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Original Article

Micro-geographic population genetic structure within Arctic cod (*Boreogadus saida*) in Beaufort Sea of Alaska

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Many marine organisms show significant levels of genetic heterogeneity on local spatial scales despite exhibiting limited genetic structure at large geographic scales which can be produced through a variety of mechanisms. The Arctic cod (*Boreogadus saida*) is a circumpolar species and is a vital species in Arctic food webs. To examine population genetic structure of Arctic cod at macro- and micro-geographic scales, we characterized variation at mitochondrial DNA (mtDNA) and microsatellite loci among Arctic cod located in the Chukchi and Beaufort seas in Alaska. We found two distinct mtDNA haplotype clusters, although there was no underlying geographic pattern ($F_{ST} = -0.001$). Congruent with this finding, microsatellite loci suggested a panmictic population ($F_{ST} = 0.001$) across northern Alaskan marine waters at a large spatial scale. However, we found slight but significant micro-geographic partitioning of genetic variation in the southern shelf of the Beaufort Sea that appeared to be associated with the western reaches of the Mackenzie River plume. This fine-scale spatial pattern was not associated with kin-associated groups, suggesting larvae cohorts are not remaining together throughout development. We hypothesize that this pattern reflects the intermixing of Pacific and Arctic origin lineages of Arctic cod.

Keywords: Arctic cod, Beaufort Sea, *Boreogadus saida*, genetic patchiness, population genetic

Introduction

Spatial and temporal heterogeneity in habitats plays an important role in shaping the distribution of genetic variation (Selkoe *et al.*, 2008; Anderson *et al.*, 2010). Some of the most extreme patterns of heterogeneity in demographic characteristics have been observed in marine environments (Roughgarden *et al.*, 1988; Navarrete *et al.*, 2008). Many marine fishes and other marine organisms exhibit population genetic structuring at both macro- (range-wide) and micro- (local) geographic scales (Knutsen *et al.*, 2012; Maas *et al.*, 2018). Such geographically based genetic heterogeneity within widely distributed and abundant marine organisms arises through a variety of mechanisms, including life-history and population dynamics, environmental and geographic features (Gaggiotti *et al.*, 2009), random evolutionary processes (e.g. genetic drift), and human disturbances (Glover *et al.*, 2012).

The physical oceanography of the Beaufort Sea Shelf is influenced by multiple processes (MBC Applied Environmental Sciences, 2003). Regionally, the waters of the Beaufort Sea in Alaska are influenced not only by the coastal boundary, but also by three oceanic regimes (Macdonald *et al.*, 1989; McLaughlin *et al.*, 1996; Hopcroft *et al.*, 2008): (i) Pacific Ocean waters, which enter the Beaufort Sea from the Chukchi Shelf via the Barrow Canyon, (ii) the offshore shelf boundary, which includes the outer shelf and the continental slope, and (iii) the Mackenzie

shelf, on the eastern boundary of the Beaufort Sea off Alaska's north coast. Furthermore, the influence of Pacific waters decreases eastward (Macdonald *et al.*, 1989; McLaughlin *et al.*, 1996; Smoot and Hopcroft, 2017), as evidenced by changes in marine community assemblages in some fauna groups (Carmack and MacDonald, 2002; Smoot and Hopcroft, 2017).

Abiotic changes in Arctic marine ecosystems may strongly impact the distribution of marine organisms and in turn, overall ecosystem dynamics. Historically, both the Chukchi and Beaufort seas were characterized by perennial sea ice. In recent years, however, they have experienced extensive sea ice loss during summer months (Comiso *et al.*, 2008). Fish species, such as Arctic cod, *Boreogadus saida*, that are sensitive to fluctuations in temperature respond to changes in ice-sea conditions by altering their distributions and abundance (Wassmann *et al.*, 2011). Shifts in the abundance of Arctic cod may adversely affect ecosystem dynamics, as the species represents an important link in Arctic marine food webs. Arctic cod are involved in up to 75% of the energy transfer between lower and higher trophic levels (Welch *et al.*, 1992). Its critical role in Arctic marine ecosystems is exemplified by the decrease in fitness of several predators, presumably linked with recent reductions in yearly availability of Arctic cod (Harwood *et al.*, 2015). Despite the importance of Arctic cod as a key prey species, our understanding of many aspects of its life history is limited (see special issue on Arctic cod in *Polar Biology* 2016 issue 6). Thus, a greater understanding of Arctic cod population dynamics, including spatial distribution of genetic diversity, is critical to evaluate responses of predicted and observed changes in ice concentration in Arctic ecosystems.

Arctic cod has a pan-Arctic distribution and is at times locally very abundant, making up to 92% of total number of fish in some areas of the Arctic (Rand and Logerwell, 2011). The species is often associated with sea ice and has evolved antifreeze proteins for life in sub-zero Celsius water temperatures (Chen *et al.*, 1997). Although found in a range of environmental conditions, physiological experiments suggest Arctic cod has a higher degree of stenothermy than other gadid species (Laurel *et al.*, 2016; Leo *et al.*, 2017). This may make acclimating to warmer temperatures difficult. Given the predicted influx of more temperate species, Arctic cod may be increasingly vulnerable to interspecies competition (Laurel *et al.*, 2016; Leo *et al.*, 2017). Given this, movements and distribution of Arctic cod, in particular eggs and larvae, are likely influenced by the synergistic effects of environmental factors such as temperature, salinity, and sea ice cover (Kessel *et al.*, 2016). However, determining the degree of dispersal is problematic in ocean environments due to the impracticality of directly observing larval-stage movements (Fauvelot and Planes, 2002). Indeed, it was only recently discovered that the Arctic cod could move large distances (190 km; Kessel *et al.*, 2017). Thus, the integration of genetic approaches can provide valuable insight into population connectivity and ultimately into factors restricting or promoting dispersal.

Here, we investigate the population genetic structure of Arctic cod within the Alaskan Beaufort and Chukchi seas using microsatellite genotype and mitochondrial (mt) DNA cytochrome *b* (*cytb*) gene sequences. Previous genetic research on Arctic cod focusing on populations in the northern Atlantic Ocean (Fevolden *et al.*, 1999; Pálsson *et al.*, 2009) and northwestern Alaskan waters (Chukchi Sea; Wildes *et al.*, 2016) found little population differentiation within these regions; although subtle large-scale global differentiation may be present (R. Nelson, unpublished data cited in Bouchard *et al.*, 2018). A recent study using microsatellites uncovered genetic partitions, associated with fjord and shelf habitats in the North Atlantic Ocean (Madsen *et al.*, 2016), that were congruent with observations in Atlantic cod (*Gadus morhua*; see Karlsen *et al.*, 2014) for which local adaptation appeared to play a role in driving divergence between ecotypes. Therefore, reassessment of the hypothesis of panmixia in Arctic cod occupying northern Alaska waters is relevant considering the predicted future environmental changes in the Arctic marine ecosystem. Due to the complex physical oceanography of the Beaufort Sea, we employed a seascape approach by mapping genetic divergences to determine potential barriers to connectivity and assess fine-scale genetic patterns among Arctic cod populations in the Alaskan Beaufort Sea which may be influenced by micro-geographic processes such as kin groups formation.

Methods

Sample collection

Fin clips or muscle were collected from Arctic cod in the southern Beaufort Sea off the northern coast of Alaska ($n = 780$) in 2008, 2011, 2013, and 2014 and in the Chukchi Sea ($n = 85$) during 2008 and 2015, and from the Gulf of St. Lawrence, Canada, from 2010 ($n = 30$) (Figure 1, Wilson *et al.*, 2018). Samples in the Beaufort Sea were collected as part of the Bureau of Ocean Energy Management (BOEM) Central Beaufort Sea Survey and US–Canada Transboundary Survey in August designed to encompass the entire continental shelf in the western, central, and eastern Beaufort Sea from Point Barrow to the Alaska–Canada Boundary. Sampling stations along Beaufort Sea transects were situated at depths between 10 and 1000 m, encompassing the inner shelf area (<50 m) and shelf-break zone (>75 m). We broadly defined regions within the Beaufort Sea as (i) western, (ii) central, and (iii) southern (Figure 1). The southern Beaufort was further subdivided into the Camden Bay and southern shelf areas. Within the Chukchi Sea, samples were collected from two general areas: (i) southern (~67°N 169°W) and (ii) eastern Chukchi Sea (~72°N 164°W). Detailed sample information is in Wilson *et al.* (2018).

Laboratory techniques

Genomic DNA was extracted from samples using procedures described in Sonsthagen *et al.* (2004) or using QIAGEN DNeasy Tissue Kit (QIAGEN, Valencia, CA). Genomic DNA concentrations were quantified using fluorometry and diluted to 50 ng ml^{-1}. PCR amplification and data processing followed protocols described in Sonsthagen *et al.* (2004).

We amplified the mtDNA *cytb* gene with primers designed using a reference mitogenome available on Genbank (Accession number AM919428) and amplified an either 818 or 1266 bp fragment of *cytb* (Supplementary Table S1). Samples were cycle-sequenced using primer pair CB115F:CB993R on LI-COR 4200LR or ABI 3730xl and trimmed to 707 bp. Sequences were processed using LI-COR eSeq and AlignIR 2.0 or Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, MI). Sequences are accessioned in GenBank (MG100209–MG100615).

Eleven microsatellite loci were amplified in four multiplexed PCR reactions (Bsa6, Bsa7, Bsa14, Bsa15, Bsa60, Bsa101, Gmo8, Gmo34, PGmo32, Tch14, and PGmo127; Supplementary Table S2). For quality control, 10% of the samples were re-extracted, amplified and genotyped. Allelic dropout, null alleles, or scoring

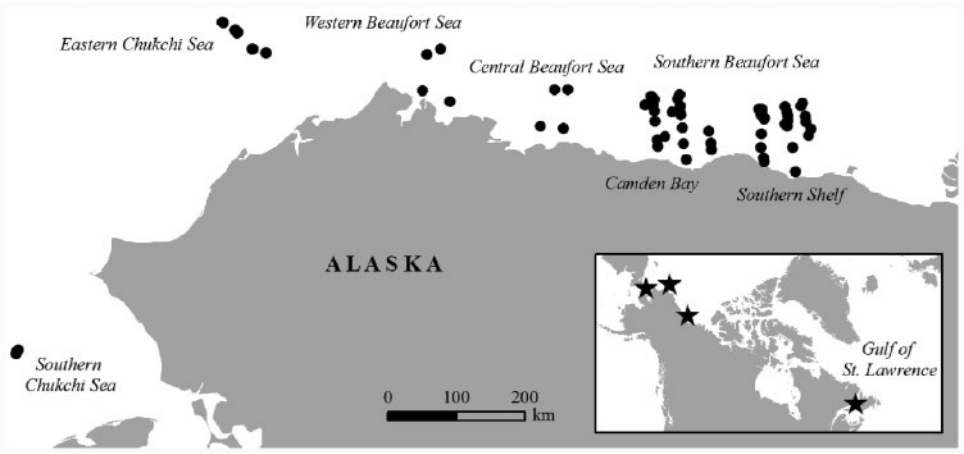

Figure 1. Map of Alaska and Canada showing general sampling locales, indicated by stars in the insert, and Beaufort and Chukchi seas sampling locales represented by black dots.

error was assessed using MICROCHECKER (Van Oosterhout *et al.*, 2004). Seven individuals possessed alleles in the range observed only in *Arctogadus glacialis* for Gmo8 (Madsen *et al.*, 2009) and therefore were assumed to be *A. glacialis* and were removed from subsequent analyses. Microsatellite genotypic data are available in Wilson *et al.* (2018).

Data analysis

Samples were collected across multiple years, therefore, we employed exact tests of population differentiation, in ARLEQUIN 3.5.2.2 (Excoffier and Lischer, 2010) to test for temporal variation in the data set. We failed to uncover significant correlation in the distribution of haplotypes or alleles ($p > 0.5$ for both tests) among years. As a result, samples were pooled across years by sea for regional level tests (see Supplementary Methods, Supplemental Figure S1).

We calculated haplotype (h) and nucleotide (π) diversity for mtDNA *cytb* using ARLEQUIN and haplotypic richness using Contrib 1.4 (Petit *et al.*, 1998). We calculated Tajima's D and Fu's Fs to distinguish between neutral evolution (genetic drift) or non-random processes (selection) and demographic expansion or contraction using ARLEQUIN. Significant negative values may indicate a recent population expansion or purifying selection. An unrooted phylogenetic tree of *cytb* haplotypes was constructed in NETWORK 4.6.1.3 (Fluxus Technology Ltd 2009) using the median joining network method.

We calculated allelic richness, observed (H_O) and expected (H_E) heterozygosities, Hardy–Weinberg expectation (HWE) and linkage disequilibrium (LD) at microsatellite loci in FSTAT 2.9.3 (Goudet, 1995). The degree of genetic subdivision among seas was assessed with pairwise F_{ST} and Φ_{ST} for mtDNA data and F_{ST} and R_{ST} for microsatellite data in ARLEQUIN. Because samples sizes varied among populations, differentiation based on χ^2 distributions of alleles or haplotypes was also estimated using GENEPOP'007 (Rousset, 2008). Tests for HWE, LD, F_{ST}, R_{ST}, and χ^2 based on microsatellite data were adjusted for multiple comparisons using Bonferroni corrections ($\alpha = 0.05$).

To further explore population structure among seas, we used the Bayesian-clustering program STRUCTURE 2.2.3 (Pritchard *et al.*, 2000) with the LOCPRIOR option, which can detect population structure in datasets with a weak signal of structure not detectable under standard models (Hubisz *et al.*, 2009). STRUCTURE assigns individuals to populations maximizing HWE and minimizing LD. The analysis was conducted on the microsatellite data set, for $K = 1$–6, where K is the number of populations, using an admixture model with 100 000 burn-in iterations and 1 000 000 Markov chain Monte Carlo (MCMC) iterations with 10 independent replicates per K. We used the ΔK method of Evanno *et al.* (2005) to determine the most likely number of groups at the uppermost level of population structure.

To identify potential genetic discontinuities between genetic and geographic locations within the Beaufort Sea, we analysed sample-specific microsatellite genetic distance and spatial location data to determine the effects of dispersal barriers on population structure. First, we calculated pairwise values of genetic chord, chi-square, and euclidean distances between all sampling stations in GenoDive (Meirmans and Van Tienderen, 2004). As genetic differences can accumulate as a function of increasing geographic distance, we tested for isolation-by-distance (IBD) using a Mantel test in the program IBD (Bohonak, 2002). If significant IBD effect was observed, the residual values from the regression were used to remove the effects of distance on genetic divergence (Manni *et al.*, 2004). We then visualized genetic distances as genetic landscapes, using Genetic Landscapes Toolbox version 10.1 with the Single Species Divergence Tool (Vandergast *et al.*, 2011) in ArcGIS 10.6 (ESRI, 2011). Pairwise genetic distances or residual values from the IBD analysis were mapped to the geographic midpoint between sampling locales. A divergence landscape surface was generated from the mapped genetic distance values at midpoints using Inverse Distance Weighted interpolation with the following settings (power = 2, variable search radius with 12 points, grid cell size 1 km^2). The generated landscape was clipped to the extent of the sampling locations in the Beaufort Sea to avoid extrapolation beyond the geographic scope of the original locations. The most divergent cells in the genetic divergence landscape ($\geq$1.5 standard deviations from the mean cell value) were used to evaluate hypothesized barriers to movement.

To examine the potential of non-equilibrium conditions contributing to divergence "hotspots" indicated in the Genetic Landscapes Toolbox, we calculated the mean pairwise relatedness within each Beaufort Sea station represented by at least 5 individuals using the relatedness measure, r_{qg}, as estimated in GenAlEx

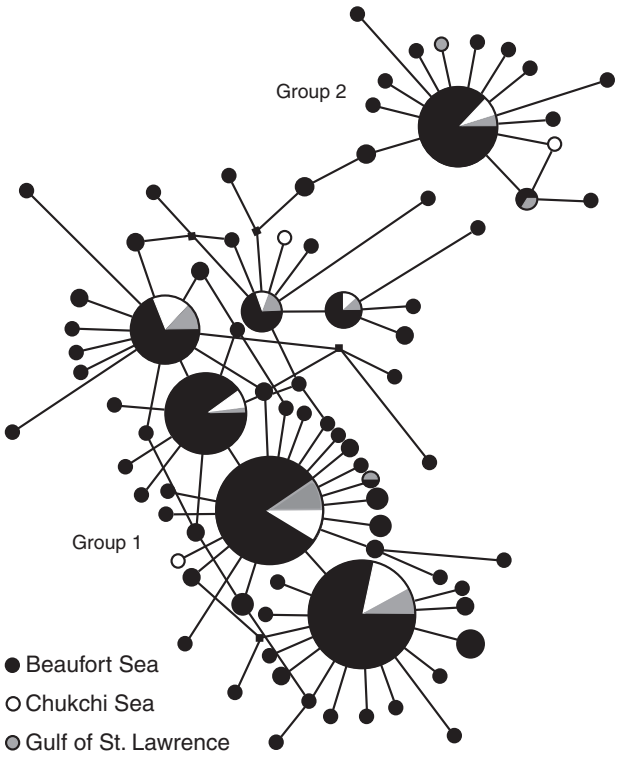

Figure 2. Parsimony network illustrating the relationships among 82 mitochondrial DNA cytochrome *b* haplotypes assayed from Arctic cod. Size of the node corresponds to the frequency of each haplotype. All line segments represent a difference at one nucleotide position between neighbouring haplotypes. Black squares represent unsampled haplotypes.

(Peakall and Smouse, 2012) with associated 95% confidence intervals determined by 1000 bootstraps. To determine the 95% confidence intervals of kinship values predicted under a panmictic model, we used a permutation test of genotypes (999 times) to calculate the predicted range of r_{qg}. In addition, HWE, H_O, and H_E were calculated for each station ($n > 5$).

Results

Genetic diversity

Eighty-two mtDNA *cytb* haplotypes characterized by 64 variable sites were observed among Arctic cod ($n = 407$) sampled from the Beaufort and Chukchi seas and the Gulf of St. Lawrence in Canada. Fifty-six (68%) of the haplotypes were represented by a single individual with all seven higher frequency haplotypes shared among seas (Figure 2). Although diversity measures were similar across regions, we observed differences in tests used to uncover changes in demographic parameters. Notably, we observed negative *Fs* for all sampling regions within the Beaufort Sea.

We obtained microsatellite genotypes from 740 individuals from the Beaufort and Chukchi seas. The average number of alleles per sampling area ranged from 6.2–11.5 alleles per locus with similar allelic richness values across regions (Table 1). Sampling transects in the southern Beaufort (Camden Bay and Southern Shelf) contain the most private alleles (9 and 20, respectively). Heterozygosities were similar across sampled locales and all locales, except the eastern Chukchi Sea ($\chi^2 = \infty$, df = 22, $p < 0.0001$), were in HWE (Table 1). Two loci, Bsa101 and PGmo32, were in LD when the analysis included all locales ($\alpha = 0.05$), however when locus pairs were analysed by location, all loci were in linkage equilibrium. We found no evidence of scoring error and no inconsistencies in genotypes among replicates. Evidence of null alleles in southern Chukchi Sea (locus Gmo34) and eastern Chukchi Sea (loci PGmo32, Gmo8, and Gmo34) was detected (Supplementary Table S3). Since those loci did not show heterozygote deficit in other populations, it was assumed the homozygote excess is not due to null alleles but rather to lack of mutation-drift equilibrium in eastern Chukchi Sea. Furthermore, we would expect three loci to be in LD by chance, therefore, all loci were retained in subsequent analyses.

Population subdivision—among seas

We observed no overall differentiation across sampling areas for either *cytb* ($F_{ST} = -0.001$, $\Phi_{ST} = -0.010$) or microsatellites ($F_{ST} = 0.001$, $R_{ST} < 0.001$) and no significant pairwise comparisons in either the microsatellite or mtDNA datasets (Supplementary Table S4). However, we found a significant difference between the distribution of microsatellite alleles in samples from southern Chukchi Sea and central ($\chi^2 = 43.7$, df = 22, $p = 0.004$) and those from southern Beaufort Sea localities (Camden Bay $\chi^2 = 52.6$, df = 22, $p = 0.0003$; southern Shelf $\chi^2 = 56.8$, df = 22, $p = 0.00007$).

In accordance with overall differentiation tests, the STRUCTURE analysis revealed little genetic structure across the Beaufort and Chukchi seas. While the most likely number of clusters (K) was two ($\Delta K = 56.9$; LnP($K = 1$) = −20 314.3, LnP($K = 2$) = −20 078.1), most samples were assigned to Cluster 1 (99.3%); only four fish from the Chukchi Sea (membership coefficient > 96%) and one fish from southern Beaufort Sea (membership coefficient = 45%) was assigned to Cluster 2 (Supplementary Figure S2).

Micro-geographic structure within Beaufort Sea

We did not find an association between genetic distance and geographic distance within the Beaufort Sea stations for all three genetic distance measures (chi-square, $r = -0.09$, $p > 0.18$; chord, $r = -0.13$, $p > 0.09$; Euclidean distance, $r = -0.14$, $p > 0.06$). Therefore, pairwise genetic distances (and not the residuals from the regression) were used to visualize genetic divergence maps. The surfaces interpolated from genetic divergence indices identified multiple areas of exceptionally high and low divergence defined by the cutoff values (> 1.5 *SD* above or below mean). All three genetic indices produced the same overall pattern; only the results based on Euclidean genetic distance (range = 0.26–2.92) are shown. Areas of high divergence were restricted to the southern Beaufort Sea (Figure 3) and associated with the inner shelf (< 50 m) and offshore shelf break zones (up to 1000 m) near the Canning River outflow in Camden Bay. Additional areas of high divergence occurred in the shelf break zone (> 50 m) in the southern shelf area near the US–Canada boundary and Mackenzie River outflow. One area of low divergence was located near the inner shelf area (depth < 50 m) and the coastal zone (depth < 20 m) of the southern shelf east of Kaktovik, Alaska.

Relatedness

The mean pairwise relatedness across all fish in the Beaufort samples was −0.002 (*SD* = 0.220; Range = −1.282 to 0.840). One station, A2-500, exhibited an average positive kinship value that exceeded the predictions of the panmictic model, and one station, TBS-750, exhibited an average negative station kinship value that

Table 1. Estimates of genetic diversity[a] of Arctic cod in the Alaskan Chukchi and Beaufort seas, including average number of alleles, allelic richness[b], observed (H_O) and expected heterozygosities (H_E), and sample size (N) calculated from 11 autosomal microsatellite loci, as well as, number of haplotypes, haplotypic richness[c], haplotype (h), and nucleotide (π) diversity, Fu's Fs, and Tajima's D calculated from mtDNA cytochrome *b*.

	Southern Chukchi	Eastern Chukchi	Western Beaufort	Central Beaufort	Southern Beaufort		St. Lawrence, Canada
					Camden Bay	Southern Shelf	
Microsatellites							
No. alleles	6.5 (4.2)	7.5 (4.6)	6.5 (4.4)	6.2 (5.0)	10.2 (6.9)	11.6 (7.3)	–
Allelic richness	6.3 (4.0)	6.0 (3.5)	5.3 (3.4)	5.2 (3.8)	5.4 (3.7)	5.7 (3.7)	–
Private alleles	2	5	2	2	9	20	–
H_O (*SD*)	52.4 (3.6)	**51.6 (2.5)**	54.9 (2.5)	54.2 (2.6)	54.2 (1.0)	55.4 (0.8)	–
H_E (*SD*)	56.6 (7.4)	**57.8 (7.0)**	53.2 (8.2)	54.1 (7.8)	54.4 (7.7)	55.7 (7.7)	–
N	18	37	38	35	236	350	–
	Chukchi[d]		**Western Beaufort**	**Central Beaufort**	**Southern Beaufort**		**St. Lawrence, Canada**
					Camden Bay	**Southern Shelf**	
mtDNA							
No. haplotypes	10	–	26	19	36	21	11
Haplotypic richness	8.2	–	15.0	11.4	12.5	10.4	10.0
h	0.83 (0.04)	–	0.92 (0.02)	0.86 (0.03)	0.88 (0.02)	0.86 (0.02)	0.85 (0.04)
π	0.0041 (0.0024)	–	0.0050 (0.0029)	0.0038 (0.0023)	0.0046 (0.0026)	0.0052 (0.0030)	0.0045 (0.0026)
Fu's *Fs*	−1.2	–	**−14.8**	**−9.2**	**−24.9**	**−6.7**	−2.1
Tajima *D*	−0.3	–	−0.5	−1.4	−1.8	−0.6	−0.1
N	36	–	62	55	117	71	30

[a]Bold values signify populations out of Hardy–Weinberg equilibrium or significant values for population demography parameters (Fu's *Fs* or Tajima's *D*). A dash indicates that marker type was not collected for that location.
[b]Allelic richness is based on 17 individuals.
[c]Haplotypic richness is based on 30 individuals.
[d]Samples from the Chukchi Sea are pooled for mtDNA analysis due to low samples with known exact locality. Therefore, the mtDNA diversity values represent the entire Alaskan Chukchi Sea which includes samples with known (eastern, $N = 2$ and southern, $N = 4$) and unknown exact location within the Chukchi Sea ($N = 30$).

exceeded the null predictions (Figure 4). After Bonferroni correction, all loci within each station were in HWE (Supplementary Table S5).

Discussion

We found different patterns of genetic variation at various spatial scales. At the broad-scale, we uncovered two mitochondrial *cytb* lineages in Arctic cod, but with no underlying geographic pattern of haplotypes. The relatively more contemporary signal based on microsatellite loci showed little overall differentiation across Arctic waters of Alaska, concordant with findings of others (Pálsson *et al.*, 2009; Wildes *et al.*, 2016), suggesting high connectivity across the Arctic with a general lack of dispersal barriers. However, we found areas of significantly higher than average levels of genetic differentiation within the southern shelf of the Beaufort Sea, manifested as differences in allelic distribution between our southernmost and easternmost sampling locales. This micro-geographic structuring may be the result of temporal or seasonal environmental heterogeneity due to the influence of the Mackenzie River and other freshwater outflows in this region of the Alaskan Beaufort Sea.

Micro-geographic genetic structure

Although often exhibiting limited levels of genetic structure across large spatial scales, marine organisms can show slight, albeit significant, localized genetic structure that can vary within and between years; that is, they show chaotic genetic patchiness (Larson and Julian, 1999; Selwyn *et al.*, 2016). Fine-scale spatio-temporal patterns are promoted by a variety of factors such as variation in reproductive success, recruitment, and micro-geographic environmental heterogeneity (Larson and Julian, 1999). Some life history characteristics, such as batch spawning and high fecundity, are conducive to generating a pattern of patchy genetic diversity as recruitment pulses of related individuals may remain together through development (larval cohesion) (e.g. *Micromesistius australis*, McKeown *et al.*, 2017). Local variability in sea surface temperature and currents may also produce a pattern of localized genetic structure in the absence of broad scale differentiation, as temporal variability in physical oceanographic process influences larval dispersal and recruitment (e.g. *Centrostephanus rodgersii*, Banks *et al.*, 2007). Although this study and others failed to find historical signatures of broad geographic genetic structuring in Arctic cod in northern marine waters of Alaska, the divergence hotspots associated within the inner shelf and offshore shelf-break zone in Camden Bay and near the Mackenzie River outflow (see Figure 3) suggest that micro-geographic processes can drive the distribution of genetic diversity.

Cohort cohesion may also promote chaotic genetic patchiness, as individuals within cohorts have stronger kin associations than across a broader region (Eldon *et al.*, 2016). Chaotic genetic

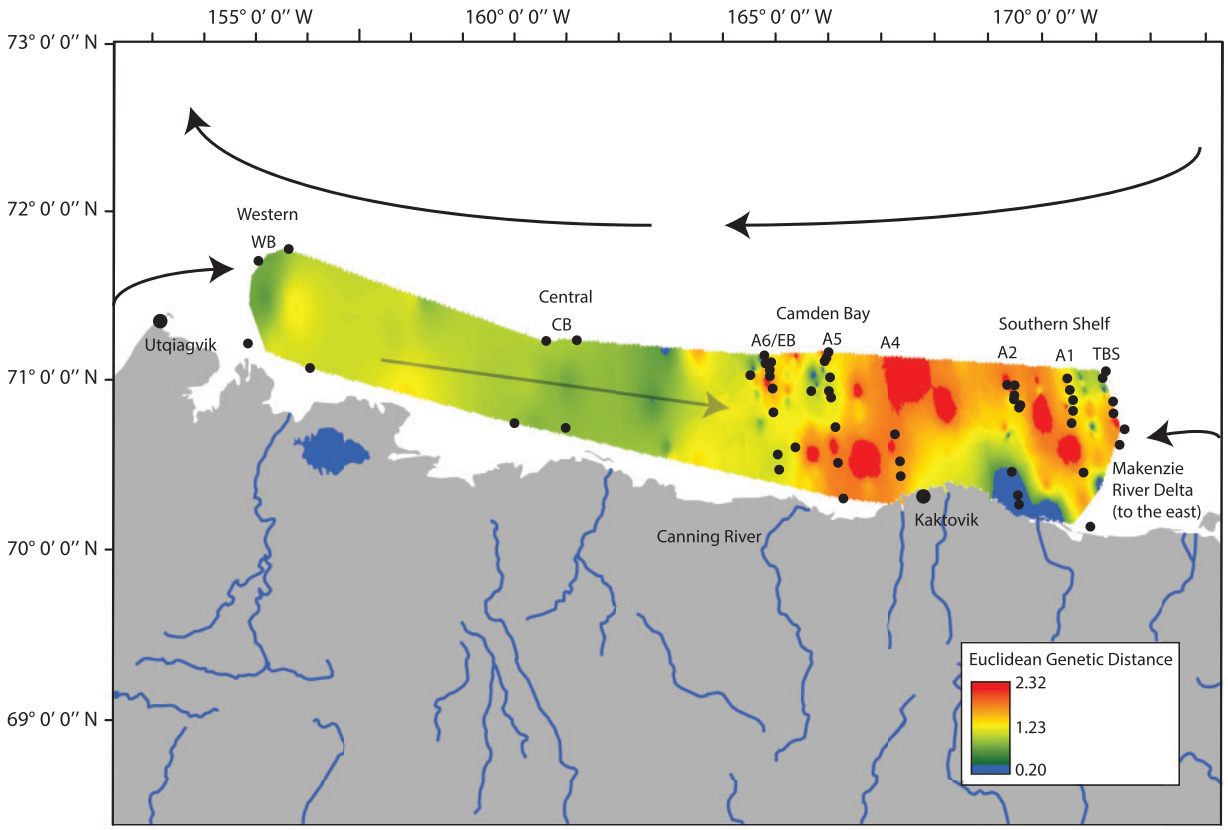

Figure 3. Genetic divergence landscape based on Euclidean genetic distances of Arctic cod. Small black circles indicate sampling stations within each of the four main sections of the Beaufort Sea: Western, Central, Camden Bay, and Southern Shelf. Main currents are depicted by arrows. Areas with relatively high genetic divergence (>1.5 *SD* from mean) are shown in red (i.e. restricting dispersal) while areas with lower than usual divergence (<1.5 *SD*) are shown in blue (promoting dispersal). All other colours indicate intermediate levels of divergence which do not indicate areas promoting or restricting connectivity.

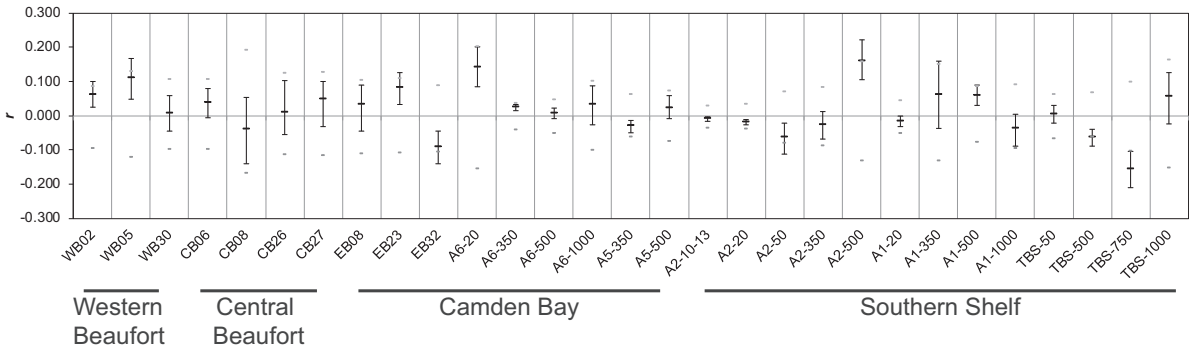

Figure 4. Mean within-station pairwise relatedness, r_{qg}, with 95% confidence intervals (black bars). The grey bars indicate the 95% upper and lower expected values for a null distribution of panmixia based on 999 permutations.

patchiness often produces a pattern in which biparentally inherited molecular markers deviate from HWEs within some locales, as well as high levels of relatedness within patches (Marino *et al.*, 2010; Selwyn *et al.*, 2016). High relatedness within cohorts in pelagic fish (Buston *et al.*, 2007; Selwyn *et al.*, 2016) have been interpreted as cohort cohesion. Although the reproductive biology of Arctic cod is not well known, the species is assumed to be a total spawner; that is, they release all eggs at once. Females lay between 9000 and 30 000 eggs, fewer than other more temperate cod species in this region (batch spawners: *Gadus chalcogrammus* up to 1 400 000 eggs; total spawners: *Eleginus gracilis* up to 690 000 eggs, *Gadus microcephalus* up to 6 400 000; see citations in Thorsteinson and Love, 2016). Arctic cod spawn under the sea ice where buoyant eggs remain on the ice–water interface (Graham and Hop, 1995); thus, dispersal of eggs and larvae likely depends on currents, wind, etc. (Norcross and Shaw, 1984). However, our

kinship analysis failed to uncover elevated levels of relatedness within stations relative to the null distribution of panmixia; therefore, cohort cohesion does not appear to explain patchiness in genetic divergence within the Beaufort Sea for Arctic cod.

Hydrographic features, such as river plumes, gyres, upwelling, and hydrographic fronts, can transport larvae from lower-suitability to higher-suitability habitat, but may also restrict larvae dispersal. The Mackenzie Delta, the second largest Arctic delta, drives productivity in the Beaufort Shelf (Emmerton *et al.*, 2008), and this region of the Beaufort Sea often represents a transition zone between Pacific and Arctic species (Carmack and MacDonald, 2002; Smoot and Hopcroft, 2017). The Mackenzie River plume causes large fluctuations in water temperature and salinity (Mulligan *et al.*, 2010; Nghiem *et al.*, 2014), and winds can transport plumes far offshore (Mulligan *et al.*, 2010), distributing heat across large areas (Nghiem *et al.*, 2014). Such temporal and spatial heterogeneity influences the distribution and diversity of fish assemblages in this region, including larval Arctic and Saffron cods (Wong *et al.*, 2013), and migratory behaviour of the Arctic cisco (*Coregonus autumnalis*; Colonell and Gallaway, 1997). Although we found no evidence of kin associations within stations located in the western reaches of the Mackenzie plume—one station (TBS-750), in fact, showed significant negative relatedness values—we found patchily distributed areas of genetic divergence comprising individuals that may belong to lineages originating from different sources (Pacific and Arctic-Canadian Beaufort Sea origin). Furthermore, negative values of Fu's F_S and larger number of alleles in southern Beaufort (Table 1) suggest historical growth and provide additional evidence that this area is a transition zone between lineages. Given that the Mackenzie River region is a transition zone with complex undercurrents flowing eastward from the Alaskan Beaufort and westward from the Canadian Beaufort (Weingartner, 2006), the pattern of patchy genetic divergence may signal cohesion of individuals with either Arctic or Pacific lineages in the area.

Conclusions

Habitat heterogeneity and oceanography conditions have a large influence on gene flow and dispersal (i.e. population connectivity) which affects the distribution of genetic diversity. A growing literature shows that local processes produce fine-scale genetic structure in many marine systems. While we failed to detect significant genetic structuring in Arctic cod in northern waters of Alaska, mapping genetic distances onto the seascape uncovered a nonrandom distribution of genetic diversity within the eastern region of the Beaufort Sea brought about by a complex physical oceanography influenced by Mackenzie River plume. Although it is unclear if this pattern is ephemeral and subject to seasonal changes in oceanic conditions, understanding the mechanisms behind such patterns are relevant to a species' life cycle, demography, ecology, and evolution (Eldon *et al.*, 2016). Thus, the application of approaches to determine potential barriers to connectivity or spatial distribution of genetic variation in Arctic cod furthers our knowledge of this ecologically important species and informs management strategies in light of future environmental changes.

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Supplementary data

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

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