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Genetics Investigations of Dolly Varden Char (*Salvelinus malma*) of the North Slope of Alaska

Part I
Population Genetic Structure of Dolly Varden Char from Beaufort Sea Drainages of Nothern Alaska and Canada

by
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Part II
Stock Origins of Dolly Varden Collected from Beaufort Sea Coastal sites of Arctic Alaska and Canada

by
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Preface

This document is the final report on genetic studies conducted by the U.S. Fish and Wildlife Service on Dolly Varden *Salvelinus malma* along the coastline of the Beaufort Sea and in the rivers and streams of the North Slope of Arctic Alaska and Canada. Conceptually the project proceeded in a two sequential steps: (1) to describe the population genetic structure of Dolly Varden, and then if population structure was present, (2) to determine the stock composition of mixture samples from along the Beaufort Sea Coast.

First, studies were conducted to determine whether Dolly Varden were organized into several populations or whether they functioned as one panmictic (random mating) population. If the former was true (several populations existed) then ecologically important, unique genetic variation could exist in each population and management would need to make separate considerations for each population. If the latter was true (one panmictic population) then management would be simplified and require the consideration of only one population that occupied a large geographical area. In this case, small perturbations of the environment would likely not threaten the entire population. The answer to this question has particular significance to the management of Dolly Varden in the Arctic National Wildlife Refuge (Arctic Refuge) where oil and gas exploration and development activities have been proposed. The results of this first step were published in *Fish Ecology in Arctic North America* (American Fisheries Society Symposium 19, Bethesda, Maryland). The data and their analysis are also presented in Chapter 2 of this report. Based on genetic data from allozyme loci, char stocks or populations exist, which are organized by drainage system.

The second phase (to describe stock contributions to mixture samples) proceeded because multiple populations were determined to be present. This part of the project was important because a subsistence fishery along the coast occurs near the Inupiat village of Kaktovik. Knowledge of which stocks contribute to the fishery would identify the populations and geographic regions that support the fishery. The proportional contribution of distant stocks, such as from Canada, was unknown. Populations that support this fishery could require special management consideration. The results of this phase are presented in Chapter 3. This chapter is intended to be submitted for a peer-reviewed publication.

Population Genetic Structure of Dolly Varden Char From Beaufort Sea Drainages of Northern Alaska and Canada[1]

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Abstract. -- Dolly Varden char (*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 char populations from Beaufort Sea tributaries. Allozyme electrophoresis was used to analyze variation at 49 loci (21 were polymorphic) in 27 collections made from 11 rivers. Genetic data from multiple collections made within single river systems were pooled based on statistical similarity and reduced the number of collections for subsequent analyses to 16. Average heterozygosity observed in the 16 collections was 0.038 (range 0.016 to 0.052). Average percent of loci 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 while 8% was due to differences among river systems and 1% due to differences within systems. Two of four collections from upstream areas or springs presumed to be resident char were genetically different from anadromous populations in the same river system. 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 spawning or overwintering areas, must consider the effects on individual populations rather than on a generalized char population that uses the Beaufort Sea.

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[1] A similar report was published as "Population genetic structure of Dolly Varden from Beaufort Sea drainages of northern Alaska and Canada." Pages 240-249 *in* J. Reynolds, editor. Fish ecology in Arctic North America. American Fisheries Society Symposium 19, Bethesda, Maryland.

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Introduction

Dolly Varden char (*Salvelinus malma*, hereafter 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 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 to 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 the spring. Juvenile char live in tributaries until three to five years of age when they begin to migrate to coastal areas to feed (Craig 1977a; McCart 1980). Mature and immature char return to fresh water in late summer and early fall, and overwinter in tributaries as marine waters become supercooled (< 0^o C) and too saline. These char typically do not spawn until age five or six (Bain 1974; Craig 1977a). Although an individual can spawn repeatedly over their lifetime, they seldom acquire enough energy reserves in one season to be able to spawn every year.

Overwintering habitat is critical to the survival of Dolly Varden char in this Arctic environment. Only about two percent of the fresh water 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 char of all life history stages. If an overwintering area fails, e.g., due to anoxia, freezing solid, or water removal, fish are not able 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 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 char populations are adapted to the physical extremes of the Arctic by long life and repeat 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 occurred within the major river drainages of the Beaufort Sea area and refute the null hypothesis that char from this region exist as a single panmictic population. The amount and pattern of genetic variation was described and compared within and among char collections from 11 river systems.

Methods

Collections. -- Char were collected at 27 sites on 11 river systems 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). 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 due to 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, presumed to have a stream resident life history, were collected from upstream of the waterfall on the Babbage River (site 26), upstream Firth River (site 23), Shublik Springs (site 9, Canning River drainage), and Sadlerochit Springs (site 12) and 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). Twentyfour enzymes were examined within white muscle, liver, and eye tissues

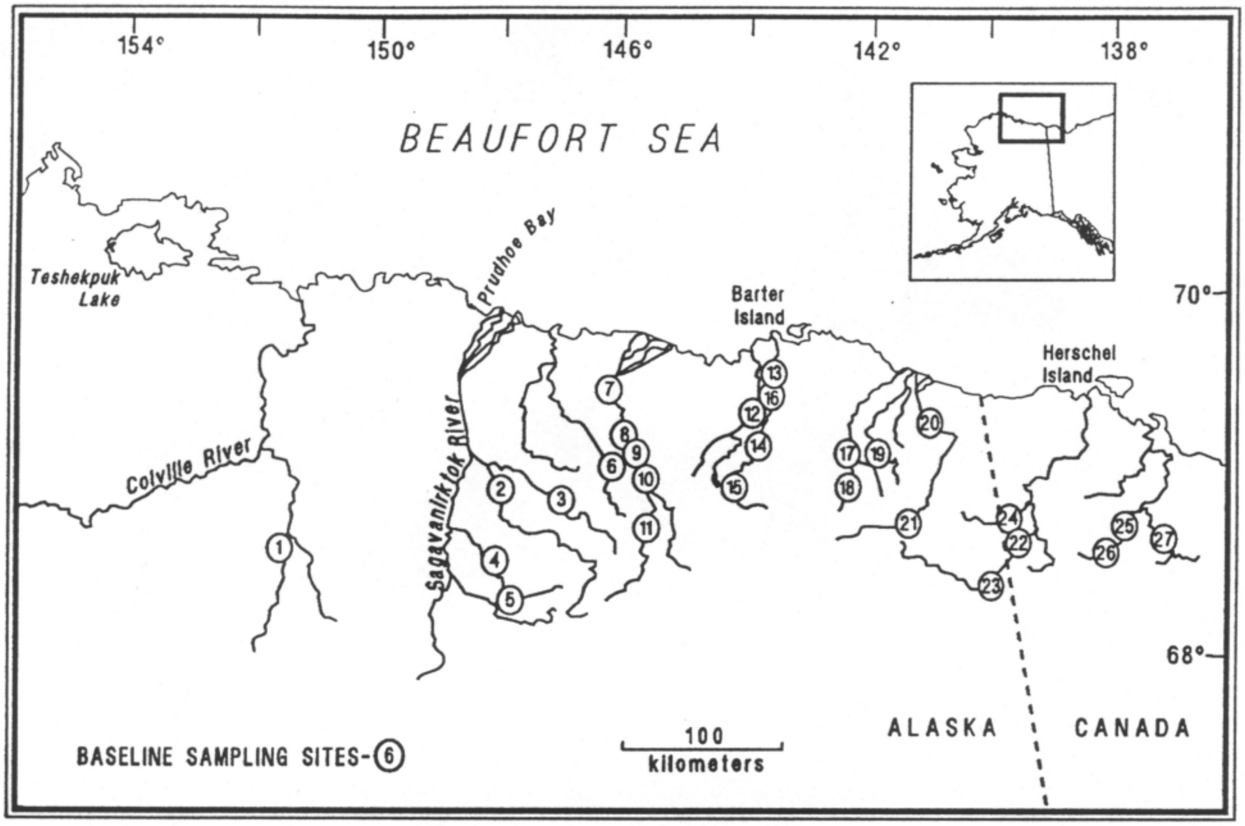

FIGURE 1. Sampling sites for Dolly Varden char collected from Beaufort Sea tributaries of Alaska and Canada from 1985-1987. Site numbers correspond to locations in Table 1.

(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*. *PGM-3,4** was variable, but not scored reliably. Putative variation was observed at *bGLUA**, 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 by 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 $P \geq 0.01$, indicating that collections were not significantly different based on a *G*-test (Sokal and Rohlf 1981; criteria of Shaklee and Phelps 1990). Based on pooling, the

TABLE 1. - Collections of Beaufort Sea Dolly Varden sampled from Alaska and Canada with site location (Universal Transverse Mercator), number of samples, and date collected (months/years). Site number corresponds 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 Zone	Latitude	Longitude	N	Date
Anaktuvuk River	1	5W	7624250	574000	40	5/86
Sagavanirktok River						
Ivishak River	2	6W	7663300	463800	50	9/86
Echooka River	3	6W	7683800	486800	24	4/86
Ribdon River	4	6W	7615250	453500	40	5/86
Lupine River	5	6W	7652130	443000	48	8/87
Kavik River	6	6W	7691000	517100	40	9/86
Canning River						
	7	6W	7652250	553250	27	5/86
	8	6W	7719500	527300	70	8/87
Shublik Spring	9	6W	7699300	533800	59	8/87
	10	6W	7687800	536000	62	8/87
Marsh Fork	11	6W	7663000	540000	29	5/86
Sadlerochit Spring	12	6W	7731300	600300	62	8/87
Hulahula River						
#1	13	6W	7740000	609500	15	10/85
#2	14	6W	7711000	602000	37	10/85
#2	15	6W	7690500	595300	59	10/85
#1	16	6W	7734300	608500	97	8/87
Aichilik River						
	17	7W	7694000	413500	40	9/86
	18	7W	7683500	417300	70	8/87
Egaksrak River	19	7W	7702500	435800	41	5/86
Kongakut River						
	20	7W	7712000	471700	40	9/86
	21	7W	7666000	463000	90	8/87
Firth River						
	22	7W	7625300	507500	64	8/87
	23	7W	7610250	494000	47	8/87
Joe Creek	24	7W	7646500	502300	50	9/86
Babbage River						
#1	25	7W	7625300	579300	53	8/87
#2	26	7W	7619500	575500	21	8/87
Canoe River	27	7W	7612500	592500	35	9/86

TABLE 2. - Enzymes, IUBNC numbers, and loci examined in samples of Dolly Varden collected from northern Alaska and Canada. Buffers include: AC (Clayton and Tretaik 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	Loci	Buffer	Tissue
Adenylate kinase	2.7.4.3	*AK-1**	AC 6.8	M
Alcohol dehyrogenase	1.1.1.1	*ADH-1**	RW	L
Aconitate hydratase	4.2.1.3	*sAH-1**	AC 6.8	L
Aspartate aminotranferase	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
b-Glucosaminidase	3.2.1.30	β-*GLUA**	AC 6.8	L
Glucose 6 phosphate isomerase	5.3.1.9	*GPI-B1,2**	RW	M
		*GPI-A1**	RW	M
Glutahione 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	1.1.1.8	*G3PDH-1*, G3PDH-2**	AC 6.1 RW	M,L
Glycyl-leucine peptidase	3.4.11	*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* LDH-C1**	RW	E
		*LDH-B2**	RW	L
Leucyl-glycyl-glycine peptidase	3.4.13	*PEPB-1**	EBT	M
Malate dehydrogenase	1.1.1.37	*sMDH-A1,2**	AC 6.1	M
		*sMDH-B1,2**	AC 6.1	M
Malate dehydrogenase (NADP-dependent)	1.1.1.40	*mMEP-1*, mMEP-2*, sMEP-1,2**	AC 6.1	M
Phosphoglucomutase	2.7.5.1	*PGM-1*, PGM-2**	RW	M
		*PGM-3,4**	AC 6.1	L,M
6-Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	AC 6.8	M,L,E
Sorbitol (iditol) dehydrogenase	1.1.1.14	*sIDDH-1,2**	RW	L
Superoxide dismutase	1.15.1.1	*sSOD-1**	RW	L
Triose-phosphate isomerase		*TPI-1*, TPI-2*, TPI-3*, TPI-4**	TG	E
Xanthine dehydrogenase	1.23.2	*XDH-1**	RW	L

data set was reduced to 16 collections from the original 27 sites; thus, some collections included data from fish collected from more than one site within a river system (e.g., data from collections at three sites in the Firth River system were combined). The amount of genetic variation within the 16 collections was described by percent of polymorphic loci (*P*) 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 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 decreased 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 cluster analysis (UPGMA) of the distance coefficients was used to construct a dendogram (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.

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**, *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 due to Type I error. Percent of polymorphic loci ranged from 7.1 to 35.7% (average 19%, SE=6.7%; Table 4). Average heterozygosity ranged from 1.6 to 5.2% and overall all collections was 3.8% (SE=1.02%). Lowest heterozygosity (1.6%) was observed in resident char collected from Sadlerochit Springs. 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, 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. Significant 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 like 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*-1237, df=143; P<<0.001).

TABLE 3. - Gene frequencies of variable loci in 16 collections or pooled collections of Dolly Varden char 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/Echooka, KA=Kavik, KO=Kongakut, LU=Lupine, RI=Ribdon, SA=Sadlerochit Spring. See Table 1 for further description of collections.

		Collections															
Locus	Allele name N	AI	AN	B1	B2	CN	CA	EG	FI	H1	H2	IV	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

TABLE 3. continued

Locus	Allele name N	AI	AN	B1	B2	CN	CA	EG	FI	H1	H2	IV	KA	KO	LU	RI	SA
		Collections															
*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

TABLE 4. - Expected average percent of fish heterozygous per locus (*H*), and percent of loci examined that were polymorphic in 16 populations of Dolly Varden char sampled from tributaries of the Beaufort Sea in Alaska and Canada. The average value of *H* over all populations were weighted by sample size (standard errors for average *H* and average % of polymorphic loci are in parentheses).

Drainage/Sites	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
Table 4. Continued				
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		1097		
Average (SE)			3.79 (1.02)	19.0 (6.7)

TABLE 5. Heterogeneity tests (*G*) of allozyme data among collections of Dolly Varden sampled at different sites and/or different years within a river system. $P > 0.01$ was used as the criterion for pooling data for further analyses. Degrees of freedom (df) 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	13/16 pooled vs. 14/15 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/Echooka pooled, Ribdon, and Lupine	2/3 pooled vs. 4, 5	1986/1987	53.60	12	<0.001

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

		Absolute Gene Diversity				Relative Diversity (%)		
Drainage	# 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

Cluster analysis of genetic distances (Nei's) between the char 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. (Figure 1 and 2). However, the correspondence between genetic and geographic distances was weak in the hierarchial groupings. For example, the western group identified above as next linked to char from Babbage #1, Babbage #2, and Canoe, the eastern-most 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 Springs char (a resident form) and all other collections next to char from the Firth River in the east. The greatest pairwise genetic distance was between the Sadlerochit Springs 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 balance of the variation observed (8%) was attributable to differences among the 11 drainages with a minor component due to differences within drainages 91%).

Discussion

Amount and Pattern of Genetic Variation

The average heterozygosity observed in Dolly Varden char (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 char than in Arctic char *Salvelinus alpinus* of North America, Ireland, Sweden, and Norway (H = 0.00 - 0.024; Kornfield et al. 1981; Ferguson 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 char 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 both other collections within that system (primarily due to 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, due to the lack of hydrographic complexity in the river system. Possibly, 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). Based on these data, more than one population of Dolly Varden char 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 char 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

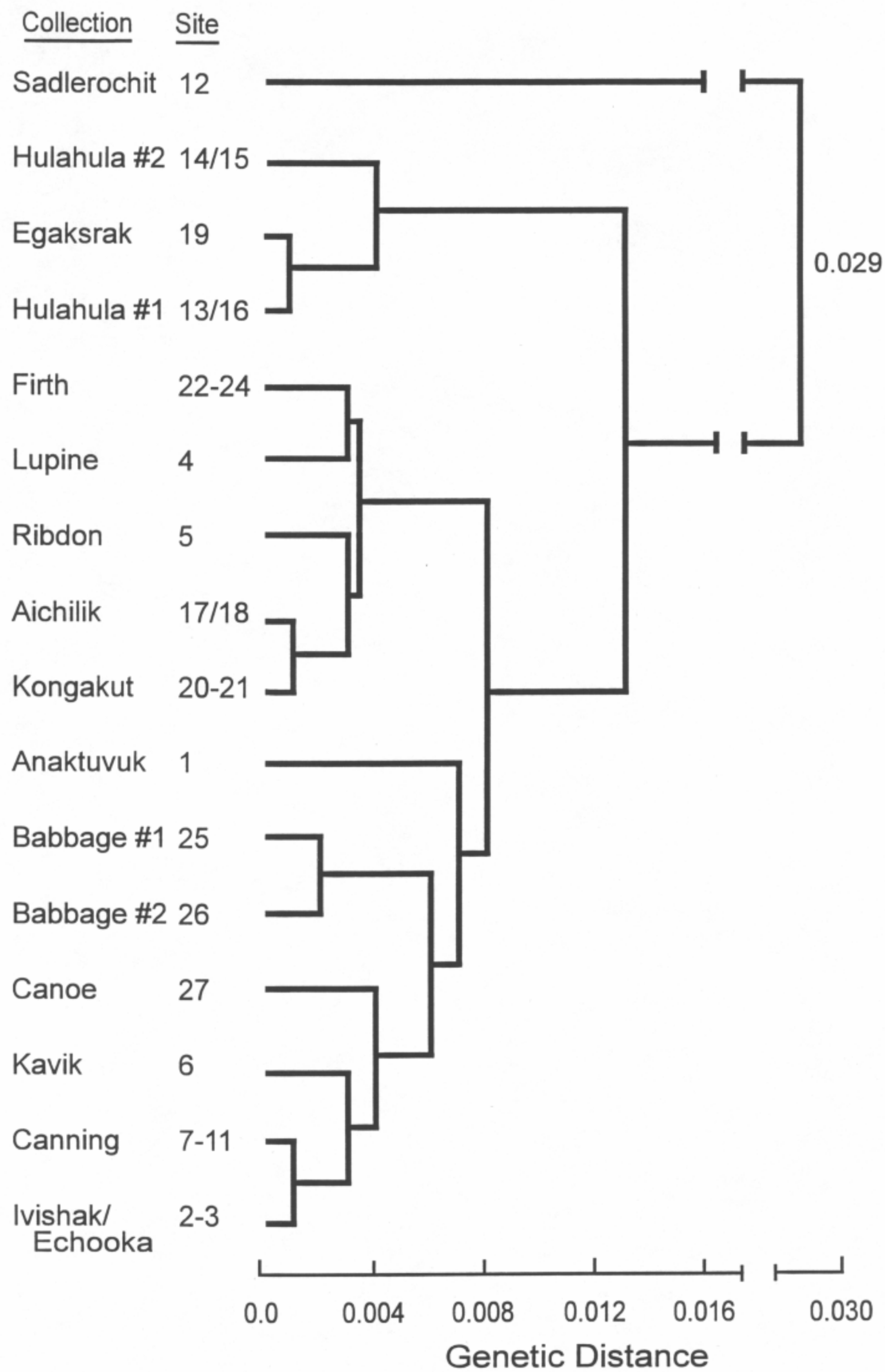

FIGURE 2. Dendogram based on cluster analysis of Nei's genetic distances based on polymorphic loci only calculated between Dolly Varden char collections from Beaufort Sea tributaries in northern Alaska and Canada. Site numbers refer to those used in Table 1 and Figure 1.

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, though one of the collection contained resident Dolly Varden char (#9, Shublik Springs).

The genetic divergence observed among Dolly Varden char populations of different river systems has likely been maintained by homing behavior (e.g., Furniss 1974; Craig and McCart 1975). Although Dolly Varden char are known to overwinter in non-natal drainages (e.g., Armstrong 1984; Craig 1977a), the pattern of relationships among stocks indicated that sufficient isolation exists to permit genetic differentiation of populations. The differentiation observed among Dolly Varden char in this study was in accord with 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 western Beaufort Sea Dolly Varden char in this study (G_{ST} = 0.09) was similar to that reported for other anadromous salmonids that have been studied (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 char (9%) was less than that of non-migratory Arctic char (14 - 53%; Kornfield et al. 1981; Andersson et al. 1983; Hindar et al. 1986), typically from isolated 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. Though 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 likely reproductively isolated from other stocks, the apparent divergence of these stocks was related to the low level of variability ($0.016 < H < 0.024$) observed rather than the presence of unique alleles. In the Babbage River system, small resident Dolly Varden char presumed to be from above the waterfall have been observed spawning with large anadromous Dolly Varden char below the falls (Bain 1974). This uni-directional downstream gene flow likely has prevented the two populations from diverging further. The resident Dolly Varden char of the Shublik Springs 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 due to the life-history distinction between resident and migratory forms, e.g., rainbow trout (Allendorf and Utter 1979), brown trout (Ryman and Stahl 1981), and Arctic char (Hindar et al. 1986). Resident Dolly Varden char of the Beaufort Sea area likely arose independently in various drainages where conditions were unfavorable or impossible for migration. Nordeng et al. (1983) found that some individuals in a brood of Arctic char (*Salvelinus alpinus*) reared in a hatchery and then released would mature early and remain as small residents while others became anadromous. Life history strategy can also be related to feeding, and thus partially explained by a growth-dependent maturity (Jonsson and Hindar 1982).

Mangement Implications

The observed pattern of differentiation among populations within and among river systems refuted the null hypothesis that Beaufort Sea Dolly Varden char are a single panmictic population. Nearly all collections of Dolly Varden char 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 indivdual populations of Dolly Varden char 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 the region's Dolly Varden char.

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Stock Origins of Dolly Varden Collected from Beaufort Sea Coastal Sites of Arctic Alaska and Canada

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Abstract. -- Anadromous northern Dolly Varden *Salvelinus malma* support a summer subsistence fishery in Beaufort Sea coastal waters. These same waters coincide with areas of oil and gas exploration and development. The purpose of this study was to assess variation in stock origins of Dolly Varden collected from sites along 400 km of Beaufort Sea coast. Mixed-stock analyses (MSA) of allozyme data were used to compare collections from four sites (Endicott near Prudhoe Bay, Mikkelsen Bay, Kaktovik, Phillips Bay-Canada), and to assess variation in stock contributions among summer months and between 1987 and 1988. MSA estimates for individual stocks were summed into estimates for three stock groups: western stocks from the area near Sagavarnirktok River and Prudhoe Bay (SAG), Arctic National Wildlife Refuge stocks (Arctic Refuge), and Canada stocks. MSA estimates of Endicott samples taken in 1987 and 1988 did not differ greatly among months in terms of contributions from local SAG stocks (range 71 to 95%). Contributions from non-local (>100 km distant) Canada and Arctic Refuge stocks were not different from zero in 1987 but contributions from Canada stocks were significant in July (17%) and August (20%) of 1988. Thus, stock contributions were different between years in the samples from Endicott. Mixture samples from the Kaktovik area in 1988 were different between months in terms of contributions from non-local SAG stocks (July 7% and August 27%). Significant contributions were made to these samples both months from Canada (25 and 17%) and local Arctic Refuge stocks (68 and 56%). Among the four coastal sites, local stocks typically contributed most to collections; however, every site had collections that contained significant contributions from non-local stocks. MSA estimates clearly revealed the movement of char between U.S. and Canada coastal waters. If local Dolly Varden stocks are affected by oil and gas development activities, distant subsistence fisheries along the Beaufort Sea coast could also be affected.

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Introduction

Dolly Varden *Salvelinus malma* use the coastal waters of the Beaufort Sea during summer months to access food resources essential for growth and reproduction. Most Dolly Varden growth occurs in the short summer season, when food such as mysids and amphipods concentrate in the highly productive marine waters (Craig 1984; Fechhelm et al. 1997). These fish return to North Slope streams in late summer to escape lethal winter sea temperatures and to overwinter in deep pools or springs. Some large fish (> 400 mm, ~ age 6-7) at this time also mature and spawn (McCart 1980; Underwood et al. 1996). Eggs incubate for 7-8 months before young emerge in the spring. Young Dolly Varden smolt in early summer, sometimes as young as age 1, but more commonly as age 3 or 4 fish (Armstrong and Morrow 1980; McCart 1980). The overwintering habitats used by char in this region are scarce and represent "critical" habitat for the species. Fish in the winter can not move between pools or out of springs because channels freeze to the stream bottom. Char must use these locations to survive and are held captive in them until spring breakup (Craig 1989a). Any oil and gas exploration and development activities (e.g., Hachmeister et al. 1991) that harm these habitats or impede migration to, or the use of, coastal waters would reduce Dolly Varden growth and abundance and be detrimental to populations.

Dolly Varden that use the Beaufort Sea during summer months have genetically identifiable populations that use homing to natal streams to maintain their identity. Allozyme studies have shown genetic differences among char collections from North Slope streams (Reist 1989; Everett et al. 1997). For example, Everett et al. (1997) analyzed variation at 21 polymorphic loci in juvenile char collected from 11 river drainages. Genetic differences in char occurred among drainage systems, and in some cases within drainages. Stock-isolating mechanisms, such as homing, are required to maintain population structure. Consistent return to rivers of prior spawning experiences has been reported for Dolly Varden in tributaries of the Chukchi Sea (DeCicco 1997), and homing to natal rivers has been reported for Dolly Varden in southeastern Alaska (Armstrong 1974, 1984). Based on the genetic population structure described for North Slope Dolly Varden and the homing reported for this species, many populations use the coastal waters during the summer, and support the fisheries of the region.

Fish and fishing provide important subsistence and cultural benefits to the people across the North Slope of Alaska. Several fish species are harvested from coastal waters near the village of Kaktovik on Barter Island in the Arctic National Wildlife Refuge (Arctic Refuge) from late June to September, and from traditional fish camps on the Hulahula River in fall and winter (e.g., Jacobson and Wentworth 1982; Craig 1989b). Many char are also harvested as part of the summer fishery in the Colville River near Nuiqsut (e.g., Pedersen and Shishido 1988). Much of the fishing during the summer months is done in near-shore coastal waters with gill nets and by angling. Year-to-year differences in the numbers of fish harvested by North Slope residents probably reflect variation in fish abundance and fishing effort (Craig 1989b).

The proportional contributions of different populations or stocks of Dolly Varden to the Beaufort Sea coastal fisheries are unknown. Although, char are typically found in the nearshore brackish waters close to their rivers-of-origin (Furniss 1975), numerous examples of extensive char movement have been documented (e.g., Glova and McCart 1974; Furniss 1975; Craig 1977; Underwood et al. 1995). Dolly Varden tagged in Beaufort Sea tributaries have been caught up to 300 kilometers away in coastal Native domestic fisheries (summarized in Craig and Haldorson 1981).

This paper describes the stock composition of Dolly Varden collections made from four widely separated locations along the Beaufort Sea coast in Alaska and Canada. Stock composition at each location was compared among different months within years, between years, and among the four sites. Mixed-stock analyses of allozyme data from coastal collections relied on baseline data of char stocks reported by Everett et al. (1997).

Methods

Sample collections. -- Dolly Varden from four sites along 400 km of Beaufort Sea coast were collected with fyke nets, except gill nets were used for the Mikkelsen Bay collection (Figure 1). At the Endicott Causeway (the most western location) near Prudhoe Bay, three collections were taken at approximately one-month intervals in 1987 and 1988. Near the Inupiat village of Kaktovik within the Arctic Refuge, collections were made in

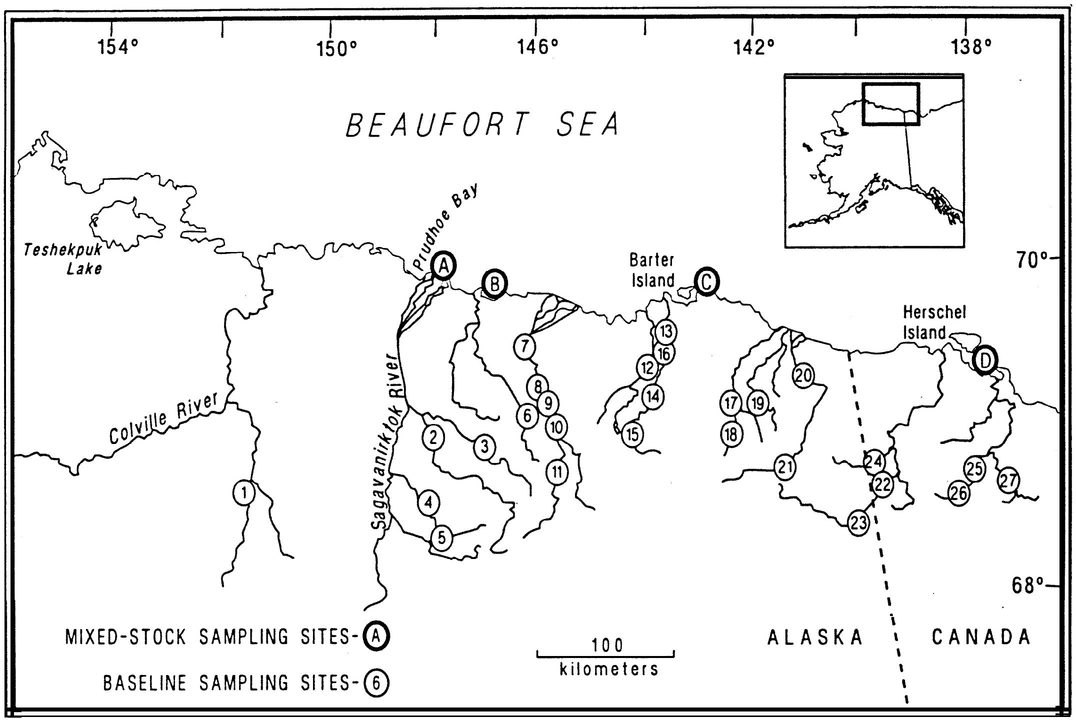

FIGURE 1. Sampling sites for Dolly Varden *Salvelinus malma* collected from Beaufort Sea coastal locations in 1987 and 1988. A = Endicott. B = Mikkelsen Bay. C = Kaktovik. D = Phillips Bay. Site numbers on tributary streams refer to collection locations of Dolly Varden that were used to generate the baseline data (Everett et al. 1997) and are listed in Table 1. Data from non-anadromous Dolly Varden were excluded from the baseline data (Shublik Spring 9-10; Sadlerochit Spring 12).

July and August of 1988. Single collections were made at Mikkelson Bay (between Endicott and Kaktovik) in August 1988 and at Phillips Bay (Canada) in September 1988. Baseline data were developed from collections of juveniles (pre-smolts) made at 27 sites on 11 North Slope tributaries that spanned approximately 600 km of Beaufort Sea coastline (Figure 1; Everett et al. 1997). Taxonomic designation of char as Dolly Varden followed that recommended by Reist et al. (1997).

Allozyme analysis. -- Electrophoretic procedures were described in Everett et al. (1997). Allozyme nomenclature used here follows that suggested by Shaklee et al. (1990). Twelve polymorphic loci were available for the mixed-stock collections (*sAH-1**, *GAPDH-3**, *GPI-B1,2**, *GPI-A1**, *mIDHP-1**, *sIDHP-1,2**, *LDH-C1**, *sMDH-A1,2**, *PGM-2**, *PGDH**, *sIDDH-1,2**, and *sSOD-1**).

Mixed-stock analyses. – Mixed-stock analysis (MSA) used the maximum likelihood procedures described by Pella and Milner (1987) as incorporated into the computer programs CONSQURT and SYMSQURT developed by personnel of National Marine Fisheries Service (Masuda et al. 1991). Isoloci were treated as one locus with four gene doses in the baseline and mixture data. MSA collections where data were missing for a locus (*GAPDH-3** data missing, Endicott July and September collections) were handled by the MSA program by simply analyzing them based on only the loci available. Bootstrap resampling was used to account for sampling error in both baseline and mixture sample data (Efron and Tibshirani 1986).

Baseline data used for MSA were configured based on the population structure described by Everett et al. (1997). Allelic frequency data for twelve baseline stocks were developed by combining data from the 27 collections as follows (site numbers in parentheses correspond to Figure 1): Anaktuvuk River (1), Sagavanirktok drainage - Ivishak and Echooka rivers (2-3), Sagavanirktok drainage – Ribdon and Lupine rivers (4-5), Kavik River (6), Canning River (7-8,10), Hulahula River (13-15), Hulahula (16), Aichilik River (17-18), Egaksrak River (19), Kongakut River (20-21), Firth River (22 and 24), and Babbage River (25 and 27). Data from non-anadromous Dolly Varden were excluded from the baseline data (Shublik Spring 9-10; Sadlerochit Spring 12; Firth River 23; Babbage River 26). Data from sites within systems were combined based on geographic proximity and non-significant differences in allelic frequencies tested by log likelihood ratio analyses (G-test; Sokal and Rohlf 1981).

Individual stock estimates from MSA of mixture samples were combined by summing estimates into three geographically broad stock groups. Stock groups were assembled based on a combination of geography and genetics. The western stocks (SAG) included char from the Anaktuvuk (Colville River drainage), Sagavarnirktok (tributaries), Kavik, and Canning rivers.

Dolly Varden from the Canning River, on the border of the Arctic Refuge, were assigned to the SAG group due to its genetic affinity with the Ivishak River (Sagavarnirktok River drainage) collection (Everett et al. 1997). The Arctic Refuge stock-group included char from the Hulahula, Aichilik, Egaksrak, and Kongakut rivers. The Canada stocks included char from the Firth and Babbage rivers. MSA estimates for individual stocks within the same stock group were added together, and the variances recalculated. Stock composition estimates were considered to be different from zero if an MSA estimate was not within two standard deviations of zero. Estimates by individual stock for each mixture sample are shown in Appendix 1.

Simulation analysis. -- The accuracy and precision of stock-group estimates were evaluated by MSA of simulated mixture samples constructed from the baseline data. Each simulation sample consisted of 200 individuals and was created from a single stock. Thus, twelve simulation samples representing each baseline stock were constructed. Each simulation sample was analyzed for its stock composition based on the 12 stocks in the baseline data set. Perfect MSA estimates of a simulation sample would equal 100% of the stock-group from which it was constructed.

To test the ability of MSA to correctly estimate the proportion of Canadian stocks in mixture samples, a series of hypothetical samples were generated from the baseline data with variable proportions of Canadian-origin fish. Samples were created composed of 0% to 100% Canadian-origin fish in 10% increments. Equal proportions of non-Canadian stocks in the baseline data made up the balance of these samples. The true proportions of Canadian-origin stocks were then plotted against MSA estimated proportions.

TABLE 1. – MSA estimates of 12 simulated Dolly Varden *Salvelinus malma* samples constructed from 100% of each of the 12 baseline stocks. Each row represents one simulation. A perfect MSA estimate would equal 100% for the stock group that originated the simulation sample. Numbers in parentheses under stock group refers to site numbers used in Figure 1 to identify locations where baseline samples were collected. Percentage MSA estimates are followed by standard deviations in parentheses.

Stock group Simulation samples	Percent by stock group SAG	 Arctic Refuge	 Canada
SAG Stocks			
Anaktuvuk (1)	97 (4.6)	0 (0.5)	3 (4.6)
Ribdon (4)/Lupine (5)	95 (4.8)	3 (3.9)	2 (3.5)
Ivishak (2)/Echooka (3)	94 (5.9)	4 (4.9)	2 (3.1)
Kavik (6)	94 (5.3)	4 (4.6)	2 (2.9)
Canning (7-8,11)	92 (6.4)	6 (6.0)	2 (2.8)
Arctic Refuge Stocks			
Hulahula-85 (13-15)	2 (2.7)	98 (2.8)	0 (0.5)
Hulahula-87 (16)	10 (9.6)	89 (9.5)	1 (1.4)
Aichilik (17-18)	6 (5.7)	93 (6.3)	1 (2.7)
Egagsrak (19)	7 (7.3)	93 (7.3)	0 (1.5)
Kongakut (20-21)	11 (8.7)	83 (10.0)	6 (6.7)
Canada Stocks			
Firth (22, 24)	7 (5.9)	5 (5.4)	88 (7.4)
Babbage (25, 27)	3 (3.3)	0 (1.0)	96 (3.3)

Results

Analysis of Simulation Samples

More than 88% of the fish in 11 of 12 simulation samples (perfect estimate = 100%) were attributed to the correct stock group (SAG, Arctic Refuge, or Canada; Table 1). MSA estimates of simulation samples were closer (≥ 92% attributed to SAG stock group) to the correct estimate of 100% than Arctic Refuge simulated samples (≥ 83%) or Canada samples (≥ 88%). Except for the simulated sample of Kongakut River fish, more than 89% of the samples created from Arctic Refuge stocks were attributed to the Arctic Refuge stock. The Kongakut River sample was incorrectly estimated to be composed of 11% SAG and 6% Canada stocks.

MSA of the 10% increment series of samples created from Canada stocks correctly identified each sample as Canadian stocks within 9% (Figure 2). Estimates were within 5% for samples with 10 to 70% Canadian-origin stocks. Overestimates of the percentage composition of the Canada stock group occurred when simulation samples were made up of low percentages of Canadian origin fish (< 20%). Underestimates occurred when samples were composed of high percentages of Canadian fish (> 40%).

Allelic Variation in Mixture Collections from Beaufort Sea Sites

Allelic variation was observed at each of the 12 allozyme loci in four or more collections of Dolly Varden collected from coastal sites (Table 2). No evidence for new alleles, not previously reported by Everett et al. (1997), was observed. Allelic variation at TPI-2* was observed in mixed-stock collections, but was not surveyed in baseline collections and therefore not included in the MSA.

Month and Year Comparisons

MSA estimates of Endicott samples taken in 1987 and 1988 did not differ greatly among months in terms of contributions from local SAG stocks (range 71 to 95%; Table 3; Figure 1). Contributions from non-local (>100 km distant) Canada and

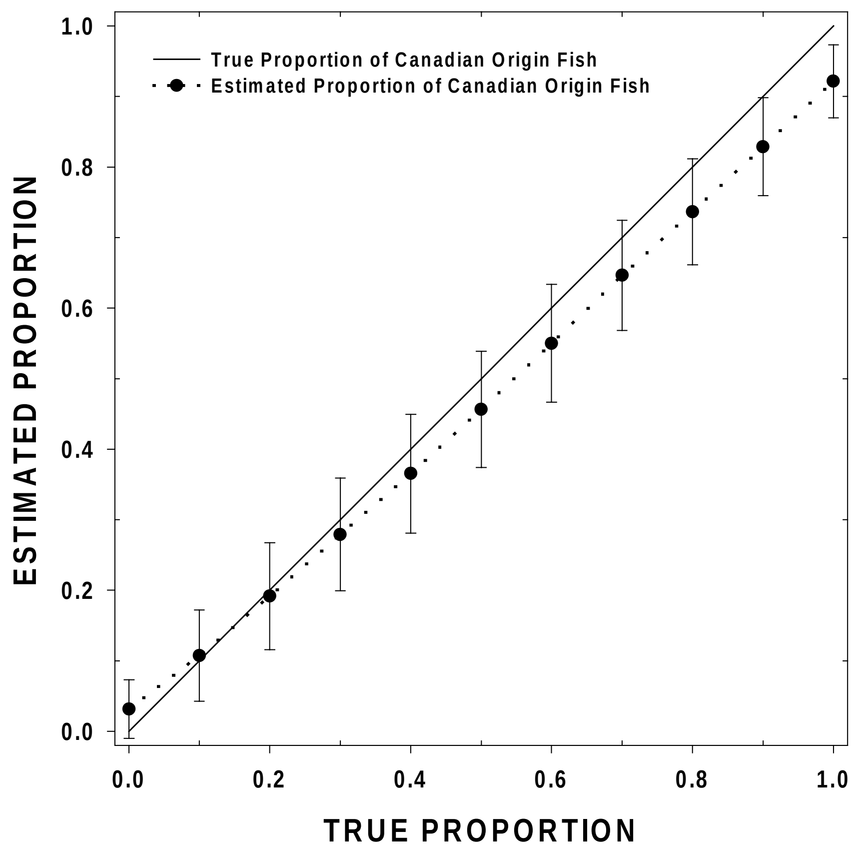

FIGURE 2. Known versus MSA proportions Dolly Varden *Salvelinus malma* stock composition of artificial simulation sample constructed from allozyme baseline data. MSA was performed on a series of simulation samples created with known percentages of Canadian-origin fish from 0% to 100% in 10% increments. Error bars around the estimates are one standard deviation.

TABLE 2. Allelic frequencies of 12 allozyme loci in the mixed-stock analyses of ten collections of Dolly Varden char from four Beaufort Sea coastal sites.

	*sAH-1**				*GPI-B1,2**			*GPI-A**		
Site	*N*	**100*	**115*	**130*	*N*	**100*	**55*	*N*	**100*	**96*
Endicott 1987										
June	207	0.568	0.191	0.241	206	0.978	0.022	206	0.769	0.231
July	123	0.480	0.228	0.292	125	0.984	0.016	124	0.790	0.210
September	164	0.564	0.186	0.250	166	0.985	0.015	165	0.773	0.227
Endicott 1988										
July	202	0.545	0.158	0.297	205	0.988	0.012	203	0.840	0.160
August	273	0.496	0.212	0.291	273	0.991	0.009	272	0.822	0.178
September	137	0.562	0.175	0.263	137	0.971	0.029	135	0.863	0.137
Mikkelsen Bay 1988	84	0.476	0.208	0.316	87	1.000	0.000	87	0.828	0.172
Kaktovik 1988										
July	199	0.580	0.181	0.239	200	1.000	0.000	199	0.819	0.181
August	178	0.562	0.222	0.216	178	0.994	0.006	177	0.833	0.167
Phillips Bay 1988	124	0.556	0.198	0.246	127	0.996	0.004	115	0.783	0.217

TABLE 2. Continued

	GAPDH-3*			mIDHP-1*			sIDHP-1,2*		
Site	*N*	**100*	**Null*	*N*	**100*	**220*	*N*	**100*	**80*
Endicott 1987									
June	191	0.992	0.008	195	0.982	0.018	208	0.993	0.007
July	0	--	--	119	0.958	0.042	126	0.988	0.002
September	0	--	--	166	0.970	0.030	166	0.994	0.006
Endicott 1988									
July	202	0.760	0.240	205	0.971	0.029	204	0.993	0.007
August	272	0.783	0.217	271	0.961	0.039	273	0.995	0.005
September	136	0.732	0.268	136	0.967	0.033	137	0.985	0.015
Mikkelsen Bay 1988	87	0.759	0.241	87	0.994	0.006	87	0.994	0.006
Kaktovik 1988									
July	194	0.621	0.379	200	0.995	0.005	200	0.978	0.022
August	177	0.599	0.401	178	0.989	0.011	178	0.972	0.028
Phillips Bay 1988	123	0.768	0.232	124	0.988	0.012	126	0.944	0.056

TABLE 2. Continued

	LDH-C*			sMDH-A1,2*			PGM-2*		
Site	*N*	**100*	**97*	*N*	**100*	**128*	*N*	**100*	**88*
Endicott 1987									
June	205	0.985	0.015	208	0.993	0.007	206	0.951	0.049
July	121	0.996	0.004	125	1.000	0.000	125	0.968	0.032
September	165	0.982	0.018	166	0.997	0.003	165	0.958	0.042
Endicott 1988									
July	205	0.978	0.022	203	0.995	0.005	205	0.990	0.010
August	272	0.978	0.022	273	0.993	0.007	273	0.995	0.005
September	137	0.938	0.062	136	1.000	0.000	137	1.000	0.000
Mikkelsen Bay 1988	87	0.989	0.011	87	1.000	0.000	87	1.000	0.000
Kaktovik 1988									
July	200	0.985	0.015	200	1.000	0.000	200	0.995	0.005
August	178	0.994	0.006	178	1.000	0.000	178	1.000	0.000
Phillips Bay 1988	127	0.949	0.051	127	1.000	0.000	127	1.000	0.000

TABLE 2. Continued

	*PGDH**			*sIDDH-1,2**			*sSOD-1**			
Site	*N*	*100	*95	*N*	*100	*43	*N*	*100	*115	*87
Endicott 1987										
June	208	0.993	0.007	155	0.935	0.065	208	0.954	0.046	0.000
July	122	1.000	0.000	122	0.967	0.033	126	0.956	0.044	0.000
September	166	0.985	0.015	165	0.952	0.048	166	0.958	0.042	0.000
Endicott 1988										
July	205	1.000	0.000	201	0.943	0.057	205	0.956	0.027	0.017
August	273	0.996	0.004	273	0.952	0.048	272	0.943	0.031	0.026
September	137	0.993	0.007	134	0.918	0.082	137	0.953	0.033	0.014
Mikkelsen Bay 1988	87	1.000	0.000	87	0.943	0.057	87	0.948	0.017	0.035
Kaktovik 1988										
July	200	1.000	0.000	199	0.950	0.050	200	0.880	0.073	0.047
August	178	1.000	0.000	178	0.944	0.056	178	0.902	0.048	0.050
Phillips Bay 1988	127	1.000	0.000	121	0.971	0.029	118	0.945	0.021	0.034

Arctic Refuge stocks were not different from zero in 1987 but contributions from Canada stocks were so in July (17%) and August (20%) of 1988.

Mixture samples from the Kaktovik area in 1988 were different between months in terms of contributions from non-local SAG stocks (July 7% and August 27 %; Table 3). Significant contributions were made to these samples both months from Canada (25 and 17%) and local Arctic Refuge stocks (68 and 56%).

Stock-group estimates from the Endicott area were different between collections made in 1987 and 1988 (Table 3). In 1987, the estimated contribution from local SAG stocks to the collections were slightly higher (mean 87%; range 82-95%) than in 1988 (mean 76%; range 71-85%). Contributions from the Arctic Refuge remained similar in 1987 and 1988. Canada stocks contributed much less in 1987 (mean 6%; range 1-14%) than in 1988 (mean 16%; range 10-20%).

Comparison Among Sample Locations

The largest estimated stock-group contribution to the coastal collections typically came from local stocks near the sample site (Table 3). However, most collections were also estimated to have significant contributions from non-local stocks. One notable exception was the 1987 Endicott collections, with estimated contributions of non-local Arctic Refuge and Canada stocks not different from zero. Also, non-local stocks contributed 65% to the Philips Bay collection in Canada. MSA estimated this collection to contain nearly equal percentages of Canada (35%), Arctic Refuge (34%), and SAG stocks (31%).

Significant contributions from Canada stocks were estimated at all collection locations in the U.S. (Table 3). When MSA estimates were pooled by year, Canadian-origin char contributed 9% (SD = 6.9%) to the 1987 collection (U.S. origin fish = 91%; SD = 6.9%) and 20% (SD = 6.1%) to the 1988 collection (U.S. origin fish = 80%; SD = 6.1%)

Discussion

One or more mixture collections from each of the four Beaufort Sea coastal sites contained significant contributions from distant (100-350 km), non-local stocks. Substantial variation in stock contributions was observed among months, and between 1987 and 1988 in Endicott collections, near Prudhoe Bay. These results suggest substantial movement along the Beaufort Sea coastline of Dolly Varden away from rivers of natal origins. Underwood et al. (1995) reported the long distance movement of char marked in Arctic Refuge coastal waters to locations to the east in Canada and west to Simpson Lagoon (20 km west of Prudhoe Bay). Similarly, fish tagged in the Firth River (Canada) were recaptured west of the Arctic Refuge in the Canning River (Craig and McCart 1975) and in the Arctic Refuge coastal waters (Craig and McCart 1976).

Extensive movements of Dolly Varden have been reported for populations southwest of our Beaufort Sea study region. DeCicco (1997) reported tag recoveries from more than 4,000 char tagged in tributaries to Kotzebue Sound of the Chukchi Sea. One fish tagged in the Noatak River system was recaptured 485 km away at Point Hope one year later. Dolly Varden tagged in the Wulik River were later recaptured in the Kobuk River (150 km), Norton Sound (570 km), and near St. Lawrence Island (530 km). Three Dolly Varden tagged in the Wulik River were recaptured in the Anadyr (two fish) and Margje rivers (one fish), Russia. The two char recaptured in the Anadyr River had traveled more than 540 km upstream, and were more than 1,560 km from the Wulik River in Alaska (DiCicco 1992, 1997).

Transboundary movement of char between Canada and the U.S. was clearly indicated by the MSA estimates of collections from all four sites (Table 3). A large percentage (65%) of U.S. stocks was estimated in the Phillips Bay (Canada) collection. Canada stocks contributed 20% to an Endicott (U.S.) collection and 25 % to the Mikkelsen Bay and Kaktovik-July samples. The results from the simulation analysis indicated high levels of accuracy for estimating proportions of Canada stocks (< 9% error), which provided further confidence in our MSA estimates of field collections. The presence of Canadian-origin Dolly Varden in U.S. waters has been reported based on tag returns (described above). Our MSA results now provide a percentage estimate for this presence of char from Canada. We conclude that Canada stocks are an important origin of char that use the Beaufort Sea coastal waters of the U.S. during the summer. Similarly, U.S. stocks from Arctic Refuge populations can comprise a large proportion of Dolly Varden that use coastal waters in Canada.

TABLE 3. Estimated stock composition from MSA of collection of Dolly Varden *Salvelinus malma* from coastal areas of northern Alaska and Canada. Individual estimates were summed into stock groups (SAG = stocks from Anaktuvuk, Sagavanirktok, Kavik, and Canning rivers; Arctic Refuge = Arctic National Wildlife Refuge rivers; Canada = stocks from the Firth and Babbage rivers). * Indicates MSA estimates more than two standard deviations from zero.

	Percent by stock group					
	SAG		Arctic Refuge		Canada	
Coastal Site	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Endicott 1987						
June	95*	11.1	4	9.0	1	4.6
July	82*	12.6	4	7.2	14	9.5
September	85*	11.7	12	9.1	3	6.6
Endicott 1988						
July	71*	9.7	12	7.3	17*	6.9
August	72*	9.0	8	6.5	20*	6.0
September	85*	10.4	5	8.9	10	5.3
Mikkelsen Bay 1988	52*	14.6	23*	11.3	25*	8.6
Kaktovik 1988						
July	7	10.4	68*	10.1	25*	5.0
August	27*	11.9	56*	11.0	17*	4.6
Phillips Bay 1988	31*	13.8	34*	11.8	35*	9.8

Management Implications

Dolly Varden that use the coastal areas of the Beaufort Sea in Alaska and Canada provide several classic fish management challenges:

- multiple genetic stocks,
- dependency on geographically discrete specialized habitats,
- mixtures of stocks vulnerable to fisheries,
- movement across international boundaries,
- multi-jurisdictional management authority (aboriginal claims, state, federal), and
- proposed regional economic development activities.

These characteristics pose a distinct challenge to effective fisheries management, as illustrated by the past failure of Pacific salmon management at some locations (e.g., National Research Council 1996). To meet this challenge, management of Dolly Varden should not be based solely on single river systems but should include multiple river systems within an area at least as large as this study used (~350 km coastline).

Populations affected by local, site-specific development activities in one region could have a widespread effect on abundance of Dolly Varden in coastal areas during the summer. For example, oil and natural gas exploration and development activities in localized areas could reduce the quality and quantity of critical over-wintering and spawning habitats for Dolly Varden. Reduced over-wintering stream habitats would affect Dolly Varden from numerous stocks because non-spawning fish often use non-natal streams as overwintering locations (e.g., Craig 1977, 1989a). Though such habitat degradation would be site specific, environmental and fishery impacts to populations could be widespread. Even more serious, damage to spawning habitats in streams could cause the reduction or extinction of local populations. Extinction would result in a permanent loss of genetic diversity for this species. In addition, these populations' contribution to coastal waters during summer months would decline and coastal fisheries affected.

Development activities and fish management in the study area must consider the principal subsistence fishery near the Inupiat village of Kaktovik. This fishery occurs primarily in the coastal waters near Barter Island in the Arctic Refuge (Craig 1989b). Tagged Dolly Varden caught in this fishery have come from fish marked in the Sagavanirktok and Canning rivers to the west and the Firth River in Canada (Craig and McCart 1976; Craig 1989b). Our study provided evidence that as much as 35% of the catch could be from non-Arctic Refuge stocks, with significant proportions coming from Canadian sources. Further oil development in the Prudhoe Bay area or new oil and gas development activities in Canada must assess not only local environmental impacts on char populations but also the potential effects on this subsistence fishery more than 150 km away.

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APPENDIX 1. Stock composition estimates of the North Slope Dolly Varden *Salvelinus malma* mixed fishery samples, 1987 and 1988.

	Endicott-1987						Kaktovik-1988			
	June		July		September		July		August	
Site	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Anaktuvuk	0.19	0.080	0.14	0.085	0.03	0.040	0.00	0.031	0.00	0.018
Ivishak/Echook	0.07	0.140	0.00	0.147	0.47	0.156	0.07	0.077	0.17	0.118
Ribdon/Lupine	0.44	0.084	0.32	0.108	0.35	0.085	0.00	0.034	0.02	0.027
Kavik	0.03	0.026	0.03	0.043	0.00	0.010	0.01	0.021	0.00	0.042
Canning	0.22	0.154	0.27	0.164	0.00	0.461	0.00	0.095	0.08	0.152
Hulahula-1985	0.00	0.003	0.00	0.021	0.00	0.023	0.07	0.091	0.04	0.086
Hulahula-1987	0.04	0.078	0.06	0.059	0.10	0.077	0.49	0.154	0.24	0.152
Aichilik	0.00	0.015	0.03	0.039	0.00	0.014	0.02	0.037	0.10	0.058
Egaksrak	0.00	0.052	0.00	0.020	0.02	0.063	0.09	0.121	0.17	0.133
Konkakut	0.00	0.034	0.00	0.022	0.00	0.029	0.00	0.023	0.00	0.028
Firth	0.00	0.010	0.00	0.059	0.03	0.040	0.00	0.012	0.00	0.006
Babbage	0.00	0.046	0.14	0.083	0.00	0.053	0.25	0.049	0.17	0.046

APPENDIX 1. Continued.

	Endicott-1988						Mikkelsen Bay-1988		Phillips Bay-1988	
	July		August		September		August		September	
Site	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Anaktuvuk	0.13	0.061	0.09	0.056	0.06	0.071	0.00	0.077	0.00	0.026
Ivishak/Echook	0.40	0.153	0.43	0.149	0.61	0.181	0.01	0.153	0.25	0.122
Ribdon/Lupine	0.17	0.070	0.20	0.071	0.18	0.074	0.05	0.055	0.05	0.081
Kavik	0.14	0.048	0.00	0.006	0.00	0.031	0.03	0.035	0.00	0.044
Canning	0.04	0.127	0.00	0.140	0.00	0.126	0.63	0.219	0.00	0.074
Hulahula-1985	0.00	0.024	0.00	0.028	0.00	0.009	0.00	0.026	0.00	0.012
Hulahula-1987	0.00	0.069	0.03	0.034	0.00	0.059	0.00	0.073	0.00	0.060
Aichilik	0.12	0.012	0.01	0.021	0.05	0.043	0.00	0.000	0.21	0.092
Egaksrak	0.00	0.042	0.03	0.053	0.00	0.053	0.02	0.096	0.13	0.091
Konkakut	0.00	0.022	0.00	0.031	0.00	0.044	0.00	0.030	0.00	0.093
Firth	0.04	0.054	0.02	0.043	0.00	0.019	0.01	0.053	0.11	0.083
Babbage	0.13	0.050	0.18	0.047	0.10	0.051	0.25	0.080	0.25	0.070