



Original Article

Feeding strategy of mackerel in the Norwegian Sea relative to currents, temperature, and prey

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High abundance of Northeast Atlantic mackerel (*Scomber scombrus* L.), combined with limited food resources, may now force mackerel to enter new and productive regions in the northern Norwegian Sea. However, it is not known how mackerel exploit the spatially varying feeding resources, and their vertical distribution and swimming behaviour are also largely unknown. During an ecosystem survey in the Norwegian Sea during the summer feeding season, swimming direction, and speed of mackerel schools were recorded with high-frequency omnidirectional sonar in four different regions relative to currents, ambient temperature, and zooplankton. A total of 251 schools were tracked, and fish and zooplankton were sampled with pelagic trawl and WP-2 plankton net. Except for the southwest region, swimming direction of the tracked schools coincided with the prevailing northerly Atlantic current direction in the Norwegian Sea. Swimming with the current saves energy, and the current also provides a directional cue towards the most productive areas in the northern Norwegian Sea. Average mean swimming speed in all regions combined was ~ 3.8 body lengths s^{-1} . However, fish did not swim in a straight course, but often changed direction, suggesting active feeding in the near field. Fish were largest and swimming speed lowest in the northwest region which had the highest plankton concentrations and lowest temperature. Mackerel swam close to the surface at a depth of 8–39 m, with all schools staying above the thermocline in waters of at least 6°C. In surface waters, mackerel encounter improved foraging rate and swimming performance. Going with the flow until temperature is too low, based on an expectation of increasing foraging rate towards the north while utilizing available prey under way, could be a simple and robust feeding strategy for mackerel in the Norwegian Sea.

Keywords: behaviour, currents, feeding, multibeam sonar, NEA mackerel, Norwegian Sea.

Introduction

Migrations of fish are often associated with exploitation of spatially and temporally varying food resources (Hoar, 1953; Harden Jones 1968; Arnold and Cook, 1984; Russell, 2008). Less than 0.01% of all fish species make long-distance migrations, but these species are also highly abundant and of substantial economic value worldwide (UNCLOS, 2009). Long-distance migrations and extensive distributions are key features of pelagic planktivorous fish species (Nøttestad *et al.*, 1999; Skjoldal *et al.*, 2004; Trenkel *et al.*, 2014). The Norwegian Sea provides a large and productive feeding ground for pelagic fish in late spring and summer (Skjoldal *et al.*, 2004; Huse *et al.*, 2012; Utne *et al.*, 2012). Mackerel (*Scomber*

scombrus L.) is a pelagic schooling fish, and the population of Northeast Atlantic (NEA) mackerel now makes extensive northward feeding migrations in the Norwegian Sea (Nøttestad *et al.*, 2016). The population has rapidly increased in abundance and expanded its geographic distribution during the last decade (Nøttestad *et al.*, 2016). Mackerel has recently been recorded as far north as Svalbard (Berge *et al.*, 2015). The recent rapid increase in stock size of mackerel has probably increased the intra- and interspecific competition for limited food resources (Olafsdottir *et al.*, 2016). Increasing temperature (Skagseth and Mork, 2012) and changing prey conditions and concentrations during the last 10–15 years in the Norwegian Sea (Skjoldal *et al.*, 2004; Prokopcuk and

Sentyabov, 2006; Huse *et al.*, 2012) may have forced mackerel to expand their feeding migration and distribution. Thus, a major driving force behind the great expansion of mackerel in the Norwegian Sea and surrounding waters could be limited available food resources, leading to pronounced density-dependent growth in the mackerel stock (Olafsdottir *et al.*, 2016). A temperature $\sim 8^{\circ}\text{C}$ has earlier been suggested to be the lower boundary of the preferred temperature range for NEA mackerel (Iversen, 2002, 2004), which may set the outer borders of maximum distribution of mackerel.

The changing distribution and migration patterns of NEA mackerel raise the question how the fish exploit the spatially varying feeding resources in the Norwegian Sea. In spring and summer, higher latitudes provide higher production of phyto- and zooplankton (Melle *et al.*, 2004; Rey, 2004) and a longer feeding period for visual feeders like mackerel (Nøttestad *et al.*, 1999). It is not known if and how mackerel localize the best feeding habitats, taking into account the energy costs of moving and the constraints with low temperatures in the northern part. Herring (*Clupea harengus* L.) is believed to use predictive orientation mechanisms based on both genetically controlled migration tendencies and learning to localize the western productive front between Arctic and Atlantic waters in the western Norwegian Sea (Fernö *et al.*, 1998). However, mackerel has a much wider geographical distribution, temperature range, and habitat use in the North Atlantic and is not specialized to utilize the food resources in the Norwegian Sea.

The energetic costs of migration in mackerel can be offset by swimming with the tidal currents (Nøttestad *et al.*, 1999; Godø *et al.*, 2004) or by taking advantage of mesoscale eddies (Simons *et al.*, 2015) in the Norwegian Sea and along the Norwegian coast (Orvik and Nüiler, 2002; Godø *et al.*, 2012). The Norwegian North Atlantic Current (Nw NAC) transports warm water in offshore waters and up along the coast of Norway, whereas cold Arctic water is brought south at the western border of the Norwegian Sea (Blindheim, 2004; Skjoldal *et al.*, 2004), but it is not known whether mackerel utilize these currents for long-distance transportation.

NEA mackerel is one of the most ecologically and economically important fish species in the Atlantic Ocean (Trenkel *et al.*, 2014), but there is notably little knowledge about its spatial dynamics, particularly at the school level. Mackerel lack a swimbladder and are difficult to detect with acoustic methods, and small loosely aggregated mackerel schools close to the surface are in the echosounder acoustic blind zone (Tenningen *et al.*, 2003; Simmonds and MacLennan, 2005). However, omnidirectional sonar has been successfully used to record migratory behaviour of schooling fish (Nøttestad *et al.*, 1996, 2004, 2007; Brehmer *et al.*, 2006), and high-frequency omnidirectional sonars have even better spatial resolution, permitting studies of mackerel behaviour (Godø *et al.*, 2004).

The main objective of this study was to investigate the swimming direction and speed of mackerel schools in the Norwegian Sea relative to the instantaneous and prevailing currents. We tested the hypothesis that mackerel would utilize the north-flowing currents to migrate to areas of the Norwegian Sea that are considered most productive. We also studied school behaviour in the different regions relative to temperature, zooplankton abundance and composition, as well as the depth distributions relative to local temperature.

Material and methods

Study area

Biological, oceanographic, and acoustic data were collected from an ecosystem survey conducted in the Norwegian Sea and surrounding

waters in July–August 2010. The combined purse-seining and pelagic trawling vessel MV “Brennholm” was used in this study. Four geographically separate regions from the predetermined cruise tracks were the focus for quantitative analysis: northwest (NW), northeast (NE), southwest (SW), and southeast (SE) (Figure 1). These regions were selected based on geographical separation in terms of latitude, longitude, sonar data quality, and mackerel abundance.

Current speed and direction

Current speed and direction were continuously measured with an RDI vessel-mounted acoustic Doppler current profiler (Teledyne RD Instruments, Inc.) at 75 kHz on narrowband with a 30° beam angle. Current speed and direction were collected in 5-min averages at 16-m depth bins. To avoid measurement noise often present in the top bin, we used the mean of bins 2 and 3 (29–62 m) that provided a good measure for the upper ocean currents. We used the data collection system VmDas, version 1.46.5 (Teledyne RD Instruments, Inc.). The ADCP data were post-processed in CODAS (http://currents.soest.hawaii.edu/docs/adcp_doc/index.html). There was no bottom track for direction reference because of very deep bottom depths, but high-quality navigation data resulted in good quality current measurements.

Temperature and plankton biomass

Temperature was recorded at ca. every 60 nautical miles at a predetermined sampling station every 1 m in the water column from the surface to a maximum depth of 500 m with an SAIV SD200 (SAIV A/S) conductivity, temperature, and depth (CTD) sensor. The depth of the 8°C isotherm was analysed in each region and compared with the mean school depths.

Zooplankton sampling was performed along with the CTD stations ~ 60 nautical miles apart. A WP-2 net (56 cm in diameter) with a $180\text{-}\mu\text{m}$ mesh size was hauled from a depth of 200 m to the surface at 0.5 m s^{-1} . The sampling range from 0 to 200 m was chosen based on the depth ranges of mackerel and other pelagic species that were the focus of the survey. This range is also the international standard for WP-2 net hauls for the International Council for the Exploration of the Sea (ICES). The samples were split into two equal parts on-board, with one preserved with formaldehyde and the second dried. Before drying, the samples were divided into size fractions (< 1000 , $1000\text{--}2000$, and $> 2000\text{ }\mu\text{m}$) by sieves filtering mesh sizes 2000, 1000, and $180\text{ }\mu\text{m}$, weighed, dried, and weighed again at the laboratory after the survey.

Biological data

Pelagic sampling was done with a large pelagic trawl towed 160–200 m behind the vessel with a vertical opening of 30–35 m and a width (distance between the trawl wings) of 55–65 m. Cruising speed between stations of predominantly 10.0 knots was reduced to 4.2–5.3 knots during trawling. Standardized pelagic trawling close to the surface for 30 min took place after a CTD profile and plankton station. Trawl data verified that mackerel was the dominant species in the area of scrutinized acoustic data and provided information on fish length and weight. Fish were sorted by species on-board after trawling, and total weight was recorded using Fishmeter measuring tools (Scantrol). 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.*, 2012).

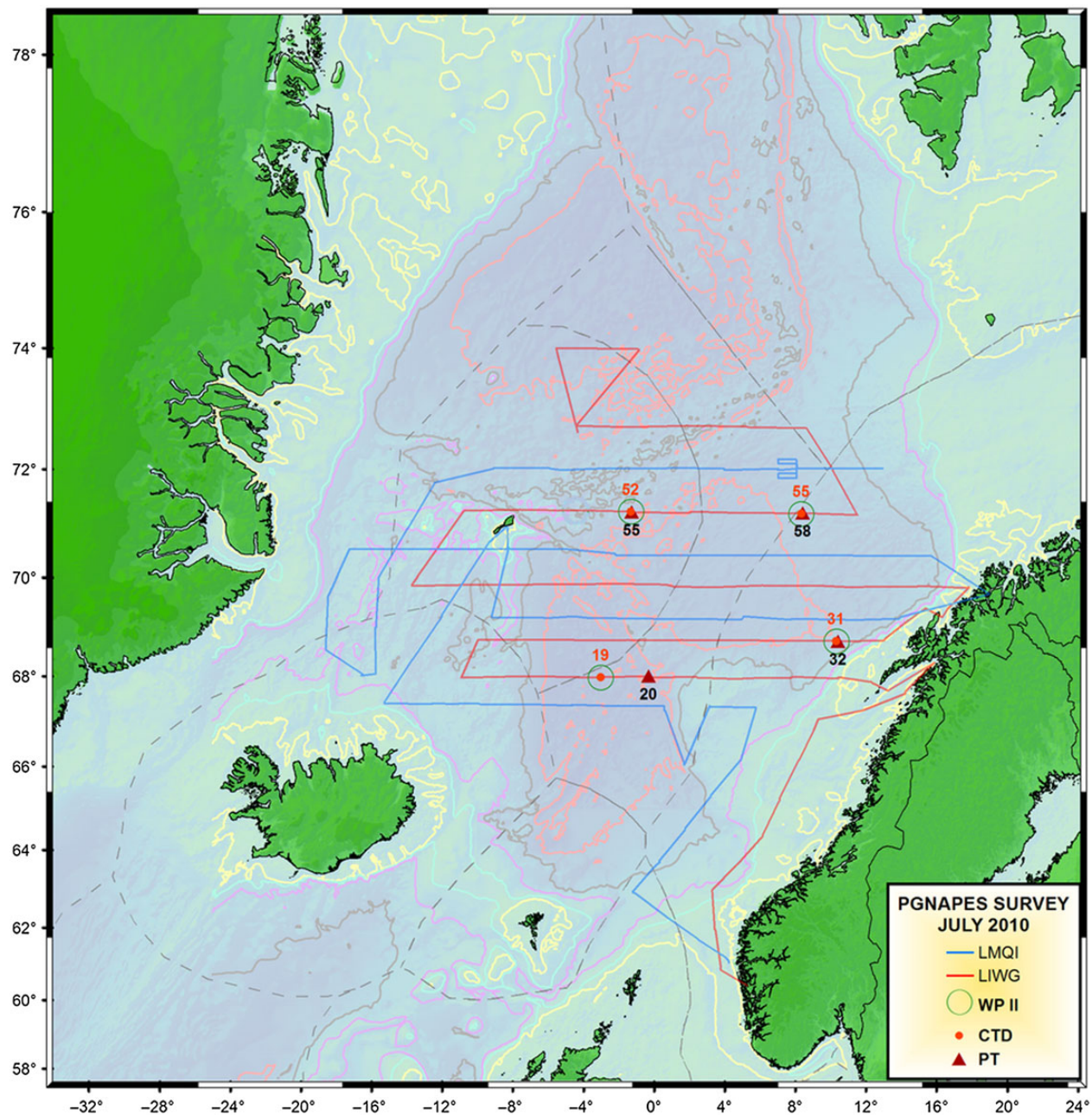


Figure 1. Cruise tracks for MV “Brennholm” (red) with pelagic trawl (PT), CTD, and plankton sampling stations (WP II) and their corresponding identification number in proximity to the transects used for sonar scrutinizing.

Acoustic data

Acoustic data were continuously recorded during the survey, but analyses of mackerel schools were only made in four geographically separate areas and only during daylight hours. The trawl catch from the nearest occurring pelagic trawl station confirmed that mackerel was the species being detected (at least 90% mackerel in all trawl hauls). Sonar data were recorded with Simrad SH80 multibeam omnidirectional sonar with a standard operating frequency of 116 kHz and 8° horizontal and 9° vertical opening angles. The sonar was operated using a 360° horizontal fan tilted down 4°. The tilted angle and range was set to obtain school detection close to the surface, minimizing surface reverberation echoes. Moreover, sound-speed profiles were used to compute realistic

sonar ray trace plots with the acoustic ray trace model Lybin (Mjølness, 2000).

Large-scale Survey System (LSSS) (www.marec.no) was used for post-processing raw acoustic data (Korneliussen *et al.*, 2006; Korneliussen, 2010). A module in the programme PROFOS can replaying and filtering raw data and distinguishing schools from noise. The preprocessing function allowed for bypassing the time-consuming process of scrutinizing the sonar manually.

To minimize potential vessel avoidance and allowing analyses of schools exhibiting natural undisturbed behaviour (Misund *et al.*, 1997), only schools within a radius of 85–300 m from the vessel were used. Furthermore, detections were excluded from the analysis based on the following criteria: (i) detections consisting of ≤ 4

consecutive pings, (ii) schools not having a “biologically reasonable” speed (ca. 1–6 BL s⁻¹, see Godø *et al.*, 2004), and (iii) schools appearing as noise caused, for example, by large waves. We excluded swimming speed measured to be >3–7 m s⁻¹ (>6 BL s⁻¹).

After the sonar data were scrutinized, PROFUS provided means on the following parameters using the ping data for each school: (i) geographical position of the school’s centre of mass (longitude and latitude maximum and minimum), (ii) depth (m) providing vertical distribution, and (iii) school speed (m s⁻¹) and direction (°). The number of pings of the detected school (number of seconds the school was detected) and time and date of the first and last detections were also recorded.

Mackerel school velocity relative to current

LSSS school output generated the speed and direction per mackerel school based on 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 taking ping-by-ping data to calculate 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. School direction and speed were 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>) presenting class intervals of 15° for the mean school direction in each region. Feather plots were used to illustrate school direction (arrow direction) and speed/velocity (arrow length).

The corresponding mackerel schools were matched with the local current from the ADCP measurements based on the time they were sampled. There was some distance (100–300 m) between the tracked mackerel schools by sonar and the current measurements originating in the hull of the vessel.

Statistical analysis

The statistical programme 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 dataset. Parametric tests (linear regression analysis, analysis of variance (ANOVA), and the Tukey *post hoc* test) were used in this analysis. The Tukey *post hoc* test was used to compare school parameters (depth and swimming speed) between regions. Non-parametric tests were used in cases when there were cases of deviation from normal distribution. All the statistical tests assumed 5% significance (95% probability).

Results

Mackerel length and weight

Mean length, weight, and condition factor (*K*) for NEA mackerel in the four different areas are shown in Table 1. Fish were larger in the north with significant differences in both length and weight between the north and the south (ANOVA, $p < 0.01$). Fish condition was

Table 1. Mean length (cm), weight (g), and condition factor (*K*) with standard deviation (\pm s.d.) based on a subsample of 100 individuals from each of the study areas.

Region	Mean length (\pm s.d.)	Mean weight (\pm s.d.)	<i>K</i> (\pm s.d.)
NW	35.03 (\pm 1.52)	393.47 (\pm 51.16)	0.91 (\pm 0.07)
NE	35.2 (\pm 1.83)	412.25 (\pm 65.11)	0.94 (\pm 0.06)
SW	33.11 (\pm 1.61)	353.39 (\pm 40.88)	0.97 (\pm 0.08)
SE	33.98 (\pm 2.40)	372.4 (\pm 77.76)	0.94 (\pm 0.08)

highest in the SW and lowest in the NW, with significant differences between all regions except between the NE and SE (ANOVA, $p < 0.01$; Tukey HSD, $p < 0.05$).

Temperature and plankton biomass

Temperature in the four regions ranged from 4.8 to 10.3°C at depths of 0–50 m (Figure 2). The NW region had generally the coldest subsurface sea temperatures and the SE region the warmest. In the NW, the 8°C isotherm that earlier has been suggested to represent the lower boundary of the preferred temperature range in mackerel occurred at a shallower depth (13 m) than in other regions (Figure 2). In the NE and SW regions, the 8°C isotherm was at 26 and 28 m, respectively, and in the SE region, it was even deeper (47 m). There was a marked seasonal thermocline in all regions except in the NW, where the temperature decreased gradually from the surface.

The NW region had the highest biomass of plankton (6.52 g m⁻²) and the SW region the lowest (3.08 g m⁻², Figure 3). Small plankton (<1000 µm) were present in all regions and dominated the NW and SE samples (Figure 3). Medium plankton (1000–2000 µm) were also present in all regions and comprised the majority fraction in the NE sample. Large plankton (>2000 µm) were present in the NW and SW regions and in a very small amount in the SE. The SW region did not have a dominant size fraction.

Acoustic data

A total of 251 mackerel schools were tracked with high-frequency multibeam omnidirectional sonar during daylight hours in the four regions ($n = 62$ in NW, $n = 52$ in NE, $n = 66$ in SW, and $n = 60$ in SE). The dataset did not have a normal distribution (Shapiro–Wilk test), and log transformation on the depth distribution and school speed was, therefore, performed.

Depth distribution of schools

Mackerel schools were generally distributed within the upper 40 m of the water column, with average depth of 18–28 m in the four regions (Figure 4). Average school depth in the NW, NE, and SE

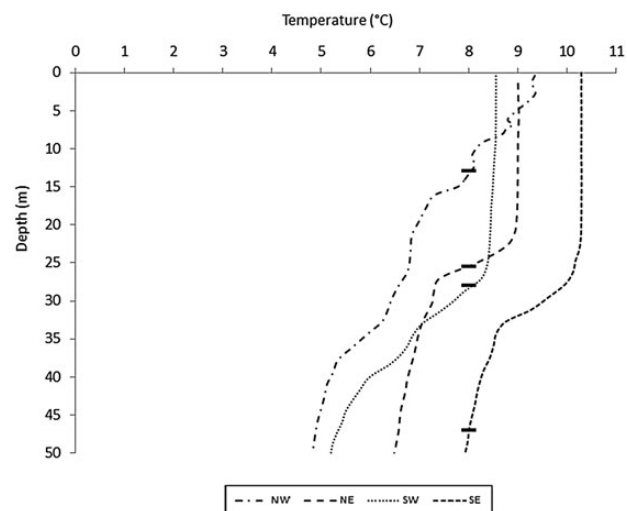


Figure 2. Temperature (°C) profiles from the surface to 50 m in the four study regions. The indicated horizontal lines indicate the depth at which the sea temperature reaches 8°C in each region [northwest (NW), northeast (NE), southwest (SW), and southeast (SE)]. The 8°C isotherm occurred at 12 m in the NW, 26 m in the NE, 28 m in the SW, and 47 m in the SE regions.

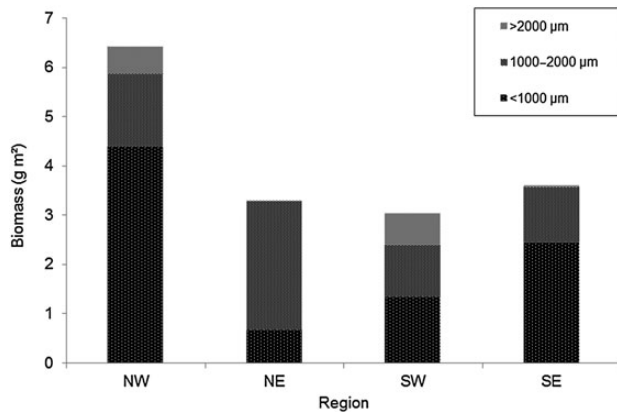


Figure 3. Plankton biomass (g m^{-2}) and size fractions within the samples ($<1000 \mu\text{m}$, $1000\text{--}2000 \mu\text{m}$, $>2000 \mu\text{m}$, and other). Other includes Amphipods, Chaetognatha, and Paraeuchaeta. These plankton species are usually not caught in the smaller WP-2 net.

regions were very similar at 20, 22, and 19 m, respectively, but a significantly deeper average school depth (26 m) was recorded in the SW region (Tukey HSD, $p < 0.05$). Except in the NW region, the majority of schools were swimming above the thermocline. The majority of schools occurred above the depth where ambient sea temperature reached 7°C , and all schools occurred in waters warmer than 6°C . In the NW region, mackerel were distributed below the 8°C isotherm, and temperature at the maximum school mean depth was 6.8°C (Figure 4). Schools in the NE and SW regions stayed above the 8°C isotherm.

School speed and direction relative to current

Average swimming speed in all regions combined was 1.33 m s^{-1} (3.8 BL s^{-1}) for a 35-cm mackerel. The majority of schools were

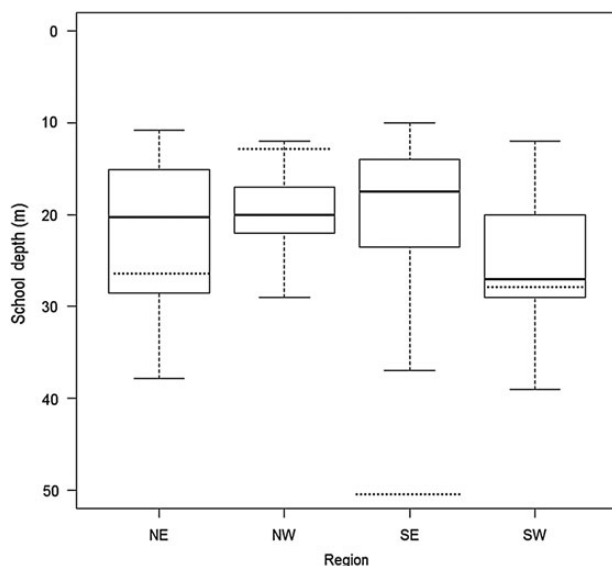


Figure 4. Box and whisker plot of the mean depth distributions (m) of mackerel schools in the four study regions. The indicated horizontal lines represent the depth for the 8°C isotherm in each region [northwest (NW), northeast (NE), southwest (SW), southeast (SE)*]. The bold line represents median value, the box is the mid-spread (including the first and third quartiles), and the whiskers are the minimum and maximum values. *The SE 7°C isotherm was 169 m.

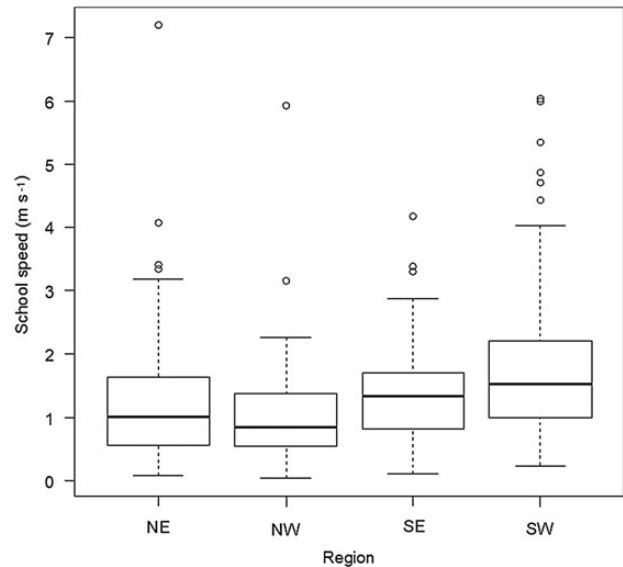


Figure 5. Range of observed average school swimming speeds (m s^{-1}). The bold line represents the median speed value, within the box is the mid-spread, the whiskers are the minimum and maximum values, and the circles are outliers.

moving between 0.72 and 2.25 m s^{-1} (Figure 5). Schools in the north moved generally slower than schools in the south (ANOVA, $p < 0.01$). The SW schools moved significantly faster than those in the NW (Tukey HSD, $p < 0.01$) and NE (Tukey HSD, $p < 0.005$) regions.

The upper ocean current velocity in the overall survey area was highly variable in both strength and direction (Figure 6). These variations could be associated with mesoscale eddies. If the cruise track crossed through the centre of an eddy, a 180° change in direction was observed, and even when the track was not through the centre, a change in current speed and direction could be recorded. For example, on the track line just south of 70° , two strong eddies with clockwise circulation (anticyclonic) were observed, one at $\sim 11^\circ\text{E}$ and one at 2°E , both with swirl speeds of $>0.5 \text{ m s}^{-1}$.

Both the local current pattern and swimming direction of the schools relative to current direction showed marked variations. A northerly current was only observed in the SW region, and schools swam in the current direction only in the NW region (Figures 7–10). Yet, in three of four studied regions, schools swam predominately northward, coinciding with the direction of the prevailing Atlantic current in the Norwegian Sea. The magnitude of mean swimming velocity was considerably slower than the general overall swimming speed due to low directional stability. Directional stability (magnitude of mean velocity divided by mean speed) ranged from 0.33 to 0.51 (Table 2), suggesting variable swimming direction between mackerel schools within a region.

Discussion

In three of four investigated regions in the Norwegian Sea, the tracked mackerel schools tended to swim in a northerly direction coinciding with the direction of the major Nw NAC. In the northwest region with highest plankton concentrations and lowest temperature, fish were largest and swimming speed lowest. Mackerel generally stayed close to the surface, with vertical distribution constrained by thermocline depth and low temperatures.

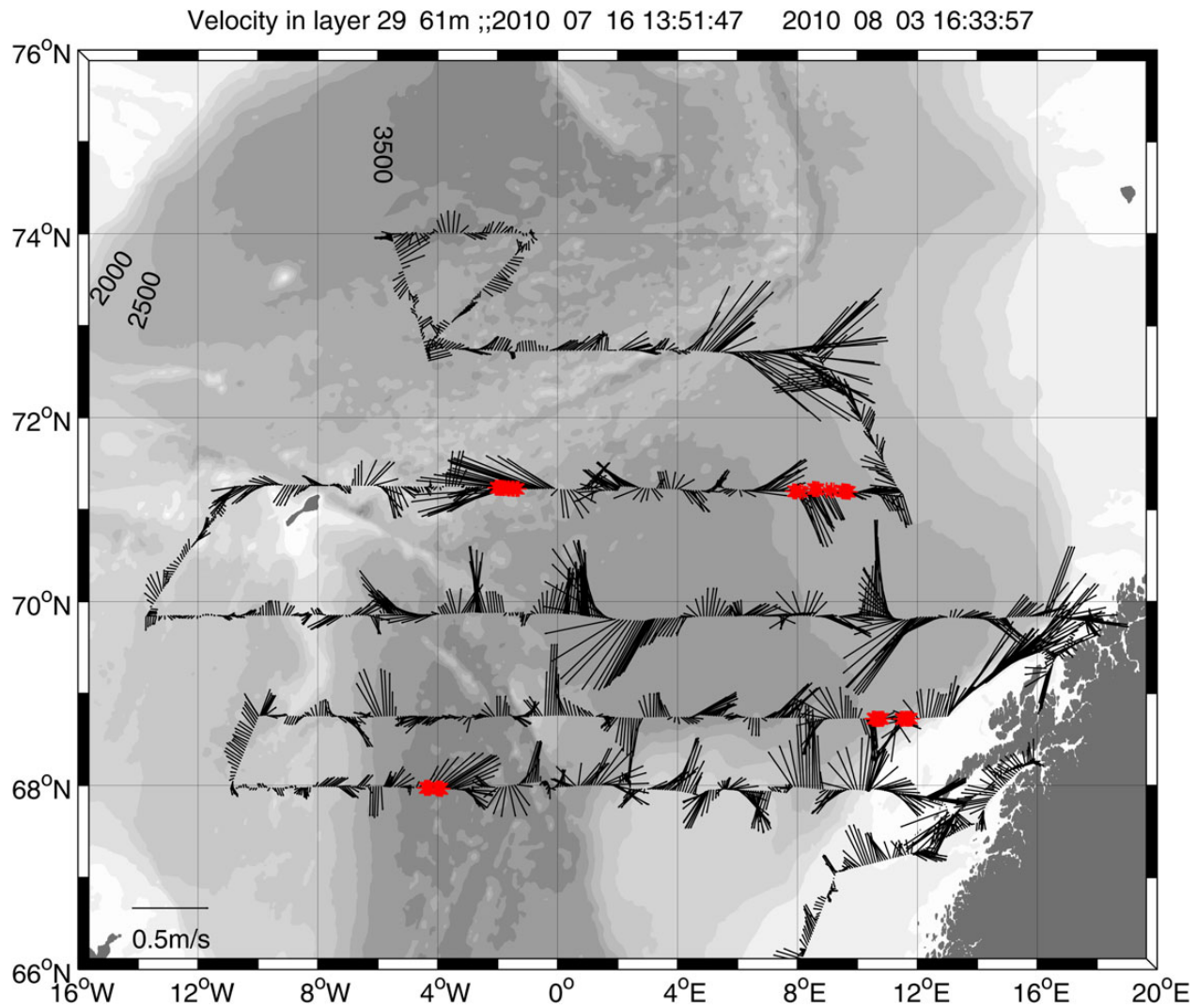


Figure 6. Measured current velocity (black arrows) in the Norwegian Sea for the entire survey with MV “Brennholm” in July 2010. The four red regions indicate where mackerel schools were tracked with multibeam sonar. Note the different cyclonic and anticyclonic mesoscale eddies of different size within the Norwegian Sea.

The analysed regions were selected after the survey to study gradients between north, south, east, and west based on inherent physical and biological differences between regions. This study illustrates the gain by using fisheries sonar in ecosystem surveys. Sonar is the only reliable acoustic methodology able to detect and track schools of pelagic fish close to the surface in the upper blind zone of the echosounder, and multibeam sonar provides more detections and thus greater accuracy than echosounders (Kvamme *et al.*, 2003; Nøttestad *et al.*, 2007). At least 50 schools within each region could be tracked for a minimum of 5 s. Tracking of schools with at least 10 pings would improve estimations of school speed, and occasionally reducing vessel speed will allow schools to be tracked for longer duration.

Horizontal and vertical distribution relative to temperature and food abundance

The northward expansion of NEA mackerel is restricted by low temperature (Berge *et al.*, 2015), but in the present study, mackerel were abundant in all studied regions including the coldest NW region. At

the time of our study, mackerel were distributed from the southern edge of the Norwegian Sea to as far north as 75°N (ICES, 2010; Nøttestad *et al.*, 2016). The availability of food should also be expected to have a strong influence on distribution during the summer feeding period (Olafsdottir *et al.*, 2016). The number of samples was limited, but the plankton biomass was nearly twofold higher in the NW than in the SW region.

Mackerel schools generally swam close to the surface at median depths of 8–39 m. Predation pressure seemed low, with only few marine mammals sighted within the four regions (Nøttestad *et al.*, 2014), so increased visibility and predation risk close to the surface should not have forced the mackerel to deeper less productive waters. All schools stayed above the thermocline in waters of at least 6°C, with the majority of schools between 7 and 11°C. The thermocline is known to stabilize water masses close to the surface and trap high concentrations of nutrients, phytoplankton, and zooplankton in summer (Rey, 2004; Nilsen and Falck, 2006). This may attract mackerel to surface waters where high light levels, including areas with midnight sun, also facilitate visual detection and capture

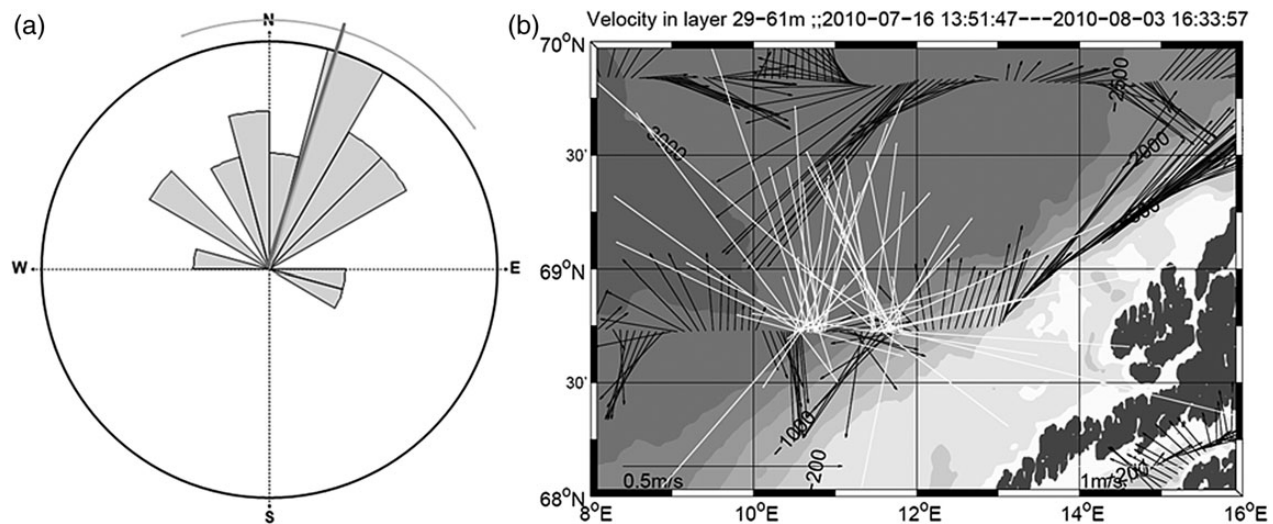


Figure 7. (a) Rose plot showing the mean swimming school speed and direction for schools of mackerel tracked with sonar in the SE region. (b) A more detailed map including current velocity and direction (black arrows) overlaid with mean swimming school speed and direction (white lines). The magnitude of the vector mean school swimming velocity (white lines) was 0.72 m s^{-1} with a direction of 6.9° . Magnitude of the vector mean current velocity (black arrows) was 0.12 m s^{-1} with a direction of 320° within the transect of tracked mackerel schools.

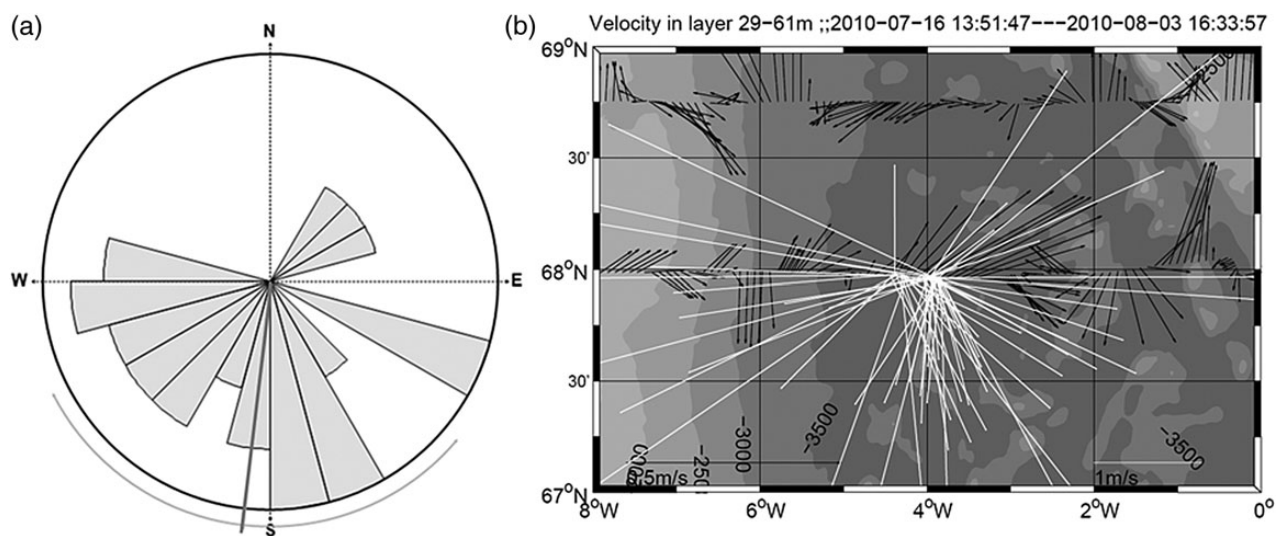


Figure 8. (a) Rose plot showing the swimming speed and direction for schools of mackerel tracked with sonar in the SW region. (b) A more detailed map including current velocity and direction (black arrows) overlaid with mean swimming school speed and direction (white lines). The magnitude of the vector mean school swimming velocity (white lines) was 0.62 m s^{-1} with a direction of 183° . Magnitude of the vector mean current velocity (black arrows) was 0.28 m s^{-1} with a mean current direction of 85° within the transect of tracked mackerel schools.

of prey (Suthers and Sundby, 1996). Higher temperature in shallow waters could, in addition, improve swimming performance (Videler and Wardle, 1991). A temperature of 8°C has earlier been suggested to be the lower boundary of the preferred temperature range for NEA mackerel (Iversen, 2004). Although temperature preference and thresholds may vary depending on fish location in their annual migration cycle, our results suggest that the preference limit should actually be 7 or even 6°C , as earlier found for mackerel in the western Atlantic (Castonguay *et al.*, 1992). Our data together with earlier studies (Berge *et al.*, 2015) strongly indicate that the distribution of mackerel is constrained by low temperatures in both the vertical and horizontal dimensions.

School swimming speed

With few exceptions, mackerel swam above the critical speed of 0.4 BL s^{-1} to avoid sinking (Wardle and He, 1988) from the upper productive waters. Schools were generally recorded by sonar to swim faster, with an average speed of 3.8 BL s^{-1} . In tank experiments, mackerel could maintain a swimming speed of 4.1 BL s^{-1} for at least 30 min at 11.7°C (Wardle and He, 1988; Dickson *et al.*, 2002), so schools should have been able to maintain their swimming speed for prolonged periods. Mackerel swimming northward at a constant velocity of 1 m s^{-1} (ca. 3 BL s^{-1}) would only take 20 d to cover the distance from 60 to 75°N of ca. 1670 km.

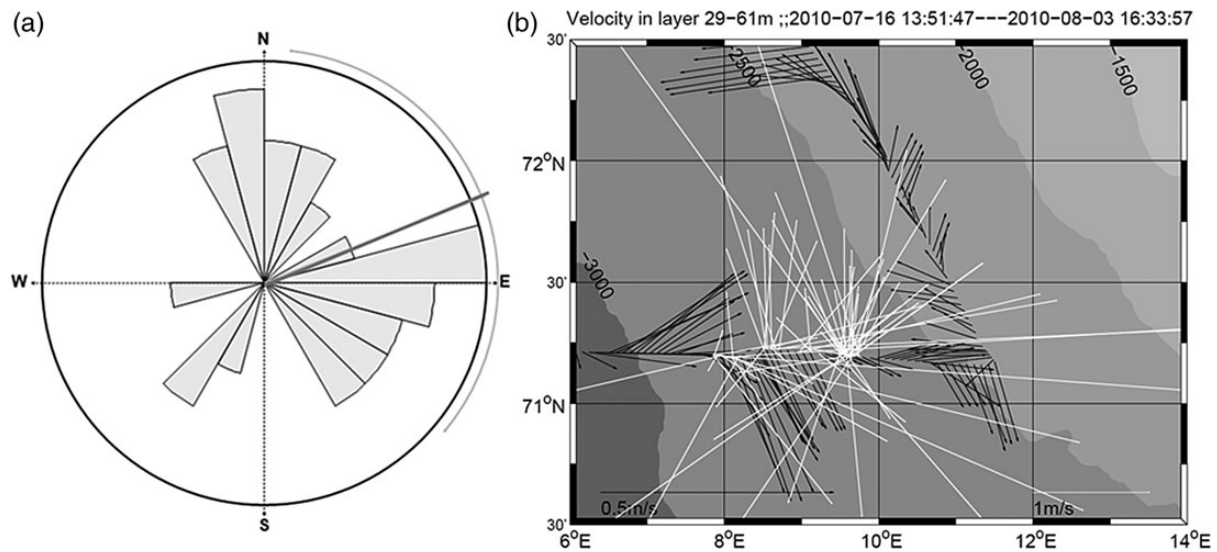


Figure 9. (a) Rose plot showing the swimming speed and direction for schools of mackerel tracked with sonar in the NE region. (b) A more detailed map including current velocity and direction (black arrows) overlaid with mean swimming school speed and direction (white lines). The magnitude of the vector mean school swimming velocity (white lines) was 0.44 m s^{-1} with a direction of 18° . Magnitude of the vector mean current velocity (black arrows) was 0.18 m s^{-1} with a direction of 183° within the transect of tracked mackerel schools.

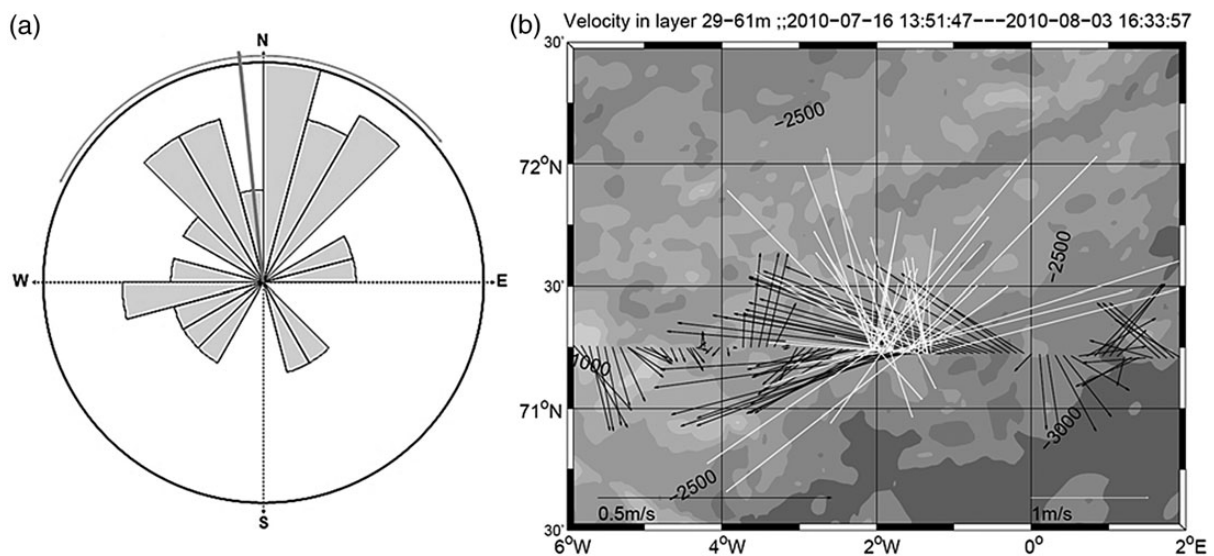


Figure 10. (a) Rose plot showing the swimming speed and direction for schools of mackerel tracked with sonar in the NW region. (b) A more detailed map including current velocity and direction (black arrows) overlaid with mean swimming school speed and direction (white lines). The magnitude of the vector mean school swimming velocity (white lines) was 0.54 m s^{-1} with a mean swimming direction of 7.3° . Magnitude of the vector mean current velocity (black arrows) was 0.44 m s^{-1} with a direction of 330° within the transect of tracked mackerel schools.

We excluded mackerel swimming speed measured to be $>3\text{--}7 \text{ m s}^{-1}$ ($>6 \text{ BL s}^{-1}$) from sonar tracking, based on our assumption that this is not biologically reasonable. This may be questioned in some cases, since mackerel are known to be fast and enduring swimmers (Wardle and He, 1988; Videler and Wardle, 1991), e.g. displaying rapid explosive avoidance reactions to predators. Uncertainties and biases involved when tracking mackerel schools may vary. Larger and denser schools probably provide more accurate and stable swimming speed measurements compared with smaller and looser mackerel shoals or aggregations as recorded in summer with weaker and less stable acoustic echoes from ping to ping.

Current system and mackerel behaviour

It is well known that prevailing ocean currents in the Norwegian Sea are northward (Poulain et al., 1996; Blindheim, 2004). The present study supports this, but additionally demonstrates a complex current system including many mesoscale eddies of varying size. The northeastern part of the Norwegian Sea is a hot spot for ocean eddies (Volkov et al., 2013). The intense eddy observed at 2°E was surveyed *in situ* in detail in July 2010 by Søiland and Rossby (2013). Whereas most eddies are transient features, they found evidence that this eddy most likely is permanent and deep reaching. Both satellite observations (Raj et al., 2015) and ocean

Table 2. Overview of mean velocity, mean direction, and swimming stability of mackerel schools and mean current speed, mean direction, and current stability.

Region	Mackerel			ADCP		
	Mean velocity (m s^{-1})	Mean direction ($^{\circ}$)	Swimming stability	Mean speed (m s^{-1})	Mean direction ($^{\circ}$)	Current stability
NW	1.10	7.3	0.49	0.44	257.2	0.99
NE	1.29	52.5	0.34	0.18	150.2	0.98
SW	1.85	183.4	0.34	0.28	52.4	0.99
SE	1.40	6.9	0.52	0.12	178.8	0.64

Stability = velocity/speed.

current modelling (Volkov *et al.*, 2015) also confirm that variations are caused by mesoscale eddies. Yet, due to the challenges to accurately relate tracked schools with *in situ* current velocity in our study, all observed current variations along the skip track are presumably not caused by eddies. Reduced vessel speed during surveys and larger number of analysed schools recorded over larger areas with synoptic sampling of the current systems could provide more detailed knowledge of how mackerel utilize mesoscale eddies with patchy distributions of prey (Parrish and Edelman-Keshet, 1999).

The small-scale picture showed large variations with a northward current observed only in one region. This demonstrates the complexity on smaller scales and illustrates the problem of pattern and scale in ecology (Levin, 1992). Schools swam in the direction of the local current only in the NW region. Still, in three of four investigated regions in the Norwegian Sea, mackerel schools tended to swim in a northerly direction coinciding with the direction of the major Nw NAC.

Feeding strategy of mackerel

Fish could reduce energy expenditure by swimming with the prevailing current, and mackerel off the coast of North America utilize the tidal cycle to reach their spawning grounds (Castonguay and Gilbert, 1995). Swimming with the current should decrease the energetic costs of migration and thus be an effective strategy for mackerel to reach the productive waters in the northern Norwegian Sea. The main North Atlantic current not only transports the fish northward but may also provide a directional cue towards a habitat with high food abundance. An interesting possibility is that predictive orientation mechanisms (Neill, 1979; Fernö *et al.*, 1998) based on current direction permit mackerel to reach productive areas. Increasing day-length farther north may provide another directional cue (Healey, 1957). Yet, schools did not always swim in the direction of the main current. First, swimming direction showed some variations (Figures 7–10). Second, schools in the NW region swam in a westerly direction, and schools in the NE and SE regions even swam southward. Third, our data on swimming stability showed that the different tracked schools were often not swimming in the same direction. All in all, this indicates an active reactive feeding or escape reaction to predators in the near field. Plankton biomass in the Norwegian Sea in the year of our study (2010) was among the lowest in 20 years, and mackerel condition was low (Huse *et al.*, 2012). Food should thus be a critical resource, and mackerel may utilize many prey types of different size (Prokopcuk and Sentyabov, 2006; Langøy *et al.*, 2012). By swimming in the direction of the main current in combination with detours when encountering food patches, fish will enter new water masses that could be exploited. When mackerel reached the most productive northern areas, they were observed to reduce their swimming speed (see also Macy *et al.*, 1998).

Concluding remarks

This study provides new knowledge about the feeding strategy of mackerel during the summer feeding migration in the Norwegian Sea based on *in situ* synoptic observations with multibeam sonar coupled with oceanographic data and biological sampling. This is the first time that mackerel schools have been tracked with simultaneous current measurement. Distribution seems to be constrained by low temperatures both in the vertical and horizontal dimensions. The major finding of our study is that mackerel tend to swim in the direction of the northward Atlantic current that brings them to the most productive areas of the Norwegian Sea. Although there are methodological challenges when estimating these parameters, high swimming speed and strong variations in observed swimming direction suggest that it is crucial for mackerel to both cover large areas and react to food patches in the near field. Based on our findings, we suggest that mackerel in the Norwegian Sea have the following simple feeding strategy based on an expectation of increasing foraging rate towards the north: go with the flow until temperature is too low, while utilizing available prey under way. The prevalence and robustness of this strategy should be further evaluated in more pinpointed studies.

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