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Population Genetic Structure of Dolly Varden from Beaufort Sea Drainages of Northern Alaska and Canada

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Abstract.—Dolly Varden *Salvelinus malma* spawn, rear, and overwinter in freshwater tributaries to the Beaufort Sea and migrate to coastal waters to feed. Oil and gas development activities that alter the freshwater or marine environments could affect char populations and the local fisheries they support. The purpose of this study was to describe the genetic relationships among Dolly Varden populations from Beaufort Sea tributaries. Allozyme electrophoresis was used to analyze variation at 49 loci (21 were polymorphic) in 27 collections made from 11 river drainages. Average heterozygosity observed was 0.038 (range: 0.016–0.052). Average percent of loci that were polymorphic was 19%. Overall heterogeneity *G*-tests indicated highly significant differences among collections ($P < 0.001$). Cluster analysis of Nei's genetic distance sometimes formed groups of geographically proximate collections; however, correspondence between genetic and geographic distances was weak in hierarchical groupings. Differences among collections within and between river systems were observed. On average, 91% of the genetic variation occurred among individuals within collections, whereas 8% was attributable to differences among river systems and 1% to differences within systems. Resident char from Sadlerochit Spring were genetically distinct from char in other collections due to low variability rather than to the presence of unique alleles. Genetic data indicated that multiple populations of char occur along the arctic coast of Alaska and Canada, often organized by major river system, and that more than one population may occur within river systems. Human activities that affect critical habitats, such as areas used for spawning or overwintering, must be considered with respect to the effects on individual populations rather than on a generalized char "population" that uses the Beaufort Sea.

Dolly Varden *Salvelinus malma* (herein also referred to as char) of the Beaufort Sea of Alaska and Canada migrate between freshwater tributaries and coastal waters, and are important in subsistence fisheries in both the United States and Canada (Craig 1989a). Oil and gas development activities that change either the freshwater or marine environments could affect char populations and the fisheries they support. The char's life history and migration patterns in this region reflect an adaptive response to the severity of the habitat and to seasonal and annual variation in habitat availability.

Char in this region spend most of their lives in tributaries of the Beaufort Sea, where they spawn, rear, and overwinter. Spawning occurs in autumn in areas often associated with springs in or near the Brooks Range (McCart 1980), and the eggs hatch in spring. Juvenile char live in tributaries until 3–5 years of age, when they begin to migrate to coastal areas to feed (Craig 1977a; McCart 1980). Mature and immature char return to freshwater in late summer and early fall and overwinter in tributaries as marine waters become supercooled (<0°C) and highly saline. These char typically do not spawn until age 5 or 6 (Bain 1974; Craig 1977a). Although an individual can spawn repeatedly over its lifetime, sufficient energy reserves are rarely acquired in one season to permit spawning every year.

Overwintering habitat is critical to the survival of Dolly Varden in this arctic environment. Only about 2% of the freshwater habitat—deep river pools and springs—remains available to fish by the end of winter (Craig 1989b), and these areas are shared by Dolly Varden of all life history stages. If an overwintering area fails (e.g., anoxia or freezing)

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fish are unable to move to a different refuge because connecting stream segments freeze to the bottom. Therefore, the availability of deep-pool habitat in tributaries is critical to the viability of Dolly Varden populations.

Char populations are potentially vulnerable to habitat perturbations such as those caused by oil and gas development activities. Though Dolly Varden populations are adapted to the physical extremes of the Arctic by long life and repeated spawning, they also rely on the availability of overwintering areas and on their ability to migrate. In freshwater habitats, water removal from overwintering sites for well drilling, road construction, or other human use could deplete the limited overwintering resource used by all life history stages of char. Construction of river crossings, channelization, or removal of material from the rivers could affect migratory corridors and spawning substrate quality. If separate populations occur in coastline tributaries, the effects of development activities could cause local extinctions and the loss of genetic diversity.

In this study, allozyme electrophoresis was used to determine if genetic data supported the contention that different populations of Dolly Varden occurred within the major river drainages of the Beaufort Sea area and to refute the null hypothesis that char from this region exist as a single panmictic population. The amount and pattern of genetic variation is described and compared within and among char collections from 11 river systems.

Methods

Collections

Char were collected at 27 sites on 11 tributaries to the Beaufort Sea in 1985, 1986, and 1987 by U.S. Fish and Wildlife Service personnel (Table 1; Figure 1). Taxonomic designation of char from this region as Dolly Varden follows the recommendations of Reist et al. (1997, this volume). Electrofishing and minnow traps were used to collect juveniles from anadromous populations and juveniles and adults from stream-resident populations. Anadromous spawning adults were not used in this study because of the extreme logistical difficulties of sampling fish during the spawning season in this region. Sample sizes at sites ranged from 15 to 97 fish. Char were also collected from upstream of the waterfall on the Babbage River (site 26), upstream Firth River (site 23), Shublik Spring (site 9, Canning River drainage), and Sadlerochit Spring (site 12); these fish were presumed to have a stream-resident life history and were included in the analysis for comparison to anadromous populations.

Electrophoretic Procedures and Locus Designations

Horizontal starch-gel electrophoresis with histochemical staining was used to identify protein products of allozyme loci (Aebersold et al. 1987). Enzymes were examined in white muscle, liver, and eye tissues (Table 2). Allozyme nomenclature follows that suggested by Shaklee et al. (1990). Allelic product mobilities were designated as gel migration distances relative to the product of the most common allele. The most common allele expressed at a locus was always designated as **100*. The *PGM-3,4** locus was variable, but not scored reliably. Putative variation was observed at *βHA** and *XDH-1**, but phenotypes were scoreable only in collections made in 1985 and 1986, when live fish were transported to the laboratory. Consistently good resolution was not obtained in 1987 collections because samples were frozen at −20°C rather than in liquid nitrogen or dry ice before shipping. Thus, out of a possible 53 loci for 24 enzymes, 49 loci that encode 22 enzymes were scored reliably.

Statistical Procedures

Conformance to Hardy–Weinberg expectations was assessed using a chi-square statistic. For each population, chi-square values from all variable loci were summed and the total was compared to a chi-square distribution. Variation at isoloci that share alleles (e.g., *sAAT-1,2**) cannot be assigned to a specific locus. This variation was assigned arbitrarily to one locus for purposes of data analysis and not examined for conformance to Hardy–Weinberg expectations.

Genetic differences among samples were assessed with percent of polymorphic loci, heterozygosity calculations, *G*-tests, and genetic distance coefficients (*D*). Data from different collections within a river system, made either at different sites or in different years, were sometimes pooled. Data were pooled when *P* was greater than or equal to 0.01, indicating that collections were not significantly different based on a *G*-test (Sokal and Rohlf 1981; see criteria of Shaklee and Phelps 1990). Because of pooling, the data set was reduced to 16 collections from the original 27 sites; thus, some collections included data from fish collected at more than one site within a river system (e.g., data from collections at three sites in the Firth River system were com-

TABLE 1.—Collections of Beaufort Sea Dolly Varden *Salvelinus malma* sampled from Alaska and Canada in 1985–1987 with site location (Universal Transverse Mercator, UTM), number of samples (*N*), and date collected. Site numbers correspond to those used in Figure 1. Numbers (#) under the collections from the Hulahula and Babbage rivers refer to the pooled sets of data used for analysis in Tables 3–6.

Collections	Site number	UTM coordinates			*N*	Date
		Zone	Latitude	Longitude		
Anaktuvuk River	1	5W	7624250	574000	40	May 1986
Sagavanirktok River						
Ivishak River	2	6W	7663300	463800	50	Sep 1986
Echooka River	3	6W	7683800	486800	24	Apr 1986
Ribdon River	4	6W	7615250	453500	40	May 1986
Lupine River	5	6W	7652130	443000	48	Aug 1987
Kavik River	6	6W	7691000	517100	40	Sep 1986
Canning River						
	7	6W	7652250	553250	27	May 1986
	8	6W	7719500	527300	70	Aug 1987
Shublik Spring	9	6W	7699300	533800	59	Aug 1987
	10	6W	7687800	536000	62	Aug 1987
Marsh Fork	11	6W	7663000	540000	29	May 1986
Sadlerochit Spring	12	6W	7731300	600300	62	Aug 1987
Hulahula River						
#1	13	6W	7740000	609500	15	Oct 1985
#2	14	6W	7711000	602000	37	Oct 1985
#2	15	6W	7690500	595300	59	Oct 1985
#1	16	6W	7734300	608500	97	Aug 1987
Aichilik River						
	17	7W	7694000	413500	40	Sep 1986
	18	7W	7683500	417300	70	Aug 1987
Egaksrak River	19	7W	7702500	435800	41	May 1986
Kongakut River						
	20	7W	7712000	471700	40	Sep 1986
	21	7W	7666000	463000	90	Aug 1987
Firth River						
	22	7W	7625300	507500	64	Aug 1987
	23	7W	7610250	494000	47	Aug 1987
Joe Creek	24	7W	7646500	502300	50	Sep 1986
Babbage River						
#1	25	7W	7625300	579300	53	Aug 1987
#2	26	7W	7619500	575500	21	Aug 1987
Canoe River	27	7W	7612500	592500	35	Sep 1986

bined). The amount of genetic variation within the 16 collections was described by percent of polymorphic loci and the average percent of heterozygous loci per individual (*H*). Expected heterozygosity for each locus was calculated with the observed allele frequencies in each collection and was based on expected random mating proportions (Hardy–Weinberg). Isoloci were treated as a single locus for these calculations (total of 42 loci or locus combinations).

Allele counts by locus were compared statistically by contingency table analysis with *G*-tests to test heterogeneity between pairs of collections (Sokal and Rohlf 1981). Because of the robustness of the test, only cells with expected values less than 1.0 were combined. The critical value used to reject the null hypothesis (no differences) for the *G*-tests was increased to account for the increase in type I error when multiple tests of the same hypothesis were made (Cooper 1968).

Pairwise genetic distance (*D*) data (Nei 1972) were calculated based on polymorphic loci only. When missing data occurred for loci, distances were calculated by assuming the allele frequencies of other collections within the same drainage (*sAAT-4** of Ribdon was assumed the same as that for Lupine, *sAAT-4** and *sAAT-1,2** of Hulahula #1 was assumed to be the same as Hulahula #2, and *GAPDH-3** of Canoe was assumed to be the same as the average between Babbage #1 and #2). Unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis of the distance coefficients was used to construct a dendrogram (Sneath and Sokal 1973).

Total gene diversity (H_T) was partitioned to estimate within-collection (H_S), between-collection (D_{ST}), and relative gene diversity (G_{ST}; Nei 1973; Chakraborty 1980). Sample data were analyzed hierarchically by sites within drainages and by collections from different drainages.

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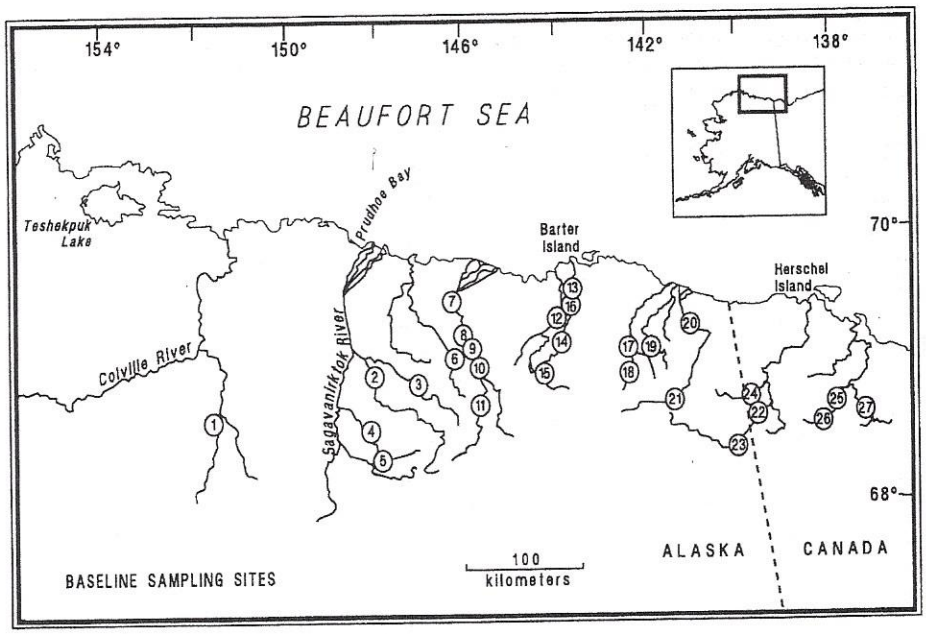

FIGURE 1.—Sampling sites for Dolly Varden *Salvelinus malma* collected from Beaufort Sea tributaries of Alaska and Canada in 1985–1987. Site numbers correspond to locations in Table 1.

Results

Genetic Variability within Collections

Forty-nine loci coding for 22 enzymes in three tissues were scored in the collections (Table 3). Of the 49 loci examined, 21 were variable and 28 were monomorphic. The 21 polymorphic loci included six isoloci (*sAAT-1,2**; *GPI-B1,2**; *sIDHP-1,2**; *sMDH-A1,2**; *sMEP-1,2**; and *sIDDH-1,2**). No evidence of departure from expected genotypic distributions (Hardy–Weinberg proportions) was observed in any collection when tests for all loci were summed in the analyses. Individual loci were out of equilibrium, but no more than expected as a result of type I error. Percent of polymorphic loci ranged from 7.1 to 28.6% (average 19%, SE = 6.7%; Table 4). Average heterozygosity ranged from 1.6 to 5.2% and over all collections was 3.8% (SE = 1.02%). The lowest heterozygosity (1.6%) was observed in resident char collected from Sadlerochit Spring. No allele substitutions were observed among stocks at any locus.

Genetic Variability among Samples

Data sets from collections of char made at different sites or in different years were not different within the Aichilik, Canning, Firth, and Kongakut drainages, nor between the Ivishak and Echooka rivers within the Sagavanirktok system, and thus these data sets were pooled ($P > 0.01$; Table 5). Similarly, char from Hulahula River sites 13 and 16 and from sites 14 and 15 were not different; however, when data from these char were pooled (Hulahula #1 and Hulahula #2, respectively) and compared, differences were detected (Table 5). Within the Sagavanirktok system, tests of the pooled data from the Ivishak and Echooka rivers against the data from char collected from the Ribdon and Lupine rivers revealed significant differences. Differences also were observed among the three collections from within the Babbage River system. No differences were observed in those *G*-tests that compared resident char from the Canning River (site 9, Shublik Springs) and Firth River (site 23) to anadromous char within each system. However, upstream resident fish from Babbage River (site 26) were different from the downstream collection (site 25) and char from a tributary (Canoe River site 27). After combining similar data sets (see "Methods"), 16 collections were used in subsequent analyses. The 16 collections were significantly different from each other, based on a *G*-test of all stocks and summed over all variable loci ($G = 1{,}237$; df = 143; $P \ll 0.001$).

TABLE 2.—Enzymes, International Union of Biochemistry-Nomenclature Committee (IUBNC) numbers, and loci examined in samples of Beaufort Sea Dolly Varden *Salvelinus malma* collected from northern Alaska and Canada in 1985–1987. Buffers include AC (Clayton and Tretiak 1972), pH 6.1 and pH 6.8; AC+ was AC with NAD; RW (Ridgway et al. 1970), pH 8.2; and EBT (was similar to that of Boyer et al. 1963), pH 8.5. Tissues include muscle (M), liver (L), and eye (E). Pairs of loci numerically separated by commas (e.g., *sAAT-1,2**) were electrophoretically indistinguishable isoloci (Allendorf and Thorgaard 1984).

Enzyme or other protein	IUBNC number	Loci	Buffer	Tissue
Adenylate kinase	2.7.4.3	*AK-1**	AC 6.8	M
Alcohol dehydrogenase	1.1.1.1	*ADH-1**	RW	L
Aconitate hydratase	4.2.1.3	*sAH-1**	AC 6.8	L
Aspartate aminotransferase	2.6.1.1	*sAAT-3*, sAAT-4**	RW	E, L
		*sAAT-1,2**	RW	M
Creatine kinase	2.7.3.2	*CK-1*, CK-2**	RW	M
		*CK-5**	RW	E
Fumarate hydratase	4.2.1.2	*FH**	AC 6.8	M
β-*N*-Acetylhexosaminidase	3.2.1.52	*βHA**	AC 6.8	L
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B1,2**	RW	M
		*GPI-A1**	RW	M
Glutathione reductase	1.6.4.2	*GR-1**	RW	L
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-3*, GAPDH-4**	AC 6.1	E
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1*, G3PDH-2**	AC 6.1 RW	M, L
Cytosol nonspecific dipeptidase	3.4.13.18	*PEPA-1**	EBT	M
Isocitrate dehydrogenase	1.1.1.42	*mIDHP-1*, mIDHP-2**	AC 6.8	M
		*sIDHP-1,2**	AC 6.1, 6.8	L, E
Lactate dehydrogenase	1.1.1.27	*LDH-A1*, LDH-A2**	RW	M
		LDH-B1, LDH-B2**	RW	E
		*LDH-C1**		
		*LDH-B2**	RW	L
Tripeptide aminopeptidase	3.4.11.4	*PEPB-1**	EBT	M
Malate dehydrogenase	1.1.1.37	*sMDH-A1,2**	AC 6.1	M
		*sMDH-B1,2**	AC 6.1	M
Malic enzyme (NADP$^+$)	1.1.1.40	*mMEP-1*, mMEP-2*, sMEP-1,2**	AC 6.1	M
Phosphoglucomutase	5.4.2.2	*PGM-1*, PGM-2**	RW	M
		*PGM-3,4**	AC 6.1	L, M
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	AC 6.8	M, L, E
L-Iditol 2-dehydrogenase	1.1.1.14	*sIDDH-1,2**	RW	L
Superoxide dismutase	1.15.1.1	*sSOD-1**	RW	L
Triose-phosphate isomerase	5.3.1.1	*TPI-1*, TPI-2*, TPI-3*, TPI-4**	TG	E
Xanthine dehydrogenase	1.1.1.204	*XDH-1**	RW	L

TABLE 3.—Ger
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collections are A
EG = Egaksrak,
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Locus	Allel nam and
*sAAT-4**	33
	N
*sAAT-1,2**	75
	129
	N
*sAH-1**	115
	130
	N
*GAPDH-3**	Null
	N
*GPI-B1,2**	55
	N
*GPI-A1**	96
	N
*mIDHP-1**	220
	N
*sIDHP-1,2**	80
	N
*LDH-C1**	97
	N
*sMDH-A1,2**	128
	N
*sMEP-1,2**	69
	N
*PGDH-1**	95
	N
*PGM-2**	88
	N
*sIDDH-1,2**	43
	N
*sSOD-1**	115
	87
	N

Cluster analysis of Nei's genetic distances between the char collections identified some groups of collections with close genetic affinity that were also geographic neighbors (Figure 2). For example, char from the Aichilik River, from the middle of the coastal area sampled, were grouped with char from the Kongakut River, located to the east approximately 10 km (Figure 1). Similarly, char from the Ivishak–Echooka, Kavik, and Canning rivers formed a group that represented collections from the western region of the coastal area sampled (Figures 1 and 2). However, the correspondence between genetic and geographic distances was weak in the hierarchical groupings. For example, the western group identified above was next linked to char from Babbage #1, Babbage #2, and Canoe, the easternmost sites in Canada. Also, char from the Lupine and Ribdon rivers of the Sagavanirktok system in the west were grouped together but were joined next to char from the Firth River in the east. The greatest pairwise genetic distance was between the Sadlerochit Spring char (a resident form) and all other collections.

Variation among individuals within collections accounted for 91% of the total gene diversity observed (Table 6). Most of the remaining observed variation (8%) was attributable to differences among the 11 drainages, with a minor component attributable to differences within drainages (1%).

Discussion

Amount and Pattern of Genetic Variation

The average heterozygosity observed in Dolly Varden (H = 0.038) from Beaufort Sea drainages was in the range typical of fish species in general (H = 0.051; Nevo et al. 1984). More variation as measured by average heterozygosity was observed in Beaufort Sea Dolly Varden than in Arctic char *Salvelinus alpinus* of North America, Ireland, Swe-

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TABLE 3.—Gene frequencies of variable loci in 16 collections or pooled collections of Dolly Varden *Salvelinus malma* sampled in 1985, 1986, and 1987 from the Beaufort Sea area of Alaska and Canada. Variants of duplicated loci were arbitrarily assigned to one locus of the pair. Only frequencies of alternate alleles other than *100** are given. Names of loci (abbreviated here) are in Table 2. No data (ND) were available from some collections at some loci. Codes for collections are AI = Aichilik, AN = Anaktuvuk, B1 = Babbage #1, B2 = Babbage #2, CN = Canning, CA = Canoe, EG = Egaksrak, FI = Firth, H1 = Hulahula #1, H2 = Hulahula #2, IV = Ivishak and Echooka, KA = Kavik, KO = Kongakut, LU = Lupine, RI = Ribdon, SA = Sadlerochit Spring. See Table 1 for more details of collections.

Locus	Allele name and *N*	Collections															
		AI	AN	B1	B2	CN	CA	EG	FI	H1	H2	I V	KA	KO	LU	RI	SA
*sAAT-4**	*33**	0.012	0.025	0.000	0.000	0.031	0.000	0.014	0.079	0.019	ND	0.000	0.000	0.000	0.000	ND	0.000
	N	80	40	53	21	179	33	35	76	80		22	37	85	45		44
*sAAT-1,2**	*75**	0.082	0.092	0.000	0.000	0.092	0.000	0.049	0.050	0.050	ND	0.034	0.000	0.088	0.044	0.050	0.133
	*129**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	ND	0.000	0.000	0.000	0.000	0.000	0.000
	N	85	38	53	21	206	35	41	130	80		72	40	85	45	40	45
*sAH-1**	*115**	0.194	0.292	0.019	0.000	0.216	0.029	0.243	0.211	0.220	0.239	0.174	0.137	0.177	0.211	0.112	0.011
	*130**	0.265	0.305	0.490	0.559	0.270	0.271	0.200	0.328	0.220	0.294	0.291	0.400	0.275	0.322	0.300	0.889
	N	85	36	52	17	183	35	35	128	91	46	72	40	85	45	40	45
*GAPDH-3**	*Null**	0.345	0.066	0.067	0.150	0.246	ND	0.500	0.177	0.440	0.675	0.225	0.294	0.286	0.233	0.270	0.000
	N	82	38	52	20	183		32	107	91	40	71	34	84	45	37	45
*GPI-B1,2**	*55**	0.000	0.050	0.010	0.000	0.002	0.000	0.000	0.019	0.000	0.000	0.007	0.000	0.000	0.000	0.077	0.000
	N	85	40	52	21	211	35	41	129	95	51	74	40	85	45	39	45
*GPI-A1**	*96**	0.241	0.100	0.154	0.000	0.123	0.371	0.171	0.306	0.158	0.140	0.088	0.012	0.282	0.411	0.333	0.156
	N	85	39	52	21	211	35	41	129	95	50	74	40	85	45	39	45
*mIDHP-1**	*220**	0.018	0.000	0.000	0.000	0.003	0.000	0.000	0.019	0.000	0.010	0.014	0.025	0.012	0.022	0.050	0.000
	N	85	37	53	21	149	35	35	129	95	51	74	40	85	45	40	45
*sIDHP-1,2**	*80**	0.122	0.000	0.000	0.000	0.035	0.000	0.014	0.053	0.027	0.073	0.007	0.100	0.059	0.000	0.000	0.000
	N	85	39	53	21	184	35	35	131	91	48	73	40	85	45	40	45
*LDH-C1**	*97**	0.054	0.000	0.000	0.000	0.005	0.014	0.071	0.027	0.011	0.059	0.027	0.012	0.035	0.000	0.077	0.000
	N	83	35	53	21	188	35	35	132	95	51	73	40	85	45	39	45
*sMDH-A1,2**	*128**	0.000	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	N	82	34	53	21	182	35	35	128	93	52	72	40	85	40	40	45
*sMEP-1,2**	*69**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000
	N	85	40	53	21	197	35	35	132	95	54	74	40	85	45	40	45
*PGDH-1**	*95**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.011	0.012	0.000
	N	85	40	53	21	197	35	35	132	95	51	74	40	85	45	40	45
*PGM-2**	*88**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.021	0.029	0.000	0.000	0.000	0.000	0.000	0.000
	N	85	35	51	21	161	28	39	128	95	51	50	40	85	45	40	45
*sIDDH-1,2**	*43**	0.035	0.125	0.000	0.000	0.088	0.000	0.014	0.015	0.086	0.000	0.087	0.000	0.041	0.011	0.000	0.000
	N	85	36	53	21	188	34	35	131	87	17	23	40	85	44	40	44
*sSOD-1**	*115**	0.053	0.000	0.000	0.000	0.026	0.015	0.057	0.004	0.086	0.093	0.028	0.000	0.024	0.089	0.112	0.000
	*87**	0.000	0.000	0.056	0.043	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	N	85	35	53	21	212	35	35	132	93	54	72	40	85	45	40	45

den, and Norway (H = 0.00–0.024; Ferguson 1981; Kornfield et al. 1981; Andersson et al. 1983; Hindar et al. 1986). Most Arctic char sampled for the studies listed above were from landlocked lake populations, but anadromous and small, resident (dwarf) stocks were also included in some cases. The amount of variation in Beaufort Sea Dolly Varden was closer to the average reported for anadromous salmonids (H = 0.041; Gyllensten 1985; and tabulated in Altukhov and Salmenkova 1991) than for Arctic char.

Evidence for separate populations within a drainage occurred in three (Babbage, Hulahula, and Sagavanirktok) of the seven river systems where more than one collection had been taken. Within the Babbage River system, the Canoe River collection was significantly different from the two Babbage River collections, similar to observations by Reist (1989). The isolated population above the waterfall on the Babbage River (Babbage #2, Site 26) was different from the other two collections within that system (primarily because of fixation of the common allele at *GPI-A1**) but was most similar to the collection below the falls (Babbage #1, site 25; Figure 2). The differences observed between collections from upstream and downstream in the Hulahula River were not expected, because of the lack of hydrographic complexity in the river system. Perhaps the series of overwintering and spawning pools (20–30 km apart) that characterize this system serves to isolate local stocks. Evidence for separate char populations also occurred within the Sagavanirktok River system (Ivishak–Echooka, Lupine, and Ribdon rivers), even though several stocks may rely on the same overwintering area in the Ivishak River (see Yoshihara 1973; Furniss 1974, 1975).

TABLE 4.—Expected average percent of heterozygosity per locus (H) and percent of loci examined that were polymorphic in 16 populations of Dolly Varden *Salvelinus malma* sampled from tributaries of the Beaufort Sea in Alaska and Canada in 1985–1987. The average value of H over all populations was weighted by sample size (SEs for average H and average percent of polymorphic loci are in parentheses).

Drainage and site	Year	N	H (%)	Polymorphic loci (%)
Aichilik River	1986, 1987	85	5.04	23.8
Colville River				
Anaktuvuk	1986	40	3.81	19.0
Babbage River				
#1	1987	53	2.48	11.9
#2	1987	21	2.43	7.1
Canoe River	1986	35	2.51	9.8
Canning River				
5 Sites	1986, 1987	212	4.13	26.2
Egaksrak River	1986	41	4.32	21.4
Firth River				
3 Sites	1986, 1987	132	4.29	28.6
Hulahula River				
#1	1985, 1987	95	4.57	23.8
#2	1985	54	4.66	22.5
Kavik River	1986	40	3.14	14.3
Kongakut River	1986, 1987	85	4.54	21.4
Sadlerochit Spring	1987	45	1.63	7.1
Sagavanirktok River				
Ivishak, Echooka	1986	74	3.62	26.2
Lupine River	1987	45	4.36	19.0
Ribdon River	1986	40	5.16	22.0
Total		1,097		
Average (SE)			3.79 (1.02)	19.0 (6.7)

Based on these data, more than one population of Dolly Varden within each Beaufort Sea river drainage should be anticipated when assessing ecological and genetic risks from development or exploitation.

River systems that exhibited no genetic differences among Dolly Varden collections included those with multiple collections from the same site in different years and from multiple sites. Allele frequencies were similar in collections from geographically close sites sampled in two different years (Aichilik, Kongakut, and Hulahula rivers). No significant differences over all loci were observed among three collections from sites #22–24 (Figure 1) on the Firth River system (this study; Table 5). However, in another study a significant difference at a single locus was reported between two char collections from the Firth River (Reist 1989). No divergence was detected among collections from multiple sites in the Canning River drainage, although one of the collections contained resident Dolly Varden (#9, Shublik Spring).

The genetic divergence observed among Dolly Varden populations of different river systems probably has been maintained by homing behavior (e.g., Furniss 1974; Craig and McCart 1975). Although Dolly Varden are known to overwinter in nonnatal drainages (e.g., Craig 1977a; Armstrong 1984), the pattern of relationships among stocks indicated that sufficient isolation exists to permit genetic differentiation of populations. The differentiation observed among Dolly Varden in this study was in accord with that of a previous study that documented genetic differences between char from the Babbage River, Firth River, and two Mackenzie River tributaries (Reist 1989).

The gene diversity observed among anadromous Dolly Varden from the western Beaufort Sea in this study ($G_{ST} = 0.09$) was similar to that reported for other anadromous salmonids (Gyllensten 1985) and corresponded to what has been considered as local differences (Ryman 1983). The level of between-stock diversity among Beaufort Sea Dolly Varden (9%) was less than that of nonmigratory Arctic char (14–53%; Kornfield et al. 1981; Andersson et al. 1983; Hindar et al. 1986), typically from isolated lake habitats. T observed corre tion (5–15%) d (Wright 1978).

TABLE 5.—Heterogeneity tests (G) of allozyme data among collections of Beaufort Sea Dolly Varden *Salvelinus malma* sampled at different sites and different years (1985–1987) within a river system. A value of P greater than 0.01 was used as the criterion for pooling data for further analyses. Degrees of freedom reflect the number of variable loci in the comparisons. Site numbers refer to those used in Table 1 and Figure 1.

Collection	Site numbers	Year	G	df	P
Aichilik	17, 18	1986, 1987	12.45	11	0.330
Babbage	25, 26, 27	1986, 1987	46.95	7	<0.001
Canning	7, 8, 9, 10, 11	1986, 1987	19.31	8	0.013
Firth	22, 23, 24	1986, 1987	11.64	13	0.458
Hulahula	13 and 16 pooled versus 14 and 15 pooled	1985, 1987	29.41	9	<0.001
Kongakut	20, 21	1986, 1987	5.71	10	0.839
Sagavanirktok					
Ivishak, Echooka	2, 3	1986	11.99	8	0.152
Ivishak and Echooka pooled versus Ribdon, Lupine	2 and 3 pooled versus 4, 5	1986, 1987	53.60	12	<0.001

FIGURE 2.—D genetic distances lated between c *malma* from Bea and Canada in 1 used in Table 1 a

TABLE 6.—Ge taries of Alaska a during 1985–198

Drainage
Babbage River
Hulahula River
Sagavanirktok
Average

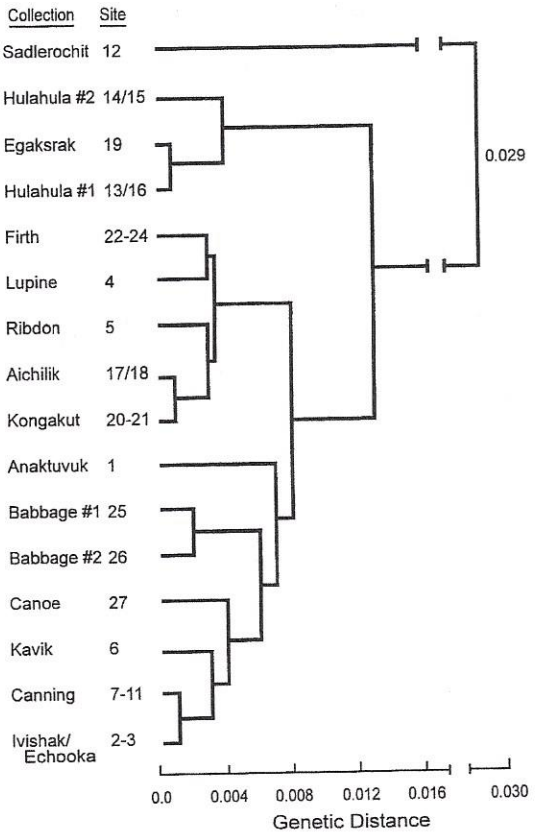

FIGURE 2.—Dendrogram of cluster analysis of Nei's genetic distances based only on polymorphic loci calculated between collections of Dolly Varden *Salvelinus malma* from Beaufort Sea tributaries in northern Alaska and Canada in 1985–1987. Site numbers refer to those used in Table 1 and Figure 1.

lake habitats. The 9% between-stock diversity we observed corresponded to the level of differentiation (5–15%) described as moderate in various taxa (Wright 1978).

Life History Differences

The general pattern of genetic variation among collections was not strongly associated with anadromous versus stream-resident life history types. Typically, more similarity was observed between collections of resident and anadromous char in the same drainage than to resident populations elsewhere. Although the Babbage River #2 collection (above the waterfall) and Sadlerochit Spring char (from a spring area not known to include anadromous individuals; Craig 1977b) were genetically distinct and probably reproductively isolated from other populations. The apparent divergence of these populations was related to the low level of variability ($0.016 < H < 0.024$) observed rather than to the presence of unique alleles. In the Babbage River system, small, resident Dolly Varden presumed to be from above the waterfall have been observed spawning with large, anadromous Dolly Varden below the falls (Bain 1974). This unidirectional downstream gene flow probably has prevented the two populations from diverging further. The resident Dolly Varden of the Shublik Spring collection were not detectably different from other collections in the Canning River drainage even though these char are isolated by a falls (McCart and Craig 1973).

In most other salmonids that have been studied, only a small percentage of the divergence among populations was attributable to the life history distinction between resident and migratory forms, for example, rainbow trout *Oncorhynchus mykiss* (Allendorf and Utter 1979), brown trout *Salmo trutta* (Ryman and Ståhl 1981), and Arctic char (Hindar et al. 1986). Resident Dolly Varden of the Beaufort Sea area probably arose independently in various drainages where conditions were unfavorable or impossible for migration. Nordeng (1983) found that some individuals in a brood of Arctic char reared in a hatchery and then released matured early and remained as small residents, while others

TABLE 6.—Gene diversity analysis among populations of Dolly Varden *Salvelinus malma* from Beaufort Sea tributaries of Alaska and Canada. The average values represent data from all 16 collections from the 11 river systems sampled during 1985–1987.

		Absolute gene diversity				Relative gene diversity (%)		
Drainage	Number of sites	Within sites	Between sites	Between drainages	Total	Within sites	Between sites	Between drainages
Babbage River	3	0.0256	0.0020		0.0276	92.9	7.1	
Hulahula River	2	0.0463	0.0009		0.0472	98.1	1.9	
Sagavanirktok	3	0.0429	0.0013		0.0442	97.1	2.9	
Average	16	0.0383	0.0004	0.0033	0.0420	91.1	0.9	8.0

became anadromous. Life history strategy can also be related to feeding and thus partially explained by a growth-dependent maturity (Jonsson and Hindar 1982).

Management Implications

The observed pattern of differentiation among populations within and among river systems refuted the null hypothesis that Beaufort Sea Dolly Varden are a single panmictic population. Nearly all collections of Dolly Varden from different river systems were genetically distinct, and several systems supported more than one population. Human activity affecting a critical habitat in localized areas, such as an overwintering area or access to Beaufort Sea coastal feeding areas in summer, could threaten individual populations of Dolly Varden from this region. For anadromous populations, changes in their distribution and abundance will affect species abundance within a broad coastal area that serves as an important fishing area. Loss of populations would reduce the overall genetic diversity of Dolly Varden in this region.

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FISH ECOLOGY IN ARCTIC NORTH AMERICA

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