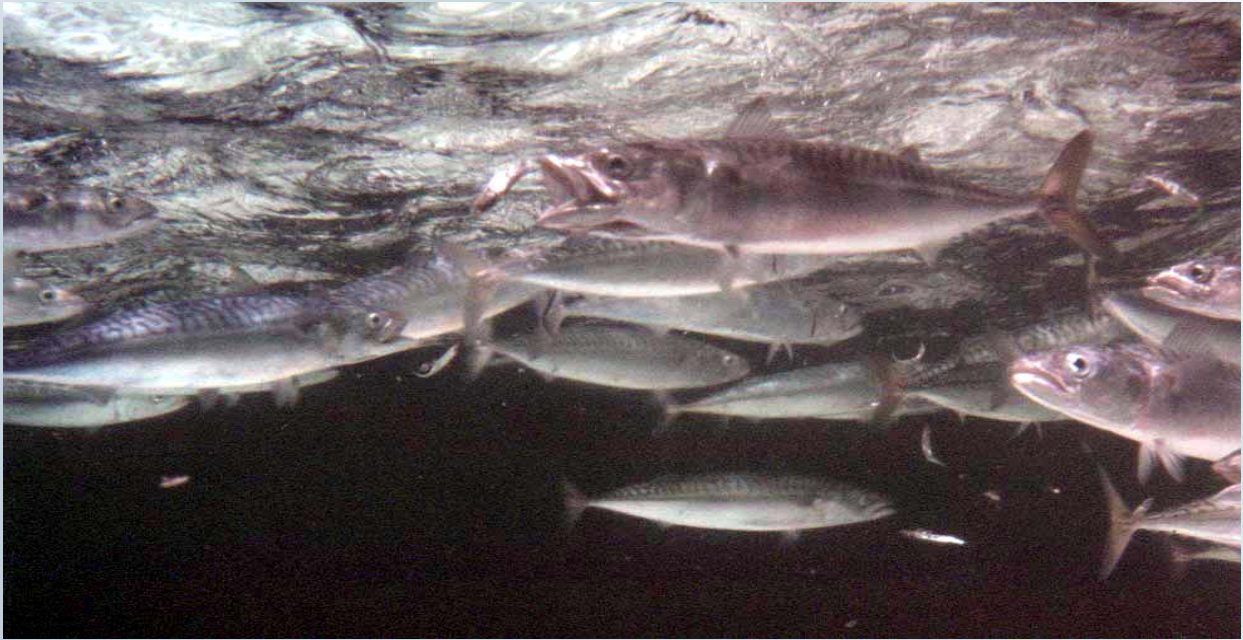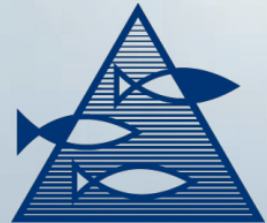# SCHOOLING DYNAMICS OF SUMMERTIME MIGRATING NORTHEAST ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) IN THE NORWEGIAN SEA USING MULTIBEAM SONAR

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Feeding mackerel school at the surface. Photo: T.G. McInnes, British Marine Life Study Society
M/V "Brennholm". Photo: Justine Diaz

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Abstract

Pelagic fish in the Norwegian Sea perform seasonal migrations from overwintering, via spawning, to feeding grounds. Northeast Atlantic (NEA) mackerel (*Scomber scombrus*) are highly migratory, fast-swimming, and an obligate schooling fish. The schooling dynamics of NEA mackerel in nature is largely unknown because they lack a swimbladder, resulting in a weak acoustic signature, and therefore are difficult to detect in the summer when swimming in loose school formations. However, high frequency omnidirectional SONAR (SOund Navigation And Ranging) is capable of detecting NEA mackerel in the acoustic echosounder blind zone close to the surface. Acoustic, biological, and temperature data were used to study the schooling dynamics of NEA mackerel in relation to temperature, zooplankton abundance and density of conspecifics in four geographically separate regions of the Norwegian Sea during summer. These results show that there were regional differences in fish size, swimming speed and direction, school depth, temperature and zooplankton abundance. The thermocline depth had a profound influence on the depth distribution of schools throughout the Norwegian Sea during summer. NEA mackerel were consistently found shallower than 40 m depth where the temperature was at least 6° C. The fish generally swam north except for in the SW region, coinciding well with prevailing current directions. Fish were significantly larger in the north than in the south, and plankton abundance was higher in the west than in the east. The observed school dynamics in relation to abiotic and biotic factors are explained in terms of the ecology of NEA mackerel during the summer feeding migration.

Keywords: schooling, NEA mackerel, Norwegian Sea, feeding, behaviour, multibeam SONAR

Contents

Introduction

Background

The Norwegian Sea is a large feeding ground and migration highway for highly abundant stocks of pelagic fish during their feeding migration in the late spring and summer months (Skjoldal *et al.* 2004; Huse *et al.* 2012; Utne *et al.* 2012). Major commercial species in this area are NEA mackerel (*Scomber scombrus* L.), Norwegian spring-spawning (NSS) herring (*Clupea harengus* L.) and blue whiting (*Micromesistius poutassou*) (Iversen *et al.* 2004; Holst *et al.* 2004; Monstad 2004). Long distance migrations and extensive distributions are key features of these and other pelagic planktivorous fish species (Nøttestad *et al.* 1999; Skjoldal *et al.* 2004). Pelagic fish stocks can be exceptionally abundant, consisting of several million tonnes and billions of individuals, and may have a great impact on the ecosystem by depleting large amounts of zooplankton (e.g. Ayón *et al.* 2008; Huse *et al.* 2012; Langøy *et al.* 2012; Utne *et al.* 2012). Migrating species, such as NEA mackerel, are important components in the food web; as major predators and prey (Iversen 2002; 2004) and competitors with other pelagic fish species (Prokopchuk and Sentyabov 2006; Huse *et al.* 2012; Langøy *et al.* 2012). They also contribute to shifting nutrients across great distances from open oceans to coastal waters (Dragesund *et al.* 1997; Varpe *et al.* 2005). The NEA mackerel stock in 2010 was estimated to be 4.5 million tonnes from trawl catches and swept area calculations north of 62° N (Nøttestad *et al.* 2010). The official spawning stock biomass according to ICES was 2.9 million tonnes (ICES 2012). Presently, neither hydro-acoustic methods with SONAR and echosounder nor the swept area methodology based on standardized pelagic trawling are properly evaluated and accepted as quantitative input series to the ICES mackerel assessment. Nevertheless, the results indicate a strong and robust mackerel population steadily increasing in the Norwegian Sea in summer (Nøttestad *et al.* 2013). This is partly a result of record high recruitment from the 2002, 2005 and 2006 year classes, coinciding with record high sub-surface temperatures (Nøttestad *et al.* 2013). However, zooplankton concentrations are steadily declining in the Norwegian Sea (Huse *et al.* 2012; ICES 2012; Utne *et al.* 2012).

Biology of NEA mackerel

Many pelagic fish species migrate annually from overwintering, via spawning, to feeding areas during their lifetime (Harden Jones 1968; Arnold and Cook 1984; Dingle 1996). NEA mackerel is a fast swimming pelagic fish with high endurance that is highly migratory, performing summer feeding migrations northwards from the spawning grounds around 40 -

60° N to 72° N via the Norwegian Sea, but has also been recorded north to 73° N (Holst and Iversen 1992; Iversen 2004) and even up to 75° N (Nøttestad *et al.* 2010). The distribution and abundance of NEA mackerel in this area has presumably varied considerably over the years and during the last decades depending on sea temperature and feeding conditions (Iversen 2004; Utne *et al.* 2012). Iversen (2004) stated that NEA mackerel prefer sea temperatures of 8° C or warmer; however, on the western side of the North Atlantic, mackerel were found to prefer to waters of at least 7° C along the east coast of North America (Castonguay *et al.* 1992). They have even been recorded down to 0° C in the Gulf of Saint Lawrence (Castonguay *et al.* 1992). NEA mackerel mainly occur in the upper 40 m of the water column during summer (Godø *et al.* 2004) and rely on light when selectively feeding on the later copepodite stages (IV-VI) of Calanoid copepods, in particular, *Calanus finmarchicus* (Iversen 2004; Prokopchuk and Sentyabov 2006; Langøy *et al.* 2012). Higher latitudes provide extended daylight hours and higher production of phyto- and zooplankton in spring and summer, and therefore, longer available feeding period for these visual feeders (Nøttestad *et al.* 1999). However, NEA mackerel are known to hunt their prey by active particulate feeding and passively filter feeding while swimming with their mouths wide open. Passive filter feeding contributes to effective plankton feeding when in less aggregated prey concentrations, and at the same time enables fish to pass more water over the gills for improved oxygen uptake needed for rapid, constant swimming (Macy *et al.* 1998; Iversen 2004).

Currents in the Norwegian Sea

The Norwegian Sea is bound by the warmer northerly Atlantic and coastal currents to the east and by the cooler southerly Arctic front to the west (Figure 1). Oceanic currents transport zooplankton, but also enforce temperature barriers. The Atlantic and coastal currents drive warm southern water up along the Norwegian coast, while the Arctic front distributes the cold Arctic water towards the surface in the western Norwegian Sea. The Gulf Stream brings warm water up the coast of Norway and cold Arctic water is brought south at the western border of the Norwegian Sea (Blindheim 2004; Skjoldal et al. 2004; Figure 1).

Energetic costs of migration can be offset by swimming with the tidal currents (Nøttestad *et al.* 1999, Godø *et al.* 2004) or taking advantage of gyres and eddies in the Norwegian Sea and along the Norwegian coast (Godø *et al.* 2012). Castonguay and Beaulieu (1993) found that mackerel utilized the tidal streams at flood tide and high tide to reach their spawning grounds

off the northeast coast of North America, and refer to this behaviour as "selective tidal stream transport" (STST). Larval organisms passively utilize the tidal streams for transportation (Castonguay and Gilbert 1995), but whether this continues into adulthood for the summer feeding migration is unknown.
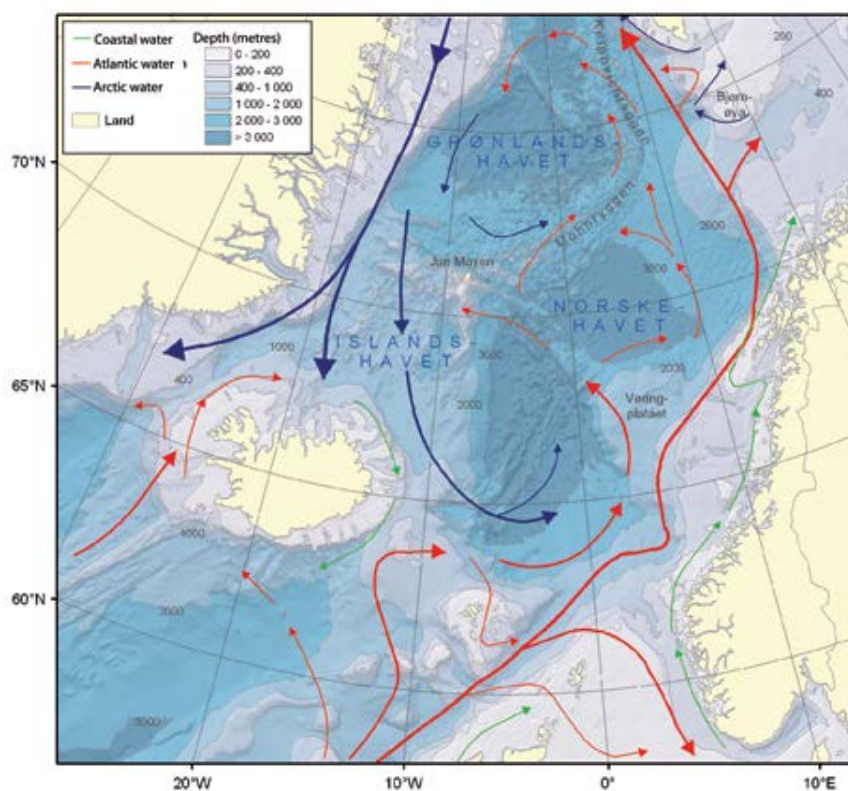

Figure 1. Coastal and oceanic water masses flowing through the Norwegian Sea and surrounding waters (Institute of Marine Research/Norwegian Coastal Administration).

Advantages of schooling

Schooling is common in pelagic fishes, and mackerel are a known obligate schooler (van Olst and Hunter 1970; Parrish *et al.* 2002). Numerous studies have been conducted on the schooling dynamics of NSS herring with regards to their macro- and meso-scale distributions (horizontal and vertical), school size, swimming speed and direction, feeding behaviour and diurnal behaviour (e.g. Misund 1993; Mackinson *et al.* 1999). These studies provide baselines for comparisons with mackerel, considering that they are also a pelagic migrating species, and thus probably exhibit similar schooling dynamics. The advantages of schooling for small planktivores include: improved hydrodynamics, enhanced food finding and protection from predators (Pitcher and Parrish 1993; Parrish and Edelstein-Keshet 1999; Krause and Ruxton 2002). Individual fish within a school modify their behaviour on a second to second basis based on individual needs, and observed behaviours are collected and linked from meters to

kilometres (Mackinson *et al.* 1999; Nøttestad *et al.* 2004). Adaptive responses to the environment contribute to the short-term gain for the individual and the long-term function of the group (Parrish *et al.* 2002). The "optimal school size" concept aims for a maximised net benefit through a balance of costs and benefits (Pitcher and Parrish 1993; Krause and Ruxton 2002). Unfortunately, the "optimal school size" is naturally unstable and determined by the balance of trade-offs to individuals within the group, where size of the group affects its performance (Clark and Mangel 1986; Parrish and Edelstein-Keshet 1999; Hoare *et al.* 2000). The spatial organization of schools also varies between spawning and feeding migrations (Nøttestad *et al.* 1996, Fernö *et al.* 1998; Nøttestad *et al.* 2007). When feeding tendency is strong and predation risk is low, schools are likely to split up and become loosely aggregated (Pitcher and Parrish 1993).

NEA mackerel are a long-lived species with a lifespan of more than 20 years (Iversen 2004), suggesting that mackerel prioritize potentially threatening situations over feeding when neccessary, as has been discussed for herring (Fernö *et al.* 1998). Individual NEA mackerel, and NSS herring, form large, dense schools to reduce their individual predation risk from whales and other predators through a dilution effect (Misund 1993; Vabø and Nøttestad 1997; Nøttestad *et al.* 2002; 2004). Diel vertical migration (DVM) from deep waters during day time to shallow water at night is a widespread behavioural strategy in the pelagic habitat (Huse and Korneliussen 2000; Holst *et al.* 2004). DVM is common in pelagic fishes to provide protection from predators by hiding in the deeper waters during the day (Nøttestad *et al.* 2002), but it is also a mechanism of following prey that also performs regular DVM.

Sampling methods

Presently, little information exists regarding the behaviour of NEA mackerel because they are difficult to detect with acoustic equipment when in small, loose schools near the surface of the water because they have no swimbladder (Tenningen *et al.* 2003; Simmonds and MacLennan 2005). Thus, the low acoustic back-scattering from lack of a swimbladder complicates proper quantification of abundances of mackerel from echosounder technology (Korneliussen and Ona 2004; Korneliussen 2010). Omnidirectional SONAR has been used successfully in the past to record migratory behaviour of schooling fish (Godø et al. 2004; Nøttestad *et al.* 1996; 2004; Brehmer *et al.* 2006; Nøttestad et al. 2007). Small schools close to the surface are located in the echosounder acoustic blind zone (a region where fish are above the sampling range of the acoustic beam). High-frequency, long range omnidirectional SONAR have better

resolution and mackerel school detection because the transducer is smaller than a low-frequency transducer (Simrad), thereby facilitating studies of mackerel behaviours (Totland *et al.* 2009).

Aims and objectives

The main objective of this thesis was to analyse the distribution, depth, swimming speed and direction, school size and clustering of NEA mackerel schools from July to August 2010 using an omnidirectional multibeam SONAR. These parameters were correlated with physical and biological data to examine their influence on schooling NEA mackerel during the summer feeding migration. It was predicted that while selectively feeding on copepod zooplankton NEA mackerel would form many small, loose aggregations evenly distributed in the upper parts of the water column. Physical (temperature, currents) and biological (prey, potential predators) differences between northern and southern and oceanic and coastal regions were also expected, hence, four geographically separate regions of the Norwegian Sea were selected for inter and intra-regional analyses. The results from this thesis can add to the understanding of behaviour, migration and schooling dynamics of NEA mackerel, as well as, contribute to the new swept area methodology for abundance estimation of NEA mackerel with standardized trawling, which uses the area of the trawl and the collected sample biomass to estimate pelagic fish abundances.

Materials & Methods

Study area

Biological, oceanographic and acoustic data were collected from an ecosystem survey in the Norwegian Sea in July - August 2010. The combined purse seining and pelagic trawling vessels M/V "Brennholm" and M/V "Libas" were employed; however, only data from M/V "Brennholm" were used in this study. Four geographically separate regions from the predetermined cruise tracks in the Norwegian Sea and surrounding waters were the focus for quantitative analysis for this thesis; northwest (NW), northeast (NE), southwest (SW) and southeast (SE) respectively (Figure 2, Nøttestad *et al.* 2010). The regions for analysis were chosen based on geographical separation in terms of latitude and longitude, SONAR data quality and mackerel abundance. Their inherent properties are outlined below (Table 1).
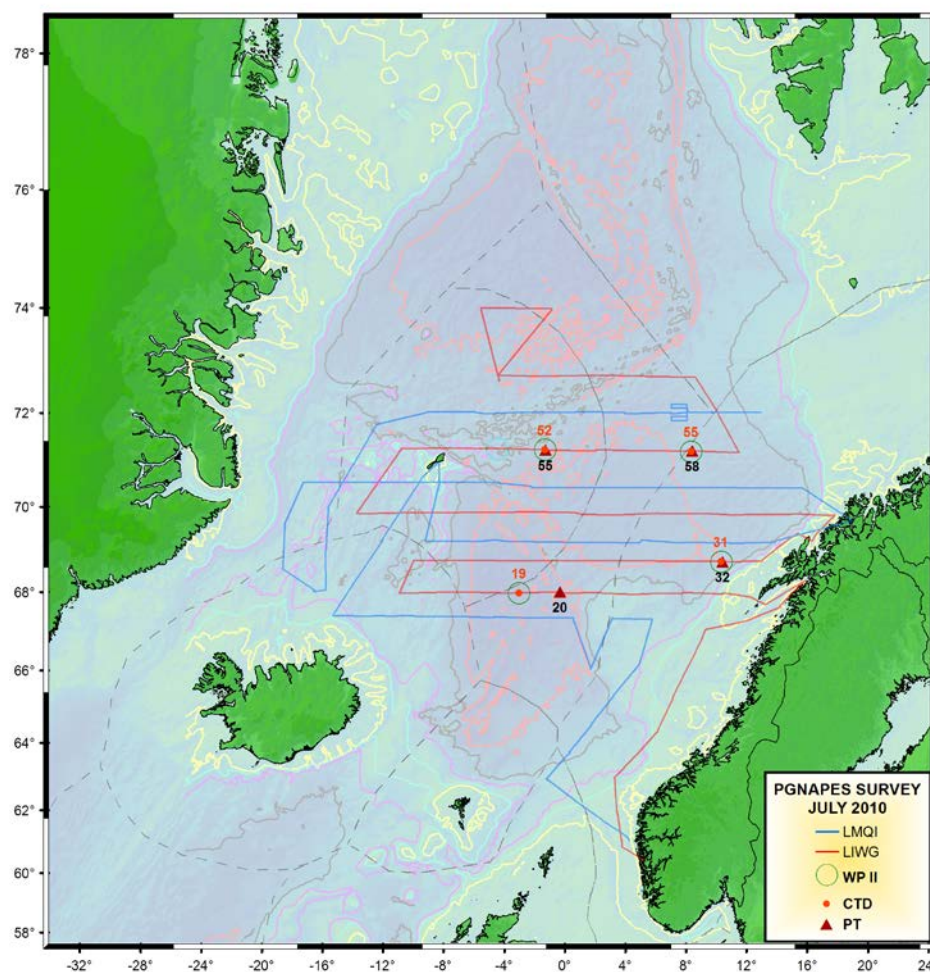

Figure 2. Cruise tracks for M/V "Brennholm" (red line) and M/V "Libas" (blue line) with pelagic trawl (▲), CTD (●) and plankton (○) sampling stations and their corresponding identification number in proximity to the transects used for SONAR scrutinizing.

Table 1. Location (latitude and longitude) of the transects used for acoustic and biological mackerel analysis in the NEA (Norwegian Sea and surrounding waters); including sampling date and bottom depth.

Region	NW	NE	SW	SE
Latitude	71° 15' N	71° 12' N	67° 57' 36" N	68° 43' 12" N
Longitude	2° 3'36" W - 1 15' W	7° 42'00" E – 8° 20'24" E (*day*) 9° 28'48" E - 9° 45'36" E (*night*)	3° 50'16" W - 4° 2'60" W	11° 26'24" E -11° 49'48" E
Date	30 July	31 July - 01 August	20 July	23 July
Bottom depth (m)	>1500 m	>1500 m	>1500 m	>1500 m

Temperature

The temperature data were recorded approximately every 60 nautical miles (nmi) at a predetermined sampling station with a SAIV SD200 (SAIV A/S) Conductivity Temperature and Depth (CTD) sensor. Temperature from the surface to a maximum 500 m depth was recorded every meter in the water column (Nøttestad *et al.*, 2010). Upcast data from 50 m depth to the surface was used for analysis. The depth of the 8° C isotherm was analysed in each region and compared with the mean school depths to evaluate the minimum temperature preference for NEA mackerel.

Acoustic data

Study areas

Four transects were acoustically analysed for NEA mackerel schools in four geographically separate regions; northwest (NW), northeast (NE), southwest (SW), and southeast (SE). These transects (NW, NE, SW, SE) were collected during daylight hours. A night time segment in the NE was located approximately 23 km east of the daytime segment, which was nearly three hours between the last sampled school of the day segment and the first sampled school of the night segment. With the prolonged daylight hours in the summer, a function in the statistical program R version 2.15.1 (R Development Core Team 2012, www.r-project.org) determined the altitude of the sun to discriminate between day and night hours (Appendix 1). The day

segment occurred from 19:26-20:23 on 31 July, and the night segment occurred from 23:12 on 31 July to 00:08 on 1 August. The trawl catch from the nearest occurring pelagic trawl station with a proportion of at least 90% mackerel was used to confirm that mackerel was the species detected acoustically.

SONAR data collection and scrutinizing

Acoustic measurements of schooling NEA mackerel and other pelagic fish species, such as NSS herring, were taken continuously throughout the survey using multi-frequency acoustics from the Simrad ER60 echosounder. The echosounder had an opening angle of 8° and operated on five frequencies (18, 38, 70, 120, and 200 kHz). The high frequency Simrad SH80 omnidirectional SONAR has 480 elements and a standard operational frequency of 116 kHz with an 8º horizontal opening angle (9º vertical) (Simrad, www.simrad.no). During the data collection, the SONAR operated from 2-6° tilt angle during collection, and the sampling range was set at 85 to 300 m radius from the vessel.

Large Scale Survey System (LSSS) (www.marec.no) was used for post-processing raw acoustic data (Korneliussen *et al.* 2006). A module in the program, PROFOS, is capable of replaying and filtering raw data, and distinguishing between detected schools and noise (noise: "*unwanted signals that are present in the medium but independent of the echosounder/SONAR transmission*," Simmonds and MacLennan 2005). The pre-processing function allowed for bypassing the time consuming process of scrutinizing the SONAR manually (Appendix 2).

To minimize any potential vessel avoidance by mackerel schools, only schools within an 85-300 m radius from the vessel were used; the goal being to detect and analyse schools exhibiting natural undisturbed swimming behaviours (Misund *et al.* 1997). Furthermore, detections under the following criteria were excluded from the analysis: consisting of four or less consecutive pings, schools not having a "biologically reasonable" speed (approximately 1 m s⁻¹ to 6 m s⁻¹) (see Godø *et al.* 2004) and those appearing as noise (i.e. exhibiting an unnatural swimming pattern, the first detection appearing behind the vessel, and extreme variations in school size).

Mackerel school parameters

After the SONAR data was scrutinized, PROFOS provided means on the following parameters using the ping data per each school: mean depth (m), mean speed (m s⁻¹), mean

direction (°), mean backscattering volume (s_v), mean area (m²), geographical school position (longitude and latitude maximum and minimum). The number of pings of the detected school (how many seconds the school was detected) and time and date of the first and last detections were also provided.

School depth was used to analyse the vertical distribution of mackerel. The SONAR provided an estimate of mean school depth ($\overline{m}$) with the range (m) of the detections from the vessel and the opening angle of the transducer (θ) (equation 1).

$$depth(m) = \frac{range(m)}{\tan \theta} \tag{1}$$

To estimate the biomass (kg) of each school, two assumptions were made:

1. The schools were ellipsoid shaped, which reduces drag for migrating schools (Himelrijk *et al.* 2010; Misund 1993; Pitcher 1993).
2. The packing density was one fish per cubic metre in every school, because the SONAR was not calibrated, thus providing an s_v value that was only a relative measure of the acoustic energy from a school (Misund 1990).

To estimate the biomass of mackerel schools in kg, the relative school volume was calculated using the provided area (m²) from the SONAR output. Given that the height (m) (*h*) was equal to the width (*z=h*) and the length was three times the height (*l = 3·h*), the area (equation 2) was used to determine the dimensions of a theoretical ellipsoid school shape (equation 3), and in turn was used to estimate a relative volume (equation 4). The volume (m³) (*V*) was equal to the number of fish in each school. The number of fish was multiplied by the average fish weight (g) (*w*) in each region and divided by 1000 kg to provide an estimated school biomass (equation 5).

$$A = \pi \cdot hlz \tag{2}$$

$$h = \sqrt{\frac{A}{3\pi}} \tag{3}$$

$$V = 4\pi \cdot h^3 \tag{4}$$

$$B = \frac{V \cdot w}{1000000} \tag{5}$$

Nearest neighbour distance (NND)

Meso-scale school clustering patterns in each region were compared using methods developed by Mackinson *et al.* (1999). The nearest neighbour distance (NND) was calculated as the two-dimensional distance from a school to its closest neighbouring school (equation 6). The mean NND ($\overline{NND}$) along approximately 10 km of transect in each region was quantified to assess regional meso-scale clustering patterns.

$$\overline{NND} = \frac{\sum_{1}^{n} \frac{n}{NND}}{n} \tag{6}$$

Mackerel school speed, direction, and currents

LSSS school output generated the speed and direction per mackerel school in each region, determined by the first and last ping detections of a school. An improved estimate was developed to give a more realistic view of the direction of each school. This method takes ping-by-ping data to calculate a mean direction and speed. The headings (°), provided by LSSS, were converted into geometric angles relative to the heading of the vessel, and converted back to degrees for the true direction of the school based on a mean value for each ping (Appendix 3). School speed is not referred to in the same sense as swimming speed in this thesis because the currents may influence the actual direction and swimming speed of a school. Therefore, the school speed includes the effect of the prevailing current, whereas the swimming speed is the result of subtracting the current from the school speed (see later).

The current speed (m s⁻¹) and direction (º) were measured continuously onboard M/V "Brennholm" with an RDI Vessel Mount Acoustic Doppler Current Profiler (ADCP) (Teledyne RD Instruments, Inc.) at 75 kHz on narrowband with a 30° beam angle. The current direction (°) and magnitude (m s⁻¹) were collected in five minute averages at 24.5 m depth to be representative of the upper layers of the water column (10 – 40 m) using a default setting of the data collection system VmDas, version 1.46.5 (Teledyne RD Instruments, Inc.) (Nøttestad *et al.* 2010). The ADCP data were reprocessed in VmDas for misalignment by 40.98° throughout the entire survey area because the transducer was changed without performing a new calibration, and there was no bottom track for direction reference due to very deep bottom depths (Nøttestad *et al.* 2010). The reprocessed data was then extracted into data sheets using WinADCP version 1.1.0 (Teledyne RD Instruments, Inc.) to assess whether mackerel schools utilize STST. However, the reprocessed data had unrealistically high current

magnitude values, therefore, the magnitude values from the raw data were coupled with the direction from the reprocessed data as a representative of the local prevailing currents.

The active swimming speed by the mackerel schools without the influence of the local prevailing currents was found by decomposing the vectors of both the mackerel schools and the local prevailing current. The x and y vectors of the average local current along each transect was subtracted from the x and y vectors of the schools. The corresponding schools were matched with the local current based on the time at which they were sampled. The resultant was considered to be the active swimming speed without the influence of the local current.

SONAR ray-trace

Various physical conditions during a survey may influence the accuracy of measurements from acoustic instruments. Adverse weather conditions and strong thermoclines can result in inaccurate acoustic measurements (Aglen 1994; Simmonds and MacLennan 2005; Nøttestad *et al.* 2010; Bernasconi *et al.* 2012). LYBIN is an acoustic ray-trace simulator of how acoustic waves propagate through the water column (Norwegian Research Defence Establishment/Forsvarets Forskningsinstitutt (FFI) Facts 2012; Nøttestad *et al.* 2010). A LYBIN ray trace was performed and combined with the CTD data from a station near the SE region (CTD station no. 29) to compare the depth results provided by the SONAR and those which were reflected on the echogram to see if acoustic ray bending occurred in this area of the survey.

Biological data

Mackerel length and weight

The cruising speed between predetermined stations was predominantly between 10.0 - 12.0 knots during the survey, with the speed was reduced to 4.2 - 5.3 knots during standardized pelagic trawling close to the surface for 30 minutes after a CTD profile and plankton station. This duration was reduced a couple of times if large schools or aggregations of fish were detected on the trawl sonde (Nøttestad *et al.* 2010). Pelagic sampling was done with a large pelagic trawl towed 160 - 200 m behind the vessel with a vertical opening between 30 - 35 m and spread 55 - 65 m (Nøttestad *et al.* 2010; 2012). Trawl data provided information on the length and weight of NEA mackerel based on subsamples of 100 individuals per trawl; and as verification that mackerel were in the area of scrutinized acoustic data. The fish were sorted by species onboard after trawling and a total weight was recorded using Fishmeter measuring tools (Scantraal) (Øvredal and Totland 2002).

A subsample of 100 individuals from each haul was used to calculate the mean total length (nearest 0.5 cm below) and wet weight (nearest gram below) of the catch (see Mjanger *et al.* 2010). Fulton's Condition Factor (K) was calculated to assess mackerel condition (equation 7) (Ricker 1975).

$$K = 100 \cdot \frac{W}{L^3} \tag{7}$$

Plankton sampling

Zooplankton sampling was performed along with the CTD stations, which were distributed approximately every 60 nmi. A WP-2 net (56 cm in diameter) with a 180 µm mesh size was towed from 200 m depth to the surface at 0.5 m s^{-1} (see Fraser 1966). The sampling range was chosen based on the depth ranges of mackerel and other pelagic species which were the focus of the survey. The sampling range from 0-200 m depth is also international standard for WP-2 net hauls in ICES. While aboard the vessel, each sample was divided in two fractions: 1) taxonomic analyses (taxonomic species, size), and 2) biomass estimates. On board, the samples were split into two equal parts, one was preserved with formaldehyde and the second was to be dried. Prior to drying, the samples were divided into size fractions (<1000 µm, 1000-2000 µm, and >2000 µm) by sieves filtering mesh sizes 2000 µm, 1000 µm and 180 µm, weighed, dried, and weighed again at the institute laboratory after the survey. The result of the >2000 µm fraction was identified, and depending on the species group the organisms

were length measured and the various groups were transferred to trays for drying, and then weighed (Nøttestad *et al.* 2010).

Marine mammal observations

Marine mammal observations were also used for ecological interpretation. Two observers were constantly on watch during daylight hours to note the species, time and location of marine mammals sighted. The priority observation periods were during the cruising periods from one trawl station to the next (Palka and Hammond 2001; Lawson and Gosselin 2009; Nøttestad *et al.* 2010).

Statistical analysis

The statistical program R version 2.15.1 was used for all statistical analyses and plotting. The Shapiro-Wilk normality test was used to test normality in the data set. Parametric tests (linear regression analysis, analysis of variance (ANOVA) and Tukey HSD were used in this analysis. Tukey HSD was used to compare school parameters (depth, swimming speed, NND and biomass) between regions. Non-parametric regression models (histograms) were used in cases when there was deviation from normal distribution. All of the statistical tests assumed 0.05 significance.

Results

Temperature

In general, the NW experienced the coldest sub-surface sea temperatures, and the SE had the warmest. The sea temperature ranged from 4.8° C to 10.3° in the four regions combined (Figure 3). In the NW, the 8º C isotherm occurred at a shallower depth (13 m) compared to the other regions (Figure 3). In the NE and SW, the 8º C isotherm was at 26 m and 28 m, respectively, whereas in the SE it occurred at 47 m depth. The temperature also decreased more rapidly with depth in the NW compared to the other three regions. The temperature distribution throughout the Norwegian Sea mapped below illustrates the decrease in temperature both from the coast towards the Arctic front and from 10 - 50 m, particularly in the western Norwegian Sea (Figure 4, Nøttestad *et al.* 2010).
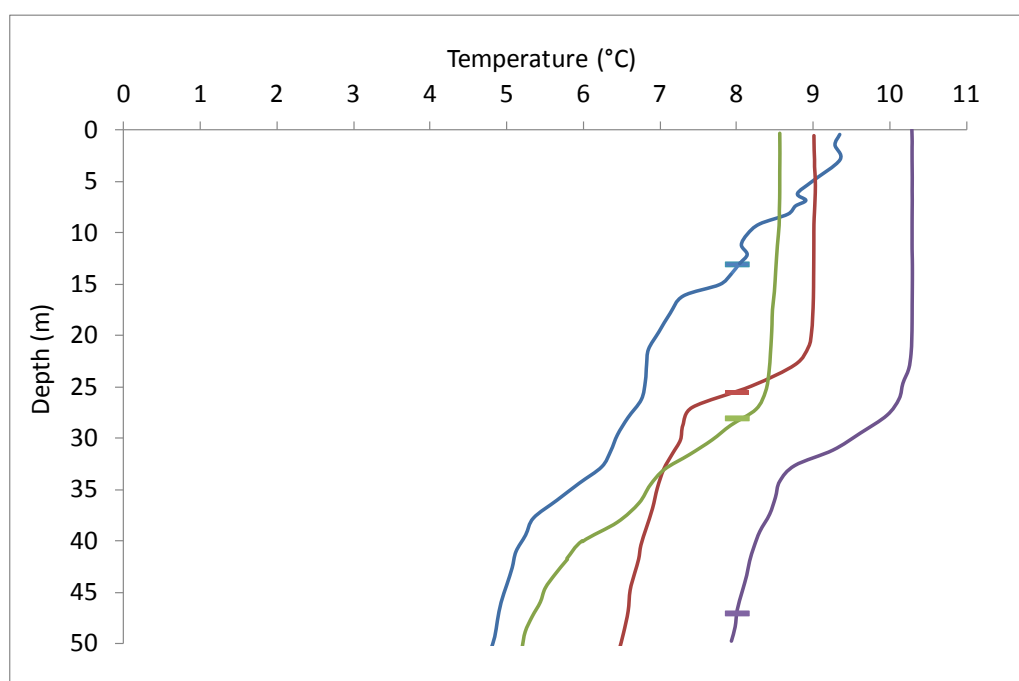

Figure 3. Temperature (°C) profiles from 50 m depth to the surface in the four study regions. The horizontal lines indicate the depth at which the sea temperature reaches 8º C in each region (blue = NW; red = NE; green = SW; purple = SE).
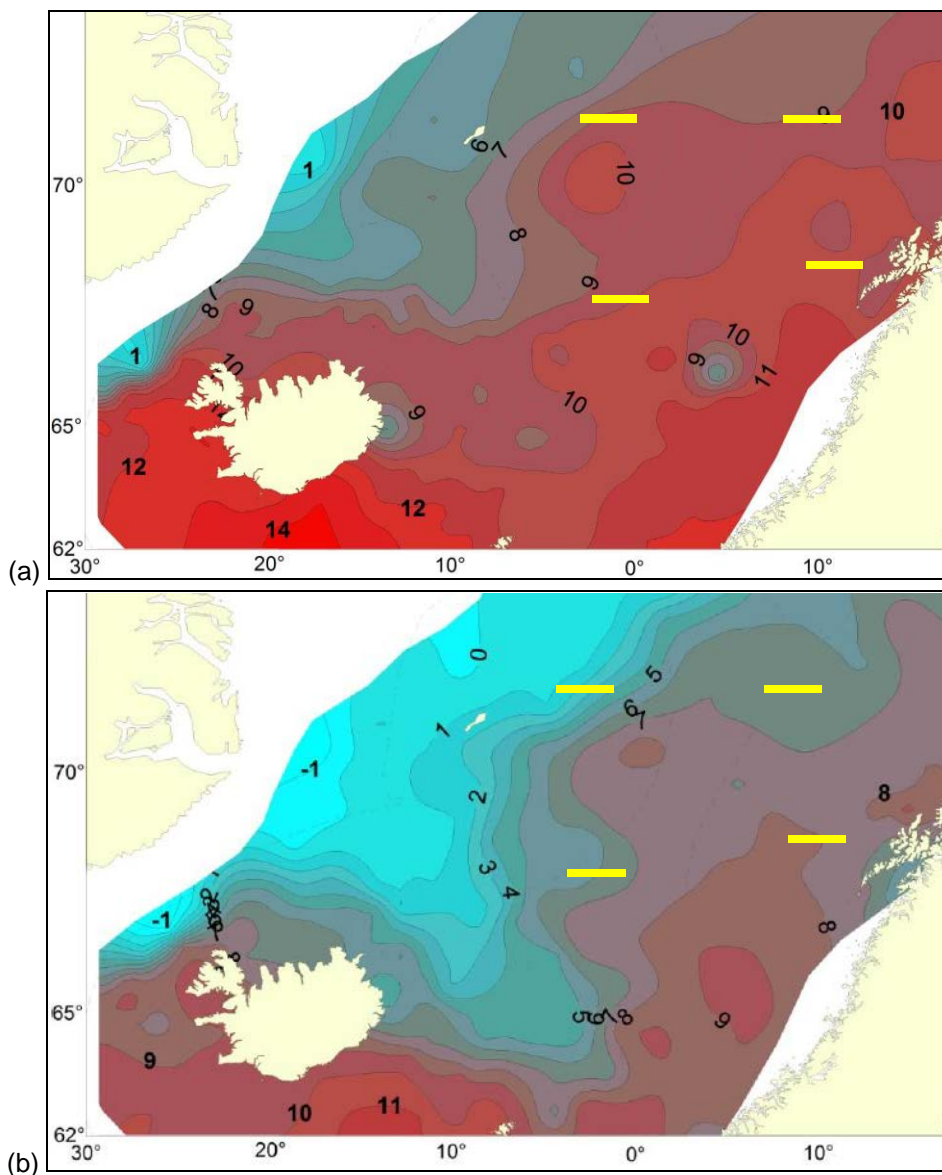
Figure 4. Mapped temperature (°C) in the NE Atlantic from the July-August 2010 ICES Ecosystem Survey at 10 m (a) and 50 m (b) depth (Nøttestad *et al.* 2010). The yellow lines represent the general geographic location of the sampling transects.

Acoustic data

A total of 276 selected mackerel schools were tracked with a high-frequency multibeam omnidirectional SONAR in this study. From those schools, 251 schools, which occurred during daytime hours, comprised the main comparisons of the regions: 62 NW, 52 NE, 66 SW, and 60 SE. For the diurnal analyses, 36 additional schools during night hours in the NE were compared with the 52 schools from the daytime transect. The data set did not have normal distribution; therefore a log transformation was performed.

Depth distribution

The depth distribution of NEA mackerel school mean depth was within the top 40 m of the water column, the mean depths ranged from 9 - 39 m between the four regions (Figure 5). The average mean school depth in the NW, NE and SE were very similar at 20, 22 and 19 m, respectively, but the average mean school depth in the SW (26 m) was significantly deeper than the other three regions (Tukey HSD, $p < 0.005$). The NW schools occurred from 12 - 29 m; a smaller distribution compared to the other regions, which all had maximum mean depths deeper than 35 m.

The majority of the schools in the NW were distributed below the 8° C isotherm, and the temperature at the maximum school mean depth (29 m) was 6.8° C (Figure 5). The schools in the NE and SW had roughly the same maximum school mean depth, and the 8° C isotherm occurred between 26 - 28 m in both regions. The majority of schools occurred above the depth where sea temperature reached 7° C, and all schools occurred in waters warmer than 6° C.
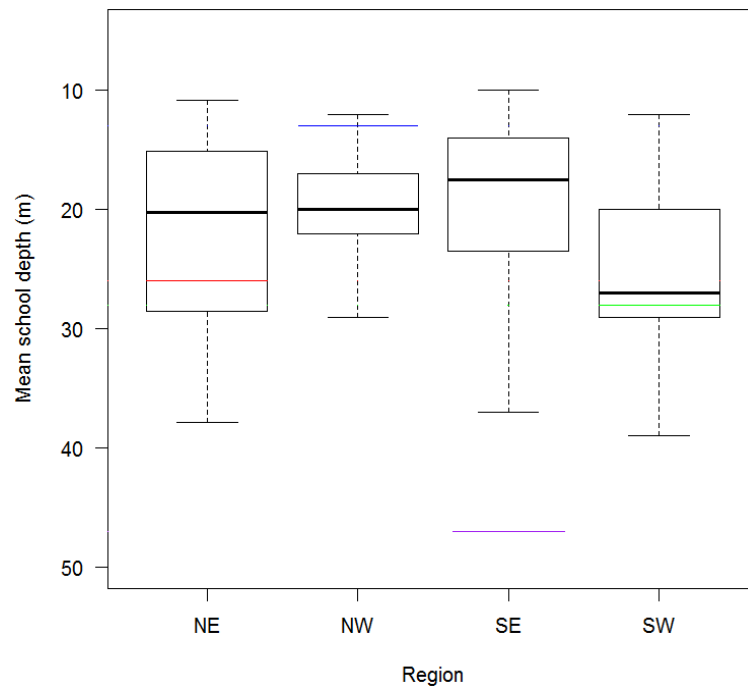
Figure 5. Box and whisker plot of mackerel school mean depths (m) in the four study regions. The coloured lines represent the depth of the 8º C isotherm in each region (blue = NW, red = NE, green = SW, purple = SE). The bold line represents the median value, the box is the midspread (including the first and third quartiles), and the whiskers are the minimum and maximum values.

Mackerel school biomass

Estimated school biomass ranged from 68 kg to 10538 kg between the four regions combined (Figure 6). The schools in the northern regions had greater mean biomass than in the southern regions (ANOVA, $p < 0.01$). The SW region had the lowest average biomass between the regions (1352 kg), as well as the smallest distribution of biomass (142 - 3797 kg) (Tukey HSD, $p < 0.01$).
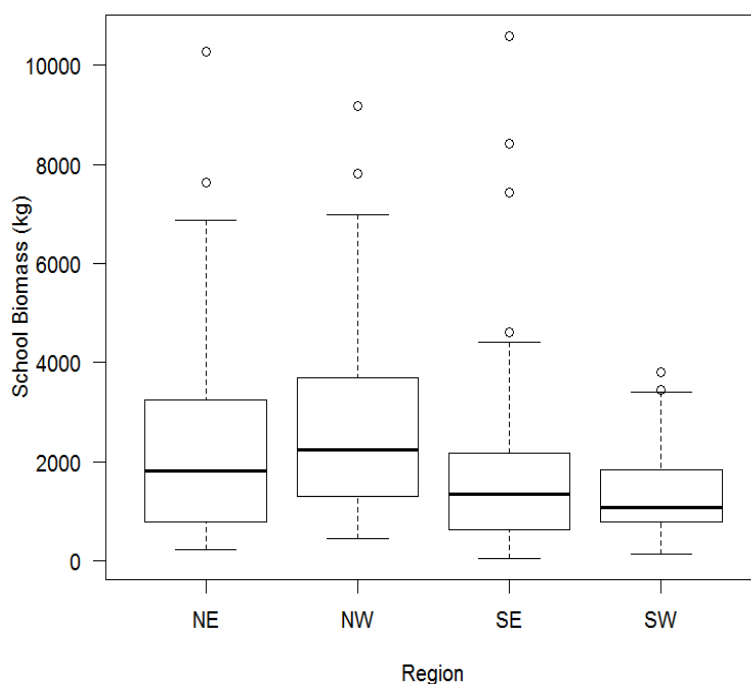

Figure 6. Estimated relative biomass (kg) of mackerel schools per region. The bold line represents the median value, box is the midspread (including the first and third quartiles), the whiskers are the minimum and maximum values, and the circles are outliers.

Nearest neighbour distance (NND)

The distribution of the tracked schools along the transects were analysed using the method developed by Mackinson *et al.* (1999). The data revealed that schools were anywhere from 39 - 1286 m from its nearest neighbour along a 10 km section (Table 2). More schools were detected along in the SW and NE (night) segments along the 10 km stretch compared to the other segments (Table 2). The SW schools had smaller $\overline{NND}$ than the other regions (ANOVA, $p < 0.001$). A smaller $\overline{NND}$ indicates schools are closer together, whilst a larger $\overline{NND}$ illustrates greater distance between one school and its nearest neighbour.

Table 2. Mean Nearest Neighbour Distance ($\overline{NND}$) of a transect segment approximately 10 km long of the scrutinized transects in each region; including: number of schools, mean, and range of $\overline{NND}$ values along the segment.

Region	Latitude	Longitude	Schools (*n*)	$\overline{NND}$ (*m*)	NND ranges (*m*)
NW	71° 14' 15.72" N 71° 14' 5.23" N	2° 4' 1.06" W 1° 48' 6.20" W	27	274	94 - 1286
NE (day)	71° 12' 10.94" N 71° 11' 44.64" N	7° 41' 8.65" E 7° 58' 7.39" E	27	254	74 - 586
NE (night)	71° 11' 53.07" N 71° 11' 27.75" N	9° 28' 54.01" E 9° 45' 12.48" E	36	244	59 - 1135
SW	67° 58' 1.36" N 67° 57' 42.14" N	4° 2' 56.53" W 3° 50' 16.31" W	46	194	39 - 429
SE	68° 43' 34.85" N 68° 43' 35.66" N	10° 29' 56.94" E 10° 45' 33.12" E	26	385	42 - 1151

Mackerel school speed, direction and currents

The mean speed is the net school speed resulting from active swimming and the influence of the prevailing current. The average mean speed in all of the areas combined was 1.44 m s^{-1} (Figure 7), approximately 4.24 body lengths per second (B.L. s^{-1}). Minimum mean school speed was 0.04 m s^{-1}, the maximum was 7.2 m s^{-1}, and the majority of the schools were moving between 0.72 and 1.79 m s^{-1}. In general, the schools in the north had a slower average mean speed than those in the south (ANOVA, $p < 0.01$). The SW schools moved significantly faster than those in the NW (Tukey HSD, $p < 0.001$) and NE (Tukey HSD, $p < 0.005$). The SW schools also displayed a wider range of mean school speeds compared to the NW schools.
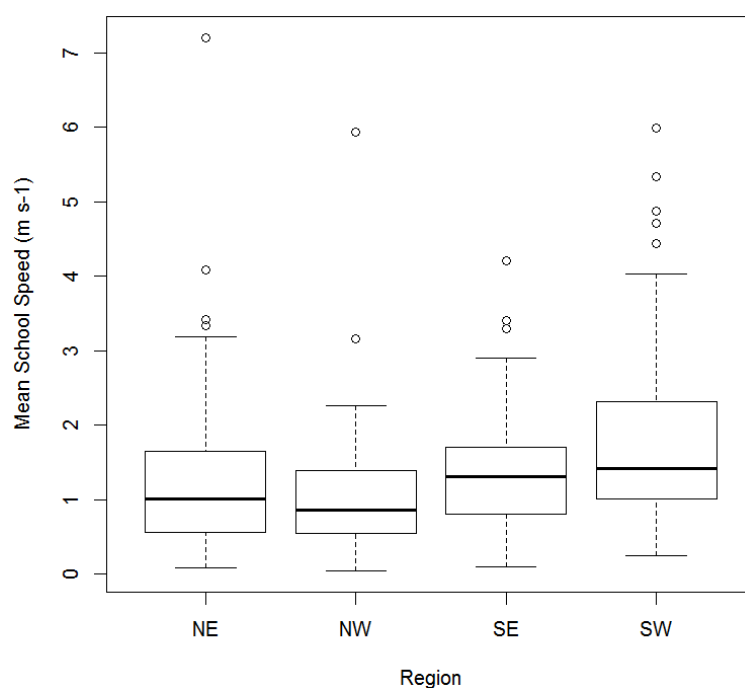

Figure 7. Range of observed mean school speeds (m s^{-1}). The bold line represents the median speed value, the box is the midspread (including the first and third quartiles), the whiskers are the minimum and maximum values, and the circles are outliers.

School direction is first illustrated as rose plot histograms using the free software Rose.Net, version 0.10 (Todd A. Thompson Software 2012, http://mypage.iu.edu/~tthomps/programs/html/tntrose.htm), and also displayed as feather plots. The rose plot histograms illustrate class intervals of 15° for the mean school direction (°) in each region (Figures 8-11 a). Feather plots were also used to illustrate the school direction (arrow direction) and speed/velocity (arrow length) (Figures 8-11 b). In the NW, NE and SE, the mean direction was north with the prevailing current (Figures 8, 9 and 11 b). However, in the SW the mean direction of the schools was to the south (Figure 10). The current speed in the NW, NE and SE was approximately 0.35 m s^{-1} in a northward direction (Figures 8, 9 and 11 c), and about 0.32 m s^{-1} in the SW in a southward direction (Figure 10 c). The current data in the SW may suggest a meso-scale oceanic eddy (Figure 10 c).

Figures 8-11 d illustrate the school speed minus the effect of the current, which is referred to as the swimming speed. The minimum and maximum speeds (or velocities) are presented as a scale of reference. The results illustrate faster school speeds for schools swimming with the currents, and slower speeds for those actively swimming against the current at that time. Most of the schools in all of the regions were swimming with the prevailing local current, thus resulting in a slightly reduced swimming speed because of the prevailing current.

Figure 8. NW mackerel school school directions are presented on a rose plot histogram; the green line represents the mean and the orange line outside the circle is the standard deviation (maximum value of axis = 7) (a). Feather plots illustrate the school direction and speed (b), current direction and magnitude (c), and the school swimming speed and direction without the influence of the current (d). Speed and direction vectors are represented as arrow length and angle. The minimum and maximum school speeds and mean current magnitude for the region are in red.
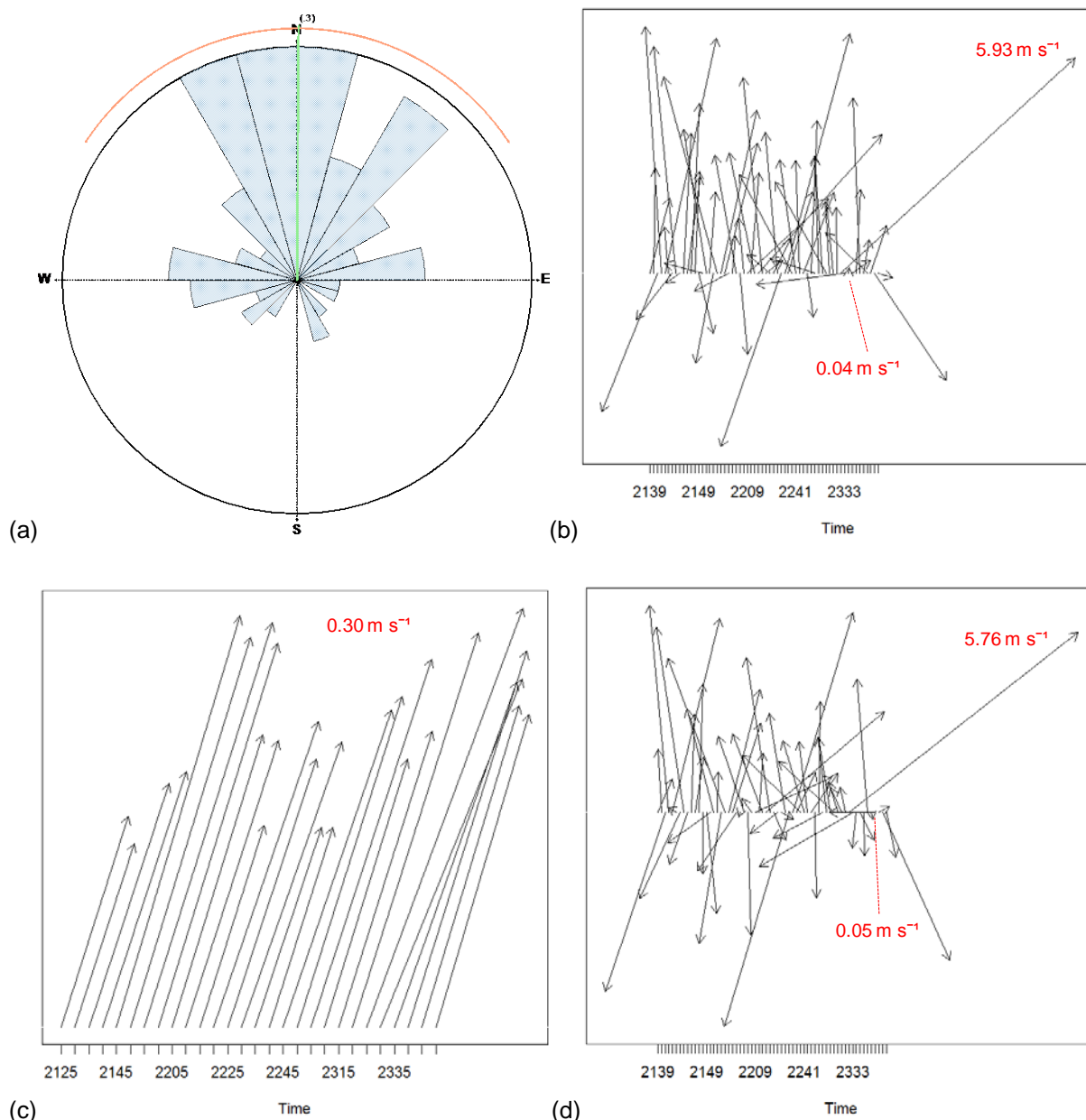
Figure 9. NE mackerel school directions are presented on a rose plot histogram; the green line represents the mean and the orange line outside the circle is the standard deviation (maximum value of axis = 9) (a). Feather plots illustrate the school direction and speed (b), current direction and magnitude (c), and the school swimming speed and direction without the influence of the current (d). Speed and direction vectors are represented as arrow length and angle. The minimum and maximum school speeds and mean current magnitude for the region are in red.
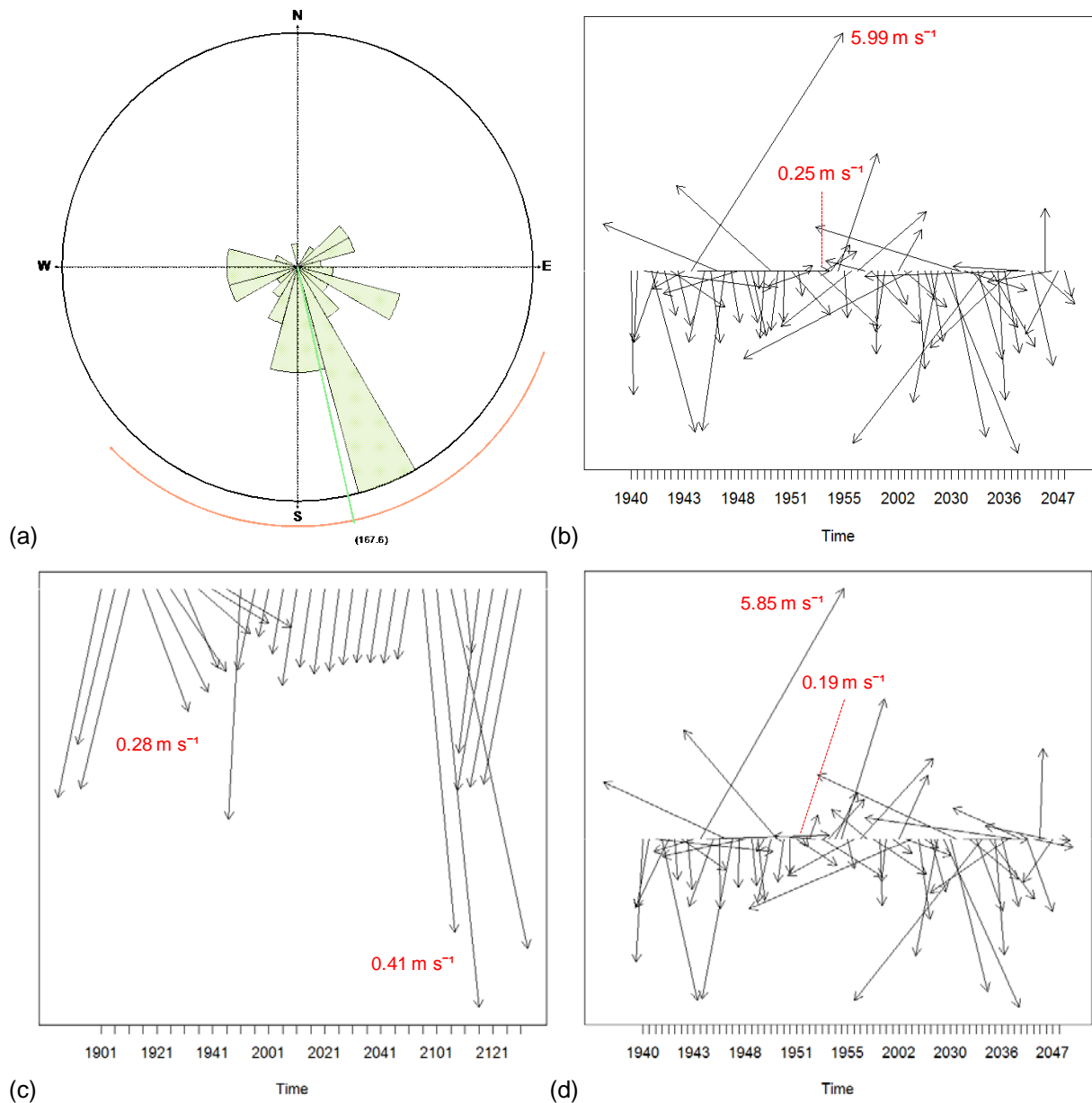
Figure 10. SW mackerel school directions presented on a rose plot histogram; the green line represents the mean and the orange line outside the circle is the standard deviation (maximum value of axis = 13) (a). Feather plots illustrate the school direction and speed (b), current direction and magnitude (in this case, split into separate segments of mean direction and magnitude) (c), and the school swimming speed and direction without the influence of the current (d). Speed and direction vectors are represented as arrow length and angle. The minimum and maximum school speeds and mean current magnitude for the region are in red.
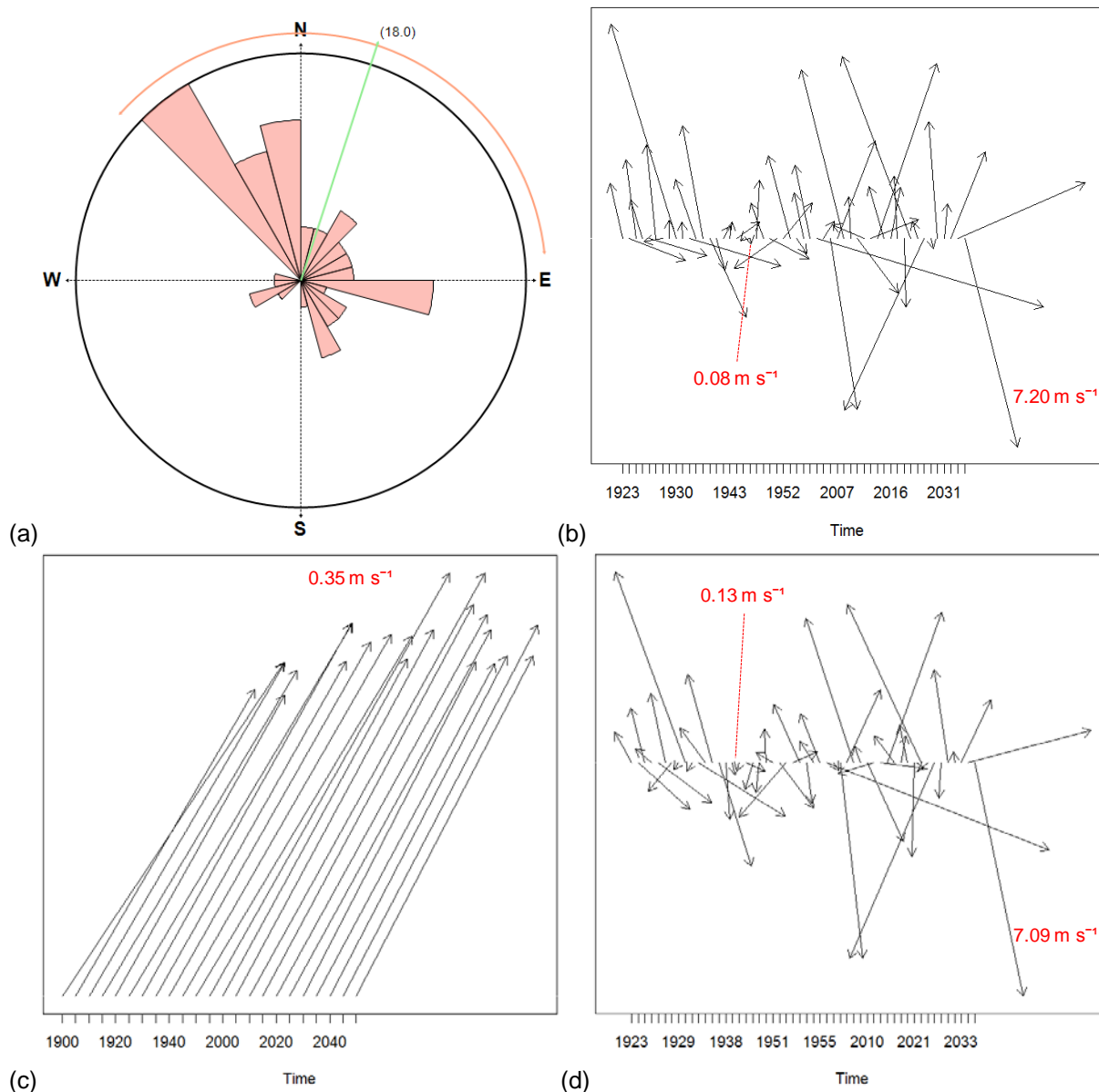
Figure 11. SE mackerel school directions are presented on a rose plot histogram; the green line represents the mean and the orange line outside the circle is the standard deviation (maximum value of axis = 9) (a). Feather plots illustrate the school direction and speed (b), current direction and magnitude (c), and the school swimming speed and direction without the influence of the current (d). Speed and direction vectors are represented as arrow length and angle. The minimum and maximum school speeds and mean current magnitude for the region are in red.
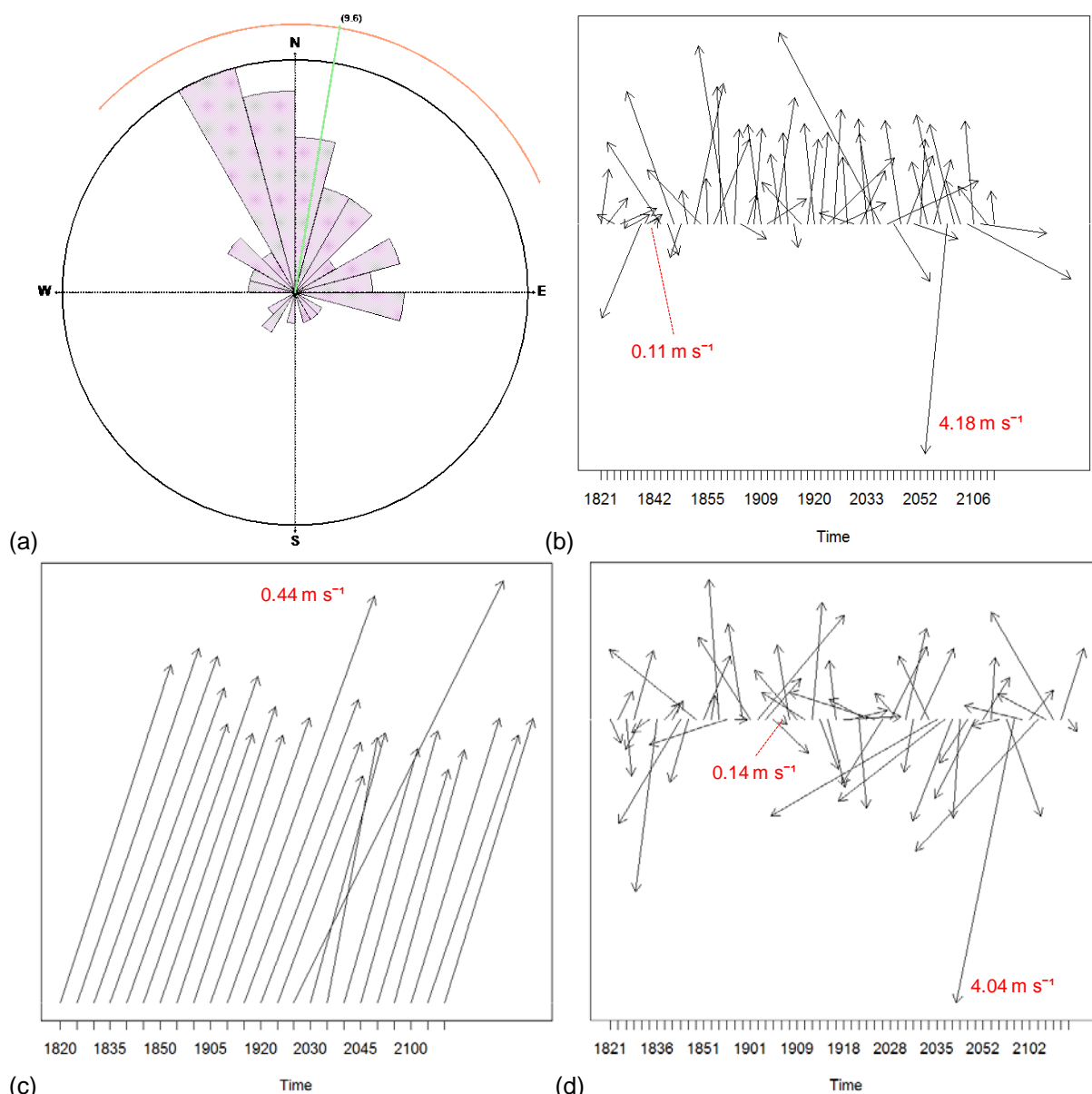
Diurnal behaviour

The mean school depth was deeper at night than during the day (ANOVA, $p < 0.001$) (Figure 12). The average mean depth during the day was 22 m (median 20 m), and 25 m at night (median 27). The depths during the day ranged from 11 - 38 m and from 9 - 36 m at night.

The biomass estimates of the tracked schools were also larger along the daytime transect than the night transect (ANOVA, $p < 0.001$) (Figure 13). The average school biomass during the night transect was 1920 kg, compared to 4150 kg during the day transect. The range of school biomass estimates was more variable during the day compared to at night. There were no observed diurnal differences in school speed, direction or NND.
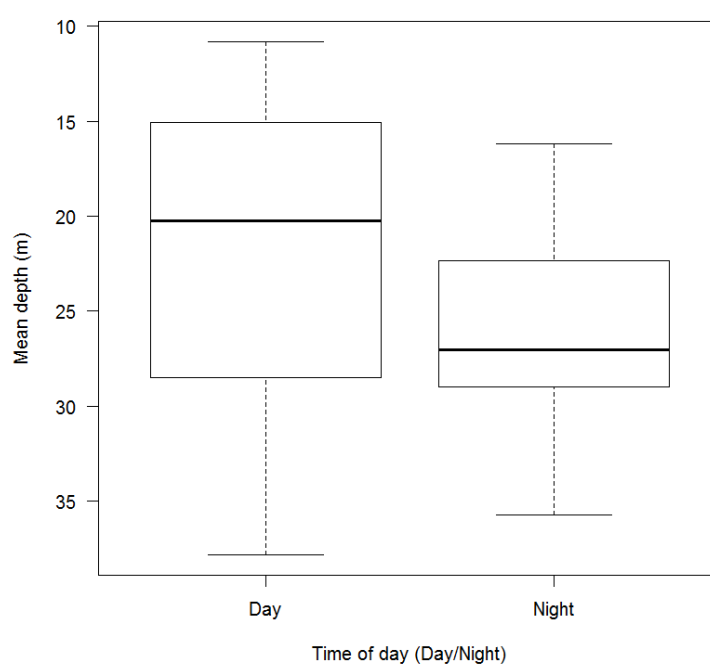

Figure 12. Mackerel school mean depths (m) in the NE (71° 15' N) at daytime (*N* =52; 19:26-20:23 31/07/2010, 7° 50' 51" E) and night (*N* = 36; 23:39 31/07/2010 – 00:08 01/08/2010, 9° 45' 12" E). The bold line represents the median depth, the box is the midspread (including the first and third quartiles), and the whiskers are the minimum and maximum values.
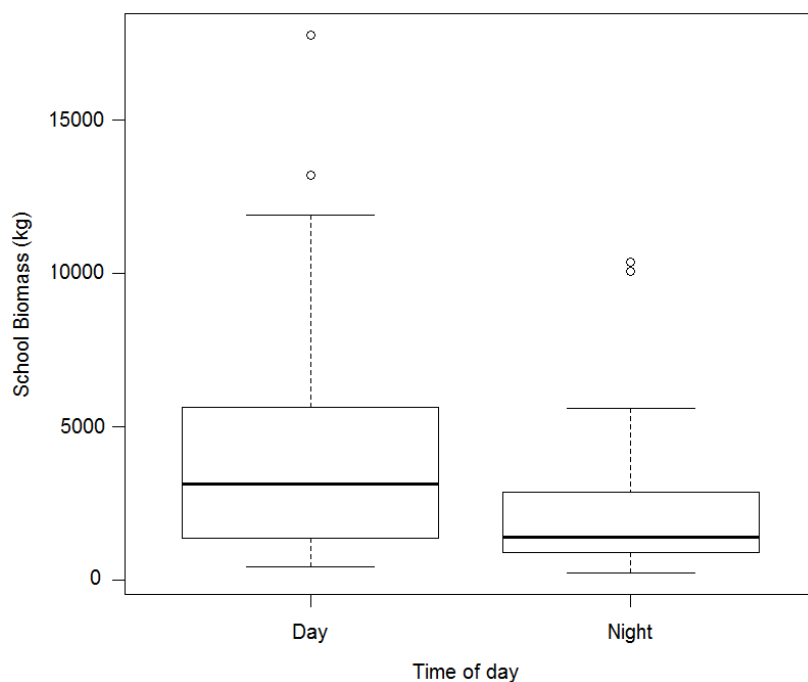
Figure 13. Estimated school biomass (kg) in the NE (71° 15' N) at daytime (N =52; 19:26-20:23 31/07/2010, 7° 50' 51" E) and night (N = 36; 23:12 31/07/2010 – 00:08 01/08/2010, 9° 45' 12" E). The bold line represents the median biomass, the box is the midspread (including the first and third quartiles), the whiskers are the minimum and maximum values, and the circles are outliers.

SONAR ray-trace

A LYBIN ray trace was performed using the CTD data from a specific station in the SE region (CTD station no. 29) where the schools were particularly difficult to detect. It illustrates the beam width at 300 m distance from the vessel, the beam stretched from approximately 30 m to the surface at 0° tilt angle (Figure 14 a). At 2° tilt, the beam spreads from 0 to 40 m depth at 300 m distance from the vessel (Figure 14 b). And at 4 ° tilt, the beam reaches approximately 50 m depth (Figure 14 c). Furthermore, at distances up to 1 km from the vessel, the beam spreads from the surface to deeper than 100 m. Due to the shape of the acoustic beam, sampling volume increases with distance from the vessel (Fréon *et al.* 1992). It also illustrates that there was no strong thermocline in this region to cause acoustic ray bending.

(a)

(b)

(c)
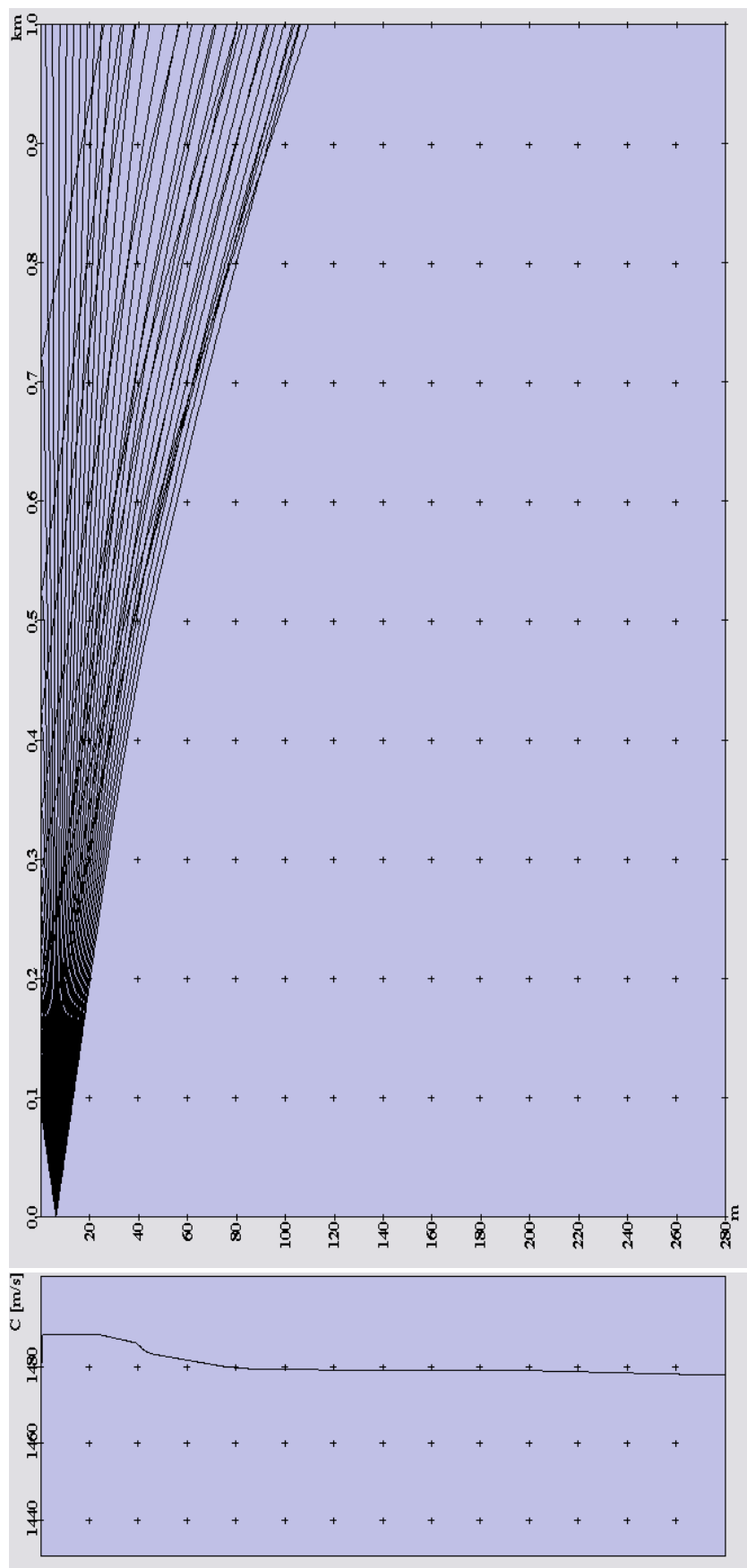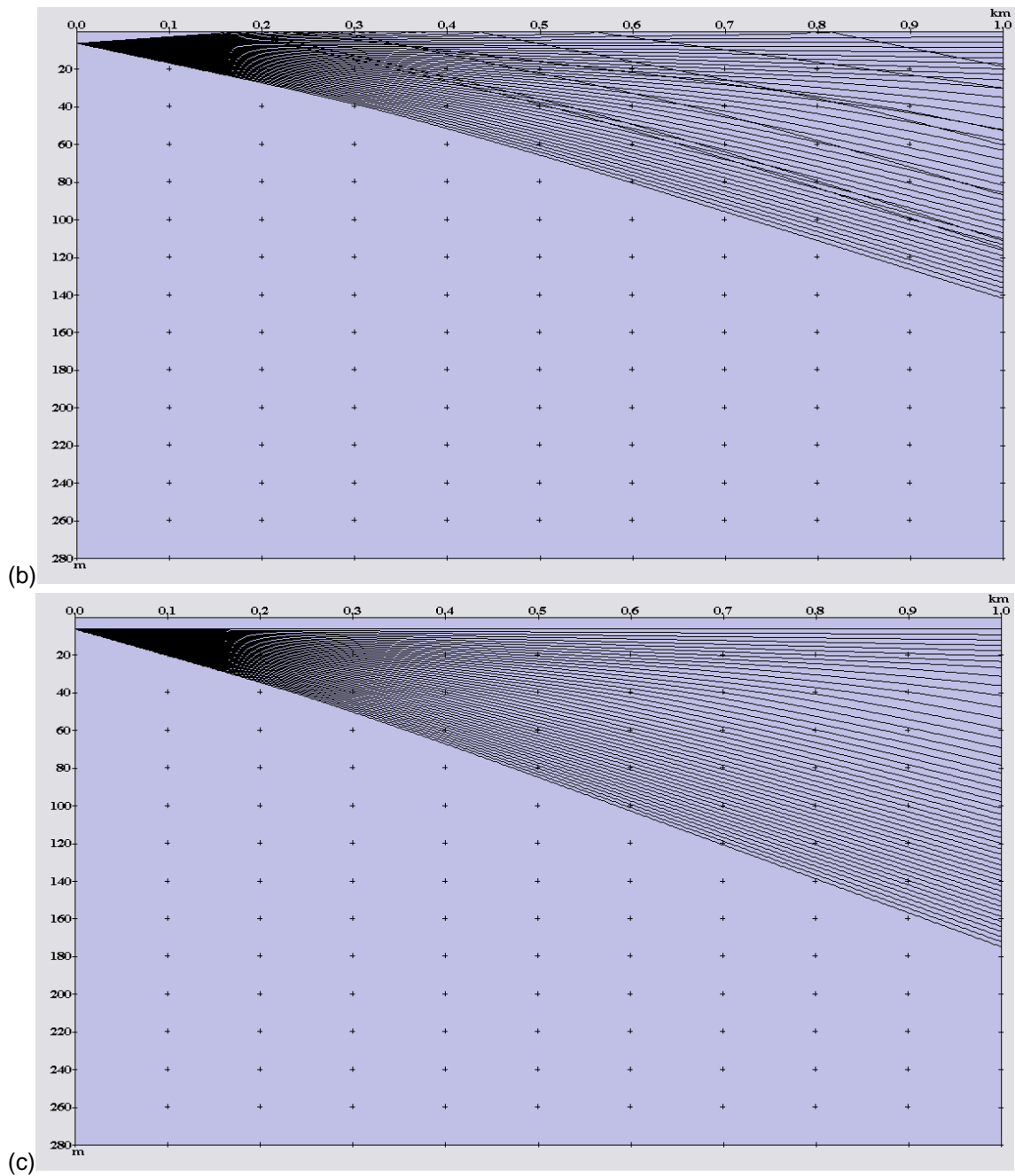
Figure 14. Sound speed profile (m s⁻¹) (a, left) and ray trace simulation for a CTD station in the SE region for the Simrad SH80 unit operating at 116 kHz at 0° (a, right), -2° (b), and -4° (c) tilt angle.

Biological data
Spatial distribution

Mackerel were present in most of the trawl catches from the predetermined stations throughout the survey period, and were dominating along the coast of Norway and central Norwegian Sea samples (Figure 15; Nøttestad *et al.* 2010). NSS herring dominated trawl samples west of 4° W and north of 72° N. The spatial overlap between mackerel and herring occurred mainly in the outskirts including southern, southwestern, and northern parts of the Norwegian Sea (Nøttestad *et al.* 2010). Blue whiting, salmon, and other (e.g. lumpsucker) were not used in this study though depicted in the figure.
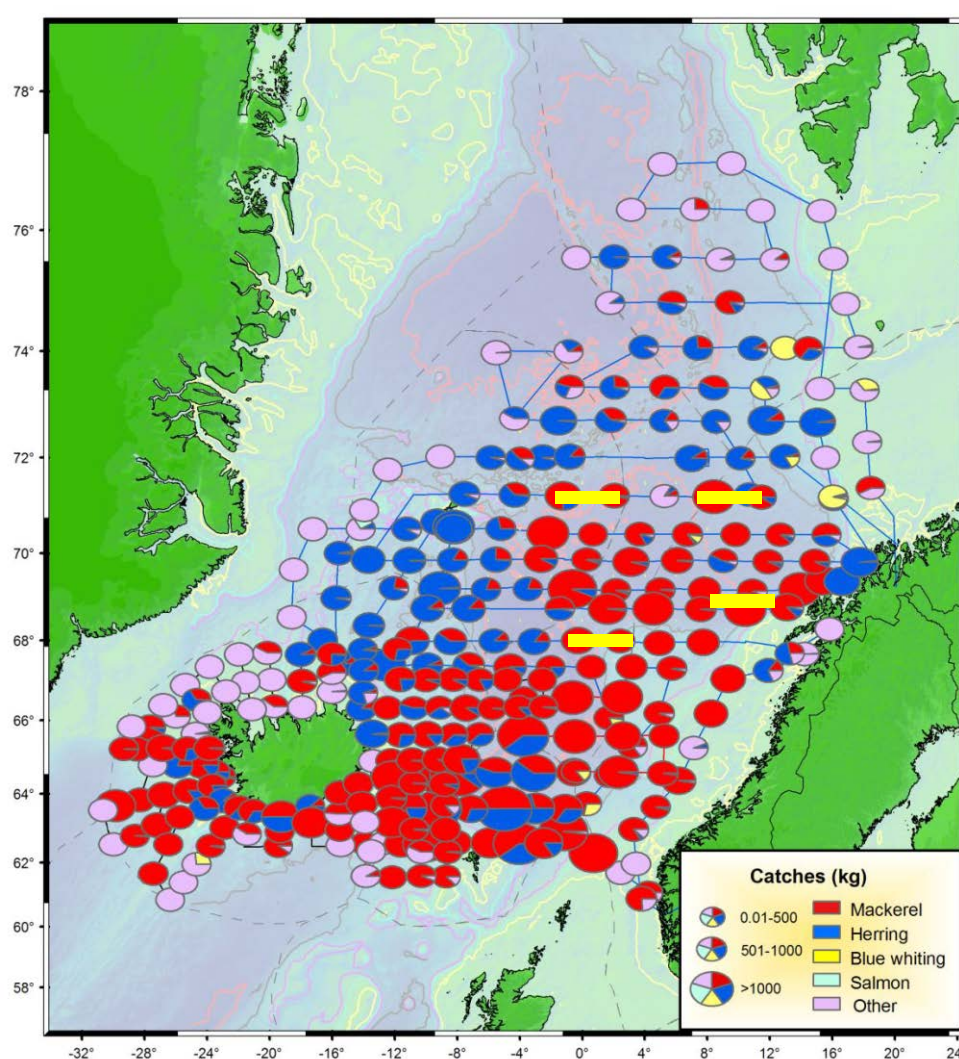
Figure 15. Distribution and spatial overlap between mackerel (red), herring (blue), blue whiting (yellow) and salmon (violet) from M/V "Libas", M/V "Brennholm", M/V "Finnur Fridi" (Faroe Islands) and M/V "Arni Fridriksson" (Iceland) in the Norwegian Sea, 15 July - 20 August 2010 (Nøttestad *et al.* 2010). The yellow lines represent the general area of each transect, not the exact transect location and length.

Mackerel length and weight

The biological data on NEA mackerel are from the pelagic trawl station, directly after the CTD and plankton stations, which was closest to the relevant transect in each region. There was a significant difference in the size (length and weight) of NEA mackerel between the north and the south (ANOVA, $p < 0.01$) (Figure 16). The mackerel in the NE region were the largest, and those in the SW were the smallest (Figure 16, Table 3). In general, the mackerel condition (K) was higher in the south than in the north (ANOVA, $p < 0.01$). In particular, K was significantly higher in the SW than in the NW (Tukey HSD, $p < 0.05$) (Table 3). The 2005- and 2006-year classes dominated the mackerel population in the Norwegian Sea and constituted 50% in 2010 (Nøttestad *et al.* 2010).
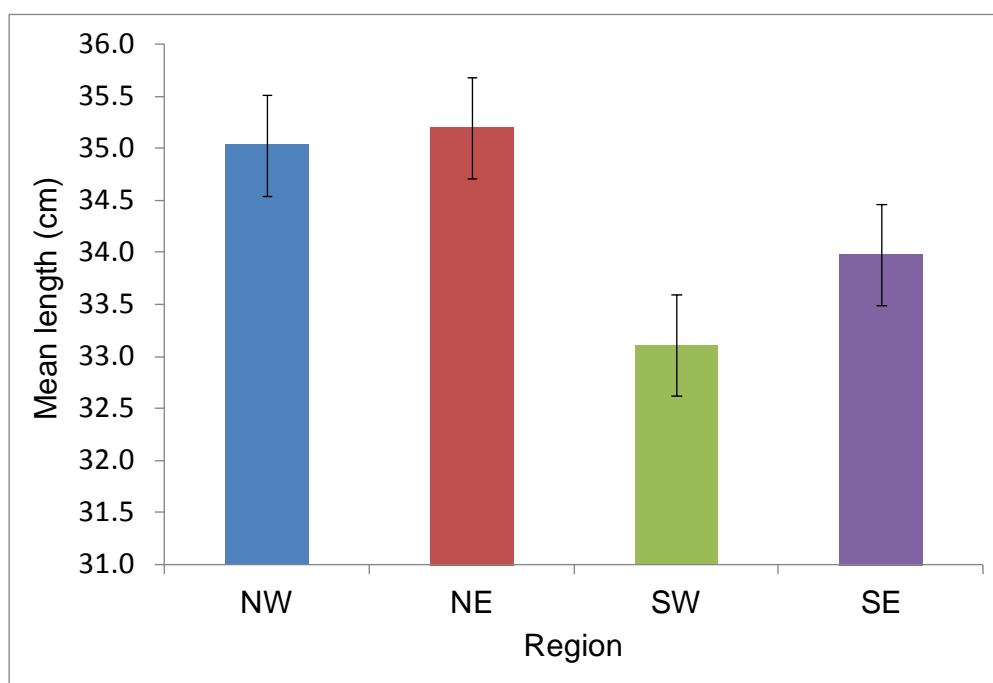
Figure 16. Mean length (±SE) (cm) of NEA mackerel in the study areas.

Table 3. Mean length (cm), weight (g) and condition factor (K) with standard deviation (±SD) based on a sub sample of 100 individuals from each of the study areas.

Region	Mean Length	Mean Weight	K
NW	35.0 ±1.5	393.5 ±51.2	0.91 ±0.07
NE	35.2 ±1.8	412.3 ±65.1	0.94 ±0.06
SW	33.1 ±1.6	353.4 ±40.9	0.97 ±0.08
SE	34.0 ±2.4	372.4 ±77.8	0.94 ±0.08

Plankton biomass

The plankton results are based on one sampling station nearest to the relevant acoustic transect. The NW region had the highest biomass of plankton per square metre (6.52 g m²), and the SW had the lowest (3.08 g m²) (Figure 17). Small plankton (<1000 μm) was present in all regions, and dominated the NW and SE samples (Figure 17). Medium plankton (1000-2000 μm) was also present in all regions, and comprised of the majority fraction in the NE sample. Large plankton (>2000 μm) was present in the NE and SW, and a very small amount in the SE (0.016 g m²). The SW did not have one particular dominant size fraction.
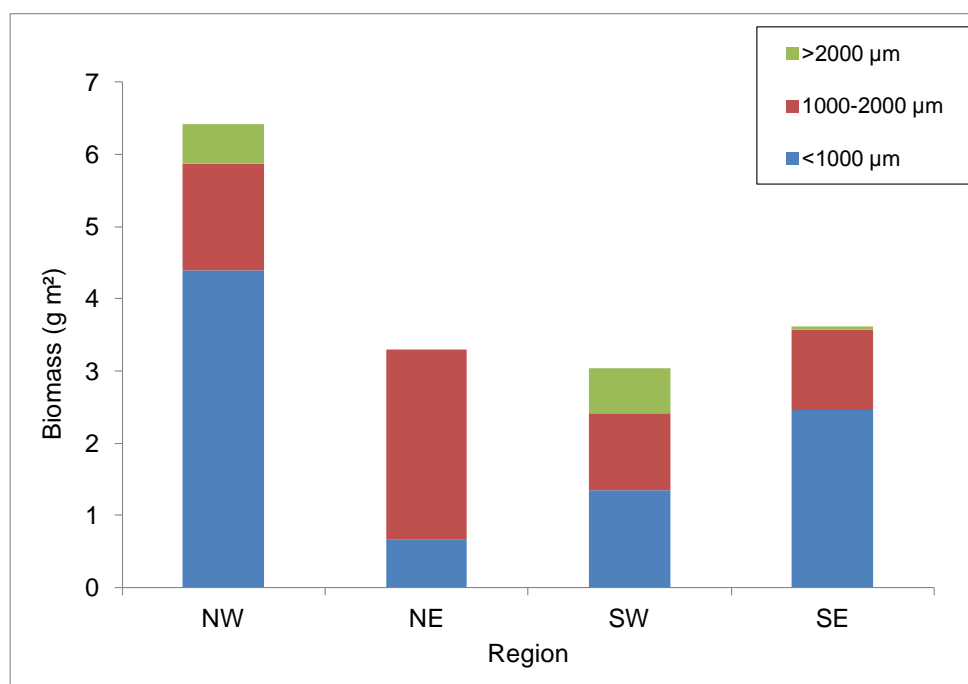
Figure 17. Plankton biomass (g m²) and size fraction (<1000 μm, 1000-2000 μm, >2000 μm) biomass within the sample from each region.

Marine mammal observations

Marine mammals were the only potential predator analysed in this study. They were observed in patches throughout the Norwegian Sea, but were not sighted along the scrutinized transects in this study (Figure 18). However, in the SE region, an individual sperm whale was sighted prior to the transect.
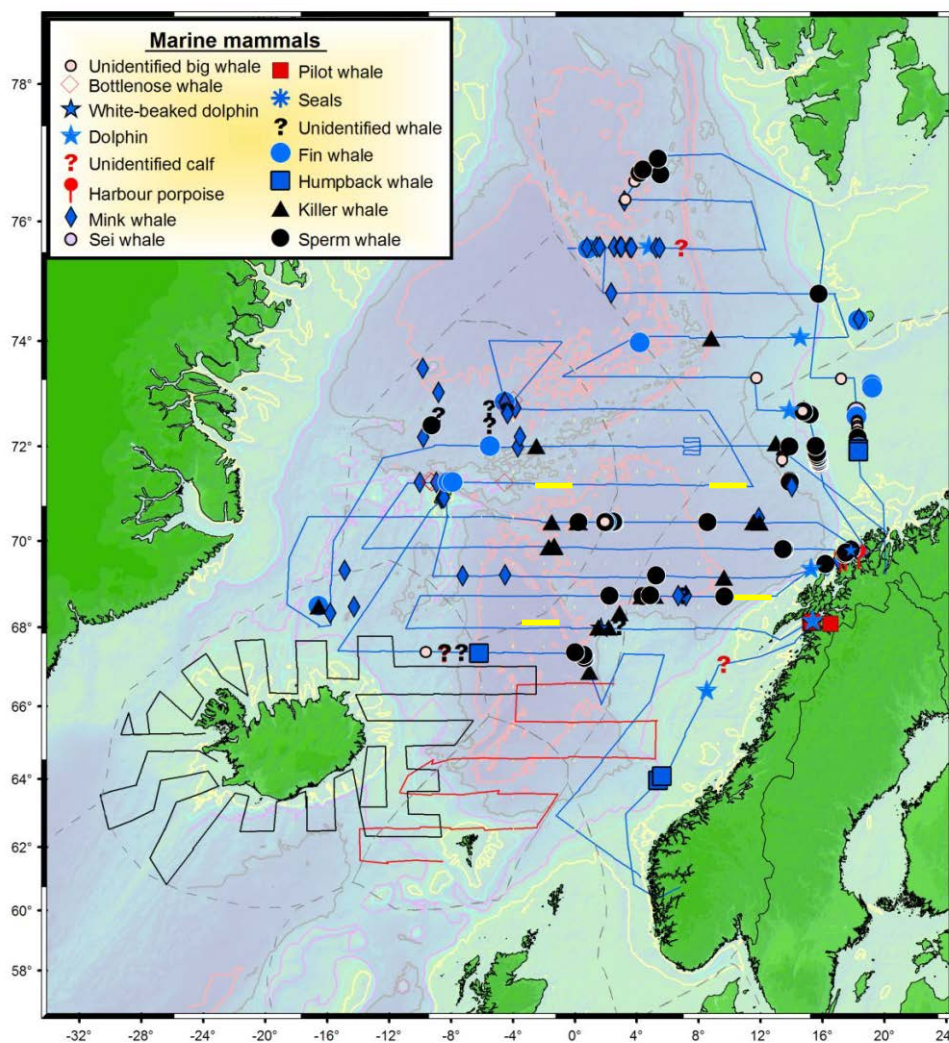
Figure 18. Marine mammals observed in the Norwegian Sea onboard M/V "Libas" and M/V "Brennholm" between stations in daylight hours, 15 July - 20 August 2010 (Nøttestad *et al.* 2010). The yellow lines indicate the location of the SONAR sampling transect.

Discussion

To the best of my knowledge, the schooling dynamics of NEA mackerel on the summer feeding migration has not been thoroughly analysed in relation to temperature, currents, and biological parameters prior to this study. Schools of mackerel flood the Norwegian Sea during the summer months for their annual feeding migration. All of the schools were detected within the upper 40 m of the water column, and most of the schools were swimming with the local prevailing current. The average mean school speed was the slowest in the NW, and significantly faster in the SW, which had a prevailing southerly current. Sea temperature, local plankton biomasses, density of conspecifics and predators are believed to affect school size, depth and swimming speed based on second-to-second individual trade-off decisions. Mackerel abundance and their schooling dynamics may therefore indicate the environmental state of the Norwegian Sea during the time of year when schooling pelagic fish are abundant.

Methodology

The survey was designed for different objectives, and was therefore not tailored specifically to the objectives of this study. The regions used in this study were chosen after the survey in an attempt to observe a gradient between north, south, east, and west based on inherent physical and biological differences. At least 50 mackerel schools were detected for a minimum of five seconds within each of the four selected study regions (NW, NE, SW, SE). The high mackerel stock in the Norwegian Sea during the summer allowed for many schools to be sampled during the survey period.

The LYBIN ray trace case study illustrated the influence of tilt angle on depth detections. Schools closer to the research vessel (e.g. < 85 m radius from the vessel) will be detected to have a shallower mean school depth, acquired from the series of school detections, than those further from the vessel. Axelsen and Misund (1997) pointed out that coupling SONAR and echosounder technology creates 3D observations of schooling dynamics for pelagic fish. Still, since mackerel are located in the upper blind zone of the echosounder close to the surface, SONAR may sometimes be the only reliable acoustic methodology to detect and track mackerel schools in summer. Individual school target tracking by multibeam SONAR will also provide more detections and thus greater accuracy in the measured school parameters (Kvamme *et al.* 2003).

The analysis of whether mackerel schools utilize STST highlighted the importance of calibrating the ADCP prior to the survey, as well as complications that can arise as a result of

having to reprocess misaligned data. The magnitude of the currents was much more reasonable in the raw data than in the reprocessed data, which provided currents up to 4 m s⁻¹. However, the direction needed to be corrected by reprocessing the data. Thus, the raw data had to be combined with the reprocessed data to accommodate more reasonable representation of the local currents.

Horizontal and vertical mackerel distribution linked to temperature

NSS herring and NEA mackerel are two highly abundant pelagic fish species performing migrations throughout the Norwegian Sea. Mackerel were distributed from the southern edge of the Norwegian Sea to as far as 75° N in July - August 2010. The majority of mackerel schools at the end of July were distributed between 67° and 72° N, including farther East along the Norwegian coast and fjords, and far west into Icelandic and Jan Mayen waters. Mackerel made up the majority of the trawl catches in most areas except along the periphery of the Norwegian Sea and surrounding waters in the west (Iceland), northwest (Jan Mayen) and northernmost regions (Bear Island) where herring dominated.

The spatial overlap between mackerel and herring within the four selected regions in my study was limited. This coincided with the low overall overlap between the two species in the entire Norwegian Sea ecosystem in July - August 2010 (Nøttestad *et al.* 2010). Utne *et al.* (2012) determined that the vertical overlap between herring and mackerel is high, but horizontal overlap was limited during the summertime from 1995 to 2006. This is probably because herring migrate through the Norwegian Sea earlier than mackerel (Broms *et al.* 2012; Holst *et al.* 2004). A major factor influencing the spatial distribution of both herring and mackerel in summertime is the oceanic front between the cold Arctic water masses in the East Iceland Current and the warmer Atlantic water in the central Norwegian Sea, which are influenced by climate variation (Misund *et al.* 1997; Varpe *et al.* 2005). During part of the summer feeding migration, herring prefer to feed in polar front areas (Nøttestad *et al.* 2007), in contrast to mackerel (Nøttestad *et al.* 1999).

In July, when mackerel have their maximum geographical distribution and expansion in the Norwegian Sea, the herring has been feeding in this ecosystem for several months. In April, the highest concentrations of herring occupy the central and eastern areas of the Norwegian Sea. These large concentrations are replaced by mackerel later in July and August, and the older herring are now distributed primarily in the northernmost part of the Norwegian Sea, west of approximately 10° E, and north of 70° N (Broms *et al.* 2012). NSS herring

distribution was found to correlate with the overwintering of *C. finmarchicus*. By the time mackerel have arrived to the Norwegian Sea, the herring have then moved farther north and west, past the 7° C isotherm and consumed the preferred stages (IV-VI) of *C. finmarchicus*, though not depleting the abundance (Melle *et al.* 2004). This west- and northward feeding migration of herring may also be influenced by fish condition (Dragesund *et al.* 1997; Nøttestad *et al.* 2004). These seasonal movements may allow mackerel to adapt and move into the Norwegian Sea in July, while both passively filter feeding and actively particulate feeding on available zooplankton concentrations.

In general, the schools occurred in the upper 40 m of the water column throughout day and night in the Norwegian Sea during my study period. NEA mackerel were distributed from 8 - 39 m depth with an average of 22 m depth. All of the schools were located above the given thermocline for each of the four regions, and occurred in waters of at least 6° C, with the majority of schools in waters between 7° - 11° C. Godø *et al.* (2004) examined aspects of schooling behaviour for mackerel during the summer feeding migration in the Norwegian Sea, but due to lack of data they were not able to substantiate the observed schooling dynamics with temperature. Therefore, this study contributes new knowledge related to physical preferences of mackerel schools. Prior to this study, 8° C was thought to be lower boundary of the preferred temperature range for NEA mackerel (Iversen 2004), but the present results indicate that this preference limit should actually be 7° C, as Castonguay *et al.* (1992) found for mackerel in the western Atlantic. In the NW, the variation in school depth, compared to the other regions, suggested that the depth distribution in this cold region was influenced by the shallower thermocline. In the warmer SE, the depth distribution of the schools was not strictly determined by temperature because the sea temperature was at least 7° C down to 160 m depth. Feeding conditions and light levels were probably the main driving forces behind the depth distribution in this region (see later).

Both the horizontal and vertical distribution of mackerel from acoustic and biological samples was found to be considerably influenced by their surrounding sea temperature. This suggests that mackerel distribution is constrained by low temperatures, both in the horizontal and vertical dimension. Temperature acts on pelagic fish as a proximate factor by affecting locomotor response, and ultimately determines the distribution (Nøttestad *et al.* 2004). Temperature preferences are main contributors in governing the large-scale distribution of planktivorous pelagic fish species (Langøy *et al.* 2012; Utne *et al.* 2012). Pelagic fish may generally move into waters slightly beyond their preferred temperature range, but ultimately

temperature will set the distribution boundary (Kvamme *et al.* 2003). Temperature may therefore be used as a proxy for maximum geographical extent for NEA mackerel during the summer by following the 6° C isotherm in the horizontal and vertical dimensions. Fish respond to temperature effects by "behavioural enviroregulation," which is when an animal adjusts its behaviour to regulate immediate environmental conditions. Mackerel utilize behavioural enviroregulation in response to changing temperature regimes both their horizontal and vertical distribution. Mackerel distribution was significantly positively correlated with temperature in accordance with an expected preference for warmer waters. Yet, mackerel are known to be able to adapt to high temperatures in its southern distribution range in more sub-tropical water masses (Uriarte and Lucio 2001) and to relatively low temperatures in the northern more Arctic waters (Nøttestad *et al.* 2013). Even though temperature often sets the physical extrinsic limit for distribution and behaviour, nonthermal factors such as photoperiod, currents, and biotic interactions may highlight the ecological importance of a temperature response (Reynolds 1977). Furthermore, nonthermal variables may act as additional proximate factors in response to temperature (Reynolds 1977).

Swimming speed and the effect of currents

The average swimming speed did not differ between the day and night in this study, which is consistent with Macy et al. (1998). Swimming speed of mackerel schools was on average 1.33 m s^{-1} with an average school speed of 1.44 m s^{-1} as a result of the prevailing currents. It could be argued that the effect of the current is relatively small, accounting for 10% of the school speed. In tank experiments, mackerel can maintain a swimming speed of 4.1 B.L. s^{-1} for at least 30 minutes at 11.7° C (Dickson et al. 2002; Wardle & He 1988); corresponding to approximately 1.44 m s^{-1} based on a 35 cm fish. School swimming speed found in this study for mackerel schools was predominantly between 0.72 and 1.79 m s^{-1} in all four regions. The mackerel schools in this study may therefore have been able to maintain their average swimming speed for prolonged periods during their feeding migration, particularly along the coastal regions as a result of warmer surrounding sea temperatures. Data accuracy of the school parameters increases with the number of pings, as schools with more than ten pings were more accurate than those with less than ten pings. Therefore, in future projects, reducing the vessel speed occasionally and/or remaining in one area, will allow schools to be tracked for longer durations, and thus, result in improved calculations of school speed and direction.

Similar results were found with NSS herring schools tracked with SONAR along the Norwegian coast (Kvamme et al. 2003).

NEA mackerel and other scombrids lack a swimbladder and must swim constantly at a speed of at least 0.4 B.L. s^{-1} to avoid sinking and maintain a constant depth (Wardle & He 1988), which is approximately 0.14 m s^{-1} based on a 35 cm long mackerel. The results coincide with earlier findings, and suggest that mackerel during summer in the Norwegian Sea maintain their movements above minimum swimming speed in order to remain in the upper most productive water masses and avoid sinking to deeper waters. The school speed was significantly higher in the SW compared to the NW and NE, which coincided with warmer sea temperatures. Decreased temperature can slow locomotor responses in fish and act on a fish through the central nervous system (Dickson et al. 2002). Fish are provided higher muscle fibre contraction in warmer temperature, as well as by a more direct action on the metabolism with slower metabolism in lower temperatures (Harden Jones 1968). Axelsen and Misund (1997) observed that NSS herring schools swam faster when the average sea temperature was higher, resembling the results on mackerel in this study. Other previous studies have also stated that metabolic rate and maximum sustainable swimming speed generally increase with temperature (Dickson et al. 2002).

The prevailing ocean currents in the NW, NE and SE regions of the Norwegian Sea were in a northern direction, whereas the current direction in the SW was predominantly to the south. Interestingly, the majority of mackerel schools were found to be swimming with the current, even in the SW. Schools rely on the prevailing currents during long-distance migrations to reduce energy expenditure via STST, in which schools swim with the prevailing current. Off the coast of North America, mackerel have previously been found to utilize the tidal cycle to reach their spawning grounds (Castonguay and Beaulieu 1993). The northward zooplankton production cycle forces pelagic planktivorous fish to follow the production cycle of zooplankton, and the concurrent prolonged day length increases the feeding period for visually feeding planktivorous fish (Nøttestad et al. 1999). Mackerel may take advantage of the currents accordingly to actively follow zooplankton prey in the summer migration to reach higher latitudes.

Since day length increases the farther north mackerel migrate, including midnight sun in the northernmost areas, mackerel as a visual predator would benefit energetically by migrating to and staying in areas where day length is longest and where plankton production is high simultaneously (Nøttestad et al. 1999). Larger fish were consistently caught in the north,

supporting the length-based hypothesis for feeding migrations in pelagic fish proposed by Nøttestad et al. (1999) and later confirmed (Utne et al. 2012; Nøttestad et al. 2013). The larger mackerel are capable of swimming greater distances probably because they are more efficient feeders (Iversen 2004) and have greater tail propulsion (Videler 1991). Large fish are also better at foraging than small individuals because they have greater visual and swimming capabilities, and therefore may out-compete the smaller individuals in direct competition for food items (Hoare et al. 2000).

NEA mackerel in the SW were moving in a southern direction with the prevailing current along the cruise track. The SW data on both current and swimming direction may indicate a meso-scale oceanic eddy. The SW region was characterized by smaller fish, smaller school biomasses, and a predominantly southwards direction by mackerel. Oceanic meso-scale eddies are considered oases for marine life because they circulate nutrients (Godø et al. 2012). Thus, eddies can create patchy and highly clumped distributions of organisms (Parrish and Edelstein-Keshet 1999). This particular area may have had a relatively high amount of plankton being trapped inside an eddy. The closest plankton sampling station was prior to the SONAR transect, so concurrent plankton data were not available in this particular area. Nevertheless, such eddies can circulate available plankton for prolonged periods (Godø et al. 2012), and the best feeding strategy for pelagic fish may be to remain in an area as long as the feeding conditions are sufficient (Kvamme et al. 2003).

Food availability and feeding behaviour

The average plankton biomass throughout the Norwegian Sea was 4.71 g/m² during the survey period. Plankton concentrations varied between the four regions from 3.08 g/m² to 6.52 g/m²; the plankton abundance was nearly twice as high in the NW compared to in the SW. Mackerel in the north were swimming slower than in the south, indicating that swimming speed was related to local food abundance. Although there were not enough plankton samples to make substantial statistical analyses, these findings support Macy *et al.*'s (1998) tank experiments, which found that fish swam slower at high food concentrations and faster at low food concentrations.

The copepod *C. finmarchicus* is an important prey item for NEA mackerel (Iversen 2004). Earlier studies in the Norwegian Sea has suggested that *C. finmarchicus* is a valued prey species for mackerel during the summer months, although not the only one (Prokopchuk and Sentyabov 2006; Langøy *et al.* 2012). During summer, *C. finmarchicus* faces large

fluctuations in both phytoplankton biomass and predator abundance (Dale and Kaartvedt 2000), and they normally begin to descend to deeper waters for overwintering by late July (Kaartvedt 2000). Planktivorous fish may affect the timing of spawning and descent and hence the number of generations per year (Kaartvedt 2000).

The plankton samples in this study were comprised of zooplankton of various size fractions. The small sized zooplankton dominated, followed by medium sized zooplankton. Smaller sized zooplankton (< 1000 μm) was the most abundant in the NW, but there were also some large zooplankton (> 2000 μ). The large percentage of small plankton in the NW suggests heavy selection by pelagic fish that had migrated through that area prior to sampling. Intense selection pressure on larger plankton species by planktivores will eliminate the large species, and the smaller species will predominate (Brooks and Dodson 1965). Still, mackerel are efficient at utilizing small planktonic prey. Langøy *et al.* (2006) found that small copepods (< 1000 μm) were numerous in the plankton samples throughout the Norwegian Sea, but were not dominant in mackerel stomach samples, suggesting that mackerel performed selective feeding.

School size, patchiness and competition

The mackerel schools in this study were generally small and estimated school biomass ranged from 200 kg to approximately 10000 kg in the four study regions. The trade-off between safety in numbers and feeding competition between co-specifics probably limit the school size of NEA mackerel during the active feeding period. Group foraging can increase the feeding rates of individuals whenever food is scarce and patchily distributed, since animals in groups find and consume food faster than lone individuals (Clark & Mangel 1986), and larger schools find food faster than smaller schools (Ward *et al.* 2011). Yet, feeding efficiency is decreased when a school is too large as a result of increased competition over the available food.

We can assume that the faster schools were denser than the slower schools, denser schools are more elongated, and slower schools are less polarized and more oblong in shape (Misund 1993; Pitcher and Parrish 1993; Himelrijk 2010). Group size and shape fluctuate as a function of resources, physiology, predominant activity, and sensing limitations (Parrish and Edelstein-Keshet 1999). Hunger and low predation pressure tends to loosen a strict school structure (Misund 1993; Mackinson *et al.* 1999), whereas high predation pressure increases the school size and density (Nøttestad *et al.* 2002). School size and structure is an obvious response to predation risk (e.g. Fréon *et al.* 1992).

Only an individual sperm whale was sighted near the beginning of the SE transect, indicating a low predation pressure from marine mammals in all of the four regions. Sperm whales do not normally constitute any immediate threat to pelagic schooling fish. Otherwise there were no sightings of marine mammals along or in the vicinity of any of the four transects. Many of the marine mammals mainly occurred in the central Norwegian Sea. A reduced amount of marine mammal predators over the years have been found in the Norwegian Sea (Nøttestad *et al.* 2013 submitted) and may have reduced the overall predation pressure on the pelagic fish stocks. Although the distribution of killer whales has been found to significantly overlap with mackerel in the Norwegian Sea (Nøttestad *et al.* 2013 submitted), the relatively small sized schools observed during the summer, indicates that the mackerel schools had low overall predation pressure and did not have to form larger schools to compromise individual feeding opportunities.

Meso-scale observations in this study revealed schools were patchy and swimming against the current. In the SW, the majority of the schools were small (less than 1350 kg on average) and the individuals within those schools were also the smallest of the four regions. The schools were more numerous in the SW, with nearly double the amount of schools along 10 km of transect compared to the other regions. Therefore, the SW had the shortest average nearest neighbour distance of the four transects. Low plankton abundance and lack of predators may have allowed for the schools to form small and loose schools in the SW, yet still remaining in proximity of a neighbouring school to join when necessary.

Diurnal behaviour

The NE region consisted of both a day and night segment 31 July - 1 August 2010 at approximately 71° N. This segment was the only suitable cruise track with "good data" in terms of multibeam SONAR data quality and pelagic trawl hauls with mackerel comprising the majority of the planktivorous fish species. Nearest neighbour distance did not differ between day and night, but schools were found to be smaller and deeper at night compared to during the day. Because of the depth range of the data, the statistical results illustrated that the schools were deeper at night than during the day; however, this difference was only by approximately four meters, which is relatively minor in terms of the possible depth range where the bottom depth exceeds 500 m. Furthermore, the following plankton station indicated greater plankton abundance farther east, so the mackerel observed during the night may have been foraging deeper in this area. Mackerel might not perform DVM during the summer;

rather, their vertical and horizontal distribution is based on prey abundance at these high latitudes with the prolonged daylight period. Approximately 20 - 24 hours of daylight at high latitudes in the Norwegian Sea should ensure more or less continuous visual feeding opportunities for the mackerel (Langøy *et al.* 2006).

Due to the midnight sun at high latitudes during spring and summer, the distinction between day and night is so reduced that the cues needed to initiate migrations could leave the copepods without a safe interval for feeding, thus eliminating the advantages of DVM (Dale and Kaartvedt 2000). The visual range of planktivores is highly sensitive to illumination (Dale and Kaartvedt 2000), and the midnight sun is a benefit for mackerel, allowing extended feeding periods at higher latitudes for these effective visual predators (Nøttestad *et al.* 1999). According to Dale and Kaartvedt (2000), the older stages of *C. finmarchicus*, preferred by mackerel, underwent DVM during the summer in the Norwegian Sea; however, this behaviour was scarce at high latitudes in oceanic waters. Still, their data displayed flexibility in copepod DVM behaviour depending on different environmental conditions.

Mackerel and herring possess very similar characteristics and the potential to occupy the same niche (Skjoldal *et al.* 2004; Dommasnes *et al.* 2004). Herring conduct DVM with varying intensity throughout the year. This is also the case for mackerel, but to a lesser extent during the summer. It can be speculated that mackerel do not have the need to perform DVM due to the midnight sun and limited predation pressure. They thrive in the upper layers of the water column where light improves their abilities to constantly feed on large copepods. Pitcher (1993) recognized that within the scombrids, several species do not display well-defined activity periods. Additional diurnal studies of mackerel behaviour should be performed during the summer to better elucidate the diel vertical behaviour and depth preferences of actively feeding mackerel schools.

Ecological context

The NW displayed a shallower thermocline, and thus cooler sub-surface sea temperatures due to the influence of the Arctic front. The thermocline depth limited the maximum depth of the schools to approximately 28 m. These cooler waters could create an optimal environment for higher biomass of larger zooplankton from input of nutrient-rich Arctic waters. Larger mackerel formed larger schools than compared to in the other regions and swam north against the current to feed in this richer and more productive region. The relatively high food abundance should reduce local competition and allow the schools to be larger than in the

southern areas with lower prey abundance. The lower range of swimming speeds in the NW could be due to a combination of the lower temperature and higher zooplankton abundance. The NE was characterized by even slightly larger fish than those in the NW, and slightly smaller average school biomass, probably in connection with lower local zooplankton biomass compared to in the NW. The deeper thermocline depth may have allowed fish to forage at slightly deeper depths where zooplankton abundance was possibly greater than in slightly shallower depths.

Mackerel occurred significantly deeper in the SW than the other regions, although the depth where temperature reached 7° C was the same as in the NE. The SW schools swam faster and in much smaller aggregations, which contained the smallest individuals of the four regions. The zooplankton biomass was the lowest in this region. In general, the mackerel schools in the south swam faster than those in the north probably due to sub-optimal feeding conditions and warmer sub-surface sea temperature. Mackerel in the SE swam in various directions in search of more food patches, where as the schools in the SW swam south within a meso-scale eddy that possibly contained rich concentrations of zooplankton.

The spatial distribution of mackerel in each region probably reflected dynamic trade-offs between available food in combination with potential predator threat and experienced temperature regime. Lack of potential marine mammal predators in all four regions during the survey period may have resulted in smaller and looser schools adapted to limited food. In the north, mackerel schools were large; a common response to predation pressure. However, food abundance was also high in the NW so it was probably not necessary to dissolve into smaller schools. In particular, in the SW the schools were relatively close together and in small aggregations that could be prepared to join a neighbouring school in response to predator attacks. Even without predation pressure in these four regions, the schools in the north probably traded off safety over maximizing feeding as a result of close to record low levels of zooplankton abundances in the Norwegian Sea in 2010 (Huse *et al.* 2012).

Conclusions

Given that NEA mackerel is one of the most important ecological and economical fish species in the Atlantic Ocean, there is notably little knowledge available regarding schooling behaviour and ecology of this species. This study has produced new data on parameters such as school size, depth, swimming speed, direction, and clustering in relation to prevailing

current systems. The observed schooling dynamics have shed new light on the ecological situation of mackerel schools during their extensive feeding migrations at high latitudes.

Large stocks of commercially important pelagic fish conduct extensive feeding migrations through the Norwegian Sea in preparation for the oncoming overwintering period. Improved knowledge of the schooling dynamics of NEA mackerel will enable scientists to predict their patterns for better understanding their ecological role in marine ecosystems. Acoustic observations using modern multibeam SONARs coupled with biological sampling at different trophic levels and oceanographic measurements, provides new genuine insight into the highly dynamic pelagic ecosystem in the Norwegian Sea. This thesis illustrated the gain by systematic use of fisheries SONAR in ecosystem surveys, as well as the drawbacks that can improve data collection, efficiency, and accuracy. The horizontal and vertical distributions, swimming direction and speed, and diurnal behaviours of the summer feeding migration exposed in this study provide a basis for more efficient SONAR detection and quantification of swept area for abundance estimation of NEA mackerel by standardized pelagic trawling.

In future projects one or more of the following tasks should be considered: 1) reduce vessel speed to perform target tracking of mackerel schools lasting at least 60 seconds for a more accurate estimation of swimming speed and direction; 2) choose a smaller dedicated study area and remain in one area for prolonged periods to design experimental field studies, including hypothesis driven behavioural and ecological process studies on diurnal time scales; 3) include data from the southern distribution of mackerel in the North Sea and west of the British Isles in summer in direct comparison with concurrent data from the Norwegian Sea to evaluate regional differences between two marine ecosystems; and 4) calibrate the ADCP prior to the survey to have more accurate direction and magnitude data for analysis of STST.

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Appendices

Appendix 1. Function developed in R to determine the altitude of the sun during the summer at high latitudes where daylight hours are prolonged.

```
alt.of.sun <- function(min=x$min, hour=x$hour, day=x$day,
month=x$month,
                  lat=x$lat, lon=x$lon, x=NULL)
{
    # altitude of sun
    UTC <- hour+min/60
    CET <- (UTC + 1) %% 24
    dayadd <- cumsum(c(0,31,28,31,30,31,30,31,31,30,31,30,31))
    cumday <- day + dayadd[month]
    K1 <- (lon - 15 - 0.4083 * sin(0.0172 * (cumday-80))
                                    - 1.7958 * cos(0.0172 *
(cumday-80))
                                    + 2.4875 * sin(0.0344 *
(cumday-80)))
    SST <- ((CET*15) + K1) / (180/pi)
    dkl <- asin(0.3979 * sin((0.0172 * (cumday - 80))
            + 0.03346 * (sin(0.0172 * cumday) - 0.98112)))
    Brq <- lat/(180/pi)
    sinush <- (sin(dkl)*sin(Brq)) -
(cos(dkl)*cos(Brq)*cos(SST))
    alt.of.sun <- asin(sinush) * (180/pi)

    # time when altitude of sun = asun.0
    asun.0 <- 0
    K2 <- (sin(dkl)*sin(Brq) - sin(asun.0/(180/pi))) /
(cos(dkl)*cos(Brq))
    K2[K2 < (-1)] <- -1        # polar night
    K2[K2 > ( 1)] <-  1        # midnight sun
    SST0 <- acos(K2)
    CET0 <- (SST0 * (180/pi) - K1) / 15
    UTC0 <- (CET0 - 1) + 24*(CET0 < 1)
    sun.rise <- UTC0%%24
    list(alt.of.sun=alt.of.sun, sun.rise=sun.rise)
}
```

Appendix 2. SH90 SONAR pre-processing settings used per region for automatic detection of schools.

Region	NW	NE	SW	SE
Tilt (degrees)	-4 to -6°	-6°	-4°	-6°
Sampling radius (m)	85 - 300	85 - 300	85 - 300	85 - 300
Alpha	0.7	0.1	0.7	0.5
Alpha radius (number of pixels used)	1	2	2	1
Time median radius (number of pings on either side)	2	3	2	2
Threshold	0.4	0.3	0.8	0.3
Min max Sv	101.5	100.5	100.5	101.3
Min area (m)	10	10	10	10
Max area (m)	20000	20000	20000	20000
Max aspect ratio	16	16	16	16

Appendix 3. R syntax using per ping data to calculate a more accurate mean fish school speed and direction.

```
xps$Speed<-as.numeric(as.character(xps$Speed)) #per school to compare
xps$Heading<-as.numeric(as.character(xps$Heading)) #per school to
compare

# Reshape time to R format
dt2<- paste(x$Date, x$Time)
dt3<-strptime(dt2, "%Y-%m-%d %H:%M:%OS")
dt3<-format(dt3, format = "%Y-%m-%d %H:%M:%OS2")
options(digits.secs = 2)
x$dt4 <- as.POSIXct(dt3,format="%Y-%m-%d %H:%M:%OS",origin="1960-01-
01", tz="GMT")

# Define a function that converts compass headings (bearings,
azimuths) into geometric angles for trigonometry.
# Examples:  For a heading = 0 degrees, vector points due north, and
angle = 90 deg.
# For a heading = 90 degrees, vector points east, and angle = 0 deg.

convert.heading.angle <- function(heading) {
num.heading <- length(heading)
angles <- rep(NA, num.heading)
for(i in 1:num.heading) {
    angles[i] <-
      ifelse((heading[i] >=0 && heading[i] <= 90), 90 - heading[i],
```

```
                    ifelse((heading[i] >=90 && heading[i] <= 180), 360 -
    (heading[i] - 90),
                        ifelse((heading[i] >=180 && heading[i] <= 270),
    180
    + (270 - heading[i]), 90 + (360 - heading[i]))
                        )
                )
      }
    return(angles)
    }  # end of convert.heading.angle()

    #create variables for loop
    pId<-unique(x$Id)
    lat0<-vector(length=length(unique(x$Id)))
    lon0<-vector(length=length(unique(x$Id)))
    posMet<-vector(length=length(unique(x$Id)))
    deltaSec<-vector(length=length(unique(x$Id)))
    res<-data.frame()

    #Calculations made from mean position (lat-long)
    library(SoDA)
    for(i in 1:length(unique(x$Id))){
    Subindex<-(pId[i])
    lat0<- mean(x$Center.lat[x$Id==Subindex])
    lon0<- mean(x$Center.lon[x$Id==Subindex])
    posMet<-geoXY(x$Center.lat[x$Id==Subindex],x$Center.lon
    [x$Id==Subindex],lat0,lon0,unit=1) #distance (m) for each detection
    to mean position

    deltaSec <- as.numeric(x$dt4[x$Id==Subindex]) -
    as.numeric(min(x$dt4[x$Id==Subindex]))#delta in time (sec)

    fit_X<-lm(posMet[,1]~deltaSec) #linear curve fitting  of distance in
    lat and long by time
    fit_Y<-lm(posMet[,2]~deltaSec)

    a<-fit_X$coefficients[[2]]     #regression slopes
    o<-fit_Y$coefficients[[2]]
    Vel<-sqrt(a^2+o^2)                  #velocity from vectors
    Theta<-atan2(o,a)*(180/pi)       #Theta angle in degrees
    Bea<-convert.heading.angle (ifelse(Theta<0,Theta+360,Theta)) #Use
    function from Heading to Bearing
    res<-rbind(res,c(Subindex, Vel, Bea))#All together in one file
      }
colnames(res)<-c("Id2","Vel","Bea")
```