

# Arctic warming will promote Atlantic–Pacific fish interchange

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**Throughout much of the Quaternary Period, inhospitable environmental conditions above the Arctic Circle have been a formidable barrier separating most marine organisms in the North Atlantic from those in the North Pacific<sup>1,2</sup>. Rapid warming has begun to lift this barrier<sup>3</sup>, potentially facilitating the interchange of marine biota between the two seas<sup>4</sup>. Here, we forecast the potential northward progression of 515 fish species following climate change, and report the rate of potential species interchange between the Atlantic and the Pacific via the Northwest Passage and the Northeast Passage. For this, we projected niche-based models under climate change scenarios and simulated the spread of species through the passages when climatic conditions became suitable. Results reveal a complex range of responses during this century, and accelerated interchange after 2050. By 2100 up to 41 species could enter the Pacific and 44 species could enter the Atlantic, via one or both passages. Consistent with historical and recent biodiversity interchanges<sup>5,6</sup>, this exchange of fish species may trigger changes for biodiversity and food webs in the North Atlantic and North Pacific, with ecological and economic consequences to ecosystems that at present contribute 39% to global marine fish landings.**

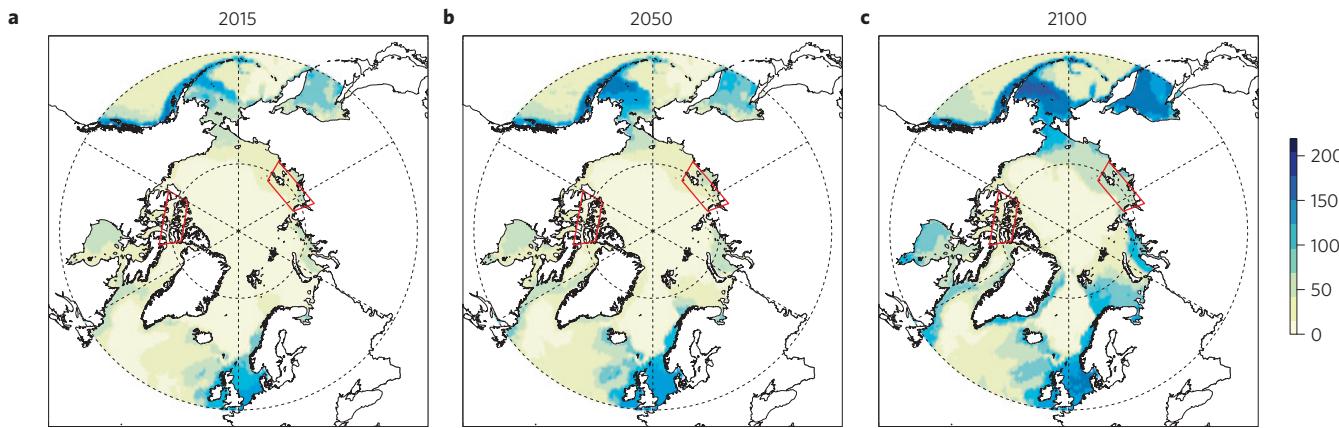
Biotic interchanges begin when barriers (land bridges, mountain ranges, waterways, and so on) existing over geologic timescales are disrupted, allowing the dispersal and exchange of species between historically isolated pools of biodiversity<sup>5</sup>. The interchange of competitors or predators between previously isolated regions can introduce new trophic interactions, resulting in the reorganization of food webs, and declines in local species populations and/or biomass<sup>5,6</sup>. Examples of interchange are known from the fossil record and contemporary marine and terrestrial ecosystems<sup>5</sup>. An illustrative recent example began with the opening of the Suez Canal, which led to the arrival of 55 Red Sea species to the Mediterranean, with a drastic impact on commercial fisheries<sup>6</sup>. The Mediterranean Basin today is dominated in abundance and biomass by non-indigenous species, whereas native species have been driven to near extirpation levels<sup>6</sup>. In contrast, the opening of the freshwater Panama Canal fostered interchange between Pacific and Caribbean watersheds, facilitating an increase in diversity in both freshwater fish faunas, but with no known extirpation of

native species<sup>7</sup>. As yet, the consequences of fish species interchange is poorly understood, especially in the Arctic region, which is a challenge because opportunities for interchange will increase in a warmer future<sup>2</sup>.

Since the initial opening of the Bering Strait in the Pliocene Epoch, perennial Arctic sea ice and cold environmental conditions throughout much of the Quaternary Period prevented many taxa from interchanging between the Pacific and the Atlantic<sup>1–3</sup>. Although suitable conditions may exist for Atlantic species in the North Pacific, and vice versa, inhospitable conditions such as low temperature and low productivity<sup>3</sup> in passages separating the seas are presumed to have been the main barriers maintaining two distinct faunas with limited overlap since the Pliocene Epoch<sup>1,8,9</sup>. Occurrence records (<http://www.iobis.org>) show that at present only 135 out of more than 800 fish species found above 50° of latitude occur on both sides of the passages, and these are from previous openings of the passages during warm periods of the Quaternary Period<sup>10</sup>. Even though arctic sea-ice cover has waxed and waned numerous times since the end of the Pliocene Epoch<sup>4,11</sup>, palaeontological evidence suggests that conditions in high-latitude seas generally limited free biotic interchange between the Atlantic and Pacific during the Quaternary Period<sup>1</sup>, resulting in long-standing isolation of molluscs<sup>1</sup>, diatoms<sup>3</sup> and most fishes<sup>4,10,12</sup>. Nevertheless, shared fish species between Atlantic and Pacific cold waters indicate that previous openings of the passage during warm periods of the Quaternary Period allowed fish interchange<sup>10</sup> (Supplementary Note). Ongoing climate change may result in accelerated Atlantic–Pacific fish interchange within the next century<sup>2</sup>.

The warming of the Arctic in recent decades is well documented<sup>13</sup> and in August 2012 the area of perennial Arctic sea ice was lower than it had been for at least 121 years<sup>14</sup>. Analyses of fisheries data show that the mean temperature of catch is increasing in the Arctic at the same rate as in the boreal ecosystems<sup>15</sup>. The reduction of sea ice is expected to increase currents that can transport propagules in coastal environments<sup>16</sup> and to increase primary production<sup>17</sup>, which could in turn lead to distributional consequences such as northward range shifts across many taxa<sup>18,19</sup>. Together the opening of the Northwest Passage (NW Passage) and the influx of increasingly warmer Atlantic currents through the Northeast

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**Figure 1 | Predicted number of high-latitude fish species in each approximately 50 × 50 km pixel of the Arctic region according to the EC-Earth model, RCP 8.5 scenario.** **a–c,** Results are shown for 2015 (**a**), 2050 (**b**) and 2100 (**c**). 515 species occurring at over 50° N latitude are considered. Numerous high-latitude coastal areas—such as the Svalbard coast, the Barents Sea, western, eastern and southern Iceland, the Faroe Islands, the Alaskan coast, Bering Strait, Eastern Greenland, the Sea of Okhotsk and Hudson Bay—are predicted to be among those to encounter the largest colonization of new fish species that will find suitable future conditions. Red boxes represent the locations of the NW and NE passages. Species at present restricted to one ocean (the North Atlantic or the North Pacific) are predicted to occur in both oceans only if >10% of the intervening passage is covered by suitable habitat for the species. Only species occurring in the NE Atlantic or the Pacific were allowed to cross the NE Passage, and only those occurring in the NW Atlantic or the Pacific were allowed to cross the NW Passage. Results from other models and scenarios are presented in Supplementary Fig. 3.

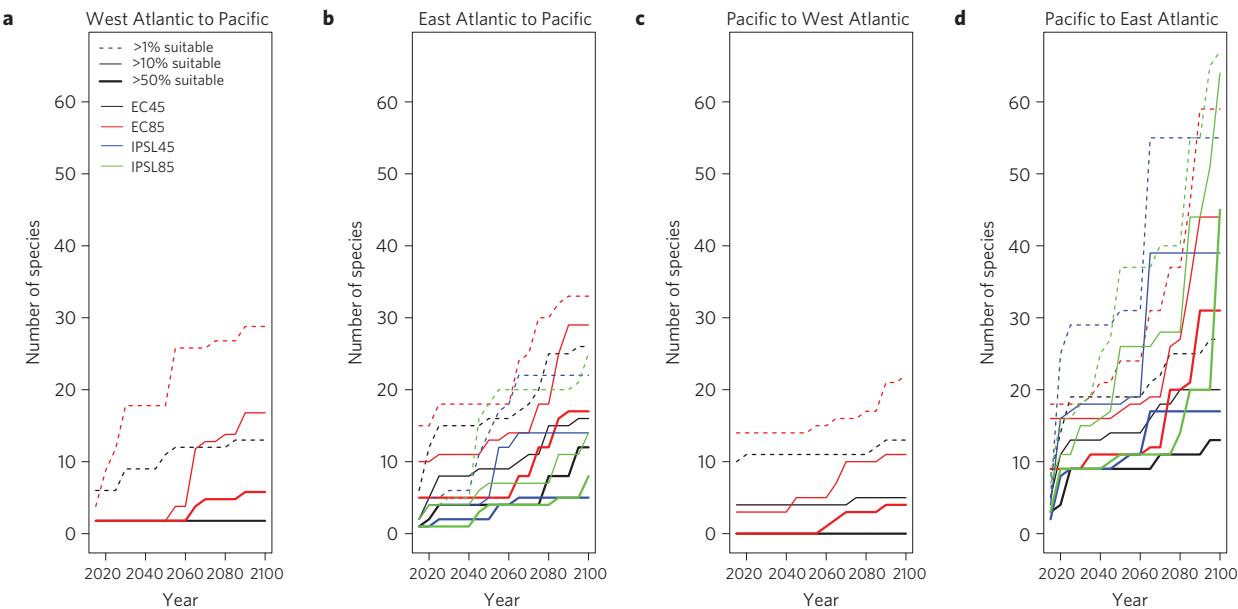
Passage (NE Passage) could facilitate the interchange of marine species between the North Atlantic and the Pacific. Moreover, as the role of the NW and NE passages in fisheries and shipping is likely to increase in the future, maritime industry could play a role in the pace of fish interchange by assisting the colonization of species, for example, during ballast water exchange<sup>20</sup>. On the basis of historical examples<sup>5,6</sup>, one can anticipate that a new Arctic interchange would have a considerable impact on species composition and trophic structure in the low-diversity Arctic ecosystems.

To evaluate the potential interchange of fish species between the North Atlantic and the North Pacific under climate change by 2100, we applied niche-based modelling tools<sup>21</sup>, implemented with fish occurrence records for 515 species (Supplementary Table 2) with sufficient number of occurrences north of 50° N latitude. We matched these records with corresponding monthly oceanographic conditions from two global climate oceanographic models for two different scenarios (moderate and extreme; EC45, EC85, IPSL45, IPSL85) for 2012–2100 (refs 22,23; Supplementary Methods). Niche-based models, as fitted here, fit species' bioclimatic requirements<sup>21</sup> and are well suited to studying species range shifts in the Arctic owing to the strong role of abiotic factors such as sea surface temperature in determining fish range limits<sup>19</sup>. These models predict a value of habitat suitability in each pixel. By assessing the proportion of pixels predicted to be occupied in an area, an overall value of predicted occupancy can be calculated for this area (for example, the NE and NW passages; Supplementary Methods). Overall, our forecasts of fish distributions under climate change (Fig. 1 and Supplementary Fig. 3) forewarn of likely ecosystem restructuring and shifts in diversity in high-latitude locations, which include fragile simple ecosystems such as the Svalbard coasts, where there at present are no recorded non-indigenous marine species<sup>20</sup>. High-latitude changes are already underway and recent years have seen the arrival of new species to, for example, the East Greenland coast<sup>24</sup>, supporting new opportunities for fisheries<sup>25</sup>.

Forecasts of suitability in the NW and NE passages indicate the potential for future mixing of parts of the Atlantic and Pacific species pools as individual species advance to higher latitudes and into the passages (Figs 1 and 2). A sensitivity analysis relating the cumulative number of potentially interchanging species (that is,

non-circumpolar species occurring in the Northeast Atlantic, the Northwest Atlantic or the Pacific, but with suitable future conditions in both oceans and in at least one accessible passage) over time reveals a progressive increase from 2012–2100 (Fig. 2 and Supplementary Fig. 5). By 2050, species will gradually approach the passages, with the majority of these being Pacific species approaching the Atlantic via the NE Passage. The number of species potentially interchanging will increase sharply by 2100 as even more Pacific species and an increasing number of Atlantic species find suitable conditions in both passages (Fig. 2 and Supplementary Fig. 5 and Table 3). Our most conservative interchange scenario (EC-Earth RCP 4.5 and requiring 50% predicted occupancy of an accessible passage) shows that, by 2100, 13 species may reach the Atlantic from the Pacific (all via the NE Passage), while 16 may reach the Pacific from the Atlantic (14 via the NE Passage, 2 via the NW Passage; Supplementary Table 3). A more relaxed version of that scenario (requiring only 10% predicted occupancy) predicts 44 species reaching the Atlantic (all 44 via the NE Passage, 11 via the NW Passage) and 41 (29 via the NE Passage, 17 via the NW Passage) reaching the Pacific via the passages by 2100 (Supplementary Table 3).

The predicted changes in the distributional patterns of species can be expected to introduce new biotic interactions and changes to community composition, potentially resulting in biomass shifts<sup>19</sup>. The Atlantic species potentially advancing into the Pacific via the NE Passage across scenarios were on average larger than those in the existing species pool (for example, EC8.5 10% predicted occupancy scenario, one-way analysis of variance (ANOVA) on log transformed maximum lengths;  $F_{1,167} = 14.7$ ,  $p < 0.001$ ), but the average trophic level did not differ from that of the native fish (for example, EC8.5, 10% interchange threshold scenario native:  $3.50 \pm 0.35$ ; interchanged:  $3.54 \pm 0.40$ ) (Supplementary Fig. 2). The average lengths and trophic levels of species advancing into the Pacific via the NW Passage and the species potentially reaching the Atlantic were not significantly different from the native fish under either of the two scenarios (ANOVA on log transformed maximum lengths and trophic levels, all  $p > 0.05$ ) (Supplementary Methods and Table 1 and Fig. 2). This suggests that interchanging species will mainly introduce a supplement to already existing trophic guilds rather than change the trophic structure or size.



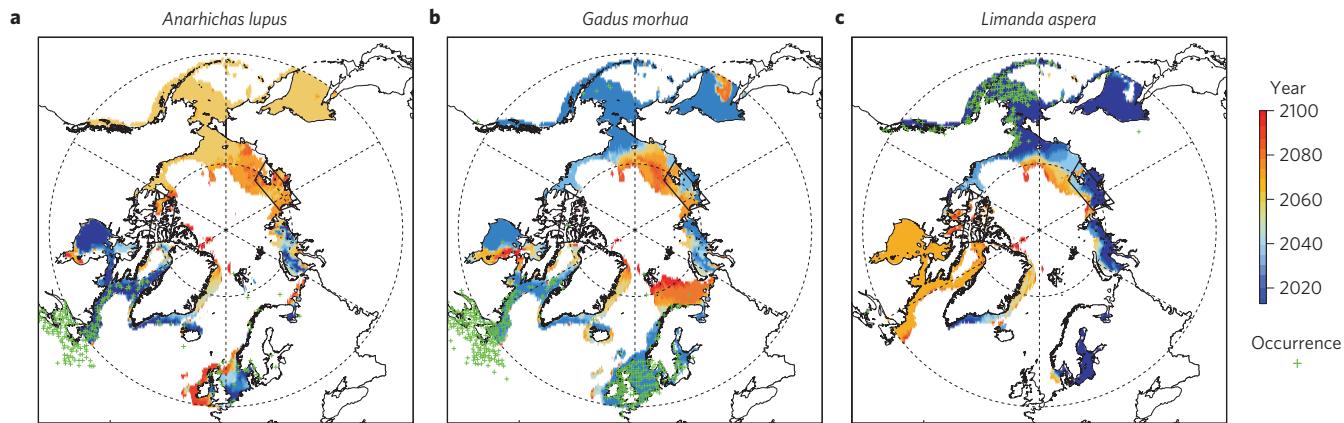
**Figure 2 | Sensitivity analysis of the interchange potential of the NE and NW passages between 2015 and 2100.** **a-d,** The number of species occurring in the NW Atlantic (**a**), the NE Atlantic (**b**) and the N Pacific (**c-d**) but predicted to reach another sea via an accessible intervening Arctic passage are reported. Three scenarios of predicted occupancy within an accessible passage (that is, 1, 10 or 50% covered by suitable conditions) are shown for two oceanographical models (EC-Earth and IPSL) and two climatic scenarios (RCP 4.5 and 8.5). Note that **a** and **c** do not show results from the IPSL model because it does not cover the NW Passage region. Further explanations concerning models and scenarios are presented in Supplementary Methods.

Few apex predators are predicted to be involved in interchange. Notable exceptions are *Gadus morhua* (Atlantic cod) and *Ophiodon elongatus* (Lingcod), which have the potential to dominate ecosystems with top-down effects (Supplementary Methods). Most potentially interchanging species are mid-trophic-level zooplanktivores, benthivores and omnivores (trophic level 3.2–3.7). Moreover, among those on our list of potential interchangers, 59 out of 91 species with known spawning strategy disperse pelagically as eggs, larvae or juveniles (Supplementary Table 5) and thus have the possibility to disperse rapidly on ocean currents to colonize newly suitable habitats as they become available (Supplementary Methods and Fig. 1). Among these, Alaska pollock (*Theragra chalcogramma*; up to 15 million eggs per fish), Atlantic cod (up to 7 million eggs per fish) and Atlantic herring (up to 200,000 eggs per fish) show among the highest reproductive and larval dispersal potential for fishes globally (Supplementary Methods 2.3). In contrast, some of our potential interchangers (that is, 36 out of 91) have few, large eggs, lack pelagic dispersal stages and may thus be slower to colonize new habitats when they become available (Supplementary Table 5). Examples include chondrichthyans and the species-rich genera *Careproctus* and *Lycodes* (Supplementary Table 5). Studies of fish phylogeography and genetic evidence show that both passages were used in the past<sup>4,26</sup>, although quantitative palaeontological evidence, particularly based on marine molluscs, shows that more species crossed the Arctic Ocean from the Pacific to the Atlantic<sup>1</sup>. There is firm evidence that these transfers occurred predominantly via the NW Passage and the northernmost Canadian coast<sup>1</sup>, and indeed, among shell-bearing molluscs, 261 species of the Arctic–Atlantic basin are of Pacific origin whereas only 34 species in the North Pacific are of Atlantic origin<sup>1</sup>. This route is also thought to have been used repeatedly by several fish families, for example, Agonidae, Cottidae, Stichaeidae and Zoarcidae<sup>10,27</sup> (Supplementary Table 4). Our results predict more movement from the Pacific to the Atlantic and suggest that many species will interchange using both passages, with a steep increase in interchange rate via the NE Passage from 2050 (Fig. 2).

Among the species predicted to colonize the NE and NW passages by 2100, ten of these are at present commercial species, including five highly commercial: saffron cod (*Eleginops gracilis*), American plaice (*Hippoglossoides platessoides*), Atlantic cod (*Gadus morhua*), yellowfin sole (*Limanda aspera*) and the Atlantic wolffish (*Anarhichas lupus*; Fig. 3 and Supplementary Fig. 4). The NW Passage does not yet support commercial fisheries, nor do the Laptev and Siberian Seas<sup>12</sup>, but climate change may yield additional opportunities for high-latitude fisheries in the future. New high-latitude fishing opportunities have already emerged; for example, Atlantic mackerel fisheries developed soon after the arrival of the species to Eastern Greenland, with 53,000 tons caught in 2013, and there are plans to extend fishing during 2014 to Greenland's west coast<sup>25</sup>. Care will be needed in fishing these high-latitude stocks, as they are likely to be very vulnerable to overexploitation<sup>12</sup>.

Fishes have been documented to have already responded to climate change by a general movement to higher latitudes<sup>15</sup>, including the Arctic<sup>12,24,25</sup>, demonstrating their capacity to track suitable climatic conditions, as assumed in this study. Fully accounting for spawning and dispersal mechanisms, interactions between species, as well as food-web changes will be important next steps to predict future community changes (Supplementary Methods)<sup>18</sup>. As distributional shifts are not predicted to be synchronized across species (Fig. 3), consistent with the expectation that each species will respond distinctly to environmental changes<sup>21</sup>, forecasting the dynamic shift in the food-web balance following species interchange<sup>18,28</sup> is the next modelling challenge.

As perennial sea ice retracts and sea temperature increases in the Arctic seas, niche-based models predict that an increasing number of fish species will find suitable conditions in both the north Atlantic and the Pacific and the intervening Arctic passages, facilitating interchanges. These results are consistent with poleward shifts detected in the distribution of fishes and other marine taxa with recent climate change<sup>15,19,29</sup>. Our predictions are of potential changes and interchange, but actual changes will depend on the food new species encounter, the predators that they may encounter and on the adaption mechanisms the species may be able to develop.



**Figure 3 | The prediction of suitable environmental conditions for three commercial species over time.** **a–c**, Colours indicate the forecasted year in which conditions become suitable for Atlantic wolffish (*Anarhichas lupus*; **a**), Atlantic cod (*Gadus morhua*; **b**) and Yellowfin sole (*Limanda aspera*; **c**). Continuous predictions of probability of occurrence in pixels were converted to binary presence-absence predictions for the seas above 50° N using the threshold that maximized the true skills statistic. Predictions are based on the EC-Earth RCP8.5 scenario, assuming a minimum of 10% predicted occupancy in an accessible intervening passage. Results from other scenarios are presented in Supplementary Fig. 4.

Arctic warming is expected to continue beyond 2100, thus one can expect that the extent of faunal interchange will continue to increase and continue to promote important marine ecosystem changes in this region also beyond the next century.

## Methods

Using a global database of dated fish occurrence records and spatially explicit variables representing oceanographic conditions for the period 1948–2012, we built niche-based models for each species and forecasted changes in suitable habitat conditions in the NW and NE passages, the North Atlantic and the North Pacific every five years from 2015 to 2100. These niche-based models fit statistical relationships between species' occurrences and environmental variables to define each species' realized niche and to project them in space and time according to scenarios of marine climate change (Supplementary Methods). Here, our variables were derived from dynamic oceanographic and climate models (1948–2100) and matched to the distinct month within the year of each observation (Supplementary Methods). To reduce the chance of unrealistic dispersal we constrained predictions so that species restricted to the Northeast or Northwest Atlantic could enter only the nearest intervening passage (Supplementary Methods) and further spread to the adjacent ocean only when conditions become favourable to the species in the passages (see interchange potential scenarios hereafter).

**Environmental data.** Ocean environmental data were extracted in part from a forced ocean hind-cast simulation using known and atmospheric forcing (1948–2012) and from two different climate models (EC-Earth and IPSLCM5A-LR) assuming two different emission scenarios RCP 4.5 (moderate) and 8.5 (high) from 2006 to 2100 (see Supplementary Methods). Here, the simulations provide monthly values for the years 1948–2100 for salinity, surface and bottom temperature, and currents (summarized as the barotropic stream function), which have been applied for a product also used in other studies of high-latitude marine ecosystems<sup>20,23</sup>. We interpolated grid cells to 0.5 × 0.5 decimal degrees (~50 × 50 km) and based our analyses on the following environmental predictors based on monthly averages: mean annual bottom temperature, minimum springtime surface temperature, annual maximum surface temperature and minimum springtime surface salinity. The spring temperatures were defined as March–May, as this is the period when light returns to the Arctic, triggering many marine ecological events, including fish spawning. In Arctic conditions, low salinity can provide warm refugia for some species when ice is formed<sup>26,30</sup>. Further to this, we included a bathymetric map derived from the National Oceanic and Atmospheric Administration.

**Fish occurrence data.** We downloaded locality records from the entire geographic range of each fish species occurring north of 50° N from the Ocean Biogeographic Information System (<http://www.iobis.org>) and the Global Biodiversity Information Facility (<http://www.gbif.org>) on 10 January 2013. Some species were represented by thousands of records, especially in commonly sampled areas, and species occurring in fewer than 50 of our 50 × 50 km grid cells were not included in the analysis. Each species was categorized into one or more of the following: Northeast Atlantic, Northwest Atlantic, or Pacific on the

basis of the geographic descriptions documented in FishBase (<http://www.fishbase.org>). We removed spatially redundant occurrences of the same species (that is, occurrences that were less than 10 km apart from neighbouring occurrences) to avoid the spurious effects of spatial autocorrelation. As environmental variables were available for each year (1948–2100), we associated environmental values to each record based on the recorded date of observation. Given that no environmental GIS layers were available before 1948, we removed records before this date from the analyses.

**Niche-based modelling.** Distributions of the 515 species were modelled using niche-based methods; among these, 118 species occur in both the North Pacific and the North Atlantic. We used an ensemble forecasting approach embedded in the modelling package biomod2 in R by combining the predictions of four modelling techniques (see Supplementary Methods). For each species and each five-year time interval, continuous predictions of probability of occurrence in pixels were converted to binary presence-absence predictions for the seas above 50° N using the threshold that maximized the true skills statistic. We defined the NW and NE passages as a rectangular area bounded by latitudes 72° N to 77° N and longitudes 120° W to 80° W in the NW Passage and latitudes 72° N to 77° N and longitudes 110° E to 150° E in the NE Passage; see Fig. 1). We counted the number of species, at a given time, for which the NW and NE passages were potentially suitable for interchange. Interchange potential was determined by the predicted occupancy—that is, the availability and amount of suitable habitat within each passage. We performed a sensitivity analysis for the scenarios to compute the number of species with suitable habitat in both seas and with various portions of predicted occupancy within the passages (1, 10 or 50% predicted occupancy). Potential changes to the community and trophic structure of the Pacific and Atlantic fish assemblages were evaluated by assessing the maximum length and fractional trophic level of the native and interchanged species, together with their impact in their native ecosystems (Supplementary Methods).

Received 23 May 2014; accepted 15 December 2014;  
published online 26 January 2015

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## Acknowledgements

The study was carried out with financial support from the Danish Agency for Science, Technology and Innovation as part of the Greenland Climate Research Centre. Support was provided by NACLIM (EU-FP7 GA n.308299), the NAACOS project (DK) to S.M.O., the Canada Excellence Research Chair, and is a contribution to the Arctic Science Partnership. We thank J. Oakley, K. Steenken and E. Shanley-Roberts for improving the manuscript.

## Author contributions

M.S.W. conceived the initial idea and designed the study with the entire co-author team. P.G., R.B.H., P.R.M., L.P. and M.S.W. gathered data on fish distribution and traits. All taxonomic affiliations were confirmed by Arctic fish taxonomist P.R.M. O.B. ran the niche-based models and analyses of sensitivity, with conceptual help from A.G. P.G. and L.P. ran the functional analyses, while P.R.M. led the compilation of historical evidence. S.M.O. and D.S. (polar oceanographers) and M.S.W. provided oceanographic and environmental data. All co-authors contributed to the text and interpretation of the results.

## 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](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to M.S.W.

## Competing financial interests

The authors declare no competing financial interests.