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PANMIXIA IN ALASKAN POPULATIONS OF THE SNOW CRAB *CHIONOECETES OPILIO* (MALACOSTRACA: DECAPODA) IN THE BERING, CHUKCHI, AND BEAUFORT SEAS

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ABSTRACT

Decreasing sea ice in the Arctic is expected to impact marine ecosystems, and to lead to increased human activity in the form of shipping traffic, fishing pressure, and mineral resource exploration and extraction. In the face of these pressures, we examine genetic population structure in the snow crab *Chionoecetes opilio* (Fabricius, 1788), throughout its distribution in Alaskan waters, to determine degrees of population connectivity between the Arctic and more southerly portions of the species' range. Snow crabs are widely distributed on the high-latitude continental shelves of North America, where they support a valuable commercial fishery in the United States and Canada. Fishing pressure in United States waters is currently concentrated in the Bering Sea, but large populations of snow crab also occur farther north in the Chukchi and Beaufort Seas. These northern stocks are not well studied, and not yet targeted by fisheries, although commercial-sized individuals were recently reported in areas of the Western Beaufort Sea. We used seven polymorphic microsatellite markers to examine tissue samples from 573 individual crabs collected at 12 sampling locations distributed across the Bering, Chukchi, and Beaufort Seas. These data indicate that Alaskan snow crabs constitute one large, panmictic population. Connectivity between fishery areas in the south and unexploited regions farther north thus appears to be substantial, perhaps due to a lengthy larval dispersal period and highly mobile adult population.

KEY WORDS: Beaufort Sea, *Chionoecetes opilio*, Chukchi Sea, fisheries, panmixia, snow crab

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INTRODUCTION

Changing climate in the Arctic is manifesting as warming temperatures and changing sea ice conditions, with consequences for marine communities (Grebmeier, 2012). Moreover, declining sea ice coverage is opening up areas of the Arctic shelves to increased human presence in the form of shipping traffic and petroleum resource extraction activities, and stimulating interest in potential exploitation of new fisheries resources. The snow crab, *Chionoecetes opilio* (Fabricius, 1788), represents one such commercially valuable species with the potential to be impacted by both fishing pressure and habitat disturbance in the Alaskan Arctic. Snow crabs occur throughout high-latitude continental-shelf regions of the North Pacific and Northwest Atlantic, and recent surveys have also documented the presence of an expanding non-native population in the Barents Sea (Alvsvåg et al., 2009; Agnalt et al., 2011). In addition, changing temperatures appear to be driving a northward range contraction in the Pacific-Arctic region (Dionne et al., 2003; Orensanz et al., 2004), as evidenced by substantial increases in snow-crab biomass and abundance in the Chukchi Sea since the 1970s (Bluhm et al., 2009). This range shift may increase population sizes in the Chukchi and Beaufort Seas, and alter dynamics of dispersal and migration in the region.

Lucrative snow-crab fisheries exist in northeastern Canada, Greenland and the United States. The US snow-crab fishery is currently limited to the eastern Bering Sea (EBS), and represents the largest and most valuable crab fishery in the country (over $155 million ex-vessel value; NPFMC, 2010). Harvest increased during the 1980s as catches of the more valuable Tanner crab, *Chionoecetes bairdi* Rathbun, 1924, began to decline (Bowers et al., 2008). Since that time, EBS stocks have undergone large inter-annual fluctuations in population size, and were declared overfished in 1999 (NPFMC, 2010).

EBS stocks are currently managed as one panmictic unit with a single harvest quota, although harvest and population dynamics are tracked in two distinct sub-districts (divided at 173°W) (Bowers et al., 2008). Mature females in the Bering Sea undergo an ontogenetic migration, moving into deeper water in a direction that is generally "upstream" with respect to local currents that may disperse larvae (Ernst et al., 2005). Males may also migrate to deeper waters following the terminal molt (Otto, 1998). Although these patterns could potentially influence patterns of gene flow, previous investigations of population structure using allozymes

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supported the current management scheme, indicating little structure within the EBS region (Merkouris et al., 1998).

Relatively little attention has been paid to snow crab stocks in the Chukchi and Beaufort Seas, where large aggregations also occur (Paul et al., 1997; Bluhm et al., 2009; Rand and Logerwell, 2011). These unexplored populations may be sources or sinks for genetic exchange with other, more intensively fished populations farther south, or farther east in Canadian waters. Movement patterns within the Chukchi and Beaufort Seas are not known; however, migrations to deeper water may be evidenced by the discovery of larger individuals (up to 119 mm carapace width, CW) at depths up to 478 m in the Beaufort Sea (Rand and Logerwell, 2011). This discovery was significant because a latitudinal cline in size-at-maturity has been well-documented in both Pacific and Atlantic populations, with morphometrically mature Chukchi Sea snow crabs typically only reaching 40 to 70 mm CW (Somerton, 1981; Burmeister and Sainte-Marie, 2010).

The large population size, degree of adult mobility, and lengthy planktonic larval period of snow crab (on the order of three to four months; Incze et al., 1984, 1987; Kogane et al., 2005) may be expected to create a genetically homogenous population over a relatively large area. Again, an earlier allozyme study did fail to detect population structure in the Bering Sea (Merkouris et al., 1998). Allozymes are less polymorphic than microsatellites, and may thus fail to detect structure in large populations. Nonetheless, microsatellite-based studies of snow crab populations in northeastern Canada also failed to detect significant population structure over similar spatial scales (Puebla et al., 2008). Genetic tools have not been applied in examining connectivity between the EBS and northern populations in Alaska, but complex ontogenetic migrations (Orensanz et al., 2004; Ernst et al., 2005) and possible hydrographic retention of larvae in some areas of the Bering Sea (Parada et al., 2010) may generate more population structure than has been accounted for in current management strategies. Alternatively, the lengthy planktonic period and predominantly northward flow in the Pacific-Arctic region (Winsor and Chapman, 2004) could be sufficient to homogenize genetic population structure throughout Alaskan waters (Fig. 1). We explore these two scenarios using microsatellite techniques to examine population structure of snow crabs collected throughout the Bering, Chukchi, and Beaufort Seas, and determine whether genetically distinct subpopulations exist despite the

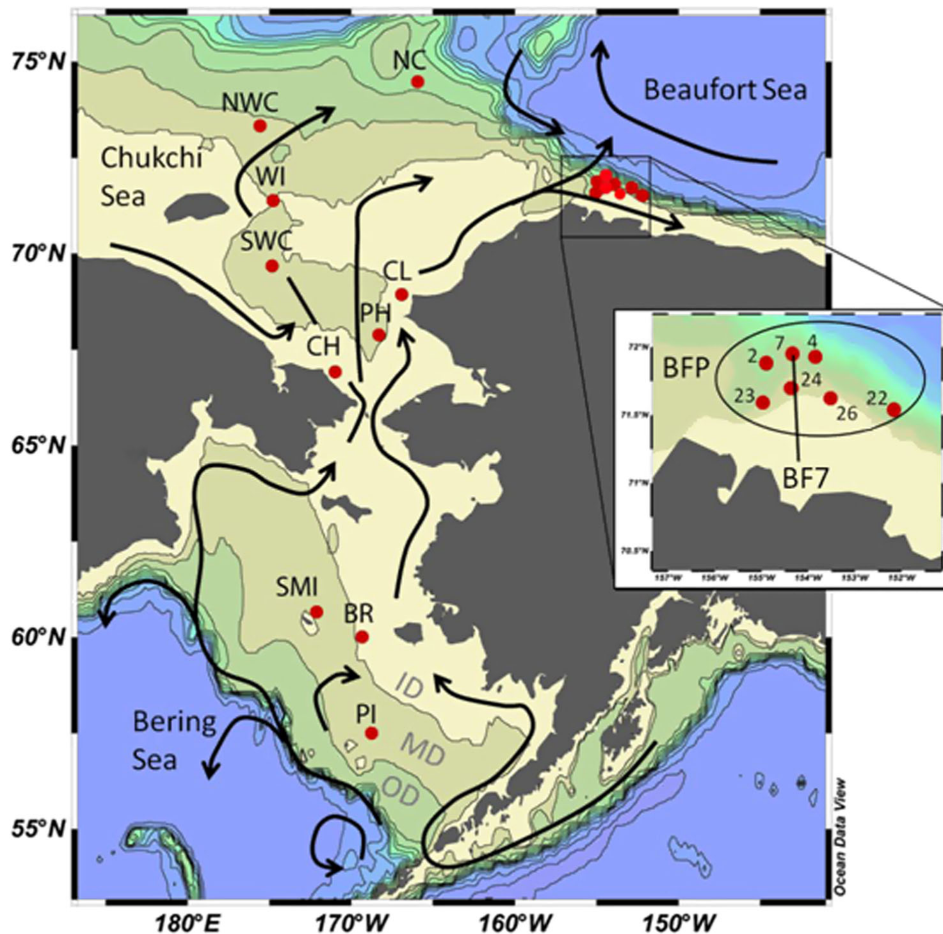

Fig. 1. Map showing sample locations (red circles). Station BFP (inset) in the Beaufort Sea is comprised of samples pooled from sites 2, 4, 22, 23, 24 and 26 (site numbers correspond to Rand and Logerwell, 2011). Idealized oceanographic flow through the study area (based on Stabeno et al., 2001; Weingartner et al., 2005; Parada et al., 2010) shown by black arrows. Site 7 (BF7) was not pooled due to the presence of larger-sized individuals at this site. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

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absence of obvious physical barriers to movement and dispersal. Specifically, we test the null hypothesis that snow crabs form a panmictic population throughout the region.

MATERIALS AND METHODS

Sample Collections

Samples of snow crab muscle tissue were collected opportunistically on a series of cruises in the Bering, Chukchi and Beaufort Seas from 2008 to 2010 (Fig. 1). Female crabs were specifically targeted for collection because snow crabs in the EBS are known to undergo sex-specific ontogenetic migrations (Ernst et al., 2005). Interpretation of results from this study could thus be complicated by these sex-specific patterns, so we attempted to eliminate sex as a variable. However, because samples were collected opportunistically, sample numbers were low at some locations. We thus pooled males and females for one location in the Bering Sea (station PI) and one location in the Chukchi Sea (station NC), and at all stations in the Beaufort Sea (Table 1; Fig. 1).

Beaufort Sea samples ($n = 105$) were collected in August 2008 on a US Minerals Management Service expedition aboard the F/V *Ocean Explorer*, using an 83-112 eastern otter trawl (for additional sampling details, see Rand and Logerwell, 2011). Whole crabs were frozen at −20°C aboard the vessel and transferred to −80°C in the home laboratory prior to tissue sub-sampling. In addition to pooling males and females, samples from six Beaufort Sea stations (2, 4, 22, 23, 24 and 26) were pooled due to low sample numbers. These samples included a range of different-sized individuals from depths ranging from 49 to 478 m, but all samples were collected in a relatively localized area (station BFP, Fig. 1). Station BF7 was also located near the pooled stations, but samples from BF7 were treated separately in our analyses because these crabs were notably larger in size (88.5 ± 15.0 mm, compared to 34.6 ± 15.2 mm avg. carapace width (CW)). Despite their larger size, these crabs had similar shell condition as the smaller individuals from nearby sites, suggesting they were of roughly the same age (Ernst et al., 2005; Fonseca et al., 2008). Thus, we were interested in determining whether these larger crabs were genetically distinct from the smaller individuals found at all the other sites.

Chukchi Sea samples ($n = 268$) were collected in September 2009 during the Russian-American Long-term Census of the Arctic (RUSALCA) cruise aboard the R/V *Professor Khromov*, using both otter and plumb-staff beam trawls. Crabs were again frozen whole aboard the vessel and sub-sampled in the home laboratory. As many as 50 females were collected from each of seven stations to encompass a broad area (Fig. 1, Table 1). The majority of individuals collected (92.4% of the females) were immature, based on width of the abdominal flap.

Bering Sea samples ($n = 200$) were collected in July 2010 aboard the National Marine Fisheries Service (NMFS) annual trawl survey cruises (for additional sampling details, see Chilton et al., 2011). Sampling was conducted aboard the F/V *Aldebaran* and the F/V *Alaska Knight* using 83-112 eastern otter trawls. Three sampling locations were chosen to encompass a broad area in the region of maximum snow crab density. Primiparous females (one molt prior to morphometric maturity) were targeted at each of three sites in order to sample an approximate age range that was consistent with samples previously collected in the Chukchi Sea. A 2.5-cm section of the 4th walking leg was sampled from each live crab on board ship, and preserved in 95% ethanol. Measurements of carapace width (Table 1) were taken at time of sampling and data were obtained from NMFS data logs.

DNA Extraction and Genotyping

Genomic DNA was extracted from tissues using Omega Bio-Tek E.Z.N.A.® and Qiagen DNeasy® extraction kits. Seven published microsatellite loci were successfully amplified: *Cop2*, *Cop3*, *Cop4*, *Cop3-4II*, *Cop24-3* and *Cop11* (Puebla et al., 2003) and *EC0106* (An et al., 2007). Attempts to amplify and analyze five additional loci (*Cop4-1* and *Cop77*; Puebla et al. 2003, and *KC030*, *KC0181* and *KC0235*; An et al., 2007) were unsuccessful.

PCR amplifications contained about 20-100 ng template DNA, 0.5 μM each primer, Qiagen hot-start *Taq* and 2× Multiplex PCR Master Mix (containing a final concentration of 3 mM $MgCl_2$), for a final volume of 10 μl. PCR conditions consisted of a 30 minute denaturation at 94°C, followed by 40 cycles of 30 seconds denaturing at 96°C, 50 seconds annealing at 55°C, and 1 minute of extension at 72°C with a final extension time of 20 minutes at 72°C. Three PCR multiplexes consisting of 2 loci each (*Cop113* and *Cop3-4II*, *Cop2* and *ECO106*, *Cop3* and *Cop4*) were used; however, *Cop24*-3 was run independently due to interference when paired with any other locus. Final PCR product was submitted to the Yale DNA Analysis Facility (available online at: http://dna-analysis.research.yale.edu//) for capillary electrophoresis on a 3730xl 96 Genetic Analyzer using Gene Scan LIZ-500 internal size standard. All samples were amplified, analyzed, and scored a minimum of two times to ensure accurate genotyping with a range of 0-8.5% missing data per locus. Alleles were scored using GeneMapper® software (version 3.7. Applied Biosystems), and all scores were visually checked to confirm binning.

Statistical Analysis

The data set containing genotypes for all 7 microsatellite loci (12 sampling locations, $n = 573$ individuals) was analyzed with MICRO-CHECKER (Van Oosterhout et al., 2004) to detect scoring incongruities and possible null alleles. Number of alleles (N_A) and allelic richness (A) were calculated for the 12 samples (i.e., geographic locations) at each locus, using the software FSTAT v. 2.9.3.2 (Goudet, 2001). A Wilcoxon signed-rank test was carried out in the statistical software package JMP (SAS institute, Cary, NC, USA) to test for significance in allelic richness between samples. Observed (H_O) and expected (H_E) heterozygosities were calculated for each sample at each locus using the software ARLEQUIN v. 3.5.1.3 (Excoffier and Lischer, 2010). Heterozygosities over loci by sample and over samples by locus were computed using the software GENETIX v.4.05.2 (Belkhir et al., 1996-2004) and FSTAT v. 2.9.3.2 (Goudet, 2001), respectively. FSTAT was also used to estimate F_{IS} (a measure of the heterozygote deficit within samples) for each locus, and across loci for each sample. F_{IS} was then tested (1000 randomizations) for significant differences from zero to assess compliance with Hardy-Weinberg equilibrium. Linkage disequilibrium (non-random association of alleles at different loci, e.g. due to physical linkage) was tested within samples between all pairs of loci using FSTAT. All probability values were adjusted for multiple comparison tests using sequential Bonferroni adjustments (Rice, 1989).

Pairwise genetic differentiation was quantified for each sample (station) pair using estimates of pairwise fixation indices (F_{ST}) based on variance in allelic frequencies (Weir and Cockerham, 1984). Values were tested for significance, based on 1320 permutations, using FSTAT. All probability values were adjusted for multiple comparison tests using sequential Bonferroni adjustments (Rice, 1989). Jost's (2008) measure of differentiation (D), which accounts for effective allele frequencies and, unlike F_{ST}, is not constrained by heterozygosity, was also calculated overall and between pairs of samples using SMOGD (Crawford, 2010). Finally, a hierarchical analysis of molecular variance (AMOVA) was carried out to partition genetic diversity among the three geographic regions (Bering Sea, Chukchi Sea and Beaufort Sea), among samples within regions, and within samples, using ARLEQUIN v. 3.5.1.3.

To test the hypothesis of panmixia across the study region, a Bayesian clustering approach was implemented using the program STRUCTURE (version 2.3.4; Pritchard et al., 2000). All possible numbers of populations (K) from 1 (panmixia) to 13 (distinct population at each sampling site) were tested using the admixture and correlated allele-frequency models. For each value of K, five runs were performed with 500 000 Markov Chain Monte Carlo (MCMC) repetitions following a 500 000 repetition burn-in period. The entire procedure was performed twice, i.e. with and without the assistance of sample geographic information (Hubisz et al., 2009). The most likely number of populations was determined based on the *ad hoc* likelihood measures $L(K)$ (Pritchard et al., 2000) and ΔK (Evanno et al., 2005) using the web-based program STRUCTURE HARVESTER (Earl and von Holdt, 2012).

RESULTS

Descriptive Statistics and Population Differentiation

The seven microsatellite markers were highly polymorphic, with alleles per locus ranging from 12 (*Cop4*) to 41 (*ECO106*; mean = 24.6 ± 8.8; Table 2). Mean within-sample allelic richness across loci (based on the smallest sample size $n = 23$) ranged from 12.5 to 14.4 (mean = 13.6 ± 0.5; Table 1). Allelic richness did not significantly differ between any two samples (Wilcoxon signed-rank test,

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Table 1. Sample collection information and descriptive statistics. Sampling location abbreviations correspond to those in Fig. 1; (N) number of males (m) and females (f) analyzed from each station; (CW) mean carapace width of all individuals collected at each sampling site ± standard deviation; (N_A) mean number of alleles by locus; (A) allelic richness for a common minimum sample size of 23; (H_O) observed heterozygosity; (H_S) gene diversity; (F_{IS}) individual diversity relative to the sample, with average CW not available for station BR; however, all females collected in the Bering Sea were between 30-65 mm CW and considered to be immature. *Significant F_{IS} values after correction for multiple tests.

Sampling location		N	Depth (m)	Lat; Long	CW (mm)	N_A	A	H_O	H_S	F_{IS}
Bering Sea										
Pribilof Islands	PI	77f, 23m	71	57.50N; 168.75E	50.5 ± 6.1	19.6	13.9	0.762	0.824	0.076*
Bering Sea Shelf	BR	50f	47	60.01N; 169.33E	*	16.9	13.9	0.790	0.806	0.020
Saint Matthew Is.	SMI	50f	61	60.66N; 172.12E	43.9 ± 4.0	16.6	13.5	0.736	0.804	0.085*
Chukchi Sea										
Chukotka Coast	CH	50f	53	66.56N; 170.59E	33.5 ± 5.7	17.0	13.6	0.757	0.797	0.051
Point Hope	PH	29f	57	67.88N; 168.31E	46.3 ± 5.1	14.6	13.7	0.721	0.809	0.111*
Cape Lisburne	CL	39f	47	68.57N; 166.55E	35.4 ± 4.5	16.6	14.0	0.765	0.812	0.058
SW Chukchi Shelf	SWC	50f	54	69.41N; 174.51E	44.1 ± 5.9	16.7	13.7	0.786	0.807	0.026
Wrangel Island	WI	26f	86	71.24N; 174.47E	45.5 ± 5.6	14.7	14.4	0.793	0.807	0.017
NW Chukchi Shelf	NW	50f	146	73.21N; 175.34E	35.6 ± 4.4	15.9	13.4	0.793	0.821	0.033
N Chukchi Shelf	NC	7f, 17m	350	74.30N; 165.57E	36.1 ± 15.3	13.7	13.5	0.815	0.810	−0.007
Beaufort Sea										
Site 7	BF7	8f, 65m	334	71.98N; 154.41W	88.5 ± 15.0	18.1	13.2	0.780	0.807	0.034
Other sites pooled	BFP	9f, 23m	45-478	71.55-71.90N; 152.20-155.05W	34.6 ± 15.2	13.7	12.5	0.772	0.791	0.024
Mean ± SD						16.2 ± 1.8	13.6 ± 0.5	0.773 ± 0.026	0.808 ± 0.009	0.044 ± 0.033

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Table 2. Characteristics of microsatellite loci; observed heterozygosity (H_O); genetic diversity (H_S); individual diversity relative to the subpopulation (in this case sampling site) with standard error estimated by jackknifing over loci (F_{IS}); subpopulation diversity relative to the total population (F_{ST}); (D) Jost's (2008) measure of differentiation; ± standard deviation. Negative F_{ST} and D values were replaced by zeros.

Locus	*Alleles*	Size range (bp)	H_O	H_S	F_{IS}	F_{ST}	D
Cop2	24	291-341	0.836	0.841	0.006	<0.001	0
Cop3	21	210-318	0.793	0.861	0.097	<0.001	0.007
Cop4	12	211-259	0.232	0.266	0.115	0	0
Cop3-4II	22	117-209	0.858	0.910	0.064	0.001	0.015
Cop24-3	27	145-253	0.908	0.925	0.023	0.002	0.037
Cop113	24	114-170	0.886	0.893	0.018	0	0
ECO106	41	187-271	0.895	0.961	0.0659	0.001	0.056
Mean/Global	24.6 ± 8.8	–	0.773 ± 0.242	0.808 ± 0.242	0.047 ± 0.013	<0.001 ± 0.001	0.017 ± 0.021

data not shown, $p = 0.12$). Overall observed heterozygosity (H_O) at each locus ranged from 0.232 (*Cop4*) to 0.908 (*Cop24-3*; mean = 0.773 ± 0.242; Table 2). Observed heterozygosity averaged across all loci for each sampling station ranged from 0.721 (sample PH) to 0.815 (sample NC; mean = 0.773 ± 0.026; Table 1).

Significant departure from Hardy-Weinberg equilibrium (HWE) was found in only one out of 84 possible population-locus pairings (sample PI at locus *Cop3*), after correction for multiple tests (see the Appendix, which can be found in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x); significant departures from HWE were observed in three samples when statistical tests were computed across loci (Table 1). All significant tests were due to heterozygote deficits. MICRO-CHECKER did not suggest technical problems related to stuttering or large allele dropout. These departures are thus likely due to random error associated with genotyping and null alleles. Tests for linkage disequilibrium (LD) revealed no significant results in any of the 252 tests at each locus combination per sample, after correction for multiple tests (not shown).

The mean (global) F_{ST} value across loci (<0.001) and the mean Jost's (2008) measure of differentiation (D) across loci (0.017) were both low (Table 2). Pairwise indices of differentiation (F_{ST}) between samples ranged from 0 to 0.005 (mean = 0.0009 ± 0.001), and no value was significantly different from zero after correction for multiple tests (Table 3). Pairwise D values ranged from 0 to 0.018 (mean = 0.003 ± 0.005), indicating that the two most divergent samples differed by less than 2% in actual relative allelic frequencies. The AMOVA analysis (Table 4) detected no significant genetic differences ($p = 0.476$) among the three regions (the Bering Sea, the Chukchi Sea, and the Beaufort Sea), as well as among sites within these regions ($p = 0.718$). Based on $L(K)$, results of the Bayesian clustering analysis performed in STRUCTURE indicated the most likely number of clusters (putative populations) is one; $K = 1$ showed the highest value (mean = −18568.86; SD = 0.22) and likelihood values decreased with increasing values of K. The delta-K method indicated $K = 3$, but this method is incapable of evaluating the possibility that $K = 1$, and examination of q-score plots (not shown) clearly favored a conclusion of $K = 1$. The results were similar whether or not sampling locations were used to assist the model (not shown). Taken together, the results strongly suggest that Alaskan snow crabs constitute one large, panmictic population.

Discussion

Analysis of seven microsatellite loci revealed genetic homogeneity in snow crab populations throughout the Alaska region. Results are consistent among all loci and locations sampled, and thus considered robust. An earlier study by Puebla et al. (2008) employed six of the same microsatellite

Table 3. Pairwise F_{ST} (above the diagonal) and D (below the diagonal) values between sampling sites. Negative values were replaced by zeros. No F_{ST} values were significant.

	PI	BR	SMI	CH	PH	CL	SWC	WI	NWC	NC	BF7	BFP
PI	*	0.0020	0	0.0001	0	0.0011	0.0006	0	0.0007	0	0	0.0008
BR	0.0043	*	0	0	0.0025	0.0003	0.0025	0	0.0019	0.0012	0.0030	0
SMI	<0.0001	0.0010	*	0	0	0.0005	0	0	0	0	0	0.0027
CH	<0.0001	<0.0001	0	*	0	0.0024	0.0004	0.0017	0.0026	0.0023	0.0022	0.0039
PH	0	0.0055	0	0	*	0	0.0001	0	0	0	0	0.0039
CL	0.0043	0.0013	0.0069	0.0129	<0.0001	*	<0.0001	0	0	0.0009	0.0018	0.0046
SWC	<0.0001	0.0111	0	<0.0001	0.0011	0.0013	*	0	0	0.0007	<0.0001	0.0007
WI	0	0	<0.0001	0.0002	0	0	0	*	0	0	0	0
NWC	0.0003	0.0081	0.0010	0.0015	<0.0001	<0.0001	0	0	*	0	0	0.0033
NC	0.0002	0.0035	0.0004	0.0028	0	0.0060	0.0050	0	0	*	0	0.0050
BF7	0	0.0077	0	0.0002	0	0.0073	0.0002	0	0	0	*	0.0024
BFP	0.0033	0.0003	0.0116	0.0129	0.0149	0.0180	0.0022	0.0011	0.0098	0.0163	0.0078	*

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Table 4. Hierarchical AMOVA partitioning genetic diversity across the three geographic regions sampled (Bering, Chukchi and Beaufort Seas), based on the seven microsatellite loci. Results shown indicated variance components and percentage of variation explained by different levels of population structure, as well as F-statistics and probability of significance.

Source of variation	df	Sum of squares	Variance components	Percentage of variation	Fixation index (F_{ST})	P (based on 1023 permutations)
Among regions	2	4.61	0.00006	0.00	0.00003	0.476 ± 0.015
Among populations within regions	9	20.57	−0.00009	0.00	−0.00004	0.718 ± 0.014
Within populations	1134	2601.82	2.29	100.00	−0.00001	0.718 ± 0.015
Total	1145	2627.01	2.29			

markers used here, along with two additional loci, in examining population structure of Atlantic snow crab populations in Northeast Canada and Greenland. Genetic homogeneity was found within each of these regions, although Canadian populations showed evidence of differentiation from those in Greenland. The global mean F_{ST} value reported by Puebla et al. was higher than in this study (0.011, compared to <0.001) and highly significant. However, all of the variation was attributed to differences between Atlantic Canada and Greenland sites; the mean F_{ST} value within Atlantic Canada samples (0.001) was comparable to the value reported here for Alaska populations.

Snow-crab populations appear to be genetically homogeneous, not only on regional scales, but over much larger scales as well. Albrecht (2011) compared the Alaskan population (data reported here, all sites pooled) to those in Atlantic Canada and Greenland (data from Puebla et al., 2008) using five microsatellite loci, and found low levels of differentiation between populations in Alaska and Atlantic Canada. Values of Jost's (2008) D indicated greater genetic similarity between Alaska and Atlantic Canada ($D = 0.0195$) than between Canada and Greenland ($D = 0.1956$). Similar evidence of connectivity between Pacific and Atlantic populations was also shown using allozyme markers (Merkouris et al., 1998). This finding is particularly noteworthy considering snow crabs are not known to occur across most of the Canadian Arctic coastline. Snow crab occur on the western Beaufort Sea shelf and slope (Rand and Logerwell, 2011), with the farthest-east reports dating back to the 1960s from the Mackenzie River delta region (Atkinson and Wacasey, 1989). The Atlantic population only extends as far west as the Labrador region, and along the southwestern coast of Greenland (Squires, 1990).

In taxa with long-lived planktonic larvae such as the snow crab, length of the larval period is widely assumed to govern dispersal distance, and extensive dispersal distance is often invoked to explain genetic homogeneity over large spatial scales (Palumbi, 1992). In Arctic regions, low temperatures may further prolong the length of the larval period (O'Connor et al., 2007) such that extremely long-range dispersal is possible. A number of Arctic invertebrate taxa with planktonic larvae have shown this pattern (reviewed by Hardy et al., 2011). However, numerous examples can also be cited wherein marine taxa do not conform to this pattern for a variety of reasons, including larval behavior and hydrographic barriers to dispersal (reviewed by Levin, 2006; Cowen and Sponaugle, 2009). Such examples can be found among other crab species in the North Pacific and elsewhere.

Populations of red king crab, *Paralithodes camtschaticus* (Tilesius, 1815) and Tanner crab, *Chionoecetes bairdi*, show evidence of genetic differentiation between Southeast Alaska, Gulf of Alaska and Bering Sea regions, and Tanner crab exhibit some structure even within the EBS (Bunch et al., 1998; Merkouris et al., 1998; Grant et al., 2011; Grant and Cheng, 2012). Regional separation is thought to be caused by oceanographic barriers created by the Aleutian Island chain and the southeastern Alaska archipelago; however, factors influencing genetic population structure of Tanner crab within the EBS are not yet identified. Current patterns and spawning-site fidelity may be responsible (Merkouris et al., 1998), although the same factors should also influence snow crabs, which show no evidence of population structure. Tanner and king crabs do inhabit coastal fjord systems (Taggart et al., 2008), whereas snow crabs are more abundant out on the open shelf; the complex hydrography of these fjord areas may influence gene flow (Grant and Cheng, 2012). Dungeness crabs, *Metacarcinus magister* (Dana, 1852) in fjord systems of British Columbia also show differentiation of local subpopulations in some isolated embayments (Beacham et al., 2008). Domingues et al. (2010) identify hydrographic barriers to dispersal within the broad native range of the shore crab. *Carcinus maenas* (Linnaeus, 1758), which generate regional genetic structuring within European waters.

Contemporary features such as current patterns that serve as barriers to dispersal may generate structure over short time scales, whereas these patterns may also be underlain by deeper genetic structure developing on geological time scales due to, for example, confinement in glacial refugia (Grant and Cheng, 2012). The distribution of Tanner and king crab in nearshore areas may have led to greater influence of glacial cycles on genetic structure, as has been observed in a number of other Arctic taxa (reviewed by Hardy et al., 2011). In contrast, genetic homogeneity of snow crab throughout the Alaska region may be explained by population expansion from the Bering Sea into the Chukchi and Beaufort Seas relatively recently, following the last glacial maximum; a similar phenomenon has been proposed in EBS red king crab (Grant et al., 2011). Merkouris et al. (1998) further suggest a general northward and eastward expansion of the population, pointing to the lower frequency of occurrence of rare alleles and reduced heterozygosity in Atlantic snow crab populations as evidence that these populations may have been founded by immigrants from the Pacific.

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Implications for Fishery Management

Genetic homogeneity found throughout the Alaska region supports the validity of the current management approach for EBS snow crab stock, which is treated as a single panmictic unit. Moreover, Arctic populations in the Beaufort and Chukchi Seas appear to be highly connected to those in the Bering Sea. Our evidence does not suggest that the significantly larger-sized crabs found at station BF7 in the Beaufort Sea are from a distinct population. Rather, exposure to warm waters known to occur at depth in the area (Pickart et al., 2005) may have influenced the size of these crabs (Orensanz et al., 2007; Burmeister and Sainte-Marie, 2010). It is unlikely that distinct snow crab populations remain undiscovered within the Alaska region, given the spatial coverage of sampling achieved here relative to the potential scales of adult migration and larval dispersal (Ernst et al., 2005; Parada et al., 2010). The absence of a clear source-sink relationship between Alaska regions and evidence of extensive genetic exchange suggest northern stocks could persist through local recruitment even if populations continue to decline in the Bering Sea (cf. NPFMC, 2010); reproductive females have been recovered from the Chukchi Sea (Paul et al., 1997; Bluhm et al., 2009 and unpublished data).

A widely distributed, panmictic population is likely to be resilient to local disturbance if recolonization can be facilitated by influx from neighboring locations. However, populations with numerous distinct units are also thought to be more resilient to local disturbance than panmictic populations such as those identified here (Schindler et al., 2010). The enhanced genetic diversity found in more structured populations may confer an advantage, because impacts of a disturbance affecting one localized subpopulation might not be felt by other distinct groups within the region that possess a slightly different genetic make-up.

Evidence of genetic homogeneity in Alaskan snow crabs should still be considered with caution when devising management and/or conservation strategies for this species. Failure to reject the null hypothesis of panmixia does not definitively confirm that populations are extensively demographically connected (Palsbøll et al., 2007). Although high levels of gene flow have been identified as the main source of genetic homogeneity in other crab species (e.g., Sotelo et al., 2008; Domingues et al., 2010), Grant and Cheng (2012) identified recent expansion from ice-age refugia as the source of apparent homogeneity in a subset of Alaskan red king crab populations. The large population size of such species may prevent divergence due to random drift, as has been shown in multiple species of lobsters (e.g., Stamatis et al., 2004; Kenchington et al., 2009). Genetic evidence should thus be corroborated with ecological data to confirm that populations are not demographically isolated.

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APPENDIX

Table S1. Descriptive statistics by sample and locus, indicating the number of individuals (N), the number of alleles (N_A), allelic richness (A, for a common minimum sample size of 23 individuals), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) and probability (p) of heterozygote deficit. * Significant p-values after sequential Bonferroni correction.

	Cop2	Cop3	Cop4	Cop3_4II	Cop24_3	Cop113	ECO106
Pribilof Islands (PI)							
N	100	97	100	96	86	100	89
N_A	19	17	11	17	21	19	33
A	12.7	12.5	6.4	13.1	15.9	13.1	23.3
H_O	0.860	0.629	0.340	0.854	0.884	0.870	0.899
H_E	0.855	0.844	0.370	0.906	0.929	0.903	0.961
F_{IS}	−0.006	0.256*	0.082	0.057	0.049	0.037	0.065
p-value	0.608	0.0006	0.107	0.067	0.080	0.160	0.008
Bering Sea Shelf (BR)							
N	50	50	50	50	44	50	50
N_A	19	16	6	17	17	13	30
A	13.8	13.5	4.6	14.5	14.9	12.2	23.6
H_O	0.820	0.880	0.200	0.960	0.909	0.860	0.900
H_E	0.823	0.878	0.257	0.914	0.916	0.889	0.963
F_{IS}	0.004	−0.003	0.223	−0.051	0.008	0.033	0.066
p-value	0.556	0.615	0.037	0.960	0.520	0.336	0.038
Saint Matthew Island (SMI)							
N	50	49	50	47	49	50	49
N_A	19	16	5	15	18	14	29
A	13.7	13.1	4.2	13.2	15.2	12.0	23.0
H_O	0.860	0.755	0.240	0.745	0.878	0.820	0.857
H_E	0.855	0.868	0.224	0.907	0.927	0.884	0.962
F_{IS}	−0.006	0.131	−0.074	0.181	0.054	0.073	0.110
p-value	0.601	0.010	1.000	0.001	0.138	0.098	0.005
Chukotka Coast (CH)							
N	50	50	50	50	49	50	50
N_A	18	13	6	16	22	14	30
A	13.3	10.6	4.7	13.2	18.0	12.3	23.2
H_O	0.740	0.780	0.260	0.760	0.918	0.920	0.920
H_E	0.816	0.800	0.258	0.907	0.937	0.894	0.965
F_{IS}	0.094	0.026	−0.010	0.164	0.020	−0.029	0.047
p-value	0.076	0.395	0.643	0.001	0.389	0.797	0.105
Point Hope (PH)							
N	29	29	29	29	25	28	28
N_A	12	13	5	12	17	15	28
A	11.1	12.2	4.6	11.5	16.4	13.9	25.9
H_O	0.793	0.724	0.172	0.690	0.880	0.893	0.893
H_E	0.826	0.857	0.283	0.901	0.931	0.893	0.974
F_{IS}	0.041	0.158	0.395	0.238	0.056	0.000	0.085
p-value	0.379	0.038	0.010	0.003	0.233	0.593	0.039
Cape Lisburne (CL)							
N	39	39	39	38	39	39	39
N_A	16	15	7	15	20	15	28
A	13.4	12.2	5.3	14.2	16.9	13.3	22.7
H_O	0.821	0.795	0.231	0.868	0.872	0.897	0.872
H_E	0.848	0.829	0.281	0.925	0.934	0.906	0.957
F_{IS}	0.033	0.042	0.182	0.061	0.068	0.010	0.090
p-value	0.388	0.343	0.098	0.153	0.107	0.503	0.016

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Table S1. (Continued.)

	Cop2	Cop3	Cop4	Cop3_4II	Cop24_3	Cop113	ECO106
SW Chukchi Shelf (SWC)							
N	49	50	50	48	47	50	48
N_A	17	15	5	17	19	14	30
A	12.9	13.0	4.1	14.7	16.1	11.7	23.1
H_O	0.816	0.900	0.180	0.813	0.936	0.920	0.938
H_E	0.836	0.868	0.240	0.923	0.931	0.885	0.961
F_{IS}	0.024	−0.037	0.251	0.121	−0.005	−0.039	0.025
p-value	0.401	0.836	0.030	0.008	0.630	0.849	0.280
Wrangel Island (WI)							
N	25	26	26	26	24	26	23
N_A	16	14	4	15	16	14	24
A	15.4	13.5	3.8	14.8	15.7	13.6	24.0
H_O	0.880	0.808	0.154	0.923	0.958	0.962	0.870
H_E	0.878	0.878	0.149	0.934	0.931	0.916	0.964
F_{IS}	−0.003	0.081	−0.036	0.012	−0.030	−0.051	0.100
p-value	0.633	0.181	1.000	0.519	0.824	0.907	0.041
NW Chukchi Shelf (NWC)							
N	50	50	50	47	38	50	49
N_A	13	15	6	15	20	15	27
A	10.6	13.1	5.0	13.6	16.9	12.8	21.9
H_O	0.900	0.780	0.320	0.894	0.921	0.800	0.939
H_E	0.838	0.883	0.322	0.917	0.932	0.892	0.960
F_{IS}	−0.075	0.118	0.007	0.026	0.012	0.104	0.022
p-value	0.949	0.024	0.554	0.356	0.452	0.042	0.333
N Chukchi Shelf (NC)							
N	24	24	24	24	23	24	24
N_A	15	15	4	12	15	13	22
A	14.7	14.7	4.0	11.9	15.0	12.8	21.6
H_O	0.958	0.792	0.208	0.958	0.957	0.875	0.958
H_E	0.873	0.870	0.269	0.897	0.906	0.895	0.957
F_{IS}	−0.100	0.091	0.228	−0.070	−0.057	0.023	−0.001
p-value	0.978	0.165	0.130	0.929	0.895	0.474	0.663
Beaufort Sea site 7 (BF7)							
N	73	72	73	72	72	73	70
N_A	16	17	6	17	21	16	34
A	11.6	12.2	4.2	13.1	16.1	12.0	23.2
H_O	0.836	0.806	0.233	0.861	0.944	0.877	0.900
H_E	0.839	0.863	0.271	0.895	0.929	0.888	0.962
F_{IS}	0.004	0.067	0.143	0.038	−0.017	0.013	0.065
p-value	0.526	0.086	0.081	0.228	0.773	0.423	0.015
Beaufort Sea other sites pooled (BFP)							
N	32	30	32	32	30	32	30
N_A	13	12	6	13	13	13	26
A	11.6	11.7	5.3	12.3	12.7	11.3	22.7
H_O	0.750	0.867	0.250	0.969	0.833	0.938	0.800
H_E	0.810	0.885	0.261	0.884	0.895	0.874	0.931
F_{IS}	0.075	0.021	0.042	−0.098	0.071	−0.075	0.142
p-value	0.224	0.458	0.464	0.983	0.201	0.939	0.005

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