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Mitochondrial DNA variability among Lake Baikal omul *Coregonus autumnalis migratorius* (Georgi)

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with 3 figures and 4 tables

Abstract : Omul, *Coregonus autumnalis*, are a commercially important coregonine fish from Lake Baikal, Siberia, Russia. In Lake Baikal, three morphotypes recognized by fishery experts occupy different zones in the lake; they are referred to as "littoral," "pelagic," and "benthic". Expressed character divergence was supported by whole-body morphometric analysis, but it is not known whether discrete genetic differences accompany the observed morphological variation. This study was designed to assess the genetic variation of three different omul morphotypes sampled from different locations in Lake Baikal that were segregated by morphotype in multivariate analysis. We surveyed genetic variation with restriction fragment length polymorphism analysis of specific gene loci amplified with the polymerase chain reaction. Sequence variation was localized in the mitochondrial control region. Though no discrete genetic markers were found, there is evidence of reproductive segregation by geographic location that corroborates geographic variation in morphological characters.

Introduction

The omul, *Coregonus autumnalis migratorius* (Georgi), is the most important fish in the Lake Baikal region, comprising a major portion of both commercial and subsistence fisheries for centuries. After decades of intense harvest, environmental modification, and technological improvements in harvest methods, omul population abundance began to decline sharply (Smirnov 1992). Virtually all populations were considered endangered by the mid-1900s and the fishery was closed from 1969–1975. Today, omul account for approximately 50% of the annual harvested biomass in the lake; commercial and subsistence fisheries are supported by wild

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populations which are supplemented by significant numbers of cultured fish (SMIRNOVA-ZALUMI & SMIRNOV 1973, BRONTE et al. 1999, SOKOLOV 2002).

Eco-morphological heterogeneity is well-recognized among Lake Baikal omul (Smirnov 1992). Three distinct morphotypes are categorized as littoral, pelagic, and benthic (SMIRNOV & SHUMILOV 1974), and differ in several morphological and behavioral characteristics including body shape, spawning time, and feeding behavior. Meristic and morphological measures are used to distinguish among forms, however similarities in overall appearance of the different morphotypes make field classification problematic (SMIRNOV & SHUMILOV 1974, BRONTE et al. 1999). The morphotypes are identified primarily by the number of gill rakers on the first gill arch as well as size at maturity (SMIRNOV & SHUMILOV 1974). In general, littoral omul have a smaller head, a shorter sharp snout, and mature at a smaller size than the pelagic or benthic forms, pelagic omul are more elongated, and benthic omul are deeper bodied than the other morphotypes. Although whole-body morphometric analysis appears to support delineation among the morphotypes (BRONTE et al. 1999), it is not known whether such physical differences are accompanied by genetic divergence.

Spawning times also differ among the three morphotypes. Pelagic omul spawn almost exclusively in the Selenga River area and different populations are segregated both temporally and spatially within the river (SMIRNOV 1992). Littoral populations appear to mix in the lake across contiguous near-shore habitat, and have different spawning times than the pelagic or benthic forms in several rivers (SMIRNOV 1969, SMIRNOV & SHUMILOV 1974). The benthic morphotype shows the greatest amount of morphological divergence from the pelagic and littoral morphotypes (BRONTE et al. 1999), but reproductive isolation may be most dependent on temporal factors in spawning rivers (SMIRNOV 1992). While temporal differences in spawning time may help to maintain genetic differences among the different morphological forms, inconsistencies in choice of sources for artificially propagated omul may break down naturally-established barriers to gene flow. This could further reduce the overall genetic variability among omul populations that have already experienced population declines.

The goal of this study is to assess genetic variation within and among collections of three omul morphotypes from different sampling locations in Lake Baikal. The morphotype assignment of these collections was corroborated by multivariate analysis of morphological measures in a truss framework (BRONTE et al. 1999). Our assignment of morphotype is derived from the results of the BRONTE et al. (1999) study. We will survey a suite of genetic characters from mitochondrial DNA gene loci to compare the level of genetic diversity among littoral, pelagic, and benthic morphotypes, as well as among populations defined by geographic location.

Material and methods

Omul were collected from five locations around Lake Baikal (Fig. 1). From the east shore of Lake Baikal, fish were sampled at Chivyrukui Bay (three morphotypes), Barguzin Bay near the mouth of the Barguzin River (littoral and pelagic morphotypes), and Selenga Delta, outlet of the Selenga River (three morphotypes). Fish were also sampled from Maloye More on the western shore (littoral and pelagic morphotypes), and from northern Lake Baikal near Nizhneangarsk at the mouth of the Upper Angara and Kichera Rivers (littoral morphotype only). Fish were captured with a universal (benthic-pelagic design) trawl by the Eastern Siberian Institute

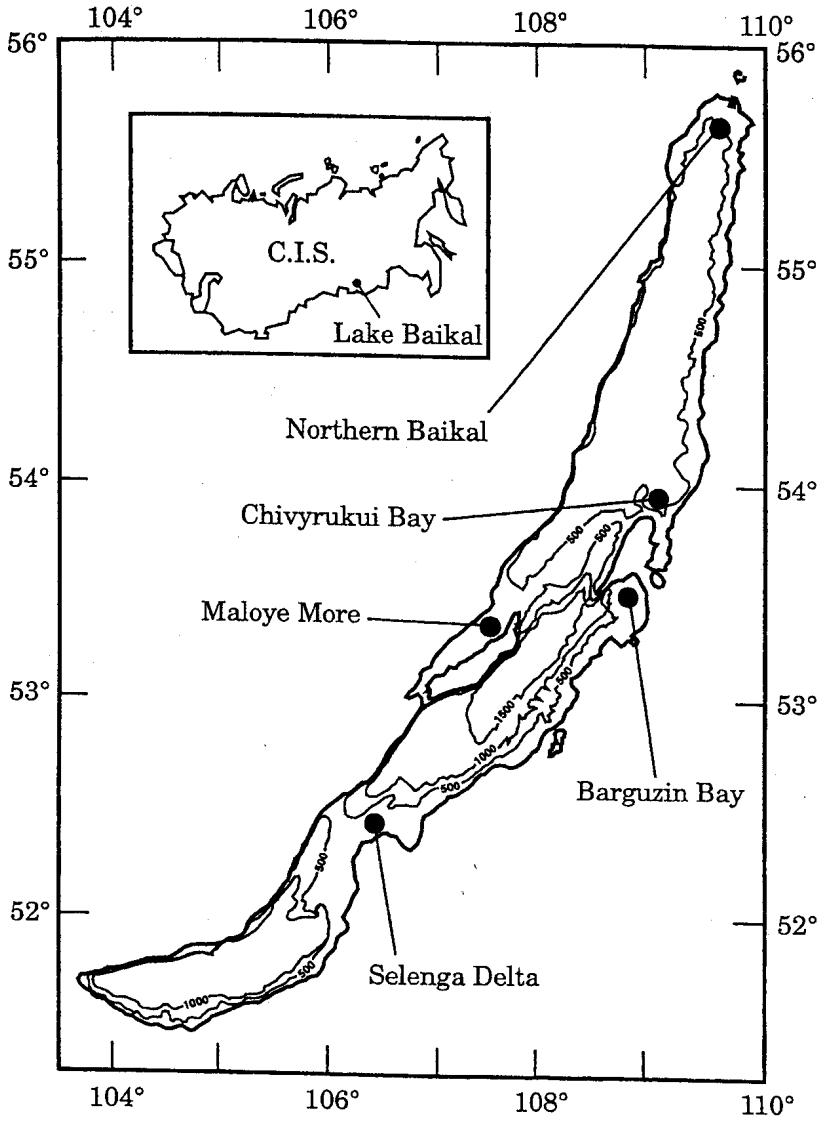

Fig. 1. Map of Lake Baikal sampling locations. The 500-, 1000-, and 1500-m depth contour lines are indicated.

of Fisheries research vessel *Ichthyolog* during June 7–22, 1995. Individual samples were categorized to morphotype in the field by sampling location and depth as well as gross morphological appearance. Fish that represented each morphotype from each netting location were photographed for morphometric analysis in a separate study. The results of the morphometric analysis corroborated morphotype assigments made in the field and were used to group fish by morphotype in this analysis.

Liver tissue was taken from individual specimens and preserved in either 95% ethanol or a modified Queen's buffer (0.25 M EDTA, 10 mM Tris buffer, 20% DMSO, saturated with NaCl, modified from SEUTIN et al. 1991), and sent to the Great Lakes Science Center for genetic analysis. We extracted total genomic DNA from tissue with the ion binding resin Chelex-100 (Bio-Rad Laboratories[1], WALSH et al. 1991). Samples were boiled in a solution of 5% weight:volume Chelex-100 resin and sterile distilled water, then snap-chilled on ice for at least 15 minutes prior to using the extract as a template to amplify specific gene products via the polymerase chain reaction (Perkin-Elmer Applied Biosystems, Foster City, California[1]). We successfully amplified mitochondrial genes for the control region (D-loop), 16S rRNA, NADH 5/6, and NADH 2. PCR amplifications were performed using Ampli-Taq DNA polymerase and PCR buffer II supplied by the manufacturer (Perkin-Elmer Applied Biosystems, Foster City, California[1]), 2.0–6.0 mM MgCl2, 200 µM dinucleotide mix, and 0.1 µM of each oligonucleotide primer, with 2.0–20.0 µl of the Chelex supernatent used as amplification target. PCR-amplified products were fractionated through 1% agarose gels and Synergel (a cellulose-based sieving agent, Diversified Biotech, St. Louis, MO[1]), 1 X TAE (0.04M Tris-acetate, 0.001M EDTA), post-stained with ethidium bromide, and visualized with long-wave ultraviolet light (SAMBROOK et al. 1983).

Following amplification of the specific gene products, the samples were surveyed for genetic variation by digesting the DNA products with a suite of type II restriction enzymes having 4- to 8-base recognition sequences. Enzymatic digestions were performed according to the manufacturer's instructions (New England Biolabs, Beverly, MA[1]). The 33 restriction enzymes used in the survey included *Acc I, Aci I, Alu I, Apa I, Asc I, Ase I, Ava II, Ban I, Ban II, Bfa I, BssA I, BssH I, BstU I, Dde I, Dpn II, Eag I, Hae III, HinP I, Kas I, Mse I, Msp I, Nae I, Nci I, Nde I, Nla III, Not I, Nsi I, Pst I, Rsa I, Sac I, Sma I, Ssp I,* and *αTaq I*. Each amplified gene locus was digested with up to 20 restriction enzymes of non-overlapping recognition sequences. Restriction digestion products were electrophoresed in 4.0% agarose gels plus Synergel, post-stained with ethidium bromide, and visualized with long-wave ultraviolet light.

Restriction site haplotypes for each locus/enzyme combination were assigned alphabetic designations in order of decreasing frequency. Restriction fragments were sized in comparison with known molecular weight and size standards. Size standards and positive and negative controls were run concurrently on each electrophoretic gel to verify size homology. Restriction sites were inferred from multiple enzyme digests for each locus. Composite haplotypes were used to define different genetic lineages for statistical analysis. Descriptive statistics (percent sequence divergence between lineages, mean number of pairwise differences, average gene diversity over loci) and analytical statistics (analysis of molecular variance) were calculated using the Arlequin Ver. 1.1 statistical software program (SCHNEIDER et al. 1997). Hierarchical groupings for AMOVA were arranged by geographic location and morphotype to address the alternative hypotheses that gene flow is affected by geographic or phenotypic factors. Clustering comparisons were performed using the NEIGHBOR option in Phylip Ver 3.5 (FELSENSTEIN 1983) with a matrix of pairwise genetic distances. Confidence estimates and a consensus branching diagram were estimated over 5000 bootstrap replicates of pairwise genetic distance matrices using the SEQBOOT, GENDIST, NEIGHBOR, and CONSENSUS options of Phylip Ver. 3.5.

[1] Mention of tradenames does not imply U.S. Government endorsement of commercial products.

Results

Most of the observed genetic variation among the omul populations sampled for this study was concentrated in the control region of mitochondrial DNA. The genetic variation defined by the RFLP analysis revealed 11 different composite haplotypes, of which only 2, OM1 and OM7 were widely distributed (Table 1). The OM1 haplotype was present in all populations except the benthic form from Chivyrukui Bay (n = 2). OM7 was present in all populations except those from the Selenga Delta. Among the samples from the Selenga Delta, OM1 and OM8 were most common; OM8 differs from OM7 by two restriction sites in the mtDNA control region. A parsimony network of the 11 mtDNA haplotypes is depicted in Figure 2.

Substructuring of populations was mainly by sample location and there was no evidence of discrete population structuring by morphotype. Heterozygosity and genetic diversity estimates for sample groups (grouped by sample location and morphotype) are listed in Table 2. The most common haplotypes (OM1, OM7, and OM8) were shared across all morphotypes, but not equally distributed across all sample locations. Differences in haplotype distributions were more noticeable across sample locations, where rare haplotypes were uniquely distributed in three of the five locations. Two locations, Barguzin Bay and Chivyrukui Bay, had the same complement of haplotypes, but slightly different frequencies (Table 3).

A hierarchical analysis of variance (AMOVA, Excoffier et al. 1992) showed that among individual groups, 88% of the variation was attributed to variation within location/morphotype combination, and 12% of the variation could be allocated between groups across all sample locations and morphotypes. When groups were defined by sample location alone, 87% of the variation was attributed to within-group variation, 5% among morphotypes within sample location, and 8% between sample locations (Table 4). A similar hierarchical analysis was performed to test the effect of morphotype on population structuring. In this AMOVA, 15% of the

Table 1. Composite haplotype and restriction site profiles for Lake Baikal omul. Restriction site profiles are grouped by restrictase in the same order as the haplotype profile. All informative variable sites were located within a 500-bp region of the mitochondrial DNA control region (CR).

	Dde I	Rsa I	Ava II	Dpn I	Mse I	Msp I	Restriction sites
OM 1	A	A	A	A	A	A	10 10 1110 110 11 11
OM 2	A	A	A	A	A	B	10 10 1110 110 11 00
OM 3	A	A	A	A	B	A	10 10 1110 110 10 11
OM 4	A	A	A	B	A	A	10 10 1110 111 11 11
OM 5	A	A	B	A	A	A	10 10 1101 110 11 11
OM 6	A	B	A	A	A	A	10 11 1110 110 11 11
OM 7	B	A	A	A	A	A	11 10 1110 110 11 11
OM 8	B	A	A	A	A	B	11 10 1110 110 11 00
OM 9	B	A	B	A	A	A	11 10 1101 110 11 11
OM 10	B	A	B	A	A	B	11 10 1101 110 11 00
OM 11	B	B	A	B	A	A	11 11 1110 111 11 11

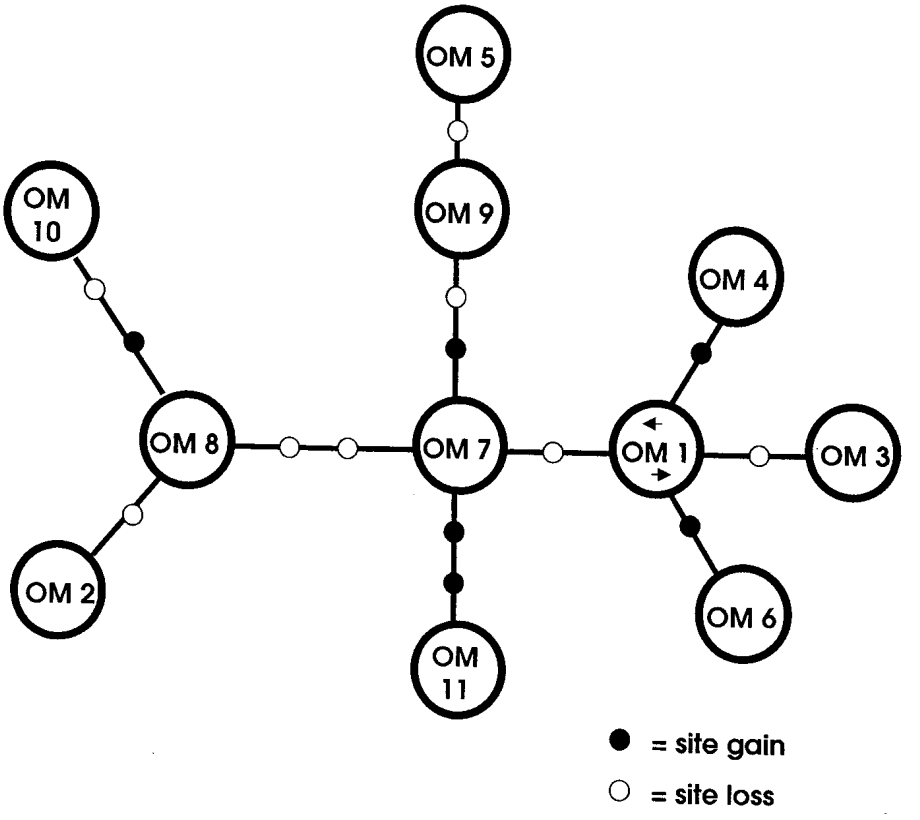

Fig. 2. Parsimony network of omul haploytpes determined from PCR-RFLP of an 800-bp segment of the mtDNA control region. Open circles represent site losses and filled circles represent site gains relative to the restriction site profile of the most common haplotype, OM1.

Table 2. Estimates of genetic diversity based on RFLP site differences in the mitochondrial DNA control region among omul sampled from Lake Baikal.

	Morphotype	Gene Diversity	Mean no. pairwise differences (π)	Nucleotide Diversity
Northern Baikal	Littoral	0.673 ± 0.123	0.982 ± 0.718	0.065 ± 0.054
Maloye More	Littoral	0.621 ± 0.087	0.864 ± 0.652	0.057 ± 0.049
	Pelagic	0.500 ± 0.136	0.923 ± 0.679	0.061 ± 0.051
Selenga Delta	Littoral	0.509 ± 0.101	1.527 ± 0.989	0.102 ± 0.074
	Pelagic	0.679 ± 0.112	2.231 ± 1.313	0.149 ± 0.098
	Benthic	0.538 ± 0.114	1.659 ± 1.037	0.111 ± 0.077
Barguzin Bay	Littoral	0.559 ± 0.083	0.632 ± 0.519	0.042 ± 0.039
	Pelagic	0.509 ± 0.101	0.509 ± 0.464	0.034 ± 0.035
Chivyrukui Bay	Littoral	0.182 ± 0.144	0.182 ± 0.253	0.012 ± 0.019
	Pelagic	0.500 ± 0.128	0.500 ± 0.466	0.033 ± 0.035
	Benthic	0	0.0	0

Table 3. Distribution of mtDNA haplotypes among Lake Baikal omul by sampling location and morphotype. Row frequencies are in parentheses.

Region	Morphotype	OM1	OM2	OM3	OM4	OM5	OM6	OM7	OM8	OM9	OM10	OM11
Northern Baikal n = 11	Littoral n = 11	6 (0.55)				1 (0.09)	3 (0.27)	1 (0.09)				
Maloye More n = 25	Littoral n = 12	6 (0.50)	1 (0.08)					5 (0.42)				
	Pelagic n = 13	9 (0.69)	3 (0.23)		1 (0.08)							
Selenga Delta n = 38	Littoral n = 11	7 (0.64)							4 (0.36)			
	Pelagic n = 13	7 (0.54)							3 (0.23)	2 (0.15)	1 (0.18)	
	Benthic n = 14	9 (0.64)							4 (0.29)			1 (0.07)
Barguzin Bay n = 28	Littoral n = 17	6 (0.35)		1 (0.05)				10 (0.59)				
	Pelagic n = 11	7 (0.64)						4 (0.36)				
Chivyrukui Bay n = 22	Littoral n = 11	10 (0.90)		1 (0.09)								
	Pelagic n = 9	6 (0.67)						3 (0.33)				
	Benthic n = 2							2 (1.00)				

variation was attributed to differences among sample locations within a morphotype. The variation between morphotypes was virtually zero (Table 4).

Relationships among the individual populations were compared in a neighbor-joining algorithm (Sneath & Sokal 1981) based on Cavalli-Sforza-Edwards chord distance among sampled populations. Figure 3 represents a consensus arrangement from 5,000 bootstrap replicates

Table 4. Hierarchical partitioning of genetic variance among Lake Baikal omul samples analyzed with AMOVA (Excoffier et al. 1992). Most of the variation was partitioned within groups identified by sample location and morphotype. Virtually no variation was partitioned among the different morphotypes across geographic location.

	df	Variance	Percent of total	P[2]	Φ statistic
Among all groups (collection site/morphotype)	10	0.07	12.22	< 0.001	Φ_{ST} = 0.122
Among collection sites	4	0.05	8.51	0.889	Φ_{CT} = 0.085
Among morphotypes within collection site	6	0.03	4.75	0.001	Φ_{SC} = 0.052
Among morphotype	2	0.00	0.00	0.889	Φ_{CT} = –0.041
Among collection sites within morphotype	8	0.08	11.00	0.001	Φ_{SC} = 0.145
Within group (collection site/morphotype)	113	0.51	87.78	< 0.001	Φ_{ST} = 0.132

[2] Probability of getting more extreme variance estimates out of 1,000 permutations.

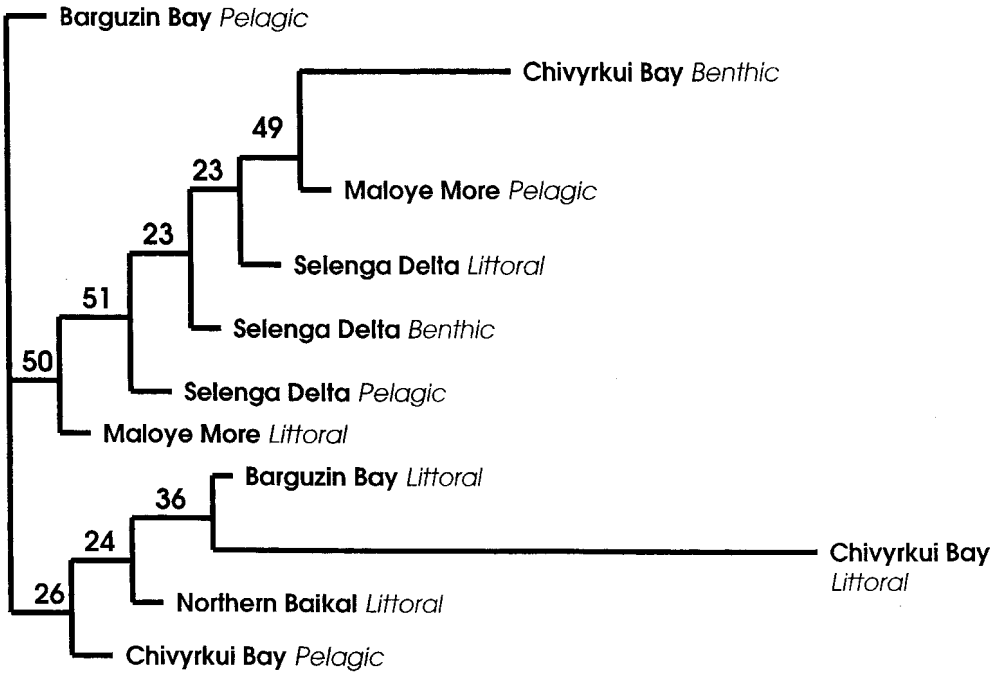

Fig. 3. Neighbor-joining dendrogram based on Cavalli-Sforza-Edwards chord distances among omul samples collected from Lake Baikal. Numbers on branches refer to the percent of trees from 5000 bootstrap replicates that showed the same arrangement.

of the genetic distance matrix generated in GENDIST from PHYLIP 3.1. There is no clear segregation of sample groups by morphotype. However, there is some minor geographic substructuring in which samples from contiguous areas Chivyrukui Bay, Barguzin Bay, and Northern Baikal littoral zones group together. In addition, all samples from Maloye More and Selenga Delta group together on a relatively well-supported branch.

Discussion

Restriction site profiles of the control region of the mitochondrial DNA among omul populations from Lake Baikal show no strict correspondence to differences in morphotype. Most of the mtDNA variation among morphotypes was characterized by slight frequency differences among the most common haplotypes. Some haplotypes that were uniquely present within a morphotype were either found in only a single individuals or among a small number of individuals from one location. In contrast, differences among geographic regions were more pronounced with the presence or absence of haplotypes closely related to haplotypes shared among a larger proportion of individuals across regions. For example, the distribution of the OM7 and OM8 haplotypes was disjunct between regions, but within a region the haplotype was com-

monly distributed across morphotypes. The greater amount of genetic partitioning among sample locations relative to that allocated between morphotypes corroborates the morphometric study (BRONTE et al. 1999) in which classification more accurately assigned individuals to sample location than to morphotype.

Previous studies of morphological variation among Lake Baikal omul (SMIRNOV et al. 1987, BRONTE et al. 1999) suggested that traditional morphological character suites could be used to categorize the different omul morphotypes, but that classification among morphotypes was most accurate within a defined geographic region. In contrast, the genetic evidence suggests that the same level of divergence has not evolved among morphotypes with respect to mitochondrial DNA genetic variation, although genetic differences are present on a geographic scale. Studies of serological, isozyme, and mtDNA variation among various omul populations have also demonstrated the presence of genetic differences on a geographic scale (TALIEV 1941, MAMONTOV & YAKHNENKO 1987, SUKHANOVA et al. 1996). As in this study, previous genetic analyses of Lake Baikal omul have shown that intrapopulation variation is responsible for most mtDNA diversity detected.

Geographic differences among the genetic characteristics of the sampled populations are also reflected in the neighbor-joining diagram (Fig. 3). The lack of discrete population definition in the neighbor-joining diagram by morphotype or geographic area more likely reflects the collection of samples from feeding aggregations rather than the spawning structure of omul populations in Lake Baikal. However, pelagic omul that feed in Maloye More are thought to spawn in the Selenga River, and samples from these two locations group together on a well-supported branch in the neighbor-joining diagram. The grouping of the littoral forms from Northern Baikal, Barguzin Bay, and Chivyrukui Bay on one branch may similarly reflect the mixing of littoral populations referred to in previous studies (SMIRNOV 1992).

The modern appearance of Lake Baikal dates to approximately 100,000 ybp (RESHETNIKOV 1980, MATS 1990). However, recent radiation of most coregonine species is considered to have occurred at the end of the Pleistocene (10–30,000 ybp; RESHETNIKOV 1992) and *Coregonus autumnalis migratorius* are thought to have colonized the Baikal region during the Quaternary from the Arctic Ocean (CHERSKY 1877 as in KOZHOVA & IZMEST'EVA 1998). We would not expect to find significant levels of divergence in mtDNA characteristics among populations that are recently diverged (DOWLING et al. 1996). Rather, differences are more likely to appear as frequency shifts than discrete presence or absence of lineages (WILSON et al. 1987, WARD et al. 1989). Our samples support this hypothesis because the haplotypes that appear to be unique to a particular location or population are related to their closest relative by one or two restriction site losses.

While our study shows that there is overlap in genetic characteristics among the three omul morphotypes, it also supports the hypothesis that some barriers to gene flow exist on a geographic scale. The apparent lack of distinct genetic divergence among populations known to spawn at different times and places (SMIRNOV et al. 1987) may be due to several factors. Our samples were not collected at specific spawning locations, but rather reflect aggregations related to resource use. Alternatively, genetic homogenization may be an artifact of recent artificial propagation efforts in which eggs for hatchery rearing are sampled across spawning locations and spawning times (SOKOLOV 2002). Further investigations of genetic divergence among *C. a. migratorius* morphotypes should proceed with additional genetic markers, such as microsatellite DNA, which are able to partition genetic variation at the population level. In addition,

questions of morphotype divergence at the population level should proceed with samples collected from spawning aggregations.

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