https://doi.org/10.17895/ices.pub.19271819

ICES Marine Science Symposia, 219: 261–270. 2003.

Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature?

K. Brander, G. Blom, M. F. Borges, K. Erzini, G. Henderson, B. R. MacKenzie, H. Mendes, J. Ribeiro, A. M. P. Santos, and R. Toresen

Brander, K., Blom, G., Borges, M. F., Erzini, K., Henderson, G., MacKenzie, B. R., Mendes, H., Ribeiro, J., Santos, A. M. P., and Toresen, R. 2003. Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? – ICES Marine Science Symposia, 219: 261–270.

The temperature of the upper 300 m of the North Atlantic increased by about 0.57°C between 1984 and 1999, but this underlying trend was overlain with substantial geographic and interannual variability. Northward shifts occurred in the distribution of many commercial and non-commercial fish species in the NE Atlantic during the 1990s. New records were established for a number of Mediterranean and NW African species on the south coast of Portugal. Red mullet (*Mullus surmuletus*) and bass (*Dicentrarchus labrax*) extended their ranges northward to western Norway and catches of the former increased throughout the 1990s in the North Sea. Abundance or relative abundance of warm-water commercial species of gadoids and flatfish generally increased during the 1990s, but like the warming trend the changes in distribution and abundance were by no means uniform and there was considerable interannual variability. There were also examples of southward shifts for some species, which can be related to local hydrographic conditions, such as upwelling. Information on distribution and abundance of Greenland cod (*Gadus morhua* L.) and Norwegian spring-spawning herring (*Clupea harengus*) during a previous warming period in the late 1920s and 1930s is also presented and compared with changes in the 1990s.

Keywords: climate change, fish distribution, Northeast Atlantic, temperature.

K. Brander: ICES, Palaegade 2–4, DK-1261 Copenhagen K, Denmark [e-mail: keith@ices.dk]. G. Blom: Department of Fisheries and Marine Biology, University of Bergen, High Technology Centre, N-5020 Bergen, Norway. M. F. Borges, H. Mendes, and A. M. P. Santos: Fisheries and Sea Research Institute, Avenida de Brasilia 1449-006, Lisboa, Portugal. K. Erzini and J. Ribeiro: CCMAR, Universidade do Algarve, 8000 Faro, Portugal. G. Henderson: FRS Marine Laboratory Aberdeen, PO Box 101, Victoria Road, Aberdeen AB11 9DB, Scotland. B. R. MacKenzie: Danish Institute for Fisheries Research, Department of Marine Ecology and Aquaculture, Kavalergården 6, DK-2920 Charlottenlund, Denmark. R. Toresen: Institute of Marine Research, PO Box 1870, N-5024 Bergen, Norway.

Introduction

Given the recent concern over global warming, it is not surprising that information about changes in distribution of fish have appeared in both popular (Brown, 2000) and scientific (Quero *et al.*, 1998; Stebbing *et al.*, 2002) sources over the past few years, and have been related to increased sea temperatures. We present evidence of changes in fish distribution from many parts of the Northeast Atlantic (Figure 1) during the 1990s and relate this to observed temperature variability. In order to avoid bias we made a particular effort to find information on distribution changes which appeared to contradict the "global warming" scenario.

Although the main aim of the article is to look at evidence of changes in distribution, some information on changes in abundance is also included. The distribution of a species is determined by the geographic area it occupies and also by its relative abundance within that geographic area. For example, an increase in abundance near the northern end of its range and/or a decrease in abundance near the southern end can be regarded as a northward shift in distribution, even if the overall range remains the same.

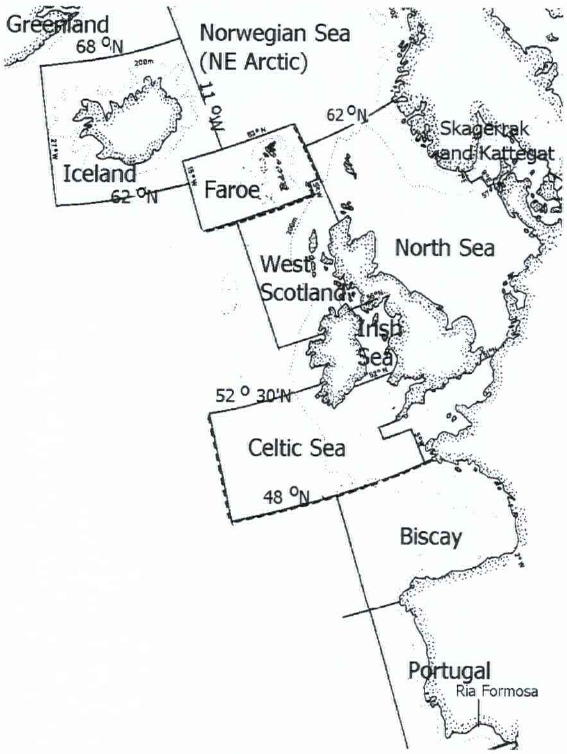

Figure 1. ICES Fishing Areas and place names referred to in the text.

Changes in distribution have many causes, but thermal effects are pervasive and reasonably well known (e.g. Welch *et al.*, 1998). We know the thermal responses and limits for many fish species (Alderdice and Forester, 1971; Magnuson and Destasio, 1997) and it is therefore possible to consider whether observed distribution changes are commensurate with the observed scale of temperature change. Changes in temperature permit extension of geographic range in some areas and limit distribution in others. Changes in temperature may also indicate changes in the movement and distribution of water masses, which transport species to new areas (Holliday and Reid, 2001).

An analysis of distribution change, restricted mainly to thermal effects, is inevitably incomplete, but there are nevertheless scientific and practical justifications for doing so. Temperature affects the rates of physiological, metabolic, and behavioural processes (Brett, 1979; Wood and McDonald, 1997) and hence the population dynamics of the species via growth (Brander, 1995), recruitment (O'Brien *et al.*, 2000), and mortality. We have better information about temperature fields than any other environmental variable affecting fish, which does not mean that we have adequate temperature information in all cases, but it is much better than for any other variable.

Given the large scale in time and space which is covered here and the limited amount of matching ambient environmental information, the analysis is mainly qualitative. Our aim is to compare observations of changes in fish distribution and abundance with changes in temperature, and to evaluate whether the response is coherent in the sense of following a common principle.

Materials and methods

Climate indicators

Although a large amount of data on sea temperature exists, no consistent, comprehensive, standardized source of information was available at the time of writing. Information about temperature variability in the eastern North Atlantic has been taken from two principal sources: sea temperature data are from the Annual ICES Ocean Climate Status Summary 2000/2001 (ICES, 2002); air temperature data are from the IPCC Data Distribution Centre, (http://ipcc-ddc.cru.uea.ac.uk/), which provides visualizations of annual mean air temperature anomalies (relative to the mean for 1961–1990).

The ICES Ocean Climate Status Summary has begun to bring together time series representing particular sea areas, but they are not presented in a standard way and most cover only a limited period of time. It is therefore difficult to obtain the necessary background information on the temperature variability over all the areas and time periods reviewed here. In order to gain a more comprehensive overview, air temperature data are included for all areas, because they are available in a standard format back to 1900. This allows comparisons between different areas over long time periods. The degree of similarity between trends in sea and air temperature can be judged by comparing them for areas for which time series of both are plotted in Figure 2.

The temperature of the upper 300 m of the North Atlantic rose by about 0.57°C between 1984 and 1998 (Figure 3). The increase was not geographically uniform, with some areas showing quite different trends; therefore a coherent response, in the sense of fish distribution behaving uniformly throughout the NE Atlantic, cannot be expected.

Mean bottom temperature data used to compare different areas are taken from Brander (1995) and from the ICES oceanographic database.

Fish population indicators

Information on fish distribution and abundance comes from catches by commercial fishing vessels

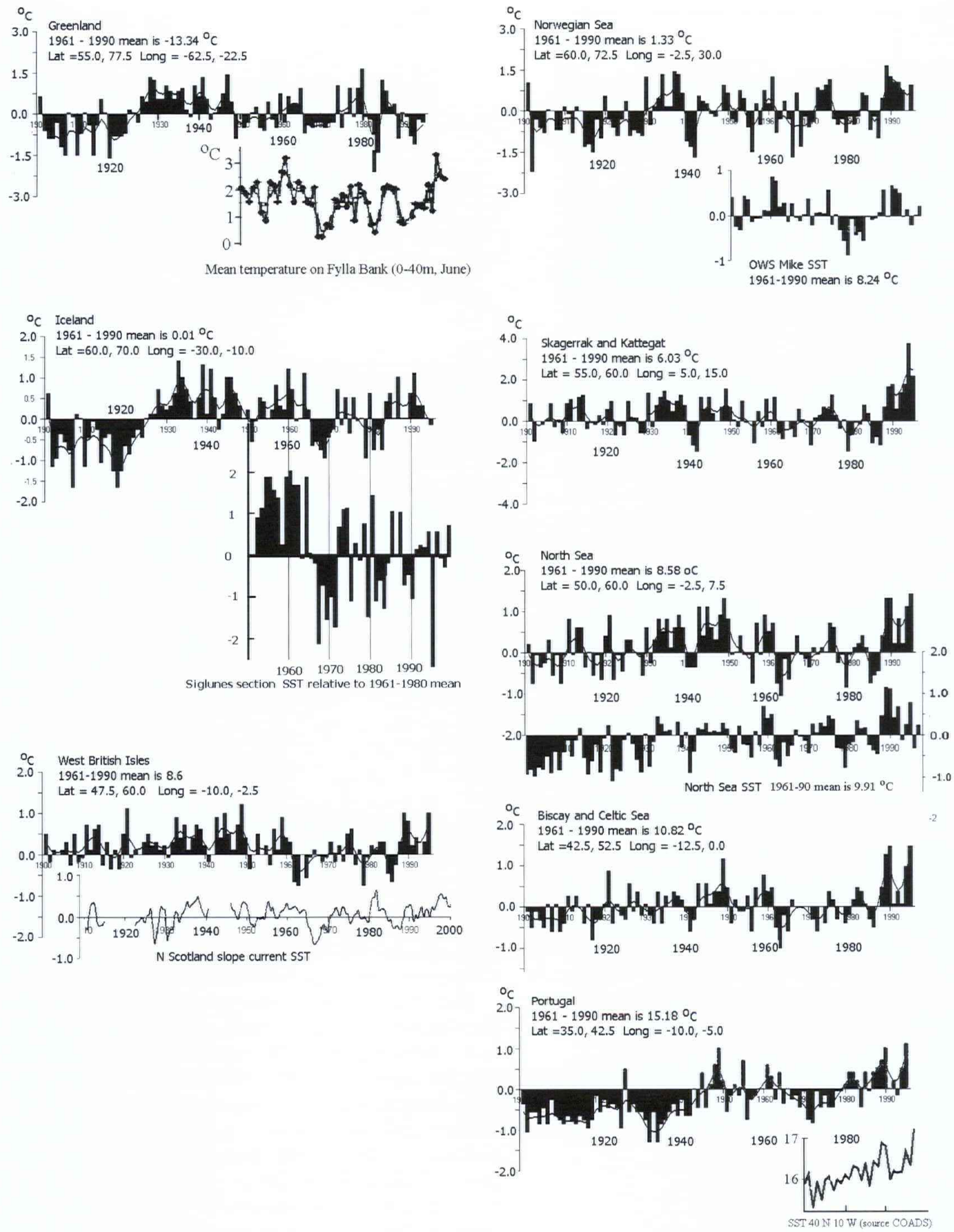

Figure 2. Mean annual air temperature and sea surface temperature (SST) anomalies for the main areas of the NE Atlantic. Air temperature data (1900–1995) are from the IPPC Data Distribution Centre, from which information concerning the mean 1961–1990 climatology and the anomaly time series can be obtained. SST data and anomalies are from the ICES Ocean Climate Status Summary (ICES, 2002).

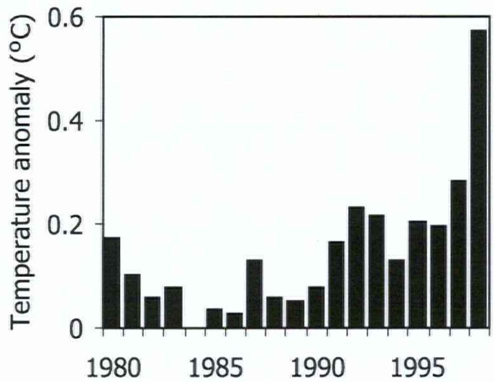

Figure 3. Volume mean temperature anomaly for the North Atlantic 0–300 m. 1984 is set to 0°C. Replotted from Levitus *et al.* (2000).

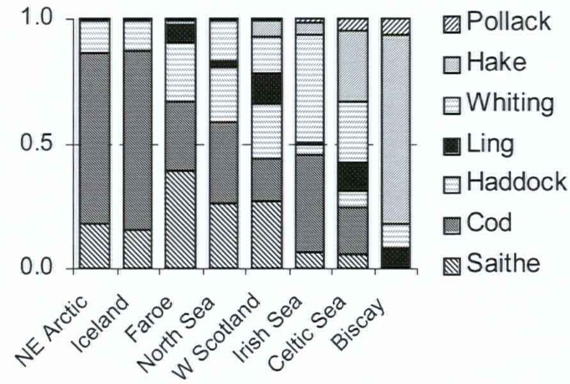

Figure 4. Proportions of seven principal gadoid species in the fishing areas of the NE Atlantic, 1973–1998.

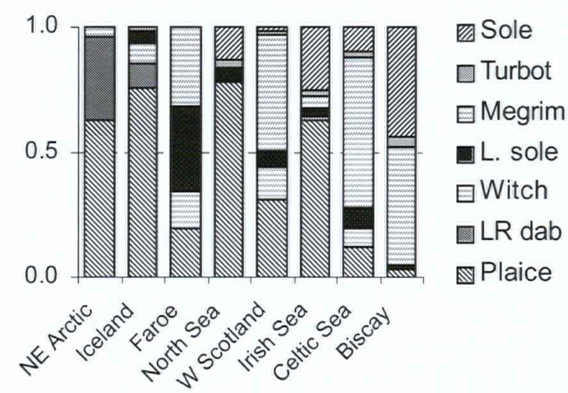

Figure 5. Proportions of the seven principal flatfish species in the fishing areas of the NE Atlantic, 1973–1998.

(catch statistics reported to ICES and available from the ICES STATLANT database http://www.ices.dk/fish/statlant.htm), research sampling and records of unusual species from a variety of sources. All of these sources have shortcomings which limit the strength and detail of interpretations drawn from them, but consistent patterns can nevertheless be derived.

Catch statistics are used here to show the varying proportion of seven principal gadoid and seven flatfish species in the areas NE Arctic, Iceland, Faroe, North Sea, West of Scotland, Irish Sea, Celtic Sea, and Biscay (Figure 1). The proportion of each gadoid species in relation to the total catch of all seven gadoids (for the period 1973–1998) is shown in Figure 4, and Figure 5 shows the same pattern for the flatfish. Since all of these species are marketed commercially and are in many cases caught in the same fisheries, the catches are a reasonable representation of their relative abundance in the different areas. Thus the absence of hake from the catches in the NE Arctic, Iceland, and Faeroe, or of saithe from the Bay of Biscay, is because they do not occur there.

Further relevant details about the nature and source of particular catch records are provided in the sections on each area below.

Results

Climate indicators

As previously mentioned, the mean temperature anomaly for the upper 300 m of the North Atlantic increased by about 0.57°C between 1984 and 1998 (Figure 3). Atlantic water along the NW European shelf edge has been warming since 1987 at a rate of 0.5°C/decade (ICES Ocean Climate Status Summary 2000/2001). The long-term trends in sea surface temperature (SST) are similar to those in air temperature for this area (Figure 2).

The pattern of temperature change on the European continental shelf from 43°N to 60°N and from 15°E to 12°W (areas marked Skagerrak and Kattegat, North Sea, West of British Isles, and Biscay and Celtic Sea in Figure 2) can be characterized as a period of positive air temperature anomalies from 1930 to 1961 (apart from a 3-year cold period from 1940 to 1942), then 2 years of rapid cooling. During the period 1964 to 1986 the temperature fluctuated about the mean, and from 1987 rose quickly to high positive anomalies.

The period of warming of the North Atlantic from 1918 to 1933 was much more marked at Greenland, Iceland, Faroe, and the Norwegian Sea than it was further south. The former three areas maintained positive air temperature anomalies until 1950 and the main cooling period was from 1963 to 1970 (Figure 2).

Fish population indicators

Ria Formosa and the south coast of Portugal

The Ria Formosa is a 55-km-long lagoon in the Algarve (southern Portugal), with a surface area of approximately 16 300 hectares. The fish fauna has been well studied, particularly by Monteiro (1989) and Monteiro *et al.* (1987, 1990). They sampled 8 stations (three replicates each) monthly over a 7-year period (1980 to 1986) using a 50-m-long, 3.5-m-high beach seine with a 14 mm mesh size. Sixty-seven species were reported and their annual patterns of abundance and migration described.

Since September 2000, sampling with beach seines has been carried out on a monthly basis in the Ria Formosa in order to evaluate changes in species composition and relative abundance. In the 9 months to May 2001, 85 fish species have been recorded in the beach seine, of which 52 were reported by Monteiro (1989). For species that were not common to the two studies, information on geographic distribution was obtained from Whitehead *et al.* (1984, 1986) and their occurrence or disappearance between the earlier period and the present was evaluated.

The increase was largely due to species not previously recorded in Portuguese waters and in particular to species whose distribution was previously limited to the Mediterranean and/or NW Africa (Whitehead *et al.*, 1984): *Parablennius incognitus* (Blenniidae), *Michrochirus boscanon* (Soleidae), *Pomadasys incisus* (Haemulidae), *Symphodus ocellatus* (Labridae), and *Bothus podas* (Bothidae). Other largely Mediterranean or NW African species, such as *Spicara flexuosa* and *Spicara maena* (Whitehead *et al.*, 1984), were found in the Ria recently, but not in 1980–1986. A few northerly species, such as the gobies *Gobius couchi* and *Pomatoschistus pictus* have apparently increased their range to the south.

Of the northerly species recorded by Monteiro (1989) but not found in 2000–2001, Portugal and/or NW Africa and the Mediterranean were the southern limits according to Whitehead *et al.* (1984). Examples are *Hyperoplus lanceolatus* (Ammodytidae), not recorded from the Mediterranean or NW Africa, *Alosa fallax* (Clupeidae), previously recorded as far south as Morocco, and *Trisopterus luscus* (Gadidae), reported from the Mediterranean and Morocco. Since the ongoing study has not completed a full annual cycle, it is possible that the species reported by Monteiro (1989), but not found recently, could be summer visitors, which may appear in catches in June–August.

The increase in diversity shown from just 9 months of data is remarkable and indicates that important changes have taken place. Given the proximity to the Mediterranean and NW Africa and the fact that the south of Portugal is a transition zone, heavily influenced in terms of oceanography by the Mediterranean in particular, these findings are not surprising.

In addition to the research trawl survey of the fish community of the Ria Formosa, information and specimens from local fishermen, who occasionally bring rare or new species to the University, also provide evidence that warm water species have been extending their range to southern Portugal. In recent years for example, a lesser African threadfin (*Galeoides decadactylus*), found between the Canary Islands and Angola (Whitehead *et al.*, 1984), was caught in a gillnet in the Algarve. Two specimens of the Atlantic lizardfish (*Synodus saurus*), primarily insular in the eastern Atlantic and Mediterranean, were also brought in by gillnet fishermen. Further evidence of a warming trend is the increasing abundance of large pelagics such as the white marlin (*Tetrapturus albidus*) and the blue marlin (*Makaira nigricans*) in the summer months. These are species generally not found in waters less than 20°C. Over the past few years they have been so abundant in Algarve coastal waters that sport fishing tournaments are now common from July to September.

West coast of Portugal

There is evidence of both northward and southward shifts in fish distribution on the west coast of Portugal. Portuguese catch statistics, estimated back to 1896 by Mendes (2001) and published here for the first time, indicate that the sardine (*Sardina pilchardus*) population has shifted southward since the late 1970s (Figure 6). The shift was also observed in egg distributions (Stratoudakis *et al.*, 2002) and is associated with increased northerly winds during the spawning season (Santos *et al.*, 2001; Borges *et al.*, 2002), which result in increased upwelling.

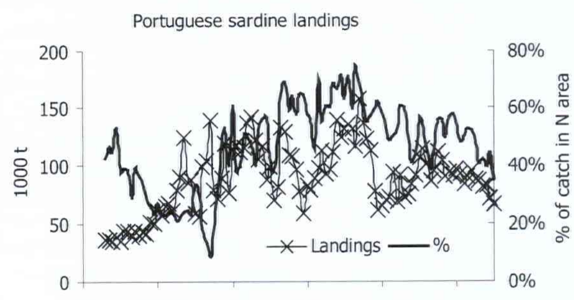

Figure 6. Landings of sardines in Portugal and landings from the northern area as a percentage of total landings.

The migratory snipefish (*Macrorhamphosus* sp.), a non-commercial species associated with warm and saline water, extended its distribution northwards during the late 1990s. Research surveys in 1979 showed that the distribution did not extend north of Lisbon (Afonso dos Santos and Moura, 1980). In September 1991, extensive schools of juvenile snipefish were found migrating from southwest of the Ormond Seamount towards the Algarve and Gulf of Cadiz and then north along the shelf edge as far as the latitude of Lisbon (Dias *et al.*, 1996). In the late 1990s, this species was observed in the trawl surveys at the extreme north of the Portuguese coast (41–42°N) and probably continuing further north along the shelf edge (Borges, 1998).

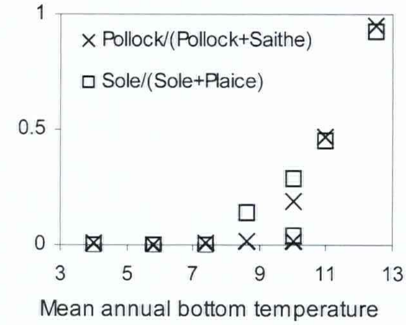

Figure 7. Proportions of "southern" vs. "northern" species in the fishing areas of the NE Atlantic. (a) Pollock vs. saithe, (b) sole vs. plaice. Mean annual bottom temperatures are Iceland 5.8°C, Faeroe 7.4°C, North Sea 8.6°C, West of Scotland 10°C, Irish Sea 10°C, Celtic Sea 11°C, Biscay 12.5°C (Brander, 1995).

European shelf edge

A variety of tropical species have extended their ranges northward along the European continental slope since the early 1960s (Quero *et al.*, 1998). A particularly striking example is the Sailfin dory (*Zenopsis conchifer*), of which 36 have been taken since it was first recorded in European waters in 1966 at 38°N off the coast of Portugal. By the early 1990s it had been found north of 55°N. The depth range of capture is 100–500 m.

Distribution and abundance of the principal gadoid and flatfish species

The relative abundance of the principal gadoid and flatfish species taken in commercial fisheries in the eastern North Atlantic varies depending on the characteristic temperature regime of the area. Cod is the principal gadoid, along with saithe and haddock in cold areas, whereas in warm areas the principal gadoid is hake, with whiting and pollock (Figure 4). For the smaller flatfish (i.e. excluding halibut and Greenland halibut) the cold-adapted species are plaice and long rough dab, while the warm-adapted species are sole and megrim (Figure 5).

The differences in species composition between areas can be expressed as a ratio of catches of warm to cold adapted species. A pair of gadoid species (pollock and saithe) and a pair of flatfish species (sole and plaice) were chosen for the analysis. They are frequently caught by the same fishing gear in areas where their distributions overlap, and may therefore be expected to undergo similar changes in fishing mortality with time. For both of these species pairs, the ratio increases from zero at the Faroes (i.e. no catch of pollock or sole) to nearly 1 in Biscay (Figure 7). The distributions are clearly related to other factors in addition to temperature (e.g. depth, distance from coast), but there is no evidence that they are related to latitude.

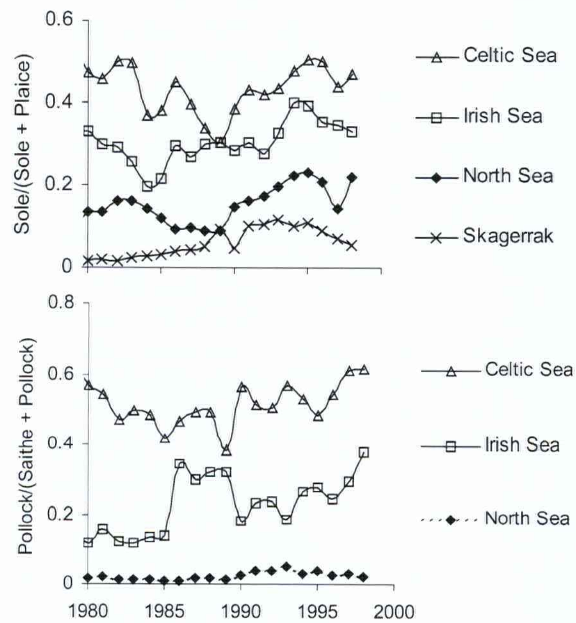

Figure 8. Temporal changes in the proportions of "southern" vs. "northern" species in the fishing areas of the NE Atlantic.

The catch ratio of warm to cold-adapted species also changes with time. Temporal trends in the ratios for areas with bottom temperatures, which lie between those of Faroes and Biscay, are shown in Figure 8. There is a general increase in the proportion of the "southern" species during the 1990s in most cases.

In the Celtic Sea the proportion of both "southern" species (pollock and sole) decreased from the late 1970s until 1989, before increasing again. In the Irish Sea there has been an underlying rise since 1973, but with substantial fluctuations. The West of

Scotland has much lower proportions of the "southerly" species and shows an increase in the proportion of sole, but not of pollock. The North Sea also shows an increase in sole relative to plaice, but pollock is always at a very low level.

Red mullet (Mullus surmuletus) *and bass* (Dicentrarchus labrax)

The ranges and fishery for these two species have been the subject of numerous articles in the popular and angling press (e.g. Brown, 2000). They are valuable, easily recognized species which have extended their ranges northwards and increased in abundance around the British Isles. The trend in commercial catches of red mullet in the English Channel and Central North Sea over the period since 1980 is particularly striking (Figure 9).

Records of catches of red mullet and bass in Scottish waters between 1984 and 2000 do not show a trend, but are not based on standard sampling (Figure 10). However, the International Young Fish Survey carried out by RV "Scotia" in February each year and covering a series of standard stations in the NW North Sea caught 1, 5, and 0 red mullet, respectively, in 1995–1997, and 98, 28, and 46, respectively, in 1998–2000 (Figure 9).

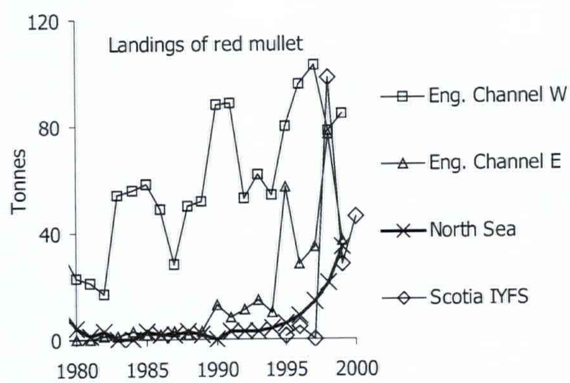

Figure 9. Annual landings of red mullet by Denmark, Ireland, The Netherlands, and UK. RV "Scotia" International Young Fish Survey (IYFS) catches are number of fish.

Red mullet and bass have recently been caught in western Norway for the first time as follows:

- Red mullet – several catches (at least 3 since 1993) in Hordaland county (ca. 60°N, 5°E)
- Sea bass – caught in Førdefjord, western Norway (61.5°N, 5.1°E) on 4 November 2000
- Other exotic fishes caught in Norwegian waters in September/October 2000 include:
- Swordfish (*Xiphias gladius*) caught in Sognefjorden, western Norway (61°N, 5°E)
- Sunfish (*Mola mola*) caught in Drammensfjorden, eastern Norway (59.7°N, 10.3°E)

Sole in the Kattegat–Skagerrak (ICES Division IIIA)

Sole have been landed in the Kattegat–Skagerrak area throughout the period for which we have catch records, but landings increased from 200 to 500 t per year during the period 1952–1985 to 1000–1400 t per year during the period 1990–1995 (Fig. 11; ICES, 2001). Landings have fallen to ca. 700 t per year since the early 1990s but are still approximately double the long-term level during the 1950s–1970s. Most (ca. 70–80%) of the sole caught in the region are captured in the Kattegat.

Sole are captured in a multispecies fishery which targets cod, plaice, and Norway lobster. Effort information is available only since the 1980s. Danish gillnet and trawler fleets in the Kattegat capture >90% of all sole in the fishery and represent the major trends in effort for the entire stock. Effort has been relatively stable, but catch per unit effort indices do not take differences in vessel power, net size, net soak time, etc., into account and cannot fully

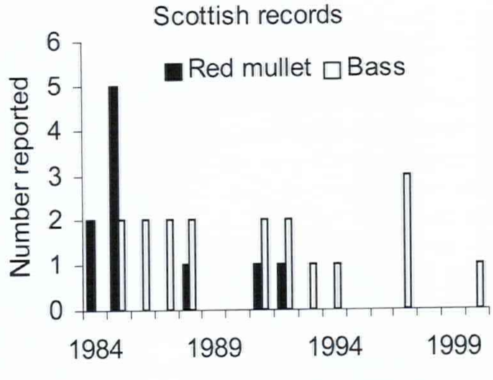

Figure 10. Numbers of bass and red mullet reported landed in Scotland.

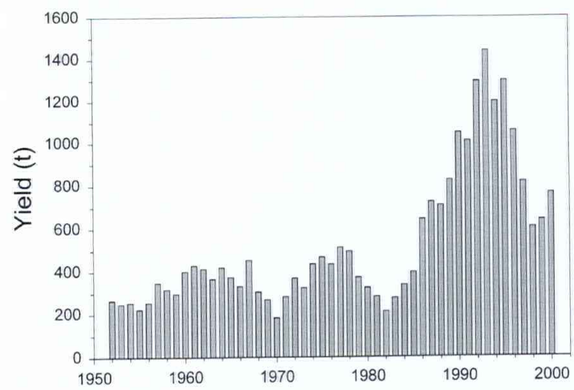

Figure 11. Annual landings of sole in the Kattegat–Skagerrak (ICES Division IIIA).

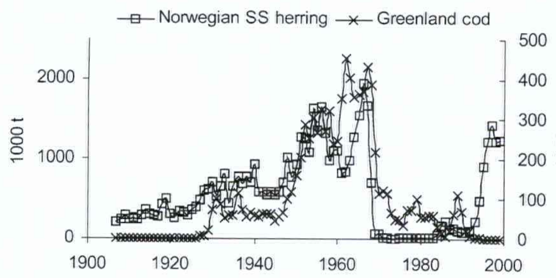

Figure 12. Annual landings of Norwegian spring-spawning herring and Greenland cod.

explain either the fluctuations in landings or fishing mortality rates during the same time period (ICES, 2001).

The environmental factors that might affect recruitment to the stock or other aspects of stock biology are poorly known (ICES, 2001). The stock is located near the edge of its geographical range (Muus and Nielsen, 1999) and therefore may be susceptible to environmental effects (Leggett and Frank, 1997; Myers, 1998; Brander, 2000). The distribution of the stock in the Baltic is limited by low salinity; sole are rare in the Belt Sea (ICES Subdivision 22) and absent in the western and eastern Baltic Sea (ICES Subdivisions 24–32; Muus and Nielsen 1999). Although good quality information on ambient temperature and other environmental factors is not available, the correspondence with the trends in air temperature and SST in the adjacent North Sea over the same period is striking (Figure 2).

Big northern stocks and the warming period of the 1920s and 1930s

The time series of catches of cod at Greenland and of Norwegian spring-spawning herring (Toresen and Østvedt, 2000) over the past century are remarkably similar (Figure 12). At their peak the catches from these stocks were so large that they constituted a significant proportion of the global pelagic and demersal catches, and in both cases the stock biomass increased and decreased by over three orders of magnitude.

The rising catch and biomass during the 1920s and 1930s was due to the warming that took place at Iceland and Greenland at this time (Figure 2) and which resulted in a poleward extension of the range of many species of fish, benthos, marine mammals, and also terrestrial fauna (Jensen, 1939).

The decline in both stocks in the late 1960s occurred during a major cooling episode, when the Polar Front moved south in the Greenland Sea and herring no longer migrated around the north coast of Iceland. Temperature on the Siglunes section north of Iceland declined by 4°C between 1964 and 1967 (Figure 2). However, both stocks were being heavily fished at the time and their collapse was probably due to a combination of lower temperature and overfishing.

The history of two stocks has been very different since the early 1970s. The Norwegian spring spawning herring recovered from a spawning biomass of less than 3000 t in 1972 to around 12 million t in 1997. It has resumed its summer feeding migration in the Norwegian Sea (Toresen and Østvedt, 2000), but does not penetrate into the area north of Iceland as it did prior to 1965. The temperature north of Iceland has not returned to the values found prior to 1965 (Figure 2).

The biomass of cod at Greenland remains low and the catch declined from 68 000 t in 1990 to less than 1000 t in 1999. Evidence from past recruitment indicates that temperatures above 1.5°C are necessary to produce big year classes (Brander, 2000); therefore it is not surprising that the stock has failed to recover. The temperature increased at West Greenland throughout the 1990s, but only exceeded 1.5°C at Fylla Bank in June in 1996, 1998, and 1999. Since cod in this area take 6 or 7 years to reach maturity, any rebuilding of the stock is likely to be slow.

Discussion

The absence of comprehensive, standard, up-to-date information on sea temperature and other hydrographic information for the NE Atlantic makes the task of explaining changes in fish distribution during the 1990s and relating it to earlier periods of the 20th century more difficult. Information on sea and air temperature is presented here (Figure 2) in an attempt to show the long-term background of temperature change, for all parts of the NE Atlantic, but a more complete and systematic treatment is needed. The ICES Ocean Climate Status Summary (ICES, 2002) has made a start on putting together such information, but to date this is fragmentary; the records are based on small numbers of stations or sections and often represent only a fraction of the depth range and seasonal cycle. The duration of the records is variable and they are not presented in a standard format.

Air and sea temperatures over most of the NE Atlantic have risen by at least 0.4°C in the decade since the late 1980s. In the northwestern part of the area, at Greenland and Iceland, the 1990s began with sea temperatures which were below the long-term average, and although temperatures rose during the decade they did not reach the levels which occurred during the warm period from the mid-1920s to 1960. The eastern parts of the North Atlantic, from the Norwegian Sea down to Portugal, were warmer during the 1990s than during previous decades of the 20th century, but the middle years of the decade were relatively cool in most areas.

Northward shifts occurred in the distribution of many commercial and non-commercial fish species during the 1990s from southern Portugal to northern Norway. The abundance of commercial gadoid and flatfish species that occur in warmer waters (e.g. pollock and sole) increased relative to colder water species (e.g. saithe and plaice) in areas where their distribution overlaps. The absolute abundance of sole doubled during the 1990s in the Skagerrak and Kattegat, which is at the cold end of its range. A few examples of southward shifts, such as the sardine distribution off Portugal, which appear to contradict the overall pattern can be related to specific local hydrographic features. The scale and geography of the northward changes in fish distribution recorded here are similar to those shown for calanoid copepods during the period from 1960–1967 to 1992–1997 (Beaugrand *et al.*, 2002).

Trends in landings and biomass of Norwegian spring-spawning herring and of cod at Greenland have followed a similar pattern since the early 20th century, with both showing very substantial increases during the late 1920s and 1930s, declining in the late 1960s, but only the herring stock recovering during the 1990s. Both of these stocks are at the lower end of their temperature range and both extended their range northward during the warm period from the mid-1920s to the early 1960s. They did not reoccupy these northern limits during the 1990s. In the case of cod around Greenland this could be because low temperatures during most of the decade restricted both spawning and range extension. Also, the stock is at an extremely low level and could take many years to recover, providing it does not suffer excessive mortality due to the existing shrimp fisheries. The Norwegian spring-spawning herring stock did recover during the 1990s but has not reoccupied its previous feeding areas north of Iceland, probably because of the low temperatures and low plankton production which persist north of the polar front.

Acknowledgements

KB was funded by the US National Science Foundation Grant OCE-0075263, the UK Ministry of Agriculture Fisheries and Food Project MF0424, the Norwegian Research Council Project 13744/120, the Canadian Department of Fisheries and Oceans, and the Icelandic Ministry of Fisheries. He was also supported by the International Council for the Exploration of the Sea.

References

Afonso dos Santos, G., and Moura, O. 1980. Abundância e distribuição do trombeteiro (*Macroramphosus scolopax*) na costa portuguesa em Novembro de 1978 e Maio, Agosto e Novembro de 1979. IPIMAR Report (unpublished).

Alderdice, D. F., and Forester, C. R. 1971. Effects of salinity, temperature and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). Journal of the Fishery Research Board of Canada, 28: 883–902.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692–1694.

Borges, L. 1998. Biologia, Distribuição e Comportamento do apara-lápis (*Macroramphosus* spp.) na costa Continental Portuguesa. Master dissertation, Instituto de Ciências Biomédicas de Abel Salazar, Porto.

Borges, M. F., Santos, A. M. P., Crato, N., Mendes, H., and Mota, B. 2002. Sardine regime shifts off Portugal: a time series analysis of catches and wind conditions. Scientia Marina. (In press.)

Brander, K. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1–10.

Brander, K. 2000. Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. Oceanologica Acta, 23: 485–496.

Brett, J. R. 1979. Environmental factors and growth. *In* Fish Physiology, vol. VIII, pp. 599–675. Academic Press, London.

Brown, A. 2000. Mediterranean fish colonise North Sea. The Observer. 17 September.

Dias, C. A., Marques V., Soares 1996. Condições oceanográficas e distribuição de juvenis de trombeteiro (*Macroramphosus scolopax*) ao largo da costa de Portugal em Setembro de 1991. IPIMAR Technical Report (unpublished).

Holliday, N. P., and Reid, P. C. 2001. Is there a connection between high transport of water through the Rockall Trough and ecological changes in the North Sea? ICES Journal of Marine Science, 58: 270–274.

ICES. 2001. Report of the Baltic Fisheries Assessment Working Group. ICES CM 2001/ACFM: 18.

ICES. 2002. The Annual ICES Ocean Climate Status Summary 2000/2001. Ed. by W. Turrell and N. P. Holliday. ICES Cooperative Research Report, No. 245. 19 pp

Jensen, A. S. 1939 Concerning a change of climate during recent decades in the Arctic and SubArctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. Det Kgl. Danske Videnskabernes Selskab. Biologiske Medd. XIV, 8: 75 pp.

Leggett, W. C., and Frank, K. T. 1997. A comparative analysis of recruitment variability in North Atlantic flatfishes: testing the species range hypothesis. Journal of Sea Research, 37: 281–299.

Levitus, S., Antonov, J. I., Boyer, T. P., and Stephens, C. 2000. Warming of the World Ocean. Science, 287: 2225–2229.

Magnuson, J. J., and Destasio, B. T. 1997. Thermal niche of fishes and global warming. Society of Experimental Biology Seminar Series 61: Global Warming: Implications for freshwater and marine fish, pp. 377–408. Ed. by C. M. Wood and D. G. McDonald. Cambridge University Press, Cambridge.

Mendes, H. 2001. Relatório de Actividades no âmbito do Projecto PO-SPACC (PRAXIS/P/CTE/1128/1998). IPIMAR Technical Report (unpublished).

Monteiro, C., Lasserre, G., and Lam Hoai, T. 1990. Organisation spatiale des communautés ichtyologiques de la lagune Ria Formosa (Portugal). Oceanol. Acta 13: 79–96.

Monteiro, C. 1989. La faune ichtyologique de la Ria Formosa; organisation spatio-temporelle. Thèse Doctorat, Université de Montpellier, France. 219 pp.

Monteiro, C., Lam Hoai, T., and Lasserre, G. 1987. Distribution chronologique des poissons dans deux stations de la lagune Ria Formosa (Portugal). Oceanologica Acta, 10: 359–371.

Muus, B. J., and Nielsen, J. G. 1999. Sea fish. First: 1–340 Hedehusene, Denmark, Scandinavian Fishing Year Book.

Myers, R. A. 1998. When do environment-recruitment correlations work? Review Fish Biol. Fisheries, 8: 285–305.

O'Brien, C. M., Fox, C. J., Planque, B., and Casey, J. 2000. Climate variability and North Sea cod. Nature, 404: 142.

Quero, J.-C., Du Buit, M-H., and Vayne, J.-J. 1998 Les observations de poissons tropicaux et le rechauffement des eaux dans l'Atlantique europeen. Oceanologica Acta, 21: 345–351.

Santos, A. M. P., Borges, M. F., and Groom, S. 2001. Sardine and horse mackerel recruitment and upwelling off Portugal. ICES Journal Marine Science, 58: 589–596.

Stratoudakis, Y., Bernal, M., Borchers, D., and Borges, M. F. 2002. Spatio-temporal changes in the distribution of sardine eggs and larvae off Portugal. Fisheries Oceanography. (In press.)

Stebbing, A. R. D., Turk, S. M. T., Wheeler, A., and Clarke, K. R. 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001) Journal of the Marine Biological Association, U.K., 82: 177–180.

Toresen, R., and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries, 1: 231–256.

Welch, D. W., Ishida, Y., and Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncoryhynchus nerka*): long-term consequences of global warming. Canadian Journal of Fisheries and Aquatic Science, 55: 937–948.

Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., and Tortonese, E. 1984, 1986. Fishes of the North-eastern Atlantic and the Mediterranean. Unesco, vols. I, II and III. 1473 pp.

Wood, C. M., and McDonald, D. G. (Eds.) 1997. Society of Experimental Biology Seminar Series 61: Global Warming: Implications for Freshwater and Marine Fish. Cambridge University Press, Cambridge. 425 pp.