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6–9 July 2010

Nantes, France



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Executive summary

WKANSARNS met in Nantes, France to investigate the phenomena of increased catches in anchovy and sardine since the mid-1990s in the North Sea and adjacent areas. The workshop attempted to increase our understanding by considering the phenomenon in terms of the processes controlling the life cycle of anchovy and sardine. It considered the historical context and synthesised across the scientific disciplines of oceanography, climatology, genetics, ecology, biophysical individual-based modelling and analysis of empirical time series.

WKANSARNS concluded that the recent increase of anchovy in the North Sea is probably due to the development of local North Sea populations, rather than a northward movement of Bay of Biscay populations. There has always been anchovy, at a low abundance, in the North Sea (spawning along the Dutch coast, Wadden Sea and estuaries). The expansion of anchovy in the North Sea is thought to be driven by pulses of successful recruitment that are controlled by relatively high summer temperature of sufficient duration followed (or preceded) by favourable winter conditions. There is probably a balance between high enough summer temperature allowing sufficient growth and winter conditions allowing sufficient survival at length. Variability in the length of these periods or in spatial extent where such conditions can be found may have a strong influence on the recruitment success.

Whilst this workshop primarily considered driving processes related to temperature, other potential mechanisms, or mechanisms that co-vary with temperature, may be important in the dynamics of North Sea anchovy.

It is probable that sardine in the North Sea is either part of one large Atlantic population or it mixes greatly with sardine further south. It appears likely that spring abundance depends on recruitment in the North Sea from summer spawning events, while autumn catches are also influenced by migrations from the west.

The conclusion of the workshop, although preliminary, was that climate-driven changes in water temperature appear to mediate the productivity of anchovy in the North Sea although the influence of climate-driven factors on sardine is less clear.

WKANSARNS will not meet again under ICES.

1 Objectives

Trawl survey and fisheries information have recently shown an increase in catches of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the North Sea from about the middle of the 1990s onwards. A few papers have been published on this increase but few have closely considered the processes that lead to this phenomenon and most have only speculated about its cause. Scientists that study the North Sea ecosystem have very little knowledge or experience of working in anchovy and sardine ecology but these two fishes are heavily studied in other parts of the world and especially in southern Europe. The management of fisheries on anchovy in the Bay of Biscay has also received much attention. The recent closure of the fishery as a result of low biomass and poor recruitment has led to speculation that perhaps the stock had moved north.

WKANSARNS was set up to address some of these issues and to investigate some hypotheses about why anchovy and sardine suddenly appeared in the North Sea and adjacent areas. Studying an organism at the edge of its range often provides insight into its dynamics at the centre of its distribution, thus WKANSARNS would not only improve our understanding of anchovy and sardine in the North Sea but also in areas where they are much more abundant.

WKANSARNS also considered the dynamics of sprat (*Sprattus sprattus*) in the North Sea, as sprat fill a similar trophic niche as anchovy and sardine in systems where they co-occur. The approach of the workshop was to consider specific ideas (hypotheses) about why anchovy, sardine and sprat exhibit their particular dynamics and synthesise all available knowledge for the provision of advice to fisheries managers and the scientific community.

The report is structured to give the background to the changes in dynamics of anchovy and sardine near their northern limits. This is followed by considerations of the oceanography and climatology of the region and considerations of the evidence for connectivity with southern populations. Then various hypotheses for the increase in abundance are investigated and we look into the future and further research needs.

2 Dynamics of anchovy, sardine and sprat in the North Sea and adjacent areas

Anchovy, sardine and sprat, are planktivorous pelagic species which have their northern-most distribution in the north-east Atlantic, more specifically in the North Sea and adjacent areas. Particularly anchovy and sardine are generally associated with warmer, southern European waters (Lusitanian ecoregion). However, sprat is also distributed from the Mediterranean and Black Sea to the southern North Sea and west of Scotland. Long-term information about the population dynamics of these three species in the North Sea and adjacent waters is relatively sparse and little reliable information is available about the stock sizes in these waters.

2.1 Anchovy

Some of the oldest records of anchovy in northern Europe are from archaeological findings from Denmark and date back to the Atlantic period (ca. 7000–3900 b.c.). However the marine environment during this period was characterised by higher temperature and salinity waters compared to today (Enghoff *et al.*, 2007). In recent more temperate times, the largest northerly anchovy spawning area was in the

Zuiderzee, a large shallow estuary in the Netherlands. A dedicated fishery targeted the spawning anchovy there during the summer months (May–August) from at least the end of the nineteenth century (Cunningham 1889/1890) until 1932 when the Zuiderzee was closed off by a dam (Boddeke and Vingerhoed, 1996; Figure 2.1.1). Although no long time series are available for that period, anecdotal evidence suggests that at the end of the 19th century anchovy were also regularly caught during the winter sprat fishery in the English Channel, along the south coast of Wales and off eastern England, sometimes in high numbers (Cunningham 1890). These anchovies were adult specimens thought to originate from the Zuiderzee spawning grounds. Particularly high numbers of anchovy were caught in the winter of 1889, when considerable numbers were also reported from as far North as the Moray Firth. The dedicated anchovy fishery in the Zuiderzee in the subsequent summer (1890) reportedly caught nearly 10 000 tonnes of anchovy, the highest number in at least that decade and by any nineteenth century standards a large fishery. This could suggest that anchovy from the Zuiderzee population and those in the Channel are related.

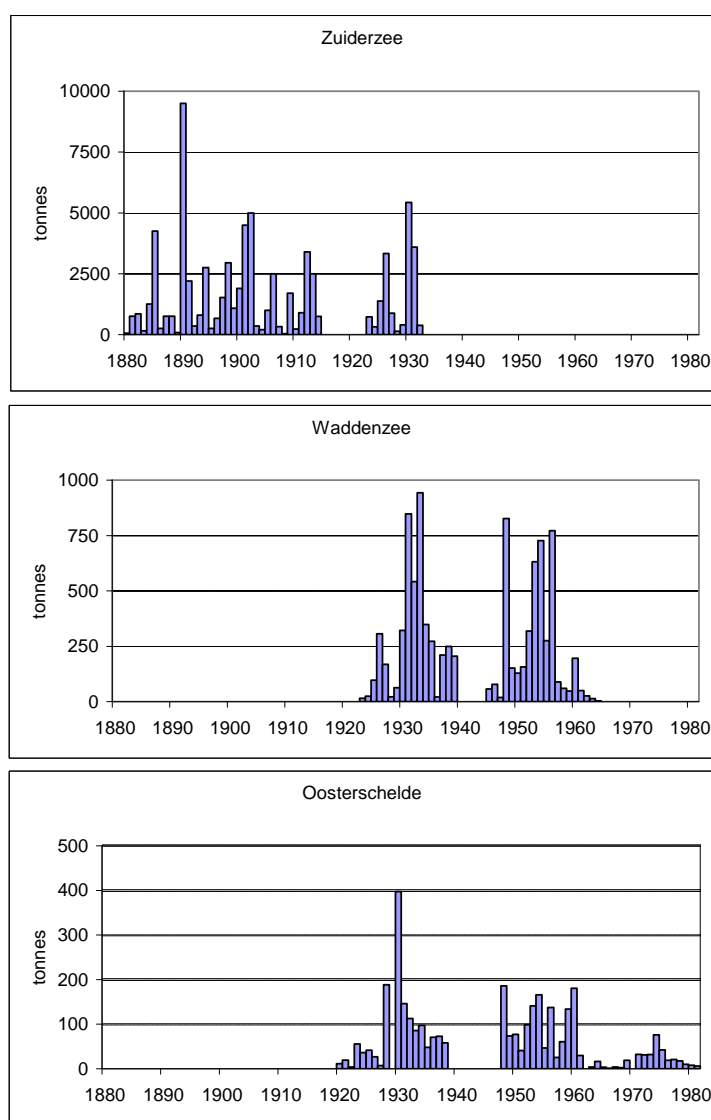


Figure 2.1.1. Dutch fishery landings of anchovy from 1880 to 1980. Data from IMARES.

It can be assumed that the Zuiderzee spawning population was the largest in the region as since its closure, numbers of anchovy in the region appeared to drop significantly. Smaller anchovy spawning areas were known from the Eastern Oosterschelde estuary in the Netherlands (Wallace and Pleasants, 1972; Boddeke and Vingerhoed, 1996; Figure 2.1.1) and in the western Dutch Waddenzee. Here the fishery landed up to 1000 tonnes a year between the 1930s and 1960s (Figure 2.1.1), after which the fishery ceased to exist. Smaller numbers of spawning anchovy were also recorded in Danish waters, the Baltic Belt area and German Bight during the 1930s (Heegaard, 1947) and 1940s (Enghoff *et al.*, 2007). Fisheries independent time series confirm that anchovy was generally very rare in the North Sea and adjacent areas. It occurred occasionally in low numbers of between the thirties and sixties in for example the northern North Sea and in the mid 1970s (Beare *et al.* 2004 a,b; Figure 2.1.2). Several different sources independently report a sudden increase in anchovy in the mid 1990s across the northern region: in the Waddenzee (SSB: 104 tonnes), southern North Sea, northeastern North Sea (Boddeke and Vingerhoed, 1996; Corten and van de Kamp, 1996; Beare *et al.* 2004 a, b), Irish Sea (Armstrong *et al.*, 1999) and German Bight (Alheit *et al.* 2007). Since then years of high abundance and evidence of spawning in northern waters have become more frequent, including in the North Sea (Beare *et al.* 2004), German Bight (Kanstinger and Peck 2009; Alheit, unpubl. data), Kattegat, Skagerrak and in the Baltic Sea (Enghoff *et al.* 2007). These various sources confirm over the last century that although generally rare when in high abundance the anchovy are widespread throughout the area with several distinct spawning locations.

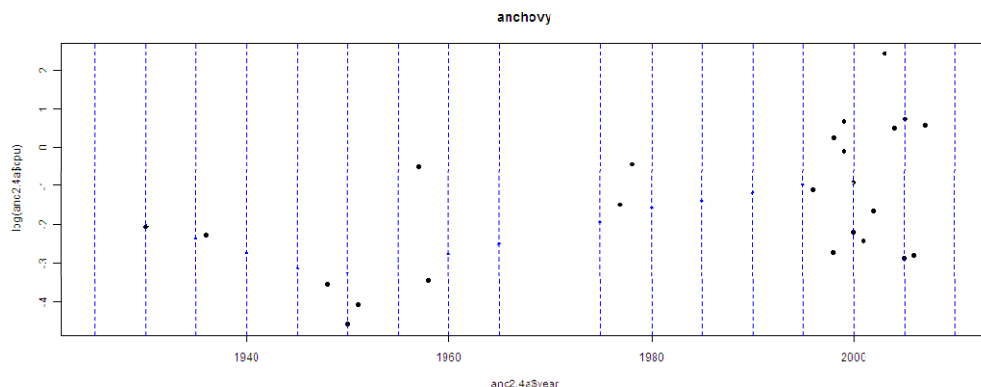


Figure 2.1.2. Trend in catches of anchovy in the North Sea by the Scottish trawl survey (Beare pers com).

2.2 Sardine

Information about sardine in the North Sea and adjacent waters is also relatively limited although several studies have been published on the English Channel populations. Anecdotal evidence suggests that European sardines, locally also known as pilchards, have been targeted by a dedicated inshore fishery in Devon and particularly Annual catches of 3000–5000 tonnes have been reported (Cushing, 1957). The first survey and probably the only dedicated fieldwork on both adult sardine and eggs and larvae in the northern part of its distribution (Cushing, 1957) explored various aspects of the population dynamics in the Channel. Large numbers of eggs were found mainly in May and June, particularly in the western parts of the Channel suggesting that the area is spawning site for this species (Cushing, 1957). This was later corroborated by a number of different studies focussing on egg/larvae abundance in the Channel based on fixed sampling stations (Southward, 1974; Southward and

Boalch, 1988; Southward *et al.*, 1988; Coombs *et al.*, 2010), plankton surveys (Wallace and Pleasants, 1972; Demir and Southward, 1974; Haynes and Nichols, 1994) and CPR data (Coombs *et al.*, 2005), as well as studies on the maturity stages of commercially landed sardines (Macer, 1974; Parnell, 1974). Most of these authors report that eggs were present in the Channel throughout the year with peaks in the summer and a second peak of spawning in the autumn (e.g. Demir and Southward, 1974; Parnell, 1974; Stratoudakis *et al.*, 2007; Coombs *et al.*, 2010). Based on eggs distribution in May, the western channel spawning site has been postulated to extend west and includes most of the Celtic Sea shelf area (Wallace and Pleasants, 1972). Other spawning areas in the northern parts of its distribution are off the south and west Irish coast during summer and autumn (Wallace and Pleasants, 1972), in spring in the southern North Sea (Taylor, 2007) and during the late summer in the German Bight (Alheit *et al.* 2007) from May to August (Kanstinger and Peck, 2009: Alheit, unpubl.data).

As has been observed in anchovy, the sardine populations in the North Sea and adjacent waters have fluctuated greatly over the last few hundred years. Landings by the Cornish sardine fishery going back to the 16th century show a strong positive association with warmer periods in the late sixteenth century (1590–1640) and twentieth century (1930–1960; Southward *et al.*, 1988). During the last century increases were observed in egg production between the nineteen thirties and sixties (Southward *et al.*, 1988, Southward and Boalch, 1988) and from the mid nineties. Apart from an increase in egg abundance and landings, these periods are also characterised by an extended distribution further east in the Channel and in the southern North Sea. From the mid nineties the summer spawning seemed to decrease in importance and higher numbers of sardine eggs were observed during warmer autumns. This shift was traditionally associated with colder periods, and be associated with a shift of high primary productivity towards the autumn (Coombs *et al.*, 2010). These same patterns as observed in annual egg abundance were corroborated by several studies investigating the catches of sardines on North Sea groundfish and IBTS surveys (Corten and van de Kamp, 1996, Beare *et al.* 2004 a, b).

2.3 Sprat

In the North Sea and adjacent seas, there is evidence that sprat abundance and distribution can vary greatly (ICES 1990; MacKenzie & Köster, 2004; Rijnsdorp *et al.*, 2010). Sprat has often been reported in commercial catches as herring, or herring as sprat, therefore it is difficult to use time series of reported catch to investigate both distributional and abundance changes (MacKenzie *et al.*, 2007; ICES 2008).

In the North Sea proper, sprat have probably been present in the south for most of last 100 years. However the abundance of sprat east of Scotland has shown large variations (ICES 1990). Currently the SSB is estimated to be approximately 0.5 million tonnes (ICES 2008). Sprat are also fairly consistently present in the English Channel and Irish Sea (with estimates of 0.5 million tonnes in the 1980s in the English Channel and 0.1–0.3 million tonnes in the Irish Sea in recent years; Milligan 1986; ICES 2008). To the west of Scotland sprat can be found throughout the area and in the sea lochs (Langham, 1968; De Silva, 1973). The biomass of sprat in the Bay of Biscay is thought to be approximately 10 thousand tonnes (Petitgas pers com.) and the biomass to the south of Ireland was 20 thousand tonnes (Grainger & Woodlock, 1981) and it occurs in other areas around Ireland (Kennedy *et al.*, 1973).

Sprat are indeterminate batch spawners (Alheit 1988). There is anecdotal information about sprat spawning in the autumn in the North Sea; however most of the information about spawning timing comes from ichthyoplankton surveys in the spring and

summer. Little sampling has occurred in autumn. In the North Sea proper, spawning takes place along the German Bight, Dutch coast, east of Scotland and central North Sea (ICES, 1990; Taylor *et al.*, 2007). In the western English Channel spawning is more inshore (Demir & Southward, 1974) and sprat spawn throughout the eastern English Channel (Milligan, 1986). In the Bay of Biscay sprat spawn in the river plumes in May (Petitgas per comm.).

Area	Start	End	Source
North Sea (North)	February	April	ICES, 1990; Taylor <i>et al.</i> , 2007
North Sea (Dutch coast)	April	May*	ICES, 1990; Baumann <i>et al.</i> , 2009
North Sea (German Bight)	May	June*	ICES, 1990; Baumann <i>et al.</i> , 2009
English Channel	Jan	July	Demir & Southward, 1974; Milligan 1986
Irish Sea	April	June	Nichols <i>et al.</i> , 1993, Fox <i>et al.</i> , 1997

* anecdotal accounts of autumn spawning sprat

2.4 Interactions

Due to the spatial overlap in distribution of these three species and their similar trophic role, there is likely to be a degree of interaction. Over the last 100 years, both sardine and anchovy seem to follow a similar pattern with fluctuations in their abundance and distribution, favouring warmer periods. There is limited spatial overlap in spawning with anchovy favouring less saline, warmer waters, often associated with estuarine environments, compared to sardine which spawns in open waters. In the North Sea and adjacent waters anchovy was found to have a relatively fixed spawning period between May and July/August, whereas sardine and sprat seem in some areas to have two peaks, one in summer and one in autumn.

3 Oceanographic and climatic variability of the north east Atlantic and the North Sea

This section considers the oceanography and climatology of the region, in relation to the changes observed in anchovy and sardine in the North Sea.

3.1 Hydrodynamic variability in the North Sea in the period 1948 to 2007

The Model Hindcast 1948–2007

A multi-decadal hindcast covering the period 1948–2007 has been carried out (Meyer *et al.* submitted) using the well-established circulation model HAMSOM (e.g., Backhaus and Hainbucher, 1987; Pohlmann, 1996, 2006; Schrum and Backhaus, 1999, Delhez *et al.* 2004). The model was driven by 6-hourly air temperature, humidity, cloud cover, precipitation, sea level pressure and near-surface wind speed and direction from the NCEP/NCAR global atmospheric reanalysis (Kalnay *et al.* 1996; Kistler *et al.* 2001). Siegmund and Schrum (2001) showed that the main features of the large-scale atmospheric circulation over the North Sea are reasonably represented by the NCEP/NCAR reanalysis.

While NCEP/NCAR atmospheric data are available on a T62 grid (approximately 210 x 210 km) only, bi-linear interpolation to the HAMSOM grid was performed. Full model output has been stored every hour, comprising two-dimensional water levels

and three-dimensional fields of temperature, salinity, and horizontal velocity components.

SST development

To illustrate the spatial variations and the differences between the periods before and after 1987, linear trends for SST were computed at every model grid points for the two periods (Figure 3.1.1). For the first period trends were mostly small (up to about 0.1 K/decade) and negative while for the second period a strong increase in the sea surface temperatures of up to 0.5 K/decade occurred over the entire North Sea. The strongest warming is found in the German Bight where the trend after 1987 corresponds to an increase in sea surface temperatures of about 1.0 K over the last 20 years. For the central North Sea somewhat smaller values in the order of about 0.3–0.4 K/decade are found, while trends are considerably smaller (about 0.1–0.3 K/decade) in the northern part of the model domain.

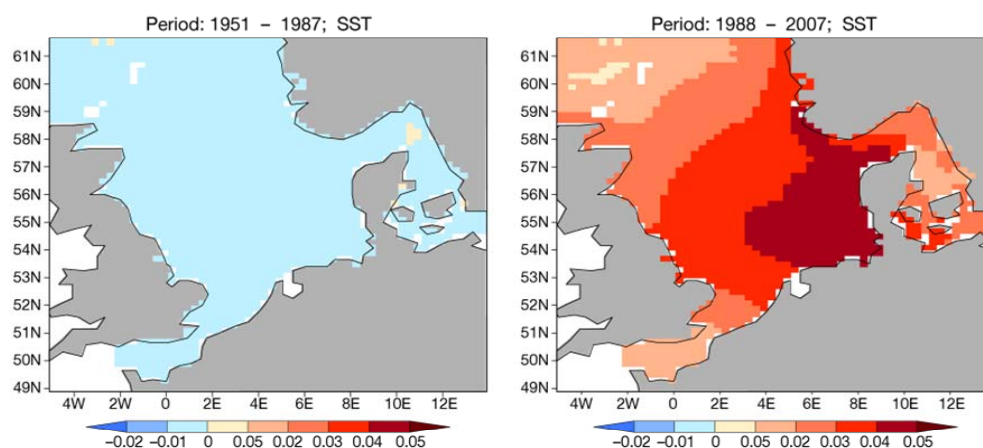


Figure 3.1.1. Linear trends 1951–1987 (a) and 1988–2007 (b) of SST [K yr⁻¹].

Thermocline structure

Long-term changes in thermocline depth and/or intensity are of central importance as a process potentially driving changes in biological productivity and/or phenology. The thermocline separates mixed surface waters from the water masses below the thermocline, which has a number of ecological implications in particular for the phytoplankton production. While in the winter season the North Sea is generally well mixed, in spring a thermocline develops over much of the North Sea area as the sea absorbs increasingly more solar radiation due to the higher altitude of the sun and reduced cloud cover. Through wind stress, turbulence is introduced which causes a downward mixing of warm water and increases the thermocline depth.

Intensive ship campaigns are necessary to investigate the structure and development of the thermocline. However, normally such observations only provide information for narrow transects and for limited time periods. Hindcasts performed with high resolution 3-d ocean models may complement such campaigns by providing a better insight into the space-time structure and long-term variability of the thermocline. In the following we use the hindcast to describe the long-term variability of the thermocline structure in the North Sea where the latter is referring to changes in thermocline depth, intensity, extension and the first day in each year at which a noticeable thermocline is observed. Here thermocline depth is defined when the vertical temperature gradient exceeds a threshold value of 0.1 K m⁻¹. Thermocline intensity is defined

as the maximum of the vertical temperature gradient provided it exceeds a threshold of 0.1 K m^{-1} and thermocline extension refers to the mean area of the grid cells, where the threshold value is exceeded. Figure 3.1.2 shows the long-term changes and variability of the thermocline structure as obtained from the multi-decadal hindcast when spatial and temporal integrated over the entire North Sea. For mean thermocline depth considerable interannual variability was found ranging from about 16 m to 24 m but no long-term trend can be inferred. Moreover, there is also no indication of stronger trends after about 1987. Similarly, the mean thermocline intensity appears to be rather stationary over the years with values ranging between 0.15 and 0.18 K m^{-1} . There is a small correlation between thermocline depth and intensity. Similar conclusions hold for the mean thermocline extension, and the first day of noticeable thermocline occurrence.

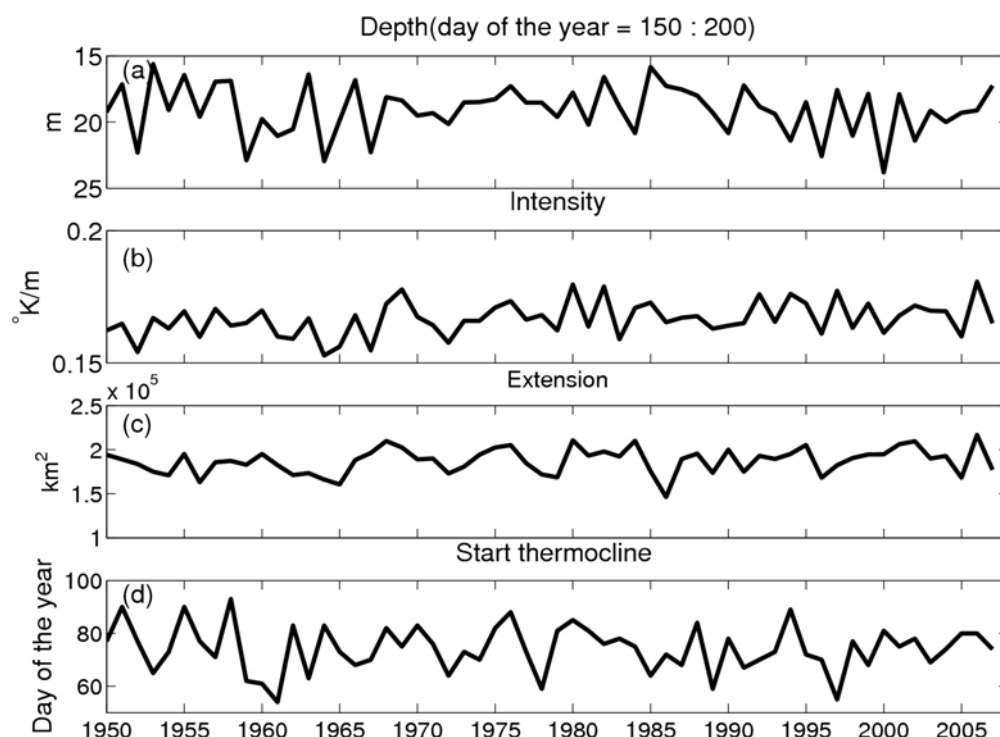


Figure 3.1.2. Volume averaged statistics of thermocline structure 1950–2007. (a) Average thermocline depth in m during the period of 150th to 200th day of the year; (b) Mean thermocline intensity in K/m ; (c) Mean extension in km^2 (d) First day of the year with volume averaged thermocline stronger than 0.1 K/m .

North Sea heat content

The heat content of the North Sea is mainly governed by solar and long-wave radiation as well as latent and sensible heat fluxes. However, under certain conditions, the advective and diffusive heat fluxes may also be relevant. The solar radiation depends on the declination of the sun and the cloud cover, whereas the long-wave radiation depends on the difference between air and sea temperature and cloud cover. Sensible and latent heat fluxes are controlled by the difference of air and sea temperature, wind speed and water vapour pressure. The sum of all four fluxes yields the total heat flux into the ocean (Pohlmann, 2006). In summer heat fluxes are generally directed into the North Sea (positive heat fluxes) while in winter negative heat fluxes over the North Sea prevail.

The annual and the seasonal mean heat content of the North Sea are shown in Figure 3.1.3. For the annual mean, values vary between about $330 \times 10^5 \text{ J m}^{-3}$ and $366 \times 10^5 \text{ J m}^{-3}$. Seasonally, heat content is largest in the summer months and smallest in winter while inter-annual variability is largest in winter ($46.6 \times 10^5 \text{ J m}^{-3}$) and spring seasons ($47.5 \times 10^5 \text{ J m}^{-3}$). For summer and autumn, inter-annual variability is somewhat smaller ($31.6 \times 10^5 \text{ J m}^{-3}$ and $37.5 \times 10^5 \text{ J m}^{-3}$, respectively). As for sea surface temperatures, there is no noticeable trend until the early 1980s, afterwards a stronger positive trend can be seen.

Additionally, Figure 3.1.4 presents the development of the North Sea heat content anomaly on a monthly basis in form of a year (y-axis) against month (x-axis) plot. Again the increase of the heat content since 1996 is clearly visible. 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 1995 where major warming occurs for the winter months.

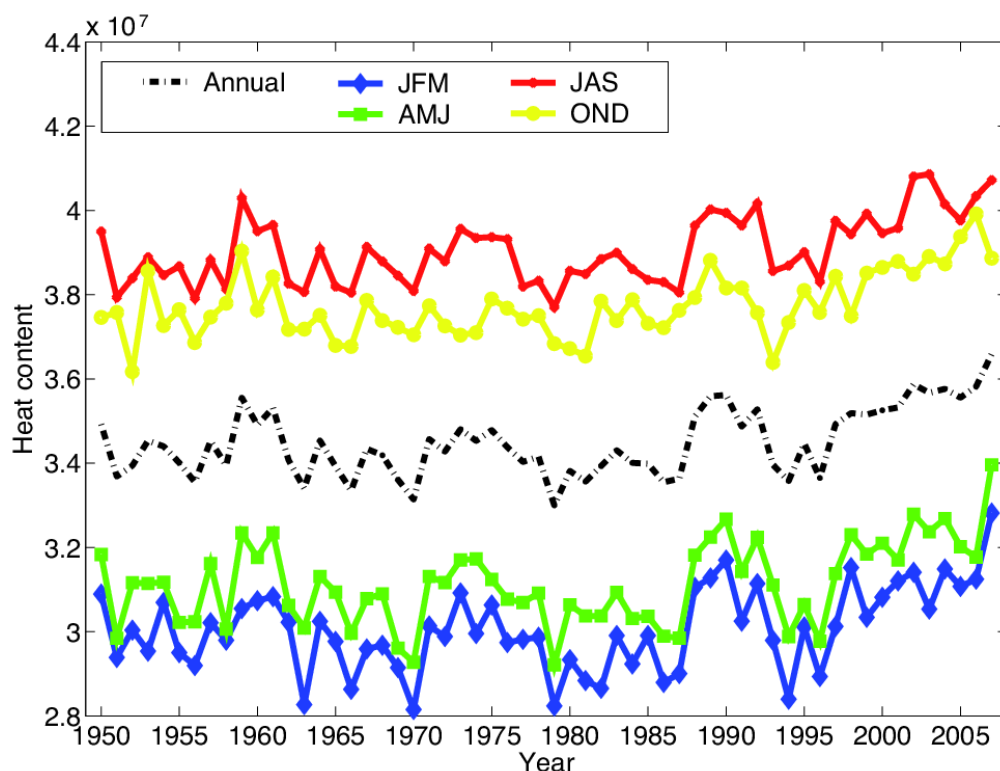


Figure 3.1.3. Annual (black) and seasonal (JFM-blue, AMJ-green, JAS-red, OND-yellow) mean North Sea heat content in 10^7 J m^{-3} .

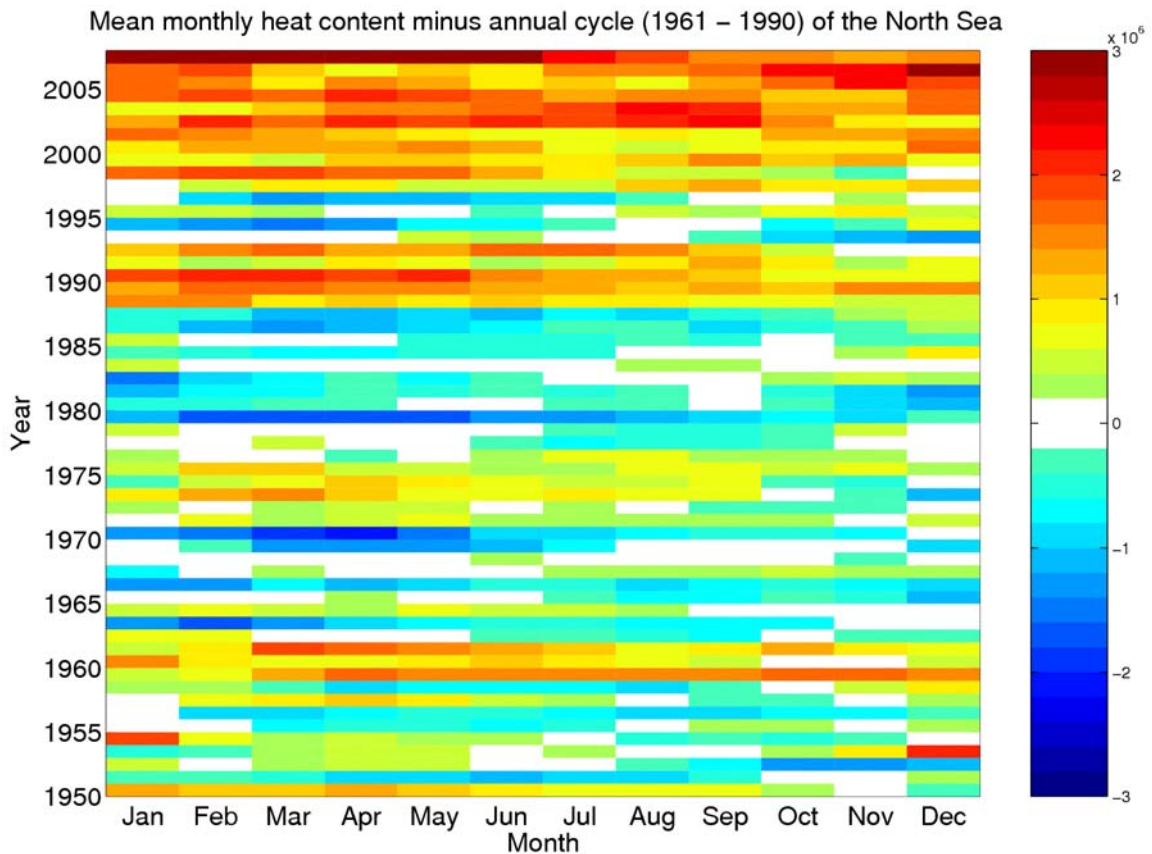


Figure 3.1.4. Anomaly of the North Sea mean heat content in 10^6 J m^{-3} . (subtracted is the climatological seasonal cycle calculated for the years 1961 to 1990).

3.2 Regime shift late 1980s

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, 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 1987–1996 was based on elevated winter temperatures (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 lar-

vae, 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 may 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. Kröncke *et al.* 2001, Reid and Edwards 2001, Reid *et al.* 2001a, Reid *et al.* 2001b; Edwards *et al.* 2001, Beaugrand *et al.* 2002, Beaugrand and Reid 2003; Beaugrand 2004; Edwards *et al.* 2004; Weijerman *et al.* 2005; Alheit *et al.* 2005; Alheit and Bakun 2010). 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.

3.3 Changes in mid-1990s

In spite of the increase in North Sea SSTs and although apparently many zooplankton species of Lusitanian origin had increased their abundances starting in the late 1980s, the warm water-adapted European anchovy and sardine did not seem to react to the strong climate signal in the late 1980s. Instead, they appeared across the North Sea much later, around 1995 (Beare *et al.* 2004), and spawning spread wider across the region (Alheit *et al.* 2007). In contrast to NAO-associated changes in the plankton, no corresponding changes were observed in the mid-1990s.

In the mid-1990s a rapid reversal of the marine climate was recorded 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 the autumn of 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 centres 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 1998/1999 (Flatau *et al.*, 2003). 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 (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). The question is how far north does the Mediterranean Outflow Water (MOW) flow and how is its extension linked to dynamics of NAO, subpolar gyre circulation and zonal shifting of the subpolar front or are all these factors linked to another process? 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). All these interactions of atmosphere and ocean in the Northeast Atlantic seem to have a global dimension. What implications did all these atmospheric and hydrographic processes

have 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 SST increased after a short dip in 1996 and reached even higher levels after 2000 than in the years following the late 1980s (Loewe, 2009). However, annual average temperatures were no longer determined by winter values since the strong westerlies had disappeared. Instead, the subtropical waters moving northward and partly replacing the subpolar gyre waters provided anomalously high summer temperatures in the North Sea through atmosphere-ocean coupling. SSTs, bottom temperatures and heat content have increased steadily since 1995 (Meyer *et al.* submitted). It is unclear if this warming has influenced anchovy and sardine, and this issue will now be further explored in chapters 4 and 5.

4 Connectivity between populations

4.1 Genetic Structure of European anchovy, sardine and sprat

In general marine fishes display high intra-population levels of genetic diversity and weak genetic differentiation among populations compared with fresh water and anadromous fishes (Ward 1994, Waples 1998, DeWoody and Avise 2000). Still, significant genetic differentiation has been identified at various geographical levels from large oceanic scale differentiation (Bentzen, 1996; Heist, 2004; O really *et al.*, 2004; Bremer *et al.* 2005), from regional (Ruzzante *et al.*, 1996; Nielsen, 2003; Rolland *et al.*, 2007) to small geographical scales with observed genetic differentiation over few tens of kilometres (Knutzen, 2003; Nielsen *et al.*, 2005; Bradbury *et al.*, 2008).

Anchovy

The European anchovy shows large amounts of genetic differentiation between populations. Most of the studies have focused on the analysis of the Mediterranean sub-basins using allozyme and mitochondrial (mt) DNA markers. Magoulas *et al.* (1996) identified two mtDNA phylogroups ('A' & 'B') representing 1.1–1.85 million years of separation. These markers indicate that anchovy populations are subdivided in the eastern Mediterranean (Bembo *et al.*, 1996; Spanakis *et al.*, 1989), but less so in the western Mediterranean (Tudela *et al.*, 1999).

An initial analysis has been carried out on the genetic structure of anchovy populations over the whole distributional range of the species by a research group of the genetics laboratory of the University of the Basque Country and Azti-Tecnalia. This study analyses 50 nuclear neutral SNP (Single Nucleotide polymorphism) markers on 790 individuals covering an extensive regions: North Sea, English Channel, Bay of Biscay, South East Atlantic coast, Canary Islands, South Africa, Alboran, West Mediterranean and East Mediterranean (Adriatic and Aegean seas).

Nei standard (Ds) distance based neighbor-joining tree, pair-wise FST comparisons and the Bayesian approach clustering method suggest that North Sea and English Channel samples are genetically homogenous, exhibiting significant genetic differences with the Bay of Biscay samples. Moreover, Bay of Biscay samples appeared to be genetically more similar to the West Mediterranean samples than to the North sea-English channel samples. **These results support that the recent increase of anchovy in the North Sea is likely due to the development of local North Sea populations, rather than a northward movement of Bay of Biscay populations** (Zarraonaindia In Prep.; Figure 4.1.1).

Sardine

Regarding sardines, a different genetic pattern has been observed showing this species not to be as genetically structured as the European anchovy. A recent genetic study conducted by Laurent *et al.* 2007 using 9 allozymes suggest that European Atlantic coast samples constitute a single population being the Azores, Madeira and Mediterranean a differentiated population (Figure 4.1.2). This result was also suggested by Silva 2003 using morphometry. However, this hypothesis of geographic structuring organized as Atlantic Ocean vs Mediterranean Sea samples was not supported by an analysis of 8 microsatellite markers (Gonzalez and Zardoya, 2007).

Sprat

In sprat, most of the analyses have focused on studying Baltic and Black sea populations. In that sense, based on mitochondrial genomic analysis Debes *et al.* (2008) found 2 'major clades' with one distributed in the eastern Mediterranean, (Adriatic and black sea) and another in the western Mediterranean, Northeast Atlantic ocean, North sea and Baltic. This author suggested a recent postglacial (13 000 to 7600) northward range expansion into the North and Baltic Sea from an Atlantic refugia. Limborg *et al.* 2009 analyzing 9 microsatellite markers suggest a recent (within last 10000 year) split between Northeast Atlantic and Baltic Sea populations. The analyses of these 9 microsatellite loci revealed a sharp genetic division separating samples from the north eastern Atlantic Ocean and North Sea (northern Kattegat, North Sea and Celtic) and the Baltic Sea concurring with a steep salinity gradient, being the Belt sea a genetically intermediate transition zone.

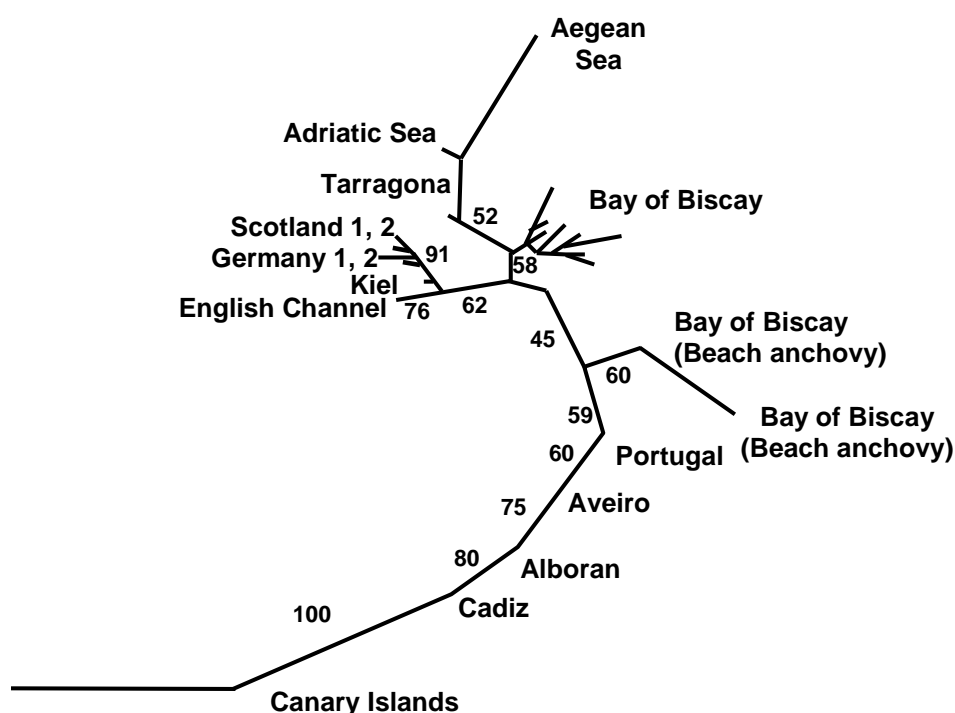


Figure 4.1.1. Nei standard (Ds) distance based neighbour-joining tree with 1000 bootstrap replicates. The line in the extreme bottom right leads to the South African populations (not shown).

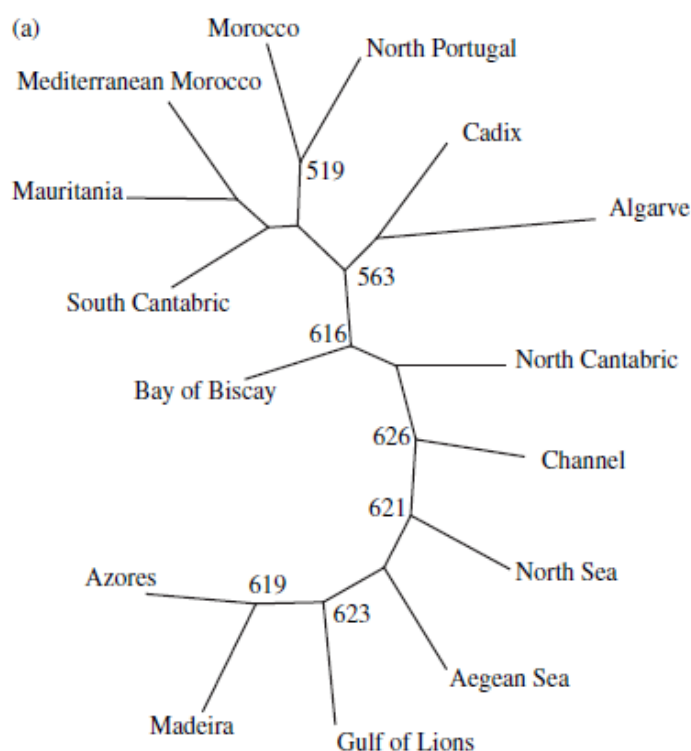


Figure 4.1.2. Neighbour-joining dendrogram showing the genetic relationship between samples of *Sardina pilchardus*. The dendrogram was based on Nei's (1972) genetic distance. Taken from Laurent *et al.*, 2007.

4.2 Oceanographic connectivity between the Bay of Biscay and the English Channel

In looking for explanations for the recent expansion of anchovy in the North Sea, two main hypothesis arise: sympatry and allopatry. Allopatry could either be due to further adult migration to the north, or increase of larval and juvenile survival into the English Channel and southern North Sea for individuals originating from Biscay spawning. Here the second hypothesis is tested using a particle tracking model.

The general residual circulation over the shelf of the Bay of Biscay is low and oriented to the north (Pingree and Le Cann, 1989), with strong seasonal variability due to wind and runoff from major rivers (Loire, Gironde and Adour). Connectivity between the Bay of Biscay and the Channel has already been reported (e.g. Kelly-Gerreyn *et al.*, 2004). Using a particle tracking model, Huret *et al.* (2010) indicated that anchovy eggs spawned in the Bay of Biscay could be transported to the Channel, but no attempt was made to quantify the strength of that potential connectivity. They also reported that, considering the seasonal shift in the circulation from northward to southward during the anchovy spawning season, and the northward progression of spawning during the season as the temperature increase (Motos *et al.*, 1996), retention of eggs in the Bay of Biscay was much more likely compared to transport to the English Channel. Here our aim is to quantify this loss of eggs into the English Channel from the Bay of Biscay.

We use the Lagrangian particle tracking model presented in Huret *et al.* (2010). Two areas are considered for describing the connectivity of the Bay of Biscay with northern regions (Figure 4.2.1). First area is north of 48°N while the second area is the eastern part of the first area with a boundary at 5°E, thus delimiting the entrance of the English Channel. Five spawning areas were defined as described in Huret *et al.*

(2010). The southern ones are where most of the spawning occurs (Motos *et al.*, 1996), particularly during the peak spawning season (May/June), whereas the northern ones are more likely end of the season locations. We released thousands of particles per spawning ground, every week over the spawning season (April to August), and track them for 50 days, a mean age at metamorphosis for Bay of Biscay anchovy. Then the fraction of particles reaching the two defined northern regions is calculated. The model is run over the period 1996 to 2009.

Figure 4.2.2 shows the mean fraction of particles arriving in both regions from the five spawning grounds. This fraction is low, from ~0% for spawning grounds 1 to 3, to 10% for spawning ground 5 in the north of the Bay (2.11% when averaged over the 5 spawning grounds). 87% of the particles lost from the Bay are entering the Channel, the rest remaining in the Celtic Sea.

Figure 4.2.3a shows the interannual variability in the connectivity to the Channel. For spawning location 5, the fraction averaged over the spawning season ranges between less than 10% (1997, 2001 to 2003 and 2005 to 2007, 2009), to more than 20% in 2008.

But most important is the seasonal variability of this fraction (Figure 3b). Indeed, all the connectivity occurs from the beginning of the season until mid-May for the northern spawning grounds. However, very few spawning is reported from the French PELGAS survey in April-May north of 46°N as well as from literature (Motos *et al.*, 1996). Connectivity is null from mid-April onward.

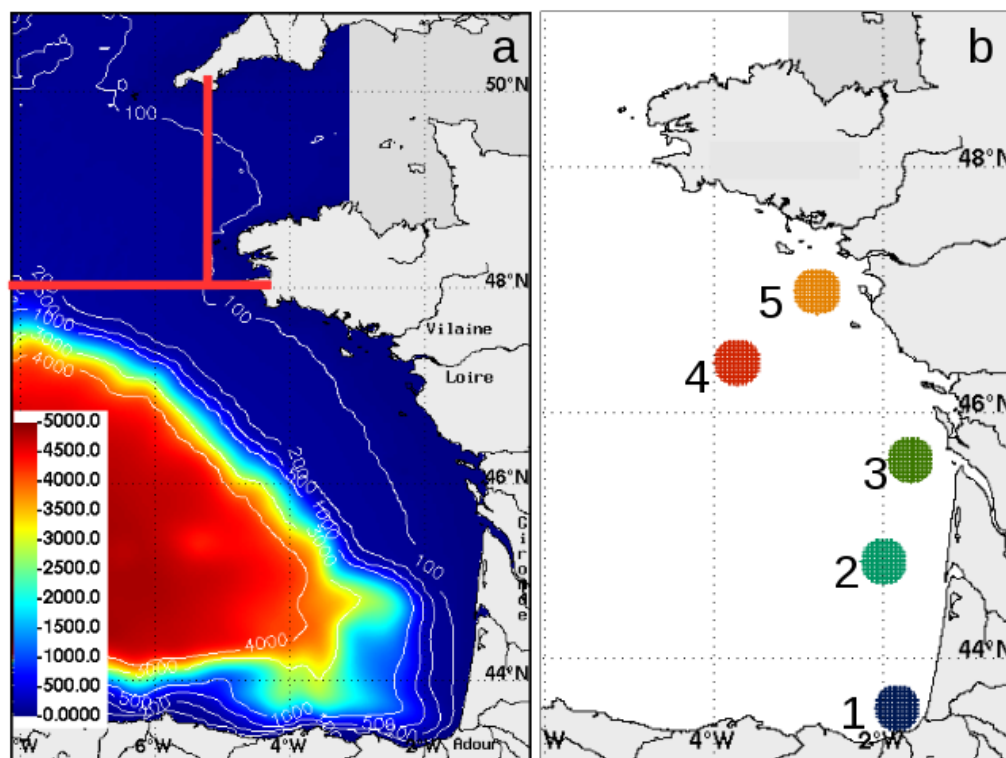


Figure 4.2.1. Model domain with boundaries of defined northern areas for the connectivity study (a), and 5 defined spawning grounds chosen in the Bay of Biscay (b).

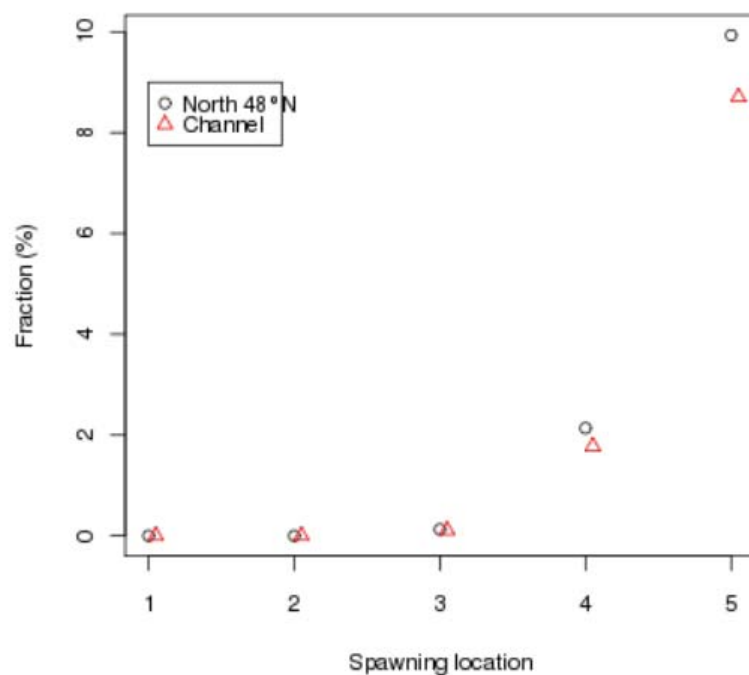


Figure 4.2.2. Variability of the connectivity (as fraction of released particles) between different spawning grounds of the Bay of Biscay and the two northern areas defined (see Figure 4.2.1).

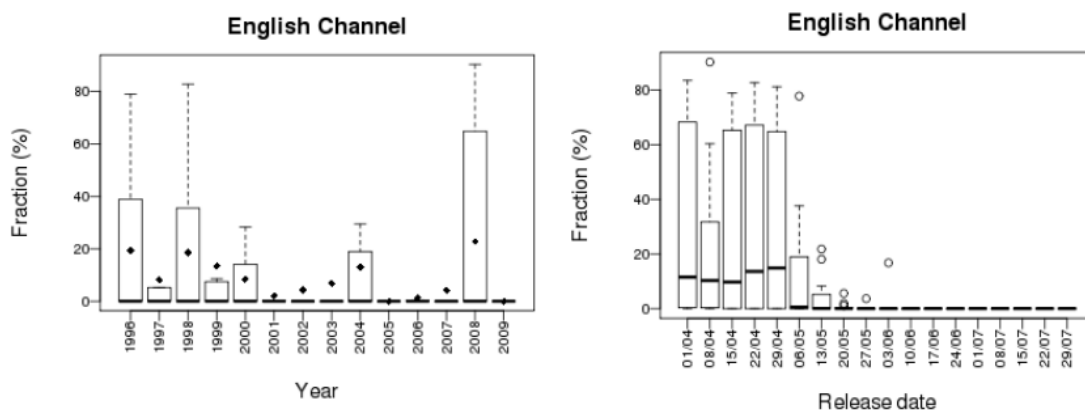


Figure 4.2.3. Interannual and seasonal variability of the fraction of particles ending up in the English Channel from spawning ground 5 in the north of the Bay of Biscay.

Our results show that the potential connectivity fraction of the Bay of Biscay to the north of 48°N is only 2%, essentially due to northern spawning in the Bay. Now considering the observed spatio-temporal spawning pattern (shift to the north as the season progress), connectivity may be considered as negligible.

In the context of climate change, Bay of Biscay surface temperature has already been observed to increase (Gomez-Gesteira *et al.*, 2008), which will likely continue. This could advance the spawning season with earlier spawning in the north of the Bay. Under the hypothesis of no other change than temperature increase (e.g. circulation patterns), this would increase the potential for connectivity with the English Channel. From climate change scenarios (temperature increase, wind change) run over the Bay

of Biscay, Lett *et al.* (2010) suggests modification of the circulation with further impact on the dispersal kernel for Bay of Biscay anchovy, among them further distance dispersed under increased stratification.

5 Hypotheses and investigations

5.1 Hypotheses for increase of anchovy and sardine in the mid 1990s in the North Sea

The expansion of a species in a given area can be explained by an allopatry hypothesis (colonizers coming from elsewhere) or a sympatric hypothesis (recruitment pulses of a relict adult population). The colonizers from elsewhere can be drifting larvae originating from spawning events outside the North Sea, or actively migrating adults. The sympatric hypothesis amounts to the good survival of larvae spawned in the North Sea. To differentiate between the different hypotheses, the implications of each hypothesis are detailed below.

H1. Relict population in the North Sea with recruitment pulses. In this case, the species has been completing its full life cycle in the North Sea and has been present at small abundances in reduced areas even before its newly recorded increase. The first signal of increased abundance is in the recruits, i.e. smaller length classes show the first increase. Genetic differences would be found between the North Sea and Bay of Biscay stocks. Lagrangian drift / particle tracking modelling would not predict transport from the Bay of Biscay into the North Sea.

H2. Allopatric population seeding the North Sea by larval drifts. The first signal of increased abundance is in the recruits, i.e. smaller length classes show the first increase. There is no genetic differentiation between the North Sea and Bay of Biscay stocks. In this case, lagrangian drift / particle tracking modelling of larvae would predict drifts into the North Sea.

H3. Allopatric population seeding the North Sea by active adult migrations. The first signal of increased abundance is in the adults. There is no genetic differentiation between the North Sea and Bay of Biscay stocks.

To tentatively address these questions, we analysed the North Sea IBTS data for spatial distribution and length structure of both species. To look for evidence of first colonizers in survey data is difficult as abundance is low and therefore sampling unreliable. We extracted from the ICES website portal the catch per unit effort (numbers) at length by species by ICES rectangle and quarter (Note that in 2007 WGFE used catch per unit effort (numbers) at length by species by haul and quarter). We further considered temperature series, genetic results and transport connectivity patterns (section 4 of this report) to find evidence in favour or against the hypotheses.

5.2 Anchovy - investigation of empirical information

Coherence in the seasonal patterns as provided by IBTS data

Averaging the length frequencies across all years shows that generally, quarter 1 anchovies are larger in size (ca. 12cm) while quarter 3 anchovy lengths are slightly bimodal with a peak at sizes of ca. 7 cm and another weaker signal at lengths of ca. 17cm (Figure 5.2.1). The variability in lengths of the catches (Figure 5.2.2) show that in quarter 1 recent years (dark blue) anchovy lengths are fairly similar while in earlier years (yellow-green-light blue) they were sometimes mostly large or mostly small. Q3

lengths are more variable, sometimes large, sometimes small, sometimes mixed, probably reflecting recruitment pulses.

According to Alheit *et al.* (2007), the anchovy spawning window is during the summer in the North Sea. Egg surveys show anchovy spawning in early May of the Dutch coast. Given that anchovy within the Bay of Biscay can obtain 7–8 cm within ca. 60–80 days, it seems likely that the anchovies caught in quarter 3 in the North Sea are juveniles born during the spring/summer of the same year (see section 5.3 below). In the now extinct Zuider Zee populations, which spawned in early May, anchovy used to reach 6–8 cm in 90–120 days (Arné, 1931). Thus quarter 3 catches probably give information mainly on recruitment but also on adults (the second peak in the length frequencies) while quarter 1 catches provide information mainly on the adult component of the population.

The averaged spatial distribution (Figure 5.2.3) shows that the anchovies are more spread out across the whole North Sea in quarter 1 than in quarter 3 when the range is more restricted to the southern North Sea and British coast. The possibility of habitat differences in q3 between juveniles and adults was investigated by comparing the map of large (>12 cm) with that of small anchovies (≤ 12 cm). The difference is small, with larger fish slightly more present in the southern North (figures not shown). Such little difference in distribution could be explained by the fact that spawning had already occurred prior to the survey and therefore the habitats are not well separated. In effect, spawning requires temperature $> 14^{\circ}\text{C}$, which occurs prior to q3 surveys, in June as can be deduced from Figure 5.2.4. (see section 5.5).

Overall, the spatial spread is fairly constant in time (as shown by the yearly gravity centres that lie close together in q1 and q3) but some years stand out as having most catches near-shore or slightly off-centre from the average of the time series. These years may be worth investigating more closely for high value catches, length distribution, or physical properties (the Dutch coastal time series might be useful to look at for more information as well). The variability in spatial spread was slightly higher in q3 than q1.

The IBTS data provided a coherent picture of the seasonal spatial patterns and length distributions of the anchovy in the North Sea. Anchovy usually (in Biscay: Massé *et al.*, 1996) forms small schools above the bottom during day time and disperses at night at the surface. Catchability by the bottom trawl GOV is probably good enough to extract the large scale patterns. We have used logarithms and presence rather than actual CPUE to make the analysis of the patterns more robust.

The seasonal spatial pattern (large coverage in q1 and into the northern North Sea, restricted coverage in q3 in more coastal waters) is compatible with a temperature dependent life cycle organisation. The recruitment signal in q3 is compatible with spawning in June above 14°C allowing larvae and juvenile high growth above 16°C .

Supporting evidence for a sympatric expansion

IBTS data : recruitment pulses

The time series of total CPUE shows that though a few anchovy were present in the 70s and early 90s, the first strong increase occurred in the mid-1990s (Figure 5.2.5; time series Q1 and Q3 anchovy $\log(\text{cpue}+1)$). Looking for the first colonizers using survey data is difficult as at low abundance survey catches can be unreliable. Therefore, we considered those years when abundance was high enough ($\log(\text{average cpue}+1) > 0.5$). The first time anchovy was seen in the North Sea since the 70s was in q3

of 1992 (Figure 5.2.5). In that year, a recruitment signal is detectable (length mode < 12 cm) but these recruits do not survive through winter: abundance in q1 of 1993 is low. **The next recruitment signal is in q3 of 1994 and recruits survive through winter: abundance is higher in q1 of 1995. This event, 1994/1995 is the first large-scale colonisation event of the North Sea since the 1970s.**

Then, in several occurrences of high abundances (94/95, 97/98, 02/03: Figures 5.2.5 & 5.2.6), the Q3 increase precedes an increase in the following year's first quarter, suggesting overwintering of young adults into the following year. Although this pattern fits with the explanation that the recruitment pulses provide the possibility for overwintering and thus high catches in the following year's first quarter, this pattern is not present in recent years (since 2003). If the suggested sequence (recruitment pulse -> high catches in following Q1) is correct, maybe other changes (e.g., spatial distribution) are responsible for the changed pattern in recent years.

The interannual variability in recruitment signal measured by IBTS (log cpue of anchovy <12 cm in q3) was related to the length of the period above 16°C in the Southern North Sea and German Bight (ECOSMO data: Figure 5.2.3). Variability in recruitment appears limited by the time window above 16°C (Figure 5.2.7). Summers with less than 65 days above 16°C seem detrimental to recruitment. Above 90 days, other factors than temperature may also control recruitment and therefore temperature is not the prime limiting factor. A high enough growth during summer is probably necessary to allow survival through winter (see section 5.4).

These results are compatible with other studies on North Sea anchovy. The interannual variability of the seasonal hydrological conditions was quantified using the hindcast of a physical bio-geochemical model (ECOSMO: Schrum *et al.*, 2006). The anchovy life cycle in the North Sea was timed to the North Sea cycle and it seemed that the summer anchovy larval period occurred at a time of important interannual variability (Petitgas *et al.*, 2009), compatible with the hypothesis of population increase via recruitment pulses. Also, the use of a bioenergetics anchovy model forced by the ECOSMO hindcast showed that the unsuitability of conditions had decreased in winter for small fish since 2000, also compatible with a higher winter survival of progeny (Struski *et al.*, 2009). **The expansion of anchovy in the North Sea is thus thought to be controlled by recruitment pulses, linked to relatively high summer temperatures of long enough duration and favourable winter conditions allowing overwinter survival. There is supposedly a balance between high enough summer temperature allowing sufficient growth and winter conditions allowing sufficient survival at of young-of-the-year fish.**

Support from transport modelling likelihood of drift

Based on the above, there is supporting evidence in the IBTS data and hind-caste environment that helps explain the expansion of anchovy in the North Sea by recruitment pulses controlled by long enough period with high enough water temperatures. Recruitment from local spawning in the North Sea is more likely than from the input of larvae drifting into the area from the English Channel and the Bay of Biscay as estimated with Lagrangian particle tracking modelling (section 4.2).

Support from spatial general additive models – covariation of environmental variables

Moreover, testing for covariation between environmental and food availability variables with anchovy CPUE showed that high net flow (Eastwards) through the Channel has a negative effect on CPUE (Raab *et al.* in prep; working document presented to workshop) which is contrary to what would be expected if these water masses

were transporting juveniles into the North Sea. Temperature had a positive effect on Q1 CPUE, suggesting in warmer winters, more anchovy are present. This may be a result of higher winter survival if cold winter temperatures limit the population.

Support from genetics

The results of the genetic analyses (see section 4.1) indicate that the Bay of Biscay anchovy (either oceanic or beach anchovy) differ from the North Sea anchovy. This makes it more likely that the North Sea population is an independent (i.e. relict) population.

The combination of the above information makes it seem likely that anchovy in the North Sea is that a low abundance level relict population that has recruitment invading pulses.

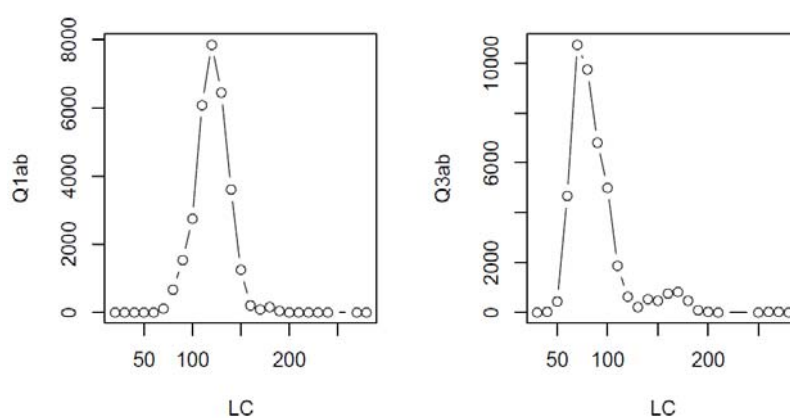


Figure 5.2.1. Average length class frequencies of anchovies per quarter in North Sea IBTS catches.

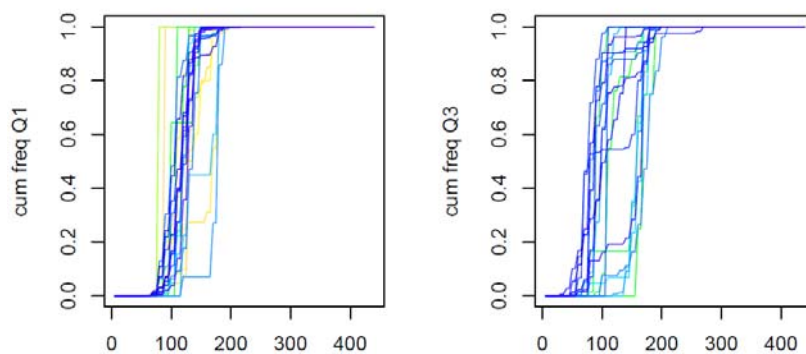


Figure 5.2.2. Cumulative frequency by length class for IBTS anchovy catches in quarter 1 and quarter 3. Different colours indicate years with darker being more recent years.

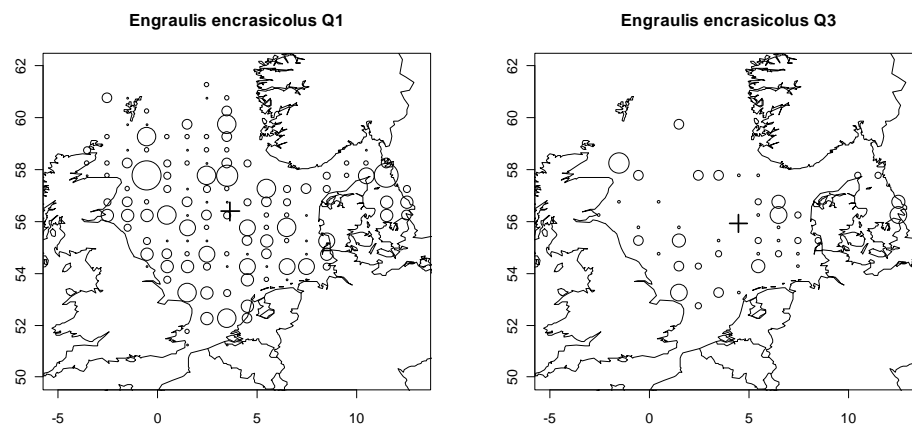


Figure 5.2.3. Probability of presence (mean count >2 individuals per ICES statistical rectangle) in q1 (left: 1973–2010) and q3 (right: 1990–2009). Averages are taken for those surveys where abundance was consistent enough (survey average Log CPUE > 0.5). The cross indicates the gravity centre.

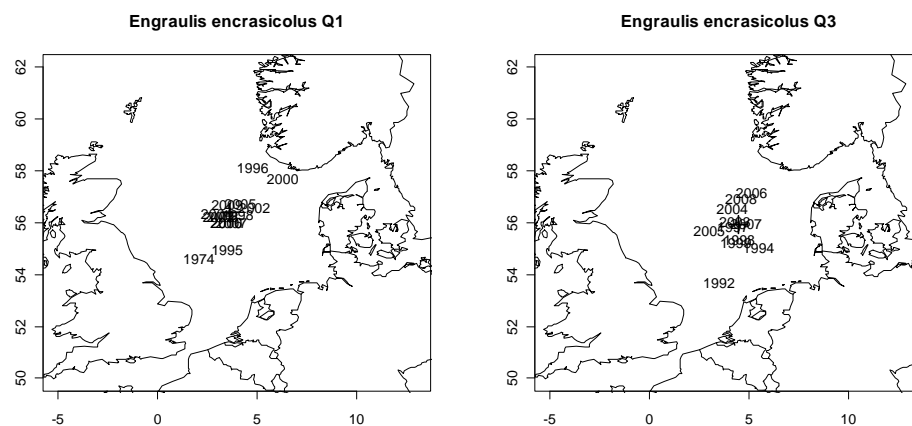


Figure 5.2.4. Variability across years in the gravity centres of the maps of probability of presence (mean count >2 individuals per ICES statistical rectangle) in q1 (left: 1973–2010) and q3 (right: 1990–2009). Averages are taken for those surveys where abundance was consistent enough (survey average Log CPUE > 0.5).

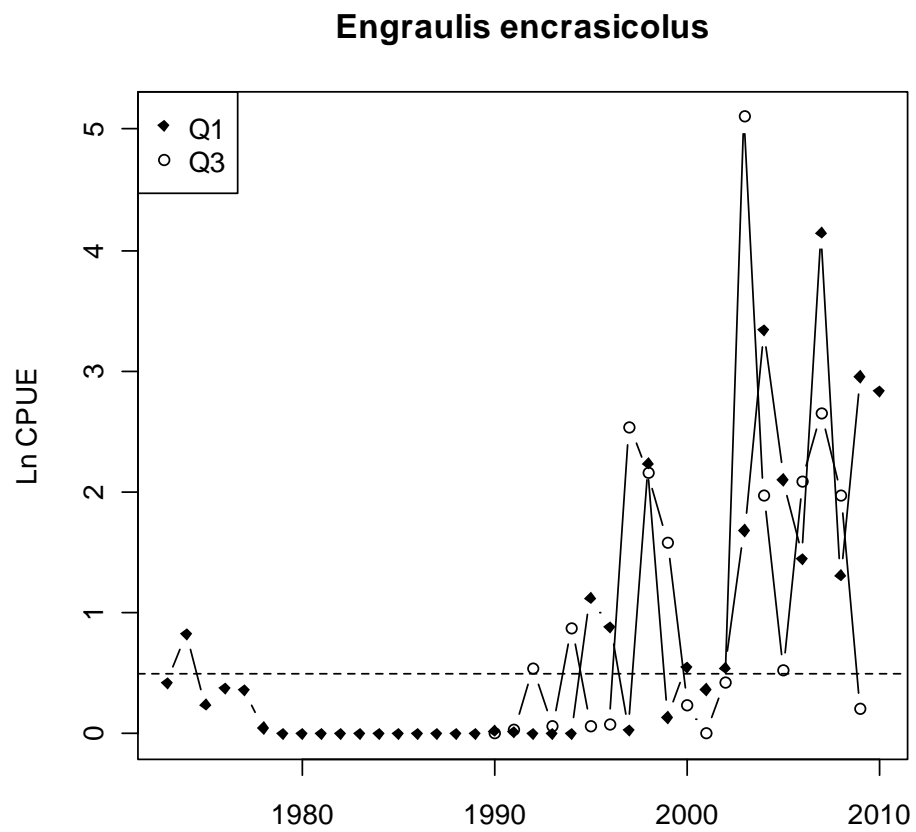


Figure 5.2.5. Anchovy abundance index [$\log(\text{cpue}+1)$] in the Q1 and Q3 North Sea IBTS.

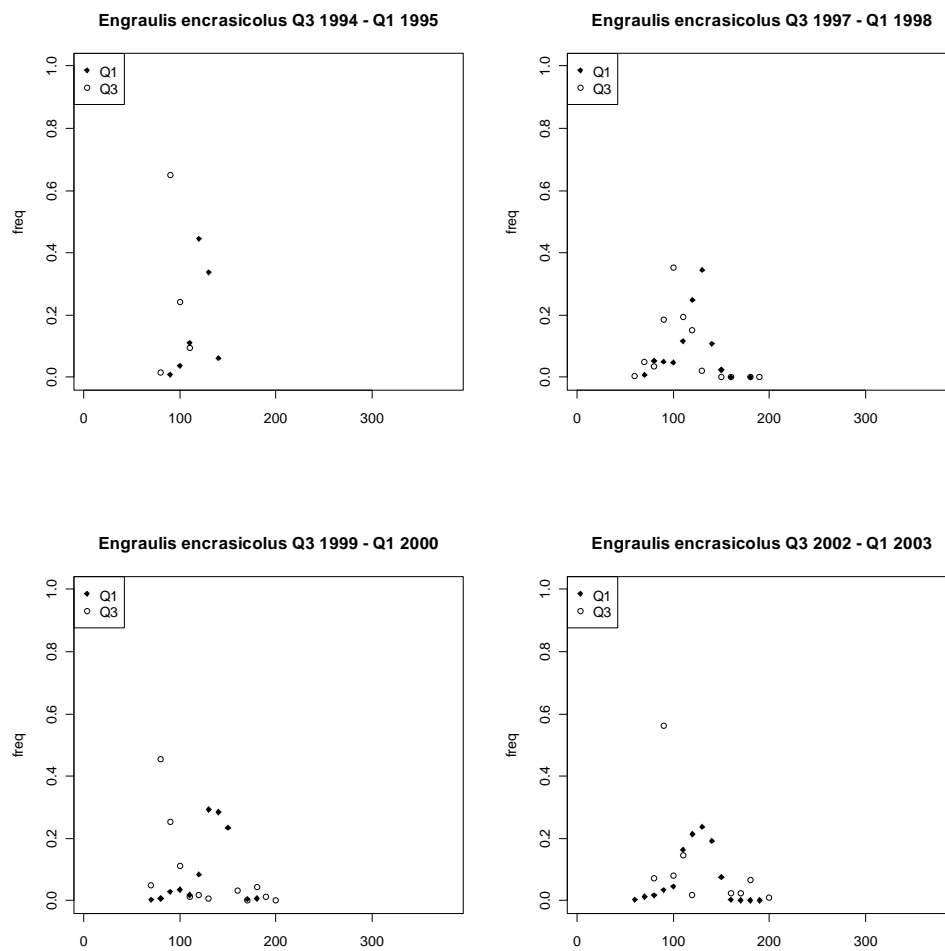


Figure 5.2.6. Length distribution in q3 and subsequent q1, showing recruitment pulse and its survival through winter at the beginning of the colonisation of the North Sea (1994–2003).

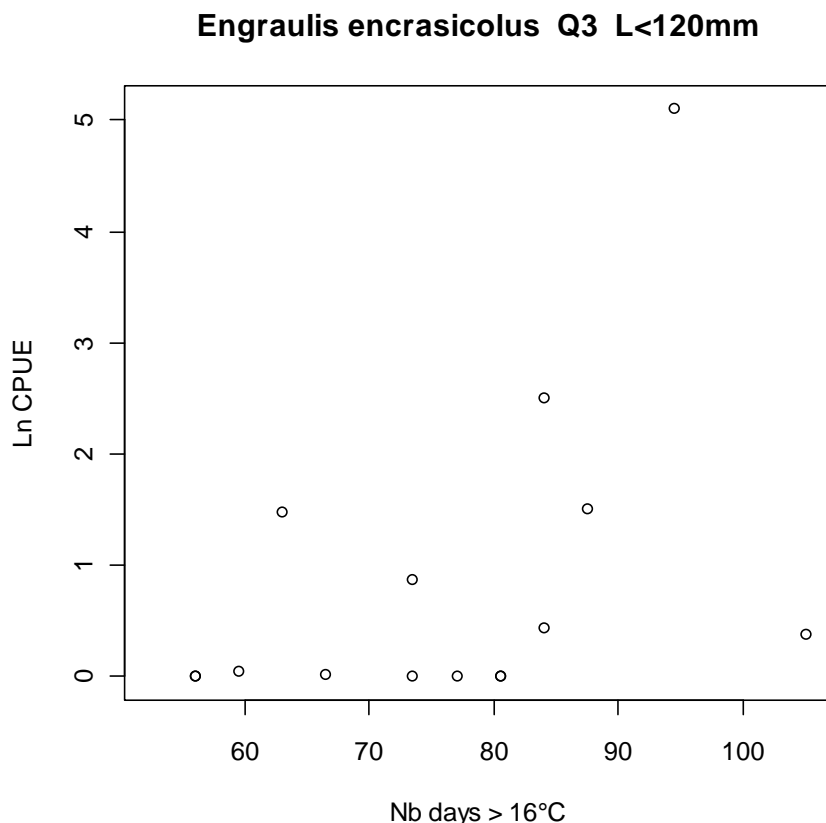


Figure 5.2.7. Relationship between the number of days above 16°C in the Southern North Sea and German Bight and the abundance index of anchovy in IBTS q3 survey.

5.3 Sardine investigation of empirical information

For sardine, the information is more sparse as the IBM model is not applicable to sardine. Statistical modelling of environmental and food availability variables for sardine are in progress. Thus most of the information is based on empirical analyses of the IBTS survey data.

The length frequencies in quarter 3 are large adults (ca. 25 cm), while in quarter 1 both smaller (ca. 12 cm) and large fish (ca. 25 cm) are present (Figure 5.3.1). Unlike anchovy, sardine young of the year are not captured in q3. The recruitment pulse is caught at an older age in q1. During the 90s, large sardines appear in q3, while negligible abundance remains in q1. Since 2000s, high abundance occurs in q3 and q1 (figure 5.3.2). The abundance series is therefore different than for anchovy. The first strong abundance event occurs in q3 of 1991 but unlike anchovy, these invading fish are adults (Figure 5.3.3). This observation supports H3 as the other two hypotheses imply the first individuals appearing should be juveniles. The first time the abundance is not negligible in q1 occurs in 1998 and this event is concomitant with a recruitment signal (Figure 5.3.3). **It could be that q1 abundance depends on recruitment in the North Sea from summer spawning events, while q3 sardine being larger is more migratory.** In addition genetic studies do not show a separate northern population.

The seasonal spatial pattern of sardine in the North Sea is similar to that of anchovy but with more pronounced differences, the distribution being more to the northwest

in q1 and occupying more area and by contrast more restricted to the southern North Sea in q3 (Figure 5.3.4).

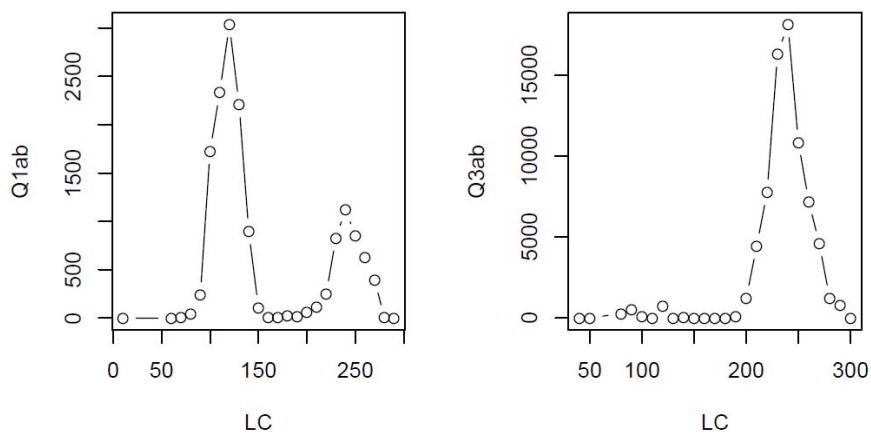


Figure 5.3.1. Average length class frequencies of sardines by quarter in North Sea IBTS catches.

Sardina pilchardus

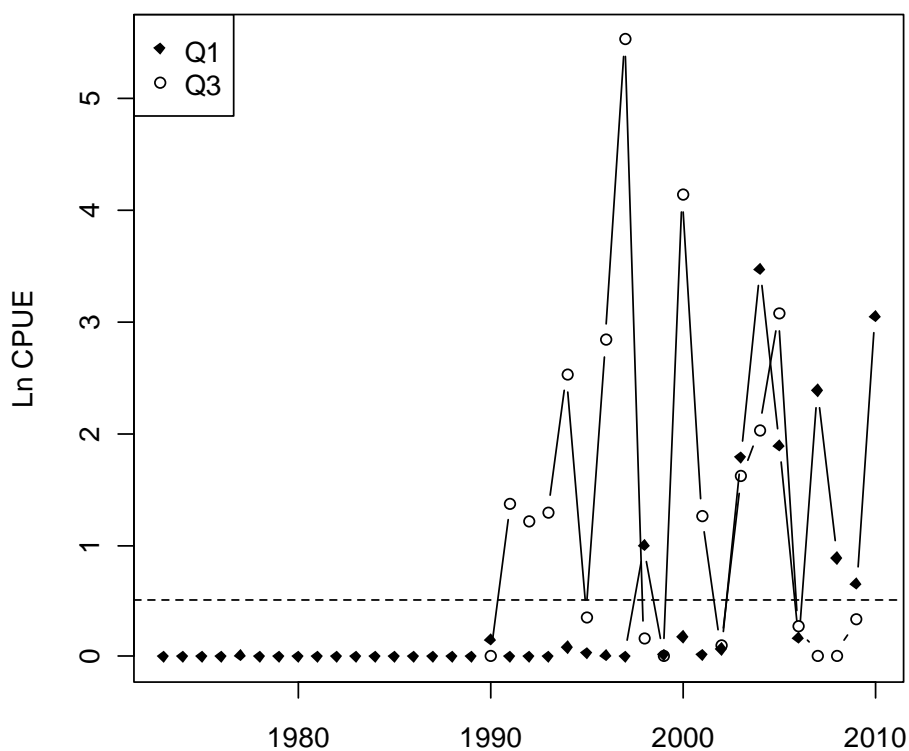


Figure 5.3.2. Sardine abundance index $[\log(\text{cpue}+1)]$ in the Q1 and Q3 North Sea IBTS.

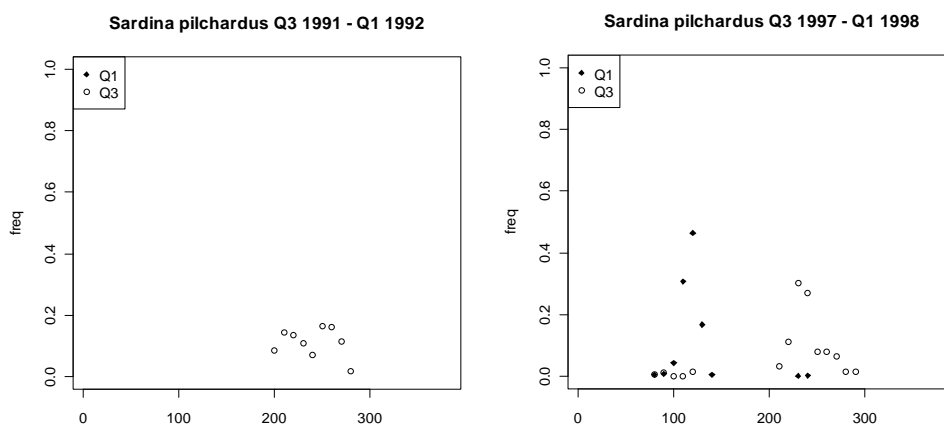


Figure 5.3.3. Length distribution of sardine in the North Sea the first time their abundance is not negligible (left: q3 in 1991) and the first time their abundance is also not negligible in q1 (right: 1998).

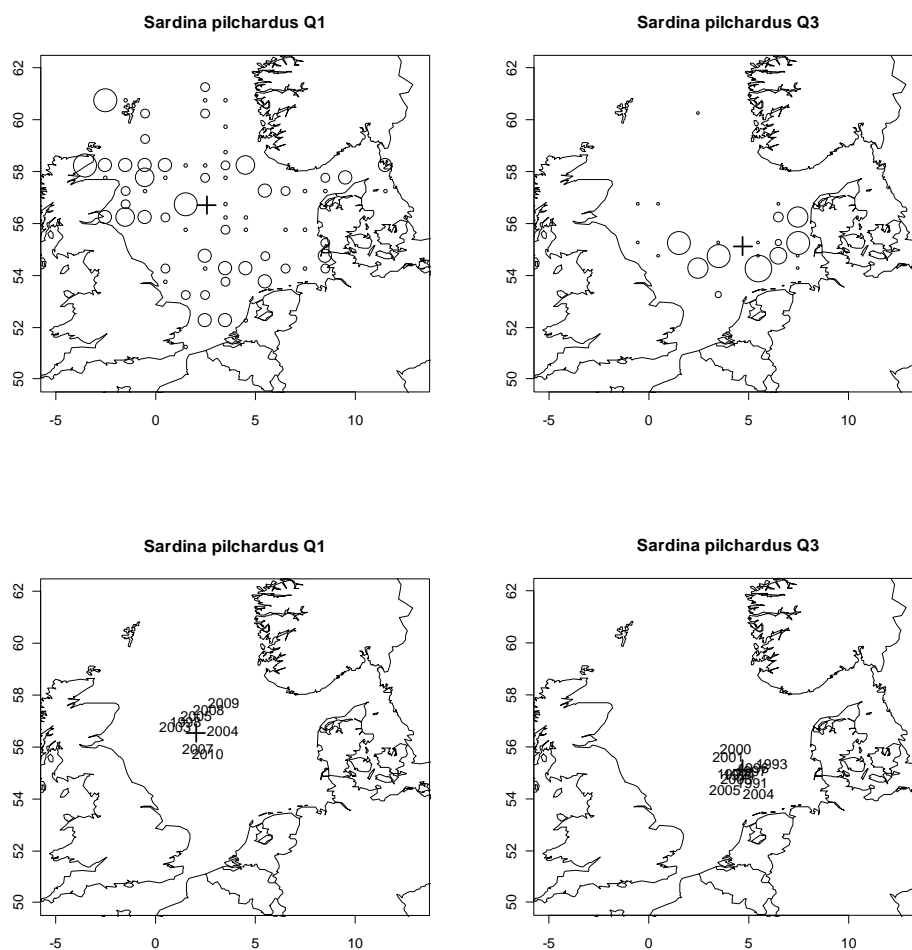


Figure 5.3.4. Seasonal spatial pattern of sardine in the North Sea in q1 (left) and q3 (right). Above: Probability of presence (>2 individuals per ICES rectangle) averaged over 1973–2010 (q1) and 1990–2009 (q3). Below: variability across years of the gravity centres in the yearly maps of presence/absence.

5.4 Closer analysis of temperature and anchovy expansion in the North Sea.

There is evidence of continuous presence of anchovies in the North Sea from the stone age onward (Enghoff *et al.*, 2007), with fisheries on the Dutch coast (Boddeke and Vingerhoed 1996) and periods of expansion (Cunningham 1891, 1895; Heegaard 1947; Beare *et al.*, 2004).

The increase of the population since the mid-nineties appears to be related to the global weather pattern change identified at that period and resulting in an increase of the average annual temperature of about 0.5 °C (see sections 3.1 and 5.2). Apparently this increase since 1995 is mainly due to higher summer temperatures (section 3.3).

An average increase of 0.5 °C is not biologically enough as to explain an increase of the population. However, the increase of temperature has to be considered in other terms than absolute increase:

- The summer warming may have increased the areas and the period where the growth period is long enough for anchovy larvae to reach a size allowing survival during the winter. According to literature in the Bay of Biscay spawning occurs mainly at temperatures higher than 14 °C (Ibaibarriaga *et al.*, 2007), although spawning starts with warming rather than an absolute temperature (Motos *et al.*, 1996). Optimum larval growth temperatures are above 16 °C (Ibaibarriaga *et al.*, 2007; Urtizberea *et al.*, 2009, Peck *et al.*, submitted). At such temperatures 40 to 50 days are needed to metamorphose (around 4–5 cm, Aldanondo 2010), and 60 to 80 days to reach a size of 7–8 cm (Aldanondo 2010) that results in higher winter survival (Boyra pers communication).
- Rather than the average temperature, the frequency of extreme thermal events (Mantzouni and MacKenzie 2010) that can be either unfavourable for anchovies (too cold) or for their competitors (too warm) needs to be considered. This second concept will be examined by the workshop participants over the next 6 months through correspondence.

Growth period

The length of the periods above 14 and 16 °C has been analysed on the output of the ECOSMO model hindcast (Schrum *et al.*, 2006a,b) which covers the period 1958–2004. Spatial averages over three different areas have been compared on a weekly basis: the southern North Sea area, the German Bight Area as well as the northern North Sea (MAP). A monthly dataset from the Wadden Sea has been analysed for an area where anchovy has been continuously recorded (Boddeke and Vingerhoed, 1996) and must therefore indicate the minimum times (degree days) required for successful growth and survival (population persistence). The length of the potential growth periods has been compared to the same type of data in the Southern Bay of Biscay (Figure 5.4.1).

Although the monthly averages do not allow for a detailed estimation, the Wadden Sea data indicate that the window of time with temperatures > 16 °C is between 2 to 3 months, with an increase in recent years (Figure 5.4.2 a). The window of time where temperatures are above 14°C is around 4 months (Figure 5.4.2 b). For comparison the same time windows in the south of the Bay of Biscay are 5 and 7 months.

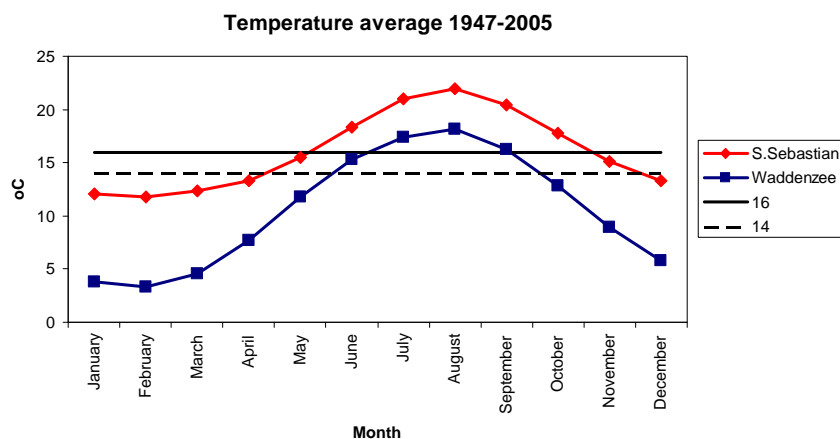


Figure 5.4.1. 1947–2005 average seasonal temperature cycle in the Waddenzee and San Sebastian. The horizontal lines indicate the lower limits for spawning and larval growth assuming a similar biology to the Bay of Biscay population (see text).

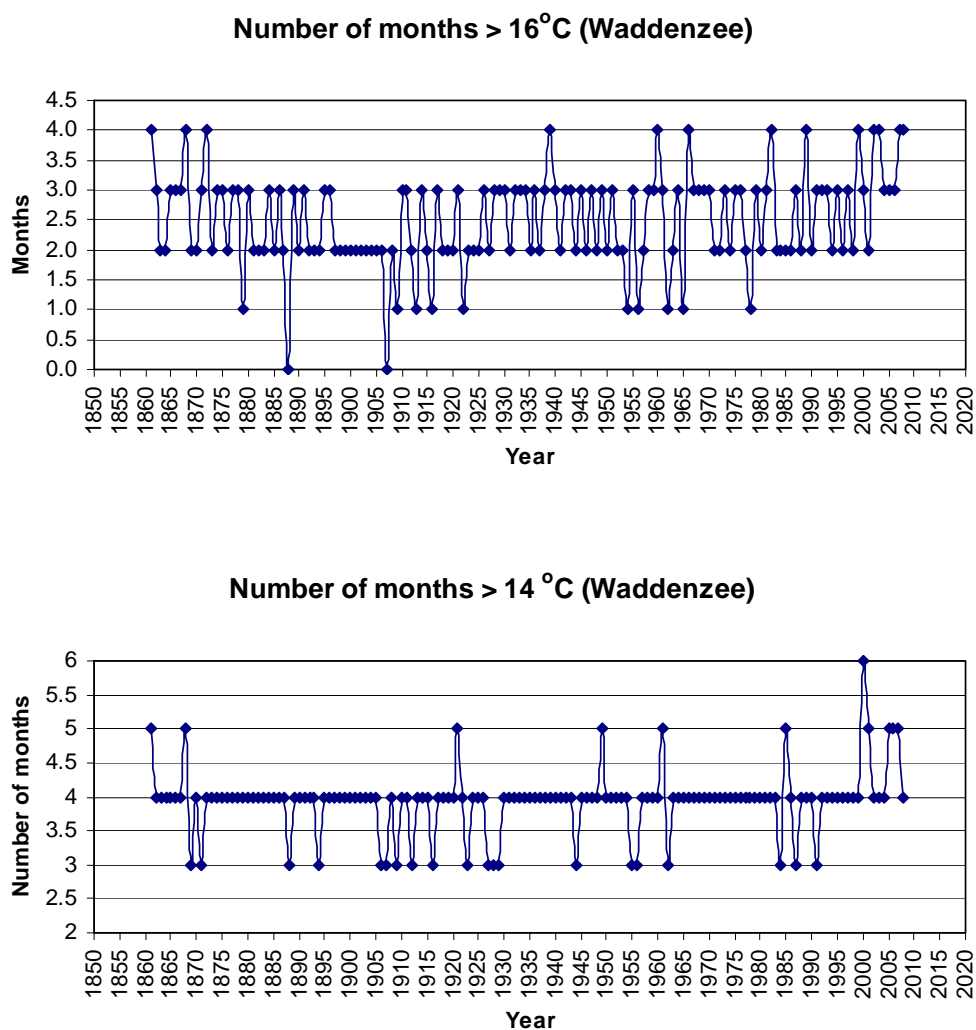


Figure 5.4.2. Number of months per year with temperatures above 16 °C (top) and 14 °C (bottom) in the Dutch Wadden Sea (Waddenzee) from 1850 to 2009.

The higher resolution data derived from the ECOSMO model confirm the previous observation for larger areas of the North Sea: southern North Sea, German Bight and Northern North Sea (Figure 5.4.3 a, b and c). In the southern areas the window of time above 14 °C is around 120 days. The window above 16 °C is around 70 to 80 days but shows higher variability than that of 14 °C (Figure 5.4.3 a and b and Table 5.4.1). In the Northern North Sea the window of temperatures above 16 °C is 15 days in average, and there are years where 16 °C are not reached (Figure 5.4.3 c and Table 5.4.1).

We also observe variability in the dates where 14 and 16 °C are reached, with a range of initial dates between 30 and 40 days (Figure 5.4.4, Table 5.4.1).

The temperatures in the southern area of the North Sea present the conditions for the anchovy to complete its life cycle as the window of time with temperatures allowing good growth conditions (assuming to be similar to the Bay of Biscay; which due to plasticity in traits of the species may not be the case, Somarakis *et al.*, 2004) is long enough. In the Northern North Sea such temperature conditions are not found. The results suggest that European anchovy in the Southern North Sea, German Bight and adjacent areas is at its northern limit in terms of temperature.

Thus, temperature has the potential to be a limiting factor as the window for growth is narrow in terms of the species' requirement, which allows little temporal margin for cohorts to be successful. Variability in the length of this "window of opportunity" or in the spatial extent where such conditions are found may have a strong influence on the recruitment success.

As mentioned above the influence of extreme temperature events will be examined over the next 6 months.

Table 5.4.1. Basic statistics per area on the average number of days above 14 and 16 °C, date of the average first day reaching those temperatures and the variation range.

	Average nb. days above 14°C (spawning)	Average nb. days above 16°C (Larval development)	First day > 14°C (mean)	First day > 14°C (variation range)	First day >16°C (mean)	First day >16°C (variation range)
Northern North Sea	73	15	186 (July 6th)	35		
Southern North Sea	119	71	173 (June 23th)	28	196 (July 16th)	35
German Bight	121	79	169 (June 19th)	28	189 (July 9th)	42

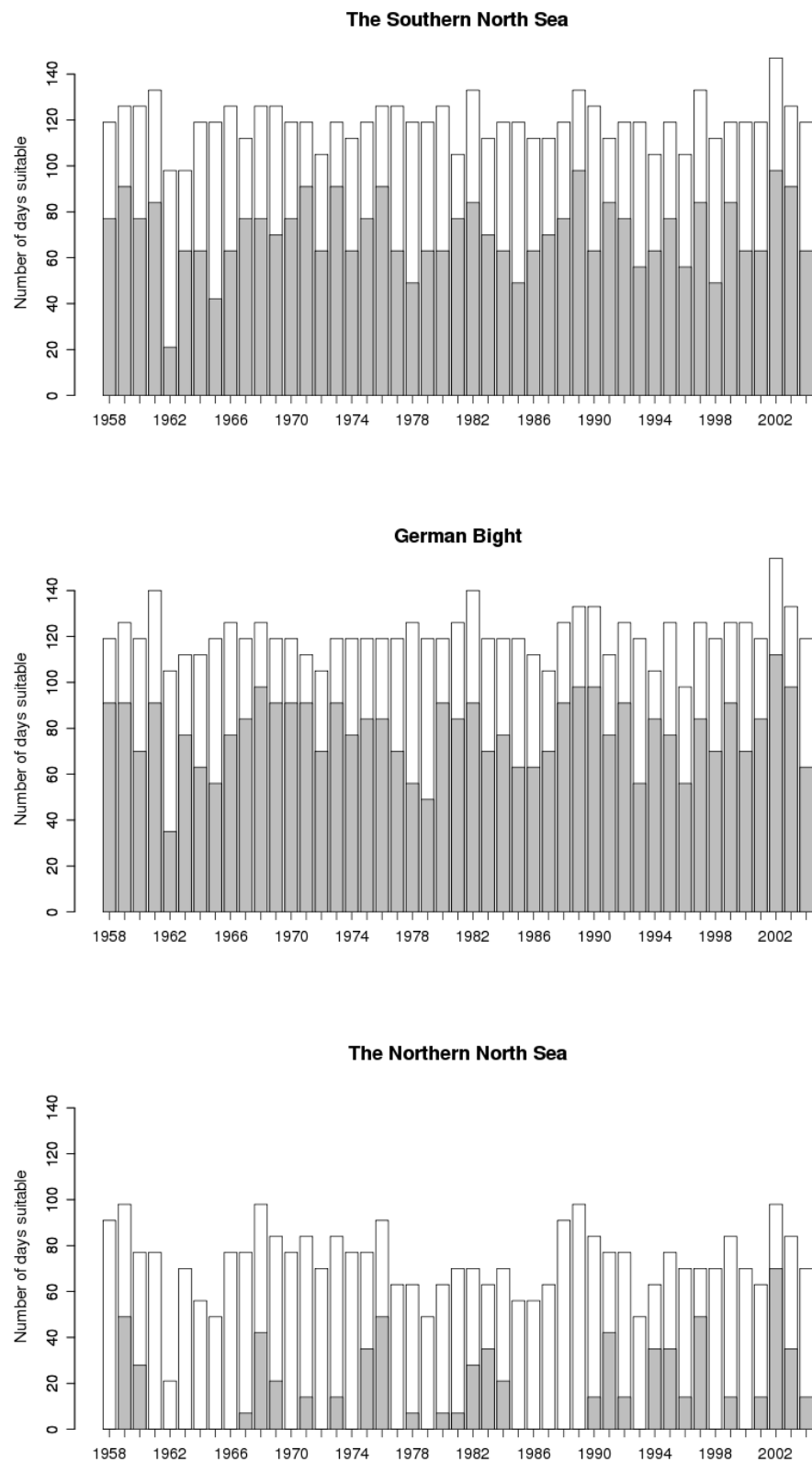


Figure 5.4.3. Number of days per year with temperatures above 16 °C (grey) and 14 °C (white) in the southern North Sea (top), German Bight (middle) and Northern North Sea (bottom). Data derived from Ecosmo.

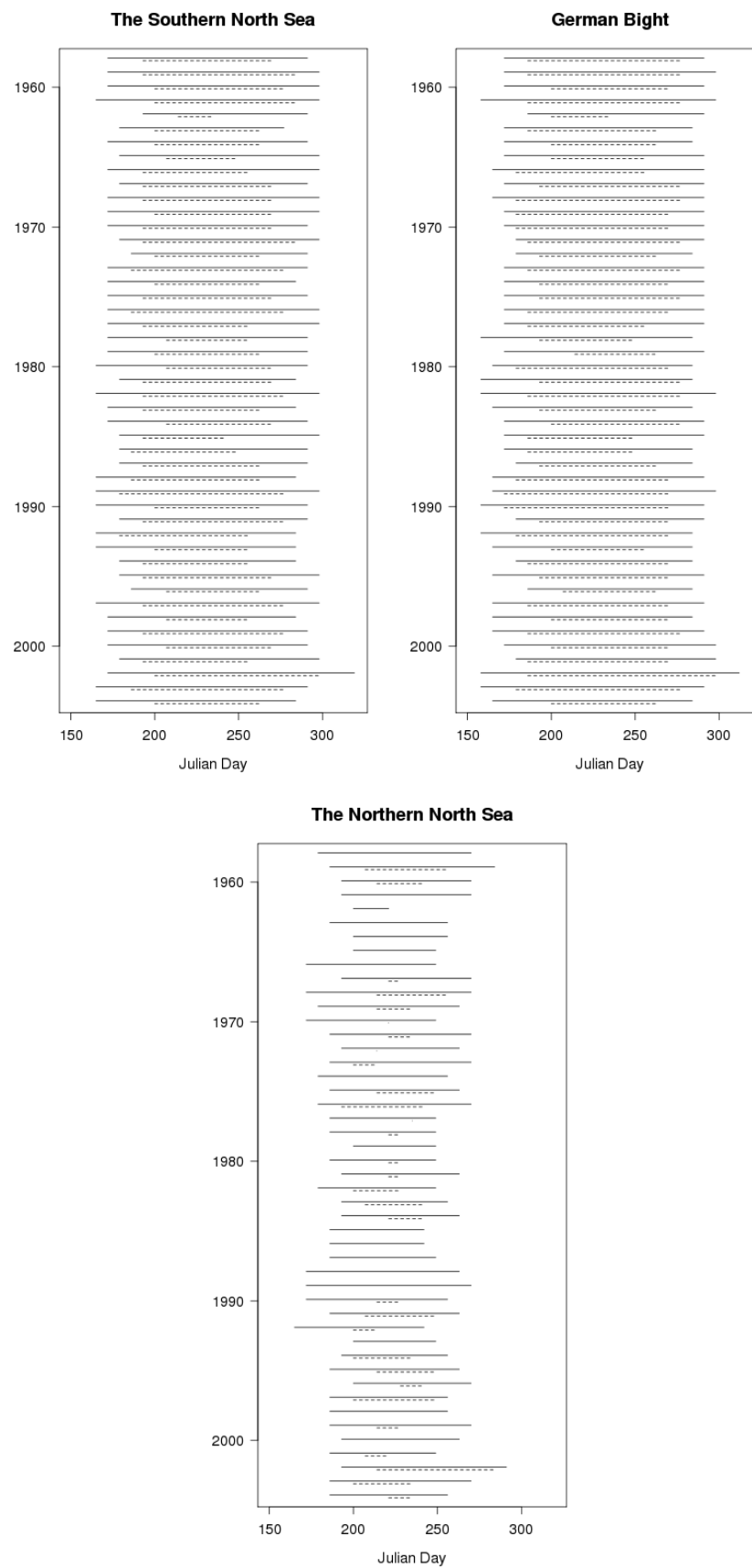


Figure 5.4.4. Julian days with temperatures above 16 °C (dots) and 14°C (continuous line) in the Southern North Sea (left) and the German Bight (right). Data from ECOSMO (Schrum, 2006).

5.5 Why does the June acoustic survey of the North Sea not observe anchovy?

The IBTS survey catches anchovy and is used as the primary indicator of trends of anchovy in the North Sea. The trends can be seen in quarter 1 and quarter 3. Why doesn't the June acoustic survey of the North Sea (see ICES WGIPS reports) catch anchovy in any numbers and thus not provide a time series. Either the methods are inappropriate to sample North Sea anchovy, or the anchovy are not there.

Anchovy in the Bay of Biscay are relatively demersal during the day, even more so in winter. This probably explains why the IBTS in quarter 1 has provided such a useful index of anchovy dynamics. If the anchovy were more demersal in the summer too, then they may not be detected by the North Sea acoustic survey which targets very pelagic sprat and herring. Although we know that anchovy in the Bay of Biscay tend to be more pelagic at night and the acoustic survey sometimes surveys in darkness. We know that the tradition spawning grounds of North Sea anchovy are the shallow more estuarine areas. So perhaps the anchovy are not in the North Sea proper in June but are inshore, spawning.

In 2010, the Netherlands initiated monthly sampling for ichthyoplankton in the southern North Sea. 100 stations will be sampled every month from April 2010 to May 2011 with a Gulf VII (Nash *et al.*, 1998). Anchovy eggs were not present in April and May, but were present in June, very close inshore by the Wadden Sea and the delta region. This suggests that the anchovy are spawning in June in very inshore areas and beyond the survey area of the acoustic survey.

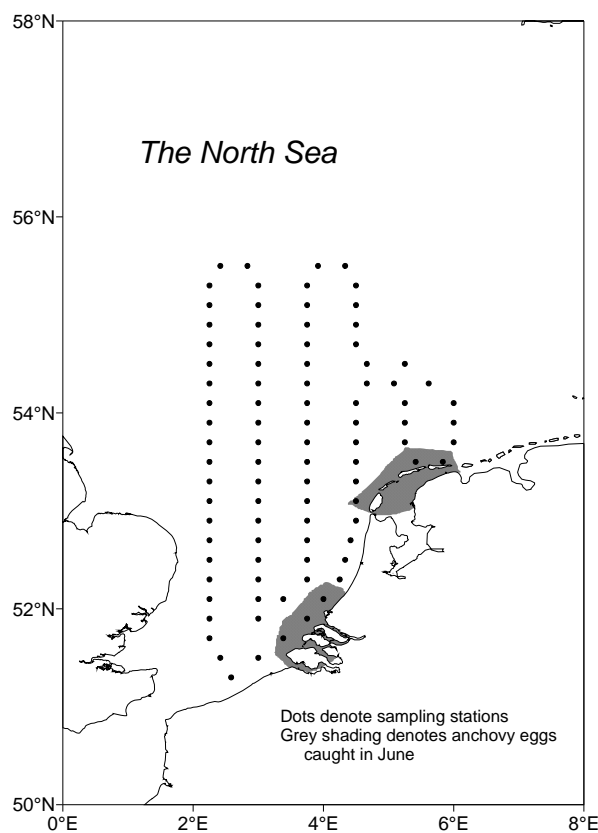


Figure 5.5.1. Anchovy spawning in Dutch waters in June 2010. Sampling grid of the Dutch ichthyoplankton survey carried out in April, May and June.

6 Multispecies interactions

All of the above considerations have assumed that each species acts in isolation and this, of course, is not the case. As planktivores, anchovy, sardine and sprat compete with other North Sea species like herring, sandeel and Norway pout. Anchovy in the North Sea are generalist planktivores and appear to be a fairly opportunistic feeder (Raab *et al.*, submitted) and are less specialised compared to sprat and especially herring (Raab *et al.*, in prep).

As forage fish, all three species are key prey species for piscivorous fish, sea mammals and birds. There are few studies that have actively investigated the relative importance of anchovy and sardine as prey in the North Sea and western Baltic. It is also likely that sardine, sprat and anchovy are all part of Predator to Prey loops (P2P; Bakun and Weeks, 2006). In the North Sea and adjacent areas, anchovy and sardine are not included in multispecies models (such as Multispecies Virtual Population Analysis; MSVPA, Vinther, 2001; Kempf *et al.*, 2006, Stochastic Multispecies model; SMS; Lewy and Vinther, 2004 and Ecopath with Ecosim; Mackinson and Daskalov, 2007) because their biomass was considered to be too low (their impact on the food-web was thought to be negligible). However, some models are currently being updated as part of ongoing EU research programs (i.e., “FACTS” Forage Fish Interactions).

There appears to be some synchrony between the dynamics of some other fish and the sardine and anchovy, such as the decline in productivity in North Sea herring in 1995 and the increase in productivity of northeast Atlantic blue whiting (*Micromesistius poutassou*) (1995 to 2007). Also, the study of historical fishing periods has indicated synchrony and alternations between dynamics of European herring and sardine fisheries (Alheit and Hagen 1997). However comparing short time series of fish dynamics and assuming a causal or longer-term correlative relationship can be very misleading, especially when processes have not been considered (see Fields *et al.*, 2009).

7 Gaps in knowledge and required further studies

This workshop was also tasked with describing the gaps in our knowledge base and suggesting future research directions. The workshop has provided some more insight into the dynamics of anchovy and sardine in the North Sea and adjacent areas. There is clearly much more that needs to be investigated before we understand the “sudden appearance” of rare species at their northern limit in the North Sea.

The information gained from the IBTS survey was useful in piecing together a possible life history pattern in the North Sea but several issues remain. Due to the fixed and limited sampling design, it is possible that low abundances of anchovy or sardine were present prior to their being recorded in the survey, leaving the “first appearance” events being poorly described. Moreover, the IBTS does not cover coastal areas where anchovy are known to be present and spawn. To refine the understanding of the first arrival events and of the spatial movements of the population, other data sources will need to be used such as coastal surveys of individual ICES nations. This would also help with elucidating the distribution of these species during quarter 2 and 4 in the years since their reappearance in the North Sea (the IBTS time series for q2 and q4 is very reduced).

Spawning and growth of anchovy and sardine in the North Sea are not well understood. In sections 5.2 and 5.3 we assumed, based on the length distributions and

likely growth time that for anchovy, q3 data reflect juveniles and adults, while q1 shows adults only. Ideally, this should be verified using otolith microstructure analysis to ascertain whether the small-sized individuals caught in quarter 3 were born the same year and to determine whether or not all of the large-sized individuals belonged to the same generation. In this regard, models of growth bioenergetics linked to physical and NPZD models (e.g., Daewel *et al.*, 2008) may also give insight into population dynamics at low abundances.

Generally, the limiting factors determining the reproductive success of anchovy and sardine in the North Sea still remain unknown. A lot of the work presented here was related to temperature in one way or another. Although understanding species (and life stage) specific thermal windows for growth is an important step towards a “cause-and-effect” understanding of distribution and productivity of species, multiple factors potentially interact to limit environments suitable for growth and survival of a species (Pörtner and Peck, In Press). How to identify and differentiate between limiting factors in summer (such as minimum temperature for spawning, or minimum number of days above or below a certain temperature threshold) versus in winter (e.g. killing temperatures for that year’s juveniles) remains an open question. Even in areas where the species has been better examined such as the Bay of Biscay, the limiting factors in the life history cycle are not fully understood (for instance, winter dynamics are poorly recorded and understood there, unlike in the North Sea where q1 is the longest time series from the IBTS). But these are crucial questions to understand why, almost from one year to the next, a resident population can expand into much broader areas. A contrasting end-to-end modelling study of anchovy in the Bay of Biscay and in the North Sea may provide useful insights into the processes that control productivity of that species.

More open questions remain about sardine as the expertise of the group was slightly biased towards anchovy. Genetic and spatio-temporal statistical modelling may improve the understanding of the origin of and the mechanisms affecting its dynamics.

It has been suggested that the decline in the productivity of other species (such as herring, Payne *et al.* 2009; or sprat) may have facilitated the increase in anchovy and sardine populations. More analyses could be done to understand how these species interact. Spatial overlap between the populations for instance shows that sprat has not changed very much and abundances have even increased.

Addressing the spatial distribution of these species may yield interesting insights in terms of the differential distribution at high or low abundances. Indeed WGFE 2007 showed that abundance and area occupied seem to be related. But has this relationship levelled off in recent years that the species have had several years of successful spawning in increasingly large areas (e.g. the German Bight and east of Denmark now too, additional to the English Channel) or is each year still as survival limited as in the early colonization phases?

It is clear that more insight into the basic biology, physiology, behaviour, growth and condition of these fish is needed. Increased sampling and collection and analysis of otoliths may help this (micro increment and chemistry analysis). The dynamics of the “ghost” populations in the delta region of the Netherlands and the Wadden Sea need to be further investigated along with their genetics (are these “beach” populations or are they the true source of the North Sea anchovy). The UK has initiated acoustic surveys of sardine in the western English Channel and the Celtic Sea. It is hoped that these surveys will be used to build up a time series of sardine abundance and distri-

bution but they will not cover the autumn spawning components of the sardine population.

There is a need for further knowledge, but potentially useful data sets exist at places such as SAHFOS and the Plymouth Marine Laboratory. Do similar sets exist in Ireland, Scotland and Denmark? This workshop has focused on and thus highlighted temperature as a controlling or limiting factor but other potentially important environmental factors (acting alone or interacting with temperature) were ignored. What are the key climate-driven factors and/or mechanisms driving changes in populations? What is the spatial scale of the relevant mechanisms / processes? Are all relevant processes related to changes in local phenomena and thus, are they difficult to detect using measures (e.g. climate indices) relevant to larger / broader spatial scales?

8 Conclusions

This workshop attempted to increase our understanding by considering the phenomenon of the “appearance” of anchovy and sardine in terms of the processes controlling the life cycle. It fitted these considerations into the historical context and synthesised across scientific disciplines. Through the use of oceanography, genetics, IBM modelling, analysis of empirical time series we conclude that:

- i) The recent increase of anchovy in the North Sea is probably due to the development of local North Sea populations, rather than a northward movement of Bay of Biscay populations.
- ii) The expansion of anchovy in the North Sea is thought to be driven by recruitment pulses, controlled by long enough duration of relatively high summer temperature and favourable enough winter conditions. Temperature has the potential to be a limiting factor as the window time for growth fits narrowly with the species requirement, allowing little margin for cohorts to be successful. There is probably a balance between high enough summer temperature allowing sufficient growth and winter conditions allowing sufficient survival at length. Variability in the length of these periods or in the area where such conditions can be found may have a strong influence on the recruitment success.
- iii) It is probable that sardine in the North Sea is either the same population or mixes greatly with sardine further south. It appears likely that spring abundance depends on recruitment in the North Sea from summer spawning events, while autumn populations are also influenced by migrations.

Climate-driven changes in key factors such as temperature thus appear to mediate the productivity of the North Sea population of anchovy although the influence of changes in climate-driven factors on North Sea sardine is less clear.

Participants of WKANSARNS will meet again in February 2011, outside the auspices of ICES, to synthesise this report into a manuscript for publication in the primary literature.

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Annex 2: WKANSARNS Terms of Reference 2009

A **Workshop on anchovy, sardine and climate variability in the North Sea and adjacent areas** [WKANSARNS] will be established (Co-Chairs: M. Dickey-Collas, UK, Pierre Petitgas, France and Jürgen Alheit, Germany) and will meet on 22–25 June 2010 in Nantes, France to:

- a) synthesise and test the potential hypotheses for the multi-decadal fluctuations of anchovy and sardine abundance in the North Sea and adjacent areas
- b) produce a working paper to be submitted for publication on the current understanding of the causes of the fluctuations of abundance relating to the hypotheses raised in a).
- c) recommend areas which required further investigation and highlight the gaps in our knowledge of the dynamics of anchovy and sardine in the North Sea for the purpose of stimulating and advising further research.

WKANSARNS will report by 15 August 2010 (via SSGRSP) for the attention of SCICOM.

Annex 3: Agenda for WKANSARNS

6–9 July 2010

IFREMER Nantes

- | | |
|--------|---|
| 6 July | 10:00 Welcome, House Keeping and Introductions |
| | 10:30 The Structure of the workshop, the Terms of Reference and developing the approach. |
| | 12:30 Lunch |
| | 14:00 Ideas – each person will be invited, and expected, to raise one or two concepts that they think are relevant to our deliberations. Each idea will have a 10 minutes allocated time. |
| | 16:30 Rounding up and the way forward for the workshop. Synthesis of ideas. |
| 7 July | 09:30 Hypotheses raised and testing. |
| | 11:30 Split into sub groups: |
| | i) Climatic and ocean wide processes |
| | ii) Local processes/habitats |
| | iii) Biology and interactions |
| | 12:30 Lunch |
| | 14:00 Continue sub groups |
| | 16:30 Sub groups report back |
| 8 July | 09:30 Overview of Progress |
| | 09:45 Split into sub groups to test and write. |
| | 12:30 Lunch |
| | 14:00 Sub groups continue |
| | 16:00 Gaps in knowledge and future investigations |
| 9 July | 09:30 Synthesise sub group findings |
| | 10:30 Outline paper structure, and fill with text |
| | 12:00 Close |

Annex 4: Recommendations

There are no following recommendations from WKANSARNS other than the recommended areas for further investigations and research (see section 7).

A synthesis manuscript for submission to a peer reviewed journal will be prepared by WKANSARNS. The members of WKANSARNS will meet in February 2011, outside the auspices of ICES, to finalise the manuscript. The work of ICES WKANSARNS will be acknowledged in the manuscript.

WKANSARNS will not meet again under ICES.