



# Warming changes the life history composition of marine fish communities at high latitudes

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**ABSTRACT:** Across marine ecosystems, species are redistributing as a response to increased sea temperatures. In the Arctic, rapid warming causes poleward shifts of boreal species. Which species are redistributing and the drivers of their movements can be related to their life history traits. Here, we aimed to characterize and analyze the spatio-temporal changes in the life history strategy (LHS) composition of fish communities in the Barents Sea (2004–2017). We performed an archetype analysis to characterize species' LHS based on their life history traits and related it to the equilibrium–periodic–opportunistic framework. Fish species in temperate ecosystems were documented to be largely distributed along the opportunistic–periodic continuum, whereas many fish species in the Barents Sea are distributed along the opportunistic–equilibrium continuum, illustrating the specificity of Arctic fish LHS. During the study period, boreal periodic species showed an increase in the central Barents Sea, a zoogeographic transition area. Simultaneously, Arctic opportunistic species retracted to cold waters, and the abundance of equilibrium strategists increased in the eastern Barents Sea. The expansion of periodic species may be explained by the configuration of their traits. This includes a high reproductive potential, broader diet, and migratory behavior. These traits might increase their tolerance and adaptive capacity to a changing environment. Fish LHS play a crucial role in fisheries management, particularly in promoting better fishing practices for vulnerable populations. By understanding the various LHS adopted by different fish species and their environmental preferences, fisheries managers can develop informed fishing strategies on a broader scale.

**KEY WORDS:** Life history strategies · Archetypal analysis · Distributional shift · Marine fish

## 1. INTRODUCTION

In marine ecosystems, climate warming causes extensive changes in fish composition driven by poleward distributional shifts (Fossheim et al. 2015, Pinsky et al. 2020). Life history and behavioral characteristics of incoming species often differ from local fish communities, resulting in a reorganization of functional traits (Dencker et al. 2017, Frainger et al. 2017, Beukhof et al. 2019c). For example, in the North Sea, pro-

nounced changes in the fish community were observed, with a substantial shift in the fish community towards an increased relative abundance of smaller, faster-growing, less-fecund, and earlier maturing species (McLean et al. 2018, Beukhof et al. 2019b). Changes in life history due to warming have important implications for demographic responses to environmental pressures and for vulnerability to human activities such as harvesting (Wang et al. 2020, Ingvaldsen et al. 2021, Otero & Hidalgo 2023).

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In the Arctic, rapid warming is causing a northward expansion of boreal species (Mueter & Litzow 2008, Fossheim et al. 2015). The incoming boreal species differ from the Arctic species due to different adaptive requirements, which affect feeding opportunities and offspring survival, among other factors (Wiedmann et al. 2014, Frainer et al. 2017). Arctic fish are often small-sized and produce few, relatively large eggs, whereas boreal species display greater variation in body size and life history traits (Wiedmann et al. 2014, Aune et al. 2018). Boreal species that respond rapidly to warming are foraging migrants which are typically large body-sized generalists (Frainer et al. 2017, 2021).

Climate impact studies on fish life history characteristics have focused on a few traits, often considered separately (Wang et al. 2020). However, many life history traits are correlated, notably through trade-offs (e.g. parental care assumes higher offspring survival rates at the cost of fecundity) (Roff 1992, Smalås et al. 2017). Addressing multiple traits jointly is a promising approach to identify life history strategies (LHS) and characterize fish community changes (Wiedmann et al. 2014, Pecuchet et al. 2017). A more comprehensive approach accounting for various LHS is based on the triangular continuum scheme of Winemiller & Rose (1992) (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m732p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m732p119_supp.pdf)). The framework identifies 3 strategies, namely equilibrium, periodic, and opportunistic (EPO), characterized by different combinations of life history trait values that are expected to exist under distinct environmental conditions (Winemiller 2005). Equilibrium strategists tend to have a large body size and thrive in a more stable environment, producing small numbers of large eggs (or live young) with high parental investment and low fecundity (Winemiller & Rose 1992). These fish species, such as sharks and rays, present a very low rate of intrinsic population increase (Thorson et al. 2023). The success of fish under this strategy is more closely related to stable environments (Winemiller & Rose 1992). The periodic LHS includes fish that delay maturation to achieve sufficient size to produce a large clutch, improving the survival rates for adults during periods of poor environmental conditions (Winemiller & Rose 1992). In this way, high larval survivorship during one good year would compensate for the bad years with low larval endurance (Rose et al. 2001). The fish species under this strategy prevail in strongly seasonal environments with high spatio-temporal predictability (Winemiller & Rose 1992, Winemiller 2005). Most commercially harvested fish (Secor 2015), such as herrings and sardines, tend

to follow this strategy (Thorson et al. 2023). Lastly, opportunistic strategists have early maturation and frequent reproduction over a prolonged spawning season, rapid larval growth, and high adult mortality (Winemiller & Rose 1992). Fish species under this strategy, such as gobies, are adapted to colonize in disrupted environments (Thorson et al. 2023).

LHS prevalence is expected to vary spatially according to environmental conditions; notably, environmental stability and predictability (Winemiller & Rose 1992). In the European seas, opportunistic strategists appear to be more successful in warmer areas with high temperature seasonality in contrast to equilibrium fish species that prevail in locations with lower temperature seasonality (Pecuchet et al. 2017). Analyzing the dynamics of fish communities according to their LHS composition provides insights into community responses to environmental and anthropogenic pressures (McLean et al. 2018, Wang et al. 2020, Hitt et al. 2020, 2022). For example, in a fish community in the North Sea, the abundance of the opportunistic and equilibrium fish strategists has increased relative to periodic species over the last 30 yr, which could be due to an increase in sea temperature and a decrease in fishing pressure (Pecuchet et al. 2017).

The Barents Sea is one of the most productive marine zones in the world (Carmack & Wassmann 2006). Its shallow continental shelves represent an important nursery and feeding area for fish, including many commercial species (Popov & Zeller 2018). The Barents Sea has a frontal area separating Atlantic and Arctic water masses, called the Polar Front, that functions as a zoogeographic transition zone (Fig. S2), with boreal species in the south and Arctic species in the north (Fossheim et al. 2015, Ingvaldsen et al. 2021, Gerland et al. 2023). To date, this marine ecosystem has experienced a significant environmental change due to climate warming (Gerland et al. 2023), and it is one of the ecosystems with the highest increase in temperature (Hu et al. 2020). Climate-driven poleward shifts of boreal species have changed the composition and structure of the Arctic fish communities in the Barents Sea (Fossheim et al. 2015, Frainer et al. 2017). Yet it is unknown whether and how the Barents Sea fish species pool, with its unique composition of Arctic and boreal species, can be distributed along the EPO continuum and whether the observed zoogeographic shift has resulted in changes in the LHS composition of the fish communities.

In this study, we quantified the Barents Sea fish life history characteristics as specified within the EPO framework and related these traits to zoogeography, environmental properties, and fish foraging-related

traits. Furthermore, we investigated the climate-driven trends of life history composition in Barents Sea fish communities. Based on fish traits and environmental preferences, we expected that boreal species would primarily exhibit a periodic strategy, whereas Arctic species would follow the opportunistic strategy. Furthermore, in light of climate warming, we expected an increase in the relative abundance of periodic strategists in northern regions, as this strategy is often found in widespread and productive fish species (King & McFarlane 2003, Secor 2015), and a decrease in opportunistic species. In line with the expectations, we found a zoogeographic distinction in EPO strategies and observed that with warming, periodic boreal species are increasing in relative abundance in the northern Barents Sea at the expense of opportunistic Arctic species.

## 2. MATERIALS AND METHODS

We used cluster analysis (archetype analysis) on species' life history traits to characterize the LHS of fish occurring in the Barents Sea and related the obtained strategies to the EPO framework. Sub-

sequently, we examined the interplay between these 3 strategies, ecological attributes, and environmental affinities. We collected trait data for 69 fish species from the Barents Sea. We analyzed spatial and temporal changes in the life history composition of the Barents Sea fish communities by using abundance data from a scientific bottom-trawl survey (2004–2017). The abundance data served as the basis for calculating the community-weighted mean (CWM) as well as determining the mean, standard deviation, and slope of the LHS. For these analyses, we used data for 59 fish taxa from the Barents Sea.

### 2.1. Study area

The Barents Sea is a shelf sea located north of the Arctic Circle on the western part of the Eurasian shelf (Jakobsen & Ozhigin 2011). It has an average depth of 230 m with a maximum depth of approximately 500 m (Sakshaug et al. 2009) (Fig. 1). The inflow of warm and saline Atlantic water brings boreal conditions to the west and southern regions, which stand in contrast to the colder and less saline Arctic waters in northern areas (Smedsrud et al. 2010, 2013) (Fig. S2). The

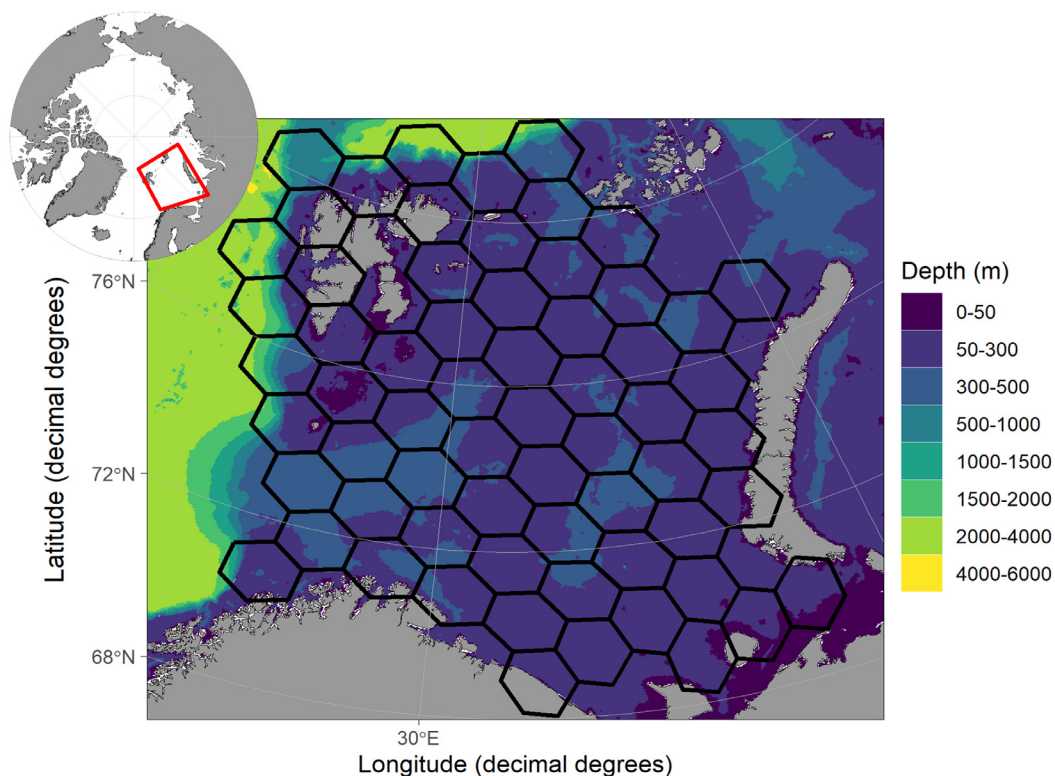


Fig. 1. Bathymetric map of the study area and its location in the Arctic Northern Hemisphere. Black grid: cells used as units in this study to calculate metrics of the life history composition of the fish assemblage. Map was created using the R package 'ggOceanMaps' (Vihtakari 2022), with bathymetric data from NOAA ETOPO1 (Amante & Eakins 2009)

Barents Sea ecosystem is productive and supports numerous commercial fish species populations (Haug et al. 2017). The rapid increase in temperature and loss of sea ice experienced during the last 3 decades (Hu et al. 2020), with more frequent marine heatwaves (Onarheim et al. 2014, Mohamed et al. 2022), threatens Arctic species like polar cod *Boreagadus saida* (Ingvaldsen et al. 2021, Kjesbu et al. 2022).

## 2.2. Fish abundance and environmental variables

Relative fish abundance data were collected during the annual ecosystem surveys, jointly conducted by the Institute of Marine Research (Norway) and the Polar Branch of VNIRO (Russia), in August and September from 2004 to 2017 (Eriksen et al. 2018). During these surveys, fish species were caught using a Campelen 1800 shrimp bottom trawl with a 22 mm stretched mesh size codend towed at approximately 3 knots for 15 min (Eriksen et al. 2018). On average, 100 fish species were caught per year on the ecosystem surveys during the study period (Wienerroither et al. 2011). However, we used 59 fish groups (containing 69 taxa) for the analyses using abundance data (Wiedmann et al. 2014), due to representativity (equally sampled throughout the study period, presence at enough stations, and lowest consistent taxonomic level). For each trawl tow (i.e. station), sampled individuals were sorted and identified to the lowest taxonomic resolution possible (mainly species level). Some individuals could not be identified at the species level and were thus pooled at a higher taxonomic resolution. For example, various *Lycodes* species and *Lyncechelys* species were grouped together at the family level, under Zoarcidae. A more detailed explanation of the species identification can be found in the supplementary information provided in Johannesen et al. (2012). In this study, we included a total of 5095 samples, with an average of 364 sampling stations per year (range: 242–590) distributed across the Barents Sea along a spatial grid with stations spaced approximately 35 nautical miles apart (Eriksen et al. 2018).

At each station, bottom depth was registered and environmental data were collected using a CTD device. Sea surface temperature (SST) was measured at 5 m depth, and sea bottom temperature (SBT) was measured close to the sea floor. Data on the duration of ice coverage (in days) were extracted from the daily sea ice extent maps from NOAA (Cavalieri et al. 1996).

Due to technical problems with the ships and/or climate events, the number of stations sampled per year varied over time (Wienerroither et al. 2011). To

account for potential between-year differences in sampling effort, we only kept cells for which at least 4 stations per year were sampled.

## 2.3. Traits data

To analyze the LHS of fish in the Barents Sea, 7 traits describing the pace of life and reproductive strategies of fish were selected based on Winemiller & Rose (1992) and following Pecuchet et al. (2017) (see Table 2). Maximum body length, longevity, length and age at maturity, fecundity, offspring size, and parental care data were collected from openly available data sets on marine fish traits (Wiedmann et al. 2014, Beukhof et al. 2019a, Froese & Pauly 2019), including our updated data used in Wiedmann et al. (2014), and are available in Table S1. In some cases, trait values were not available at the species level and were then imputed using values from primary literature averaged at the genus or family level (Beukhof et al. 2019a). According to Wiedmann et al. (2014), several taxa, including *Ammodytes* sp., *Careproctus* sp., *Gymnelus* sp., and *Icelus* sp. were categorized at the genus level due to the difficulties in trait data collection at the species level. Despite having distinct data for *Sebastes norvegicus*, *S. mentella*, and *S. viviparus*, numerous individuals (especially juveniles) within the *Sebastes* genus could not be identified to species, resulting in the aggregation of data under the *Sebastes* sp. taxon. Hereafter, we refer to different taxa, although identified from the species to the family level, simply as species. The insufficient trait data for certain species or taxa, especially in terms of longevity, maximum body size, and reproductive data, could potentially result in biased estimates of the LHS of fish species. We used 69 taxa for which complete trait information was available and were thus kept for the LHS and community analyses (Table 1 and Table S1).

## 2.4. Ecological attributes and environmental affinities data

We used additional ecological attributes to characterize and understand *a posteriori* the distribution of the Barents Sea fish species across the LHS continuum. Notably, we investigated the differences between Arctic and boreal fish by characterizing species according to their zoogeographic affinity. The data used were gathered from the literature (Johannesen et al. 2012, Mecklenburg et al. 2018) and con-

Table 1. Barents Sea fish species and their association to a life history strategy (LHS) represented by equilibrium (E), periodic (P), and opportunistic (O). The ID number represents the fish species in Fig. 2. Species that are closely related to a specific strategy are denoted by **bold**, capital letters (outside the center triangle of Fig. 2), those more distant to the strategies' endpoint (inside the center triangle in Fig. 2) are displayed in roman, lowercase letters

ID	LHS	Species name	ID	LHS	Species name	ID	LHS	Species name
1	<b>E</b>	<i>Amblyraja hyperborea</i>	24	<b>P</b>	<i>Gadus morhua</i>	47	<b>P</b>	<i>Macrourus berglax</i>
2	<b>E</b>	<i>Amblyraja radiata</i>	25	<b>P</b>	<i>Gaidropsarus argentatus</i>	48	<b>O</b>	<i>Mallotus villosus</i>
3	<b>O</b>	<i>Ammodytes</i> sp. <sup>a</sup>	26	<b>O</b>	<i>Gasterosteus aculeatus</i>	49	<b>O</b>	<i>Maurolicus muelleri</i>
4	e/p	<i>Anarhichas denticulatus</i>	27	<b>P</b>	<i>Glyptocephalus cynoglossus</i>	50	<b>P</b>	<i>Melanogrammus aeglefinus</i>
5	e	<i>Anarhichas lupus</i>	28	<b>O</b>	<i>Gymnelus</i> sp. <sup>a</sup>	51	<b>P</b>	<i>Merlangius merlangus</i>
6	p	<i>Anarhichas minor</i>	29	<b>O</b>	<i>Gymnocanthus tricuspis</i>	52	<b>P</b>	<i>Micromesistius poutassou</i>
7	<b>O</b>	<i>Anisarchus medius</i>	30	<b>P</b>	<i>Hippoglossoides platessoides</i>	53	<b>P</b>	<i>Microstomus kitt</i>
8	p	<i>Arctogadus glacialis</i>	31	<b>P</b>	<i>Hippoglossus hippoglossus</i>	54	<b>P</b>	<i>Molva molva</i>
9	p	<i>Arctozenus risso</i>	32	<b>O</b>	<i>Icelus</i> sp. <sup>a</sup>	55	<b>O</b>	<i>Myoxocephalus scorpius</i>
10	p	<i>Argentina silus</i>	33	<b>O</b>	<i>Leptagonus decagonus</i>	56	<b>O</b>	<i>Paraliparis bathybius</i>
11	<b>O</b>	<i>Artediellus atlanticus</i>	34	<b>O</b>	<i>Leptoclinus maculatus</i>	57	<b>P</b>	<i>Pleuronectes platessa</i>
12	<b>O</b>	<i>Aspidophoroides olrikii</i>	35	<b>P</b>	<i>Limanda limanda</i>	58	<b>P</b>	<i>Pollachius virens</i>
13	<b>E</b>	<i>Bathyraja spinicauda</i>	36	<b>O</b>	<i>Liparidae</i> <sup>a</sup>	59	<b>E</b>	<i>Rajella fyllae</i>
14	<b>O</b>	<i>Benthose maglaciale</i>	37	<b>O</b>	<i>Lumpenus fabricii</i>	60	<b>P</b>	<i>Reinhardtius hippoglossoides</i>
15	<b>O</b>	<i>Boreogadus saida</i>	38	o	<i>Lumpenus lampretaeformis</i>	61	<b>E</b>	<i>Sebastes marinus</i>
16	<b>P</b>	<i>Brosme brosme</i>	39	<b>O</b>	<i>Lycenchelys kolthoffi</i>	62	<b>E</b>	<i>Sebastes mentella</i>
17	<b>O</b>	<i>Careproctus</i> sp. <sup>a</sup>	40	o	<i>Lycodeses markii</i>	63	<b>E</b>	<i>Sebastes</i> sp.
18	<b>P</b>	<i>Clupea harengus</i>	41	<b>O</b>	<i>Lycodesveudipleurostictus</i>	64	e	<i>Sebastes viviparus</i>
19	<b>O</b>	<i>Cottunculus microps</i>	42	<b>O</b>	<i>Lycodes gracilis</i>	65	<b>E</b>	<i>Somniosus microcephalus</i>
20	p	<i>Cyclopterus lumpus</i>	43	<b>O</b>	<i>Lycodes pallidus</i>	66	<b>O</b>	<i>Triglops murrayi</i>
21	<b>P</b>	<i>Enchelyopus cimbrius</i>	44	o	<i>Lycodes reticulatus</i>	67	<b>O</b>	<i>Triglops nybelini</i>
22	<b>O</b>	<i>Eumicrotremus spinosus</i>	45	<b>O</b>	<i>Lycodes rossi</i>	68	<b>O</b>	<i>Triglops pingelii</i>
23	<b>O</b>	<i>Gadiculus argenteus</i>	46	<b>O</b>	<i>Lycodesse minudus</i>	69	<b>O</b>	<i>Trisopterus smarkii</i>

<sup>a</sup>Taxa with uncertain identities often were identified to the family or genus level. *Ammodytes* sp. predominantly comprised *A. marinus*. *Icelus spatula* and *I. bicornis* were pooled as *Icelus* sp. *Gymnelus* sp. was mainly dominated by *G. retrodorsalis*, and all *Liparids* sp. were treated at the family level as *Liparidae*. Among the 3 species found in the Barents Sea, *Careproctus kidoi*, *C. micropus*, and *C. reinhardti* were combined as *Careproctus* sp. For additional information regarding the taxa that have been grouped at family and genus level, see Johannesen et al. (2012)

sisted of 4 subcategories: Arctic, Arctic–boreal, boreal, and widely distributed species.

Furthermore, we assessed the relationship between a species' LHS and feeding niche and mobility (Table 2). The feeding niche was characterized by trophic level and diet breadth. Trophic level was obtained from the literature (Wiedmann et al. 2014, Pecuchet et al. 2017, Beukhof et al. 2019a, Froese & Pauly 2019). Diet breadth (generalist, intermediate, and specialist) was categorized solely based on the data taken for the Barents Sea food web from Planque et al. (2014). We used the trait body shape as a proxy for fish mobility, as the shape of a fish has a significant impact on the swimming ability (Videler 1993). For example, the fusiform body shape, as seen in cod, is a streamlined, torpedo-like body, which is ideal for fast, continuous swimming (Burton & Burton 2018). Body shape data was extracted from Wiedmann et al. (2014).

In addition to the species' zoogeography, we also assessed the relationships between the species' LHS and their environmental affinities. Environmental af-

finites refer to the preference or adaptation of a species to certain environmental conditions. Understanding these affinities can help predict where a species could be found and how it may respond to changes in its habitat (Belmaker et al. 2013). The environmental affinities of fish species in the Barents Sea were obtained from fish distributional data and spatial environmental measurements (described in Section 2.2). The affinities were calculated by averaging the environmental data (depth, ice coverage, and bottom temperature), weighted by each species' abundance. The definitions of traits, ecological attributes, and environmental affinities are listed in Table 2, and their data values are listed in Tables S1 & S2.

## 2.5. LHS

We performed the unsupervised cluster method of archetypal analysis (AA) to characterize the LHS of fish species from the Barents Sea and interpret it ac-

Table 2. Ecological attributes utilized to classify the distribution of the Barents Sea fish species within the life history strategy continuum

Parameter	Definition
<b>Life history traits</b>	
Maximum body length	Maximum length ever recorded for a species (cm) (Froese & Pauly 2019)
Fecundity	Average number of offspring produced per adult female (Froese & Pauly 2019)
Offspring size	Average values of the egg diameter, egg case, or size of offspring released into the water (mm) (Froese & Pauly 2019)
Age at maturity	Age at which 50% of a cohort spawn for the first time (year) (Froese & Pauly 2019)
Longevity	Maximum age recorded in a species (year) (Froese & Pauly 2019)
Length at maturity	Average length at which fish spawn for the first time (cm) (Froese & Pauly 2019)
Parental care	Investment of fish individuals into the survival of their young (Balon 1984)
1. Non-guarders	Fish that release eggs in the water masses or on a substrate (pelagic and benthic eggs)
2. Hiders	Fish that hide their brood
3. Guardians	Fish that guard their eggs or young
4. Bearers	Fish that fertilized eggs internally and the young develop inside the maternal body
<b>Ecological attributes</b>	
Zoogeography	Represents the total geographic range of a species (Mecklenburg et al. 2018).
Arctic	Species occurring and reproducing in the Arctic region and rarely found in sub-arctic waters
Arctic–boreal	Species occurring and reproducing in both Arctic and boreal ecosystems
Boreal	Species typically occurring and reproducing in boreal ecosystems and rarely found in Arctic waters
Widely distributed	Species that occur in boreal and temperate but also in subtropical and warm waters
Trophic level	Ranging from 2.9 to 4.41
Feeding behavior	Complex behavior that is closely associated with food intake (Volkoff & Peter 2006)
Specialist	Less than 5 prey species
Intermediate	Between 5 and 20 prey species
Generalist	More than 20 prey species
Body shape	Proxy of fish mobility (Videler 1993)
DEEP	Deep and short bodies
EEL	Eel-shape
ELS	Elongated shape
FS	Flat shape
NS	Normal shape or fusiform shape

According to the EPO LHS framework. In contrast to most cluster analyses that use average or median to group multivariate data sets, AA identifies extreme points within the multivariate data, i.e. archetypes (Eugster & Leisch 2009). In this study, these archetypes characterize species with extreme life history trait combinations and can represent the LHS endpoints (Pecuchet et al. 2017). Once the archetypes are identified (used hereafter interchangeably as equilibrium, periodic, opportunistic, or more generally, LHS), all the other points can be characterized as a mixture of the LHS based on the proximity of each strategy endpoint and be expressed as proportions (Cadwell 2012). Thereby, in line with the life history continuum framework, species may have life history configurations that are intermediate between alternative LHS (e.g. a species following both the opportunistic and periodic strategy, with each a proportion of 0.5). The sum of the proportions across the obtained LHS adds to one.

The 'archetypes' R package (Eugster & Leisch 2009) was used on the 7 life history traits. Prior to the calculation, trait values (except parental care) were log

transformed due to skewness and scaled for equal weights in the AA. To assess the optimal number of LHS needed to summarize the Barents Sea species' traits data, we performed AA with a definite number of strategies ( $K$ ) ranging from 1 to 10; for each  $K$ , we conducted 5 iterations and calculated the residual sum of squares (RSS). Archetypes are represented by  $K$  which, in our study, correspond to the strategies. Following Eugster & Leisch (2009), values of  $K$  needed to effectively summarize the life history variation were decided based on visual inspection of the plot of the RSS against  $K$  using the 'elbow criterion' (Fig. S3; Legendre & Legendre 2012). We represented the Barents Sea fish species LHS by plotting them in a ternary plot according to their EPO proportions. In the ternary plot, a fish positioned at a triangle corner follows a strategy with a proportion of 1 (i.e. 100%) and thus does not follow any of the other 2 strategies (i.e. proportion of 0). The match with an LHS decreases linearly with increasing distance from its corner, e.g. a fish that follows the 3 EPO strategies equally will be placed in the center of the triangle. The ternary

plots displaying the LHS, the ecological niche, and the environmental affinities were obtained using the 'ggtern' package (Hamilton & Ferry 2018).

## 2.6. Spatial and temporal patterns in LHS and environmental conditions

For the spatio-temporal data analyses, we specified 64 equal-area hexagonal grid cells (cell area: 23 322 km<sup>2</sup>; cell center spacing: 165 km<sup>2</sup>) containing a minimum of 4 sampling stations per year using the R package 'dggridR' (Barnes 2018).

To assess spatial and temporal patterns in the LHS composition within the fish communities, we first calculated for each grid cell and year the mean abundance-weighted proportion of each strategy. To do so, we calculated the community-weighted mean of the life history strategy (CWM LHS) per grid cell and year as the average proportion of a given strategy (i.e. periodic, opportunistic, or equilibrium strategy) weighted by the relative abundance of the fish species.

To investigate spatial patterns, we computed the grid cell mean of each CWM LHS over the study period (2004–2017). The interannual variability within each grid cell was calculated as the standard deviation of the CWM LHS over the study period. To investigate temporal trends in the CWM LHS, we estimated the slope of a beta linear regression (with beta error distribution accounting for the proportional character of the data) over time per grid cell. The model's assumptions, including normality and heteroskedasticity, were assessed by regression diagnostics (visual inspection of regression diagnostics plots and test statistics). The beta linear regressions were obtained with the 'betareg' function from the 'betaregression' package (Cribari-Neto & Zeileis 2010).

Spatial and temporal patterns of environmental characteristics were studied based on annual grid cell estimates of the mean, spread (measured by the standard deviation), and slope for SST, SBT, and ice coverage for each year of the study period. The linear regression for the environmental variables was computed using the 'lm' function from the 'stats' package in R (R Core Team 2013).

## 3. RESULTS

### 3.1. LHS and trait combination

Following the elbow criterion on the RSS, the optimal value of  $K$  that permitted a large part of the trait

variability to be encompassed while keeping the complexity low was determined to be 3 (Fig. S3). The life history configurations of the 3 archetypes were consistent with the EPO LHS, as proposed by the original framework (Fig. 2). Most fish species in the Barents Sea were clustered close to the archetypes or were distributed along the axes connecting pairs of strategies, with few species being intermediate to all 3 strategies. Among 69 species analyzed, there were 32 opportunistic strategists, 18 periodic strategists, 8 equilibrium strategists, and 11 intermediate species (Table 1). Many species were positioned on the opportunistic–periodic continuum, a common pattern in previous LHS studies. However, Fig. 2 also reveals that several Arctic species were positioned along the opportunistic–equilibrium axis.

The 3 obtained archetypes were characterized by different combinations of trait values (bar plots of the 3 LHS in Fig. 2). The opportunistic strategy, represented by *Triglops nybelini* (bigeye sculpin), had the lowest values in all traits except for parental care. The opportunistic strategists were thereby the smallest fish, maturing at smaller lengths, producing small and few eggs, and living short lives. In contrast with the opportunistic strategist presented by other studies, some of the species related to this strategy showed parental care. The periodic strategists, represented by *Gadus morhua* (cod), were characterized by no parental care, medium to large body size and lifespan, high fecundity, and small egg size. The equilibrium strategists, represented by *Bathyraja spinicauda* (spinytail skate), were characterized by high values in all traits except fecundity, i.e. highest parental investment in fewer large offspring, large body size, long lifespan, and reproducing at a late age.

The zoogeographical patterns of the fish pool showed that most of the Arctic and Arctic–boreal species were located at the opportunistic endpoint. The periodic strategists were predominantly boreal species, whereas equilibrium strategists did not have a specific zoogeographic affiliation (Fig. 2).

The species' ecological attributes and environmental affinities appeared to be related to the species' LHS (see Figs. 3 & 4). Generally, opportunistic strategists were also specialist feeders with a narrow diet, feeding on 5 or fewer prey taxa (Fig. 3A). These species also tend to occupy lower trophic levels (Fig. 3B) and were mostly characterized by eel-shaped and elongated body forms (Fig. 3C). By contrast, the larger periodic and equilibrium strategists were associated with a generalist feeding behavior, corresponding to predatory fish with broader diet (Fig. 3A), located at medium to high trophic levels (Fig. 3B). The periodic

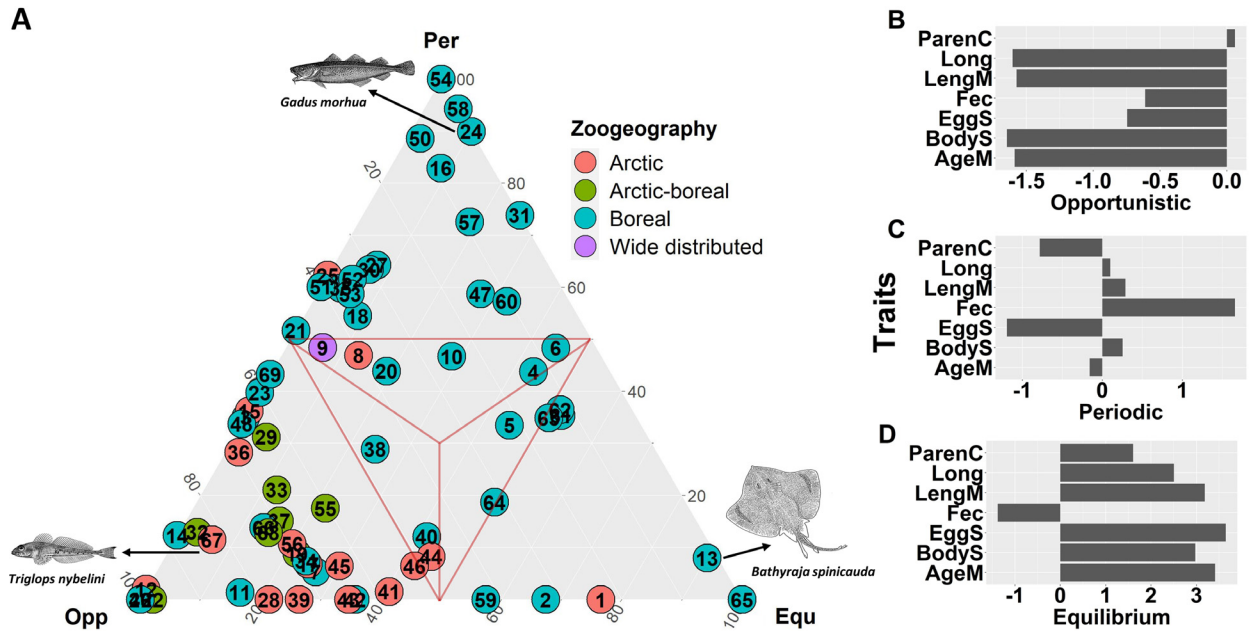


Fig. 2. Life history strategy (LHS) of the fish community from the Barents Sea, based on Winemiller & Rose's (1992) equilibrium, periodic, and opportunistic (EPO) concept. (A) Inside the ternary plot, the dots within the EPO space represent each species used in this study and are categorized by their zoogeographic affinity. In the ternary plot, a fish positioned at a triangle corner follows a strategy with a proportion of 1 (100%) and thus does not follow any of the other 2 strategies (0%). The match with an LHS decreases linearly with increasing distance from its corner. Inside the red triangle, species are intermediate to all 3 strategies; e.g. a fish that follows the 3 EPO strategies equally with a proportion of 0.33 for each will be placed in the center of the triangle. We selected 3 iconic species from the Barents Sea fish community to represent the 3 strategies: *Triglops nybelini* (bigeye sculpin) represents the opportunistic strategy, *Gadus morhua* (cod) represents the periodic strategy, and *Bathyraja spinicauda* (spinytail skate) represents the equilibrium species. Each species is associated with a number inside the circles; the corresponding species names can be found in Table 1. The histograms represent the relative trait values of the (B) opportunistic, (C) periodic, and (D) equilibrium strategy for parental care (ParenC), longevity (Long), length at maturity (LengM), fecundity (Fec), egg or offspring size (EggS), maximum body length (BodyS), and age at maturity (AgeM)

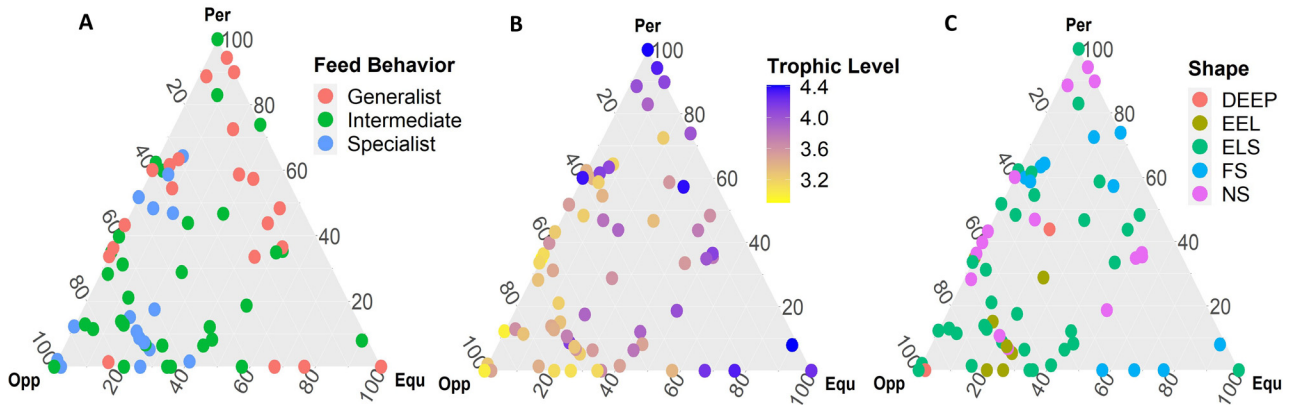


Fig. 3. Ecological attributes of the fish species from the Barents Sea and their relationships with the species life history strategy (LHS). (A) Feeding behavior of the fish species according to their LHS. (B) Trophic level of the fish species, with blue dots indicating species at higher trophic level (4.4) and yellow dots indicating species at lower trophic level (2.5). (C) Mobility of fish species as proxied by their body shape (abbreviations defined in Table 2)

species displayed variation in body shape, with the species closest to the periodic strategy endpoint having intermediate and elongated body forms (Fig. 3C).

Equilibrium species generally had a medium to broad diet and medium to high trophic levels, as well as flat and elongated body shapes (Fig. 3).



Opportunistic species displayed a higher affinity for shallower waters (Fig. 4A) and for colder, ice-covered waters (Fig. 4B,C). Periodic strategists generally showed a preference for shallower, warmer waters and ice-free regions (Fig. 4). Equilibrium strategists had a general preference, albeit with variations, for deeper, warmer waters and ice-free areas (Fig. 4).

### 3.2. Spatial patterns, interannual variability, and temporal trends in the environment

On average, there were more days with ice cover in the north than in the south of the Barents Sea (min.: 0; max.: 362 days with ice cover). The interannual variability of days with ice cover was highest in the northern parts of the Barents Sea. During the study period, the number of days with ice cover decreased in the northern Barents Sea (Fig. 5A). The southern areas had warmer SST compared to the north of the Barents Sea (min.:  $-1.74^{\circ}\text{C}$ ; max.:  $13.73^{\circ}\text{C}$ ), with higher interannual variability observed in the northwest and southeast areas. SST increased during the study period in a few grid cells in the northwest areas around Svalbard, while it appears to have decreased in the southern Barents Sea (Fig. 5B). SBT was warmer across the western areas compared to the northeast of the Barents Sea (min.:  $-1.61^{\circ}\text{C}$ ; max.:  $9.36^{\circ}\text{C}$ ), with higher interannual variability observed in the northwest and east areas of the Barents Sea. During the study period, SBT increased in the eastern area and a few grid cells near Svalbard, while it slightly decreased across the north and central areas of the Barents Sea (Fig. 5C).

### 3.3. Spatial patterns, interannual variability, and temporal trends of fish community

The proportion of periodic strategists was generally higher in the south, central, and northwest areas of the Barents Seas (Fig. 6A). The opportunistic strategists were more prevalent in the northeast, decreasing in proportion in the southern areas (Fig. 6A). The proportion of equilibrium strategists was higher in areas from northwest to southwest and decreased towards the east (Fig. 6A). Interannual variability was similar for both periodic and opportunistic strategies, with higher variability in the central Barents Sea and lower variability north and south of these areas (Fig. 6B). Higher interannual variability was observed in the northwest and southwest areas for equilibrium species, and little variability around the eastern areas (Fig. 6B). The relative proportion of periodic fish increased in the central area of the Barents Sea, whereas it did not display significant trends in the southern and the northern areas (Fig. 6C). The relative proportion of opportunistic species decreased in the most central areas while it did not change significantly in the southern and the northern areas, revealing a negative correlation between these 2 strategies (Fig. 6C). The relative proportion of the equilibrium strategy increased in the northwest, central-east, and down to southwest parts of the Barents Sea (Fig. 6C). The most abundant species influenced the signals in the spatial-temporal analyses were *Hippoglossoides platessoides* (long rough dab), representing the periodic strategy; *Boreogadus saida* (Polar cod), representing opportunistic strategy; and *Sebastes mentella* (beaked redfish), representing

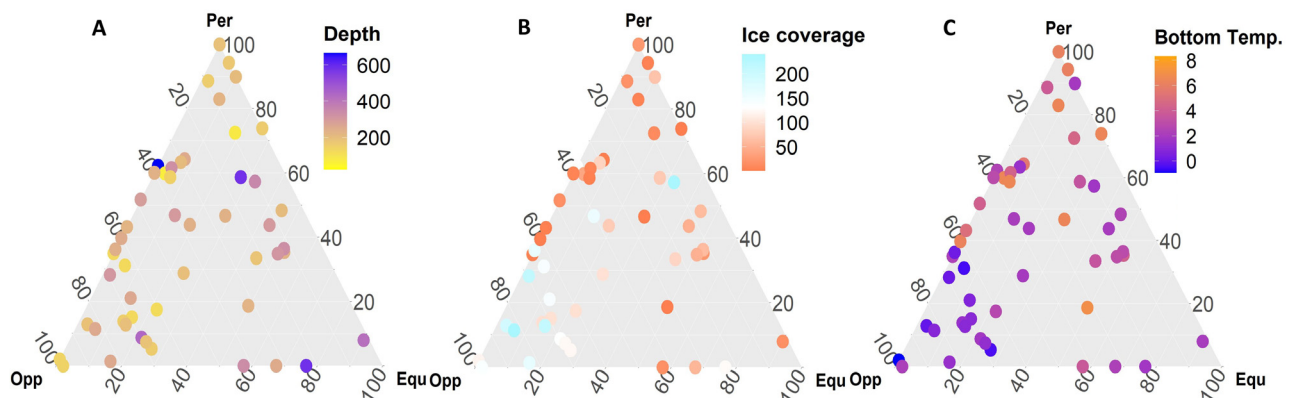


Fig. 4. Environmental affinities of fish species in the Barents Sea. (A) Averaged depth distribution of fish species, from fish distributed preferentially in shallow waters to deep waters. (B) Ice coverage affinity of fish species in terms of number of days covered by ice, with light blue dots representing species with the highest affinity for ice-covered areas and orange dots representing species with the lowest affinity for ice-covered areas, i.e. preference for ice-free areas. (C) Bottom temperature affinity of fish species, from fish distributed preferentially in cold water (dark blue dots) to warmer waters (orange dots)

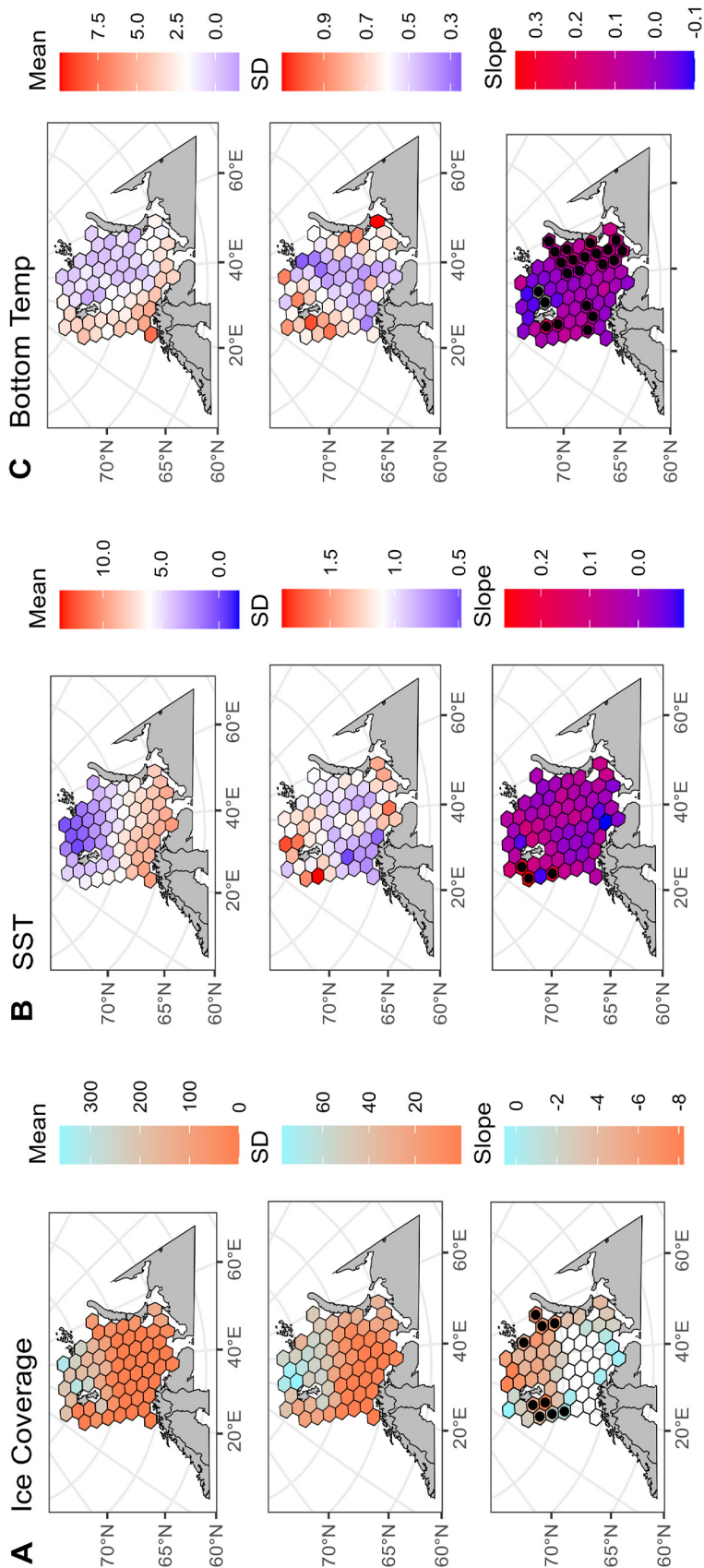


Fig. 5. Spatial patterns and temporal changes of the Barents Sea ice cover, sea surface temperature (SST), and sea bottom temperature (SBT). (A) mean ice cover (days) across the study period; the standard deviation (SD) of ice coverage represents the interannual variability and the slope represents the temporal trends of the number of days with ice cover. The white polygons in the temporal trend plot represent the grid cells that are mostly ice-free throughout the study period. (B) Average, interannual variability, and temporal trends of SST (in °C). (C) Average, interannual variability, and temporal trends of SBT (in °C). For the temporal changes (all lower panels), black dots indicate a clear temporal trend ( $p < 0.05$ ). In the legend of SST and SBT, the mean and SD midpoint (in white) is equal to the average values across the grid cells

equilibrium strategy. It is important to highlight that if this study was based on biomass data (instead of abundance), spatial and temporal analysis could present a different response. Small opportunistic fish species may be relatively abundant but with low individual weights in contrast to equilibrium species with high individual weights and low abundances.

#### 4. DISCUSSION

We found that the LHS of fish species in the Barents Sea can be summarized according to 3 endpoint strategies consistent with the EPO framework (Winemiller & Rose 1992). Equilibrium species, with very low fecundity and low generational turnover, varied in zoogeographic affiliation and were generalist species at higher trophic levels, inhabiting deeper waters. Opportunistic species, with small body size, early maturation, and low fecundity, were mainly found in ice-covered, cold Arctic waters and displayed specialized diets and low trophic levels. Periodic species, with large body sizes and high fecundity, were primarily boreal species inhabiting shallower, ice-free, and warmer waters, and were mostly generalists with a high trophic level. Interestingly, several Arctic species were aligned along the opportunistic–equilibrium continuum. The zoogeographic transition zone coinciding with the Polar Front separated the boreal, periodic species in warm Atlantic waters from the Arctic, opportunistic species in Arctic water masses. In deeper waters to the south and west, equilibrium strategists dominated the fish communities. The rapid warming experienced during the study period induced a poleward redistribution of boreal fish that increased the importance of

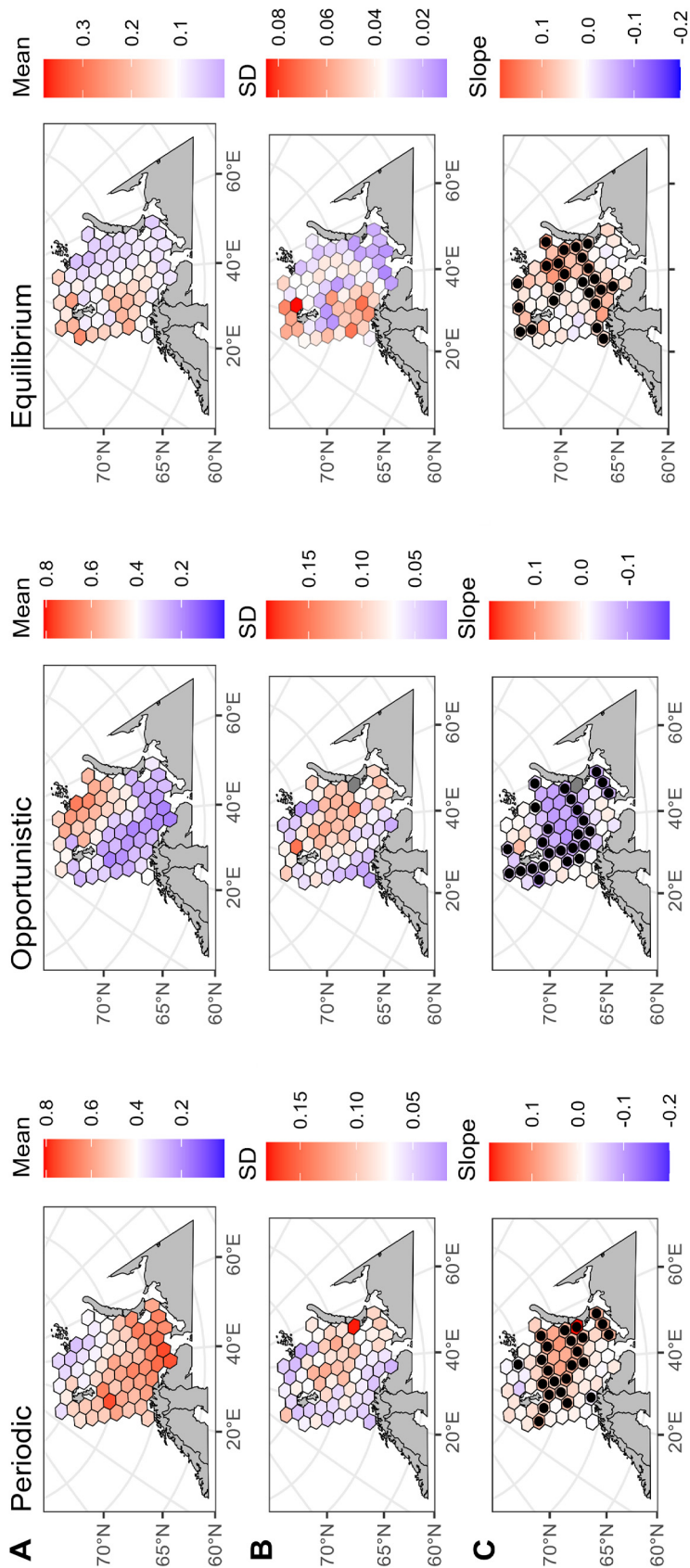


Fig. 6. Mean across years, interannual variability, and temporal trends of the life history strategy (LHS) proportion of the Barents Sea fish community for 2004–2017. (A) Mean proportion across the years for periodic (first column), opportunistic (middle column), and equilibrium strategists (left column). (B) Interannual variability, in terms of between-year standard deviation (SD) for periodic, opportunistic, and equilibrium strategies. (C) Temporal trends of the LHS relative proportion, expressed in terms of the rate of change (slope), for periodic, opportunistic, and equilibrium strategies. For the temporal changes (all lower panels), black dots indicate a clear temporal trend ( $p < 0.05$ ). To allow for comparison, the legend values are the same for the periodic and opportunistic strategies, but not for the equilibrium strategy mean and SD due to its lower abundance

the periodic strategy in the central Barents Sea region. The deep-water equilibrium strategists moved east towards shallower waters with warming ocean waters. The most rapid changes in life history composition were observed in areas adjacent to the Polar Front, which displayed a substantial change in water temperature. The documented rapid change in life history composition is relevant to climate adaptation of fisheries and environmental planning.

The Barents Sea fish life history configuration relates to the EPO framework, with species clustering according to zoogeographic affiliation. Many species from the Barents Sea, and especially boreal species, were primarily periodic or aligned along the opportunistic–periodic axis, a pattern already observed in temperate marine fish (Pecuchet et al. 2017). A large proportion of Arctic species are found along the opportunistic–equilibrium axis, a novel pattern emerging from our study. The Arctic fish are small and mature early, in line with the opportunistic strategy, but some of the Arctic species produce relatively few and large eggs (Dolgov 1994) and display parental care, which is more consistent with the equilibrium strategy. According to the EPO framework, the opportunistic and equilibrium species are favored under different environmental conditions, with the opportunistic species being favored in highly variable and unpredictable environments, whereas equilibrium species are favored in more stable and predictable environments with low productivity (Winemiller & Rose 1992, Rose et al. 2001, Mims & Olden 2012). The Arctic Barents Sea is characterized by strongly fluctuating environmental conditions, including ice cover and primary production (Wassmann et al. 2020), which

tends to favor opportunistic species. Yet the strong Arctic seasonality, with long periods of low production, is relatively predictable, which may favor equilibrium strategists. For example, the timing of the phytoplankton blooms in Arctic waters is tightly coupled to the timing of sea-ice retreat and has historically been relatively constant across the years, although climate-driven changes in phytoplankton phenology in the Arctic are now occurring (Kahru et al. 2011, Ardyna & Arrigo 2020).

The distribution of species in the EPO life history continuum was related to ecological attributes and environmental affinities. The low productivity and food availability experienced in the Arctic region for most parts of the year select for large energy allocation to each egg to ensure that offspring have sufficient resources for survival and growth (Stearns 1977, Roff 1992). The opportunistic life history configuration, associated with bottom dwelling and a specialist benthivore diet, is well documented in polar regions (North & White 1987, von Dorrien 1996), and has emerged repeatedly in recent evolution among fish colonizing Arctic lakes after the last glaciation (Smalås et al. 2017). Parental care helps to further promote offspring survival (Mahon 1984), a phenomenon also seen in small species of fish in Antarctica (North & White 1987). Larger periodic species are not found year-round in the Arctic due to the low pelagic productivity, which does not provide sufficient food to cover energy demands, and the limited amount of small planktonic prey for their planktivorous larvae (Gerland et al. 2023). Some periodic species, like cod, are foraging migrants that move north during the Arctic productive season in the summer months (Fossheim et al. 2015). The equilibrium strategists are large species, including sharks and skates such as the spinytail skate *Bathyraja spinicauda*, that feed on higher trophic levels in deep waters. Deep waters are usually relatively stable environments with low productivity (Danovaro et al. 2004, Emblemståg et al. 2022b).

In the Barents Sea, the LHS distribution contrasts with previously described patterns in the Northern Hemisphere and European seas. In the Northern Hemisphere, shallow and warmer regions are primarily dominated by species in the 'fast' end of the life history continuum (i.e. species with rapid growth, early maturation, and short lifespan) and thus related to the opportunistic strategy (Beukhof et al. 2019c). LHS analyses in European seas revealed that the proportion of opportunistic species was high in warmer areas, especially in the Baltic Sea, the southern North Sea, and the Mediterranean (Pecuchet et al. 2017). Fish communities found in colder, deeper waters

characterized by stable environments were documented to have a higher abundance of species following strategies at the 'slow' end of the continuum, which comprises slow-growing fish that mature late and have a long lifespan (Beukhof et al. 2019c) and are more related to the periodic and equilibrium strategies. Whereas the proportion of periodic species prevailed in areas such as southern Iceland and northern offshore of the North Sea and Celtic Sea, the equilibrium species had a relatively higher abundance within high latitudes seas; for example, around Iceland and Greenland but also in the Balearic and Irish Seas (Pecuchet et al. 2017). These waters with a higher equilibrium proportion tend to be colder, deeper, or less seasonal (Pecuchet et al. 2017). In the Northern Hemisphere, species with a 'slow' LHS that could be considered equilibrium strategists are also typically found in relatively stable, deeper waters (Beukhof et al. 2019c). The documented spatial pattern of the 'slow' and equilibrium life history in the northern Atlantic is consistent with the spatial pattern found in this study, with the equilibrium strategists in the Barents Sea found primarily in the deeper, western areas.

The climate-driven redistribution of species that took place during the study period changed the spatial configuration of LHS. Periodic species expanded their distribution to the north and east of the Barents Sea, increasing in importance in the central, mixed-water areas and to a lesser extent in the northeast, Arctic region. The proportion of opportunistic species declined significantly in areas coinciding with an increase in periodic species, except for a small Arctic region in the north that remained cold and ice-covered. The poleward distributional shift by boreal species associated with warming and Atlantification leads to the observed compositional change towards increasing dominance of periodic species (Ingvaldsen et al. 2021). The borealization of Arctic fish assemblages leads to a zoogeographic shift in functional traits including life history characteristics (Frainer et al. 2017). In the North Atlantic, the same process of climate-driven fish functional borealization has been observed in Greenland (Emblemståg et al. 2022a) and taxonomic borealization has been documented in the Bering Sea (Mueter & Litzow 2008). We observed that equilibrium strategists expanded their distribution eastward to shallower waters. In deeper waters, equilibrium strategists could be expected to experience more stable environmental conditions and slower climate-driven change. However, recent findings from Greenland show that warming and borealization can also have a fast pace in deep waters (Emblemståg et

al. 2022b). The latter might explain the eastward increase of equilibrium strategists in the Barents Sea. In the North Sea, at lower latitudes, fish communities have also undergone compositional changes, both in terms of species composition and trait composition (Perry et al. 2005, Simpson et al. 2011, Beukhof et al. 2019b, McLean et al. 2019). Some of the species moving north have life history characteristics consistent with the opportunistic strategy (i.e. faster life cycles and smaller body sizes) (Perry et al. 2005). Overall, in the North Sea, the relative abundance of periodic species appears to have declined, possibly due to warming, whereas the opportunistic species and equilibrium strategists have shown a slight increase in relative abundance (Pecuchet et al. 2017).

In this study, we documented temporal changes in the LHS proportion within the fish communities by using a short time series of about 14 yr. Using short time series can be problematic for assessing ecological changes; for example, the slope (i.e. rate of change) of short time series can be overestimated. In addition, ecological responses to warming might be lagged and thus not observed in short time series. Here, however, we are investigating mobile fish species with documented rapid changes in spatial distribution (Fossheim et al. 2015) that appear to respond to abrupt extreme temperature events by relocating to favorable habitats (Jacox et al. 2020, Husson et al. 2022).

The documented changes in LHS have implications for climate adaptation of fisheries management (King & McFarlane 2003). The Barents Sea is a significant area for the fisheries sector (Shevelev et al. 2011) and, together with other Arctic and Subarctic marine ecosystems, accounts for 15% of the world's fish catch (Huntington 2013, Zeller et al. 2016). The southern Barents Sea fish communities, dominated by periodic species, many of which have high commercial value (Fig. S4), experience substantial fishing pressure in addition to rapid warming. In the Arctic region of the Barents Sea, species are not yet exposed to fisheries, with few exceptions such as polar cod and Arctic flounder *Liopsetta glacialis*. However, under warmer conditions, fisheries activities are expected to increase northward (Fauchald et al. 2021). The Arctic species are vulnerable to fisheries due to their low fecundity and are already being negatively impacted by climate change (Fossheim et al. 2015). An increase in their mortality through fisheries bycatch or direct exploitation could thus have significant negative effects.

**Acknowledgements.** L.P. and R.P. acknowledge financial support from the European Union's Horizon Europe research and innovation program project 'B-USEFUL' (ID:

101059823). We thank all the individuals and organizations that have contributed to this research paper. Also, a special thanks to all the scientists and crew members engaged in the Barents Sea ecosystem surveys.

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Editorial responsibility: Alistair Hobday,  
Hobart, Tasmania, Australia  
Reviewed by: L. Rutterford, C. Möllmann and  
1 anonymous referee

Submitted: June 8, 2023  
Accepted: January 17, 2024  
Proofs received from author(s): March 15, 2024