Genetic and Morphological Differentiation between Dwarf and Normal Size Forms of Lake Whitefish (*Coregonus clupeaformis*) in Como Lake, Ontario[1]

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Normal and dwarf size forms of lake whitefish (*Coregonus clupeaformis*) from Como Lake, Ontario, were sampled at spawning time and examined for differences in electrophoretic, mtDNA, and morphological characteristics to test the hypothesis of reproductive isolation and provide clues regarding evolutionary origin. Of the 36 enzyme loci examined, 33 were fixed for the same alleles in both dwarf and normal lake whitefish. At the three polymorphic loci, allele frequencies were not statistically different between dwarfs and normals. mtDNA analysis revealed five different haplotypes. The same mtDNA haplotype was the most common in both dwarf and normal lake whitefish, but there was a statistically significant difference in haplotype frequencies between the two size forms. Discriminant and principal component analyses demonstrated highly significant morphological differences between dwarfs and normals. Because the two size morphs spawn in the same place at the same time, it is most likely that genetic differences, not different rearing environments, underly the observed morphological differences. mtDNA haplotypes derived from both the Mississippi and Atlantic glacial refugia are present in Como Lake lake whitefish, raising the possibility of an allopatric divergence for the two forms; however, this hypothesis requires testing by genetic comparisons of other sympatric populations in Ontario.

On a échantillonné les formes normale et naine du grand corégone (*Coregonus clupeaformis*) du lac Como (Ontario) au moment de la fraye, et l'on a examiné les différences de migration électrophorétique, l'ADNmt et les caractéristiques morphologiques, afin de vérifier l'hypothèse relative à l'isolement reproductif et d'obtenir des indices concernant leur origine évolutive. Sur les 36 loci enzymatiques étudiés, 33 présentaient les mêmes allèles chez les formes naine et normale du grand corégone. Dans le cas des trois loci polymorphes, on n'a pas observé de différence statistique entre les fréquences des allèles chez les deux formes. L'analyse de l'ADNmt a révélé la présence de cinq haplotypes différents. On a constaté que le même haplotype d'ADNmt était le plus commun à la fois chez les grands corégones nains et ceux de taille normale, mais qu'il y avait une différence statistique importante dans la fréquence des allèles chez les deux formes. Les analyses discriminantes et les analyses en composantes principales indiquent qu'il existe des différences morphologiques très importantes entre les formes naine et normale. Ces formes de taille différente frayant toutes deux au même endroit et au même moment, il est fort probable que les différences morphologiques observées soient dues à des différences génétiques plutôt qu'à des différences dans les milieux où se produit l'alevinage. Les haplotypes d'ADNmt provenant du refuge glaciaire naturel du Mississippi et de celui de l'Atlantique sont présents chez le grand corégone du lac Como, ce qui indique la possibilité d'une divergence de nature allopatrique chez les deux formes; toutefois, cette hypothèse doit être vérifiée par des comparaisons génétiques avec d'autres populations sympatriques en Ontario.

Many salmonid species include sympatric populations, which are often characterized by distinct life histories and can be separated by their morphology and/or genetic properties (Behnke 1972). The origin and isolating mechanisms of these sympatric populations are of particular interest in the study of speciation mechanisms. The two con-trasting views of speciation for such sympatric populations are that they have either developed in sympatry or are the result of secondary contact between two forms which diverged allopatrically.

The lake whitefish (*Coregonus clupeaformis*) in North America constitutes a species complex with five glacial races (Bernatchez and Dodson 1991; Bodaly et al. 1992; Foote et al. 1992). The races have distinct genetic characters and their distribution is mainly allopatric. In addition, several instances of sympatric lake whitefish forms within the same lake are known (Lindsey et al. 1970; Bodaly 1979; Bernatchez and Dodson 1990a). Most of these forms are easily recognizable by differ-

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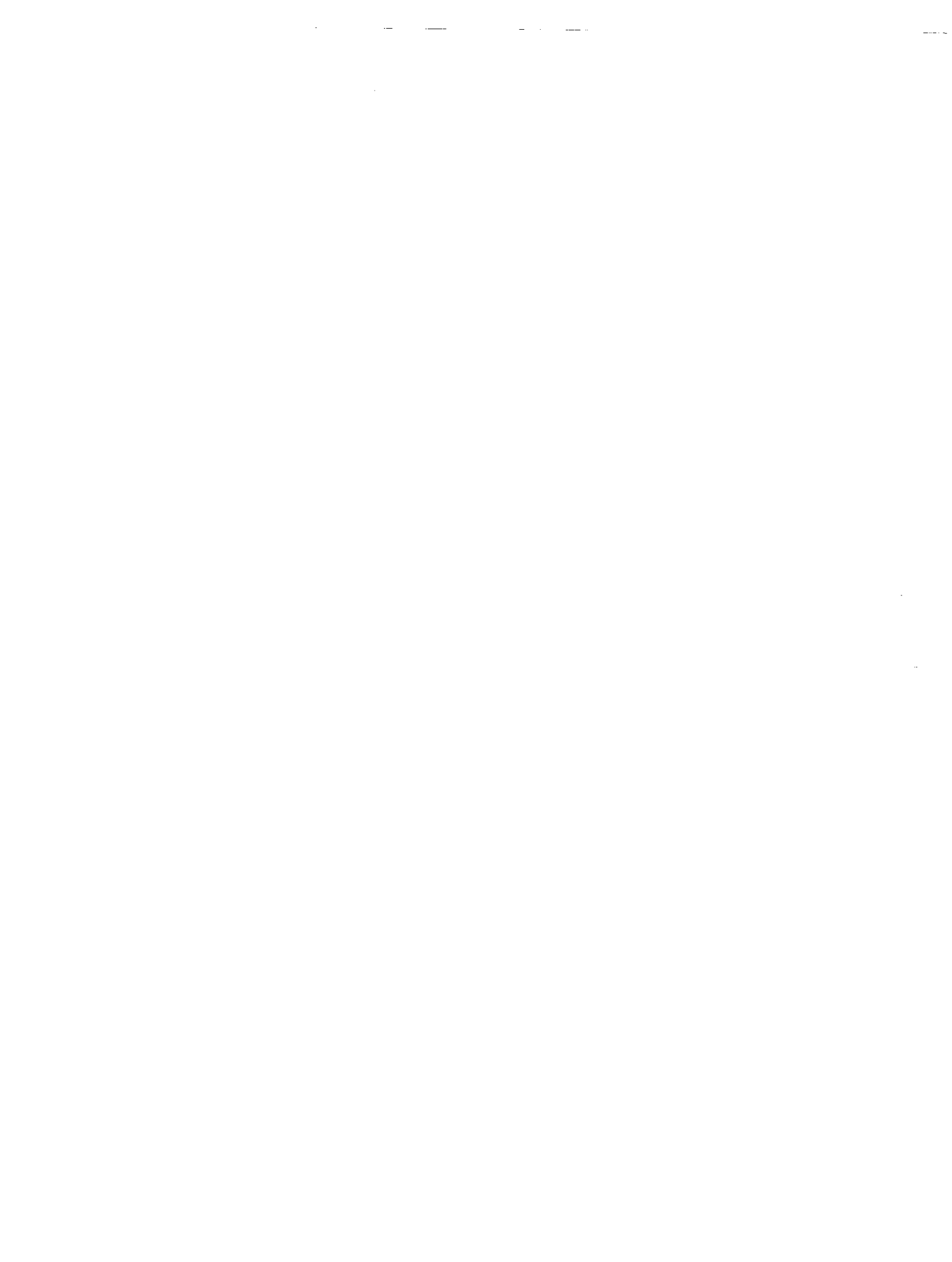
ences in their size and gill raker count. The presence of an additional sympatric pair of lake whitefish was recently documented in Como Lake (Bodaly et al. 1991a). The size distribution of spawning fish was distinctly bimodal with modes at 170–179 and 280–289 mm fork length. For both forms, the modal gill raker count was 24, but dwarfs had significantly lower mean gill raker counts (24.4 versus 25.0). Besides size, dwarfs and normals also differed significantly in growth rate, reproductive age, and generation length. Dwarfs grew much slower, matured earlier, and their generation length was short compared with normals (Bodaly et al. 1991a). Thus, dwarfs compensate their lower fecundity by earlier maturity and shorter generation length. The objective of this study was to investigate genetic (isozyme and mtDNA) and morphological differences between the sympatric lake whitefish populations in Como Lake in order to (1) test the hypothesis that the sympatric populations are reproductively isolated and (2) provide clues regarding the evolutionary origin of the sympatric pairs.

Materials and Methods

Como Lake is located in northern Ontario (47°55′N, 83°30′W), near the town of Chapleau, in the Michipicoten River basin tributary to Lake Superior. It has a surface area of 1596 ha, a mean depth of 9.4 m, and a typical coolwater fish community, with the exception that no ciscoes are present (Bodaly et al. 1991a).

Lake whitefish were captured with gill nets of mesh sizes 3.8–13.3 cm stretched measure on a spawning shoal overnight on 25–26 October 1989. Additional samples for mtDNA analyses were captured on 28–30 August 1990 with similar gill nets, away from spawning areas. Fish were immediately placed on ice and frozen within 12 h of capture. Eggs were stripped from 44 normals and 36 dwarfs and transported on ice to the laboratory for mtDNA extraction.

The isozyme products of 36 genetic loci were analyzed by starch gel electrophoresis as described in Bodaly et al. (1991b). The enzyme loci scored were the same as given in Bodaly et al. (1991b) except for the omission of CK-B and LDH-C, expressed in eye tissue, and the addition of esterase (EST) which is most strongly expressed in liver.

mtDNA was purified from liver and egg tissues by a rapid extraction method (Bernatchez et al. 1988). mtDNA aliquots were digested with eight hexameric (DraI, HindIII, PvuII, SmaI, XmnI, BglI, PstI, BamHI), four multihexameric (AvaI, BanI, HaeII, HincII), and one multipentameric (AvaII) restriction enzymes. mtDNA fragments were electrophoretically separated on 0.8 and 1.2% agarose gels at 25 V run overnight. Restriction fragments were revealed by either ethidium bromide staining or hybridization with a highly purified radiolabelled total mtDNA probe (Bernatchez and Dodson 1990b). Fragments were sized by comparison with digests of phage lambda DNA with HindIII and EcoRI–HindIII double digest. No attempt to visualize fragments less than 350 base pairs was made. Distinct single endonuclease patterns were identified by a specific letter in order of appearance. Each fish was assigned a multiletter code which described its composite mtDNA genotype. Intrapopulation diversity of mtDNA lineages was estimated with Nei and Tajima's (1981) nucleon diversity index. Heterogeneity in the frequency of genotypes between populations was analyzed using the likelihood ratio chi-square test (G^2, SAS statistical package).

Nine meristic variables were counted as shown in Fig. 1C and 1E: LLS (lateral line scales), SPS (suprapelvic scales), ULS (scales above the lateral line), DRC (dorsal ray count) (Lindsey 1962), ARC (anal ray count), PEC (pectoral ray count), PVC (pelvic ray count) (Hubbs and Lagler 1974), UGR (upper gill raker count), and LGR (lower gill raker count) (Bodaly 1979).

Twenty morphometric variables were measured (Fig. 1A, 1B, 1D, 1E). The following were measured between topographic features but parallel to the long axis of the body to the nearest 0.1 mm using dial calipers: POL (preorbital length: tip of the snout to the anterior fleshy margin of the orbit), OOL (orbital length: anterior fleshy margin of the orbit to the posterior fleshy margin), PSL (postorbital length: posterior fleshy margin of the orbit to the most posterior projection of the bony operculum), TTL (trunk length: posterior end of the operculum to the origin of the dorsal fin), DOL (dorsal fin length: origin of dorsal fin to the posterior edge of the fin behind the final ray), LUL (lumbar length: end of the dorsal fin to the origin of the anal fin), ANL (anal fin length: origin of anal fin to the posterior edge of the fin), CPL (caudal peduncle length: end of anal fin to the end of the body (structural base of the caudal rays as indicated by a crease when the tail rays are flexed) (Lindsey 1962)), and STL (standard length) (Lindsey 1962). The following variables were measured parallel to the vertical axis of the body: HDD (head depth: vertical depth through the pupil of the eye from the dorsal surface of the cranium to the ventral edge of the gular region), BDD (body depth: vertical depth from the dorsal origin to the ventral surface of the body, and CPD (caudal peduncle depth) (Hubbs and Lagler 1974). IOW (interorbital width), MXL (maxillary length), MXW (maxillary width), and GRL (lower gill raker length) followed Lindsey (1962). The following variables were measured along the axis of the individual body element: PCL (pectoral length: most basal part of the first ray distally to the end of the fin when it is laid flat against the body), PVL (pelvic length: most basal part of the first ray where it forms a crease with the body distally to the most posterior point of the fin when laid flat against the body), ADL (adipose length: distance from the point where skin and scales meet at the anterior end of the fin posteriorly to the free margin of the fin), and LAL (lower arch length) (Bodaly 1979).

Morphometric variables were standardized relative to fish size using both ratios of body part to standard length and analysis of covariance with standard length as the covariate. Residual values, the difference between the observed and predicted size of the body part, from the within-groups regression line for both forms were used to estimate the size of body parts relative to a standard common to both forms (Reist 1985, 1986). The meristic and size-adjusted data sets were analyzed univariately (t-tests) and multivariately (discriminant analysis and principal components analysis) to test the hypothesis of identity of the two forms. To ensure that sexual differences did not bias results, all data were initially examined for differences between sexes.

Results

Electrophoresis

Only three of the 36 genetic loci examined were polymorphic, namely G3PDH-1* and isoloci sMDH-B1,2*. For both enzyme systems, variation conformed to Hardy–Weinberg expectations. Allele frequencies were almost identical in dwarf and normal lake whitefish at the G3PDH-1* locus and were not significantly different at isoloci sMDH-B1,2* (Table 1). In the remaining 33 loci, both size forms were fixed for the same alleles. Both forms
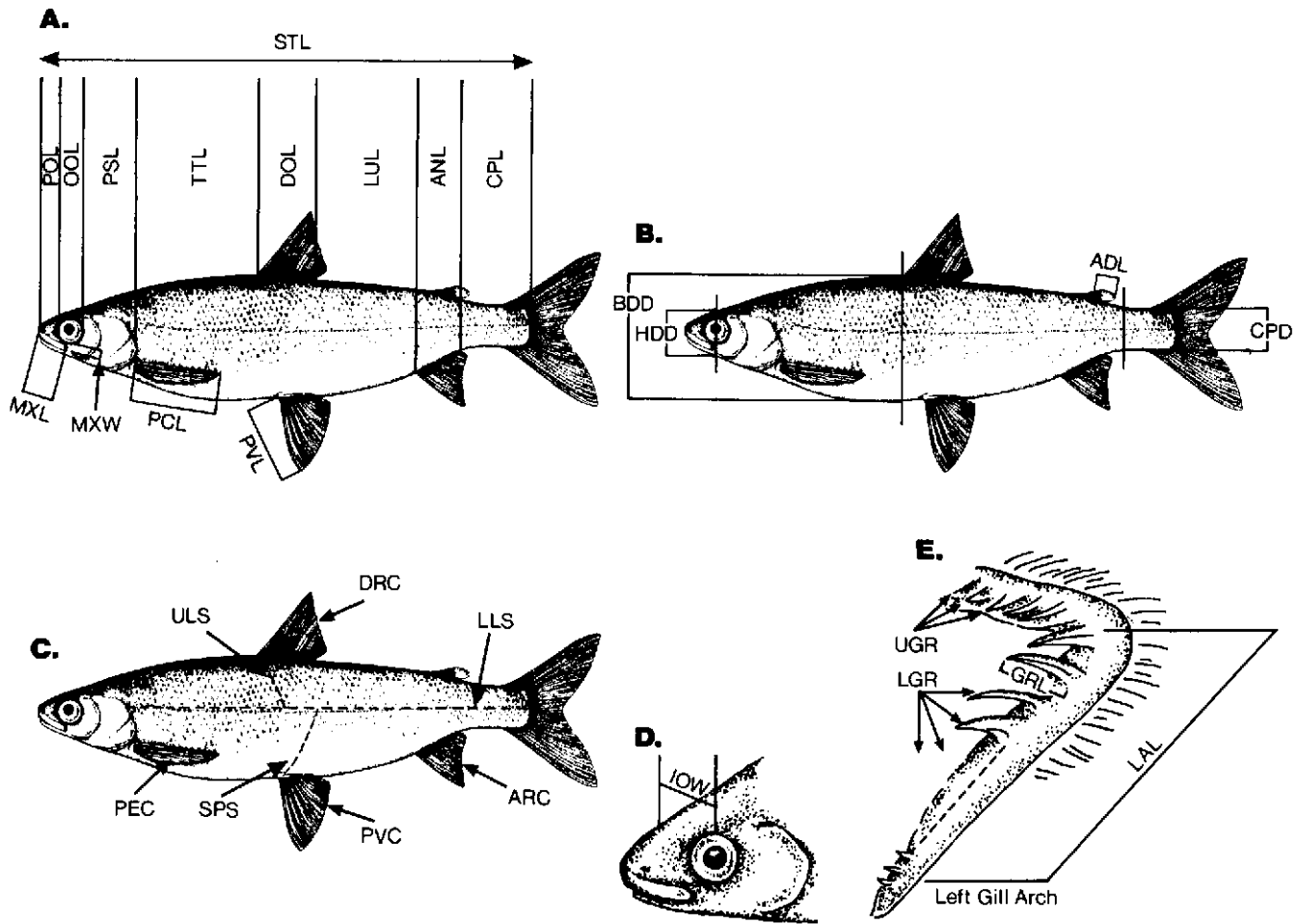
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FIG. 1. Meristic and morphometric measurements. See text for abbreviations.

TABLE 1. Allele frequency estimates for dwarf (n = 51) and normal (n = 50) lake whitefish in Como Lake, Ontario. The remaining 33 loci were fixed for the same allele in both forms. Allele frequencies at *sMDH-B1,2** isoloci were estimated from the maximum likelihood procedure of Waples (1988). Allele frequencies at these isoloci were not significantly different between dwarfs and normals (first locus, G statistic = 3.15, P > 0.05; second locus, G statistic = 0.38, P > 0.05).

Locus and allele	Dwarf	Normal
G3PDH-1*		
0	0.69	0.69
−85	0.31	0.31
sMDH-B1,2* isoloci		
First locus		
100	0.27	0.39
120	0.73	0.61
Second locus		
100	0.80	0.76
120	0.20	0.24

TABLE 2. Definition and frequency distribution of mtDNA haplotypes, sample sizes, and estimated nucleon diversity index for dwarf and normal lake whitefish in Como Lake. Composites represent the following order of restriction enzymes: *Ava*I, *Ava*II, *Hinc*II. Corresponding fragment patterns are described in Bernatchez and Dodson (1991) except for *Ava*II "M" which differs from "A" by a single site loss. Other enzymes were fixed for fragment pattern "A."

Haplotype		Dwarf	Normal
1	AAA	30	35
2	AAB	1	8
3	AFA	0	1
4	CAA	4	0
5	AMA	1	0
Total		36	44
Nucleon diversity		0.30	0.34

The alleles present in both lake whitefish forms were those that are either fixed or common in lake whitefish that survived Wisconsin glaciation in the Mississippi, Atlantic, and Acadian glacial refugia (Bodaly et al. 1991b, 1992).

MtDNA Analysis

Five mtDNA haplotypes were observed among the 80 lake whitefish analyzed (Table 2). All haplotypes were only slightly differentiated, differing by one or two restriction sites. The first four corresponded to haplotypes 1, 17, 23, and 24, respectively,

showed quite low genetic variability, lacking the *G3PDH-1*(210)*, *slDHP-3*(125)*, and *slDHP-4*(118)* alleles which are common in other Ontario lake whitefish populations. The average expected heterozygosity was only 0.04 for both dwarfs and normals; allozyme genetic diversity was much lower than in other nearby lake whitefish populations (Bodaly et al. 1992).

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as described in Bernatchez and Dodson (1991). Haplotype 5 had not been observed previously and differed from haplotype 1 by a single *Ava*II site loss. Three haplotypes (3, 4, 5) have been observed only in Como Lake lake whitefish. mtDNA diversity values were intermediate between values observed for Mississipian and Atlantic populations (Bernatchez and Dodson 1991). Significant heterogeneity in the distribution of mtDNA haplotypes was revealed by the likelihood ratio chi-square test $(G^2 = 14.099, P = 0.007, df = 4)$.

Meristic Counts and Morphometric Measurements

The distribution of sexes in the samples was 25 male and 26 female dwarfs and 26 male and 24 female normals. Two-way analysis of variance (form and sex as levels) indicated that only lateral line scales, anal rays, anal length, caudal peduncle depth, and pelvic fin length differed between sexes when the effects of form were held constant. Within forms, only lateral line scales were significantly different between sexes for normals and dorsal fin origin, anal length, caudal peduncle depth, and pelvic fin length were different between sexes for dwarfs. These results, together with the nearly equal sex ratios within both forms, indicate that the results below are free from biases due to sexual differences.

Five of the nine meristic variables were significantly different $(P < 0.05)$ between forms based on univariate analysis (Table 3). In all cases, the dwarf form exhibited a lower count than the normal form. Results obtained by nonparametric testing were similar. The multivariate test of the hypothesis of identity indicated a highly significant difference between the two forms $(P < 0.0001)$ (Table 3). The variables contributing most substantially to the discriminant axis were those exhibiting the greatest univariate differences: ULS, LLS, LGR, UGR, and PEC in decreasing order. A posteriori classification accuracy using the discriminant function was high for the normal form (47 of 49, 96% of fish classified correctly) but lower for the dwarf form (20 of 29, 69% of fish classified correctly). This implied substantial overlap of the groups as was evident in the plots of discriminant scores (Fig. 2) and as was confirmed by principal components analysis.

Fourteen of 19 morphometric variables (residuals) were significantly different $(P < 0.05)$ between forms based on univariate analysis (Table 4). The multivariate test of the hypothesis of identity indicated a highly significant difference between the two forms $(P < 0.0001)$ (Table 4). A posteriori classification accuracy of the discriminant function was high

for both forms (48 of 50, 96% correct for normals and 51 of 51, 100% correct for dwarfs). This implies very minimal overlap between forms in terms of body morphometry (Fig. 2), which is confirmed by principal components analysis and plots of scores on components.

Discussion

Our results indicate that lake whitefish in Como Lake show genetic differences and are therefore probably structured into two largely or wholly reproductively isolated subpopulations: dwarfs and normals. This conclusion is supported by significant differences in the frequency of mtDNA haplotypes between the two forms. Morphological differences observed also imply genetic differences between the two forms. Morphological variation in fish, both meristic and morphometric, is known to be influenced by both genetic and environmental factors. Therefore, the two forms differ in the genetic background of these characters, or in environments occupied at least during some critical time during development, or in both of these aspects. Because the two forms appear to spawn at the same time and together in at least some spawning locations (Bodaly et al. 1991a) and are therefore exposed to the same environment during development, genetic differences between them are probably at least partly responsible for the observed morphological differences. And dwarf and normal lake whitefish clearly exhibit different life histories with different growth rates, reproductive ages, and generation lengths. Parallel life history variation in Arctic char (*Salvelinus alpinus*) has been shown to have a genetic basis (Svedäng 1990). It seems likely that genetic differences also underly the life history differences between the Como Lake dwarf and normal lake whitefish.

The sympatric forms in Como Lake appear to have diverged to a lesser degree than other sympatric lake whitefish populations, which show divergence in allele frequency distributions and time and/or place of spawning in addition to morphological and life history characteristics (Fenderson 1964; Lindsey et al. 1970; Kirkpatrick and Selander 1979; Bodaly et al. 1988, 1992). This suggests that the divergence of the two forms is relatively recent. Furthermore, reproductive isolation may be incomplete and the two forms may still be exchanging genes. Because the two lake whitefish forms in Como Lake appear to spawn in the same place at the same time, differences in spawning behaviour, perhaps acting in concert with selection against hybrids or hybrid sterility, are most likely the basis for their reproduc-

TABLE 3. Meristic comparison of dwarf and normal lake whitefish in Como Lake. ns = nonsignificant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

| Variable | Mean | | t-test significance | Standard discriminant coefficient | Unstandardized discriminant coefficient |
	Dwarf	Normal			
LLS	74.7	77.7	***	0.549	0.177
SPS	7.8	7.9	ns	0.237	0.617
ULS	9.5	10.2	***	0.770	1.373
DRC	11.6	11.7	ns	0.205	0.335
ARC	11.9	12.2	ns	0.067	0.094
PEC	16.3	16.7	*	0.024	0.033
PVC	11.3	11.5	ns	0.090	0.171
UGR	7.9	8.2	*	0.283	0.500
LGR	16.4	16.7	*	0.320	0.493
Constant					-51.877
λ				0.885	

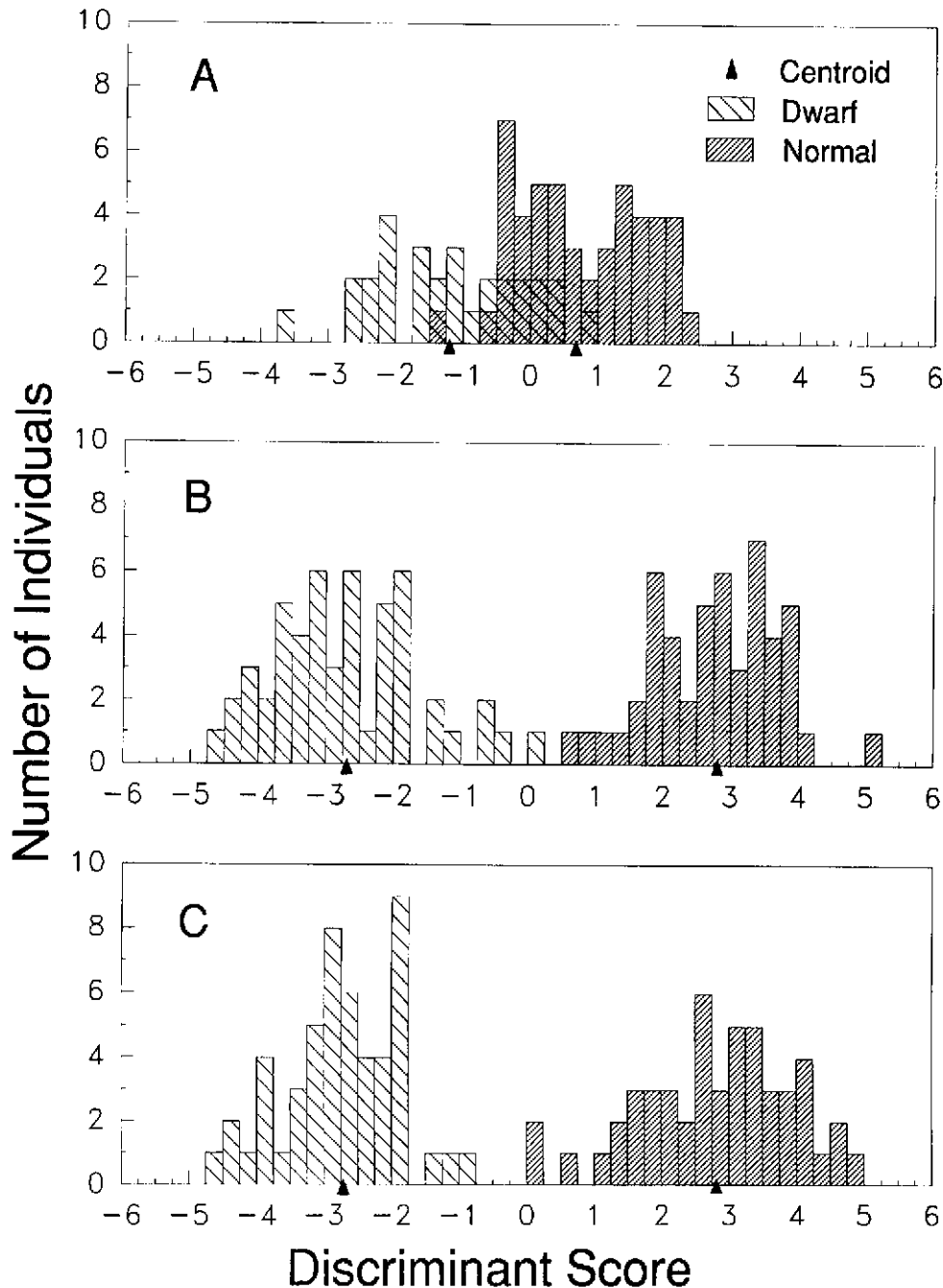*Can. J. Fish. Aquat. Sci., Vol. 50, 1993*

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Fig. 2. Discriminant analysis of (A) meristics, (B) ratios of morphometric variables, and (C) residuals.

tive isolation. The two forms may have preferences for different sizes of mates, similar to the presence of alternative reproductive strategies in landlocked and anadromous sockeye salmon (*Oncorhynchus nerka*) (Foote 1988). Selection will tend to favour more complete reproductive isolation if hybrid individuals are less fit than either of the parental types. Size preferences by spawning individuals can provide the explanation for both a mechanism of reproductive isolation following allopatric divergence and a mechanism of reproductive isolation for sympatric divergence. Further studies on spawning biology are necessary to establish the mechanism for reproductive isolation between the dwarf and normal lake whitefish in Como Lake.

Partial reproductive isolation also accounts for the distribution of differences between the two forms. A low level of nuclear gene flow can prevent differences in isozyme frequen-

cies. However, due to the maternal inheritance of mtDNA, nuclear genes could be passed from one form to the other without flow of mtDNA. Given a genetic basis for the size differences between forms, morphological differences may also be preserved in the face of gene flow.

Regarding the mode of origin of the Como Lake sympatric lake whitefish forms, there is both precedent and evidence which would tend to favour both of the contrasting hypotheses: recent divergence (i.e. postglacial) either sympatrically or during deglaciation and allopatric divergence in separate glacial refugia followed by secondary contact. Bodaly et al. (1992) examined sympatric lake whitefish populations in a number of Canadian lakes, utilizing allozyme allele frequencies, and concluded that the data best supported postglacial origins for such pairs. Allozyme data are, however, not definitive in determin-

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TABLE 4. Morphometric comparison of dwarf and normal lake whitefish in Como Lake. Sig. = univariate significance with ns = nonsignificant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; STD = standardized, UNSTD = unstandardized.

Variable	Residual Mean Dwarf	Residual Mean Normal	Sig.	Ratio (× 100) Mean Dwarf	Ratio (× 100) Mean Normal	Sig.	Discriminant coefficients Residual STD	Discriminant coefficients Residual UNSTD	Discriminant coefficients Ratio STD	Discriminant coefficients Ratio UNSTD
POL	0.115	−1.311	***	5.3	5.5	*	0.030	0.029	0.389	78.721
OOL	0.719	−0.416	***	5.9	4.7	***	0.076	0.112	−0.715	−195.629
PSL	0.149	−0.381	*	11.6	11.5	ns	0.239	0.191	0.092	15.195
TTL	−4.127	2.861	***	22.0	23.8	***	0.661	0.270	0.567	47.975
DOL	1.679	1.211	ns	11.6	11.6	ns	0.094	0.042	−0.170	−16.102
LUL	−1.313	4.309	***	19.2	19.8	ns	0.226	0.057	0.205	11.205
ANL	0.719	−0.699	***	9.3	9.5	ns	−0.326	−0.175	0.198	21.166
CPL	−3.391	−2.701	ns	11.7	11.1	*	0.571	0.218	−0.222	−16.381
HDD	0.909	−0.199	***	10.1	9.7	**	−0.045	−0.041	0.135	24.138
BDD	−2.047	−1.414	ns	22.7	24.0	***	0.197	0.088	0.412	36.672
CPD	0.481	0.462	ns	7.5	7.6	ns	0.287	0.306	0.111	23.637
IOW	0.028	−1.485	***	5.9	5.8	ns	−0.470	−0.497	0.017	3.327
MXL	1.401	−0.181	***	6.7	6.1	***	−0.388	−0.582	−0.271	−74.194
MXW	0.283	0.116	*	2.1	2.1	ns	0.226	0.599	0.102	56.318
PCL	2.714	−1.009	***	18.7	18.2	**	−0.306	−0.164	0.007	0.776
PVL	2.811	0.321	***	19.3	18.5	***	−0.172	−0.113	−0.091	−10.517
ADL	−0.518	2.430	***	6.8	5.9	***	0.489	0.199	−0.549	−45.937
GRL	0.169	−0.265	***	2.5	2.5	ns	−0.090	−0.191	0.222	96.332
LAL	0.063	0.041	ns	8.5	7.8	***	0.567	0.580	−0.309	−67.572
Constant								0.722		−8.660
λ							7.809		7.676	

ing racial origin for sympatric pairs which possibly involve the Mississippi, Atlantic, and Acadian glacial refuge races, such as those in Como Lake, because these races are less differentiated allozymically than other adjacent races such as the Mississippi and Bering (Bodaly et al. 1992). The allozyme evidence does tend to favour a recent origin for the Como Lake forms on the basis of their small genetic divergence and quite low heterozygosities. Low heterozygosities may indicate genetic drift during a founder event immediately following deglaciation and subsequent sympatric divergence. Numerous other salmonid species appear to have diverged locally into sympatric forms, including Arctic char, brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*) Atlantic salmon (*S. salar*) (see Foote et al. 1989 for a review and references), and, in the coregonid fishes, vendace (Vuorinen et al. 1981).

In contrast with this support for an hypothesis of recent, sympatric divergence, Bernatchez and Dodson (1990a, 1991) concluded, on the basis of mtDNA analyses, that sympatric dwarf and normal lake whitefish in the Allegash basin, Maine, have an allopatric origin representing two separate glacial races, namely the Atlantic and Acadian races. For the sympatric forms in Como Lake, the mtDNA evidence suggests an allopatric origin for the two morphs in the Mississippi and Atlantic refugia. One haplotype (No. 2, Table 2), which occurs predominantly in the normal morph, is characteristic of lake whitefish populations found in southeastern Quebec and is indicative of fish that probably survived the last continental glaciation in an Atlantic refugium (Bernatchez and Dodson 1991). An hypothesis of allopatric origin of the Como Lake forms would predict that the normal size form in other Ontario lakes supporting sympatric morphs (i.e. Opeongo and hopefully others to be discovered) would, like the Como Lake normal form, also show mtDNA haplotype 2. Also, haplotype 2 should be found

in a corridor between southern Quebec and Como Lake (and beyond), following a dispersal route utilizing glacial Lake Nippissing I (Underhill 1986).

These results have implications for the management and preservation of these two forms. The phenomenon of size variation in coregonids that results in sympatric forms as in Como Lake is not unique but is relatively uncommon. Therefore, management steps should be taken to ensure preservation of both forms of lake whitefish. Dwarf lake whitefish survive only in the absence of ciscoes (Bodaly et al. 1988). The introduction of ciscoes into Opeongo Lake, Ontario, appears to have resulted in a reduction in the abundance of the dwarf lake whitefish (Bodaly et al. 1991a). Also, the spread of rainbow smelt (*Osmerus mordax*) into lakes in Maine has apparently reduced the normal form of lake whitefish in lakes supporting two forms (L. Bernatchez, unpubl. data). Therefore, preservation of sympatric lake whitefish forms will require vigilance against the introduction of new species into lakes such as Como Lake.

Ackowledgments

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