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Original Article

Genetic differentiation between inshore and offshore populations of northern shrimp (*Pandalus borealis*)

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Many marine organisms have a permanent presence both inshore and offshore and spawn in multiple areas, yet their status as separate populations or stocks remain unclear. This is the situation for the northern shrimp (*Pandalus borealis*) around the Arctic Ocean, which in northern Norway represents an important income for a small-scale coastal fishery and a large-vessel offshore fleet. In Norwegian waters, we uncovered two distinct genetic clusters, viz. a Norwegian coastal and a Barents Sea cluster. Shrimps with a mixed heritage from the Norwegian coastal and the Barents Sea clusters, and genetically different from both, inhabit the fjords at the northernmost coast (Finnmark). Genetic structure between fjords did not display any general trend, and only the Varangerfjord in eastern Finnmark displayed significant genetic structure within the fjord. Shrimps in the Finnmark fjords differed in some degree from shrimps both in the adjacent Barents Sea and along the rest of the coast and should probably be considered a separate management unit.

Keywords: coastal and offshore populations, fjord populations, genetic clusters, management unit, microsatellite DNA, *Pandalus borealis*, *Pandalus eous*.

Introduction

The presence of multiple stocks within fishery represents a common problem in fishery management. Genetic research has revealed stock substructure in many or most marine fishes and other organisms, also at small geographical scales (Hauser and Carvalho, 2008, and references therein). Management has mainly been focusing on the bigger offshore fisheries, where management units typically have been defined by geographical and economic boundaries rather than by biological populations. However, correctly identifying biological populations of fish and shellfish is essential in fishery management (Reiss *et al.*, 2009; Kerr *et al.*, 2017). In the West-Atlantic, Smedbol and Stephenson, (2001) demonstrated the importance of managing within-species diversity in cod and herring fisheries. Assessing only a portion of a biological population may bias analyses of growth, recruitment, and mortality which are key parameters when making forecasts and estimating yields. On the other hand, assessing a biological population and making inferences about stock status of its different components may also give biased results if the sub-groups are demographically independent. Finally, not taking into account the possibility of a management unit consisting of several genetic sub-populations might result in overexploitation of local populations, leading to loss of intraspecific genetic variation and adaptive potential (Hauser and Carvalho, 2008; Kerr *et al.*, 2017). Genetic differences between offshore and coastal populations have been detected in several marine organisms, including

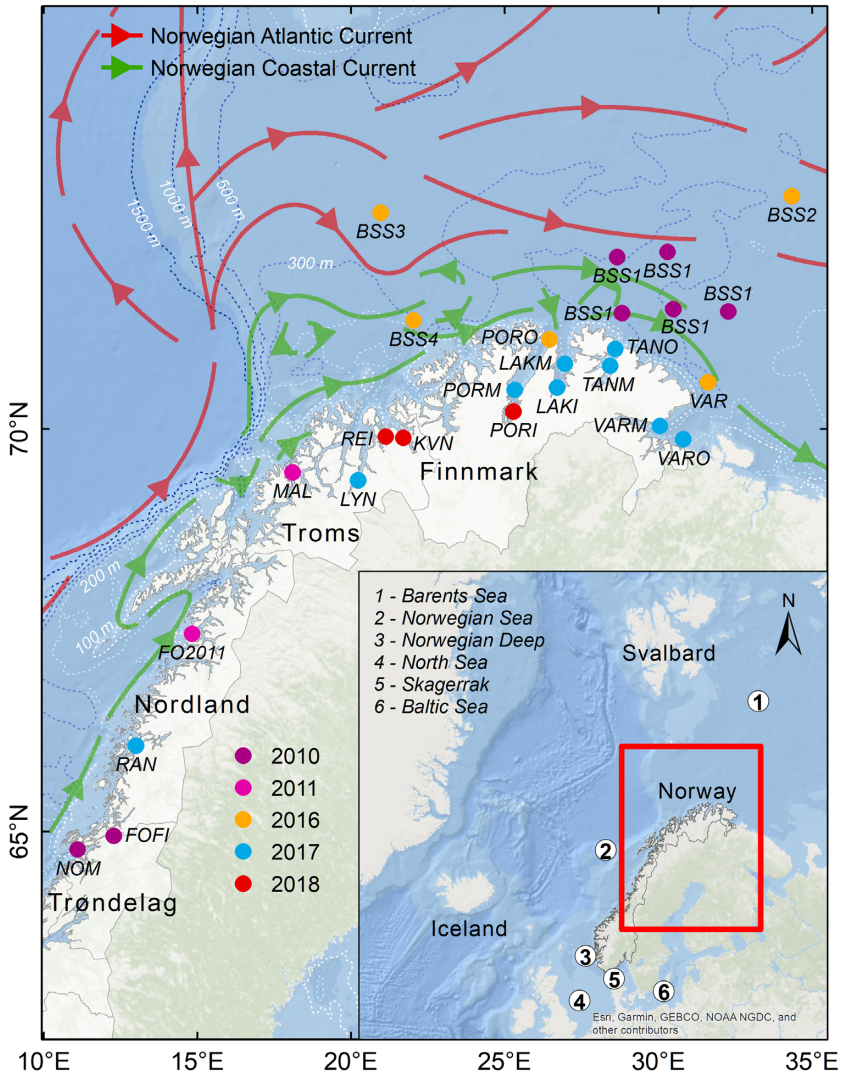

Figure 1. Map of the study and sampling area of *P. borealis*. Sampling localities (= sample names) given as abbreviated names; full names are given in Table 1. Colours indicate sampling year. The sample from Vancouver Island (Pacific Ocean) is not included in the map. The main pathways of the Norwegian Atlantic current (NAC) and the Norwegian Coastal Current (NCC) are displayed in the map.

European sprat (*Sprattus sprattus*), Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Ruzzante *et al.*, 1996; Westgaard and Fevolden, 2007; Pampoulie *et al.*, 2011; Berg *et al.*, 2017; Johansen *et al.*, 2018; Quintela *et al.*, 2020; Berg *et al.*, 2021).

The northern shrimp, *Pandalus borealis* is a circumpolar species common on the continental shelves in boreal waters. In the Northeast (NE) Atlantic, it is found from the Skagerrak to north of Svalbard (Shumway *et al.*, 1985; Bergström, 2000) (Figure 1). Two subspecies are recognised: *P. borealis borealis* Krøyer, 1838 in the Atlantic Ocean and *P. borealis eous* Makarov, 1935 in the Pacific Ocean (Garcia, 2007; Rasmussen and Aschan, 2011). The latter was raised to species level as *Pandalus eous* by Squires, (1992), but this division has not been universally accepted (Bergström, 2000; Garcia, 2007). *P. borealis* is a protandric hermaphrodite, functioning first as male, before passing through a transitional phase and becoming female (Shumway *et al.*, 1985). The larvae hatch in the spring (Shumway *et al.*, 1985), and the five pelagic larval stages drift with ocean currents before settling on the bottom (Pedersen *et al.*, 2003; Ouellet and Allard, 2006; Rasmussen and Aschan, 2011). The relatively long larval stage renders possible extensive dispersal (Drengstig *et al.*, 2000), which may tend to genetically homogenize populations.

In the NE Atlantic, *P. borealis* is the most abundant and commercially important shrimp species (Shumway *et al.*, 1985; Garcia, 2007). The two economically most important stocks of northern shrimp in Norwegian waters are found in the Barents Sea, and in the Skagerrak and Norwegian Deep (Garcia, 2007; NAFO and ICES, 2020) (Figure 1). While these offshore stocks are annually monitored and assessed, the patchily distributed populations along the Norwegian coast have received little scientific attention, yet they represent an important source of income for a small-scale fishery. There is presently an increasing focus on the coastal shrimp populations from both management and the general public, particularly in connection with the vulnerability of shrimp to chemical sea lice controlling agents used in salmon aquaculture along the Norwegian coast (e.g. Bechmann *et al.*, 2017; Bjørkan and Rybråten, 2019; Bechmann *et al.*, 2020). The present distribution and abundance, and the genetic stock structure of the Norwegian fjord populations of shrimp are to a large extent unknown. Earlier mapping of commercial shrimp grounds through interviews of local fishers

Table 1. Location (name and geographic coordinates), sampling year, and number of genotyped individuals (*n*) of all samples of *P. borealis*, where *t* = total number analysed.

Region or county	Locality	Sample	Year	Position	n/t
Barents Sea	Barents Sea south	BSS1[a]	2010	71°15`N 28°48`E	19/20
	Barents Sea south	BSS1[a]	2010	71°17`N 30°28`E	18/20
	Barents Sea south	BSS1[a]	2010	71°16`N 32°15`E	18/20
	Barents Sea south	BSS1[a]	2010	71°52`N 30°17`E	19/20
	Barents Sea south	BSS1[a]	2010	71°49`N 28°39`E	11/11
	Barents Sea south	BSS2	2016	72°26`N 34°19`E	91/94
	Barents Sea south	BSS3	2016	72°16`N 20°57`E	50/51
	Barents Sea south	BSS4	2016	71°10`N 22°01`E	40/43
Finnmark	Varangerfjord outer	VARO	2017	69°52`N 30°47`E	92/94
	Varangerfjord middle	VARM	2017	70°01`N 30°02`E	90/94
	Outside Vardø	VAR	2016	70°30`N 31°36`E	92/94
	Tanafjord outer	TANO	2017	70°52`N 28°35`E	91/94
	Tanafjord middle	TANM	2017	70°41`N 28°24`E	92/94
	Laksefjord middle	LAKM	2017	70°42`N 26°56`E	90/94
	Laksefjord inner	LAKI	2017	70°27`N 26°41`E	92/94
	Porsangerfjord outer	PORO	2016	70°58`N 26°26`E	89/94
	Porsangerfjord middle	PORM	2017	70°25`N 25°18`E	75/94
	Porsangerfjord inner	PORI	2018	70°11`N 25°15`E	92/94
Troms	Kvænangen	KVN	2018	69°53`N 21°42`E	91/94
	Reisafjord	REI	2018	69°54`N 21°07`E	92/94
	Lyngen	LYN	2017	69°25`N 20°13`E	91/94
	Malangen	MAL	2011	69°30`N 18°05`E	91/96
Nordland	Folda	FO2011	2011	67°35`N 14°49`E	96/96
	Ranfjord	RAN	2017	66°09`N 12°59`E	92/94
Trøndelag	Follafjord inner	FOFI	2010	64°56`N 12°16`E	94/96
	Tviberg	NOM[a]	2010	64°45`N 11°05`E	96/96
Canada	Vancouver Island	VANC	2015	49°20`N 123°27`E	85/96

[a]The data set includes some samples analysed by Jorde *et al.,* (2015). The BSS1 sample consists of five subsamples following the sampling scheme of Jorde *et al.,* (2015), where shrimp were collected from several trawl hauls to sample a site representatively.
Sample names are most often composed of three letters referring to fjord/area, and a fourth letter referring to locality within fjords (outer, middle, inner) or a figure numbering the samples (Barents Sea samples).

(Fiskeri, fiskeridir.no) revealed isolated pockets of shrimp in several fjords. New insights on possible population subdivision and locally adapted shrimp are highly relevant to fisheries management as preservation of genetic resources is critical to sustain stocks continuation (Hauser and Carvalho, 2008).

Earlier analyses of the genetic population structure of *P. borealis* in the NE Atlantic found evidence of genetic differentiation between shrimp from the Barents Sea and Svalbard area, and shrimp in the Norwegian fjords and around Jan Mayen (Drengstig *et al.*, 2000; Martinez *et al.*, 2006). In the Pacific Ocean, an allozyme study by Kartavtsev *et al.,* (1993) on *P. borealis* in the Sea of Japan, the Sea of Okhotsk, and the Bering Sea revealed within-sea-basin genetic homogeneity, and statistically significant heterogeneity among samples from the different seas. Microsatellites developed for *P. borealis* (Pereyra *et al.*, 2012) revealed only weak genetic structure among oceanic *P. borealis* samples from the Skagerrak and the Norwegian Deep (Knutsen *et al.*, 2015), in accordance with the current management regime of one single stock (ICES, 1990; NAFO and ICES, 2020). In a large-scale study across the whole North Atlantic, using the same microsatellite markers, marked genetic clustering was detected and attributed to regional differences in bottom temperature (Jorde *et al.*, 2015). The study included 21 samples from waters off the USA, Canada, Greenland, Iceland, Jan Mayen, and Norway (including Svalbard). In Norwegian waters, the study found little if any genetic differences between shrimp in the Norwegian Deep and along the coast of the Trøndelag county (Figure 1), but profound and significant differences between these samples on one hand and shrimp in the Barents Sea region on the other hand. Thus, together the studies by Knutsen *et al.*, (2015) and Jorde *et al.*, (2015) found that there is only weak and non-significant genetic structuring among northern shrimp sampled along the southern Norwegian coast, from the Skagerrak to the Trøndelag county.

The main objective of the present study is to test for population genetic structure of northern shrimp along the Norwegian coast, focusing on northern areas (i.e. the region within the red frame in Figure 1), while emphasizing the following research questions: (i) where is the genetic border between coastal shrimp and the Barents Sea shrimp located?, (ii) is there any genetic differentiation between fjord populations?, (iii) is there any genetic population structure within fjords?, and (iv) is there any genetic difference between *Pandalus* shrimp in the Atlantic and Pacific Ocean? Using the same set of microsatellite markers as in Jorde *et al.,* (2015) allowed us to combine our data with this previous study. Specifically, we combined the sample from the Trøndelag county and one sample from the Barents Sea from Jorde *et al.*, (2015) with new samples from the Norwegian coast and the southern Barents Sea (Table 1).

Material and Methods

Study area

Water masses in the Norwegian coastal areas and fjords are heavily influenced by offshore water (Figure 1). The northward flowing Norwegian Coastal Current (NCC) interacts with surface waters in

Table 2. Characteristics of the sampled fjords (with data presented for respectively the inner, middle, and outer parts of the Porsangerfjord due to its size and internal variations in hydrography), with fjord length in km, maximum and sill depth in m, and temperature (minimum, average and maximum) in °C.

County	Fjord	Length	Maximum depth	Sill depth	Minimum temperature	Average temperature	Maximum temperature	Connection to offshore waters
Finnmark	Varangerfjord	95	250	No sill	2.2	4.3	7.4	1
	Tanafjord	70	300	No sill	2.3	4.6	7.4	1
	Laksefjord	90	330	250	2.0	4.2	6.9	1
	Porsangerfjord-inner	30	110	15	−1.6	1.4	4.9	2
	Porsangerfjord-middle	45	250	250	0.7	3.4	6.7	2
	Porsangerfjord-outer	60	250	160	2.8	4.9	7.4	1
Troms	Kvænangen	70	400	No sill	2.0	3.9	6.9	2
	Reisafjord	60	297	230	1.9	4.0	6.5	2
	Lyngen	125	260	100	2.2	4.5	6.4	2
	Malangen	65	250	150	3.6	5.5	7.8	1
Nordland	Folda	75	540	300	3.4	5.9	8.4	1
	Ranfjord	100	520	300	4.0	6.0	8.0	2
Trøndelag	Follafjord	105	520	150	3.6	6.5	8.6	2
	Tviberg	50	570	400	4.5	6.8	10.3	1

Data on length and depths are from Norgeskart, while temperature data are from the coastal model NorKyst800 (Asplin *et al.*, 2020). Connection to offshore waters is based on visual inspection of TS-diagrams (Supplementary Figure 7) and given as either (1) fjord water mass is well connected to offshore properties or (2) fjord water mass is only partly connected to offshore properties.

the fjords and mixes with the brackish water originating from river outflows. The NCC originates in the Skagerrak (Sætre, 2007) and acts as a boundary between oceanic water and surface inshore low-saline water along the entire Norwegian coast into the Barents Sea. At intermediate depths, above fjord sill levels but below the surface layer, coastal areas and fjords are influenced by Atlantic Water (AW) masses from the Norwegian Atlantic Current (NAC) and are subject to variability and climatic trends in the AW properties (Eilertsen and Skarðhamar, 2006). The Barents Sea is a shelf sea covering about 1.4 million km^2 with an average depth of 230 m. Circulation in the Barents Sea is dominated by an inflow of warm AW in the southwest and by colder water masses in northern areas. In addition, the NCC continues eastward along the Norwegian and Russian coasts.

Fjords and fjordscapes in the Trøndelag and Nordland counties (Figure 1) are characterized by steep mountains and deep basins with sills, which generally characterize Norwegian fjords (Myksvoll *et al.*, 2014a) (Table 2). Although Troms and Finnmark from January 2020 belong to the same county, they will hereafter be referred to as two separate regions because of their differences in topography and bathymetry. Length, depth, width, and sill depth vary considerably between the larger fjords in Troms and Finnmark (Wassmann *et al.*, 1996) (Table 2). (All fjords mentioned in the text can be identified on the map in Figure 1 by their three characters long abbreviated name, see Table 1). Except for Malangen (MAL), most fjords in Troms are narrow with relatively shallow sills where maximum sill depths are less than 200 m, and some of the fjords are connected with the offshore waters through narrow inlets (Wassmann *et al.*, 1996). In contrast, all the main fjords in Finnmark (except from the Altafjord, located between KVN and POR: Figure 1) are relatively wide, with lengths of 80–100 kilometres (km), and with a maximum width of 10–20 km (Wassmann *et al.*, 1996). The wide entrance and resemblance to a bay makes the circulation in the Varangerfjord (VAR) structurally different from the other fjords (Pedersen *et al.*, 2009). The Porsangerfjord (POR) is divided into three parts, the inner part separated from the middle part by a 30 m shallow sill, the middle part separated from the outer part by an island, and the outer part with a relatively shallow sill of 180 m (Myksvoll *et al.*, 2012). The outermost part is well connected with the offshore waters (Myksvoll *et al.*, 2012). Normally, fjord basins have stagnating water masses due to sills, and the length of the stagnating period may vary from weeks to several years depending on the fjord topography and external conditions such as offshore density variability, tides etc. Whether a fjord area and potential habitats for northern shrimp are subject to exchange of offshore water or stagnating basin water will potentially affect the physical environment, including temperature.

Sampling

Shrimp samples for genetic analyses were collected along the coast and in fjords from the Trøndelag county to the Varangerfjord, and in the southern part of the Barents Sea during the period 2010–2018 (Figure 1, Table 1). The samples were collected during research cruises by the Norwegian Institute of Marine Research (IMR) or by local fishers. One outgroup sample was collected off Vancouver Island in Pacific Canada in 2015 (Table 1) by scientists at the Department of Fisheries and Oceans Canada (DFO). The samples NOM and BSS1 from 2010 were analysed in Jorde *et al.*, (2015). To standardize our work with earlier genetic investigations on northern shrimp in Norwegian waters only female shrimps were collected (Jorde *et al.*, 2015; Knutsen *et al.*, 2015). As northern shrimp is a hermaphroditic species and as the female portion of the population consists of several year classes, female samples should yield a better representation of the adult shrimp population and avoid biasing samples with a single, perhaps unrepresentative, male cohort. Tissue samples were collected at sea during cruises and preserved in 96% ethanol. Samples were stored at 4°C until DNA extraction at IMR's facilities in Tromsø. For commercial samples, fishermen froze shrimp for later tissue and DNA extraction at IMR. All the samples were collected using bottom/shrimp trawl.

Genetic screening

DNA was isolated from ethanol-fixed muscle tissue. DNA was isolated according to the Omega E-Z 96 Tissue DNA manual (Omega Bio-Tek Inc., Norcross, GA, USA). The polymerase chain reaction (PCR) was performed in 5 microliter (μl) reaction volume compromising 2 × Qiagen Multiplex Mastermix, dH_2O, 0.06–0.59 μM primers ([10 μM]), and 1 ng/μl DNA. A total of 12 microsatellite loci, developed by Pereyra *et al.*, (2012), were organized in three different multiplexes. Target DNAs were amplified with PCR in a MiniAmp thermal cycler (Thermo Fisher Scientific). Alleles were separated by size in an ABI3500 Genetic Analyzer (Thermo Fisher Scientific). GeneMapper 6.0 (Thermo Fisher Scientific) software was used for quality check and genotyping. Some samples in the data set were analysed and genotyped prior to the present study (Table 1). One locus, PbA108, amplified only sporadically and was removed from the dataset after genotyping.

Statistical analysis

Genotypes were tested for departures from Hardy–Weinberg Equilibrium (HWE) separately in each sample using Genepop 1.1.4 (Rousset, 2008) in R (R core Team, 2020). All corrections for multiple testing was performed according to the Benjamini–Hochberg procedure with a q-value of 0.05 as a threshold for significance (Benjamini and Hochberg, 1995). Observed and expected heterozygosity (H_o and H_e) within each sample and in each locus were calculated in Genepop. The locus Pba104a was significantly out of HWE after false discovery rate (FDR) corrections in 8 of 23 samples due to deficiency of heterozygotes (data not shown) and was removed from further analysis. Weighted average F_{ST} between all pairwise samples were calculated in ARLEQUIN 3.5 (Excoffier and Lischer, 2010) and tested for significance using 10 000 permutations, and corrected for multiple tests.

Independent allele frequency and no admixture model with the locprior option in STRUCTURE 2.3.4 (Pritchard *et al.*, 2000) was used to identify major clusters in the microsatellite data with six independent runs and ten repetitions for each value of *K* (groups or populations) and with a burn-in of 300 000 iterations followed by 1000 000 Markov chain Monte Carlo (MCMC) iterations. Group estimates were made on all sampled stations pooled. Delta *K* and the best *K*-value for the dataset created in STRUCTURE were identified with STRUCTURE HARVESTER (Earl and vonHoldt, 2012), using the Evanno method (Evanno *et al.*, 2005). A Clumpp infile file with the appropriate *K* was downloaded from the webpage. Clumpp 1.1.2 (Jakobsen and Rosenberg, 2007) was used to generate a permuted outfile. A STRUCTURE bar plot, based on the outfile created with Clumpp, was generated with the R package "ggplot 2." Pie-charts were made by the average STRUCTURE Q-value for each sample and each *K* and plotted on the geographical location of each sample on a map (ArcGIS). R Adegenet 2.1.1 (Jombart and Ahmed, 2011) was used to perform Discriminant Analysis of Principal Components (DAPC) on the full dataset, as well as on all samples except VANC.

We explored the ability of STRUCTURE to discriminate between mechanical mixing and hybridization between shrimp populations by creating artificial mechanical mixtures and hybrids with the HYBRIDLAB 1.0 (Nielsen *et al.*, 2006). The mechanical mixtures were composed of 50 randomly selected individuals each from the Barents Sea group (orange) and the homogeneous coast group (blue), then run through HYBRIDLAB to create artificial hybrids between the groups.

Table 3. Mean total observed heterozygosity (H_o), expected heterozygosity (H_e), and F_{is} averaged over loci for each sample of *P. borealis*.

Sample	H_o	H_e	F_{is}
BSS1	0.746	0.761	0.020
BSS2	0.726	0.753	0.036
BSS3	0.746	0.753	0.009
BSS4	0.775	0.768	-0.010
VARO	0.736	0.757	0.028
VARM	0.721	0.742	0.028
VAR	0.740	0.758	0.023
TANO	0.717	0.750	0.044
TANM	0.734	0.747	0.018
LAKM	0.710	0.731	0.029
LAKI	0.733	0.742	0.013
PORO	0.719	0.732	0.018
PORM	0.731	0.744	0.017
PORI	0.744	0.743	-0.001
KVN	0.680	0.702	0.032
REI	0.726	0.729	0.005
LYN	0.692	0.709	0.025
MAL	0.699	0.716	0.024
FO2011	0.634	0.705	0.101
RAN	0.692	0.722	0.040
FOFI	0.699	0.713	0.019
NOM	0.668	0.732	0.088
VANC	0.765	0.812	0.058

A positive F_{is} indicates heterozygote deficit; and a negative F_{is} indicates heterozygote excess. Sample names given as abbreviated names; full names are given in Table 1.

The possible effect of temperature differences on genetic structure (cf. Jorde *et al.*, 2015) was explored by linear regression. Ocean temperatures (Supplementary Figures 1, 2) were extracted from representative locations from all fjords and offshore sites, based on the coastal model NorKyst800 (Asplin *et al.*, 2020) and a large-scale model (Lien *et al.*, 2014) for the Nordic Seas for the inshore and offshore sites, respectively. Daily temperatures during April–June for the years 2010–2017 were used to calculate an average temperature for each location (pooling the Barents Sea samples) at 50 m depth and close to the sea floor. We used pairwise F_{ST} as response variable and temperature differences (at bottom or 50 m) and geographic distances between pairs of localities as explanatory variables in linear regressions, carried out in the R statistical software (R Core Team, 2020). Data from NorKyst800 (daily averaged temperatures and salinities from 50 m depth from April, May, and June from 2012–2017) were also used for making TS-diagrams for characterizing the hydrography of all sampled fjords and adjacent offshore areas.

Results

Ten of 12 loci were successfully scored for 1989 shrimps. For the ten loci, 16 of 230 tests deviated significantly from HWE after FDR adjustment, apparently randomly distributed across samples/loci (Supplementary Table 1). There was a general tendency to a weak, and statistically non-significant, heterozygote deficit (positive average F_{IS}-value) in most samples, except for BSS4 and PORI (Table 3). Heterozygote deficits occurred at all loci, except for PbC105 and SD3-62 (Supplementary Table 1).

The Pacific Ocean sample (VANC) differed significantly in all the pairwise comparisons between samples (Table 4). Significant differences were also found between the Barents Sea samples (BSS1, BSS2, BSS3, and BSS4) and every sample south and west of the Tanafjord, as well as the inner parts of the Tanafjord (TANM) and Varangerfjord (VARM). Kvænangen (KVN) and samples farther south were all significantly different from all samples from the Finnmark fjords except for VARM and LAKI, for which the differences did not quite reach significance (*P*-values ranging from 0.051 to 0.2). Genetic differentiation within fjords was found only in the Varangerfjord (VARO and VARM).

The STRUCTURE analysis (Figure 2) revealed the same trend as the pairwise comparisons and divided the samples into three main groups (Supplementary Figure 3). VANC and the Barents Sea samples were clearly different from the fjord samples (Figure 2). The Barents Sea samples appeared to be homogenous, with all sampled shrimp from this area belonging to a single genetic group. The third group (blue) encompassed all the fjord samples from Kvænangen (KVN) and southwards, while the samples from the Finnmark fjords revealed a tendency of being more mixed and resembled both the blue and the orange group. A close resemblance was found between shrimp from outside the city Vardø (VAR) and shrimp in the Barents Sea. Similarly, the outer Varangerfjord (VARO) and outer Tanafjord (TANO) samples had high proportions of shrimp belonging to the Barents Sea group. The STRUCTURE analysis visualized as pie-charts on a map (Figure 3), display the geographic distribution of the genetic clusters.

We performed a HYBRIDLAB analysis as an aid in interpreting the STRUCTURE pattern for the Finnmark fjords, by comparing HYBRIDLAB results with the actual pattern observed in the fjords. The results (Supplementary Figure 4) indicate that STRUCTURE was unable to distinguish between the hypotheses of (1) mechanical mixing of fjord and Barents Sea shrimp, and (2) the result of gene flow/hybridization between the two stocks.

A pattern of genetic structuring similar to that observed in the STRUCTURE plot, can be seen in the DAPC plots (Figure 4). The VANC individuals separated from the rest of the samples (Figure 4A) with almost no overlap. Barents Sea individuals, on one hand, and all the samples from Troms to the Trøndelag county, on the other hand, differed from each other, with the Finnmark fjord samples positioned between the two (Figure 4B). A DAPC plot of only the coastal samples (Supplementary Figure 5) showed that the outer eastern Finnmark samples (VARO, VAR, and TANO) differed from those farther south, in Troms to Trøndelag.

We found that the variable that explained most of genetic divergence (F_{ST}) among samples was the geographic distance separating sample locations, with only a weak, and non-significant contribution from bottom temperature differences and none from temperature differences at shallower (50 m) depth (Supplementary Figure 6).

Seven of the 12 sampled fjords can be characterized as having water masses well connected with offshore water mass properties (Supplementary Figure 7, Table 2). This pertains to all the Finnmark fjords, but in Porsangerfjord only the outer part has good connection with offshore water. The fjords Malangen and Folda farther south along the coast also have water masses well connected with offshore water mass properties, as has the location Tviberg, which is situated at the outer coast.

Discussion

The main finding of the present study was the division of shrimp in Norwegian waters into a Barents Sea group and the Troms-Trøndelag fjords group. The outgroup sample from the Pacific Ocean (Vancouver Island) was genetically different from all samples from Norwegian waters and the Barents Sea. Our findings regarding shrimp in the Finnmark fjords can be summarized as comprising a genetically distinct group, with shared characteristics with both the offshore (Barents Sea) and the Troms-Trøndelag fjord populations. Moreover, this mixed group appears fairly homogenous among fjords, except for the outer parts of Tanafjord (TANO) and Varangerfjord (VARO) which display a closer relationship with the offshore Barents Sea shrimps. The present data did not allow a clear conclusion regarding the origin of this Finnmark fjords component and the possible extent of hybridization between stocks.

Differences between coastal and offshore shrimp

The results indicate that the border between the Barents Sea and the coastal shrimp (the Troms-Trøndelag group) could be somewhere between Kvænangen (KVN) and the Porsangerfjord (POR). In Finnmark, pairwise comparisons between groups revealed that the Varangerfjord middle (VARM), Tanafjord middle (TANM), and samples west and south of the Tanafjord differed significantly from the Barents Sea samples. This suggests that there exists a second genetic border, between Barents Sea shrimp on one hand and Finnmark shrimp on the other hand, and that this border is located just off the coast of Finnmark. The lack of non-significant differences between outer fjord samples in eastern Finnmark (VARO and TANO) and the Barents Sea shrimp, and the resemblance between the sample from just outside the city of Vardø (VAR) and the Barents Sea samples suggest that the border is close to the coast in this area and may not be clear-cut.

The Norwegian coast experiences different oceanic retention regimes, and there is often large retention within fjords, intermediate at the outer coast and little or no retention offshore (Myksvoll *et al.*, 2014b). This implies that planktonic organisms are more often advected northwards with the NCC and NAC when advected from coastal and offshore areas. Larval drift by the strong NCC promotes genetic homogeneity, but appears ineffective across large temperature gradients (Jorde *et al.*, 2015). From a genetic perspective, there are indications of transportation of shrimp from the coast from Trøndelag to Troms into the Barents Sea, displayed by some proportions of coastal shrimp in the Barents Sea samples but not at quantities that affect the genetic structure found in the Barents Sea. Hence, both the food availability during the transport and the final environment may be sub-optimal for the larvae drifting from the coast into the Barents Sea (Palumbi, 1994).

The open nature of the Finnmark fjords may explain the genetic structure found in these fjords, which was also noted by Drengstig *et al.*, (2000). The TS-diagrams indicate that the water masses in the Finnmark fjords are well connected with offshore water masses. If there were continuous gene flow from the Barents Sea into the fjords in Finnmark, and thus a continuous hybridization between coastal and Barents Sea shrimp, the shrimp in the Finnmark fjords would eventually resemble the Barents Sea shrimp. Because they do not, but instead also retain a genetic resemblance to fjord shrimp farther south, this indicates that there is limited gene flow and hybridization with Barents Sea shrimp in the Finnmark fjords. An

Table 4. Pairwise genetic distances (F_{ST}) for *P. borealis* among all samples.

	BSS1	BSS2	BSS3	BSS4	VARO	VARM	VAR	TANO	TANM	LAKM	LAKI	PORO	PORM	PORI	KVN	REI	LYN	MAL	FO2011	RAN	FOFI	NOM	VANC
BSS1		0.179	0.064	0.072	0.121	**<0.001**	0.086	0.161	**0.015**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
BSS2	0.001		0.705	0.17	0.179	**<0.001**	0.161	0.406	**0.003**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
BSS3	0.003	−0.001		0.304	**0.025**	**<0.001**	0.12	0.17	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
BSS4	0.003	0.002	0.001		0.135	**<0.001**	0.304	0.453	**0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
VARO	0.002	0.001	0.004	0.003		**0.024**	0.357	0.517	0.775	**<0.001**	**0.008**	**0.03**	0.111	0.137	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
VARM	0.011	0.01	0.015	0.01	0.003		**<0.001**	**0.006**	0.4	0.658	0.754	0.866	0.651	0.714	**0.018**	0.097	**0.007**	**0.021**	**0.034**	0.105	**0.008**	**0.004**	**<0.001**
VAR	0.002	0.001	0.002	0.001	0.001	0.007		0.567	**0.027**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
TANO	0.002	0.001	0.002	0	0	0.004	0		0.237	**<0.001**	**<0.001**	**0.004**	**0.001**	**0.011**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
TANM	0.003	0.005	0.009	0.005	−0.001	0	0.003	0.001		**0.007**	0.176	0.434	0.348	0.796	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
LAKM	0.013	0.017	0.02	0.016	0.007	0	0.011	0.007	0.004		0.315	0.199	**0.01**	**0.046**	**0.043**	**0.021**	**0.008**	**0.006**	**0.017**	**0.027**	**0.023**	**0.018**	**<0.001**
LAKI	0.01	0.012	0.015	0.011	0.004	−0.001	0.007	0.007	0.001	0.001		0.52	0.472	0.686	**0.002**	0.124	**0.003**	**0.007**	**0.004**	0.051	0.065	0.208	**<0.001**
PORO	0.008	0.01	0.015	0.01	0.003	−0.001	0.008	0.004	0	0.001	0		0.318	0.481	**0.003**	**0.011**	**<0.001**	**<0.001**	**<0.001**	**0.013**	**0.002**	**0.05**	**<0.001**
PORM	0.009	0.008	0.013	0.009	0.002	0	0.005	0.006	0.001	0.004	0	0.001		0.341	**<0.001**	**0.002**	**0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**
PORI	0.006	0.006	0.011	0.009	0.001	−0.001	0.004	0.003	−0.001	0.002	−0.001	0	0.001		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**
KVN	0.024	0.029	0.035	0.028	0.015	0.003	0.022	0.017	0.009	0.003	0.005	0.004	0.007	0.007		0.652	0.81	0.642	0.843	0.359	0.756	0.171	**<0.001**
REI	0.022	0.025	0.029	0.022	0.013	0.002	0.018	0.015	0.007	0.003	0.002	0.003	0.005	0.005	0		0.523	0.622	0.566	0.243	0.768	0.317	**<0.001**
LYN	0.027	0.03	0.036	0.028	0.016	0.004	0.023	0.019	0.01	0.004	0.004	0.006	0.006	0.008	−0.001	0		0.349	0.4	0.774	0.555	0.065	**<0.001**
MAL	0.024	0.028	0.035	0.027	0.015	0.003	0.022	0.017	0.01	0.004	0.004	0.005	0.007	0.006	0	0	0.001		0.52	0.063	0.52	0.191	**<0.001**
FO2011	0.026	0.03	0.038	0.03	0.016	0.003	0.023	0.021	0.011	0.004	0.004	0.006	0.008	0.007	−0.001	0	0.001	0		0.097	0.358	**0.017**	**<0.001**
RAN	0.021	0.024	0.03	0.022	0.012	0.002	0.019	0.015	0.006	0.003	0.002	0.003	0.005	0.006	0.001	0.001	−0.001	0.002	0.002		0.297	0.454	**<0.001**
FOFI	0.025	0.03	0.034	0.028	0.016	0.004	0.023	0.019	0.01	0.003	0.002	0.005	0.006	0.007	−0.001	−0.001	0	0	0.001	0.001		0.157	**<0.001**
NOM	0.016	0.022	0.027	0.023	0.01	0.004	0.016	0.014	0.006	0.004	0.001	0.003	0.006	0.004	0.002	0.001	0.002	0.001	0.004	0	0.002		**<0.001**
VANC	0.054	0.055	0.059	0.054	0.044	0.041	0.049	0.052	0.045	0.047	0.042	0.048	0.044	0.045	0.057	0.046	0.052	0.052	0.054	0.048	0.051	0.05	

P-values above the diagonal and F_S below. Significant values are given in bold. *P*-values are FDR corrected. Sample names given as abbreviated names; full names are given in Table 1.

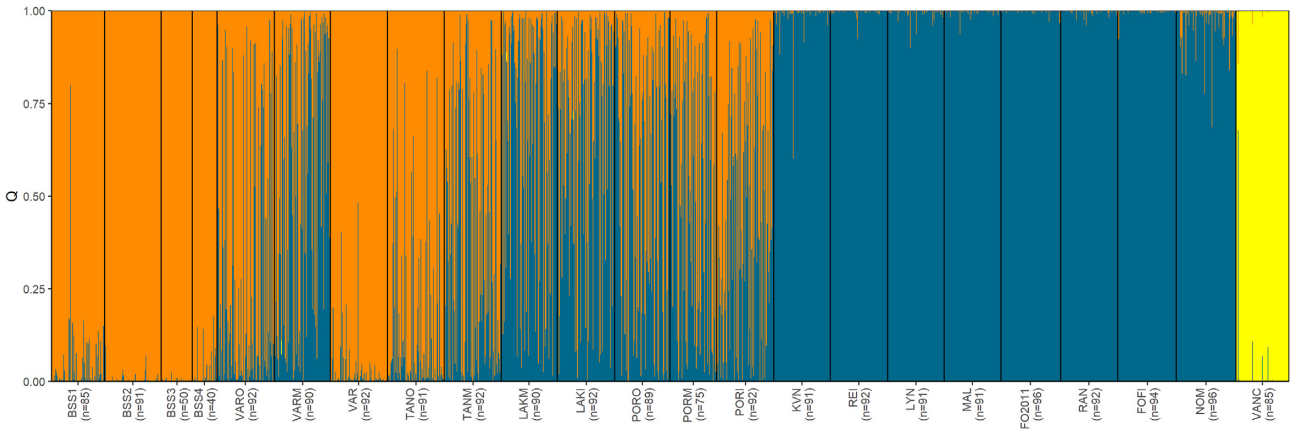

Figure 2. Estimated probability of individual shrimp (*P. borealis*) being assigned to different groups by STRUCTURE 2.3.4 (Pritchard *et al.*, 2000). Samples are distributed into three clusters/groups. Each vertical coloured line (orange, blue, yellow, or mixed) presents an individual shrimp. *Q*-values give individual score to each group. Sample names given as abbreviated names; full names are given in Table 1.

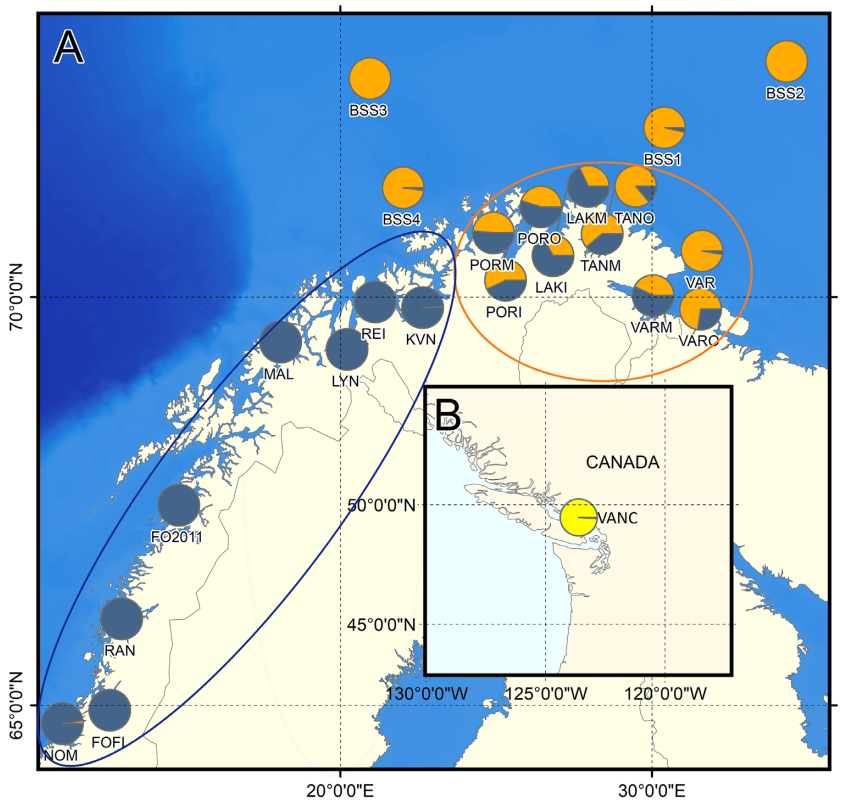

Figure 3. Pie charts of average *P. borealis* assigned to each cluster per sample, along (A) the Norwegian coast and the Barents Sea, and (B) the North-Pacific, based on the *Q*-values from STRUCTURE 2.3.4 (Pritchard *et al.*, 2000). Pie charts placed on the approximate geographic position of each sample. Sample names given as abbreviated names; full names are given in Table 1. The blue ring encircles all fjord samples from the Trøndelag county to Kvænangen; the orange ring encircles all the Finnmark fjord samples.

alternative explanation may be that gene flow from the Barents Sea is balanced with gene flow from the fjord populations farther south, perhaps carried northwards and into the Finnmark fjords by the NCC. The influence from the Barents Sea shrimp stock seems to be strongest in the outer parts of the Varangerfjord and Tanafjord, the two easternmost Finnmark fjords. Pedersen *et al.*, (2003) found that temporal and spatial variations in the hydrodynamics of the Barents Sea seem to govern the pattern of larval settlement of *P. borealis*. In their larval drift studies conducted for three consecutive years (1996–1998), they found that the main area of settlement was in the northern Barents Sea around the Polar Front. From this, it seems that larvae hatching in the open Barents Sea generally are transported northwards and to a lesser extent into fjords and coastal areas.

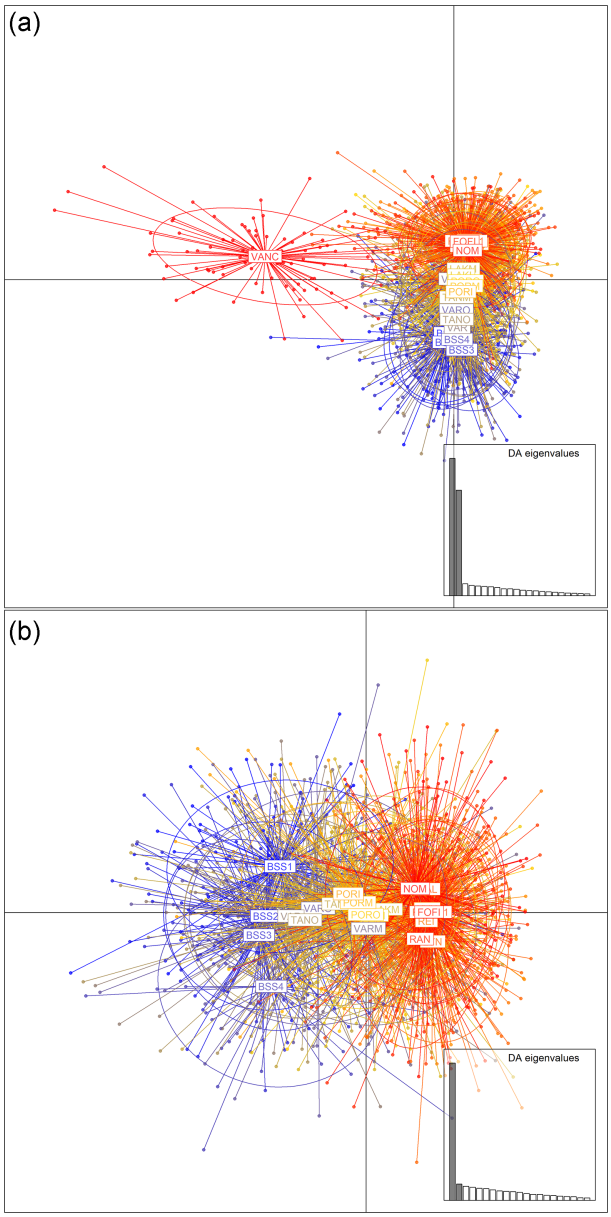

Figure 4. (A) DAPC plot for all samples of *P. borealis*. (B) DACP plot without the Vancouver Island sample. Discriminant Analysis (DA) eigenvalues display the number of discriminant functions retained. Sample names given as abbreviated names; full names are given in Table 1.

Genetic population structure between fjords

For fjords along the coast of Norway, from the Trøndelag county to the Varangerfjord, our study resolved two main groups of shrimp. The results did not reveal any clear genetic population structure between neighbouring fjords, except between Kvænangen (KVN) and the Porsangerfjord (POR). A less clear structure was found between the Laksefjord and Porsangerfjord which are located next to each other, where the two Laksefjord samples (LAKM and LAKI) displayed lower proportions of Barents Sea genes than did the Porsangerfjord samples (PORI, PORM, and PORO). No difference was observed between any of the fjords from the Trøndelag county to Troms. In contrast, in the Skagerrak region in southern Norway, shrimp in four of seven investigated Skagerrak fjords displayed significant but weak genetic differentiation (Knutsen *et al.*, 2015). The lack of differentiation in our present study may be caused by transport of larvae, as indicated above, by the method used (see below), or it may be a result of which fjords we chose to study. Drengstig *et al.* (2000), using allozymes, found genetic differentiation between fjords in Troms and two fjords in north western Norway (located south of our southernmost sample site Tviberg). In a different species, Quintela *et al.*, (2020) found no genetic structuring between fjord populations of European sprat along the Norwegian coast, from Oslo to north of the Ranfjord (RAN).

Genetic structure within fjords

The Varangerfjord (VARO and VARM), which is the widest of all Norwegian fjords, resembling a bay more than a fjord, was the only fjord in our study with significant genetic variation within the fjord. A study of capelin (*Mallotus villosus*) larvae revealed that larvae that hatched farther west (in Troms-Finnmark) were more rapidly transported offshore compared to the situation farther east where larvae were transported downstream along the shelf and into the Varangerfjord (Pedersen *et al.*, 2009). This scenario may also apply to shrimp larvae, as they are carried by the same currents. In addition, eddies in the Varangerfjord area may retain some of the larvae (Pedersen *et al.*, 2009). The process of retention may be one of the explanatory factors for the difference between outer and inner parts of the Varangerfjord.

We found no significant differences between shrimp from the inner and outer parts of the Porsangerfjord, even though the hydrography of the inner, isolated basins differs markedly from the rest of the fjord, experiencing strong cooling throughout a large part of the year with temperatures around 0°C (Myksvoll *et al.*, 2012). The environment in the inner part resembles that of an arctic ecosystem (Myksvoll *et al.*, 2012), and the basins harbour several Arctic benthic invertebrate species (Oug and Fuhrmann, 2013). The shrimp population here stands out from other coastal populations by a very high density and a life cycle seemingly out of phase with shrimp in the rest of the fjord (Søvik *et al.*, 2020). However, we were not able to detect a noticeable effect of temperature on genetic structure beyond the effect of geographic distance alone. In other marine species, contrasting salinity regimes have led to genetically distinct sub-populations (Johannesson *et al.*, 2020; Quintela *et al.*, 2021).

Lack of genetic differentiation between fjord samples as well as between shrimp sampled at different localities within fjords (e.g. between the inner and outer parts of the Porsangerfjord) may be caused by low statistical power for the genetic markers used. Future studies may explore a wider set of genetic markers (singe nucleotide polymorphic markers, SNPs) that have proven successful in elucidating weak population structure in other species. This by increasing statistical power of detection, either from the use of a larger number of markers or by uncovering genomic regions with more pronounced differentiation, perhaps caused by local adaptation.

The Pacific Ocean sample

The Pacific sample (VANC) was included in the present study as an outgroup and to test for genetic differences across the Arctic Ocean. This sample differed significantly from all other samples from the Barents Sea, and the Norwegian fjords and coast and was the genetically most distinct sample in our study. This indicates that there is

presently no connection or genetic drift between the Pacific and Atlantic populations. On the other hand, levels of genetic divergence for the Vancouver Island sample (pairwise F_{ST} ranging from 0.041 to 0.059: Table 4) were not excessive relative to the differences between the coastal and Barents Sea samples in the Atlantic Ocean (range 0.016–0.038), yielding little support to the notion of separate species status for the Pacific populations (cf. Squires, 1992). Instead, our data suggest that *Pandalus eous* (alternatively *P. borealis eous*) in the Pacific Ocean and *P. borealis* in the Atlantic Ocean are closely related, conspecific populations.

Implications for management

Our genetic study contributes valuable insights for the resource management of northern populations of *P. borealis*. Presently, *P. borealis* in Norwegian waters is divided into two management units: the Skagerrak and Norwegian Deep shrimp stock (shared with Sweden and Denmark), and shrimp north of 62°N (shared with Russia). Our results reveal, however, that the shrimp in fjords and coastal areas in northern Norway (from Trøndelag county to Varangerfjord) are genetically distinct from shrimp in the Barents Sea. Furthermore, our results, taken together with the results of Knutsen *et al.,* (2015) and Jorde *et al.,* (2015), indicate that coastal shrimp north to Kvænangen belong to a common stock with the Skagerrak and Norwegian Deep shrimp.

Shrimp landings from the coastal areas are small compared to the landings from the Barents Sea. Total landings from along the whole Norwegian coast (within 12 nm) in 2020 were 3959 tons, of which 1113 tons were from 62°N to the Varangerfjord (data from the Norwegian Directorate of Fisheries), while total landings in the Barents Sea and Svalbard zone increased from 20 000 tons in 2013 to 76 083 tons in 2019, and were predicted to reach 53 000 tons by the end of 2020 (NAFO and ICES, 2020). Fjord populations are, thus, of less economic value than the Barents Sea and the Skagerrak and Norwegian Deep stocks, but are nevertheless important for the coastal fishery and not least for maintaining genetic variability and biocomplexity of the species in Norwegian waters (Knutsen *et al.*, 2015).

While the Barents Sea shrimp stock is estimated to be well above any precautionary reference points and exploited sustainably (NAFO and ICES, 2020), stock status of the coastal shrimp is to a large extent unknown, and there is no regular assessment. Presently, there are no quotas for the Norwegian shrimp fishery north of 62°N (NAFO and ICES, 2020), but under a possible future scenario with quotas restricting the fishery one might envisage local overfishing of small coastal populations if they continue to remain part of the present, large management unit. Extending the southern management unit farther north to reflect the biological population is probably not an option as the Skagerrak and Norwegian Deep stock is shared between Norway, Sweden, and Denmark, and is part of international quota negotiations for the North Sea fish stocks.

A separate management unit encompassing the fjords and coast from 62°N and northwards would ensure a locally adapted management regime. Our results suggest, however, at least two coastal shrimp management units. If there is a mixture of two biological populations in the Finnmark fjords, the shrimp fisheries there are exploiting a mixed population, possibly leading to overexploitation of the less-abundant population. Alternatively, if shrimp in the Finnmark fjords represent a distinct biological population, in close kinship with both the coastal and the Barents Sea populations, it will be important to manage this population separately from those in the Barents Sea and the fjords farther south, to conserve genetic diversity.

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Data Availability

The data underlying this article are available on https://hdl.handle.net/11250/2770119.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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