Dispersal routes of marine range expansions into the Arctic

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As a result of ocean warming, the species composition of Arctic habitats has begun to shift in an Atlantic direction. One ecosystem exposed to such a change is the Arctic Northeast Greenland shelf. However, the dispersal route taken by boreal fauna to this area is unknown. This knowledge is essential to predict to what extent boreal biota will dominate and alter Arctic ecosystems. We show that Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*), and deep-sea shrimp (*Pandalus borealis*) specimens recently found on the Northeast Greenland shelf originate from the Barents Sea, and suggest that a likely dispersal route is via advection across the Fram Strait. Our results indicate that boreal invasions of Arctic habitats can be driven by the dispersal of pelagic offspring, and that the fauna of the Barents Sea can project into adjacent habitats with unknown consequences to the structure and function of putatively isolated Arctic communities.

Introduction

The Arctic is warming more rapidly than any other geographical region[1]. Increases in water temperature and loss of sea-ice[2,3] are expected to induce a northward expansion of boreal fauna[4–6], a phenomenon that is already apparent in the Barents Sea[7–9]. Atlantic mackerel (*Scomber scombrus*) exemplifies this trend, having recently displayed an exceptional northward shift in distribution to Spitsbergen[10]. Such predatory newcomers and competitors pose a genuine threat to native Arctic fauna and thus to Arctic ecosystems, as they may restructure trophic relationships[8,11,12].

In 2015 and 2017, boreal species, i.e. juvenile Atlantic cod (*Gadus morhua*), juvenile beaked redfish (*Sebastes mentella*), and adult deep-sea shrimp (*Pandalus borealis*), were observed on the Northeast (NE) Greenland shelf (latitudes 74–77 °N, Fig. 1) for the first time since surveying began in 2002[13]. This was well outside of their known distribution ranges[4,14,15] (Fig. 2a,d,g). However, the route by which the three species had reached NE Greenland was unknown. The present study aims to determine their population of origin using genetic markers. This knowledge will allow us to infer the dispersal routes taken by these species – information that is important to forecast (e.g. [5]) which species will likely ensue, and to what extent boreal fauna will modify Arctic habitats[16].

We consider two main routes of dispersal to NE Greenland, either 1) via migration against the East Greenland Current[17] from Iceland, or 2) via advection[18] from the Barents Sea by the westbound Return Atlantic Current[17,19,20] (Fig. 1) across the abyssal plains of the Fram Strait. The Norwegian Atlantic Current, along the Norwegian coast, and the West Spitsbergen Current[17,20], along the Barents Sea shelf-break, are already known to result in the advection of cod, redfish, and shrimp offspring from the Norwegian coast and the Barents Sea proper to Spitsbergen, east of the Fram Strait[21–23].

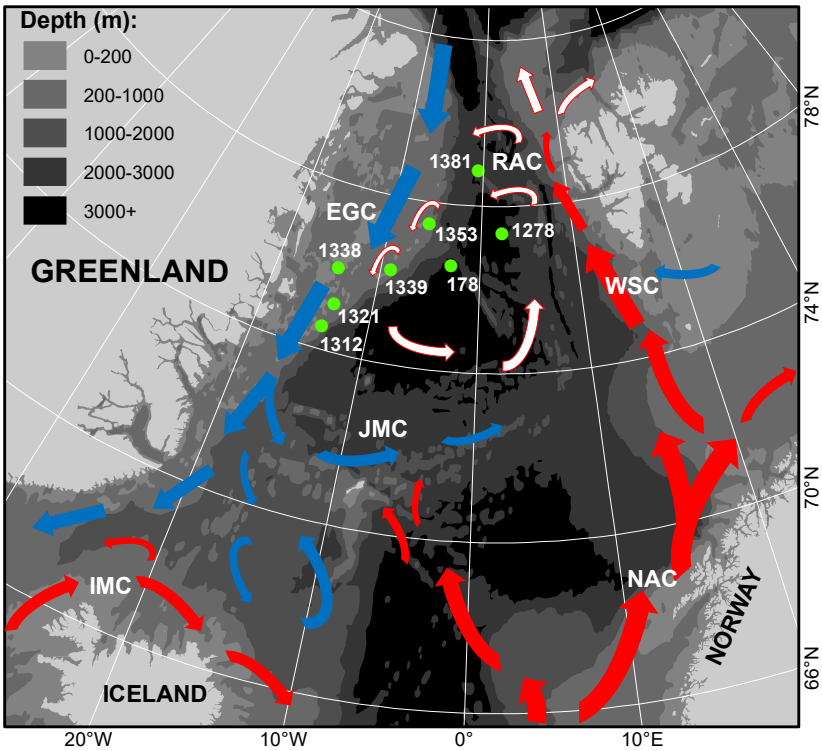

Fig. 1. Stations (green full circles) of observation for Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis*) (Methods, Table 1). Arrows indicate ocean currents (Source[17,24]). Atlantic surface currents (red arrows): IMC (Irminger Current), NAC (Norwegian Atlantic Current), WSC (West Spitsbergen Current), RAC (Return Atlantic Current). Atlantic sub-surface water (white arrows). Arctic surface currents (blue arrows): EGC (East Greenland Current), JMC (Jan Mayen Current). Arrow size indicates velocity. Map created using ESRI ArcMap (v. 10.6, www.arcgis.com).

Results

We find that all cod (n = 10), and 95% of redfish (n = 61 out of 64) caught on either the NE Greenland shelf or in the Fram Strait, are genetically assigned to the Barents Sea North East Arctic Cod (NEAC) population (Fig. 2c), and Norwegian Shallow (NSH) redfish population (Fig. 2f), respectively. All shrimp (n = 40) caught on the NE Greenland shelf, are genetically assigned to the Spitsbergen West (SPW) shrimp population (Fig. 2i). Assignment with STRUCTURE was supported by high membership probabilities (q >0.8), which suggests that the three species on the NE Greenland shelf are likely to originate from the Barents Sea.

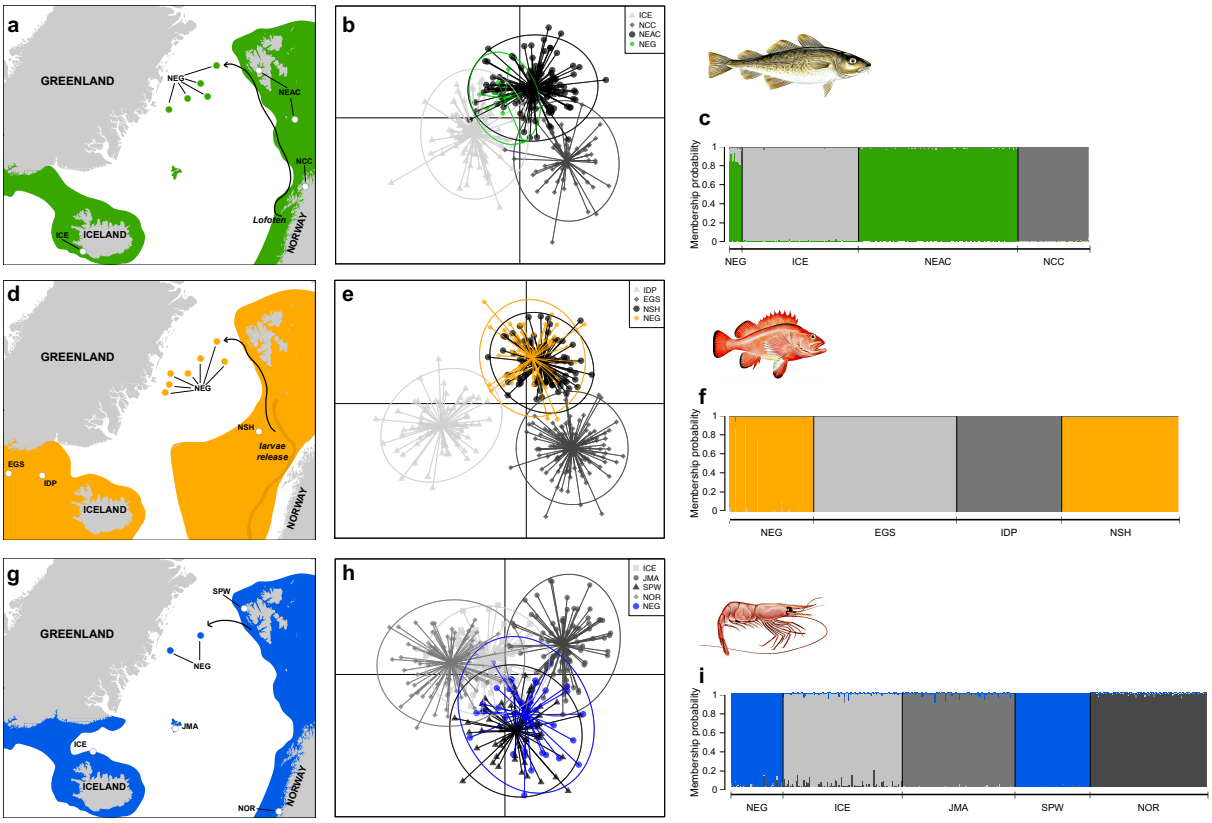

Fig. 2. Genetic evidence of Atlantic cod (*Gadus morhua)* (**a**, **b**, **c**), beaked redfish (*Sebastes mentella)* (**d**, **e**, **f**) and deep-sea shrimp (*Pandalus borealis)* (**g**, **h**, **i**) specimens found off Northeast Greenland originating from the Barents Sea. Maps (**a**, **d**, **g**) show species known distribution extent (shaded colours) in the Northeast Atlantic, catch sites of individuals in Northeast Greenland (NEG) waters (full circles), reference samples (hollow circles) and a proposed dispersal route (arrow). DAPC scatterplots (**b**, **e**, **h**) show how the NEG groups relate to the reference populations of the Northeast Atlantic Ocean. DAPC cluster ellipses were set to contain 95% of genotypes. DAPC scatterplots explain 94% (**b**), 92% (**e**) and 97% (**h**) of the total variation observed. STRUCTURE barplots (**c**, **f**, **i**) show membership probabilities (q) for NEG individuals based on the reference populations used. For abbreviations refer to Methods Table 2. Maps were created using ESRI ArcMap (v. 10.6, www.arcgis.com).

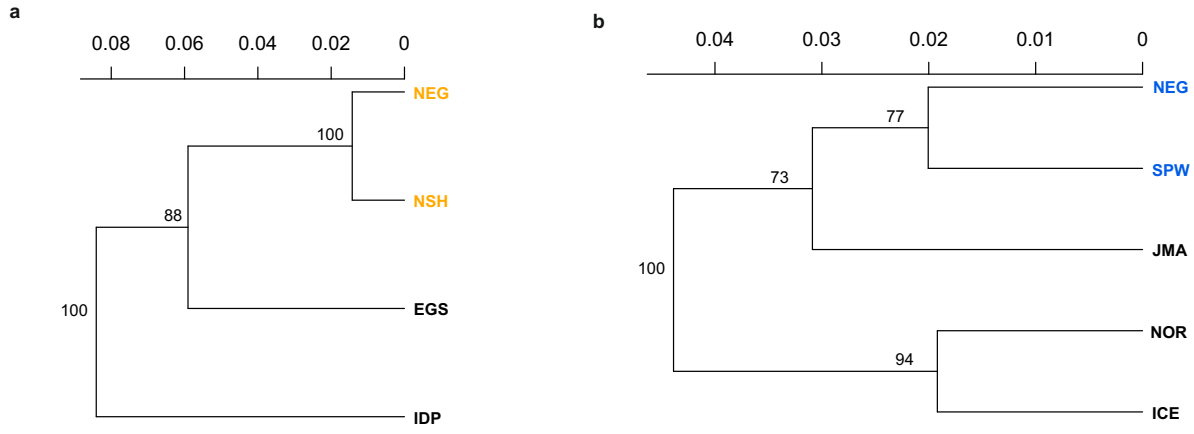

Fig. 3. Neighbour-joining trees utilising Nei's distance, for beaked redfish (*Sebastes mentella*) (**a**) and deep-sea shrimp (*Pandalus borealis*) (**b**) NE Greenland (NEG) groups and reference populations. For abbreviations refer to Methods Table 2. Bootstrap values (>88% and >73%) on both trees suggest good reproducibility

There was high consistency in the inferred population of origin between the assignment methods (STRUCTURE and *snapclust*), where 90% of cod, 98% of redfish and 75% of shrimp formed a consensus (Supplementary S5, Table S5). All individuals of these three species were assigned with a greater probability to populations in the Barents Sea than from any other location. The exception was three out of 64 (5%) redfish individuals (Supplementary S5, Table S5.2).

Discriminant Analysis of Principle Components (DAPC) strongly support the assignment results by clustering the NE Greenland specimens with the corresponding Barents Sea populations (Fig. 2b,e,h). The 95% DAPC cluster ellipses between NE Greenland and the population clusters overlapped considerably, though overlap was also evident between the reference populations, most significantly for the cod and shrimp clusters. The redfish and shrimp neighbour-joining tree's resulted in the same grouping as the assignment and DAPC analyses, and report a Nei's Distance of <0.02 between the redfish caught in NE Greenland and the Norwegian Shallow population (Fig. 3a). Nei's Distance was comparatively low (0.02) between the Norwegian and Icelandic shrimp reference populations as between the shrimp specimens of NE Greenland and the Spitsbergen West population (Fig. 3b).

Discussion

Our results show that the NE Greenland shelf is readily reached by cod, redfish and shrimp from the Barents Sea, probably advected across the Fram Strait by the Return Atlantic Current, supporting recent simulation studies[25–27]. Advection plays an important role in the northward transport of plankton in the Barents Sea, via the West Spitsbergen Current[18] and because up to 50% of this water is estimated to cross the Fram Strait[28–30], the Return Atlantic Current provides a connection between the Barents Sea and the NE Greenland shelf ecosystems. The inflow of Atlantic water to the Barents Sea has doubled since 1980[31], resulting in an increase in the West Spitsbergen Current temperature[32]. Hence, there is reason to believe that the faunal connection across the Fram Strait has tightened concordantly in recent years.

While the NE Greenland shelf is dominated by Arctic water carried southward by the East Greenland Current, higher temperatures may explain declining sea-ice[2,3], and the occurrence of boreal species such as cod, redfish and shrimp, along the NE Greenland shelf and shelf break. The copepod *Calanus finmarchicus* is the major prey for young cod[33] and its abundance during the last warm period in the North Atlantic (1920–1965) has likely driven the range expansion of cod and other boreal species[34]. Low abundances of *Calanus finmarchicus* were observed on the NE Greenland shelf in autumn 2006[35], but in light of the West Spitsbergen Current warming, its abundane will likely increase in the Fram Strait and on the NE Greenland shelf in the future[36], thus providing ample food for boreal predators.

North East Arctic Cod (NEAC), the population of origin for the NE Greenland specimens, spawns along the Norwegian coast[37] (latitudes 62–71 °N) during March and April where pelagic offspring drift by surface currents[38] northwards and eastwards into the Barents Sea[39]. Depending on local wind-forcing, up to 1/3 of 0-group year-classes may advect off the Norwegian and Barents Sea shelf and disperse over the Norwegian Sea[38]. Our results suggest that 0-group cod advected off the shelf by wind-forcing[27,40] either outside of their spawning grounds, or at any point until their northern-most report west of Spitsbergen[21], are likely to cross the Fram Strait by the Return Atlantic Current (Fig. 2a). By October, when cod are >80 mm in total length (TL), they gain motility, descend out of the pelagic layer, and become demersal[42]. Therefore, for

our theory to hold true, 0-group cod from the Norwegian coast/Barents Sea must advect to the NE Greenland shelf by October of their spawning year. The observations of 0-group cod off the NE Greenland shelf with a genetic signature of the NEAC population, in September 2007 and 2017, demonstrate that this is happening.

Redfish larvae are extruded along the continental shelf break of the Norwegian and Barents Seas from latitudes 64–74 °N between March and June[42]. Redfish larvae have been observed in Atlantic water west of the continental shelf, and as far north as Spitsbergen[23,43]. We observed large numbers of 0-group redfish over the Fram Strait with a genetic signature of the Norwegian Shallow population. Juvenile redfish are pelagic until 40–50 mm TL at age 4–5 months when they gain motility and descend to deeper waters[44]. We propose that the 0-group redfish found over the Fram Strait in September 2017 were advected north to Spitsbergen along the shelf break by the West Spitsbergen Current, before crossing the Fram Strait by the Return Atlantic Current. The juvenile redfish had then reached the NE Greenland shelf along this route (Fig. 2d) by the time they were 4–5 months old.

Shrimp on the NE Greenland shelf also originated from the Barents Sea (see sampling of [27]). Shrimp spawn in autumn throughout the Barents Sea and the meroplanktonic larvae hatch in spring. Shrimp larvae are highly-mobile, distributed according to currents until 2–3 months of age when they settle as post-larvae[14]. We find it more likely that shrimp larvae from the north-west Barents Sea, i.e. Spitsbergen, will reach the NE Greenland shelf than larvae from the northern Norwegian Coast or central-eastern Barents Sea, due to Spitsbergen's close proximity to the Return Atlantic Current connection (Fig. 2g).

The NE Greenland shelf ecosystem is severely understudied and biodiversity baselines are fragmentary with no timeline[45]. It is therefore difficult to establish whether our findings reflect a recent shift driven by ocean warming or constitute a common component of the NE Greenland Shelf fauna. Nonetheless, the Barents Sea is the most productive ecosystem in the NE Atlantic[47] and presently supports the historically largest cod population[41]. In addition, Atlantic herring (*Clupea harengus*), Atlantic haddock (*Melanogrammus aeglefinus*) and Atlantic mackerel (*Scomber*

scombrus) are nowadays abundant in Spitsbergen waters. Therefore, in the future we could expect to find more boreal species on the NE Greenland shelf, exemplified by a recent observation of capelin (*Mallotus villosus*) in this area[13]. The three species studied herein are clearly not exceptional in being capable of entering the NE Greenland shelf. A recent simulation study[27] demonstrates that between 2.4% and 12% of 0-group NEAC may be transported northwest along the proposed route (Fig. 2a). Advection has therefore the potential to restructure Arctic ecosystems[18] and the route identified here suggests that a boreal faunal invasion of NE Greenland shelf from the Barents Sea is plausible. As a result, trophic relationships are likely to be strongly modified[12] as boreal generalists such as cod is favoured by climate scenarios[5]. Cod feeds on polar cod (*Boreogadus saida*), Arctic seabed fishes and zoobenthos[11], and as a figurehead of boreal range expansions into the Arctic, gives a glimpse of what is to come for native Arctic fauna.

This is the first report to disclose the genetic origin of boreal species in Arctic waters and the connection between Atlantic and Arctic ecosystems. Our findings support the hypothesis that cod, redfish, and shrimp indeed disperse from the Barents Sea across the Fram Strait to the NE Greenland shelf. Due to a lack of time series, we cannot conclude if this is a new phenomenon, or not. In any case, predators and food competitors from lower latitudes alter trophic relationships and impact native Arctic fauna and, with a warming ocean in mind, we suggest that the NE Greenland shelf is likely to become invaded by a larger proportion of Atlantic species.

Methods

Specimens of juvenile cod (*Gadus morhua*, *n* = 7, body weight [bw]: 206–762 g), juvenile redfish (*Sebastes mentella*, *n* = 32, bw: 12–82 g), and adult shrimp (*Pandalus borealis*, *n* = 40) were caught via bottom trawl (c.f.[14]) from 2007 to 2017 on the Northeast (NE) Greenland shelf (latitudes 74–79 °N), well outside of their known distributional range (Table 1). In addition, 0-group cod (*n* = 3) and 0-group redfish (*n* = 32) were caught via mid-water trawls ("Harstad" trawl, ~20 min, ~3 Knots) over the Fram Strait (Table 1) and are included in the analysis to support dispersal route hypotheses. Gill or muscle tissue samples from each specimen were preserved at sea

in 96% ethanol and stored at -20 °C until further processing. Sampling was conducted using the R/V *Helmer Hanssen* as part of the TUNU-Programme[47]. A subset of (0-group) redfish and shrimp was used for genotyping, otherwise, genotyped individuals represent all specimens caught in the area.

Table 1. Details of assignment samples for each species. Station: p = Pelagic, b = Bottom, Year/Month = time of sampling. Totals for each species represent the number of genotyped individuals. Mean temp. = *in situ* sampling temperature obtained from CTD-sensor (Seabird 911).

Station #	Latitude	Longitude	Year	Month	Mean temp. (°C)	Mean depth (m)	Cod	Redfish	Shrimp
178 p	76.55N	03.03W	2007	10	2.0	29	1	-	-
1312 b	74.33N	14.08W	2015	8	1.8	300	-	11	-
1321 b	75.09N	13.38W	2015	8	1.1	213	5	2	-
1339 b	76.14N	09.03W	2015	8	1.6	280	1	7	-
1353 b	77.28N	05.49W	2015	8	0.3	385	1	11	7
1278 p	77.37N	02.24E	2017	9	5.6	34	-	16	-
1338 b	76.00N	14.18W	2017	9	0.1	350	-	1	33
1381 p	78.86N	00.63W	2017	9	1.2	26	2	16	-
Genotyped individuals in total							10	64	40

Genotyped reference populations (Table 2) for the Northeast Atlantic were obtained from several studies[16,26,48]. To ensure the major populations of each species in the Northeast Atlantic were well represented, the cod reference populations were supplemented by genotyping a representative cod population from Iceland, following the same procedure as listed below.

Table 2. Details of reference samples for each species. Abbr. = the abbreviated population name, Year/Month = time of sampling. *n* = sample size (number of genotyped individuals).

Species	Population	Abbr.	Year	Month	*n*	Latitude	Longitude
Cod	Iceland	ICE	2013	4	93	63.57N	20.61W
	Norwegian Coastal Cod	NCC	2002	4	86	69.30N	18.65E
	North East Arctic Cod	NEAC	2005	12	47	74.10N	21.10E
	North East Arctic Cod	NEAC	2001	12	90	78.22N	14.65E
Redfish	Iceland Deep	IDP	2012	8	87	65.46N	30.39W
	South East Greenland Slope	EGS	2011	3	133	64.24N	35.14W
	Norway Shallow	NSH	2006	10	91	72.18N	10.25E
Shrimp	Iceland	ICE	2011	7	92	67.28N	22.67W
	Jan Mayen Island	JMA	2011	10	88	70.61N	08.43W
	Norway	NOR	2010	10	94	64.75N	11.10E
	Spitsbergen West	SPW	2010	8	85	79.51N	10.29E

DNA was isolated from ethanol-fixed gill or muscle tissue using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) or the E-Z 96 Tissue DNA Kit (Omega Bio-Tek Inc., Norcross, GA, USA) following the manufacturer's instructions.

Microsatellite loci were arranged in multiplexes (Supplementary Table S1), and amplified using polymerase chain reaction (PCR). PCR reactions (2.5 µL) contained ca. 1 x Qiagen Multiplex Master Mix, 0.1–1.0 µm primer, and 15–25 ng DNA. The 5′ end on the forward primers was labelled with a fluorescent dye by the manufacturer (Applied Biosystems, Foster City, CA, USA). Amplification was performed in a GeneAmp 2700 or 9700 thermal cycler (Applied Biosystems). PCR profiles were applied as per published protocols[16,48,49] (Supplementary S1). PCR products were separated using an ABI 3130XL sequencer and GeneScan 500-LIZ (Applied Biosystems) was used as internal size standard. Alleles were automatically binned using GENEMAPPER software (v. 3.7, Applied Biosystems) and double-checked manually. Negative controls employed for extraction, amplification and fragmentation reported no contamination between samples. Replicates (33%) reported the repeatability and consistency of genotyping to be 100%.

Prior to analysis, reference genotypes that showed no amplification in >10% of loci were removed. This achieved amplification success >98% for each locus. All microsatellite loci were assessed for the presence of potential scoring errors, deviation from Hardy-Weinberg equilibrium (HWE), and non-neutrality (Supplementary S1). As the presence of scoring errors such as null alleles may introduce ambiguity around the true origin of the NE Greenland specimens, we ran analyses under two conditions, (1) removing loci showing potential scoring errors, and (2) inclusive of all loci (Supplementary S1, Table S1). This enabled us to retain loci subject to potential scoring errors where both conditions produced concurrent results, and to therefore minimise the loss of statistical power.

To increase the power of assignment (see Supplementary S2 for evaluation), only individuals with membership coefficients (q) lower/higher than 0.2/0.8 were used to establish reference population datasets (c.f. [50], Supplementary S3, Table S3). As weak population differentiation was expected within all datasets, we adopted a conservative approach to infer q[51] using a no-admixture model as implemented in the

Bayesian clustering method, STRUCTURE (v.2.3.4)[52]. This approach has been shown not to bias the true structuring in datasets with weak genetic differentiation[51]. STRUCTURE was run assuming no admixture (NOADMIX = 1), correlated allele frequencies (FREQSCORR = 1) and utilising locality data (LOCPRIOR = 1). The program was run using K = number of reference populations, for 10 iterations, each with a burn-in period and MCMC replicates of 500,000. CLUMPAK[53] was used to merge runs (merged barplots: Supplementary S3, Fig. S3), and reported similarity scores >0.95.

STRUCTURE was employed as the principle tool to assign the NE Greenland individuals to previously identified populations. For this, STRUCTURE was run under the assignment mode (POPFLAG = 1), and assumed no admixture (NOADMIX = 1), correlated allele frequencies (FREQSCORR = 1) and utilised locality data (LOCPRIOR = 1). The program was run using K = number of reference populations, for 10 iterations, each with a burn-in period and MCMC replicates of 500,000. CLUMPAK reported run similarity scores >0.95. STRUCTURE barplots were visualised in R (v. 3.2.3)[54] using the *pophelper* package (v. 2.2.5)[55].

The maximum-likelihood clustering tool *snapclust*[56], within the R package *adegenet* (v. 2.1.1)[57], was used to corroborate the membership probabilities output by STRUCTURE. The function `snapclust` was run without optimization, and priors for the NE Greenland individuals were set to the reference population identified by STRUCTURE as the most probable origin. Runs used zero iterations (max.iter = 0) and membership coefficients were interpreted as output.

As an exploratory tool, Discriminant Analysis of Principle Components (DAPC)[58], within the R package *adegenet*, was used to explore how the NE Greenland individuals relate to the reference populations. DAPC is a geometric clustering method free of HWE and linkage disequilibrium (LD) assumptions, that attempts to maximise the inter-variation between clusters while minimising the intra-variation observed within clusters.

DAPC clusters were set *a priori* to the number of reference populations plus one, including NE Greenland individuals as part of the DAPC model. The `x.val` function indicated the number of principle components (PC's) to retain, but when this method resulted in the selection of too many PC's, which would lead to overfitting, the `optim.a.score` function was preferred, based on an initial selection of all PC's before refinement. All discriminant functions were retained due to the few clusters present (c.f. [57]).

To identify the genetic distance between the NE Greenland individuals and reference populations, neighbour-joining trees were produced using the `aboot` function in the R package *poppr* (v. 2.3.0)[59]. This method utilised Nei's Distance[60] and 1000 bootstrap replicates. Due to the small sample size of NE Greenland cod, neighbour-joining trees were only produced for redfish (n = 64) and shrimp (n = 40) data.

Pre-analysis testing where loci subject to potential scoring errors were removed from analyses resulted in the same outcome as analysis retaining all loci (Supplementary S4). We therefore suggest that potential scoring errors had little impact on assignment and thus present our analyses utilising all loci available.

References

1. IPCC Intergovernmental Panel on Climate Change. *Climate Change 2013: The Physical Science Basis*. Working Group II Contribution to the IPCC 5th Assessment Report (2013).
2. Polyakov, I.V., Pnyushkov, A.V., Alkire, M.B., Ashik, I.M., Baumann, T.M., Carmack, E.C., Goszczko, I., Guthrie, J., Ivanov, V.V., Kanzow, T. & Krishfield, R. Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science* **356**(6335), 285-291 (2017).
3. Smedsrud, L.H., Halvorsen, M.H., Stroeve, J.C., Zhang, R. & Kloster, K. Fram Strait sea ice export variability and September Arctic sea ice extent over the last 80 years. *The Cryosphere* **11**(1), 65-79 (2017).
4. Drinkwater, K.F. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science* **62**(7), 1327-1337 (2005).
5. Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R.E.G., Zeller, D. & Pauly, D. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16**(1), 24-35 (2010).
6. Hollowed, A.B., Planque, B. & Loeng, H. Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. *Fisheries Oceanography* **22**, 355-370 (2013).

7. Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M. & Dolgov, A.V. Recent warming leads to rapid borealization of fish communities in the Arctic. *Nature Climate Change* **5**, 673-678 (2015).
8. Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V. & Aschan, M. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B* **282**(1814), 20151546 (2015).
9. Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E.H., Høines, Å.S., Hoel, A.H., Ingvaldsen, R.B., Jørgensen, L.L., Knutsen, T. & Loeng, H. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fisheries Research* **188**, 38-57 (2017).
10. Mecklenburg, C.W., Lynghammar, A., Johannesen, E., Byrkjedal, I., Christiansen, J.S., Dolgov, A.V., Karamushko, O.V., Møller, P.R., Steinke, D. & Wienerroither, R.M. *Marine Fishes of the Arctic Region Volume 1*. Conservation of Arctic Flora and Fauna (2018).
11. Christiansen, J.S. No future for Euro-Arctic ocean fishes?. *Marine Ecology Progress Series* **575**, 217-227 (2017).
12. Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A.V., Fossheim, M. & Aschan, M.M. Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences* **114**(46), 12202-12207 (2017).
13. Christiansen, J.S., Bonsdorff, E., Byrkjedal, I., Fevolden, S.E., Karamushko, O.V., Lynghammar, A., Mecklenburg, C.W., Møller, P.D., Nielsen, J., Nordström, M.C. & Præbel, K. Novel biodiversity baselines outpace models of fish distribution in Arctic waters. *The Science of Nature* **103**, 8 (2016).
14. Bergström, B.I. The biology of *Pandalus*. *Advances in Marine Biology* **38**, 55-245 (2000).
15. Saha, A., Johansen, T., Hedeholm, R., Nielsen, E.E., Westgaard, J.I., Hauser, L., Planque, B., Cadrin, S.X. & Boje, J. Geographic extent of introgression in *Sebastes mentella* and its effect on genetic population structure. *Evolutionary Applications* **10**(1), 77-90 (2017).
16. Murphy, E.J., Cavanagh, R.D., Drinkwater, K.F., Grant, S.M., Heymans, J.J., Hofmann, E.E., Hunt Jr, G.L. & Johnston, N.M. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. *Proceedings of the Royal Society B* **283**, 20161646 (2016).
17. Håvik, L., Pickart, R.S., Våge, K., Torres, D., Thurnherr, A.M., Beszczynska-Möller, A., Walczowski, W. & von Appen, W.J. Evolution of the East Greenland current from Fram Strait to Denmark strait: synoptic measurements from summer 2012. *Journal of Geophysical Research*: *Oceans* **122**(3), 1974-1994 (2017).
18. Hunt Jr, G.L., Drinkwater, K.F., Arrigo, K., Berge, J., Daly, K.L., Danielson, S., Daase, M., Hop, H., Isla, E., Karnovsky, N. & Laidre, K. Advection in polar and sub-polar environments: Impacts on high latitude marine ecosystems. *Progress in Oceanography* **149**, 40-81 (2016).
19. Bourke, R.H., Weigel, A.M. & Paquette, R.G. The westward turning branch of the West Spitsbergen Current. *Journal of Geophysical Research: Oceans* **93**,14065-14077 (1988).

20. Eldevik, T., Nilsen, J.E.Ø., Iovino, D., Olsson, K.A., Sandø, A.B. & Drange, H. Observed sources and variability of Nordic seas overflow. *Nature Geoscience* **2**(6), 406 (2009).
21. Foyn, L., von Ouillfeldt C.H. & Olsen E. Miljø- og ressursbeskrivelse av området Lofoten - Barentshavet [A description of the marine environment and resources in the area Lofoten -Barents Sea]. *Fisken og Havet* **6,** 83 (2002) (In Norwegian).
22. Pedersen, O.P., Aschan, M., Rasmussen, T., Tande, K.S. & Slagstad, D. Larval dispersal and mother populations of *Pandalus borealis* investigated by a Lagrangian particle-tracking model. *Fisheries Research* **65**(1-3), 173-190 (2003).
23. Drevetnyak, K. & Nedreaas, K.H. Historical movement pattern of juvenile beaked redfish (*Sebastes mentella* Travin) in the Barents Sea as inferred from long-term research survey series. *Marine Biology Research* **5**(1), 86-100 (2009).
24. Koltermann, K.P. & Luethje, H. *Hydrographic atlas of the Greenland and northern Norwegian Seas (1979-1987)* Deutsches Hydrographisches Institut, Hamburg, Germany (1989).
25. Koszalka, I., LaCasce, J.H., Andersson, M., Orvik, K.A. & Mauritzen, C. Surface circulation in the Nordic Seas from clustered drifters. *Deep Sea Research Part I: Oceanographic Research* Papers **58**(4), 468-485 (2011).
26. Jorde, P.E., Søvik, G., Westgaard, J.I., Albretsen, J., André, C., Hvingel, C., Johansen, T., Sandvik, A.D., Kingsley, M. & Jørstad, K.E. Genetically distinct populations of northern shrimp, *Pandalus borealis*, in the North Atlantic: adaptation to different temperatures as an isolation factor. *Molecular Ecology* **24**(8), pp.1742-1757 (2015).
27. Strand, K.O., Sundby, S., Albretsen, J. & Vikebø, F.B. The Northeast Greenland shelf as a potential habitat for the Northeast Arctic cod. *Frontiers in Marine Science* **4**, 304 (2017).
28. Rudels, B. On the mass balance of the Polar Ocean, with special emphasis on the Fram Strait. *Norsk Polarinstitutt skrifter* **188**, 1-53 (1987).
29. Manley, T.O. Branching of Atlantic Water within the Greenland-Spitsbergen Passage: An estimate of recirculation. *Journal of Geophysical Research: Oceans* **100**, 20627-20634 (1995).
30. de Steur, L., Hansen, E., Mauritzen, C., Beszczynska-Möller, A. & Fahrbach, E. Impact of recirculation on the East Greenland Current in Fram Strait: Results from moored current meter measurements between 1997 and 2009. *Deep Sea Research Part I: Oceanographic Research Papers* **92**, 26-40 (2014).
31. Oziel, L., Sirven, J. & Gascard, J.C. The Barents Sea frontal zones and water masses variability (1980–2011). *Ocean Science* **12**(1), 169 (2016).
32. Beszczynska-Möller, A., Fahrbach, E., Schauer, U. & Hansen, E. Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES Journal of Marine Science* **69**(5), 852-63 (2012).
33. Sundby, S. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* **85**(4), 277-298 (2000).
34. Drinkwater, K.F. The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography* **68**(2-4), 134-151 (2006).
35. Svensen, C., Seuthe, L., Vasilyeva, Y., Pasternak, A. & Hansen, E. Zooplankton distribution across Fram Strait in autumn: Are small copepods and protozooplankton important? *Progress in Oceanography* **91**(4), 534-544 (2011).

36. Weydmann, A., Walczowski, W., Carstensen, J. & Kwaśniewski, S., 2018. Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Global Change Biology* **24**(1), 172-183 (2018).
37. Sundby, S. & Nakken, O. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science* **65**(6), 953-962 (2008).
38. Sundby, S., Bjørke, H., Soldal, A.V. & Olsen, S., 1989. Mortality rates during the early life stages and year class strength of the Arcto-Norwegian cod (*Gadus morhua* L.). *Rapports et procès-verbaux des Réunions. Conseil permanent international pour l'Exploration de la Mer* **191**, 351-358 (1989).
39. Vikebø, F., Sundby, S., Ådlandsvik, B. & Fiksen, Ø., 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science* **62**(7), 1375-1386 (2005).
40. Vikebø, F., Jørgensen, C., Kristiansen, T. & Fiksen, Ø., 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. *Marine Ecology Progress* Series **347**, 207-220 (2007).
41. Yaragina, N.A., Aglen, A., & Sokolov, K.M. Cod. In: Jakobsen, T. & Ozhigin, V.K. (ed.) *The Barents Sea ecosystem, resources, management, Half a Century of Russian–Norwegian Cooperation*. Tapir Academic Press, Trondheim, Norway 225-270 (2011).
42. Cadrin, S.X., Bernreuther, M., Daníelsdóttir, A.K., Hjörleifsson, E., Johansen, T., Kerr, L., Kristinsson, K., Mariani, S., Nedreaas, K., Pampoulie, C., Planque, B., Reinert, J., Saborido-Rey, F., Sigurðsson, T. & Stransky, C. Population structure of beaked redfish, *Sebastes mentella*: evidence of divergence associated with different habitats. *ICES Journal of Marine Science* **67**, 1617-1630 (2010).
43. Hylen, A., Korsbrekke, K., Nakken, O. & Ona, E. Comparison of the capture efficiency of 0-group fish in the pelagic trawls. In: Hylen, A. (ed.) *Precision & relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea and adjacent waters, proceedings of the sixth IMR-PINRO symposium, Institute of Marine Research, Bergen, Norway*, 145-156 (1995).
44. Kelly, G.F. & Barker, A.M. Vertical distribution of young redfish in the Gulf of Maine. *ICNAF Special Publications.* **3**, 220-233 (1961).
45. Christiansen, J.S., Mecklenburg, C.W. & Karamushko, O.V. Arctic marine fishes and their fisheries in light of global change. *Global Change Biology* **20**(2), 352-359 (2014).
46. Wassmann, P. Arctic marine ecosystems in an era of rapid climate change. *Progress in Oceanography* **90**(1–4), 1-17 (2011).
47. Christiansen, J.S. The TUNU-Programme: Euro-Arctic marine fishes—diversity and adaptation. In: di Prisco, G. & Verde, C (ed.) *Adaptation and evolution in marine environments, vol. 1, From pole to pole.* Springer, Berlin Heidelberg, Germany 35–50 (2012).
48. Westgaard, J.I. & Fevolden, S.E. Atlantic cod (*Gadus morhua* L.) in inner and outer coastal zones of northern Norway display divergent genetic signature at non neutral loci. *Fisheries Research* **85**(3), 306-315 (2007).
49. Pereyra, R.T., Westgaard, J.I., Dahl, M., Johansen, T., Knutsen, H., Ring, A.K., Søvik, G. & André, C. Isolation and characterization of nuclear microsatellite

loci in the northern shrimp, *Pandalus borealis*. *Conservation Genetics Resources* **4**(1), 109-112 (2012).
50. Vähä, J.P. & Primmer, C.R. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. *Molecular Ecology* **15**(1), 63-72 (2006).
51. Hubisz, M.J., Falush, D., Stephens, M. & Pritchard, J.K. Inferring weak population structure with the assistance of sample group information. *Molecular Ecololgy Resources* **9**, 1322-1332 (2009).
52. Pritchard, J.K., Stephens, M. & Donnelly, P. Inference of population structure using multilocus genotype data. *Genetics* **155**(2), 945-959 (2000).
53. Kopelman, N.M., Mayzel, J., Jakobsson, M., Rosenberg, N.A. & Mayrose, I. Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources* **15**(5), 1179-1191 (2015).
54. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: www.r-project.org (2018).
55. Francis, R.M. POPHELPER: an R package and web app to analyse & visualize population structure. *Molecular Ecology Resources* **17**(1), 27-32 (2017).
56. Beugin, M.P., Gayet, T., Pontier, D., Devillard, S. & Jombart, T., A fast likelihood solution to the genetic clustering problem. *Methods in Ecology and Evolution* **9**(4), 1006-1016 (2018).
57. Jombart, T. adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**(11),1403-1405 (2008).
58. Jombart, T., Devillard, S. & Balloux, F., 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* **11**(1), 94 (2010).
59. Kamvar, Z.N., Brooks, J.C. & Grünwald, N.J. Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Frontiers in Genetics* **6**, 208 (2015).
60. Nei, M. *Molecular Evolutionary Genetics*. Columbia University Press, New York, USA (1987).

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