Abstract.—We used allozyme analyses to investigate genetic variation among commercially exploited populations of *Chionoecetes bairdi* (Tanner) and *C. opilio* (snow) crabs in Alaskan waters. Data were collected from 34 presumptive loci in 1002 *C. bairdi* and 539 *C. opilio* sampled throughout the commercially important range of each species in Alaska. Average observed heterozygosities were 0.027 for *C. bairdi* and 0.013 for *C. opilio*. Low levels of geographic differentiation were detected among populations of *C. bairdi* and *C. opilio*, and our data suggest that subpopulations of *C. bairdi* exist within the Bering Sea. Further, evidence of gene introgression was found between *C. bairdi* and *C. opilio* in the Bering Sea. We also included a geographic isolate, North Atlantic *C. opilio*, in the analyses. Little differentiation was found, and no private alleles were detected in North Atlantic *C. opilio* despite significant geographic separation from Alaskan *C. opilio*.

Low levels of genetic diversity in highly exploited populations of Alaskan Tanner crabs, *Chionoecetes bairdi*, and Alaskan and Atlantic snow crabs, *C. opilio**

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Manuscript accepted 24 October 1997.
Fishery Bulletin 96:525–537 (1998).

Five species of the genus *Chionoecetes*, Majidae, are described from the North Pacific region (Rathbun, 1925; Garth, 1958). The nearly circumpolar range of *C. opilio* (snow crab) includes the Bering Sea, the Arctic Ocean, the western North Pacific coast of Asia, and the northern Atlantic Ocean. *Chionoecetes bairdi*, *C. angulatus*, and *C. tanneri* are widespread in the eastern North Pacific (Garth, 1958). *Chionoecetes japonicus* is found only in the western North Pacific along the coast of Asia. In the Alaskan waters of the Bering Sea, the distribution of *C. bairdi* is strongly associated with the continental slope areas along the coast of the Alaska Peninsula, and the Pribilof Islands (Otto, 1982), and there is considerable overlap in the distribution of *C. bairdi* and *C. opilio* (Karinen, 1974).

Commercial fisheries for male *C. bairdi* and *C. opilio* in Alaska, along with king crabs (*Paralithodes* and *Lithodes*) have long been the world's most abundant sources of crabs and have considerable current and historical commercial importance in Alaska (Otto, 1990). *Chionoecetes bairdi* are faster growing, larger, and more valuable than *C. opilio*. Commercial harvests of *C. bairdi* in the Bering Sea and Gulf of Alaska fisheries peaked in the late 1970s, declined throughout the 1980s, and although some populations of *C. bairdi* have recently rebounded, many fisheries remain closed owing to low abundance (Kruse, 1993). Rapid development of the Bering Sea *C. opilio* fishery coincided with the decline of *C. bairdi* fisheries, and although *C. opilio* have dominated landings of Bering Sea crabs since the mid-1980s, catches have also declined dramatically in recent years (ADF&G, 1994).

Declining abundances of Bering Sea and Gulf of Alaska crab populations have intensified competition for the remaining resources and have lead to re-evaluation of crab fishery management practices. Gen-

* Contribution number PP-123 of the Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Juneau, Alaska.

erally when a population or stock is modeled, the assumption is made that the individuals within the population are uniform, but it is important that this assumption be verified (Cobb and Caddy, 1989). In practice, a stock is often defined as 1) a production or management unit about which conclusions can be made without regard for differences within the group and exchanges with other groups, or as 2) biologically, a genetically discrete population (reviewed in Cobb and Caddy, 1989). However, stock identity of decapod populations has been largely ignored or problematic (Cobb and Caddy, 1989; Kruse, 1993).

Existing shellfish management units in Alaska were originally established according to historical fishing grounds of red king crab. Current area lines for *C. bairdi* and *C. opilio* were based on mark-and-recapture data, natural geographic barriers, and areas of stock abundance grouped by major fishing grounds. Although genetic surveys were not conducted on unexploited *Chionoecetes* populations in Alaska, the establishment of a genetic baseline is critical for verifying current fishery management units and for monitoring potential fishery-induced genetic changes. Additionally, the genetics of *C. bairdi* and *C. opilio* populations in the Bering Sea is complicated by the presence of hybrids of these two species. *Chionoecetes bairdi* and *C. opilio* appear to have many similar morphological, physiological, and reproductive features (Watson, 1970; Slizkin, 1990) that allow them to hybridize in areas of range overlap (Karinen and Hoopes, 1971; Somerton, 1981; Hoopes et al.[1]).

Many studies suggest that commercial fishing activities may have significant genetic effects on fish stocks without reducing them to near extinction (for example, see reviews in Allendorf et al., 1987; Thorpe, 1993), and genetic selection against fast growth may result from intense fishing pressure (Kruse, 1993; Stevens et al., 1993); however, these effects can be assessed only if there are comparative baseline data.

In 1990 we began genetic investigations of *C. bairdi* and *C. opilio* populations in Alaska using allozyme electrophoresis. Our objectives were 1) to assess genetic variation in exploited populations of *C. bairdi* and *C. opilio* in Alaska and 2) to determine if significant differentiation exists to warrant re-examination of current management units.

Materials and methods

Population sample collections

Samples of *C. bairdi* and *C. opilio* were obtained between 1989 and 1993 from population assessment trawl and pot survey catches, test fishery pot catches, and dockside commercial pot catches. Crabs caught in pots set in adjacent areas were pooled into a single collection (Table 1). *Chionoecetes bairdi* were collected from sites ranging from Seymour Canal in Southeast Alaska to northwest of the Pribilof Islands in the Bering Sea (Table 1; Fig. 1). *Chionoecetes opilio* were collected from sites in the Bering Sea. In addition, we obtained a collection of *C. opilio* from the North Atlantic for comparison with Bering Sea samples. Eighteen collections of *C. bairdi* and nine collections of *C. opilio* were analyzed in this study.

Table 1
Collection information for *Chionoecetes* specimens.

Location number	Location[1]	Date	*n*
Chionoecetes bairdi			
1[2]	Bristol Bay	Jun 90	50
	Bristol Bay	Jun 91	50
2[2]	Bering Sea and Pribilof Islands	Jul 90	50
	Bering Sea and Pribilof Islands	Apr 91	75
	Bering Sea and Pribilof Islands	Jul 92	30
	Bering Sea and Pribilof Islands	Mar 93	50
	Bering Sea and Pribilof Islands	Jul 93	80
3	Port Moller	Jun 90	42
4	Sand Point and Pavlof Bay	Aug 90	50
5	Kodiak N. Mainland	Feb 90	50
6	Kodiak S. Sitkalidak Strait	Feb 90	50
7	Kamishak Bay	Jun 90	50
8	Montague Strait	Jul 90	50
9	Kachemak Bay	Jun 90	50
10	Prince William Sound	Aug 90	50
11	Sullivan Island	Jul 93	100
12	Seymour Canal	Sep 89	50
	Seymour Canal	Jul 93	75
Chionoecetes opilio			
I[2]	Bering Sea	Apr 91	75
	Bering Sea	Mar 93	50
II[2]	St. Matthew Island	Jul 90–Aug 90	100
	St. Matthew Island	Jul 92–Aug 92	100
III[2]	Pribilof Island	Jul 90	44
	Pribilof Island	Aug 90	50
	Pribilof Island	Jul 92	40
	Pribilof Island	Jun 93–Jul 93	80
	Nova Scotia, North Atlantic	Sep 91	97

[1] Latitude and longitude locations available from authors.
[2] Collections within geographic location pooled for analyses; *C. bairdi* collection sites in the Bering Sea and Pribilof Islands were overlapping.

[1] Hoopes, D. T., J. F. Karinen, and M. J. Pelto. 1970. King and Tanner crab research. International North Pacific Fisheries Commission Annual Rep. 1970:110–120.

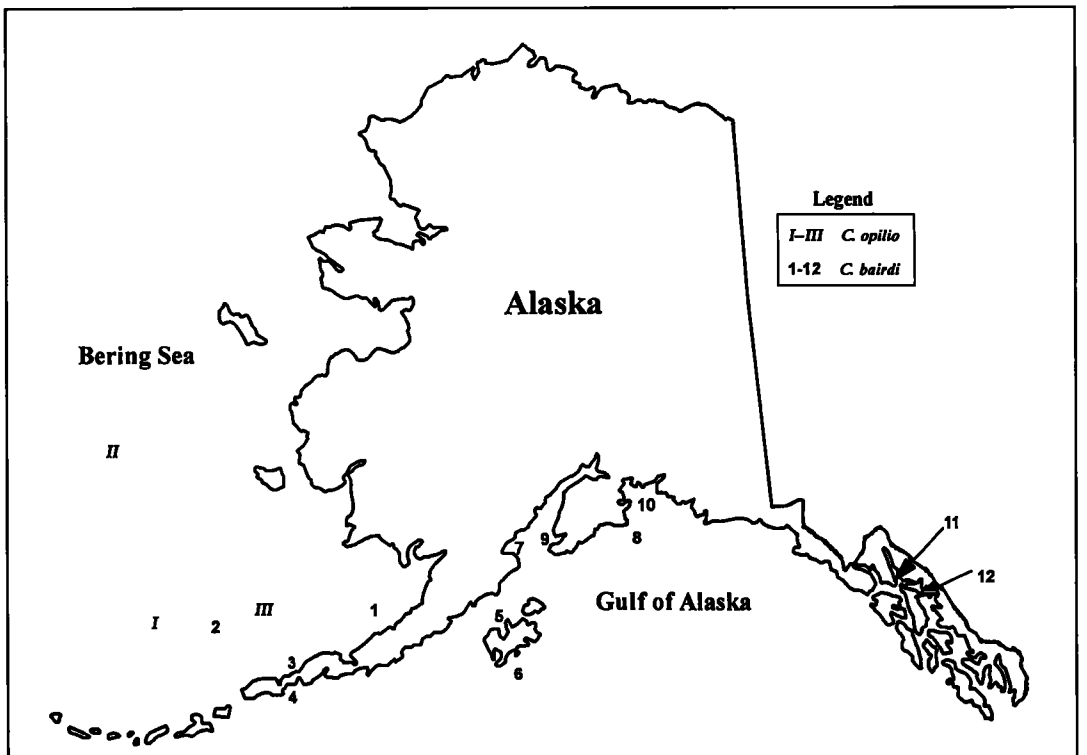

Figure 1

Locations of samples of *C. bairdi* and *C. opilio* in Alaska analyzed for genetic variation. Numbers correspond to populations described in Table 1. *C. bairdi* sample locations are labelled 1–12. *C. opilio* sample locations are labelled *I–III*.

Tissues (muscle, gill, hepatopancreas, and heart) were dissected from each individual, placed in a labelled tube, which was chilled on wet ice, capped, and frozen at –15°C (1989–90 collections) or in liquid nitrogen (1991–93 collections). Freezing generally occurred within 20 minutes after dissection but in some cases was as long as 1 hour. Tissues were transported to the laboratory on dry ice or liquid nitrogen and stored at –80°C until analysis. Several locations were sampled in multiple years.

Allozyme electrophoresis

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976) and Aebersold et al. (1987). Activity reflecting 34 presumed loci were resolved with the following buffers (Table 2): 1) N-(3-aminopropyl)-morpholine, citrate (AC, pH 6.1, 6.9) (Clayton and Tretiak, 1972); 2) Tris, borate, citrate, lithium hydroxide (TBCL, pH 8.7) (Ridgway et al., 1970); 3) Tris, citrate (TC, pH 7.0) (Shaw and Prasad, 1970); 4) Tris, citrate (TC, pH 8.0) (Selander et al., 1971); and 5) Tris, borate, EDTA (TBE, pH 8.5) (Boyer et al., 1963). Gene nomenclature followed Shaklee et al. (1990). Allelic standards were used to compare relative mobilities between species.

Genetic differentiation

We estimated allele frequencies, calculated average observed heterozygosities, and tested conformation of genotype frequencies to Hardy-Weinberg expected frequencies with log-likelihood ratios (modified from Weir, 1990) for each collection (α=0.05, adjusted for multiple tests [Rice, 1989]). Samples of *C. bairdi* collected from the Bering Sea and Pribilof Island areas were pooled because sample sites were overlapping. Interannual heterogeneity of multiple-year collections in Bristol Bay, Bering Sea, St. Matthew Island, Pribilof Islands, and Seymour Canal was tested by using log-likelihood statistics (Sokal and Rohlf, 1995). Multiple-year collections within a site were pooled for further analyses if no significant heterogeneity existed (P<0.01). We estimated degree of population subdivision by using Wright's (1978) nonhierarchical F statistics and a hierarchical log-likelihood analysis. We used FSTAT (version 1.2)(Goudet, 1995) to

Table 2

Allozyme protocols to resolve enzyme coding loci in *Chionoecetes* samples. Enzyme nomenclature follows Shaklee et al. (1990), and locus abbreviations are given. Tissue abbreviations are: (M) muscle, (H) heart, (G) gill, and (P) hepatopancreas. Buffers are described in the text.

Enzyme or protein	Enzyme number	Locus	Tissue	Buffer
Aspartate aminotransferase	2.6.1.1	*AAT-1*, AAT-2**	M	TBE
Aconitate hydratase	4.2.1.3	*AH-2**[2]	M	TC7.0
		*AH-3**	M	TC7.0
Adenosine deaminase	3.5.4.4	*ADA-1*, ADA-3**	G,M,H	TBCL
		*ADA-2**	P	TBCL
Alanine aminotransferase	2.6.1.2	*ALAT**	M	TBCL
Cytochrome-b5[1]	1.8.1.4	*CBYR**	M	TBCL
β-N-Acetylgalactosaminidase	3.2.1.53	*βGALA**	G,P	TBCL, TBE
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH**	M	AC6.1
N-Acetyl-β-glucosaminidase	3.2.1.30	*βGLUA**	G,P	TBCL
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**	M	TC7.0
		*G3PDH-2**	H,M	TC7.0
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A1**	M	TBCL
Isocitrate dehydrogenase (NADP+)	1.1.1.42	*IDHP-1**	H	TC7.0
Malate dehydrogenase	1.1.1.37	*MDH-A1*, MDH-A2**	M	AC6.1
Malic enzyme (NADP+)	1.1.1.40	*MEP-1**	H	TC7.0
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	M	TBE
Dipeptidase	3.4.-.-	*PEPA**	H,P	TBE
Proline dipeptiase	3.4.13.9	*PEPD-2**	G,P	TBCL
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	H	TC7.0
Phosphoglucomutase	5.4.2.2	*PGM-1**	M,H	TC7.0
General (unidentified) protein		*PROT-1*, PROT-2*, PROT-3**	M	TBCL
Superoxide dismutase	1.15.1.1	*SOD-1**[2]	M	TBCL
Triose-phosphate isomerase	5.3.1.1	*TPI-1**	M	TBE

[1] This locus expressed with both CBYR* and GR*; preferential stain is CBYR*.
[2] Used in *C. opilio* statistical analysis only.

test significance of F_{ST} values (2000 permutations). Allele frequencies were used to generate distance matrices of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards, 1967). Computations were made with *S-Plus* analytical software (MathSoft Inc., 1997).

Results

Chionoecetes bairdi

Twenty-seven loci were scored consistently in *C. bairdi* populations and were used in the data analyses. Temporal variation was examined for multiple-year collections of *C. bairdi* from Bristol Bay, the Bering Sea and Pribilof Islands area, and Seymour Canal (Table 1). No significant interannual differences ($P<0.01$) were found within each geographic location; therefore these collections were pooled for subsequent analyses.

Fifteen loci, *AAT-1**, *AAT-2**, *AH-3**, *ALAT**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, and *TPI-1** were polymorphic (Table 3). At four loci, *G3PDH-1**, *GPI-A1**, *IDHP-1**, and *PEPA**, the most common allele had a frequency of ≤0.95 in at least one population. Twelve monomorphic loci, *ADA-1**, *ADA-2**, *ADA-3**, *βGALA**, *GAPDH**, *βGLUA**, *MDH-A2**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2** were included in the 27-locus analyses. Seven monomorphic loci, *AH-2**, *mMDH-1**, *PEPD-1**, *SOD-1**, *SOD-2**, *TPI-2**, and *XO** were not scorable in all populations and were not included in our analyses. We could not interpret the genetic basis for the variation we observed in two consistently resolved zones of esterase activity; therefore those data were excluded.

Three collections of *C. bairdi*, Sand Point and Pavlof, Port Moller, and Prince William Sound, with sample sizes of <25 at informative loci, *AH-3** and *IDHP-1**, were not included in the population data analyses; however, we report allele frequencies in Table 3.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all sam-

Table 3

Allele frequency estimates for *Chionoecetes bairdi* and *C. opilio* collections. ND indicates no data. Dashed lines indicate frequency of 0.000.

	*AAT-1**					*AAT-2**				*AH-2**			
Population[1]	*n*	*100	*64	*210	*120	*n*	*100	*131	*69	*n*	*100	*110	*83
Chionoecetes bairdi													
Bristol Bay pooled	100	0.995	—	—	0.005	100	1.000	—	—	ND			
Bering Sea pooled	283	1.000	—	—	—	274	0.998	—	0.002	280	1.000	—	—
Port Moller 1990	42	1.000	—	—	—	42	1.000	—	—	42	1.000	—	—
Sand Pt/Pavlof 1990	37	1.000	—	—	—	47	1.000	—	—	ND			
Kodiak N. 1990	48	1.000	—	—	—	48	0.990	0.010	—	38	1.000	—	—
Kodiak S. 1990	43	0.988	—	—	0.012	43	0.988	0.012	—	36	1.000	—	—
Kamishak 1990	50	0.990	0.010	—	—	50	1.000	—	—	50	1.000	—	—
Montague St. 1990	42	1.000	—	—	—	49	1.000	—	—	50	1.000	—	—
Kachemak Bay 1990	50	1.000	—	—	—	50	0.990	0.010	—	50	1.000	—	—
Prince Wm. Sd. 1990	50	1.000	—	—	—	50	1.000	—	—	50	1.000	—	—
Sullivan Is. 1993	100	1.000	—	—	—	100	0.995	0.005	—	100	1.000	—	—
Seymour C. pooled	125	1.000	—	—	—	123	1.000	—	—	125	1.000	—	—
Chionoecetes opilio													
Bering Sea pooled	124	0.992	—	0.004	0.004	123	1.000	—	—	115	0.991	0.009	—
St. Matt. Is. pooled	192	0.992	—	—	0.008	193	0.987	0.005	0.008	200	1.000	—	—
Pribilof Is. pooled	211	0.991	0.005	—	0.005	193	0.995	0.003	0.003	214	0.993	0.002	0.005
Atlantic O. 1991	97	1.000	—	—	—	97	0.995	0.005	—	97	1.000	—	—

	*AH-3**					*ALAT**			*CBYR**			*G3PDH-1**			*G3PDH-2*[2]			
Population[1]	*n*	*100	*94	*91	*106	*n*	*100	*87	*n*	*100	*117	*n*	*100	*117	*n*	*100	*86	*111
Chionoecetes bairdi																		
Bristol Bay pooled	100	0.005	0.995	—	—	100	1.000	—	100	1.000	—	96	0.974	0.026	100	1.000	—	—
Bering Sea pooled	279	0.014	0.982	0.004	—	283	0.998	0.002	285	0.998	0.002	265	0.958	0.042	196	0.949	0.008	0.043
Port Moller 1990	42	—	1.000	—	—	42	1.000	—	42	1.000	—	41	0.976	0.024	20	0.950	0.025	0.025
Sand Pt/Pavlof 1990	3	—	1.000	—	—	ND			50	1.000	—	1	1.000	—	ND			
Kodiak N. 1990	38	0.013	0.987	—	—	50	1.000	—	50	1.000	—	46	0.967	0.033	50	0.990	—	0.010
Kodiak S. 1990	33	0.015	0.985	—	—	50	1.000	—	50	1.000	—	37	0.946	0.054	42	1.000	—	—
Kamishak 1990	50	—	1.000	—	—	50	1.000	—	50	1.000	—	49	0.990	0.010	50	1.000	—	—
Montague St. 1990	49	—	1.000	—	—	49	1.000	—	50	1.000	—	50	0.970	0.030	31	1.000	—	—
Kachemak Bay 1990	50	—	1.000	—	—	50	1.000	—	50	1.000	—	50	0.950	0.050	50	0.970	—	0.030
Prince Wm. Sd. 1990	50	—	0.990	0.010	—	50	1.000	—	50	1.000	—	50	0.970	0.030	47	1.000	—	—
Sullivan Is. 1993	95	0.011	0.979	0.011	—	97	1.000	—	50	1.000	—	89	0.933	0.067	49	0.980	—	0.020
Seymour C. pooled	122	0.004	0.992	0.004	—	125	1.000	—	100	1.000	—	122	0.959	0.041	109	1.000	—	—
Chionoecetes opilio																		
Bering Sea pooled	124	0.923	0.077	—	—	123	1.000	—	125	0.996	0.004	125	0.988	0.012	96	0.995	—	0.005
St. Matt. Is. pooled	197	0.939	0.058	—	0.003	195	1.000	—	200	1.000	—	198	0.990	0.010	174	0.994	—	0.006
Pribilof Is. pooled	213	0.937	0.063	—	—	214	1.000	—	214	1.000	—	214	0.998	0.002	183	0.992	0.003	0.005
Atlantic O. 1991	95	0.937	0.063	—	—	97	1.000	—	97	1.000	—	97	1.000	—	94	1.000	—	—

continued

ples were from single panmictic populations. Average observed heterozygosities ranged from 0.016 to 0.035.

Among-population variation

Various measures indicated a low level of population differentiation. F_{ST} values were low, however two loci, *G3PDH-2** and *PEPA** with respective F_{ST} values of 0.0137 (P=0.0005) and 0.0154 (P=0.0020), and the overall F_{ST} value of 0.0046 for 15 polymorphic loci (P=0.0295) differed significantly from zero. A comparison of all *C. bairdi* populations with a hierarchical log-likelihood analysis, indicated significant heterogeneity at four loci, *G3PDH-2**, *IDHP-1**, *PEPA**, and PROT-3*; however the overall statistic was not significant (Table 4). In contrast, when populations

Table 3 (continued)

Population[1]	*GPI-A1**								*IDHP-1**					*MDH-A1**			
	n	*100	*142	*60	*158	*9	*55	*19	*n*	*100	*81	*119	*90	*n*	*100	*79	*128
Chionoecetes bairdi																	
Bristol Bay pooled	100	0.970	—	0.020	—	0.005	—	0.005	79	0.633	0.278	0.082	0.006	100	1.000	—	—
Bering Sea pooled	283	0.971	0.005	0.018	—	0.002	0.002	0.002	275	0.562	0.358	0.074	0.006	283	0.995	0.005	—
Port Moller 1990	42	0.988	—	0.012	—	—	—	—	9	0.611	0.389	—	—	42	1.000	—	—
Sand Pt/Pavlof 1990	50	0.980	—	0.010	—	0.010	—	—	34	0.691	0.162	0.147	—	8	1.000	—	—
Kodiak N. 1990	49	0.959	0.010	0.031	—	—	—	—	49	0.592	0.357	0.051	—	49	1.000	—	—
Kodiak S. 1990	50	0.930	0.020	0.030	—	0.010	—	0.010	36	0.722	0.264	0.014	—	39	1.000	—	—
Kamishak 1990	50	0.990	—	—	—	0.010	—	—	30	0.683	0.267	0.050	—	50	1.000	—	—
Montague St. 1990	50	1.000	—	—	—	—	—	—	50	0.510	0.430	0.060	—	50	1.000	—	—
Kachemak Bay 1990	50	0.980	—	0.010	—	0.010	—	—	28	0.571	0.286	0.107	0.036	50	1.000	—	—
Prince Wm. Sd. 1990	49	0.990	—	—	—	0.010	—	—	7	0.643	0.214	0.143	—	50	1.000	—	—
Sullivan Is. 1993	100	0.985	—	0.015	—	—	—	—	82	0.634	0.341	0.024	—	99	1.000	—	—
Seymour C. pooled	124	0.992	—	0.004	—	0.004	—	—	122	0.574	0.348	0.078	—	125	0.996	—	0.004
Chionoecetes opilio																	
Bering Sea pooled	125	0.984	0.004	0.004	0.004	—	0.004	—	125	1.000	—	—	—	125	0.992	0.008	—
St. Matt. Is. pooled	200	0.988	0.013	—	—	—	—	—	196	1.000	—	—	—	200	0.973	0.027	—
Pribilof Is. pooled	214	0.986	0.012	0.002	—	—	—	—	207	0.990	0.005	0.005	—	213	0.986	0.014	—
Atlantic O. 1991	97	0.974	0.026	—	—	—	—	—	97	1.000	—	—	—	97	0.990	0.010	—

Population[1]	*MDH-A2**			*PEPA**				*PGDH**					*PGM-1**						
	n	*100	*65	*n*	*100	*138	*64	*n*	*100	*112	*124	*91	*n*	*100	*82	*114	*103	*88	*75
Chionoecetes bairdi																			
Bristol Bay pooled	100	1.000	—	92	0.940	0.022	0.038	92	0.995	0.005	—	—	100	0.995	—	—	0.005	—	—
Bering Sea pooled	283	1.000	—	279	0.991	0.004	0.005	269	0.996	—	0.004	—	268	0.996	0.004	—	—	—	—
Port Moller 1990	42	1.000	—	39	0.987	—	0.013	18	1.000	—	—	—	42	1.000	—	—	—	—	—
Sand Pt/Pavlof 1990	8	1.000	—	40	0.975	—	0.025	47	1.000	—	—	—	13	1.000	—	—	—	—	—
Kodiak N. 1990	49	1.000	—	48	0.990	0.010	—	40	1.000	—	—	—	47	0.989	—	—	—	—	0.011
Kodiak S. 1990	40	1.000	—	43	0.977	0.012	0.012	34	1.000	—	—	—	38	0.987	0.013	—	—	—	—
Kamishak 1990	50	1.000	—	49	1.000	—	—	45	1.000	—	—	—	50	0.980	0.010	—	—	—	0.010
Montague St. 1990	50	1.000	—	50	1.000	—	—	49	1.000	—	—	—	42	1.000	—	—	—	—	—
Kachemak Bay 1990	50	1.000	—	50	1.000	—	—	46	0.989	—	—	0.011	50	1.000	—	—	—	—	—
Prince Wm. Sd. 1990	50	1.000	—	47	0.989	—	0.011	49	1.000	—	—	—	50	1.000	—	—	—	—	—
Sullivan Is. 1993	99	1.000	—	92	0.995	—	0.005	84	0.994	—	0.006	—	99	0.995	0.005	—	—	—	—
Seymour C. pooled	125	1.000	—	118	0.983	0.004	0.013	119	0.992	—	0.008	—	125	0.992	—	—	—	0.008	—
C. opilio																			
Bering Sea pooled	125	1.000	—	125	0.992	0.008	—	123	0.980	—	0.020	—	125	0.992	0.008	—	—	—	—
St. Matt. Is. pooled	200	0.998	0.002	187	1.000	—	—	183	0.970	—	0.030	—	198	0.982	0.005	0.003	0.003	0.008	—
Pribilof Is. pooled	214	1.000	—	199	0.997	0.003	—	196	0.967	0.008	0.025	—	214	0.993	0.002	—	—	0.005	—
Atlantic O. 1991	97	1.000	—	97	0.995	0.005	—	97	0.985	0.005	0.010	—	97	0.964	—	—	—	0.036	—

Population[1]	*PROT-3**			*SOD-1**			*TPI-1**			
	n	*100	*88	*n*	*100	*109	*n*	*-100	*100	*-41
Chionoecetes bairdi										
Bristol Bay pooled	100	0.010	0.990	125	1.000	—	100	1.000	—	—
Bering Sea pooled	283	0.016	0.984	273	1.000	—	284	0.996	—	0.004
Port Moller 1990	42	—	1.000	39	1.000	—	42	1.000	—	—
Sand Pt/Pavlof 1990	50	—	1.000	50	1.000	—	47	0.979	—	0.021
Kodiak N. 1990	50	—	1.000	50	1.000	—	50	0.990	—	0.010
Kodiak S. 1990	50	—	1.000	50	1.000	—	47	1.000	—	—
Kamishak 1990	50	—	1.000	50	1.000	—	49	1.000	—	—
Montague St. 1990	50	—	1.000	50	1.000	—	50	1.000	—	—

continued

Table 3 (continued)

Population[1]	*PROT-3**			*SOD-1**			*TPI-1**			
	n	*100	*88	*n*	*100	*109	*n*	*-100	*100	*-41
Chionoecetes bairdi, continued										
Kachemak Bay 1990	50	—	1.000	50	1.000	—	50	1.000	—	—
Prince Wm. Sd. 1990	50	—	1.000	50	1.000	—	50	1.000	—	—
Sullivan Is. 1993	100	—	1.000	ND			100	1.000	—	—
Seymour C. pooled	125	—	1.000	125	1.000	—	125	1.000	—	—
Chionoecetes opilio										
Bering Sea pooled	124	0.992	0.008	122	1.000	—	125	0.992	0.004	0.004
St. Matt. Is. pooled	196	0.997	0.003	198	0.997	0.003	198	0.995	0.002	0.002
Pribilof Is. pooled	214	0.986	0.014	211	0.998	0.002	214	1.000	—	—
Atlantic O. 1991	97	1.000	—	97	1.000	—	97	0.990	0.010	—

[1] Port Moller, Sand Point/Pavlof Bay, and Prince William Sound *C. bairdi* populations not included in analyses.
[2] *G3PDH-1*87* was pooled with **100*.

were grouped by major geographic regions (Bering Sea, Gulf of Alaska, and Southeast Alaska) for comparison, the overall log-likelihood statistic was highly significant ($P<0.01$, Table 4). *G3PDH-2** and *PROT-3** contributed most to the observed among-region heterogeneity. Within the Bering Sea, pooled samples collected from Bristol Bay (east of approximately 162°45'W long.) were significantly different from pooled samples from the Bering Sea and Pribilof Island areas (west of approximately 167°00'W long.). In this comparison, *G3PDH-2**, *IDHP-1**, and *PEPA** allelic frequencies differed significantly.

The following were the low-frequency alleles detected according to their respective major geographic regions: 1) Bering Sea, *AAT-2*69*, *ALAT*87*, *CBYR*117*, *G3PDH-2*86*, *GPI-A1*55*, *MDH-A1*79*, *PGDH*112*, *PGM-1*103*, and *PROT-3*100*; 2) Gulf of Alaska, *AAT-1*64*, *PGDH*91*, and *PGM-1*75*; and 3) Southeast Alaska, *MDH-A1*128* and *PGM-1*88*. The *PROT-3*100* allele, likely an introgressed *C. opilio* allele, contributed significantly to the overall heterogeneity observed among the major geographic regions of Bering Sea, Gulf of Alaska, and Southeast Alaska. Genetic distance measurements (Cavalli-Sforza and Edwards, 1967) within *C. bairdi* populations ranged from 0.031 to 0.059.

Chionoecetes opilio

Twenty-nine loci were scored consistently in all collections and were used in the data analyses. No significant temporal variation ($P<0.01$) was found within multiple-year collections in the Bering Sea, St. Matthew Island, and the Pribilof Islands. We pooled these collections for further analyses.

Seventeen loci, *AAT-1**, *AAT-2**, *AH-2**, *AH-3**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *MDH-A2**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, *SOD-1**, and *TPI-1**, were polymorphic in at least one population (Table 3). Twelve monomorphic loci were *ADA-1**, *ADA-2**, *ADA-3**, *ALAT**, *βGALA**, *GAPDH**, *βGLUA**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2**. One polymorphic locus, *AH-3**, was variable at a frequency of ≥0.05 in at least one population.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all samples were from single panmictic populations. Average observed heterozygosities were lower than those for *C. bairdi* and ranged from 0.012 to 0.013 in Alaskan populations; the average heterozygosity was 0.010 in Atlantic Ocean *C. opilio*.

Among-population variation

F_{ST} of 17 polymorphic loci was not significantly different from zero for Alaskan populations ($P=0.4270$) or when the Atlantic Ocean collection was included ($P=0.7130$). However, the F_{ST} value for *PGM-1** was highly significant ($P=0.0050$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. A hierarchical log-likelihood analysis of these loci revealed very low levels of heterogeneity among all *C. opilio* (Table 5). In this analysis, *PGM-1** was also highly significant ($P=0.0071$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. Among all *C. opilio*, *PGM-1** was significant ($P=0.0361$). The overall log-likelihood statistic for all loci among all *C. opilio* was significant ($P=0.0382$)(Table 5). Low-frequency alleles detected in Alaskan collections were *AAT-1*64*, **210*, and **120*, *AAT-2*69*, *AH-2*110* and **83*, *AH-3*106*, *CBYR*117*, *G3PDH-1*117*, *G3PDH-2*86* and **111*, *GPI-A1*60*,

*158, and *55, IDHP-1*81 and *119, MDH-A2*65, PGM-1*82, *114, and *103, PROT-3*88, SOD-1*109, and TPI-1*-41. Differing PGM-1* alleles and allele frequencies contributed most to the overall levels of differentiation observed between Alaskan and Atlantic Ocean *C. opilio* populations. Multilocus between-population chord distance measures ranged from 0.029 to 0.033 in Alaskan collections and increased to 0.043 when we added the Atlantic Ocean population.

Comparison of *C. bairdi* and *C. opilio* from Alaska

A total of 27 loci, *AAT-1*, AAT-2*, AH-3*, ADA-1*, ADA-

Table 4

Hierarchical log-likelihood analysis for *Chionoecetes bairdi*.

	df	*AAT-1**	df	*AAT-2**	df	*AH-3**	df	*ALAT**
Total	16	13.10	16	12.70	16	14.72	8	2.21
Among	2	1.23	2	6.35*	2	1.90	1	1.60
Within	14	11.87	14	6.35	14	12.82	7	0.61
Bering Sea	2	2.69	2	0.62	2	2.54	1	0.61
Gulf of Alaska	12	9.18	12	5.73	12	10.28	6	0.00
Among	2	1.49	2	0.10	2	1.54	1	0.00
Within	10	7.69	10	5.63	10	8.74	5	0.00
Northern Gulf	8	7.69	8	4.83	8	5.38	4	0.00
Southeast	2	0.00	2	0.80	2	3.36	1	0.00
	df	*CBYR**	df	*G3PDH-1**	df	*G3PDH-2**	df	*GPI-A1**
Total	8	2.21	8	8.25	16	43.07**	40	37.66
Among	1	1.61	1	0.31	2	13.82**	5	3.89
Within	7	0.60	7	7.94	14	29.25**	35	33.77
Bering Sea	1	0.60	1	1.01	2	16.84**	5	3.50
Gulf of Alaska	6	0.00	6	6.93	12	12.41	30	30.27
Among	1	0.00	1	1.16	2	0.49	5	6.25
Within	5	0.00	5	5.77	10	11.92	25	24.02
Northern Gulf	4	0.00	4	3.85	8	9.94	20	21.57
Southeast	1	0.00	1	1.92	2	1.98	5	2.45
	df	*IDHP-1**	df	*MDH-A1**	df	*PEPA**	df	*PGDH**
Total	24	38.63*	16	10.40	16	30.30*	24	15.60
Among	3	3.79	2	5.96	2	4.55	3	2.87
Within	21	34.84*	14	4.44	14	25.75*	21	12.73
Bering Sea	3	3.56	2	1.82	2	14.04	3	3.91
Gulf of Alaska	18	31.28	12	2.62	12	11.71	18	8.82
Among	3	5.51	2	0.78	2	2.62	3	0.77
Within	15	25.77	10	1.84	10	9.09	15	8.05
Northern Gulf	12	20.83	8	1.84	8	8.22	12	7.13
Southeast	3	4.94	2	0.00	2	0.87	3	0.92
	df	*PGM-1**	df	*PROT-3**	df	*TPI-1**	df	Overall
Total	32	27.40	8	18.22*	8	6.29	256	280.75
Among	4	6.43	1	17.83**	1	0.58	32	72.71**
Within	28	20.97	7	0.39	7	5.71	224	208.04
Bering Sea	4	3.87	1	0.39	1	1.21	32	57.22
Gulf of Alaska	24	17.10	6	0.00	6	4.50	192	150.82
Among	4	3.01	1	0.00	1	0.77	32	24.49
Within	20	14.09	5	0.00	5	3.73	160	126.33
Northern Gulf	16	13.38	4	0.00	4	3.73	128	108.40
Southeast	4	0.71	1	0.00	1	0.00	32	17.93

* Test is significant at $\alpha = 0.05$.
** Test is significant at $\alpha = 0.01$.

2, ADA-3*, ALAT*, CBYR*, βGALA*, GAPDH*, βGLUA*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, MEP-1*, MPI*, PEPA*, PEPD-2*, PGDH*, PGM-1*, PROT-1*, PROT-2*, PROT-3**, and *TPI-1**, were scored in all *C. bairdi* and *C. opilio* populations analyzed; 16 loci, *AAT-1*, AAT-2*, AH-3*, ALAT*, CBYR*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, PEPA*, PGDH*, PGM-1*, PROT-3**, and *TPI-1**, were polymorphic in at least one population of either species. Eleven loci, *ADA-1*, ADA-2*, ADA-3*, βGALA*, GAPDH*, βGLUA*, MEP-1*, MPI*, PEPD-2*, PROT-1**, and *PROT-2**, were monomorphic for the identical allele. Significant differences ($P<0.01$) between the two species were detected at eight loci, *AH-3*, G3PDH-1*, GPI-A1*, IDHP-1*, MDH-A1*, PEPA*, PGDH**, and *PROT-3**. Two loci, *AH-3** and *PROT-3**, were particularly informative with nearly fixed differences for alternate alleles (Table 3). In addition, with the exception of *C. opilio* from the Pribilof Island area collections, *C. opilio* expressed only the *IDHP-1*100* allele, whereas *C. bairdi* were highly variable. Several low-frequency variants ($P<0.05$) also contributed to the overall differences between the species. Numerous low-frequency alleles detected in only Bering Sea collections of *C. bairdi* were also detected in Alaskan *C. opilio* collections, including the following: *AAT-2*69, CBYR*117, G3PDH-2*86, GPI-A1*55, MDH-A1*79, PGM-1*103*, and *PROT-3*88*. Also, a rare allele, *PGDH*112*, was detected only in Bristol Bay *C. bairdi* and in Pribilof Island and Atlantic Ocean *C. opilio*.

Multilocus variation between species was estimated by genetic-distance measures. Between-species genetic-distance measures ranged from 0.222 to 0.251. The largest genetic distance was between Atlantic *C. opilio* and two northern Gulf of Alaska *C. bairdi* populations, those of Kachemak Bay and Montague Strait. The smallest between-species genetic distance was that for Pribilof Island and Bering Sea *C. opilio* compared with that for Bering Sea and Pribilof Island *C. bairdi*.

Table 5

Hierarchical log-likelihood analysis for *Chionoecetes opilio*.

Source	df	Overall
Total	96	121.93*
Among	32	41.63
Within	64	80.30
Bering Sea	64	80.30
Atlantic Ocean	0	0.00

* Significant value ($P<0.05$)

Chiocoetes bairdi × *C. opilio* hybrids

Hybrids between *C. bairdi* and *C. opilio* crabs in the Bering Sea have been identified morphologically and genetically (Karinen and Hoopes, 1971; Johnson, 1976; Grant et al., 1978; Hoopes et al.[1]). Several collections in our study had allele frequencies suggesting either low levels of introgression between the species or the inclusion of hybrid or backcross individuals in the collection. For example, low frequencies of *PROT-3*100* were observed in *C. bairdi* crabs from Bristol Bay, the Bering Sea, and the Pribilof Islands. *PROT-3*100* was not observed in *C. bairdi* from non-Bering Sea collections. Similarly, *PROT-3*88* was observed in *C. opilio* collections from the Bering Sea, St. Matthew Island, and the Pribilof Islands, and low frequencies of *IDHP-1*81* and **119* were observed in Pribilof Island *C. opilio* collections; these alleles were not observed in *C. opilio* collected from the Atlantic Ocean.

Discussion

Allozyme electrophoresis techniques have been used extensively to describe evolutionary relationships within genera of decapod crustaceans (Bert, 1986; Bert and Harrison, 1988; Busack, 1989; Abdullah and Shukor, 1993); however, these techniques have generally revealed very low levels of intraspecific genetic variation (Nelson and Hedgecock, 1980; Smith et al., 1980; Busack, 1988; Seeb et al., 1990b). Exceptions to this generalization are found in species that occur over broad geographic areas or in widely different environments (Nelson and Hedgecock, 1980; Mulley and Latter, 1981; Kartavtsev et al., 1991). Significant population heterogeneity has been found in species that exhibit highly specialized life history attributes (Stevens, 1991) and in some freshwater species (Macaranas et al., 1995; Fetzner et al., 1997). Within a marine species, Seeb et al. (1990a) discriminated populations of red king crab from major geographic areas of the Gulf of Alaska and Bering Sea. Allozyme techniques have also been used to examine seasonal variability of decapod larval, megalopal, and adult allelic frequencies (Kordos and Burton, 1993).

Davidson et al. (1985) examined population structure in North Atlantic *C. opilio* using allozymes and interpreted their observed esterase polymorphisms as phenotypic expressions of probable genotypic differences. However, we feel caution should be used in interpreting their data until genetic transmission of these markers can be shown by inheritance studies because we were unable to interpret the genetic basis of observed esterase activity.

The importance of tissue quality for allozyme studies is well documented (e.g. Utter et al., 1987) but is particularly critical for crustacean tissue, which degrades more rapidly than finfish tissue. Laboratory analysis revealed obvious differences in enzyme resolution for several loci that resulted in conservative allele pooling and loss of some population data. Optimal sample handling may have increased detectable variation.

Population diversity of *C. bairdi*

We detected differences among *C. bairdi* populations of the three major geographic regions: Bering Sea, Gulf of Alaska, and Southeast Alaska. Most notably, we detected population subdivision within the Bering Sea. Samples collected in Bristol Bay (east of approximately 162°45'W long.) were statistically different from samples collected near the Pribilof Islands (west of approximately 167°00'W long.).

Other biological data support our inference that subpopulations of *C. bairdi* occur within the Bering Sea. Using trawl survey data from 1974 onward, Otto (1982) reported size-frequency distributions of *C. bairdi* in the Pribilof Islands that were different from those in the area north of the Alaska Peninsula, including Bristol Bay. Further, as National Marine Fisheries Service (NMFS) trawl assessment surveys expanded westward, it became evident that crabs in the Pribilof area were larger in size compared with those along the continental slope north and west of the Pribilof Islands. Somerton (1981) found size differences among large females from the eastern Bering Sea seemed to partition into two subareas along 167°15'W long. The mean size of adult females was quite constant in the eastern subarea (east of 167°15'W long.) but decreased steadily in the western subarea. Although both investigators speculated upon the possibility of genetic or environmental factors causing these differences, the species has been considered a single Bering Sea stock for management purposes (Otto, 1982). In our study, we lacked *C. bairdi* specimens from west of approximately 173°W long. and thus were unable to test whether crabs collected from near the Pribilof Islands differed from crabs collected near the continental slope. Although there does not appear to be a precise correlation between our findings and the observations of Otto (1982) and Somerton (1981), all data seem to suggest that *C. bairdi* in the Bering Sea may not be composed of a single panmictic population.

However, any conclusions we may draw from biochemical data should be confirmed by other types of data. The American lobster (*Homarus americanus*) is a case in point. Tracey et al. (1975) noted genetic and morphological differences between inshore and offshore populations. In tagging studies, Fogarty et al. (1980) demonstrated limited movement of lobsters released at inshore stations, in contrast with extensive seasonal migrations by lobsters tagged at offshore locations. These studies indicated that despite the potential for genetic exchange during seasonal mixing, the inshore and offshore populations retained their genetic identity.

The planktotrophic larvae of *Chionoecetes* may spend up to two months in surface waters (Slizkin, 1990), raising the possibility that larvae released in one area may become recruits in another. Further, most of what is known or hypothesized about migration of Bering Sea *C. bairdi* is based upon abundance and distribution estimates from annual NMFS trawl surveys and subsequent fishery captures.[2] Migration studies of *Chionoecetes* in Alaska have been hindered by tag losses after molting. Development of a permanent tag for *Chionoecetes* would provide a valuable tool for examining population migration and further for evaluating the null hypothesis of panmixia. Our findings of regional and within-Bering Sea heterogeneity among *C. bairdi* populations merit further investigation.

Population diversity of *C. opilio*

We detected only small differences between Bering Sea and North Atlantic *C. opilio*, primarily in *PGM-1** allele frequencies. The low-frequency alleles of other loci observed in Alaskan *C. opilio* did not contribute significantly to overall differences. Although sampling error may have been a factor (Gregorius, 1980) in detection of rare alleles, no private alleles were found in the North Atlantic. The minimal genetic differentiation among this circumpolar species contrasts with findings in halibut (*Hippoglossus*), herring (*Clupea*) and cod (*Gadus*) (Grant, 1987) where significant differentiation has been described across a similar geographic range. The close genetic affinity of the Bering Sea *C. opilio* collections with the collection from the North Atlantic and the detection of low-frequency Bering Sea *Chionoecetes* alleles in the North Atlantic suggest recent or ongoing gene flow. This possibility is supported by Garth (1958) whose range description includes a distribution of *C. opilio* northward (from the Bering Strait) and eastward through the Beaufort Sea and Davis Strait to the North Atlantic. This species tolerates very low temperatures; the optimum temperature for immature individuals has negative values even in the summer (Slizkin, 1990). Thus, it is plausible to hypoth-

[2] Morrison, R. 1997. Alaska Dep. Fish and Game, P.O. Box 920587, Dutch Harbor, AK 99692. Personal commun.

esize gene flow through these northern seas even in the presence of sea ice pack. Alternatively, it is possible that gene flow is restricted, but that the differentiating forces of drift, selection, and mutation have not yet produced significant detectable genetic divergence.

Species differentiation, hybrids, and gene introgression

The morphological criteria for differentiating *C. bairdi* and *C. opilio* have been well described (Rathbun, 1925; Garth, 1958; Karinen and Hoopes, 1971). However, a few crabs in our study that met one or more morphological criteria were probably hybrid or recombinant individuals. Their composite genotypes were atypical of the parental species and were instead indicative of F_1 hybrids or backcross matings. Species differentiation in allelic frequencies was observed between *C. bairdi* and *C. opilio*, most notably for *AH-3**, *IDHP-1**, and *PROT-3**. The unusual composite genotypes were most clearly differentiated by the *PROT-3*100* allele in *C. bairdi* collections, and conversely, by the *PROT-3*88* allele in the *C. opilio* collections from the Bering Sea. The *PROT-3*100* allele contributed significantly to the among-regional differences in *C. bairdi*. This marker is also very useful for investigation of hybridization between these species.

Gene flow and geographic barriers

Our findings are consistent with previous electrophoretic studies that infer that decapod crustaceans, especially large, mobile species, exhibit low levels of variation at allozyme markers (Nelson and Hedgecock, 1980). The high dispersal potential of marine species is often used to explain the low levels of variation detected among populations (Avise, 1994). Such distribution appears to be the case with *Chionoecetes* as well as with other marine organisms with similar geographic distributions in the North Pacific, Gulf of Alaska, and Bering Sea, such as Pacific halibut (Grant et al., 1984), Pacific herring (Grant and Utter, 1984), Pacific cod (*Gadus macrocephalus*) (Grant et al., 1987), Pacific ocean perch (*Sebastes alutus*) (Seeb and Gunderson, 1988), and red king crab (*Paralithodes camtschaticus*) (Seeb et al., 1990a).

Limits to the actual dispersal of marine species, despite high dispersal potential, may periodically or continuously limit gene flow in some directions (Avise, 1994 and references therein). The Alaska Peninsula–Aleutian chain appears to be a significant barrier to gene flow in some species, such as Pacific ocean perch (Seeb and Gunderson, 1988), Pacific herring (Grant and Utter, 1984), rock sole (*Pleuronectes bilineatus*) (Mulligan et al., 1995) and red king crab (Seeb et al., 1990a).

The Alaska Peninsula–Aleutian Chain appears to limit gene flow among *C. bairdi* populations as evidenced by the differentiation detected among regions above and below this geographic barrier. The lack of introgressed *C. opilio* alleles in the Gulf of Alaska and Southeast Alaska populations studied also supports this view. Our findings suggest that the numerous rare alleles observed in Bering Sea, and not Atlantic, populations of *Chionoecetes* may be ancient alleles that have been maintained over time in the large populations that have inhabited these waters; however, larger sample sizes of Atlantic Ocean *C. opilio* are needed to confirm this hypothesis. Detection of low-frequency Bering Sea *Chionoecetes* alleles in North Atlantic *C. opilio* and the lower heterozygosity of North Atlantic *C. opilio*, coupled with the lack of congeners in the North Atlantic, allow speculation that the genus *Chionoecetes* may have arisen in the North Pacific.

Acknowledgments

The authors thank the following Alaska Department of Fish and Game personnel for population sample collections: Dean Beers, Cathy Bothelo, Bill Donaldson, Wayne Donaldson, Lee Hammarstrom, Ken Imamura, Dave Jackson, Al Kimker, Tim Koeneman, Al Spalinger, Dan Urban, and especially Donn Tracy, Ken Griffin, and Rance Morrison. We thank the National Marine Fisheries Service personnel for collections: Pete Cummiskey, Jan Haaga, John Karinen, Rich MacIntosh, Eric Munk, and Brad Stevens, and we thank Bob Otto for his efforts in coordinating the Atlantic *C. opilio* collection. We also thank Dave Armstrong of the University of Washington, and M. John Trembley of the Canadian Department of Fisheries and Oceans for their assistance. Penny Crane and three anonymous reviewers provided critical reviews. This research was funded in part by a cooperative agreement with the National Oceanic and Atmospheric Administration (award NA37FL0333).

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