Dispersal routes of climate-induced marine range expansions into the Arctic

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As a result of climate change, the species composition of Arctic habitats has begun to shift in an Atlantic direction[1–3]. 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 fauna will dominate Arctic habitats, and alter ecosystems[4]. 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[2,5,6].

The Arctic is warming more rapidly than any other geographical region[7]. Increases in water temperature and loss of sea-ice[8,9] are expected to induce a northward expansion of boreal fauna[10–12], a phenomenon that is already apparent in the Barents Sea[1–3]. Atlantic mackerel (*Scomber scombrus*) exemplifies this trend, having recently displayed an exceptional northward shift in distribution to Spitsbergen[13]. Such predatory newcomers, as Atlantic mackerel, pose a considerable threat to native Arctic fauna and thus to Arctic ecosystems, as they may restructure trophic relationships[2,5,6].

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[14]. This was well outside of their known distribution ranges[10,15,16] (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, required by climate models e.g. [11] to predict which species will likely ensue, and to what extent boreal fauna will dominate Arctic habitats[4].

We consider two main routes of dispersal, either via migration against the East Greenland Current[17] and along the East Greenland shelf from Iceland, or from the Barents Sea via advection[18] by the 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, is known to result in the advection of cod, redfish, and shrimp offspring from the Norwegian coast and the Barents Sea proper to Spitsbergen[21–23]. Cod, redfish, and shrimp offspring from Iceland are also known to advect with the East Greenland Current and via the Irminger Current to East/West Greenland[24,25].

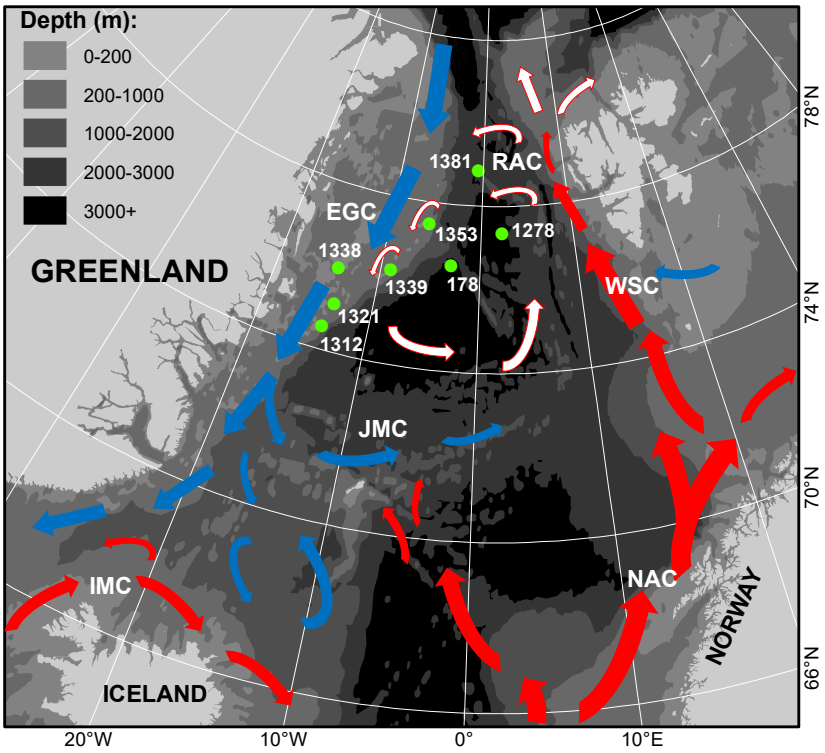

Fig. 1. Stations (green full circles) of observation for Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis*) (Methods, Table 1). Arrows indicate ocean currents (Source[17,26]). Atlantic surface currents (red arrows): IMC (Irminger Current), NAC (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).

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.

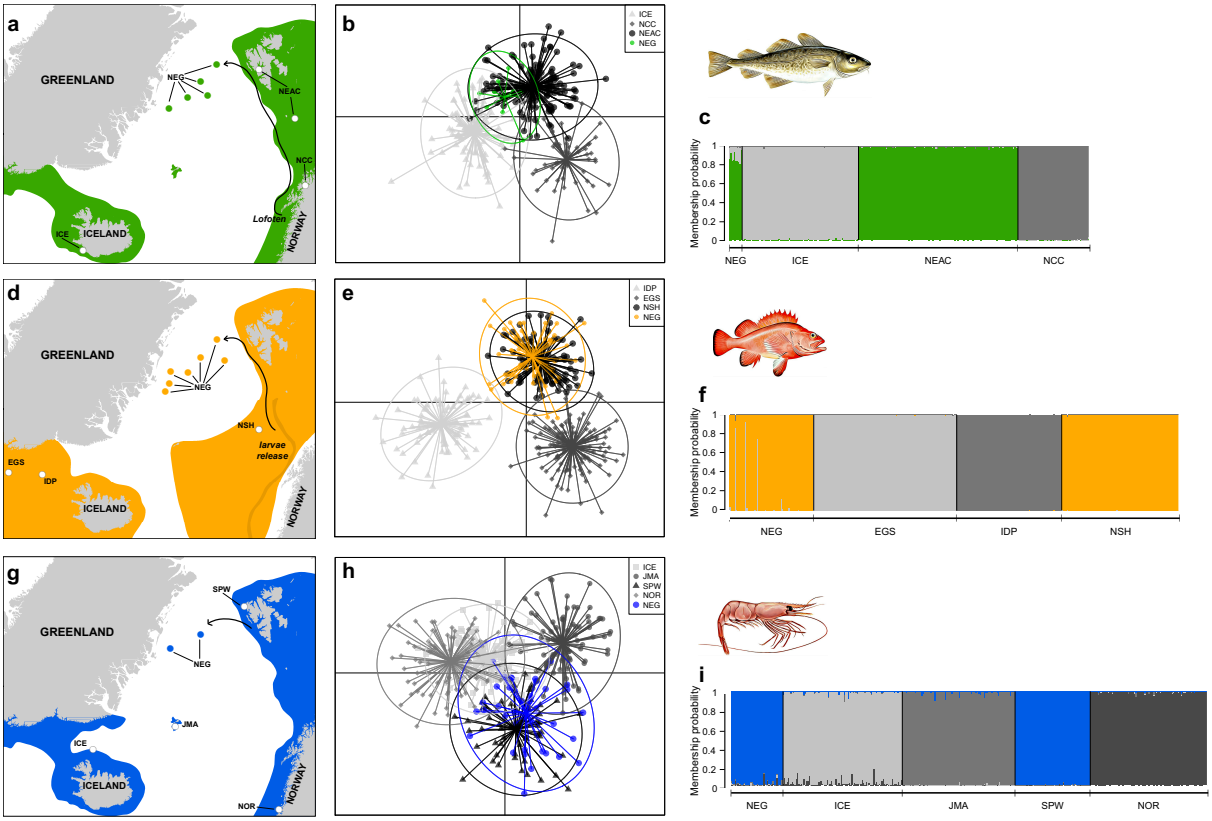

Fig. 2. Genetic evidence of Atlantic cod (*Gadus morhua)* (**a**, **b**, **c**), beaked redfish (*Sebastes mentella)* (**d**, **e**, **f**) and deep-sea shrimp (*Pandalus borealis)* (**g**, **h**, **i**) specimens found off Northeast Greenland originating from the Barents Sea. Maps (**a**, **d**, **g**) 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 colonisation 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).

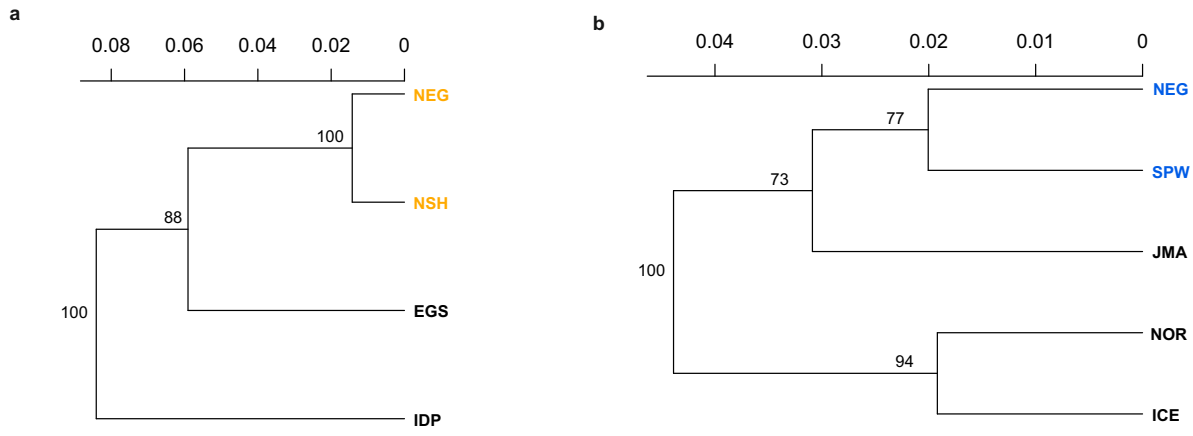

Fig. 3. Neighbour-joining trees utilising Nei's distance, for beaked redfish (*Sebastes mentella*) (**a**) and deep-sea shrimp (*Pandalus borealis*) (**b**) NE Greenland (NEG) groups and reference populations. For abbreviations refer to Methods Table 2. Bootstrap values (>88% and >73%) on both trees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

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[27–29]. 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[30–32], the Return Atlantic Current provides a connection between the Barents Sea and the NE Greenland shelf ecosystems. The inflow of Atlantic water in the Barents Sea has doubled since 1980[33], resulting in an increase in the West Spitsbergen Current temperature[34]. 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, an increase in water temperature may explain the loss of sea-ice[8,9], 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[35] and its abundance during the last warm period in the North Atlantic (1920–1960) has likely driven the range expansion of cod and other boreal species[36]. Relatively low abundances of *Calanus finmarchicus* were observed on the NE Greenland shelf in autumn 2006[37], but in light of the West Spitsbergen Current warming, its abundance will likely increase in the Fram Strait and on the NE Greenland shelf in the future[38], 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[39] (latitudes 62–71 °N) during March and April where pelagic offspring drift by surface currents[40] northwards and eastwards into the Barents Sea[41]. 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[40]. Our results suggest that 0-group cod advected off the shelf by wind-forcing[29,42] 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[43]. 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[44]. Redfish larvae have been observed in Atlantic water west of the continental shelf, and as far north as Spitsbergen[23,45]. 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[46]. 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 found on the NE Greenland shelf had reached their destination 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 [28]). 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[15]. 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 via the Return Atlantic Current connection (Fig. 2g).

The NE Greenland shelf ecosystem is severely understudied and biodiversity baselines are fragmentary with no timeline[47]. It is therefore difficult to establish whether our findings reflect a recent shift driven by climate change or constitute a common component of the NE Greenland Shelf fauna. The Barents Sea is the most productive ecosystem in the Northeast Atlantic[48] and presently supports the historically largest cod population[43]. 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[14]. The three species studied herein are clearly not alone in being capable of entering the NE Greenland shelf. A recent simulation study[29] 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 to be expected. As a result, trophic relationships are likely to be strongly modified[6] as boreal generalists such as cod will be favoured by climate scenarios[11]. Cod feeds on polar cod (*Boreogadus saida*), Arctic seabed fishes and zoobenthos[5], and as a figurehead of boreal range expansions into the Arctic, gives a glimpse of what is to come for native Arctic fauna.

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 become invaded by a larger proportion of Atlantic species.

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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[49]. 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[16,28,50]. 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[16,50,51] (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. [52], Supplementary S3, Table S3). As weak population differentiation was expected within all datasets, we adopted a conservative approach to infer *q*[53] using a no-admixture model as implemented in the Bayesian clustering method, STRUCTURE (v.2.3.4)[54]. This approach has been shown not to bias the true structuring in datasets with weak genetic differentiation[53]. 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[55] 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)[56] using the *pophelper* package (v. 2.2.5)[57].

The maximum-likelihood clustering tool *snapclust*[58], within the R package *adegenet* (v. 2.1.1)[59], 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)[60], 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. [59]).

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)[61]. This method utilised Nei's Distance[62] 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.

Methods Only References

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