UiT
THE ARCTIC UNIVERSITY OF NORWAY

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

# Climate-induced range expansions of marine fauna into the Arctic – what is the most likely colonisation route?

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**Adam Jon Andrews**

*BIO-3950 Master's thesis in Biology, May 2018*


**Main supervisor:** Dr. Kim Præbel (NFH, UiT)

**Co-supervisors:** Dr. Jørgen Schou Christiansen (AMB, UiT)

Dr. Jon-Ivar Westgaard (IMR, Tromsø)

UNIVERSITY OF TROMSØ

# Abstract

As a result of climate change, the Arctic faunas of the Northeast Atlantic have begun to shift in an Atlantic direction. One system exposed to such a change is the Northeast Greenland (NEG) Shelf. However, the colonisation route taken by boreal fauna to the NEG shelf is unknown. This knowledge is essential to predict to what extent boreal fauna will dominate Arctic habitats, and alter ecosystems in the future. For the species under study here, colonisation is possible from either the Barents Sea via a northern route, or via southern expansion from Iceland and Jan Mayen Island. Here, we used microsatellite markers and established reference population genetic data from Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis*) to determine the most likely origin of specimens of these species recently collected at the NEG shelf. We demonstrate that all three species originate from the Barents Sea, and suggest that a likely colonisation route is via advection across the Fram Strait. Our results show that the species composition of Arctic habitats can be shaped by the dispersal of pelagic larvae, and that the fauna of the Barents Sea can project on to adjacent Arctic habitats with unknown consequences to the structure and function of putatively isolated Arctic communities.



***Keywords:*** Atlantic cod**,** Barents Sea, climate change, population genetics, range expansion of fishes

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# Preface

This thesis is written in the form of an extended draft of a scientific article, intended to be later submitted to a peer-review journal. Prior to the article itself is a General Introduction – tasked with familiarising the reader with the species, study site and techniques utilised therein. After the article is a reflective Future Perspectives section, outlying how the work could be extended.

I would like to take the opportunity to formally thank my supervisors, Kim, Jørgen and Jon-Ivar, fellow co-authors, Shripathi and Christophe, and the NFH Group for Genetics (lead by Kim). I've enjoyed two wonderful years of study under your guidance, and wherever the future takes me, I will look back with fond memories. I wish to especially thank Kim and Jørgen. Kim, for his keenness to involve me in other projects which gave me the opportunity to learn additional skills and experience that I am truly grateful for, and Jørgen, for his interest in me as a person. I will miss your humour and support.

This work is a contribution to the TUNU-Programme, UiT The Arctic University of Norway and was part-funded by a Small Research Grant from The Fisheries Society of the British Isles.

# General Introduction

This thesis uses microsatellites, a type of genetic marker, to understand how boreal fauna in the Northeast Atlantic can disperse or migrate into the Arctic habitats of the Northeast (NE) Greenland shelf. This General Introduction aims to introduce the reader to the study site of the NE Greenland shelf, the three species under study; Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis)*, the field of population genetics, and how genetic tools are used in the context of this thesis.

**The Northeast Greenland Shelf – Study site**

Much of the NE Greenland shelf is ice-covered for 10 months of the year, and dominated by the cold southward-flowing East Greenland Current from the Arctic Ocean (Fig. 1, Håvik et al. 2017). As a result, it is poorly productive (Wassmann 2011) and thus supports a low abundance of fishes – of solely 'Arctic' description (i.e. fishes that spawn only at sub-zero temperatures) (Christiansen 2012). Compared to their boreal counterparts (e.g. Atlantic cod), Arctic fishes are seldom harvested. Currently, only Russia exploit stocks of but a few species, namely, polar cod (*Boreogadus saida*), navaga (*Eleginus nawaga*) and Arctic flounder (*Liposetta glacialis*), and are limited by their jurisdictional boundaries to the Barents, White and Kara Seas (Karamushko 2012, Hop & Gjøsæter 2013). Hence, commercial fisheries have not yet been established on the NE Greenland shelf and thus a lack of interest (and its associated funding) has resulted in a lack of historical knowledge of the site (Christiansen et al. 2014). Since 2002, the TUNU-Programme, UiT The Arctic University of Norway, has undertaken bi-annual expeditions to the shelf (Christiansen 2012), where ice-conditions have become favourable to allow access.

In general, recent warming (Hoegh-Guldberg & Bruno 2010) has resulted in a loss of sea-ice for the entire Arctic (NSIDC 2018). For the NE Greenland shelf, this has resulted in the September (Arctic sea-ice extent minimum) marginal-ice zone shifting north-westwards. In relation to the stations where the sampling was conducted for this thesis, only five out of 17 years so-far this century would have sea-ice covering those

stations – with a sea-ice extent that typifies the mean of the 20th century. Thus, in recent years, such as those when the sampling for this thesis took place, much of the south and east of the shelf was ice-free in September (Fig. 1).

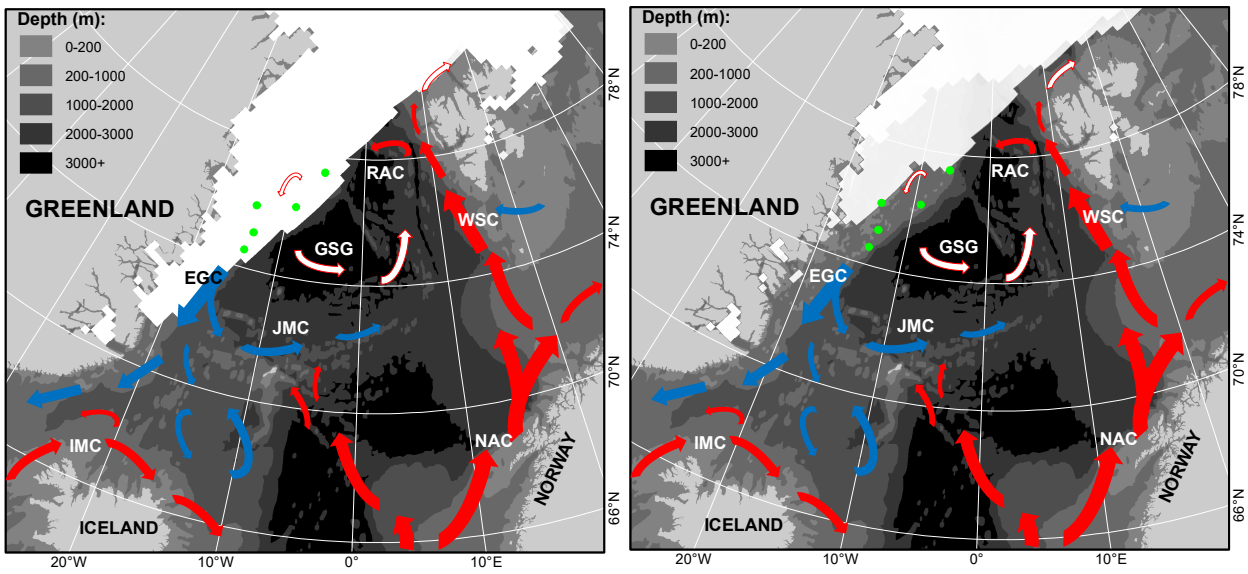


**Fig. 1.** Thesis sampling stations (green circles) in relation to the mean sea-ice extent for September (white shading, source: NSIDC 2018), where one or more stations were ice covered this century (**left**, years: 2000, 2006, 2007, 2009 & 2012), and in the years where Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis*) were observed on the Northeast Greenland shelf (**right**, years: 2015 & 2017). Arrows indicate currents (source: Koltermann & Lüthje 1989, Håvik et al. 2017). Atlantic surface currents (red arrows): IMC (Irminger Current), NAC (Norwegian Atlantic Current), WSC (West Spitsbergen Current), RAC (Return Atlantic Current). Atlantic sub-surface currents (white arrows): GSG (Greenland Sea Gyre). Arctic surface currents (blue arrows): EGC (East Greenland Current), JMC (Jan Mayen Current). Arrow size indicates velocity. Maps were created using ESRI ArcMap (v. 10.6, www.arcgis.com).

Changes to water temperature and sea-ice extent raise questions of how both native Arctic fauna, and the fauna of adjacent systems (i.e. the Icelandic and Barents Sea) will respond. The previous warm period (1920–1960) saw a general northward shift of boreal fauna driven by increased primary production (Drinkwater 2006), and while this was never evaluated for the NE Greenland shelf, we cannot conclude that it did not occur.

If the current warming trend continues, productivity in the Arctic and its adjacent seas is predicted to increase (Wassmann 2011, Hollowed et al. 2013, Wiedmann et al. 2014). Thus, the large NE Greenland shelf, with similar depths to the Barents Sea

(~300 m) may have the potential to support a host of boreal species favoured by climate scenarios (Cheung et al. 2010). This could impact native Arctic fauna two-fold, directly via restructuring trophic relationships (Hollowed et al. 2013, Fossheim et al. 2015, Frainer et al. 2017) and indirectly due to the attraction of fisheries (Christiansen 2017). Potential newcomers to NE Greenland, such as those studied herein are commercially important species (Haug et al. 2017). Fisheries may look to capitalise on these new stocks and as there is a large proportion of benthic fauna on the shelf (e.g. Cottoids, Liparids and Zoarcids, Christiansen 2012), Arctic fauna will turn up as bycatch (Christiansen et al. 2014) and habitats will face destruction (Wiedmann et al. 2014) if trawling methods akin to those in sub-Arctic fisheries are employed (CAFF 2013, Lynghammar et al. 2013). Though, it is also worth mentioning that top-down processes (i.e. enhanced competition with newcomers) are likely to drive Arctic species northwards, as observed during the previous warm period (Drinkwater 2006).

**Study species and their population structure within the Northeast Atlantic**

Atlantic cod (*Gadus morhua*, hereafter "cod"), beaked redfish (*Sebastes mentella*, hereafter "redfish") and deep-sea shrimp (*Pandalus borealis*, hereafter "shrimp") are among the most economically important commercial fish and invertebrate species, having been exploited for centuries (Haug et al. 2017) – hence, the elucidation of their population structure has been of interest for management. They are all widely distributed throughout the NE Atlantic, co-habiting continental shelves of the Barents Sea and Iceland (Bergström 2000, Drinkwater 2005, Saha et al. 2017). The pelagic redfish are also distributed off the shelves of the Norwegian Sea (Saha et al. 2017). All three species have been reported around Jan Mayen Island (Nilssen & Aschan 2009, Wienerroither et al. 2011) at latitude ~71 °N. On the East Greenland Shelf, the northernmost report of shrimp is at latitude 70 °N (Bergström 2000) while cod and redfish are present south of latitude 67 °N, and 66 °N, respectively (Magnusson & Magnusson 1995, Jørgensen et al. 2015).

Several studies have revealed their population structure within these distribution limits, using genetic tools. Within the Norwegian and Barents Seas, two populations of cod have been genetically described: Norwegian Coastal Cod (NCC), and North East Arctic Cod (NEAC) (Westgaard & Fevolden 2007). NEAC (Norwegian = *skrei*) is

characterised by its long-distance spawning migrations, from feeding areas in the Barents Sea to spawning locations – mainly off the Norwegian Lofoten Islands (latitude ~68 °N, Sundby & Nakken 2008). NCC, by contrast, spawn along the entire Norwegian coast (Nordeide 1998), inhabiting coastal waters and fjords, and performing, in general, relatively short migrations (Hylen 1964). In addition, two populations of cod have been genetically described in Icelandic waters (Pampoulie et al. 2015)—Frontal and Coastal cod—differing whereby the Frontal ecotype descends deeper than its Coastal equivalent to feed at thermal fronts (Neuenfeldt et al. 2013). Cod from Iceland is well known to migrate to and from West Greenland, thus only Jan Mayen Island remains as a potential fifth population of cod in the NE Atlantic. This remains unstudied, though tagging experiments suggest that it represents a fragmented sub-population of Iceland (Neuenfeldt et al. 2013).

The population structure of redfish is complex, and, in the past has been clouded by uncertainties in the taxonomic classification of the genus *Sebastes*, driven by significant hybridisation between described species (Roques et al. 2001). Currently, three populations are genetically described in the NE Atlantic, a Norwegian “shallow” population that includes redfish distributed throughout the Barents Sea, Norwegian Sea and west to Jan Mayen Island, an Icelandic “deep” population inhabiting mostly deep waters of the Irminger Sea, southwest of Iceland, and an East Greenland “slope” population inhabiting mainly continental slope areas surrounding the Irminger Sea (Saha et al. 2017). The populations are named according to how they are assessed by the International Council for the Exploration of the Sea (ICES 2015) and how samples clustered in analysis (following Saha et al. 2017), not solely due to their depth strategies.

Deep-sea shrimp populations of the NE Atlantic are considered to have high gene flow, as a function of high connectivity. Martinez et al. (2006) report how shrimp of three areas show genetic divergence, namely, the Barents Sea and Spitsbergen, Norwegian Fjords, and Jan Mayen Island. Jorde et al. (2015) confirmed this and demonstrated further how shrimp from Iceland can also be differentiated from those described, and suggest that while high gene flow is apparent, temperature is the isolating factor driving population divergence in shrimp.

**An Introduction to population genetics**

Population genetics is the study of genetic variability (polymorphism) at various levels, i.e. among individuals, within populations and among populations. Genetic variability is driven by four major evolutionary forces: *natural selection*, *genetic drift*, *mutation*, and *gene flow* (dispersal between populations). These forces can be understood by applying the Hardy-Weinberg principle, the equation to which, is expressed as:

$$p^2 + 2pq + q^2 = 1$$

where p and q are the frequencies of dominant or recessive alleles in a two-allele system, thus $p^2$ and $q^2$ represent the frequencies of dominant and recessive homozygous genotypes, respectively, and 2pq, the frequency of heterozygous genotypes.

The Hardy-Weinberg principle or equilibrium (HWE) states that genotype frequencies in a population will remain constant from generation to generation in the absence of evolutionary forces. Thus, a population not in HWE is subject to evolutionary force(s) and depending on the frequency of alleles within a population, the forces at play can be identified. For example, mutation and gene flow introduce new alleles into a population, natural selection change genes frequencies, and genetic drift changes allele frequencies randomly (only in small populations).

Genetic software tools, such as those utilised herein (STRUCTURE, Pritchard et al. 2000, and *snapclust*, Beugin et al. 2018) cluster individuals into groups whereby the aim is to maximise the HWE within the groups depending on Bayesian or maximum-likelihood probabilities (Beugin et al. 2018). This clustering allows the inference of relationships between groups and uses groups to describe populations according to their variability. Alternatively, with prior ecological knowledge of a species under study we can pre-emptively collect samples in different locations thought to each represent a population, and then compare the relationships between those pre-defined groups.

The term genotype relates to the genetic make-up of an individual and can be obtained via a variety of markers (genes or DNA sequences). This section covers microsatellites, as used in this thesis, though more commonly used are SNPs (Single

Nucleotide Polymorphisms) (see Syvänen 2001). Microsatellites are regions on the genome where DNA is repeated in tandem sequences (e.g. CACACACA) (Selkoe & Toonen 2006). Repeat units vary, but are generally di-, tri-, tetra- or penta-nucleotide. Most importantly, the repeat length varies between individuals and populations i.e. they are polymorphic. It is this repeat length that is "scored" whereby the genotype of an individual is made up of the allele (variant form of a gene/DNA sequence) length of the repeat unit on one chromosome, and another (for diploid organisms).

Variability in repeat length is driven by mutations, which not only occur through the classical substitution of one nucleotide for another, but "step-wise", whereby a repeat unit is inserted or deleted during replication by the slippage of DNA polymerase (Ellegren 2004). This results in high levels of mutation, and since microsatellites are sequences in non-coding regions (introns), there is no selection pressure acting upon them, so mutations are retained, though, microsatellites can be subject to so-called "hitch-hiking" selection, acting on a nearby gene (Schlötterer 2003). High mutation rates translate to high levels of polymorphic variation, which allows the differentiation of individuals and populations. High mutation rates themselves are useful in studying recent population divergence (Selkoe & Toonen 2006). Microsatellites also enable the distinction between homozygotes (allele of the same repeat length) and heterozygotes (alleles of two different repeat lengths) and are polymerase chain reaction (PCR)-based, thus only small amounts of DNA are required, which can be highly degraded (e.g. ancient DNA). A major disadvantage of microsatellites is homoplasy – that two identical genotypes may be observed but may not be identical-by-descent (Estoup et al. 2002). This occurs due to high mutation rates whereby a single repeat unit is gained or lost, and results in an underestimation of population differentiation.

**Use of population genetic tools to assign individuals to populations**

Population genetic information can be used to answer a variety of questions, for example as herein to identify the population origin of unknown individuals. Here, it is explained how genetic tools can be used to address this. The population genetic structure of the species under study here has been elucidated (c.f. Westgaard & Fevolden 2007, Jorde et al. 2015, Saha et al. 2017). Those populations can be used to "assign" individuals of an unknown population i.e. how closely do the genotypes of each unknown individual resemble each species known population.

This task is complicated by low-levels of population differentiation (Nielsen et al. 2001), as expected for studies utilising microsatellites on marine species (e.g. $F_{ST}$ <0.01, Ward et al. 1994). This is linked to a variety of factors e.g. high gene flow among populations, huge effective population sizes resulting in almost no genetic drift and thereby very limited divergence among populations, and overlapping spawning areas, which are often in transit (Ward et al. 1994, Hauser & Ward 1998). Despite population differentiation being 'weak' for a variety of species (e.g. Atlantic herring *Clupea harengus*: McPherson et al. 2001, American lobster *Homarus americanus*: Benestan et al. 2015), including those under study here (Westgaard & Fevolden 2007, Jorde et al. 2015, Saha et al. 2017), it has been shown to be statistically significant. Thus, high assignment success is possible, if the study design is optimal. This often means the use of many markers (e.g. >15 microsatellites recommended) and large sample sizes (e.g. $n$ = ~100) to capture the entire genotypic variation within a population (Hansen et al. 2001). Nielsen et al. (2001) and Roques et al. (1999) are examples of assignment using microsatellites, for cod, and redfish, respectively.

A disadvantage of microsatellites not yet mentioned is that they are subject to scoring errors. These impact the validity of the data as they obscure the true genotype (DeWoody et al. 2006, Selkoe & Toonen 2006). There are three forms of scoring errors: null alleles, stuttering and large allele dropout. Null alleles occur because of mutations at a primer site which cause an allele to not amplify during PCR and thus, to not be represented. This results in an individual falsely appearing as a homozygote (Selkoe & Toonen 2006). Stuttering is caused by the slippage of DNA polymerase during PCR, resulting in an allele appearing to have less repeats than in reality (Selkoe & Toonen 2006). Large allele dropout occurs as a result of low-annealing efficiency for large fragments (alleles) during PCR, also causing genotypes to appear, falsely, as homozygotes (Wang et al. 2012). Software tools (e.g. MICROCHECKER, Van Oosterhout et al. 2004) have been designed to identify scoring errors (Selkoe & Toonen 2006) though, null alleles are notoriously difficult to detect as there is no difference between them and homozygotes – which occur naturally in populations to varying degrees (Dakin & Avise 2004, Van Oosterhout et al. 2004). Despite some studies (e.g. Carlsson 2008) that claim null alleles are unlikely to impact the outcome of assignment analysis, it is often routine to omit these microsatellites (DeWoody et al. 2006).

The screening process for scoring errors is often extended to other sources of bias, biases that cause the misrepresentation of the genome, rather than the incorrect typing of it. These include, but are not limited to, linkage disequilibrium, non-neutrality, and deviation from HWE. If two or more markers are correlated or non-randomly associated, they are said to be in linkage disequilibrium (Manel et al. 2005). Non-neutrality, as previously mentioned, are cases where markers are subject to natural or sexual selection – for microsatellites, this is an indirect process (Schlötterer 2003). Non-neutrality is an issue for population genetic studies if markers under selection are not correlated with neutral markers. Hence, they do not serve as a neutral representation of the genome of an individual. Finally, deviation from HWE is often explored, which can be an alternative method to identify an excess of homozygotes i.e. null alleles (e.g. Jorde et al. 2015). Studies differ in how they treat potential sources of bias due to a trade-off between retaining suspect markers and therefore statistical power, or the inverse (DeWoody et al. 2006).

Several genetic tools are routinely used to assign individuals to populations. These are either model-based methods, such as STRUCTURE, *snapclust* and GeneClass2 (Piry et al. 2004), or geometric methods such as Discriminant Analysis of Principle Components (DAPC) (Jombart et al. 2010). Model-based methods compute a likelihood (Bayesian or Maximum-likelihood) probability that unknown genotypes belong to a group/population, given a population structure and model of evolution (HWE) (Pritchard et al. 2000, Beugin et al. 2018). These methods provide group membership probabilities that genuinely reflect the probability that an unknown individual belongs to each group/population (Beugin et al. 2018). In contrast, DAPC aims to visualise cluster (group/population) diversity in a reduced space and estimate group assignment probabilities. DAPC probabilities, therefore, reflect genetic proximities, and cannot be interpreted as the probability that an individual belongs to a given population (Beugin et al. 2018). Hence DAPC should not be used principally as an assignment tool (e.g. Bonanomi et al. 2016).

# Climate-induced range expansions of marine fauna into the Arctic – what is the most likely colonisation route?

Adam J. Andrews[1,2]*, Shripathi Bhat[2], Jon-Ivar Westgaard[3], Jørgen S. Christiansen[1], Christophe S. Pampoulie[4], Kim Præbel[2*]

[1]Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Norway
[2]The Norwegian College of Fishery Science, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Norway
[3]Institute of Marine Research, Tromsø, Norway
[4]Marine and Freshwater Research Institute, Reykjavik, Iceland

*Authors to whom correspondence should be addressed, E-mail: adamjonandrews@gmail.com, kim.præbel@uit.no

***Keywords:*** Atlantic cod**,** Barents Sea, climate change, population genetics, range expansion of fishes

**As a result of climate change, the Arctic faunas of the Northeast Atlantic have begun to shift in an Atlantic direction (Fossheim et al. 2015, Kortsch et al. 2015, Haug et al. 2017). One system exposed to such a change is the Arctic Northeast Greenland Shelf. However, the colonisation 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, in the future (Murphy et al. 2016). Here we show that Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*), and deep-sea shrimp (*Pandalus borealis*) specimens found on the Northeast Greenland shelf originate from the Barents Sea, and suggest that a likely colonisation route is via advection across the Fram Strait. Our results indicate that the species composition of Arctic habitats can be shaped by the dispersal of pelagic larvae, and that the fauna of the Barents Sea can project onto adjacent Arctic habitats with unknown consequences to the structure and function of putatively isolated Arctic communities (Kortsch et al. 2015, Christiansen 2017, Frainer et al. 2017).**

# Introduction

The Arctic is warming at twice the global average rate (Hoegh-Guldberg & Bruno 2010). Increases in water temperature and loss of sea-ice (Polyakov et al. 2017, Smedsrud et al. 2017) are expected to expand the distribution of boreal fauna northwards (Drinkwater 2005, Cheung et al. 2010, Hollowed et al. 2013), and that has already become apparent in the Barents Sea (Fossheim et al. 2015, Kortsch et al. 2015, Haug et al. 2017). Atlantic mackerel (*Scomber scombrus*) exemplify this trend, having recently displayed an exceptional northward shift in distribution to Spitsbergen (Berge et al. 2015, Mecklenburg et al. 2018). Novel species in the Arctic, such as the predatory Atlantic mackerel, pose a considerable threat to native Arctic fauna and thus to the Arctic ecosystem, as they restructure trophic relationships (Kortsch et al. 2015, Christiansen 2017, Frainer et al. 2017).

In 2015, 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) for the first time since sampling began in 2002 (Christiansen et al. 2016). This was well outside of their known ranges of distribution (Bergström 2000, Drinkwater 2005, Saha et al. 2017). However, the route which the species took to colonise the site, was unknown. This study adds to Christiansen et al.'s (2016) observations with further finds of the same species in 2017 and aims to determine their population genetic origin. This knowledge will allow us to infer the colonisation routes taken by the three species, required by climate models (e.g. Cheung et al. 2010) to predict which species will likely ensue, and to what extent boreal fauna will dominate Arctic habitats in the future (Murphy et al. 2016).

Atlantic cod (hereafter, "cod"), beaked redfish (hereafter, "redfish") and deep-sea shrimp (hereafter, "shrimp") are widely distributed throughout the NE Atlantic, co-habiting continental shelves of the Barents Sea and Iceland (Bergström 2000, Drinkwater 2005, Saha et al. 2017). In addition, redfish is also distributed off the shelves of the Norwegian Sea (Saha et al. 2017). All three species have been reported around Jan Mayen Island (Nilssen & Aschan 2009, Wienerroither et al. 2011) at latitude ~71 °N. On the East Greenland Shelf itself, the northernmost report of shrimp

is at latitude 70 °N (Bergström 2000) while cod and redfish have only been found as far north as latitudes 67 °N, and 66 °N, respectively (Magnusson & Magnusson 1995, Jørgensen et al. 2015) – over 1000 km south of our observations in NE Greenland.

We consider the NE Greenland shelf to be subject to colonisation along two main routes, either via migration against the East Greenland Current (Håvik et al. 2017), along the East Greenland shelf from Iceland, or from the Barents Sea via advection (Hunt et al. 2016) by the Return Atlantic Current (Bourke et al. 1988, Eldevik et al. 2009, Håvik et al. 2017) – the physical connector between Spitsbergen and NE Greenland, across the abyssal plains of the Fram Strait. High connectivity within the Barents Sea, driven by the Norwegian Atlantic Current along the Norwegian coast, and the West Spitsbergen Current (Eldevik et al. 2009, Håvik et al. 2017) along the Barents Sea shelf-break, is well documented to result in the advection of cod, redfish, and shrimp larvae from the Norwegian coast and the Barents Sea proper to Spitsbergen (Føyn 2002, Pedersen et al. 2003, Drevetnyak & Nedreaas 2009). On the other hand, cod, redfish, and shrimp larvae from Iceland are known to advect with the East Greenland Current and via the Irminger Current to West Greenland (Magnusson & Magnusson 1995, Hedeholm et al. 2017). Moreover, as neither cod, redfish, nor shrimp are known to migrate as juveniles (Drevetnyak & Nedreaas 2009, Ottersen et al. 2014), we hypothesize that the three species found on the NE Greenland shelf are advected across the Fram Strait by the Return Atlantic Current and therefore originate from the Barents Sea.

# Materials & Methods

## Sampling

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. Christiansen et al. 2016) from 2007 to 2017 on the Northeast (NE) Greenland shelf (latitudes 74–79 °N), well outside of their known distributional range (Table 1, Fig. 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, Fig. 1) and are included in the analysis to support colonisation 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 (Christiansen 2012). A subset of redfish fry 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 |

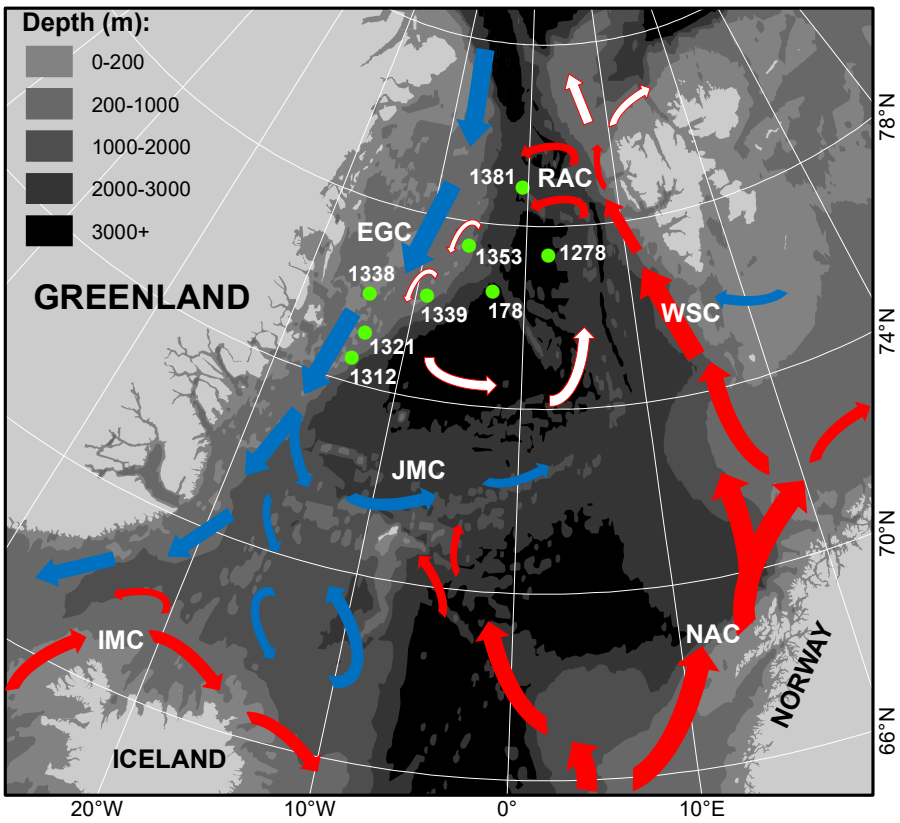


**Fig. 1.** Stations (green circles) of observation for Atlantic cod (*Gadus morhua*), beaked redfish (*Sebastes mentella*) and deep-sea shrimp (*Pandalus borealis*) (Table 1). Arrows indicate currents (Source: Koltermann & Lüthje 1989, Håvik et al. 2017). Atlantic surface currents (red arrows): IMC (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).

## Reference data

Genotyped reference populations (Table 2) for the Northeast Atlantic were obtained from several studies (cod: Westgaard & Fevolden 2007, redfish: Saha et al. 2017, shrimp: Jorde et al. 2015). To ensure the major populations of each species in the Northeast Atlantic were well represented, the cod reference populations were supplemented by genotyping to obtain 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 |

## Microsatellite genotyping

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 (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 (cod: Westgaard & Fevolden 2007, redfish: Saha et al. 2017, shrimp: Pereyra et al. 2012, Appendix 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%.

**Reference data screening**

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 (Appendix 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 (Appendix 1, 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 Appendix 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. Vähä & Primmer 2006, Appendix S3, Table S3). As weak population differentiation was expected within all datasets, we adopted a conservative approach to infer *q* (Hubisz et al. 2009) using a no-admixture model as implemented in the Bayesian clustering method, STRUCTURE (v.2.3.4, Pritchard et al. 2000). This approach has been shown not to bias the true structuring in datasets with weak genetic differentiation (Hubisz et al. 2009). 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 of 500,000 and 500,000 MCMC replicates. CLUMPAK (Kopelman et al. 2015) was used to merge runs (merged barplots: Appendix S3, Fig. S3), and reported similarity scores >0.95.

**Assignment tests**

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 of 500,000 and 500,000 MCMC replicates.

CLUMPAK reported run similarity scores >0.95. STRUCTURE barplots were visualised in R (v. 3.2.3, R Core Team 2018) using the *pophelper* package (v. 2.2.5, Francis 2017).

The maximum-likelihood clustering tool *snapclust* (Beugin et al. 2018), within the R package *adegenet* (v. 2.1.1, Jombart 2008), 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.

**Discriminant and distance tests**

As an exploratory tool, Discriminant Analysis of Principle Components (DAPC) (Jombart et al. 2010), 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. Jombart 2008).

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, Kamvar et al. 2015). This method utilised Nei's Distance (Nei 1987) 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.

**Impact of potential scoring errors on assignment**

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

# Results

Overall, we find that all cod (*n* = 10), and 95% of redfish (*n* = 61) caught on either the NE Greenland shelf or in the Fram Strait, are genetically assigned by STRUCTURE to the 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 it is high-likely that the three species on the NE Greenland shelf originate from the Barents Sea.

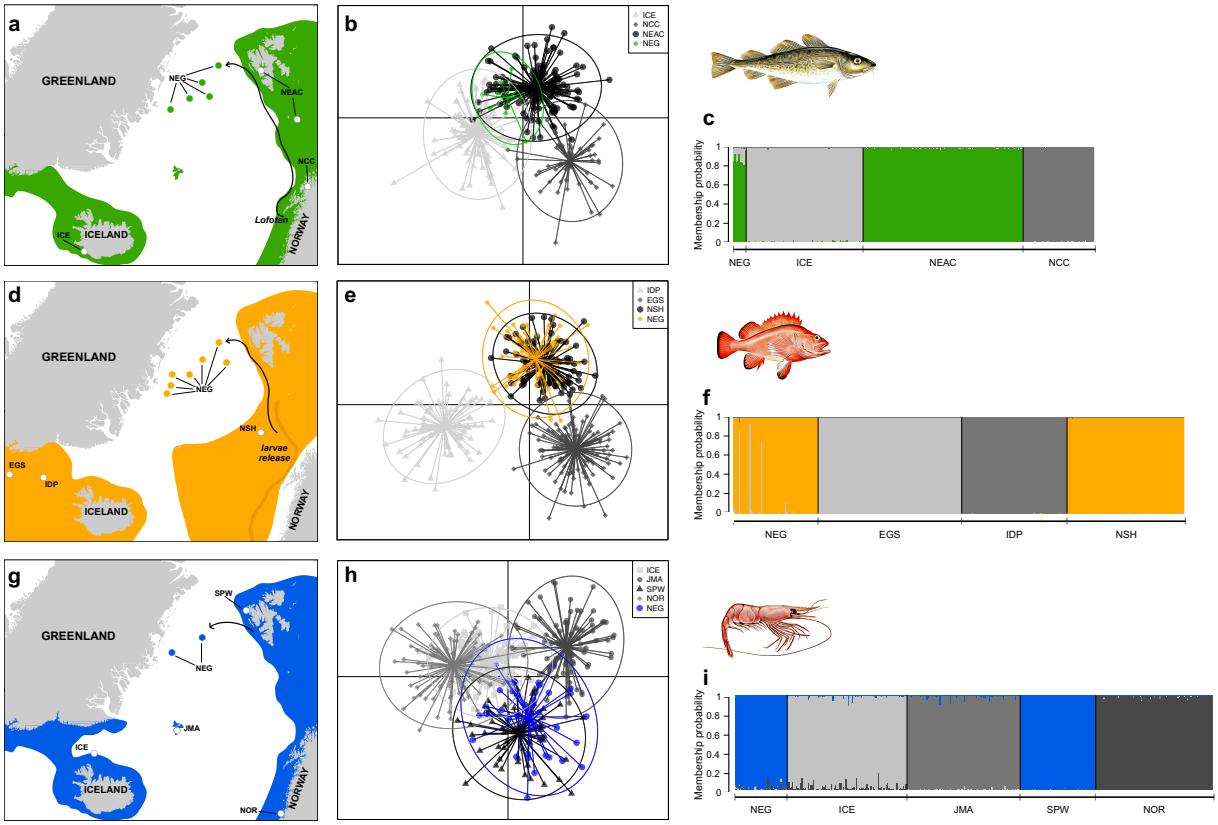


**Fig. 2.** Genetic evidence of Atlantic cod (*Gadus morhua)* (**a**, **b**, **c**), beaked redfish (*Sebastes mentella)* (**d**, **e**, **f**) and deep-sea shrimp (*Pandalus borealis)* (**g**, **h**, **i**) specimens found off Northeast Greenland originating from the Barents Sea. Maps (**a**, **d**, **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 Table 2. Maps were created using ESRI ArcMap (v. 10.6, www.arcgis.com).

Individual assignment tests with STRUCTURE were generally highly consistent with those of *snapclust*, where 90% of cod tests, 98% of redfish tests and 75% of shrimp tests formed a consensus between the two approaches (Appendix S5, Table S5). Of those consistent tests, all individuals of the three species under study were assigned with a greater probability to populations in the Barents Sea than populations from any other location. The exception was three out of 60 (5%) of redfish individuals (Appendix S5, Table S5.2). There was no difference in the assignment outcome between cod or redfish individuals caught on the NE Greenland shelf and in the Fram Strait, as such, they are presented as a single group.

DAPC clustered the NE Greenland group of the three species closely with the corresponding Barents Sea populations as indicated by the assignment testing (Fig. 2c,f,i). The 95% DAPC cluster ellipses between NE Greenland and these population clusters overlapped considerably, though overlap was also evident between the reference population clusters, most significantly for the cod and shrimp clusters. The ellipse centre for the NE Greenland redfish and shrimp groups falls most closely to the centre of their Barents Sea population clusters whereas the ellipse centre for the NE Greenland cod falls closer to the extremes of the NEAC population than its centre (Fig. 2b). The redfish and shrimp neighbour-joining tree's resulted in the same grouping as the assignment testing and DAPC scatterplots, 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 NE Greenland group and Spitsbergen West population (Fig. 3b). Bootstrap values (>88% and >73%) on both trees suggest good reproducibility.

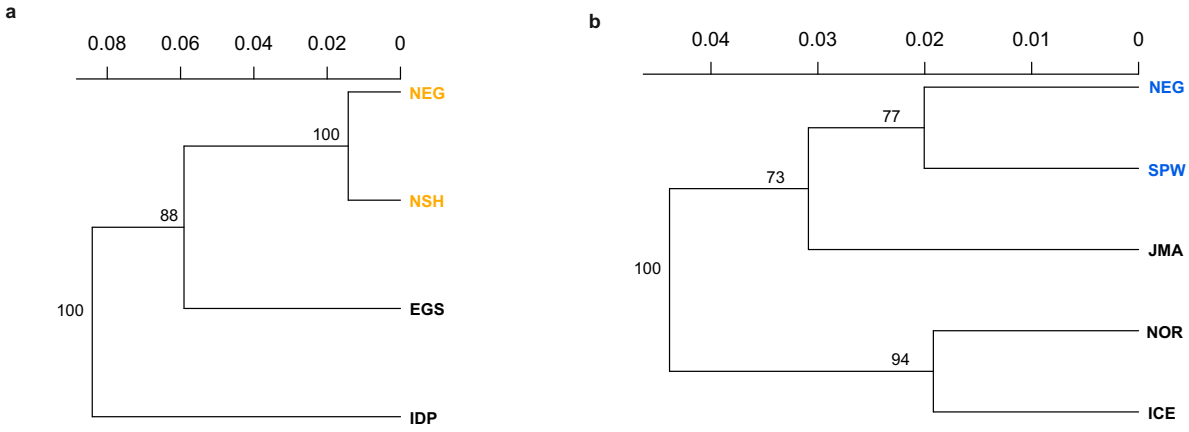


**Fig. 3.** Neighbour-joining trees utilising Nei's distance, for beaked redfish (*Sebastes mentella*) (**a**) and deep-sea shrimp (*Pandalus borealis*) (**b**) NE Greenland (NEG) groups and reference populations. For abbreviations refer to Table 2. Branches are labelled with bootstrap values using 1000 iterations.

# Discussion

### The Northeast Greenland Shelf–Barents Sea connection

Our results show that the NE Greenland shelf is readily colonized by cod, redfish and shrimp from the Barents Sea, probably advected across the Fram Strait by the Return Atlantic Current, as shown by recent simulation studies (Koszalka et al. 2011, Jorde et al. 2015, Strand et al. 2017). Advection plays an important role in the northward transport of plankton in the Barents Sea, via the West Spitsbergen Current (Hunt et al. 2016) and because up to 50% of this Atlantic water is estimated to cross the Fram Strait (Rudels 1987, Manley 1995, de Steur et al. 2014), the Return Atlantic Current is a likely connector between the Barents Sea and the NE Greenland shelf. The inflow of Atlantic water in the Barents Sea has doubled since 1980 (Oziel et al. 2016), resulting in an increase in the West Spitsbergen Current temperature (Beszczynska-Möller et al. 2012), 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 (Polyakov et al. 2017, Smedsrud et al. 2017), and the occurrence of boreal species such as cod, redfish and shrimp, along the eastern portion of the NE Greenland shelf and shelf break. The copepod *Calanus finmarchicus* is the major prey for young cod (Astthorsson & Gislason 1995, Sundby 2000) 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 (Drinkwater 2006). Svensen et al. (2011) report *C. finmarchicus* in relatively low abundance on the NE Greenland shelf in autumn, but in light of the West Spitsbergen Current warming it is likely that the abundance of this important prey species will increase in the Fram Strait and on the NE Greenland shelf (Weydmann et al. 2018).

### Life histories and colonisation routes

North East Arctic Cod (NEAC), the population origin of the cod found on the NE Greenland shelf, utilises the Barents Sea as a nursery and feeding area and undertakes a counter-current migration against the Norwegian Atlantic Current to the spawning grounds along the Norwegian coast (latitudes 62–71 °N) (Sundby & Nakken

2008). Spawning occurs during March and April in relatively shallow water, where eggs and larvae drift by surface currents (Sundby et al. 1989), such as the Norwegian Atlantic Current, and disperse northwards and eastwards into the Barents Sea (Vikebø et al. 2005). Until late September, the pelagic larvae (0-group) are highly-mobile and retained in the upper-mixed layer. Depending on weather patterns and thus local wind-forcing, up to 1/3 of some 0-group year-classes is advected off the Norwegian and Barents Sea shelf and disperses over the Norwegian Sea (Sundby et al. 1989). 0-group cod have also been observed west of Spitsbergen (Føyn 2002).

We propose that 0-group cod advected off the shelf by wind-forcing (Vikebø et al. 2007, Strand et al. 2017) either outside of their spawning grounds, or at any point until their northern-most report west of Spitsbergen are likely to cross the Fram Strait by the Return Atlantic Current. In October, when cod larvae are >80 mm in total length (TL), they gain motility, descend out of the pelagic layer, and become demersal (Yaragina et al. 2011). 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. Our observations of 0-group cod just off the NE Greenland shelf, in September of 2007 and 2017, demonstrate that this is achievable.

Redfish, on the other hand, are ovoviviparous, i.e. eggs are fertilized, develop and hatch internally and larvae are extruded (Sorokin 1961). Larval extrusion occurs along the continental shelf break of the Norwegian and Barents Seas from latitudes 64–74 °N between March and June (Sorokin 1961, Cadrin et al. 2010) peaking in mid-April (Saborido-Rey & Nedreaas 2000). Larvae are extruded at different depths, resulting in transport to all directions, with most believed to drift north along the continental shelf break (Saborido-Rey & Nedreaas 2000). However, like cod, redfish larvae have been observed in Atlantic water west off the continental shelf, and as far north as Spitsbergen (Hylen et al. 1995, Drevetnyak & Nedreaas 2009). In this study, we observed large numbers of 0-group redfish over the Fram Strait with a genetic signature of the Norwegian-Barents Sea population. Redfish larvae are pelagic until 40–50 mm TL at age 4–5 months when they gain motility and descend to deeper waters by the autumn of their first year (Kelly & Barker 1961). The pelagic larval phase enables long distance dispersal of redfish dictated by currents.

We propose that the 0-group redfish found over the Fram Strait 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 by the time they were 4–5 months old.

Shrimp found on the NE Greenland shelf were shown to originate from the Barents Sea as a whole (see sampling of Jorde et al. 2015). Shrimp spawns in autumn throughout the Barents Sea and their larvae hatch in spring, ascending from the bottom to depths between 0–50 m within a 24-hour period (Pedersen et al. 2003, Garcia 2007). Shrimp larvae are highly-mobile and are distributed according to currents until they are 2–3 months of age when they settle as post-larvae (Shumway et al. 1985, Bergström 2000). Pedersen et al. (2003) simulated shrimp larval drift within the Barents Sea, over three years and demonstrated that larvae were moved maximum distances of 330 km before settling, but often much less owing to a relatively short pelagic larval phase. Thus, we find it more likely that the NE Greenland shrimp originates from the north-west Barents Sea, i.e. at Spitsbergen, than the northern Norwegian Coast or central-eastern Barents Sea. If we assume this to be true, the most likely colonisation route is via the Return Atlantic Current, as is the case with cod and redfish.

**Retention or homing?**

What becomes of cod, redfish and shrimp arriving at the NE Greenland shelf? The most likely scenario, for fishes, is that the NE Greenland shelf functions as a nursery ground, while the Barents Sea remains the preferred spawning habitat. This implies both species are able to home, long-distance and return to the Barents Sea as adults – and would explain why, so far, we have only observed juvenile fish on the NE Greenland shelf.

Cod undertakes counter-current spawning migrations of ~1000 km in both the Barents Sea (Sundby & Nakken 2008), and from West Greenland to Iceland (Jamieson & Jónsson 1971). Although the Fram Strait represents a barrier with depths of >3000 m, cod are able to perform pelagic migrations (Neuenfeldt et al. 2013). This behaviour has been noted from tagging experiments where specimens found at Jan Mayen

Island and the Norwegian coast migrated over deep water to Iceland and the Faroe Islands, respectively (Iversen 1934, Holden 1960). Redfish are not known to perform long-distance migrations (Sorokin 1961), although they are pelagic as adults and do move between the Barents Sea and Jan Mayen Island over deep water of the Norwegian Sea (Saha et al. 2017). Hence, it is possible that as adults, redfish seek deeper waters of the Greenland Sea and return to the Barents Sea.

Shrimp is the only species we observed as adults, and with eggs, implying that they have, or will form a fragmented sub-population. Our results show the genetic distance between NE Greenland and Barents Sea shrimp to be similar to that between Icelandic and Norwegian shrimp which is either a function of high connectivity or an indication of a recently established sub-population of NE Greenland shrimp – and we are unable to rule out either possibility.

**Climate change and range expansions**

Prior to a discussion on climate-driven change, a historical perspective can be insightful, to first avoid misperceptions, but also to understand how ecosystems were resilient to change in the past and, therefore how likely they will be effected by change in the future (Drinkwater 2006). The case study of cod allows the best understanding of this. Studies from the current warm period (1990–present) allude to cod distribution within the Barents Sea shifting north as a result of warming (Wassmann et al. 2011, Fossheim et al. 2015, Vihtakari et al. 2018). Upon inspection, however, this should be understood as a reoccurring phenomenon since cod has supported a substantial fishery in the north-west Barents Sea since the 1870's (e.g. ~50 million individual cod landed per year in the late 19$^{th}$ century, Iverson 1923). Likewise, cod were distributed throughout the northern Barents Sea during the last warm period of the 1920–1960's (Drinkwater 2006). Moreover, the recent find of a 450-year-old cod in multi-year ice in the Canadian High-Arctic (Crawford et al. 2018) may further indicate how far north this species was distributed in the past.

In contrast to the Barents Sea, the NE Greenland shelf is severely understudied (Christiansen et al. 2014). Because of this, biodiversity baselines are fragmentary with no timeline (Christiansen 2012), and it is difficult to establish whether our observations reflect a recent shift driven by climate change or constitute a common component of

the NE Greenland Shelf fauna not previously observed due to a lack of sampling. Despite this, the Barents Sea is the most productive ecosystem in the Northeast Atlantic (Wassmann 2011) and presently supports the historically largest stock of cod (Yaragina et al. 2011). Therefore, in the future we could expect to find more boreal species, and greater numbers thereof, on the NE Greenland shelf. Christiansen et al. (2016) observed the novel finding of a fourth species on the NE Greenland shelf, capelin (*Mallotus villosus*), which was not analysed as part of this study. In addition, Atlantic herring (*Clupea harengus*), Atlantic haddock (*Melanogrammus aeglefinus*) and Atlantic mackerel (*Scomber scombrus*) are present in Spitsbergen waters. So, the three species studied herein are clearly not alone in being capable of entering the NE Greenland shelf. The simulation study by Strand et al. (2017) demonstrates that, depending on year, between 2.4% and 12% of 0-group North East Arctic Cod year classes may be transported northwest along the proposed route (Fig. 2a), which suggests that there is potential for a "boreal invasion" of NE Greenland in the future along this route, if conditions promote survival.

**Implications and future work**

Advection has the potential to restructure Arctic ecosystems (Hunt et al. 2016) and the route identified here suggests that the boreal fauna of the Barents Sea may be further projected onto the NE Greenland shelf by advection in the future. As a result, we can expect trophic relationships to be restructured (Frainer et al. 2017) as boreal generalists such as cod are favoured by climate scenarios (Cheung et al. 2010, Wisz et al. 2015a). Cod, as an example, is a species well-known to predate polar cod (*Boreogadus saida*), other Arctic fishes and zoobenthos (Link et al. 2009, Christiansen 2017), and so, as a figure-head of boreal range expansions into the Arctic, gives a glimpse of what is to come for native Arctic fauna.

The colonisation mechanisms identified here form a drive to improve our understanding of pelagic ecosystem function and structure which is needed to predict the impact of change (Murphy et al. 2016). Further work on this subject should utilise these mechanisms to predict the composition, structure and function (e.g. Frainer et al. 2017) of the Arctic. This work should account for a variety of factors but most notably should consider how likely habitats such as the NE Greenland shelf are to sustain incoming species (c.f. Drinkwater 2006). Recent studies on the zooplankton

present on the NE Greenland shelf (e.g. Svensen et al. 2011), for example, are limited. In addition, studies should consider the impact of ocean warming on spawning location (c.f. Sundby & Nakken 2008), ontogeny, and larval development, as the NE Greenland shelf may become out of range to larvae before conditions there promote enhanced growth (Young et al. 2018). Clearly observations in the understudied seas of the Arctic are needed, especially through non-invasive means, e.g. using acoustic surveys and environmental DNA sampling, and must ensure that this information is made available for inclusion in models to achieve accurate forecasts (Ingvaldsen et al. 2015, Wisz et al. 2015a,b). Finally, bettering our understanding of dispersal routes and ecosystem function, as attempted here, is crucial to model (Murphy et al. 2016) and manage the vulnerable Arctic ecosystems of the future (Harris et al. 2018).

**Conclusion**

Our findings support the hypothesis that cod, redfish, and shrimp are dispersed from the Barents Sea across the Fram Strait and settle on the Northeast Greenland shelf. Due to a lack of time series, we are unable to decipher if this is a new phenomenon, or not. In any case, these boreal generalists may impact native Arctic fauna and with a warming ocean in mind, we suggest that the Northeast Greenland shelf is likely to take on a larger proportion of Atlantic species from Barents Sea origin.

# Future perspectives

If this study were to be extended, with no limitations, it should seek the use of genetic markers, such as SNPs, that have the potential for increased power (Putman & Carbone 2014). It is widely accepted that while microsatellites are more powerful than SNPs by number, they are time-consuming and expensive to develop, hence, relatively few (e.g. ~10–15) microsatellites are commonly used, and as a result, datasets often lack the power to differentiate populations (Hansen et al. 2001, Putman & Carbone 2014). This was observed in the present study e.g. DAPC reference population clusters overlapped in some cases and $F_{ST}$ was low (~0.1) for cod and shrimp data. The fourth species of interest in the planning of this study, capelin, was not analysed for this reason (data not shown). Instead, a reasonable number of SNPs (e.g. ~1000) could be utilised to differentiate populations effectively (Putman & Carbone 2014), achieve greater assignment success, and therefore increase the support of our conclusions.

Alternatively, dispersal routes could be assessed directly via the use of tagging. 0-group fishes could be caught outside of their spawning grounds, in the Norwegian Sea, for example, and tagged before attempted recapture surveys were made. This, though, may prove problematic for two reasons, first, captured redfish are usually non-viable (Drevetnyak & Nedreaas 2009), and second, due to a relatively small proportion of Barents Sea fishes (e.g. 2.4% to 12% of 0-group cod year classes, Strand et al. 2017) expected to disperse to the Northeast Greenland shelf, this method would require large effort and extensive fishing – likely to impact native Arctic fauna. On the other hand, 0-group fish surveys (e.g. Føyn 2002) conducted in the Greenland Sea, would not impact Arctic bottom fauna, and could utilise both sonar and active pelagic fishing. Finally, environmental DNA (eDNA) surveys conducted over the shelf could elucidate the presence or absence of species using metabarcoding or quantitative PCR (e.g. Thomsen et al. 2012) with no impact to fauna. In addition, state-of-the-art eDNA haplotype analysis (e.g. Stat et al. 2017) offers a promising application to population genetic studies, and thus assignment studies of this type in the future.

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# Appendices

## Appendix S1

### PCR Profiles

The PCR profile for cod (from Westgaard & Fevolden 2007) consisted of an initial denaturation step at 95 °C for 15 min, followed by 22 cycles of 95 °C for 30 s, 56 °C for 3 min and 72 °C for 1 min. The PCR reactions ended with a final elongation step of 60 °C for 30 min.

The PCR profile for redfish (from Saha et al. 2017) consisted of an initial denaturation step at 95 °C for 15 min, followed by 25 cycles of 95 °C for 30 s, 56 °C for 90 s and 72 °C for 1 min. The PCR reactions ended with a final elongation step of 60 °C for 45 min.

The PCR profile for shrimp (from Pereyra et al. 2012) consisted of an initial denaturation step at 95 °C for 15 min, followed by 35 cycles of 95 °C for 30 s, 56 °C for 3 min and 72 °C for 1 min. The PCR reactions ended with a final elongation step of 60 °C for 30 min.

### Microsatellite loci evaluation

*Methods:*

MICRO-CHECKER (v. 2.2.3, Van Oosterhout et al. 2004) was used to identify large allele drop-out, null alleles, and stuttering scoring errors. Locus-wise deviation from HWE was analysed using GENEPOP (v. 4.2.1, Rousset 2008) using exact tests (Guo & Thompson 1992), in addition to Linkage Disequilibrium (LD) identification between loci. In addition, BAYESCAN (v. 2.1, Foll & Gaggiotti 2008) and ARLEQUIN (v. 3.5.2.2, Excoffier & Lischer 2010) were used to test loci neutrality with default settings. ARLEQUIN simulations examined the joint distribution of $F_{ST}$ and heterozygosity under a hierarchical island model (Beaumont & Nichols 1996). All results were judged for significance under the false discovery rate (FDR) approach (Benjamini & Yekutieli 2001) at the 5% level. Loci were not considered to be non-neutral unless both approaches reported them as such.

*Results:*

There was no evidence of large allele dropout in any loci. Several cases of stuttering and significant LD were reported, though these were deemed as non-genuine since genuine stuttering and LD are expected to affect all populations equally (Dormontt et al. 2014). Loci were deemed to be subject to null alleles if null alleles were present in more than a single population. This applied to one locus of each species (cod: Gmo35, redfish: Spi6, shrimp: PbA104a). No loci deviated from HWE in more than a single population. No loci were consistently reported as non-neutral outliers under both approaches utilised.

**Table S1.** Microsatellite loci are shown in amplification multiplexes (MP's) and as utilised under both screening conditions and analyses (following: Westgaard & Fevolden 2007, Pereyra et al. 2012, Saha et al. 2017).

| Species | Condition 1 | All loci |
|---|---|---|
| Cod | MP1: Gmo8, Gmo19, Gmo35, Gmo37, Tch11<br>MP2: Gmo2, Gmo3, Gmo34, Tch13, Gmo132 | MP1: Gmo8, Gmo19, Gmo35, Gmo37, Tch11<br>MP2: Gmo2, Gmo3, Gmo34, Tch13, Gmo132 |
| **Total** | **9** | **10** |
| Redfish | MP1: Sal1, Sal3, Sal4, Smen05<br>MP2: Spi4, Spi10, Smen10<br>MP3: Seb09, Seb25, Seb31, Seb33, Seb45 | MP1: Sal1, Sal3, Sal4, Smen05<br>MP2: Spi4, Spi6, Spi10, Smen10<br>MP3: Seb09, Seb25, Seb31, Seb33, Seb45 |
| **Total** | **12** | **13** |
| Shrimp | MP1: PbC8, PbC105, SD2-14<br>MP2: PbA1, PbA110, PbC109, PbD9<br>MP3: SD1-41, SD2-68, SD3-62 | MP1: PbA104a, PbC8, PbC105, SD2-14<br>MP2: PbA1, PbA110, PbC109, PbD9<br>MP3: SD1-41, SD2-68, SD3-62 |
| **Total** | **10** | **11** |

## Appendix S2

### Reference dataset evaluation

*Methods:*

To test the power of assignment, the function `predict.dapc` in the R package *adegenet* was used to re-assign all reference samples back to their original *a priori* population clusters. The `x.val` function indicated the number of principle components to retain. ARLEQUIN was used to calculate pairwise $F_{ST}$ values (Weir & Cockerham 1984) between the reference populations. Only results for the all-loci condition of analysis are shown.

*Results:*

DAPC reassignment reported reference samples were successfully re-assigned to their original cluster (population) in 97% (cod) and 93% (redfish & shrimp) of cases. $F_{ST}$ values ranged from 0.011 to 0.040 and were all highly significant ($P$ <0.001) (Table S2).

**Table S2.** Pairwise $F_{ST}$ values and $P$-values. The values in boldface are significant after false discovery rate control at $P$ = 0.05. For abbreviations refer to Table S3.

| Species | | | | | |
|---|---|---|---|---|---|
| Cod | | ICE | NCC | NEAC | |
| | ICE | - | **0.000** | **0.000** | |
| | NCC | 0.024 | - | **0.000** | |
| | NEAC | 0.014 | 0.023 | - | |
| Redfish | | NSH | EGS | IDP | |
| | NSH | - | **0.000** | **0.000** | |
| | EGS | 0.031 | - | **0.000** | |
| | IDP | 0.037 | 0.040 | - | |
| Shrimp | | NOR | SPW | ICE | JMA |
| | NOR | - | **0.000** | **0.000** | **0.000** |
| | SPW | 0.031 | - | **0.000** | **0.000** |
| | ICE | 0.011 | 0.019 | - | **0.000** |
| | JMA | 0.038 | 0.024 | 0.025 | - |

## Appendix S3

## Reference population structure

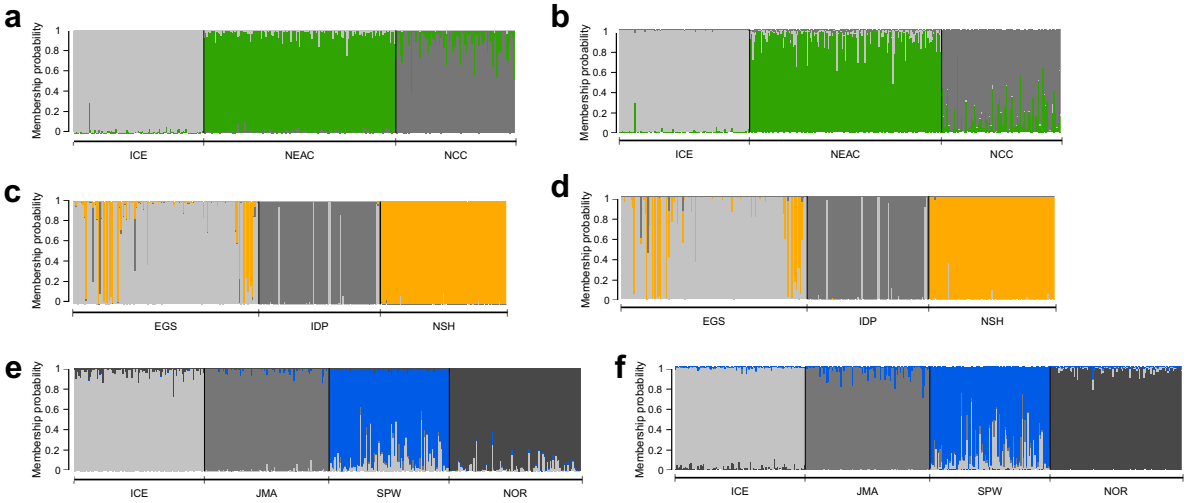


**Fig. S3.** STRUCTURE barplots showing Atlantic cod (*Gadus morhua*) (**a**, **b**), beaked redfish (*Sebastes mentella*) (**c**, **d**) and deep-sea shrimp (*Pandalus borealis*) (**e**, **f**) reference population membership probabilities (*q*) prior to the removal of individuals with a threshold of *q* lower/higher than 0.2/0.8. Barplots (**a**, **c** & **e)** utilised a reduced number of loci (Condition 1). Barplots (**b**, **d** & **f**) utilised all loci available regardless of potential scoring errors identified. For abbreviations refer to Table S3.

**Table S3.** Details of reference populations for each species, post removal of individuals with a threshold of *q* lower/higher than 0.2/0.8 and, under both analyses conditions. Abbr. = the abbreviated population name, *n* = sample size (number of genotyped individuals).

| Species | Population | Abbr. | Condition 1 *n* | All loci *n* |
|---|---|---|---|---|
| Cod | Iceland | ICE | 92 | 92 |
| | Norwegian Coastal Cod | NCC | 67 | 57 |
| | North East Arctic Cod | NEAC | 136 | 126 |
| Redfish | Iceland Deep | IDP | 80 | 80 |
| | South-East Greenland Slope | EGS | 111 | 109 |
| | Norway Shallow | NSH | 91 | 90 |
| Shrimp | Iceland | ICE | 90 | 92 |
| | Jan Mayen Island | JMA | 87 | 87 |
| | Norway | NOR | 87 | 91 |
| | Spitsbergen West | SPW | 45 | 58 |

## Appendix S4

### Evaluation of the impact of potential scoring errors on assignment

When using the datasets where loci subject to potential scoring errors (specifically, null alleles) were removed, individual assignment using STRUCTURE resulted in the same outcome as when analysing the data utilising all loci available, regardless of scoring errors. STRUCTURE barplots (Fig. S4) show that 100% of cod, 95% of redfish and 80% of shrimp tests resulted in the genetic assignment of individuals to a population within the Barents Sea, with a high membership probability ($q$ >0.8) suggesting a high-likelihood that specimens of the three species found off Northeast Greenland originate from the Barents Sea.

DAPC clustering using datasets where loci with potential scoring errors were removed resembled the results when using all loci available (Fig. S4a,c,e). The NE Greenland group of all three species clustered closely with the same Barents Sea populations as indicated by the assignment testing (Fig. S4b,d,f). The 95% DAPC cluster ellipses between NEG and these population clusters overlapped considerably, though overlap was also evident between the reference population clusters, most significantly for the cod and shrimp clusters. The distance between the NE Greenland group clusters and clusters they were assigned to using STRUCTURE only differed for the shrimp data. Here, there is a greater distance between the NE Greenland shrimp group and Spitsbergen West shrimp group, than when analysed using all loci available.

Therefore, we suggest that the impact of potential null alleles on assignment was minimal and that utilising all loci available regardless of null alleles did not bias the assignment outcome.

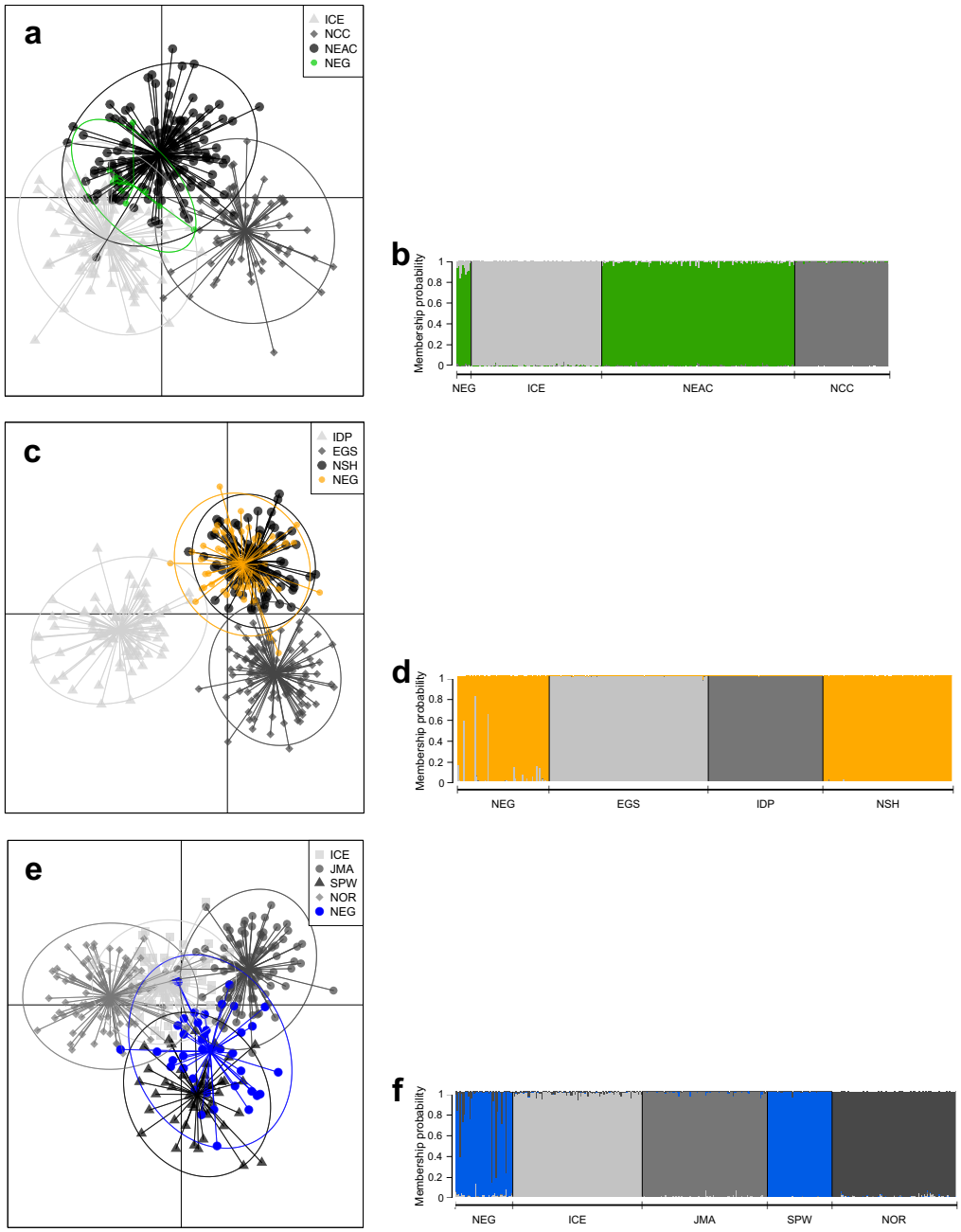


**Fig. S4.** Genetic analysis using a reduced set of loci that accounted for potential scoring errors, that we termed 'Condition 1', for Atlantic cod (*Gadus morhua*) (**a**, **b**), beaked redfish (*Sebastes mentella*) (**c**, **d**) and deep-sea shrimp (*Pandalus borealis*) (**e**, **f**) data. DAPC scatterplots (**a, c**, **e**) show how the NE Greenland groups relate to the reference populations of the Northeast Atlantic Ocean. DAPC cluster ellipses were set to contain 95% of genotypes. DAPC scatterplots explain 91% (**a**), 94% (**c**) and 99% (**e**) of the total variation observed. STRUCTURE barplots (**b**, **d**, **f**) show membership probabilities (*q*) for NE Greenland individuals based on the reference populations used. For abbreviations refer to Table S3.

## Appendix S5

### Assignment membership probabilities

STRUCTURE and *snapclust* membership probabilities (*q*) for cod (Table S5.1), redfish (Table S5.2) and shrimp (Table S5.3) specimens caught off Northeast Greenland are shown, and summarised with the most probable assignment origin indicated for both methods.

**Table S5.1.** STRUCTURE and *snapclust* identified population origin and membership probabilities (*q*) for Northeast Greenland (NEG) cod individuals using all loci. Bold typeface indicates the *q* values supporting the most probable origin of each individual. For abbreviations refer to Table S3.

| Sample | STRUCTURE origin | *snapclust* origin | STRUCTURE *q* values | | | *snapclust q* values | | |
|---|---|---|---|---|---|---|---|---|
| | | | ICE | NEAC | NCC | ICE | NEAC | NCC |
| NEG Cod 1 | NEAC | NEAC | 0.133 | **0.852** | 0.015 | 0.230 | **0.630** | 0.140 |
| NEG Cod 2 | NEAC | NEAC | 0.074 | **0.925** | 0.001 | 0.056 | **0.943** | 0.001 |
| NEG Cod 3 | NEAC | NEAC | 0.158 | **0.839** | 0.003 | 0.388 | **0.601** | 0.011 |
| NEG Cod 4 | NEAC | NEAC | 0.148 | **0.848** | 0.003 | 0.380 | **0.605** | 0.015 |
| NEG Cod 5 | NEAC | NEAC | 0.063 | **0.935** | 0.002 | 0.092 | **0.887** | 0.021 |
| NEG Cod 6 | NEAC | NEAC | 0.160 | **0.835** | 0.005 | 0.373 | **0.620** | 0.007 |
| NEG Cod 7 | NEAC | NEAC | 0.144 | **0.840** | 0.016 | 0.284 | **0.631** | 0.085 |
| NEG Cod 8 | NEAC | NEAC | 0.171 | **0.825** | 0.004 | 0.466 | **0.520** | 0.014 |
| NEG Cod 9 | NEAC | ICE | 0.188 | **0.802** | 0.010 | **0.557** | 0.326 | 0.117 |
| NEG Cod 10 | NEAC | NEAC | 0.038 | **0.962** | 0.000 | 0.036 | **0.962** | 0.002 |

**Table S5.2.** STRUCTURE and *snapclust* identified population origin and membership probabilities (*q*) for Northeast Greenland (NEG) redfish individuals using all loci. Bold typeface indicates the *q* values supporting the most probable origin of each individual. For abbreviations refer to Table S3.

| Sample | STRUCTURE origin | *snapclust* origin | STRUCTURE *q* values | | | *snapclust q* values | | |
|---|---|---|---|---|---|---|---|---|
| | | | EGS | IDP | NSH | EGS | IDP | NSH |
| NEG Redfish 1 | NSH | NSH | 0.044 | 0.000 | **0.956** | 0.217 | 0.001 | **0.782** |
| NEG Redfish 2 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.016 | **0.983** |
| NEG Redfish 3 | NSH | NSH | 0.003 | 0.002 | **0.995** | 0.036 | 0.056 | **0.908** |
| NEG Redfish 4 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.004 | 0.001 | **0.995** |
| NEG Redfish 5 | EGS | EGS | **0.870** | 0.052 | 0.079 | **0.553** | 0.226 | 0.221 |
| NEG Redfish 6 | NSH | NSH | 0.004 | 0.000 | **0.996** | 0.044 | 0.000 | **0.956** |
| NEG Redfish 7 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 8 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 9 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 10 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 11 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |
| NEG Redfish 12 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.012 | 0.001 | **0.987** |
| NEG Redfish 13 | EGS | EGS | **0.919** | 0.000 | 0.081 | **0.990** | 0.000 | 0.010 |
| NEG Redfish 14 | NSH | NSH | 0.027 | 0.002 | **0.971** | 0.017 | 0.032 | **0.801** |
| NEG Redfish 15 | NSH | NSH | 0.003 | 0.000 | **0.997** | 0.023 | 0.000 | **0.977** |
| NEG Redfish 16 | NSH | NSH | 0.003 | 0.001 | **0.996** | 0.031 | 0.061 | **0.908** |
| NEG Redfish 17 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 18 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.001 | **0.998** |
| NEG Redfish 19 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.002 | 0.000 | **0.998** |
| NEG Redfish 20 | NSH | NSH | 0.005 | 0.000 | **0.995** | 0.063 | 0.000 | **0.937** |
| NEG Redfish 21 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.009 | 0.000 | **0.991** |
| NEG Redfish 22 | EGS | EGS | **0.746** | 0.001 | 0.253 | **0.953** | 0.002 | 0.045 |
| NEG Redfish 23 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.023 | 0.003 | **0.974** |
| NEG Redfish 24 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.033 | 0.003 | **0.964** |
| NEG Redfish 25 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 26 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.009 | 0.000 | **0.991** |
| NEG Redfish 27 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 28 | NSH | NSH | 0.006 | 0.000 | **0.994** | 0.048 | 0.000 | **0.952** |
| NEG Redfish 29 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.005 | 0.000 | **0.995** |
| NEG Redfish 30 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.001 | **0.998** |
| NEG Redfish 31 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.007 | 0.000 | **0.993** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| NEG Redfish 32 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.002 | 0.000 | **0.998** |
| NEG Redfish 33 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **0.999** |
| NEG Redfish 34 | NSH | NSH | 0.008 | 0.000 | **0.992** | 0.076 | 0.000 | **0.924** |
| NEG Redfish 35 | NSH | NSH | 0.009 | 0.001 | **0.990** | 0.028 | 0.024 | **0.948** |
| NEG Redfish 36 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.004 | 0.000 | **0.996** |
| NEG Redfish 37 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.026 | 0.003 | **0.971** |
| NEG Redfish 38 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.002 | 0.000 | **0.998** |
| NEG Redfish 39 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 40 | NSH | EGS | 0.120 | 0.000 | **0.880** | **0.693** | 0.000 | 0.307 |
| NEG Redfish 41 | NSH | NSH | 0.022 | 0.000 | **0.978** | 0.023 | 0.000 | **0.977** |
| NEG Redfish 42 | NSH | NSH | 0.004 | 0.000 | **0.996** | 0.176 | 0.005 | **0.819** |
| NEG Redfish 43 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |
| NEG Redfish 44 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.001 | **0.999** |
| NEG Redfish 45 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 46 | NSH | NSH | 0.028 | 0.000 | **0.971** | 0.127 | 0.002 | **0.871** |
| NEG Redfish 47 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.012 | 0.000 | **0.988** |
| NEG Redfish 48 | NSH | NSH | 0.001 | 0.002 | **0.997** | 0.005 | 0.045 | **0.950** |
| NEG Redfish 49 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.007 | 0.000 | **0.993** |
| NEG Redfish 50 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.001 | **0.999** |
| NEG Redfish 51 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.001 | **0.999** |
| NEG Redfish 52 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.001 | 0.000 | **0.999** |
| NEG Redfish 53 | NSH | NSH | 0.004 | 0.000 | **0.996** | 0.175 | 0.000 | **0.825** |
| NEG Redfish 54 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |
| NEG Redfish 55 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |
| NEG Redfish 56 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.285 | 0.000 | **0.715** |
| NEG Redfish 57 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |
| NEG Redfish 58 | NSH | NSH | 0.002 | 0.000 | **0.998** | 0.107 | 0.001 | **0.892** |
| NEG Redfish 59 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.001 | **0.999** |
| NEG Redfish 60 | NSH | NSH | 0.001 | 0.000 | **0.999** | 0.025 | 0.000 | **0.975** |
| NEG Redfish 61 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.004 | **0.996** |
| NEG Redfish 62 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.016 | 0.010 | **0.974** |
| NEG Redfish 63 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.007 | 0.000 | **0.993** |
| NEG Redfish 64 | NSH | NSH | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | **1.000** |

**Table S5.3.** STRUCTURE and *snapclust* identified population origin and membership probabilities (*q*) for Northeast Greenland (NEG) shrimp individuals using all loci. Bold typeface indicates the *q* values supporting the most probable origin of each individual. For abbreviations refer to Table S3.

| Sample | STRUCTURE origin | *snapclust* origin | STRUCTURE *q* values | | | | *snapclust q* values | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | ICE | JMA | SPW | NOR | ICE | JMA | SPW | NOR |
| NEG Shrimp 1 | SPW | ICE | 0.027 | 0.027 | **0.938** | 0.008 | **0.451** | 0.439 | 0.096 | 0.014 |
| NEG Shrimp 2 | SPW | SPW | 0.008 | 0.000 | **0.976** | 0.016 | 0.063 | 0.012 | **0.751** | 0.175 |
| NEG Shrimp 3 | SPW | SPW | 0.008 | 0.015 | **0.977** | 0.000 | 0.301 | 0.253 | **0.445** | 0.002 |
| NEG Shrimp 4 | SPW | NOR | 0.003 | 0.02 | **0.914** | 0.063 | 0.010 | 0.168 | 0.207 | **0.615** |
| NEG Shrimp 5 | SPW | SPW | 0.015 | 0.001 | **0.982** | 0.002 | 0.197 | 0.022 | **0.772** | 0.009 |
| NEG Shrimp 6 | SPW | SPW | 0.007 | 0.008 | **0.962** | 0.023 | 0.135 | 0.132 | **0.534** | 0.200 |
| NEG Shrimp 7 | SPW | NOR | 0.006 | 0.000 | **0.979** | 0.015 | 0.159 | 0.009 | 0.257 | **0.575** |
| NEG Shrimp 8 | SPW | SPW | 0.011 | 0.001 | **0.983** | 0.005 | 0.169 | 0.018 | **0.715** | 0.098 |
| NEG Shrimp 9 | SPW | SPW | 0.004 | 0.000 | **0.996** | 0.000 | 0.028 | 0.012 | **0.958** | 0.001 |
| NEG Shrimp 10 | SPW | SPW | 0.007 | 0.000 | **0.987** | 0.006 | 0.137 | 0.001 | **0.805** | 0.057 |
| NEG Shrimp 11 | SPW | SPW | 0.002 | 0.013 | **0.967** | 0.018 | 0.008 | 0.349 | **0.584** | 0.058 |
| NEG Shrimp 12 | SPW | SPW | 0.000 | 0.000 | **0.998** | 0.002 | 0.001 | 0.003 | **0.967** | 0.028 |
| NEG Shrimp 13 | SPW | SPW | 0.000 | 0.001 | **0.999** | 0.000 | 0.000 | 0.098 | **0.900** | 0.001 |
| NEG Shrimp 14 | SPW | SPW | 0.001 | 0.000 | **0.998** | 0.001 | 0.002 | 0.002 | **0.991** | 0.005 |
| NEG Shrimp 15 | SPW | SPW | 0.005 | 0.001 | **0.990** | 0.004 | 0.023 | 0.026 | **0.832** | 0.119 |
| NEG Shrimp 16 | SPW | ICE | 0.042 | 0.003 | **0.954** | 0.001 | **0.798** | 0.013 | 0.188 | 0.002 |
| NEG Shrimp 17 | SPW | JMA | 0.000 | 0.042 | **0.958** | 0.000 | 0.001 | **0.707** | 0.290 | 0.002 |
| NEG Shrimp 18 | SPW | SPW | 0.001 | 0.014 | **0.985** | 0.000 | 0.003 | 0.273 | **0.716** | 0.007 |
| NEG Shrimp 19 | SPW | SPW | 0.002 | 0.001 | **0.997** | 0.000 | 0.042 | 0.018 | **0.933** | 0.007 |
| NEG Shrimp 20 | SPW | SPW | 0.001 | 0.007 | **0.992** | 0.000 | 0.008 | 0.437 | **0.555** | 0.000 |
| NEG Shrimp 21 | SPW | SPW | 0.008 | 0.004 | **0.986** | 0.001 | 0.208 | 0.171 | **0.551** | 0.070 |
| NEG Shrimp 22 | SPW | SPW | 0.007 | 0.001 | **0.992** | 0.000 | 0.180 | 0.055 | **0.751** | 0.014 |
| NEG Shrimp 23 | SPW | SPW | 0.001 | 0.001 | **0.999** | 0.000 | 0.007 | 0.033 | **0.960** | 0.001 |
| NEG Shrimp 24 | SPW | SPW | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | 0.028 | **0.971** | 0.000 |
| NEG Shrimp 25 | SPW | SPW | 0.004 | 0.002 | **0.993** | 0.001 | 0.052 | 0.095 | **0.846** | 0.007 |
| NEG Shrimp 26 | SPW | NOR | 0.013 | 0.001 | **0.824** | 0.162 | 0.017 | 0.004 | 0.038 | **0.942** |
| NEG Shrimp 27 | SPW | SPW | 0.004 | 0.008 | **0.979** | 0.009 | 0.041 | 0.126 | **0.776** | 0.057 |
| NEG Shrimp 28 | SPW | SPW | 0.007 | 0.002 | **0.990** | 0.001 | 0.112 | 0.050 | **0.828** | 0.010 |
| NEG Shrimp 29 | SPW | NOR | 0.004 | 0.000 | **0.924** | 0.072 | 0.022 | 0.001 | 0.212 | **0.765** |
| NEG Shrimp 30 | SPW | SPW | 0.005 | 0.003 | **0.976** | 0.016 | 0.079 | 0.037 | **0.751** | 0.132 |
| NEG Shrimp 31 | SPW | SPW | 0.003 | 0.005 | **0.991** | 0.001 | 0.021 | 0.201 | **0.769** | 0.009 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| NEG Shrimp 32 | SPW | SPW | 0.011 | 0.003 | **0.985** | 0.001 | 0.203 | 0.144 | **0.645** | 0.008 |
| NEG Shrimp 33 | SPW | JMA | 0.005 | 0.026 | **0.945** | 0.024 | 0.029 | **0.587** | 0.273 | 0.111 |
| NEG Shrimp 34 | SPW | SPW | 0.003 | 0.000 | **0.996** | 0.001 | 0.183 | 0.004 | **0.798** | 0.016 |
| NEG Shrimp 35 | SPW | SPW | 0.004 | 0.000 | **0.996** | 0.000 | 0.128 | 0.002 | **0.869** | 0.002 |
| NEG Shrimp 36 | SPW | ICE | 0.052 | 0.008 | **0.837** | 0.103 | **0.504** | 0.016 | 0.069 | 0.411 |
| NEG Shrimp 37 | SPW | SPW | 0.000 | 0.000 | **1.000** | 0.000 | 0.000 | 0.001 | **0.999** | 0.000 |
| NEG Shrimp 38 | SPW | SPW | 0.004 | 0.003 | **0.993** | 0.000 | 0.013 | 0.238 | **0.749** | 0.000 |
| NEG Shrimp 39 | SPW | SPW | 0.002 | 0.002 | **0.996** | 0.000 | 0.030 | 0.109 | **0.851** | 0.010 |
| NEG Shrimp 40 | SPW | JMA | 0.008 | 0.054 | **0.937** | 0.001 | 0.094 | **0.680** | 0.225 | 0.002 |

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**Acknowledgements** Thanks are extended to the Government of Greenland and the crew on board R/V *Helmer Hanssen* for access to the Greenland Sea. We thank Tanja L. Hanebrekke for laboratory assistance. This study is part of the TUNU-Programme, UiT The Arctic University of Norway, and was part-funded by a Small Research Grant from The Fisheries Society of the British Isles.