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Horizontal distribution and overlap of planktivorous fish stocks in the Norwegian Sea during summers 1995-2006

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Abstract:

The Norwegian Sea harbours several large pelagic fish stocks, which use the area for feeding during the summer. The period 1995–2006 had some of the highest biomass of pelagic fish feeding in the Norwegian Sea on record. Here we address the horizontal distribution and overlap between herring, blue whiting and mackerel in this period during the summers using a combination of acoustic, trawl and LIDAR data. A newly developed temperature atlas for the Norwegian Sea is used to present the horizontal fish distributions in relation to temperature. The centre of gravity of the herring distribution changed markedly several times during the investigated period. Blue whiting feeding habitat expanded in a northwestern direction until 2003, corresponding with an increase in abundance. Strong year classes of mackerel in 2001 and 2002 and increasing temperatures throughout the period resulted in an increased amount of mackerel in the Norwegian Sea. Mackerel was generally found in waters warmer than 8°C, while herring and blue whiting were mainly found in water masses between 2 and 8°C. The horizontal overlap between herring and mackerel was low, while blue whiting had a large horizontal overlap with both herring and mackerel. The changes in horizontal distribution and overlap between the species are explained by increasing stock sizes, increasing water temperature and spatially changing zooplankton densities in the Norwegian Sea.

Keywords: Herring, mackerel, blue whiting, temperature, competition, interaction

1. Introduction

1.1 The pelagic fish stocks in the Norwegian Sea

The Norwegian Sea harbours some of the largest fish stocks in the world, including two species sustaining among the highest yields globally, namely Norwegian spring spawning (NSS) herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*). Mackerel (*Scomber scombrus*) also spend the summer feeding in the Norwegian Sea (Fig. 1). These planktivorous stocks can then have substantial spatial (Kaartvedt 2000) and diet (Prokopchuk & Sentyabov 2006) overlap. By virtue of their high abundances, they can potentially have a strong ecological impact on the ecosystem and each other (Skjoldal et al. 2004). The planktivorous stocks have varied strongly in biomass during the last decades. Presently, the NSS herring and mackerel stocks are large, while the blue whiting stock is decreasing due to poor recruitment since 2005 and a high fishing pressure (ICES 2010). The three fish species in focus here all prey heavily on *Calanus finmarchicus*, with a preference for the latest copepodite stages and the adult stage (Prokopchuk & Sentyabov 2006). Their abilities to utilize other types of prey vary and are mainly determined by the availability of the different prey species.

1.2 Top-down control by planktivorous fish

Planktivorous fish populations can be very abundant and have a great impact on the ecosystem through depletion of zooplankton (Koslow 1981, Hassel et al. 1991). In small lakes planktivorous fish can change the ecosystem structure completely by depleting the zooplankton population (Carpenter et al. 1985). Planktivorous fish can further reduce the zooplankton biomass in restricted marine areas such as the southeast Bering Sea (Ciannelli et al. 2004), the Baltic Sea (Arrhenius & Hansson 1994), the Black Sea (Oguz & Gilbert 2007) and the Barents Sea (Manteufel 1941, Hassel et al. 1991, Skjoldal et al. 1992, Dalpadado et al. 2003).

Strong feeding pressure on the *C. finmarchicus* stock in the Norwegian Sea one year seems to result in a low population size the following year (Skjoldal et al. 2004, Olsen et al. 2007). This happened after 1995, when a peak in the NSS herring biomass together with the strong 1995 cohort of blue whiting resulted in a low *Calanus* population in 1996 and 1997 (Melle et al. 2004). In recent years we have witnessed some of the highest biomasses of fish feeding in the Norwegian Sea area on record (ICES 2009). At the same time the zooplankton abundance in the Norwegian Sea has been steadily declining and is now at a historically low level (Anon 2009). This has actualized interactions among the planktivorous fish stocks. The stocks comprise major fish resources and information about their interactions is crucial for ecosystem-based management of the Norwegian Sea. To understand the regulations of such complex ecosystem it is necessary to know the fish species spatial distribution and the interactions between the species. Despite its potential importance for ecosystem functioning, there have been few studies addressing interactions between planktivorous fish stocks, and the topic remains a major challenge in marine ecology.

1.3 Spatial overlap

Competition occurs when individuals of one species suffer a reduction in growth due to their shared use of a limiting resource with another species (Begon 2006). Competition can be demonstrated by population or individual growth patterns, diet composition and aggressive interactions. There is potential for feeding competition if species are present in the same area at different times, or if populations in two different areas utilize the same water masses that are displaced by currents and general water movement. In these situations interaction can lead to competition for mutual food resources. In order to demonstrate feeding competition, it must be shown that the fish stocks occupy the same water masses and utilize the same food resources. Competition for space is strongly time and density dependent. Increasing stock size will normally extend the spatial distribution, but also the age distributions of the stock will play a role since juvenile and adult fish often prefer different habitats. In the Norwegian Sea, herring enters the southern feeding ground earlier in the year than the blue whiting and mackerel, which start feeding when herring has already started a northwards migration (Prokopchuk & Sentyabov 2006). The interactions are thus strongly dependent on season and are also expected to vary between years due to changes in hydrographical conditions and stock sizes.

Data in 3D is a requirement for spatial analyses. In this paper we only focus on horizontally distributed data while the paper by Huse et al (this issue) addresses the vertical aspect.

1.4 Objectives

Several earlier publications have presented the historical distribution of herring (e.g. Devold 1963, Røttingen 1990, Jakobsson & Østvedt 1999, Holst et al. 2002), blue whiting (e.g. Zilanov 1968, Bailey 1982) and mackerel (e.g. ICES 1987, Belikov et al. 1998, Iversen 2002), but no work has been done on how the historical distribution of the pelagic species has changed within and between seasons in relation to varying stock sizes of other planktivorous fish and water temperature. Furthermore there has been little work on the most recent period characterized by high biomasses of all three stocks and low zooplankton abundance. The objectives of this study are to describe the horizontal distribution in the Norwegian Sea for NSS herring, blue whiting and mackerel in relation to temperature in early and late summer for the period 1995 – 2006. Furthermore we assess the horizontal overlap between the species during feeding and the potential for feeding interactions.

2. Material and methods

2.1 Dataset

Acoustic data from 37 trawl acoustic surveys were used to present the horizontal distribution of herring, while 35 of these surveys were used to present the horizontal distribution of blue whiting (Table 1, Table A.1). For mackerel however, acoustic surveys are at present quite unreliable (Korneliussen & Ona 2002) and catch data together with LIDAR (Light Detection and Ranging) data were the best data set available. The horizontal distribution of mackerel was based on catch data from 22 trawl surveys (Table A.2.) and 9 aerial surveys. Such a large dataset will have certain errors, and the strategy was therefore to extract the best data, transform it to a standardized resolution and then evaluate the potential sources of bias.

2.2 Herring and blue whiting

2.2.1 The surveys

Horizontally resolved data from Norwegian, Icelandic and Faroese PGNAPES (Planning Group for Northeast Atlantic Pelagic Ecosystem Surveys) surveys in May were gathered for the time period 1995-2006. In addition, data were available from some Icelandic and Norwegian surveys in July/August. The surveys were separated into two main periods covered in most years. The first period (Early Summer, ES) is in May, but the whole time period for surveys starting in late April and/or ending in early June were used. The second period (Late Summer, LS) is from mid July to the end of August. The main purpose of the surveys differed, but mapping the spatial distribution of herring and estimating the stock size were always main goals. In most surveys the spatial distribution of blue whiting could be obtained but as this was usually not the main purpose of the surveys, the whole stock was usually not covered. Overall, the data set is large and available for analyzing the horizontal distribution during periods with possible interactions between the species.

2.2.3 Acoustic recordings and biological sampling

The acoustic recordings were done with a calibrated SIMRAD 38 kHz EK60 or EK500 split-beam echo sounder. The vertical range of data recordings was set to 0-500 m. Trawl hauls where frequently taken in all surveys to obtain information about the species and their length/weight composition. To allocate the area backscattering strength to species, the acoustic recordings were scrutinized during the surveys according to depth and density appearance on the echogram and the trawl catches. The BEI data were stored on different resolutions, varying with common practice at each time. From 2001 to present, the common resolution was 1 nm horizontal and 10 m vertical resolution.

The general procedure was to take trawl hauls at predetermined locations and/or on locations with changes in the acoustic recordings, which were large changes in s_A values, the vertical position of the fish or target strength values. Normally Norwegian vessels used the “Åkra trawl” with an opening dimension of 30 x 30 m (Valdemarsen & Misund 1995) and a cod end with mesh size of 20 mm. Different midwater trawls with broadly similar fishing properties (ICES 2008) were used by other vessels. A random sample of 100 individuals was taken from each station for length, weight and age determination (Mjanger et al. 2007).

2.3 Mackerel

For mackerel, catch data from scientific surveys were used in the analyses. Since mackerel rarely enters the Norwegian Sea in ES due to spawning activity further south in May, only the late summer data is included in this analysis. Pelagic trawl hauls and biological sampling were done at predetermined locations. A detailed description of the purpose and time for the various surveys are given in Table A.2. For the mackerel catches, the catch per unit effort (CPUE) was calculated and used in the horizontal distribution maps. In addition, mackerel observation (LIDAR) from Russian aerial surveys in central parts of the Norwegian Sea from 1997-2005 are presented. LIDAR is a laser beam transmitted towards the surface penetrating up to 50 m into the water column (Tenningen et al. 2006). The light reflected back to the transmitter is recorded and can be used for abundance estimation of epipelagic stocks such as mackerel. When the LIDAR is attached to an airplane, huge areas can be covered and an estimate of the abundance and distribution of mackerel can be obtained. All fish detected by the LIDAR are assumed to be mackerel since other possible species like blue whiting form layers which will not be detected (Churnside et al. 2009).

2.4 Temperature Atlas

Gridded temperature fields for May and July-August, where prepared for the years 1995-2006. In ES the temperature at 100 m depth is presented together with the herring recordings, and the temperature at 300 m depth with the blue whiting recordings. For LS the temperature at 10m, 50m and 200m depth is used for mackerel, herring and blue whiting, respectively. The temperature fields employed here are derived from a larger temperature archive (or atlas) for the Norwegian Sea constructed by Ottersen (2010). The archive spans the area 20°W-20° E 60°-80°N and currently the years 1990-2006. It is based upon more than 58 200 CTD and Nansen bottle stations compiled from different sources including the NISE (Norwegian Iceland Seas Experiment) (Nilsen et al. 2006) project dataset, the hydrographical database maintained by ICES (www.ices.dk) and the World Ocean Database 2005 (WOD05, http://www.nodc.noaa.gov/OC5/WOD05/pr_wod05.html) (Boyer et al. 2006).

All data were gathered from trustworthy data bases, and have already been subject to the quality checking routines employed by the respective institutions (e.g., see http://www.ices.dk/Ocean/odmsoft/index.htm for an overview of ICES procedures). Also, since only the period from 1990 is covered, possible technical and methodological problems of older data were avoided. The only thorough quality control employed was to remove a significant number of duplicate data stations.

The spatially scattered stations were interpolated to systematic grids with one value in each square by means of a straightforward algorithm that uses a combination of Laplace and cubic spline interpolation in the horizontal plane and pure linear interpolation in the vertical (Taylor 1976, Ottersen 1991). The system has been applied to, and proven well suited for interpolation of hydrographical data for a variety of purposes (Martinsen et al. 1992, Engedahl et al. 1998, Ottersen et al. 1998).

2.5 Horizontal spread of data

The number of squares (dimension: 0.5° longitude, 0.33° latitude) with herring and blue whiting recordings was calculated from the Norwegian survey data in order to investigate any changes in the habitat range irrespective of geographical position for herring and blue whiting. Data of spawning stock biomass (SSB) for herring and total stock biomass (TSB) for blue whiting was retrieved from ICES (2007). The correlations between stock size and habitat range were calculated.

2.6 Overlap index

The first analyses of the fish distribution data focused on how the overlap changed with the horizontal resolution of the acoustics data. Mackerel data could not be included in this analysis as there was no echo sounder data available. A possible correlation between two observed species is dependent on the resolution used (Rose & Leggett 1990), and choosing the correct scale to use is important for the quality and relevance of the results. As a first test of whether overlap changed with scale, the following equation was used:

$$ov = \sum_{i=1}^{n} Pi,h * Pi,bw \qquad (1)$$

where *ov* is overlap, *Pi,h* is the proportion of total herring abundance in group number *i*, and *Pi,bw* the proportion of total blue whiting abundance in group number *i*. The abundance of herring and blue whiting recorded in a group of surveyed nautical miles were divided by the total abundance of herring and blue whiting recorded during the survey. The following groups were used: 1, 2, 5, 10, 25, 50, 100, 200 nm, in order to calculate any change in overlap with spatial scale (Krebs 1989). To calculate overlap between herring and blue whiting the simplified Morisita index (Horn 1966) was used, as studies suggest that this index has a low bias compared to other overlap measures (Smith & Zaret 1982). The index was calculated by the following equation:

$$Ch = \frac{2\sum Pi,h * Pi,bw}{\sum(Pi,h)^2 + \sum(Pi,bw)^2} \qquad (2)$$

where *Ch* is the simplified Morisita index of overlap. This calculation was done for each year in the study.

2.7 Ambient temperature

All acoustic data used in the analyses for this section was gridded into a 0.33 degree latitude and 0.5 degree longitude grid for each 10 m depth bin. If more than one acoustic recording was observed within a square the mean value of the recordings was used.

The ambient temperature for herring and blue whiting was calculated by using the Norwegian survey data in May and the temperature atlas. As the atlas only had information of temperature for standard depths, vertical linear interpolation had to be done for the 10 m bins lacking temperature data. When calculating the ambient temperature, the different temperature measures were weighted according to the fish abundance in the respective grid cell. The ambient temperature in LS was not calculated since some of the surveys in LS did not cover the entire herring and blue whiting populations.

3. Results

3.1 Temperature atlas

The temperature atlas provides temperature data of high quality for this area. However, since there are monthly and interannual variations in the location of the CTD-stations, some areas have missing temperature in areas with fish registrations. The temperature is therefore presented in the maps as interpolated values with a maximum geographical range of 1° latitude/longitude.

3.2 Horizontal fish distribution

During the time period 1995-2006 there were large changes in the feeding migrations for the fish. There were no abrupt changes in the horizontal distribution between years, but rather a gradual change feeding area between the different years. The whole time period was divided into three main periods, 1995-1998, 1999-2002 and 2003-2006. The acoustic data are presented as circles along the cruise transect (Fig 2-7), where circle size and colour are proportional to the magnitude of the s_A-values (NASC - nautical area scattering coefficient, m^2 nm^{-2}). The temperature profile from a temperature atlas for the given time period and year of the acoustic data underlie the acoustic densities on the maps. The depths of the temperature profiles are selected from mean preferred depth of the fish species at the time of the year according to survey reports and previous knowledge.

1995-1998

Herring was located in the south-central and south western part of the Norwegian Sea during ES these four years. The population was uniformly distributed over a large area with water temperature in the range 4-8°C at 100 m depth. The distance from the spawning areas to the feeding grounds was short. In LS there was more variation between the years. In 1995 the herring was found widespread very close to the Norwegian coast. In 1996 and 1997 the surveys probably didn't cover the whole herring population and the highest densities were found around 69-73.5°N and 6-15°E, northeast of the feeding areas used during ES. In 1998 the highest densities were found in the north-western areas between Jan Mayen and Bear Island. During this period more or less the whole herring stock was horizontally distributed in the boundary between Atlantic and Polar water masses in temperatures down to 0°C at 50 m depth.

Only low densities of blue whiting, restricted to southern parts, were located in the Norwegian Sea during ES in 1995 and 1996. In 1997 and 1998 blue whiting had increased the habitat range and were now found further north in the central Norwegian Sea. Most of the blue whiting were located in areas with water temperature in the range 2-6°C at 300 m depth. In LS blue whiting were horizontally distributed over a larger area than in ES. The northward extent of the horizontal distribution was limited and the highest densities were found outside the southern and central Norwegian coast.

In this period the abundance of mackerel in the Norwegian Sea was low (Figs. 2,3 and 8). Generally the highest densities were found in the southern Norwegian Sea and the migrations didn't exceed 70-72°N, except for a few catches. The LIDAR data give a centre of mass at around 68° N (Fig. 8a and b). Mackerel were only caught in water masses warmer than 8°C at 10 m depth.

1999-2002

In these years the survey area coverage was good both during ES and LS (Fig 4-5). The water temperatures were higher than in 1995-1998 resulting in a potential increased habitat range for the feeding pelagic fish.

Herring were now located in the central Norwegian Sea during ES and did not use the southern areas at all. The population gradually moved northwards in ES these years until 2001. There were higher densities in the western part of the distribution area than in the eastern, but in 2002 this pattern was not present and herring had a rather uniform horizontal distribution. The population was mainly found in water masses with temperature in the range 4-8°C at 100 m depth, as it was in 1995-1998. The whole population was found extremely far north during LS for all these years, mainly from 70°N and up to Svalbard.

Blue whiting were now found over a much larger part of the Norwegian Sea both in ES and LS, in correspondence with the increase in stock size. The surveys, which were mainly aimed for mapping the herring population, probably failed to cover the entire blue whiting population. The highest densities were found in the southern areas in ES while the population had a uniform horizontal distribution in LS. In 2001 and 2002, the two years with the best survey coverage, medium to high blue whiting densities were found everywhere in water masses warmer than 2°C from Icelandic and Faeroes waters to Svalbard.

The trawl catches of mackerel were very low in 1999-2000 and high in 2001-2002. The highest densities in these two latter years were found further north than the previous years, and were now in the central Norwegian Sea. The northern border of the mackerel habitat was around 70-72°N as it was in 1995-1998. The low catches of mackerel in 1998 and 1999 probably don't reflect the actual abundance of mackerel in these years as the LIDAR data indicate that the mackerel was distributed over an extensivearea these years (Fig. 8).

2003-2006

These years had the highest water temperatures in the whole time period. The survey coverage during ES was generally good but with some interannual variation (Fig 6-7). There were no surveys using echo sounder to map the spatial distribution of fish in LS after 2003.

There was variation in the horizontal distribution of herring in ES these four years. The population was located in the central and northern Norwegian Sea in 2003 and 2004, with the highest densities close to the Norwegian coast. The main difference compared to the time period 1999-2002 was the increase in horizontal spread of the population, with parts of the population found in Icelandic and Faroese waters. The density of herring in this area increased in 2005-2006 and resulted in the stock being separated into two parts, one part close to the northern Norwegian coast and one part east of Iceland and north of the Faroe Islands. In LS 2003 herring was found in the same area as in 1999-2002, which was between 70°N and Svalbard.

During the period 2003-2006, the abundance of blue whiting feeding in the Norwegian Sea decreased. From covering large parts of the Norwegian Sea in 2003, the blue whiting density gradually decreased with habitat borders moving south-eastwards during these four years. As for herring, the blue whiting population was separated into two parts in the end of the period with low densities in the central Norwegian Sea. One part of the blue whiting population was close to the northern Norwegian coast, while the other one was found in Faroese and Icelandic waters.

The increased abundance of mackerel in the Norwegian Sea starting in 2001 and 2002 continued in this period. Medium to high densities of mackerel were found over large parts of the Norwegian Sea. In this period the highest mackerel densities was found further west than the previous years. The habitat range in 2003-2005 is unknown as the surveys had limited coverage north and westwards, but mackerel catches close to Jan Mayen are indication of increased habitat range towards west. Further indication of increased habitat range was seen in the survey in 2006, which had a good spatial coverage, where mackerel was caught close to the eastern Icelandic coast.

3.3 Range of horizontal distribution

The changes in habitat range during the period were different for herring and blue whiting (Fig. 9). There was a positive correlation between TSB and the area occupied by blue whiting (Pearson's correlation test, $r = 0.74$, $p < 0.01$), but not between SSB and the area occupied by herring (Pearson's correlation test, $r = 0.37$, $p = 0.24$). Both species had a very low habitat range in 1995, but it expanded for both species the following years. While herring mostly occupied 150-200 squares of 0.5 degrees longitude and 0.33 degree latitude, blue whiting expanded its habitat range and occupied nearly 350 squares in 2003.

3.4 Overlap index

There was a linear relationship between the spatial resolution in terms of nautical miles (log transformed values) (Eq. 1) and the horizontal overlap (log transformed values) between herring and blue whiting. This shows that the species did not aggregate horizontally at a certain distance from each other and the applied spatial resolution in equation 2 was therefore irrelevant. Groups of five nautical miles were used in the analyses. There was substantial interannual variation in the horizontal overlap between the species (Fig. 10). The highest overlap was in 1998 and 1999, but 2005 and 2006 were also years with high overlap. The lowest overlap was in 1995 and 1996, in addition to 2000 and 2001. The horizontal overlap increased throughout the study period and was correlated with the total biomass of herring and blue whiting (herring SSB and blue whiting TSB) (Spearmans rank correlation test, cor = 0.62, p = 0.03).

3.5 Ambient temperature

The estimates of ambient temperature for herring and blue whiting varied in May 1995-2006 (Fig. 11) and were not correlated (Spearman correlation test, $p > 0.05$). The inter-annual variation was 3.7-7.0˚C for herring compared to 4.4-5.7˚C for blue whiting. The inter-annual variation temperature was thus much higher for the herring than for the blue whiting. This partly reflects that the herring stays shallower than the blue whiting in waters with greater temperature variation. But it also reflects the greater inter-annual variation in horizontal distribution of the herring compared to the blue whiting. In particular the low ambient temperatures in May are associated with westerly distribution of the herring in 11 of the 12 years (Spearman rank correlation test, cor = 0.13-0.81, $p < 0.001$, (Figs. 11 and 12)).

4. Discussion

4.1 Horizontal distribution

4.1.1 Herring

Herring shifted its centre of gravity in ES continuously during the period from 1995 to 2006. After inhabiting south-western parts of the Norwegian Sea in the beginning of the period, the stock centre moved northeast until 2001 (Fig. 12). Thereafter the centre of gravity moved in a southwest direction again, and the stock started to separate into two components, one component outside the northern Norwegian coast and the other one in Faeroese and Icelandic waters. In ES herring fed southwest of the areas used as feeding grounds during LS, as herring have a clockwise migration pattern (Holst et al. 2002). The exception was 1998 when the population moved north-westward from ES to LS. In years with a southerly herring distribution during ES, such as in 1995 and 1996, the herring was also distributed further south during LS than in years with a northerly herring distribution during ES.

In contrast to the 1950s and 1960s when the stock was mainly feeding to the west of 5°W (Røttingen 1990), the stock mainly utilized the feeding grounds east of 5°W after the stock collapse in the late 1960s (Dragesund et al. 1997), until 2005 when a substantial part of the stock again initiated their feeding west of 5°W. Two important factors driving the migration pattern for herring is temperature and food availability (Fernö et al. 1998). Due to increasing temperatures in the Norwegian Sea, herring had the opportunity to migrate further north and west during the investigated period. This made new habitats available for herring. An alternative reason for the north-western migration of the herring stock is reduced interspecific competition with blue whiting as compared to further southeast.

4.1.2 Blue whiting

The increasing blue whiting stock extended its habitat range during the study period. The stock size increased from 1995 – 2004 due to strong recruitment, whereas the stock size decreased thereafter (ICES 2007). With a larger stock, the horizontal distribution in the Norwegian Sea during the feeding period increased. This caused blue whiting to switch from inhabiting the southern part of the Norwegian Sea to cover areas west and north in the Norwegian Sea as long as the water temperature was above 2°C at 200-300 m depth. The highest densities were found close to the continental slope supporting earlier findings (Monstad 2004), and the stock inhabited areas further southeast in ES compared to LS. This is probably related to the blue whiting stock size, as large parts of the blue whiting stock had not started feeding in the Norwegian Sea in May after spawning west of the British Iles (Bailey 1982). The stock separation documented for herring in 2005-2006 also occurred for blue whiting, with one component outside the northern Norwegian coast and another component in Icelandic and Faroese waters.

4.1.3 Mackerel

Mackerel moved northwards during the period 1995-2006, a change in distribution pattern that started already in the beginning of the 1990s (Holst & Iversen 1992). This resulted in an increased abundance of mackerel using the Norwegian Sea as a preferred feeding ground. This is most likely both due to an increased stock size and warmer water in the Norwegian Sea. A relatively strong year class was recruited to the stock in 2001, and a very strong year class in 2002 (ICES 2007). At the same time the habitat range extended further north and west, and the density increased throughout the southern and central part of the Norwegian Sea.

Mackerel migrating into the Norwegian Sea seems to prefer the central part of the warm northwards flowing Atlantic water masses with a very narrow east-west distribution. It has been speculated whether the inflow strength of Atlantic water affects the abundance of mackerel entering the Norwegian Sea (Walsh & Martin 1986). Warm Atlantic water flowing into the Norwegian Sea has high salinity, and mackerel are typical found in these water masses. The salinity might influence mackerel distribution in addition to temperature (Walsh et al. 1995), but we do not know the mechanisms involved. Swimming abilities and thus migration range increase with fish length (Nøttestad et al. 1999), and the largest fish migrate farthest north in the Norwegian Sea (Holst & Iversen 1992, Nøttestad et al. 1999). Thus, the mackerel's horizontal distribution in the Norwegian Sea is also strongly affected by the age composition of the stock. Since research vessels have a higher pelagic trawling fishing efficiency for small mackerel (Slotte et al. 2007), there was probably also an underestimation of large mackerel in the catches. This could have caused an underestimation of mackerel in the northern part of the habitat range.

Even if several of the surveys included in our study did not directly aim at mapping the horizontal distribution of mackerel, the results seem to be applicable. The surveys in 1999 and 2000 probably underestimated the abundance of mackerel since the main focus on other species. Still, mackerel was one of the target species in these surveys and the trawl hauls were taken fairly close to each other. The agreement between the LIDAR data and the catch data varied between years. This can be explained by different times of sampling and the limited extent of the LIDAR survey. The comparison supports that mackerel was underestimated in the catches taken in 1999 and 2000, as the LIDAR results for these years were not very different from the other years.

4.1.4 Stock separation

Both the herring and blue whiting stocks were separated into two components at the end of the time period. There are two likely reasons for this stock separation, difference in the age structure of the stocks and spatial differences in prey densities. Herring in Faroese and Icelandic waters were larger and older than the herring outside the northern Norwegian coast

(ICES 2003). Large and experienced herring are better than the young ones to find the best feeding locations, due to better swimming abilities (Videler 1993, Nøttestad et al. 1999) and memory of earlier feeding locations (Corten 2000). Young herring follow the more experienced individuals towards feeding areas (Mcquinn 1997), when they are large enough to keep up with the fast swimming large individuals. Young individuals probably did not have the swimming ability to follow the older herring during the long distance to Icelandic and Faroese waters, but found sufficient prey densities outside the northern Norwegian coast and remained feeding in that area. There has not been reported any similar learning behaviour for blue whiting. The blue whiting stock consisted also mainly of young individuals due to the strong fishing pressure when the stock size was high (Standal 2006). Juvenile blue whiting, which inhabit the Norwegian Sea throughout the year, probably found high prey densities off northern Norway in this period, while the adults stopped in Icelandic and Faroese waters when migrating from the spawning areas to the feeding grounds. The stock separation for both blue whiting and herring is thus probably driven by heterogeneous zooplankton densities, and the effect was magnified for herring due to demographic differences in the stock.

4.2 Overlap between the species

4.2.1 Mackerel – herring

Herring and mackerel both stay in the upper epipelagic region (Kvamme et al. 2003, Iversen 2004, Langøy et al. this issue) during LS and the vertical overlap is potentially high. However, mackerel are mainly located south of the herring stock leading to a low horizontal overlap between the species. Even when herring are located far south in LS, as it was in 1995, the species do not horizontally overlap due to east-west differences in where herring and mackerel are feeding. Our observations agree with Monstad *et al.* (1998), concluding that there was little overlap between herring and mackerel in the middle of the 1990ies. The amount of mackerel in the central Norwegian Sea has increased during the studied time period, especially since 2002. In the same period herring has gradually been feeding further north until 2003 when parts of the stock were found in Icelandic and Faroese waters, where the water temperature was too low for mackerel. Thus, the horizontal overlap between herring and mackerel has remained low throughout the study period.

4.2.2 Mackerel – blue whiting

Blue whiting were distributed far south and east in periods with low stock size, and throughout the entire Norwegian Sea when the stock size was large. The horizontal overlap between blue whiting and mackerel was therefore extensive. However, mackerel is normally found close to the surface, whereas blue whiting has a larger vertical span ranging from the surface down to >400 m (Huse et al. this issue). This variation may be explained by preferences for different temperature ranges independent of depth (Monstad 2004). Blue whiting is located high in the water column in the north-western part of the Norwegian Sea where the water is too cold at greater depths. In the eastern and southern parts of the Norwegian Sea, the water is warmer further down in the water column and blue whiting inhabit greater depths (Huse et al. submitted). Hence, even if the horizontal overlap can be considerable, blue whiting and mackerel do not occupy the same depth preventing direct overlap. The direct overlap may increase in years with large amounts of juvenile blue whiting like in the early 2000s, as juvenile are located higher in the water column than adult blue whiting (Huse et al. submitted).

4.2.3 Blue whiting – herring

Blue whiting and herring both inhabit the Norwegian Sea during the entire summer, but the degree of overlap differed between early and late summer. After spawning west of the British Islands (Bailey 1982), blue whiting enter the Norwegian Sea either east and/or west of the Faroe Island (Hátun 2007). In ES there is mainly juvenile blue whiting in the Norwegian Sea, probably mixed with some adults in the southern region. However, both juvenile and adult individuals are present in LS and are found over a larger area, especially further north and west than in ES. The low blue whiting stock size in 1995 and 1996 conceded with low horizontal spread and low overlap with herring. With increasing stock size in 1997 the horizontal distribution increased and blue whiting inhabited most of the area also used by herring, although herring was spread over a larger area. In 1998 and 1999, blue whiting and herring were concentrated in the same areas during ES, mainly in the central Norwegian Sea. In 1999, the herring stock started to migrate northwards, but a steadily growing blue whiting stock also began to inhabit the central part of the Norwegian Sea. This resulted in a high horizontal overlap both in 1998 and 1999. In 2000 and 2001 the herring had its northernmost centre of gravity during the investigated period and was mainly located northwest of the blue whiting stock, which continued to use the traditional feeding grounds in the central Norwegian Sea and along the Norwegian coast. The overlap decreased markedly compared to the previous years, and these are the years with the lowest overlap. In 2002-2004, high densities of herring in the north-western areas were not present anymore, and the stock dispersed in the north-south direction. The number of blue whiting individuals was the highest ever on record, and blue whiting was distributed across the entire Norwegian Sea. This resulted in an increased overlap with other pelagic species. In 2005 and 2006, both herring and blue whiting were abundant outside the northern Norwegian coast with low densities of both species in central areas. The overlap between herring and blue whiting therefore remained relatively high. With increasing biomass of herring and blue whiting the horizontal overlap between the species increased. This is probably caused by two factors, habitat expansion of blue whiting and a higher degree of spatial patchiness of zooplankton. As the zooplankton abundance was reduced, the fish had to aggregate in the areas which still had relatively high densities of prey. No matter the reason for the declining zooplankton abundance, it is safe to conclude that the interactions between the stocks increase with increasing fish abundance.

4.4 Range of horizontal distribution

There was a positive correlation between blue whiting TSB and the habitat range, but not between herring SSB and the habitat range. As blue whiting seems to prefer a temperature around 5°C, the vertical distribution is concentrated around water masses with this temperature. With increasing water temperatures in the Norwegian Sea, blue whiting could expand into new areas which earlier had too cold water throughout the water column. A larger blue whiting stock is expected to expand its habitat range, due to density dependent competition for food. The spatial distribution of herring is on the other hand less determined by water temperature and it is capable of concentrating in areas with high prey densities, due to memory of prior good feeding areas (Corten 2000) and social learning (McQuinn 1997, Corten 2002). Furthermore, the loosely aggregated schooling behaviour of herring during the feeding season also facilitates localization of productive areas (Blaxter 1985). The schooling dynamics of blue whiting is not yet fully understood, but individual search behaviour is assumingly more common.

4.5 Horizontal fish distribution and climate changes

Water temperature can restrict the horizontal distribution of pelagic fish in the North Atlantic and the spatial distribution of herring in the Norwegian Sea is to a large extent limited by water temperature (Melle et al. 1994, Misund et al. 1997, Misund et al. 1998). Herring prefer waters warmer than 2°C (Jakobsson & Østvedt 1999, Nøttestad et al. 2007). This could limit the access to high densities of *Calanus* sp in the colder Arctic water masses (Broms et al. 2007), but herring can tolerate lower temperatures for a short period of time, enabling them to migrate into the Arctic water masses if necessary (Østvedt 1965, Nøttestad et al. 2007) as well as in cold and deep waters (Mackinson et al. 1999). From 1995 to 2001 the centre of gravity of herring in May moved northwards. We wanted to find out if there was a relationship between the northern displacement of the herring stock and the increase in water temperature. The ambient temperature showed that herring generally stayed in the same temperature range as blue whiting, but with marked interannual variations, indicating that temperature is not that important as a driving force for herring in the Norwegian Sea. The northern displacement concurring with increasing water temperatures are probably related to changes in the horizontal distribution of prey organisms. The most important prey for herring, *C. finmarchicus* (Gislason & Astthorsson 2002), has an affinity for colder water masses (Planque & Taylor 1998). When the water temperature increases *C finmarchicus* shows a northwards displacement following the cold water and are replaced in the south by *C helgolandicus* (Planque & Fromentin 1996), which is a less favorable prey for pelagic fish.

As for herring, not only water temperature but also zooplankton abundance determines the spatial distribution of feeding blue whiting. A larger blue whiting stock needs to expand the habitat range to reduce intraspecific competition as the advantages with schooling, reduced predation risk and improved searching for prey, is low at the great depth blue whiting inhabits. Blue whiting is usually found below 200 m and is vertically distributed according to the temperature profile (Monstad & Blindheim 1986, Huse et al. submitted). The preferred temperature is 5-7°C, but blue whiting tolerates temperatures between 0-8°C in the Nordic

Seas (Monstad & Blindheim 1986), although it seems to avoid temperatures below 2°C (Blindheim et al. 1971, Blindheim & Jakupsstovu 1976). Even though the habitat range increased with increasing blue whiting stock size, the use of areas further north did not influence the ambient temperature. The standard deviation of the ambient temperature in 2004, when the stock size was near its maximum level (ICES 2008), was one of the lowest (1.18°C) during the whole time series, indicating that blue whiting did not have to migrate into too cold water even though the intraspecific competition was high. It can be concluded that blue whiting usually stays in water masses around 5 °C irrespective of depth but may be found in colder or warmer waters depending on spatial differences in prey abundance. Increasing water temperature allows blue whiting to expand its habitat range.

Although Castonguay *et al.* (1992) observed mackerel in the Gulf of St Lawrence in water masses as low as 0°C, mackerel generally avoid temperatures below 8°C, and stays in the warm upper water layers with high concentration of zooplankton during the feeding period (Iversen 2004). The horizontal distribution maps show a clear preference for "warm" water with the main parts of the stock staying in waters well above 8°C. However, mackerel was caught in colder waters in 1998, 2005 and 2006. By cross-checking the catch positions with the temperature atlas file, mackerel were recorded in waters down to 6-6.5°C these years. In 2005, and to some extent 2004, the trawling stations did not seem to cover the whole horizontal distribution, especially in colder western and northern waters. The trawling coverage was better in 2006, and the horizontal distribution was limited by water colder than 6°C northern and western areas. As the Norwegian Sea gradually got warmer during the study period, larger thermal habitats became available for mackerel. As for herring, mackerel will also find the best feeding areas further north when areas with high density of prey organisms shifted gradually northwards. In the time period 1995-1998 only very low densities of mackerel was found in the central and northern Norwegian Sea, although the water temperatures were high enough for mackerel in this area. As the zooplankton abundance in the Norwegian Sea was high in this period (Anon 2009), we suggest that mackerel found good feeding condition in the south making it unnecessary to migrate further north. As the overall zooplankton abundance has decreased in the Norwegian Sea the last 10 years (Anon 2009), mackerel had to migrate further north to find suitable feeding areas. Mackerel is a fast swimming predator (Iversen 2004) and able to feed on smaller prey than herring (Prokopchuk & Sentyabov 2006, Langøy et al. this issue). Thus, mackerel could still feed in the central and southern parts of the Norwegian Sea but to reduce intraspecific competition parts of the stock migrated further north and west. In recent years we have seen a substantial western expansion of the feeding area of mackerel, which probably results from a combination of the increased temperature in the waters around Iceland and low abundance of prey in most of the central and western parts of the Norwegian Sea.

As a conclusion, the main pelagic fish stocks in the Norwegian Sea migrated northwards in the period 1995-2006 for two reasons. First, the increasing pelagic fish stocks needed to increase their habitat range to reduce intraspecific competition when the zooplankton abundance decreased. Warmer waters enabled the species to migrate north and westwards using a larger part of the Norwegian Sea during the feeding period. Secondly, the distribution of *C finmarchicus* shifted northwards due to its affinity for colder waters causing the fish to follow its most important prey. This main conclusion is partly in agreement with Perry et al. (2005) who stated that a northern displacement of both demersal and pelagic fish have occurred in the North Sea due to increased temperatures.

4.6 Acknowledgements

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Table 1. Number of surveys for each of the two summer periods (May and July/August) for the respective species; Norwegian springs-spawning herring, northeast Atlantic blue whiting and northeast Atlantic mackerel. Most surveys were targeted for NSS herring, but blue whiting was also focused.

Year	Early summer		Late summer		
	Herring	Blue whiting	Herring	Blue whiting	Mackerel
1995	4	3	2	2	2
1996	2	1	1	1	2
1997	3	3	1	1	2
1998	3	3	1	1	2
1999	3	3	1	1	1
2000	3	3	1	1	1
2001	3	3	3	3	4
2002	3	3	2	2	3
2003	3	3	1	1	3
2004	3	3	0	0	2
2005	4	4	0	0	2
2006	3	3	0	0	2

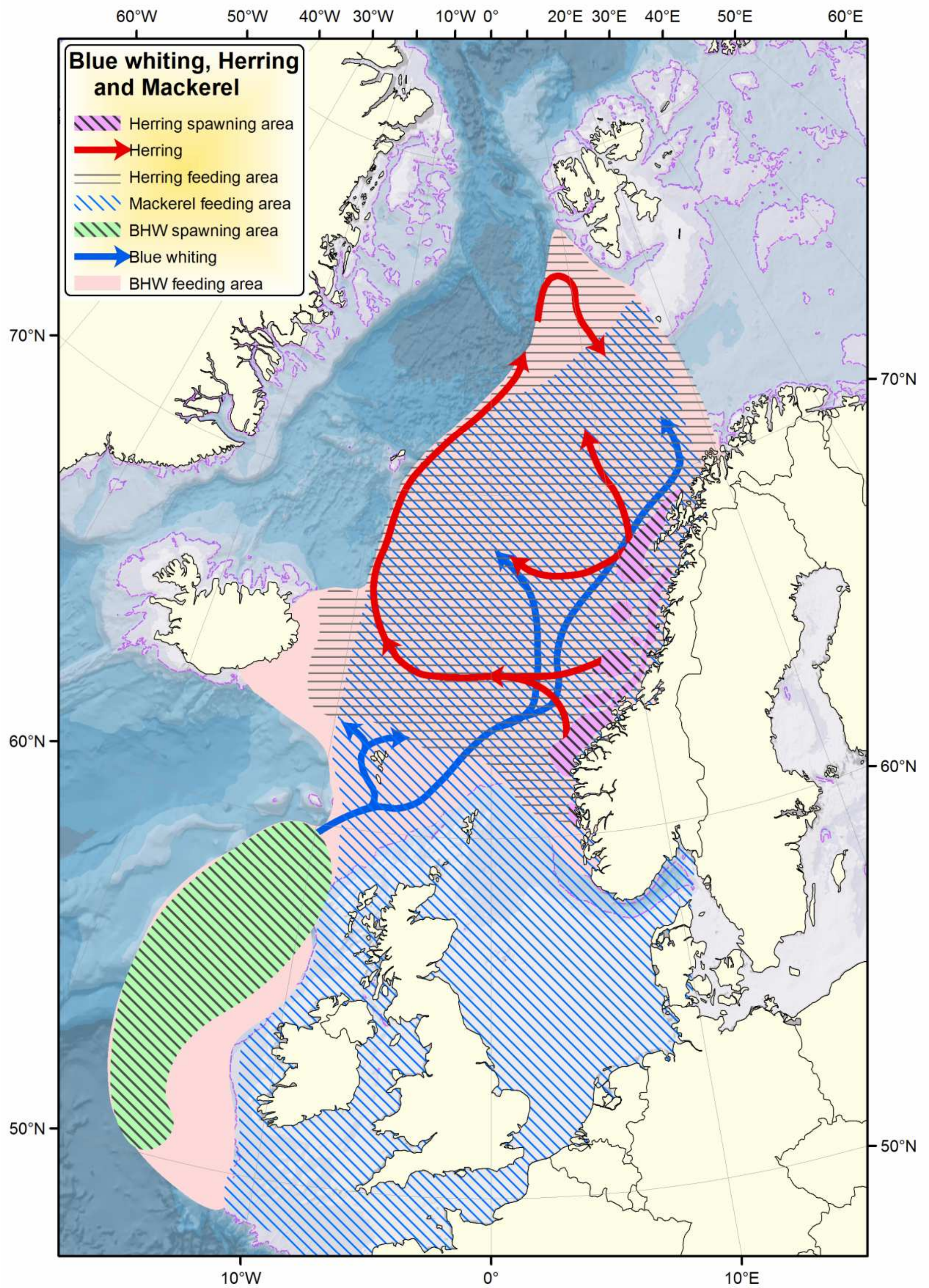

Figure 1. Schematic horizontal distributions of pelagic fish species in the Nordic Seas and their different long-distance migration patterns.

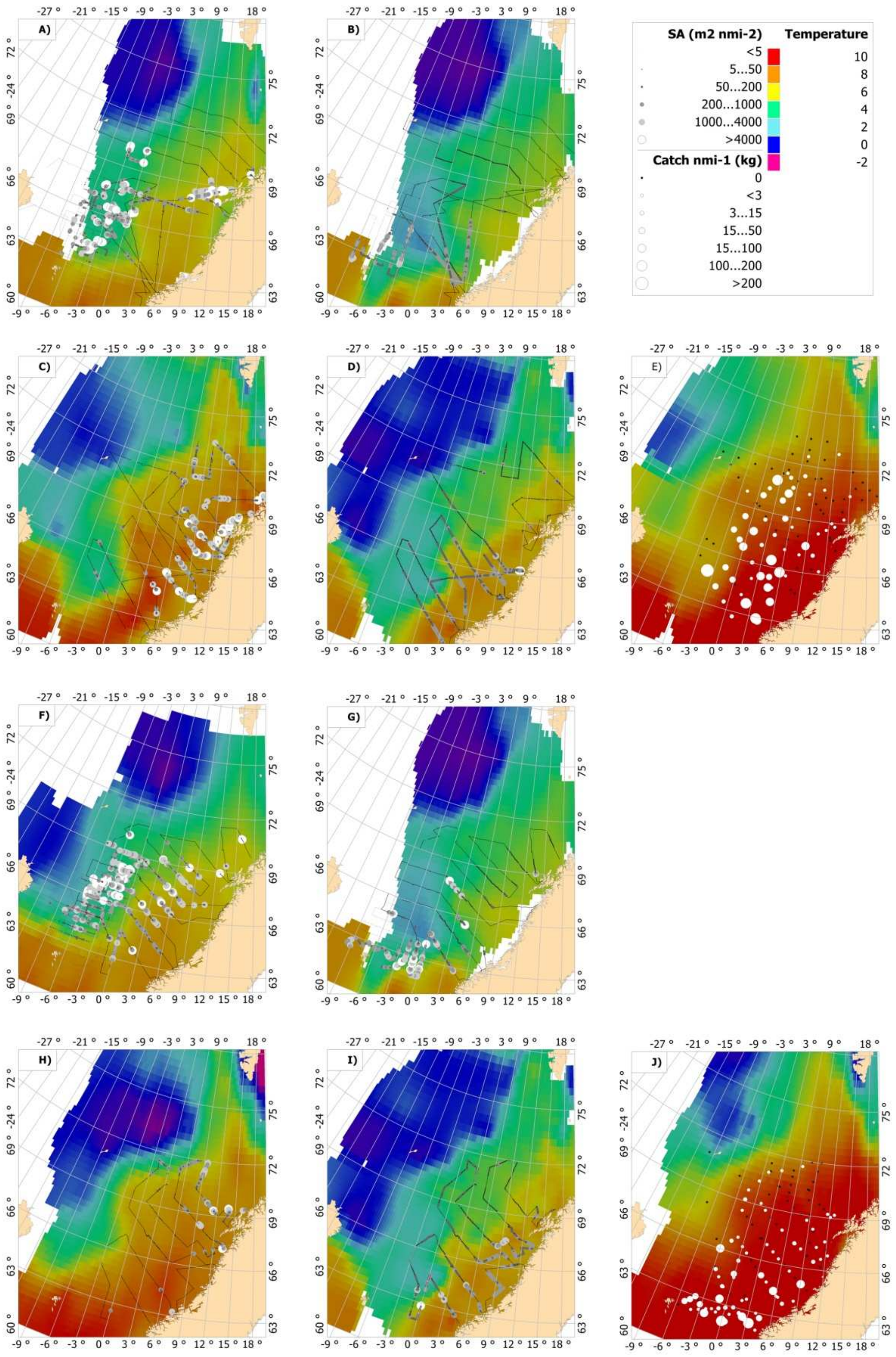

Figure 2. Horizontal distribution of A) herring ES 1995, B) blue whiting ES 1995, C) herring LS 1995, D) blue whiting LS 1995, E) mackerel LS 1995, F) herring ES 1996, G) blue whiting ES 1996, H) herring LS 1996, I) blue whiting LS 1996, J) mackerel LS 1996.

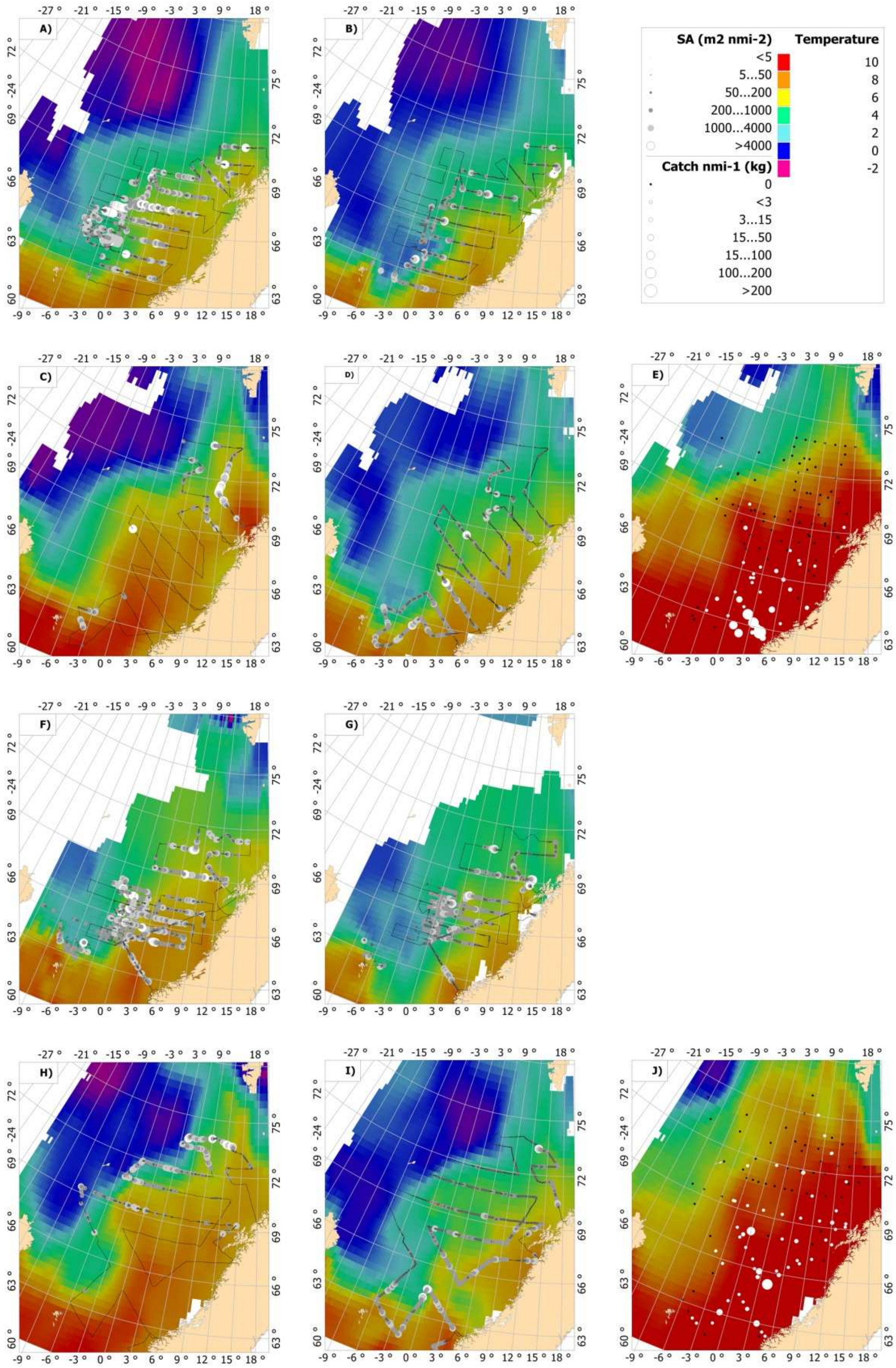

Figure 3. Horizontal distribution of A) herring ES 1997, B) blue whiting ES 1997, C) herring LS 1997, D) blue whiting LS 1997, E) mackerel LS 1997, F) herring ES 1998, G) blue whiting ES 1998, H) herring LS 1998, I) blue whiting LS 1998, J) mackerel LS 1998.

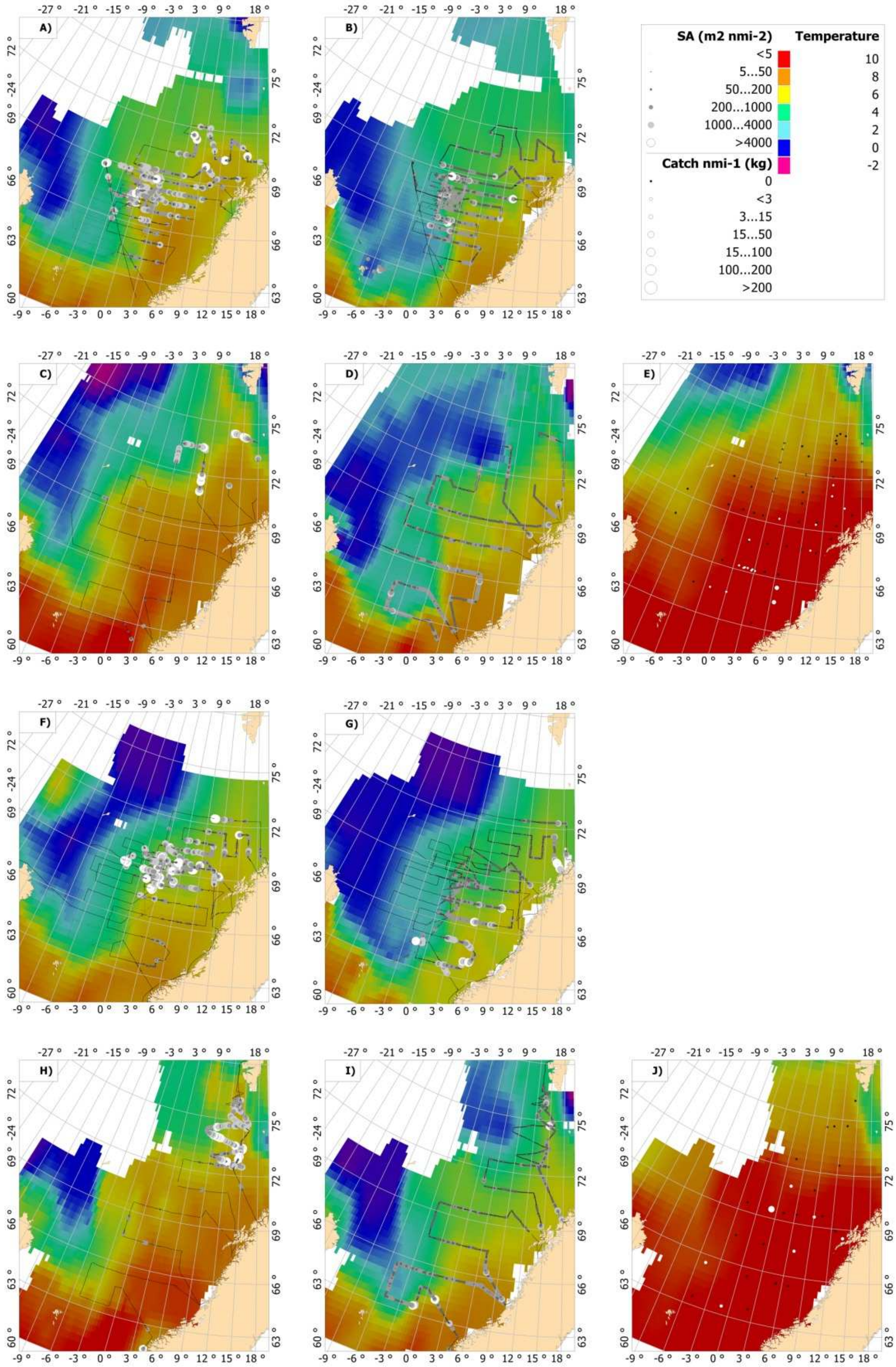

Figure 4. Horizontal distribution of A) herring ES 1999, B) blue whiting ES 1999, C) herring LS 1999, D) blue whiting LS 1999, E) mackerel LS 1999, F) herring ES 2000, G) blue whiting ES 2000, H) herring LS 2000, I) blue whiting LS 2000, J) mackerel LS 2000.

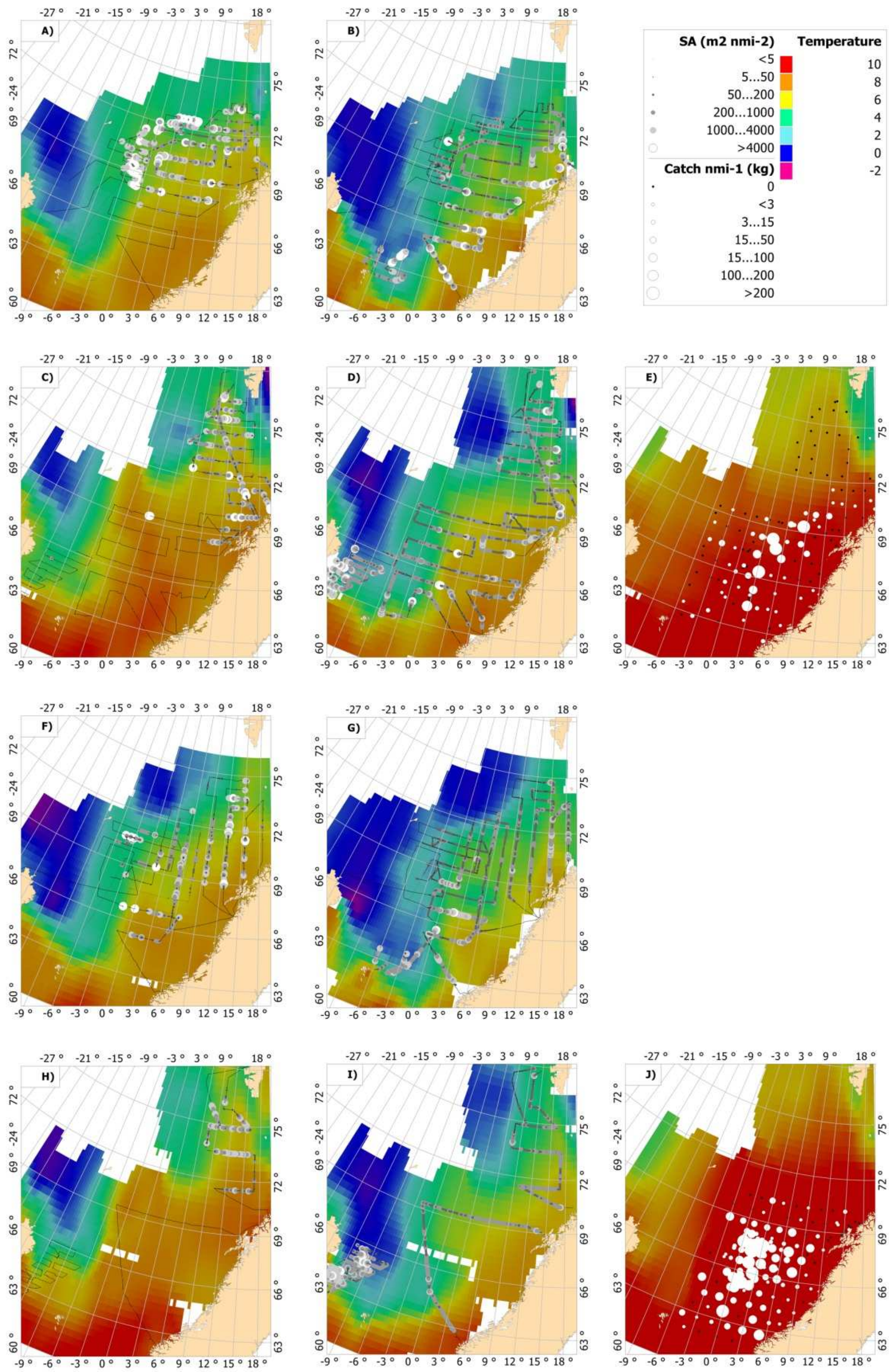

Figure 5. Horizontal distribution of A) herring ES 2001, B) blue whiting ES 2001, C) herring LS 2001, D) blue whiting LS 2001, E) mackerel LS 2001, F) herring ES 2002, G) blue whiting ES 2002, H) herring LS 2002, I) blue whiting LS 2002, J) mackerel LS 2002.

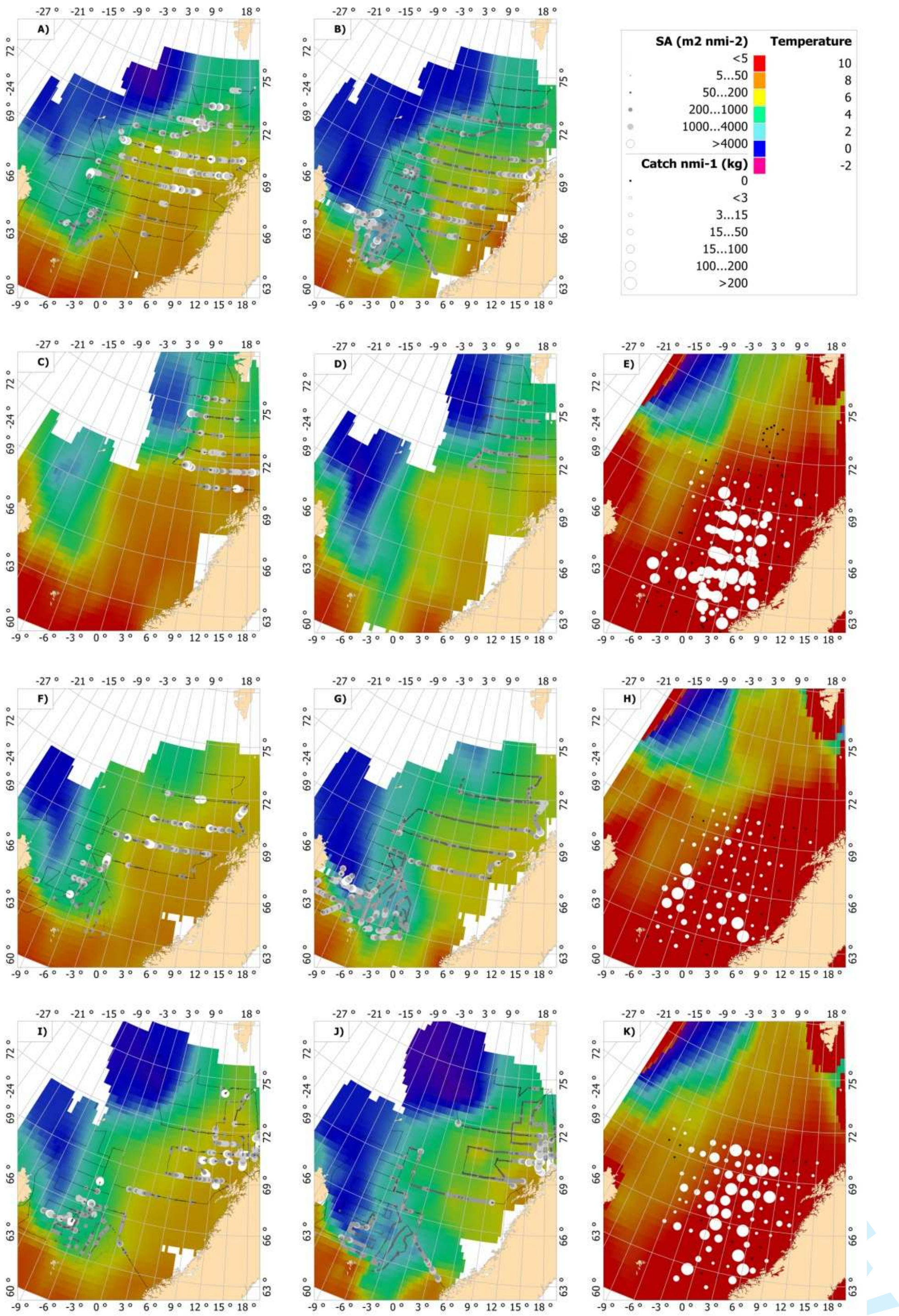

Figure 6. Horizontal distribution of A) herring ES 2003, B) blue whiting ES 2003, C) herring LS 2003, D) blue whiting LS 2003, E) mackerel LS 2003, F) herring ES 2004, G) blue whiting ES 2004, H) mackerel LS 2004, I) herring ES 2005, J) blue whiting ES 2005, K) mackerel LS 2005.

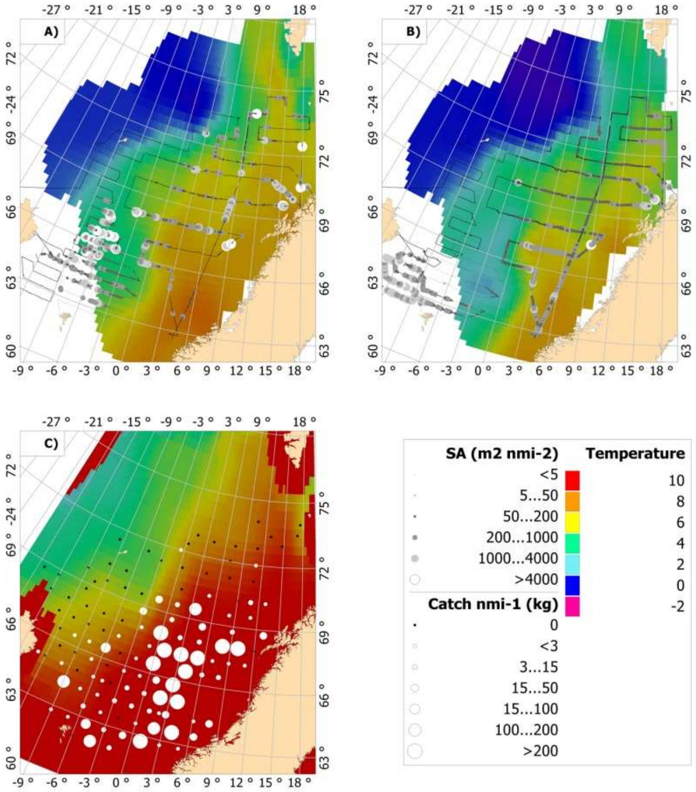

Figure 7. Horizontal distribution of Norwegian spring-spawning (NSS) herring, blue whiting and mackerel in 2006, A) herring ES 2006, B) blue whiting ES 2006, C) herring LS 2006,

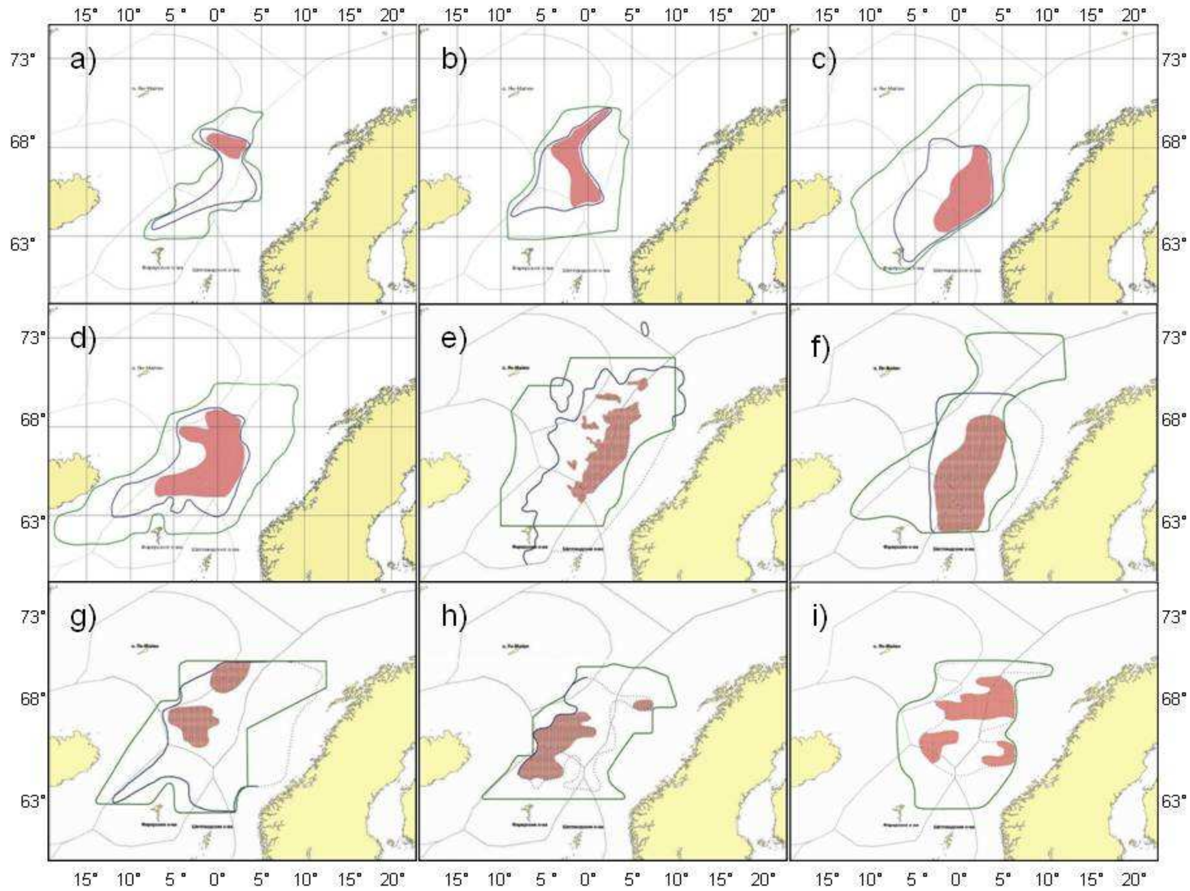

Figure 8. Horizontal distribution of mackerel in June-August; a) 1997, b) 1998, c) 1999, d) 2000, e) 2001, f) 2002, g) 2003, h) 2004, i) 2005, as measured by LIDAR in Russian aerial surveys. Main concentration of mackerel (shaded red area), boundary of the mackerel distribution (blue line) and boundary of the area surveyed (green line) shown.

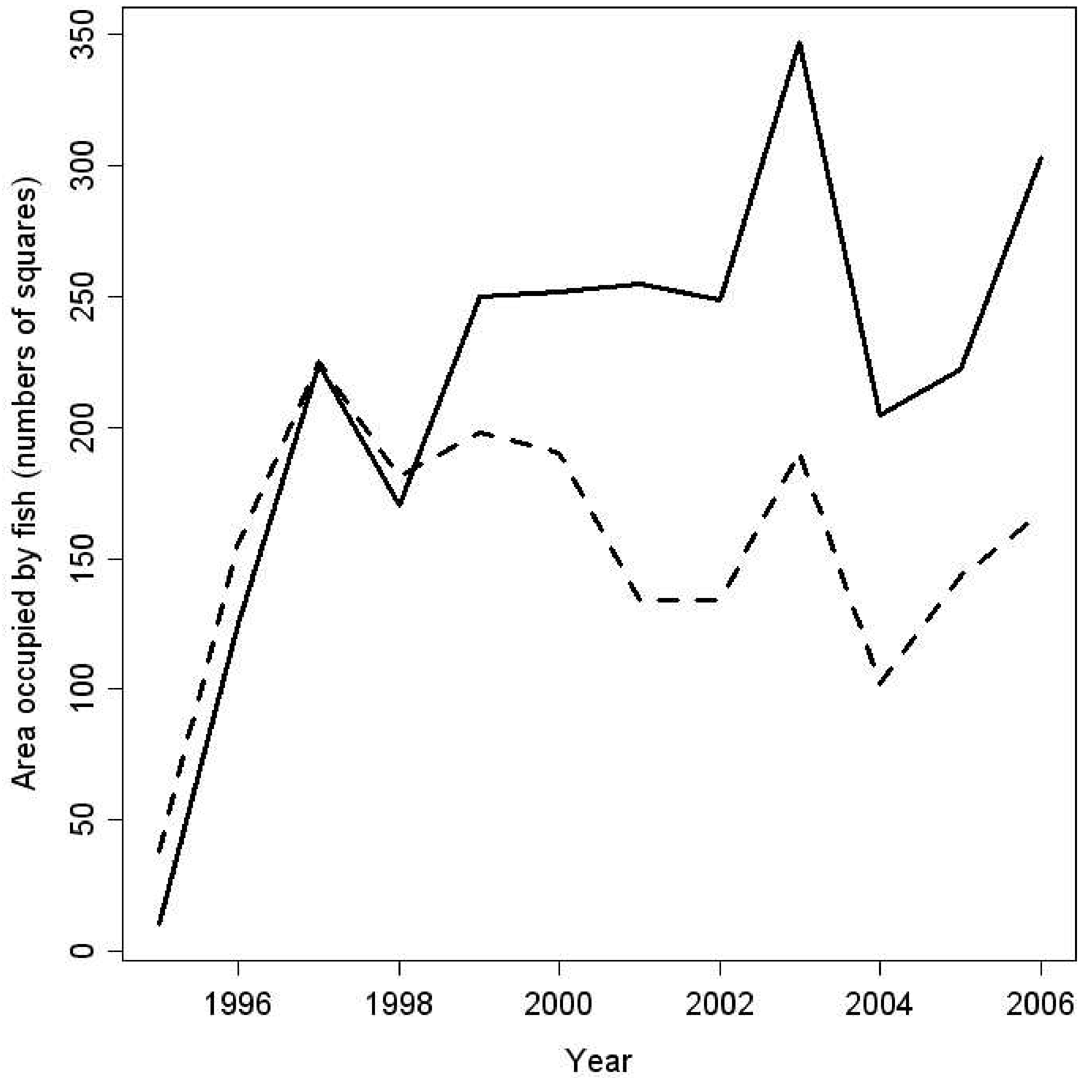

Figure 9. Number of squares (1/2 longitude, 1/3 latitude) with recordings of NSS herring (dashed line) and blue whiting (solid line). One Norwegian survey shown for each year 1995-2006.

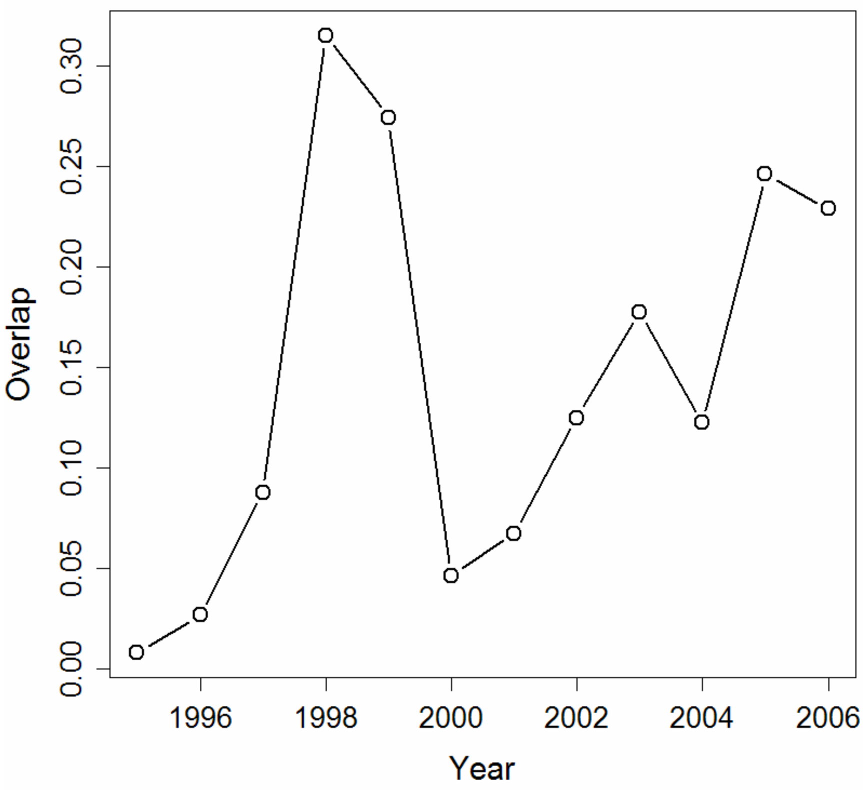

Figure 10. Development of the Morisita simplified overlap index for the horizontal overlap between NSS herring and blue whiting for 1995-2006.

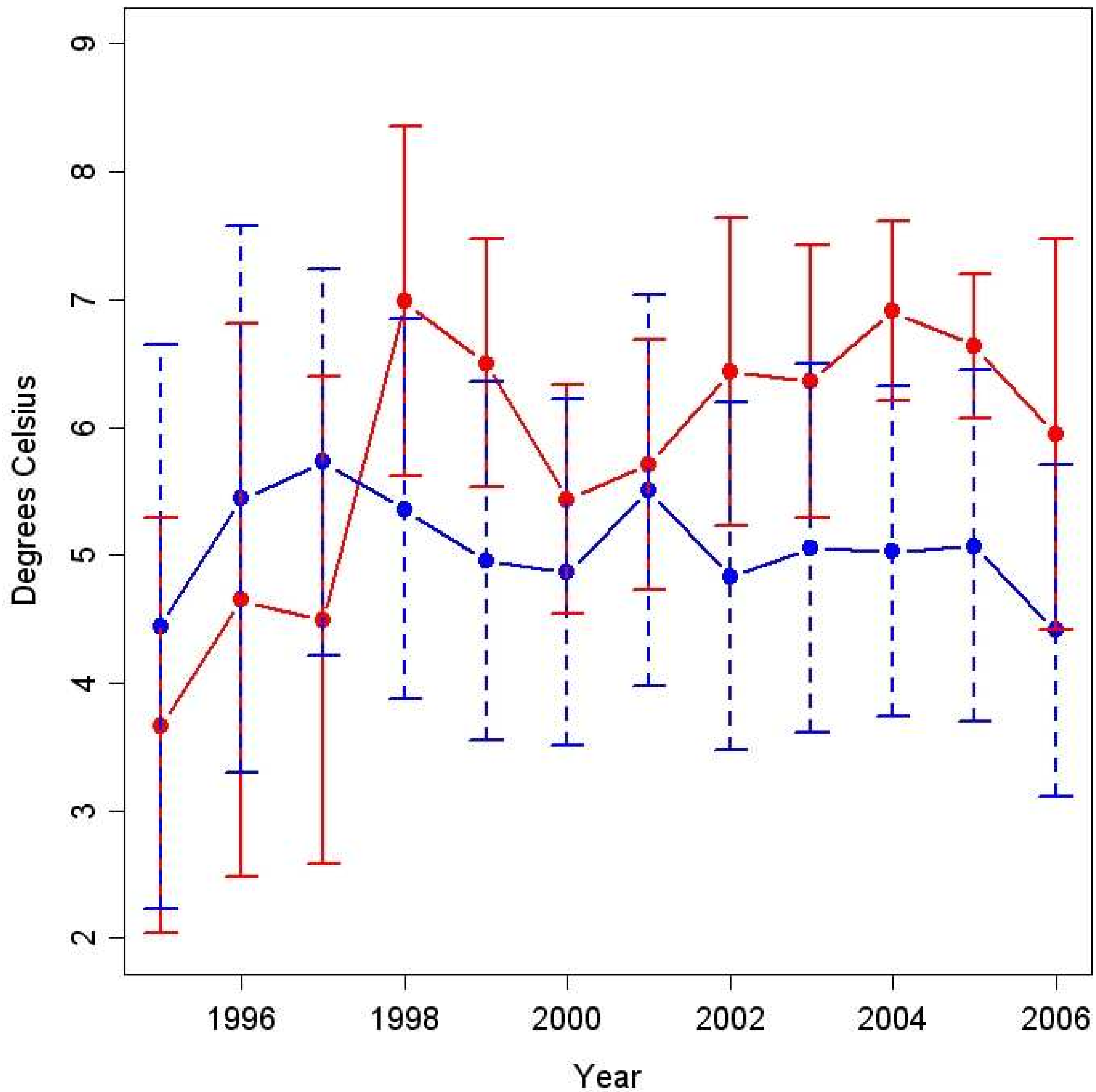

Figure 11. Ambient temperature for herring (red line) and blue whiting (blue line) with standard deviation (SD) in May 1995-2006.

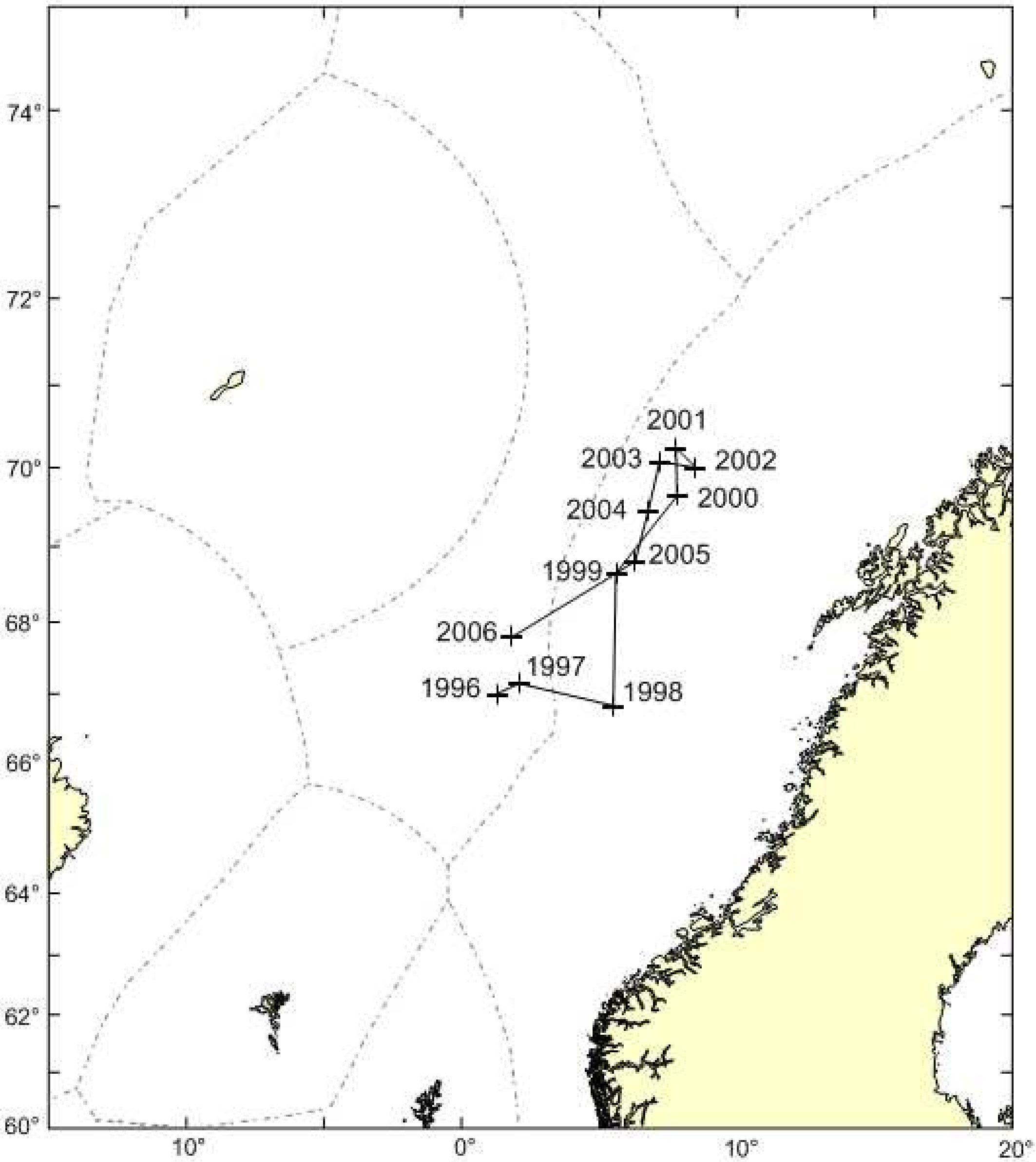

Figure 12. Centre of gravity for herring during 1996-2006 derived from acoustic values. Figure modified from ICES (2006).

APPENDIX

Table A.1. Overview of surveys with acoustic registrations used in the presentation of herring and blue whiting horizontal distribution.

Year	Vessel	Time, ES	Time, LS
1995	RV "G.O.Sars"	18 - 27 April	
	RV "G.O.Sars"	26 May - 22 June	
	RV "Árni Fridriksson"	11 - 28 May	
	RV "B. Saemundsson"	24 April - 2 May	
	RV "G.O.Sars"		29 July - 15 Aug
	RV "Johan Hjort"		7 July - 2 Aug
1996	RV "G.O.Sars"	29 April - 28 May	
	RV "Magnus Heinason"	03 - 21 May	
	RV "Árni Fridriksson"	3 - 29 May	
	RV "G.O.Sars"		19 July - 15 Aug
1997	RV "Magnus Heinason"	1 - 21 May	
	RV "Árni Fridriksson"	2 - 27 May	
	RV "G.O.Sars"	1 May - 1 June	
	RV "G.O.Sars"		20 July - 17 Aug
1998	RV "G.O.Sars"	21 April - 21 may	
	RV "Árni Fridriksson"	5 - 29 May	
	RV "Magnus Heinason"	1 - 19 May	
	RV "Johan Hjort"		30 June - 29 july
1999	RV "G.O.Sars"	28 April - 2 June	
	RV "Magnus Heinason"	30 April - 25 May	
	RV "Árni Fridriksson"	5 - 22 May	
	RV "Johan Hjort"		15 July - 9 Aug
2000	RV "G.O.Sars"	28 April - 2 June	
	RV "Magnus Heinason"	6 - 28 May	
	RV "Árni Fridriksson"	8 - 26 May	
	RV "G.O.Sars"		20 July - 17 Aug
2001	RV "Johan Hjort"	3 - 28 may	
	RV "Magnus Heinason"	2 - 27 May	
	RV "Árni Fridriksson"	25 May - 8 June	
	RV "G.O.Sars"		19 July - 12 Aug
	RV "Johan Hjort"		21 July - 19 Aug
	RV "Árni Fridriksson"		17 July - 30 Aug
2002	RV "G.O.Sars"	25 April - 29 May	
	RV "Magnus Heinason"	15 - 28 May	
	RV "B. Saemundsson"	22 - 28 May	
	Icelandic Survey		19 - 30 July
	"RV G.O.Sars"		27 July - 15 Aug
2003	"RV G.O.Sars"	24 April - 10 June	
	RV "Magnus Heinason"	30 April - 28 May	

	RV "Árni Fridriksson"	21 - 29 May	
	RV "G.O.Sars"		25 July - 14 Sep
2004	RV "G.O.Sars"	2-27 May	
	RV "Magnus Heinason"	28 April - 26 May	
	RV "Árni Fridriksson"	22 May - 3 June	
2005	RV "G.O.Sars"	28 April - 5 June	
	RV "Magnus Heinason"	3 - 17 May	
	RV "Árni Fridriksson"	10 - 31 May	
	RV "Johan Hjort"	10 May - 8 June	
2006	RV "G.O.Sars"	27 April - 1 June	
	RV "Magnus Heinason"	3 - 17 May	
	RV "Árni Fridriksson"	9 May - 1 June	

Table A.2. Overview of surveys with mackerel catches used in the presentation of mackerel distribution. The trawl column show number of trawl hauls taken and the number of trawl hauls with mackerel catches.

Year	Vessel	Time	Trawl	Survey purpose
1995	RV "G.O. Sars"	29 July-15 Aug	18/59	Pelagic fish survey
	RV "Johan Hjort"	7 July - 2 Aug	42/95	PGNAPES-survey, pelagic fish
1996	RV "G.O. Sars"	19 July-15 Aug	54/131	Pelagic fish survey
	RV "Johan Hjort"	4 June-19 July	18/44	Mackerel migrations
1997	RV "G.O. Sars"	20 July-17 Aug	27/110	Pelagic fish survey
	RV "Johan Hjort"	19 June - 16 July	10/42	Salmon and mackerel survey
1998	RV "Johan Hjort"	30 Jun-29 July	42/117	Pelagic fish survey
	RV "Johan Hjort"	1 Aug- 23 Aug	12/23	? Greenland Sea/ Norwegian Sea
1999	RV "G.O. Sars"	21 July- 21 Aug	18/64	PGNAPES-survey, pelagic fish survey
2000	RV "G.O. Sars"	20 July-15 Aug	7/27	PGNAPES-survey, pelagic fish survey
2001	RV "G.O. Sars"	19 July- 12 August	30	Pelagic fish survey
	RV "Johan Hjort"	1-17 June	5	Salmon and mackerel survey
	RV "Johan Hjort"	21 July-19 Aug	11	PGNAPES-survey, pelagic fish survey
	CV "Selvåg Sen."	2-8 August	15	Pelagic fish survey
2002	RV "Johan Hjort"	20 June - 6 July	50	Salmon and mackerel survey
	CV "Narvik"	15 - 26 July	36	Mackerel survey to support LIDAR
	CV "Trønderbas"	15-28 July	28	Mackerel survey to support LIDAR
2003	RV "Johan Hjort"	22 June - 6 July	66	Salmon and mackerel survey
	CV "Endre Dyrøy"	15 - 30 July	42	Mackerel survey to support LIDAR
	CV "Kings Bay"	17 - 30 July	30	Mackerel survey to support LIDAR
2004	CV "Endre Dyrøy"	18 - 29 July	39	Ecosystem survey, pelagic fish included
	CV "Libas"	19 - 29 July	33	Ecosystem survey, pelagic fish included
2005	CV "Møgsterbas"	16 - 29 July	34	Ecosystem survey, pelagic fish included
	CV "Libas"	17 July - 11 Aug	49	Ecosystem survey, pelagic fish included
2006	CV "Endre Dyrøy"	16 July - 4 Aug	36	Ecosystem survey, pelagic fish included
	CV "Libas"	15 July - 11 Aug	41	Ecosystem survey, pelagic fish included