms the biomass-only approach does not preclude the conceptual possibility of numbers declining faster than biomass. Thus, for higher trophic levels, it is necessary to simultaneously keep track of both numbers and biomass over time, potentially compromising the need for simplification.

MSVPA (a multispecies extension of the classical Beverton and Holt numerical population dynamics model) is a relatively well known form of model which tracks both numbers and biomass and deals with predation interactions between the constituents, in this case, fish guilds. However, growth of fish in the MSVPA is represented logistically (eg. von Bertalanffy growth curve), hence there is no requirement for biological boundary condition data on prey other than those represented explicitly in the model. MSVPA therefore has nothing to offer on how environmental changes expressed through lower trophic levels may impact on the explicitly represented fish species (or vice versa).

The requirement for a number&biomass tracking model capable of interacting with lower trophic levels requires an underlying dynamic physiological model to drive individual growth and development. Parameterisation of such a 'physiological engine' is a difficult task and there are fundamental decisions to be made at the construction stage. For example, three possible options are:

- 1 - parameterise the engine to represent some composite of a group functionally similar species.
- 2 - adopt one major species to act as an archetype of a number of functionally similar species,
- 3 - explicitly represent one (or more) species, in parallel with a simple biomass-only representation or static loading for all the functionally similar species.

An underlying assumption of the above options is that, in one way or another, it is necessary to take account of the full predation loading on any trophic level in order to capture the essence of any feedbacks between the species or taxa of primary interest and the surrounding trophic levels. Clearly, the approach adopted must depend on the questions being addressed. Consider two examples:

Example a) One wishes to ask questions about the role of *Pseudocalanus* sp. in an ecosystem. First, one asks whether this species constitutes the bulk of the biomass of small calanoid copepods. Very likely, the answer would be yes. In that case, an age or stage structured representation of all small calanoid copepods, parameterised as if all such copepods were *Pseudocalanus* (option 2), might be adequate.

Example b) One wishes to ask questions about the growth rates of adult cod in an ecosystem (eg North Sea), where cod constitute only a tiny fraction of the total demersal fish biomass. An age or size structured cohort model seems appropriate. However, option 2 will not be acceptable. Option 1 is likely to be very unsatisfactory because of the very wide range of maximum sizes and feeding strategies of demersal fish. Option 3 is feasible, but still difficult to implement because the biomass-only or static loading representation of all other demersal fish will dominate over the cod cohort in the model.

In addition, if one implements an age or stage structured representation of a species or functional group in a model, then care must be taken to avoid creating artificial competition between age groups or stages, as an artefact of the degree of resource differentiation in the lower trophic level. For example, there may be problems associated with implementing a stage structured copepod model where the main food source for each stage is a single undifferentiated phytoplankton category, unless some clever implicit caricature of functional or size differentiation in the phytoplankton is also included. The extent to which biological detail at trophic levels surrounding that of interest needs to be included cannot easily be determined beforehand due to inherent non-linearities in competing predator systems. This area is a prime target for numerical experimentation to achieve the optimum balance between dynamic representation and external forcing.

Finally, there are specific problems associated with combining spatial resolution and a number&biomass representation. Basically, a good physiological engine should dictate that an animals' growth response to the ingestion of a particular amount of food is dependent on multi-dimensional characteristics, for example age or development stage, and present condition expressed by the ratio of reserve biomass to total biomass. Incorporating spatial resolution necessitates consideration of the dispersal of animals, and potential mixing of animals with different histories at each grid point in a model. Schemes for dealing with this problem are not readily available.

The above discussion includes some of the considerations which need to be taken into account if one wishes to include a representation of particular species within an ecosystem context. Essentially, there

are trade offs to be made between the need for simplification and the retention of sufficient detail to be able to recognise the key features of interest. At the same time, there may be a limit to which secondary details can be discarded or replaced by simple forcing functions. The correct balance may only be found by experimentation. At the same time, it is of paramount importance to carefully pose the questions to be addressed by any modelling exercise.

Three candidate ecosystem frameworks to form the basis for cod and copepod models

In this section three types of approach to ecosystem modelling are briefly outlined, together with an indication of their potential for forming the 'underlying context' of models of particular species.

Box-model system. The ERSEM (European Regional Seas Ecosystem Model), is an example of the box-modelling approach which could form the template for supporting representations of particular species of zooplankton and fish. Briefly, biological dynamics are modelled in 15 spatial compartments covering the whole North Sea in the horizontal and vertical domains. Physical exchanges (advection and diffusion) between compartments are driven by spatially and temporally integrated output from a 3-dimensional general circulation model of the NW European Shelf. The chemical and biological ecosystem is represented by some 50 state variables and a series of ordinary differential equations in each compartment, covering pelagic and benthic nutrients, phytoplankton, zooplankton, fish, benthos and detritus. An attempt has already been made to explicitly represent three fish species (herring, whiting and mackerel) by age structured cohort models superimposed on the main ecosystem model and operating in parallel to static loading representing the residual mortalities inflicted by other planktivorous, pelagic piscivore and demersal fish. At present, recruitment is represented simply by a driving function. Experimentation with the model has shown that body growth rates of herring in the system are responsive to changes in biomass forced through inflicted removal by fishing, suggesting that herring growth is strongly resource limited. Historical data from the North Sea show an inverse relationship between size at age 3 and stock biomass of herring over the period 1947-1991. The initial results therefore suggest that although the approach is not without many of the problems outlined earlier, but is clearly feasible.

Particle tracking systems. Extensive work has already been carried out in several shelf seas (eg. North Sea, Georges Bank, Barents Sea, Scotian Shelf) using Lagrangian particle tracking models driven by a variety of general circulation models. So far these have been used to explore the potential for dispersal of fish larvae, copepods, river discharges or contaminants under different vertical distribution/behaviour scenarios and thus cannot really be considered as ecosystem models. However, this approach may have possibilities for development along ecological lines, by prescribing background chemical/biological conditions either as forcing data or from a separate model and then introducing categories of particles representing various taxa and allowing them to interact. This approach is analogous to a 3-dimensional cellular automata, and could be considered to be an Individually Based Model (IBM) approach. Several groups of investigators are actively developing such systems and some versions are already in use (eg. OPEN programme). However, the computational problems appear to be considerable, due to the need for an extensive database of behavioural options under the various scenarios encountered by particles in the system. The approach is therefore attractive, but may not yield results in the short term.

Size spectrum systems. The 'Sheldon size spectrum' approach has been available for many years as a framework for assembling biomass and predator-prey relations across entire ecosystems. Essentially, the numerical abundance of taxa is assumed to decline in a characteristic way with body size across the full range of organisms in the system. Assuming fixed relationships between prey size and predator size, various predictions about higher trophic level production can be made on the basis of information about low trophic level productivity, or vice versa. Recently, this generic approach has received new

attention in relation to the survival of target species, survival strategies in the presence of seasonal pulses of primary production, and analysis of fish predation strategies. Although the Sheldon approach has been extensively discussed in relation to models of ecosystem dynamics it has apparently not yet been fully applied to any particular system. There would seem to be considerable scope for adoption of the principle as a setting or context for more detailed species models, especially given recent developments giving the capability of incorporating spatial and temporal dynamics.

Appendix G

The use of size structured biological data for interpreting predation characteristics of whiting (*Merlangius merlangus*) in the North Sea

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Beyer (1989) elaborated on the so-called 'Sheldon spectrum' idea that there exists a characteristic relationship between numbers and body size for organisms in an ecosystem. The approach allows a number of valuable simplifying conclusions to be drawn concerning rates of mortality in the system, assuming some size-based relationship between predators and prey.

The large scale ICES stomach sampling programme carried out on a quarterly basis has shown that in the second quarter of the year, when herring larvae are undergoing metamorphosis, 0-group herring form a significant component of the diet of whiting. This lead to a hypothesis that metamorphosis is a critical stage in the early life of herring, attracting enhanced predation by whiting. The ecosystem size spectrum approach has been used to interpret the predation impact of whiting in the North Sea on herring larvae from field sampling.

Four sampling boxes forming a transect across the North Sea from the east coast of Scotland to the Skagerrak were studied in April 1989. The timing was chosen to coincide with the expected time of metamorphosis of herring larvae in the eastern North Sea. In each area, replicate demersal and pelagic trawls, Methot-Isaac-Kidd trawls and plankton net tows were carried out. Frequency distributions (number/m²/log-wet weight interval) of all constituent species were estimated from body length measurements and length-wet weight regression relationships. At the same time, the stomach contents of approximately 800 whiting were examined and the contents classified as far as possible in terms of species and wet body weight.

The size spectra of all pelagic organisms in the ecosystem of two of the study areas are shown in Figure G1. Herring larvae were present in both areas (log weight approximately -1), but in the Skagerrak, metamorphosed and partly metamorphosed larvae were also present. Whiting were present in both areas in the range 0.5-2 log weight. The slope of the size spectrum was characteristically steeper off the east of Scotland, possibly implying that the transfer efficiency of biomass up the food chain was less efficient in that area.

Comparison of the size distribution of items in whiting stomach contents with the distribution of items in the water was effected by calculating Chesson's alpha (Chesson, 1978) which is a form of prey preference index. A wide range of prey sizes were ingested by the whiting (overall acceptable window of log prey wt - log pred wt, -3.5 to -1). Off the east of Scotland, Chesson's alpha suggested that the whiting had a strong preference for the large tail of this distribution (Figure G2). However, this result was not replicated in the other regions. The conclusion was that size alone was not a good discriminator of the prey composition of whiting.

The next stage of the analysis was to examine the species composition of items in the water falling within the acceptable size window for each size class of whiting, and compare this with the importance of each species in the stomach contents. Chesson's alpha calculated on a species basis showed some strong correlations between areas (Figures G4, G6). First, transparent organisms such as chaetognaths and fish larvae (including herring) were effectively ignored by the whiting, even when present as an appreciable proportion of the items within the acceptable size window. Second, organisms such as euphausiids, mysids and amphipods were consumed approximately in proportion to their abundance in the water but the whiting showed no strong preference for them. Finally, sandeels (when present) and smaller whiting were consumed with a strong preference. When sandeels were absent from the system,

Norway pout were preferentially ingested. Metamorphosed herring (when they occurred) were also subject to strong selection. The implication is that the feeding strategy of whiting is to seek and destroy small pelagic fish (sandeels, smaller whiting, pout, and metamorphosed herring). The results also indicated that metamorphosis is indeed a critical stage in the development of herring, at which they become subject to increased predation pressure.

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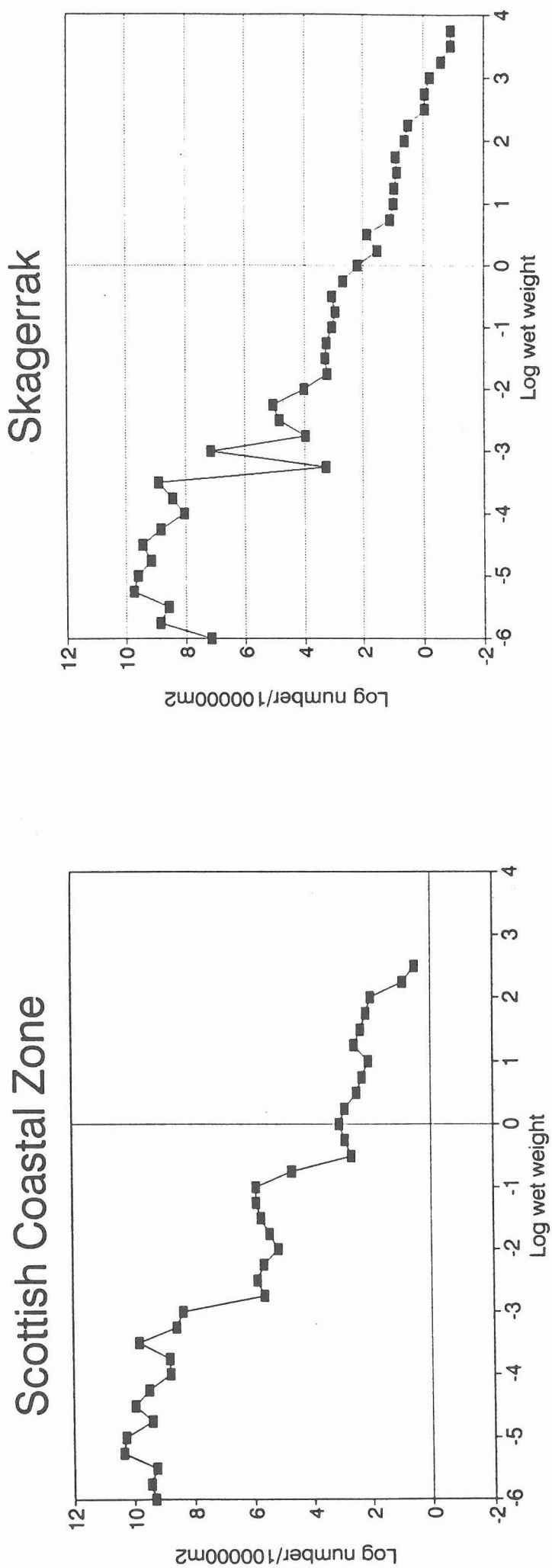
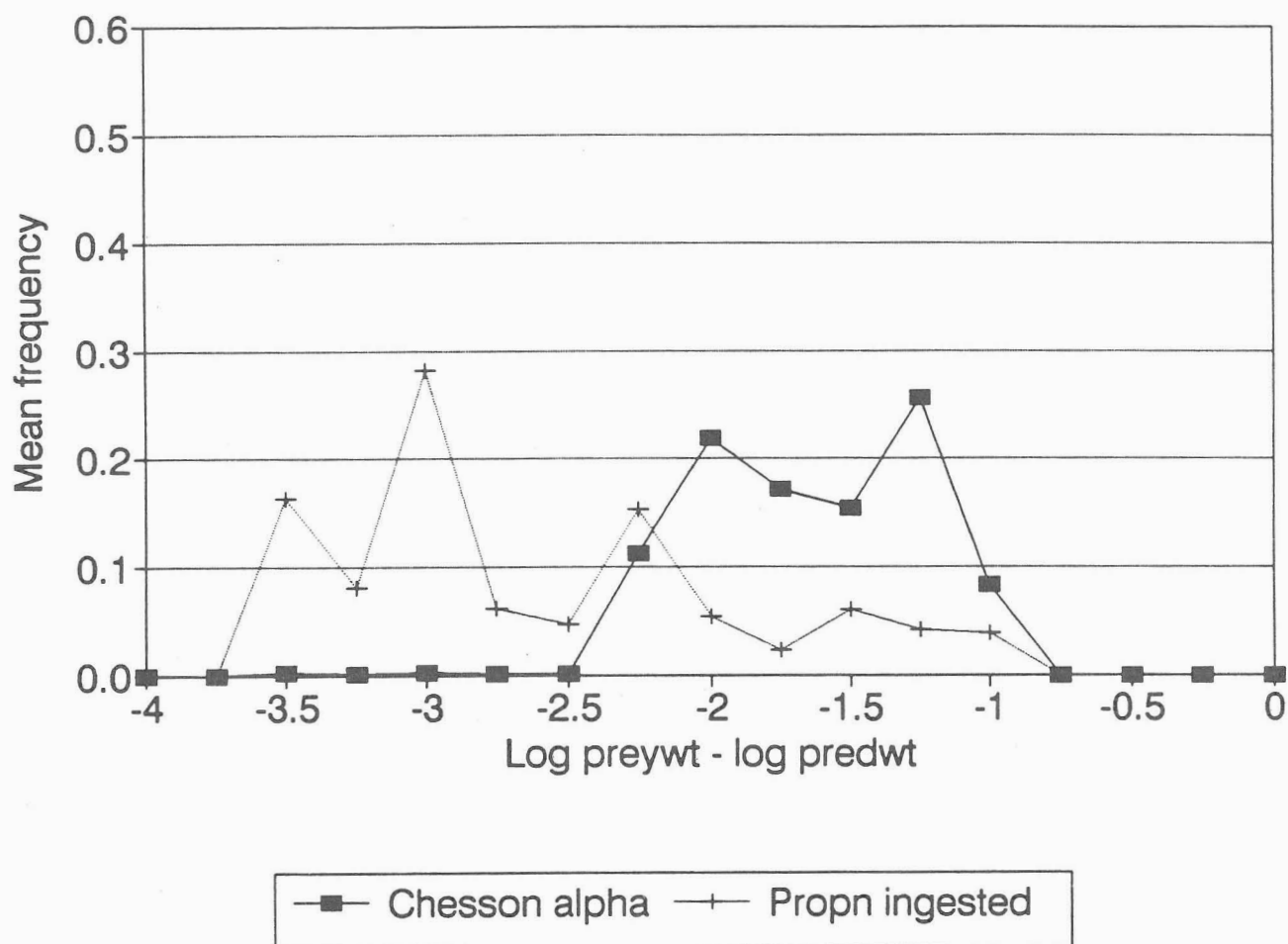


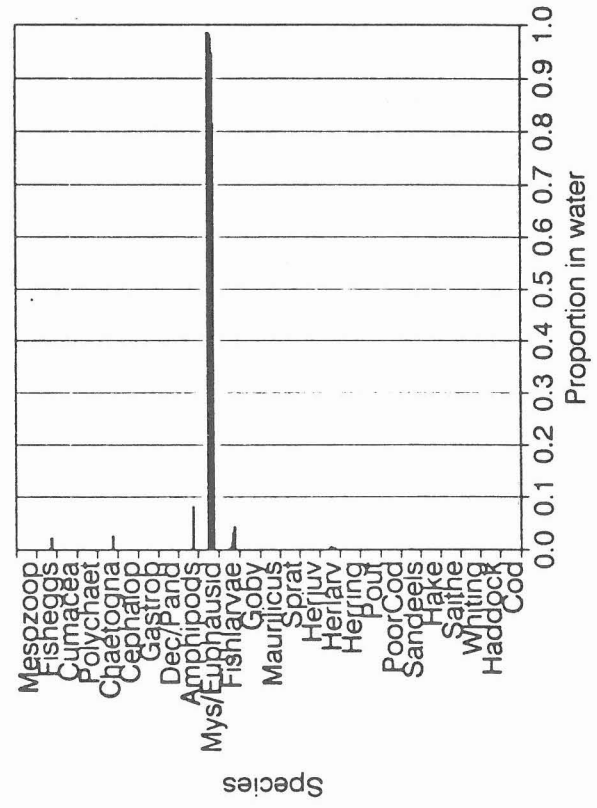
Figure G1

Figure G2

Scottish Coastal Zone



Scottish Coastal Zone



Scottish Coastal Zone

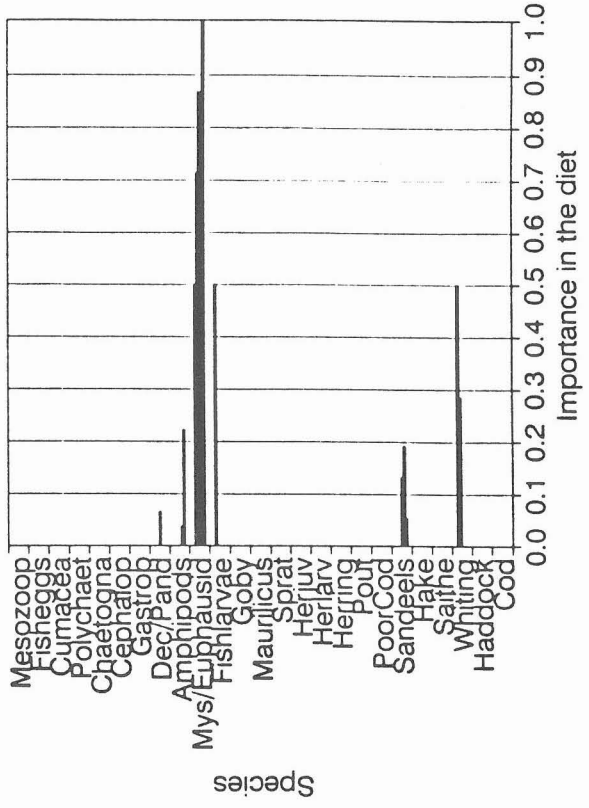
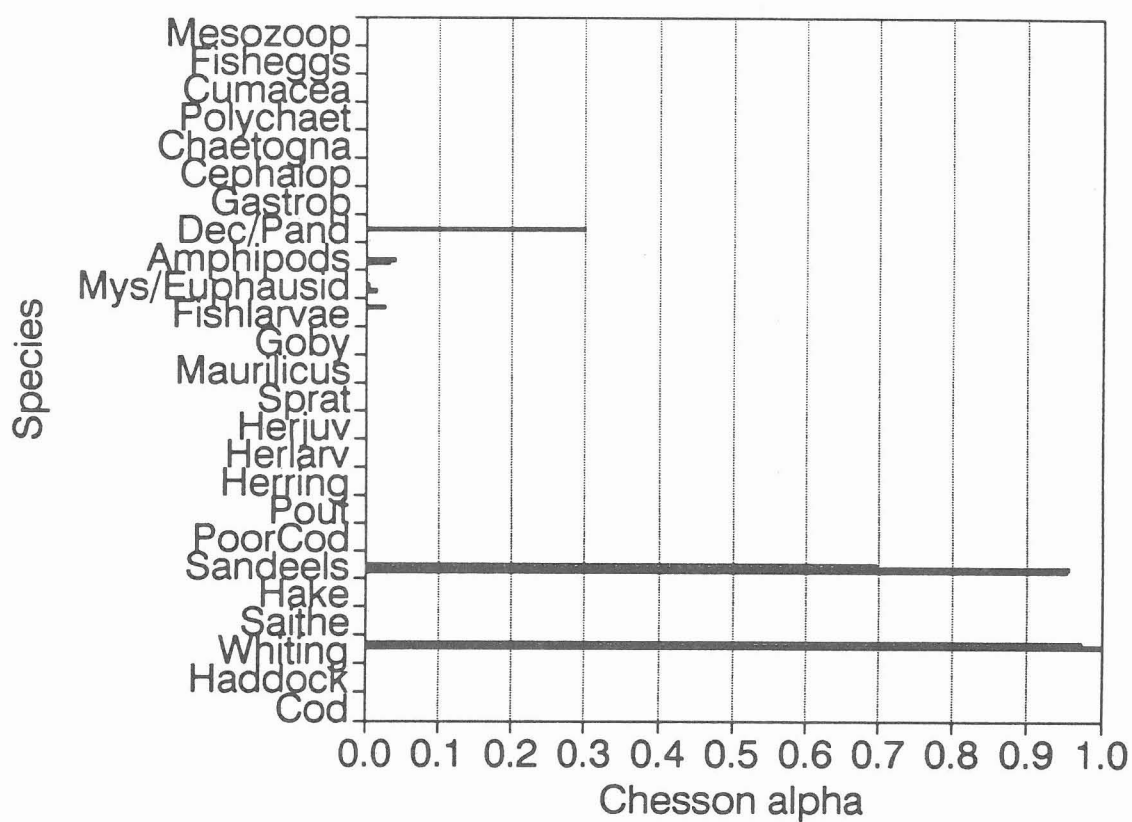


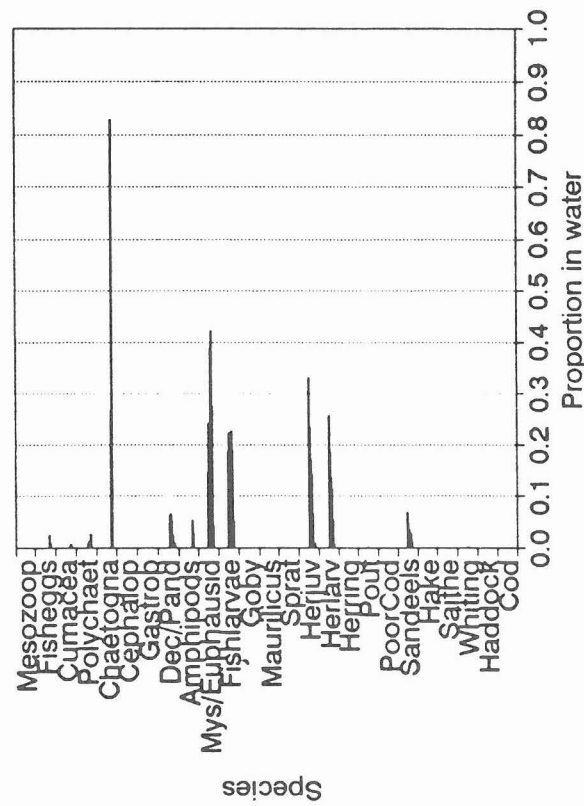
Figure G3

Figure G4

Scottish Coastal Zone



Skagerrak



Skagerrak

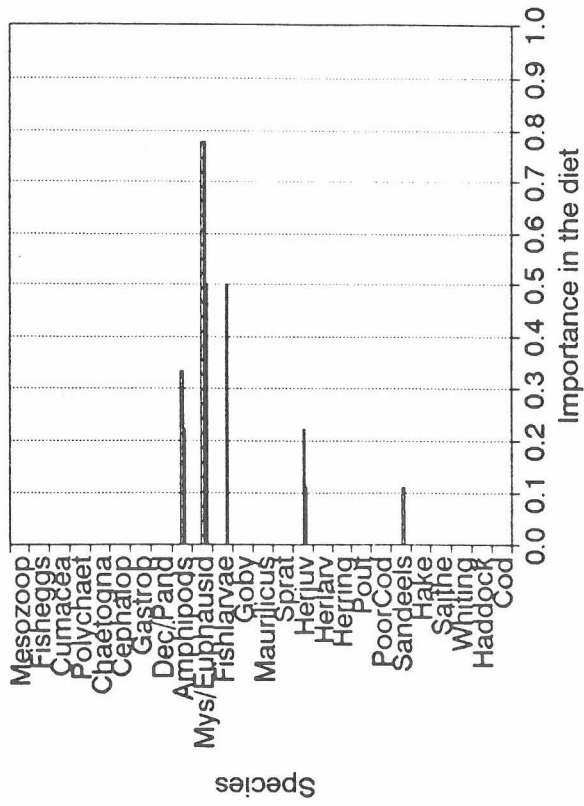
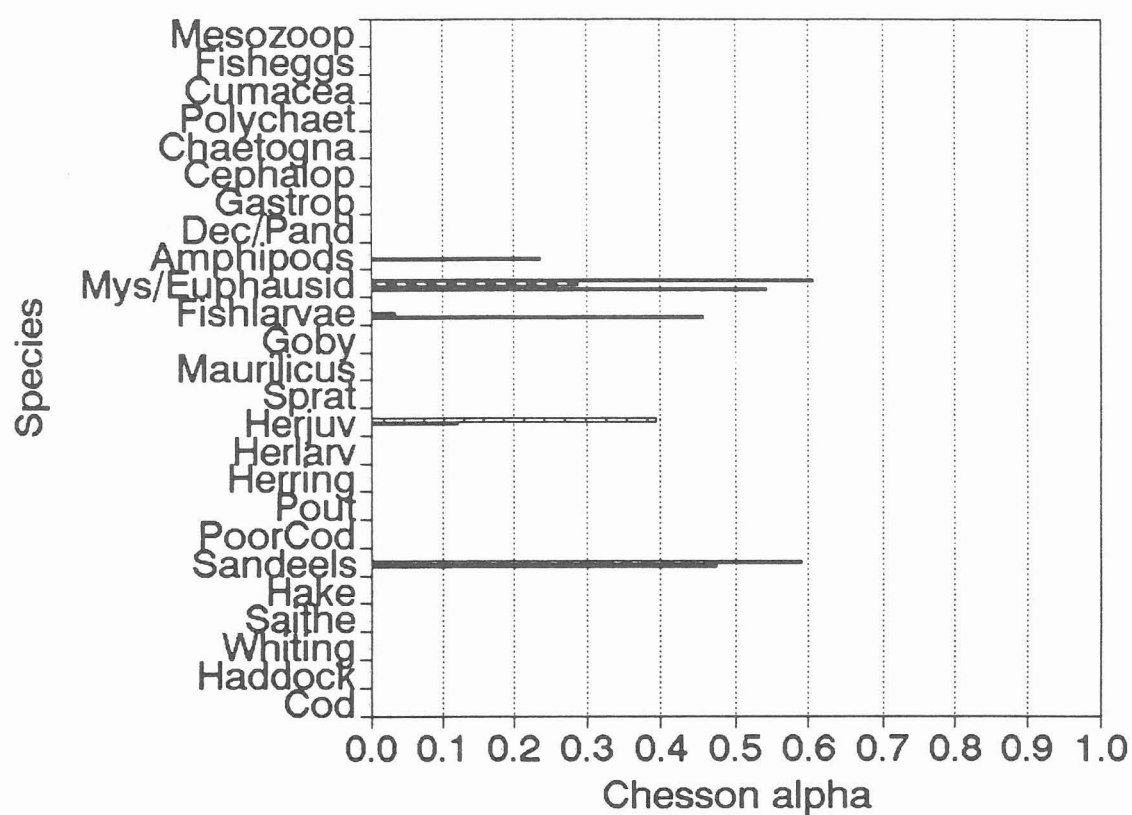


Figure G5

Figure G6

Skagerrak



Appendix H

Variability in plankton food web dynamics in the Orkney-Shetland area off northern Scotland

M Heath,
Marine Laboratory Aberdeen

The Orkney and Shetland Isles form the exposed parts of a reef projecting northwards off the north of Scotland. Tidal mixing over the reef is intense, and the water column remains vertically mixed throughout the year. However, in the deeper water on either side seasonal thermal stratification develops, so that strong tidal fronts lie across the Fair Isle Channel between Orkney and Shetland in the summer.

The Fair Isle Channel is also an area where outer shelf water enters the North Sea as a strong coastal current driven partly by latitudinal sea level gradients established by far-field wind conditions (Figure H1). The so called 'Fair Isle Current' flows through the gap between Orkney and Shetland and is delineated by salinity values in the range 34.9 - 35.1 ppt. During the summer, surface isohalines representing the track of the Fair Isle Current, lie approximately perpendicular to the isotherms marking the boundary of the tidal mixing zone (Figure H2). Thus, the stratified coastal current must destratify in the mixing zone and restratify on entering the North Sea. The effect of the system is to act as a nutrient pump, injecting new nutrients into the euphotic zone on the downstream side of the mixing zone. The system behaves like a chemostat culture, and enhanced primary production is maintained throughout the summer months, when low production is found in the surrounding surface stratified waters (Figure H3). Traverse times of the mixing zone are in the range 5-10d (35-40km), and the system thus has a spatial scale approximately equal to the grid scale of the main hydrodynamic circulation model in use in the North Sea (20km) (Backhaus, 1985).

Detailed observations in the Fair Current were carried out in June 1988. A comprehensive sampling grid of CTD, chlorophyll and nutrient observations was combined with selective measurements (10 sites) of phytoplankton and zooplankton size compositions, species composition and physiological rates (uptake, growth and excretion). The data were assembled to form carbon budgets for the pelagic ecosystem for four areas forming a transect down the axis of the Fair Isle Current. The budgets are shown diagrammatically in Figure H4, where biomass (mgC/m^2) is proportional to the area of square symbols, production ($\text{mgC}/\text{m}^2/\text{d}$) to the area of circles, and flux between trophic groups ($\text{mgC}/\text{m}^2/\text{d}$) to the area of arrow stems. Nanozooplankton refer to heterotrophic flagellates, ciliates and tintinnids; microzooplankton to mainly copepod eggs and nauplii; mesozooplankton mainly to copepods, and macroplankton to euphausiids, chaetognaths and other carnivorous predatory organisms captured by plankton nets. The data indicate dramatic and fundamental shifts in the pathway of carbon through the food web as the Current traverses the mixing zone. The main signatures are a shift of the phytoplankton population towards small cell species (microflagellates), accompanied by an increase in phytoplankton production per unit biomass. At the same time, the diet of mesozooplankton changed from being approximately 60% of algae to only 20% algae, the balance being made up by carnivorous feeding on smaller zooplankton. Zooplankton on the upstream side of the mixing zone apparently consumed all of the daily primary production, but only a small proportion was consumed on the downstream side, the remainder presumably contribution to an enhanced flux to the sediments.

The enhanced summer production in the Orkney Shetland area is believed to represent a 'hot-spot' in the northern North Sea, and to be the main contributor to the high carbon content of sediments in the Fladen deposition basin some 100km to the southeast. The area therefore probably plays an important role in the carbon dynamics of the wider northern North Sea, but is almost certainly too small to explicitly resolve in any wide area ecosystem model of the region.

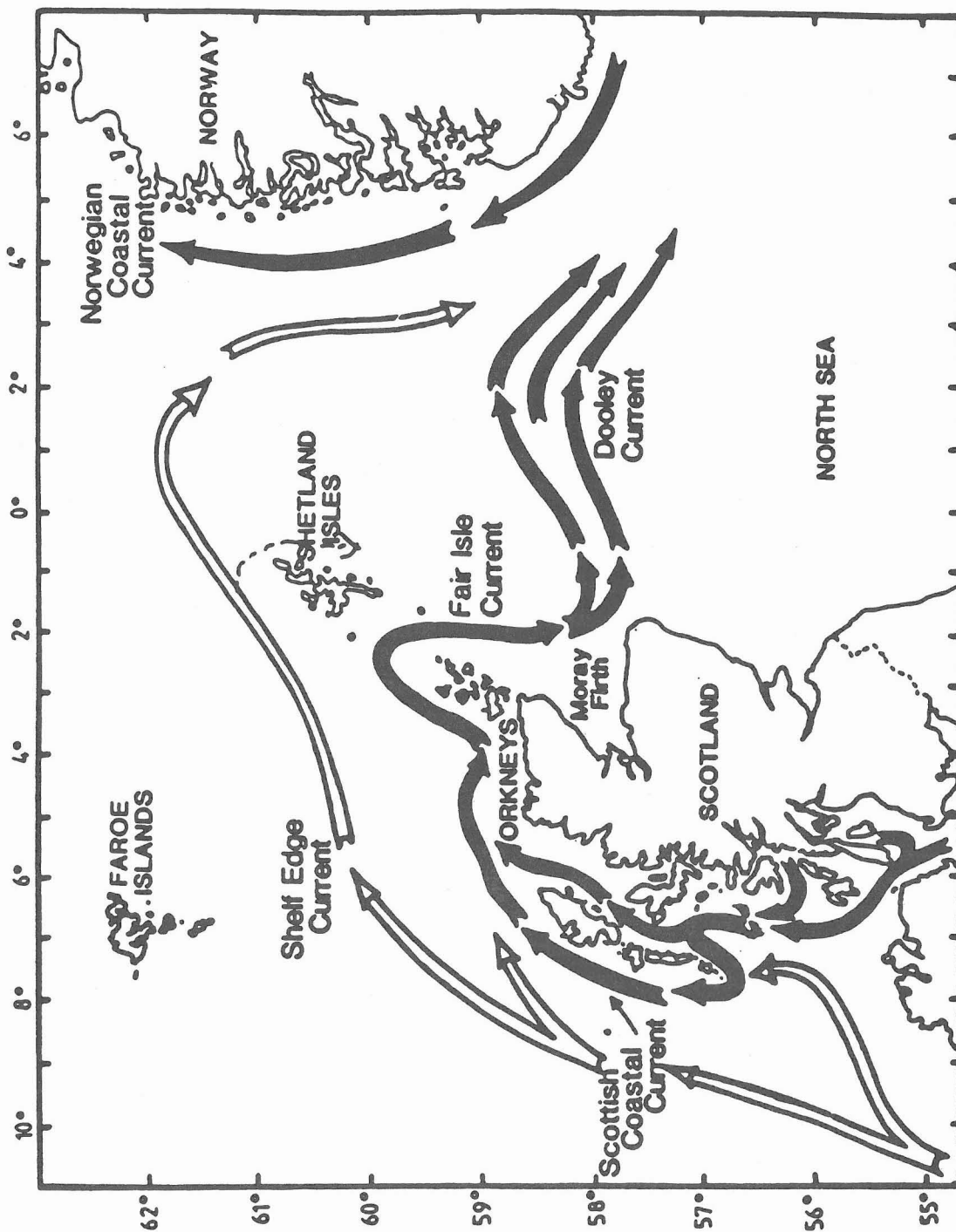


Figure H1

Figure H2

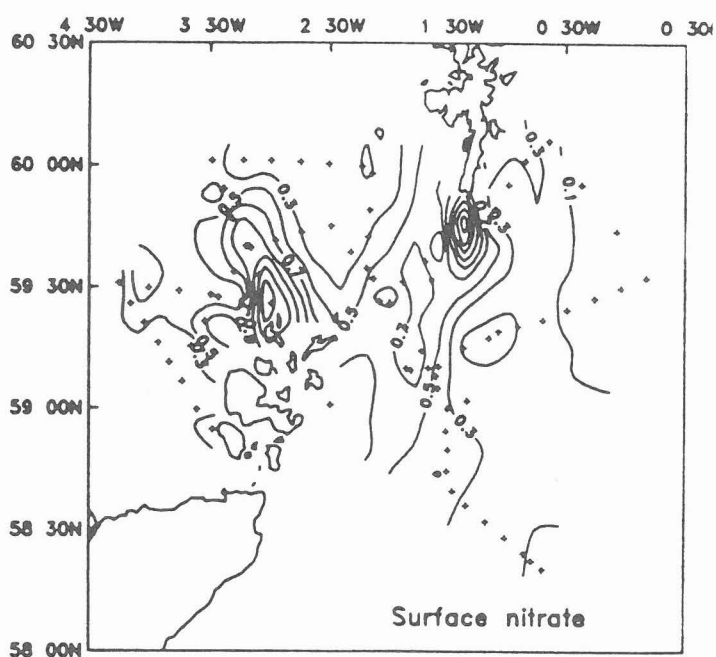
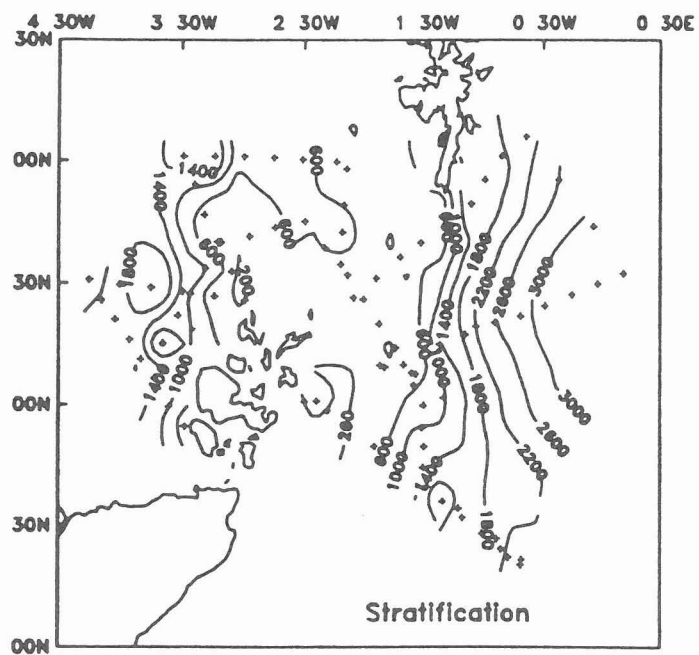
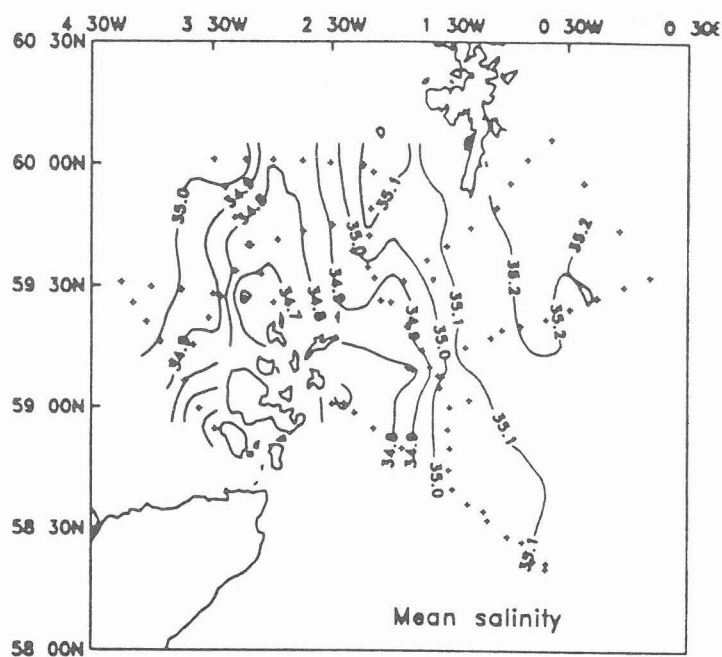
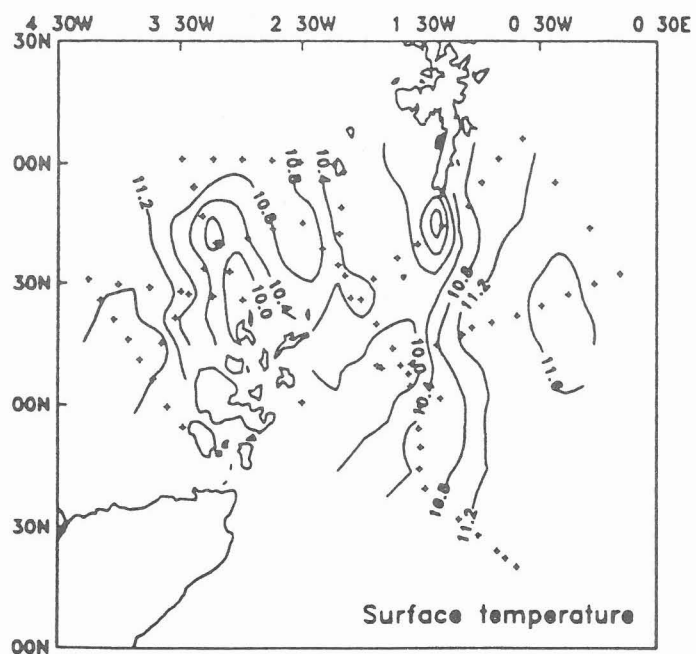


Figure H3

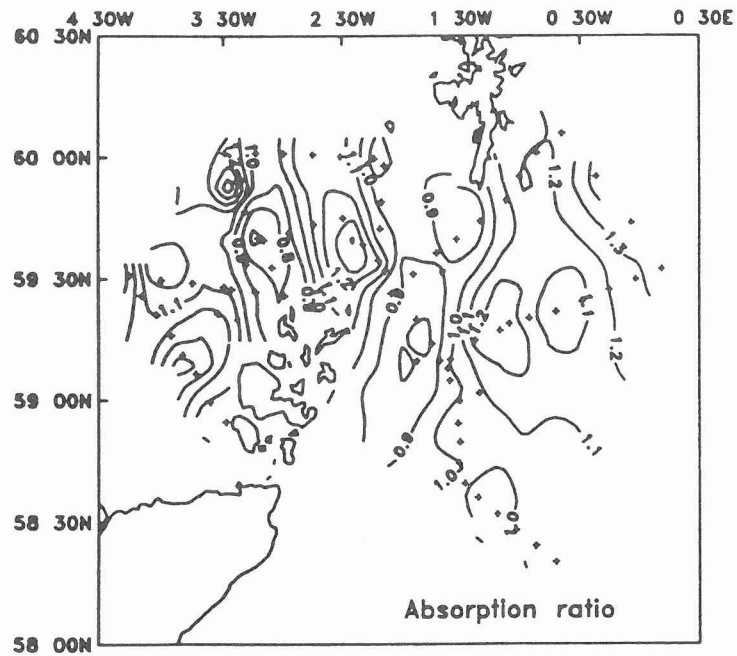
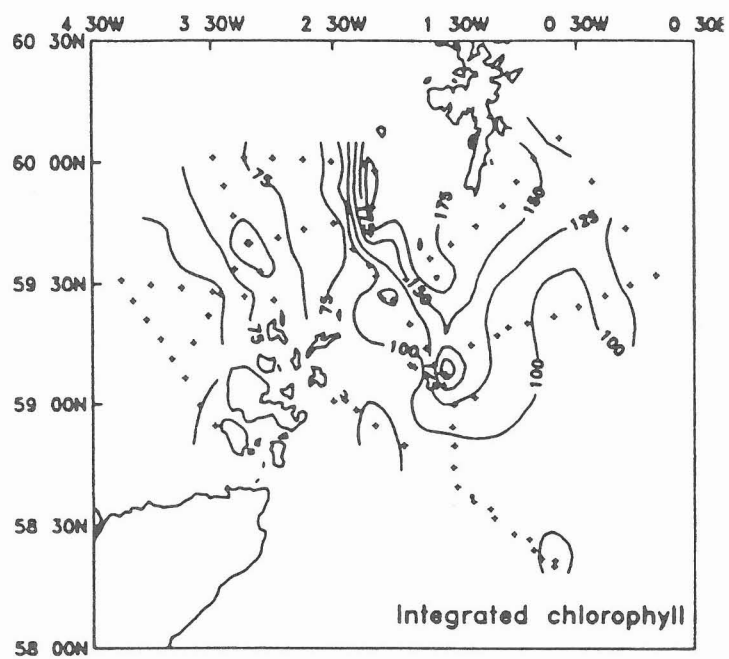
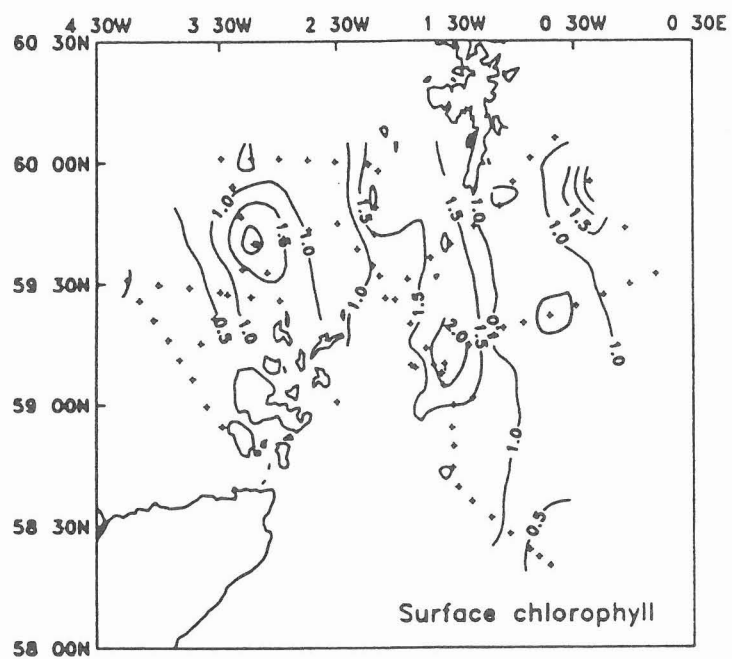
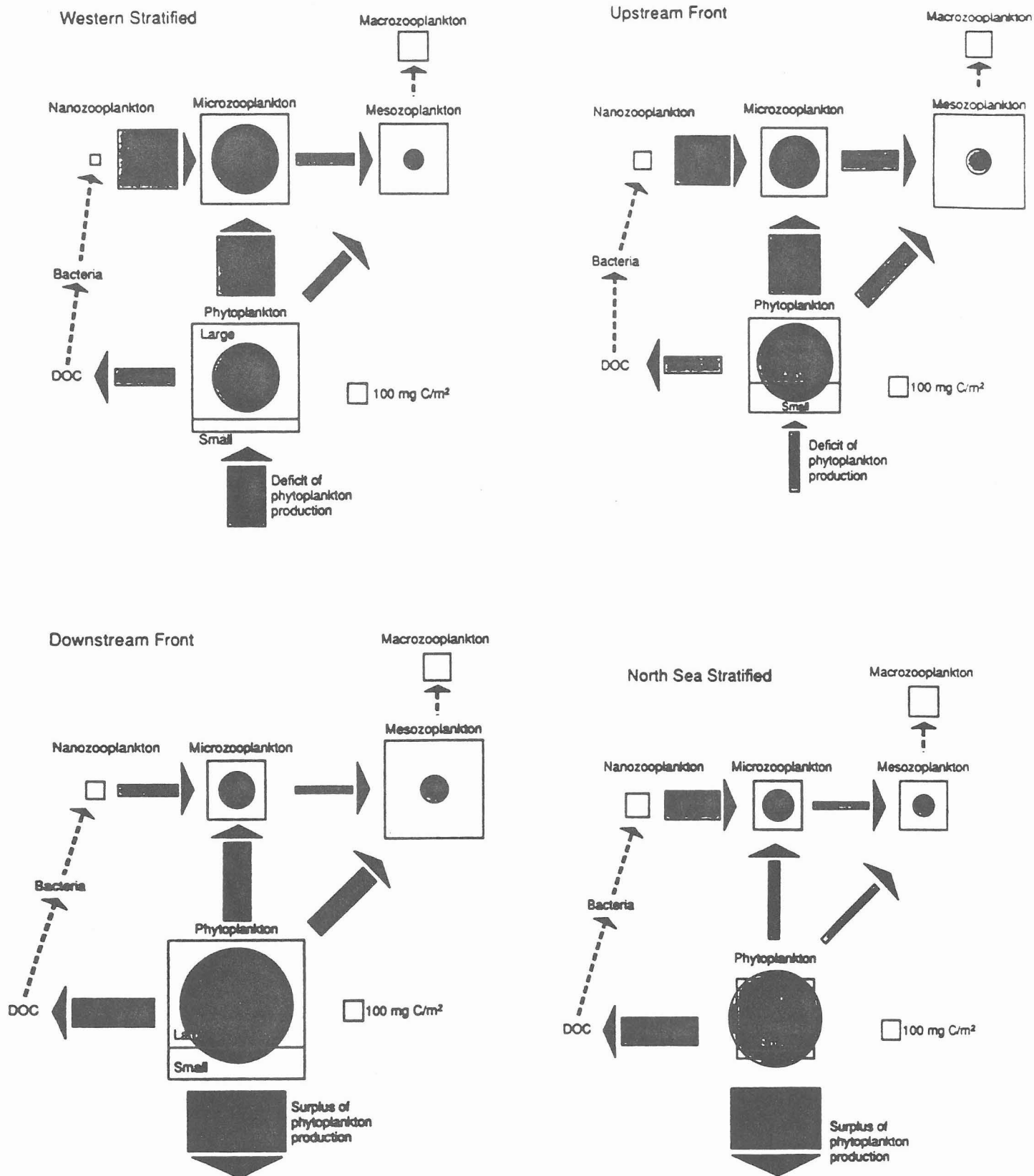


Figure H4



Appendix I

A STUDY OF THE EFFECTS OF VARIATIONS IN CIRCULATION ON THE DISTRIBUTION AND ABUNDANCE OF FISH EGGS AND LARVAE

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Temporal changes in the spatial distribution of fish eggs in Conception Bay, a system of approximately 1000 square kilometers, are being studied using a combination of ichthyoplankton surveys and observations of surface currents obtained from CODAR (Coastal Ocean Dynamics Application Radar) measurements. Resolution of the current field is fine in both space (1km) and time (1 hour averages). Hourly observations of the surface circulation field are input into an advection and diffusion model designed to track the movement of particles in the system.

Model runs are being initialized from a Laplacian interpolation of a 15 station ichthyoplankton survey. We are performing 5 day simulations which correspond to the time between surveys. The accuracy of model predictions is evaluated by contrasting the observations from a second survey with the interpolated field estimated using the simulation's output. Residuals are used to assess overall bias in model predictions as well as spatial patterns that might be indicative of model inadequacies or mortality.

Results indicate that advective losses of fish eggs at the mouth of Conception Bay are sufficient to account for almost all changes in abundance observed between surveys. There is little evidence of a significant spatial pattern in residuals when we contrast model predictions with observations. The combination of these results suggests that dynamic physical models can be useful in predicting changes in the distribution of planktonic organisms. However, experiments in which we alter the scale (in time or space) over which the average currents are calculated reveal that predictions of both changes in the abundance and in the distribution of fish eggs can be substantially influenced by the scale of measurement. As the grid becomes coarser, the overall accuracy of predictions decreases. There is evidence that small eddies, a few kilometers in diameter, can contribute significantly in determining the retention and loss of ichthyoplankton from Conception Bay. The factors that determine the appropriate scale to use in model simulation are under study.

Appendix J
Recruitment: MSVPA, Size Spectra and Size-Specific Cohort Dynamics

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MSVPA: How many juvenile fish are there in the sea. It is not surprising that the most important insight gained from MSVPA is that the rates of natural mortality are much higher than previously estimated and variable from year to year. The real problem is simply that fish stock assessment for many years has been based on an assumption of a constant and low rate of natural mortality for all age groups. There was no direct estimates of M available for the younger age groups. In lack of anything better, it is simply Beverton and Holt's (1957) estimation of $M=0.1 \text{ yr}^{-1}$ for adult plaice and $M=0.2 \text{ yr}^{-1}$ for adult haddock in the North Sea that has been adopted in the VPAs. These mortality figures refer to very old fish eg. the survival of 5 year old plaice in pre-war samples to age 13 yrs in post-war samples.

The point here is that the complex book-keeping of who eats whom in MSVPA is not necessary for showing that the traditional value of 0.2 represents a tremendous underestimate of juvenile fish mortality. What is needed is only a small but important exercise in spatial and temporal integration. The underlying reasoning has been known for many years. It does not takes place by considering the million of events underlying the realization of multidimensional, trophodynamics subgrid processes that determine the actual components of mortality at various life-history stages in the sea. It simply takes place by switching the attention from all the underlying spatial and temporal events to the average outcome of the entire process: the 2 survivors that, on average, are needed in the generation replacement.

Examples of these derived survival-considerations are given below. Although simple, the result emerging from such explanatory survival scenarios cannot be disputed: MSVPA still severely underestimates the rates of natural mortality for juvenile fish! Some of the reasons for this fact are equally clear. Stock assessment in virtual population analyses are based on knowledge of the number of live fish that are removed from the sea. At present it is estimated by MSVPA that the North Sea fishery removes ca. 2.5 mio. tonnes annually and that the same amount of small fish are taken by the five major, commercially important fish-eaters: cod, whiting, saithe, mackerel and haddock. The 2.5 mio. tonnes represents an underestimate in both cases. Considerable discards are not accounted for in the human consumption fishery and the daily rations used for the piscivorous fish in MSVPA are most likely based on very conservative estimates of food consumption. Furthermore, available stomach data etc. has not permitted to include a description of the predation losses of 0-group fish. Finally, the impact of equally important non-commercial fish-eaters such as scad, gurnard, rays, birds, seals and other mammals are not yet accounted for properly in MSVPA. This is not a criticism of the Multispecies Assessment WG. It merely illustrates that the development of MSVPA is a big and long-term task. The MSVPA-WG is very much aware of all these problems and the stomach sampling project in 1991 was also designed to provide the next important platform for improving and elaborating on the estimates of the consumption of small fish in the sea. However, it should come as no surprise if the result will be an annual removal of ca. 10 mio. tonnes small fish by all parties combined. Thus, the numbers of juvenile fish in the North Sea is

most likely at least twice as high as the present result of MSVPA indicates (based on the 5 million tonnes annual removal figure).

How to explain the one in a million survival ? The survival to maturation is in the order of $10^{-6} = \exp(-13.8)$ for most species because, on average, only two eggs of the total number of eggs produced by an adult fish survive and develop into two mature fish. The cumulative mortality through the first three to four years of life (T_m) must, then, be about 13.8, ie.

$$\int_0^{T_m} M_{\text{age}}(t) dt = -\ln(S_{\text{age}}(T_m, 0)) = 13.8; \quad S_{\text{age}}(T_m, 0) = 10^{-6} \quad (1)$$

where $S_{\text{age}}(T_m, 0)$ denotes the age-specific survivorship from age 0 to T_m , the age of (massive) maturation. As an example put $T_m = 3$ yrs. If the rate of natural mortality remains constant throughout life, then the mortality level required to explain the one in a million survival must be $M = 4.6 \text{ yr}^{-1}$ ($1.3\% \text{ d}^{-1}$) giving a mean age of 79 days and an annual survival rate of $\exp(-4.6)$ or 1%. Such a high level of natural mortality exceeds estimated total mortality (incl. fishing) for age group 2 or 3 in most cases. Consequently, M -at-age is not constant but must be much higher for juvenile and small fish than for older and bigger fish. If, for example, $M=1$ for 2-group and $M=2$ for 1-group then the cumulative mortality for 0-group fish must be 0.8 to explain average survival in the present example.

As an example of a continuously decreasing mortality, Fig. 1b depicts a situation with M inversely proportional to age ie. using $M(t)=3/t$ in Eq. (1):

$$S_{\text{age}}(t_1, t_0) = (t_1/t_0)^{-3}; \quad M_{\text{age}}(t) = 3/t \text{ yr}^{-1} \quad (2)$$

The survivorship for an increase in age by a factor of ten ($t_1=10t_0$) is simply 10^{-3} . Thus, the survivorship from the onset of feeding at age, say 2 weeks to 4.6 months (20 weeks or 0.38 yr) is 0.001 and equals the survivorship from 0.38 to 3.8 yrs of age. The model can therefore explain a survival in the order of 10^{-6} from the onset of feeding to maturation. The mortality at first feeding (2 weeks = $1/26 \text{ yr}$) in this description is 78 yr^{-1} (0.21 d^{-1}) but diminishes by one half in the course of two weeks. Perhaps such a high larval mortality may be considered sensible since we have not accounted for mortality during the egg and yolk-sac stages. However, the mortality rate is still 1 yr^{-1} at three years of age or five times the traditional value of 0.2.

Moving from age to size. It seems much more sensible to describe mortality as a function of body-size instead of age because of the underlying size-dependent mechanisms involved in spatial integrated predation processes. For this purpose, let $g(L)=dL/dt$ denote the growth rate ie. $dt = dL/g(L)$ gives the time required to grow through dL . The cumulative mortality for growing through the length interval from L_0 to L_1 is thus obtained by a simple t to L variable substitution in Eq. (1):

$$\int_{L_0}^{L_1} \frac{M_{\text{length}}(L)}{g(L)} dL = -\ln S_{\text{length}}(L_1, L_0) \quad (3)$$

If L_0 is larval length and L_1 is length at maturation then this cumulative mortality must also be required to produce 13.8 in the present example ie. to explain a length-specific survival, S_{length} of 10^{-6} . Note that it is the rate ratio of mortality to growth that determines the cumulative mortality and, hence, survival for a given growing-up interval. Thus, the effect of eg. doubling M is the same as the effect of halving the growth rate. The result in both cases is a doubling of the cumulative mortality.

As an example, we first consider the consequences of the classical Beverton and Holt (B&H, 1957) model with constant mortality and the von Bertalanffy growth rate:

$$S_{\text{length}}(L_1, L_0) = \left[\frac{L_{\infty} - L_1}{L_{\infty} - L_0} \right]^{M_{\infty}/K} ; M_{\text{length}}(L) = M_{\infty} ; g(L) = K(L_{\infty} - L) \quad (4)$$

That is, the survivorship equals the ratio of the growth rates at the end and at the beginning of the length interval to the power of M_{∞}/K . The symbol M -infinity is here introduced to replace the traditional constant $M = 0.2$ which, as noted above, refers to estimates for very old fish. The whole point is again that the traditional models (in absense of fishery) cannot explain the small survival in the sea. Using for example B&H's estimates for North Sea cod, $K = 0.2 \text{ yr}^{-1}$ ie. $M_{\infty}/K = 1$, $L_{\infty} = 126 \text{ cm}$ ($W_{\infty} = 20 \text{ kg}$) the survival to grow from $L_0 = 0$ to a certain length, L , becomes $1 - L/126$. Hence, almost 30% of cod larvae are still alive about 6 years later at length 90 cm.

Mortality inversely proportional to body-length. Refining the mortality model we may tentatively multiply M_{∞} by L_{∞}/L ie. the mortality is still M_{∞} for very old fish but increases in inverse proportion to body-length for smaller fish. Inserting this new size-specific mortality model in Eq. (3) and integrating, we obtain, maintaining the von Bertalanffy growth model:

$$S_{\text{length}}(L_1, L_0) = \left[\frac{L_{\infty}/L_1 - 1}{L_{\infty}/L_0 - 1} \right]^{M_{\infty}/K} ; M_{\text{length}} = M_{\infty} * L_{\infty} / L \quad (5)$$

That is, the survivorship now equals the ratio of the specific rates of growth to the power of M_{∞}/K . With the values for cod the mortality-at-length(cm) becomes $25.2/L \text{ yr}^{-1}$ eg. 84, 8.4 and 0.84 at lengths 3 mm, 30 mm and 30 cm, respectively. The survivorship to increase ten-fold in length from metamorphosis, say from 30 mm to 30 cm, becomes ca 8% hereby accounting for a cumulative mortality of only ca 2.5. Survival from 3 mm to 90 cm (ca 10 kg) is ca 0.001 corresponding to a cumulative mortality of ca 7. Thus, the model can at best explain only half the required cum. mortality. This merely indicates that the von Bertalanffy growth equation is not adequate for larval fish. The maximum growth rate in the model is $K * L_{\infty}$ or 0.7 mm d^{-1} for the cod and will in practice govern growth through the entire larval stage because $L \ll L_{\infty}$. A constant daily growth within 0.1 to 0.3 mm is often the result of larval investigations in the North Sea. Inserting in Eq (3), the resulting survivorship is easily obtained in the case of a constant rate of growth:

$$S_{\text{length}}(L_1, L_0) = (L_1, L_0)^{-M_{\infty}/K} ; M_{\text{length}} = M_{\infty} * L_{\infty} / L ; g(L) = K * L_{\infty} \quad (6)$$

Note again that this model virtually produces the same results as Eq (5) with the von Bertalanffy growth at small lengths ie. mathematically, neglecting the minus one's in Eq. (5) produces Eq. (6). In the cod case, $M_{\infty} / K = 1$ implying that the survivorship simply becomes L_0/L_1 ie. the (instantaneous) rate of mortality equals the specific (instantaneous) rate of growth (in length) so the total length (not mass) of all individuals in the cohort remains constant. In other words, numbers are decimated in inverse proportion to length in this special case. One in ten larvae survive increasing their length ten-fold eg. from 3 mm to 30 mm. Reducing the growth rate by a factor of four, $K_{\text{larvae}} = K/4 = 0.05 \text{ yr}^{-1}$ gives a daily growth of the right magnitude (0.17 mm) which implies that the power in the survivorship, Eq. (6), increases by a factor of four. Thus, survival, growing from 3 mm to 30 mm, is now reduced from 10^{-1} to 10^{-4} . It simply takes the larvae 4 times longer to grow through any length interval and the cumulative mortality is consequently also increased by a factor of four. The conclusion is that a simple size-specific mortality model operating on all life-history stages can explain the one in a million survival if K in the traditional growth model is reduced by a factor of 3-4 for the larval stage. Since the power in the weight-length relationship for larval fish also usually appears to be in the range of 3-4 it follows that the specific rate of growth in weight will be (3-4 times the specific rate of growth in length and hence) of the same magnitude as the rate of mortality. The larval biomass of the year-class will remain constant if the specific rates are exactly the same. Note in particular that it is the mortality-growth parameter ratio, M_{∞} / K , which determines the power in the survivorship. It is, thus, a delicate balance between high rates of growth and high rates of mortality that determines the increase of year-class biomass, in particular during the larval stage. It is for the same reason that, in principle, it is not difficult to explain the degree of variability in recruitment (resulting from VPAs) by comparatively small year-to-year variations in predation mortalities. We have actually more reason to be astounded at the stability of recruitment than at its variability.

Stock & Recruitment: A problem of spatial and temporal integration. The size-specific analysis above is still traditional in the sense that a one to one correspondance is assumed between size and age. Thus, members of a year-class are incorrectly treated as being identical. Nevertheless, the introduction of the simple size-specific mortality model completely alters our conception of the traditional, age-specific B&H and Ricker S-R curves. Fig. 2 gives an example of the effect on the S-R curves of introducing a simple type of density-dependent growth. It is clearly a consequence of the identical member-at-age assumption that the effect of food competition cannot be dealt with properly because all surviving members eat and grow in exactly the same manner. This is one of the most important draw-backs of all traditional methods used in fish stock assessment including MSVPA. We may, in particular, expect that the heterogeneous composition of a year-class of larval fish affects its dynamics. IBMs based on stochastic simulation support this statement. The ultimate and necessary model will be stochastic, not deterministic. However, as a first important refinement of the traditional discrete basis (ie. the identical member assumption), there is a need for a continuous, deterministic approach. Extremely simple considerations based on the size spectrum of all individuals in the sea may here serve as the very first step for acquiring overview at the ecosystem level and gaining insight because all levels of particle sizes are basically described within the same level of detail - see the illustration in Fig. 3.

The importance of body-size in describing ecosystem properties was recognised already in the 1920s. The size of an organism was actually considered as the single most important attribute. Fig. 3 is furthermore stimulated by the empirical evidence for the smaller plankton presented

by Sheldon in the early '70s. Each live animal or particle in the sea contributes to the spectrum. For every species one may imagine that cohorts or year-classes of animals are represented by continuous size-distributions. Integrating crosswise of species or functional categories creates the spectrum. Moving up the spectrum towards smaller particle sizes, the underlying number of species increases almost exponentially. Fish in general accounts for only a small part of the spectrum. It is within this scenario of all particle sizes in the sea that it seems promising to reconsider the S-R problem as a general question concerning the fundamental stability of marine life at all size-levels of the spectrum.

I suggested in 1988 that the solution to the S-R problem could very well be a general one of predator-prey control or, in principle, mass balance at various temporal and spatial scales. This suggestion appears to offer a new angle to the ecological controversy (which was raging in particular during the 1950-60s) concerning various conceptions of the balance of nature: The opponents of the density-dependent school expressed that single neat control mechanisms are unlikely to explain fluctuations in populations, that no female alive now, in any species or in any location, will be replaced by precisely one female alive a generation from now. The arguments were that all populations are continuously changing in abundance, that the environments of organisms are constantly changing with changes on different time scales (diurnal, seasonal, long-term) going on simultaneously etc. Both schools or arguments are substantially correct within the spectrum representation in Fig. 3. The stability of populations refer here to the balance in the predation-food-consumption process between interspecies size categories. Thus, it is advocated that the amazing degree of stability in nature is caused mainly by a temporal and spatial integrated prey-predation balance between size-structured populations crosswise of species. The degree of spatial and temporal stability which we are likely to observe depends on the position at the size spectrum. The smallest unicellular organisms with their tremendous diversity and densities and small regeneration times will show high stability in abundance at the bucket of water scale on an hourly basis. The temporal and spatial scales generating stability gradually increase moving down the spectrum. In this way the small-scale stability for small particles has a direct impact on the larger-scale stability of larger particles. At the size window in which we find fish, the basic stability of marine life shows up on the sea or supergrid scale on a long-term or decadal basis.

The basic idea is thus that the Sheldon type of stability is caused by predator-prey interactions mainly governed by size-structured processes but, clearly, other types of functional population grouping may play an important role as well. Long-term recruitment stability for a particular fish-species is in this explanation caused by density-dependent processes but the adult stock plays a minor role in determining the densities involved. The famous but unknown density-dependent mechanisms are in this suggestion presented by Fig. 3 conceiving the marine ecosystem as tending towards a steady-state.

The intraspecies recruitment variations can in this scenario be explained alone by small annual changes in the average vital rates during early life. Such changes represent the outcome of interannual variations in the physical and biological settings of larval prey and larval predator trophodynamics at subgrid scale. This is not represented by Fig. 3. The key issue is here how to integrate subgrid trophodynamic processes spatially to obtain an adequate picture of the dynamics of a cohort of larval fish developing into juvenile fish.

Size-Specific Cohort Dynamics. One way of integrating age- and size-specific cohort dynamics with the spectrum idea is shown in Fig. 4. Logarithmic weight groups give the vertical dimension (i) of the matrix whereas species and age groups determine the horizontal dimension (j). The beginning point is a simple one column matrix ie. the complete size spectrum of the pelagic ecosystem is represented by numbers or densities at size in the first column (j=1). Year-classes or entire life-histories for species groups can now be pulled out for a detailed, dynamic analysis in columns 2,3,4..., ie. numbers in the spectrum or environment in column 1 must be reduced accordingly.

Fig. 4 shows an example with three species. The last one could be cod or codfish and is represented by five age groups, ie. columns $j = 10, 11, \dots, 14$. Column 10 is 0-group fish which are transferred to column 11 on their one year birthday etc. Columns 13 and 14 combined are all the 3+ groups and represent age-mature fish. Size is also considered as a criterion for maturation. Thus, during the spawning season it is only the codfish that has grown into the hatched area (in column 13) that will spawn. Once a fish has spawned it is transferred to column 14 of spent-fish with reduced body-weight. Eggs enter simultaneously into the two hatching boxes at the top of the "species-hanger". Fishing and predation take place as size-dependent processes. Cod is believed to prefer prey of 1/100 of its own weight. This means that a cod in the tableau prefers to eat prey four size-groups or rows up the spectrum. Preference on either side of the preferred size is described by tails of a normal distribution (which due to the log-weight scale is equivalent to a log-normal preference curve). Different degrees of species-specific vulnerability to predation can also be incorporated. Competition can be taken into account by distributing the total amount of food consumed by an age-size group according to some probability distribution and derive growth accordingly etc. The model was in the old days run on a time-discrete weekly basis. 50-100 yrs runs were used for long-term recruitment studies.

By taking not 3 but ca 10 species into the system (ie. out of the environmental column, $j=1$), the model becomes equivalent to Andersen and Ursin's North Sea Model extended with the size-dimension. If the dynamics of food consumption, growth and recruitment (eggs, larvae etc.) are neglected the model becomes a sizespecific elaboration of forecast-MSVPA with "other or external food" and "predation from non-commercial species" represented by the environmental column. In the extreme that all species or functional groups were accounted for in the system, the environmental column should contain zeroes only. The size spectrum of the ecosystem is in every case and at any moment of time obtained by summing over all species/age groups ($j=1,2,3,\dots$) and in this way projecting the entire matrix crosswise of species into the first column.

Comments. The few references given below reflect that I was politely asked by the chairman to produce an appendix on some of my work with size-dependent models.

Figs 2 and 3 are from my publication in Dana, vol. 7, pp. 45-147, 1989 which also includes the examples on age-specific and size-specific survival and the general theory: see, in particular, Comment 1 on age (p. 52), Comment 4 on size (p. 55), Comment 5 on R-variations (p. 57), Comment 7 on Ricker S-R curve (p. 58), Comment 10 (p. 64) together with the final Comment (p. 71) on spectrum and allometric vital rates, and the associated Examples 1, 4, 5, 7 and 10 for details.

The biomass spectrum and its possible relation to the S-R problem was presented at the ICES Early Life History Symposium in 1988. The age- and size-specific multispecies model in Fig. 4 was presented at various symposia in USA, Canada and Europe in the mid 1970s. A simplified version is described in my book: *Aquatic ecosystems*, Univ. Wash. Press. 315 pp., 1981. However, the situation in the 1970s was not ripe for models of more complexity than the age-structured North Sea Model. Many researchers doubted that it would ever become possible to estimate the parameters involved in the North Sea Model. The model was reduced to its bare bones to create the operational MSVPA and the stomach programme began. Now, 20 years later, as the data are becoming available, the development of MSVPA is beginning to move in the direction of the old North Sea Model principle of maintaining mass balance in the sea eg. including also the non-commercial fish-eaters and the other side of predation, the dynamic of food-consumption and growth in MSVPA. The next step, I'm convinced, will move the focus towards the dynamics of growth and mortality of the very small fish and other functional groups in the same size-range. It is difficult to see how one can escape the importance of body-size in the models at this stage in year 2000.

I believe that the apparent slow rate of development is due to underestimates of the problems (and, hence, money) involved in understanding the dynamics of the spectrum of particles in the sea (inner space), lack of an effective interdisciplinary dialogue in developing quantitative building-stones and, perhaps, first of all, the distinction between visible and non-visible particles and mechanisms. The effect of fishing, for example, has been much more visible than the much greater effect of predation. The stomach programmes etc. are now making predation visible ie. that mechanism can be included in the virtual analyses. The Coulter counter made some of the smaller planktons visible for Sheldon. Other small particles are not even visible through the light microscope or eg. the Coulter counter etc. Millions of dollars are going to be spent on data collection including, at present, the unattractive job of working up tonnes of half-digested stomach material. Yet, comparatively little effort goes into the development of the necessary theories. The area of temporal and spatial integration is the most important one and the present S.G. initiative, laying the general ground, should be followed up by a series of very specific, case-oriented activities.

FIGURE CAPTIONS

Fig. 1. Mortalities required to explain the one in a million survival, ie. a cumulative mortality of 13.8 until maturation. a: Even rather high M_s for 1+ groups imply that the cumulative mortality for the 0-group must exceed 10! b: $M=3/t$ can explain the average survival. c: Constant growth rate, $g = K * L_{\infty}$ ($K=0.05 \text{ yr}^{-1}$ and $L_{\infty}=126 \text{ cm}$ for cod) and $M = M_{\infty} * L_{\infty} / L$ ($M_{\infty} = 0.2 \text{ yr}^{-1}$) results in a cumulative mortality of 9.2 in the larval stages (3 mm to 30 mm). d: Using von Bertalanffy's growth model with a four times higher K -value for the juvenile and adult stages explains a cumulative mortality of 4.6 in growing from 3 cm to 90 cm. Note that the M/g -curve attains a pronounced flat minimum (of $4M_{\infty} / L_{\infty} / K = 0.03175 \text{ cm}^{-1}$) at length $L_{\infty} / 2 = 63 \text{ cm}$. M/g reaches 0.1 at length 115 cm and, increases to 1 at length 125 cm before it goes on to infinity.

Fig. 2. Recruitment curves when the initial mortality rate is 7% per day and thereafter decreases in inverse ratio to the cubic root of weight, ie. to length. The rate of growth in weight is inversely proportional to the initial number (N_0) but increases in direct proportion to the $2/3$ -power of weight ie. a constant rate of growth in length. a: The shape of the age-specific recruitment curve changes with increasing age of recruitment from case 1 to 4. Recruitment after 40 days (case 1) bears an increasing relationship to N_0 . Recruitment to age ca 2 months (case 2) resembles the B&H-type of curve. After 3 months, the first part of the recruitment curve is shaped like the Ricker curve (case 3). Asymptotes are shown by dotted lines. Recruitment to age one year (case 4) looks like a Ricker curve. The same four recruitment curves are drawn in b: The Ricker recruitment curve (heavy outlined) to gain a factor of 200 in weight. The effect of density-dependent growth is here the same as the effect of density-dependent mortality (ie. the traditional S-R consideration) because it is mortality divided by growth that determines survival in size-specific theory. All the size-specific recruitment curves in the present example will be Ricker curves.

Fig. 3. The theoretical number spectrum of the pelagic ecosystem, see Beyer (1989) p. 71 and p. 136 for details.

Fig. 4. Group tableau of an age- and size-specific multispecies model. Index i denotes log-weight classes while index j specifies age-groups for selected species or functional groups. The first column thus represents the environmental number spectrum. In this example, the remaining 13 columns are used to describe age- group dynamics of three selected species; see text for details.

Figure J1

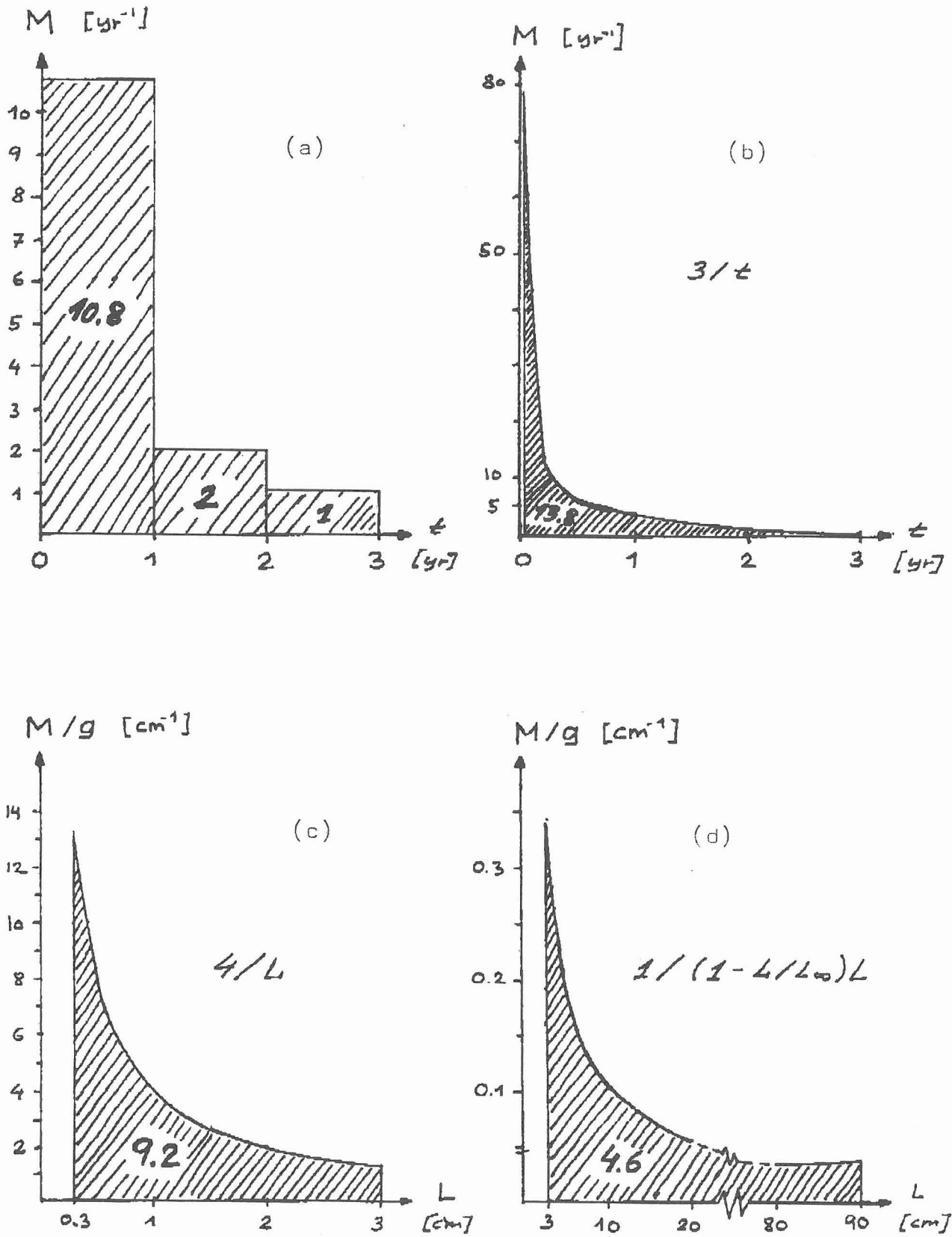


Figure J2

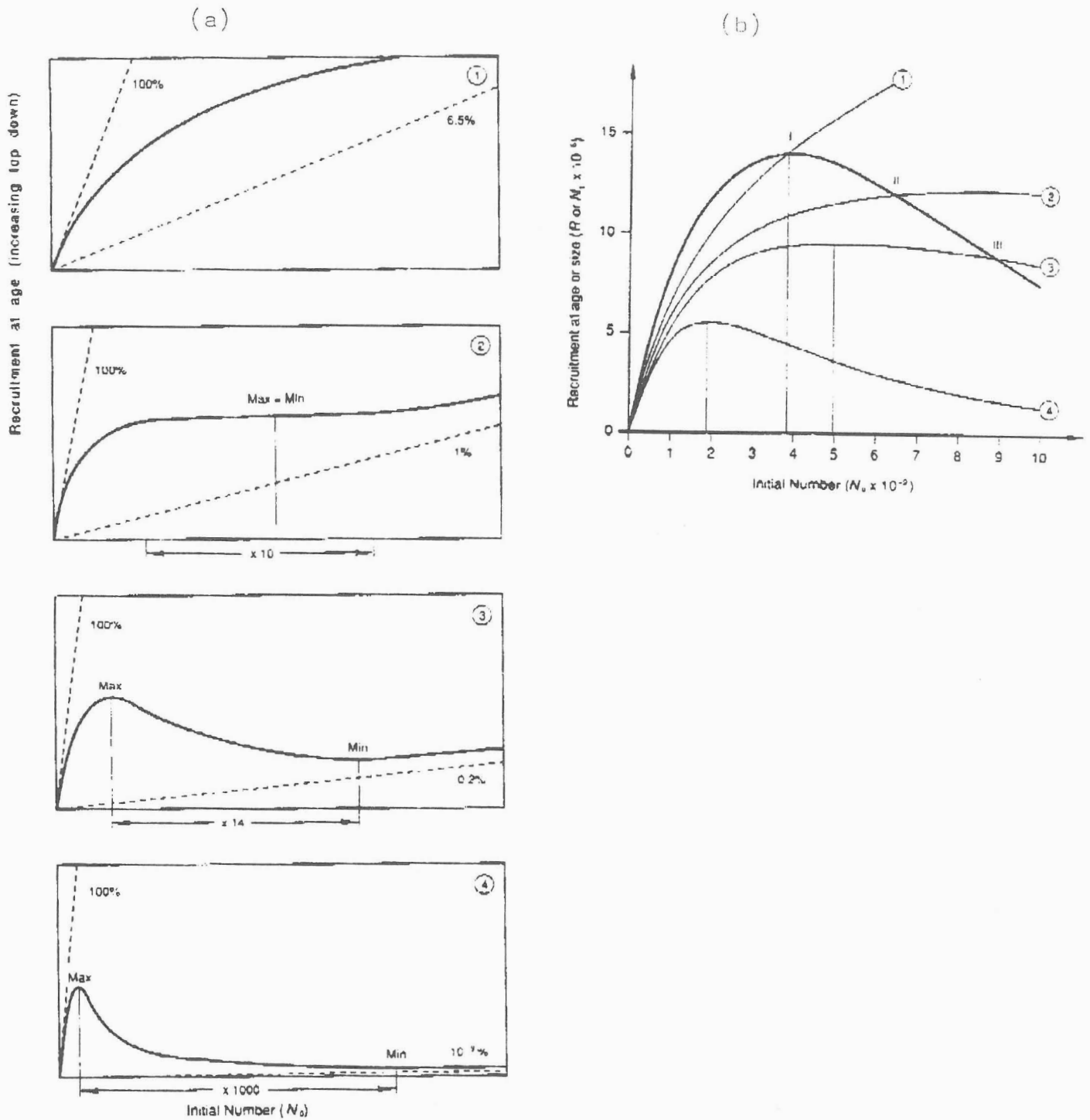


Figure J3

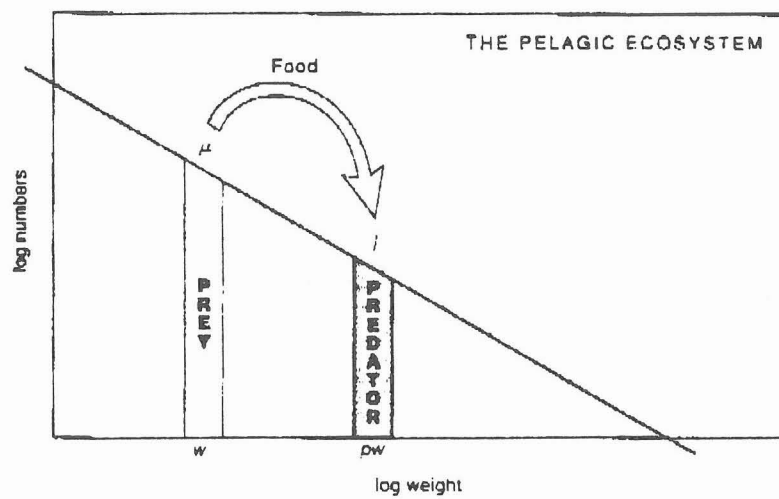


Figure J4

w gram	i	1	2	3	4	5	6	7	8	9	10	11	12	13	14
10^{-8}	1														
$3 \cdot 10^{-8}$	2														
10^{-7}	3														
$3 \cdot 10^{-7}$	4														
10^{-6}	5														
$3 \cdot 10^{-6}$	6														
10^{-5}	7														
$3 \cdot 10^{-5}$	8														
10^{-4}	9														
$3 \cdot 10^{-4}$	10														
10^{-3}	11														
$3 \cdot 10^{-3}$	12														
10^{-2}	13														
$3 \cdot 10^{-2}$	14														
10^{-1}	15														
$3 \cdot 10^{-1}$	16														
1	17														
3	18														
10	19														
30	20														
10^2	21														
$3 \cdot 10^2$	22														
10^3	23														
$3 \cdot 10^3$	24														
10^4	25														
$3 \cdot 10^4$	26														
10^5	27														

Appendix K

Spatial variation, description and interpolation using the variogram

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There are a number of ways of describing spatial variation from data, geostatistics provides one way of describing the spatial variability using a variogram. This provides, both a description of spatial variability, an interpolation method determined from the data and an estimate of variance at all points on the surface. All this information is useful when trying to understand variation of a phenomena in space.

Driving data for an ecological model may be required at a different space scale than that which has been used for data collection. It may be necessary to assign values to grid points for which there is no data by interpolation. Alternatively it may be necessary to change the volume or area over which the data is averaged to match the model. In both these cases correct interpretation of sampling error and spatial autocorrelation will provide more accurate spatial representation of the data. Ignoring the information on spatial variability makes simple but possibly unwarranted assumptions. For example raising data by a stepwise surface approximation or using linear interpolation are spatial models, but models without any justification. It should be remembered that while estimates of total populations within an area may not be affected much by taking into account the spatial variability the individual values used as driving data may depend considerably on the method chosen for interpolation.

The variogram is defined as:

$$\gamma(d) \equiv \frac{1}{2n_d} \sum_i (X_i - X_{i+d})^2$$

Where x_i is the value of the variable at location i

X_{i+d} is the value of the variable distance d from location i

n_d is the number of point pairs with spacing d

This function can describe in statistical terms sampling error at a point, (the nugget), the extent of local positive autocorrelation, patch size and patch spacing the presence of trend or non-stationarity. Figure K1 illustrates the general properties of the variogram. The experimental variogram which is calculated from data values from known spatial locations, can be used to define an algebraic function using fitting procedures.

In order to carry out interpolation correctly the detail of the variogram function can be important. Figure K2 shows a simulated linear process with statistical properties similar to those of a herring population in the North Sea both the underlying surface and 40 samples taken using a systematic sampling strategy are shown in the figure. The surface values represent the transect sums from parallel transects constructed across an area. Figure K3 shows the cloud of point pair estimates of variance (780 values) from these 40 samples. The experimental variogram derived from distance aggregated means of the point pair estimates and the underlying function measured over the whole surface are shown as continuous lines. There is variability at a point in space or in the transect estimate illustrated by an intercept on

the y axis. In addition there is some short range positive autocorrelation and the variogram reaches a plateau region extending to a distance of about 250, this is the result of the major patch covering a similar distance (see Figure K2). The smaller scale undulations are the result of smaller patches within the overall structure. For comparison both spherical and exponential variogram models, including nugget, have been fitted by least squares.

The fine detail of the variogram function near the origin may make significant differences to the interpolation process. Figure 3 illustrates the differences between the underlying process, the experimental variogram and the fitted variogram models. This disparity results from insufficient samples. It would be helpful if more detail was available on both the size of the nugget effect (the y intercept) and the slope near the origin. Simulations indicate that the fitted models depend a great deal on the particular data sample that have been acquired during the survey. Therefore additional sample information may be helpful, particularly at short distance.

If the object is to obtain good short scale interpolation, often the case for driving data or validation data, there are implications for data collection. It may be that under some circumstances additional samples can be obtained at small cost. There are a number of possibilities:

1. Duplicate sampling at stations. If simultaneous or sequential deployment of samplers can be carried out, at small additional cost at each station, considerable information on the nugget effect may be available.
2. Additional small scale sampling. Redeployment of some data collection effort for close distance sampling (sub data grid) may provide some additional information. However, the region or regions selected for close sampling must be typical of the whole.
3. Slightly Random Sampling. Systematic sampling provides the best estimate of a data field with local positive correlation. A spatial sampling strategy with systematic strata to give two random samples per strata may be one method of obtaining more information at close distance at the expense of locating stations on the regular grid.

The success of these different strategies should be compared before altering existing sampling procedures.

Good interpolation is likely to be an important factor in obtaining good driving data and geostatistics is ideally suited to this task.

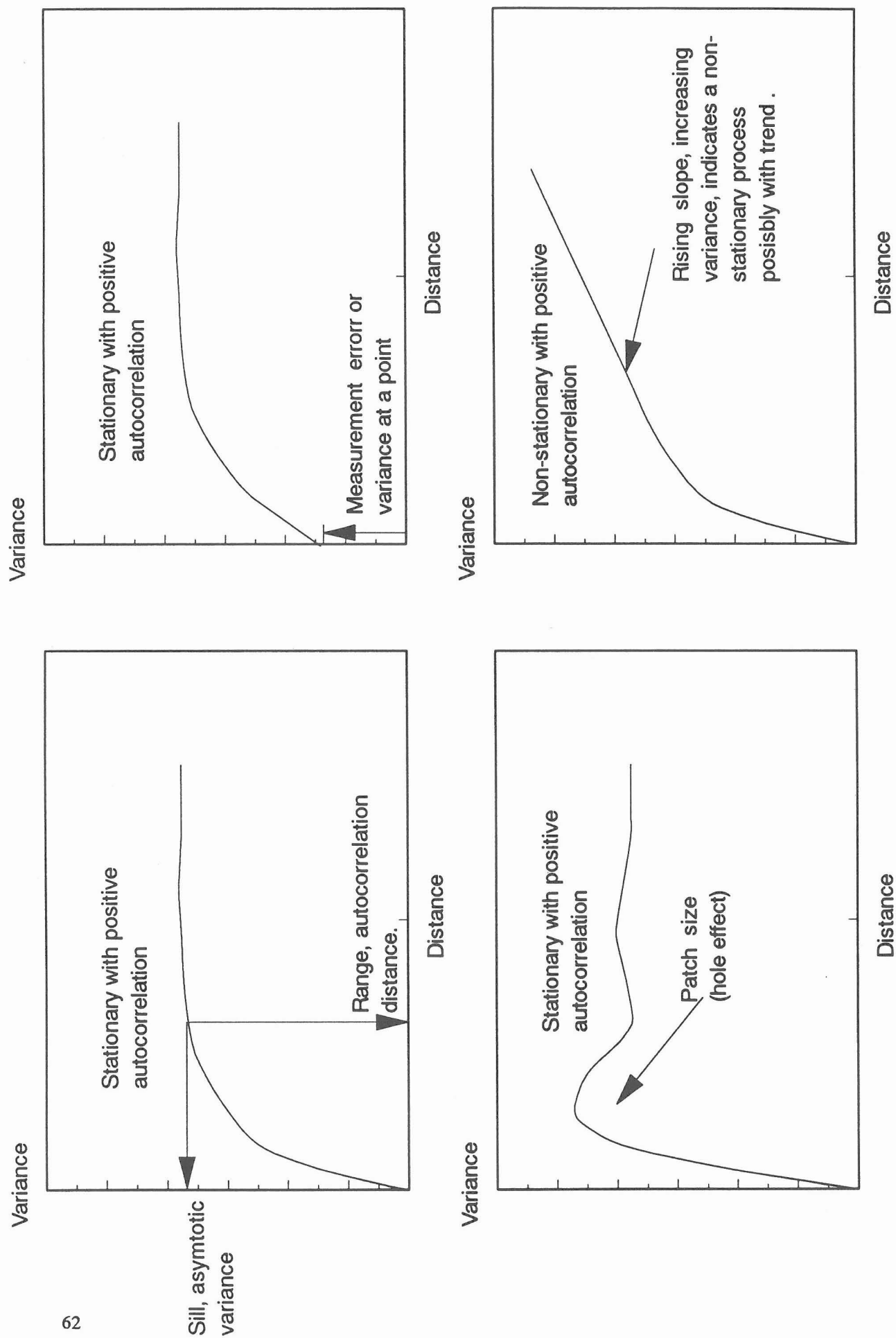


Figure 1. The main features of the variogram

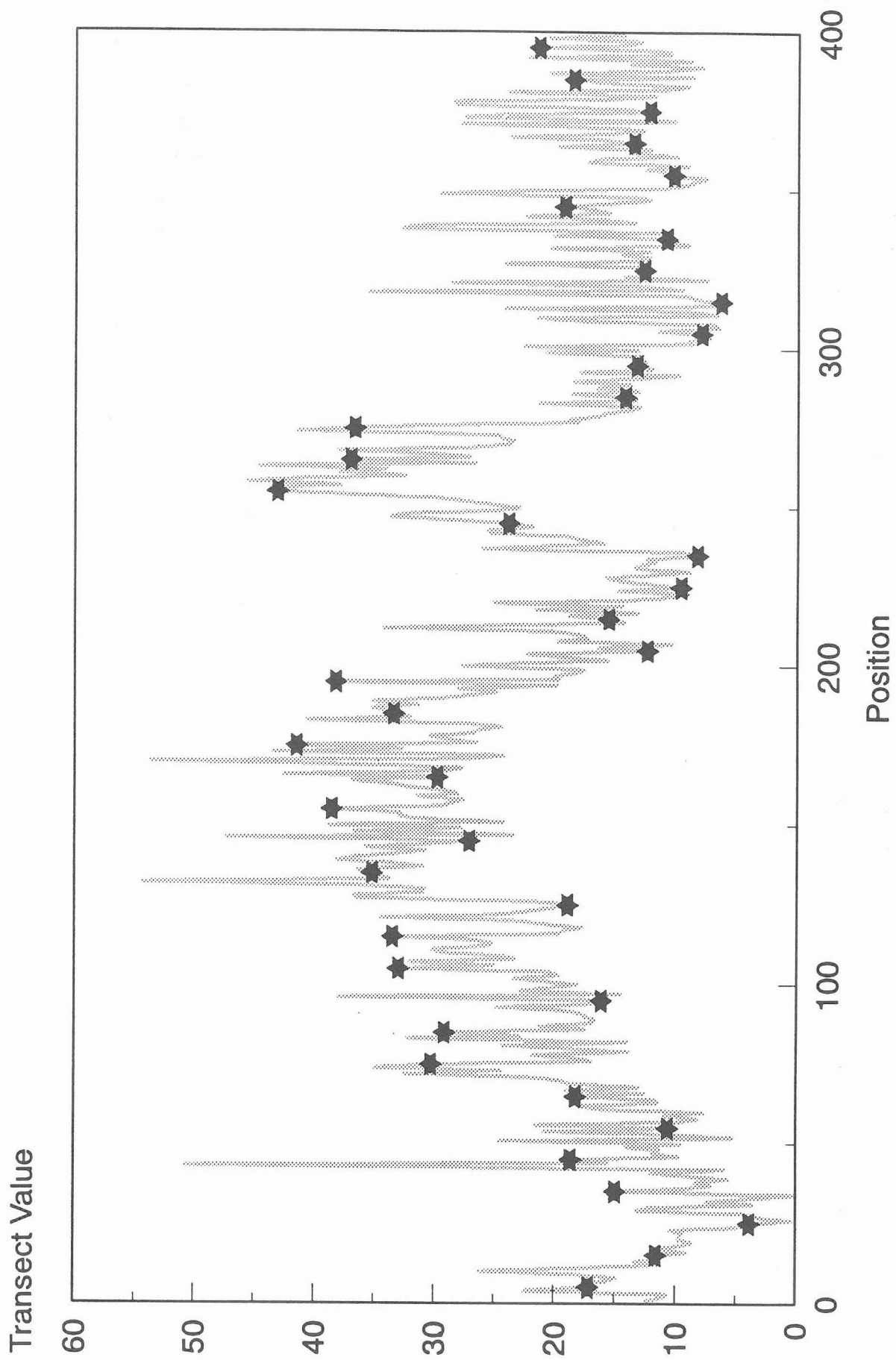


Figure 2. A simulated surface with statistical properties similar to North Sea herring and sample values for obtained using a systematic sampling strategy

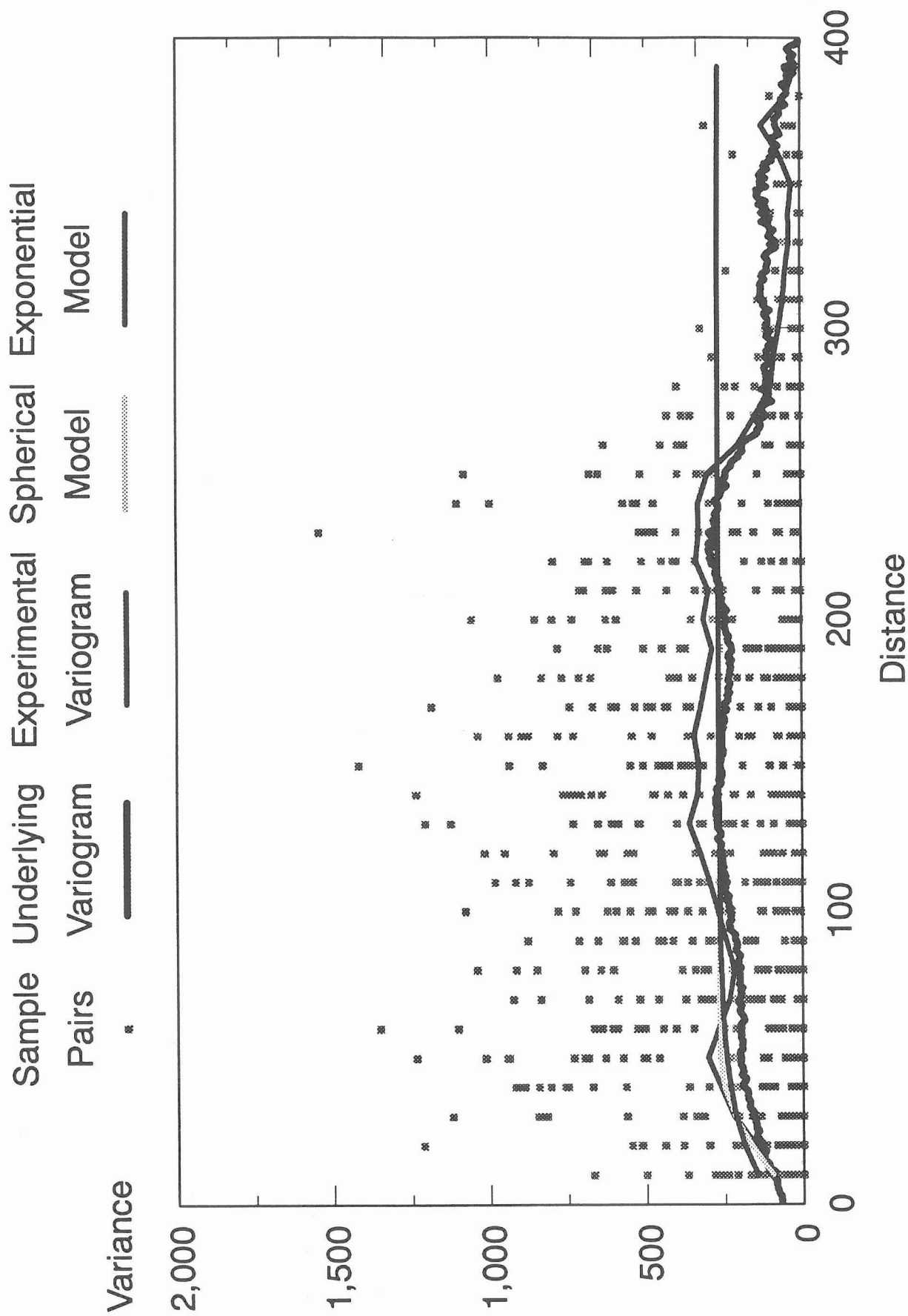


Figure 3. The experimental variogram compared with variance values computed from sample pairs, the variogram of the underlying surface and models fitted by least squares.

APPENDIX M

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Appendix N

Influence of the internal structure of a population in relation to the environmental variability on the pattern of abundance fluctuations

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Global annual abundance estimations per age group are available for the most part of the exploited fish stocks. Practical reasons lead us to consider an internal homogeneity of the population and to estimate global abundance indices. But it is well admitted that the internal structure (patchiness, degree of isolation of local patches) determines strongly the variability level and the pattern of temporal fluctuations of the population considered as a whole. Following the "spreading of risk" concept, the degree of patchiness in relation to the environmental heterogeneity, the immigration and emigration patterns, the individual behaviour and dispersion rates affect the temporal evolution of the "composite" population abundance.

Studies on the recruitment of the Bay of Biscay sole (*Solea solea* L.) revealed some interesting elements concerning the organisation of the population. Figure N1 shows the seasonal evolution of the spawning period in different areas of the bay. A shift of about two months appears between the Southern and the Northern part. Sea temperature alone is not sufficient to explain these differences. The hydrology of these three areas is strongly influenced by different environmental features. The oceanic inflow over the narrow continental shelf of the Southern part of the bay affects the hydrological conditions during winter and early spring. In the Northern part important river plumes (Loire, Gironde river) affect the hydrology over the wider continental shelf. Thus reproduction and early life stages survival are submitted to regional environmental structures with different characteristics.

Relatively important diffusion processes were revealed by the study of the pelagic stages transport towards the coastal nurseries (fig. 2). The dispersion of the spawning products over the continental shelf smooths local anomalies to some extent. In addition the distribution of 0, 1 and 2-group juveniles is principally marked by high concentrations in the coastal nurseries (estuaries and protected bays). At the end of the juvenile stage, in late autumn, they start their pre-spawning emigration towards deeper and more stable waters. This phase is also characterized by an important dispersion of the individuals all over the shelf (fig.3). This diffusion process compensates local anomalies in growth and mortality occurred in the highly variable environment of the nursery grounds.

These elements suggest that diffusive processes may increase the stability of this "composite" population. In fact, if the regional (three areas of the bay) or local (isolated nurseries) environmental dynamics are not very similar the risk of wide fluctuations is spread unequally over the population components. The probability of exceptional year classes (good or bad) decreases. In addition diffusion mechanisms are in general robust. The explanation of abnormally high or low year classes may be very difficult if the environmental heterogeneity is neglected and an average value of the population strength index is considered. The probability of occurrence of perturbations large enough in space and time to affect the entire population

of the pre-recruitment stages is very low. But exceptional years may result from spatial and temporal coincidences at smaller scales. Therefore it will be interesting to evaluate the probability of a succession of local anomalies coinciding with peak densities of the local components of the population.

The internal organisation of a population must be considered as a crucial parameter examined in parallel with the environmental heterogeneity. The study of processes characterising the population (ontogenic migrations, individual movements, seasonal evolution), with a special emphasis to diffusion mechanisms, is determinant for the analysis of the variability level and the pattern of abundance fluctuations of the entire population.

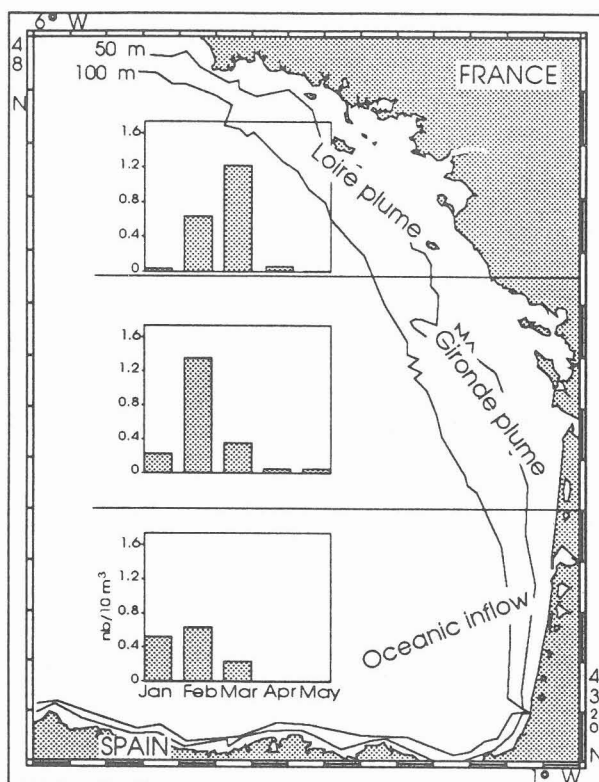


fig. 1

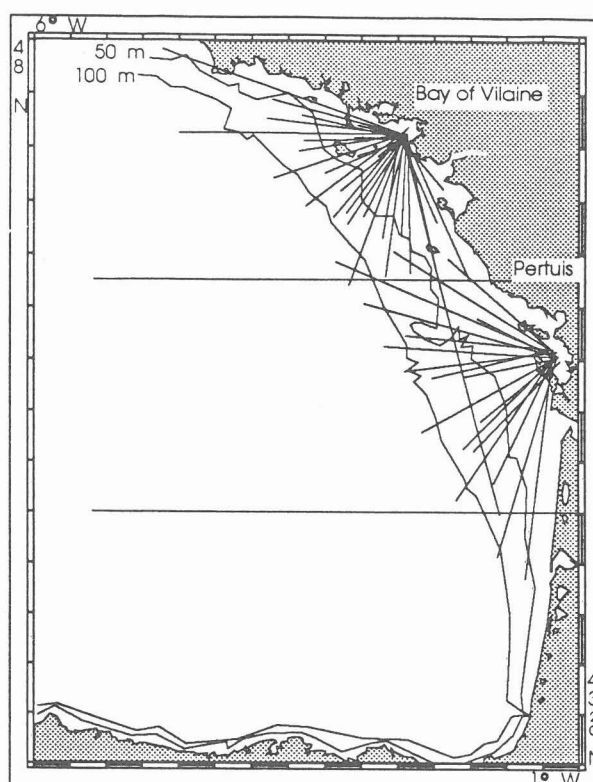


fig. 3

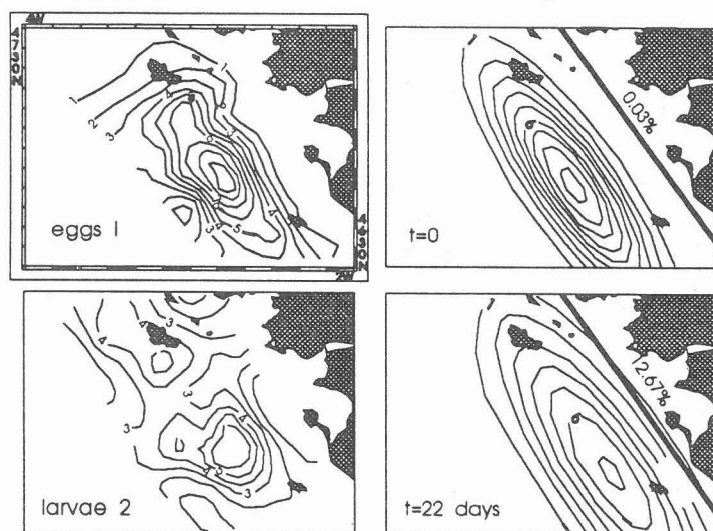


fig. 2

Fig. 1. Time related changes of Dover sole (*Solea solea* L.) egg production in 1982 for three areas of the Bay of Biscay. The main environmental features affecting hydrology in these regions are also presented.

Fig. 2. (left) Mean spatial distribution of two pelagic stages of Dover sole obtained from 13 cruises realized between 1986 and 1989 in the main egg production area in front of the Loire estuary. Numbers indicate relative abundance. (right) A simple model describing the temporal changes of the spatial distribution of the pelagic stages. The initial conditions ($t=0$) corresponding to the eggs I distribution are based on a two dimensional normal distribution. The mean (advection) and variance (diffusion index) of this distribution after 22 days (mean age of stage 2 larvae) were obtained by a 9 Argos drifting buoys tracking experiment realized in the centre of the spawning area in 1987. Thick lines correspond to the entrance of the coastal zone and the numbers behind present the fraction of the specific stage population reaching this limit.

Fig. 3. An illustration of the summarized results of the 1981 and 1992 tagging experiments. Lines link the tagging and recapture positions. Tagging operations were carried out in the Bay of Vilaine and the nursery ground of Pertuis in autumn, in order to follow the offshore prespawning migration of the 2 and 3-group individuals. The presented results is a synthesis of the main characteristics of migration patterns obtained between autumn and the following spring.

