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How different life-history strategies respond to changing environments: a multi-decadal study of groundfish communities

Jón Sólmundsson[1]✉, Ólafur Á. Sigurðsson[2], Ingibjörg G. Jónsdóttir[1] & Steingrímur Jónsson[1,2]

In recent decades, climate variability has led to significant shifts in the distribution and prevalence of various fish species in the North Atlantic. These changes are well documented for several groundfish species within the zoogeographical transition waters surrounding Iceland, coinciding with variations in seawater temperature. This study analyses groundfish assemblage structure through the frameworks of life-history theory and biogeography. Utilizing annual bottom trawl survey data from 1987 to 2024, groundfish species in the continental shelf waters around Iceland were categorized into three primary life-history strategies: periodic, opportunistic, and equilibrium, based on their life-history traits. Over the study period, these strategies demonstrated distinct responses to environmental changes, influenced by the biogeography of the species. Increased water temperatures were accompanied by an influx of Atlantic and Boreal species, while species richness for Arctic fish remained similar or decreased. Boreal periodic species emerged as the most prominent in Icelandic waters, maintaining long-term stability in abundance and distribution. However, environmental conditions in recent decades have favoured southerly warmer-water (Atlantic) species across life-history strategies, while most Arctic species have experienced declining abundance trends. Opportunistic strategists exhibited the most pronounced temporal changes during the warming period.

Keywords Demersal fish, Life-history traits, Biogeography, Climate variability, Species richness, North Atlantic

The Arctic and Subarctic regions of the Atlantic Ocean host several stocks of marine fish and invertebrates that sustain some of the world's largest fisheries[1]. In these areas, research on climate-driven changes in distribution and abundance have focused on iconic species such as Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) (e.g.[2,3]). Additionally, studies have explored environmental impacts on fish assemblages based on their biogeography, thermal preferences, functional traits, or life-history characteristics[4–12]. Rapid changes have been documented for fish communities in the Barents Sea, where small-sized, bottom-dwelling Arctic benthivores were being replaced by larger, longer-lived and more piscivorous Boreal species, causing functional reorganization of the ecosystem[7,12,13]. Similarly, poleward shifts and borealization of fish communities were observed along the coast of Norway[14]. In the North Sea, changes in the relative prevalence of different life-history strategies were attributed to rising temperatures and reduced fishing effort[6].

Zoogeographical transitional areas, where different ecosystems interact, are of particular importance for analysing animal redistributions due to their variable environmental conditions. With comprehensive long-term investigations, at the boundary between warm, saline Atlantic water and cold, lower-salinity Arctic water, the sea around Iceland is ideal for monitoring changes in the ichthyofauna[15]. Since 1996, these waters have been relatively warm, and pronounced changes have been observed in pelagic and demersal marine fish communities, which have been proposed to be induced by increased inflow of warmer Atlantic water[16,17]. The pelagic Atlantic mackerel (*Scomber scombrus*) extended its feeding grounds from European seas northwest into Icelandic and Greenlandic waters, which sparked the development of significant mackerel fisheries in these areas[18,19]. At the same time, the distribution of capelin has shifted westward, towards East-Greenland, leading to a decline in abundance and reduction in the capelin fishery[3]. Since 2017, sprat (*Sprattus sprattus*) has emerged as a new forage fish, having colonized shallow waters south and west of Iceland[20,21]. Likewise, oceanographic changes have led to various developments in the distribution and abundance of groundfish species. Haddock

[1]Marine and Freshwater Research Institute, Hafnarfjörður, Iceland. [2]University of Akureyri, Akureyri, Iceland. ✉email: jon.solmundsson@hafogvatn.is

(*Melanogrammus aeglefinus*) and monkfish (*Lophius piscatorius*) saw a spike in abundance in the early 2000s and extended their northern distribution considerably, as well as the fisheries targeting them[22,23]. Concurrently, many non-commercial species were reported for the first time in the sea around Iceland[24].

The biotic and abiotic changes observed around the turn of the century are likely linked to large-scale circulation dynamics causing temperature fluctuations in the Northeast Atlantic. Environmental conditions in Icelandic waters appear to correspond with phases of the Atlantic Multidecadal Oscillation (AMO), an index for sea-surface temperature in the North Atlantic Ocean[1,25]. Additionally, the physical properties of seawater and the strength of surface currents south of Iceland are believed to be influenced by the Atlantic subpolar gyre (SPG), which underwent a notable shift in the late 1990s[26]. A variety of biological changes south of Iceland[27] and Greenland[28] have been linked to shifts in SPG dynamics.

Community-wide approaches have proven effective in predicting the large-scale impacts of environmental change on fish assemblages. Applying species traits and their combinations offers a more comprehensive assessment of environmental and anthropogenic forcing on fish communities[5,6,29], which may be important in understanding the mechanisms behind distributional changes and species invasions[30]. Understanding life-history composition and turnover is crucial for fisheries management, as fisheries selectively target species with specific traits, potentially altering these compositions[31,32]. Regardless of whether shifts are driven by fishing or environmental factors, monitoring functional composition is essential for effective fisheries management[6,33].

According to the r/K selection theory[34], species can be classified as r-selected or K-selected based on their life-history traits, which correlate with different ecological and environmental conditions. The r/K model suggests that life-history strategies exist along a continuum defined by two end points: the r-strategy providing greatest fitness in unpredictable environments due to fast growth and high reproductive rates, and the contrasting K-strategy having greater fitness in more stable environments. Winemiller and Rose[35], extended this linear model, identifying three primary life-history strategies among fish, that reflect trade-offs among traits fundamental to feeding, survival and reproduction. Their trilateral continuum model provides a foundational framework for understanding the relationship between fish life-history traits and environmental changes.

The objective of this study is to investigate shifts in abundance and distribution of Icelandic groundfish communities, adopting a community-wide perspective and studying periods with contrasting environmental conditions. To achieve this, we analysed standardized groundfish survey data collected over multiple decades, categorizing species into distinct groups based on biogeography and life-history strategies. Building upon the framework of Winemiller and Rose[35], we examined spatio-temporal variations in fish communities in Icelandic waters, paying particular attention to environmental dynamics.

Material and methods

Survey and study area

We use data from a standardized Icelandic groundfish survey conducted annually since 1985[36]. The survey monitors groundfish species and environmental factors, providing data on abundance and distributional changes of both commercial and non-commercial fish species over the study period. The research area is the continental shelf of Iceland down to depths of around 500 m (Fig. 1). Given high seasonal environmental variability in the area, standardization and consistency in timing makes the survey ideal for studying long-term changes in fish

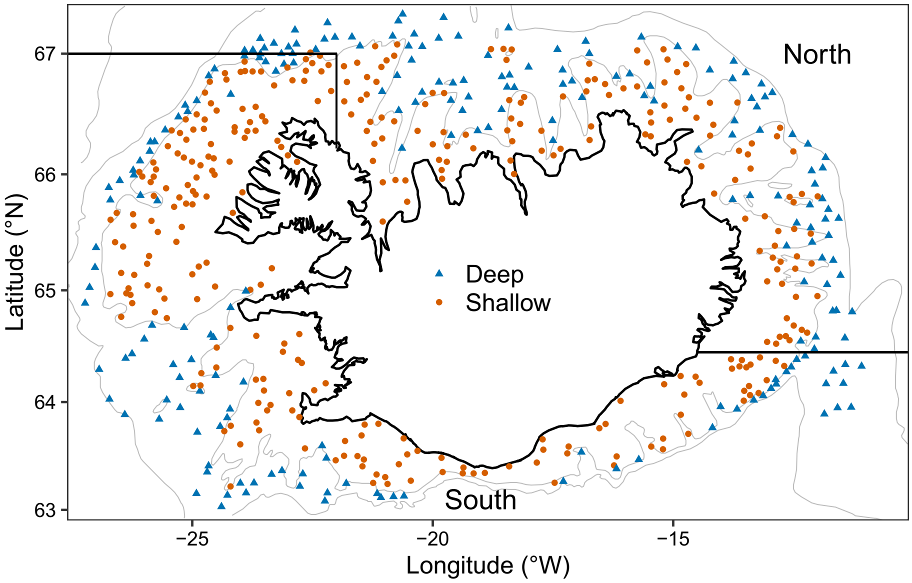

Fig. 1. Locations of stations in the Icelandic Groundfish Survey and division of the study area into two subareas; North and South. Shallow (15–200 m) stations are shown as red dots, deep (> 200 m) stations as blue triangles.

distributions. However, this means that the study only provides information for a limited period of the year and is constricted to the continental shelf.

Data were collected at fixed stations using standardized bottom trawls, both day and night in the period 27 February-20 March (99% of stations were collected within this period), with tows of 4 nautical miles and towing speed of around 3.8 knots. The front and middle sections of the trawl have mesh sizes of 135 and 80 mm, respectively, and the codend is covered inside with a 40 mm net[36]. Information about each tow include time, location, bottom temperature, and depth. Fish were measured for length and counted, with sampling criteria, particularly regarding length measurements and otolith collection, varying across species[36]. The study focuses on the period 1987–2024, as data for some fish species and temperature for part of the study area in 1985–1986 are incomplete. Fixed stations that were sampled < 30 times in the 38-years study period were omitted. The survey was carried out in compliance with permits and regulations of the Icelandic government, as authorized to the Marine and Freshwater Research Institute.

The study area was divided into two subareas, hereafter referred to as North and South (Fig. 1). This division mirrors the boundary between the Arctic and Boreal ichthyofaunal regions[15], and roughly correlates to differences in average hydrographic conditions. In the South subarea relatively warm and saline Atlantic water prevails, but the North subarea represents the colder waters where mixing of Atlantic and Polar water has taken place. In the south, bottom temperatures are considerably higher than in the north, due to the presence of relatively homogeneous warm Atlantic water, which extends to depths of over 500 m.

Survey stations were categorized as either shallow (15–200 m) or deep (> 200 m) (Fig. 1). Bottom temperatures tend to differ between the two depth zones, especially north and east of Iceland where deep near-bottom areas are affected by water masses of Polar origin, but the influence of Atlantic water over the north Icelandic shelf usually does not extend deeper than 200 m[16]. In the South subarea, March temperatures are usually lower in the shallow than in the deep depth zone, due to surface cooling during the winter months. The shallow part of the North subarea is influenced by Atlantic water entering through Denmark Strait but along its path it is cooled and mixes with cold Arctic waters from the north. Out of all the samples (stations) in the refined dataset (n = 20 222), 55% are within the South subarea, and 60% are from shallow depths.

Species data

Most fish species that are not classified as groundfish or had some sampling uncertainty for the first years of the study (e.g. capelin), were omitted from the analyses. However, some species which are typically pelagic or benthopelagic, such as herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*), were included, due to their prevailing presence in the demersal habitats. Species observed less than six times in the study period were omitted. Various species of coldwater eelpouts (*Lycodes reticulatus*, *L. esmarkii*, *L. seminudus*, *L. eudipleurostictus*, *L. pallidus, L. squamiventer*) were grouped together at the genus level (*Lycodes*) due to inconsistent species identifications in the first years of the survey. For the same reason, the species *Arctozenus risso*, *Paralepis coregonoides*, and *Magnisudis atlantica* were grouped together at the family level as Paralepididae (barracudinas), and the species *Ammodytes tobianus*, *A. marinus*, and *Hyperoplus lanceolatus* were grouped together at the family level as Ammodytidae (sandeel).

Abundance, diversity and evenness

For each species at each station, abundance was defined as the number of individuals per towed nautical mile. The mean abundance for different groups of fish each year was calculated by dividing their total abundance by the total number of stations. The abundance variable does not account for biomass and therefore does not differentiate between large and small species, or between different sizes (e.g. juveniles vs. adults) within species.

Species richness was calculated for each group of fish per year, either as the total number of species recorded per subarea and depth zone, or the average number of species per station within different subareas and depth zones. Abundance of species within different groups of fish was used to calculate Shannon–Wiener index of diversity (H') which combines species richness and their relative abundances to determine the level of diversity, where *s* is the total number of species collected, and *pi* is the relative abundance of species *i*.

$$H' = -\sum_{i=1}^{s} p_i \ln(p_i)$$

Species evenness within different groups was calculated using Pielou's index (J') which quantifies how evenly individuals are distributed among species. The evenness index is calculated as:

$$J' = \frac{H'}{\ln(s)}$$

Pielou's evenness values range from 0 to 1, where 0 indicates that one species dominates completely, and 1 indicates that all species are equally abundant.

Weighted means were used to determine the average environmental conditions in which species were found (i.e. depth, temperature, and latitude), using non-transformed abundances as weights. A list of species used in the analyses is given in Supplement 1, along with their calculated mean abundance and associated environmental factors.

Biogeographic groups

Species were classified into three biogeographic groups referred to here as *Atlantic*, *Boreal*, and *Arctic*, based on their spatial distribution in the survey. This categorization took notice of the Arctic/Boreal ichthyofaunal boundary described by Mecklenburg et al.[15]. First, subarea-specific abundance (North and South) was calculated for each species using data for the period 1987–2006. Then, proportional abundance within the two subareas was used to classify species as Arctic (≥ 90% within the North subarea), Atlantic (≥ 90% within the South subarea), and the remaining species with intermediate distribution as Boreal. By using data from the first 20 years of the study, we aimed to capture different environmental conditions without the dominance of either cold or warm periods. Five species first recorded after 2006 were all classified as Atlantic, since they were solely observed in the South area.

Life-history strategies

Species were assigned pre-defined values (proportions, hereafter LHS values) for different life-history strategies, based on their life-history traits. For 28 species we used LHS values directly from Pecuchet et al.[6], which utilized archetypal analysis (AA) to characterize fish species in European seas. The method is similar to cluster analysis, first identifying extreme values (archetypes) within the trait space, and then assigning proportional values (0–1) to species based on their proximity to each archetype. Six traits were used by Pecuchet et al.[6]: maximum length, lifespan, trophic level, fecundity, offspring size, and parental care (see Pecuchet et al.[6] for further information on the six traits). LHS values for a few northerly species (n = 5), not available in[6], were derived from Bernardo et al.[4] using the same method. For species where LHS values were available from both studies (n = 41) we used the average of the two studies. Finally, for species where no LHS values were available (n = 12), we used values for closely related species (see Supplement 1).

The three life-history strategies identified by Pecuchet et al.[6] and Bernardo et al.[4], and their relations with traits, corresponded closely to the theoretical model of Winemiller and Rose[35], namely the equilibrium, periodic, and opportunistic strategies. The equilibrium life-history strategy is characterized by species with high trophic levels, long lifespan, large size, low fecundity but large offspring size and high parental care, e.g. skates/rays and sharks/dogfish such as starry ray (*Amblyraja radiata*) and spiny dogfish (*Squalus acanthias*). The periodic strategy is characterized by species with medium-to-long lifespan and length, as well as high trophic levels and fecundity but low parental care and offspring size, such as the Atlantic cod and other relatively large gadoids. The opportunistic strategy is characterized by species with low trophic levels, small size, short lifespans, and intermediate fecundity, e.g. Norway pout (*Trisopterus esmarkii*) and eelpouts (*Lycodes* spp.).

In this study, following Bernardo et al.[4], we categorized species into groups of life-history strategies (hereafter LHS groups) based on the framework described above. The criteria for categorization were as follows: If a species had a value for one strategy which was equal or greater than the sum of the other two (≥ 0.5), then it was categorized according to the dominating strategy. A fourth LHS group, “mixed “, was assigned to species with no life-history value ≥ 0.5. See Fig. 2 for visual representation of the classification into LHS groups.

There is some relationship between species taxonomic order and life-history strategies. Species within the Rajiformes and Squaliformes orders are characterized by equilibrium strategy, although some Rajiformes species also have opportunistic and/or periodic traits (Fig. 2). In contrast, species of the orders Gadiformes and Pleuronectiformes are generally categorized as periodic strategists, or align along the periodic-opportunistic spectrum, with some small-sized Gadiformes species classifying within the opportunistic LHS-group. Species within order Scorpaeniformes have more varied life-history strategies, most of them classified within the opportunistic or mixed LHS-groups.

The annual mean abundance of the nine most abundant species from each LHS group was calculated, to analyse species composition and variance within each group. To evaluate the effects of retaining all LHS values for each species, instead of implementing division into LHS groups, we multiplied species abundance by their respective LHS values. The products were then summed across species, years, and biogeographic groups providing an estimate of LHS prevalence within the fish community over time.

Statistical analysis

To assess whether temporal trends in abundance for different biogeographic/LHS groups were statistically significant we fitted generalized additive mixed models (GAMM) using the *mgcv* package[37] written in the R language[38]. We fit a separate GAMM for each LHS group wherein the response variable was log-transformed abundance, and predictor variables included a smoother of year, biogeographic group, and their interaction via group-specific smooths. A first-order autoregressive correlation structure (AR(1)) was included in the GAMM using the *nlme* package[39] to account for potential temporal autocorrelation within each biogeographic group. Model residuals were inspected using autocorrelation function (ACF) plots to confirm that autocorrelation was adequately accounted for. Interaction effects were examined to determine whether abundance varies across different levels of biogeography, by comparing models with and without interaction terms using AIC and likelihood ratio tests.

Non-metric multidimensional scaling ordination (NMDS) was used to identify temporal patterns in mean abundance among different biogeographic/LHS groups, using years (1987–2024) as “sites” and the 12 biogeographic/LHS group combinations as “species”. NMDS was based on Bray–Curtis dissimilarity, using the function “metaMDS” in the R package *vegan*[40], with parameters: k = 3 (number of dimensions) and trymax = 100 (maximum number of random starts in search of a stable solution).

Heatmaps with hierarchical clustering analysis of different species across years were used to visualize temporal relationships among opportunistic species. The heatmaps and clustering were created using the R package *pheatmap*[41], with Euclidian distance metric and Ward’s clustering method[42]. To reduce the effects of chance observations of rare species, we excluded data for species where only one individual was caught at a

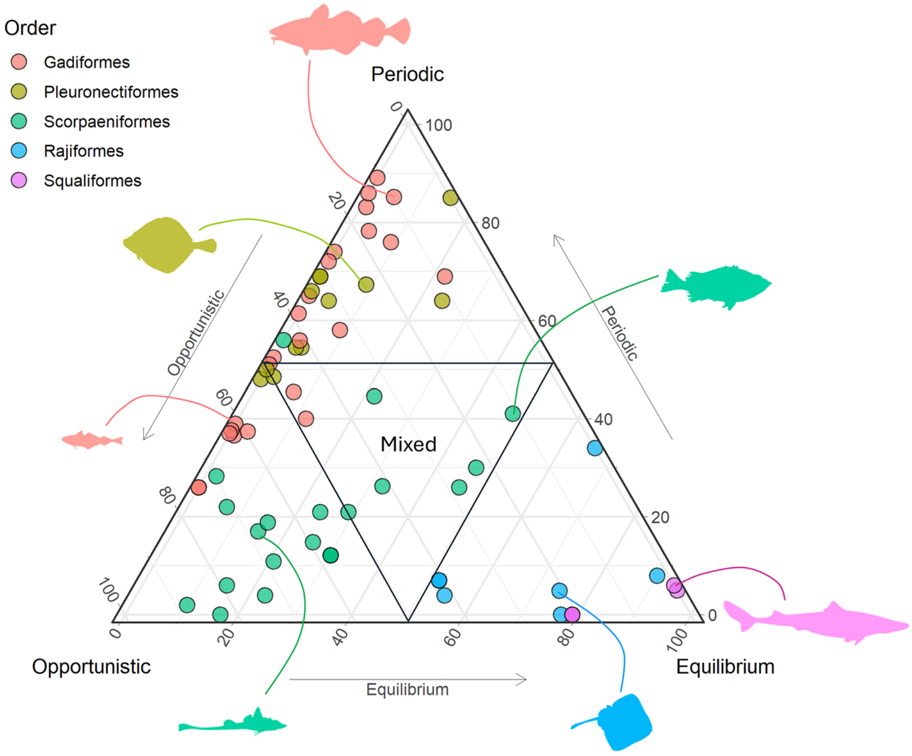

Fig. 2. Relative life-history strategy values derived from Pecuchet et al.[6] and Bernardo et al.[4] of selected species within five taxonomic orders (shown with different colours) plotted as trilateral continuum of traits based on Winemiller and Rose[35]. Taxonomic orders are represented by iconic demersal species on the Icelandic continental shelf: Atlantic cod and European plaice (periodic), Norway pout and Atlantic poacher (opportunistic), starry ray and spiny dogfish (equilibrium), and golden redfish (mixed). Triangles indicate grouping of species into four LHS groups. Angles of each axes values indicates what gridline to follow.

station. For the resulting dataset, we excluded species caught in less than six years. Values analysed were log abundance per year and scaling was done by rows, meaning that all species have the same overall abundance weight. Hierarchical clustering with dendrogram was constructed on rows.

Figures were plotted using the R package *ggplot2*[43]. The "geom_smooth" function (method = 'gam', formula = y ~ s(x)) was used for gam smoothing, unless otherwise stated.

Results

Bottom temperature

Bottom temperature measured in the survey varied considerably from year to year (Fig. 3). A marked increase in mean temperature was observed in the period 1995–2005, but since 2005, no further upward trend has been detected. In the North subarea, mean bottom temperatures are generally lower than in the South, both in shallow and deep areas. Specifically, in the North subarea, bottom temperatures are lower in the deeper zone, whereas in the South subarea the deeper zone is warmer. As a result, the difference between North and South is more pronounced in the deeper depth zone (Fig. 3a).

A clear trend of rising bottom temperature is observed across all regions covered by the groundfish survey (Fig. 3b, Supplement 2). There was a distinct cross-shelf variation between years with the lowest annual mean temperature in the dataset (1989 and 1995), as compared to years with the highest annual mean temperature (2003 and 2013). In 2003, the northern and eastern shelf had noticeably high bottom temperatures, indicating strong inflow of Atlantic water (Fig. 3b).

Species richness by biogeographic groups

The adapted dataset included a total of 86 species/groups (hereafter referred to as species), of which 15 were classified as Arctic, 35 as Boreal, and 36 as Atlantic (Table 1). Out of the 20 most abundant species, 12 were classified as Boreal, six as Atlantic, but only two as Arctic (Supplement 1). The number of Arctic species was relatively stable throughout the study period in all subarea/depth zone combinations (Fig. 4). Atlantic species were uncommon in the North subarea before 2000, but their number increased considerably after the turn of the century. In fact, the number of Atlantic species increased in all subareas and depth zones around that time. These trends result in higher number of Atlantic vs. Arctic species in the shallow part of the North subarea after 2010. Boreal species had the highest species richness of the three biogeographic groups in all subarea/depth zone combinations. Their number saw an upward trend in 2000–2010 and has remained high since then (Fig. 4).

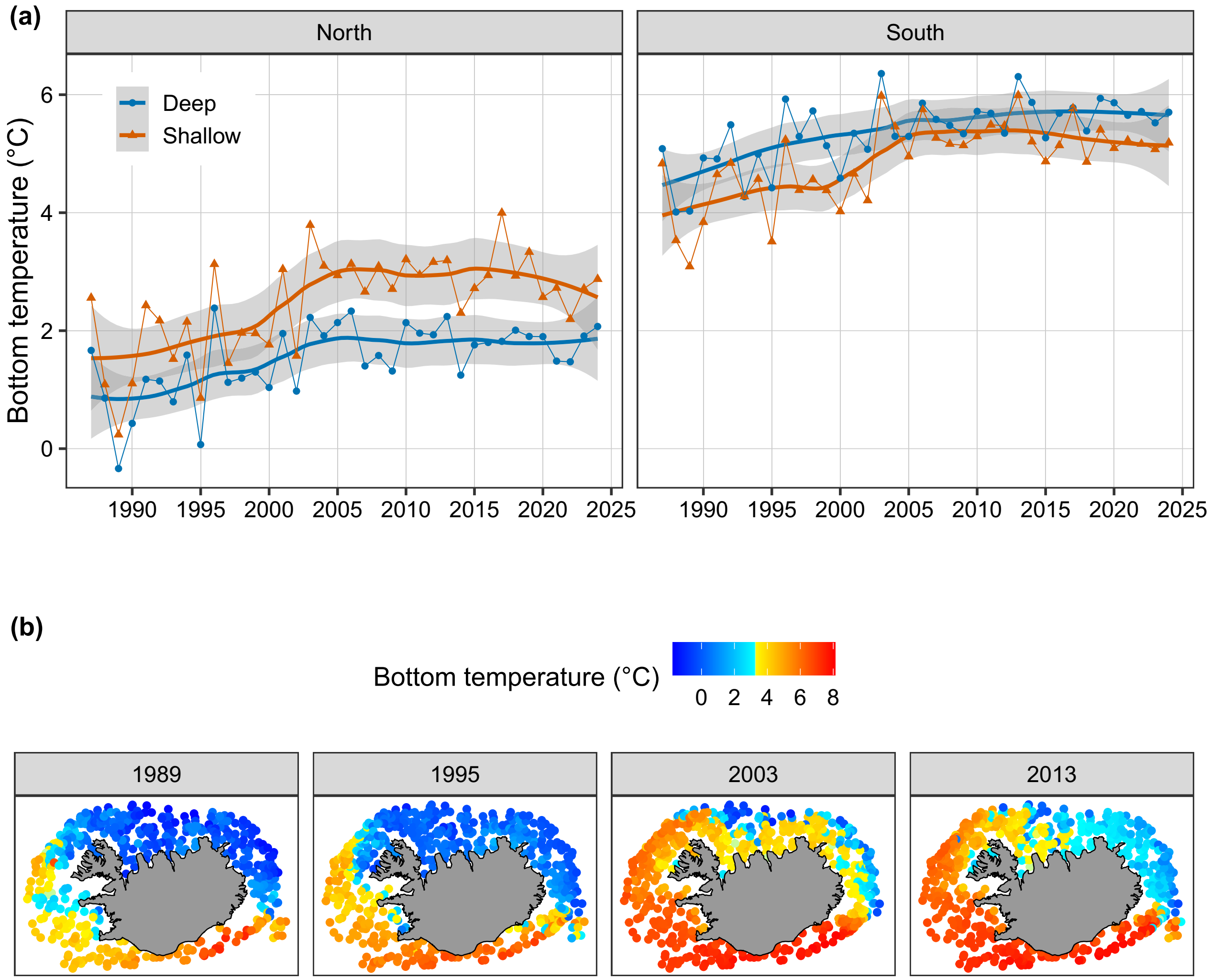

Fig. 3. (**a**) Mean bottom temperatures measured in the Icelandic groundfish survey, arranged by subareas and depth zones (Shallow, 15–200 m, Deep, > 200 m). Smoothed lines and 95% confidence bands are based on loess smoothing. b) Bottom temperature (°C) at stations in the Icelandic groundfish survey. Years selected were those with the lowest (1989 and 1995), and highest (2003 and 2013) mean bottom temperatures in the study period. Bottom temperature per station for years 1989–2024 is shown in Supplement 2.

	Arctic	Boreal	Atlantic
Equilibrium	1	5	5
Periodic	1	13	12
Opportunistic	12	9	12
Mixed	1	8	7

Table 1. Number of species by biogeographic groups and LHS groups.

The average number of species per station shows a similar temporal pattern as the total number of species over the whole subareas/depth zones. However, the analysis by stations highlights a greater difference between the Boreal vs. the Atlantic and Arctic groups (Supplement 3), indicating a more widespread distribution of Boreal species within each subarea/depth zone. For Arctic and Boreal species in the two subareas and depth zones, species evenness fluctuated throughout the period without a clear temporal trend (Supplement 4). Species evenness for Atlantic species in the South subarea has shown a downward trend.

Species abundance and diversity within LHS groups

The equilibrium group stands out as the most scarce among the four LHS groups, comprising only 11 species (Table 1) based on our criteria for species selection, and exhibiting low Shannon–Wiener diversity and Pielou evenness indices ($H' = 0.41$, $J' = 0.17$) when analysing the whole survey period. Among the nine most abundant

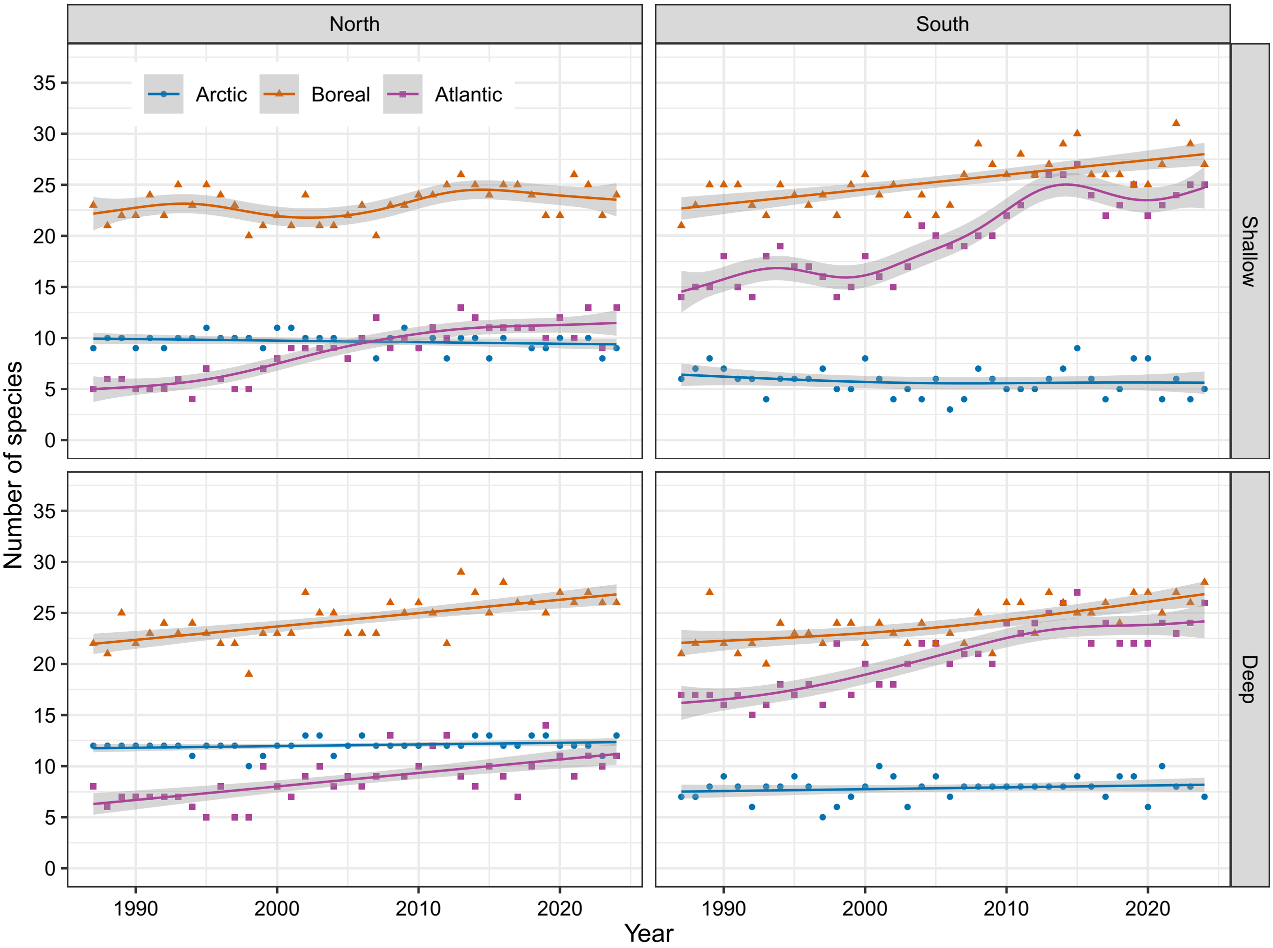

Fig. 4. Temporal changes in species richness of different biogeographic groups by subareas and depth zones. Smoothed lines are based on gam smoothing.

species within the equlibrium group, four are classified as Atlantic and four as Boreal (Supplements 1 and 5). The periodic group consists of 26 species and has the highest diversity and evenness indices of the four groups ($H' = 1.57$, $J' = 0.48$). The group contains many abundant species, and out of the nine most abundant, seven are classified as Boreal (Supplements 1 and 5). The opportunistic group has the highest species richness, with 33 species in total, but has relatively low diversity ($H' = 0.52$) and evenness ($J' = 0.15$) scores. Among the nine most abundant opportunistic species, six species are Arctic, but the opportunistic group also contains abundant Atlantic species (Supplements 1 and 5). The mixed LHS group consists of 16 species in total based on our criteria and has relatively high diversity and evenness indices ($H' = 1.18$, $J' = 0.43$). Out of the nine most abundant species within the mixed LHS group, five classify as Boreal (Supplements 1 and 5).

Distribution and abundance of LHS groups

Abundance of various LHS groups changes with bottom temperature, and the direction of the change is closely tied to biogeographic groups (Supplement 6), as would be expected. Bottom temperatures and depth, for which different species were on average associated with, varied considerably (Fig. 5). Opportunistic species were observed across a wide range of conditions, thriving in both deep and shallow and in cold and warm waters (Fig. 5). Within the colder and deeper part of the study area, opportunistic species were the most prevalent. Periodic species are relatively abundant and are found at various depths and bottom temperatures. However, some periodic species are prominent outliers, such as the Greenland halibut (*Reinhardtius hippoglossoides*), which prefers deeper, colder conditions. The equilibrium species are few and dispersed across the temperature-depth spectrum. Mixed species exhibited considerable variability in their average depths, although none had an average temperature below 2 °C.

Changes in the abundance of LHS groups reveal a rise in Atlantic opportunistic species, with their abundance increasing almost a 100-fold between 1995 and 2012 (Fig. 6). An increase in the abundance of Boreal opportunistic species was observed after 2005. In contrast, Arctic opportunistic strategists, which were the dominant species within this LHS group for most of the 1990s, have experienced a decline. The overall abundance of equilibrium species has remained relatively stable (Fig. 6). Within the periodic LHS group, Boreal species have remained consistently abundant, reaching a peak around year 2005. In contrast, Atlantic periodic species have exhibited a

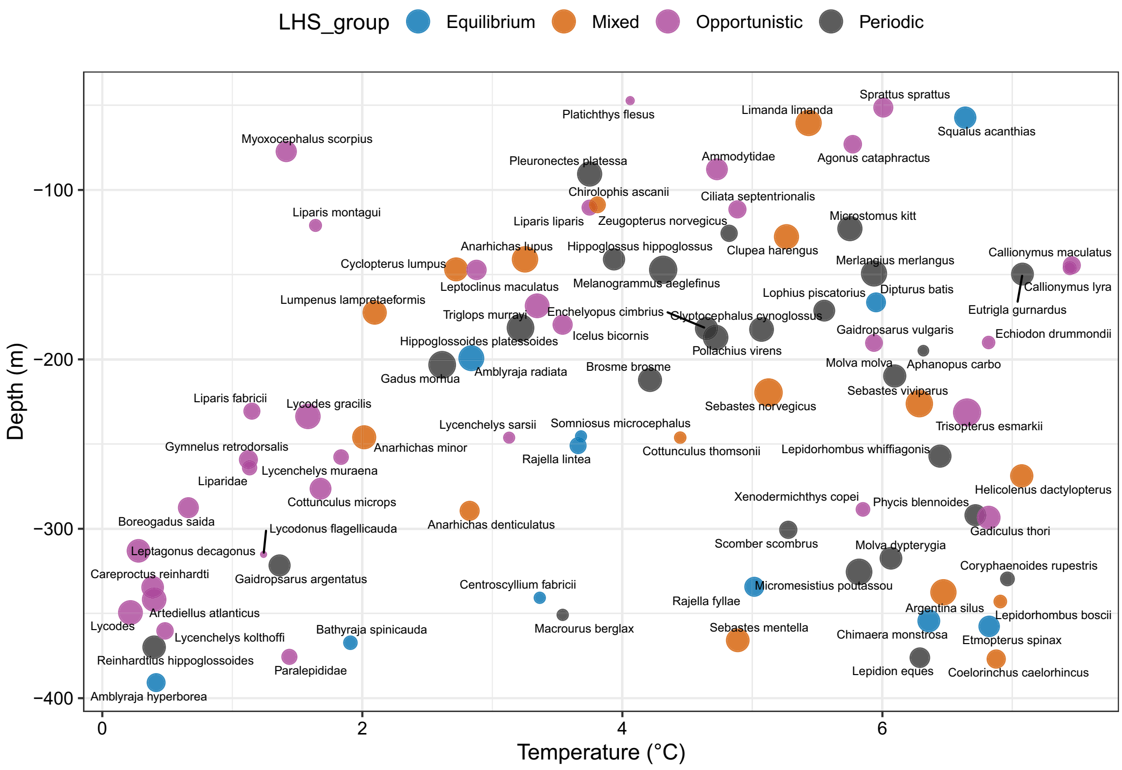

Fig. 5. Weighted means of depth and bottom temperature for different species. Colour of dots represents groups of life-history strategies, and size represents log abundance.

long-term upward trend, while the abundance of Arctic periodic species has declined. For the mixed LHS group, a decline has been observed for Arctic fish, but a gradual upward trend for Atlantic fish. The approach of using all LHS values in the calculations, instead of classifying species into distinct LHS groups, gave similar results as described above (Supplement 7).

For most biogeographic/LHS-groups, GAMM models revealed significant temporal trends in log abundance (Table 2a). The exceptions were Boreal fish of equilibrium and periodic strategies. Model comparison indicated that allowing for group-specific temporal trends significantly improved model fit compared to a model with a single smooth for year (Table 2b), suggesting that abundance trends differed significantly between biogeographic groups for most LHS groups. For equilibrium fish, however, there were no significant differences in abundance trends among biogeographic groups. Residual diagnostics showed no evidence of remaining temporal autocorrelation, indicating that the AR(1) structure adequately accounted for within-group temporal dependence.

A sharp increase in the abundance of Boreal periodic species in 2003–2005 (Fig. 6) occurred all around Iceland but was particularly pronounced in shallow parts of the North subarea (Supplement 8). Boreal species with mixed life-history strategies are most abundant in deeper waters west of the country. Atlantic opportunistic fish disappeared almost completely from the northwestern part of Iceland in the cold year of 1995. Their subsequent rise started in the south and southwest and gradually extended towards the northwest. At the same time, the abundance of Arctic opportunistic species in the offshore areas north and east of Iceland declined (Supplement 8).

The spatial distribution of the most abundant biogeographic/LHS group combinations, expressed as the percentage of stations occupied, indicates a notable expansion of Atlantic fish populations (Fig. 7a). Atlantic opportunistic species were present at fewer than 20% of the stations in the early 1990s, but by 2010–2024, their distribution expanded to approximately 50% of the stations. A similar trend is evident in Atlantic mixed life-history strategists, whose occurrence increased from under 50% to nearly 80% after 2010. For Boreal species, mixed and periodic strategists were found at nearly all stations throughout the survey period, while equilibrium species are found at 80–90% of the stations, with no significant long-term trend. In contrast, Boreal opportunistic fish have extended their range, with their occurrence rising from one-third to more than half of the stations (Fig. 7a). Focusing on stations where more than ten fish were caught per biogeographic/LHS group reveals a similar pattern, with Atlantic species expanding and Arctic fish contracting around the year 2000. The contrasting spatio-temporal distribution of Arctic and Atlantic opportunistic fish is shown in Fig. 7b and Supplement 8, revealing a gradual expansion of Atlantic opportunistic strategists.

NMDS ordination reveals a distinction between biogeographic groups, although the distribution of LHS-groups within each biogeographic group varies (Fig. 8). The main pattern highlights a separation of Arctic fish from Atlantic fish along NMDS1, where Arctic fish are predominantly associated with earlier years, while Atlantic

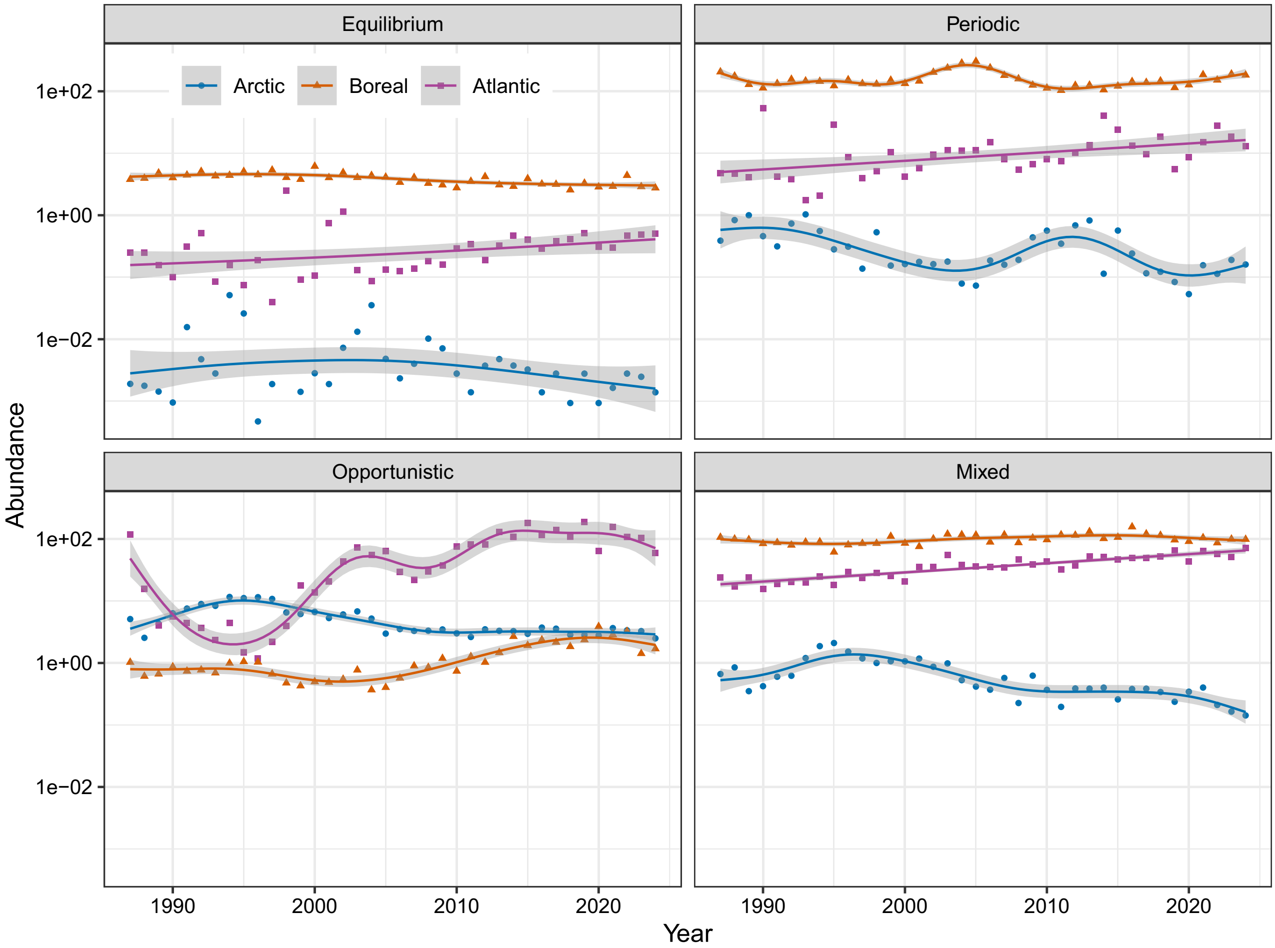

Fig. 6. Temporal changes in abundance (plotted on a log scale) of LHS groups, shown for each biogeographic group. Lines are based on gam smoothing.

fish are linked to intermediate or later years. Notably, Atlantic and Boreal opportunistic fish are separated from Arctic fish. The second NMDS component further distinguishes between years, highlighting greater variation during the earlier period compared to the later years (Fig. 8). Changing the number of NMDS dimensions to two or four, instead of three, did not affect the observed distinction between biogeographic groups (Supplement 9).

Heatmaps identified three clusters of opportunistic species, differentiated by their biogeographic abundance patterns (Fig. 9). One group of fish primarily consists of Arctic species that were relatively abundant during the initial colder period. This group contrasts to the other two; one of which consists mainly of Atlantic species which have been most abundant since around 2010, and the other of Boreal and Arctic species which show no clear temporal trends in abundance or were most abundant during both the early and late periods of the study (Fig. 9).

Discussion

Changes in abundance, distribution, and species richness of different LHS groups were found to be closely tied to the biogeography of the fish, where Atlantic and Boreal species appear to have benefitted from the warming trend, while Arctic fish have experienced reductions. This community turnover coincides with a period of increased flow of warm and saline Atlantic water towards the North Icelandic shelf[16,17], which has triggered various biological changes in the marine habitats[10,23,24,44–46]. These changes are likely linked to large-scale oceanographic variability in the Northeast Atlantic, as environmental conditions in Icelandic waters are in phase with the Atlantic Multidecadal Oscillation (AMO)[1] and associated with shifts in the subpolar gyre[26,27]. Our study suggests that the relatively stable temperatures observed over the past two decades have promoted a general stability of fish communities as compared to the swift changes around the turn of the century.

We observed an increased abundance and northern expansion of Atlantic opportunistic species, and a simultaneous reduction of most Arctic opportunistic species, mirroring changes in fish compositions in the Barents Sea and along the coast of Norway[4,7,13,14]. A similar trend has been noted for demersal fish communities in the more southern European seas, where the proportion of opportunistic strategies increased[6]. This period also saw a rise in overall species richness due to an increase in Atlantic and Boreal species. However, in the deeper and colder parts of the North subarea, the average number of species per station has not increased, suggesting

(a)

LHS group	Biogeographic group	edf	Ref.df	F	*P*
Equilibrium	Arctic	2.091	2.091	3.707	0.031
	Boreal	1.000	1.000	1.169	0.282
	Atlantic	1.000	1.000	5.601	0.020
Periodic	Arctic	5.844	5.844	6.651	< 0.001
	Boreal	1.000	1.000	0.002	0.962
	Atlantic	1.000	1.000	15.678	< 0.001
Opportunistic	Arctic	1.000	1.000	8.691	0.004
	Boreal	2.552	2.552	9.472	< 0.001
	Atlantic	7.574	7.574	26.373	< 0.001
Mixed	Arctic	7.615	7.615	34.718	< 0.001
	Boreal	1.000	1.000	4.714	0.032
	Atlantic	1.000	1.000	108.355	< 0.001

(b)

LHS group	Model	df	AIC	BIC	logLik	L.Ratio	*P*
Equilibrium	1	11	268.5	298.5	−123.3		
	2	7	268.9	288.0	−127.5	8.38	0.079
Periodic	1	11	204.7	234.8	−91.4		
	2	7	211.5	230.7	−98.8	14.8	0.005
Opportunistic	1	11	136.6	166.7	−57.3		
	2	7	158.3	177.5	−72.2	29.7	< 0.001
Mixed	1	11	21.3	51.4	0.33		
	2	7	59.6	78.7	−22.8	46.2	< 0.001

Table 2. (a) Summary results from generalized additive mixed models (GAMM) testing temporal trends in log abundance across biogeographic groups. The models include separate smooth terms for year within each group (s(year):biogeo) and an AR(1) correlation structure to account for temporal autocorrelation. *P*-values indicate whether temporal trends were significant within each group. (b) Model comparisons (likelihood ratio test) between a full model (Model 1) and a simpler model with a shared smooth term (s(year)) across biogeographic groups (Model 2).

that increased species richness is confined to specific parts of this subarea. While rising species richness has been linked to increased temperatures in many habitats, e.g. along the entire Norwegian coast[14], some deep-water communities, such as those in East Greenland, have experienced decreased species richness and total abundance with rising bottom temperatures[47].

The study classified species into groups based on life-history strategies while also observing individual species trends. Overall, the abundance of the primary periodic species remained relatively stable throughout the study period, with a notable spike around 2005, largely attributed to haddock. In the early years, haddock was predominantly found in the warmer waters to the south and west of Iceland, but over the past two decades, its presence has increased in northern areas[23]. Opportunistic species saw a significant rise in abundance around 2000, particularly in the southern region, a change primarily driven by Norway pout. An overall reduction in the abundance of equilibrium species is mainly due to a gradual decline in starry ray, the most abundant equilibrium species. However, less abundant Atlantic equilibrium strategists have shown increases since 2000. Increased temperatures appear to benefit mixed-strategy species such as golden redfish (*Sebastes norvegicus*), Norway haddock (*Sebastes viviparus*), and greater argentine (*Argentina silus*), which thrive in the warmer waters to the south and west of Iceland, in contrast to spotted wolffish (*Anarhichas minor*) and snakeblenny (*Lumpenus lampretaeformis*), which have more northerly distributions[48].

The opportunistic LHS group exhibited the most pronounced and swift temporal changes in abundance during the warming period, as expected given that opportunistic species are particularly responsive to environmental change or habitat disturbances[35]. Heatmap analysis of opportunistic species confirms significant variations in abundance patterns across different years, with notable differences between Atlantic/Boreal and Arctic species. Capelin is an opportunistic species[4] that plays a key ecological role in the Arctic-Boreal transition zone of the North Atlantic[49]. Similar to our observations for other Arctic opportunistic fish such as eelpouts and polar cod (*Boreogadus saida*), capelin abundance at the Icelandic continental shelf has reduced due to changed environmental conditions[3]. Although capelin was not included in our study due to inconsistent sampling in the early years of the groundfish survey, the reduced abundance of this important forage fish shows that climate-driven changes may affect the whole fish community, not only through direct environmental forcing, but also through species interactions and food webs.

For opportunistic fish, hierarchical clustering revealed a clear distinction between Atlantic and most Arctic and Boreal fish. However, a few opportunistic Arctic species appear to have increased in abundance despite the warming trend. While some of these are both small and rare, leaving open the possibility that chance may

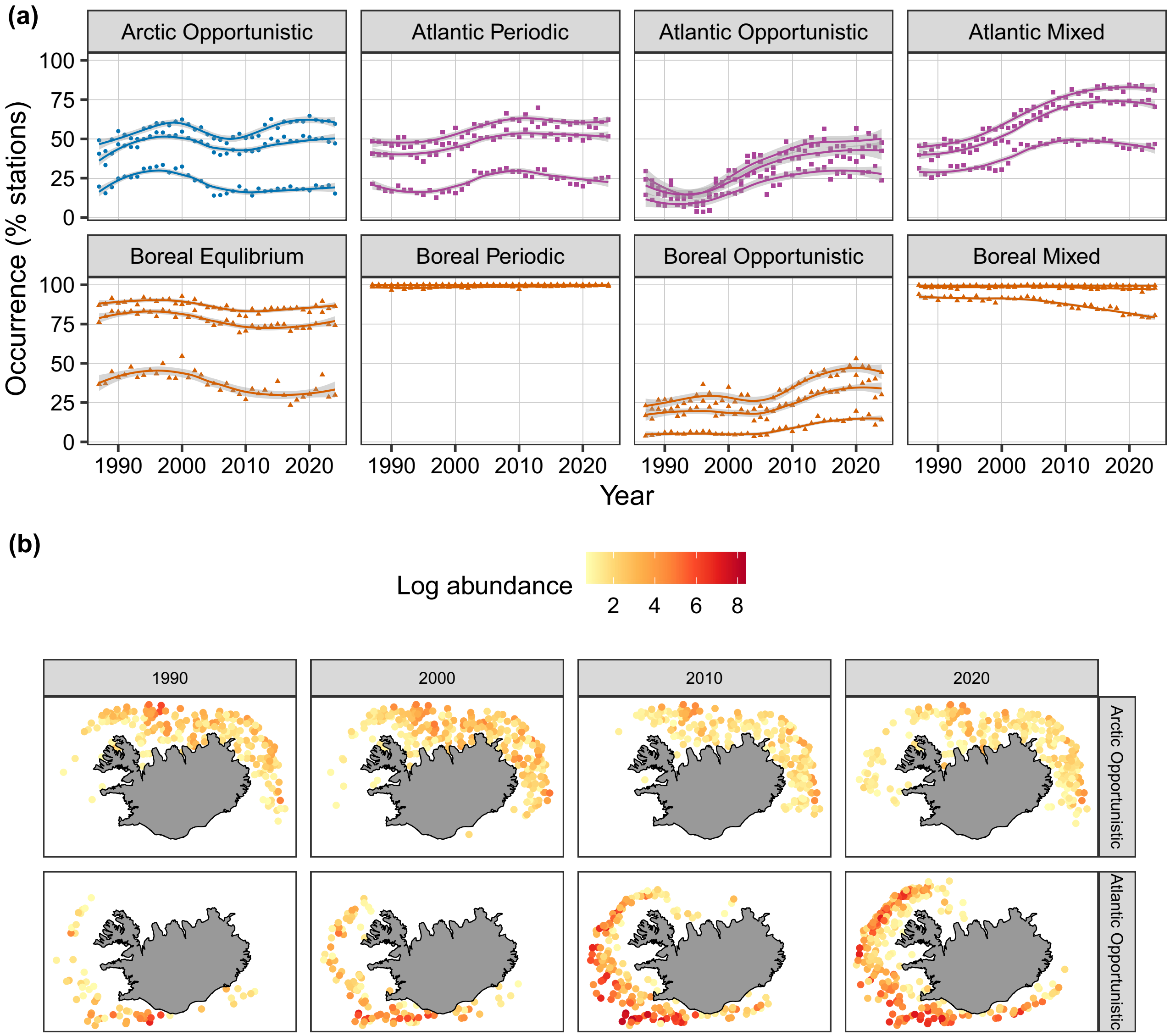

Fig. 7. (**a**) Temporal changes in spatial distribution of different biogeographic and LHS groups shown as the percentage of stations occupied by each group. Upper lines show occurrence for all fish, middle lines are based on stations where more than one fish per group was caught, and the lower lines where more than ten fish were caught per group. Lines are based on gam smoothing. b) Spatial distribution of Arctic and Atlantic opportunistic fish in four years, excluding tows where only one fish per group was caught (see Supplement 8 for more groups and years).

influence their abundance estimates, the sea tadpole (*Careproctus reinhardti*) and polar sculpin (*Cottunculus microps*) are frequently captured in cold waters and have shown a recent upward trend. Possibly, reduced predation pressure or less competition from co-occurring species may have benefited certain Arctic species. Therefore, despite observable biogeographic patterns, the responses to environmental changes are not clear-cut.

Most opportunistic species were small-sized and non-commercial, in contrast to periodic species which are predominantly commercially exploited, consistent with observations in the Barents Sea[4]. In Iceland, the primary commercially exploited demersal fish; cod, haddock, and saithe (*Pollachius virens*)[50], exhibit periodic life-history strategies. Within the study area, these Boreal gadids display a centralized spatial distribution and a preference for moderate temperatures and may therefore be less sensitive to environmental fluctuations than Arctic or Atlantic species[10]. However, their periodic traits, such as medium-to-long lifespan and length, suggest that they may be vulnerable to high fishing pressure, as larger, later-maturing species tend to be less resilient to fishing than smaller, early maturing ones[32]. While a negative effect of North Sea fishing effort on the equilibrium strategy has been documented, fishing effort was not a good predictor for the periodic or opportunistic strategies[6]. For commercially exploited equilibrium species, the negative effects of fishing effort would be expected, as they are particularly vulnerable due to their low fecundity and slow growth[6,9]. It should be noted that assessing the relative impacts of fisheries on different groups of fish is challenging, as non-commercial fish can be indirectly affected through bycatch, habitat disturbance from towed gear, or shifts in predator populations, which may be

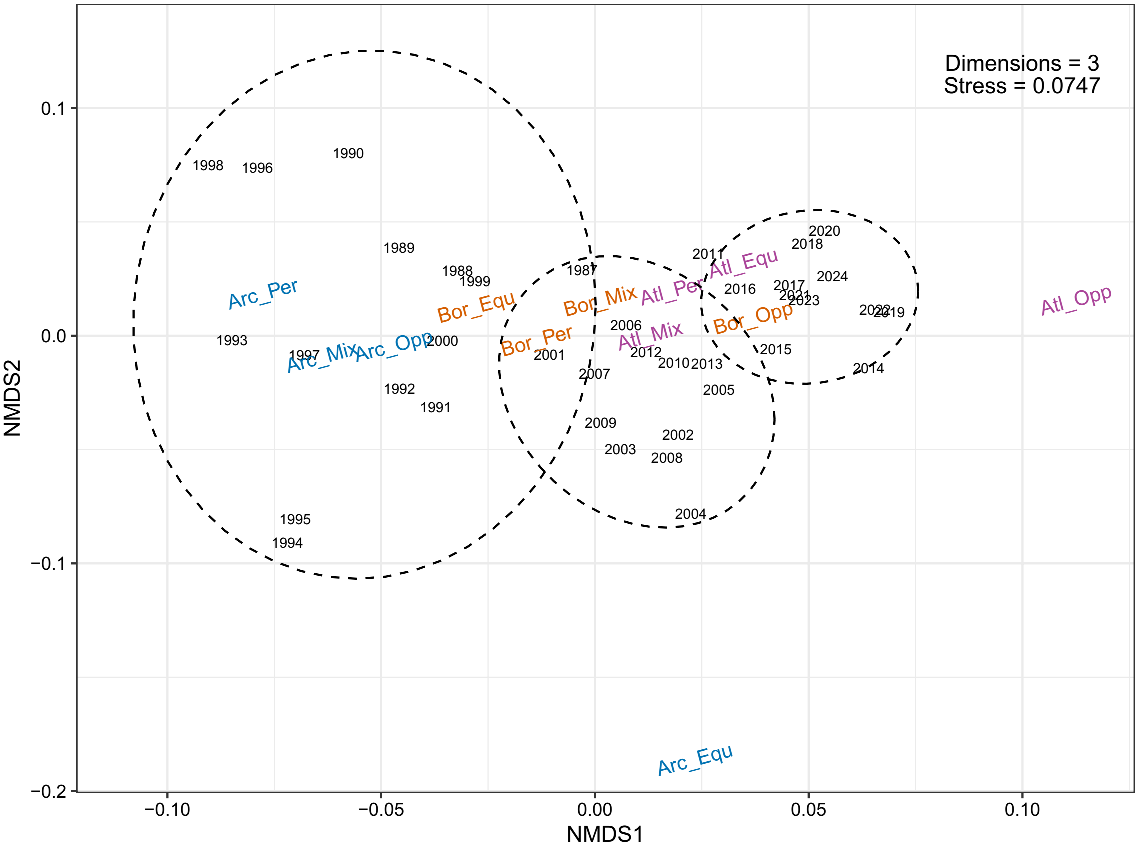

Fig. 8. NMDS ordination on mean abundance (log) of 12 biogeographic/LHS groups by years. Broken lines indicate 90% confidence ellipses for three periods; 1987–1999 (left), 2000–2012 (middle), and 2013–2024 (right). Arc = Arctic, Bor = Boreal, Atl = Atlantic, Equ = Equilibrium, Per = Periodic, Opp = Opportunistic, Mix = Mixed.

commercially targeted. This is complicated further by the fact that fisheries usually target medium-to-large fish but not the juveniles.

The drastic increase in the abundance of Atlantic opportunistic fish coinciding with rising temperatures, and the concurrent decrease in Arctic species, indicates a climate-driven transition in the fish community. In this regard, Icelandic waters have become increasingly similar to the warmer more southern European waters, where the proportion of opportunistic species is high[6]. Species-specific fluctuations within LHS groups indicate that life-history strategies do not uniformly predict fish responses to changing temperatures, where higher temperatures are clearly more advantageous to Atlantic than to Arctic species. While the LHS approach is useful for studying changes in groundfish communities in zoogeographic transitional areas, the species' traits do not provide a complete picture, as evidenced by the differing responses of biogeographic groups within each LHS group.

Our findings are consistent with previous research suggesting poleward shifts in Icelandic groundfish species following warming[10,11]. These studies forecasted changes in fish distribution in response to elevated temperatures over the Icelandic continental shelf. However, our observations indicate relatively small changes in bottom temperatures and fish assemblage structure over the past 10–15 years. Contrary to trends expected elsewhere globally, recent investigations suggest that future instability of the Atlantic Meridional Overturning Circulation (AMOC) may lead to significant cooling in the areas between Iceland, the British Isles, and southern Greenland[51]. This potential cooling would reverse the poleward trends in fish distribution and abundance. Under this scenario, conditions might become beneficial for Arctic species, while Atlantic and Boreal opportunistic fish would retreat swiftly from these regions.

The period since 1996 bears similarities to the warm phase between the mid-1920s and mid-1960s, regarding elevated AMO indices[52] (see Supplement 10), increased water temperatures around Iceland, and boreo-tended changes in fish assemblages[53]. During 1925–1945, at least 37 species of fish were thought to show evidence of changes linked to warmer waters, with many Atlantic species either expanding their range or becoming more abundant[53]. In light of these historical patterns, the recent temperature-driven shifts in distribution and abundance of groundfish in Icelandic waters appear to be primarily driven by inter-decadal oceanographic variability.

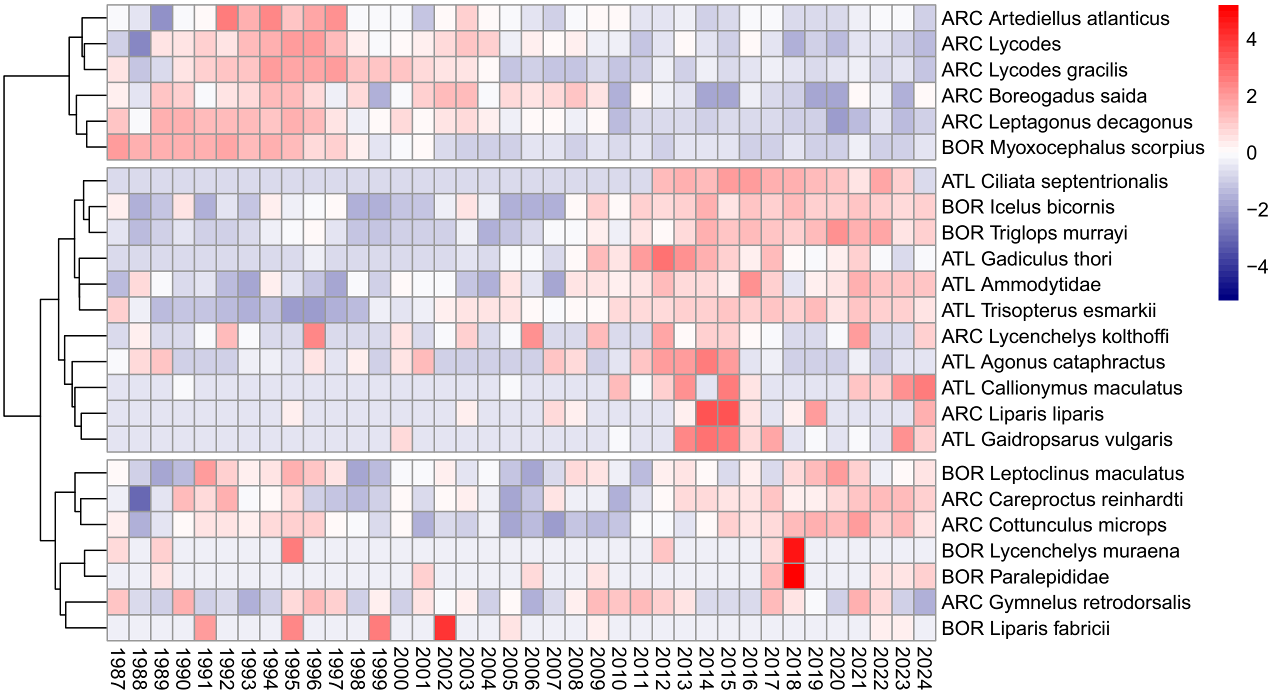

Fig. 9. Heatmap showing temporal patterns of opportunistic species abundance across years, with the colour scale indicating the degree of deviation from the mean abundance (standardized Z-scores) for each species. Prefixes in front of species names indicate biographic groups: ARC = Arctic, BOR = Boreal, ATL = Atlantic.

Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

J.S. led the writing of the paper, J.S. and Ó.A.S. analysed the data, and all authors were involved in conceiving the study, writing, and editing, and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to J.S.

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