

Morphological Variation of Siscowet Lake Trout in Lake Superior

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Abstract.—Historically, Lake Superior has contained many morphologically distinct forms of the lake trout *Salvelinus namaycush* that have occupied specific depths and locations and spawned at specific times of the year. Today, as was probably the case historically, the siscowet morphotype is the most abundant. Recent interest in harvesting siscowets to extract oil containing omega-3 fatty acids will require additional knowledge of the biology and stock structure of these lightly exploited populations. The objective of this study was to determine whether shape differences exist among siscowet populations across Lake Superior and whether these shape differences can be used to infer stock structure. Morphometric analysis (truss protocol) was used to differentiate among siscowets sampled from 23 locations in Lake Superior. We analyzed 31 distance measurements among 14 anatomical landmarks taken from digital images of fish recorded in the field. Cluster analysis of size-corrected data separated fish into three geographic groups: the Isle Royale, eastern (Michigan), and western regions (Michigan). Finer scales of stock structure were also suggested. Discriminant function analysis demonstrated that head measurements contributed to most of the observed variation. Cross-validation classification rates indicated that 67–71% of individual fish were correctly classified to their region of capture. This is the first study to present shape differences associated with location within a lake trout morphotype in Lake Superior.

A variety of morphotypes of the lake trout *Salvelinus namaycush* were historically present in the Laurentian Great Lakes (Strang 1854; Smith and Snell 1891; Lawrie and Rahrer 1973; Brown et al. 1981; Goodier 1981). However, with the exception of Lake Superior, most of this morphological diversity has been eliminated by predation of the sea lamprey *Petromyzon marinus* and overfishing (Krueger and Ihssen 1995). Similar morphological diversity has been recently described in large lakes in Canada (Blackie et al. 2003; Alfonso 2004; Zimmerman et al. 2006), which suggests that this is a common feature of lake trout biology in large, deep lakes. The siscowet lake trout, first described by Sweeny (1890), is the most abundant lake trout morphotype found in Lake Superior (Bronte et al. 2003). The siscowet is characterized by a short, convex snout; high fat content in the flesh and viscera; deep body; and short, thick caudal peduncle (Agassiz 1850; Thurston 1962; Eschmeyer and Phillips 1965;

Moore and Bronte 2001). These and other characteristics distinguish it from the two other principal morphotypes found in Lake Superior, the lean and humper lake trout, although there is considerable overlap in some features (Crawford 1966; Khan and Qadri 1970; Burnham-Curtis 1993; Burnham-Curtis and Smith 1994; Moore and Bronte 2001). Siscowet lake trout are principally found in waters with depths greater than 80 m (Sweeny 1890; Eschmeyer 1955; Lawrie and Rahrer 1973; Goodier 1981; Bronte et al. 2003) but appear to move to shallower water in late summer (Bronte et al. 2003). The fish are presumed to spawn over deep reefs (Hansen et al. 1995), but actual locations have not been identified. Spawning times vary from April to November (Sweeny 1890; Eschmeyer 1955; Bronte 1993). Siscowet populations are increasing in abundance and expanding their range into shallower waters typically inhabited by lean lake trout. The population increase may be associated with a return to a previously unrecognized state that existed before intense exploitation and sea lamprey predation (Bronte et al. 2003).

Interest in the life history, biology, and stock structure of the siscowet lake trout has increased in recent years. Siscowets were a part of the historical commercial harvest in Lake Superior, and at one time

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consumers preferred them over lean lake trout (Goode 1884), but demand for them has decreased. Siscowet lake trout contain very high levels of omega-3 fatty acids (Wang et al. 1990), which has human health benefits and may promote increased exploitation of the siscowet for fish oil. These populations, presently lightly exploited, represent a high degree of remnant genetic diversity (Page et al. 2004) among extant lake trout. Additional knowledge of their biology and stock structure is required to manage any fishery expansion properly.

Homings and site imprinting are behavioral stock-isolating mechanisms found in many salmonines, including lean lake trout (Pycha and King 1975; Horrall 1981). Recaptures of tagged lean lake trout in the Great Lakes indicate localized movements (Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007), suggesting that historical populations were probably composed of many spatially isolated stocks. Genetic evidence also suggests that many stocks existed historically (Krueger and Ihssen 1995) and still exist today (Page et al. 2004). In Lake Superior, wild populations of lean, humper, and siscowet lake trout differ significantly in microsatellite allele frequency (Page et al. 2004). Most of the variation observed was due to among-morphotype differences, but there is some evidence of geographic structuring of populations within morphotypes, which corroborates previous allozyme surveys (Dehring et al. 1981; Ihssen et al. 1988). It is likely that multiple stocks of siscowet lake trout exist in Lake Superior.

We previously quantified shape differences among the lean, humper, and siscowet lake trout in Lake Superior (Moore and Bronte 2001) via whole-body morphometrics. As an extension of this work, we used this same technique to investigate the potential stock structure of siscowet populations throughout Lake Superior. Similar efforts have been executed for other species (i.e., Winans 1984; Rauchenberger 1988; Bronte et al. 1999; Cheng et al. 2005; Sheehan et al. 2005). An important assumption of this technique is the genetic basis for morphological differences among populations that are segregated at reproduction. Our objective was to determine whether shapes of the siscowet differ across geographic areas of Lake Superior (i.e., whether geographic variation could serve as a precursor to stock identification).

Methods

Specimen and data collection.—Siscowets were captured in 1-night sets of gill nets during spring and summer from 1992 to 1995 in 22 sampling locations across Michigan waters and 1 location in the Minnesota waters of Lake Superior (Figure 1) during cruises of the

R/V *Siscowet*. Distances between adjacent sampling locations ranged from 10 to 70 km. Fish were caught with bottom-set gill net gangs (length, 91 m; height, 1.8 m) made of multifilament nylon twine with equal lengths of stretch mesh (sizes were 114, 127, 139, and 152 mm). All fish were taken at depths ranging from 80 to 140 m at each location, as siscowet are the most common morphotype found at these depths (Bronte et al. 2003); however, they can be mixed with humpers in the Isle Royale area (Moore and Bronte 2001). Morphotype identification was based on previously described characteristics (Khan and Qadri 1970; Lawrie and Rahrer 1973; Moore and Bronte 2001). Ambiguous fish were not included in the analysis.

Where possible, 20 siscowets were randomly selected for study from each sample location. Before rigor mortis, fish were photographed on black and white film (Kodak T-Max 100) with a 35-mm camera mounted on a tripod. The fish were placed in a natural position on a white background; the pectoral and pelvic fins were oriented parallel to the body, and the caudal and dorsal fins were extended. Each photograph included an identification number to allow cross-referencing of biological data as well as a millimeter scale for calibration. All photographic images were scanned and digitized before morphometric analysis.

The truss protocol of morphometric analysis was used to describe the shape of a fish through distances measured between anatomical landmarks (Strauss and Bookstein 1982; Bookstein et al. 1985). Each measured distance constituted a truss element. We measured 31 truss elements from 14 landmarks similar to those of Moore and Bronte (2001; Figure 2a). All truss measurements were made on digital images using image measurement software (Sigma Scan). Calibration was achieved for each specimen by measuring a known distance on a millimeter scale in each photograph.

Data analysis.—All truss measures were \log_e transformed to approximate normal distributions of the variates (Krzanowski 1988; Yandell 1995) without affecting the allometries (Jolicouer 1963). The total length (TL) of fish ranged from 232 to 878 mm, but the TL of most fish was between 450 and 650 mm (mean, 545; SD, 104); however, the mean TL differed significantly among sample locations ($F = 5.28$, $P < 0.0001$). We adjusted for size differences before all statistical analyses by regressing each transformed truss element separately on the first principal component of all truss elements from all fish, which is a multivariate measure of size. The residuals from these regressions, which express variation in the truss measures free from size effects, were used in all subsequent statistical analyses (dos Reis et al. 1990). Correlation analysis

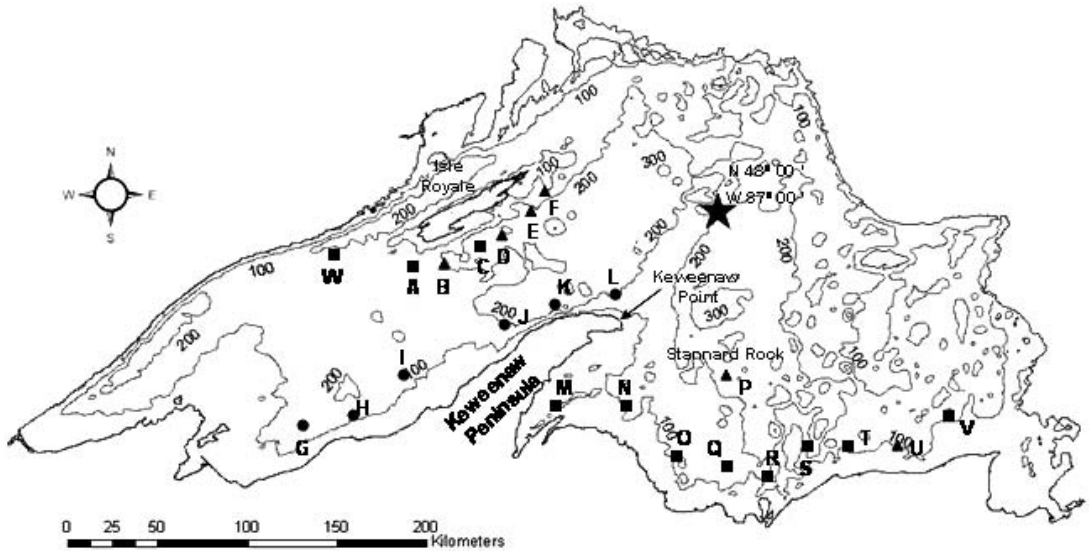


FIGURE 1.—Map showing the sampling locations for siscowets captured during spring and summer 1992–1995 and the bathymetry of Lake Superior. Locations with the same indicator shape (circle, square, or triangle) were grouped in the same cluster and have similar morphology.

was used to identify highly covarying truss elements and remove them from the analysis. One variable was removed from each pair of truss elements with a correlation coefficient greater than 0.5 (least 25% of the variability explained by the paired variable) and significance at an α of less than 0.05 (Cohen 1988).

Cluster analyses of the size-adjusted data were used to identify potential large-scale geographic regional associations (regions) of siscowets from the capture locations. Because of the large number of specimens analyzed ($N = 532$), means were calculated for each truss element by location and these were used in the analysis. A hierarchical cluster tree from a single linkage clustering method (Ward 1963) was used to indicate the locations that had siscowets with similar means of truss element measurements. Locations where fewer than 10 fish were captured were not used in the analysis.

Morphometric data were then pooled for all fish from individual capture locations into the regions identified by cluster analysis. Multivariate analysis of variance (MANOVA) was used to test for shape differences among clustered capture locations. Separate pairwise comparisons were conducted for each regional grouping to test for significant shape differences. For significance tests, we used the Bonferroni-adjusted alphas to conservatively account for multiple comparisons. Data were subjected to backward stepwise discriminant function analysis (Williams 1983). This method is preferred when the prospective number of

variables is fewer than 15 (Johnson 1998). A probability-based selection criterion was used with an alpha-to-enter at 0.01 and an alpha-to-remove at 0.05. The objectives were to identify the truss variables that best separated the fish to each cluster region and then to determine how well siscowets could be classified to the regions from which they were captured. To determine how well the fish could be classified to each region, classification error matrices were calculated using a jackknife procedure that sequentially removes one observation from the data set and classifies it using functions computed from the remaining data (Lackenbruch holdout procedure). All statistical analyses were done using SAS version 8-e.

Results

We collected truss measures on 532 siscowet lake trout from the 23 sampling locations (Figure 1). Six truss variables were highly correlated with other trusses and removed from subsequent analyses (Table 1). Cluster analysis on the retained 25 truss elements indicated three primary lake regions that had siscowets with similar morphologies (Figure 3). The first group contained four locations along Isle Royale, Michigan (locations B, D, E, and F), along with Stannard Rock (P), which is an isolated submerged offshore reef about 45 km east of Keweenaw Point, and a location in eastern Lake Superior northeast of Grand Marais, Michigan (U) (hereafter referred to as the “Isle Royale region”). Within this group, most Isle Royale locations

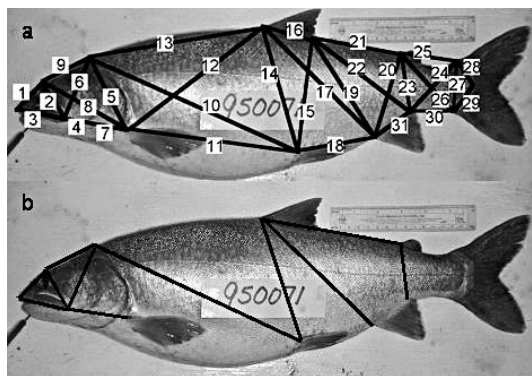


FIGURE 2.—Panel (a) shows all of the truss elements used in this study, namely, (1) anterior tip of snout to top of cranium at midpoint of the eye, (2) top of cranium at midpoint of eye to posterior end of maxillary, (3) posterior end of maxillary to anterior tip of snout, (4) anterior tip of snout to origin of pectoral fin, (5) posterior aspect of neurocranium to origin of pelvic fin, (6) posterior aspect of neurocranium to posterior end of maxillary, (7) posterior point of maxillary to origin of pectoral fin, (8) origin of pectoral fin to top of cranium at midpoint of eye, (9) top of cranium at midpoint of eye to posterior aspect of neurocranium, (10) posterior aspect of neurocranium to origin of pelvic fin, (11) origin of pelvic fin to origin of pectoral fin, (12) origin of pectoral fin to origin of dorsal fin, (13) origin of dorsal fin to posterior aspect of neurocranium, (14) origin of dorsal fin to origin of pelvic fin, (15) origin of pelvic fin to insertion of dorsal fin, (16) origin of dorsal fin to insertion of dorsal fin, (17) origin of dorsal fin to origin of anal fin, (18) origin of anal fin to origin of pelvic fin, (19) origin of anal fin to insertion of dorsal fin, (20) origin of anal fin to origin of adipose fin, (21) insertion of dorsal fin to origin of adipose fin, (22) insertion of dorsal fin to insertion of anal fin, (23) insertion of anal fin to origin of adipose fin, (24) insertion of anal fin to anterior attachment of dorsal membrane of caudal fin, (25) origin of adipose fin to anterior attachment of dorsal membrane of caudal fin, (26) origin of adipose fin to anterior attachment of ventral membrane of caudal fin, (27) anterior attachment of dorsal membrane from caudal fin to anterior attachment of ventral membrane from caudal fin, (28) anterior attachment of dorsal membrane from caudal fin to distal margin midpoint of caudal peduncle, (29) distal margin of caudal peduncle to anterior attachment of ventral membrane from caudal fin, (30) anterior attachment of ventral membrane from caudal fin to insertion of anal fin, and (31) origin of anal fin to insertion of anal fin. Panel (b) shows the truss elements that best separated siscowet lake trout by region of Lake Superior, according to a backward stepwise discriminant function analysis.

were clustered at Ward's Euclidian distance 0.04, as were the two Michigan locations (P and U). The second group, which was more distinct than the first group, contained six adjacent stations west of the Keweenaw Peninsula (G–L) in Michigan waters (hereafter referred to as the “western region”), with two clusters (Euclidian distance, 0.022) that represented adjacent

TABLE 1.—Results of the correlation analysis and the six truss elements excluded from subsequent analysis of siscowets in Lake Superior. See Figure 1 for locations of trusses.

Truss element pair	Pearson correlation coefficient	P-value	Truss element removed
1, 4	0.724	<0.001	4
8, 4	0.863	<0.001	4
7, 8	0.788	<0.001	8
10, 11	0.743	<0.001	11
14, 15	0.872	<0.001	15
21, 22	0.787	<0.001	22

sites in the southwestern (G, H, and I) and northeastern (J, K, and L) areas of this region. The third cluster included eight stations (M, N, O, Q, R, S, T, and V) east of the Keweenaw Peninsula, two from Isle Royale (A and C), and one from Minnesota waters (W) (hereafter the “eastern region”). Within this group, regional geographic affinities were less evident because geographic outlier locations were mixed in with the body of adjacent locations east of the Keweenaw Peninsula that made up 73% of the group. Multivariate analyses of variance to test for shape differences among regions were all significant: eastern versus western ($F = 8.72$, $df = 422$, $P < 0.0001$), eastern versus Isle Royale ($F = 8.56$; $df = 328$; $P < 0.0001$), and western versus Isle Royale ($F = 9.29$; $df = 280$; $P < 0.0001$).

Cross-validation matrices from discriminant function analysis classified most fish to their cluster region of capture corresponding to the cluster diagram (Table 2). Correct classification rates were 70% for Isle Royale fish, 71% for western fish, and 67% for eastern fish. Eastern fish were more likely to be misclassified as western fish (20%) than as Isle Royale fish (13%). Western fish were almost equally likely to be grouped with eastern (16%) or Isle Royale (13%) fish, and Isle Royale fish were misclassified more frequently as eastern (20%) than as western (10%) fish.

Head measures (trusses 1, 2, 3, 6, 7, and 9), body depth measures (10, 14, and 17), the length from of the insertion of the dorsal fin to the origin of the adipose fin (21), and caudal peduncle thickness (23) (Table 3) were useful in predicting geographic region (Figure 2b). Eastern region fish had a longer distance from the midpoint of the eye to the insertion of the opercle (9) but shorter anterior head measures (2, 3, 6) than fish from the Isle Royale and western regions (Table 3). Western region fish had larger and deeper heads (1, 2, 6), longer bodies (10), and the narrowest caudal peduncle (23). Isle Royale Region fish had longer jaws (3), wider bodies (14), and thicker caudal peduncles (23) than fish from other regions.

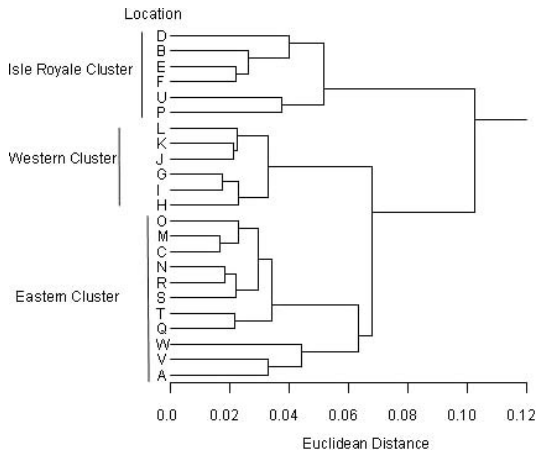


FIGURE 3.—Dendrogram from Ward's cluster analysis indicating regional and subregional groupings of capture locations for siscowets of similar shape. The letter designations refer to the sample locations in Figure 1.

Discussion

Our results suggest the presence of stock structure of siscowets at moderate spatial scales that correspond to subtle differences in head measures and body depth. The western region group had well-defined location aggregations, but finer geographic scales of stock structure were also suggested by clustering of proximate locations. The Isle Royale and eastern region groups were less clearly defined, but the majority of locations within these regions had fish of similar body shape. Lack of complete regional association may suggest finer scales of shape associations that may have an environmental basis or represent a range in possible shapes that vary from site to site. We speculate that Minnesota and Wisconsin waters may also exhibit similar geographic associations.

Head measures were key variables that separated fish from different lake regions. Cranial bones are important taxonomically for salmonines (see Burnham-Curtis and Smith 1994). The dorsal opercular notch and radii of the supraethmoid differ between the lean and

siscowet morphotypes in Lake Superior (Burnham-Curtis and Smith 1994). Head measurements were also important in separating the three morphotypes in Lake Superior (Moore and Bronte 2001), and within-morphotype variation of head measurements shown here for siscowet lake trout add further significance to such metrics.

We speculate that the degree of relatedness among adjacent stocks is associated with the bathymetric habitat present in those areas of Lake Superior. Stock definition was more pronounced in the Isle Royale and western region groups, which were associated with more a homogenous bathymetric habitat. In contrast, the eastern region stock is located in a bathymetrically diverse area (Figure 1), where smaller local stocks could be present. The topography of the eastern basin would facilitate the presence of smaller local stocks isolated by the many peaks and valleys in the lake bottom. Although the present-day bathymetry provides no physical obstacles to prevent siscowet subpopulations from mixing, some reproductive isolation may have occurred when lake levels were lower historically (Burnham-Curtis 1993). As water levels increased approximately 8,000 years ago, isolated populations could have reestablished contact. The population near Stannard Rock (site P) was clustered with most of the Isle Royale sites. All these sites are similarly distanced from the mainland compared with the remaining locations and may suggest a habitat-specific association of morphology and lead to finer scales of stock structure.

Circulation patterns may also be important in explaining the stock structure. Hypothetical spring and fall circulation patterns create subbasin eddies in Lake Superior (Murty and Rao 1970; Figure 4) that are consistent with the patterns of morphological association we report here. The circulation pattern is clockwise

TABLE 3.—Standardized means of truss elements important in discriminating siscowets to capture regions identified by cluster analysis. See Figure 1 for locations of trusses.

Truss	Truss length (mm) by region		
	Isle Royale	Western	Eastern
1	36.1	37.4	36.5
2	44.9	45.2	44.8
3	49.4	48.8	48.6
6	69.6	69.8	69.4
7	58.4	59.6	60.9
9	54.4	54.8	56.5
10	216.8	218.5	218.0
14	113.8	110.6	111.4
17	155.1	154.5	153.9
21	98.9	102.7	103.0
23	54.2	52.8	53.7

TABLE 2.—Classification matrix from backward stepwise discriminant functions calculated from 11 truss elements of siscowets from three regions of Lake Superior. The values shown are percentages; see text for definitions of regions.

Actual region	Classified region		
	Isle Royale	Western	Eastern
Isle Royale	70	10	20
Western	13	71	16
Eastern	13	20	67

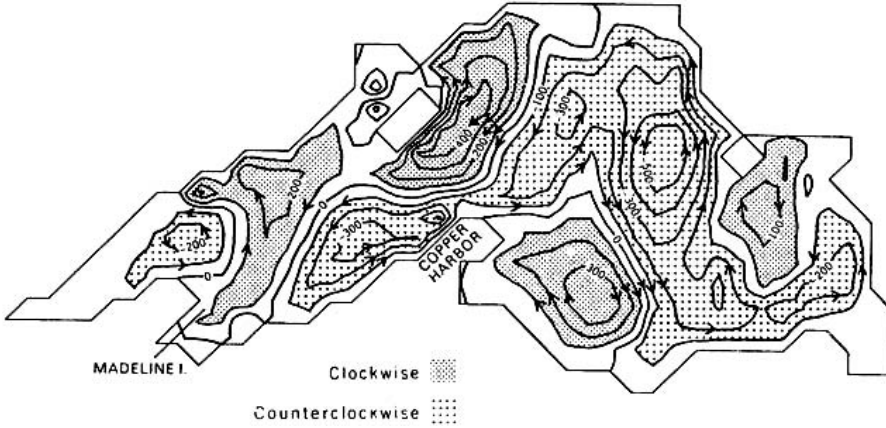


FIGURE 4.—Subbasin surface water circulation patterns in Lake Superior from Murty and Rao (1970).

along the southeastern shore of Isle Royale and east of the Keweenaw Peninsula, counterclockwise along the west side of the Keweenaw Peninsula, and mixed in far-eastern Lake Superior. Lean lake trout must swim to the surface to fill their swim bladders adequately (Tait 1960), and although not much is known about the early life history of the siscowet, we presume that the same behavior is required for this morphotype. If swim-up occurs at a time of high surface current flow, the majority of fry could be maintained in the circulation eddy and hence remain in a general geographic area that would lead to some degree of isolation, although some transport or movement to areas outside the eddy can always occur at this and other life stages.

The causes of the morphological diversity indicated here for the siscowet are presently unknown. Potential explanations include phenotypic plasticity due to differing local environments, random genetic drift, and fidelity to spawning areas that leads to mating of individuals that are phenotypically similar. Resource polymorphism also explains phenotypic plasticity when intraspecific competition is great, as has been proposed for across-morphotype comparisons in lake trout in Great Bear Lake (Blackie et al. 2003). Reproductive success as a result of body shape characteristics may be dependent on localized environmental conditions in the areas inhabited by fish (Dynes et al. 1999; Peres-Neto and Magnan 2004), implying a mechanism for local adaptation as suggested by the association of bathymetric diversity and clusters of sampling locations. Other salmonines are known to exhibit phenotypic plasticity influenced by distinctly different environments; these include brook trout *S. fontinalis* (Imre et al. 2002; Proulx and Magnan 2002). Atlantic salmon *Salmo salar* (Niecieza 1995), Pacific

salmon *Oncorhynchus* spp. (Winans 1984; Swain et al. 1991), and Arctic char *S. alpinus* (Adams and Huntingford 2002; Adams et al. 2003). Phenotypic plasticity has potential for evolutionary success (Day et al. 1994), and degrees of plasticity exist within groups of a species that are geographically separated. Hence, it is likely that geographically distant populations exhibit more dissimilar morphologies than proximate populations, which we have demonstrated here for siscowet lake trout. It is unlikely that environmental differences or resource polymorphism can account for the subtle differences in morphology seen here, since habitat features and available forage are relatively similar across the locations sampled.

Morphological differences may develop as populations become spatially or temporally isolated. Siscowet spawn at various times of the year, ranging from April to November (Eschmeyer 1955; Bronte 1993), so some temporal isolation of stocks is suggested. Lean lake trout show some degree of fidelity to specific spawning areas (Eschmeyer 1955; Pycha and King 1975). Recaptures of tagged wild and hatchery-reared lake trouts in Lakes Michigan and Superior are usually within 80–100 km from tagging locations (Eschmeyer et al. 1953; Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007), which indicates relatively small home ranges in proportion to the total lake size. This temporal and spatial isolation of spawning may contribute to nonrandom gene selection, which can lead to groups of fish exhibiting distinct phenotypic characteristics (Dehring et al. 1981; Dynes et al. 1999). Eschmeyer and Phillips (1965) and Burnham-Curtis (1993) showed that some morphological traits in the siscowet are heritable. Therefore, it is likely that morphological differences among siscowets are a

combination of both heritable characters and phenotypic plasticity from reproductive isolation.

Further studies that contribute a more detailed understanding of the life history of siscowet lake trout and the specific locations of spawning reefs would improve our ability to interpret these results and would lead to a more informed strategy for managing any developing fishery. Our results suggest stock structure on a small scale, which should be reflected in managing the harvest at similar spatial scales to prevent sequential overfishing of stocks that has plagued other species in Lake Superior in the past (Lawrie and Rahrer 1973).

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