



**Allozyme Analysis of Population Structure in Arctic Cisco (*Coregonus autumnalis*)
from the Beaufort Sea**

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ALLOZYME ANALYSIS OF POPULATION STRUCTURE IN ARCTIC CISCO (*COREGONUS AUTUMNALIS*) FROM THE BEAUFORT SEA.—Arctic ciscoes (*Coregonus autumnalis*) are anadromous salmonid fishes, and their range includes the nearshore Arctic Ocean of Europe, Siberia, and western North America (Gallaway et al., 1983). During the winter, the North American populations of Arctic ciscoes avoid entrapment in the Beaufort Sea ice pack by overwintering in refugia at the deltas of the Mackenzie River of the Northwest Territories in Canada and the Colville River of the Alaskan North Slope. As summer arrives, Arctic cisco aggregations in the Colville and Mackenzie deltas disperse to nearshore feeding habitat, which extends along the Beaufort Sea from Point Barrow, Alaska to Bathurst Inlet, Canadian Northwest Territories (Gallaway et al., 1983).

The spawning of the Canadian and Alaskan populations of the Arctic cisco from the Beaufort Sea has only been reported in tributaries of the Mackenzie River drainage system of the Northwest Territories in Canada. The apparent geographic restriction of spawning runs to this river system is the primary basis for the formulation of the "Mackenzie hypothesis," that all North Slope Arctic cisco aggregations are derived from one (or more) breeding stock(s) associated with the Mackenzie River system (Gallaway et al., 1983). In a study of population variation of Arctic ciscoes from Alaska and Canada, Bickham et al. (1989) concluded that genetic data do not provide evidence of significant genetic divergence between Alaskan and Canadian aggregations and, therefore, supported the "one stock" hypothesis of the Mackenzie origin of these fishes. Deviations from Hardy-Weinberg proportions observed in coastal samples was assumed to be due to the pooling of individuals from different breeding stocks within the Mackenzie River system. We examined an increased number of coastal samples and spawning site localities in tributaries of the Mackenzie River to reevaluate the results of Bickham et al. (1989) and to reexamine the hypothesis of the Mackenzie River system as the sole source of Arctic ciscoes in the Beaufort Sea.

Materials and methods.—During July through Aug. 1988, a total of 126 *Coregonus autumnalis* were sampled from the following coastal sites

(numbers correspond with Fig. 1): (1) Point Barrow; (2) Kogru River; (3) Colville River; (4) Sagavanirktok River; (5) Kaktovic/Jago Lagoon in Alaska; (6) Stokes Point in the Yukon Territory; and (7) Atkinson Point in the Northwest Territories. These samples were compared to 130 *C. autumnalis* from the following spawning site localities: (8) Peel River, (9) Arctic Red River, (10) Mountain River, (11) Carcajou River, and (12) Liard River, all tributaries of the Mackenzie River drainage system. Specimens collected from coastal sites in the Beaufort Sea were mostly adults or subadults. Specimens collected from the spawning runs in the Mackenzie River system were adults, estimated from known growth rates in these fishes (Schmidt et al., 1989).

Specimens were frozen on dry ice in the field. Liver tissue samples were taken in the laboratory and stored directly at -70°C prior to processing for electrophoresis. Additional details of the electrophoretic methods used followed the protocol described by Bickham et al. (1989). Arctic cisco, as other members in the family Salmonidae, is a tetraploid species (Allendorf and Thorgaard, 1984) and expresses some duplicate loci as isoloci. Our locus nomenclature has been developed to consider this fact. Assayed allozymes were encoded by the following protein systems that were representative of at least 19 putative enzymatic loci: aconitase hydratase (AcoH-1,2; E.C. 4.2.1.3), alcohol dehydrogenase (Adh-1; E.C. 1.1.1.1), glycerol-3-phosphate dehydrogenase (G3pdH-1,2; E.C. 1.1.1.8), isocitrate dehydrogenase (NADP^{+}) (Idh-1,2; E.C. 1.1.1.42), cytosol aminopeptidase (Ap-1,2; E.C. 3.4.11.1), L-lactate dehydrogenase (Ldh-1,2; E.C. 1.1.1.27), malate dehydrogenase (oxaloacetate-decarboxylating) (NADP^{+}) (MdhP-1,2; E.C. 1.1.1.40), malate dehydrogenase (Mdh-1,2; E.C. 1.1.1.37), mannose-6-phosphate isomerase (Mpi-1; E.C. 5.3.1.8), phosphogluconate dehydrogenase (decarboxylating) (Pgdh-1; E.C. 1.1.1.44), glucose-6-phosphate isomerase (Gpi-1; 5.3.1.9), and transferrin (Trf-1).

Using the computer package BIOSYS-1 (Swofford and Selander, 1981), we computed allele frequencies, chi-square test for conformity to Hardy-Weinberg proportions, and Modified Rogers' (1972) Genetic Distance. A Principal Component Analysis was performed on the correlation matrix of the genotypic frequencies to depict patterns of nonhierarchical associations among the samples, using the procedure PRINCOMP of the Statistical Analysis

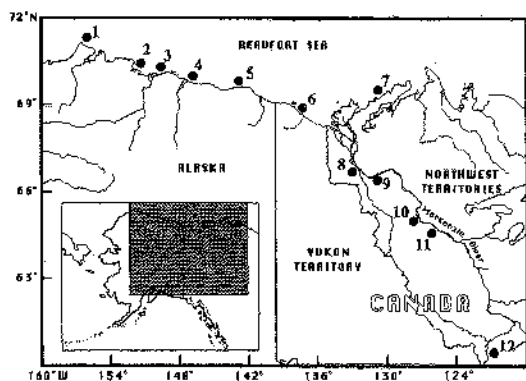


Fig. 1. Localities of aggregations of Arctic cisco sampled in this study. (1) Point Barrow, (2) Kogru River, (3) Colville River, (4) Sagavanirktok River, (5) Kaktovic/Jago Lagoon, (6) Stokes Point, (7) Atkinson Point, (8) Peel River, (9) Arctic Red River, (10) Mountain River, (11) Carcajou River, (12) Liard River.

Systems package (SAS, 1988). The computer package BIOSTAT-1 (Pimentel and Smith, 1986) was used to test differences in allele frequencies using Fisher's Exact Test of independence (FET). Allelic values from each polymorphic locus were compared between two populations, and the sum of twice the negative natural logarithm ($\ln p$) of the exact probability values were computed. This value was compared to a chi-square distribution with $2K$ degrees of freedom in which K = number of independent tests (Sokal and Rohlf, 1981). Initial tests were performed between populations with the greatest genetic distance values and were continued until a nonsignificant level was reached. Levels of population subdivision were tested using F -statistics (Nei and Chesser, 1983; Van Den Bussche et al., 1986). A chi-square test was used to evaluate the null hypothesis $F_{ST} = 0$, for single locus F_{ST} values:

$$\chi^2 = 2NF_{ST}(k - 1); \quad df = (k - 1)(s - 1)$$

where N is the total number of individuals sampled, k is the number of alleles at the locus, and s is the number of populations (Waples, 1987). Significance levels for tablewise comparisons of Hardy-Weinberg proportions were adjusted with the sequential Bonferroni technique according to Rice (1989). Significance levels for the F_{ST} chi-square test was $\alpha = 0.05$.

Results.—Five of the 19 presumptive gene loci examined were polymorphic. Chi-square tests for deviation of genotypic frequencies from Hardy-Weinberg expectations revealed significant departures from random mating proportions for the *Gpi-1* locus. Among the coastal

samples, significant deficiencies of heterozygotes were observed for this locus at Colville ($P = 0.007$); and for the spawning localities at the Mackenzie drainage system, *Gpi-1* presented a significant deficiency of heterozygotes ($P = 0.001$) at the Peel River. Observed genotypic distributions are presented in Table 1.

Rogers' distance values for all pairwise comparisons of populations revealed very small differences among all samples, with the exception of those involving Point Barrow. Genetic distances among samples exclusive of Point Barrow range from 0.026 between the Peel River and Sagavanirktok samples to 0.104 between Kogru and Kaktovic. Genetic distances between Point Barrow and the other samples range from 0.212–0.282. The FET for pairwise comparison of allele frequencies among populations revealed significant differences in all comparisons between Point Barrow and the other samples. None of the other pairs was significantly different.

Because geographic variation may take many nonhierarchical or semihierarchical forms, such as clinal and reticular patterns (Lessa, 1990), a Principal Component Analysis was performed on the correlation matrix of genotypic frequencies to detect whether any of such patterns were apparent among our samples. A projection of the population scores on the first two principal components is depicted in Figure 2. These two components account for about 51% of the total variation among our samples. The largest difference observed is between the Point Barrow sample and all the other samples along Principal Component 1. Nevertheless, along Principal Component 2, some evidence of genotypic frequency differences is apparent among the other samples. Whereas most spawning populations with the exception of the Arctic Red River population (sample 9) form a tight cluster along both components, some coastal populations (Colville, Kaktovic/Jago Lagoon, and Stokes Point) depart conspicuously along the second component, suggesting a different genotype composition with respect to the Mackenzie River system spawning populations. However, no geographic trend is apparent among the samples. Chi-square analyses on Hardy-Weinberg proportions including first all populations and then, without the Point Barrow sample, resulted in significant departures in both cases for the *Gpi-1* locus, suggesting that in fact our samples are composed from more than the gene pool from the Mackenzie River system.

Values of F_{ST} for the five polymorphic loci were estimated once with all the samples included, and then with the exclusion of Point

TABLE 1. GENOTYPIC DATA FOR FIVE POLYMORPHIC LOCI FROM COASTAL AND SPAWNING POPULATIONS OF *Coregonus autumnalis*. Locality numbers correspond to (1) Point Barrow, (2) Kogru River, (3) Colville River, (4) Sagavanirktok River, (5) Kaktovic/Jago Lagoon, (6) Stokes Point, (7) Atkinson Point, (8) Peel River, (9) Arctic Red River, (10) Mountain River, (11) Carcajou River, (12) Liard River.

Locus	Geno- type	Sample locality											
		1	2	3	4	5	6	7	8	9	10	11	12
G3pdh-1	aa	0	1	3	1	1	1	0	2	5	4	1	5
	ab	0	2	9	13	4	3	8	10	7	2	5	16
	ac	3	1	0	0	0	1	1	2	0	2	1	1
	ad	0	2	2	0	2	2	2	4	2	3	2	3
	bb	0	11	1	2	4	5	4	6	8	4	8	2
	bc	2	0	0	3	0	2	3	2	0	2	0	1
	bd	0	2	4	3	1	0	6	2	4	2	4	1
	cc	3	0	0	1	0	0	0	0	0	0	0	0
	cd	2	1	0	0	0	0	0	0	0	0	0	0
	dd	1	0	1	1	0	1	0	0	0	0	0	1
Mpi-1	aa	7	0	1	1	2	1	2	2	0	1	2	1
	ab	4	6	7	9	2	9	7	8	4	8	12	12
	ac	0	0	0	0	1	0	0	0	1	0	1	0
	bb	0	14	11	14	7	5	14	18	13	8	6	17
	bc	0	0	1	0	0	0	1	0	0	1	0	0
Adh-1	aa	10	18	19	23	12	15	22	28	26	19	20	28
	ab	0	2	1	1	0	0	2	0	0	0	1	0
	ac	1	0	0	0	0	0	0	0	0	0	0	0
Idh-1	aa	0	0	0	0	0	0	0	0	0	0	1	0
	ab	0	4	4	4	1	0	2	1	3	2	1	5
	bb	10	16	13	20	10	15	21	26	23	17	19	24
	bc	1	0	2	0	1	0	1	0	0	0	0	0
Gpi-1	aa	0	1	2	2	0	0	0	3	3	1	1	1
	ab	0	1	0	2	0	4	3	1	7	5	5	6
	an	0	0	1	0	2	0	0	0	0	0	0	0
	bb	8	18	10	20	7	11	21	24	15	13	13	22
	bn	2	0	1	0	3	0	0	0	0	0	0	0
	nn	1	0	0	0	0	0	0	0	0	0	0	0

Barrow. F_{ST} values ranged from 0.020 (Adh-1) to 0.133 (Mpi-1). When Point Barrow was excluded from the analysis, F_{ST} values ranged from 0.018 (Adh-1) to only 0.031 (Mpi-1). Significant heterogeneity ($F_{ST} > 0$, $P < 0.05$) occurred across all samples (including Point Barrow) for the loci G3pdh-1 ($F_{ST} = 0.079$), Mpi-1 ($F_{ST} = 0.133$), and Gpi-1 ($F_{ST} = 0.048$). Excluding Point Barrow, significant heterogeneity among samples occurred only at the Gpi-1 locus ($F_{ST} = 0.041$). Multilocus F_{ST} values for the five polymorphic loci were 0.061 across all samples, and 0.009 without the Point Barrow sample. Finally, the allele frequencies of the loci G3pdh-1^c and Mpi-1 for the Point Barrow sample, are more similar to those reported by Bickham et al. (1989) for a Bering cisco sample from the Yukon River, than to the other samples of Arctic cisco analyzed in this study. The allele G3pdh-1^c had a frequency of 0.55 for the Yukon River (Bick-

ham et al., 1989) and 0.59 for Point Barrow in this study. In all the other samples of Arctic cisco surveyed, this allele had frequencies ranging from 0–0.11. The allele Mpi-1^a presented frequencies of 0.8 and 0.82 in the Yukon River and Point Barrow, respectively, and ranged from 0.14–0.41 in all other samples of Arctic cisco.

Discussion.—This study, as well as that of Bickham et al. (1989), reports slight divergence among Arctic cisco populations from spawning site localities in the Mackenzie River system but suggests that coastal aggregations might include individuals from a source other than the Mackenzie River. Genetic distance values among all samples excluding Point Barrow were very small, and there was minimal evidence of significant allele frequency differences among samples. Thus, samples from Kogru, Alaska, east to Atkinson Point, Northwest Territories, Canada,

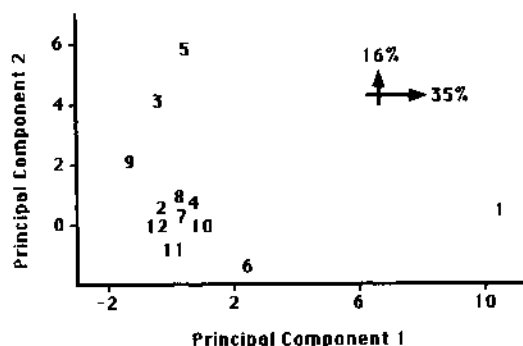


Fig. 2. Projection of the population scores on the first two principal components based on the correlation matrix of genotypic frequencies. Sample numbers as in Figure 1.

conform with expectations from the "one stock" hypothesis (Gallaway et al., 1983).

The sample of Arctic cisco from Point Barrow apparently represents a separate population from the one in Mackenzie River. Bickham et al. (1989) compared three individuals from Point Barrow to other samples of Arctic cisco from coastal sites and spawning areas and to one sample of Bering cisco from the Yukon River. Their results were inconclusive regarding the population affinity of the Point Barrow sample. Our results suggest that supposed Arctic cisco specimens from Point Barrow may be more closely related to Bering ciscoes (*Coregonus laurettae*) from the Yukon River, than to Arctic ciscoes of the Beaufort Sea and Mackenzie drainage.

McPhail (1966) suggested that the number of gill rakers on the lower limb of the first gill arch could be used to separate Arctic and Bering cisco (26–30 for *C. autumnalis*; 21–25 for *C. laurettae*) and concluded that these were different species. On this basis, we identified the sample from Point Barrow as *C. autumnalis*. Dillinger (1989), however, considered the Arctic and Bering ciscoes to be conspecific. If our sample of "Arctic cisco" from Point Barrow is in fact more closely related to the population from the Yukon River, as Dillinger (1989) suggested, then gill rakers might not be a reliable diagnostic character. The sample from Point Barrow possibly was composed of Bering cisco, or it may have represented Arctic cisco from a population other than the one spawning in the Mackenzie River system. The former seems likely because Point Barrow is within the range of Bering cisco (Craig, 1989).

Nevertheless, the distribution of rare alleles provides further evidence that samples from coastal sites include individuals from places oth-

er than the Mackenzie River system. Allele Idh-1^c was present in some coastal samples but was absent in all 130 specimens of Arctic cisco so far analyzed from the spawning site samples in the Mackenzie River system. Allele Adh-1^c was found only in the Point Barrow sample, and allele Gpi-1^a is found only at Point Barrow, Colville River, and Kaktovic/Jago Lagoon.

It appears that the Alaskan coastal aggregations of Arctic cisco consist mostly of individuals from the Mackenzie River system. However, the aggregations also contain individuals from a western population representing either a different population of Arctic ciscoes, or a population of Bering ciscoes that are morphologically difficult to distinguish from Arctic ciscoes. This western population appears to decrease in numbers from west to east.

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- JUAN CARLOS MORALES, BRIAN G. HANKS, JOHN W. BICKHAM, JAMES N. DERR, *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843*; and BENNY J. GALLAWAY, *LGL Ecological Research Associates, Inc., 1410 Caviit Street, Bryan, Texas 77801*. Present Addresses: (JCM) *Department of Anthropology, Columbia University, New York, New York 10027*; and (JND) *Department of Animal Science, Texas A&M University, College Station, Texas 77843*. Send reprint requests to JWB. Submitted 6 Sept. 1991. Accepted 11 July 1992. Section editor: D. G. Buth.
- nibalism is an interesting biological phenomenon because it may involve eating individuals that carry genes related by common descent and thus be detrimental to individual fitness. This should be strongly selected against, unless there are benefits that counter the costs of removing related genotypes from the next generation. A number of benefits have been proposed, including energy gain, survival during periods of food scarcity, removal of potential competitors or predators, and even a group selection argument for population self-regulation (Fox, 1975; Polis, 1981). Regardless of cannibalism's evolutionary role, however, one problem with many studies is that it is difficult to document and quantify under natural conditions. Consequently, in some groups, the importance of the trait in wild populations is unknown.
- Cannibalism has been reported to occur in several poeciliid (livebearing) fishes in nature including *Gambusia affinis* (Seale, 1917; Krumholz, 1948; Harrington and Harrington, 1982; some of these populations were undoubtedly *G. holbrooki*), *Poeciliopsis monacha* (Thibault, 1974), and *Belonesox belizanus* (Belshe, 1961; Miley, 1978). Several other species are known to cannibalize in captivity, including *Poecilia reticulata* (Shoemaker, 1944); *Poeciliopsis occidentalis* (Meffe, 1984); and *Poecilia latipinna*, *Heterandria formosa*, and *Xiphophorus variatus* (GKM, pers. obs.). Unfortunately, laboratory observations only indicate a physical capacity to ingest members of the same species and may be an artifact of captivity. Therefore, such reports may be misleading with respect to the trait in nature.
- A number of gambusiine fishes have been shown to cannibalize under laboratory conditions (Walters and Legner, 1980; Harrington and Harrington, 1982; Hubbs, 1991), but no large scale study has been conducted specifically to document the occurrence and frequency of the behavior in wild populations. In this study, we document rates of cannibalism in three wild populations of the eastern mosquitofish (*G. holbrooki*) in South Carolina by dissection of over 1800 individuals to search for evidence of its occurrence.

Methods.—Fish were collected from three habitats on the United States Department of Energy's Savannah River Site, a federal nuclear production facility located near Aiken, in west-central South Carolina. Pond C is a 67-ha reactor cooling reservoir that periodically received thermal effluent from 1958 to April 1988. Since then the system has been at ambient temperature. During both thermal and ambient periods, mosquitofish are among the most abun-

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