

# Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities

D. J. Beare\*, F. Burns, A. Greig, E. G. Jones, K. Peach, M. Kienzle,  
E. McKenzie, D. G. Reid

Fisheries Research Services, Marine Laboratory, PO Box 101, Victoria Road, Torry, Aberdeen AB11 9DB, UK

**ABSTRACT:** Observations made in the scientific and popular literature suggest that the characteristics of both marine and terrestrial ecosystems are changing rapidly due to increasing global air and sea temperatures. Here, we examine the hypothesis that fish species with more 'southern' distributions are increasing in the northern North Sea over time. In order to do this, 2 important databases on fish abundance collected by trawl on research cruises are interrogated. When combined, the databases cover both the entire North Sea and the Scottish west coast and span a period of 80 yr (1925 to 2004). The data take the form of length-frequencies for all species caught (>300 different species), while additional information (e.g. age, sex, weight and stage of sexual maturity) is available for the commercially important component (e.g. cod). The trawl data suggest that the North Sea is experiencing waves of immigration by exotic, southern species (e.g. red mullet, anchovy and pilchard). The purpose of this paper is to describe and document these changes.

**KEY WORDS:** Anchovy · Sardine · Horse mackerel · Mackerel · Long-term · North Sea · Climate

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Long-term and seasonal changes in the abundance and distribution of fish have been noted since fishing activity by humans began. Over the last millennium, fluctuations of pelagic, demersal and shellfish stocks all around the globe have been regularly observed. There are numerous records, for example, of herring, mackerel, sardine and anchovy fisheries suddenly emerging in certain areas only to disappear again (Cunningham 1889–90, Parrish & Saville 1965, 1967, Southward et al. 1988, Alheit & Hagen 1997). Similarly, demersal fish stocks have experienced population expansions followed by rapid collapses. In the mid-1960s the 'gadoid explosion' led to unusually high landings of cod, haddock and whiting (Cushing 1984, Hislop 1996) around British coasts, while in the mid-1990s the once prolific cod fisheries of the Grand Banks completely ceased to exist in many areas (deYoung & Rose 1993).

In the last decade, global air and sea temperatures have begun to rise due to greenhouse warming (Levitus et al. 2000). At the same time, scientists have begun

to note profound changes in the composition of both marine and terrestrial ecosystems at all trophic levels (Crick et al. 1997, Myneni et al. 1997, McCleery & Perrins 1998, Dunn & Winkler 1999). The abundance of the boreal copepod *Calanus finmarchicus* has fallen in the North Sea, whereas numbers of its Lusitanian relative, *C. helgolandicus*, have increased. Unlike *C. helgolandicus*, *C. finmarchicus* must descend into deep offshore water, where its metabolic rate slows, in order to survive the winter. Reductions in the volume and depth of the upper surface of Norwegian Sea Deep Water since the 1960s, resulting in unfavourable conditions for this important over-wintering stage by *C. finmarchicus*, has been promulgated as an explanation for its decline (Heath et al. 1999, Greene et al. 2003). Changes in the species diversity of the North Atlantic copepod community have been discovered using continuous plankton recorder data which have been linked to a warmer 'dynamic equilibrium' (Beaugrand et al. 2000) and simultaneous modifications of water masses, currents and atmospheric forcing. Recent (1998) influxes into the North Sea of warm-water

\*Email: d.beare@marlab.ac.uk

doliolids are connected to unusual incursions of oceanic water caused by changes in the North Atlantic Oscillation (Edwards et al. 1999).

Higher than average sea temperatures are correlated with low recruitment of cod at the latitudinal limits of its range (Planque & Frédou 1999, O'Brien et al. 2000). Reid et al. (2001) related abrupt changes in the abundance and composition of the plankton and fish community ca. 1988 to recent increases in the North Sea horse mackerel fishery. Pronounced increases in tropical fish in the Bay of Biscay area have been noted (Quero et al. 1998) by scientists in France, while Swaby & Potts (1999) made the first British record of the sailfin dory *Zenopsis conchifer*, noting that the species is advancing northwards along the continental shelf west of the British Isles at a rate of 60 km per decade. Other studies show similar patterns. Information on first records of southerly fish species caught in Cornish waters has been collated and published (Stebbing et al. 2002), and nearly 20 completely new species have been recorded (by 2001). The fish species noted include big-eyed tunny *Thunnus obesus*, sailfin dory *Zenopsis conchifer*, short-nosed seahorse *Hippocampus hippocampus* and barracuda *Sphyraena sphyraena*. In the Irish Sea, the occurrence of the warm-water species, anchovy *Engraulis encrasicolus*, has increased between 1990 and 1998 according to trawl data from research surveys (Armstrong et al. 1999). British commercial fishermen have also noted change. The spider-crab *Maia squinado* fishery, for example, is advancing steadily further northwards (Anonymous 2003).

In 1996, a paper was published describing the long-term variation in the abundance of southern species in the southern North Sea (Corten & van de Kamp 1996) in relation to hydrography. Two periods of increase in the prevalence of southern species were described (mid-1970s and 1990) using data from the International Bottom Trawl Surveys (IBTS). Both periods coincided with positive temperature anomalies, which in turn correlated with southerly winds over The Netherlands, indicating increased flow of Atlantic water through the Dover Strait. The authors concluded that the increases were not part of a systematic long-term trend, but the result of increased transport of southern fish species into the North Sea and favourable winter temperatures. The aim of this paper is to use the Corten & van de Kamp (1996) approach as a basic template. This time, however, Scottish trawl survey data will also be used to extend the information for the northern North Sea further back in time than is possible using the IBTS data alone. Our scientific goal is to ascertain whether the increases noted by Corten & van de Kamp in the early 1990s in the southern North Sea extend into the northern North Sea, and whether or not they actually do appear to be part of a 'systematic long-term trend'.

## MATERIALS AND METHODS

For this study we used 2 trawl survey databases. The first is maintained by Fisheries Research Services (FRS), Aberdeen, UK. FRS is responsible for managing Scottish commercial fisheries and has been collecting data on fish distribution and abundance in the seas around Scotland since the late 19th century. The FRS data were originally stored in the form of paper notebooks built up over time on a cruise-by-cruise basis, making them difficult to interrogate. Recently, however, all available trawl survey data have been organised into a single computer database, which can be searched quickly. The database represents an extremely rich ecological resource and contains information on the long-term spatial and seasonal distributions of over 300 different fish species, extending back to 3 March 1925.

The second database examined is known as the IBTS (International Bottom Trawl Survey) database and is maintained by ICES (International Council for the Exploration of the Sea) in Copenhagen, Denmark. Data for the North Sea, collected by 10 European countries (Denmark, France, Germany, The Netherlands, Norway, Sweden, Russia, England, Wales and Scotland) are routinely submitted to ICES for inclusion. The IBTS data are patchy prior to 1983 and do not extend back past the year 1965. For the majority of years, only first quarter (where January to March = Quarter 1) data are available, although for a period in the mid-1990s surveys were done during each of the 4 quarters. The FRS data also have a rather patchy distribution in space and time. Nevertheless, the FRS data do contain useful information on fish abundance during other parts of the year than is the case for the IBTS data alone. Some of the FRS data are duplicated in the IBTS database (e.g. all the Quarter 1 surveys) but, as yet, many Scottish trawl survey data are not submitted to ICES.

During IBTS and FRS trawl surveys a standard protocol is followed. At each station, a Grande Overture Verticale (GOV) otter trawl is towed at 3 to 4 knots for a pre-defined duration, set at 1 h for all hauls before 1990 and half an hour subsequently. Once on board, the fish catch from the codend is processed by sorting to species and then weighing each component. All species present in relatively low numbers (typically <1 basket) are counted and measured from the tip of the head to the tip of the tail. In the case of very large catches, subsamples are taken and the resulting data 'raised' to the level of the entire catch. Information on age, sex and state of sexual maturity is usually only taken for the commercially important component only.

In both databases (IBTS and FRS), methods of storage are essentially similar: data being recorded as

length-frequencies caught by haul for all species. An additional 'haul information' or 'chronological' table provides detailed data on the location, timing, gear parameters, vessel, country and duration of every trawl haul which is used to estimate catch per unit effort. Time-series were constructed by dividing the data into 3 ICES Fishing Areas (4A, 4B and 4C; Fig. 1), within which the total numbers of individuals caught per hour during each year and quarter were calculated. High variability and data skewness meant that long-term trends were easier to interpret after transformation. Hence, data were either square-root or log-transformed in an ad hoc manner depending on the histogram properties of the relevant dataset. Maps were constructed at the level of ICES statistical rectangle (30 nautical miles square), within which the total number of fish of each species caught were summed and then divided by the total amount of fishing effort (in this case total trawl duration in hours).

The following fish species were classified as 'southern' by Corten & van de Kamp (1996): lesser weever *Echilichthys vipera*; poor cod *Trisopterus minutus*; bib *T. luscus*; anchovy *Engraulis encrasicolus*; tub gurnard *Trigla lucerna*; red mullet *Mullus surmeletus*; John dory *Zeus faber*; bass *Dicentrarchus labrax*; black sea bream *Spondylusoma cantharus*; sardine *Sardina pilchardus*; horse mackerel *Trachurus trachurus*; and mackerel *Scomber scombrus*. A fish species gained southern status if either its abundance was greater in the southern North Sea during the summer months or its distribution was restricted to the southern North Sea. The 'Atlas of North Sea Fishes' (Knijn et al. 1993) was used to determine the distributional range of each fish species. The same group of fish species was examined here, but in addition the occurrence of the relatively deepwater species, bluemouth *Helicolenus dactylopterus* and red gurnard *Aspitrigla cuculus*, were examined because of their affinities for shelf edge, and therefore typically warmer water. Bass and black sea bream were not examined due to their extreme rarity in both the FRS and IBTS databases.

## RESULTS

### Long-term trends

The locations of the 3 standard ICES fishing areas are displayed in Fig. 1. Long-term trends in the abundance of the 4 'southern' pelagic fish species are fairly consistent across all 3 areas (ICES Areas 4A, 4B and 4C). Anchovy and sardine were each almost totally absent from any part of the North Sea until the mid-1990s. It should be noted, however, that small numbers



Fig. 1. ICES Fishing Areas 4A, 4B and 4C

of anchovy have been caught occasionally in ICES Area 4A since 1925 (Fig. 2).

Anchovy has a much more distinct morphology than sardine and there is some plausible concern that sardine may have been incorrectly identified in the past, either as young herring or perhaps sprat. We have less confidence, therefore, in the reliability of the data for sardine than we do for anchovy.

Time-series summarising research vessel catches of horse mackerel and mackerel in ICES Areas 4A, 4B and 4C have 2 main peaks (see Figs. 2 & 3): the first during the mid- to late 1950s and the second since the mid-1990s. In the case of mackerel, the earlier peak (mid-1950s) is larger than the latter one, while the reverse is true for horse mackerel, with the recent peaks being larger (Fig. 2). These changes are reflected in both the FRS and IBTS databases, although the most recent (since 1990) changes are more pronounced in the IBTS data (Fig. 4). The IBTS data for mackerel suggest a significant peak centred on 1970, which can also be discerned from the FRS data (Fig. 2).

Bluemouth were largely absent from the northern North Sea between 1925 and 1990, although a few were noted in 1955. In 1991, bluemouth appeared suddenly in the North Sea in much larger numbers than usual (Fig. 5) (Heessen et al. 1996).

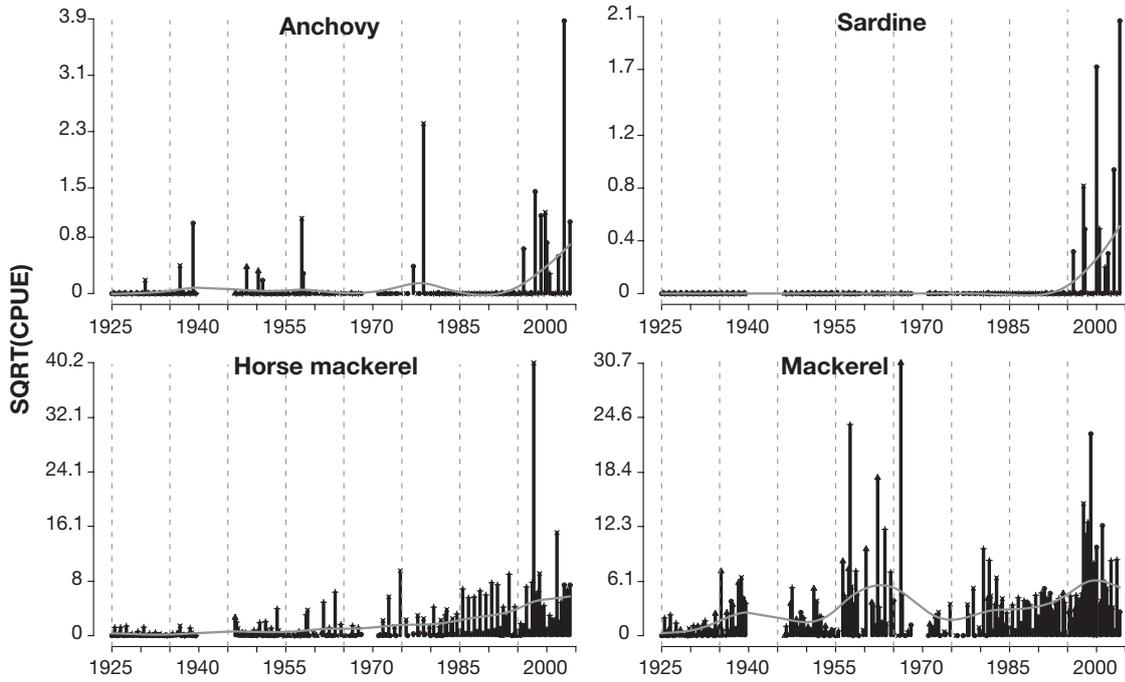


Fig. 2. Numbers of anchovy, sardine, horse mackerel and mackerel caught per hour in ICES Area 4A between 1925 and 2004. Estimates were made using FRS (Fisheries Research Services) data only and are square-root transformed (SQRT). CPUE: catch per unit effort. Grey lines represent smooth functions of CPUE data

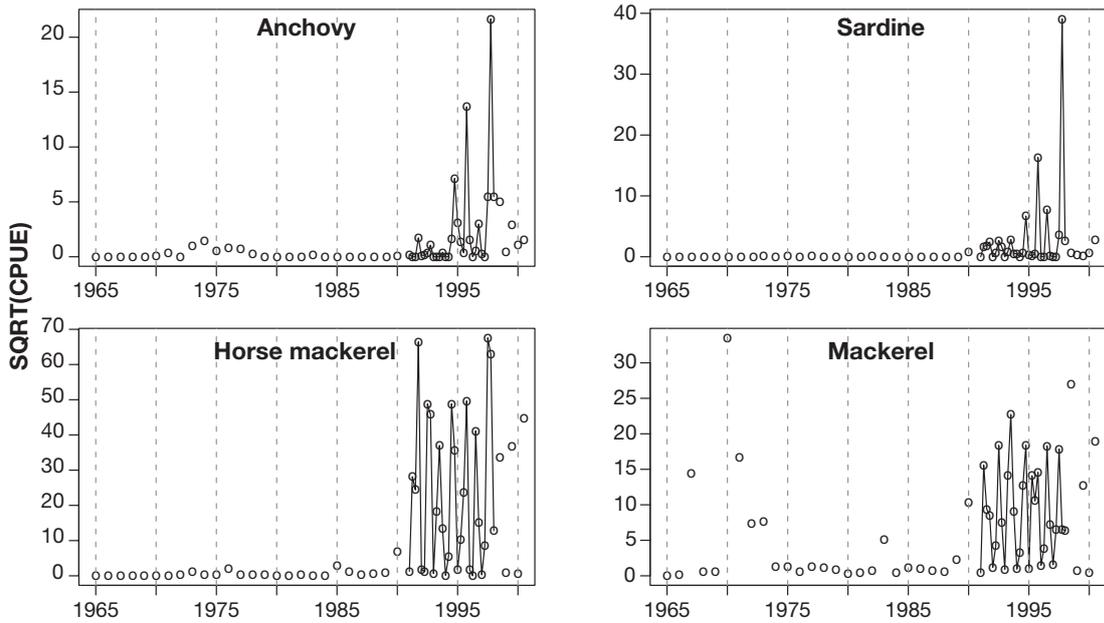


Fig. 3. Numbers of anchovy, sardine, horse mackerel and mackerel caught per hour in ICES fishing Area 4B between 1965 and 2000. Estimates were made using IBTS (International Bottom Trawl Survey) data only and are square-root transformed (SQRT). CPUE: catch per unit effort

Following this incursion, numbers of bluemouth increased up until 2001, and then begun to decline, a process which is continuing into 2004. Bib, John dory, poor cod, red gurnard, red mullet, lesser weever and tub gurnard all have similar long-term patterns (Fig. 4)

and all have increased since 1990. Some of the lesser peaks in the time-series are also consistent between species. Bluemouth, John dory, red gurnard and red mullet abundance, for example, also peaked during the mid-1950s.

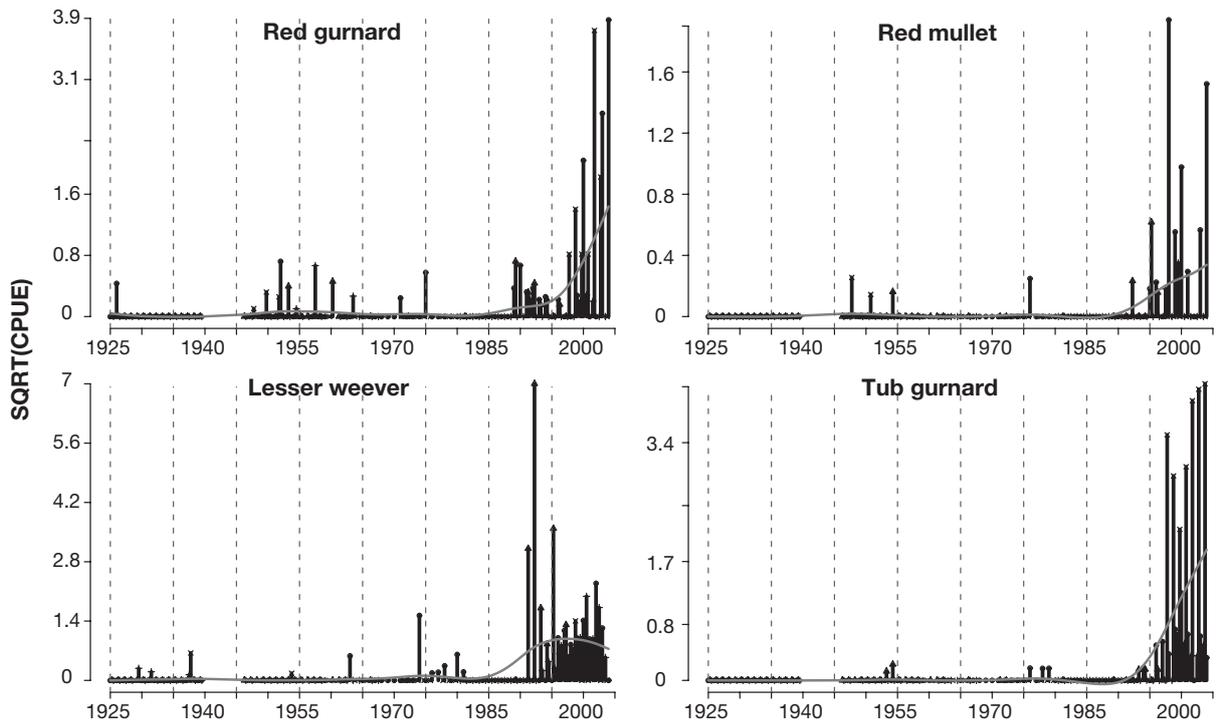


Fig. 4. Numbers of red gurnard, red mullet, lesser weever and tub gurnard caught per hour in ICES Fishing Area 4B between 1925 and 2004. Estimates were made using FRS data only and are square-root transformed (SQRT). CPUE: catch per unit effort. Grey lines represent smooth functions of CPUE data

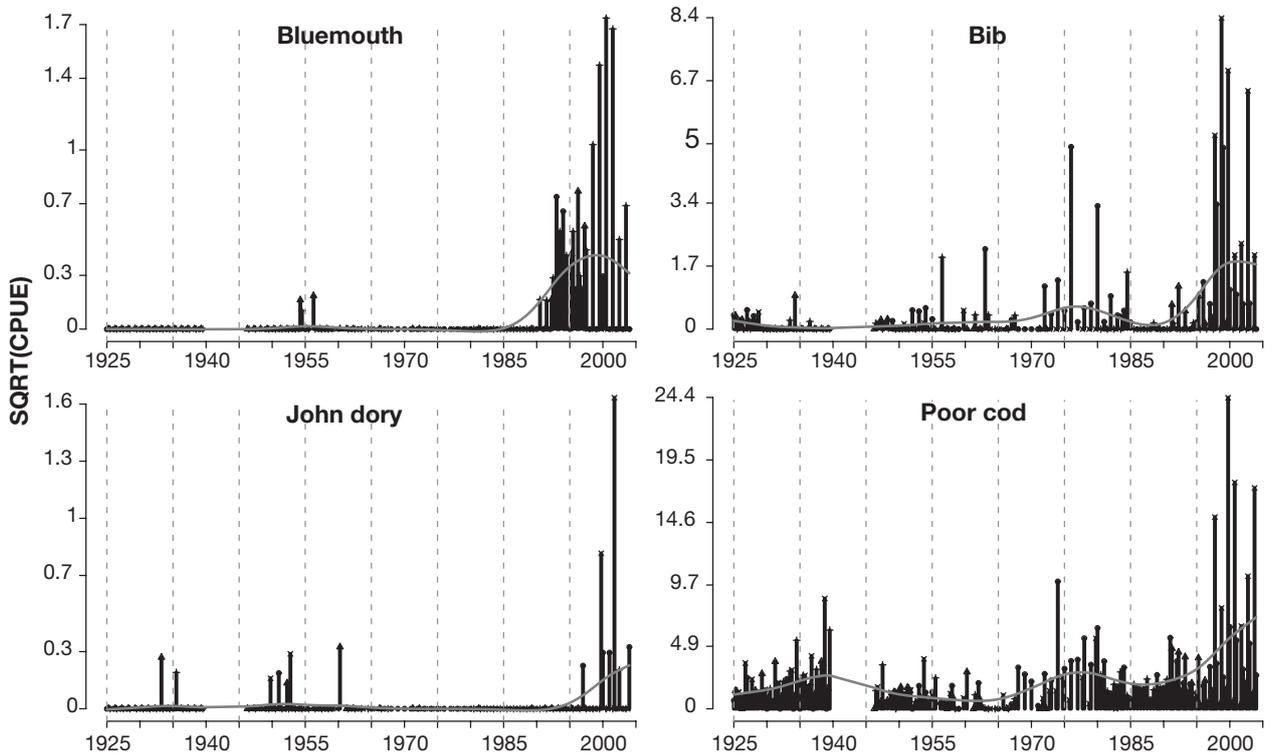


Fig. 5. Numbers of bluemouth, bib, John dory and poor cod caught per hour in ICES Fishing Area 4B between 1925 and 2004. Estimates were made using FRS data only and are square-root transformed (SQRT). CPUE: catch per unit effort. Grey lines represent smooth functions of CPUE data

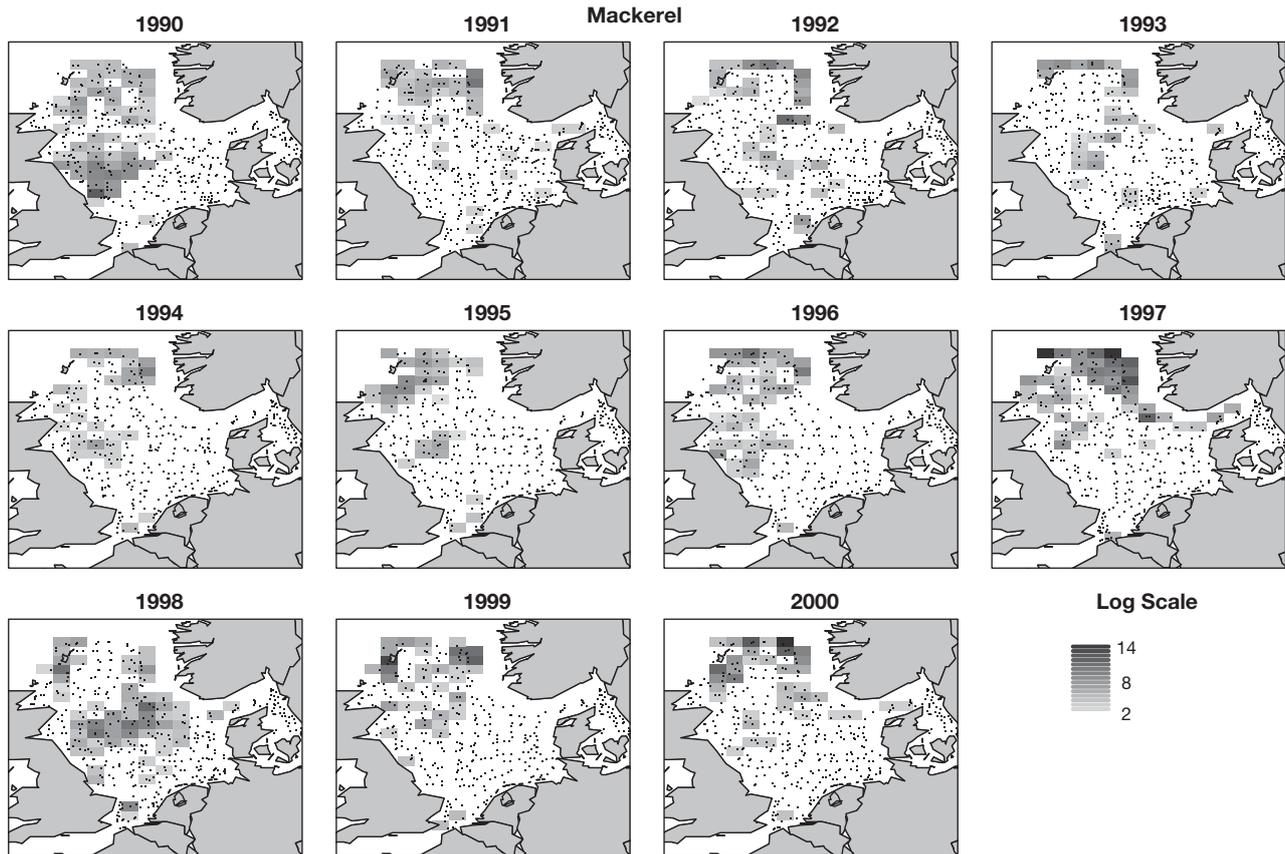


Fig. 6. *Scomber scombrus*. Mackerel abundance (log CPUE) during Quarter 1 (January to March) between 1990 and 2000 estimated using IBTS (International Bottom Trawl Survey) data only. Dots show trawl positions

### Spatial distributions

The spatial distributions of all the fish species studied were plotted on maps for each year and quarter combination. They are complex and it is difficult to produce useful generalisations since the patterns vary inter-annually and seasonally. In spite of this, there were some aspects of geographical distribution that were common to different groups of the southern species. Anchovy, sardine, horse mackerel, mackerel, red mullet and tub gurnard all tended to aggregate along the northeast coast of Britain during Quarter 1, whereas by Quarter 3 they all seemed to have moved into the southeastern North Sea, being present in warm, shallow water along northern coast of Europe (see example of mackerel in Figs. 6 & 7).

The second group comprise bluemouth, John dory, and red gurnard, which are only ever found in the far northern parts of the North Sea in both Quarters 1 and 3 (see Fig. 8). Bib and lesser weever are, in contrast, confined year-round to the southern North Sea (Fig. 9), whereas poor cod is concentrated year-round in the shallow coastal areas of the North Sea all the way along the British eastern and northern continental coasts.

### DISCUSSION AND CONCLUSIONS

The trawl data suggest that profound changes are occurring in the ecosystem of the northern North Sea. Most species classified in this paper as having southern biogeographic affinities show sudden, almost exponential, increases in abundance since the mid-1990s. These increases are common to what is a diverse range of fish species, encompassing a variety of taxa and feeding habits. Furthermore, the fish species described here have different spatial and seasonal patterns of abundance. The lesser weever, for example, is always confined to shallow, southern parts of the North Sea and the bluemouth is a deep-water shelf-edge species, yet both have shown similar increases since 1990. The changes appear to be part of a systematic long-term trend, contradicting the conclusions of Corten & van de Kamp (1996). The main long-term pattern of recent increases is particularly noticeable in the case of anchovy, sardine, red mullet, lesser weever and bluemouth. Poor cod, John dory, horse mackerel, mackerel, tub gurnard, and red gurnard abundances have also risen over the past decade, but there were also peaks in the mid- to late

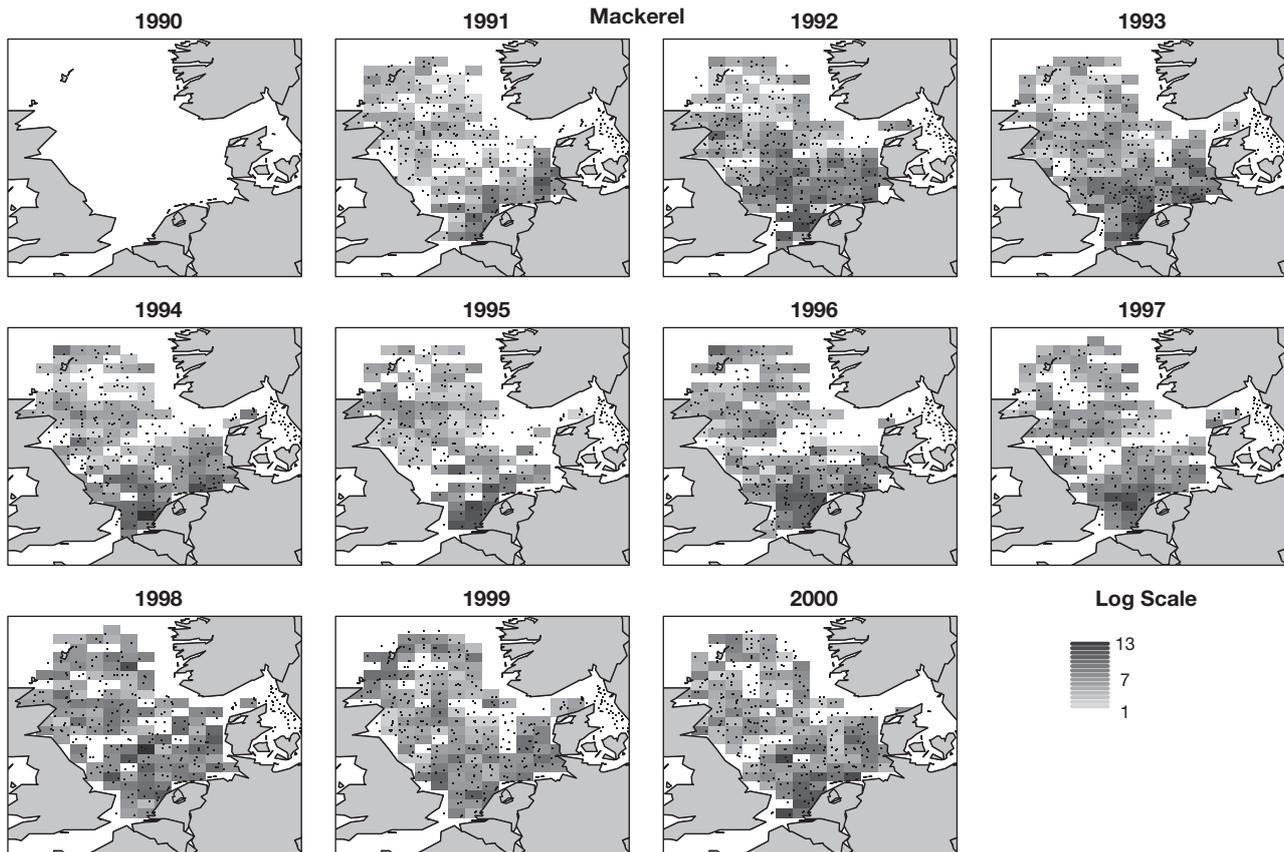


Fig. 7. *Scomber scombrus*. Mackerel abundance during Quarter 3 (July to September) between 1990 and 2000 estimated using IBTS data only. Dots show trawl positions

1950s, and mid-1970s, in addition to those observed more recently.

The IBTS data covering the entire North Sea suggest that anchovy, sardine, horse mackerel, mackerel, red mullet and tub gurnard are concentrated in different areas of the North Sea at different times of the seasonal cycle. In the FRS data, anchovy, sardine and red mullet were only recorded in Quarter 1 with none being caught in Quarter 3 despite extensive surveying at that time of year. This is because, as the IBTS data show, anchovy, sardine and red mullet are in the southeastern North Sea at that time of year. There are various scenarios that might explain these observations. It is possible that the fish migrate north in wintertime and south in summertime, reflecting the seasonal temperature gradient in the North Sea (Beare et al. 2002), which is warmer in the far north in winter due to the influence of the North Atlantic current. Mackerel and horse mackerel are known to make lengthy seasonal migrations (Coombs & Mitchell 1981, Reid et al. 1997, Iversen et al. 1998) and it is possible that anchovy, sardine and red mullet behave similarly. Another possibility is that the fish simply move into the northern North Sea in Quarter

1 via the north coast of Scotland, and into the southern North Sea via the English Channel during Quarter 3. This process would require high catches of these species both along the Scottish west coast, and in the English Channel in the preceding months. When FRS data for the Scottish west coast during Quarter 4 were examined, however, very few anchovy, sardine or red mullet appeared to be present. Data for the English Channel were unavailable during the current study.

The total numbers of mackerel caught per hour have increased since 1990 in ICES Areas 4A, 4B and 4C. By using the FRS data only, which extend further back in time than the IBTS data, it can be seen that there was also an important peak in both Areas 4A and 4B between the mid-1950s to the late 1960s. The decline of the North Sea mackerel stock into the 1970s and 1980s was well documented and, at the time, it was attributed solely to overfishing during autumn and winter. Nevertheless, Postuma (1972) showed that recruitment to the North Sea started to reduce after 1958, i.e. before the period of most intense fishing (Postuma 1972, Corten & Lindley 2003). The mackerel stock collapsed due to overfishing in the early 1970s,

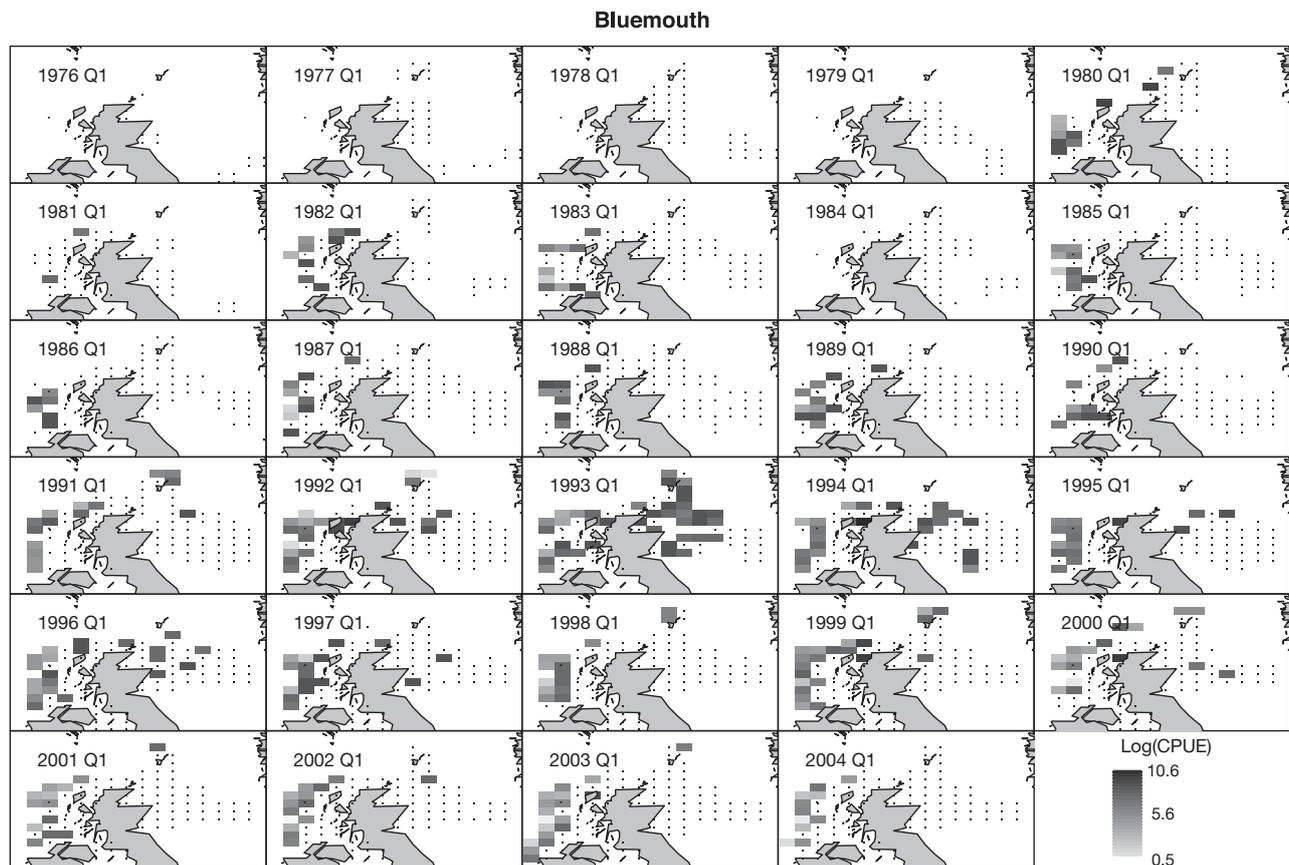


Fig. 8. *Helicolenus dactylopterus*. Bluemouth abundance during Quarter 1 between 1976 and 2004 estimated using FRS survey data only. Black dots represent stations sampled. Log(CPUE): log catch per unit effort

when it subsequently recovered, and effective management has maintained its spawning stock biomass at around 2.5 million tonnes. This has been done by keeping mortality due to fishing at a fairly consistent and low level of between  $F = 0.15$  and  $0.35$ . The increase in mackerel prevalence observed in the North Sea is not due to an overall expansion in the size of the stock, but rather to changing patterns of migration caused perhaps by environmental stimuli.

Since the 1980s, an important commercial fishery for horse mackerel has formed in the northeastern North Sea, which is reflected in the survey data summarised here. The increase in horse mackerel has been connected to a simultaneous increase in 'Phytoplankton Color Index' from Continuous Plankton Recorder data (Reid et al. 2001).

The invasion of the northern North Sea by bluemouth has been noted previously by Dutch scientists (Heessen et al. 1996). This study now extends that time-series to 2004. The main invasion of bluemouth into the North Sea took place in 1991, after which the abundance increased steadily up until the late 1990s. Abundance then began to diminish, and no bluemouth were

recorded in Quarter 1 of 2004 (FRS survey data only available). Examination of the length-frequency data for bluemouth suggests that there have been 2 main recruitments of bluemouth into the northern North Sea. The first occurred in 1991 and the second in 1998. Each 'pulse' is discernible due to the presence of only relatively small fish of less than 7 cm in length. A plot of the length-frequency data in time shows a clear progression of length modes in the bluemouth population. This pattern suggests that the bluemouth that arrived in the northern North Sea in 1991 and 1998 are individuals from one of only 2 cohorts, which then remained on the North Sea grounds to feed and grow. The other, much less likely, possibility is that the wider bluemouth population along the continental shelf edge also consists only of 2 cohorts, and we see a regular overspill of that population. Heessen et al. (1996) suggested that the large pulse of oceanic water that entered the North Sea in 1990 (Heath et al. 1991) might have transported bluemouth eggs and larvae into the area, which then developed gradually within the North Sea. The present study adds further weight to that theory since the influx of small bluemouth individuals noted in 1998 were

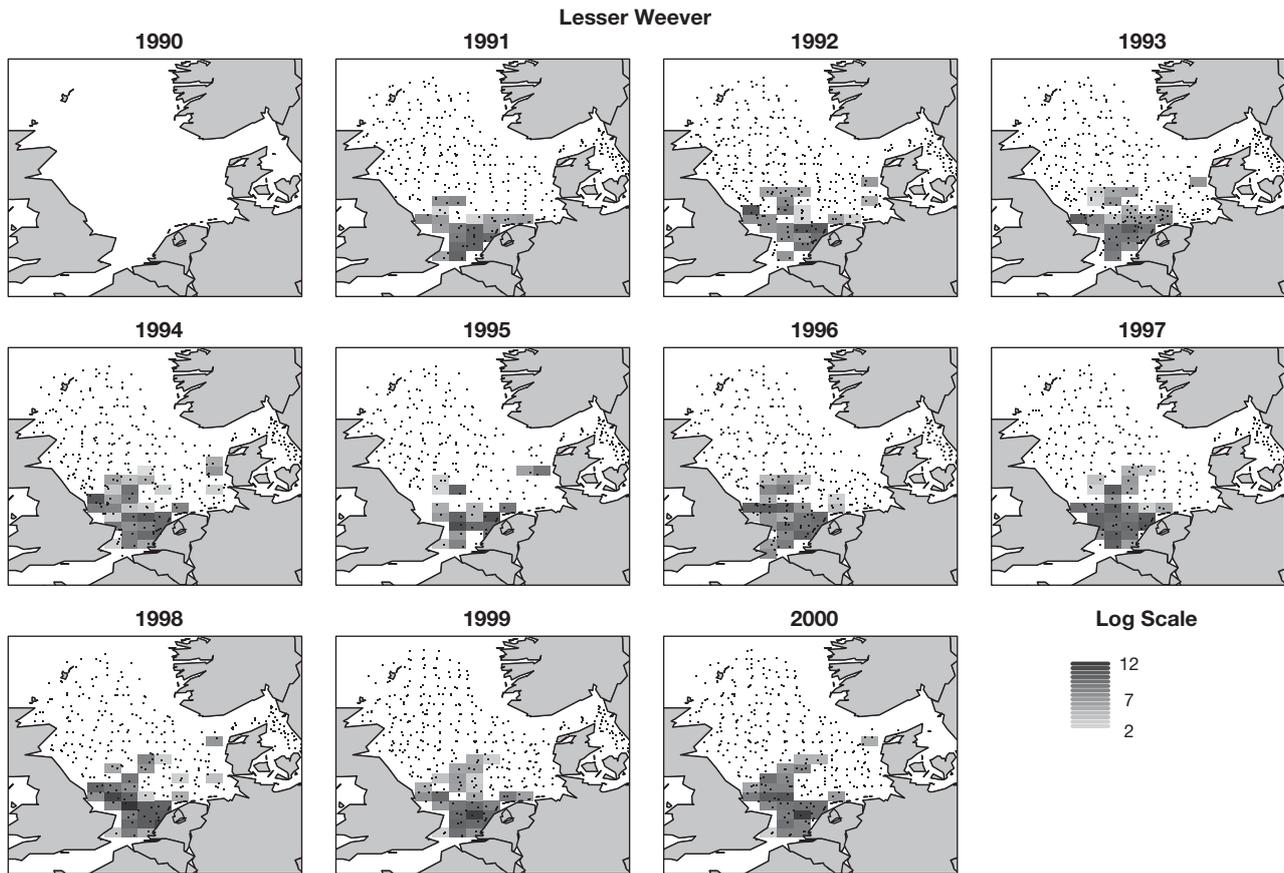


Fig. 9. *Echilichthys vipera*. Abundance of lesser weever during Quarter 3 between 1990 and 2000 estimated using IBTS data only. Dots show trawl positions

probably related to eggs and larvae transported by another large Atlantic input that occurred during November and December 1997 (Edwards et al. 1999).

It is also clear that sea temperatures have risen and it is likely that these rises are related to the population increases of all species examined. During this study, quarterly average sea surface temperatures for the relevant areas were computed and compared to the catch per unit effort data for each species. In only one instance, however (red gurnard, Quarter 1 data, ICES Area 4A), was a weak significant relationship observed ( $R^2 = 49\%$ ). The data are possibly too noisy and sparse for significant correlations to emerge. Alternatively, it could be that temperature-fish relationships are non-linear, or that the effect of temperature on fish abundance interacts with other factors (e.g. windspeed) not investigated. A further point is that such a simple 'correlative' approach is unlikely to work because the effects of potential predictor variables such as temperature on the abundance of relatively long-lived animals such as fish are likely to be cumulative over entire life cycles. In other words, temperature effects might be critical at the egg and

larval stages and relatively unimportant when the fish are adults.

Interpretation of both the FRS and IBTS datasets is hampered by non-random trawl sampling in space and time. It is known that season, depth, time of day, type of fishing gear and research vessel used can all affect or bias the results of trawl surveys. The FRS data series begins in 1925 and encompasses a large range of gear and vessel changes. The IBTS data, on the other hand, are more consistent in terms of the trawl gears used but have been collected by at least 40 different research vessels. During this study, we did not attempt to standardise the relative catch rates of different trawl and gear combinations because we believe this is difficult, if not impossible, to achieve reliably in practice. All IBTS groundfish surveys since 1983 have been done using a standard otter trawl design known as the GOV (Grand Ouverture Verticale). Most of the interesting features described here have occurred since 1990 and they are clearly detectable in both FRS and IBTS datasets. We remain, therefore, confident that the changes described are genuine and not caused, for example, by a sudden increase in fishing efficiency since the mid-1990s.

In conclusion, profound changes are taking place within the fish ecosystem of the North Sea, perhaps in response to climate change. We cannot relate them directly to temperature since the changes observed are complex and also likely to be influenced by associated changes in other components of the marine fauna caused by either natural (weather) or anthropogenic (fishing) fluctuations.

*Acknowledgements.* We would like to thank the many staff at Fisheries Research Services between 1925 and the present day who collected the trawl data upon which this study is based. Ian Thurlbeck (Department of Statistics and Modelling and Modelling Science, Strathclyde University, Glasgow, UK) helped organise the FRS database. Comments on the manuscript from N. Bailey were also valuable. Opensource software packages (Linux, PERL, R & PostGRESQL) were used exclusively for data preparation, interrogation, and visualisation and we would like to thank all who have contributed to their development.

#### LITERATURE CITED

- Alheit J, Hagen E (1997) Long-term climate forcing of European herring and sardine populations. *Fish Oceanogr* 6: 130–139
- Anonymous (2003) Lovelorn spider crabs invade the beaches but kill price. In: Oliver T (ed) *Fishing news*. Heighway, London, p 5
- Armstrong MJ, Dickey-Collas M, McAliskey M, McCurdy W J, Burns CA, Peel JAD (1999) The distribution of anchovy *Eugralis encrasicolus* in the northern Irish Sea from 1991 to 1999. *J Mar Biol Assoc UK* 79:955–956
- Beare DJ, Batten SD, Edwards M, Reid DG (2002) Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. *J Sea Res* 48:29–49
- Beaugrand G, Reid PC, Ibañez F, Planque B (2000) Biodiversity of North Atlantic and North Sea calanoid copepods. *Mar Ecol Prog Ser* 204:299–303
- Coombs SH, Mitchell CE (1981) Long-term trends in the distribution, abundance and seasonal occurrence of larvae of mackerel (*Scomber scombrus* L.) around the British-Isles, 1948–1978. *J Mar Biol Assoc UK* 61:343–358
- Corten A, Lindley JA (2003) The use of CPR data in fisheries research. *Prog Oceanogr* 58:285–300
- Corten A, van de Kamp G (1996) Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind. *ICES J Mar Sci* 53: 1113–1119
- Crick QP, Dudley C, Glue E, Thomson DL (1997) UK birds are laying eggs earlier. *Nature* 388:526
- Cunningham JT (1889–90) Anchovies in the English channel. *J Mar Biol Assoc UK* 1:328–339
- Cushing DH (1984) The gadoid outburst in the North Sea. *J Cons Int Explor Mer* 41:159–166
- deYoung B, Rose GA (1993) On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Can J Fish Aquat Sci* 50:2729–2741
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding data of tree swallows throughout North America. *Proc R Soc Lond B* 266:2487–2490
- Edwards M, John AWG, Hunt HG, Lindley JA (1999) Exceptional influx of oceanic species into the North Sea late 1997. *J Mar Biol Assoc UK* 79:737–739
- Greene CH, Pershing AJ, Conversi A, Planque B and 10 others (2003) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Prog Oceanogr* 58:301–312
- Heath MR, Henderson EW, Slesser G, Woodward EMS (1991) High salinity in the North Sea. *Nature* 352:116
- Heath MR, Backhaus JO, Richardson K, McKenzie E and 11 others (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fish Oceanogr* 8(Suppl 1):163–176
- Heessen HJL, Hislop JRG, Boon TW (1996) Short communication. An invasion of the North Sea by blue-mouth, *Helicolenus dactylopterus* (Pisces, Scorpaenidae). *ICES J Mar Sci* 53(5):874–877
- Hislop JRG (1996) Changes in North Sea gadoid stocks. *ICES J Mar Sci* 53(6):1146–1156
- Iversen SA, Skogen MD, Svendsen E (1998) Influx of Atlantic water and feeding migration of horse mackerel. *ICES CM* 1998/R:18
- Knijn RJ, Boon TW, Heessen HJL, Hislop JRG (eds) (1993) Atlas of North Sea fishes. In: *ICES Cooperative Research Report*, ICES, Copenhagen, p 194–268
- Levitus S, Antonov JI, Boyer TP, Stephens C (2000) Warming of the world ocean. *Science* 287:2225–2229
- McCleery RH, Perrins CM (1998) Temperature and egg-laying trends. *Nature* 391:30–31
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- O'Brien CM, Fox CJ, Planque B, Casey J (2000) Climate variability and North Sea cod. *Nature* 404:142
- Parrish BB, Saville A (1965) The biology of the north-east Atlantic herring populations. *Oceanogr Mar Biol Annu Rev* 3:323–373
- Parrish BB, Saville A (1967) Changes in the fisheries of North Sea and Atlanto-Scandian herring stocks and their causes. *Oceanogr Mar Biol Annu Rev* 5:409–447
- Planque B, Frédou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 56: 2069–2077
- Postuma KH (1972) On the abundance of of mackerel (*Scomber scombrus* L.) in the northern and northeastern North sea in the period 1959–1969. *J Cons Int Explor Mer* 34:455–465
- Quero JC, Du Buit MH, Vayne JJ (1998) Les observations de poissons tropicaux et le rechauffement des eaux dans l'Atlantique européen. *Oceanol Acta* 21:345–351
- Reid DG, Turrell WR, Walsh M, Corten A (1997) Cross shelf processes north of Scotland in relation to the southerly migration of western mackerel. *ICES J Mar Sci* 54: 168–178
- Reid PC, de Fatima Borges M, Svendsen E (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish Res* 50:163–172
- Southward AJ, Boalch GT, Maddock L (1988) Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *J Mar Biol Assoc UK* 68:423–445
- Stebbing ARD, Turk SMT, Wheeler A, Clarke KR (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). *J Mar Biol Assoc UK* 82:177–180
- Swaby SE, Potts GW (1999) The sailfin dory, a first British record. *J Fish Biol* 54:1338–1340