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Marine climate and mackerel distribution

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Content

Abstract

During fall 2012, the Polar research institutes in Russia (PINRO) and the Faroe marine research institute (FAMRI) continued the collaboration and the scientific work initiated in Tórshavn March 2006 on how the marine climate in the southern Nordic Seas might influence the spatial distribution of the mackerel stock in the Nordic Seas. Commercial catch data from the Russian fleet were analyzed together with a selection of comprehensive spatio-temporal oceanographic and biological observations. Pronounced sub-decadal variability is found both in the physical and the biological data, and the apparent synchronicity between these allows us to hypothesize three plausible mechanistic linkages. Much of the variability is ascribed to the spatially shifting Iceland-Faroe Front, and metrices for these fluctuations are presented. Our analysis should merely be regarded as ground work, upon which more detailed and finalized work could be conducted. We suggest continued Russian-Faroese collaboration, to further pursue these important questions.

1. Introduction

The Northeast Atlantic mackerel (*Scomber scombrus*) is a highly migratory species that, after spawning along the European shelf, gradually moves northwards, (ICES, 2014) into the summer feeding areas in the Norwegian Sea (Iversen, 2004; Uriarte et al., 2001). 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 (ICES 2014; 2015).

Here, we focus on the aspects of the mackerel migration during the summer feeding in the southern Nordic Seas. In the southeastern corner of the Nordic Seas, warm northward flowing Atlantic water masses meet colder subarctic water masses from the west (Fig. 1a). This establishes two main fronts, the U-shaped Iceland-Faroe Front (IFF), which starts at the Icelandic slope and continues towards Norway, and the meridional Jan-Mayen Front farther northwest (Fig. 1b). The density contrast across the IFF is strong, especially near Iceland, while the temperature and salinity contrasts across the Jan-Mayen front almost compensate in density and the gradient is small (Fig. 1b).

The IFF is, like most oceanic fronts, a highly productive region (Allen et al., 2005) which mackerel enters around June for feeding (Langoy et al., 2012). The frontal position might shape the mackerel distribution through thermal barriers and/or food

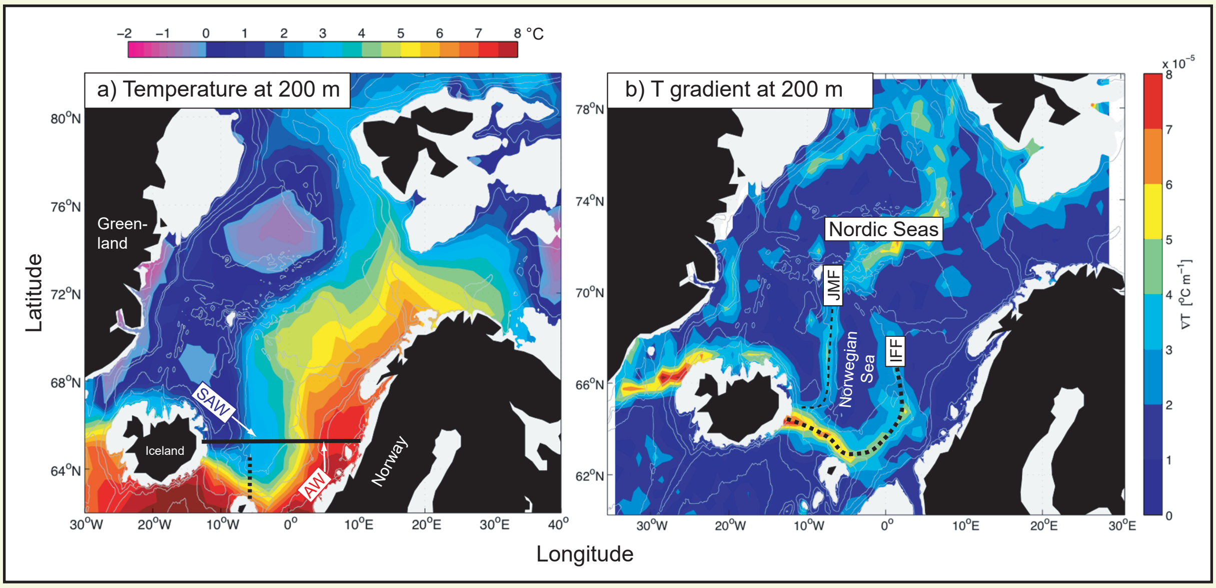

Fig. 1 Climatological hydrography at 200 m depths (Jan-Dec, 1950-2000). a) Temperature and b) temperature gradient. The solid line in a) refers to the section presented in Fig. 2 and the dashed line in a) shows the section, from where the C. finmarchicus *data present in Fig. 11 are sampled. Abbreviations: AW (Atlantic Water), SAW (SubArctic Water), IFF (Iceland-Faroe Front) and JMF (Jan-Mayen Front).*

production. It is, however, not clear which aspects of the frontal dynamics are the most important. A well developed and relatively warm mixed layer is a prerequisite for the presence of mackerel, but since these waters always are well stratified and probably over the thermal tolerance level for mackerel during June (Utne et al., 2012), temperature per se is probably not the only limiting factor.

The copepod *Calanus finmarchicus* is the most abundant zooplankton species in the subpolar Atlantic (Melle et al., 2014). The parent generation (G_0) resides deep in the cold subarctic water masses during winter, ascends to the near-surface around March-April and produces the next generation (or generations, G_1 and maybe G_2), which descend again into diapause around August (Heath et al., 2000).

Mackerel preys during June-August mainly on large stages of the new generation of *C. finmarchicus* (Langoy et al., 2012, Prokopchuk and Sentyabov 2006; Debes et al. 2012). The abundance of this prey during the main feeding season must be determined by *i)* the size of the overwintering stock (G_0)(many large females produce many eggs) and *ii)* the local/regional near-surface growth conditions through the summer. The relative importance of these two factors is not well understood.

The largest source of oceanographic variability in the Norwegian Sea is the marked southeast-northwest shifts of the major fronts (Blindheim et al., 2000). The fronts identified in remotely sensed temperature and chlorophyll, especially the IFF, are just the surface outcropping of a three dimensional thermocline (pycnocline), which bounds the Atlantic Water (AW, red in Fig. 1a) and the sub-arctic water (SAW, blue in Fig. 1a) and intersects the seafloor along the Iceland-Scotland Ridge in south and the Norwegian Slope in east (Fig. 2)(Hansen and Østerhus, 2000). Major frontal shifts in the ocean are most often observed along vertical transects, as idealistically illustrated in Figure 2. A westward shift entails an increased area of AW and a decreased area of SAW (Fig. 3a), and vice versa for an eastward shift (Fig. 3b)(Mork and Blindheim 2000). Observations of sea surface temperature (SST) would reveal an increase region with elevated temperatures during a westward shift, but since the near-surface signature in summer is blended with the upper mixed layer (Fig. 2a) this signal will be rather noisy. The identification of the front is sharper at depth, and in situ hydrography at about 300 m (Fig. 2) would also be a good metric – temperature and salinity increase during westward shifts.

The sea surface is not ‘flat’, but bulges due to oceanographic variability. The sea surface height (SSH) in the deep Norwegian Basin is primary regulated by thermal expansion, also called steric height (Hátún and McClimans, 2003). This is directly related to the average density of the entire water column, which in this region is largely determined by temperature (Siegismund et al., 2007). The frontal shift and the large density contrast between the AW and SAW, induces particularly large SSH variability in the frontal zone (Fig. 3)(Richter et al., 2012). A westward shift results in a large volume of AW water in the water column (red colour with green rectangle in Fig. 3a), larger depth averaged temperatures, lower average densities and thus a higher SSH, and opposite for an eastward shift (Fig. 3b).

We here present a preliminary investigation of how climatic indices, valuable for the mackerel distribution question, can be produced for the southern Nordic Sea. Some of the resulting time series have the potential for giving a long-term (back to the 1950s) perspective, but we will focus on the period around 1990-2008, when clear sub-decadal variability was observed.

2. Mackerel

Mackerel does not show clearly in acoustic surveys as it lack a gas-filled swim bladder, so we mostly have to rely on commercial or scientific catch data.

2.1 Catches by all nations

Data on the international fishery for mackerel by ICES statistical squares by quarter in 1977-2008 is compiled in the database of the North Eastern Atlantic Fisheries Commission (NEAFC, 1998) and later in ICES (ICES 2015). The all-year averaged distribution of this fishery during the third quarter (July-September) is shown in Fig. 4. This illustrates the historically large fishery within the North Sea and in the southeastern part of the Norwegian Sea (red colours), confirming the expected large presence of mackerel in this productive frontal region. The quarterly segregated catch data from

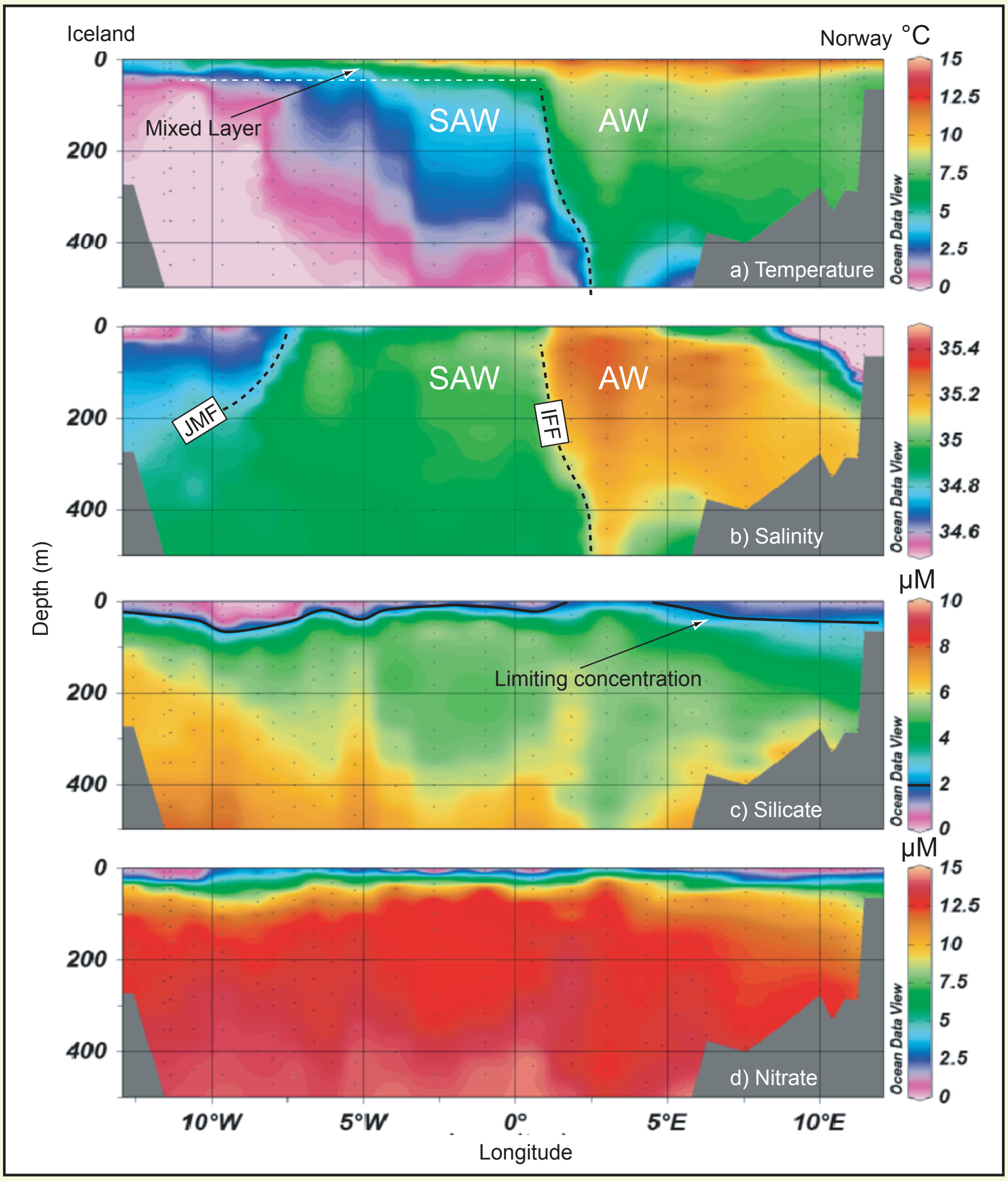

Fig. 2 A zonal cross-section along 66°N, viewed from the south, of a) temperature, b) salinity, c) silicate and d) nitrate. The observations were made during July in 2002. Abbreviations: Atlantic Water (AW), Sub-Arctic Water (SAW), Iceland-Faroe Front (IFF) and Jan-Mayen Front (JMF).

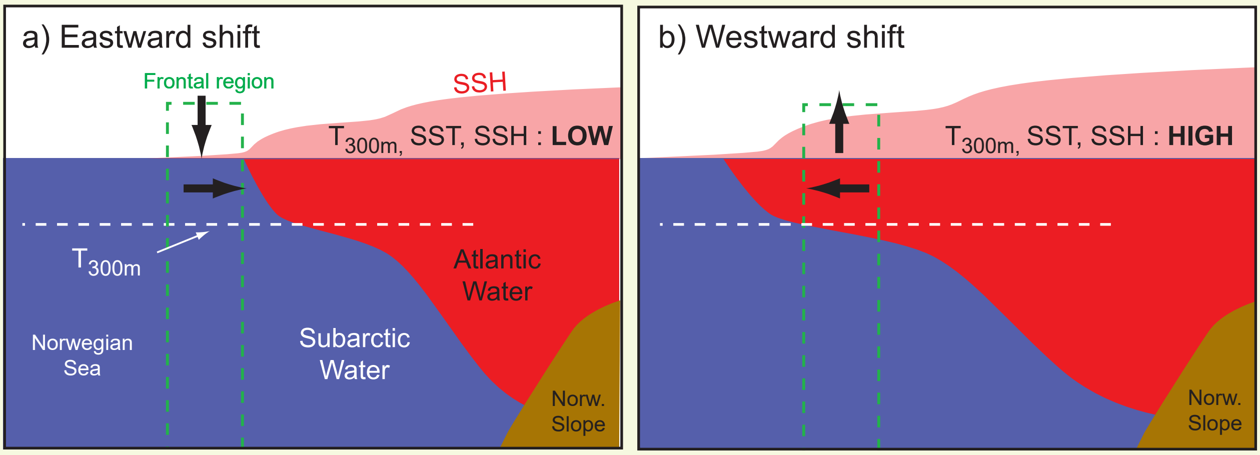

Fig. 3 Sketch of the frontal shift along a vertical westward from the Norwegian slope, viewed from the south (see Fig. 1). a) A situation when the atmospheric forcing is weak (e.g. NAO-low), and the Atlantic water spreads far west and b) a situation when the atmospheric forcing is strong (e.g. NAO-high), and the main front shifts towards Norway. The green dotted box represents the frontal area with the highest variation in SSH dependent on the east-west shift in the atmospheric forcing (thick black arrows).

the NEAFC database are, however, too coarse for a more detailed analysis.

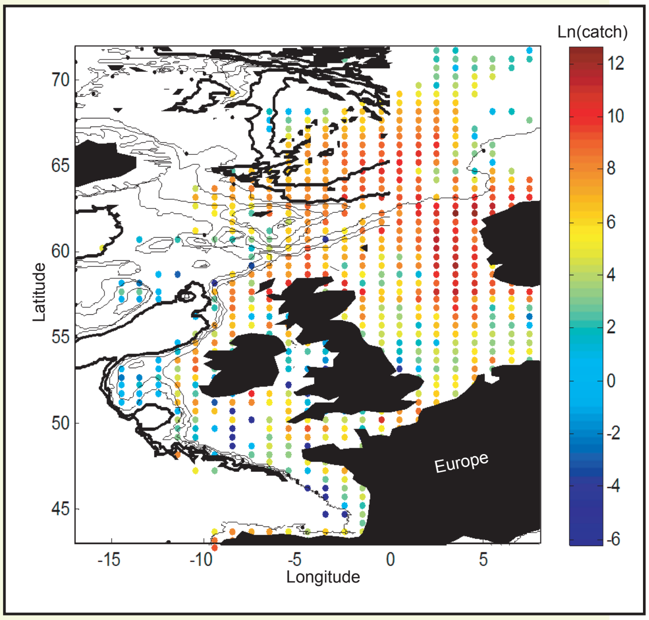

Fig. 4 Catches of mackerel by all nations. Long-term averages (1977-2008) over the months July-September (3rd quarter, from the NEAFC database). Natural logarithmic values (10 =22.000 tons).

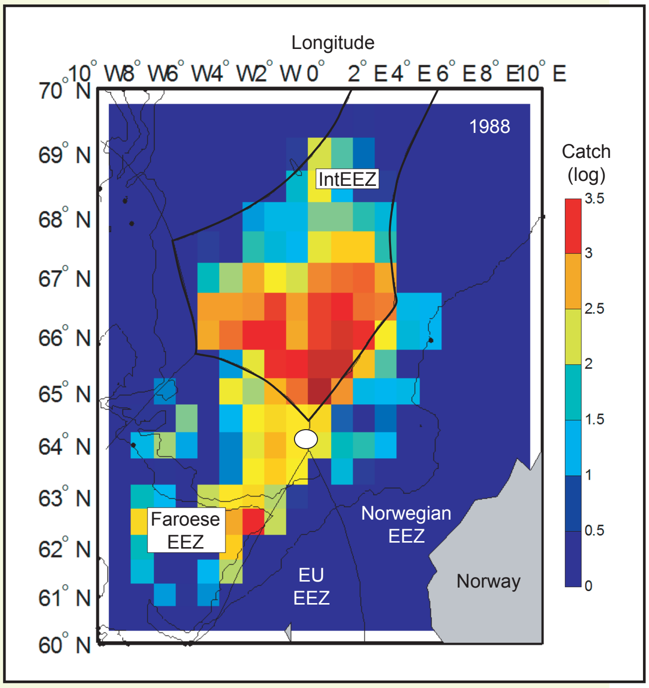

Fig. 5 Total Russian catches in 1988 (on a log scale). The EEZ borders are shown with black lines, with the IntEEZ, and the nodal point between the EEZs, emphasized.

2.2 Russian catches – a mackerel index

The rich biological data from the International Ecosystem Summer Survey in the Nordic Seas (IESSNS)(Nottestad et al., 2016) are of rather short duration (started in 2007), so the only data source with sufficient spatio-temporal coverage to elucidate the marked sub-decadal variability after 1990 is the Russian mackerel catch data. The Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) data consist of logbook data from the Russian fleet fishing for mackerel in the Norwegian Sea compiled into catch in tonnes per ICES rectangle by month and year (Belikov et al., 1998). Under the collaboration between Russia (PINRO) and the Faroe Islands (FAMRI), these data have been updated (Fig. 5). The nodal point between four Exclusive Economical Zones (EEZ's) is situated near the region of maximum frontal variability (Fig. 5). The international zone lies to the north (IntEEZ), the Faroese and Norwegian zones to the west and east, respectively, and the EU zone to the south. Russian vessels have fished mackerel in the IntEEZ since 1980 and in Faroese waters since 1981 (Belikov et al., 1998). First as by-catch in the blue whiting and herring fishery, and after 1987 as a direct mackerel fishery. This has shown high catch rates, especially in the months June-August, and that mackerel in many years has been distributed over a wide area. The main feeding distribution is on average situated near the nodal point between all four EEZ's, as illustrated with the total catches in 1988 (Fig. 5). It appears as if the fishery is 'pressed up' against the Norwegian EEZ boundary, and it might be postulated that high concentrations of mackerel might be found in the Norwegian zone close to the border – i.e. in the frontal region, which the international catches also seem to indicate (Fig. 4). If it is assumed that mackerel has an affinity for the warmer side of the frontal zone, one should expect increased mackerel abundances, and thus a larger fishery within the IntEEZ, during periods when the front is shifted towards west. We use the total Russian catches within the IntEEZ for each year as a crude proxy record for the expected east-west mackerel shifts. This 'mackerel index' is tested against plausible physical drivers below.

3. Environmental variability

With sufficient spatio-temporal data, the traditional vertical sectional view (Fig. 2) can be extended to a horizontal map view. Chlorophyll concentrations (phytoplankton) and SST can be mapped from satellite observations, optimally interpolated with available in-situ data. These fields are noisy, but the data coverage is good. The temperature variability at 300m depths (T_{300m}) is obtained from large hydrographic databases – the signal is clearer, but the coverage is much sparser. SSH data from the altimetry satellites (www.jason.oceanobs.com) reveal a depth-integrated signal of the density/buoyancy/water mass structure, and the data coverage has been very comprehensive since 1993. This is therefore a very strong data source, and its usefulness has been demonstrated by e.g. producing the gyre index (Häkkinen and Rhines, 2004; Hátún et al., 2005), against which a larger number of biological time series have been successfully compared (Hátún et al., 2009a; Hátún et al., 2009b). If output from numerical models is found to satisfactorily reproduce the main oceanographic features and signals, then these give a unique 4-D (time and space) context with all physical variables, in which to interpret the observations. We have used output from the same version of MICOM (Miami Isopycnal Coordinate Ocean Model) as was used in (Hátún et al., 2005; Sandø and Furevik, 2008).

3.1 Elevated variability along the frontal zone

The region experiencing the strongest deep shifts in the boundary between AW and SAW in the southeastern Norwegian Sea is identified with the SSH variability, calculated as the standard deviation of the altimetry data over the period 1993-2012 (Fig. 6a). Applying an Empirical Orthogonal Function

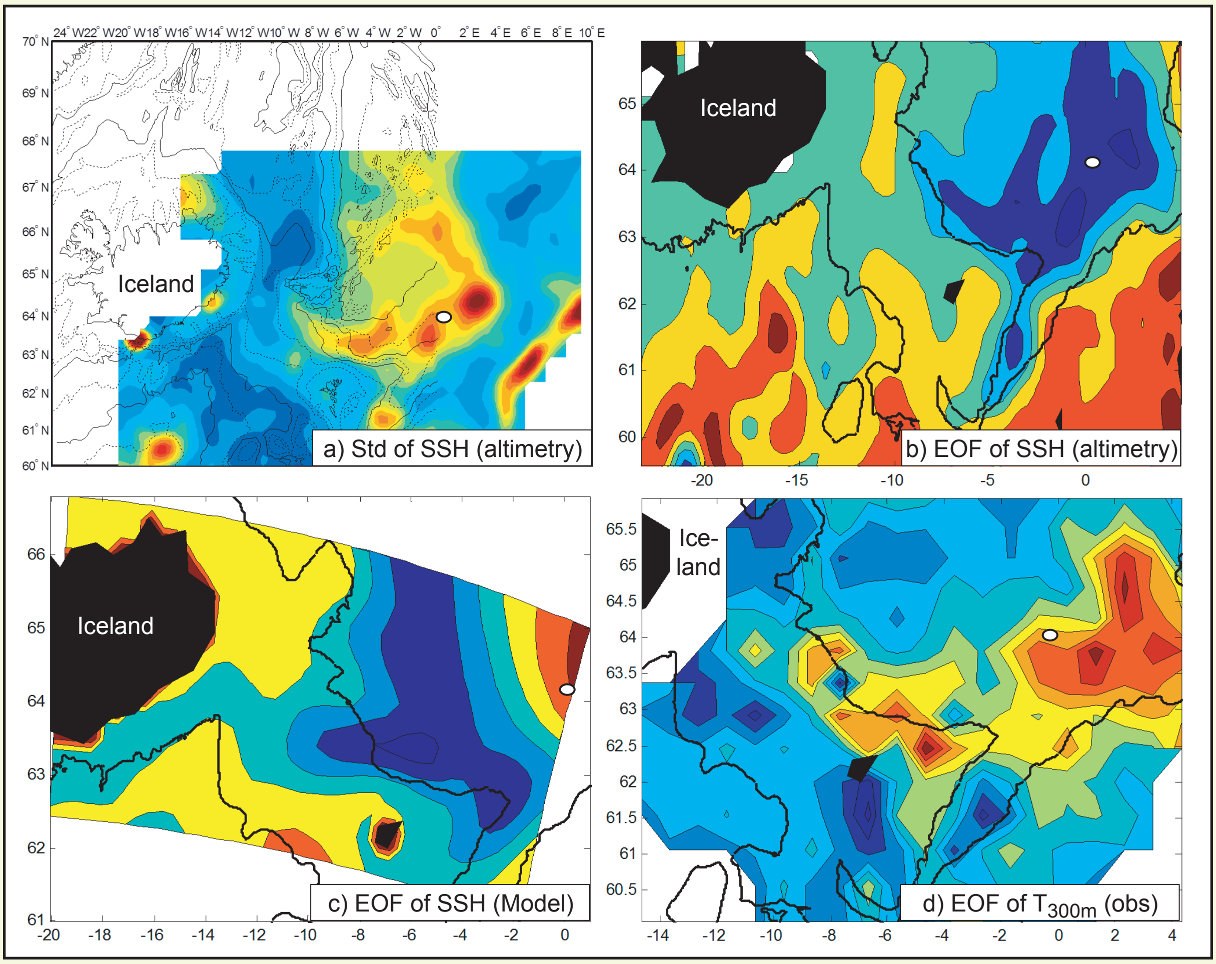

Fig. 6 Region of maximum variability along the Iceland-Faroe Front. a) Standard deviation of observed sea surface height (SSH) (1993-2009). High and low variability is red and blue, respectively. Spatial patterns associated with the leading EOF modes SSH, based on b) altimetry (1993-2009) and c) simulations (MICOM model, 1960-2003). The blue region reflects areas of maximum frontal variability. d) The EOF of the observed temperatures at 300 m depths, where now the red region reflects areas of maximum frontal variability. The nodal point between the EEZs (Fig. 5) is emphasized with a white oval.

(EOF)(Preisendorfer, 1988) analysis to annual averages of the same data, gives a leading mode of variability (Richter et al., 2012), whose spatial pattern resembles the standard deviation map (Fig. 6b), and whose temporal development (principal component) shows marked sub-decadal variability (Fig. 7a). Taken together, this mode reflects low SSH in the frontal zone, and thus an eastward shift (cf. Fig. 3) in 1995 and 2000 and high SSH and a westward frontal shift during 1996-1997 and 2003-2004 (Fig. 7a). A corresponding analysis was applied to the simulated annually averaged SSH (MICOM) over the period 1960-2003, rendering a qualitatively similar spatial pattern (Fig. 6c), and a longer term principal components, whose post-1990 fluctuations closely match the observations (Fig. 7a).

Temperature data at 300m depths (T_{300m}, cf. Fig. 3) have been extracted from the Norwegian and Iceland Seas Experiment (NISE) dataset (Nilsen et al., 2008) and spatially interpolated, giving an averaged map for each year. The spatial pattern associated with the leading EOF mode of T_{300m} (Fig. 6d) resembles the SSH pattern (Fig. 6b), and reflects large temperature changes along the IFF. Although this analysis should be refined before basing any conclusions on it, it is clear that the strong fluctuations are also captured in this dataset (Fig. 7b).

An SST index for the same region, based on a monthly dataset provided by NOAA/OAR/ESRL PSD, Boulder ('NOAA_OI_SST_V2')(Reynolds et al., 2007), likewise shows the fluctuations after 1990 (Fig. 7b). Therefore, it is safe to state that the characteristic post-1990 sub-decadal variability is a true and dominant feature of this frontal system.

3.2 A long-term perspective – environment and mackerel

The total Russian catches within the IntEEZ (the mackerel index) are compared to the physical indices (Fig. 7b). This indicates higher catches during periods with expanded volume of AW and a westward shifted front, reflected in higher temperatures and SSH (1996-1997 and around 2003). The catches are generally lower when the front is shifted east, although extreme eastward position in 1999-2000 was first seen in the mackerel distribution a year after. The period before 1990 is not representative in the mackerel index, since this period was based on by-catches only.

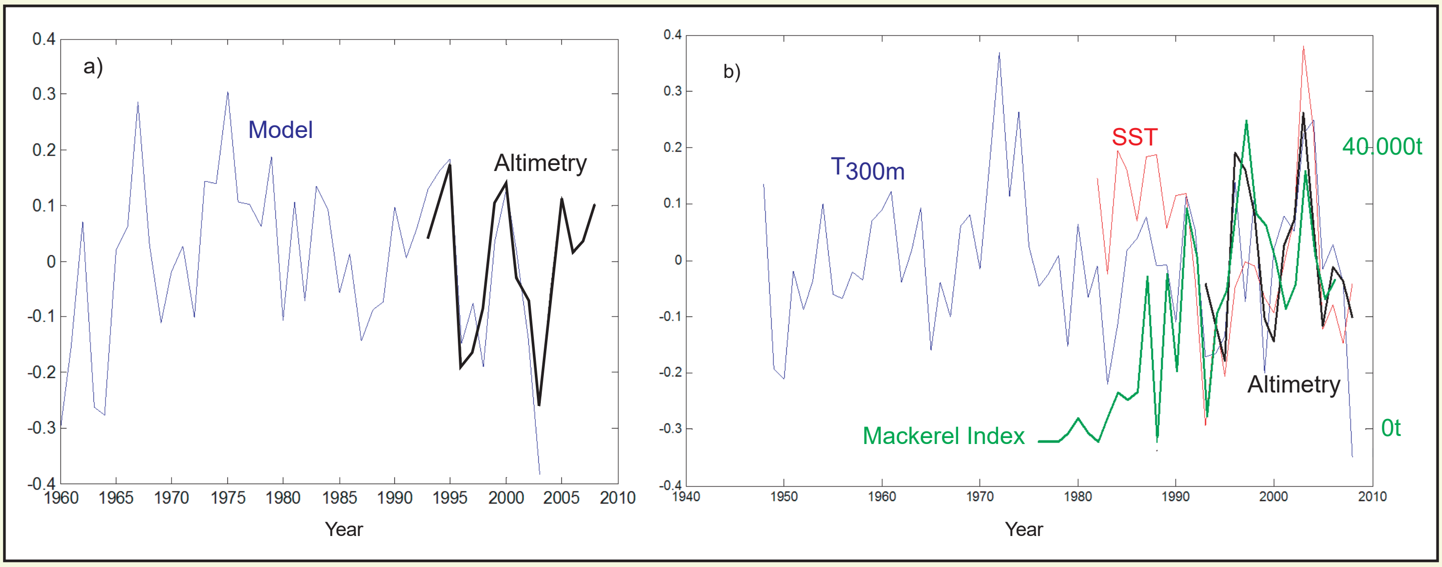

Fig. 7 Temporal development. a) Principal components (PC) associated with leading EOF modes of observed (black), altimetry and simulated SSH (blue)(no unit). b) The altimetry PC (inverted, black), the T_{300m} PC (blue, associated with the pattern in Fig. 6d), a representative sea surface temperature (SST) time series (red) and the total Russian mackerel catches within the International zone (tons, green).

4. Nutrients across the Norwegian Sea

Diatoms are the dominant phytoplankton species in the North Atlantic and a preferred food of *Calanus finmarchicus* (Meyer-Harms et al., 1999). For growth of diatoms, in addition to nitrate and phosphate, sufficient silicate concentrations are necessary for building their shells (Egge and Aksnes, 1992).

During the summer period, when mackerel arrive to the feeding grounds in the Nordic Seas, silicates and nitrates (Figs. 2c and 2d) are already at low concentrations or are even depleted in the surface layer. Depletion is most severe close to and at the shelves both on the east and west side of the presented cross-basin section. Silicate concentrations above the limiting 2 μM level (Egge and Aksnes, 1992) (black line in Fig 2c) are only found at 1°-4°E in the region where the IFF was positioned in June 2002. Nitrate concentrations are also increased at the IFF and to a lesser extent at the JMF. Replenishment of nutrients at the front might prolong phytoplankton production and the diatom bloom into summer season along this front (Allen et al., 2005). This supplies prolonged good feeding conditions for *Calanus finmarchicus* which consequently might attract mackerel (Pacariz et al., 2016). It also implies that good feeding conditions and possibly higher abundance of mackerel will shift together with the front.

5. Phytoplankton

There is a clear relation between the concentration of chlorophyll (phytoplankton) and the biomass of zooplankton (mainly *Calanus finmarchicus*) in this region (Niehoff et al., 1999). The spatio-temporal variability of chlorophyll can be illustrated utilizing satellite based Ocean Color data (Ferreira et al., 2015). These data were downloaded from the European Node for Global Ocean Colour (GlobColour Project, http://www.globcolour.info/).

5.1 Average near-surface concentrations

The mixing of water masses and the secondary vertical circulation along the IFF brings up nutrients (especially silicates, Figs. 2c and 2d)(Allen et al., 2005) enabling enhanced primary production and

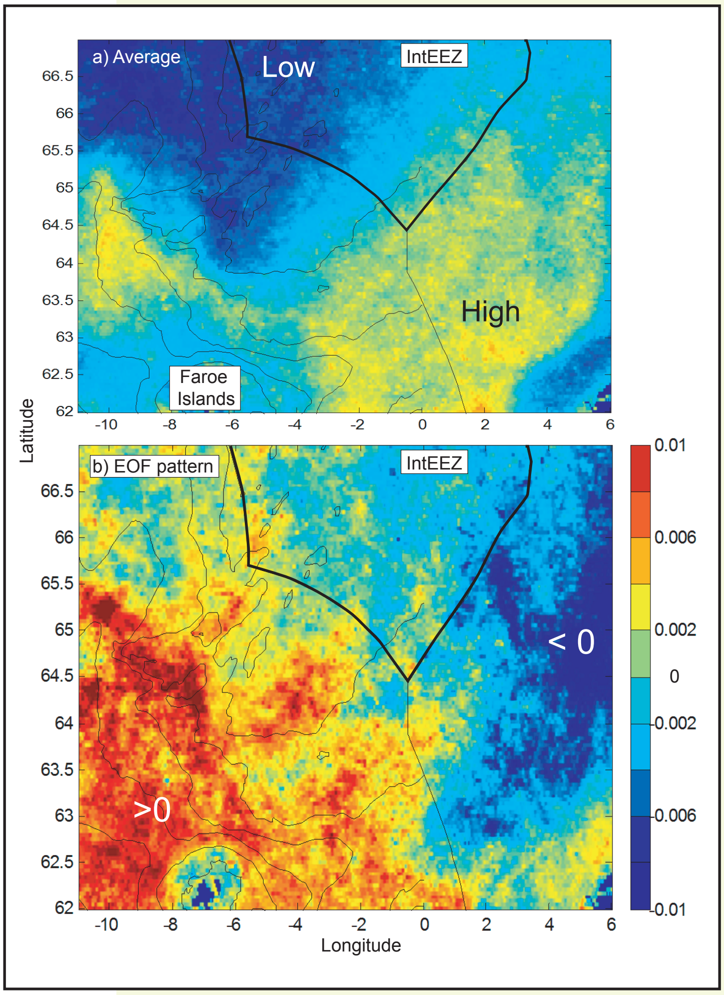

Fig. 8 Near-surface chlorophyll concentrations from Ocean Color satellites. a) The average values (1997-2011, yellowish colors show high values) and b) spatial pattern associated with the leading EOF mode. The borders of the International and the Norwegian EEZ's are shown with black lines.

thus increased phytoplankton abundances along this front throughout the summer. The Ocean Color climatology, averaged over the productive months (March-September) during all years (1998-2011), demonstrates this fact (Fig. 8a). The largest concentrations of near-surface chlorophyll are observed within the Norwegian and Faroese EEZ, while only the southeastern part of the IntEEZ (where also the largest fisheries typically are located, Fig. 5) has high concentrations on average.

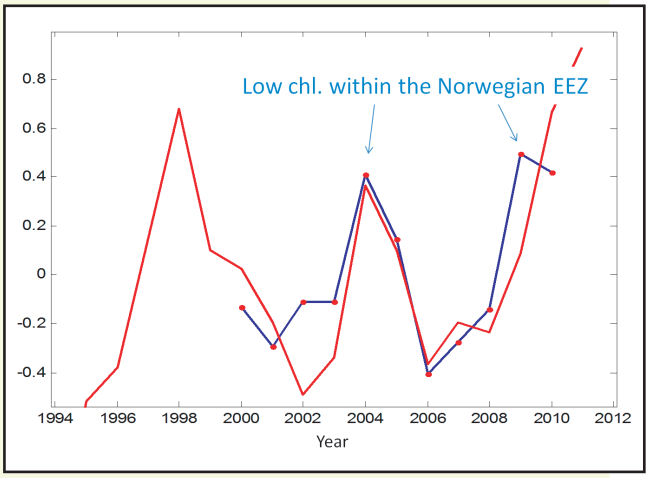

Fig. 9 Chlorophyll and mackerel. Russian catches of mackerel within the International zone (red, shifted one year backward in time, normalized values) and the chlorophyll principal component (blue), associated with the pattern in Fig. 8b. A high chlorophyll index means low values within the Norwegian EEZ.

5.2 Phytoplankton and mackerel

The spatial pattern associated with the leading EOF mode (see Section 3.1) of the Ocean Color data shows that there is a clear asynchrony between the chlorophyll concentrations within the Norwegian and the Faroese EEZs, respectively (Fig. 8b). When levels are high within the Norwegian EEZ, they are low within the Faroese zone, and vice versa. This pattern, however, shows no particular contrasts in the IntEEZ. The associated principal component does roughly correlate with the mackerel index (Fig. 9) – large abundances of mackerel are encountered in the IntEEZ when the chlorophyll concentrations in the Norwegian EEZ are lower than average.

6. Zooplankton

6.1 Average distribution of *Calanus finmarchicus*

The largest abundances of overwintering *C. finmarchicus* resting in deep cold water masses are observed near the Norwegian slope (Fig. 10a), from where they ascend to the surface during the second quarter of the year (Heath et al., 2000). The climatological near-surface concentrations of adult (CV-CVI) *C. finmarchicus* , derived from the Continuous Plankton Recorder (CPR)(Batten et al., 2003) survey show a comparable distribution – high concentrations in the southeastern Norwegian Sea (Fig. 10b). All months have been included in the CPR distribution, which therefore represents both the overwintering stock, and the new generation(s). Since *C. finmarchicus* is the principal food species for mackerel, it is not surprising that the main fishing grounds for mackerel have historically been found along this front during the third quarter of the year (primarily July-September, Fig. 4).

6.2 *C. finmarchicus* and the gyre index

It has previously been hypothesized that increased volumes of SAW in the southern Norwegian Sea (bluish colors in Fig. 1a) increases the abundance of overwintering *C. finmarchicus*, and of its larger sibling, *Calanus hyperboreus* (Kristiansen et al., 2015).

The variable volume of SAW induces the marked SSH variability in this region, which is captured by the leading SSH EOF mode (Fig. 6). This mode is closely linked to the gyre index, calculated in the same way but including the entire North Atlantic (Larsen et al., 2012). The gyre index has clear peaks around 1994-95, 2000, 2008-2009 and in 2012 (Fig. 11a).

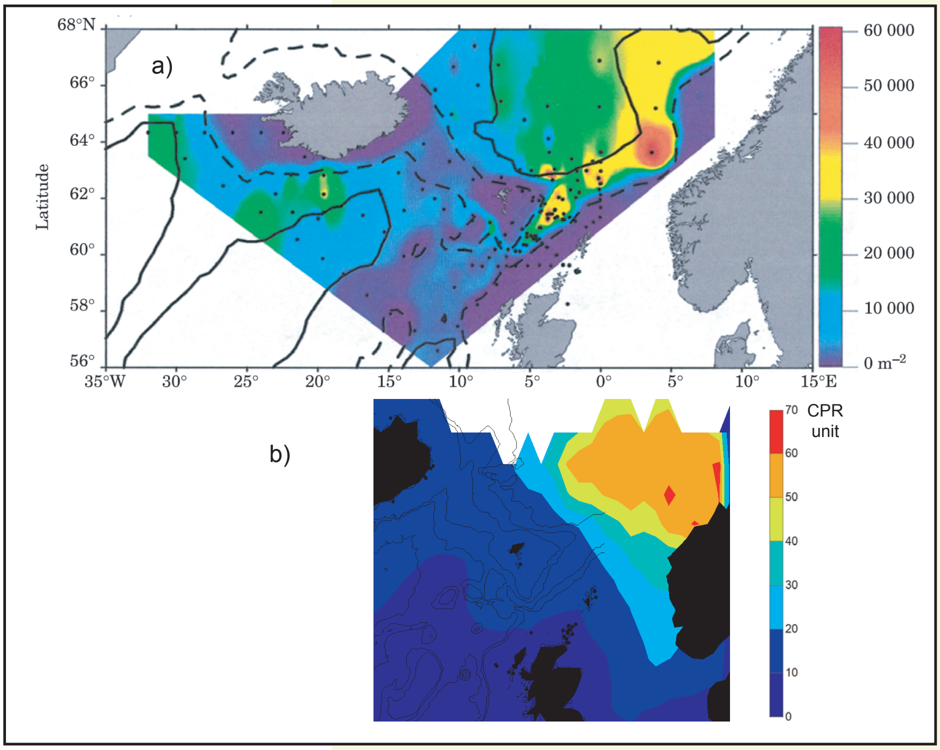

Fig. 10 Average distribution of the zooplankton species Calanus finmarchicus. *a) Abundance of overwintering* C. finmarchicus *during the months November-December (1994-1999)(Heath et al., 2000), and b) annually averaged near-surface abundances from the Continuous Plankton Recorder (CPR, 1958-1985).*

The abundance of overwintering *C. finmarchicus* (CIV+, G_o) in May have been sampled in the SAW domain of a standard section, extending north from the Faroe slope (Fig. 1a) (Kristiansen et al., 2015). Large peaks in the parent (G_o) stock are observed in 1995 and 2001, and smaller peaks in 2008 and 2012 (Fig. 11). The apparent synchrony with the gyre index, supports the hypothesized association between SAW and the G_o generation (Kristiansen et al., 2015).

Large volumes of SAW, associated with an eastward shifted IFF, influenced strongly the southeastern Norwegian Sea during the mid-to-late 1970s (Blindheim et al., 2000). This is also reflected as a pronounced dip in the long-term, simulated, gyre index (Hátún et al., 2005) (Fig. 12). The spatially averaged adult *C. finmarchicus* (CV-CVI) in this region (0-7°E, 63-66°N) from the CPR survey shows markedly increased abundance during this period, again supporting a link between the volume of SAW and the abundance of large stages of Calanus. The CPR survey coverage of this region was unfortunately terminated after the mid-1980s.

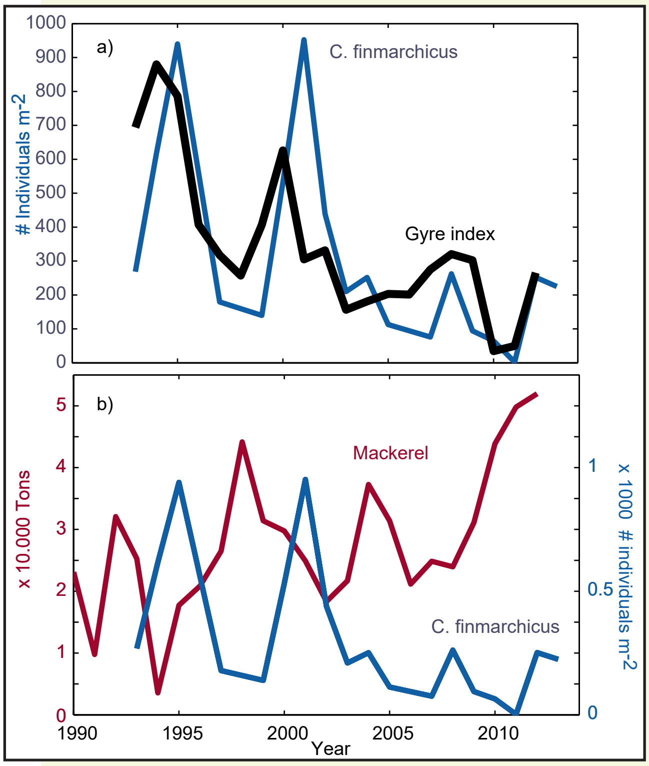

Fig. 11 Abundance of large Calanus finmarchicus *stages (CIV-CVI) (blue) with a) the altimetry-based gyre index (black) and b) the mackerel catches within the international zone (red). The* C. finmarchicus *observations are made north of the Iceland-Faroe Front during May (Kristiansen, 2015).*

6.3 *C. finmarchicus* and mackerel

Somewhat counter-intuitively, there seems to be an out-of-phase relation between the mackerel index

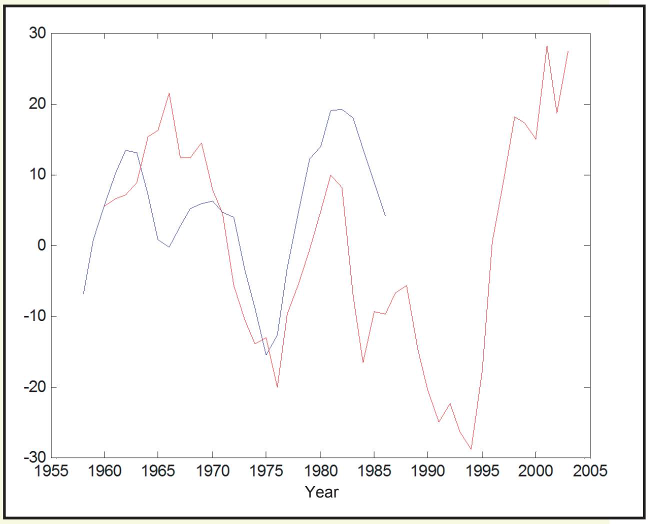

Fig. 12 Abundance of large Calanus finmarchicus *(stages CV and CVI, inverted, anomalies blue) and the long-term gyre index from the MICOM model (red). The* C. finmarchicus *record is obtained by spatially averaging the CPR data (all months) over the high-concentration region in the southeastern Norwegian Sea (0-7°E, 63-66°N).*

and the above presented abundance of large *C. finmarchicus* at the Faroese section (Fig. 11b). The interpretation of this apparent linkage is, however, not straight forward, because this zooplankton record is from early May, while mackerel arrives later, as mentioned, and mainly exploit the recruits and adults of the second generation which are dominating upon their arrival. Potential linkages are discussed below.

7. Discussion

This report presents some key environmental metrics to be considered, when studying the variable distribution of feeding mackerel in the Nordic Seas. We do not identify a single link between variability in the marine climate and the mackerel distribution, on the contrary we suggest some potential candidates. This is a preliminary study, and should not be regarded as a finalized scientific work – merely as a primer for conducting more focused and detailed investigations. Focus is devoted to the period 1990-2008, when both the physical and the biological records show particularly pronounced variability. If causal links are to be identified between the highly complex marine climate and ecosystems, based on the limited and noisy data availability, the most pragmatic approach is to focus on periods exhibiting the strongest contrasts. The recent-most period after 2006, when the mackerel stock increased dramatically and expanded towards Greenland (Pacariz et al., 2016) is not emphasized here.

The sub-decadal shifts in the frontal position are most likely real. Although much more uncertainty is associated with the mackerel catches, the similar sub-decadal variations in the mackerel index suggest a bottom-up coupling. It was a priori expected that the mackerel distribution should be warped by shifts of a major oceanic front, but the actual causal relation is difficult to ascertain with the existing data. Our results indicate that increased catches within the IntEEZ are associated with higher SST and SSH, a westward shifted front, resulting from more outspread AW in the southeastern Norwegian Sea. We will refer to such periods as 'AW-states'.

An AW-state might decrease the parent stock of *C. finmarchicus* (G_o) in the IntEEZ, due to reduced deep horizontal influx of overwintering animals in the SAW (Kristiansen et al., 2015)(Fig. 11a), but it is also likely to induce a phenological shift to an earlier onset of, and prolonged, productive season and the production of one or perhaps two new generations (G_1 and G_2), as opposed to the single generation during ‘SAW-states’. Kristiansen et al. (2015) suggested that the local growth conditions (stability, temperature, primary production) in the SAW north of the IFF are of most importance for the late summer *C. finmarchicus* stock size, and overcompensates for the size of the preceding overwintering parent stock. An AW-state might therefore result in increased and extended food availability for mackerel in the IntEEZ (Kristiansen et al., 2015).

On a larger spatial scale, *C. finmarchicus* is expected to decrease in the AW domain in the northeastern Atlantic during periods with increased northward transport of subtropical water and resulting warming (Fromentin and Planque, 1996; Hátún et al., 2009a; Planque and Fromentin, 1996). The seeding from overwintering stocks in adjacent subarctic waters (both the subpolar gyre and the Norwegian Sea gyre) might be most critical in these warmer waters, while increasing production rates resulting from additional temperature rise might be of inferior importance. If this holds for our study region, then the late July abundance of *C. finmarchicus* in AW domains should decrease during an ‘AW-state’.

If we disregard the influence of competition between the large pelagic fish stocks in this region (mackerel, herring and blue whiting), and learning aspects, and furthermore assume that the total mackerel stock size does not change markedly on the discussed relatively short, dominant subdecadal time scale, then we suggest that two opposite drivers could regulate the abundance of mackerel within the IntEEZ: Attraction/allowance to the IntEEZ or by repulsion/‘push’ from the AW-domain (Norwegian EEZ). The attraction aspect can, furthermore, be caused by food abundance or the marine climate. Plausible reasons for the apparently increased abundances within the IntEEZ during AW-states can, based on the discussion above, be summarized in the following three hypotheses (Table 1):

	Attraction	Repulsion
Food	H2 • Production of *C. finmarchicus* recruits (G_1 and perhaps G_2)	H3 • Overwintering *C. finmarchicus* (G_0) stock • Nutrient limitation
Oceanography	H1 • Temperature • A stabilized upper mixed layer	Probably not relevant

H1) Attraction-oceanography

An ‘AW-state’ shifts potential temperature barriers northwestwards, allowing mackerel to follow. It is also associated with weaker air-sea forcing and a generally well established and relatively warm upper mixed layer throughout the Norwegian Sea. Since mackerel is dependent on the establishment of such a layer, this opens up for a wide migration during late summer. The opposite would take place during a ‘SAW-state’.

H2) Attraction-food

If the reproduction rates of zooplankton are most important, an ‘AW-state’ would increase the abundance of the main prey item, large stages of new *C. finmarchicus* generations (G_1, G_2) in the IntEEZ, attracting the food-seeking mackerel to occupy this region.

H3) ‘Push’

The abundance of *C. finmarchicus* is lower in the AW domain of the study region during AW-states, and the food-seeking mackerel must continue farther northwest into the IntEEZ.

This hypothesis can be further broken down to nutrient limitation and less contribution from the overwintering stock, respectively. Nutrient limitation impacts mostly the AW region, and thus the Norwegian EEZ, while the SAW in the IntEEZ is probably more nutrient replete (Figs. 2c and 2d). An ‘AW-state’ is generally associated with lower nutrient concentrations (Rey, 2012) and especially the silicate concentration might become more severely limiting for the growth of diatoms in the Norwegian EEZ. An AW-state is likely associated with a smaller overwintering stock (G_0, Fig. 11a). If this contribution dwarfs the effect of increased growth rates in the AW domain (see above), it would result in less zooplankton during the July-August feeding season.

We shall now consider which of the suggested hypotheses are supported by our preliminary results.

- The covariability between frontal position/SSH/temperature and the mackerel index (Fig. 7) would support H1.

- The low nutrients levels in the AW domain of the study region (Figs. 2c and 2d) would support H3.

- The apparent linkage between the near-surface chl concentration within the Norwegian EEZ and the mackerel index (low/high chl concentrations → high/low mackerel index, Figs. 8 and 9), would support H3.

- The out-of-phase relation between a large overwintering stock (G_0) north of the Faroe Islands in May and the mackerel index (Fig. 11b) could support H3.

- But the relation in Fig. 11b could also just be apparent, since the G_0 record also is closely associated with the water mass composition (Fig. 11a) during the preceding year. The true linkage being that a year with low G_0 abundances in May reflect an AW-state, which in turn increases the production rate of the new generation. This would support H2. Data on *C. finmarchicu*s recruits between May and August are needed to justify this.

We shall not here judge which hypothesis is the most plausible. We suggest continued collaboration between PINRO and FAMRI, where the full richness (zooplankton, mackerel size distribution etc.) of Russian, Faroese and international data is better utilized. This might enable us to better make a judgment between the suggested hypotheses in the near future.

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