



Nutrient-driven poleward expansion of the Northeast Atlantic mackerel (*Scomber scombrus*) stock: A new hypothesis

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Abstract

The Northeast Atlantic mackerel (*Scomber scombrus*) stock has increased and expanded its summer feeding migration west- and northwards since 2006, entailing large geopolitical challenges for the countries harvesting this species. A common perspective is that climatic warming opens up new regions for biota in the north. It has also been suggested that the presently large pelagic fish stocks deplete prey resources in the eastern North Atlantic during their summer feeding phase, forcing the stocks west towards the Irminger Sea in their search for food. Here, we suggest that the declining nutrient (silicate) concentrations observed along the northern European continental slope reduce primary and thus secondary production, exacerbating food scarceness in the east and adding to the incentive to migrate westward. The new westward feeding route requires that the fish cross the Iceland Basin, which during the summer season quickly becomes nutrient-depleted and thus might act as a barrier to migration after the spring bloom. Using mackerel and zooplankton abundance data from the International Ecosystem Summer Surveys in the Nordic Seas, we suggest that the oligotrophic waters in the central Iceland Basin force the fish to migrate through a narrow 'corridor' along the south Iceland shelf, where nutrients are replenished and both primary and secondary production are higher.

Introduction

The Northeast Atlantic mackerel (*Scomber scombrus*) is a highly migratory species that, after spawning along the European shelf, gradually moves northwards (Figure 1a) into the summer feeding areas in the Norwegian Sea (Uriarte et al., 2001; Iversen, 2002; ICES, 2014a). A portion of the stock also migrates southwards and into the North Sea. After 2006, the mackerel stock has been steadily increasing and expanding northwards into the northern parts of the Norwegian Sea, and westwards into Icelandic waters. Since 2013, it has also been observed in the Irminger Sea (Figure 1a; ICES, 2014d; 2015).

Mackerel is a temperate species, thus one of the reasons considered to induce the expansion is the increasing sea surface temperature (SST) in recent years (Hughes et al., 2014), which might make new regions in the north available for mackerel to occupy. However, the position of the 6–7 °C isotherm, the lower bound of the temperature niche of mackerel (Utne et al., 2012), has been relatively stationary throughout the period 2010–2014 (ICES, 2014b). Thus it appears that average summer temperatures (July–August) in the Norwegian Sea have not changed enough to explain the post-2006 expansion of the feeding area. On the contrary, recent studies have shown that the expansion areas in the Irminger Sea, Icelandic waters and the northern Norwegian Sea have, for decades, had summer temperatures not only tolerable (> 5 °C), but well in the temperature range that mackerel occupy (Astthorsson et al., 2012; Utne et al., 2012; MacKenzie et al., 2014).

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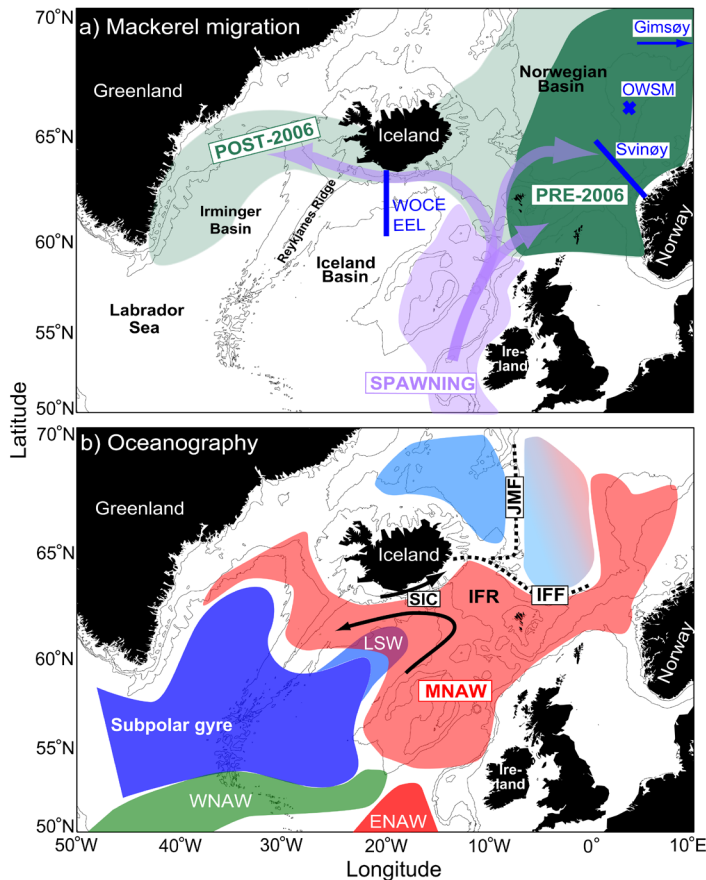


Figure 1

Geographical overview of the mackerel stock dynamics.

a) Illustrated are the mackerel spawning areas (purple shading) along the European shelf and the post-spawning and summer feeding migrations (purple arrows). The pre-2006 mackerel summer feeding areas are shown as dark green with the post-2006 expansion in light green. The standard WOCE/EEL section at 20°W (where summer silicate data were sampled; Figure 4) and the standard sampling sites: Svinøy section, Ocean Weather Station Mike (OWSM) and Gimsøy section (where the pre-bloom silicate concentrations were sampled; Figure 7) are marked in blue. b) Shown are important oceanographic features: Modified North Atlantic Water (MNAW), Eastern North Atlantic Water (ENAW), Western North Atlantic Water (WNAW), Labrador Sea Water (LSW), Jan Mayen Front (JMF), Iceland-Faroe Front (IFF), Iceland-Faroe Ridge (IFR) and South Iceland Current (SIC). Polar waters, and their admixture with the Atlantic water in the Nordic Seas, are shown in light blue colours. Emphasized currents for the present analyses are illustrated with black arrows and fronts with dashed lines.

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Stock size indices as well as the density of mackerel have been steadily increasing from 2007 to 2014 (Nøttestad et al., 2016), and food stress, which arises when the amount of food-per-fish declines, will increase as the mackerel stock size increases. This statement holds for a hypothetically constant zooplankton prey stock, but even more so considering a likely declining zooplankton stock in the Norwegian Sea (ICES, 2015) due to grazing by the large pelagic fish stocks (Fauchald et al., 2006). This top-down mechanism is referred to as *density dependence*. There are clear indications of a declining food-per-fish ratio resulting in decreased growth of juvenile and early adult Northeastern Atlantic mackerel, as tracked by the metrics *length-* and *weight-at-age* (Jansen and Burns, 2015; Ólafsdóttir et al., 2015). It has been suggested that, in recent years, increased stock size in the eastern feeding region, through density dependence, has forced the mackerel stock north- and westwards (Ólafsdóttir et al., 2015).

The copepod *Calanus finmarchicus* is the principal mackerel prey species (Langøy et al., 2006; Prokopchuk and Sentyabov, 2006) and the most important zooplankton species in the subpolar Atlantic. The total zooplankton biomass in the Nordic Seas is reported to have declined during the initial years of the westward mackerel expansion (2000–2009). In a recent study, Hinder et al. (2014) pointed out that the *C. finmarchicus* decline cannot be attributed solely to SST, and elucidated the need to consider food availability for the zooplankton stock as a causal factor along with changes in other parts of the life cycle. *C. finmarchicus* prefer the fast-growing diatoms as a food source (Planque and Fromentin, 1996; Melle et al., 2014). The spring bloom in the North Atlantic is typically dominated by diatoms, which, in addition to nitrate and phosphate, require sufficient concentrations of silicate to build their frustules (Egge and Aksnes, 1992; Brzezinski et al., 1998). One of the most fundamental principles in biological oceanography is nutrient limitation of primary production. This principle is widely acknowledged for lower latitude oligotrophic waters, where only upwelling regions can support strong and persistent biological production (Behrenfeld et al., 2006; Polovina et al., 2008). In the higher latitude subpolar waters in the North Atlantic these fundamental dynamics have been largely overlooked, probably because the most commonly studied essential nutrient, nitrate, seldom reaches limiting concentrations (Allen et al., 2005). However, these waters become silicate-limited, restricting persistent late-summer production of the fastest growing diatom algae to upwelling *hot spots* (Brzezinski et al., 1998; Allen et al., 2005).

In the spawning region of mackerel, the subtropical water masses, already low in nutrients, become oligotrophic towards the end of the spawning period (Polovina et al., 2008; Dave et al., 2015) limiting primary production (Hartman et al., 2010), and thus the production of zooplankton (Planque and Fromentin, 1996).

During spawning, mackerel seem to be feeding more sporadically, while towards the end of spawning mackerel become meagre and start to feed (Lockwood et al., 1981; ICES, 2014c). This oligotrophic environment probably cannot provide sufficient food, which each summer may force mackerel to migrate to more productive waters further north. On an interannual time scale, it is interesting to note that silicate concentrations have been declining in the eastern Norwegian Sea since the early 1990s (Rey, 2012). This change is potentially associated with an increased influence of low nutrient subtropical waters as the size of the subpolar gyre and the strength of the circulation declined (Hakkinen and Rhines, 2004; Hátún et al., 2005).

We propose *bottom-up* control as an additional driver of the movement of mackerel in their search for food after the spawning. Elucidating the importance of food availability for the zooplankton prey stock, we introduce the viewpoint of oligotrophic forcing from southeastern waters to the mackerel discussion. In this study, silicate concentrations are used as a proxy for the general food availability for mackerel. Although this approach comes with caveats, it circumvents the inherent limitations in the spatio-temporal plankton records due to grazing effects, infrequent sampling, etc. The paper is divided into two main parts: first, we propose and test a new hypothesis that mackerel migration through the Iceland Basin is restricted by food (zooplankton) availability caused by nutrient (silicate) limitation to primary production; second, we generalize the findings from this test and discuss the post-2006 large-scale westward expansion in a nutrient limitation context.

Oceanographic overview

Saline and nutrient-poor Eastern North Atlantic Water and less saline and nutrient-richer Western North Atlantic Water meet and mix at the mackerel spawning grounds west of the British Isles (Figure 1). The resulting Modified North Atlantic Water (MNAW) flows polewards along the Norwegian slope, and through the Iceland Basin. The MNAW meets subarctic water masses north of the Iceland-Faroe Ridge, establishing first the Iceland-Faroe Front (IFF) and, farther downstream, after clockwise circulation within the Norwegian Sea and subsequent cooling, the Jan Mayen Front (JMF). In the Iceland Basin, a variable volume of Labrador Sea Water (LSW) underlies the warmer MNAW. The general flow of MNAW is cyclonic in this region (Valdimarsson and Malmberg, 1999), but near the southeastern Icelandic slope, there is a swift eastward flow, the South Iceland Current (Logemann et al., 2013). The large density difference between the MNAW and the LSW in the central Iceland Basin (Yashayaev et al., 2007) impedes deep winter convection, and thus restricts the replenishment of nutrients, during winter. In April-May, the subpolar Atlantic switches from losing heat to the atmosphere to receiving heat. Without any mixing agent, the near-surface will therefore become increasingly stratified and nutrient-depleted throughout the summer. Generally, the three main mixing agents continuously fuelling primary production by replenishment of nutrients are: *i*) vertical motion along major fronts, *ii*) large-scale convection and *iii*) turbulence over underwater topography like major ocean ridges and continental slopes.

Materials and methods

Nutrient data

The available nutrient data in the studied region have poor spatial and temporal coverage. A climatological nutrient distribution (Figure 2a) at 50 m depth for 1960–2013, based on data downloaded from the World Ocean Database (WOD, <https://www.nodc.noaa.gov>; Garcia et al., 2001), however, gives a useful large-scale overview despite its coarseness ($1^\circ \times 1^\circ$).

To investigate the nutrient gradients through the Iceland Basin at finer resolution, we selected data from the most frequently sampled standard hydrographic section in the region, along the longitude 20°W (Figure 1a). Data were obtained from the World Ocean Circulation Experiment (WOCE) data archive, downloaded from CLIVAR and Carbon Hydrographic Data Office (CCHDO, <http://cchdo.ucsd.edu>), from the Extended Ellett Line (EEL, quality checked using the method detailed in Johnson et al., 2013) and from the above mentioned WOD. Measurements are temporally sparse; all silicate observations from the period 1970–2013 were used to calculate monthly averages for the summer season (May–August).

Lastly, we used winter (pre-bloom) silicate data from three locations in the Norwegian Sea (Svinøy section, OWS Mike and Gimsøy section; Figure 1a), collected mostly during March when the winter vertical mixing is at its maximum. The average values of nutrients were calculated using the observations from the surface down to 200 m or in the upper mixed layer. Data were adopted from Rey (2012) and updated for recent years. Egge and Aksnes (1992) showed that irrespective of season, diatom dominance occurred as long as silicate concentrations were above $2 \mu\text{M}$. In our study we chose to use $1.5 \mu\text{M}$ as a level expected to limit the growth of diatoms.

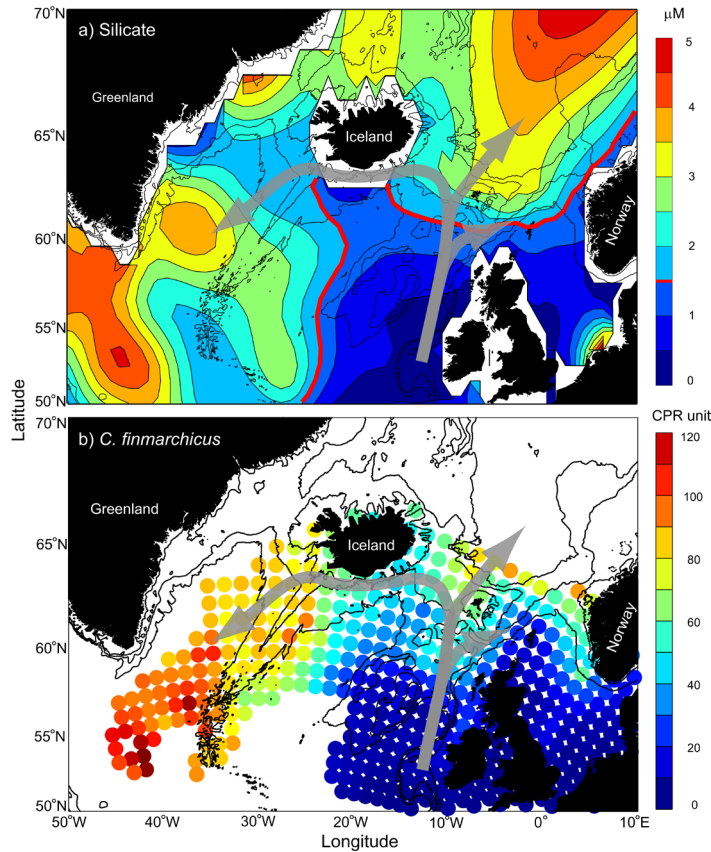


Figure 2

June silicate and *C. finmarchicus* climatology.

a) Shown are near-surface (50 m) silicate concentrations averaged over the period 1960–2013. The thick red contour line emphasizes the diatom-limiting level of 1.5 μM . b) *C. finmarchicus* abundances (stages V and VI) from the near-surface continuous plankton recorder (CPR) survey are shown for the period 1958–2005. The general mackerel feeding migration is illustrated with grey arrows.

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Chlorophyll a from satellite data

Gridded near-surface satellite chlorophyll data were downloaded from the GlobColour Project, ACRI-ST (<http://www.globcolour.info>). Eight-day temporal averages of Level 3, merged (SeaWiFS, MODIS, MERIS, VIIRS), GSM-gridded (Maritorena et al., 2002) chlorophyll (CHL1) data were used on a 4-km horizontal grid for the period 1998–2015.

Continuous plankton records

Zooplankton data were obtained from the Continuous Plankton Recorder (CPR) survey for the period 1958–2005 (Batten et al., 2003). The survey is a monitoring program that uses the CPR sampling device towed at ~10 m depth behind ships of opportunity on standard routes. As the CPR samples are highly variable in space and time, spatial interpolation using the inverse squared distance method (Lam, 1983) was applied to obtain gridded datasets for further analysis (Hátún et al., 2009). Only data for the adult *C. finmarchicus* stages CV and CVI were used in this study, representing the overwintering stock (Figure 2b).

Mackerel surveys

Snapshots of the zooplankton and mackerel distributions were obtained from the International Ecosystem Summer Surveys in the Nordic Seas (IESSNS) surveys during July and the beginning of August since 2010. The IESSNS is a swept-area trawl survey where mackerel are sampled using a pelagic trawl at the surface at predefined geographical positions. Not all participating vessels used the same trawl gear in the first years; however, since 2012 the survey gear and procedures have been standardized (Nøttestad et al., 2016). Zooplankton samples were collected using a WP2 net (mesh size 180 μm or 200 μm) that was towed vertically from 200 m depth to the surface. The methodology of surveys and sampling is described in more detail in Nøttestad et al. (2016).

The spatial extent of these surveys was mainly determined by the zero-catch line, although this approach has not always been possible due to increasing stock size and expanding distribution. However, during most of the surveys, the zero line was reached at the oceanic stations in the Iceland Basin. The coverage of the surveys has varied throughout the years, generally covering the Norwegian Sea, western Icelandic waters (since 2010) and east Greenlandic waters (since 2013). Here, data from surveys for the period 2010–2014 were used, since these surveys cover the western expansion area. Westward coverage (to about 30°W) of zooplankton

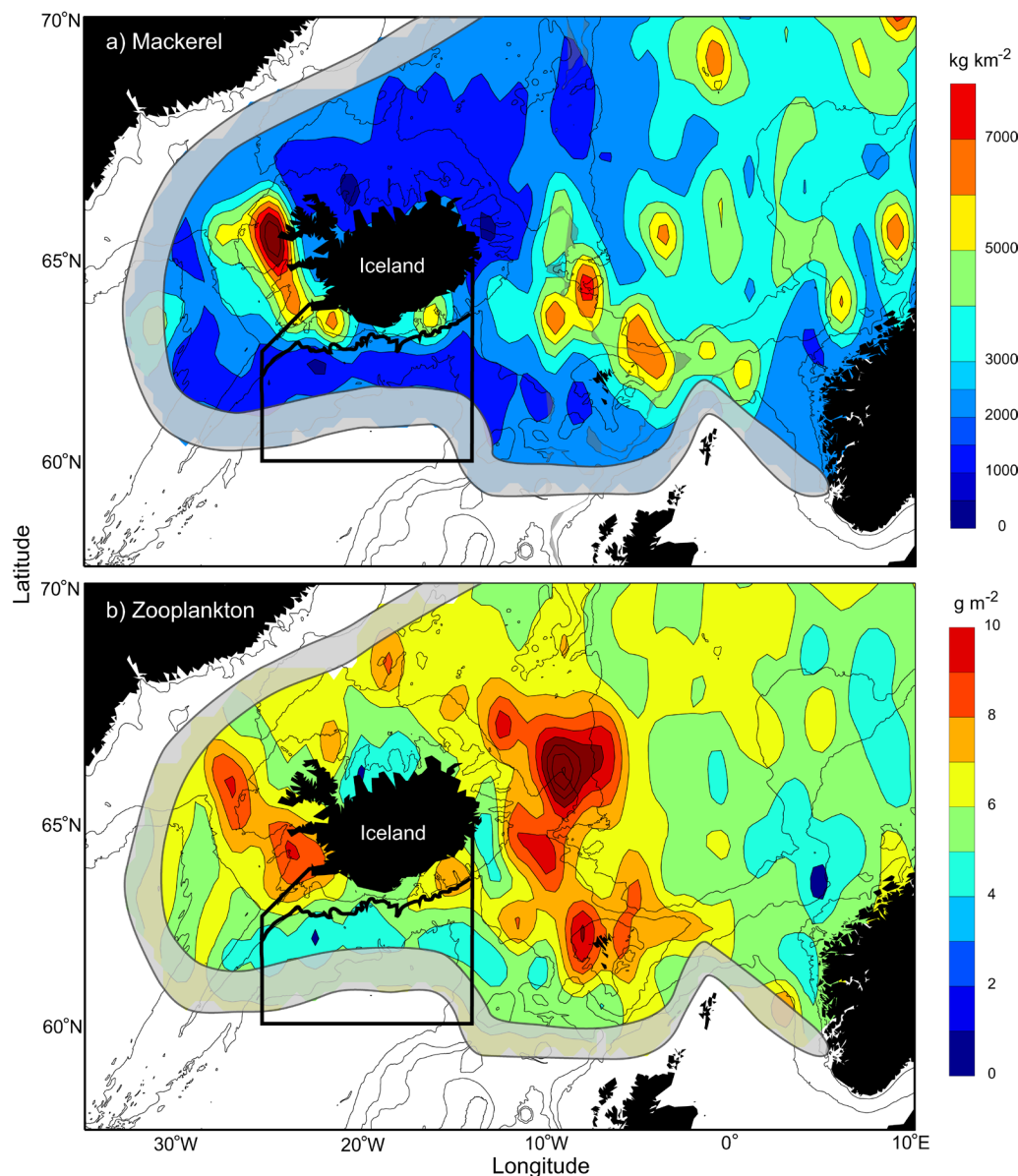


Figure 3
Mean mackerel and zooplankton abundances.

a) Average mackerel catches (kg km^{-2}) and b) average zooplankton dry weight (g m^{-2} in the upper 200 m) from the International Ecosystem Summer Surveys in the Nordic Seas (IESSNS) from the period July–August. Averages are over the period 2010–2014 and gridded onto a regular grid (0.25° latitude \times 0.5° longitude; see Material and methods). A border has been overlaid (gray shading) where the maps are less reliable due to the spatially limited data distribution. The black polygon denotes the region in the south of Iceland used in the statistical analysis (Figure 6 and Table 1). The *on-shelf* region is the area from the coast out to the 500 m isobath, while the *off-shelf* region extends from 500 m isobath southwards to 60°N .

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was first obtained in 2011, and then thereafter. The data from each of the IESSNS were first gridded onto a regular (0.25° latitude \times 0.5° longitude) grid using Objective mapping (Böhme and Send, 2005), and regions with sparse sampling, where the associated error map exceeded a selected threshold, were trimmed off. The presented averages (Figure 3) were thereafter calculated for the grid points where three or more data points were available. Since the surveys in the Irminger Sea were only obtained during two years, this region was excluded from the present analysis.

On- and off-shelf analyses

We selected a region covering a portion of the south Iceland shelf and the Iceland Basin (Figure 3), with comprehensive coverage of silicate, chlorophyll, zooplankton and mackerel data (see above). *On-shelf* averages were calculated from all stations in the selected region out to the 500 m isobath, while *off-shelf* averages included stations from the 500 m isobath southwards to 60°N . Chlorophyll, zooplankton and mackerel are presented as July averages for the years 2011–2015.

These data were supplemented with silicate data obtained from the EEL, WOCE and WOD. However, measurements are temporally sparse, and hence robust yearly values for July cannot be calculated. As such, all silicate observations obtained in the near-surface waters (0–50 m, 1970–2013) were used to calculate monthly averages for the summer season (May–August) for the *on-shelf* and *off-shelf* domain. We standardised

Table 1. Tests of the hypothesis that the summer (July) concentrations and abundances of silicate, chlorophyll, zooplankton and mackerel on the south Iceland shelf (< 500 m) are higher than those *off-shelf* in the Iceland Basin (> 500 m)^a

Variable	Test type	Difference (on-off)	<i>p</i> -value	N _{on}	N _{off}
Silicate	Wilcoxon rank sum test with continuity correction	1.49 μM	< 0.0001	4113	1002
Chlorophyll	Welch two-sample <i>t</i> -test	1.16 mg chl m ⁻³	< 0.0001	15759	88990
Zooplankton	Welch two-sample <i>t</i> -test	2.72 g m ⁻²	< 0.0001	34	56
Mackerel	Wilcoxon rank sum test with continuity correction	6.20·10 ³ kg m ⁻²	0.0014	38	58

^aN_{on} and N_{off} represent the total number of data points on and off the shelf, respectively.

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the averages for all variables by subtracting the full domain average (*on-shelf* and *off-shelf*) for months and years, accordingly. The mean over all months or years were calculated for silicate and the three other variables, respectively.

To test the significance of the *on-shelf* and *off-shelf* differences in silicate, chlorophyll, zooplankton and mackerel concentrations and abundances, statistical tests were performed (Table 1). Zooplankton and chlorophyll data exhibited normality properties after log-transformation and the Welch two sample *t*-test was applied. A non-parametric Wilcoxon rank sum test with continuity correction was applied to the silicate and mackerel data since these are highly non-Gaussian. To exclude inter-annual variability we used standardised variables (see above) in the statistical tests.

Results

Nutrient gradient and mackerel migration

The climatological upper-ocean silicate concentrations during June, when the mackerel are searching for food, showed oligotrophic conditions in the spawning region west of the British Isles and towards the south Iceland coast, and high silicate concentrations within the central Norwegian Basin and in the western subpolar gyre (Figure 2a). The climatological upper-ocean abundances of *C. finmarchicus* in June showed a qualitatively similar pattern, with relatively low abundances in the Northeastern Atlantic and high abundances in the southern Norwegian Basin and in the western subpolar gyre (Figure 2b). This coarse relationship between silicate concentration and the distribution of *C. finmarchicus* supports our hypothesis that the fish will migrate along local gradients of some property in the ocean that reflects their food stocks, which we suggest to be silicate. Mackerel might be forced poleward from the oligotrophic spawning region during summer in order to find sufficient food stocks. Hence, as a food proxy, the positive silicate gradients might explain migration patterns towards the Norwegian Basin and the subpolar gyre in the west. The pre-2006 northeastward migration route is direct, while in order to reach the silicate- and zooplankton-rich Irminger Sea, fish are challenged to cross the Iceland Basin where both nutrient concentrations and zooplankton abundances are low during summer (Figure 2).

Mackerel and zooplankton distribution in July

The average mackerel distribution from the IESSNS data (Nøttestad et al., 2016) revealed generally high abundances of mackerel in the Norwegian Sea, with highest concentrations in the western frontal region (JMF and IFF; Figure 3a). High abundances were also observed west of Iceland, which after 2012 continued southwards into the Irminger Sea (not shown, see Material and Methods; ICES, 2014b). The July zooplankton abundances were likewise highest in the western Norwegian Sea frontal zone, around the Faroe Plateau and southwest of Iceland, while lower abundances were observed along the Norwegian slope and in the central Iceland Basin (Figure 3b). This main pattern roughly reflects the climatological silicate concentrations and *C. finmarchicus* distributions discussed above (Figure 2). Another very pronounced feature in both mackerel and zooplankton distributions are the strong gradients between high abundance on the south Iceland shelf and low and/or zero abundance in the oceanic stations in the Iceland Basin (Figure 3). The zooplankton abundances yielded a more diffuse pattern, compared to the mackerel data, likely related to the higher inherent noise in the WP2 data.

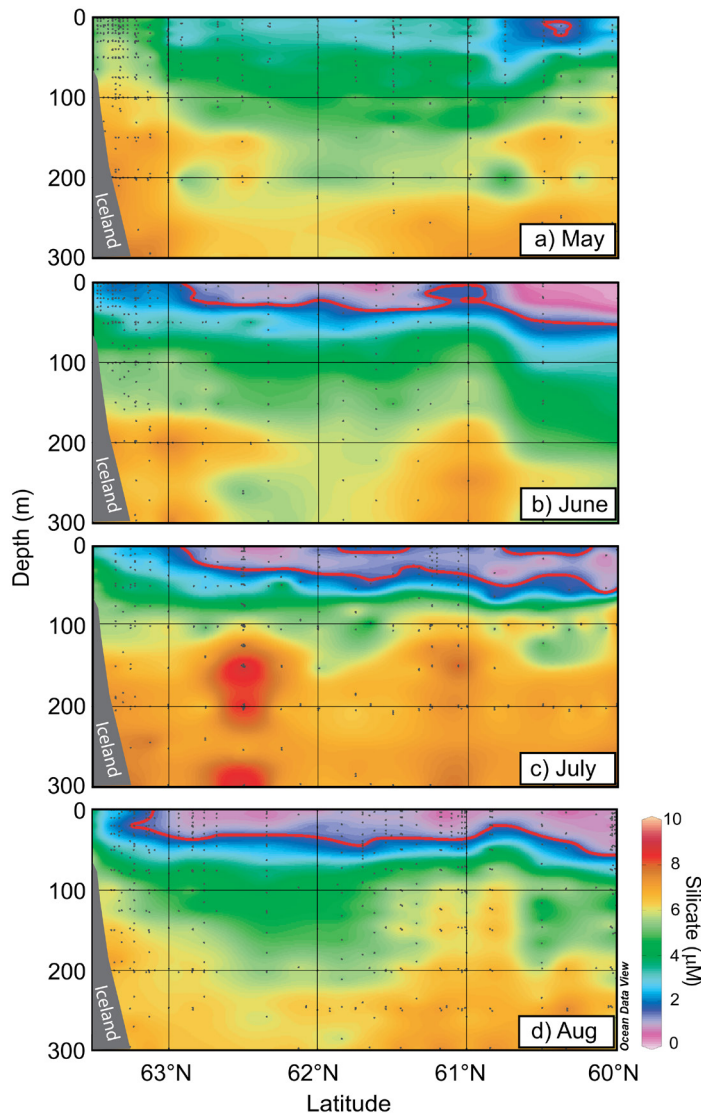


Figure 4

Silicate concentrations (μM) along the meridional section for the summer months.

a) May, b) June, c) July and d) August silicate concentrations were obtained from available WOD/ WOCE/EEL data. Latitudes from the Iceland coast to 60°N along longitude 20°W (Figure 1a). The thick red contour line emphasizes the limiting silicate concentration of $1.5 \mu\text{M}$.

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The narrow 'corridor' south of Iceland

Nutrient concentrations along the meridional section at 20°W (Figure 1a), extending from the south Iceland shelf southwards into the Iceland Basin, gave a clearer in-depth picture of the ocean-shelf contrast. Due to the variable timing of the surveys, data from several years were required to explore seasonal variability. Oceanic stratification was established in May, and silicate concentrations started to decline in the Iceland Basin (Figure 4a). The oceanic stratification intensified through the summer (May–August), and the silicate levels continued to decline in the central basin (Figure 4a–c). However, the silicate levels on the shelf remained higher through the summer, likely replenished by topographically induced mixing, although the 'corridor' of elevated silicate levels narrowed during the June to August period (Figure 4b–d). Satellite-based chlorophyll climatology (Figure 5) revealed high concentrations of chlorophyll in the vicinity of the IFF and on the south Iceland shelf, in contrast to low values in the central-eastern Norwegian Sea and central Iceland Basin. The difference between the 'on-shelf' and 'off-shelf' regions increased markedly throughout summer, as exemplified by eight-day time segments of chlorophyll data, starting in late June and ending in late July (Figure 5). The rather qualitative observations were statistically tested for the region south of Iceland, which demonstrated that the concentrations and abundances of silicates, chlorophyll, zooplankton and mackerel were all significantly higher on-shelf than off-shelf ($p < 0.001$; Figure 6, Table 1). This test supports our hypothesis that mackerel avoid the central Iceland Basin during July due to food limitation (zooplankton) caused by nutrient limitation, and thus congregate along the shelf (Figure 3a).

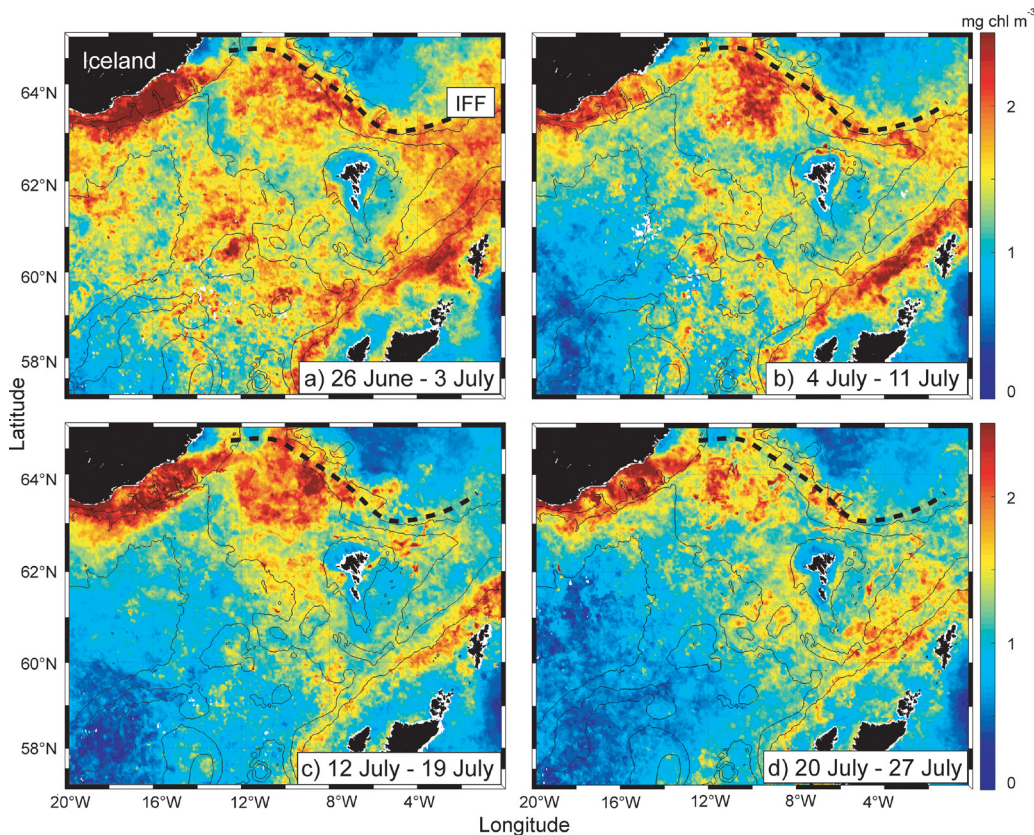


Figure 5
Average near-surface chlorophyll distribution (mg chl m^{-3}).

Climatological averages (1998–2015) over four eight-day time segments from late June to late July are shown (see Material and methods). Dotted black line defines the Iceland-Faroe Front (IFF).

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A silicate decline and the westward post-2006 mackerel expansion

Our findings from the Iceland Basin were subsequently extrapolated to discuss the post-2006 mackerel north-westward expansion, in a nutrient decline context. The winter, pre-bloom, silicate concentrations along the Norwegian slope have been persistently declining since the early 1990s with about $0.6 \mu\text{M}$ per decade (Figure 7; update from Rey, 2012). An unpublished time series of silicate concentrations based on data from EEL show a similar decline of $0.7 \mu\text{M}$ per decade in the Iceland Basin (C. Johnson, pers. comm.). Considering that diatoms are outcompeted by other smaller and slower-growing phytoplankton species when the silicate concentrations approach $2 \mu\text{M}$ (Egge and Aksnes, 1992), the reduction from $6 \mu\text{M}$ to about $4.5 \mu\text{M}$ silicate could be expected to lead to a generally earlier switch in species dominance. Assuming that the diatoms are important food items for *C. finmarchicus* (Planque and Fromentin, 1996; Melle et al., 2014), an earlier switch would likely have an impact on both the zooplankton biomass, and thus the mackerel stock dynamics.

Discussion

Here we suggest that the general migration pattern of the Northeastern Atlantic mackerel stock may be related to the near-surface silicate concentrations, which we utilize as a coarse proxy for the mackerel food stock of zooplankton (Figure 2). The surface layer in the main spawning area west of Ireland, in the Iceland Basin and along the Norwegian slope is dominated by relatively warm and saline MNAW (Figure 1b). This relatively light water mass, which also has lower nutrient concentrations than waters further westward and northward, adds stability to the water column enhanced by atmospheric heat input to the ocean during the summer months. Although this stability enables a strong spring bloom, the stratification also impedes vertical mixing and renewal of silicates, and hence strong diatom-based primary production cannot be sustained for weeks. The surface layer becomes oligotrophic (Figure 2a), and the resulting lack of food will presumably force mackerel to move towards the regions with better feeding conditions. Poleward shifts of biota have previously been linked to expanding oligotrophic gyres in both the Atlantic and the Pacific Oceans (Polovina et al., 2001, 2008). By simply assuming that mackerel will continue to migrate as long as they experience food (and by inference nutrient) limitation, and that their movement will be in the direction of positive (food/nutrient) gradients, the general migration routes into the Norwegian and Irminger Seas could be explained by the effect of silicate concentrations on prey distribution (Figure 2a).

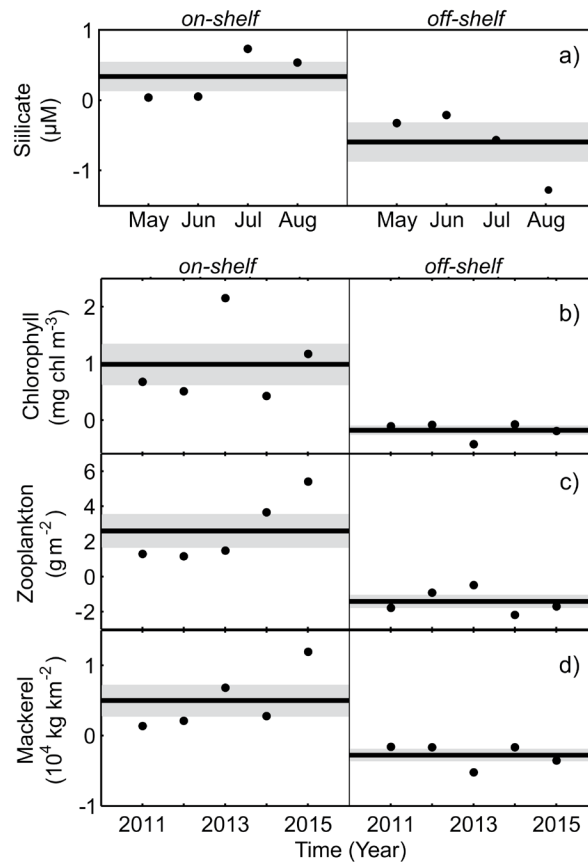


Figure 6
On-shelf and *off-shelf* standardized average differences.

Shown are *on-shelf* (left) and *off-shelf* (right) values, averaged over the respective domain (see Figure 3) and the selected time intervals (dots). Values were standardized by subtracting the full domain average (*on-shelf* and *off-shelf*) for months and years, accordingly (see Material and methods): a) monthly averaged near-surface (0–50 m) silicate concentrations (μM), based on available data from May to August during the period 1970–2013 (WOD, WOCE, EEL); b) chlorophyll concentrations (mg chl m^{-3}), averaged over July for the years 2011–2015; c) zooplankton abundances (g m^{-2}) and d) mackerel catch (kg km^{-2}) averaged over the data from the (July) IESSNS surveys of 2011–2015. Also shown are the mean (black line) over all months (a), or years (b, c and d) and associated standard error (shaded gray).

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On a smaller spatial scale (50–100 km), it appears that the fish congregate towards shelves, fronts and convective regions which, due to increased mixing and thus replenishment of nutrients, can sustain high productivity longer during the summer (Mann and Lazier, 2006). Satellite-based chlorophyll climatology revealed high concentrations on the south Iceland shelf and along the IFF frontal zone, in contrast to decreasing concentrations from late June to late July in the central Iceland Basin and central-eastern Norwegian Sea (Figure 5). During the IESSNS surveys (Figure 3a), the highest mackerel catches were made *i*) in the IFF and in the junction between the IFF and the JMF, *ii*) along the south Iceland shelf – especially on the western side, and *iii*) in the Irminger Sea after 2012. Relatively high catches were also made throughout the Norwegian Sea. The zooplankton samples from the IESSNS surveys confirmed the richness in food in these regions (Figure 3b). Diatoms thrive by utilizing deep water silicate brought to the surface by the unstable IFF (Allen et al., 2005); upwelling and potentially riverine silicate input enrich the south Iceland shelf (Stefánsson and Ólafsson, 1991). In the region southwest of Iceland winter deep convection supplies nutrients, such that the central Irminger Sea is nutrient-rich until end of June (Henson et al., 2006).

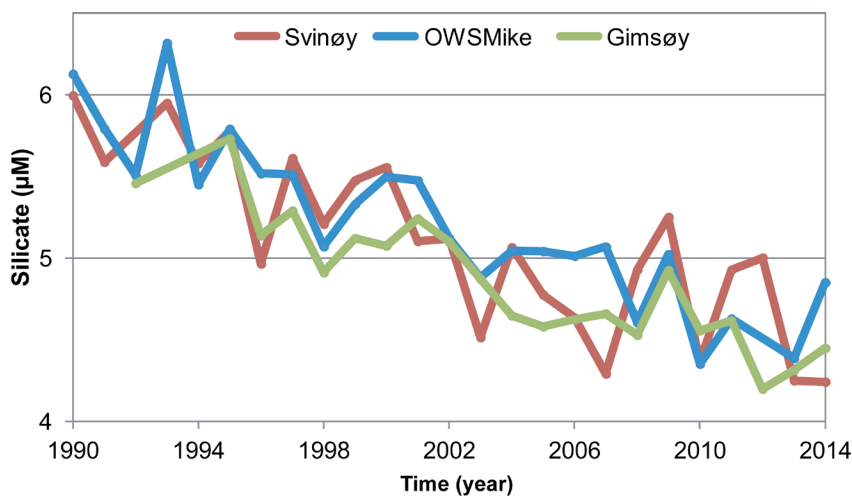


Figure 7
 Time series of winter (pre-bloom) silicate concentrations (μM).

Observed silicate concentrations from the mixed layer at three standard sampling sites in the Norwegian Sea: the Svinøy section, Ocean Weather Station Mike (OWSM) and the Gimsøy section shown in Figure 1a, updated from Rey (2012).

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Since the northern Iceland shelf is generally dominated by low temperatures intolerable for mackerel (Utne et al., 2012), mackerel will have to migrate south of Iceland in order to reach the western post-2006 expansion regions (Figure 1a). Low nutrient concentrations in the central Iceland Basin might limit primary production as early as May (Figure 4a). On the shelf, the nutrient replenishment will likely sustain strong primary production (Figure 4–6; Zhai et al., 2013), which might in turn create a zooplankton rich ‘corridor’ for the mackerel (Figures 3b and 6). The ‘corridor’ narrows during summer (June–August) as the nutrient-depleted surface layer extends northwards (Figure 4). Statistical tests on the concentrations and abundances of silicate, chlorophyll, zooplankton and mackerel show that the south Iceland shelf is more productive than the open ocean Iceland Basin (Figure 6, Table 1), supporting this hypothesis. This difference in productivity might also explain the conundrum of why the Iceland Basin is so biologically poor, with low nutrient, chlorophyll, phytoplankton, zooplankton and fish abundances/concentrations (Gudfinnson et al., 2008; Painter et al., 2014). According to logbooks, little fishery activity has historically taken place in the Iceland Basin (G. J. Óskarsson, pers. comm.) and pelagic fish surveys (redfish, mackerel, blue whiting, herring) all end at the border of the Iceland Basin (ICES, 2013, 2015).

Preliminary results from the survey in 2015 (ICES, 2015) show that, compared to the previous years, catches of mackerel were lower in the Irminger Sea, and higher in the Iceland Basin during this year. High abundances also stretched further offshore in the Iceland Basin. Convection was very deep in the Labrador–Irminger Seas during winter 2014–2015 (F. de Jong, pers. comm.), resulting in very low SST (<https://www.ncdc.noaa.gov/sotc/global/201508>) and, by inference, less stratified and nutrient-richer waters. According to mechanisms such as advection of the LSW into the Irminger Sea and exchange flows across the front (H. Hátún, pers. comm.), these conditions should have resulted in higher productivity in the open ocean surface layer, which was found to be the case during the IESSNS 2015 survey (ICES, 2015). In this sense, the ‘corridor’ on the south Iceland shelf might have also included the offshore Iceland Basin for a longer period of time during summer 2015. Furthermore, the stations in the Iceland Basin were sampled in early July during the 2015 survey, while previous surveys (2009–2014) covered this region during late July, more than two weeks later. The change in survey timing could also have contributed to the higher offshore mackerel catches, as the width of the ‘corridor’ noticeably reduces during these three–four weeks in July (Figures 4 and 5a, d). Although mackerel has been found further offshore in the central Iceland Basin in 2015, the catches at the Iceland shelf were still significantly higher than in the open ocean (Figure 6d).

A general poleward movement of biogeographical provinces, such as the post-2006 mackerel expansion, are most often linked to the ongoing global warming (Stenseth et al., 2002; Richardson and Schoeman, 2004) as *allowing* species to access new feeding grounds at higher latitudes. However, the most pronounced temperature increases in upper layer in the region did not occur in 2006, but rather around 1996–1998 and 2002–2003 (Hátún et al., 2005; Holliday et al., 2015). Subsequently the temperatures have remained high and even declined somewhat since 2010 (Larsen et al., 2012). Further, the near-surface summer temperatures south of Iceland, in the Iceland Basin and Irminger Sea, have been within the range that the mackerel occupies, and in the range that the mackerel prefers, for several decades (Astthorsson et al., 2012; MacKenzie et al., 2014). Hence we find it unlikely that temperature in itself has induced the recent mackerel expansion.

An assumption of passive drift in local currents cannot explain the expansion of the mackerel from the spawning grounds into the Iceland Basin, nor the observed near-shore affinity of mackerel in the northern Iceland Basin. Such an assumption would be based on a general anti-clockwise surface circulation of the Iceland Basin water masses (Valdimarsson and Malmberg, 1999). Nevertheless, in the narrow ‘corridor’ on the shelf, the mackerel would have to oppose the eastward flow of the South Iceland Current (Figure 1b; Logemann et al., 2013) in order to reach the highly productive regions further west.

One could, of course, question our assumption of the simplified ‘food chain’, silicate to *C. finmarchicus* to mackerel. This trophic pathway is justifiable during the spring bloom, when the fast-growing diatoms are an important food source for the ascending overwintering stock of *C. finmarchicus*. However, the linkage is more complex during mid- to late summer after the diatoms are generally outcompeted by other phytoplankton species and when the second *C. finmarchicus* generation (after the overwintering stock) constitutes the main zooplankton stock (Figure 2b). It is plausible, though, that good feeding conditions during zooplankton ascent and reproduction would generally increase the secondary production through the season (Kristiansen et al., 2015). It should be mentioned that nitrate levels are also declining in the northern North Atlantic and Nordic Seas (Rey, 2012; Johnson et al., 2013), which should reduce the production of most phytoplankton species, as already evident for the phytoplankton abundance in the Norwegian Sea (Naustvoll et al., 2010) and diatoms in the Irminger Sea (Zhai et al., 2013).

It might, furthermore, seem counterintuitive to suggest nutrient regulation of the pelagic complex, since the total biomass of the main pelagic fish stocks in the Northeastern Atlantic (mackerel, blue whiting and herring) has increased much during the last twenty years (ICES, 2014b), all while the nutrient concentrations have been declining (Figure 7; Rey, 2012). The total zooplankton biomass in the Nordic Seas is reported to have declined during the initial years of the westward mackerel expansion (2000–2009) and was lower again in 2015 (ICES, 2015). However, Hinder et al. (2014) showed that the *C. finmarchicus* decline could not be explained solely by SST and pointed out that food availability for zooplankton needs to be considered. Thus,

the presently reported declining nutrient concentrations could have contributed to this downward trend, in addition to the suggested grazing effect of the large pelagic fish stock (Ólafsdóttir et al., 2015). As nitrate and phosphate concentrations have also decreased in the spawning region in the Rockall Trough since the late 1990s (Johnson et al., 2013), limiting levels of the nutrients will have been reached earlier in the summer during recent years. The oligotrophic horizon is therefore likely to have shifted polewards and westward earlier during the season. Thus the observed nutrient decline may also impact the timing and distribution of the spawning, which in turn could have an impact on the post-spawning migration. Mackerel might therefore start spawning earlier and continue spawning farther north, which indeed has been observed (ICES, 2014c). The fish are likely then to reach the Iceland Basin earlier in the season, when the nutrient replete ‘corridor’ is broader (Figure 4a), and the nutrient- and zooplankton-rich regions in the Irminger Sea are more accessible. Although much remains to be understood before rigorously linking nutrients to fish, it seems likely that large-scale changes in the level of two major nutrients – silicate, as we have presented here, and nitrate as already documented (Rey, 2012; Johnson et al., 2013) – will impact higher trophic levels in some way. Hence we find it important to introduce this mechanism to the discussion of the post-2006 mackerel expansion.

Conclusions

Here we have added a potentially important *bottom-up* perspective to the discussion on the distribution of the Northeastern Atlantic mackerel stock and why it has expanded its summer feeding area westwards since 2006. Previous discussions have focused mainly on *top-down* density-dependent effects and on the impact of rising temperatures. By compiling rather disparate, but relevant, data on silicate concentrations, zooplankton and mackerel abundances, we have illustrated that during the summer, mackerel congregate at zooplankton-rich feeding *hot spots* near topography and oceanic fronts, while avoiding nutrient-poor Atlantic water. Evidence of the impact of nutrient limitation on mackerel migration has been illustrated, and statistically supported in the Iceland Basin. This study indicates that the ongoing nutrient decline, together with the west-east (high-low) horizontal nutrient gradient, might have added to the density-dependent depletion of food resources in the east, forcing mackerel to migrate farther north- and westwards in their search for food. We suggest that future mackerel surveys be augmented so that nutrient concentrations are sampled as well.

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Contributions

- Contributed to concept and main ideas: SP, HH
- Contributed to compilation of available data: SP, HH, SKE
- Contributed to new observations: JAJ, CJ, FR
- Contributed to analysis and interpretation of data: SP, HH, SKE
- Drafting the article: SP, HH
- Revising and finally approving the version to be published: SP, HH, JAJ, CJ, FR, and SKE

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Competing interests

The authors declare no competing interests.

Data accessibility statement

Only previously published data were used.

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