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Climate Variability drives Anchovies and Sardines into North and Baltic Seas

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Abstract

European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are southern, Lusitanian species needing warmer temperatures than boreal ones. After about 40 years of absence, they were observed again in increasing quantities in the North and Baltic Seas. Sardines re-invaded the North Sea around 1990, probably as a response to warmer temperatures associated with the strengthening of the North Atlantic Oscillation (NAO) in the late 1980s. However, surprisingly, increasing numbers of anchovy eggs, larvae, juveniles and adults were recorded only since the mid-1990s, indicating that the temperature rise in the winter months due to the NAO was not sufficient for triggering the re-appearance and spawning of this species in more northern waters. Presumably, changes in current structures and increased summer temperatures since the mid-1990s, in association with the contraction of the subpolar gyre, were responsible for the expansion of the anchovy distributional range into the North Sea. Apparently, climate variability drives anchovies and sardines into North and Baltic Seas. We will discuss, which atmospheric (e.g., AMO, East Atlantic Pattern) and oceanographic (e.g. contraction of subpolar gyre) drivers might be responsible for the occurrence of anchovies and sardines in North and Baltic Seas and other changes observed in fish populations at the same time.

Key words: climate variability, anchovies, sardines, North Sea

Introduction

Recently, a number of reports have been published on the extension of areas of distribution of fish with southern affinities (Quero 1988, Stebbing et al. 2002, Brander et al. 2003, Perry et al. 2005). A spectacular example is the re- invasion of the North Sea by anchovies and sardines since the 1990s (Beare et al. 2004a, Beare et al. 2004b), which have established spawning populations in this northern shelf sea (Alheit et al. 2007), and the penetration of the western Baltic Sea by anchovies which have frequently been captured in the central Baltic Sea over the last years (Draganik and Wyszynski 2004). This northern extension of southern fish species has been frequently linked to climate and warming. North Atlantic marine ecosystems are exposed to the forcing of several climatic phenomena, such as the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO) and global warming. The interdependence between these different climate phenomena and their individual as well as their combined impact on marine ecosystems are poorly understood. The dramatic changes in distribution and abundance of small pelagics seem to be associated with recurrent climatic events or periods, oscillations, rather than with global warming. The objective of this article is to demonstrate, why anchovies and sardines resettled spawning populations in the North Sea, and to elucidate the mechanism of their invasion into this and adjacent regions.

Results

North Sea: Temperature and wind dynamics

During the period 1980-2005, sea temperatures in the North and Baltic seas were determined to a large extent by two climatic oscillations: the NAO and the AMO and associated atmosphere/ocean coupling. In the late 1980s, the NAO index entered a phase of very positive values (Fig. 1) (Hurrell 1995). Variability in the winter NAO (January/February) index is clearly mirrored by surface temperatures of the North Sea (Helgoland Roads Series) and the Intermediate Winter Water (IWW) of the central Baltic Sea (Fig. 1). There is a strikingly coherent increase in the values of all three time series from 1987 to 1989. Since 1989, with the exception of the cold year 1996, the values of all three time series have been comparatively high. The AMO is in a warm phase since the mid-1990s (www.aoml.noaa.gov/phod/amo_faq.php) (Fig. 2).

As temperature dynamics are different in the southern and northern part of the North Sea, annual vertically and spatially average minimum and maximum temperatures were studied separately for both regions for the period from 1980 to 2005. The southern region is defined as the area between Dover Strait and 55°N. The northern region is north of 55°N and separated into an upper (above 30 m depth) and a lower part, based on the observation that 30 m is the average depth of the thermocline in the North Sea.

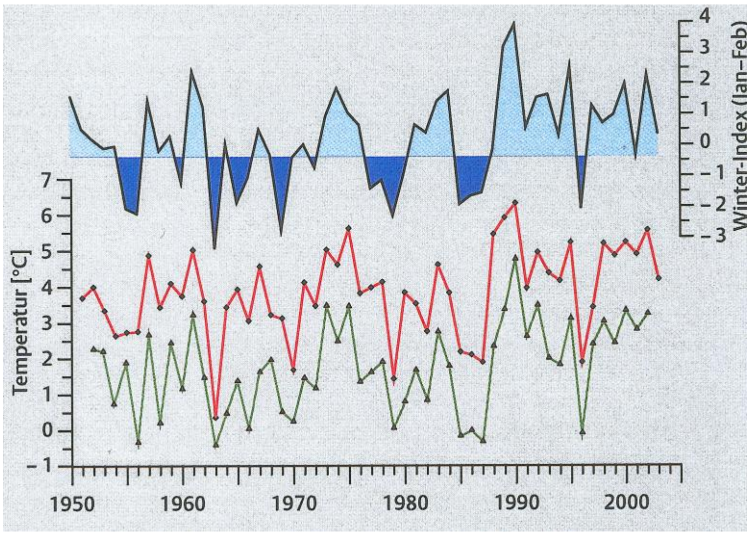


Fig. 1: NAO winter index (modified from http://www.cru.ues.ac.uk), annual temperature minimum (green line) in the Intermediate Winter Water (IWW) of the Bornholm Basin, Station K2, and mean winter SST (red line) (January to March) at Helgoland Roads (Loewe et al. 2003).

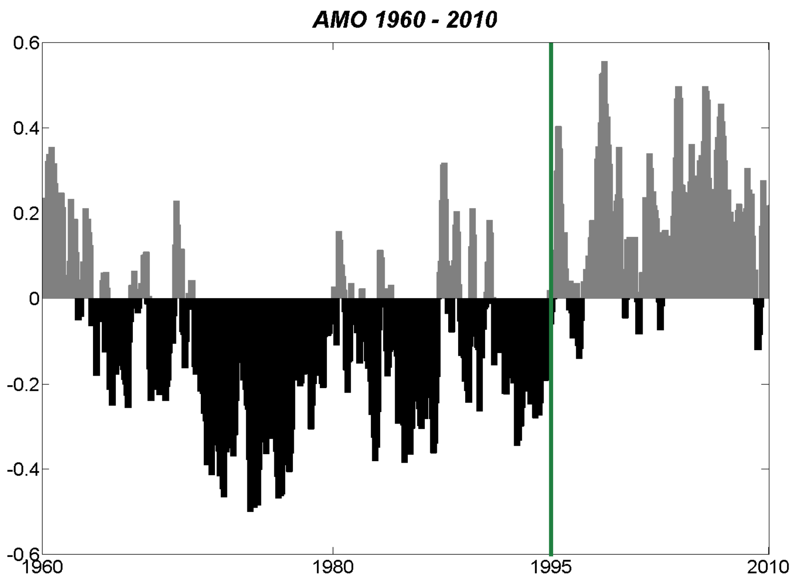


Fig. 2: Atlantic Multidecadal Oscillation. Source: www.esrl.noaa.gov/psd/data/correlation/amon.us.long.data

Southern North Sea

In the late 1980s, minimum temperatures rose rapidly from very low values in 1987 to extremely high values in 1990, which were not recorded in any previous year during the observation period (Fig. 3). Maximum temperatures also increased, but not to such an extent. Minimum temperatures decreased thereafter and maximum temperatures did not change much until winter 1994/95, when both increased again and maximum temperatures reached values of over 18°C, which had not been recorded previously. With the exception of 1996, minimum and maximum temperatures stayed on high values. Maximum temperatures were exceptionally high and reached 18.8°C in summer 2003.

Northern North Sea, above thermocline

Temperature dynamics from 1985 to 1990 were as in the southern North Sea, on a lower level, of course (Fig. 4). A different situation was observed in the mid-1990s. The winters 1993/94 and 1995/96 were very cold with a rather warm winter 1994/95. However, summer 1995 was not as outstanding as in the southern North Sea. An exceptionally period of very warm summers began in 1997.

Northern North Sea, below thermocline

Minimum and maximum temperatures increased from 1987 until 1989 and stayed on high levels until 1992 (Fig. 5). Then, minimum temperatures were rather low until 1996/97, even in 1995/96, when compared to the previous period. However, in summer 1995, maximum temperatures were rather high and they have increased steadily since summer 1996, but showed unprecedented values only since 2003.

Heat content

The annual and the seasonal mean heat content of the North Sea is shown in Fig. 6. For the annual mean, values vary between about 330×10^5 J m^{-3} and 366×10^5 J m^{-3}. Seasonally, the heat content is largest in the summer months and smallest in winter, while inter-annual variability is largest in winter (46.6×10^5 J m^{-3}) and spring seasons (47.5×10^5 J m^{-3}). For summer and autumn, inter-annual variability is somewhat smaller (31.6×10^5 J m^{-3} and 37.5×10^5 J m^{-3}, respectively). As for sea surface temperatures, there is no noticeable trend until the early 1980s, a stronger positive trend can be seen afterwards. Another interesting feature is the fact, that since 1997 the summers tend to show a stronger warming than the months of the other seasons, which is different from the situation in the years from 1987 to 1994, when major warming occurs particularly in the winter months.

Wind data

A comparison of the wind density functions of the years 1988/89, 1994/95 and 1995/96 (Dec – Feb) with the long-term mean from 1970 to 1985 (Fig. 7) shows, that there was an extreme increase in west-southwesterly winds in winter 1988/89 and southwesterly winds in 1994/95, because of a strong NAO index in these winters (Fig. 1). In contrast, in winter 1995/96, westerly winds were extremely weak, whereas the southeasterly wind density component shows a strong positive anomaly, in agreement with the low NAO index, which was observed in this winter for the last time (Fig. 1).

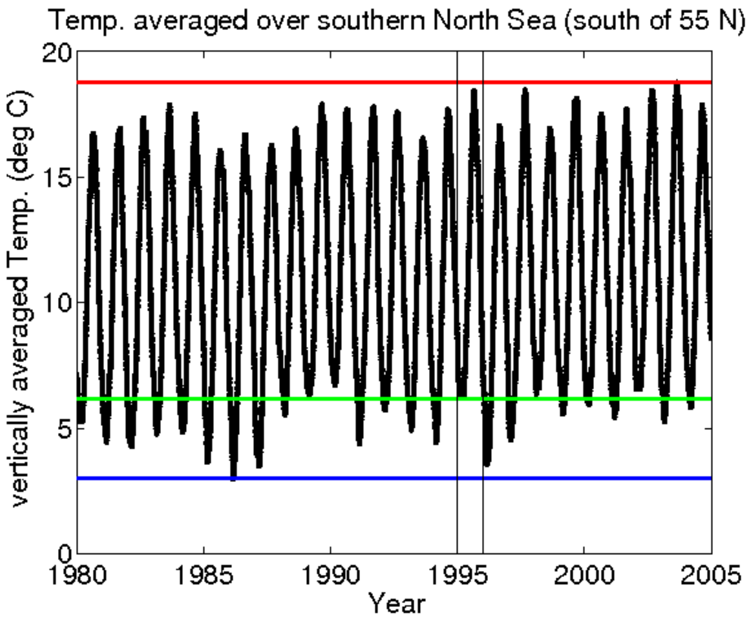


Fig. 3: Vertically and spatially averaged temperature for southern North Sea. The red and blue lines are annual maximum and minimum temperatures. The green line depicts minimum winter temperature in 1995. The year 1995 is marked by two black lines.

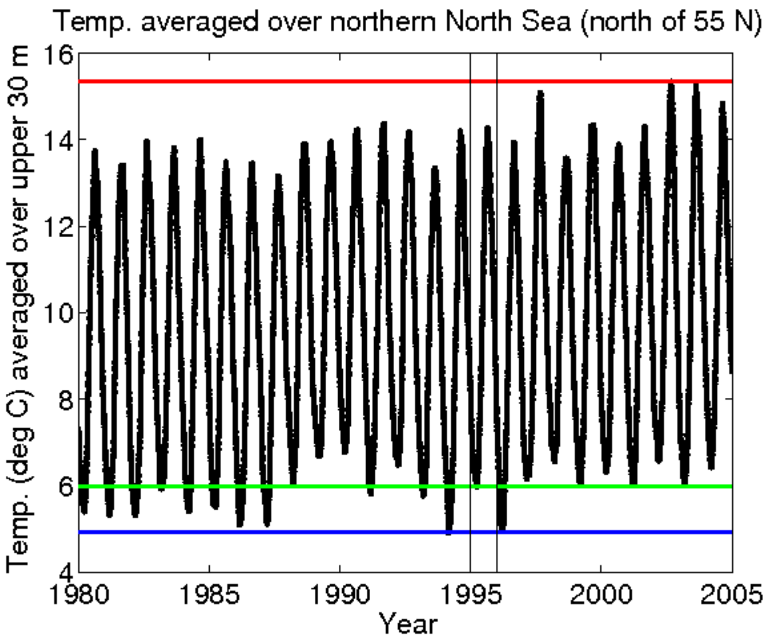


Fig. 4: Vertically and spatially averaged temperature for northern North Sea, above thermocline. For explanation see legend in Fig. 3.

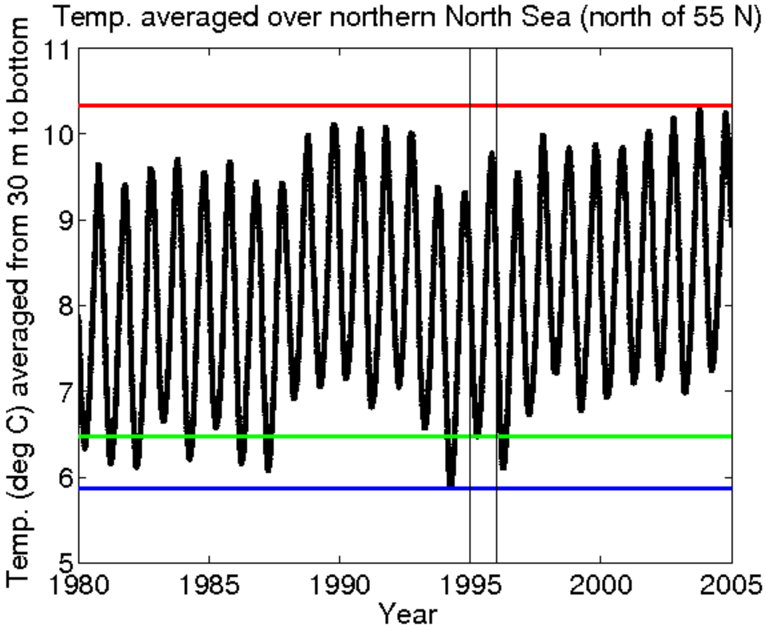


Fig. 5: Vertically and spatially averaged temperature for northern North Sea, below thermocline. For explanation see legend in Fig. 3.

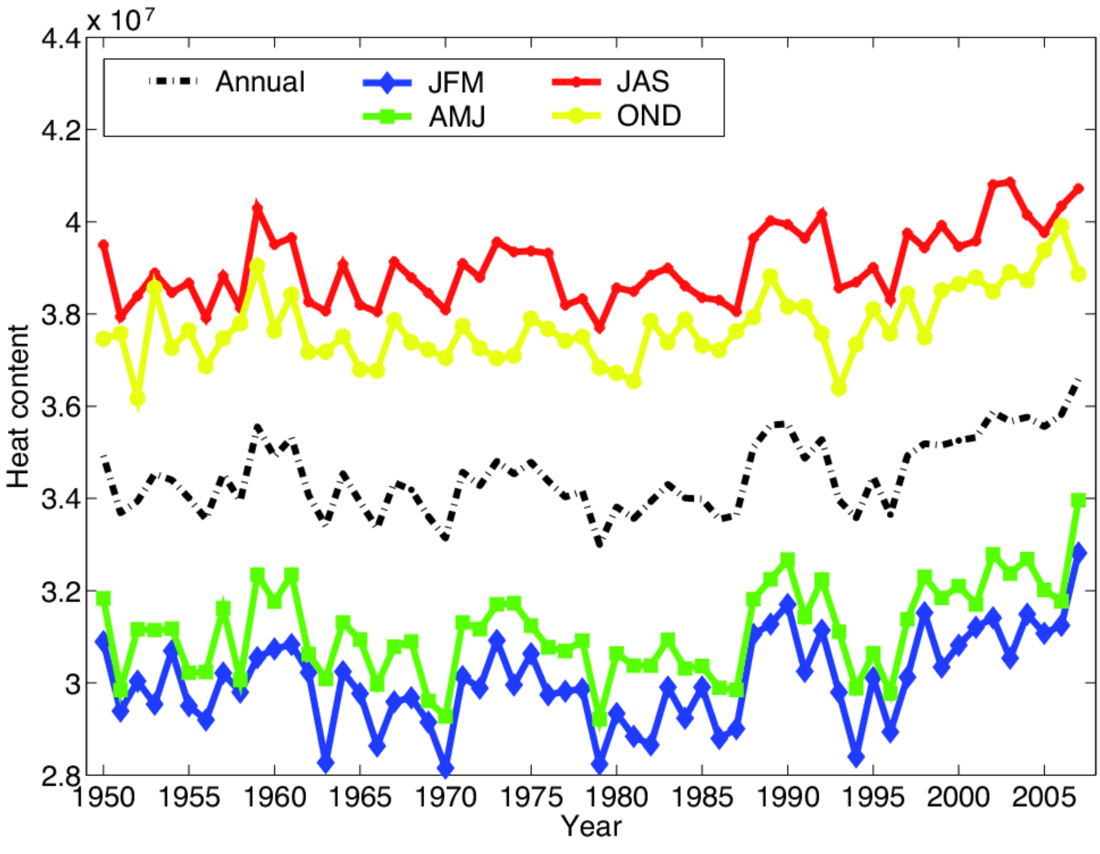


Fig. 6: Annual (black) and seasonal (JFM-blue, AMJ-green, JAS-red, OND-yellow) mean North Sea heat content in 10^7 J m^{-3}.

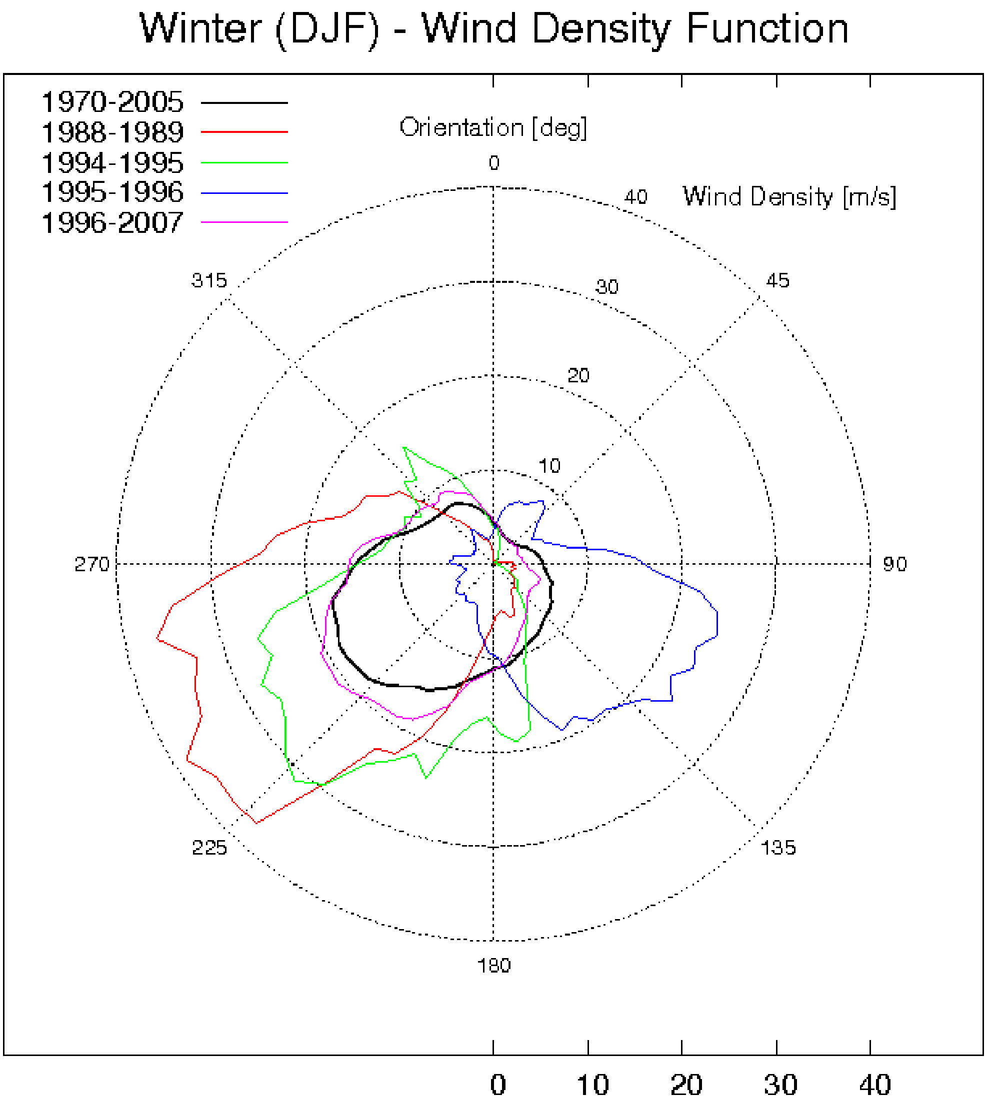


Fig. 7: Wind density function for winter (Dec - Feb) averaged over the entire North Sea.

Occurrence of anchovies and sardines in North Sea

1. Adults

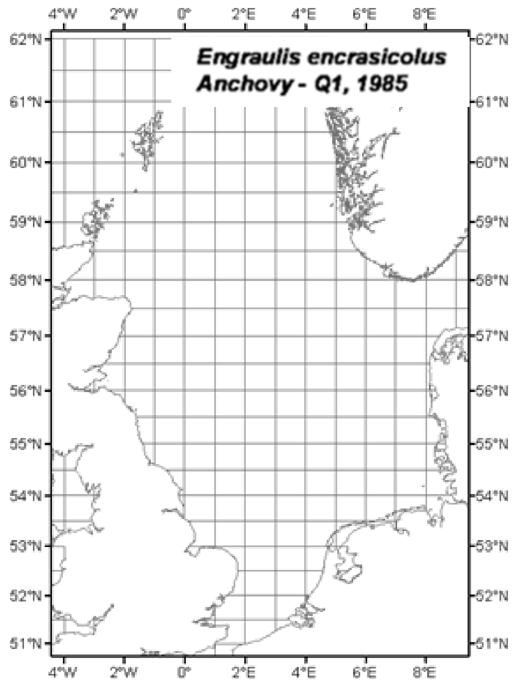
Open sea: Anchovy and sardine were not found on the International Bottom Trawl Survey (IBTS) since 1970 in the entire North Sea, except for small numbers encountered occasionally. They were collected in larger quantities since 1990 (sardines) and 1995 (anchovies) and thereafter (Beare et al. 2004a, b) (Fig. 8). In quarter 1, they tended to be aggregated along the east coast of Britain, whereas in quarter 3, they had moved to the southeastern North Sea (Beare et al. 2004a, b).

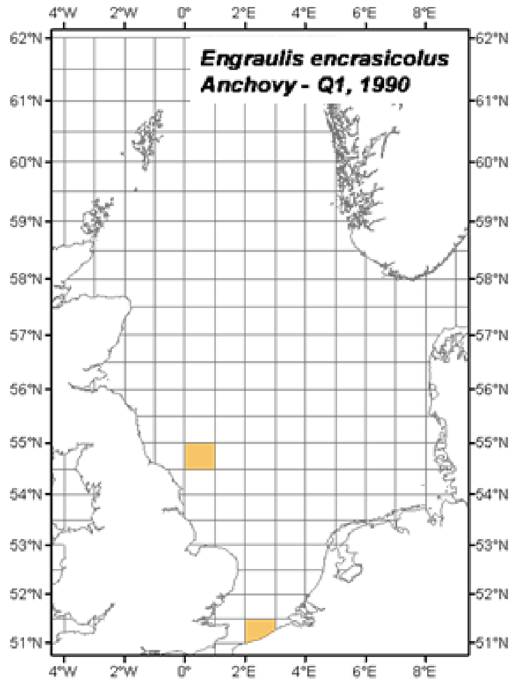
Wadden Sea: Occurrence of anchovies and sardines in the eastern Wadden Sea off the German coast was studied by collecting fish with a Hamen net since 1991 in the Meldorf Bight. Anchovies were recorded for the first time in 1997 and then every year until 2002, when time series ended (Fig. 9) (Vorberg 2003), (exception: 1992, Fig. 10).

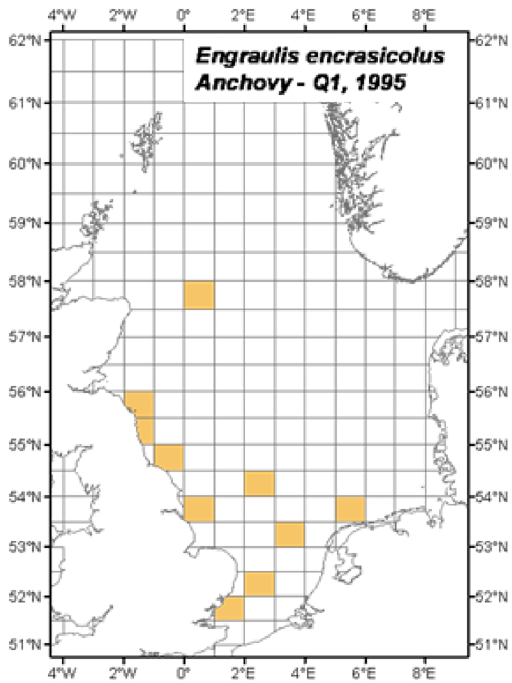
2. Juveniles

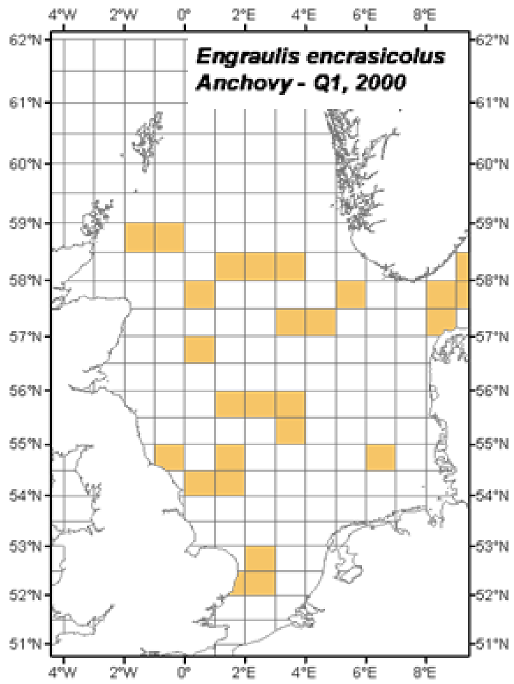
Wadden Sea: Juveniles were encountered at various sampling points of the Wadden Sea programme from 2002 to 2007, for example in August at Meldorf Bight with sizes between 5 to 7 cm (Fig. 10) (Vorberg 2003).

3. Eggs and Larvae at Helgoland Roads, CalCOFI net: The CalCOFI-net collections from the Helgoland roads time series were analyzed for larvae of sprat, anchovy and sardine









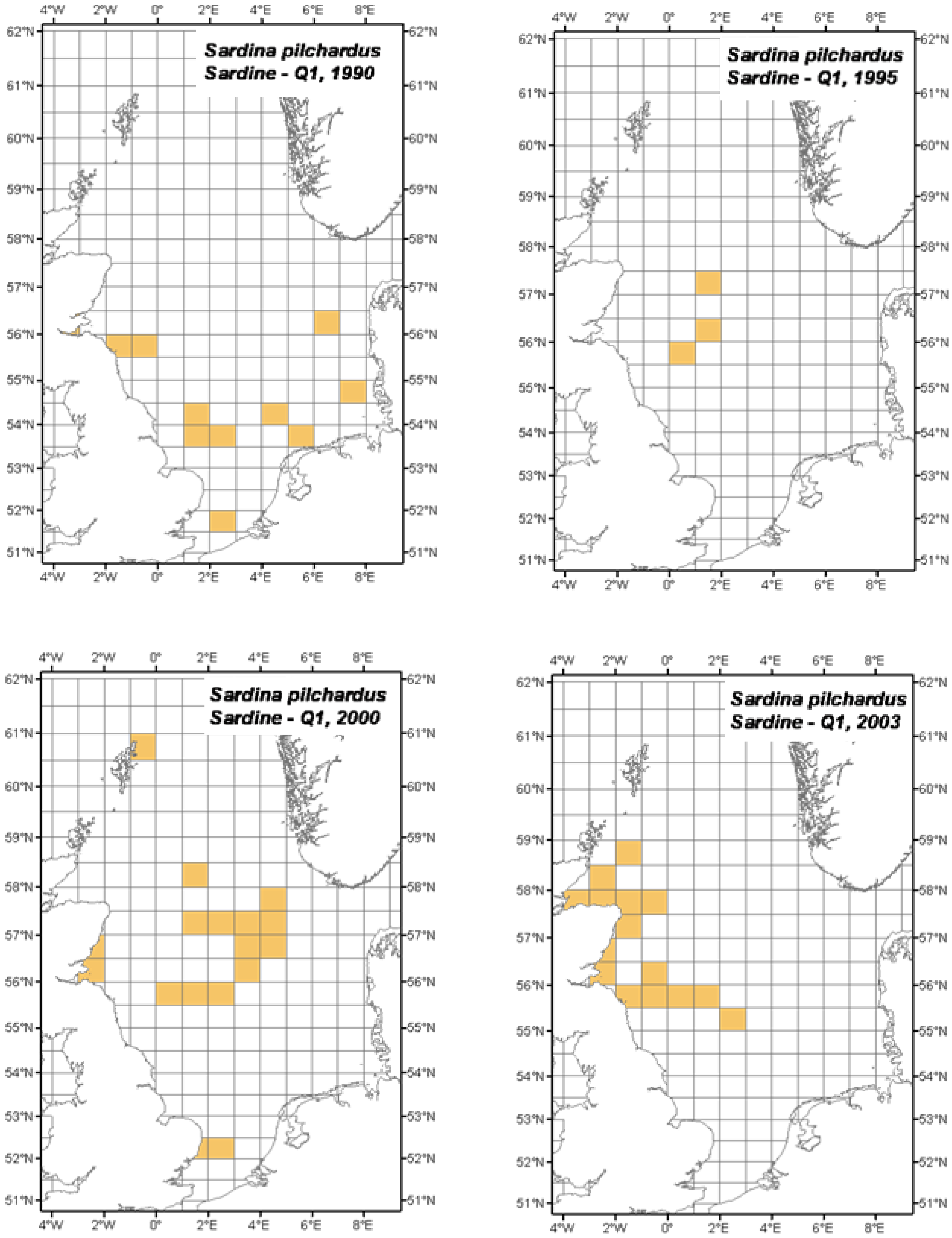


Fig. 8: Occurrence of adult anchovy and sardine in the North Sea (Quarter 1).

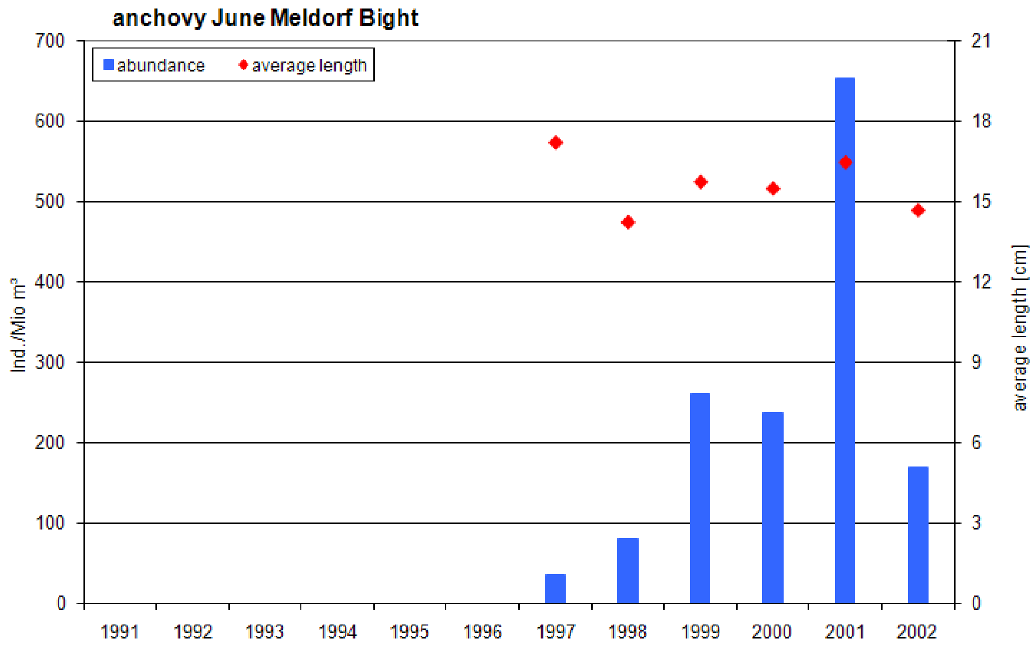


Fig. 9: Adult anchovy collected in Meldorf Bight, eastern Wadden Sea off German coast.

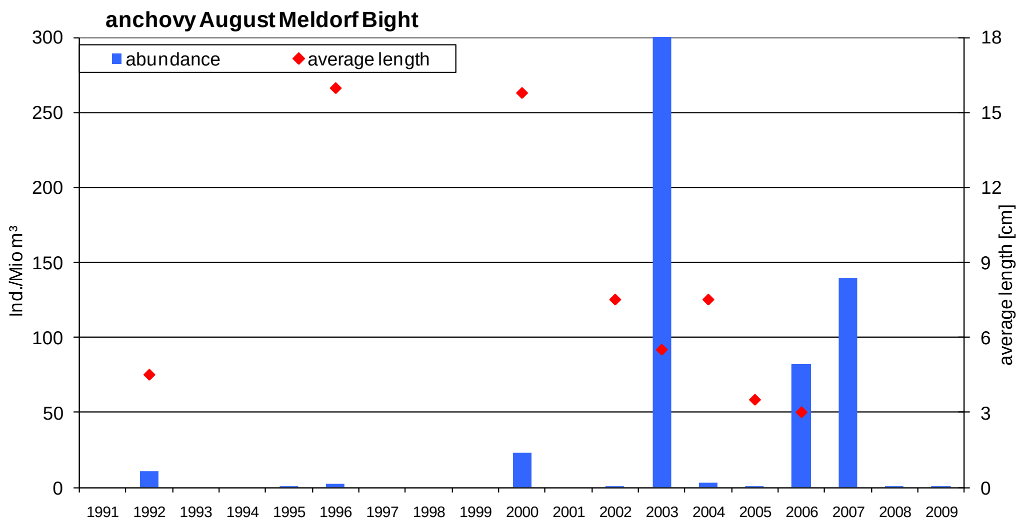


Fig. 10: Juvenile and postlarval anchovy collected in Meldorf Bight, eastern Wadden Sea off German coast.

(1990, 1993-1999) and anchovy and sardine eggs (1993-1995, 1998-1999). Sardine larvae were found in larger quantities throughout the entire sampling period from June to August with a peak usually around late June-early July (Fig. 11). The highest numbers were collected in 1990, 1996 and 1999. No sardine larvae were recorded in April, hardly any in May. No anchovy larvae were encountered from 1990-1993, very small numbers in 1994 and moderate numbers in 1996, 1998 and 1999 (Fig. 12). No sardine eggs were encountered in 1993 and very few in 1994. Larger quantities were sampled in 1995 and, particularly, in 1999 (Fig. 13). Very low quantities of anchovy eggs were found in 1993 and 1994 (Fig. 14). Numbers had increased considerably in 1995, 1998 and 1999. They were encountered from late June until

August. Sardine spawn was found throughout the entire sampling period with considerably increasing numbers since 1996. Anchovy spawn was encountered in larger quantities since 1995. For reasons of comparison, sprat larvae were sorted from the same samples. In contrast to anchovies and sardines, their abundances were significantly higher before 1996 (Fig. 15).

German Bight, GLOBEC Project: Between 2003 and 2005, during the German GLOBEC Project, anchovy and sardine eggs and larvae were regularly encountered in large quantities in the German Bight (Fig. 16) (Alheit et al. 2007).

Wadden Sea: Anchovy postlarvae of 3.5-4.0 cm length were found in 2002-2004 (Fig. 9).

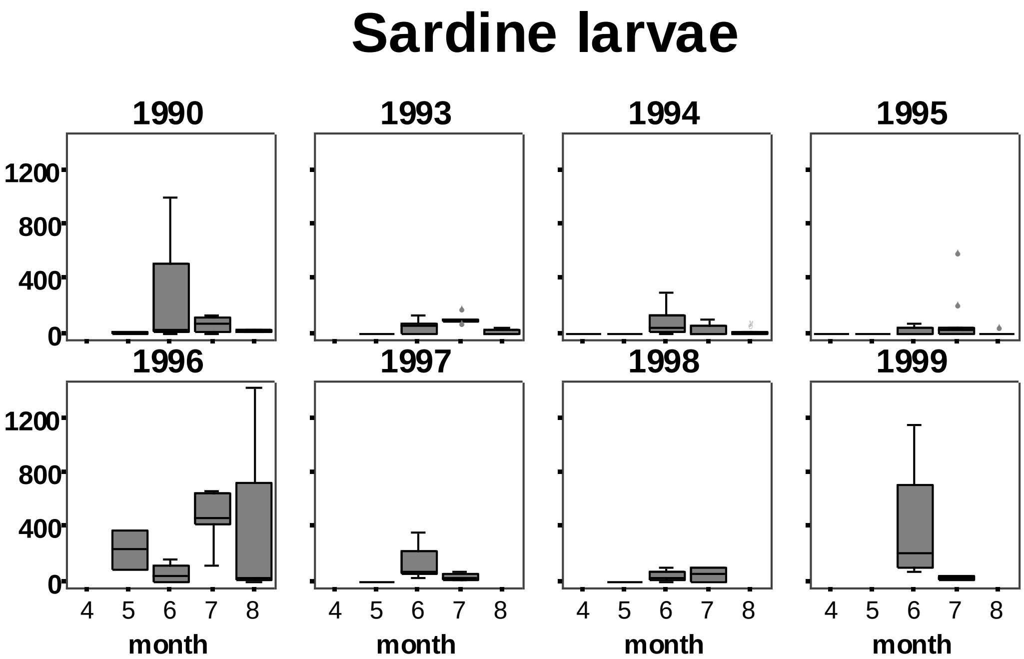


Fig. 11: Abundances of sardine larvae (1000/m^3) collected at Helgoland with CalCOFI net.

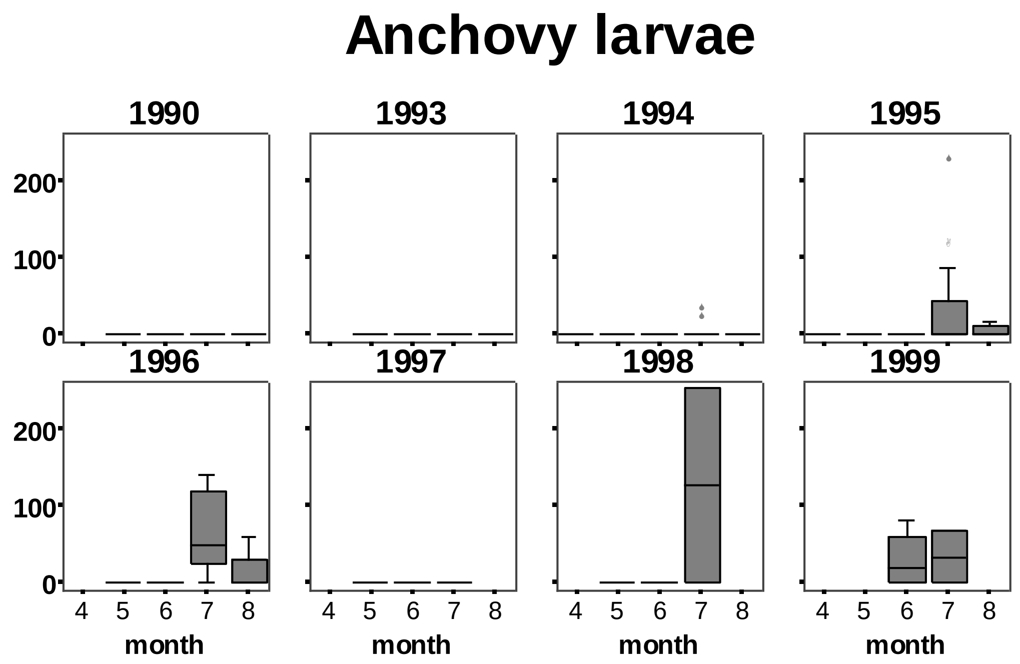


Fig. 12: Abundances of anchovy larvae (1000/m^3) collected at Helgoland with CalCOFI net.

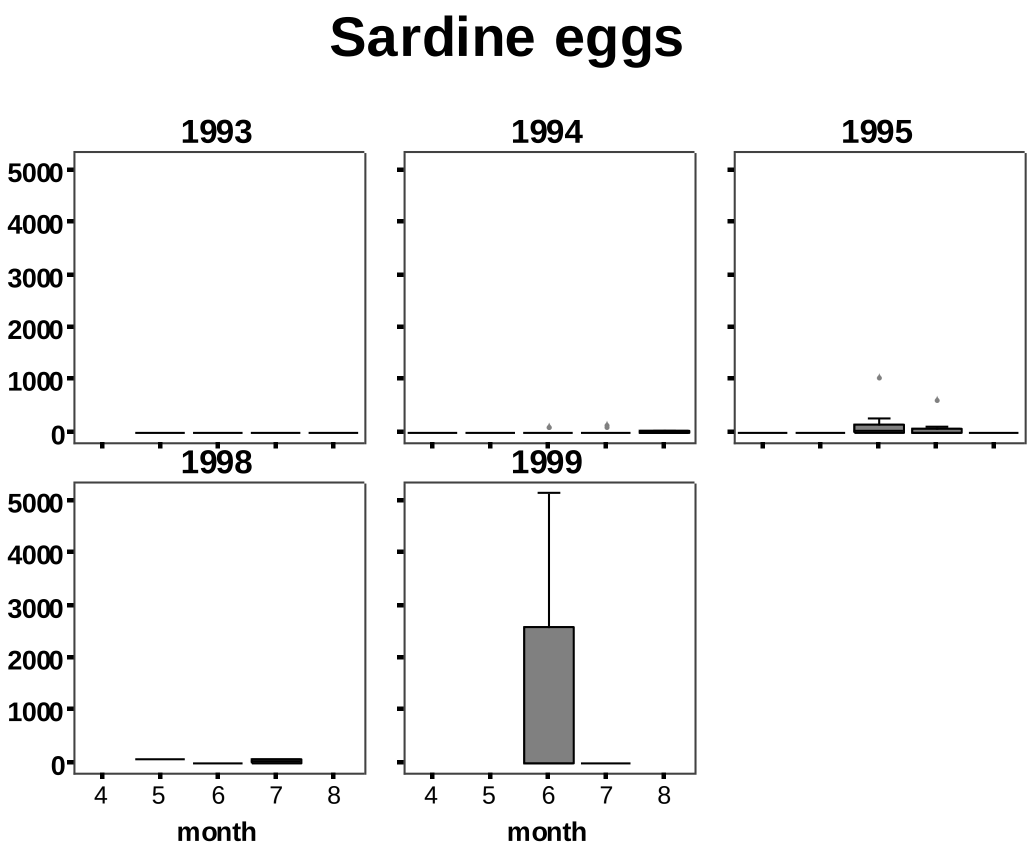


Fig. 13: Abundances of sardine eggs (1000/m^3) collected at Helgoland with CalCOFI net.

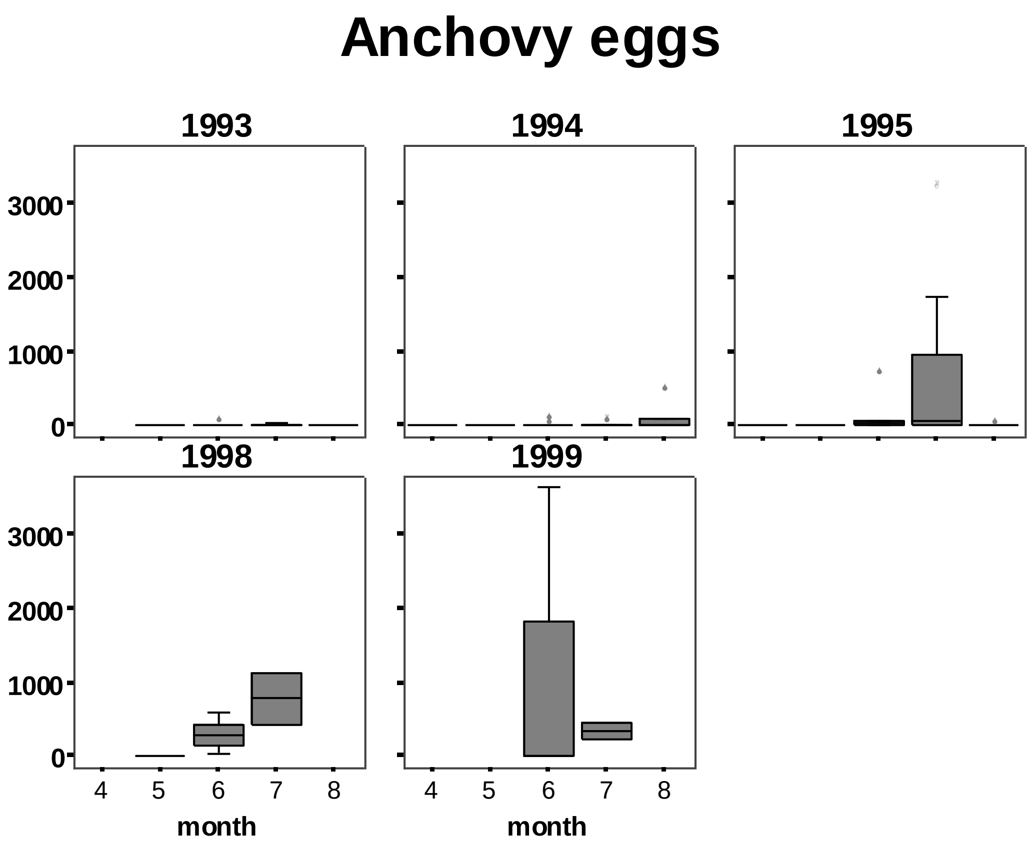


Fig. 14: Abundances of anchovy eggs (1000/m^3) collected at Helgoland with CalCOFI net.

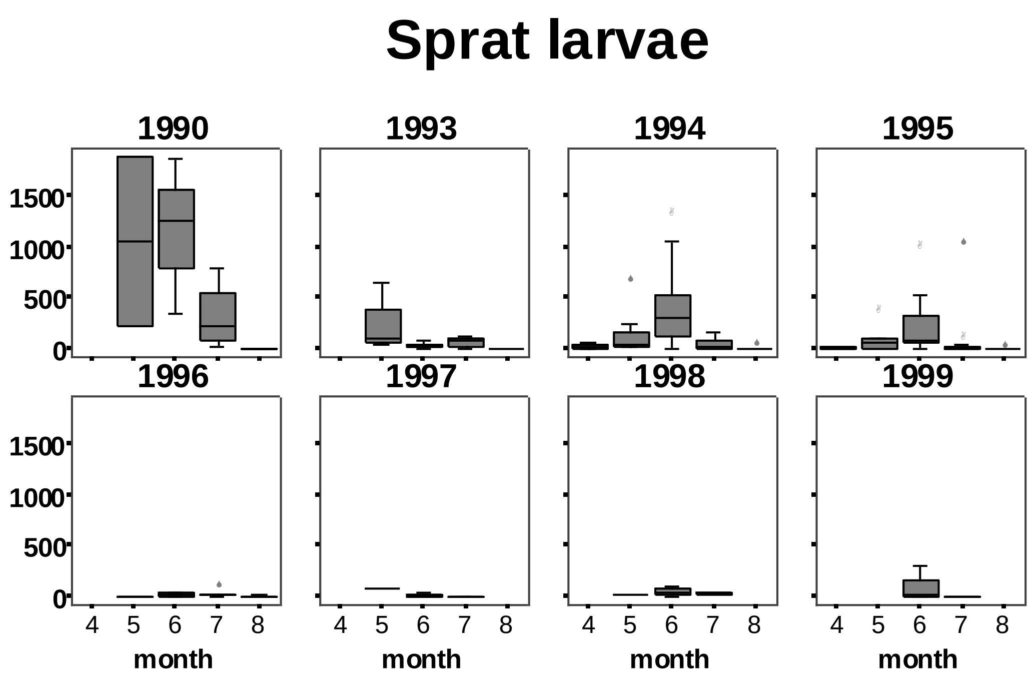


Fig. 15: Abundances of sprat larvae (1000/m^3) collected at Helgoland with CalCOFI net.

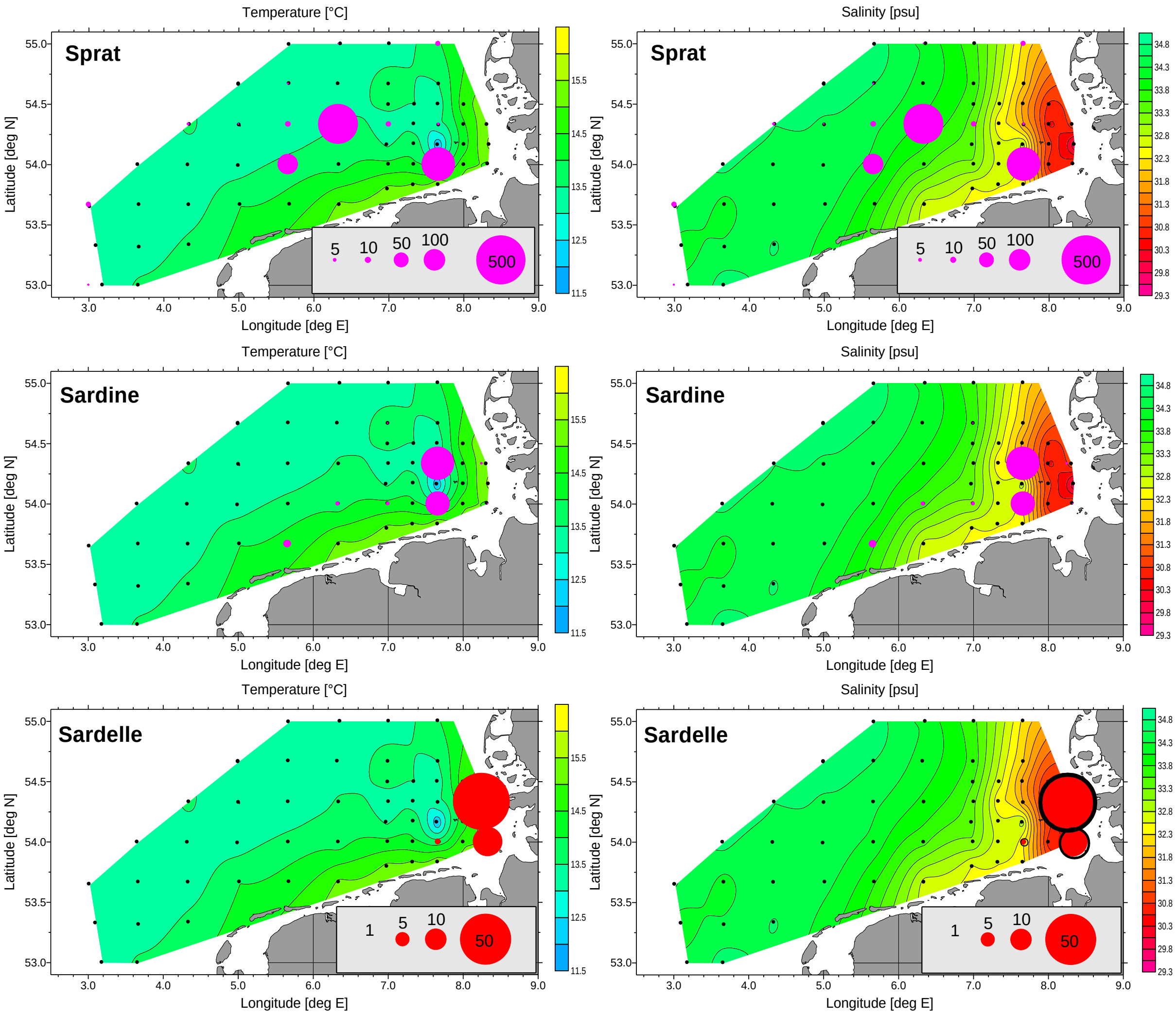


Fig. 16: Distribution of sprat, anchovy and sardine eggs 18 – 23 June 2004.

Occurrence of anchovies and sardines Baltic Sea, Skagerrak, Kattegat and English Channel

Skagerrak, Kattegat: International Beam Trawl Surveys (IBTS) were carried out in SD 20 and 21 in the 1st quarter since 1972 and in the 3rd quarter since 1991. Anchovies were found in a short period from 1974-1978 in the 1st quarter (Fig. 17). After not encountering anchovies for 17 years, they were caught again in 1995, in the 1st quarter, and then regularly until 2007 (end of time series). Similarly, they were collected in the 3rd quarter over the same period (except in 2000, when no survey was caried out in SD 21) with the largest quantities between 2003 to 2006. Sardines were found sporadically between 2001 and 2007 (Fig. 17).
Baltic Proper: Poland conducts two annual trawl surveys in its EEZ, in autumn and winter. The first single specimen of anchovy was found in 1996. More anchovies were encountered in 1998 and larger quantities in 2003 and 2004 (Draganik and Wyszyński 2004).

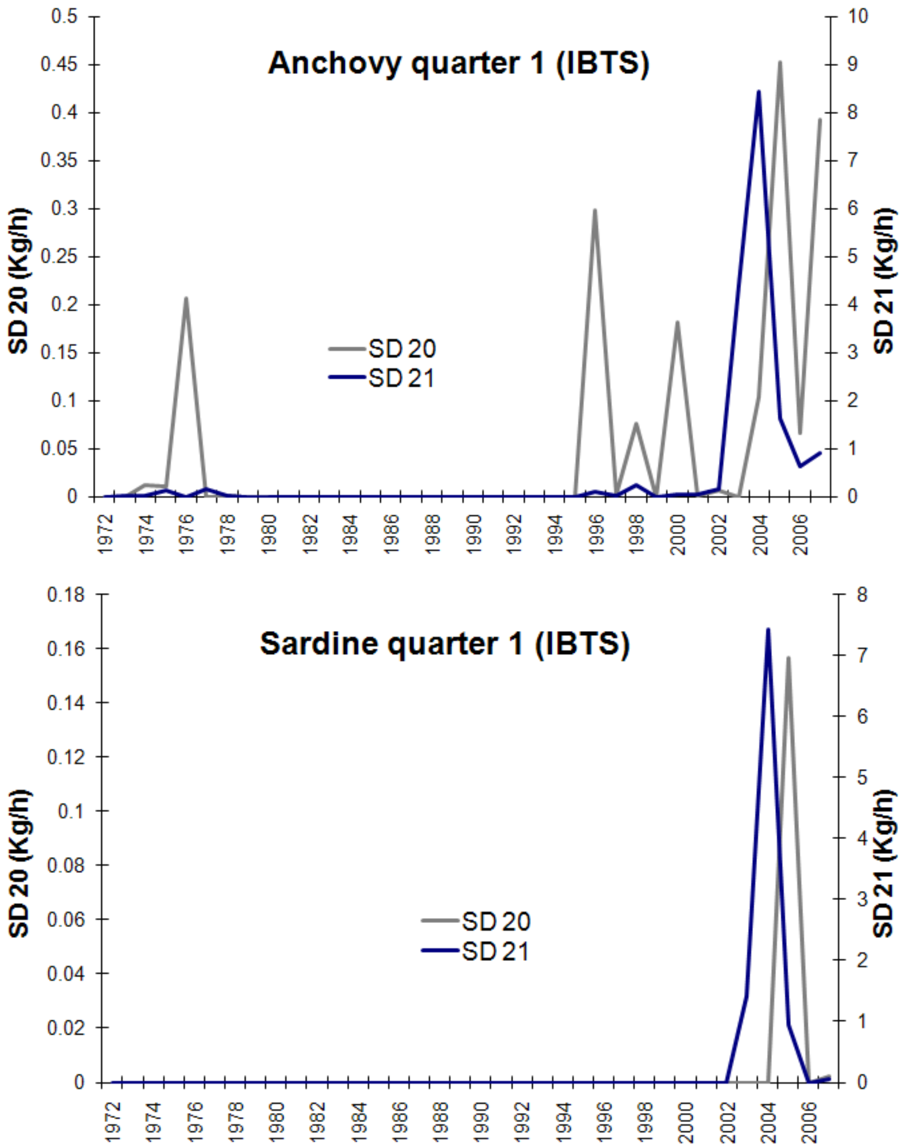


Fig. 17: Occurrence of anchovies and sardines in samples of ICES International Beam Trawl Survey in Skagerrak and Kattegat.

English Channel, Irish Sea

Irish Sea: Since 1995, research cruise catches of anchovies have increased considerably. Also, anchovies have become more widespread in the region (Armstrong and Dickey-Collas 1999).

English Channel: Coombs et al. (2010) report relatively high catches of sardines from 1988 – 1995 and particularly low ones from 2003 – 2007. Sardine eggs have been found consistently since the late 1988 at the western English Channel at station L5, whereby the abundance of autumn spawned eggs has increased conspicuously since 1995 (Coombs et al . 2010).

Discussion

Up to the late 1980s, the northern boundary of anchovies and sardines was in the English Channel (sardines) and in Dutch waters in the southwestern corner of the North Sea (anchovies). Sardines have always been spawning in the Channel (Coombs et al. 2005, 2010) and the same is probably true for anchovies in the Schelde estuary and, until 1932 when it was closed by a dam, in the Zuider Sea (Boddeke and Vingerhood 1996). Stray specimen of both species have been observed occasionally at other areas of the North Sea or the western Baltic, but large quantities were not reported since the 1960s. Recent results demonstrate convincingly that, during the 1990s, these Lusitanian species, anchovy and sardine, have successfully invaded the entire North Sea and adjacent regions, such as the Irish Sea, Skagerrak, Kattegat and western and central Baltic. Historical reports show that similar invasions have occurred in the late 19th and the early 20th century (Aurich 1950, 1953). Since the 1990s, anchovy and sardine are found all over the North Sea and complete their entire life cycle there, as can be concluded from multiple observations reporting eggs, larvae, juveniles, adults and ripe, running female and male anchovies and sardines. Spawning has been reported only from the southern North Sea, in the case of the anchovy particularly from the Dutch and German parts of the Wadden Sea (Boddeke and Vingerhood 1996; Alheit et al. 2007). Interestingly, whereas sardine larvae (Fig. 11) and adults (Fig. 8) have been found in larger quantities from about 1990 on, increased abundances of anchovy larvae (Fig. 12) and adults (Fig. 8) were reported several years later, in the mid-1990s.

It is assumed that habitat expansion and contraction and migrations of clupeoid fishes are linked to climate and that climatic oscillations on the decadal and multidecadal scale might be the drivers (Hunter and Alheit 1995, Alheit and Hagen 1997, Alheit et al. 2007). The most pronounced climate signal over the North Atlantic on decadal time scales is the North Atlantic Oscillation (Hurrell and Deser 2010). The NAO index increased conspicuously in the late 1980s with strong consequences for the North Sea ecosystem. Thereafter, SSTs were elevated (Fig. 1), the average monthly wind speed increased from October to March, and the wind showed a preference for west-southwesterly directions (Siegismund and Schrum 2001). These west-southwesterly winds provided a mild winter climate for central and northern Europe. The resulting increase of the annual SSTs in the North Sea from 1987-1995 was mainly based on elevated winter temperatures (Fig. 3, 4, 5) (Loewe 2009). The increased strength of westerly winds is also supposed to have increased the inflow of oceanic water into the northern North Sea (Drinkwater et al. 2003, Reid et al. 2003). Around the time of the increase of the NAO index, the North Sea experienced rapid changes in many biological and ecosystem processes including the linkages between different components of the ecosystem, such as phytoplankton, zooplankton, benthos, fish and seabirds. The North Sea plankton community directly responded to the environmental changes in the late 1980s. The zooplankton community shifted from a typical cold-boreal community to a warm-temperate community (Beaugrand et al. 2002, Beaugrand et al. 2004). These changes were associated with a shift in the proportion of cold and warm water species of *Calanus* (Reid et al. 2003), an influx of oceanic species (Lindley et al. 1990), an increase in warm water zooplankton species (Beaugrand et al. 2002) and a shift from holoplankton to meroplankton dominance (Kirby et al. 2007). The increasing abundance of meroplankton, particularly of echinoderm larvae, was related to warmer conditions occurring earlier in the year and increased phytoplankton abundance since the late 1980s. Also, a significant decrease of zooplankton biomass was observed (Beaugrand 2004), due to the decline of some of the key taxa typical of cold waters. Warmer water temperatures have induced changes in the phenology of many plankton species the seasonal peak occurrences of which shifted to earlier or later dates within the annual cycle (Greve *et al.*, 2001; Edwards & Richardson, 2004; Edwards *et al*., 2006a). Phenological relationships have been decoupled, leading to trophic mismatch situations between phyto-, zooplankton and fish (Edwards and Richardson 2004, Beaugrand et al. 2003). A large number of studies have reported a regime shift in the North Sea in the late 1980s (e. g. Alheit et al. 2005, Alheit and Bakun 2010, Beaugrand 2004, Beaugrand and Reid 2003, Edwards et al. 2001, Beaugrand et al. 2002, Edwards et al. 2004, Kröncke et al. 2001, Reid and Edwards 2001, Reid et al. 2001a, Reid et al. 2001b, Weijerman et al. 2005). Weijerman et al. (2005) applied principal component analysis and regime shift analysis to a set of about 100 biological and physical variables and demonstrated that 1988/89 was a major breakpoint in the data. This coincided with the change in the winter NAO index indicating a possible relationship between climate, temperature and the regime shift.

A refined study of temperature dynamics showed that average annual minimum and maximum temperatures increased considerably in the entire water coloumn in the southern and the northern North Sea (Fig. 3, 4, 5). However, the most conspicuous increase was measured in winter time, and winter temperature in the North Sea has been much elevated since 1988 with a few exceptional years. It seems that conditions prevalent in the North Sea since around 1990 were favourable again for sardine to expand their range, probably from the Channel area into the entire North Sea. During quarter 1 sardines aggregated along the northeast coast of England as, in winter, the northern North Sea is warmer than the southern part (Beare et al. 2004a, b). During quarter 3, they had moved toward the southeastern part of the North Sea where temperatures were higher than in the north. It seems that the first invasive pulse of sardines from the Channel into the North Sea was triggered by the strengthening of the NAO in the late 1980s.

In spite of the increase in North Sea temperatures, and although apparently many zooplankton species of Lusitanian origin had increased their abundances starting in the late 1980s, the warm water-adapted European anchovy did not react to the strong climate signal of the NAO in the late 1980s. Instead, they invaded the North Sea much later, around 1995 (Beare et al. 2004a, b), and established spawning populations there (Alheit et al. 2007) as demonstrated by the appearance of eggs and larvae off Helgoland (Fig. 12, 14). At the same time, anchovies were observed in increasing quantities in the Irish Sea (Armstrong et al. 1999) and in the Skagerrak-Kattegat region (Fig. 17). It follows, that the increase of annual temperatures in the North Sea in the late 1980s was not sufficient for the anchovy to move from the southwest corner of the North Sea towards east and north. To understand, why the European anchovy became a North Sea resident only in 1995 and not earlier, it is important to look at temperature dynamics. Anchovy has a rather high temperature treshold for spawning, higher than sardine. Consequently, it starts spawning later in summer than sardine. In contrast to sardine, it spawns preferentially in shallow waters such as the German Wadden Sea where salinity is lower and temperature higher than in the more offshore spawning grounds of sardine (Fig. 16). Summer temperatures in the southern North Sea reached unprecedented high values in 1995 and in most years since maximum temperatures have surpassed those from the period of 1989 to 1994, when temperatures were elevated because of the strenghtened NAO (Fig. 3). Also, after 1995, the NAO index decreased and did not reach anymore the extreme values as observed from 1987 to 1989. The question arises, why were summer temperatures very high after 1994 (exception 1996), although the NAO index had decreased again.

A very rapid reversal of the marine climate was recorded in the mid-1990s, which resulted in a hydrographic regime, which was comparable to that of the 1960s (Hátún et al. 2007). With respect to the atmosphere, the Icelandic Low and the Azorian High migrated north-eastward and the NAO index changed rather suddenly from highly positive values to negative in fall

1995 (N.B.: Many biologists presenting correlations between biological variables and the NAO index are not aware of the fact, that, since the mid-1990s, the NAO index does not reflect anymore the difference in the pressure anomalies between the centers of the pressure cells, but a value determined from the same fixed stations as before). The predominantly positive trend of the index switched to a negative phase until winter 1998/99 (Flatau et al. 2003). At the same time, the Atlantic storm track migrated east (Häkkinen and Rhines 2004). Since 1996, the NAO shows fluctuations of decreasing amplitude with a decline of amplitude (Häkkinen and Rhines 2004). These atmospheric processes were accompanied by a number of changes in North Atlantic current structure, which occurred simultaneously (Häkkinen and Rhines 2009): the subpolar gyre weakened and contracted (Fig. 8) (Häkkinen and Rhines 2004), and the subarctic front in the eastern subpolar gyre moved westward (Bersch 2002), which allowed a northward surge of highly saline Mediterranean waters along the eastern margin (Johnson and Gruber 2007). Using historical hydrographic data, Lozier and Stewart (2008) suggest, that there is a temporally varying northward penetration of Mediterranean Outflow Water (MOW). There seems to be general consensus that warm and salty MOW flows northward from the Strait of Gibraltar as a coherent mid-depth boundary current along the eastern coast of the basin. This boundary current continues along the Iberian Peninsula into the Bay of Biscay and onward toward Porcupine Bank (Lozier and Stewart 2008). The question is, how far north does the MOW flow and how is its extension linked to dynamics of NAO, subpolar gyre circulation and zonal shifting of the subpolar front. Strong prevailing westerlies as recorded during the high NAO phase in the early 1990s spin up and expand the subpolar gyre and the eastern limb of the subpolar front shifts eastward toward the British Isles (Bersch et al. 2002). Lozier and Stewart (2008) propose, that during prolonged low NAO phases, when the subpolar gyre contracts, the subpolar front moves westward, facilitating the northward penetration of MOW into the Rockall Through. Conversely, when the NAO is in a high phase, the subpolar gyre expands and the subpolar front moves eastward to the European continental shelf and so blocks the pathway of the MOW to the north. There is a correlation between the location of the subpolar front and the NAO (Lozier and Stewart 2008). During low NAO periods, the subpolar front retreats westward, whereas it shifts eastward during high NAO phases. All these interactions of atmosphere and ocean in the Northeast Atlantic seem to have a global dimension. Loewe (2009) speculates that they might be related to a poleward shift of the Hadley Circulation observed in 1997 (Hu and Fu 2007). What were the implications of all these atmospheric and hydrographic processes for the North Sea? Although the pressure cells over Iceland and the Azores had left their locations and the strong westerlies in winter weakened, annual average temperatures increased again after a short dip in 1996 and even reached higher levels after 2000 than in the years following the late 1980s (Loewe 2009). However, the rather high annual average temperatures in the North Sea were not anymore determined by winter values, as the strong westerlies had decreased. Instead, the subtropical waters moving northward and replacing partly the subpolar gyre waters provided anomalously high summer temperatures in the North Sea through atmosphere-ocean coupling. Temperatures and heat content in the North Sea have increased steadily since 1995 (Fig. 3, 4, 5).

With respect to the temperature in the southern North Sea, 1995 was definitely an exceptional year. The winter temperature in 1995 was extremely high (Fig. 3). Up to 1995, only the winters 1989 and 1990 have been warmer. But what makes 1995 really outstanding is the fact that the averaged summer temperature shows a maximum value of 18.4 °C, which was then an all time high, at least for our simulation period from 1950 to 1995 (full period not shown here). Even at the end of the 1980s, around the time of the regime shift in the North Sea, average temperatures in the southern North Sea only reached a maximum value of 17.9 °C (summer 1989). The high temperatures in 1995 were not only caused by the NAO, as demonstrated by the wind density function for winter (December, January, February) averaged over the entire North Sea (Fig. 7). Obviously, the winter 1986/87 shows an extreme increase of the westerly wind component caused by the increased NAO, which explains the mild winter of that year. Westerly winds were also dominating in winter 1994/95, however, they were significantly weaker than in 1986/87. This indicates that the NAO was not the major driving mechanism behind the exceptional warming in the mid-1990s.

As a consequence of the warming in 1995 and subsequent years (exception: 1996), temperatures in the German Wadden Sea and the German Bight were high enough from late June to early August for anchovy to spawn. As in the late 1980s, the climatic event in the mid-1990s was reflected in North Sea communities. So far, in contrast to the late 1980s, only few changes have been reported for zooplankton populations. The main reason is probably that, in the mid-1990s, there was no inflow of Atlantic water masses into the North Sea. Conspicuous changes were observed in the fish community. Abundances of eggs of sprat, a clupeoid species with more northern affinity than anchovy and sardine, decreased significantly after 1995 (Fig. 15). This could indicate, that soon a change in the composition of the small pelagics community might occur as already reported from the Mediterranean. In addition to anchovies and sardines, a number of pelagic and demersal fish species of Lusitanian origin have shown sudden, almost exponential increases in abundances in area 4B of the North Sea since the mid-1990s, such as mackerel (*Scomber scombrus*), Red Gurnard (*Aspitrigla cuculus*), Red Mullet (*Mullus barbatus*),Tub Gurnard (*Chelidonichthys lucerna*), Bluemouth (*Helicolenus dactylopterus*), Bib (*Trisopterus luscus*), John Dory (*Zeus faber*), Poor Cod (*Trisopterus minutus*) (Beare et al. 2004a). Similar observations on bottom fish assemblages were reported from other parts of the North Sea (A. Sell, pers. comm.). Also, a deepening of several species was observed around the mid-1990s (van Hal, pers. comm., abstracts from the 44th Marine Biology Symposium, 7-11 Sept., Liverpool, UK).

Summing up, it seems that anchovies and sardines expanded their area of distribution from the Channel and the southwest corner of the North Sea into the entire North Sea and established spawning populations there with the entire life cycle closure in this region. This happened as a reaction to climatically induced temperature elevations triggered by diffent climatic oscillations. Temperature increase in the late 1980s associated with strengthening of the NAO led sardines to expand and spawn in the North Sea. The temperature increase then was mainly in the winter period, when annual minimum temperatures were conspicuously elevated. In contrast, since the mid-1990s, it were particularly the summer temperatures which increased, allowing the anchovy to expand and to spawn in the German Bight. Whereas climate forcing through the NAO in the late 1980s affected particularly phyto- and zooplankton, the impact of the AMO in the mid-1990s was mainly visible in the fish communities.

Assuming the temperature increase in the North Sea will continue by global warming and an AMO in the positive phase, it will have profound consequences for dynamics of small pelagics. Sardines and, particularly, anchovies, will increase their population abundances, maybe locally up to commercial sizes. Sprat will spawn earlier in the season and its population size will depend on the match/mismatch situation with its food sources. In any case, drastic changes in the dynamics of small pelagics will occur with concomitant problems for fisheries management. Small pelagics have shown to be good indicators of changes of entire ecosystems.

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