



OPEN ACCESS

EDITED AND REVIEWED BY
Ming Li,
University of Maryland, College Park,
United States

*CORRESPONDENCE
Hjálmar Hátún
hjalmarh@hav.fo

SPECIALTY SECTION
This article was submitted to
Physical Oceanography,
a section of the journal
Frontiers in Marine Science

RECEIVED 05 October 2022
ACCEPTED 11 October 2022
PUBLISHED 26 October 2022

CITATION
Hátún H, Silva TSG, Skagseth Ø
and Grønkjær P (2022) Editorial:
Physical drivers of biogeographical
shifts in the Northeastern Atlantic –
and adjacent shelves.
Front. Mar. Sci. 9:1062204.
doi: 10.3389/fmars.2022.1062204

COPYRIGHT
© 2022 Hátún, Silva, Skagseth and
Grønkjær. This is an open-access article
distributed under the terms of the
[Creative Commons Attribution License
\(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or
reproduction in other forums is
permitted, provided the original
author(s) and the copyright owner(s)
are credited and that the original
publication in this journal is cited, in
accordance with accepted academic
practice. No use, distribution or
reproduction is permitted which does
not comply with these terms.

Editorial: Physical drivers of biogeographical shifts in the Northeastern Atlantic – and adjacent shelves

Hjálmar Hátún^{1*}, Teresa Sofia Giesta da Silva²,
Øystein Skagseth³ and Peter Grønkjær⁴

¹Faroe Marine Research Institute (FAMRI), Environmental Division, Tórshavn, Faroe Islands, ²Marine and Freshwater Research Institute (MFRI), Pelagic Division, Reykjavik, Iceland, ³Institute of Marine Research (IMR), Oceanography and Climate Division, Bergen, Norway, ⁴Department of Aquatic Biology/Arctic Research Centre, Aarhus University, Århus, Denmark

KEYWORDS

ecological indicators, physical drivers, biogeography, climate, North Atlantic

Editorial on the Research Topic

Physical drivers of biogeographical shifts in the Northeastern Atlantic – and adjacent shelves

Climate change is affecting ecosystems, both marine and terrestrial, and this makes it critically important to improve our understanding of couplings between environmental change – natural or human-induced - and the biology and ecology of marine organisms. As illustrated in the logo associated with the present Research Topic (RT), this theme is inspired by the dynamics of the North Atlantic subpolar gyre (SPG) and its interaction with the Atlantic inflow (poleward arrow) and the returning cold subarctic water masses (equatorward arrow) - collectively referred to as the Atlantic Meridional Overturning Circulation (AMOC). During the last ~15 years, research has shed light on the importance key physical drivers, such as the SPG, on the dynamics of all trophic levels in the subpolar North Atlantic (SPNA). The present RT elaborates on linkages between the changing physical and biogeochemical environment and the organisms inhabiting this mid- to high latitude area.

The concept of biogeographical zones and ecoregions with large areas sharing similar physical, biogeochemical and biological characteristics is presently making a come-back in marine science. When two different water masses rest against each other they create frontal zones delineating biogeographic boundaries across which the physical properties and biological assemblages change rapidly over short distances. The outlines of oceanic gyres are determined by such water mass boundaries, and therefore constitute frontal zones and biogeographical boundaries. Changes in gyre size and circulation strength warp the biogeographic morphology directly, as well as regulating the transport of water between biomes. This justifies our inclusion of the word 'biogeography' in the title of this RT.

The 19 papers compiled in this RT cover the entire SPNA, from the Labrador Sea in southwest, the North Sea and Skagerrak in southeast to the Barents Sea, Svalbard and the

Iceland Sea in the north. All trophic levels are represented, with *physical oceanography and biogeochemistry* here referred to as the 0-th level, *primary producers* (e.g. phytoplankton, 1st level), *secondary producers* (e.g. zooplankton, 2nd level) and *fish/predators* (3rd level). Unfortunately, no contribution has addressed sea mammals or seabirds. In this editorial, we will introduce each paper by a categorization into the following five recurrent themes: 1) *Phenology*, 2) *Spatial segregation*, 3) *Biological hotspots*, 4) *Regime shifts* and 5) *Long-term trends*. The papers generally discuss more than one of these themes, and after their initial introduction, this will be referred to by in-text citations. The trophic levels addressed will also be noted, with several papers addressing more than one level.

Phenological change

Phenology is the study of periodic events in a biological life cycle, and the timing of these events are influenced by seasonal and interannual variations. This RT clearly documents the phenological changes occurring in the SPNA and its potential effects on the linkages between trophic levels.

Using two models based on satellite observations of surface chlorophyll-a, light and temperature, [Richardson and Bendtsen](#) (level 1) show that the seasonal pattern and distribution of primary production differ in the SPG south of the Greenland-Scotland ridge and surrounding water masses probably due to differences in mixed layer depth. [Silva et al.](#) (levels 0 and 1) segregate the Barents Sea, Norwegian Sea and the North Sea into smaller regions with similar climatological and interannual trends in phytoplankton bloom onset, peak day and duration based on remote sensing data. Moving one trophic level up to zooplankton, [Falkenhaug et al.](#) (level 2) show that the annual abundance peak in the copepod species *Calanus finmarchicus* and *Calanus helgolandicus* in Skagerrak have advanced by about a month since 1994. In addition, the seasonal pattern of *C. helgolandicus* switched from a unimodal to a bimodal pattern, around the year 2002, with a small additional peak also appearing in spring. While these key copepods have advanced their phenological cycle, the Norwegian spring spawning herring has prolonged their feeding period into the late autumn, especially in a feeding hotspot east of Iceland ([Homrum et al.](#), level 3). This clear shift after 2005, could be caused by the emergence of a second generation of their preferred prey, *C. finmarchicus*, appearing in the autumn.

Biogeographical segregation within the SPNA

Using sediment samples along a zonal transect along 59.50°N, from the Labrador Sea to the Faroe-Shetland Channel, [Sahoo et al.](#) (level 1) were able to assign planktonic foraminifera assemblages

into three main groups: A cold/polar group in the Labrador Sea, a mixed (both cold and warm) group in the Irminger Sea, and a warmer temperate group in the eastern part of the transect. Spatial segregation of phytoplankton groups and traits is also discussed by the already introduced studies by [Richardson and Bendtsen](#), and [Silva et al.](#) Sharp lateral contrasts in zooplankton abundances and species composition are observed east of Iceland ([Kristiansen et al.](#) levels 0,2,3), with high biomass composed of overwintering stages of *C. finmarchicus* and *Calanus hyperboreus* in subarctic waters, contrasted with smaller stages of *C. finmarchicus* and absence of *C. hyperboreus* in the Atlantic water immediately south of the Iceland-Faroe Front. This segregation is also evident in the stomach content of herring in this region.

Water mass boundaries similarly govern the spawning distribution of blue whiting west of the British Isles ([Miesner et al.](#) levels 0, 3), as this boreal species has an affinity for the relatively warm Atlantic waters and avoids the subarctic waters, which can flush the Rockall-Hatton Plateau during periods when the SPG is strong.

As well as being separated laterally, water masses are also 'stacked' upon each other. The biomes are therefore structured in three dimensions; latitude, longitude and depth. Around the Faroe Plateau, Atlantic waters are overlying both Arctic intermediate waters deriving from the Iceland and Greenland Seas, and very cold overflow waters – the deep branch of the AMOC. This sharp 3-D biogeographical structure is utilized by e.g. anglerfish, which seek the main interface between warm and cold waters during the winter/spring spawning period, and migrate to central parts of the Faroe shelf during the summer/fall feeding period ([Ofstad et al.](#) levels 0 and 3).

Connectivity and predictability

The biogeographic boundaries are associated with large current systems, which induce down-stream connectivity, advective time lags and thus potential predictability as evidenced by [Miesner et al.](#) They show that shifting water mass distribution and water mass advection induce predictability of the environmental conditions in the spawning area of blue whiting in the Rockall Region by about one year ahead ([Miesner et al.](#)).

The major currents systems in SPNA create a broad, but spatially variable, boreal biome and pelagic fish species like blue whiting and mackerel migrate from the Rockall region towards the down-stream fringes of this biome. Strong hydrographic anomalies, recurrently manifesting in the Rockall region, can impact sea-ice coverage and primary production in the Barents Sea after a time lag of 4-5 years ([Koul et al.](#) levels 0, 1 and 3), which subsequently impacts the biomass of cod in this northerly region.

Like water masses and biogeographic zones, connectivity also has a depth dimension. The cold, low-saline and nutrient and zooplankton rich subarctic waters from the Iceland/

Greenland Seas slide iso-pycnally eastwards under the Atlantic inflow. This transports nutrients and large and energy-rich zooplankton (*C. finmarchicus* and *C. hyperboreus*) species to intermediate depths along the north Faroe slope (Kristiansen et al.), and east towards the Norwegian slope (Skagseth et al. levels, 0 and 2). Skagseth et al. suggest that the amount of Arctic waters and its concentration of nutrients and zooplankton are more important for the Norwegian Basin ecosystem functioning than the - more frequently discussed - temperature of the Atlantic waters. The connectivity from the East Iceland Current might even reach south into the Norwegian Trench, and thus have an impact on the zooplankton composition on the south Norwegian shelf (Falkenhaug et al.). There is, furthermore, a tight correlation between the oceanic conditions just downstream from the East Icelandic Current (proxied by the sea surface height) and the overflow transport through the Faroe Bank Channel (Hátún et al. level 0).

Biological hotspots

Elevated primary production and the confluence of water masses at ocean fronts collectively lead to increased abundances of zooplankton, and this attracts higher trophic level predators. Using a spatio-temporally comprehensive plankton production dataset (phytoplankton and spawning activity and egg production rates of *C. finmarchicus*) covering the Faroe shelf (1997-2020), Jacobsen et al. (levels 0, 1 and 2) demonstrate that the highest production takes place in the main inflow branch of oceanic water onto the permanently well mixed inner shelf. The confluence of subarctic and Atlantic waters east of Iceland also creates a feeding hotspot, where - before 1999 and after 2004 - older year-classes of herring did tightly congregate during the early seasonal feeding period (Eliassen et al., 2021, level 3). Into the late autumn months, the herring have shifted their main feeding area closer to the East Iceland shelf, into the main inflow branch of Atlantic water (Homrum et al.). A similar confluence of water masses with contrasting properties likely induced a biological hotspot west of Ireland, which can explain why large fish stocks such as blue whiting and mackerel select this region as their main spawning domain (Miesner et al.).

Regime shifts in the SPNA

Oceanic regime shifts are large, sudden changes in the marine climate that entails changes in the internal dynamics and feedbacks of an ecosystem and last substantial periods of time. Previous research described major shifts in the SPNA during the mid-1990s (e.g. Hátún et al., 2009). Many papers in the present RT report on similar marked changes during the early 2000s. During this period, the subpolar gyre circulation became historically weak, which led to high temperatures and salinities in the spawning region

of blue whiting (Miesner et al.). This translated downstream to a temperature increase in the waters on the Iceland-Faroe Ridge (Hátún et al.) and all the way to the Barents Sea (Koul et al.). In concert, the Norwegian Sea gyre weakened abruptly during 2002-2003, which caused the Atlantic inflow/boreal zone to widen and led to a transport peak in the Faroe-Bank Channel overflow (Hátún et al.). The influx of western waters (both Arctic Intermediate Water and Modified East Icelandic Water) into the southern Norwegian Sea weakened (Hátún et al.; Skagseth et al.), and the abundance of the Arctic calanoid *C. hyperboreus* decreased both north of the Faroes (Kristiansen et al.) and along the Norwegian slope (Skagseth et al.). Skagseth et al. therefore refer to the post-2003 years as an *Atlantic period*. The abundances of *C. finmarchicus* and *C. helgolandicus* changed on the south Norway shelf, and the seasonality of *C. helgolandicus* shifted from a unimodal fall peak to a bimodal pattern, with an emerging spring peak around 2002 (Falkenhaug et al.). As mentioned, herring started to congregate near the East Iceland Current during May (Eliassen et al.) and prolonged their feeding activity near the east Icelandic slope after 2003 (Homrum et al.). Whether this is a sign of food deprivation during the early feeding season or increased food abundance later in the season remains an unresolved question. The feeding of Atlantic salmon post smolts also changed dramatically after the early 2000s shift, whereafter the stomach fullness of this species, consisting primarily of copepods, amphipods and fish larvae, was considerably reduced (Utne et al. levels 1,3)

On the Faroe shelf, the growth of the long-lived clam *Arctica islandica* decreased after 2003 (Matras et al. levels 0-3), which the authors ascribe to reduced advection of zooplankton from the East Icelandic Current - a hypothesis that involves trophic interaction with the on-shelf bloom and grazing pressure from juvenile fish. Oppositely there was a major boom in the abundance of the boreal anglerfish on the Faroe shelf during the warm early 2000s (Ofstad et al.). The *early 2000s shift* is so broad and consistent, that it justifies the term regime shift. However, while many of the mentioned ecological changes have persisted since around 2003, some merely portrayed a peak around this time.

After 2016, the southern Norwegian Sea has shifted back from the Atlantic period to a more (sub)Arctic period, with stronger influx of Icelandic waters (Skagseth et al.), more subarctic zooplankton species (Kristiansen et al.) and improved feeding conditions for Atlantic salmon (Utne et al.). However, while salinity indeed has decreased much, temperatures have remained high since 2016.

Long-term trends

Observations of uni-directional trends can be due to relatively short records of natural cycles with long periodicities (e.g. the Atlantic Multi-decadal Oscillation) or real trends in the system, potentially caused by anthropogenic influence (e.g. climate change). Based on satellite data series, Konik et al. (level 1), find that the

Svalbard fjords have become darker (reduced light availability) during the last two decades, and suggest that this likely is a symptom of transformations in the environment. Also based on remote sensing data, [Silva et al.](#) report on a rapid delay in the onset and increased biomass of the summer blooms during the past 21 years throughout most of the Barents, Norwegian and North Seas. Regarding zooplankton, individual egg production rates and the fraction of spawning females of *C. finmarchicus* have declined throughout the Faroe shelf since 1997 ([Jacobsen et al.](#)). Since this last finding is based solely on zooplankton data from late April, it is uncertain whether this reflects a change in phenology or if this represents the annual reproduction of this species.

Two papers do not fit into our categorization above. Northward shifts in host-parasite related infectious diseases, with human health and socio-economic impacts, have been linked to climate warming stress. [Højgaard et al.](#) (level 2) describe infection of Atlantic mackerel (*Scomber scombrus*) for the years 2017 and 2018 by the myxozoan parasite *Kudoa thyrsites*, leading to myoliquefaction that renders this fish commercially unviable. It is hypothesized that the infection has occurred in the southern spawning areas, and that infected fish migrate north. [Pedersen](#) (levels 1-4) presents a comparison of trophic position estimates from stable-isotopes and an Ecopath mass-balance food web model for the Barents Sea. This study, based on a broad selection of animal species, generally shows good correspondences between the two analysis approaches.

This RT on physical drivers in the SPNA provides a 'bottom-up' perspective on observed marked ecosystem changes in this biologically productive region. This is a limitation because commercial fisheries and other human-induced 'top-down' effects do also play major roles. However, since the projected climate changes are expected to primarily disturb bottom-up processes, we find it urgently important to expand our knowledge on this interplay.

Reference

Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., and Sandø, A. B. Drange, H. (2009). Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the

Author contributions

HH composed the first version of this Editorial, which TS, ØS and PG have commented on, and contributed to. All authors contributed to the article and approved the submitted version.

Funding

HH was supported by the Faroese Research Council, project number 8013 and ØS was supported by the Research Council of Norway, (grant no. 299554). We wish to thank Dr. Guðmundur Óskarsson, head of the pelagic division at the MFRI, for his support to this Research Topic.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography* 80 (3-4), 149-162. doi: 10.1016/j.pocean.2009.03.001