Reprint of "Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic"

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ABSTRACT

Dynamics of abundance and migrations of populations of small pelagic clupeoid fish such as anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), sardinella (*Sardinella aurita*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the eastern North and Central Atlantic between Senegal and Norway vary in synchrony with the warm and cool phases of the Atlantic Multidecadal Oscillation (AMO). This is shown by compiling retrospective data on fish catches and anecdotal observations, which in some cases date back to the mid-19th century. The AMO is defined as the de-trended mean of North Atlantic (0–60°N) sea surface temperature anomalies. However, it is not primarily the temperature which drives the dynamics of the small pelagic fish populations. Instead, the AMO seems to be a proxy for complex processes in the coupled atmosphere–ocean system of the North Atlantic. This is manifested in large-scale changes in strength and direction of the current system that move water masses around the North Atlantic and likely involves the North Atlantic Oscillation (NAO), the Atlantic Meridional Overturning Circulation (AMOC), the Mediterranean Overflow Water (MOW) and the subpolar gyre (SPG). The contractions and expansions of the SPG apparently play a key role. This was particularly obvious in the mid-1990s, when the SPG abruptly contracted with the result that warm subtropical water masses moved to the north and east. Small pelagic fish populations in the eastern North and Central Atlantic, including those in the Mediterranean responded quickly by changing abundances and migrating northwards. It seems that the complex ocean–atmosphere changes in the mid-1990s, which are described in the text in detail, caused a regime shift in the ecosystems of the eastern North and Central Atlantic and the small pelagic clupeoid fish populations are the sentinels of this shift.

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1. Introduction

"The fauna of the southern North Sea exhibits clear changes. Particularly conspicuous is the increase of Mediterranean fish species and the occurrence of sardine eggs and larvae. There is no doubt, that these observations are associated with the climate change which has been shown to occur since several decades, and which, over the last years,

has had important consequences for fisheries: decrease of catches, northwards shift of fishing grounds, adaptation to fisheries for different species. ...particularly interesting questions are: will climate change continue and, also, shifts and changes of fish stocks, how long will this last, and which are the consequences, if this trend reverses?" This is not a recent statement, but is the translation of the introduction of H.J. Aurich's (1953) paper on "Distribution and spawning relationships of anchovy and sardine in the southeastern North Sea and the changes as the consequence of climate change" published 60 years ago.

The North Atlantic was in a warm state in the 20th century from about 1925 to about 1965, very similar to the situation we have been observing since about the mid-1990s. The increased surface air temperatures (SAT) during both periods, particularly in the Arctic, have been highlighted by Johannessen et al. (2004). Elevated sea temperatures,

reduced sea-ice conditions and enhanced Atlantic inflow in northern regions were reported for the former period (Drinkwater, 2006). In his review, Drinkwater (2006) describes the extensive ecosystem changes with respect to the northern regions of the North Atlantic associated with this period, such as the northwards migration of zooplankton, fish and benthos and changes in the phenology. Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*) expanded farther north, whereas colder-water species withdrew from their southern ranges. New spawning sites were established farther north and more southern species appeared occasionally or were frequently observed in regions where they had been unknown before the warming. As the ecosystem changes were so significant, The International Council for the Exploration of the Sea (ICES) conducted its first scientific meeting on climate change (ICES, 1949) as reported by Drinkwater (2006). The North Atlantic experienced a regime shift during this warming period according to Drinkwater (2006). The conspicuous biological events have already been described by Cushing (1982) in the chapter called "The Recent Period of Warming" of his famous monograph on "Climate and Fisheries" where he refers to four major events: (i) the northwards movement of animals between the 1920s and 1940s, (ii) the spread of intertidal organisms, (iii) the rise and decline of the West Greenland cod fishery, and (iv) the Russell Cycle, a series of changes, particularly in the plankton community, in the waters off Plymouth, UK, between the 1930s and the 1970s (Coombs and Halliday, 2011; Hawkins et al., 2003; Mieszkowska et al., 2014-in this issue; Southward, 1980; Southward et al., 2005).

Apparently, what has been described by Cushing (1982) and Drinkwater (2006) and what was the theme of the ICES meeting in 1949 was the warm phase of the Atlantic Multidecadal Oscillation (AMO) in the first half of the 20th century. The term AMO was coined by Kerr (2000) in an editorial article for Science to describe a multidecadal oscillation of alternating warm and cold periods of the North Atlantic over the last 150 years. The AMO is defined as the de-trended, 10-year running mean of North Atlantic (0°–60°N) sea surface temperature (SST) anomalies (Alexander et al., 2014-in this issue). It swings between cool and warm phases that may last for 20–40 years, where the difference between extremes is ~0.5 °C (Alexander et al., 2014-in this issue). The approximate period of the oscillation based on the instrumental records of the past 130 years is estimated to be 60–80 years (Deser et al., 2010; Guan and Nigam, 2009; Schlesinger and Ramankutty, 1994; Ting et al., 2014-in this issue. Knudsen et al. (2011) found a quasi-persistent 55–70 year signal in a number of different paleo-proxies, concluding that the AMO is a regular, but intermittent, feature throughout most of the Holocene (Kilbourne et al., 2014-in this issue). The AMO seems to be related to a number of climatic phenomena including Atlantic sector hurricane frequency (Goldenberg et al., 2001), precipitation in North America (Enfield et al., 2001) and rainfall over the African Sahel zone and Northeast Brazil (Knight et al., 2006). It is also suggested that the AMO has a hemispheric-wide influence, including the Tibetan Plateau and the Indian monsoon (Feng and Hu, 2008). Retrospective research indicates five major phases of the AMO over the last 150 years (Fig. 1). A mainly positive phase from about the mid- to late19th century, a negative phase until 1925, another positive phase until 1965, a negative phase until 1995, and a still lasting positive phase since (Deser et al., 2010).

The AMO impacts the long-term development in fish populations like the Norwegian spring-spawning herring (Toresen and Østvedt, 2000), the Northeast Arctic cod (Nakken, 2002) and the English Channel sardines (Edwards et al., 2013). Moreover, shifts in distributions of plankton to fish have been shown to occur over multidecadal time periods (Beaugrand et al., 2002; Drinkwater, 2006; Genner et al., 2004, 2010; Hawkins et al, 2003; Southward et al., 1988; Sundby and Nakken, 2008). The aim of this study is to continue the studies of Aurich (1953) and Cushing (1982) and to complement the observations from the northern North Atlantic reported by Drinkwater (2006) with past and recent observations from more southern regions. The targets
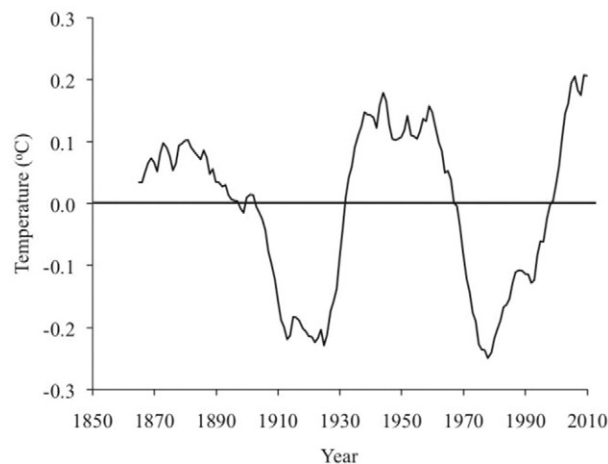

Fig. 1. Atlantic Multidecadal Oscillation.
The data are from: Enfield et al. (2001).

of this investigation are the large populations of clupeoid fish species such as anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), round sardinella (*Sardinella aurita*), Norwegian spring spawning herring and sprat (*Sprattus sprattus*) in the large region of the continental margin from Senegal in the South to Norway in the North, including the Mediterranean, the North Sea and the Baltic Sea (Fig. 2). Particular importance is given to old literature from about 1880 to 1950, first as these old publications highlight what happened during the warm AMO phases in the 19th and 20th centuries and, second, to ensure that this important information will not be lost. The possible impact of the coupled ocean–atmosphere system is discussed in detail to highlight its importance for the dramatic changes in the dynamics of ecosystems and fish populations.

2. Material and methods

In order to compare long-term changes of the small pelagic fish species in this study, multidecadal records were assembled for the different regions of the eastern North Atlantic and Mediterranean, each series covering a different time span.

- Data on Spawning Stock Biomass (SSB) and catches (landings) for Norwegian spring spawning herring during 1907–2010 were based on a combination of Toresen and Østvedt (2000) reporting virtual population analyses (VPA) from 1907 to 1998 and ICES (2011) reporting stock assessment data with VPA tuned with acoustic estimates and larval indices from 1988 to 2010. In order to get a full time series data were taken from Toresen and Østvedt (2000) from 1907 to 1987 and merged with the ICES (data) from 1988 to 2010.
- Sardine eggs sampled off Plymouth since 1924, with intermittent breaks, were used as a proxy for the sardine stock in the western English Channel (Coombs and Halliday, 2011).
- Landing data for round sardinella from Northwest Africa were used from 1990 to 2010 (FAO, 2011).
- Landing data for anchovy and round sardinella from the western Mediterranean caught by the Spanish fisheries were from 1945 to 2010 (Abad et al., 1991; Giráldez and Abad, 2000). Data for 2000 onwards were recovered from FROM (Fondo de Regulacion y Ordenacion de los Mercados de la Pesca) fisheries sales report sheets provided by different fisheries organisations of the different Spanish autonomic governments.
- For round sardinella in the Aegean Sea data from 1928 to 2009 (with an interruption between 1950 and 1962) were used. In order to compensate for changes in purse seine effort, the catches were transformed as a ratio of round sardinella to combined
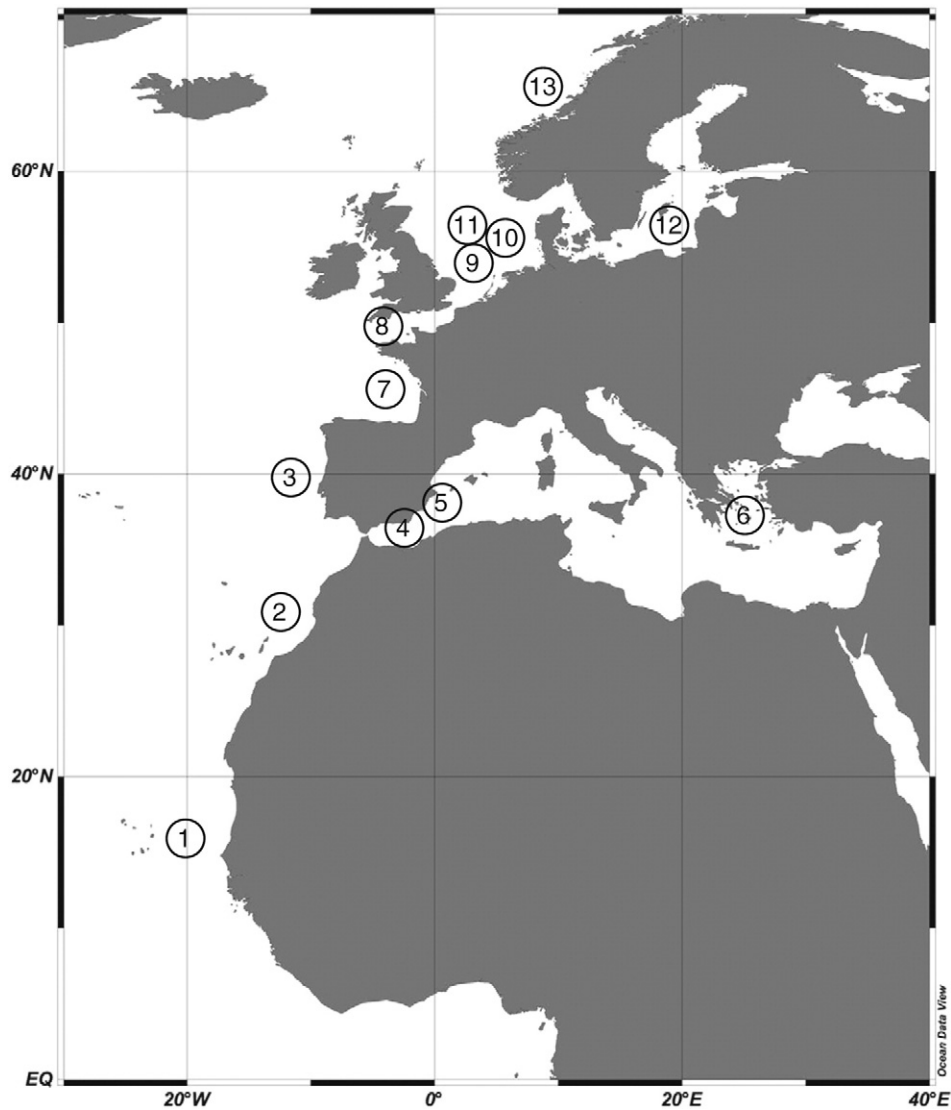
Fig. 2. Map showing location of small pelagic fish populations. 1 — Sardinella in upwelling region off NW Africa, 2 — sardine in upwelling region off NW Africa, 3 — sardine in upwelling region off Portugal, 4 — sardinella off Spain in Mediterranean, 5 — anchovy off Spain in Mediterranean, 6 — sardinella off Greece in Mediterranean, 7 — anchovy in Bay of Biscay, 8 — sardine in English Channel, 9 — anchovy in North Sea, 10 — sardine in North Sea, 11 — sprat in North Sea, 12 — sprat in Baltic Sea, 13 — Norwegian Spring Spawning Herring. The map is from: Schlitzer (2013).

sardine and anchovy catches. For data from 1928 to 1939 see Moutopoulos and Stergiou (2011); for data from 1964 to 2009 see National Statistical Service of Greece (1967–2011).

• Sea surface temperature (SST) records from the Hadley Center (the British Atmospheric Data Center—BADC HADISST 1.1 dataset) from 1930 to 2010 were used to assess long-term hydroclimatic changes in different regions of the eastern North Atlantic and Mediterranean. Yearly averages were obtained from monthly SST records for the Nordic Seas, Baltic Sea, North Sea, Celtic Sea and Bay of Biscay shelf, Iberian upwelling, western Mediterranean and eastern Mediterranean, where the regions were those defined by Philippart et al. (2007).

A principal component analysis (PCA) was carried out on the above data sets of small pelagics, excluding sardinella from Northwest Africa (data set too short). Missing data of the western English Channel sardine and Aegean sardinella were calculated using an algorithm that takes into account the long-term trends of the series (Ibanez and Conversi, 2002). From the PCA the first principal component (PC1) was used for correlation with the AMO, correcting the number of

degrees of freedom for temporal autocorrelation according to Pyper and Peterman (1998).

3. Results

3.1. Long-term temperature series in study regions

The overall trend of SST for the period 1930–2010 is similar in all seven regions (Fig. 3): elevated temperatures up to about the early 1960s followed by a cooler period in the 1970s and 1980s and another period of elevated temperatures starting between the late 1980s and the mid-1990s, reflecting more or less the AMO dynamics. However, detailed inspection of the temperature curves shows some clear regional differences. All regions, except the eastern Mediterranean, exhibited a series of cold years in the early 1940s. The three northern regions had a series of warm years in the first half of the 1970s. All regions except the Mediterranean showed a temperature increase in the late 1980s followed by a temperature minimum in the mid-1990s, both events due to strengthening and collapsing of the North Atlantic Oscillation (NAO). In all regions, a period of lasting high SSTs started in the mid-1990s.
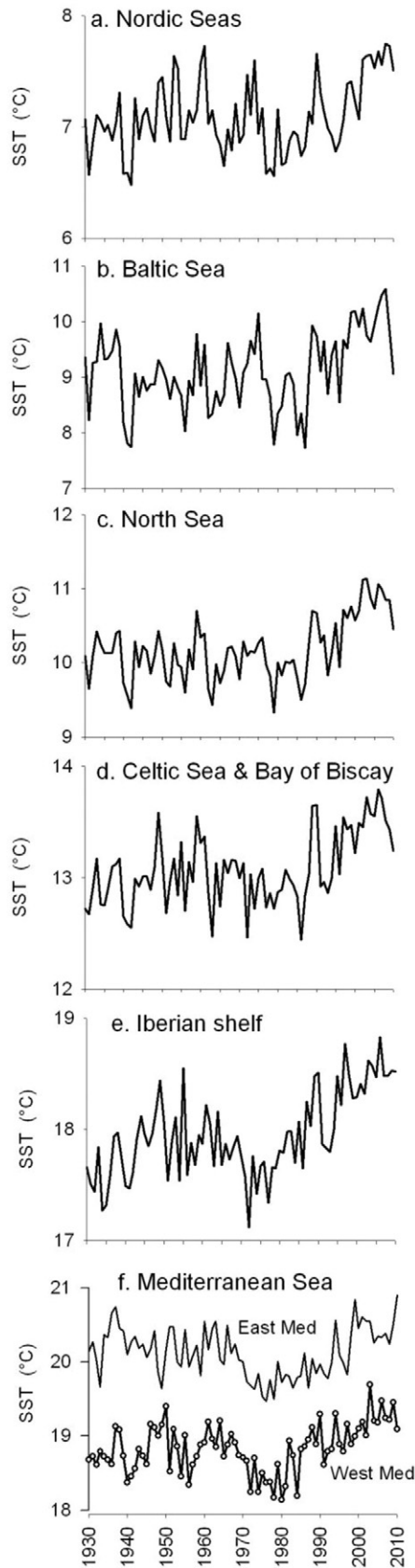
Fig. 3. Sea Surface Temperature (SST) time series from 1930 to 2010 from regions under investigation. a. Nordic Seas, b. Baltic Sea, c. North Sea, d. Celtic Sea and Bay of Biscay shelf, e. Iberian upwelling region, f. western and eastern Mediterranean.

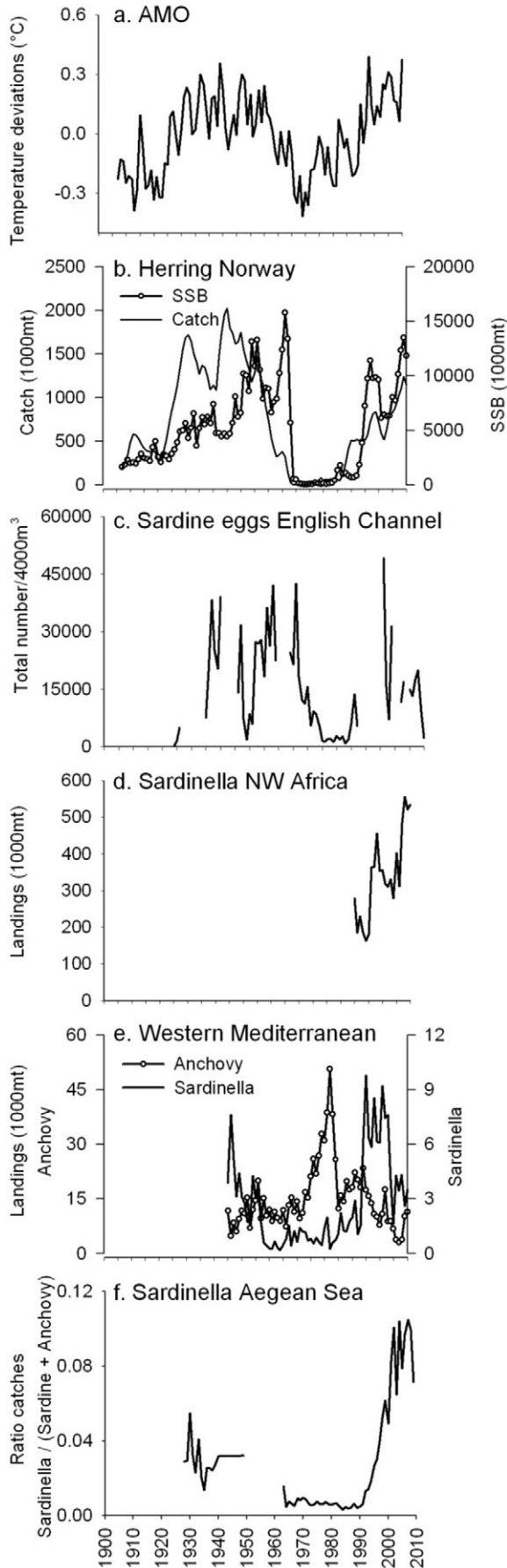### 3.2. Historical data on dynamics of small pelagic fish populations

In the following, the focus is on the description of changes in distribution and abundance of small pelagic fish populations in association with warm AMO phases. In some instances, the association with cool AMO phases is also presented.

3.2.1. Anchovy

3.2.1.1. Positive AMO phase mid- to late 19th century. During the cold AMO phases, the most northern occurrence of the anchovy is the English Channel area and the southeastern edge of the North Sea. However, during the warm periods, anchovies move farther north. Ehrenbaum (1892a) reported that anchovy occurred along the European Atlantic coast from Gibraltar to 60°N off Bergen, Norway, where it was caught frequently in summer. Occasionally, it was encountered in the western Baltic in September and October, and, sometimes, in winter, anchovies were caught in the Baltic Sea off the town of Eckernförde, Germany.

An economically important anchovy fishery existed in the summer (May–August) in the Dutch Zuiderzee for a long time, until this estuary was closed by a dam in 1932 (Boddeke and Vingerhoed, 1996). Catch records from the Zuiderzee are given for several years: 1858–1891 (Ehrenbaum, 1892b) and 1895–1914 (Redeke, 1916). Also, anchovies were fished in the eastern Oosterschelde, an estuary southwest of the Zuiderzee. Apparently, anchovies came from the Channel area between May and August to spawn in the very shallow parts (2–3 m) of the Zuiderzee (Redeke, 1916), and as water temperatures were rather high there in summer, up to 20 °C and higher (Cunningham, 1895; Redeke, 1916), the spawning threshold temperature for anchovy must have been reached. It is not clear where the anchovies spent the remainder of the year. Several authors assumed that these anchovies stayed at the western end of the Channel in autumn and winter (Aurich, 1953; Cunningham, 1895; Redeke, 1916). According to Cunningham (1890), it was long known that anchovies occur off the south coast of England. However, anchovy eggs and larvae have never been found near Plymouth (S. Coombs, pers. comm.) with adult anchovies being very rare in the summer (Cunningham, 1895; and routine trawl survey data of the Marine Biological Association). In some years, the anchovies moved further east along the coast, towards the German Wadden Sea and were caught in the Dollart, the estuary of the river Ems, and in the Jadebusen (Ehrenbaum, 1892a; Meyer, 1930).

Several anecdotal reports from German and English researchers indicate the occurrence of anchovies and sardines in the North Sea during the second half of the 19th century. In the German Dollart, anchovies were caught from 1884 to 1892 (Ehrenbaum, 1892b) and the size of catches of the fishermen from Ditzum is given for the years from 1889 to 1891 (Ehrenbaum, 1892a). According to earlier anecdotal reports of fishermen at that time, the anchovy yield in German coastal waters 30–40 years previously (around 1850–1860) had been much better (Ehrenbaum, 1892b) and in 1859 anchovy catches were so large, that the fish were used as manure in agriculture (Ehrenbaum, 1892a). The regular anchovy fishery in the Zuiderzee, which usually lasted from May to June, was important for Holland, however, annual catch rates and market prices fluctuated considerably (Ehrenbaum, 1892a). There was a record catch in 1890 in the Dutch Zuiderzee (Ehrenbaum, 1892a) as well as in the German Dollart (Ehrenbaum, 1892b). Ehrenbaum (1892a) also mentions that anchovies were encountered off the English and Scottish coasts, which were not marketable, as they were caught in the winter months and, consequently, did not have enough fat. Cunningham (1890) believed that these anchovies, which were caught in considerable quantities in January 1890 in the Moray Firth on the east coast of Scotland, were permanent residents in the North Sea. Ehrenbaum (1892a) and Ehrenbaum and Heincke (1900) reported that anchovy eggs were never encountered around the island of Helgoland, but a large amount of them (16,000) was collected 7 nm off the island of Norderney, off the German Wadden

Fig. 4. Time series of AMO and small pelagic fish stocks from eastern North Atlantic. a. AMO index, b. catches and spawning stock biomass (SSB) of Norwegian spring spawning herring (*Clupea harengus*), c. abundance of sardine (*Sardina pilchardus*) eggs in English Channel, d. catches of round sardinella (*Sardinella aurita*) off Northwest Africa, e. catches of anchovy (*Engraulis encrasicolus*) and round sardinella (*S. aurita*) from western Mediterranean, f. ratio of catches of round sardinella (*S. aurita*) to combined sardine (*S. pilchardus*) and anchovy (*E. encrasicolus*) catches.

Sea. This was in 1891, the year after the record anchovy catches in the Zuiderzee. Interestingly, a Piscatorial Atlas published in 1883 claims that anchovies occurred in this year along the entire coastline of the North Sea including eastern Scotland and southern Norway. An engraving originating from Cornwall and dating back to at least 1860 shows that anchovy together with sardine, herring and sprat seem to have been caught at the same time off the coast of Cornwall. Bahr (1933) mentions that Möbius and Heincke stated in their book "Fische der Ostsee (1883)" that anchovies had been found in the western Baltic Sea.

Spurred by the success of the Dutch anchovy fishery and because of the almost regular occurrence of anchovies as a by-catch in the German coastal fisheries in the second half of the 19th century, there were hopes to achieve similar results in German and British waters and respective trial fisheries were initiated by scientific laboratories in 1891/92 off Plymouth (Calderwood, 1892; Ehrenbaum, 1892a,b) and in 1892 in the German river Ems (Ehrenbaum, 1892b, 1932). However, these were not successful.

3.2.1.2. Positive AMO phase mid-1920s–late 1960s

3.2.1.2.1. Mediterranean. Spanish records since 1945 show that catches of anchovy were very low until the early 1970s, but then increased in the mid-1970s (Fig. 4) (Abad and Giráldez, 1990; Abad et al., 1991; Giráldez and Abad, 2000).

3.2.1.2.2. Iberian upwelling. Portuguese catches are known since 1943, mainly from the upwelling region, partly from the Algarve coast (ICES, 2010a). They were more or less stable, but abruptly decreased after 1967.

3.2.1.2.3. Bay of Biscay. Data on anchovy catches for the entire bay are available since 1940. They show a steady increase from the early 1950s to peak catches in the first half of the 1960s reaching a maximum in 1965 and then decreasing rapidly (Borja et al., 2008; Cendrero, 2002; ICES, 2010a; Villamor and Abaunza, 2003). Junquera (1986) shows a movement of the population and catches from the Cantabrican coast in the southwest to the Basque coast in the southeast from the 1950s to the 1970s, which he explains by respective warmer temperatures.

3.2.1.2.4. North Sea. In 1930 and 1931, Dutch anchovy catches increased considerably when compared to previous years and large quantities were encountered in Dutch waters, in the Zuiderzee as well as in the Schelde estuary and in Haringslivet, the estuarine area of the rivers Maas and Rhein (Ehrenbaum, 1932). Catches were seven times as high as the average from 1922 to 1929 (Aurich, 1953). Catches in the Dutch Waddensea were high from about 1926 to 1960 (ICES, 2010b; Petitgas et al., 2012). Further east, in German waters, in the German Bight, from the Dollart up to the Elbe estuary, where anchovies were hardly known previously, relatively large catches were reported from 1930 to 1934, 1938, 1948, and 1949 (Aurich, 1953; Bahr, 1950; Ehrenbaum, 1932; Hagmeier, 1939; Hass, 1938; Meyer, 1930, 1932, 1933). Catches along the East Frisian coast more than tripled (Aurich, 1953). Trial fisheries for anchovies, with the aim of marketing them on a regular basis, were carried out in 1939 and 1949 in the German Bight but did not lead to a regular fishery targeting anchovy (Bahr, 1950). Also, anchovy eggs and larvae were found in July and August in the Jadebusen, around the island of Helgoland, off the East-Frisian islands and in the Elbe estuary (Ehrenbaum, 1932). Anchovies were also caught from May to June 1948 and 1949 in the German part of the East Frisian Wadden Sea (Aurich, 1950). From late May to the end of July 1949, anchovy eggs were recorded in large quantities in the German Wadden Sea (Fig. 5) (Aurich, 1953). Later in the year, up to October, anchovy larvae were also found. The anchovy encountered in
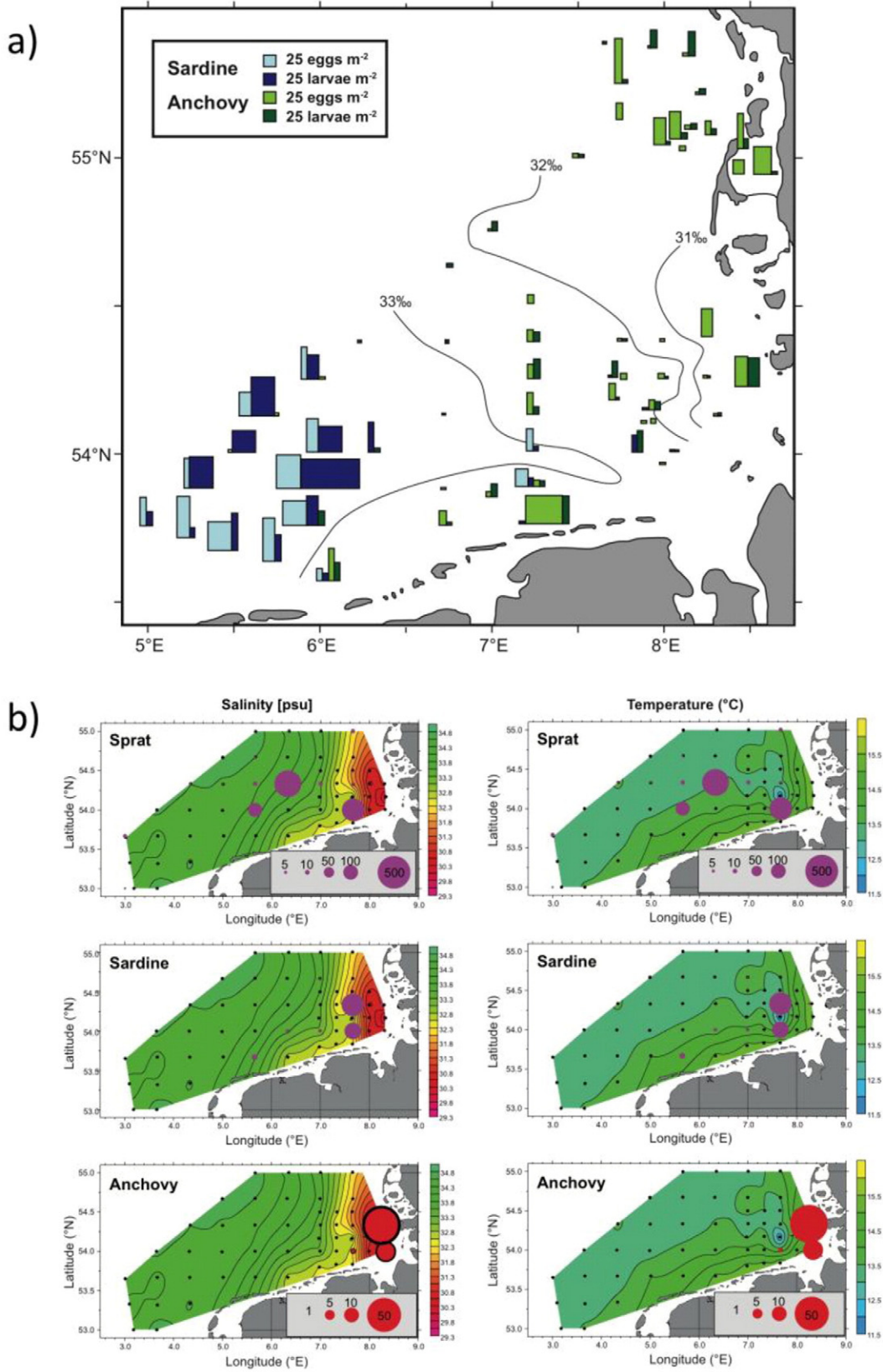
Fig. 5. Distribution and abundance of anchovy, sardine and sprat eggs and larvae in German Bight. a. Anchovy (green columns) and sardine (blue columns) eggs and larvae in 1950 (Aurich, 1953). b. Anchovy, sardine and sprat eggs in 2003 and temperature isolines (Alheit et al., 2007).

the German Wadden Sea shares the same meristic characteristics as the Zuider Sea population (Aurich, 1953). Regular ichthyoplankton surveys in the German Bight from 1948 until 1952 yielded a clear picture of anchovy spawning (Aurich, 1953). Anchovy spawned in a broad band from the Dutch to the Danish coast throughout the German Bight (Fig. 5) (Alheit et al., 2007). Anchovy eggs appeared when temperature surpassed 13 °C, usually in late May. Spawning peak was from mid-June to mid-July between 15 and 20 °C. Spawning ceased again in mid-August. Larvae were encountered from June to October when they had reached a length of up to 41 mm. Egg and larval densities reached maximum values of 3885/m^2 and 594 individuals/m^2, respectively, much higher than reported from the Zuiderzee.

3.2.1.2.5. Baltic Sea. In November/December 1933 large schools of anchovies were found in the western Baltic in the bights of Kiel, Lübeck and Mecklenburg, up to the island of Rügen, and landed in the ports of Eckernförde, Kiel, Travemünde, Warnemünde, Sassnitz and Stralsund (Fischer, 1935; Meyer, 1933). Some anchovies were even caught in November 1933 further east, off the now Russian enclave of Kaliningrad, which is located between Latvia and Poland (Bahr, 1933). Meyer (1933) assumed that the anchovies had entered the Baltic as adults, as at least up to 1933, the year of his publication, no anchovy eggs or larvae had been found in the Baltic. In summer and autumn 1938, considerable numbers of anchovies were found when catching sprat in the western Baltic and a single anchovy egg was collected in July 1938 to the east of the island of Fehmarn (Kändler and Wattenberg, 1940). Also, a few anchovy eggs were collected in June and July of 1938–1940 from Danish light-vessels in the southern Kattegat and in the Great Belt (Heegard, 1947).

3.2.1.3. Recent warm AMO period mid-1990s onwards

3.2.1.3.1. Mediterranean. Catches increased from 1970 to a peak 1980 (Giráldez and Abad, 1991; Giráldez and Alemany, 2002) (Fig. 4). By the mid-1990s, catches had decreased to levels observed prior to the 1970s and reached a historic minimum between 2005 and 2008.

3.2.1.3.2. Bay of Biscay. After relatively low catches in the 1980s, catches increased again at the end of the 1980s and particularly in the mid-1990s but collapsed dramatically in the early 2000s due to serious recruitment failure. This is particularly visible in the SSB data (Borja et al., 2008).

3.2.1.3.3. Irish Sea. Since 1995, research cruise catches of anchovies have increased considerably showing that anchovies have become more widespread in the region (Alheit et al., 2012; Armstrong et al., 1999).

3.2.1.3.4. English Channel. Significant amounts of anchovies were on occasions caught in MBA research cruises (S. J. Hawkins, pers. comm.).

3.2.1.3.5. North Sea. Anchovies were not found on the International Bottom Trawl Surveys (IBTS) for the period 1970 to 1990 throughout the entire North Sea, except for some occasional stray individuals. However, since 1995, they have been caught in larger quantities (Alheit et al., 2012; D.J. Beare et al., 2004; D. Beare et al., 2004; Petitgas et al., 2012). Also, juveniles were encountered in the Wadden Sea since 1997 and anchovy eggs and larvae were collected in larger quantities in the Helgoland Roads series since 1995 (Alheit et al., 2012). During 2003–2005, anchovy eggs and larvae were encountered regularly (Alheit et al., 2007, 2012) and their distribution was almost identical to that described by Aurich for 1951 (1953) (Fig. 5).

3.2.1.3.6. Skagerrak, Kattegat. After not having been encountered for 17 years, anchovies were caught again from 1995 onwards (Alheit et al., 2012).

3.2.1.3.7. Baltic Sea. Anchovies have been found since 1996 (Draganik and Wyszynski, 2004).

3.2.2. Sardine

The sardine has a continuous distribution along NE Atlantic coasts from Senegal (16°N) to the North Sea (60°N) (Binet et al., 1998). However, the northern and southern boundaries change in sequence with decadal climate trends. Interestingly, northern and southern stocks

(respectively, northern Portugal to the North Sea and off NW Africa) display antagonistic fluctuations when compared with the AMO signal.

3.2.2.1. Positive AMO phase mid- to late19th century

3.2.2.1.1. English Channel. Between 1860 and 1880, sardines were found in Lyme Bay (Edwards et al., 2013; Southward et al., 1988).

3.2.2.2. Positive AMO phase mid-1920s–late 1960s

3.2.2.2.1. NW Africa. Population fluctuations and long-term abundance trends of sardine off NW Africa are difficult to interpret because of (i) climatically induced expansions and contractions of distribution ranges, (ii) historically different beginnings for the various national fisheries and (iii) movements of the fisheries' fleets (Zeeberg et al., 2008). Kifani (1998) gives a good description of changes of the northern stock between Cape Spartel and Agadir Bay observed from the 1960s to the 1990s. Catches were low during the warm AMO period from 1936 until the 1960s, then started to increase with the beginning of the cold AMO period, peaked in the mid-1970s and were low again from the early 1990s on (Alheit et al., 2010; Kifani, 1998). Dynamics of the northern part of the central stock are similar (Fig. 4 in Kifani, 1998). Also, the central stock seems to have contracted its area of distribution towards the south in the 1970s (Kifani, 1998). The southern boundary of the southern stock has fluctuated very much over the last decades, due to extensions and contractions (Kifani, 1998). There were two conspicuous southwards extensions, from the late 1960s to around the mid-1970s and between the mid-1980s and the early 1990s (Binet et al., 1998).

Iberian upwelling: In contrast to the sardine catches off NW Africa, those off northern Portugal (ICES Subdivision IXa Central, 41°50′N 37°00′N) were high from about the late 1920s to the late 1960s and have declined since (Borges, 2013; Borges et al., 2003; Carrera and Porteiro, 2003; ICES, 2012), displaying opposite fluctuations when compared with NW African stocks. Sardine landings at Vigo, a Spanish port just north of the Portuguese border, show the same picture, with strong increases in catches in the late 1920s and decreases in the early 1960s, and low catches in between (Carrera and Porteiro, 2003; Guisande et al., 2004).

3.2.2.2.2. English Channel. There has been an important sardine fishery at the western end of the English Channel for several hundred years and its fluctuations have been well documented (Alheit and Hagen, 1997; Southward et al., 1988). Herring as well as sardines occur in the Channel and both species are fished. Herring are predominant in the east and sardines towards the west off the south coast of Cornwall and Devon (Southward et al., 1988). The herring fishery flourishes in cold periods and extends farther to the west, whereas, in warm periods, the sardine fishery only extends to the west up to Lyme Bay, as observed between 1930 and the mid-1960s, but is restricted to west Cornwall during cold periods. After 1930, the Plymouth herring fishery declined drastically and the herring population off south Devon and southeast Cornwall was replaced in the late 1920s and early 1930s by large numbers of sardines. Binet et al. (1998) reported that during the 1950s the French sardine fishery was bountiful and large quantities were caught all the way to the North Sea. Meyer (1951) pointed out that in the winter of 1950/51 the German fisheries' fleet caught sardines in quantity for the first time. Those sardines were from the Channel and, when landed on German markets, they were believed to be small herring, as fresh sardines were not known in Germany. Between 1930 and 1960, sardines exhibited high abundances around Cornwall, as shown both by echo-sounder surveys and by the numbers of planktonic eggs (Southward et al., 1988). Dynamics of the Channel sardine population are reflected by an almost continuous collection of sardine eggs at the ICES monitoring station L5, southwest of Plymouth, which was started in the 1920s (Hawkins et al., 2003). Egg abundances increased conspicuously in 1935, decreased considerably around the late 1960s

and remained at low values until the 1980s (Fig. 4) (Coombs and Halliday, 2011; Hawkins et al., 2003). These faunal changes in the English Channel, which include many zooplankton and ichthyoplankton species, have been termed the Russell Cycle (Russell et al., 1971), which can now be related to the AMO cycle in the North Atlantic.

3.2.2.2.3. North Sea. There were no records of sardines from the North Sea before the 1930s (Aurich, 1953). Cushing (1957) reported that there was some evidence that, since 1935, sardines extended their range from the Channel into the Central North Sea. In the 1930s, sardines became more frequent in the North Sea and, after 1946 there was a stronger increase of sardine abundance with records from different areas such as off the Norwegian coast, off Lowestoft and Yarmouth, and from the German Bight (Aurich, 1953). Catch statistics showed the first sardine catches in 1936 with increasing tendencies in the late 1940s and decreases in the mid-1960s (Postuma, 1978). Meyer (1949) reported large amounts of sardines caught in the German Bight in 1949. In spite of many ichthyoplankton surveys from 1891 to the late 1930s, sardine eggs and larvae were never found in the southern North Sea (Aurich, 1953). First records of sardine eggs in the German Bight stem from 1949 and relatively high egg and larval concentrations were encountered until 1952, when the surveys were discontinued (Fig. 5) (Aurich, 1953).

3.2.2.3. Recent warm AMO period mid-1990s onwards

3.2.2.3.1. English Channel. After low abundances between about 1970 and 1990, high numbers of eggs similar to those caught in the period between 1925 and 1965 were collected after 1995, particularly in autumn (Coombs and Halliday, 2011; Hawkins et al., 2003).

3.2.2.3.2. North Sea. Sardines were not found in the International Bottom Trawl Surveys (IBTS) between 1970 and 1990, except for occasional stray individuals, but then turned up in larger quantities since 1990 (Alheit et al., 2012; D. Beare et al., 2004). Sardine eggs and larvae were found in the Helgoland Roads series from 1990 to 1999 with numbers increasing considerably since 1996 (Alheit et al., 2012). Between 2003 and 2005, sardine eggs and larvae were encountered regularly in the German Bight (Alheit et al., 2012), where their distribution was very similar to that reported by Aurich (1953) (Fig. 5).

3.2.2.3.3. Baltic Sea. After a long absence, sardines were found sporadically between 2001 and 2007 in the Skagerrak/Kattegat area (Alheit et al., 2012).

3.2.3. Sardinella

3.2.3.1. Positive AMO phase mid-1920s–late 1960s

3.2.3.1.1. Mediterranean. Landings of round sardinella in the western Mediterranean were rather high from the mid-1940s, especially in the Alborán Sea, but decreased in the late 1950s (Instituto Español de Oceanografía, unpublished data) (Fig. 4). Historical records of round sardinella catches in the Aegean, eastern Mediterranean, (Moutopoulos and Stergiou, 2011) show that its biomass was higher from 1928 to 1948 when compared to the 1964–1990 period (Fig. 4) (the catches are plotted as a ratio of round sardinella over combined sardine and anchovy catches, in order to correct for fishing effort).

3.2.3.2. Recent warm AMO period mid-1990s onwards

3.2.3.2.1. NW Africa. Off Morocco, after rather low catches from 1970 to 1995, when conditions were generally cooler (Zeeberg et al., 2008), catches have increased considerably (Alheit et al., 2010). Total catches of *S. aurita* off NW Africa (FAO, 2011) show an increase starting around the mid-1990s (Fig. 4) Catches of *S. aurita* around the Canary Islands in the waters off NW Africa show an increase around the mid-1990s and several studies have shown that *S. aurita* has replaced *S. pilchardus* in these waters. The sardine used to be the second most important small pelagic species (after mackerel) while the round sardinella was an
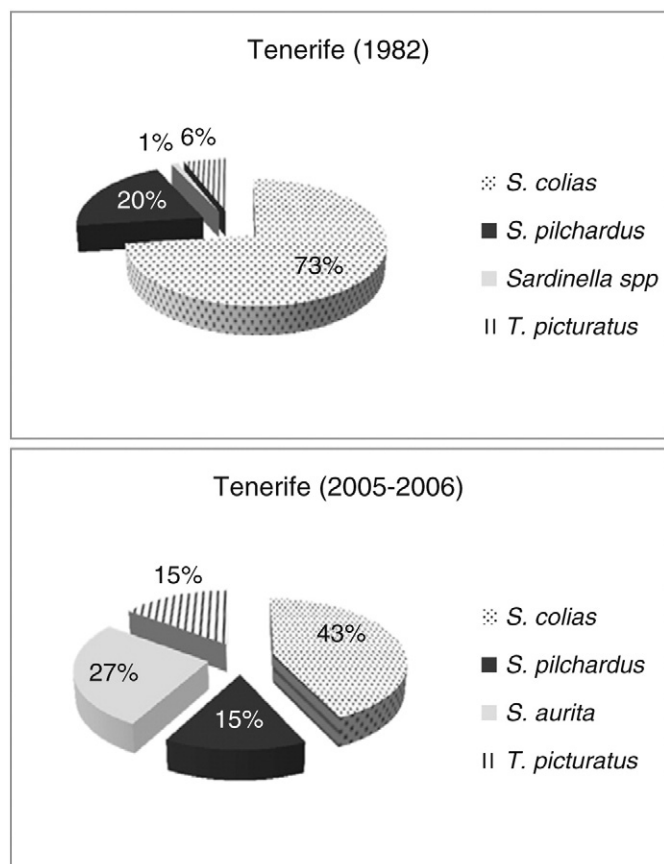

Fig. 6. Percentages of catch distribution of small pelagic fishes off Tenerife in 1982 and 2005/2006.

accessory species. For example, in 1982, sardines comprised 20% of the total catch, whereas sardinellas made up only 1%. In 2005/2006 the situation had reversed. *S. aurita* represented 27% and *S. pilchardus* only 15% of total small pelagic catches off the island of Tenerife (Santamaría et al., 2008) (Fig. 6). Herrera Rivero et al. (2008) confirmed this by demonstrating that, when comparing only catches of the two species, those of the round sardinella increased from 22% in 1978/1979 to 96%, while those of the sardine decreased at the same time from 78% to 4%.

3.2.3.2.2. Mediterranean. *S. aurita* is particularly frequent in the warm waters of the eastern and southwestern parts of the Mediterranean (Sabatés et al., 2006). However, recently, it has been reported to migrate to more northern areas such as the northern Aegean (Tsikliras, 2008; Tsikliras and Antonopoulo, 2006), the northern Adriatic (Sinovic et al., 2004), the Gulf of Lion (Francour et al., 1994) and the western Mediterranean (Sabatés et al., 2006, 2009), thereby increasing abundance and establishing spawning populations in these more northerly regions. A significant positive relationship was described between round sardinella landings and temperature anomalies for the western (Sabatés et al., 2006) and eastern (Tsikliras, 2008) Mediterranean. The increase of landings and the northwards distributional shift coincide with the start of a period of positive temperature anomalies in the mid-1990s in the western as well as in the eastern Mediterranean (Fig. 4) (Sabatés et al., 2006; Tsikliras, 2008).

3.2.4. Herring

3.2.4.1. Positive AMO phase mid- to late 19th century

3.2.4.1.1. Nordic Seas. For centuries one of the mysteries in Norwegian waters was the unforeseen fluctuations in the winter fishery of herring along the Norwegian coast. Løberg (1864) summarised the

fluctuations in the fishery from the 15th to the 18th century. He also referred to reports of fluctuating herring fisheries from the 9th century throughout the 14th century. However, it was during the 15th century, when the process of salting and storing of herring became common, that the herring fishery started to expand significantly. Løberg reported that the herring disappeared from the coast after 1567, and that the fishery did not start again until the first part of the 17th century. Herring disappeared again during the period 1650–1700. There was an important fishery from the beginning of the 18th century, and the years between 1740 and 1760 were particularly rich, but after 1784 the herring were once more absent along the coast. The subsequent herring period was between 1808 and 1873, with the main fishery moving northwards towards the end of the 19th century (Boeck, 1871; Hjort, 1914; Løberg, 1864; Sars, 1879), after which the landings declined again. The historic catches up through the 19th century correspond quite well with the AMO, being higher during the warm phases, whereas, interestingly, herring at the southern edge of its area of distribution, in the English Channel, were not very common during this period (Hawkins, pers. comm.). The clear link between periodicity of herring populations in relation to warm and cold periods has also been used to explain the alternation of fishing periods of the Norwegian spring spawning herring and the Swedish Bohuslän herring (Alheit and Hagen, 1997; Cushing, 1982; Devold, 1963), which can be traced back for centuries.

3.2.4.2. Positive AMO phase mid-1920s–late 1960s

3.2.4.2.1. Nordic Seas. The historic data on Norwegian spring spawning herring demonstrate a clear overlap between the positive AMO phase, from the mid-1920s to the late 1960s, and herring biomass landed. (Again, herring in the English Channel had increased during the previous cool period, but declined rapidly in the early 1930s during the onset of the warm phase, but did not recover again after the warm period Hawkins et al., 2003). The large fishery occurring during this positive AMO phase was in fact a result of very good recruitment and large incoming year classes which already started during the negative AMO phase. Hjort's (1914) research on year class strength in herring, based on ageing of scales, revolutionised the understanding of fluctuations in the fishery of this population and also set the agenda for research on other fish populations. He demonstrated that the fishery depended heavily on the recruitment of large year classes, which could be traced over multiple years in the fishery. In 1904, there was a large year class of herring (Hjort, 1914) during a negative AMO phase, when the AMO index was at its lowest, which formed the basis for the very rich herring fishery that developed in the following years (Devold, 1963; Lea, 1930; Runnstrøm, 1941). The understanding of how well this population recruited during the positive AMO phase until the late 1960s reached a new level when a VPA series of abundance was developed running back to 1907 (Toresen and Østvedt, 2000). This study demonstrated, that after the 1904 year class entered the spawning in 1911 and 1912, spawning stock biomass (SSB) increased to 5 million tonnes, following a decrease to levels of 2 million tonnes in 1920 due to low recruitment. However, entering into a new positive AMO phase in the 1930s, a few abundant year classes were born leading to a record high SSB of 16 million tonnes in 1945. After this herring SSB declined and, despite the abundant year classes 1950 and 1959, the stock collapsed in the 1960s reaching levels below 100 thousand tonnes in the 1970s. This happened after a very heavy fishery in combination with a period of low recruitment, when the AMO index started to decline again and entered a negative phase. Model simulations have demonstrated that the main reason for the collapse was the uncontrolled fishery (Fiksen and Slotte, 2002). Simulations show that, if the present harvest control rules and management regime were run, the full collapse in the 1960s could have been avoided and the population would have levelled off at about

4 million tonnes after a long period with low recruitment (Røttingen and Tjelmeland, 2011). The effect of the fishery may also be seen as the historic landings lag behind the SSB (Fig. 4), which may serve as a good example of the uncertainty connected with landings when used as a proxy for abundance as in the present study.

As during the previous warm phase, herring catches were taken farther to the north during the 1950s and 1960s (Cushing, 1982; Devold, 1963). In addition to the dramatic changes in abundance, large-scale distributional changes were observed during this warm period (Dragesund et al., 1980, 1997; Drinkwater, 2006). From their spawning locations on the west coast of Norway and their nursery areas in the western Barents Sea herring migrated to feeding grounds off northeastern Iceland. They also moved farther eastwards to feed in the area off southwestern Svalbard. When the population declined in the 1960s, the herring no longer migrated out to the Norwegian and Greenland Seas but remained near the Norwegian coast for feeding and spawning (Dragesund et al., 1980, 1997; Drinkwater, 2006). However, the changes in migration pattern were not necessarily a direct consequence of environmental changes. The observed changes in migration and distribution are mainly attributed to changes in population density (Dragesund et al., 1980, 1997) and population structure (Huse et al., 2002, 2010; Slotte, 1999, 2001; Slotte and Fiksen, 2000). At increasing population size the feeding area and spawning area are extended. Wintering areas and spawning areas may change, when large incoming year classes recruit to the spawning stock, and the distance migrated to feed and spawn may increase, as the herring grows to be larger and vary inter-annually with condition.

3.2.4.3. Recent warm AMO period mid-1990s onwards

3.2.4.3.1. Nordic Seas. The Norwegian spring-spawning herring SSB was at very low levels throughout the 1970s and early 1980s. During this negative AMO phase, but shortly after the AMO index started to increase again, the high recruitment of the 1983, 1991 and 1992 year classes led to a rebuilding of the stock. After the AMO index entered the positive phase, further closely spaced strong year classes occurred, such as for 1998, 1999, 2002 and 2004. The SBB reached levels above 10 million tonnes during this warm AMO phase, but after a period with low recruitment since the 2004-year class, the stock is now declining. (Fig. 4). After the collapse of the stock in the late 1960s very strict management regimes were set, and the stock was harvested in a very conservative manner relative to SSB and incoming recruitment during the rebuilding phase. Hence, during this period there was no lag between the SSB and landings. Landings increased with the bursts in SSB around the mid-1990s and around 2005 to a maximum of about 1.5 million tonnes in 2009 (Fig. 4). With the strong development in stock abundance in the 1990s, the herring again migrated to Iceland for feeding and changed wintering areas from coastal to oceanic (Dragesund et al., 1997; Drinkwater, 2006; Huse et al., 2010), again more as an indirect response of increased density and variable population structure related to the new and yet variable recruitment to the stock.

3.2.5. Sprat

3.2.5.1. Negative AMO phase until mid-1920s

3.2.5.1.1. Bay of Biscay. High catches were reported for the time between the two world wars (Cendrero, 1998), particularly between 1923 and 1929 (Anadon, 1950).

3.2.5.2. Positive AMO phase mid-1920s–late 1960s

3.2.5.2.1. Skagerrak, Kattegat. The period between 1936 and 1956 could be considered as a time of high stock abundance (ICES, 1990).
3.2.5.2.2. Baltic Sea. Higher catches were reported from 1930 to 1937 (Eero, 2012).

3.2.5.3. Negative AMO phase late 1960s–mid-1990s

3.2.5.3.1. Mediterranean. The Adriatic catches spanning 1950 to 1995 showed high values from about 1960 to 1990 (Grbec et al., 2002). Catch data from the fishery off Spain (Levantina, Tramontana), available from 1973 to 1984, show an increase from 1981 to 1984 (Anon, 1971–1986).

3.2.5.3.2. Bay of Biscay. Catch data from the fishery off Cantábria (Spain), available from 1973 to 1984, show high values until 1981 and then a decrease to very low numbers (Anon, 1971–1986).

3.2.5.3.3. North Sea. Catches started to increase considerably in 1971 to very high values in the mid-1970s and decreased again between 1980 and 1982 (ICES, 1990). Also, the distribution changed markedly, as the coastal sprat were widely dispersed in the North Sea, including eggs and larvae (ICES, 1990). During the decline, the centre of abundance shifted from the central to the southern and southeastern North Sea.

3.2.5.3.4. Skagerrak, Kattegat. The landings from 1966 to 1986 show high catches between 1973 and 1982 (ICES, 1990). Thereafter, the stock decreased to very low levels.

3.2.5.3.5. Baltic Sea. Landings show elevated values from 1969 until around 1980 and then again since the late 1980s (Eero, 2012; ICES, 1990). However, the earlier increase in biomass was recorded only in the northern Baltic, in ICES areas 26–32, whereas the recent increase occurred throughout the Baltic Sea (Eero, 2012).

3.2.5.4. Recent warm AMO period mid-1990s onwards

3.2.5.4.1. Baltic Sea. Catches since the mid-1990s have been particularly high (Eero, 2012).

3.3. Synchronicity of fish population and AMO dynamics

The analysis of long-term data available between 1945 and 2010, suggests that the fluctuations of small pelagic clupeoid fish stocks in the Central and Eastern North Atlantic and in the Mediterranean significantly respond to the different phases of the AMO. The 1st principal component (PC1), representing 53% of small pelagic fish long-term variability, is indeed highly and positively correlated with the AMO (r Pearson = 0.67** from 1945 to 2010 and r = 0.72** in 1985–2010, where ** indicates $p < 0.001$) (Fig. 7). The PC scores indicate that PC1 is mainly driven, in decreasing order of importance, by Norwegian spring spawning herring, western Mediterranean anchovy, Aegean sardinella, western Mediterranean sardinella and sardines from the Eastern Channel. Overall, during warm AMO phases the stocks of herring, sardine and sardinella tend to increase, while the western Mediterranean anchovy stock tends to decrease.

4. Discussion

Abundance of fish populations is determined both by natural processes, such as climate variability, trophic interactions or diseases, as well as by anthropogenic influences such as fishing activities. As the estimation of biomass has not been possible until recent decades and is still not available in some cases, often due to the high costs involved, we have used catch data as a proxy for comparative purposes, in spite of the disadvantages of this metric. In the case of the Norwegian spring spawning herring, we have demonstrated the time lags between catches and SSB with respect to their respective dynamics. However, as life spans and recruitment to the fisheries of the other clupeoid species are much shorter, these time lags are minimal.

The target of this study was to integrate the dynamics of the entire complex of clupeoid groups in the eastern North and Central Atlantic, including herring, sprat, anchovy, sardine and sardinella, over a wide geographic area from Senegal and Morocco in the south to the Nordic Seas in the north, including the Mediterranean, thereby covering a multitude of different ecosystems (Fig. 2). Several populations of these species were not included in this analysis because either their time series were too short (for example North Sea sprat), there was no information on catch (for example the four North Sea herring populations), or their catch statistics seemed dubious. Coherent information on the catch of the species included in this analysis is available for about the last 150 years in the case of the Norwegian spring spawning herring but for shorter time periods with respect to the other species. A large number of publications over the last hundred years or so have demonstrated that these species, which usually are the basis of important fisheries for the respective coastal human populations, exhibit large variations in abundance and catches on the multidecadal scale (for example: Alheit and Hagen, 1997; Alheit and Bakun, 2010; Toresen and Østvedt, 2000). Central to the present study was to relate the multidecadal fluctuations of clupeoid populations to the multidecadal variations of the AMO.

The study of historical time series has demonstrated that several populations of these small pelagic clupeoid fish distributed in the large area between Senegal and Norway exhibit synchronous multidecadal changes in abundance and distribution. These synchronous changes can be associated with the AMO, which is a climatic oscillation of the North Atlantic defined by surface SST. Statistical analysis using PCA indicates that major clupeoid populations in the NE Atlantic are positively (sardinella in the western and eastern Mediterranean, sardine in the English Channel and Norwegian spring spawning herring) correlated with the AMO index; conversely, there was a negative correlation with the AMO for the western Mediterranean anchovy (Fig. 7). Other clupeoid populations (i.e. round sardinella off Northwest Africa) show the same
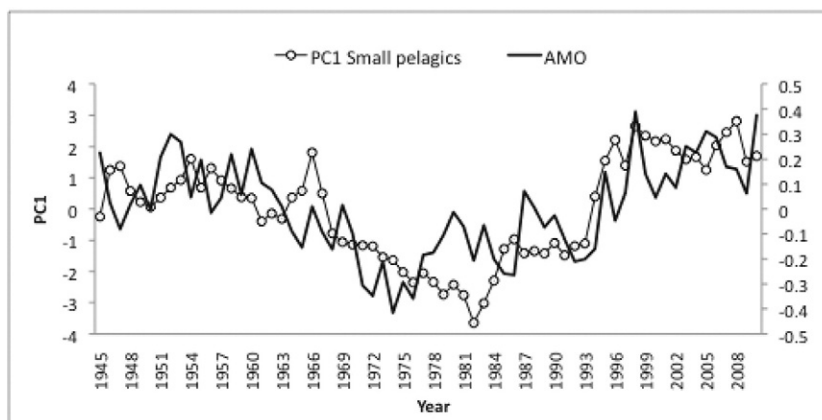

Fig. 7. First principal component (PC1) based on the main long-term data sets of small pelagics available in the Eastern Atlantic and Mediterranean between 1945 and 2010. The Atlantic Multidecadal Oscillation (AMO) is superimposed.

tendency but their time series were either incomplete or too short to be included in the statistical analysis.

The rise in SST associated with the most recent AMO phase was particularly marked in the Nordic Seas, Celtic Sea and Bay of Biscay shelf, Iberian upwelling region and western Mediterranean; in all those regions since 1995 the yearly SST mean has been ≥ 0.5 °C higher than in the previous 65 years. Temperature changes associated with the AMO are likely to be proxies for other variables in the coupled ocean–climate system, such as changes in ocean circulation patterns and advection of water masses with different physical, chemical and biological properties (Hátún et al., 2009b). Consequently, a more thorough study of changes in the waters and the overlying atmosphere of the North Atlantic, which occurred synchronously with AMO dynamics, is required. A useful starting-point might be the mid-1990s when the AMO index surged upwards.

A large number of publications report observations of changes in North Atlantic waters and atmosphere at this time, some rather drastic. These are closely tied to (i) the shift of the Icelandic Low with an associated large decrease of the NAO index, (ii) the weakening of the Atlantic Meridional Overturning Circulation (AMOC) and (iii) the contraction of the subpolar gyre (SPG). Basically, these three events observed at the mid-1990s caused a substantial re-distribution of water masses in the Northeast Atlantic which affected most ecosystems in this region, including the Mediterranean. In particular, the SPG was recently the focus of a number of physical and biological studies because of its high variability and importance for North Atlantic climate and ecosystems (Hátún et al., 2009a,b; Lohmann et al., 2009a,b; Robson et al., 2012; Yeager et al., 2012).

The key processes leading to these events can briefly be described as follows. From the mid-1960s to the mid-1990s, the winter NAO index increased from very negative to very positive values (Hurrell and Deser, 2010). During this period, the northwesterlies over the Labrador Sea were strengthening thereby causing an enhancement of winter heat loss to the atmosphere and so favouring the intensity of local deep convection (Bersch et al., 2007; Sarafanov, 2009). This resulted in cooling and freshening of the subpolar North Atlantic, but warming and salinization of the subtropical North Atlantic (Bersch et al., 2007; Cannaby and Hüsrevoğlu, 2009). The intensification of the North Atlantic Current (NAC) increased the eastwards advection of cold and fresh subarctic water on its northern side and warm and saline subtropical water on its southern side (Bersch et al., 2007). The increasingly strong NAO conditions leading up to the mid-1990s resulted in a decades-long spin-up of the AMOC (Yeager et al., 2012).

In the winter of 1995/96 the westerly winds weakened drastically and the NAO index dropped conspicuously, and both have remained in a more or less neutral situation since then (Bersch et al., 2007; Robson et al., 2012). The zonal transport of the NAC decreased, the subpolar front (SF) shifted northwards and westwards in the Iceland and West European basins, indicating a contraction of the SPG. The weakening of the westerly winds in association with the decline of the NAO index in the mid-1990s to the mid-2000s resulted in a reduction of the deep convection intensity in the Labrador Sea, a slowing and contraction of the SPG, a northwestwards shift of the SF in the east and a corresponding northwards advance of warm saline sub-tropical waters (Sarafanov, 2009). The drastic decline in the NAO index was associated with the establishment of a blocking high-pressure cell over Scandinavia in the winter of 1996 with the result that southerly winds replaced the strong westerly winds above the northeastern North Atlantic (Bersch, 2002). As the SPG is a region of intense interaction between ocean and atmosphere (Häkkinen and Rhines, 2004), its dynamics played a key role in the events in the mid-1990s. In general, the SPG controls the flow trajectory of the NAC. When the gyre is strong and extends far eastwards, a branch of the NAC drags cold, low-salinity sub-arctic waters over the Rockall Plateau (Hátún et al., 2009b). When the gyre weakens and shifts westwards, it allows sub-tropical water to spread to the north and west, leading to much warmer and more saline conditions. The SPG has warmed substantially since the mid-1990s, especially in the eastern sector (Sarafanov et al., 2008). This rapid warming

is primarily a result of a surge in northwards heat transport in the mid-1990s (Robson et al., 2012) and is linked to the slowdown of the SPG circulation (Häkkinen and Rhines, 2004; Robson et al., 2012). Between 1970 and 1995, there was a steady rise in advective heating of the SPG region which was largely counterbalanced by surface cooling, so that the heat content tendency remained generally low (Yeager et al., 2012). However, the weak NAO in winter 1995/96 coincided with an extreme positive heat content in the SPG, since the surface cooling was insufficient to match the strong advective heating. Thus, both surface and advective heat fluxes played crucial roles in the SPG warming (Yeager et al., 2012). As the strength of the SPG declined in the mid-1990s, it also contracted (Bersch et al., 2007) with a northwestwards shift of the SF (Hátún et al., 2005; Robson et al., 2012; Sarafanov et al., 2008).

During extended periods when the SF moved eastwards with a strengthened NAO (Lozier and Stewart, 2008; Sarafanov, 2009), the SPG blocked the northwards flowing Mediterranean Overflow Water (MOW). However, when the SF moved westwards during extended weak NAO periods, the MOW penetrated farther to the north. This is confirmed by Hátún et al. (2005), who showed from modelling that a westwards contraction of the SPG allows high-salinity sub-tropical waters to flow northeastwards towards the Nordic Seas (Häkkinen and Rhines, 2009). According to Hátún et al. (2005), the source of these saline waters is in the eastern Atlantic. The warm saline waters from the sub-tropics originate mostly in the upper layers of the eastern North Atlantic and from the MOW (Sarafanov, 2009). The increase of temperature and salinity of the eastern SPG is considered as strong evidence for increasing inflow from sub-tropical regions (Häkkinen and Rhines, 2009).

The question of the possible mechanisms leading to the contraction of the SPG is of particular interest with respect to potential predictability of the gyre contraction and, maybe, to the dynamics of small pelagics. There are basically two different views about the primary driver for SPG circulation changes: (i) wind forcing and (ii) buoyancy forced deep convection (Robson et al., 2012).

(i) The usual pattern of air masses is a cyclonic rotation north of the Atlantic jet and an anti-cyclonic one south of the jet whereby this type of wind forcing maintains the North Atlantic gyre circulations (Woollings, 2011). According to Häkkinen et al. (2011) this system can be blocked by a stationary anti-cyclone which leads to a reversal of the usual pattern resulting in a contraction of the subpolar gyre (Woollings, 2011).

(ii) Buoyancy driven deep convection is essential for the decrease in size and strength of the SPG since the mid-1990s (Bersch et al., 2007; Häkkinen and Rhines, 2004; Lohmann et al., 2009a; Robson et al., 2012). The AMOC increased from the 1960s to the first half of the 1990s due to strengthening of the NAO (Bersch et al., 2007). The dynamics of the SPG are tightly connected to the dynamics of the NAO. The NAO was in a very positive state from about 1980, and particularly from 1989, on to 1995. Under the persistent decadal-scale forcing of the very positive NAO the AMOC, particularly the NAC region, due to the formation of intermediate to deep water masses in the SPG (Lohmann et al., 2009a), and also the SPG strengthened. This caused the subtropical gyre (STG) to advect warm more saline water from lower latitudes into the eastern part of the SPG region which was reinforced by an anomalous wind stress curl in the northeastern North Atlantic. This, in turn, counteracted the buoyancy forcing of the SPG. This resulted in an abrupt weakening and contraction of the SPG in the winter of 1995/96 which was enforced by the sudden drop of the NAO in winter 1995/96 (Lohmann et al., 2009a,b; Robson et al., 2012).

In conclusion, a chain of very complex processes occurred in the North Atlantic starting in the mid-1960s and culminating around the mid-1990s, which had far-reaching consequences for the ecosystems in the eastern North and Central Atlantic and their biota, including

small pelagic fish populations. The dynamics of the AMO are an indicator of these processes and the Atlantic SSTA are a proxy. Understanding the mechanism behind the variability of the SPG is essential as it might potentially allow a prediction of North Atlantic climate (Lohmann et al., 2009a) and associated variability of ecosystems and plankton and fish populations (Hátún et al., 2009a).

Oceanographic processes in the 1920s and 1930s seem to have been very similar to conditions observed since the mid-1990s. During the positive AMO phase in the last century, a dramatic warming of air and sea temperatures was recorded during the 1920s and 1930s in the northern North Atlantic and the high Arctic, whereby the most drastic changes were recorded north of 60°N (Drinkwater, 2006; Johannessen et al., 2004). Sea temperature was also higher in the North Sea, the English Channel and the Baltic Sea. The elevated sea temperatures were not caused by the rising air temperature alone, but also by apparent large-scale changes in ocean circulation which brought more warm water northwards (Drinkwater, 2006). The warming was associated with atmospheric changes causing increased transfer of heat from low to high latitudes (Drinkwater, 2006). At the same time, the Icelandic Low was noted as having moved to the east (Overland et al., 2004).

It is not surprising that populations of small pelagic fish in the Mediterranean also exhibit AMO-related dynamics. Marullo et al. (2011) revealed that Mediterranean annual SST time series have a significant oscillation with a period of about 70 years, whereby the warm and cold phases correspond closely to those in the North Atlantic. Marullo et al. (2011) estimated the magnitude squared coherence (MSC) (Wang et al., 2004), which measures the strength of association and relative linearity between stationary processes, between the Mediterranean SST time series and four time series of the Atlantic Ocean, namely: the NAO, AMO, subpolar gyre region SST and subtropical gyre SST. They demonstrated that all the Atlantic time series are significantly coherent with the Mediterranean time series. Marullo et al. (2011) explored the potential mechanism of the connection between the multidecadal variability of both oceans and, inter alia, point out a possible role of the Mediterranean Overflow Water (MOW), the northwards penetration of which might be connected to the location of the subpolar front (Lozier and Stewart, 2008).

Garcia-Soto and Pingree (2012) have shown that the long-term time series of SST and SSTA in the Bay of Biscay exhibit AMO-like cycles and that the AMO explains about 25% of the interannual variability of the annual SST anomaly in the Bay of Biscay during the last 150 years, whereas different indices of the NAO explain only ≤1% of the long-term record. While the NAO is a high frequency climate mode, the AMO can modulate low frequency changes. Garcia-Soto and Pingree (2012) also point out that AMO-like variability is reflected in at least four mesoplankton components of the Russell Cycle, these being the abundance of two chaetognath species, the copepod *Calanus helgolandicus*, as well as larval decapods sardine eggs.

As with the regions farther north, the upwelling area off Northwest Africa experienced a climatic shift around 1995 (Zeeberg et al., 2008). SST increased and SSTA in summer–autumn in 2002–2003 were 3 °C higher than the long-term average. The climate shift was also associated with changes in the pressure field and winds. The effect of the climate shift was an extension of the habitat favourable for sardinellas from Senegal to Mauretania and Morocco accompanied by a strong rise in abundance (Zeeberg et al., 2008), whereas environmental conditions for sardines apparently became unfavourable.

Long-term time series on sprat abundance are available from the Mediterranean in the south to the North Sea and Baltic Sea in the north. Interpretation of changes in sprat in relation to the AMO dynamics is not straightforward, as, in contrast to the other clupeoid species, sprat dynamics do not seem to be well correlated with the AMO. The different sprat stocks show high catches during negative (mid-1960s to mid-1990s) (Mediterranean, Grbec et al., 2002) as well as during positive (recent) AMO periods (Baltic, Eero, 2012). Sprat stocks in the Bay of Biscay, North Sea, Kattegat/Skagerrak and Baltic Sea all had

high catches from about the late 1960s to the early 1980s (Anon, 1971–1986; ICES, 1990), when the AMO index was negative. On the other hand, record catches were reported from the Baltic Sea since 1995 (Eero, 2012), when the recent warm AMO period started. The picture becomes clearer when we look separately at different latitudes. In the south, in the Adriatic, sprat abundance was high during the negative (cold) AMO period (Grbec et al., 2002). In the far north, for the Skagerrak/Kattegat area and Baltic Sea, sprat catches were high during the positive (warm) periods (Eero, 2012). MacKenzie and Köster (2004) have pointed out that sprat recruitment is positively related to temperature in the north but negatively in the south. Overall, the relation between AMO and sprat dynamics is not conclusive. In the case of sprat, catch data might not reflect very well the true abundance, mainly for two reasons. First, it is very difficult to separate sprat from young herring, unless one checks each individual separately. Second, with the exception of the Baltic Sea, where sprat is the most important species in terms of biomass at present (Alheit et al., 2005), there is no other targeted fishery for sprat.

Summing up, the changes observed in the circulation of the North Atlantic and in its overlying atmosphere in the mid-1990s affected the biota of most, probably even all ecosystems of the northeastern Atlantic from the upwelling region off Senegal and Morocco up to the Nordic Seas, including semi-enclosed seas such as the Mediterranean and the Baltic Sea. This is particularly clear in the dynamics of small pelagic clupeoid fish populations many of which exhibited drastic changes in abundance and/or distribution in the mid-1990s. Small pelagic fish can be viewed as sentinels of these oceanographic and atmospheric processes, which are very pronounced for the Mediterranean. Thus, the increase of sardinella off the northern coasts of the Mediterranean was accompanied by a decrease of sardine and anchovy populations since the 1990s, whereas sprat has disappeared from commercial catches (Calvo et al., 2011; Palomera et al., 2007; Sabatés et al., 2006; Sinovic et al., 2004). Drinkwater (2006) suggests that the dramatic changes observed in plankton, fish and benthos in northern waters in the 1920s were a large-scale ecosystem regime shift. Our study demonstrates that far-reaching changes also took place in the mid-1990s in the current system of the North Atlantic in association with the contraction of the subpolar gyre and the AMO dynamics which strongly affected the dynamics of small pelagic fish populations from the upwelling region off NW Africa to the Nordic Seas. Similar changes in distribution and abundance around the mid-1990s have been reported for plankton and other groups of fish (Beaugrand and Reid, 2012; Hátún et al., 2009a). Consequently, we state that a large-scale climatically induced regime shift occurred in the ecosystems of the eastern North and Central Atlantic in reaction to complex processes indicated by the AMO signal that seem to govern multidecadal dynamics of these ecosystems and their biota in synchrony with the dynamics of the AMO.

Acknowledgements

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