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Overwintering Patterns of Dolly Varden, *Salvelinus malma,* in the Sagavanirktok River in the Alaskan North Slope Inferred Using Mixed-Stock Analysis

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Overwintering Patterns of Dolly Varden *Salvelinus malma* in the Sagavanirktok River in the Alaskan North Slope Inferred Using Mixed-Stock Analysis

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Abstract

Tagging data from previous studies indicate that anadromous Dolly Varden, *Salvelinus malma,* in the North Slope of Alaska use their natal drainage for both spawning and overwintering. This differs from other regions of the state where Dolly Varden overwinter in mixtures comprising stocks from multiple drainages. We used mixed-stock analysis to estimate the origin of overwintering Dolly Varden sampled from the Ivishak River, a tributary of the Sagavanirktok River, which drains into the Beaufort Sea. Our objective was to use mixed-stock analysis to test whether Dolly Varden show philopatry to their natal drainage to overwinter, as suggested by tagging data, and to determine if the extent of mixing differs between two maturity/size classes. We assayed genetic variation at seven microsatellite loci in 10 populations from six drainages on the North Slope and used these data to estimate the contribution of North Slope drainages to predominantly immature (200–400 mm fork length (FL)) and predominantly mature (>400 mm FL) Dolly Varden. Our results indicate that mature fish comprise Dolly Varden originating from the Sagavanirktok drainage, but that 10% of the immature sample originated from the Canning River and 4% from the Anaktuvuk River. These data support previous tagging studies indicating interdrainage exchange in Dolly Varden for overwintering is rare and underscore the importance of natal drainages for all freshwater life history stages for Dolly Varden in North Slope streams.

Introduction

In the North Slope of Alaska, anadromous Dolly Varden, *Salvelinus malma,* use coastal streams between the Colville River and the US/Canada border for both spawning and overwintering (Figure 1). These streams originate in the Brooks Range. Flow is due to surface runoff with maximum discharge in the spring from snow melt (Craig and McCart 1975). Streams may cease to flow in late fall and winter. During the winter, streams freeze to a depth of about 2 m, reducing stream habitat by 95% (Craig 1989a). Therefore, both spawning and overwintering in these streams is restricted to spring fed areas which flow year round (Craig and McCart 1976; Craig 1989a). It is, therefore, generally regarded that Dolly Varden popu-

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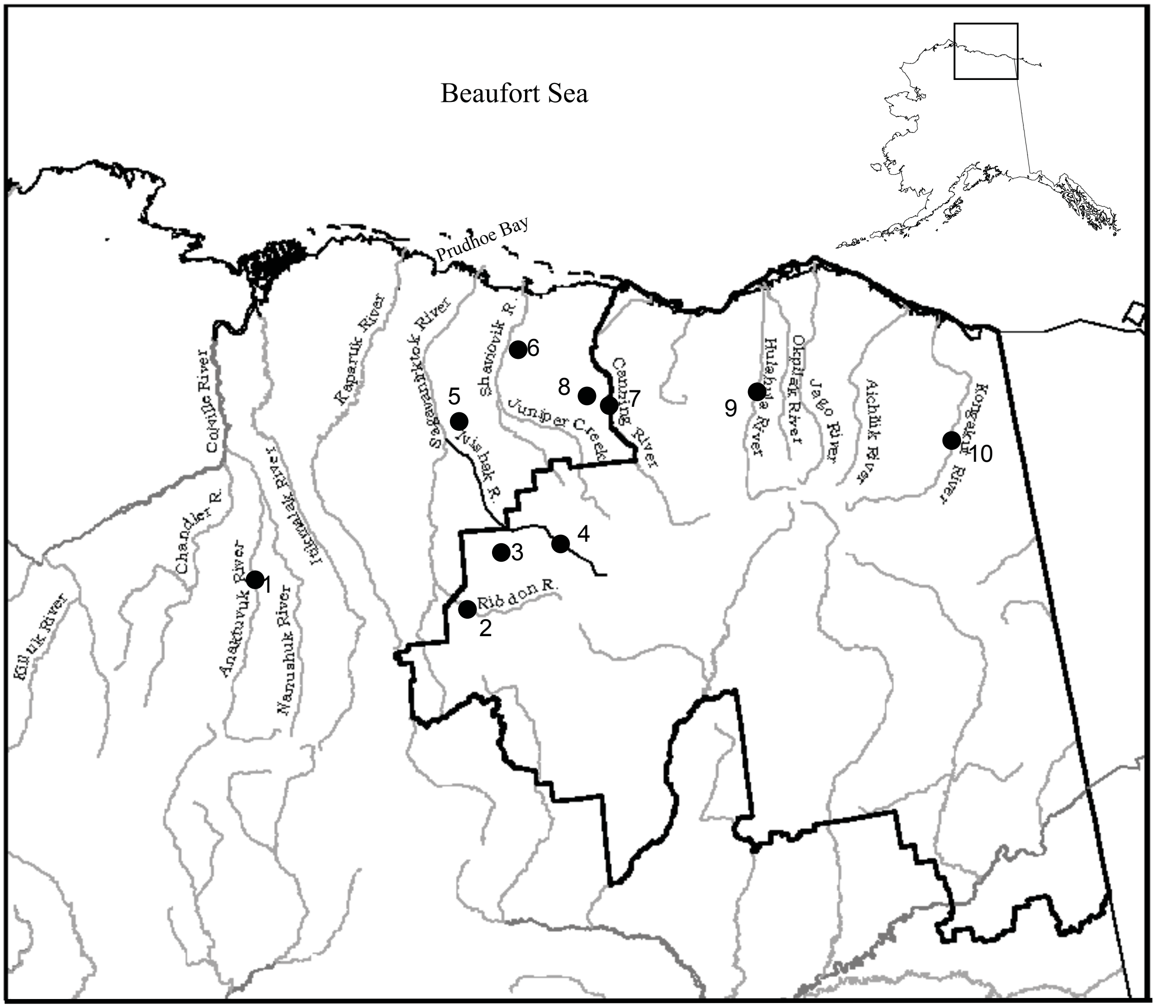

Figure 1. Sampling locations of Dolly Varden collected in Beaufort Sea drainages and surveyed for genetic variation at microsatellite loci. The dark lines indicate the borders of the Arctic National Wildlife Refuge. Numbers correspond to collection locations described in Table 1.

lations on the North Slope are limited by the availability of overwintering habitat (e.g., Power 1997).

Tagging studies conducted on anadromous Dolly Varden throughout Alaska show that Dolly Varden home to their natal streams to spawn (e.g., Armstrong and Morrow 1980; Bernard et al. 1995; DeCicco 1997; Lisac and Nelle 2000). These studies also illustrate that overwintering areas are used by stocks from multiple drainages and overwintering behavior varies greatly from region to region. For example, southern form Dolly Varden, *S. m. lordi*, distributed from the Southeast Alaska panhandle to the Alaska Peninsula, use lakes when overwintering in freshwater, but can also remain at sea in winter (Bernard et al. 1995). When southern form Dolly Varden return to freshwater to overwinter, they show philopatry to the lacustrine watershed used in previous years. Overwintering areas are utilized by stocks from multiple drainages and are not too distant from spawning areas (Armstrong and Morrow 1980; Bernard et al. 1995). Northern form Dolly Varden, *S. m. malma*, distributed from the Alaska Peninsula to the Mackenzie River in Canada, also overwinter in mixed-stocks, but differ from the southern form in that they overwinter in river mainstems or spring areas, do not show philopatry to overwintering sites, and may undertake more extensive migrations between overwintering and spawning areas. For example, Dolly Varden overwintering in the Wulik River north of Kotzebue Sound have later been recovered in other Kotzebue Sound drainages, Norton Sound, St. Lawrence Island, and several locations in the Russian Far East (DeCicco 1997).

The life history of anadromous Dolly Varden on the North Slope of Alaska is similar to Dolly Varden in other regions of the state in that spawning occurs in natal areas (e.g., Furniss 1975), but differs in that overwintering aggregates may not comprise stocks from multiple drainages (Furniss 1975; Craig and McCart 1976). Only four Dolly Varden tagged in the Sagavanirktok, Kavik, Canning, and Firth rivers during extensive tagging studies in 1972 to 1973 were recovered in drainages other than where they were tagged. Craig (1989a) argued that there maybe little flexibility in fall migration patterns and selection of overwintering habitat, an adaptation to the drastic reduction of habitat available in winter and the precise timing necessary to find overwintering habitat before stream beds dry or freeze. Conversely, interdrainage exchange may be more common than these studies suggest; the few instances detected of interdrainage exchange may be due to sampling bias because the majority of recapture efforts were conducted in the streams where Dolly Varden were originally tagged (Craig and McCart 1976).

An understanding of overwintering ecology is essential to Dolly Varden management and conservation. First, Dolly Varden, along with whitefish, *Coregonus sp.*, are the most ubiquitous species in the Alaskan Arctic (Craig and McCart 1976). Dolly Varden comprise 45% of the sport fish harvest in the region (Burr 2004) and are an important subsistence resource for residents of Kaktovik, Nuiqsut, and Anaktuvuk Pass (Craig 1989b; Alaska Department of Fish and Game 2001). Second, documentation of current patterns of overwintering are important to evaluate potential effects on Dolly Varden populations due to the affects of oil and gas exploration, increased sport fishing pressure, or of climate change which is predicted to have the most extreme effects at high latitudes (Rhydderch 2001; Burr 2004).

Because natal homing leads to genetic differences among spawning aggregates, mixed-stock analysis methods (MSA) have been used to estimate migration patterns and gene flow for Dolly Varden on the Alaskan and Yukon North Slope. Everett et al. (1997) found significant variation at allozyme loci among Dolly Varden sampled from drainages distributed from the Colville River in Alaska to the Firth River in Canada. Krueger et al. (1999) used these data to estimate the nearshore migration patterns of Dolly Varden stocks in the Beaufort Sea. Rhydderch (2001) used individual-based analyses to evaluate the extent of isolation among anadromous, stream resident, and above-barrier isolate forms and between immature and mature life history stages in Dolly Varden from the Firth River in the Yukon North Slope.

In this study, we surveyed genetic variation of Dolly Varden from six drainages in the North Slope at seven microsatellite loci and used MSA to estimate the contribution of six North Slope drainages to Dolly Varden sampled from overwintering aggregates in the Ivishak River in 2003. The Ivishak River, a tributary of the Sagavanirktok River (Figure 1), is the largest overwintering area for Dolly Varden in the Alaskan North Slope with annual aerial survey estimates ranging from 8,000 to 26,000 (Arvey 1991). Our objectives were to quantify stock contributions to test 1) whether Dolly Varden show philopatry to their natal drainage as suggested by tagging data, and 2) for potential differences in stock composition between two maturity/size classes of Dolly Varden. Dolly Varden sexually mature only after 3–5 seaward migrations and may be more likely to disperse greater distances and utilize overwintering areas not in their drainage of origin before sexual maturity (DeCicco 1997). Our results indicate that predominantly mature fish >400 mm fork length (FL) are largely from the Sagavanirktok drainage, but that immature fish 200–400 mm are a mixture of Anaktuvuk (4%), Sagavanirktok (80%), and Canning River (10%) fish. These results hint that overwintering movements may differ between immature and mature Dolly Varden and underscore the dependency of North Slope Dolly Varden populations on their natal drainage for all portions of their freshwater life history and the critical nature of spring habitat in this region.

Methods

Sample collection

Baseline samples—Fin tissue was collected from Dolly Varden at 10 locations in drainages of the Alaskan North Slope (Table 1, Figure 1). Fin tissue was taken from prespawning adults, recently emerged young-of-the-year, and juveniles. Prespawning adults were collected by seine net or hook-and-line in spawning areas. Young-of-the-year and juvenile fish were captured using baited minnow traps or small dip nets in spawning areas which also serve as

Table 1. Collection location, date, sample size (*N*), and life history stage for Dolly Varden sampled for genetic analysis on the North Slope, Alaska.

Location	Date	*N*	Life history
Colville River			
Anaktuvuk River	July12–14, 2002	227	YOY, J
Sagavanirktok River			
Ribdon River	September 17–20, 2002	25	A
	September 17, 2003	6	A
		58	J
Saviukviayak River	September 15–23, 2001	55	A
	September 16, 2003	45	A
Ivishak River	September 21, 2000	101	A
	September 19, 2003	26	A
Echooka River	September 19, 2001	94	A
Kavik River	September 18–21, 2002	100	A
Canning River			
Main Fork	31 July 2002	150	J
Marsh Fork	29 July 2002	150	J
Hulahula River	August 4–7, 2004	200	J
Kongakut River	August 17–18, 2000	72	A
		23	J

juvenile rearing habitat (Yoshihara 1974, Furniss 1975). Possible family effects of sampling young-of-the-year and juveniles (Allendorf and Phelps 1981) were minimized by sampling at multiple locations in rearing areas within a given stream. Fin clips were stored in individually labeled vials with 90% ethanol.

Mixture samples—Fin clips were collected from 500 Dolly Varden captured in the Ivishak River using seine nets from 14 September to 21 September 2003. Dolly Varden were sampled from an area between Echooka River and Flood Creek. This site is the largest overwintering area for Dolly Varden in the Alaskan North Slope and is spatially separated from spawning areas further upstream (Furniss 1975). Fork lengths of sampled fish were measured to the nearest 5 mm.

Laboratory analysis

Total genomic DNA was isolated from fin tissue using the Qiagen 96-well Dneasy® procedure. Individuals were assayed for genetic variation at seven microsatellite loci developed for Dolly Varden: *Sma-3*, *-5*, *-10*, *-17*, *-21*, *-22*, *-24* (Crane et al. 2004). PCR amplification of microsatellite loci was carried out in 10µl reaction volumes: approximately 100ng DNA, 1.5 mM $MgCl_2$, 8mM dNTPs, 0.5 U Taq DNA polymerase (Promega), 0.4uM unlabeled/labeled forward primer, and 0.4uM reverse primer, using an MJResearch™ DNA Engine™ PCT-200. Cycling conditions were 2 min at 92°; 30 cycles of 15 sec at 92°, 15 sec at T_a, and 30 sec at 72°; with a final extension for 10 min at 72°. Annealing temperatures (T_a) were 55° for *Sma-5*, *-10*, and *-22*; 56° for *Sma-17* and *-21*; and 58° for *Sma-3*. Microsatellites were separated on 64-well denaturing polyacrylamide gels and visualized and scored using a Li-Cor IR2® scanner with Li-Cor Saga™ GT ver 2.0 software (Lincoln, NE). Li-Cor 50–350bp or 50–500 size standards were loaded in the first and last lanes and at intervals of 14 lanes or less across each gel. Positive controls, consisting of 2–10 alleles of predetermined size, were loaded in three lanes distributed evenly across the gels to ensure consistency of allele scores. Two researchers scored alleles independently. Samples with score discrepancies between researchers were re-amplified at the loci in question and rescored.

Statistical Analysis

Population analysis and evalution for MSA—Unless noted, all calculations were made using FSTAT version 2.9.3 (Goudet 2001). Allele frequencies were calculated for each collection and homogeneity of allele frequencies between samples collected in the same tributary in different years were compared using likelihood ratio statistics. Significance of the likelihood ratio statistic was evaluated using a randomization test through 1820 permutations of genotypes between samples. Samples were pooled if no significant differences were detected after adjusting for four multiple tests using the sequential Bonferroni technique (Rice 1989).

Observed and expected heterozygosities and allele richness (number alleles observed per locus corrected for sample size) were used to describe within-sample diversity. For each locus in each collection, deviation of genotypic frequencies from Hardy-Weinberg expectation was evaluated by testing for a deficit of heterozygotes, $F_{IS}>0$. Significance was assessed by 1400 permutations of alleles among individuals within samples; *P*-values over all loci were calculated according to Goudet (2001). Conformation to Hardy-Weinberg expectation was evaluated by adjusting the table-wide α=0.05 for 10 multiple tests using the sequential Bonferroni technique (Rice 1989).

Homogeneity of allele frequencies among locations was tested using likelihood ratio statistics, and the significance was evaluated using a randomization test through 900 permutations of genotypes between samples. *P*-values were adjusted for four multiple comparisons using the sequential Bonferroni technique. F_{ST} was computed to quantify the amount of population subdivision following the method of Weir and Cockheram (1984). A randomization-based test was used to determine if F_{ST} was greater than zero with the null distribution created through 1000 permutations of genotypes among populations.

Cavalli-Sforza & Edwards (CSE; 1967) chord distances were calculated from allele frequencies between all pairwise combinations using MSA (Dieringer and Schlötterer 2003). Genetic similarity among collections was visualized using a UPGMA phenogram.

Maximum likelihood estimation of artificial mixtures was used to determine population groupings of Dolly Varden from the North Slope that can be reliably identified in mixtures. Prior to the simulation analysis, alleles in the baseline populations were binned using the program OptiBin (Bromaghin and Crane, In press) to reduce the effects of sampling error and rare alleles. Briefly, for each locus, bins were determined by using exact tests of homogeneity to test if allele pairs were similarly distributed across populations along with Monte Carlo simulation to estimate significance. Log-likelihood ratios were used as the test statistic and the binning procedure executed until $P<0.25$.

The program SPAM version 3.7 (Debevec et al. 2000; Alaska Department of Fish and Game, Gene Conservation Laboratory, available at http://www.cf.adfg.state.ak.us/geninfo/research/genetics/software) was used for the simulation analysis. For each population, 1000 artificial mixtures of 400 genotypes were randomly constructed using Hardy-Weinberg expectations from the baseline allele frequencies. Conditional maximum likelihood estimates and 90% symmetric confidence intervals of the mixture compositions were estimated for the mixtures using randomly resampled baseline allele frequencies to account for sampling error in the baseline. Bayesian estimates of baseline allele proportions (Rannala and Mountain 1997) were used to further reduce the effects of sampling error in the baseline allele frequencies. Mean contribution estimates for the population under study should approximate 100%. Populations were aggregated until mean contribution estimates exceeded 90%, generally considered extremely robust for mixture analysis (Teel et al. 1999; Kondzela et al. 2002).

MSA of Overwintering Samples—One hundred fifty Dolly Varden each were randomly subsampled from the total number of fish collected from overwintering aggregates in the Ivishak River in 2003 for two size classes (200–400 mm, predominantly immature fish that have completed at least one seaward migration; >400 mm, predominantly mature fish that have spawned or will spawn in the following year; Yoshihara 1974) for genetic analysis. Markov chain Monte Carlo samples of stock proportions were generated for Anaktuvuk, Sagavanirktok-Ribdon, Sagavanirktok-Ivishak tributaries, Kavik, Canning, Hulahula, and Kongakut rivers for the two size classes to determine the proportion of non-Sagavirktok stocks and if greater mixing is present in the predominantly immature sample. The initial proportion for the chains (N=5,000) for a given regional group were 95%, with the 5% distributed evenly among the remaining six groups. Values for genetic prior parameters were determined as described in Pella and Masuda (2001). The Rafferty and Lewis (1996) diagnostic was used to verify that chain lengths were sufficiently long. Convergence was determined using the Gelman and Rubin (1992) diagnostic. The mean, standard deviation, and posterior quantiles of sample stock composition estimates were generated after a burn-in of 2,500 samples.

Results

Population analysis and evaluation for MSA

All seven loci were polymorphic in all collections with the exception of *Sma-5* (Appendix 1). The number of alleles observed at each variable locus ranged from 3 to 40 (Appendix 1). No allele frequency heterogeneity was detected between collections made in different years from the Ivishak River 2000 and 2003 (P=0.7445), Saviukviayak River 2001 and 2003 (P=0.0385), and Ribdon River 2002 and 2003 (P=0.0621) or between Kongakut River adult and juvenile collections (P=0.9357), after adjusting for four multiple tests. Therefore, duplicate collections at these sites were pooled for subsequent analyses.

Mean expected heterozygosities ranged from 0.60 in the Ribdon River to 0.65 in the Kongakut River (Appendix 1). Allele richness ranged from 8.7 in the Anaktuvuk River to 12.8 in the Ivishak River (Appendix 1). When adjusted for multiple tests, two significant deviations of genotypic frequencies from Hardy-Weinberg expectation were detected for the Kongakut River and Main Fork Canning River (P=0.007).

Significant differences in allele frequencies were detected among all pairwise combinations of populations (P<0.001). F_{ST} among all populations was 0.03 (P<0.0001). Genetically similar populations in the UPGMA phenogram tended to be populations that are geographically adjacent (Figure 2). Two exceptions were the Ribdon River, which did not group with other populations from the Sagavanirktok drainage (Ivishak, Saviukviayak, and Echooka rivers), and the Kavik River.

In simulation experiments, mean contribution estimates for mixtures composed of artificial genotypes from tributaries exceeded 90%, with the exception of the Main and Marsh forks of the Canning River (87% and 85%, respectively), and the Ivishak, Saviukviayak, and Echooka rivers (82%, 86%, and 87%, respectively). Misallocation for the Main and Marsh Forks was within the Canning River, and similarly, misallocation for the Ivishak, Saviukviayak, and Echook rivers was within these three Ivishak River sites. When simulations were conducted with a Canning River stock aggregate and an Ivishak tributaries stock aggregate, all mean contribution estimates exceeded 90% (Figure 3).

Mixed-stock analysis

The mean FL of 300 Dolly Varden randomly sampled for stock composition estimates was 344 mm (range: 245–829 mm; see Figure 4 for a length frequency histogram of all samples). Markov chain Monte Carlo estimates of stock contributions indicated that the majority of samples >400 mm FL originated from the Sagavanirktok River (Ivishak tributaries=0.94, S.D.=0.05; Table 2). The majority of the immature samples <400 mm FL originated from the Sagavanirktok River (Ivishak tributaries=0.68, S.D.=0.07 and Ribdon River=0.13,

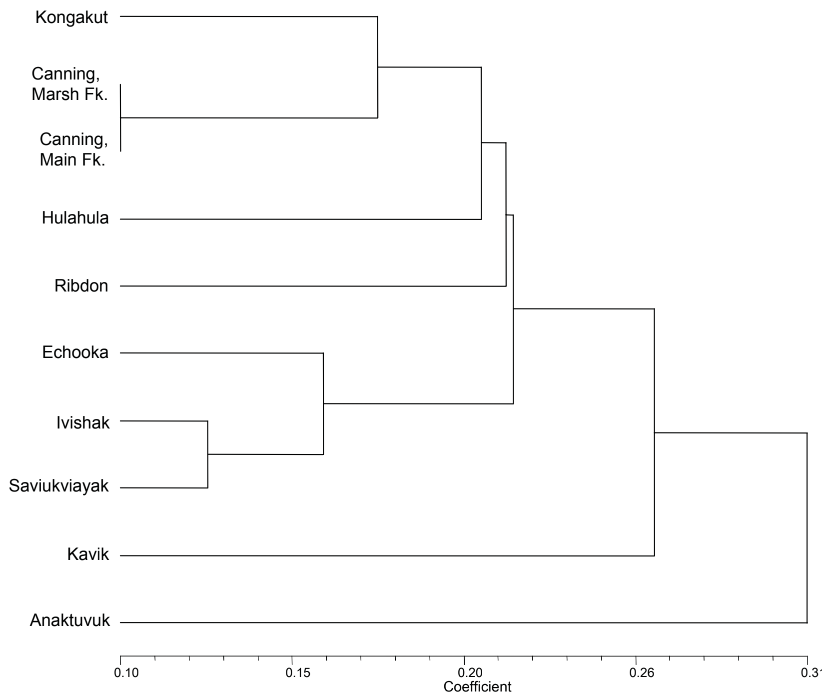

Figure 2. UPGMA phenogram of genetic similarity among Dolly Varden populations sampled from the North Slope, Alaska.

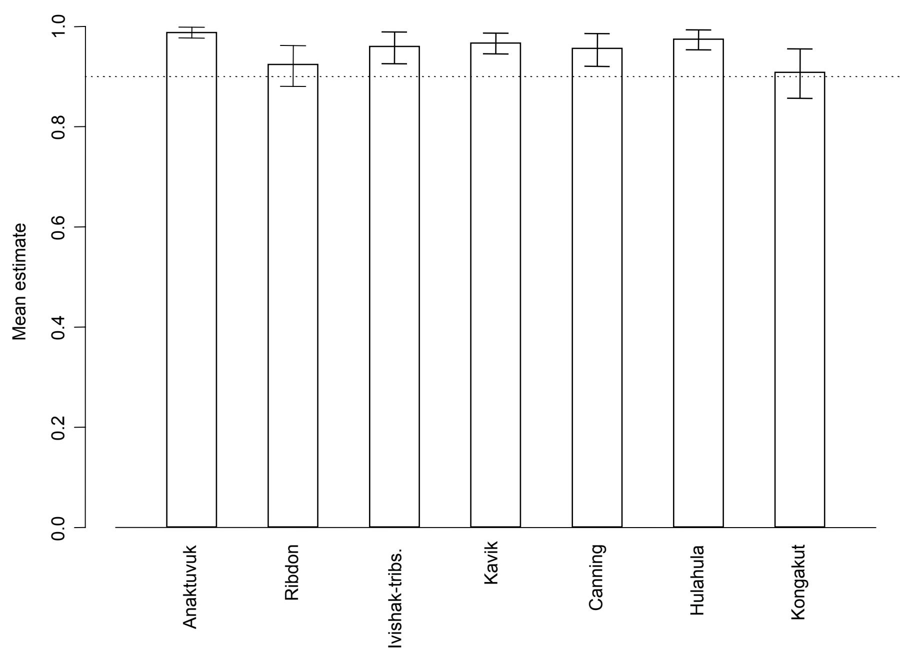

Figure 3. Mean conditional maximum likelihood estimates and 90% symmetric confidence intervals of stock contributions to mixtures comprised of randomly generated genotypes from stock aggregates of Dolly Varden in the North Slope, Alaska. Mean estimates greater than 90% (dotted line) are considered robust for mixture analysis.

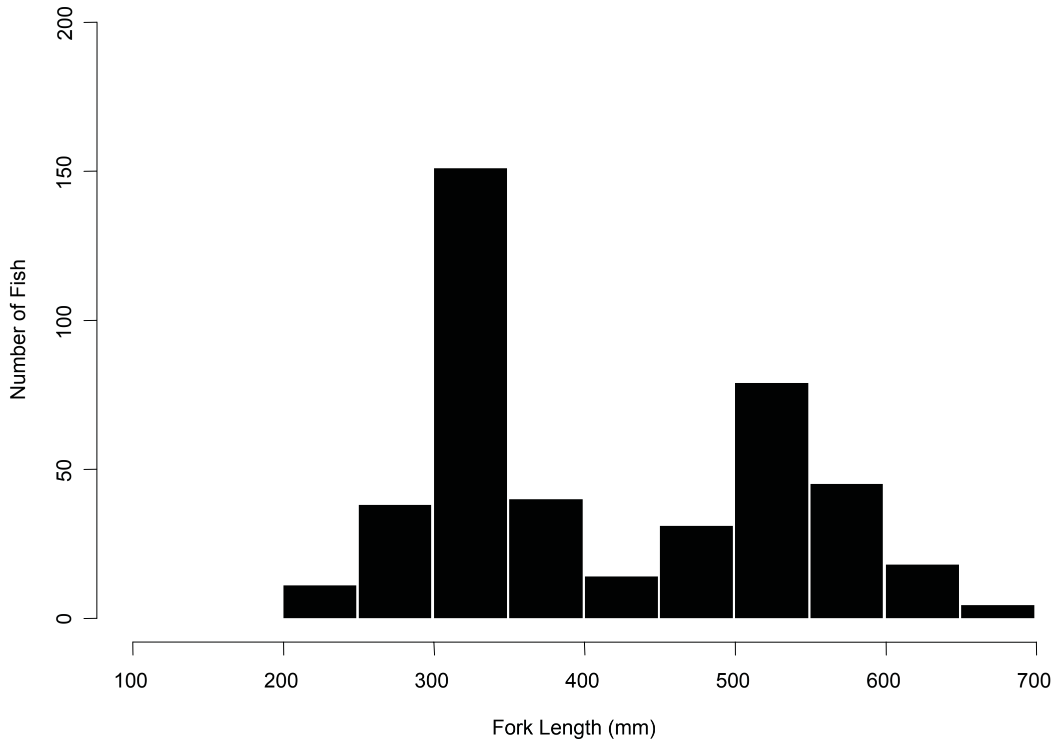

Figure 4. Histogram of fork lengths measured to nearest 5 mm for Dolly Varden collected overwintering in the Ivishak River.

S.D.=0.06), but contributions were also made from the Anaktuvuk River (0.04, S.D.=0.02) and the Canning River (0.11, S.D.=0.05).

Discussion

Population analysis and evaluation for MSA

Sampling Dolly Varden (and other anadromous *Salvelinus* species) to test for genetic evidence of population subdivision is particularly challenging because Dolly Varden returning to spawn may mix with Dolly Varden originating from other drainages returning to freshwater to overwinter. We minimized this potential source of error by only sampling Dolly Varden in prespawning condition near or on the spawning grounds or young-of-the-year and juveniles. We believe that the juvenile samples were representative of spawning aggregates in the drainages they were sampled because movement among river systems cannot occur until smoltification. Juveniles may move among tributaries within drainages, and we may have lost some power to detect differences among tributaries. The use of juveniles can introduce error through non-random sampling if family groups are collected, inflating the chance of significant differences between populations (Allendorf and Phelps 1981; "Allendorf and Phelps effect", Waples 1998). This error was minimized by sampling at several locations in spawning/juvenile rearing areas.

Table 2. Markov chain Monte Carlo means, standard deviations (S.D.), and posterior quantiles for stock proportions for two size classes of Dolly Varden overwintering in the Ivishak River in 2003.

			Posterior Quantiles		
Region	**Mean**	**S.D.**	**2.50%**	**Median**	**97.50%**
200–400 mm					
Anaktuvuk	0.0401	0.0226	0.0053	0.0371	0.0922
Ribdon	0.1277	0.0556	0.0136	0.1264	0.24
Ivishak tributaries	0.6788	0.0674	0.5449	0.6785	0.8086
Kavik	0.0128	0.0123	0	0.0093	0.0451
Canning	0.1083	0.0502	0.0139	0.1064	0.2139
Hulahula	0.0118	0.0212	0	0.0005	0.0755
Kongakut	0.0204	0.0332	0	0.0017	0.1159
>400 mm					
Anaktuvuk	0.0062	0.0116	0	0.0002	0.0414
Ribdon	0.0339	0.0424	0	0.0143	0.1415
Ivishak tributaries	0.9366	0.0493	0.8201	0.947	0.9986
Kavik	0.0017	0.0049	0	0	0.016
Canning	0.0156	0.0238	0	0.0041	0.0832
Hulahula	0.0039	0.0085	0	0.0001	0.03
Kongakut	0.0021	0.0062	0	0	0.0211

No significant allele frequency differences occurred between samples collected in multiple years or between life history stages sampled in a single drainage, supporting these arguments. Further, population relationships evaluated in this study are highly concordant with those from a survey of allozyme variation in Dolly Varden populations in the Alaskan and Yukon North Slope conducted by Everett et al. (1997). Everett et al. (1997) found highly significant allele frequency differences among all drainages, but only found allele frequency heterogeity within three of seven drainages where multiple sites were sampled. One of these drainages was the Sagavanirktok River, where genetic differences were detected within upriver samples (Ribdon, Lupine rivers) and between upper and lower river (Ivishak, Echooka rivers) samples. Similarly, we found differences among all drainages, and genetic diversity within the Sagavanirktok drainage. In both these studies, the general pattern of genetic structure followed expectations based on geography.

Average expected heterozygosity (0.625) and allele richness (11.3) were very similar to a population survey of Dolly Varden in Northwestern Alaska using the same loci (H_E=0.664, A_R=11.2; Crane et al. 2005), possibly indicating population stability in North Slope systems in spite of extreme climate conditions and habitat constraints.

Data from 12 allozyme loci and traditional maximum likelihood estimation used by Krueger et al. (1999) provided enough power to estimate the origin of Beaufort Sea mixtures to two U.S. stock aggregates (Anaktuvuk to Canning and Hulahula to Kongakut) and one Canada stock aggregate (Firth to Babbage). In this study, the combination of six microsatellite loci and Bayesian modelling of allele frequency distributions provided enough power to estimate the origin Dolly Varden to individual drainages. The use of highly polymorphic loci, particularly when combined with Bayesian methods, often allows the use of fewer markers in mixture analysis. For example, Winans et al. (2004), using Bayesian methods, found that simulations using allele frequency data from five highly polymorphic microsatellite loci provided similar power to distinguish four stock groups of steelhead, *Oncorhynchus mykiss,* as data from 32 allozyme loci.

Mixed-stock analysis

The baseline used in this study included samples from six major drainages in the Alaskan North Slope: Colville, Sagavanirktok, Kavik, Canning, Hulahula, and Kongakut. Significant spawning aggregates of Dolly Varden are also found in the Sadlerochit, Aichilik, and Egaksrak rivers in the Alaskan North Slope, and in the Firth, Babbage, and Mackenzie rivers in the Yukon North Slope. The lack of Yukon North Slope samples in the baseline dataset used in this study likely is not a source of significant bias. Krueger et al. (1997) documented that Canadian stocks migrated to the Endicott Canal in Prudhoe Bay, near the outlet of the Sagavanirktok River in 1987 and 1988. Though these stocks comprised up to 20% of mixture sampled, their presence in Endicott Canal declined in September and increased at sites sampled in more eastern locations, indicating that these stocks are migrating east in August and September. The Sadlerochit River is adjacent to the Hulahula River, and the Aichilik and Egaksrak Rivers are between the Hulahula and Kongakut Rivers. Given the strong geographic substructuring of Dolly Varden populations detected in this study and Everett et al. (1997), it is likely that Dolly Varden from these U.S. systems lacking in the baseline would misallocate to the Hulahula or Kongakut Rivers, and the contributions of these two streams to overwintering Dolly Varden in the Ivishak River were not significantly different from zero.

The MSA estimates of stock proportions of Dolly Varden overwintering in the Ivishak River show that the majority originated from the Sagavanirktok drainage, concordant with historic tagging data (e.g., Furniss 1975). These results are in contrast to overwintering aggregates in other regions in Alaska that comprise stocks from multiple drainages. For example, tagging studies conducted on the Wulik River in Northwestern Alaska have documented the presence of Dolly Varden originating from the Kivalina River, Wulik River, several Noatak River tributaries, and from streams in Norton Sound (DeCicco 1997). Further, using MSA, Crane et al. (2005) documented that over 28% of Dolly Varden sampled from the Wulik River in 2001 originated from Norton Sound. These results support the suggestion of Craig (1989a) that there is a selective advantage of philopatry to natal drainages for overwintering in the North Slope Dolly Varden due to severe habitat constraints and the precise timing necessary to locate overwintering areas. The results also illustrate the adaptability of this species to habitat and climate variation and the importance of the natal drainage to all freshwater life history stages for Dolly Varden in the Alaskan North Slope.

We found that approximately 15% of Dolly Varden 200–400 mm FL were from other North Slope drainages. Immature fish must complete several seaward migrations before returning to natal streams to spawn and are not as constrained to remain near natal streams as mature fish may be (DeCicco 1997). Further, some straying among drainages for overwintering by immature fish may be a trade off between reducing the risk of overwintering mortality by using multiple systems (non-philopatry) and ensuring that a segment of the population always finds overwintering habitat (philopatry).

Management Implications

Our data from MSA of Dolly Varden overwintering in the Ivishak River are limited to one year of data. We recommend repeated sampling to determine if our results hold true in other years and drainages. However, based on our results and those of previous tagging studies, we note the following management and conservation implications:

1) Aerial surveys of Dolly Varden overwintering in the Ivishak River can be considered as abundance indices for the Sagavanirktok River Dolly Varden.

2) Growing sport fisheries along the Dalton Highway that target Dolly Varden during their migrations to and from saltwater are primarily targeting Dolly Varden originating from the Sagavanirktok River.

3) Dolly Varden populations subdivide by drainage on the North Slope and depend on natal streams for both spawning and overwintering. Conservation of spring areas used for overwintering in North Slope drainages is as critical as conservation of spawning habitat because Dolly Varden do not exploit overwintering habitat in non-natal drainages unlike Dolly Varden in other regions of Alaska.

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Appendix 1. Allele frequency, allele richness (A_R), expected heterozygosity (H_E), observed heterozygosity (H_O), and P-values for tests of conformation to Hardy-Weinberg expectations (P-HW) for Dolly Varden collections from Beaufort Sea drainages.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
Sma-10										
140	0.0071	0.0000	0.0000	0.0000	0.0000	0.0204	0.0000	0.0000	0.0000	0.0213
144	0.0000	0.0000	0.0000	0.0081	0.0106	0.0000	0.0100	0.0134	0.0000	0.0000
148	0.0000	0.0000	0.0156	0.0161	0.0266	0.0000	0.0000	0.0000	0.0000	0.0000
152	0.1691	0.0000	0.0000	0.0000	0.0053	0.0255	0.0433	0.0638	0.0127	0.0266
156	0.0024	0.0438	0.0000	0.0040	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
160	0.0333	0.0000	0.0052	0.0040	0.0053	0.0357	0.0133	0.0067	0.1624	0.0266
164	0.0381	0.0250	0.0052	0.0000	0.0160	0.0255	0.0200	0.0134	0.0914	0.0904
168	0.1357	0.0375	0.0208	0.0161	0.0213	0.1684	0.0633	0.0336	0.0533	0.0479
172	0.3262	0.6063	0.5052	0.4919	0.4575	0.2908	0.3833	0.4161	0.4518	0.3457
176	0.0000	0.0250	0.1458	0.1452	0.1436	0.1225	0.1367	0.1376	0.0178	0.0479
180	0.0000	0.0563	0.0156	0.0081	0.0000	0.0051	0.0167	0.0067	0.0102	0.0319
184	0.0000	0.0188	0.0000	0.0242	0.0372	0.0102	0.0133	0.0034	0.0330	0.0000
188	0.0214	0.1063	0.0677	0.0847	0.1064	0.0306	0.1833	0.1644	0.0152	0.0585
192	0.1476	0.0125	0.0156	0.0403	0.0106	0.0918	0.0233	0.0470	0.0228	0.0798
196	0.0024	0.0500	0.0000	0.0161	0.0160	0.0765	0.0267	0.0067	0.0482	0.1011
200	0.0000	0.0000	0.0052	0.0040	0.0000	0.0000	0.0000	0.0034	0.0000	0.0053
204	0.0000	0.0000	0.0000	0.0121	0.0160	0.0000	0.0033	0.0067	0.0000	0.0000
208	0.0000	0.0000	0.0104	0.0081	0.0000	0.0612	0.0000	0.0101	0.0330	0.0053
212	0.0452	0.0063	0.0313	0.0282	0.0372	0.0000	0.0033	0.0168	0.0152	0.0000
216	0.0000	0.0000	0.0625	0.0242	0.0266	0.0000	0.0033	0.0000	0.0178	0.0106
220	0.0000	0.0063	0.0052	0.0121	0.0266	0.0357	0.0400	0.0403	0.0025	0.0372
224	0.0714	0.0000	0.0677	0.0403	0.0372	0.0000	0.0100	0.0067	0.0051	0.0532
228	0.0000	0.0063	0.0208	0.0121	0.0000	0.0000	0.0067	0.0034	0.0076	0.0053
232	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0053

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
N	210	80	96	124	94	98	150	149	197	94
A_R	10.4	12.8	15.1	18.1	16.5	13.7	15.9	16.1	15.4	17.2
H_E	0.8165	0.6142	0.7113	0.7260	0.7550	0.8531	0.7934	0.7735	0.7538	0.8449
H_O	0.8048	0.5625	0.6354	0.5887	0.7340	0.7755	0.6000	0.6376	0.6396	0.6702
P-HW	0.3479	0.0879	0.0186	0.0007	0.3193	0.025	0.0007	0.0007	0.0007	0.0007
Sma-17										
105	0.000	0.006	0.000	0.000	0.000	0.000	0.037	0.042	0.013	0.005
107	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.022
109	0.018	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000
111	0.000	0.058	0.036	0.046	0.037	0.015	0.060	0.053	0.025	0.000
113	0.000	0.000	0.046	0.017	0.021	0.000	0.003	0.007	0.091	0.016
115	0.190	0.397	0.276	0.275	0.282	0.227	0.297	0.239	0.264	0.242
117	0.003	0.032	0.010	0.004	0.027	0.000	0.027	0.021	0.000	0.016
119	0.000	0.006	0.000	0.000	0.000	0.020	0.013	0.014	0.000	0.005
121	0.318	0.051	0.026	0.063	0.000	0.086	0.010	0.014	0.000	0.022
123	0.069	0.019	0.056	0.046	0.085	0.056	0.023	0.039	0.071	0.049
125	0.005	0.000	0.077	0.029	0.027	0.020	0.043	0.042	0.063	0.038
127	0.390	0.385	0.388	0.413	0.367	0.470	0.410	0.475	0.383	0.555
129	0.005	0.026	0.056	0.079	0.149	0.106	0.073	0.053	0.071	0.027
131	0.000	0.019	0.020	0.025	0.000	0.000	0.000	0.000	0.000	0.000
139	0.003	0.000	0.005	0.000	0.000	0.000	0.003	0.000	0.000	0.000
141	0.000	0.000	0.005	0.004	0.000	0.000	0.000	0.000	0.000	0.000

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
N	195	78	98	120	94	99	150	142	197	91
A_R	7.0	9.9	11.5	10.2	8.8	8.0	10.8	10.7	8.9	10.7
H_E	0.7076	0.6901	0.7609	0.7411	0.7571	0.7086	0.7326	0.7077	0.7618	0.6308
H_O	0.7282	0.6154	0.7143	0.6917	0.7872	0.7071	0.7200	0.7183	0.7665	0.6484
P-HW	0.7757	0.0636	0.1407	0.0971	0.7871	0.535	0.4064	0.6457	0.6021	0.715
Sma-21										
113	0.0000	0.0000	0.0000	0.0043	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
115	0.3720	0.4870	0.4849	0.3932	0.3641	0.4192	0.4700	0.4301	0.4975	0.3956
117	0.0000	0.0000	0.0152	0.0086	0.0109	0.0000	0.0067	0.0070	0.0000	0.0220
127	0.3454	0.2208	0.2121	0.2778	0.1576	0.1364	0.2500	0.3392	0.3597	0.3022
129	0.0000	0.0195	0.0152	0.0128	0.0707	0.0051	0.0100	0.0210	0.0051	0.0220
131	0.0000	0.0000	0.0051	0.0214	0.0000	0.0000	0.0100	0.0000	0.0434	0.0220
133	0.2440	0.1494	0.0455	0.0641	0.1304	0.2475	0.1633	0.1434	0.0765	0.1319
135	0.0362	0.0000	0.0253	0.0128	0.0054	0.1465	0.0100	0.0105	0.0000	0.0604
137	0.0000	0.0000	0.0606	0.0513	0.0652	0.0000	0.0000	0.0035	0.0000	0.0000
141	0.0024	0.0455	0.0101	0.0086	0.0109	0.0000	0.0000	0.0000	0.0000	0.0055
145	0.0000	0.0000	0.0000	0.0043	0.0054	0.0051	0.0067	0.0035	0.0000	0.0000
149	0.0000	0.0000	0.0000	0.0000	0.0109	0.0000	0.0000	0.0000	0.0000	0.0000
151	0.0000	0.0714	0.1010	0.1197	0.1576	0.0404	0.0733	0.0420	0.0179	0.0385
153	0.0000	0.0065	0.0253	0.0086	0.0109	0.0000	0.0000	0.0000	0.0000	0.0000
155	0.0000	0.0000	0.0000	0.0128	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
N	207	77	99	117	92	99	150	143	196	91
A_R	4.4	7.0	10.7	12.8	11.5	6.5	8.2	7.7	5.6	8.8
H_E	0.6831	0.6887	0.7057	0.7492	0.7953	0.7250	0.6864	0.6795	0.6167	0.7322
H_O	0.7295	0.7013	0.7475	0.8120	0.7391	0.8283	0.6533	0.6923	0.5918	0.7143
P-HW	0.9471	0.6771	0.8986	0.975	0.0993	0.9971	0.1886	0.6707	0.2379	0.375
Sma-22										
148	0.0000	0.0063	0.0000	0.0042	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
164	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0077	0.0000
168	0.0000	0.0000	0.0000	0.0042	0.0000	0.1042	0.0034	0.0172	0.0000	0.0053
172	0.0000	0.0000	0.0000	0.0000	0.0000	0.0052	0.0000	0.0000	0.0000	0.0000
176	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0206	0.0103	0.0102	0.0213
180	0.0048	0.0000	0.0000	0.0042	0.0108	0.0000	0.0343	0.0207	0.0077	0.0160
184	0.0643	0.0823	0.0354	0.0417	0.0108	0.0521	0.0480	0.0345	0.0102	0.0638
188	0.0024	0.0190	0.1010	0.0792	0.1022	0.1250	0.0685	0.0793	0.0332	0.0532
192	0.0024	0.1582	0.1111	0.1250	0.0807	0.0156	0.1370	0.1207	0.0510	0.0957
196	0.0214	0.1013	0.1616	0.1500	0.1667	0.0521	0.0719	0.0931	0.0893	0.1330
200	0.0643	0.0696	0.0707	0.0958	0.0860	0.0104	0.1267	0.1621	0.0689	0.1064
204	0.0476	0.1582	0.1212	0.1417	0.1290	0.0521	0.1473	0.1448	0.1837	0.1330
208	0.2786	0.0570	0.1111	0.1042	0.1667	0.2604	0.0993	0.1241	0.1199	0.1170
212	0.1167	0.1329	0.0808	0.0833	0.0753	0.1563	0.0685	0.0828	0.0918	0.0798
216	0.0833	0.0317	0.1212	0.0500	0.0860	0.0833	0.0890	0.0276	0.1786	0.0319
220	0.1262	0.0760	0.0455	0.0792	0.0591	0.0365	0.0377	0.0379	0.0485	0.0426
224	0.0762	0.0443	0.0051	0.0250	0.0108	0.0208	0.0034	0.0172	0.0485	0.0426

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
228	0.0310	0.0127	0.0202	0.0042	0.0000	0.0260	0.0240	0.0138	0.0204	0.0106
232	0.0167	0.0000	0.0152	0.0042	0.0054	0.0000	0.0206	0.0069	0.0153	0.0213
236	0.0310	0.0000	0.0000	0.0042	0.0000	0.0000	0.0000	0.0000	0.0026	0.0053
240	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0106
244	0.0310	0.0317	0.0000	0.0000	0.0000	0.0000	0.0000	0.0069	0.0026	0.0000
248	0.0024	0.0063	0.0000	0.0000	0.0108	0.0000	0.0000	0.0000	0.0000	0.0053
252	0.0000	0.0063	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0053
256	0.0000	0.0063	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0102	0.0000
N	210	79	99	120	93	96	146	145	196	94
A_R	14.6	16.8	12.8	14.8	13.7	13.7	15.0	16.3	16.8	19.2
H_E	0.8680	0.9024	0.8986	0.9011	0.8912	0.8679	0.9079	0.8993	0.8916	0.9159
H_O	0.9000	0.8987	0.9192	0.9000	0.8710	0.8854	0.8973	0.8759	0.8776	0.9362
P-HW	0.955	0.5164	0.8007	0.5257	0.3329	0.7636	0.3636	0.2207	0.2936	0.8229
Sma-3										
120	0.4500	0.2000	0.0859	0.1371	0.1170	0.2727	0.2500	0.2740	0.1751	0.3807
122	0.5500	0.8000	0.9040	0.8468	0.8351	0.7273	0.7467	0.7260	0.8249	0.6193
124	0.0000	0.0000	0.0101	0.0161	0.0479	0.0000	0.0033	0.0000	0.0000	0.0000
N	220	80	99	124	94	99	150	146	197	88
A_R	2.0	2.0	2.9	3.0	3.0	2.0	2.5	2.0	2.0	2.0
H_E	0.4961	0.3220	0.1761	0.2650	0.2881	0.3987	0.3812	0.3992	0.2897	0.4742
H_O	0.4909	0.3000	0.1919	0.2500	0.2340	0.4040	0.4200	0.4247	0.2792	0.3523
P-HW	0.5129	0.3829	1	0.285	0.0279	0.6493	0.9086	0.8471	0.3893	0.0171

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
Sma-5										
N	220	80	100	127	94	100	150	149	197	94
90	1	1	1	1	1	1	1	1	1	1
A_R	1	1	1	1	1	1	1	1	1	1
H_E	0	0	0	0	0	0	0	0	0	0
H_O	0	0	0	0	0	0	0	0	0	0
P-HW										
Sma-24										
158	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0053
166	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0034	0.0000	0.0000	0.0000
170	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0025	0.0000
178	0.0000	0.0000	0.0000	0.0041	0.0000	0.0000	0.0000	0.0000	0.0254	0.0000
182	0.0000	0.0263	0.0361	0.0207	0.0163	0.0000	0.0000	0.0069	0.0381	0.0106
186	0.0255	0.0461	0.0052	0.0165	0.0217	0.0000	0.0034	0.0000	0.0178	0.0053
190	0.0204	0.0132	0.0000	0.0083	0.0109	0.0000	0.0101	0.0035	0.0000	0.0000
194	0.0204	0.0395	0.1237	0.1074	0.0598	0.0368	0.0203	0.0517	0.0127	0.0160
198	0.0383	0.0132	0.0464	0.0455	0.0054	0.0211	0.0135	0.0379	0.0355	0.0160
202	0.0153	0.0000	0.0155	0.0331	0.0326	0.0421	0.0135	0.0276	0.0584	0.0160
206	0.0663	0.0461	0.0103	0.0537	0.0272	0.0000	0.0439	0.0448	0.0228	0.0319
210	0.0332	0.0395	0.0052	0.0124	0.0054	0.0842	0.0034	0.0241	0.0178	0.0213
214	0.0587	0.0921	0.0670	0.0331	0.0652	0.0474	0.0372	0.0379	0.0482	0.0585
218	0.2755	0.0526	0.0103	0.0165	0.0109	0.0790	0.0101	0.0241	0.0584	0.0106
222	0.0459	0.0263	0.0155	0.0496	0.0435	0.1842	0.1014	0.0621	0.0432	0.0745
226	0.0561	0.0263	0.0670	0.0207	0.0598	0.0158	0.1419	0.0448	0.0736	0.0532

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Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
230	0.0561	0.0395	0.0773	0.0826	0.1033	0.0000	0.0068	0.0069	0.0355	0.0479
234	0.0332	0.0395	0.0361	0.0455	0.0489	0.0053	0.0304	0.0138	0.0406	0.0798
238	0.0102	0.0395	0.0464	0.0413	0.0326	0.0526	0.0270	0.0621	0.0152	0.1277
242	0.0026	0.0658	0.0670	0.0455	0.0380	0.0737	0.0642	0.0586	0.0330	0.0585
246	0.0383	0.0987	0.0516	0.0413	0.0435	0.0105	0.0608	0.0586	0.0635	0.0372
250	0.0842	0.0395	0.0773	0.0579	0.0380	0.0526	0.0608	0.0655	0.0406	0.0585
254	0.0128	0.0526	0.0309	0.0165	0.0326	0.1421	0.0439	0.0379	0.0432	0.0319
258	0.0383	0.0132	0.0206	0.0372	0.0109	0.0474	0.0642	0.0586	0.0305	0.0266
262	0.0000	0.0066	0.0000	0.0207	0.0924	0.0211	0.0439	0.0586	0.0330	0.0053
266	0.0000	0.0263	0.0516	0.0455	0.0109	0.0053	0.0405	0.0241	0.0711	0.0106
270	0.0051	0.0066	0.0258	0.0455	0.0326	0.0316	0.0237	0.0414	0.0330	0.0053
274	0.0026	0.0263	0.0567	0.0289	0.0544	0.0316	0.0372	0.0241	0.0051	0.0106
278	0.0128	0.0329	0.0258	0.0041	0.0163	0.0053	0.0203	0.0172	0.0076	0.0372
282	0.0026	0.0395	0.0155	0.0165	0.0380	0.0000	0.0237	0.0276	0.0127	0.0372
286	0.0000	0.0066	0.0103	0.0165	0.0272	0.0105	0.0000	0.0138	0.0203	0.0266
290	0.0459	0.0263	0.0052	0.0083	0.0054	0.0000	0.0101	0.0069	0.0279	0.0585
294	0.0000	0.0132	0.0000	0.0165	0.0000	0.0000	0.0203	0.0310	0.0127	0.0106
298	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0101	0.0069	0.0076	0.0053
302	0.0000	0.0000	0.0000	0.0083	0.0054	0.0000	0.0034	0.0069	0.0000	0.0053
306	0.0000	0.0000	0.0000	0.0000	0.0109	0.0000	0.0034	0.0069	0.0000	0.0000
310	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0035	0.0051	0.0000
318	0.0000	0.0066	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
322	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0034	0.0035	0.0025	0.0000
326	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0051	0.0000

Continued on next page.

Appendix 1. Continued.

	Location									
Locus	Anaktuvuk	Ribdon	Saviuk-viayak	Ivishak	Echooka	Kavik	Main Fk. Canning	Marsh Fk. Canning	Hulahula	Kongakut
N	196	76	97	121	92	95	148	145	197	94
A_R	21.4	29.0	25.2	29.7	29.1	20.3	28.2	30.1	30.8	29.7
H_E	0.8921	0.9570	0.9449	0.9554	0.9537	0.9153	0.9421	0.9590	0.9597	0.9485
H_O	0.9184	0.9342	0.9072	0.9421	0.9783	0.9579	0.9324	0.9517	0.9391	0.8191
P-HW	0.9421	0.2329	0.08	0.2914	0.9343	0.975	0.3757	0.3921	0.0936	0.0007
Overall										
A_R	8.7	11.2	11.3	12.8	12.0	9.3	11.7	12.0	11.5	12.6
H_E	0.6377	0.5963	0.5996	0.6197	0.6343	0.6384	0.6348	0.6312	0.6105	0.6495
H_O	0.6531	0.5732	0.5879	0.5978	0.6205	0.6512	0.6033	0.6143	0.5848	0.5915
P-HW	0.9536	0.0407	0.1357	0.0121	0.11	0.8407	0.0007	0.055	0.0014	0.0007