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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 scarcity 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

33 also migrates southwards and into the North Sea. After 2006, the mackerel stock has been steadily
34 increasing and expanding northwards into the northern parts of the Norwegian Sea, and westwards
35 into Icelandic waters. Since 2013, it has also been observed in the Irminger Sea (Figure 1a; ICES,
36 2014d; 2015) .

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

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

58 The copepod *Calanus finmarchicus* is the principal mackerel prey species (Langøy et al., 2006;
59 Prokopchuk and Sentyabov, 2006) and the most important zooplankton species in the subpolar
60 Atlantic. The total zooplankton biomass in the Nordic Seas is reported to have declined during the
61 initial years of the westward mackerel expansion (2000–2009). In a recent study, Hinder et al. (2014)
62 pointed out that the *C. finmarchicus* decline cannot be attributed solely to SST, and elucidated the
63 need to consider food availability for the zooplankton stock as a causal factor along with changes in
64 other parts of the life cycle. *C. finmarchicus* prefer the fast-growing diatoms as a food source
65 (Planque and Fromentin, 1996; Melle et al., 2014). The spring bloom in the North Atlantic is typically
66 dominated by diatoms, which, in addition to nitrate and phosphate, require sufficient concentrations of
67 silicate to build their frustules (Egge and Aksnes, 1992; Brzezinski et al., 1998). One of the most

68 fundamental principles in biological oceanography is nutrient limitation of primary production. This
69 principle is widely acknowledged for lower latitude oligotrophic waters, where only upwelling
70 regions can support strong and persistent biological production (Behrenfeld et al., 2006; Polovina et
71 al., 2008). In the higher latitude subpolar waters these fundamental dynamics have been largely
72 overlooked, probably because the most commonly studied essential nutrient, nitrate, seldom reaches
73 limiting concentrations (Allen et al., 2005). However, these waters become silicate-limited, restricting
74 persistent late-summer production of the fastest growing diatom algae to upwelling *hot spots*
75 (Brzezinski et al., 1998; Allen et al., 2005).

76 In the spawning region of mackerel, the subtropical water masses, already low in nutrients, become
77 oligotrophic towards the end of the spawning period (Polovina et al., 2008; Dave et al., 2015) limiting
78 primary production (Hartman et al., 2010), and thus the production of zooplankton (Planque and
79 Fromentin, 1996). During spawning, mackerel seem to be feeding more sporadically, while towards
80 the end of spawning mackerel become meagre and start to feed (Lockwood et al., 1981; ICES, 2014c).
81 This oligotrophic environment probably cannot provide sufficient food, which each summer may
82 force mackerel to migrate to more productive waters further north. On an interannual time scale, it is
83 interesting to note that silicate concentrations have been declining in the eastern Norwegian Sea since
84 the early 1990s (Rey, 2012). This change is potentially associated with an increased influence of low
85 nutrient subtropical waters as the size of the subpolar gyre and the strength of the circulation declined
86 (Hakkinen and Rhines, 2004; Hátún et al., 2005).

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

97 *Oceanographic overview*

98 Saline and nutrient-poor Eastern North Atlantic Water and less saline and nutrient-richer Western
99 North Atlantic Water meet and mix at the mackerel spawning grounds west of the British Isles (Figure
100 1). The resulting Modified North Atlantic Water (MNAW) flows polewards along the Norwegian
101 slope, and through the Iceland Basin. The MNAW meets subarctic water masses north of the Iceland-
102 Faroe Ridge, establishing first the Iceland-Faroe Front (IFF) and, farther downstream, after clockwise

103 circulation within the Norwegian Sea and subsequent cooling, the Jan Mayen Front (JMF). In the
104 Iceland Basin, a variable volume of Labrador Sea Water (LSW) underlies the warmer MNAW. The
105 general flow of MNAW is cyclonic in this region (Valdimarsson and Malmberg, 1999), but near the
106 southeastern Icelandic slope, there is a swift eastward flow, the South Iceland Current (Logemann et
107 al., 2013). The large density difference between the MNAW and the LSW in the central Iceland Basin
108 (Yashayaev et al., 2007) impedes deep winter convection, and thus restricts the replenishment of
109 nutrients, during winter. In April-May, the subpolar Atlantic switches from losing heat to the
110 atmosphere to receiving heat. Without any mixing agent, the near-surface will therefore become
111 increasingly stratified and nutrient-depleted throughout the summer. Generally, the three main mixing
112 agents continuously fuelling primary production by replenishment of nutrients are: *i*) vertical motion
113 along major fronts, *ii*) large-scale convection and *iii*) turbulence over underwater topography like
114 major ocean ridges and continental slopes.

115

116 Materials and methods

117 *Nutrient data*

118 The available nutrient data in the studied region have poor spatial and temporal coverage. A
119 climatological nutrient distribution (Figure 2a) at 50 m depth for 1960–2013, based on data
120 downloaded from the World Ocean Database (WOD, <https://www.nodc.noaa.gov>; Garcia et al.,
121 2001), however, gives a useful large-scale overview despite its coarseness ($1^\circ \times 1^\circ$).

122 To investigate the nutrient gradients through the Iceland Basin at finer resolution, we selected data
123 from the most frequently sampled standard hydrographic section in the region, along the longitude
124 20°W (Figure 1a). Data were obtained from the World Ocean Circulation Experiment (WOCE) data
125 archive, downloaded from CLIVAR and Carbon Hydrographic Data Office (CCHDO,
126 <http://cchdo.ucsd.edu>), from the Extended Ellett Line (EEL, quality checked using the method
127 detailed in Johnson et al., 2013) and from the above mentioned WOD. Measurements are temporally
128 sparse; all silicate observations from the period 1970–2013 were used to calculate monthly averages
129 for the summer season (May–August).

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

137

138 *Chlorophyll a from satellite data*

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

143

144 *Continuous plankton records*

145 Zooplankton data were obtained from the Continuous Plankton Recorder (CPR) survey for the period
146 1958–2005 (Batten et al., 2003). The survey is a monitoring program that uses the CPR sampling
147 device towed at ~10 m depth behind ships of opportunity on standard routes. As the CPR samples are
148 highly variable in space and time, spatial interpolation using the inverse squared distance method
149 (Lam, 1983) was applied to obtain gridded datasets for further analysis (Hátún et al., 2009). Only data
150 for the adult *C. finmarchicus* stages CV and CVI were used in this study, representing the
151 overwintering stock (Figure 2b).

152

153 *Mackerel surveys*

154 Snapshots of the zooplankton and mackerel distributions were obtained from the International
155 Ecosystem Summer Surveys in the Nordic Seas (IESSNS) surveys during July and the beginning of
156 August since 2010. The IESSNS is a swept-area trawl survey where mackerel are sampled using a
157 pelagic trawl at the surface at predefined geographical positions. Not all participating vessels used the
158 same trawl gear in the first years; however, since 2012 the survey gear and procedures have been
159 standardised (Nøttestad et al., 2016). Zooplankton samples were collected using a WP2 net (mesh size
160 180 µm or 200 µm) that was towed vertically from 200 m depth to the surface. The methodology of
161 surveys and sampling is described in more detail in Nøttestad et al. (2016).

162 The spatial extent of these surveys was mainly determined by the zero-catch line, although this
163 approach has not always been possible due to increasing stock size and expanding distribution.
164 However, during most of the surveys, the zero line was reached at the oceanic stations in the Iceland
165 Basin. The coverage of the surveys has varied throughout the years, generally covering the Norwegian
166 Sea, western Icelandic waters (since 2010) and east Greenlandic waters (since 2013). Here data from
167 surveys for the period 2010–2014 were used, since these surveys cover the western expansion area.
168 Westward coverage (to about 30°W) of zooplankton was first obtained in 2011, and then thereafter.
169 The data from each of the IESSNS were first gridded onto a regular (0.25° latitude x 0.5° longitude)
170 grid using Objective mapping (Böhme and Send, 2005), and regions with sparse sampling, where the

171 associated error map exceeded a selected threshold, were trimmed off. The presented averages (Figure
172 3) were thereafter calculated for the grid points where three or more data points were available. Since
173 the surveys in the Irminger Sea were only obtained during two years, this region was excluded from
174 the present analysis.

175

176 *On- and off-shelf analyses*

177 We selected a region covering a portion of the south Iceland shelf and the Iceland Basin (Figure 3),
178 with comprehensive coverage of silicate, chlorophyll, zooplankton and mackerel data (see above).

179 *On-shelf* averages were calculated from all stations in the selected region out to the 500 m isobath,
180 while *off-shelf* averages included stations from the 500 m isobath southwards to 60°N. Chlorophyll,
181 zooplankton and mackerel are presented as July averages for the years 2011–2015.

182 These data were supplemented with silicate data obtained from the EEL, WOCE and WOD. However,
183 measurements are temporally sparse, and hence robust yearly values for July cannot be calculated. As
184 such, all silicate observations obtained in the near-surface waters (0–50 m, 1970–2013) were used to
185 calculate monthly averages for the summer season (May–August) for the *on-shelf* and *off-shelf*
186 domain. We standardised the averages for all variables by subtracting the full domain average (*on-*
187 *shelf* and *off-shelf*) for months and years, accordingly. The mean over all months or years were
188 calculated for silicate and the three other variables, respectively.

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

195

196 **Results**

197 *Nutrient gradient and mackerel migration*

198 The climatological upper-ocean silicate concentrations during June, when the mackerel are searching
199 for food, showed oligotrophic conditions in the spawning region west of the British Isles and towards
200 the south Iceland coast, and high silicate concentrations within the central Norwegian Basin and in the
201 western subpolar gyre (Figure 2a). The climatological upper-ocean abundances of *C. finmarchicus* in
202 June showed a qualitatively similar pattern, with relatively low abundances in the Northeastern
203 Atlantic and high abundances in the southern Norwegian Basin and in the western subpolar gyre
204 (Figure 2b). This coarse relationship between silicate concentration and the distribution of *C.*

205 *finmarchicus* supports our hypothesis that the fish will migrate along local gradients of some property
206 in the ocean that reflects their food stocks, which we suggest to be silicate. Mackerel might be forced
207 poleward from the oligotrophic spawning region during summer in order to find sufficient food
208 stocks. Hence, as a food proxy, the positive silicate gradients might explain migration patterns
209 towards the Norwegian Basin and the subpolar gyre in the west. The pre-2006 northeastward
210 migration route is direct, while in order to reach the silicate- and zooplankton-rich Irminger Sea, fish
211 are challenged to cross the Iceland Basin where both nutrient concentrations and zooplankton
212 abundances are low during summer (Figure 2).

213

214 *Mackerel and zooplankton distribution in July*

215 The average mackerel distribution from the IESSNS data (Nøttestad et al., 2016) revealed generally
216 high abundances of mackerel in the Norwegian Sea, with highest concentrations in the western frontal
217 region (JMF and IFF; Figure 3a). High abundances were also observed west of Iceland, which after
218 2012 continued southwards into the Irminger Sea (not shown, see Material and Methods; ICES,
219 2014b). The July zooplankton abundances were likewise highest in the western Norwegian Sea frontal
220 zone, around the Faroe Plateau and southwest of Iceland, while lower abundances were observed
221 along the Norwegian slope and in the central Iceland Basin (Figure 3b). This main pattern roughly
222 reflects the climatological silicate concentrations and *C. finmarchicus* distributions discussed above
223 (Figure 2). Another very pronounced feature in both mackerel and zooplankton distributions are the
224 strong gradients between high abundance on the south Iceland shelf and low and/or zero abundance in
225 the oceanic stations in the Iceland Basin (Figure 3). The zooplankton abundances yielded a more
226 diffuse pattern, compared to the mackerel data, likely related to the higher inherent noise in the WP2
227 data.

228

229 *The narrow 'corridor' south of Iceland*

230 Nutrient concentrations along the meridional section at 20°W (Figure 1a), extending from the south
231 Iceland shelf southwards into the Iceland Basin, gave a clearer in-depth picture of the ocean-shelf
232 contrast. Due to the variable timing of the surveys, data from several years were required to explore
233 seasonal variability. Oceanic stratification was established in May, and silicate concentrations started
234 to decline in the Iceland Basin (Figure 4a). The oceanic stratification intensified through the summer
235 (May–August), and the silicate levels continued to decline in the central basin (Figure 4a-c).
236 However, the silicate levels on the shelf remained higher through the summer, likely replenished by
237 topographically induced mixing, although the 'corridor' of elevated silicate levels narrowed during
238 the June to August period (Figure 4b-d). Satellite-based chlorophyll climatology (Figure 5) revealed
239 high concentrations of chlorophyll in the vicinity of the IFF and on the south Iceland shelf, in contrast

240 to low values in the central-eastern Norwegian Sea and central Iceland Basin. The difference between
241 the ‘*on-shelf*’ and ‘*off-shelf*’ regions increased markedly throughout summer, as exemplified by eight-
242 day time segments of chlorophyll data, starting in late June and ending in late July (Figure 5). The
243 rather qualitative observations were statistically tested for region south of Iceland, which
244 demonstrated that the concentrations and abundances of silicates, chlorophyll, zooplankton and
245 mackerel were all significantly higher on-shelf than off-shelf ($p < 0.001$; Figure 6, Table 1). This test
246 supports our hypothesis that mackerel avoid the central Iceland Basin during July due to food
247 limitation (zooplankton) caused by nutrient limitation, and thus congregate along the shelf (Figure
248 3a).

249

250 *A silicate decline and the westward post-2006 mackerel expansion*

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

262

263 Discussion

264 Here we suggest that the general migration pattern of the Northeastern Atlantic mackerel stock may
265 be related to the near-surface silicate concentrations, which we utilize as a coarse proxy for the
266 mackerel food stock of zooplankton (Figure 2). The surface layer in the main spawning area west of
267 Ireland, in the Iceland Basin and along the Norwegian slope is dominated by relatively warm and
268 saline MNAW (Figure 1b). This relatively light water mass, which also has lower nutrient
269 concentrations than waters further westward and northward, adds stability to the water column
270 enhanced by atmospheric heat input to the ocean during the summer months. Although this stability
271 enables a strong spring bloom, the stratification also impedes vertical mixing and renewal of silicates,
272 and hence strong diatom-based primary production cannot be sustained for weeks. The surface layer
273 becomes oligotrophic (Figure 2a), and the resulting lack of food will presumably force mackerel to
274 move towards the regions with better feeding conditions. Poleward shifts of biota have previously

275 been linked to expanding oligotrophic gyres in both the Atlantic and the Pacific Oceans (Polovina et
276 al., 2001; 2008). By simply assuming that mackerel will continue to migrate as long as they
277 experience food (and by inference nutrient) limitation, and that their movement will be in the
278 direction of positive (food/nutrient) gradients, the general migration routes into the Norwegian and
279 Irminger Seas could be explained by the effect of silicate concentrations on prey distribution (Figure
280 2a).

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

295 Since the northern Iceland shelf is generally dominated by low temperatures intolerable for mackerel
296 (Utne et al., 2012), mackerel will have to migrate south of Iceland in order to reach the western post-
297 2006 expansion regions (Figure 1a). Low nutrient concentrations in the central Iceland Basin might
298 limit primary production as early as May (Figure 4a). On the shelf, the nutrient replenishment will
299 likely sustain strong primary production (Figure 4–6; Zhai et al., 2013), which might in turn create a
300 zooplankton rich ‘corridor’ for the mackerel (Figures 3b and 6). The ‘corridor’ narrows during
301 summer (June–August) as the nutrient-depleted surface layer extends northwards (Figure 4).
302 Statistical tests on the concentrations and abundances of silicate, chlorophyll, zooplankton and
303 mackerel show that the south Iceland shelf is more productive than the open ocean Iceland Basin
304 (Figure 6, Table 1), supporting this hypothesis. This difference in productivity might also explain the
305 conundrum of why the Iceland Basin is so biologically poor, with low nutrient, chlorophyll,
306 phytoplankton, zooplankton and fish abundances/concentrations (Gudfinnson et al., 2008; Painter et
307 al., 2014). According to logbooks, little fishery activity has historically taken place in the Iceland
308 Basin (G. J. Óskarsson, pers. comm.) and pelagic fish surveys (redfish, mackerel, blue whiting,
309 herring) all end at the border of the Iceland Basin (ICES, 2013; 2015).

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

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

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

343 One could, of course, question our assumption of the simplified ‘food chain’, silicate to *C.*
344 *finmarchicus* to mackerel. This trophic pathway is justifiable during the spring bloom, when the fast-

345 growing diatoms are an important food source for the ascending overwintering stock of *C.*
346 *finmarchicus*. However, the linkage is more complex during mid- to late summer after the diatoms are
347 generally outcompeted by other phytoplankton species and when the *C. finmarchicus* second
348 generation (after the overwintering stock) constitutes the main zooplankton stock (Figure 2b). It is
349 plausible, though, that good feeding conditions during zooplankton ascent and reproduction would
350 generally increase the secondary production through the season (Kristiansen et al., 2015). It should be
351 mentioned that nitrate levels are also declining in the northern North Atlantic and Nordic Seas (Rey,
352 2012; Johnson et al., 2013), which should reduce the production of most phytoplankton species, as
353 already evident for the phytoplankton abundance in the Norwegian Sea (Naustvoll et al., 2010) and
354 diatoms in the Iceland Basin (Zhai et al., 2013).

355 It might, furthermore, seem counterintuitive to suggest nutrient regulation of the pelagic complex,
356 since the total biomass of the main pelagic fish stocks in the Northeastern Atlantic (mackerel, blue
357 whiting and herring) has increased much during the last twenty years (ICES, 2014b), all while the
358 nutrient concentrations have been declining (Figure 7; Rey, 2012). The total zooplankton biomass in
359 the Nordic Seas is reported to have declined during the initial years of the westward mackerel
360 expansion (2000–2009) and was lower again in 2015 (ICES, 2015). However, Hinder et al. (2014)
361 showed that the *C. finmarchicus* decline could not be explained solely by SST and pointed out that
362 food availability for zooplankton needs to be considered. Thus, the presently reported declining
363 nutrient concentrations could have contributed to this downward trend, in addition to the suggested
364 grazing effect of the large pelagic fish stock (Ólafsdóttir et al., 2015). As nitrate and phosphate
365 concentrations have also decreased in the spawning region in the Rockall Trough since the late 1990s
366 (Johnson et al., 2013), limiting levels of the nutrients will have been reached earlier in the summer
367 during recent years. The oligotrophic horizon is therefore likely to have shifted polewards and
368 westward earlier during the season. Thus the observed nutrient decline may also impact the timing
369 and distribution of the spawning, which in turn could have an impact on the post-spawning migration.
370 Mackerel might therefore start spawning earlier and continue spawning farther north, which indeed
371 has been observed (ICES, 2014c). The fish are likely then to reach the Iceland Basin earlier in the
372 season, when the nutrient replete ‘corridor’ is broader (Figure 4a), and the nutrient- and zooplankton-
373 rich regions in the Irminger Sea are more accessible. Although much remains to be understood before
374 rigorously linking nutrients to fish, it seems likely that large-scale changes in the level of two major
375 nutrients – silicate, as we have presented here, and nitrate as already documented (Rey, 2012; Johnson
376 et al., 2013) – will impact higher trophic levels in some way. Hence we find it important to introduce
377 this mechanism to the discussion of the post-2006 mackerel expansion.

378

379 Conclusions

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

392

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539

540 Contributions

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

547

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557 Competing interests

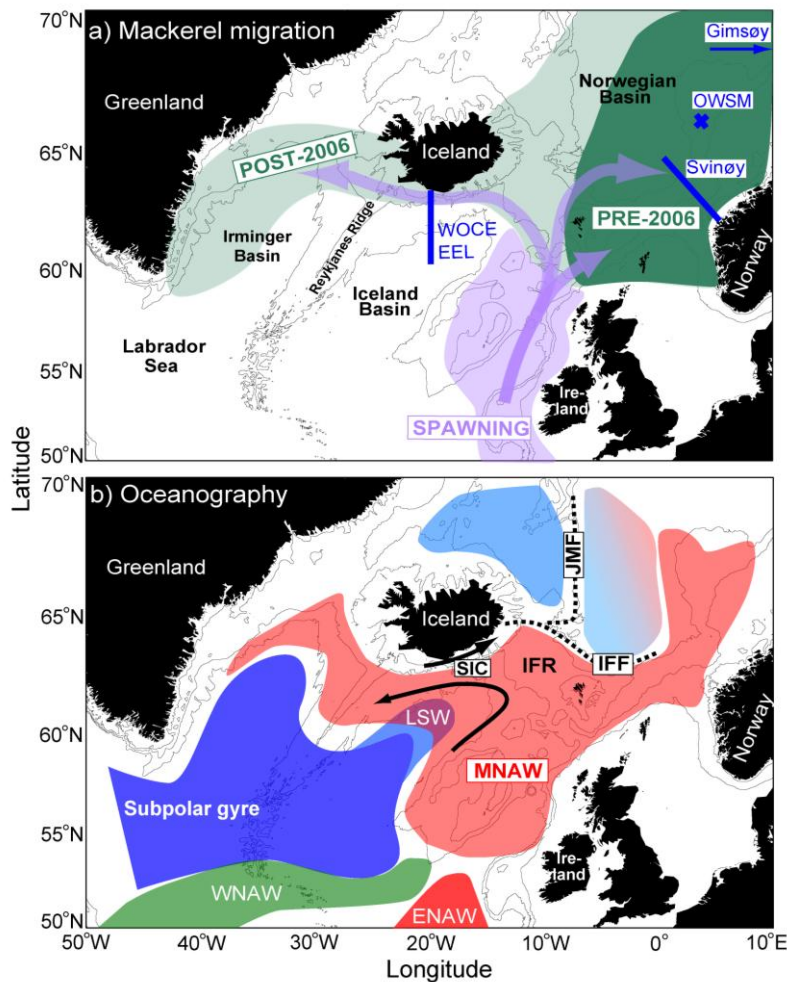
558 The authors declare no competing interests.

559 Data accessibility statement

560 Only previously published data were used.

561

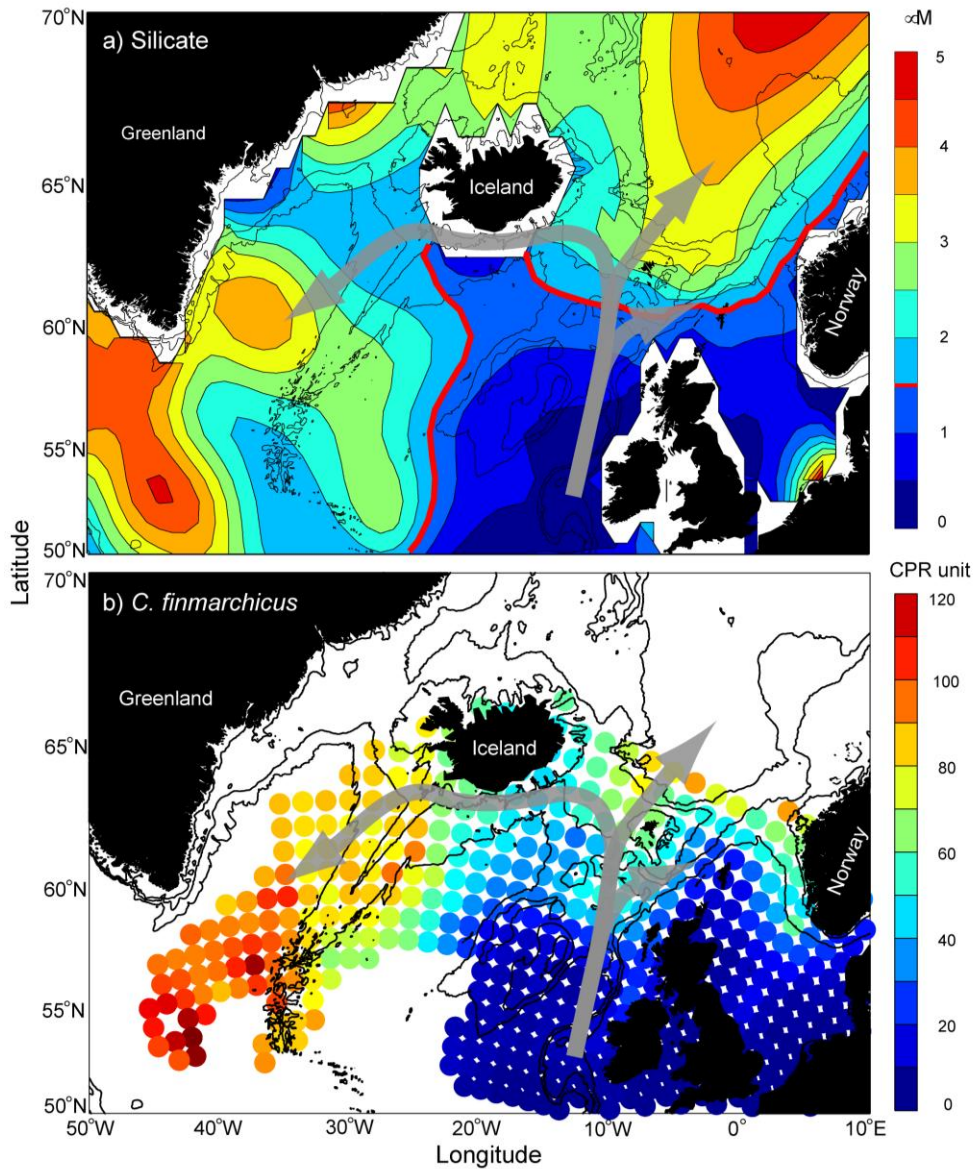
562 Figure titles and legends



563

564 **Figure 1. Geographical overview of the mackerel stock dynamics.**

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

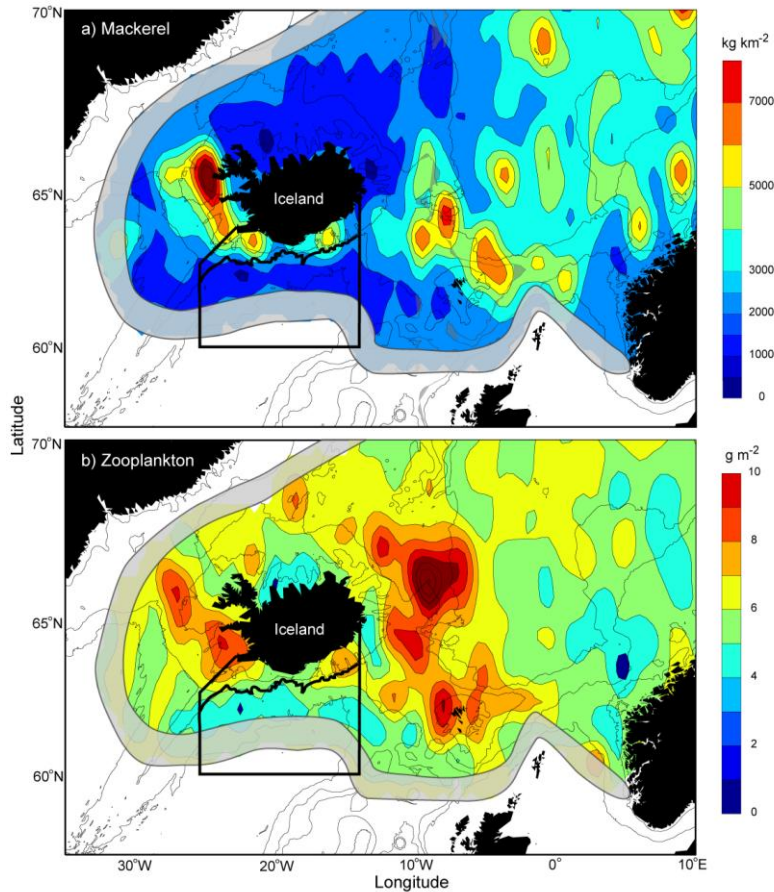


578

579 **Figure 2. June silicate and *C. finmarchicus* climatology.**

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

584

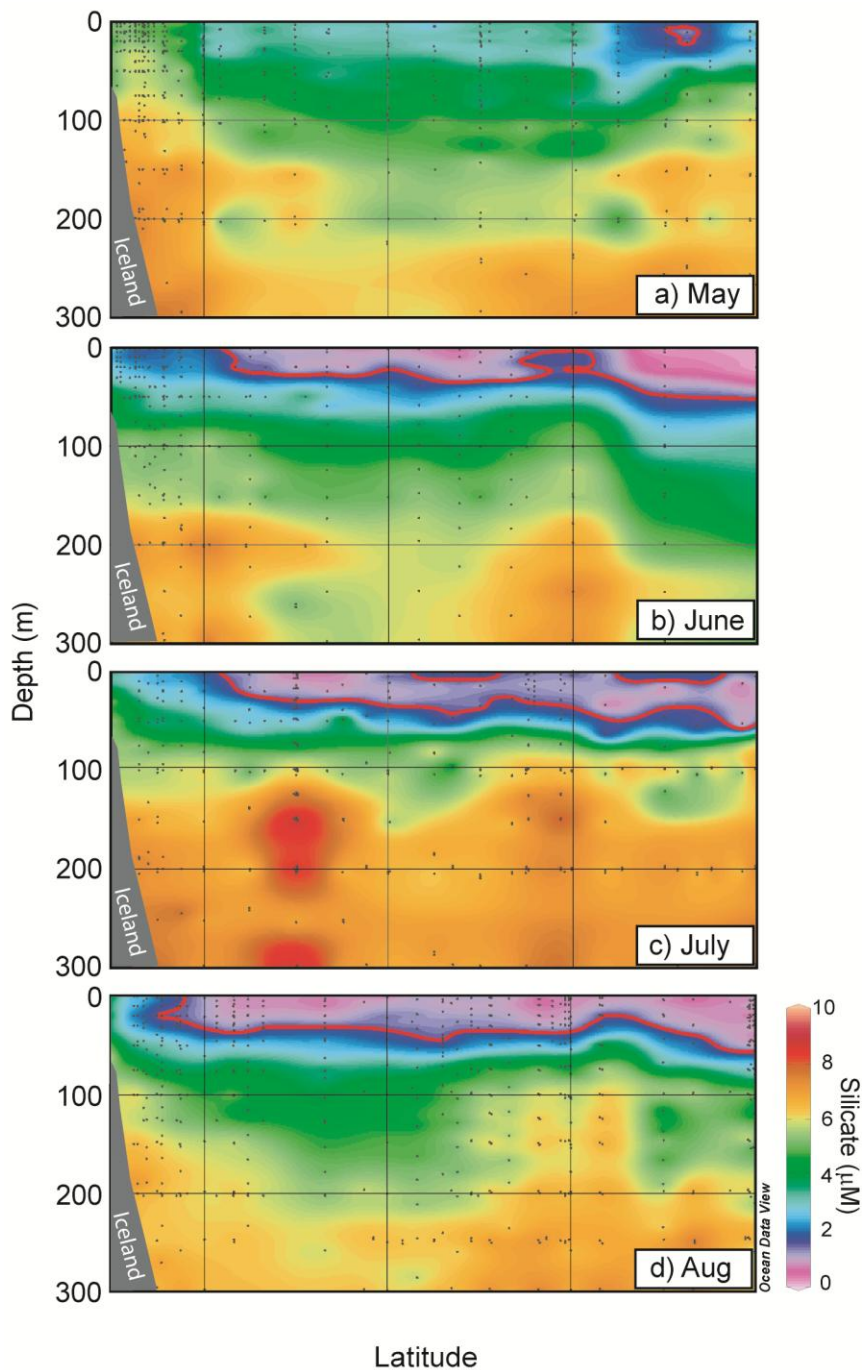


585

586 **Figure 3. Mean mackerel and zooplankton abundances.**

587 a) Average mackerel catches (kg km^{-2}) and b) average zooplankton dry weight (g m^{-2} in the upper 200
 588 m) from the International Ecosystem Summer Surveys in the Nordic Seas (IESSNS) from the period
 589 July–August. Averages are over the period 2010–2014 and gridded onto a regular grid (0.25° latitude
 590 $\times 0.5^\circ$ longitude; see Material and Methods). A border has been overlaid (gray shading) where the
 591 maps are less reliable due to the spatially limited data distribution. The black line denotes the region
 592 in the south of Iceland used in the statistical analysis (Figure 6 and Table 1). The *on-shelf* region is the
 593 area from the coast out to the 500 m isobath, while the *off-shelf* region extends from 500 m isobath
 594 southwards to 60°N .

595



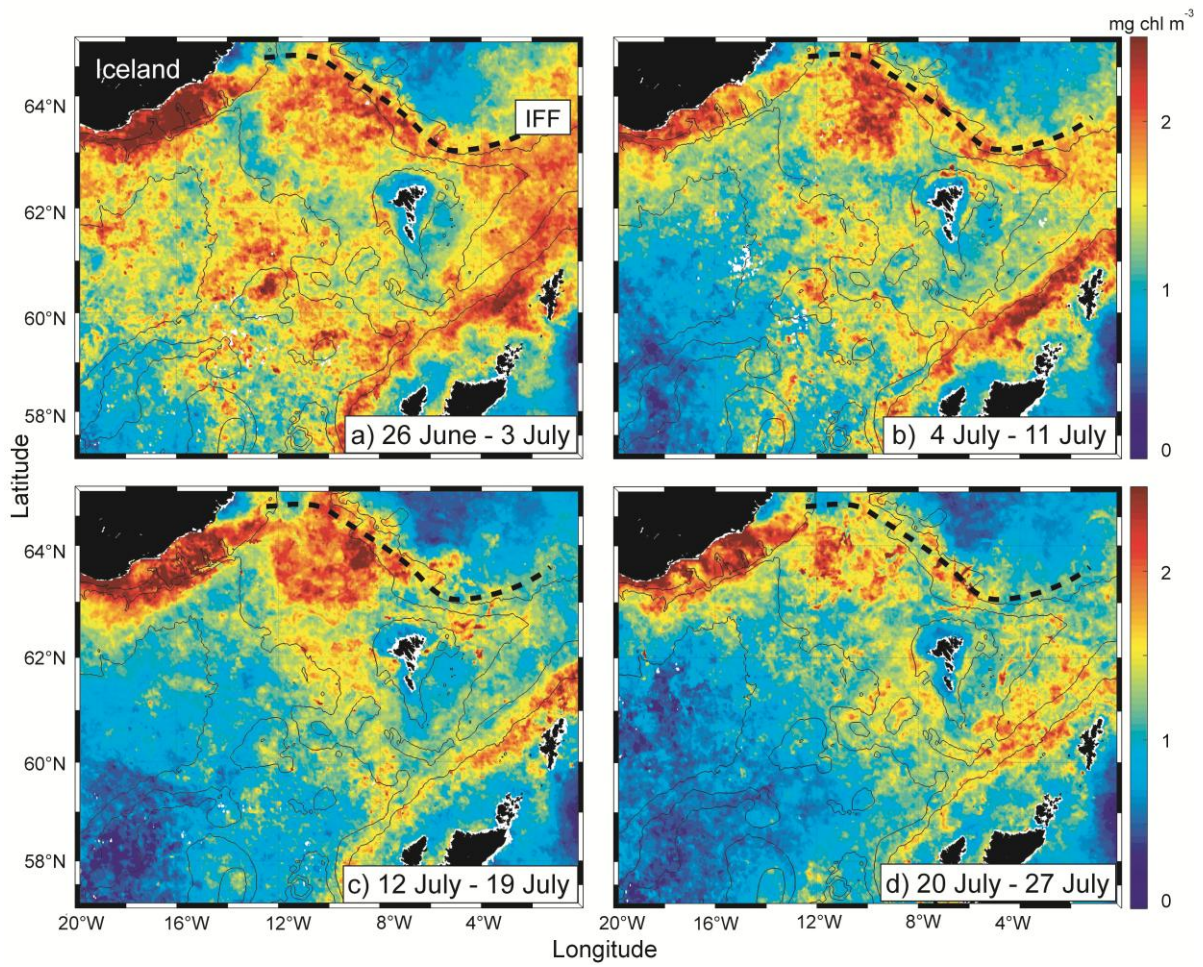
596

Latitude

597 **Figure 4. Silicate concentrations (μM) along the meridional section for the summer months.**

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

601



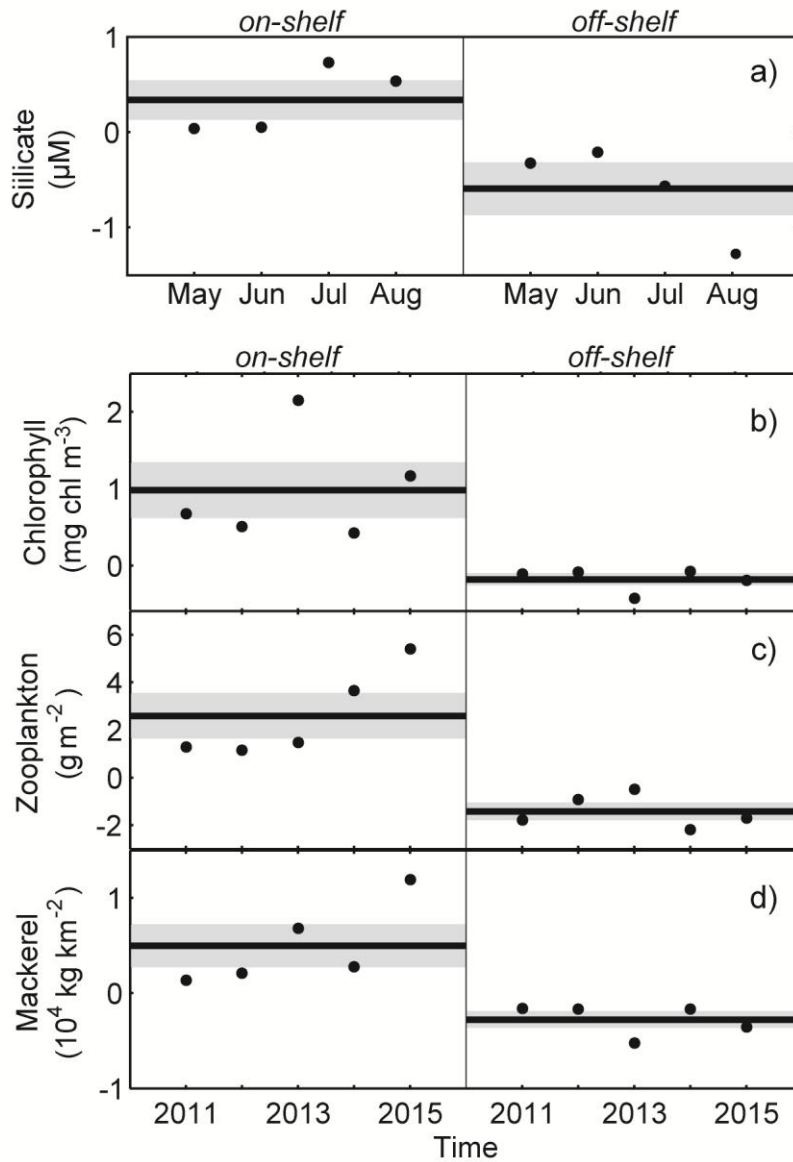
602

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

604 Climatological averages (1998–2015) over four eight-day time segments from late June to late July

605 are shown (see Material and Methods). Dotted black line defines Iceland-Faroe Front (IFF)

606

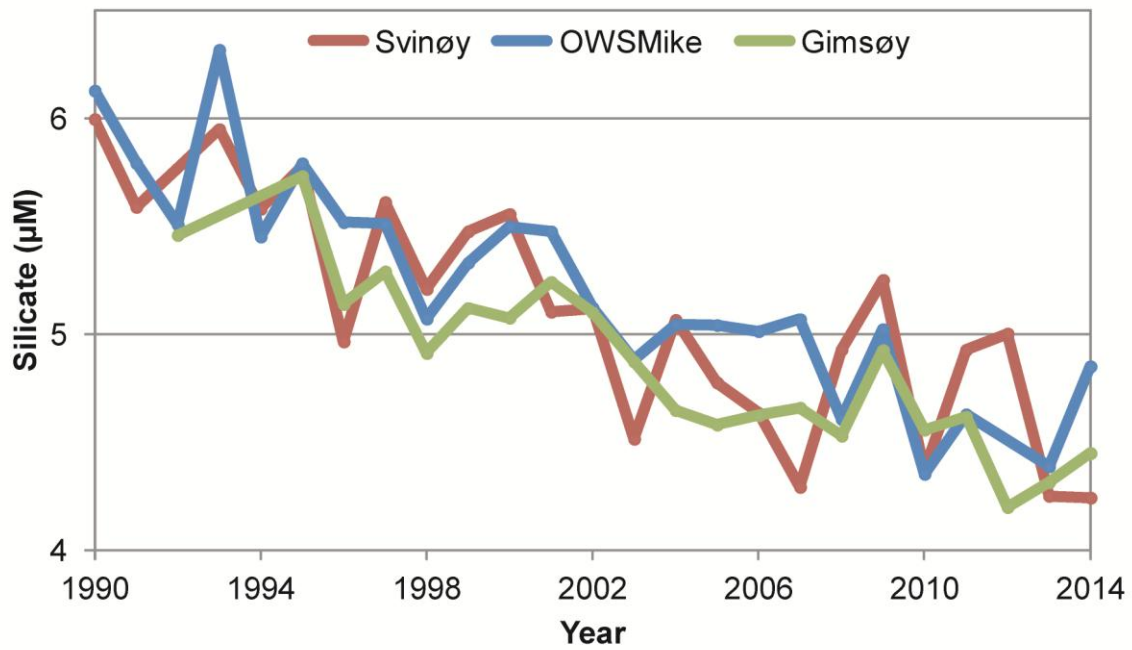


607

608 **Figure 6. *On-shelf* and *off-shelf* standardised average differences**

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

618



619

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

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

624

625

626

627 Tables

628

629 **Table 1.** Tests of the hypothesis that the summer (July) concentrations and abundances of silicate,
 630 chlorophyll, zooplankton and mackerel on the south Iceland shelf (< 500 m) are higher than those *off-*
 631 *shelf* in the Iceland Basin (> 500 m). N_{on} and N_{off} , represent the total number of data points on and off
 632 the shelf, respectively.

633

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	$6.20 \cdot 10^3 \text{ kg m}^{-2}$	0.0014	38	58

634