Changes in North Sea gadoid stocks

John R. G. Hislop

Abundance and biomass of the major gadoid species in the North Sea have undergone large changes in the present century. During the gadoid outburst of the 1960s and 1970s, cod, haddock, whiting, and Norway pout produced some of the largest (as well as some of the smallest) year classes on record. Food requirements of the enhanced populations may have been some three to four times as large as current and previous levels. Although growth rates of cod did not change, there is evidence that food for juvenile haddock, and possibly whiting, was in short supply during the periods of maximum population density. The environmental factors that led to this increase in reproductive success have not been identified. Indices of recruitment for the whole North Sea, as provided by VPA, represent the pooled contributions of separate spawning units and may not be the most appropriate data to use when modelling the relationship between stock, recruitment, and environmental variables. Analysis of historical data indicates that recent levels of spawning-stock biomass of cod and haddock are close to their historic minima and fishing mortality rates are at (cod) or near (haddock) an historic maximum. Measures to reduce fishing mortality and improve exploitation patterns should be given the highest priority.

J. Hislop: SOAEFD Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 8DB, Scotland.

Introduction

This brief review is divided into three parts. The first section describes major changes in North Sea gadoid stocks, with emphasis on changes during the last 35 years. The second section considers a number of factors that may have been responsible for the gadoid outburst, and the final section attempts to put recent events into an historical perspective.

1. The changes

Indirect evidence that the abundance of a number of gadoid species in the North Sea may have undergone large changes is provided by the commercial fishery statistics collected by ICES (Figs 1 and 2). For the first 60 years of the present century the combined annual landings of cod, haddock, whiting, and saithe from the North Sea were in the range 200–300 thousand tonnes (Fig. 1). Landings increased very rapidly during the mid-1960s and remained at a high level (600–1200 thousand tonnes) for approximately two decades. They began to decline in the mid-1980s, and by the early 1990s were only approximately 50% higher than in the late

1940s and throughout the 1950s. Not all demersal fisheries behaved in this way. Landings of the two most important commercially exploited flatfish species (plaice and sole) increased slowly but steadily, and by the late 1980s had risen to double their post-war weight (Fig. 2).

Landings statistics do not necessarily give a true picture of changes in the abundance of the species because they are also influenced by factors such as changes in consumer demand, fluctuations in fishing effort, the implementation of management measures (e.g. TACs, fishery closures), and the circumvention of these (e.g. non-reporting, misreporting). However, fisheries-independent research vessel survey data indicate that there have been real, and very substantial, fluctuations in the abundance of cod (Daan, 1978; Daan *et al.*, 1994), haddock and whiting (Jones and Hislop, 1978; Sahrhage and Wagner, 1978), and Norway pout (Richards *et al.*, 1978).

The large and sudden increase in the abundance of several gadoid species at the beginning of the 1960s is well documented (Cushing, 1980, 1982, 1984). Indeed, the "gadoid outburst" was already slightly past its peak at the time of the previous Århus Symposium (Hempel,
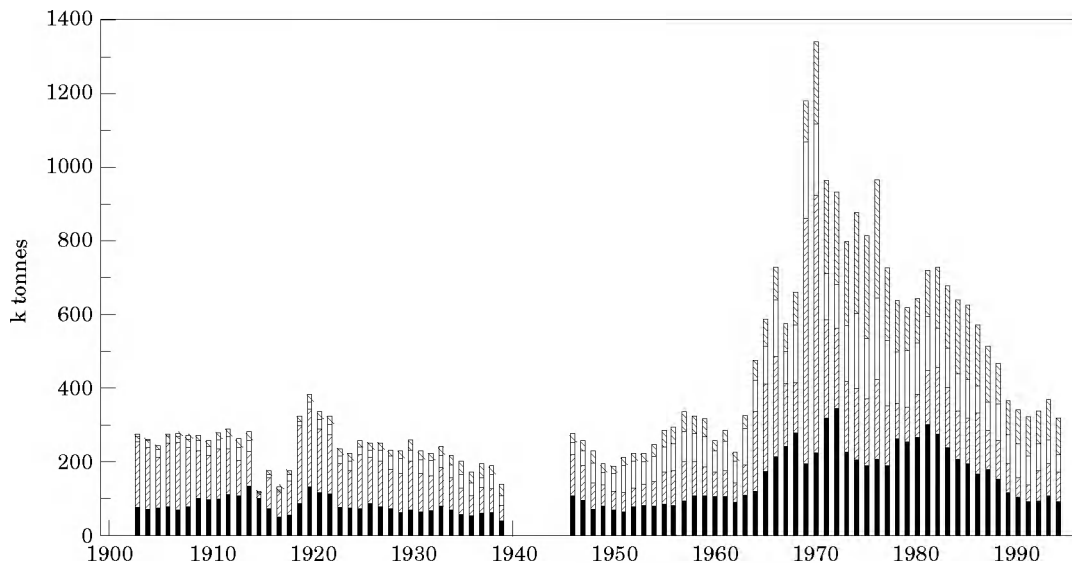
Figure 1. Landings (nominal catches) of cod (■), haddock (▨), whiting (☐), saithe (◩) from the North Sea, 1903–1993, including industrial by-catch. *Source*: ICES Bulletins Statistiques and ICES (1996b).
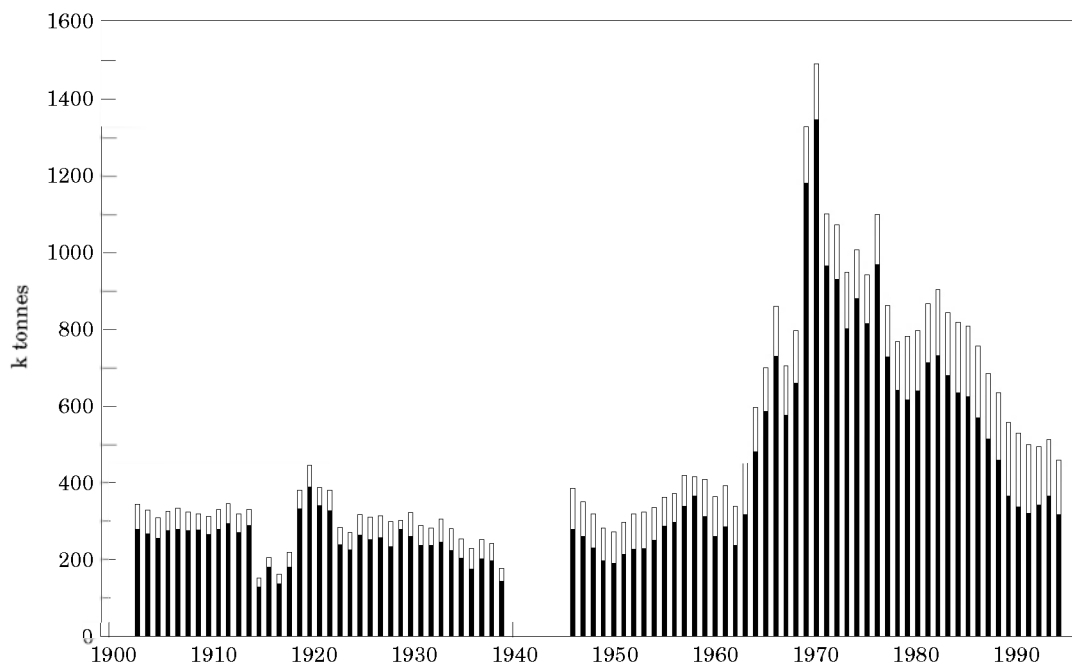

Figure 2. Landings (nominal catches) of principal gadoid species (cod, haddock, whiting, and saithe (■)) and flatfish (plaice, sole (☐) from the North Sea, 1903–1993. *Source*: ICES Bulletins Statistiques and ICES (1996b).

1978). It began in 1962, when both haddock and whiting produced an extremely strong year class. Although cod produced above-average year classes in each of the years 1963–1966, the first exceptionally strong cod year class was in 1969 (Daan, 1978). During the next two decades haddock, cod, whiting, and Norway pout each produced

one or more outstanding year class. However, despite the fact that these four species have a number of reproductive traits in common, all of them being high-fecundity winter/spring spawners with pelagic eggs and larvae (Hislop, 1984), their relative year-class strengths did not coincide. Jones (1977) compared recruitment

indices of cod, haddock, whiting, Norway pout, and saithe over the period 1959–1974. Only three pairings (haddock/whiting, haddock/Norway pout, whiting/saithe) were correlated at the 5% level of significance. Thus, during the 1960s and 1970s conditions improved for the gadoids in general, but conditions in a given year suited only one or two species.

The immediate manifestation of the gadoid outburst was a five- or sixfold increase in biomass, which reached record levels. Conventional ICES assessments based on virtual population analysis (VPA) give estimates of total-stock biomass of cod, haddock, whiting, and saithe for the years 1963–1993, indicating large fluctuations (Fig. 3). Total-stock biomass and spawning-stock biomass of haddock varied by factors of 19.5 and 13.5, respectively. The equivalent factors for cod (4.1, 5.0) and whiting (3.0, 2.3) are lower, but still substantial.

One important ecological consequence of these large changes in biomass is that there must have been changes, on a similar scale, in the quantities of food required to support the populations. Estimates of the weight of food eaten by cod, haddock, whiting, and saithe during the period 1974–1992, derived from multi-species virtual population analysis, are given in ICES (1996a). Average annual consumption by these four species combined has ranged from approximately 4 million tonnes in 1990–1992 to 13 million tonnes in 1974–1976 (slightly after the peak of the gadoid outburst). No data are available for the 1950s, but food consumption at that time was probably somewhat lower than recent levels. An analysis of growth data led Jones (1983) to conclude that the food of juvenile haddock may have been in short supply during periods of high abundance. Jones showed that there had been a long-term increase in the mean lengths-at-age of haddock; growth rates in the 1960s were in general higher than in the 1950s and considerably higher than in the 1920s. The growth rates of the two very strong year classes (1962, 1967) and the two very weak year classes that immediately succeeded them (1963, 1968) were initially very slow, comparable to the growth of haddock in the 1920s. However, when the fish reached a length of about 28 cm their growth increased to a rate typical of the 1950s. In contrast, the year classes of 1961 and 1966, both of which lived all but the first year of their lives during a period when haddock were exceptionally abundant, grew very rapidly. The effects of any intraspecific competition for food were therefore felt mainly by the individuals of the strong year classes and their younger conspecifics. Length-at-age data in Jones and Hislop (1978) indicate that the strong whiting year classes of 1962 and 1967 may have grown more slowly than average in some parts of the northern North Sea during their first three years of life, but the difference is by no means clear cut. Growth rates of cod in the 1960s were similar to those in the pre-war period (Daan, 1978). Apparently, adult gadoids were able to find sufficient food to support normal growth, even during periods of maximum abundance.

It is still not known whether the increase in gadoid biomass was only possible because there was an increase in the availability of suitable food or whether food has always been superabundant. One striking development in the North Sea fishery after World War II is the expansion of the industrial fishery, which catches small, short-lived species for reduction to fish meal and fish oil. The principal target species are sandeels, Norway pout, and sprat, all of which are preyed on by gadoids (Daan, 1989; Hislop, in press). The industrial fishery expanded very rapidly in the early 1960s (Fig. 4) and since the early 1970s this fishery has contributed approximately 50% of the total weight of fish landed from the North Sea. The increased landings could reflect an increase in the abundance of the industrial species, the increased exploitation of a previously underutilized resource, or both. It has already been mentioned that Norway pout participated in the gadoid outburst by producing several strong year classes in the 1960s. Although there are insufficient data from which to judge whether there were also substantial changes in the abundance of sandeels and sprats, stomach content analyses suggest that sandeels formed a smaller part of the diet of haddock and whiting in the 1930s and 1940s (Jones, 1954) than in the 1980s and 1990s (Daan, 1989; Hislop, in press).

The maturation of the strong year classes resulted in a general increase in spawning-stock biomass of cod, haddock, and whiting. Figure 3 illustrates the large contributions made by the strong year classes of 1962 and 1967 (haddock) and 1962, 1967, 1972, and 1974 (whiting) to the respective spawning-stock biomasses. It also demonstrates very clearly that in each case the effect was of short duration. Strong year classes were rapidly fished out.

The main feature of the gadoid outburst was that recruitment levels were high, in the sense that a greater proportion of the year classes were larger than the 30-year average (Fig. 5). However, recruitment was not consistently successful. Extremely small haddock and whiting year classes often followed abundant ones. It should be noted that spawning-stock biomass of both species was well above average during these years of poor recruitment, and that it was below average in 1962, when the first really large year classes were produced. Data for saithe and Norway pout are not directly comparable with those for the other three gadoids, because internally consistent series of recruitment indices do not span the entire period. However, unpublished Scottish data indicate that Norway pout produced strong year classes in 1959, 1961, 1962, and 1967.

There is evidence that recruitment of some species follows a cycle (Fig. 5). Thus cod have produced a relatively strong year class every 2 or 3 years (Daan, 1978). Haddock year classes have followed a 3 or 4 year
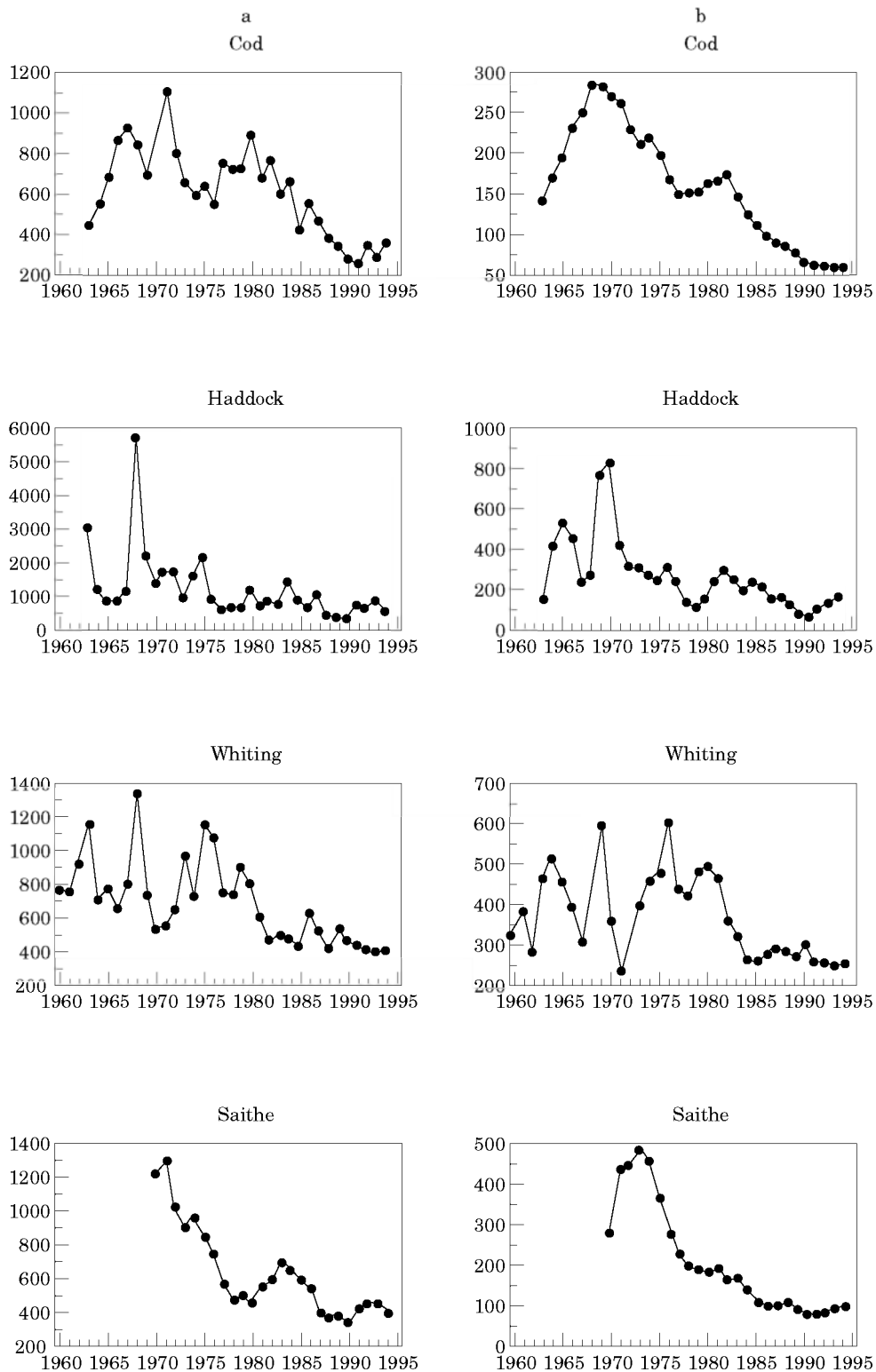
Figure 3. VPA estimates in thousands of tonnes of (a) total-stock biomass and (b) spawning-stock biomass of cod, haddock, whiting, and saithe. *Source*: ICES (1996b); N.B. saithe data are not available prior to 1970.
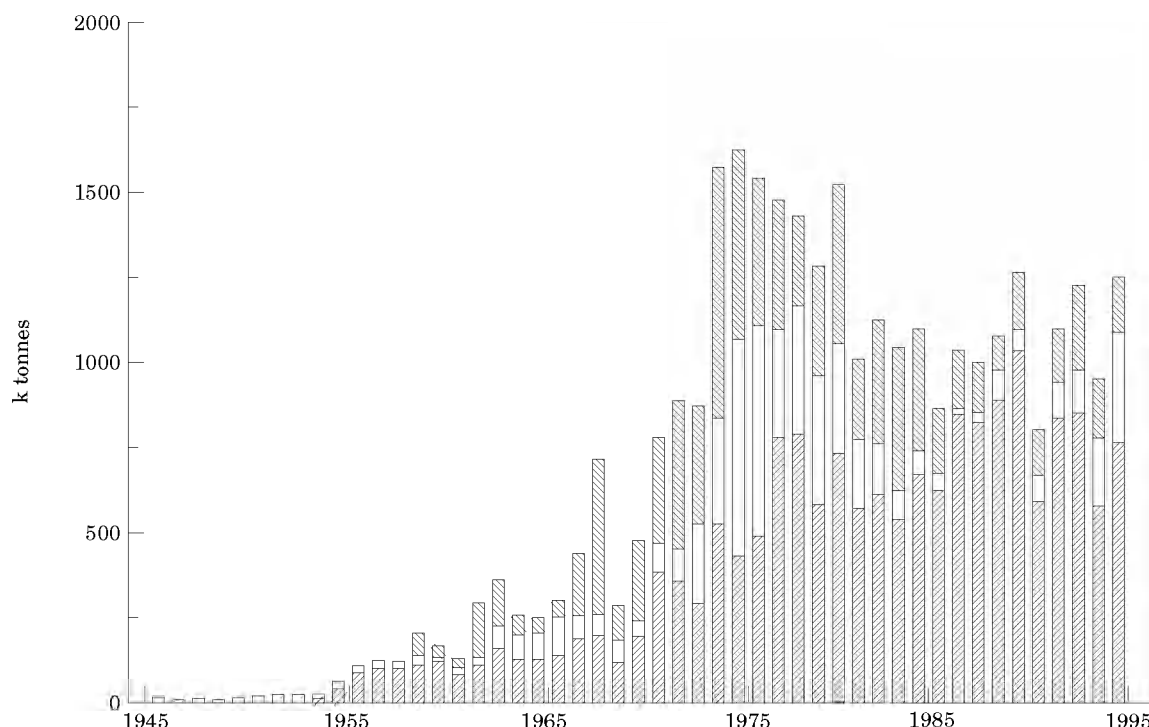
Figure 4. Landings of principal "industrial" species from the North Sea, 1946–1993. *Source*: ICES (1995b) (sandeel ▨, sprat ☐, Norway pout ◺).

cycle throughout most of the century (Jones and Hislop, 1978; Sahrhage and Wagner, 1978). Very strong haddock year classes are frequently followed by very weak ones (Cook and Armstrong, 1986). At least in the case of haddock, these cycles do not appear to be simple and persistent relationships between stock and recruitment (Sahrhage and Wagner, 1978) and they may have an underlying density-dependent component. This increases the difficulty of establishing correlations between recruitment and environmental parameters.

Although it is generally accepted that the gadoid outburst began in the early 1960s, it is more difficult to ascertain when it ended. Above-average cod year classes persisted until the mid-1980s, whereas a reduction in the number of strong haddock and whiting year classes started in the late 1970s (Fig. 5). Three strong saithe year classes were produced in the early 1980s.

Figure 5 also summarizes VPA estimates of recruitment to some other major North Sea fish stocks. It is clear that several species of fish, whose adults have differing life styles and who employ a range of reproductive strategies, experienced large changes during the last 30 years. Bearing in mind that data are included from a very heterogeneous group, it is hardly surprising that there was no single year in which recruitment was outstandingly successful, or unsuccessful, for all species.

Figure 5 illustrates an important point that has already been made by Cushing (1980, 1982, 1984) and Rothschild (1994). The increase in gadoid recruitment at the beginning of the 1960s did not exactly coincide with the decline in herring recruitment which, in conjunction with high levels of fishing mortality, led to a rapid reduction in stock biomass and the closure of the herring fishery in 1977. Recruitment to the herring stocks in the central and southern North Sea began to decline in the 1950s (Burd, 1978), and was very low in the early 1960s. However, the decline in these areas was partially offset by high recruitment in the northern North Sea. In consequence, total herring recruitment remained at near-average levels until the late 1960s (ICES, 1995a).

2. Possible causes

Although fishing must have had a considerable influence on the ecological balance between fish stocks in the North Sea, it seems likely that some of the major changes that have taken place since the war are attributable to environmental, rather than anthropogenic, factors. For example, although it is generally accepted that overfishing was ultimately responsible for the collapse of the herring stocks, the recovery may have been delayed, despite the drastic management measures
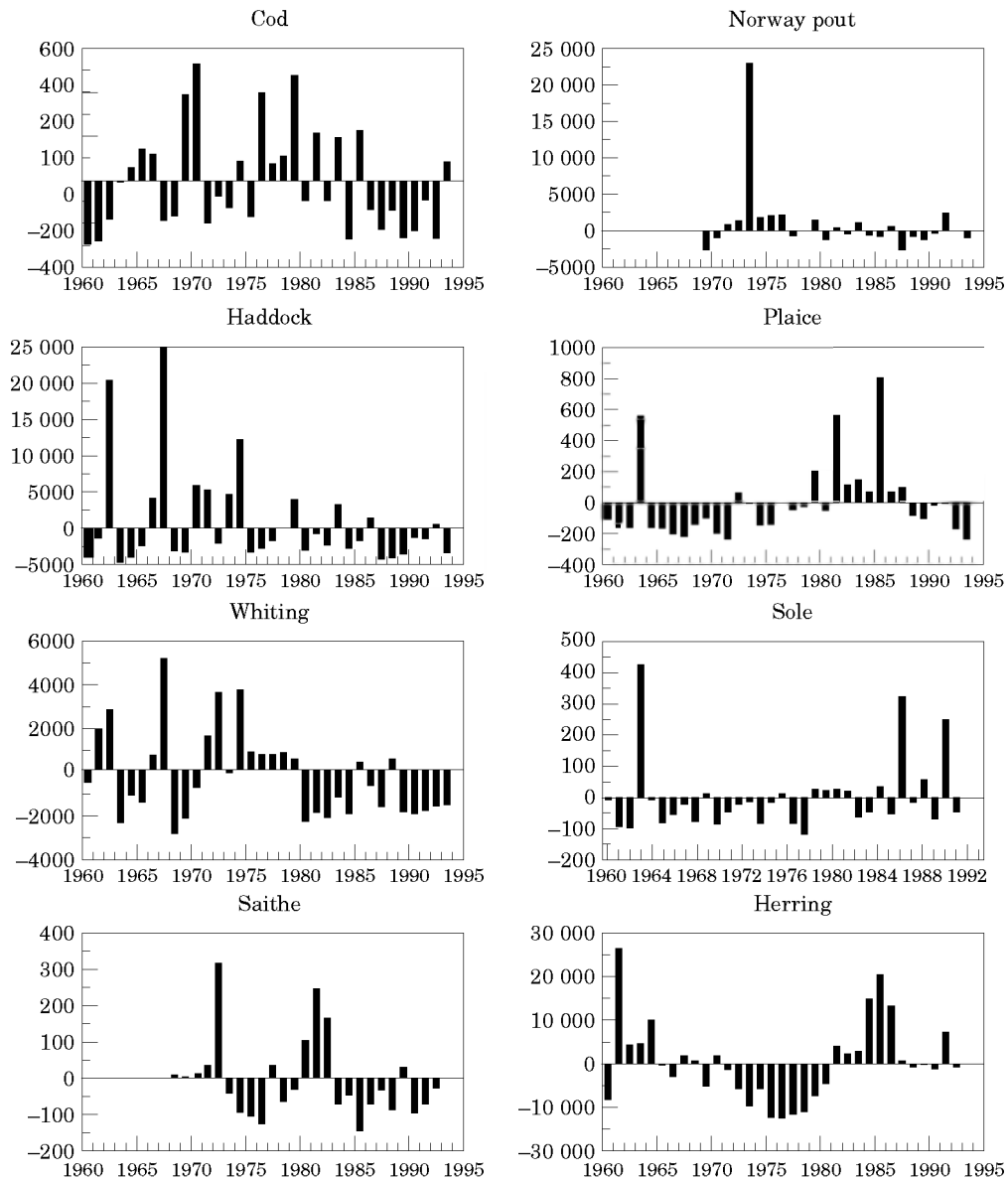
Figure 5. VPA estimates of year-class strengths (millions of 1-group fish), shown as deviations from the long-term arithmetic average. *Source*: ICES (1995a, b, 1996b).

that were taken (a complete closure of the herring fishery), because abiotic environmental factors were unfavourable during the late 1970s (Corten, 1986, 1990). Recruitment increased only when conditions improved, and the herring stock started to rebuild. Strong year classes were seen again in the mid-1980s but at that time the herring stock had recovered to an extent that a limited fishery had already been opened. Also, although fishing mortality experienced by cod and haddock in the late 1950s and early 1960s was markedly lower than current levels (Pope and Macer, 1996), there is no

evidence of a marked change in exploitation rate at that time which might explain the gadoid outburst. However, there is no doubt that mankind is capable of accelerating environmentally driven declines and of failing to take advantage of favourable developments. The rapid elimination, through overexploitation, of several outstanding haddock and whiting year classes (Fig. 3) is a good example of the latter.

Both the physical and the biological characteristics of the North Sea have undergone considerable changes in the last few decades that may have affected recruitment.

Thus the Great Salinity Anomaly of the late 1970s has come and gone (Dickson *et al.*, 1988b). Trends have been detected in the prevalence of northerly winds (Dickson *et al.*, 1988a), westerly winds (Aebischer *et al.*, 1990; Corten, 1986; Turrell, 1992), windstress and winter cooling (Svendsen and Magnusson, 1992). The Continuous Plankton Recorder data show medium to long-term changes in the abundance of phytoplankton and zooplankton (Colebrook *et al.*, 1984; Lindley *et al.*, 1995).

Although common sense dictates that some or all of these variates are likely to have a bearing on gadoid recruitment, it has not yet been possible to develop predictive models that stand the test of time. The correlation between wind function and haddock recruitment described by Carruthers *et al.* (1951) is a well-known example of a model that showed initial promise but was later shown to be unreliable (Saville, 1959). More recently, empirical models incorporating physical and meteorological data from the northern and central North Sea (Svendsen *et al.*, 1991) accounted for a large part of the variance in the recruitment of cod, saithe, whiting and herring (as determined by VPA). However, when evaluated as predictive tools (using environmental data to forecast the last three years of VPA data) the models were not altogether successful. Furthermore, it is ironic that environmental data from the core spawning area of haddock in the northern North Sea did not explain recruitment variability in this species, whereas the same data did explain recruitment variability in cod and whiting, both of which spawn throughout the North Sea, and in saithe, which spawns along the edge of the continental shelf.

One factor that may affect our ability to explain variations in year-class strength is the way in which recruitment is measured. The usual current practice is to model recruitment as defined by VPA estimates of the numbers of young fish in the sea. However, although the North Sea is treated as a single management unit for stock assessment purposes, it contains several more or less discrete sub-populations of cod, haddock and whiting (Daan, 1978; Jamieson and Birley, 1989; Jones, 1972; Kabata, 1967; Hislop and MacKenzie, 1976). Also, some haddock and saithe recruits may originate from spawning grounds outwith the official boundary of the North Sea (Saville, 1959; ICES, 1996c). The relative contributions made by these individual spawning aggregations may vary from year to year, depending on local environmental conditions, but this information cannot be retrieved from the aggregated data used for VPA. It might therefore be preferable to use research vessel indices of local (relative) recruit abundance and/or to apply VPA to fisheries data that have been disaggregated by area.

It has for many years been accepted that the year-class strengths of the gadoids are largely determined by conditions encountered within the first few months of life, i.e. during the pelagic phase (Hjort, 1914). There may be some additional adjustment during the demersal phase, mediated by factors such as predation, including cannibalism in the case of cod and whiting (Daan, 1989; Hislop *et al.*, 1991), and competition for food between newly-demersal juveniles and the members of older cohorts in the case of haddock (Jones, 1983; Cook and Armstrong, 1984). On the premise that events during the pelagic phase hold the key to recruitment, three possible explanations for the "gadoid outburst" are discussed below.

Changes in hydrography

Oceanographic changes are undoubtedly important to the recruitment of some species. For example, herring have well-defined spawning grounds, often situated a considerable distance from their nursery areas (Burd, 1978; Corten, 1986). Corten (1986, 1990) argued that the recruitment failure of herring in the northern and central North Sea during most of the 1970s could be attributed to changes in the water circulation that affected the transport of young herring from the spawning grounds to the nursery areas. But the early life histories of gadoids differ from those of herring. Some gadoids do not have specific nursery grounds (haddock, whiting, Norway pout). The early bottom-living stages of cod and saithe have a predominantly coastal or inshore distribution, but these "nurseries" are very extensive. Gadoid recruitment could therefore be less sensitive to changes in currents. However, it would be unreasonable to suppose that oceanography has no effect on the recruitment of gadoids. A proportion of the juvenile haddock and saithe in the North Sea originates from spawning grounds off the north and west coasts of Scotland and, as in the case of herring (Corten, 1990), the extent to which the larvae are advected to the North Sea will depend on the strength and direction of currents.

Changes in timing and strength of the spring productivity cycle

Cushing (1975) suggested that recruitment was governed by the extent to which the production of larvae coincided with the production of their prey (match–mismatch hypothesis). Cushing (1984) examined the relationship between *Calanus* abundance and cod and haddock recruitment, concluding that cod recruitment moved from a mismatched condition in 1949 to 1961 to a matched one in 1962 to 1978. Peak abundance of *Calanus* tended to occur later in the year during the latter period, which increased the availability of these copepods to young cod. There was no clear evidence of a similar relationship between haddock recruitment and
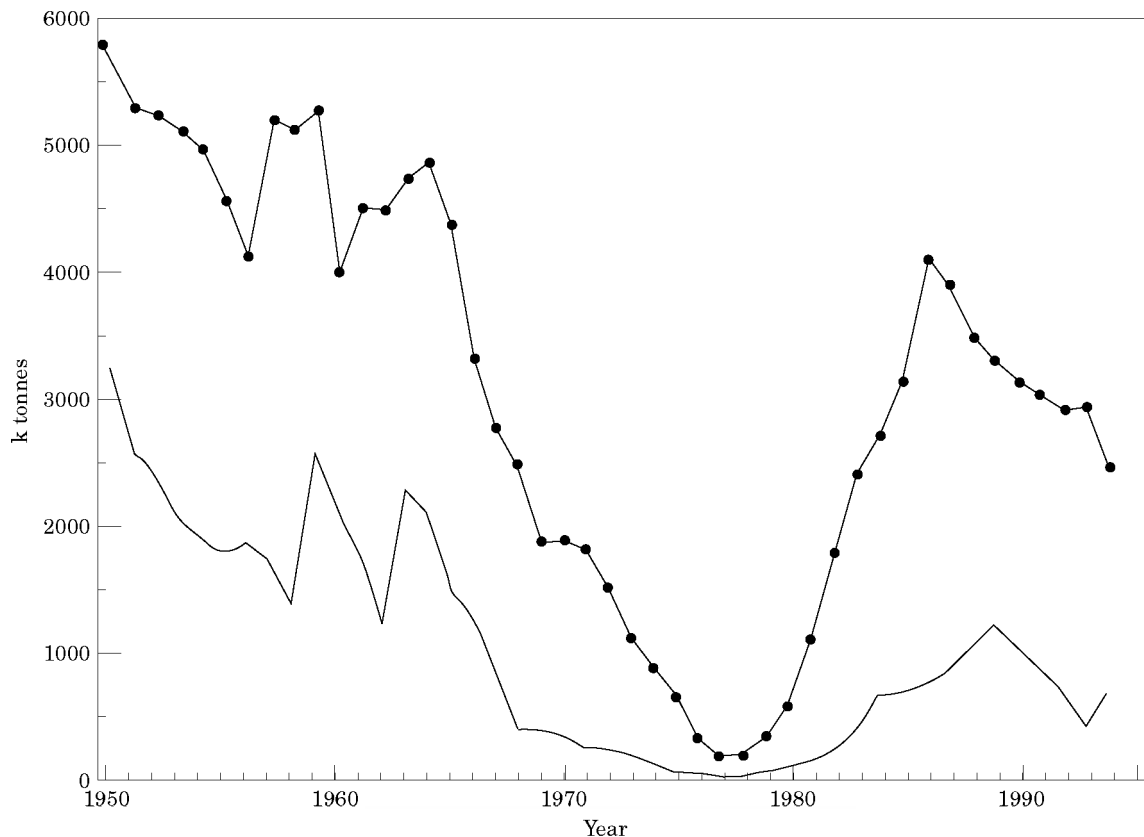
Figure 6. North Sea herring – total-stock biomass (TSB (—●—) and spawning-stock biomass (SSB (——) 1950–1993. *Source*: ICES (1995a).

the timing of the peak in *Calanus* production. Cushing postulated that all but the strongest haddock year classes might have been modified by cod predation.

Species interactions

There are two principal ways in which pelagic species may interact with the pelagic stages of gadoids. First, they prey on the eggs and juveniles of gadoids and pleuronectids (Garrod and Harding, 1981; Daan *et al.*, 1985; Daan, 1989; Kŏster and Schnack, 1994). Second, there is considerable overlap in the diets of larval and post-larval gadoids (Bromley *et al.*, 1995; Cushing, 1980; Robb, 1980; Robb and Hislop, 1980) and adult herring (Last, 1989) and mackerel (Daan, 1989; Hislop, in press). Hence, there may be competition for planktonic food. The large decrease in the abundance and biomass of North Sea herring and mackerel that occurred in the 1960s and 1970s could therefore have opened a "window of opportunity" for the gadoids by reducing predation mortality during the pelagic phase and/or increasing the amount of food available to young gadoids. However, the timing of the various events does not fully support

this hypothesis. The abundance of herring in the central and southern North Sea was already much reduced in the mid-1950s (Burd, 1978) but there is no evidence that the recruitment of cod and whiting, which have important spawning populations in the central and southern North Sea, increased earlier than the recruitment of haddock, which spawns mainly in the northern North Sea. Secondly, the first very large haddock year class in 1962 cannot be explained by a reduction in predation by, or competition with, herring and mackerel. Although the total biomass of herring was declining in the early 1960s (Fig. 6), herring were still relatively abundant in the northern North Sea in 1962 (Burd, 1978). Also, there was still a large biomass of mackerel (1–2 million tonnes) in the northern North Sea in the first half of the 1960s (Hamre, 1978, 1980).

Despite these incongruencies, the recent period of below-average recruitment of all gadoid species coincides with improved recruitment of herring (Fig. 5). In addition, although the North Sea mackerel stock is still extremely small, the western mackerel stock has invaded the northern North Sea during the 1980s and the mackerel biomass in this area during the feeding
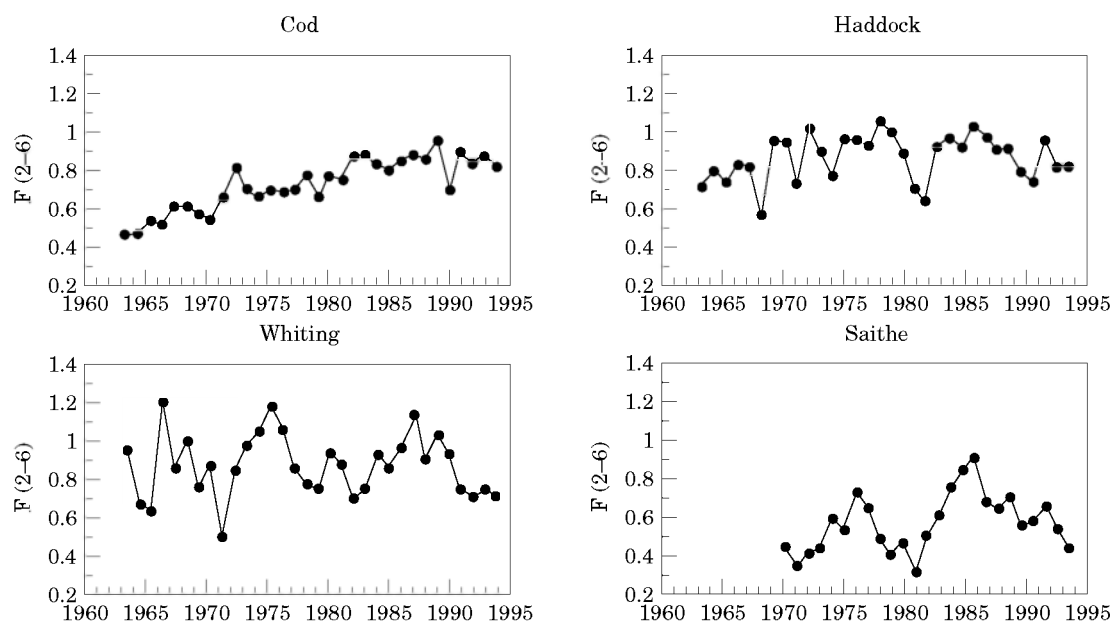
Figure 7. VPA estimates of fishing mortality rate of cod, haddock, whiting, and saithe. *Source*: ICES (1996b). N.B. saithe data are not available prior to 1970.

period is estimated at 2 million tonnes (ICES, 1996a). Thus, the overall fish fauna composition appears to have largely returned to pre-1960 conditions, whether or not as a result of species interactions.

In this context it is also important to remember that the North Sea fish fauna does not consist only of gadoids, herring and mackerel. Other species, such as sprat and sandeels, may also have responded to abiotic changes in the North Sea or taken advantage of opportunities created by the reduction in the biomass of herring and mackerel. As discussed earlier, we have no firm evidence that such changes occurred at the onset of the gadoid outburst, but Figure 4 clearly suggests that Norway pout and sprat have become less abundant since the mid-1970s, whereas sandeels have maintained high catch levels.

In conclusion, it appears that 30 years after the onset of the gadoid outburst we are no closer to understanding its causes than at the time of the previous Århus Symposium (Hempel, 1978). However, whatever the direct causes may have been, the relative dominance of the different species appears to have now largely returned to the original conditions, suggesting that the developments have not been irreversible.

3. The current situation – where are we now?

The routine application of VPA to commercial catch-at-age data, which provides estimates of the absolute numbers and biomass of cod, haddock, and whiting in

the North Sea, began in the early 1960s. The VPA time series shows a more-or-less continuous decline in the biomass of cod and haddock since the late 1960s (Fig. 3). This gives the impression that stocks of these species may have decreased to unusually low levels. However, because gadoids have been prime targets for North Sea fishermen throughout most of the present century, it is appropriate to consider these comparatively recent changes from an historical perspective. To this end Holden (1991) analysed landings statistics for the years 1920 to 1989, concluding that the VPA assessments started at a time when the stocks were at an unusually high level and that the decline in spawning-stock biomass throughout the 1980s should be regarded as a return to normal levels. More recently, data from commercial fisheries and from research vessel surveys have been used to estimate historic (i.e. pre-VPA) levels of recruitment, spawning-stock biomass, and fishing mortality for cod and haddock (Daan *et al.*, 1994; Cook, 1995; Pope and Macer, 1996). The results of these reconstructions support Holden's hypothesis that the biomass of both cod and haddock was relatively high in the 1960s, following a period of enhanced recruitment, and they indicate that levels of recruitment in the early 1990s were low, but not exceptionally so. However, the spawning-stock biomasses observed in 1990 and 1991 appear to be close to (haddock) or below (cod) their historic minima. This cannot be regarded as "normal".

It is possible that the recent decline in the recruitment and stock biomass of gadoids has an underlying environmental cause and represents a natural change in

the ecosystem. If this is so, it is unlikely that even the most drastic fishery management regime could restore gadoid stock biomass to the levels attained in the "golden age" of the 1960s and 1970s. However, this does not mean that no improvement is possible. The fishing mortality of cod and haddock has increased in recent years (Fig. 7), and in the case of cod it has probably reached an historic maximum (Daan *et al.*, 1994; Pope and Macer, 1996). The fact that the strong cod year classes in the 1970s produced large increases in total-stock biomass and fishery yield, but had comparatively little impact on spawning-stock biomass, is attributable to increased fishing mortality. Most of the fish were caught before they reached maturity (Daan *et al.*, 1994). Furthermore, the present exploitation pattern of all the gadoids is such that the spawning stocks consist largely of small, young adults. This has several consequences. Because the spawning-stock biomass is made up of a small number of cohorts, it is very responsive to the strength of each incoming year class and is likely to undergo large changes from year to year. Also, there may be subtle changes in both the quantity and the quality of the eggs produced by a "young" spawning stock, because the relative fecundity (i.e. the number of eggs produced per unit weight of spawning biomass) of recruit spawners is low and their eggs are small and light (Hislop, 1988). In addition, a reduction in the number of older, larger spawners may influence the timing and shorten the duration of the spawning season (Hutchings and Myers, 1993). Although the very strong haddock and whiting year classes of 1962 were the offspring of relatively small spawning populations, comprised mainly of young fish, the variability of recruitment may increase when a spawning stock is in this state (Mertz and Meyers, 1994). There is, therefore, cause for concern. We cannot manipulate the environment in order to enhance gadoid recruitment, but it should be possible to constrain fishing mortality, and to improve the exploitation pattern of North Sea gadoids by regulating mesh sizes. The attainment of these objectives should be given the highest priority.

Acknowledgements

References

Aebischer, N. J., Coulson, J. C., and Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature, 347: 753–755.

Broekhuizen, N., and MacKenzie, E. 1995. Patterns of abundance for *Calanus* and smaller copepods in the North Sea: time series decomposition of two CPR data sets. Marine Ecology Progress Series, 118: 103–120.

Bromley, P. J., Watson, T., and Hislop, J. R. G. 1995. Feeding interactions and the development of food webs in pelagic 0-group gadoids (cod, haddock, whiting, saithe and Norway pout) in the northern North Sea. ICES CM 1995/G: 29.

Burd, A. C. 1978. Long-term changes in North Sea herring stocks. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 137–153.

Carruthers, J. N., Lawford, A. L., Veley, V. F. C., and Parrish, B. B. 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. Nature, London, 168: 317–319.

Colebrook, J. M., Robinson, G. A., Hunt, H. G., Roskell, J., John, A. W. G., Bottrell, H. H., Lindley, J. A., Collins, N. R., and Halliday, N. C. 1984. Continuous Plankton Records: a possible reversal in the downward trend in the abundance of the plankton of the North Sea and the North-east Atlantic. Journal du Conseil International pour l'Exploration de la Mer, 41: 304–306.

Cook, R. M. 1995. A simple model for the analysis of research vessel data to determine stock trends. ICES CM 1995/D: 12.

Cook, R. M., and Armstrong, D. W. 1986. Stock related effects in the recruitment of North Sea haddock and whiting. Journal du Conseil International pour l'Exploration de la Mer, 42: 272–280.

Corten, A. 1986. On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972–1978. Journal du Conseil International pour l'Exploration de la Mer, 42: 281–294.

Corten, A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. Netherlands Journal of Sea Research, 25: 227–235.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge. 278 pp.

Cushing, D. H. 1980. The decline of herring stocks in the North Sea and the gadoid outburst. Journal du Conseil International pour l'Exploration de la Mer, 39: 70–81.

Cushing, D. H. 1982. Climate and fisheries. Academic Press, London.

Cushing, D. H. 1984. The gadoid outburst in the North Sea. Journal du Conseil International pour l'Exploration de la Mer, 41: 159–166.

Daan, N. 1978. Changes in cod stocks and cod fisheries in the North Sea. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 39–57.

Daan, N. (Ed.) 1989. Data base report of the stomach sampling project in 1981. ICES Cooperative Research Report 164.

Daan, N., Heessen, H. J. L., and Pope, J. G. 1994. Changes in the North Sea cod stock during the twentieth century. ICES Marine Science Symposia, 198: 228–243.

Daan, N., Rijnsdorp, A. D., and Overbeeke, G. R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Transactions of the American Fisheries Society, 114: 499–506.

Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., and Cushing, D. H. 1988a. North winds and production in the eastern North Atlantic. Journal of Plankton Research, 10: 151–169.

Dickson, R. R., Meincke, J., Malmberg, S.-A., and Lee, A. J. 1988b. The "Great Salinity Anomaly" in the northern North Atlantic, 1968–1982. Progress in Oceanography, 20: 103–153.

Garrod, C., and Harding, D. 1981. Predation by fish on the pelagic eggs and larvae of fishes spawning in the west central North Sea in 1976. ICES CM 1981/L: 11.

Hamre, J. 1978. The effect of recent changes in the North Sea mackerel fishery on stock and yield. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 197–210.

Hamre, J. 1980. Biology, exploitation and management of the Northeast Atlantic mackerel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 212–242.

Hempel, G. (Ed.) 1978. North Sea fish stocks – recent changes and their causes. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 449 pp.

Hislop, J. R. G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. *In* Fish reproduction: strategies and tactics, pp. 311–329. Ed. by G. W. Potts and R. J. Wootton. Academic Press, London.

Hislop, J. R. G. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. Journal of Fish Biology, 32: 923–930.

Hislop, J. R. G. In press. Data base report of the stomach sampling project in 1991. ICES Cooperative Research Report.

Hislop, J. R. G., and MacKenzie, K. 1976. Population studies of the whiting *Merlangius merlangus* (L.) of the northern North Sea. Journal du Conseil International pour l'Exploration de la Mer, 37: 98–111.

Hislop, J. R. G., Robb, A. P., Bell, M. A., and Armstrong, D. W. 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. ICES Journal of Marine Science, 48: 139–156.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 20: 1–228.

Holden, M. J. 1991. North Sea cod and haddock stocks in collapse or the end to the "gadoid outburst"? ICES CM 1991/G: 41.

Hutchings, J. A., and Myers, R. A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science, 50: 2468–2474.

ICES. 1995a. Report of the Herring Assessment Working Group for the Area South of 62°N. ICES CM 1995/Assess: 13.

ICES. 1995b. Report of the Working Group on the Assessment of Norway Pout and Sandeel. ICES CM 1995/Assess: 5.

ICES. 1995c. Report of the Saithe Study Group. ICES CM 1995/G: 2.

ICES. 1996a. Report of the Multispecies Assessment Working Group. ICES CM 1996/Assess: 3.

ICES. 1996b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES CM 1996/Assess: 6.

Jamieson, A., and Birley, A. J. 1989. The distribution of transferrin alleles in haddock stocks. Journal du Conseil International pour l'Exploration de la Mer, 45: 248–262.

Jones, R. 1954. The food of the whiting, and a comparison of that of the haddock. Marine Research, Scotland 1954, No. 2.

Jones, R. 1972. The sub-division of demersal stocks within the North Sea. ICES CM 1972/F: 13.

Jones, R. 1977. Some inter-relations between North Sea fish species. ICES CM 1977/F: 36.

Jones, R. 1983. An investigation of North Sea haddock (*Melanogrammus aeglefinus*) length-at-age data, with particular reference to the effects on growth of the outstanding year classes of 1962 and 1967. Journal du Conseil International pour l'Exploration de la Mer, 41: 50–62.

Jones, R., and Hislop, J. R. G. 1978. Changes in North Sea haddock and whiting. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 58–71.

Kabata, Z. 1967. Whiting stocks and their gall-bladder parasites in British waters. Marine Research, Scotland, 1967, No. 2.

Köster, F. W., and Schnack, D. 1994. The role of predation on early life stages of cod in the Baltic. Dana, 10: 179–210.

Last, J. M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. Journal of Fish Biology, 34: 489–501.

Lindley, J. A., Gamble, J. C., and Hunt, H. G. 1995. A change in the zooplankton of the central North Sea (55° to 58°N): a possible consequence of changes in the benthos. Marine Ecology Progress Series, 119: 299–303.

Mertz, G., and Myers, R. A. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. Fisheries Oceanography, 3: 236–245.

Pope, J. G., and Macer, C. T. 1996. An evaluation of the stock structure of North Sea cod, haddock and whiting since 1920 together with a consideration of the impacts of fisheries, ecosystem and environmental effects on their biomass and recruitment. ICES Journal of Marine Science, 53: 1157–1169.

Richards, J., Armstrong, D. J., Hislop, J. R. G., Jermyn, A. S., and Nicholson, M. D. 1978. Trends in Scottish research vessel catches of various fish species in the North Sea, 1922–1971. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 211–224.

Robb, A. P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. Journal of Fish Biology, 18: 183–194.

Robb, A. P., and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. Journal of Fish Biology, 16: 199–217.

Rothschild, B. J. 1994. Decadal transients in biological productivity, with special reference to the cod populations of the North Atlantic. ICES Marine Science Symposia, 198: 333–345.

Sahrhage, D., and Wagner, G. 1978. On fluctuations in the haddock population of the North Sea. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 72–85.

Saville, A. 1959. The planktonic stages of the haddock in Scottish waters. Marine Research Scotland, 1959, No. 3.

Svendsen, E., Aglen, A., Iversen, S. A., Skagen, D. W., and Smedstad, O. 1991. Influence of climate on recruitment and migration of fish stocks in the North Sea. ICES CM 1991/H: 12.

Svendsen, E., and Magnusson, A. K. 1992. Climatic variability in the North Sea. ICES Marine Science Symposia, 195: 144–158.

Turrell, W. R. 1992. New hypotheses concerning the circulation of the northern North Sea and its relation to North Sea fish stock recruitment. ICES Journal of Marine Science, 49: 107–123.