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# Recent warming leads to a rapid borealization of fish communities in the Arctic

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**Arctic marine ecosystems are warming twice as fast as the global average[1]. As a consequence of warming, many incoming species experience increasing abundances and expanding distribution ranges in the Arctic[2]. The Arctic is expected to have the largest species turnover with regard to invading and locally extinct species, with a modelled invasion intensity of five times the global average[3]. Studies in this region might therefore give valuable insights into community-wide shifts of species driven by climate warming. We found that the recent warming in the Barents Sea[4] has led to a change in spatial distribution of fish communities, with boreal communities expanding northwards at a pace reflecting the local climate velocities[5]. Increased abundance and distribution areas of large, migratory fish predators explain the observed community-wide distributional shifts. These shifts change the ecological interactions experienced by Arctic fish species. The Arctic shelf fish community retracted northwards to deeper areas bordering the deep polar basin. Depth might limit further retraction of some of the fish species in the Arctic shelf community. We conclude that climate warming is inducing structural change over large spatial scales at high latitudes, leading to a borealization of fish communities in the Arctic.**

Marine ectotherms are found to fully occupy their latitudinal ranges with regard to thermal tolerance, and are therefore predicted to expand at their poleward range boundaries and contract at equatorward boundaries under climate warming[6]. Poleward shifts in distributions of marine species have been extensively documented[2,7], particularly in fish[8,9]. Marine taxa track local climate velocities[5]—thus areas with above global average increases in temperatures should show pronounced shifts in species and assemblages. Marine fish without limits to dispersion typically respond to warming via abundance changes[10], and depth and geographic shifts[9,11,12]. However, species differ with regard to sensitivity to climate warming (for example, thermal tolerance), dispersal capacity (for example, migratory versus non-migratory) and ability to exploit new resources (generalists versus specialists), thereby exhibiting different rates and magnitudes of responses in abundance and distribution[1,5]. Species originally inhabiting an area might be displaced by incoming species. This might ultimately lead to local extinctions. Community-wide changes on large spatial scales are therefore expected in marine fish[3]. These changes are anticipated at high latitudes due to rapid increases in temperature and the expected strong impact of sea-ice retreat on polar ecosystems[1,13].

The Barents Sea, a shelf sea bordering the Arctic Ocean (Supplementary Fig. 1), with a hydrographical frontal zone coinciding with a zoogeographical divide, provides ideal conditions to study community-wide geographic shifts induced by climate warming. In the past decade, water temperatures in the subarctic Barents Sea have been the warmest on record[4], and the sea ice has retreated[14]. The polar frontal zone where Atlantic and Arctic water masses meet also separates boreal from Arctic fish species, which differ with regard to thermal affinities[15]. In recent years this frontal zone has ceased being a strong biogeographic border for boreal fish species. We thus investigated whether the current rapid local climate velocity is reflected in poleward shifts of fish communities. Further, we addressed whether generalist, migratory boreal fish species were responsible for the observed shifts, as expected on the basis of their higher dispersal ability and dietary flexibility.

Since 2004 we surveyed the Barents Sea (approximately 65 km between stations) annually with regard to bottom hydrography and demersal fish species in late summer (minimal ice coverage). In the period 2004–2012, bottom temperatures in the Barents Sea increased and the mixed-water area expanded (Fig. 1a,b and Supplementary Fig. 4). For the study period, the start and end year also represent the extremes of lowest water temperature and most ice (2004), and warmest water temperature and least ice (2012; Supplementary Fig. 3). The observed hydrographic changes were caused by an increased inflow of warmer Atlantic water[16], leading to a strong reduction of sea ice[14]. Concurrent with these climate-induced changes, many fish species changed their ranges, and expanded their distributions northwards and eastwards. To reduce the effect of inter-annual variation in single species, we focused on the community level by identifying well-defined fish communities based on species abundance profiles (Supplementary Fig. 5). Since 2004 the transition areas between the Atlantic and Central communities and the Central and Arctic fish communities moved northwards and eastwards (Fig. 1c,d and Supplementary Fig. 7). Whereas the Atlantic community was identified on stations steadily further north through time, the Arctic community was identified on ever fewer stations. The southern boundary of the Arctic community gradually moved north, towards the shelf edge and northern margin of the surveyed area (Fig. 1c,d and Supplementary Fig. 7).

The Atlantic shallow sub-community, found in the shallowest areas and at the highest temperatures (mean depth = 201 m, mean bottom temperature = 3.46 °C, Supplementary Fig. 9 and Supplementary Table 3), markedly expanded its area coverage north-eastwards (Fig. 2). From 2004 to 2012 the community centre of distribution moved 141 km (Fig. 2). In addition to new areas in the north, eastern areas south of Novaya Zemlya became occupied by the Atlantic shallow sub-community, in contrast to the beginning of the study period[15]. As well as the ubiquitous species

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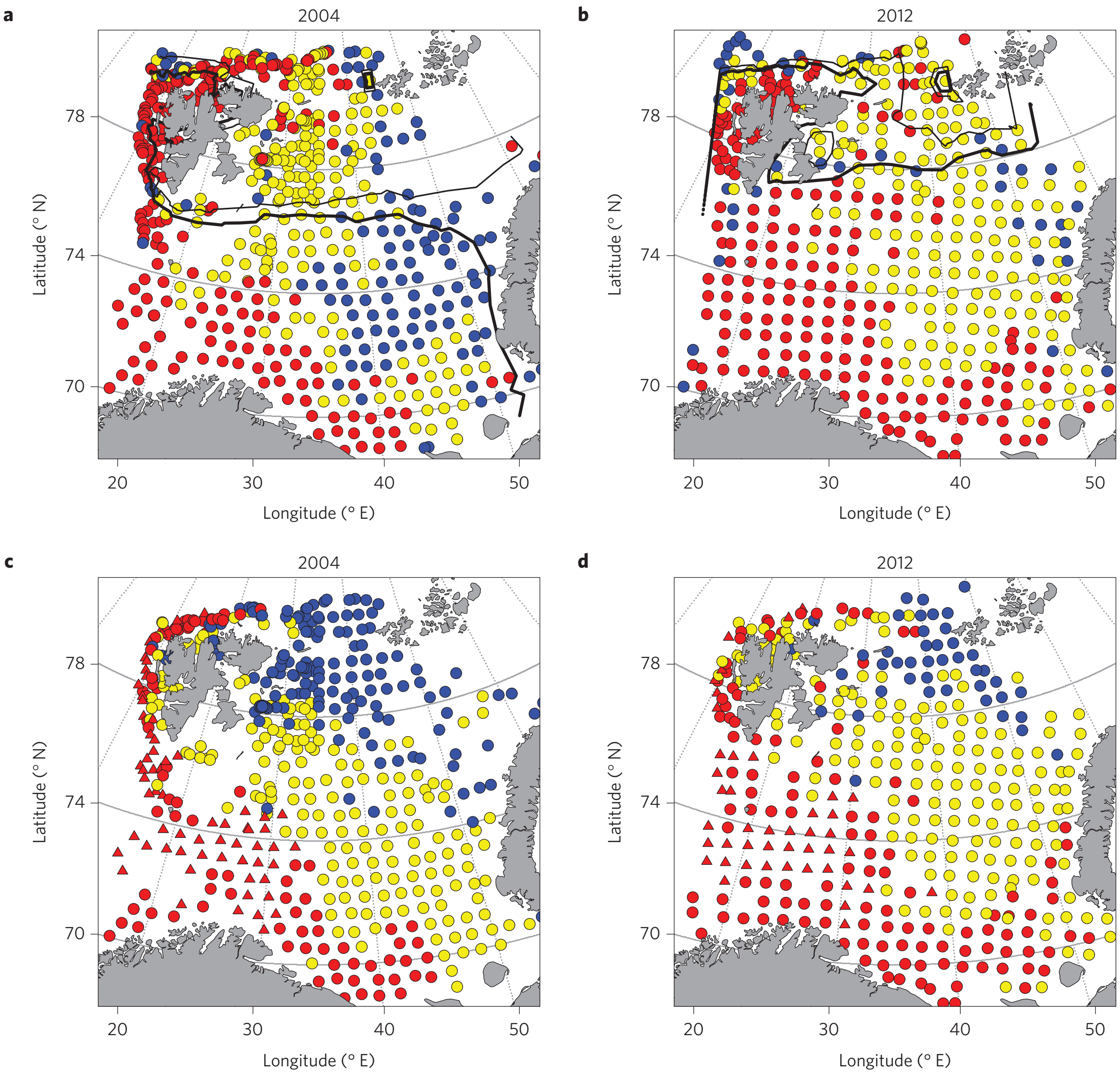

**Figure 1 | Environmental conditions and fish communities in the Barents Sea. a,b**, Water masses and ice presence in 2004 (**a**) and 2012 (**b**): Atlantic Water (red, $T > 2\,^{\circ}\mathrm{C}$), Arctic Water (blue, $T < 0\,^{\circ}\mathrm{C}$) and mixed-water masses (yellow, $0\,^{\circ}\mathrm{C} < T < 2\,^{\circ}\mathrm{C}$). Ice-presence isolines are given in number of days with ice present during the year: 120 days, bold line and 180 days, fine line. **c,d**, Fish communities identified on bottom trawl stations in 2004 (**c**) and 2012 (**d**). Atlantic, Arctic and Central communities: red, blue and yellow symbols, respectively. Circles: shallow sub-communities, triangles: deep sub-communities. Maps for all years in Supplementary Figs 4 and 7 (Supplementary Methods).

long rough dab (*Hippoglossoides platessoides*), this community is dominated by cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*; Supplementary Fig. 5), which are commercially exploited species. The Atlantic deep sub-community (mean depth = 389 m, Supplementary Fig. 9 and Supplementary Table 3), did not show a geographic shift, but remained confined to the deeper basin in the southwestern Barents Sea throughout the study period.

The Arctic community, found in cold areas with the most ice (mean bottom temperature = 1.08 °C, mean ice presence = 224 days, Supplementary Fig. 9 and Supplementary Table 3), retracted and was confined to the northernmost reaches of the surveyed area by the end of the study period (Fig. 1d and Supplementary Fig. 7). The community centre of distribution moved 159 km north through the study period (Fig. 2). This community is dominated by bigeye sculpin (*Triglops nybelini*), Greenland halibut (*Reinhardtius hippoglossoides*) and snailfish (*Liparis* spp.; Supplementary Fig. 5). In addition to its northward retraction within the study area, the Arctic community was found on stations north and east of the standardized survey area. The northern shelf edge stations are deeper than stations in the study area, implying that the retracting Arctic community in recent years occupies increased mean depths (Supplementary Fig. 7), a response also observed in the North Sea for deep dwelling species with cool temperature affinity[11,12].

As the Arctic community retracted, the Central community moved northwards (Fig. 1c,d and Supplementary Fig. 7). To investigate whether there was a mixing of the two communities or whether the Arctic community was retracting from the northern Barents Sea, we calculated which species increased or decreased in abundance relative to 2004 in the Arctic area (Fig. 3). Several species with northern affinity (*Reinhardtius hippoglossoides*, *Icelus* spp., *Liparis* spp.) exhibited a reduced mean abundance, whereas more boreal species increased in abundance (Fig. 3). Thus, the observed trends in community area coverage can be characterized as a 'take-over' by boreal species. With further ocean warming and sea-ice loss, Arctic shelf species might become locally extinct as they run out of shelf habitat[17]. These species might move eastwards to other Russian shelf seas.

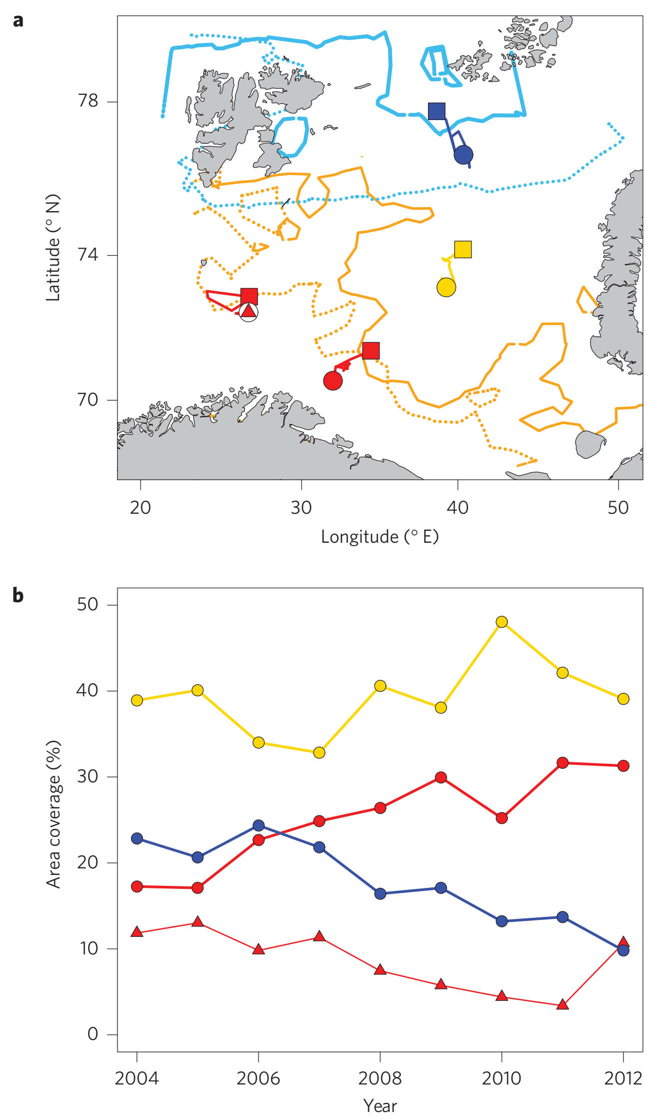

**Figure 2 | Distributional changes of fish communities from 2004 to 2012.** **a**, Centre of distribution (circle: 2004, square: 2012) and track line for different communities: Atlantic shallow sub-community in the south (red circle to red square, displacement of community centre: 141 km), Atlantic deep sub-community in the west (circle with red triangle to red square, 51 km), Arctic community in the north (blue circle to blue square, 159 km) and Central community in the central/east (yellow circle to yellow square, 131 km). Northern boundary of Atlantic water (orange, dotted line: 2004, solid line: 2012) and southern boundary of ice presence isolines (light blue, dotted line: 2004, solid line: 2012). Ice presence isolines are 180 days with ice present during the year. **b**, Area coverage for fish communities: Atlantic shallow sub-community (red bold line, $R^2 = 0.83$, $p < 0.01$), Atlantic deep sub-community (red fine line), Central community (yellow line) and Arctic community (blue line, $R^2 = 0.82$, $p < 0.01$).

The changes observed in the Barents Sea document how quickly marine fish species can track the environmental changes driven by climate warming[8]. The pace of range shifts in marine fish species is globally projected to 40 km decade$^{-1}$ on average[3], but varies considerably depending on climate modelling scenarios. Our results on shifting community centres of distribution are not directly comparable to an average for single species (for example, Arctic community shifting centre of distribution at $>$159 km decade$^{-1}$). Nevertheless, our results show how species may shift northwards at a higher pace than predicted by existing models even under a high-range climate scenario (expected shift in centre of species' range: median = 79 km, 25th to 75th percentiles = 24–179 km; ref. 3). Our estimates also exceed previous community-wide northward shifts observed in the subarctic Bering Sea (34 km, 1982–2006; ref. 3), and are comparable to the fastest shifting species in the North Sea (*Micromesistius poutassou*, 169 km decade$^{-1}$ in 1977–2001; ref. 11).

Different species shift their abundances and distribution ranges at different rates owing to unequal sensitivity to climate warming, dispersal capacity and ability to exploit new resources. The northward shifts of communities are probably driven by behavioural responses of seasonally migrating species, and by changes in their abundance[10]. Several large predatory, seasonal migrants increased in abundance and expanded their distribution towards the northern Barents Sea in the study period. Cod, the main commercial species, reached a record high population size that had not been observed since the 1950s, owing to synergies between a favourable climate and a lowered fishing pressure[18]. Recently, high abundances have also been recorded for haddock, the other main commercial species, and for long rough dab, a very common and widespread species in the Barents Sea. A poleward expansion of cod and haddock, and a north-eastward displacement of beaked redfish (*Sebastes mentella*) have been suggested[13,19], and are confirmed by this study. The increased abundance and expanded distribution area of the above-mentioned abundant species could possibly be a sufficient explanation for the apparent community-wide northward shifts. However, removing these dominant predators from the analyses did not change the main results; a northward shift in communities is still observed (Supplementary Figs 11 and 12). The latter results indicate that the observed ecological changes are extensive, with many fish species being involved.

A change in phenology (that is, timing of life history events) for migrating species, such as cod and haddock, could account for the observed northward shifts of boreal fish when the survey data are fixed. The delayed ice formation observed in the north in recent years (by approximately one month, Supplementary Fig. 2), could contribute to a later return of migrating species. However, other data sources suggest that species such as cod and haddock have also expanded their distributions northwards in winter time[20,21], implying that the northward shifts are all year round.

The increased incidence of large boreal species, such as cod in the northern Barents Sea during summer, implies increased predation pressure on small Arctic fish species and intensified competition for the few large predators such as Greenland halibut and Arctic skate (*Amblyraja hyperborea*). Greenland halibut had the largest decrease in mean abundance from 2004 to 2012 (*Reinhardtius hippoglossoides*, Fig. 3), followed by a few of the Arctic small demersal fish species. Considering that the northern reaches of the Barents Sea have become more productive through the study period[22], with an increased abundance of fish (nearly fourfold increase from 2004 to 2012), it is remarkable that some of the Arctic species have declined (Fig. 3). We interpret this as being a consequence of increased competition and predation from boreal species in addition to an effect of habitat loss for Arctic species.

The observed rapid borealization of the northern Barents Sea was influenced by a northward expansion of the thermal habitat for boreal species and by its deterioration for Arctic species. However, species replacements due to alterations of thermal habitats are not necessarily the sole explanation of the abundance changes observed[23]. Changes in fish prey composition and in energy pathways might also have contributed to the observed decreased importance of Arctic species in the northern part of the Barents Sea (Fig. 3). Climate warming is increasing the importance of Atlantic zooplankton in the northern Barents Sea[24]. Arctic zooplankton species are typically larger and fattier than Atlantic species[25], and the latter thus constitute a less energetic food source. Compositional changes in northern plankton communities might therefore be

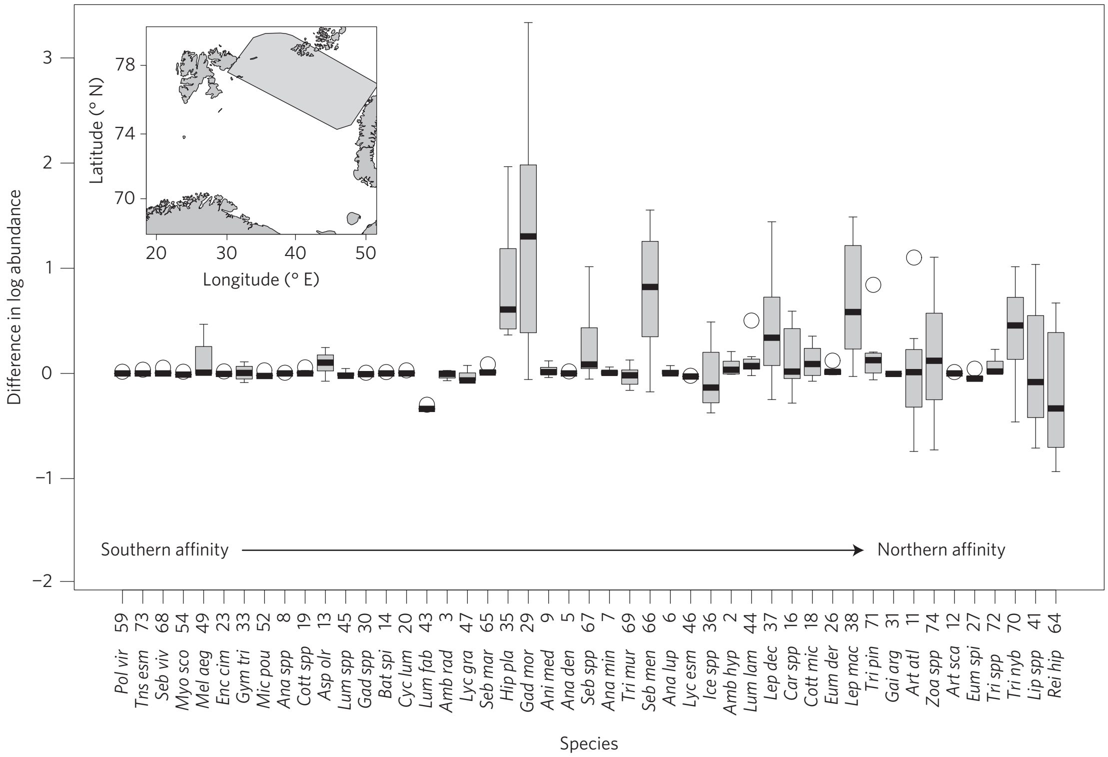

**Figure 3 | Changes in fish abundance in the northern Barents Sea (calculated area shown on map).** Abundance deviations from 2004 for the period 2005–2012, species sorted according to northern affinity (S → N). The box is delimited by the 25th and 75th percentiles, the thick black line shows the median. The whiskers show the minimum and maximum abundance difference from 2004 (excluding outliers shown by circles). Species affinity to latitude was calculated as abundance-weighted mean latitude throughout the study period 2004–2012. The species abbreviations on the *x*-axis are short Latin species names. Full species names and latitudinal affinities are given in Supplementary Table 1 according to the species number.

unfavourable for Arctic fish species. Furthermore, a shift in main energy pathways from benthic to pelagic associated with sea-ice retreat has been predicted for Arctic shallow seas[26], which will have a negative effect on Arctic benthivore fish species. Decreasing sea ice reduces the benthic fallout of ice algae and thus the supply for benthic production. Many Arctic fish species are bottom-dwelling benthivore specialists, such as bigeye sculpin and snailfish. This makes them more vulnerable to climate change than boreal species that are characterized by broader diets[27]. Thus, changes in food available for Arctic versus Atlantic species might help explain the boreal 'take-over'.

The observed changes in community structure have implications for biodiversity, food-web configuration and trophic pathways. In the northern Barents Sea, the increased importance of large boreal piscivores and small planktivores[28], and the loss of small benthivores, increases the relative importance and diversity of the pelagic food web. Also, sea-ice retraction impacts ice-associated species such as polar cod (*Boreogadus saida*), which plays a key role in Arctic food chains[29]. The documented reorganization of fish communities results in changes of fish functional characteristics, affecting functional diversity in the area[30]. This illustrates how climate-induced structural change brought about by community-wide poleward shifts can affect ecosystem functioning and vulnerability.

This study shows how boreal shelf fish species expand their distribution ranges northwards as the Arctic is warming. These large, migratory fish predators are possibly able to take advantage of increased production and prey unfavoured by Arctic fish species, as the food chain is becoming increasingly similar to subarctic ecosystems further south. Arctic fish species, on the other hand, suffer from increased competition and predation from boreal species and are retracting northwards and eastwards. The structural changes in fish communities and reconfiguration of ecological interactions result in a borealization of the Arctic ecosystem.

## Methods

Methods and any associated references are available in the online version of the paper.

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## Author contributions

M.F., R.P. and E.J. contributed to the formulation of hypotheses and approach. M.F., R.P. and R.B.I. performed the data analysis. All authors participated in writing the manuscript.

## Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.F.

## Competing financial interests

The authors declare no competing financial interests.

## Methods

The Barents Sea is a shelf break sea (1.6 mill. km$^2$, average depth: 230 m), located north of Norway and Russia (Supplementary Fig. 1). Since 2004, a joint ecosystem survey with Norwegian and Russian research vessels has covered the Barents Sea in summer–early autumn, during minimum ice coverage. Stations were allocated on a standardized grid (35 nautical miles between stations). At each station a demersal trawl (Campelen 1800) was towed for 15 min at 3 knots (0.75 nautical miles ∼1,400 m). The catch was sorted (identified to lowest possible taxonomic level), counted and weighed. Environmental information was sampled with a conductivity–temperature–depth (CTD) profiler at most stations. Sea-ice data were obtained from SSM/I passive microwave remote sensing from the National Snow and Ice Data Center[31] (http://www.nsidc.org). Ice presence was calculated as number of days with ice present during each year.

The annual cycle of temperature along the Kola section and the sea-ice coverage in the Barents Sea are shown in Supplementary Fig. 2. The Kola section, 0–200 m depth layer, represents a proxy for the temperature development of the Barents Sea (Supplementary Fig. 2a), and the first decade of the 21st century was the warmest ever recorded[32] (since the start of the survey in 1900). The duration of the ice-free season increased through the study period (Supplementary Fig. 2b). The timing of the survey was consistent through the study period 2004–2012, with only a week's delay in later years (and an expanded survey period in 2010).

To calculate yearly averages in Barents Sea bottom-water temperature, and relative areas covered by different water masses (Atlantic Water, $T < 2\,^{\circ}\mathrm{C}$; mixed-water masses, $0\,^{\circ}\mathrm{C} < T < 2\,^{\circ}\mathrm{C}$; Arctic Water, $T < 0\,^{\circ}\mathrm{C}$) and sea ice, the environmental data were first spatially interpolated on a regular grid (grid size, 50 × 50 km) by Kriging[33], and the yearly estimates (Supplementary Fig. 3) were based on the gridded data to avoid sampling bias and facilitate between year comparisons.

More than 220 fish species are known to occur in the Barents Sea, and approximately 100 fish species are regularly caught on the ecosystem surveys. However, owing to a changing taxonomic identification protocol, several species were merged on a higher taxonomic level. A further species reduction due to very low occurrence (one station only) and removal of pelagic species left us with 74 taxonomic groups identified similarly throughout the study period (Supplementary Table 1). The catches in the survey trawl were standardized to a given tow distance (1 nautical mile). From 2004 to 2012 the ecosystem surveys sampled 4,463 bottom trawl stations—of these 3,940 were included in our analyses. Stations were removed because they were repeated successively (572—for example, diurnal stations), were of low quality (96—for example, trawl hauls mostly containing mud), had tow time less than 10 min (64—unrepresentative sampling) or more than 60 min (11—various test stations), or were sampled on unrepresentative depths (54 less than 50 m and 287 more than 500 m). Following the removal of pelagic species, some stations were left empty or with an occurrence of only one species (monostations). These 11 stations were removed, leaving 3,940 stations for our analyses.

To classify the different fish communities in the Barents Sea in 2004 (start of ecosystem survey), we performed a cluster analysis (based on Bray–Curtis dissimilarities and Ward linkage). Visual inspection of the dendrogram revealed three well-separated clusters (that is, fish communities), as shown by the large interval of Bray–Curtis dissimilarity between the splits into two, three and four clusters[34] (Supplementary Fig. 6a), and by the clear separation of the clusters when plotted onto an ordination diagram[35]. The species abundance profile of each fish community was calculated by averaging individual species abundances across stations classified to that community in 2004 (Supplementary Fig. 5). The different stations were mapped with colour coding denoting cluster affiliation (Supplementary Fig. 6b). The Barents Sea open waters clearly comprise three distinct fish communities (here called Atlantic, Central and Arctic), with a spatial pattern suggesting that community structure is influenced by water masses and habitat characteristics (Supplementary Fig. 4).

The Atlantic community comprises two different sub-communities (shallow Atlantic and deep Atlantic) that are related to different depth habitats. In the figures, the two Atlantic sub-communities are identified by using different symbols (Figs 1c,d and 2 and Supplementary Figs 7,11 and 12) or colours (Supplementary Figs 5,6,8 and 10), and are treated separately when assessing distributional shifts and changes in areal coverage because of the expected differences in response to climate warming of deep versus shallow fish communities. A discriminant analysis was applied to reveal which species contribute most to the separation of the clusters (Supplementary Fig. 6c), and the resulting discriminant functions were used to classify fish communities sampled over the study period. The similarities of the two maps show the predictive capability of the discriminant function (Supplementary Fig. 6b,d). Mapping the classified stations in the Barents Sea allowed us to track changes in distribution of the Atlantic, Central and Arctic communities (Fig. 1c,d and Supplementary Fig. 7).

Estimates of areal coverage and position of community distributions are biased by sampling effort and distribution, which vary between years. To overcome sampling bias we gridded the data (Supplementary Fig. 8). The grid size was 50 × 50 km (∼27 nautical miles), ensuring approximately one station per grid cell. The grid cells were then classified according to the community affiliations of the stations found in the cells. Cells missing stations were assigned the community from the closest nearby station (Supplementary Fig. 8). This approach yields a conservative assignment when stations are missing in the margin of the surveyed area. To investigate possible changes in community distribution through time with regard to position (geographical shift) and areal coverage (expanding or retracting), for each community we calculated the centre of distribution (weighted average longitude and latitude) and the proportion of area covered relative to the total area considered, based on the gridded data (Fig. 2). Temporal trends in community area coverage were estimated by linear regression, fitting general linear models, and F-tests were used to evaluate trends' significance (Supplementary Table 2).

We also assessed community affinity to environmental characteristics such as bottom depth, water temperature and ice presence (Supplementary Fig. 9 and Supplementary Table 3). Affinities to environmental conditions were addressed using binomial generalized linear models (GLMs; Supplementary Fig. 10 and Supplementary Table 4). For each community, the GLMs were estimated based on the presence–absence data and on the environmental conditions at each station, an approach akin to species distribution modelling[36], but here applied to the distribution of communities rather than individual species. The models' output allowed us to characterize affinities (in 2004 and for all years). The environmental variables included as predictors in the GLMs showed some degree of collinearity, but even the strongest correlation detected ($r = -0.31$, between water temperature and ice presence in 2004) had an absolute value far below $|r| = 0.7$, which is considered a threshold level beyond which collinearity may seriously distort model estimation[37]. Another problem afflicting models of distributional data is spatial autocorrelation, which may lead to overly optimistic standard error estimates[36,38]. This is primarily a concern for predictive modelling purposes, which are not a goal of this study. In our data, inspection of correlograms of the binary response variables showed significant positive correlation for lag distances of up to about 300 km, but the positive autocorrelation was effectively reduced in correlograms of the GLMs residuals, indicating that the environmental predictor variables could account for most of the spatial autocorrelation in the response. The latter implies that spatial autocorrelation should not be a concern in our GLMs (ref. 38).

To investigate the change in abundance of individual fish species within the specified Arctic area (Fig. 3 inset map), the abundances in 2004 were subtracted from those of each year in the period 2005–2012. The abundance deviations were plotted by sorting species according to their geographic affinity (average latitude of a species distribution, all years), from south to north (Fig. 3).

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