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Patterns of morphological diversity in ciscoes distributed within three of Manitoba's glacial relict lakes, with reference to Shortjaw Cisco (*Coregonus zenithicus*)

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Shortjaw Cisco, *Coregonus zenithicus*, show exceptional levels of phenotypic diversity occurring in numerous postglacial lakes in North America. Here, we contrast the morphological diversity of the species from its type locality in Lake Superior to three continental lakes (Reindeer, Athapapuskow, and George lakes) in Manitoba using traditional morphological methods. In particular, we investigate if morphological variation exists among and within lakes given the potential for distinct morphologically adapted groups. Discriminant function analyses based on 26 morphological variables revealed that *C. zenithicus* from Lake Superior represents a distinct morph relative to putative conspecifics in Manitoba, and that morphological structure is strongly mediated by geography (i.e., location) and morphometry of the lake. Gill-raker counts, a highly heritable trait, showed nearly discrete distributions for up to three sympatric general cisco morphs within a lake; only a single morph from Reindeer Lake had similar gill-raker counts to *C. zenithicus* in Lake Superior despite obvious morphological differences (e.g., a smaller standard length). Consequently, morphotypes may be highly divergent in ecological habits, and thus have important management and conservation implications, but more broad-scale research is required. This study provides corroborating evidence to support the variability of *C. zenithicus* across its range, and highlights the necessity for re-evaluating the alpha taxonomy of *C. zenithicus* and closely-related Cisco (*C. artedii*) species.

Tendances en matière de diversité morphologique chez les ciscos répartis dans trois des reliquats de lacs glaciaires du Manitoba par rapport au cisco à mâchoires égales (*Coregonus zenithicus*)

RÉSUMÉ

Le cisco à mâchoires égales, *Coregonus zenithicus*, présente une diversité phénotypique exceptionnelle dans de nombreux lacs postglaciaires de l'Amérique du Nord. Ici, nous opposons la diversité morphologique d'individus provenant de la localité type de l'espèce dans le lac Supérieur à celle d'individus de trois lacs continentaux (lacs Reindeer, Athapapuskow et George) au Manitoba à l'aide de méthodes conventionnelles d'étude morphologique. Plus particulièrement, nous vérifions si la variation morphologique est présente entre et parmi les lacs, compte tenu de la possibilité qu'il y ait des groupes distincts adaptés sur le plan morphologique. Les analyses discriminantes des données basées sur 26 variables morphologiques révèlent que *C. zenithicus* du lac Supérieur présente une morphologie distincte par rapport à ses congénères putatifs du Manitoba, et que la structure morphologique est fortement fonction de la géographie (c.-à-d. emplacement) et de la morphométrie du lac. Le nombre de branchiospines, un trait fortement héréditaire, affiche une répartition quasiment discrète pour un maximum de trois morphologies générales de ciscos sympatriques dans un lac; une seule morphologie de cisco dans le lac Reindeer présentait un nombre de branchiospines différent par rapport à *C. zenithicus* du lac Supérieur, malgré des différences morphologiques évidentes (p. ex., une plus petite longueur standard). En conséquence, les morphotypes peuvent diverger fortement dans des habitats écologiques. Ils ont donc un effet important sur la gestion et la conservation, mais il faut mener d'autres recherches à plus grande échelle. Cette étude fournit des éléments probants à l'appui de la variabilité de *C. zenithicus* dans son aire de répartition, et elle souligne la nécessité de réévaluer la taxonomie principale de *C. zenithicus* et des espèces de ciscos y étant étroitement liées (*C. artedii*).

INTRODUCTION

The Shortjaw Cisco (*Coregonus zenithicus*) is a widespread species in the salmonid subfamily, Coregoninae, which occurs in central North America from the Great Lakes to the Northwest Territories (Houston 1988; Scott and Crossman 1998; Todd and Steinhilber 2002). The current distribution of *C. zenithicus*, like most Canadian fishes, was affected by advancing and retreating continental glaciers (Scott and Crossman 1998; Dyke et al. 2003). Details regarding the distribution of the species across most of its range remain poorly understood, and known localities outside the Laurentian Great Lakes may not adequately reflect the distribution of the species due to taxonomic uncertainty (see below). The species was originally described from Lake Superior by Jordan and Evermann (1909) and, as of the most recent edition of the American Fisheries Society's standard reference, Common and Scientific Names of Fishes (Nelson et al. 2004), remains formally recognized. Fourteen species of ciscoes are recognized in North America (Scott and Crossman 1998; Nelson et al. 2004), however, eight of these, the most morphologically variable species (*C. alpenae*, *C. artedi*, *C. johanna*, *C. hoyi*, *C. kiyi*, *C. nigripinnis*, *C. reighardi* and *C. zenithicus*), have been referred to as the "*Coregonus artedi*" complex in recognition of the difficulties in identification (McPhail and Lindsey 1970; Turgeon and Bernatchez 2003). For the remainder of this study, however, putative *C. zenithicus* from outside the type locality in Lake Superior are regarded as *Coregonus* spp. Generally similar to the Lake Herring or Cisco (*C. artedi*), *C. zenithicus* is elliptical in shape, laterally compressed, and has been reported to be distinguished from other sympatric ciscoes by a combination of morphological characters including gill-raker counts of 32–46; the mandible is usually shorter than the premaxilla when the mouth is closed; the premaxillary angle is high (but not in all individuals); the mouth projects slightly downward; body is deepest at the center; olive green or brown dorsal colouration, transitioning to white ventrally (Nelson and Paetz 1992; Scott and Crossman 1998; Muir et al. 2011).

The paucity of taxonomic-informative characters within and among closely related cisco species is directly related to the variability of ciscoes from lake to lake. As such, the taxonomy of ciscoes is notoriously complex and problematic because they are characterized by polymorphism and high morphological plasticity. These varied morphological features often lead to an appearance of hybridized forms in natural populations further confounding species identification (Svärdson 1965; Reist et al. 1992). It is generally accepted that multiple conspecific morphotypes or ecotypes exist within and among lakes, sometimes even in the absence of complete isolation (Bodaly 1979; Svärdson 1979; Vuorinen et al. 1993; Bernatchez et al. 1996; Amundsen et al. 2004; Vecsei et al. 2012). Accordingly, ample evidence suggests phenotypic diversification through an adaptive radiation within lakes as the outcome of divergent selection related to resource partitioning, particularly among postglacial fishes (see Schluter 1996; Lu and Bernatchez 1999; Turgeon et al. 1999). Such diversity is observed in the distinction between pelagic and benthic forms of numerous fishes, including ciscoes. Different forms are typically separated by differences in gill rakers (comblike structure that projects from the branchial arch and is involved in food sieving) and are often characterized by distinct life histories (Bodaly 1979; Svärdson 1979; Bodaly et al. 1991; Bernatchez et al. 1996; Svärdson 1998; Sandlund et al. 2002; Amundsen et al. 2004). In *C. artedi*, for example, co-existing benthic and limnetic forms have commonly been found to differ in gill-raker number (Bodaly 1979; Bernatchez et al. 1996). Morphs with the lowest gill-raker number are usually benthivorous and adapted to larger prey, whereas those with high gill-raker numbers are planktivorous, efficiently adapted to retaining smaller prey (Link and Hoff 1998). In some species, including *C. zenithicus*, the gill-raker number represents the primary character for species identification (Todd and Steinhilber 2002). In juvenile coregonines, the number of gill rakers increases with fish size up to an asymptotic value in adults complicating taxonomic interpretations based on gill-raker differences (Muir et al. 2013), and this value may vary among coregonid species (Todd 1998).

Given the continuing uncertainty regarding cisco taxonomy using traditional morphological characters, molecular methods have been used to explore group structure. Contemporary genetic methods have generally provided inconsistent evidence of taxonomic structure, and often reflect geographic structure rather than phylogenetic relationships (Reed et al. 1998; Steinhilber et al. 2002; Turgeon and Bernatchez 2003). For example, Turgeon and Bernatchez (2003) demonstrated a close genetic relationship among *C. artedi*, *C. zenithicus*, and *C. hoyi* using polymorphisms assayed in the mitochondrial D-loop region and with seven microsatellite loci. The two lineages correspond to Mississippian and Atlantic refugial races (Turgeon and Bernatchez 2001); however, species composition was not reciprocally monophyletic confirming the lack of correspondence between taxonomy and genetics within the *C. artedi* complex. Similar studies have shown that divergent forms of postglacial fishes exhibit little genetic differentiation, suggesting that morphological divergence can proceed more rapidly than neutral genetic divergence (Bernatchez and Wilson 1998; Schluter 2000). This may be partially explained by environmental effects (e.g., plastic responses; Reed and Frankham 2001), such as water temperature and salinity during ontogeny (Lindsey 1981; Todd 1998; Loy et al. 1999).

In light of morphological and genetic studies, continued taxonomic uncertainty surrounding ciscoes (*Coregonus* spp.) is retained as the central dogma. This group of fishes represents the most widely distributed, phenotypically variable, and taxonomically challenging of all Canadian freshwater fishes (Scott and Crossman 1998). A rigid delimitation and determination of taxonomic, ecological, and morphological cisco forms within lakes remains to be established and may be impossible within a strict Linnean hierarchy. Furthermore, this information collected among lakes is necessary to establish geographic range and explore interlacustrine diversification of *Coregonus* spp. Hence, the following study focuses on deepwater cisco morphotypes in the genus *Coregonus* with specific reference to *C. zenithicus* in an attempt to provide species identification and pattern recognition in three of Manitoba's continental lakes.

The present study closely links to a previous study by Todd and Steinhilber (2002) examining the morphological diversity in *C. zenithicus* in North America, using specimens collected from nine locations across Canada (including Athapapuskow, George, and Reindeer lakes). Todd and Steinhilber (2002) revealed that some lakes were distinct from others, but patterns among the variation could not be detected due to the degree of overlap between the four characters examined (i.e., snout angle, jaw angle, gill-raker area, and gill-raker number) restricting clear understanding of patterns among the variation. These patterns were explored using few morphological characters and the variability within each lake was not closely examined. The aim of the present study was to compare the morphology of *C. zenithicus* from its type locality in Lake Superior to *Coregonus* spp. – identified as *C. zenithicus* based on historical collection records – distributed inland in three of Manitoba's glacial relict lakes (Athapapuskow, George, and Reindeer lakes). The objectives of this study were to investigate: 1) if morphological variation exists within and among lakes based on a suite of 26 morphological characters, and 2) whether patterns of morphological diversity between lakes are similar given the potential for distinct morphologically adapted groups.

METHODS

Ciscoes were collected in 2000 and 2001 by gillnetting conducted in three glacial relict lakes in Manitoba, distributed over more than 900 km², where *C. zenithicus* were previously reported (Gibson and Johnson 1969; Clarke 1973; Scott and Crossman 1998; Figure 1). Sampling efforts in Reindeer, Athapapuskow, and George lakes were conducted across various depths in each lake, however, the greatest sampling efforts focused on the deeper regions where suitable *C. zenithicus* habitat is likely to occur (Scott and Crossman 1998). Morphometric and meristic characters were measured on all ciscoes following Vuorinen et al. (1993), including the premaxillary angle (PMA) according to Clarke (1973; Figure 2). Only fish larger than 140 mm

fork length were used in the analyses, since gill-raker development appears to be incomplete and gill-raker number may increase with increasing size in juvenile fish (Todd 1998; Sandlund et al. 2002). Additional phenotypic data representing *C. zenithicus* from its type locality in Lake Superior were assessed from previous cisco collections in 2007-2009 (Pratt and Chong 2012). A total of 743 individuals from Reindeer Lake ($n = 296$), Lake Athapapuskow ($n = 64$), George Lake ($n = 54$), and Lake Superior ($n = 329$) were included in subsequent univariate and multivariate analyses.

Morphological characters (see acronyms in Table 1) were initially examined using a Pearson correlation matrix to determine relationships to body size and to test for effects of allometry. There were no strong correlations (correlation coefficient <0.8) observed between meristic characters and standard length (STL) of samples. However, morphometric variables (with the exception of PMA, MXL, and GRL) were strongly linearly correlated (correlation coefficient >0.8) with STL. Therefore, to remove the confounding effects that size has on shape, particularly when comparing groups of organisms with indeterminate growth, morphometric data were transformed according to procedures outlined by Reist (1986). Accordingly, residual variates were calculated using a standard size variable (i.e., STL) measured from the tip of the snout to the end of the caudal peduncle on each fish. A Pearson correlation matrix with all size-adjusted variables as well as STL was then re-calculated to ensure the data transformation was effective in removing the effect of size among variables. This size standard was retained in subsequent analyses as a potential discriminating variable between groups. The premaxillary angle was not standardized as it is a bound variable (i.e., there are only a finite number of values possible with inherent order).

The morphological data for each lake were subsequently analysed using two independent discriminant functions analyses (DA) to achieve the greatest separation or discrimination among groups. Initially, groups were established based on geography to test for variation between lakes (Figure 3). A subsequent DA analysis examined morphological variation within each of the three Manitoban lakes (Figure 4) based on groups of fishes (or morphotypes) determined by a visual inspection of total gill raker counts (Figure 5). The initial visual inspection of total gill-raker counts for all of the Manitoban ciscoes revealed three modes (results not shown). Modal distributions for each of the lakes were defined as either a sparsely-rakered (≤ 31), moderately-rakered ($32 \leq x \leq 38$), or a densely-rakered (≥ 39) morphotype. Additionally, unstandardized canonical factor scores were plotted to help visualize variability using DA and to explore potential cisco assemblages within lakes. The total number of gill rakers (TGR) was excluded from the DA of morphotypes to avoid the circularity of basing groups upon this character and then subsequently discriminating groups based on this variable. A cross-validation classification (the leave-one-out method) matrix was calculated for each DA analysis to predict the accuracy rate of specimen reassignment to their respective group. Morphological variation between lakes, and between morphotypes was assessed using an ANOVA. All statistical analyses were calculated using SPSS version 11.0.1 for Windows.

RESULTS

A total of 26 variables (21 morphometric and five meristic) were used in multivariate DA tests (Table 1). The initial DA test comparing cisco morphology by lake revealed three clusters, with visual separation between *C. zenithicus* in Lake Superior and other inland *Coregonus* spp. (Figure 3). A Wilkes Lambda Test indicated a significant separation of lakes based on morphology (Wilkes Lambda = 0.023, $\chi^2 = 2725.6$, $df = 78$, $P < 0.001$), and 98.1% of cross-validated grouped cases were classified to their correct lake (Table 2). *C. zenithicus* in Lake Superior and Manitoban inland ciscoes were separated by canonical factor (CF) 1. George Lake ciscoes appear most similar to ciscoes in Lake Athapapuskow, and are only slightly different along CF 1. Additionally, the distinction among ciscoes from Reindeer Lake compared to

George and Athapapuskow lakes was apparent along CF 2. These first two canonical axes accounted for 87.4% of the variance among lakes (CF 1 = 63.2% and CF 2 = 24.2%). Standard length (STL; 0.568) and TGR (0.497) had the highest loadings on the first axis while HDD (0.506) and BDD (0.479) were important on the second (Table 3). Summaries of morphological characters with the highest canonical loadings for this and subsequent DA analysis are reported based on non-transformed data to facilitate potential field identification (Table 4). Notable findings with respect to among-lake comparisons suggest that STL in *C. zenithicus* from Lake Superior is higher (mean = 217.0 ± standard deviation 29.2) compared to *Coregonus* spp. from Athapapuskow (152.7 ± 14.5), George (149.9 ± 12.8), and Reindeer (163.2 ± 16.2) lakes. Moreover, *Coregonus* sp. in Reindeer Lake typically have a lower adjusted HDD compared to Athapapuskow and George lakes, however, this difference is not evident among mean absolute morphological values (Table 4).

A frequency distribution of TGR counts in *C. zenithicus* from Lake Superior revealed a unimodal distribution and the majority (88.8%) of specimens characterized as being a densely-rakered morph (i.e., TGR ≥ 39). In Manitoba lakes, however, the modal distribution of TGR counts in *Coregonus* spp. varied, confirming the presence of one or more different morphotypes in each waterbody (Figure 5). Lake Athapapuskow contained both sparsely-rakered and moderately-rakered morphs based on a bimodal TGR frequency distribution. Two individual specimens from Lake Athapapuskow grouped with the densely-rakered morph; however, each was contained within the normal distribution of those ciscoes defined as a moderately-rakered morph (Table 3). George Lake contained a single moderately-rakered morph (based on a unimodal distribution) despite three specimens contained within the sparsely-rakered group (see explanation above). Reindeer Lake contained three (sparsely-rakered, moderately-rakered, and densely-rakered) morphs based on a trimodal frequency distribution for TGR.

A second DA test compared cisco morphology based on an *a priori* grouping of gill-raker counts in Athapapuskow, George, and Reindeer lakes. Samples from Lake Superior were excluded from this analysis since their taxonomic identification as *C. zenithicus* (Pratt and Chong 2012) is currently undisputed and predominantly conform to the densely-rakered morph. The DA test revealed three significantly different clusters (Wilkes Lambda = 0.186, $\chi^2 = 668.8$, df = 50, $P < 0.001$), and 86.2% of cross-validated grouped cases were classified to their correct morphotype (i.e., sparsely-, moderately-, and densely-rakered morphs; Table 2). Despite an intergradation of morphological characters, each morphotype could be discriminated by CF 1 and CF 2. These two axes accounted for 100% of the variance among morphotypes (CF 1 = 74.1% and CF 2 = 25.9%). Gill-raker length (GRL; 0.739) and BDD (-0.529) had the highest loadings on the first axis, and MXL (0.741) and GRL (-0.504) had the highest loadings on the second axis (Table 3). In general, there is increasing GRL between sparsely-rakered (4.2 ± 0.6), moderately-rakered (5.1 ± 1.7), and densely-rakered (7.0 ± 1.4) morphs. Similarly, there is increasing MXL between sparsely-rakered (14.3 ± 1.5), moderately-rakered morphs (15.3 ± 2.3), and densely-rakered morphs (16.9 ± 2.7).

DISCUSSION

The differences in morphological variables, particularly standard length (STL) and total gill-raker count (TGR), between lakes revealed that specimens collected from historical collection sites in Manitoba do not correspond to *C. zenithicus* from Lake Superior. Continental Manitoba ciscoes typically have a smaller STL and slightly larger TGR than *C. zenithicus* in Lake Superior despite both groups being referred to the densely-rakered morph category. Rather, *Coregonus* spp. collected in Manitoba appear to be more similar to each other. This is inconsistent with the results of Todd and Steinhilber (2002), who suggested that specimens from Lake Superior are more similar to those in Athapapuskow and Reindeer lakes, than any are to George Lake. It is possible that historical *C. zenithicus* samples from Lake Superior were different in morphological

characters and gill-raker count especially compared to contemporary collection. However, historical *C. zenithicus* samples by Todd and Steinhilber (2002) show remarkable similarity in STL and TGR compared to the most recent collection of Pratt and Chong (2012) (234.7 ± 18.4 versus 217.0 ± 29.2 mm, and 40.9 ± 2.5 versus 40.8 ± 2.1 , respectively). Furthermore, the data suggest that *Coregonus* sp. from George Lake are more similar to those specimens collected from Lake Athapapuskow than either are to Reindeer Lake or Lake Superior. Once again, this is inconsistent with Todd and Steinhilber (2002), who found a clear distinction of *Coregonus* sp. in George Lake from any other lakes. The data, however, are congruent with Todd and Steinhilber (2002) suggesting distinctions among *C. zenithicus*-like assemblages across the Canadian Shield. This high level of phenotypic plasticity in these ciscoes highlights their sensitivity to environmental perturbation and variation.

The most notable finding was that within-lake morphological variation supported up to three morphotypes based on an *a priori* visual classification of gill-raker numbers. Three morphs were found in Reindeer Lake, two in Lake Athapapuskow, and a single morph in George Lake. Morphotypes were strongly in accordance with the morphometric measures best discriminated by gill-raker length, body depth, and maxillary length. Moderately-rakered forms were supported in all three Manitoban lakes, whereas sparsely-rakered forms were limited to Athapapuskow and Reindeer lakes. Aoki and Bodaly (2003) also identified two morphs in Lake Athapapuskow. They identified two cisco forms as *C. artedi* based on a bimodal gill raker distribution with modes at 38/39 and 44/45, and dismissed the possibility of *C. zenithicus* being present despite an earlier report (Clarke 1973). The current data support the identity of two morphs, however, the resulting modes (27/28 and 33/34) are lower than those reported by Aoki and Bodaly (2003). Additionally, two specimens were collected with relatively high gill-raker counts (41 and 42). It is possible that these two specimens as well as those pertaining to the moderately-rakered morph correspond to the two forms of *C. artedi* reported by Aoki and Bodaly (2003). It is, however, unlikely that the sparsely-raker morph corresponds to those previously reported, and may represent a third morphotype. Furthermore, it is unknown whether morphologically distinct moderately-rakered morphs in other lakes (i.e., George and Reindeer lakes) correspond to a common intraspecific taxon.

In addition to its collection from Lake Athapapuskow, the sparsely-rakered morph was found in greatest abundance from Reindeer Lake. With the exception of its size, the only nominal cisco species with morphology (specifically gill-raker counts) that conforms to the Athapapuskow and Reindeer lakes sparsely-rakered form is the Deepwater Cisco (*C. johanna*) (Scott and Crossman 1998). This species, contained within the *C. artedi* complex, is the largest of the ciscoes endemic to the Great Lakes and has gill-raker counts ranging from 25 to 36. However, it is believed to have gone extinct, as there have been no recent reports of *C. johanna* in the Great Lakes, and it has not been collected in Lake Michigan since 1957 (Scott and Crossman 1998). It is unknown whether sparsely-rakered morphs in Athapapuskow and Reindeer lakes represent previously unrecognized *C. johanna* outside of the Great Lakes, or a variant of another congener.

The gill-raker counts of the densely-rakered morph corresponding to *C. zenithicus* from Lake Superior are paralleled by one of three morphs in Reindeer Lake. This densely-rakered morph in Reindeer Lake is the closest representation of *C. zenithicus* from Lake Superior, despite its other morphological differences – primarily in STL.

Smith and Todd (1984), Todd and Smith (1992), Scott and Crossman (1998), and Todd and Steinhilber (2002) accepted the presence of inland *C. zenithicus* distributed beyond the Great Lakes. Generally, the morphology of the specimens examined conforms to Great Lake *C. zenithicus* in gill-raker number, pigmentation, and jaw morphology. It remains unclear to what extent morphological distinctions among and within lakes represents species-level designation, as well as their relation to *C. zenithicus* from Lake Superior. The obvious question, as posed by

Todd and Steinhilber (2002), is whether each of these morphotypes corresponds to a common intraspecific taxon or represents independent and convergent morphotypes. Similar to Todd and Steinhilber (2002), the current data do not permit clarification of this issue without a firm understanding of whether these traits are genetically or environmentally mediated.

Different morphs of coregonines have traditionally been identified by the number of gill rakers (Svärdson 1952; Lindsey 1981). Gill rakers are considered by several authorities to be a heritable, ecologically important, and stable trait (Svärdson 1979; Link and Hoff 1998; Todd and Steinhilber 2002). However, gill-raker numbers are labile within a range of variability for individual species and are strongly associated with growth rate (Todd 1998; Sandlund et al. 2002; Muir et al. 2013). It is not known to what extent growth rate affects gill-raker counts within and among the three Manitoban lakes. However, it is possible that morphotypes have evolved repeatedly in at least two lakes (Athapapuskow and Reindeer lakes) based on the similar distribution of gill rakers and the morphological similarities between lakes. Gill-raker divergence is a general pattern in adaptive radiations of postglacial fishes (Kahilainen et al. 2011), and environmental and ecosystem variability within and among lakes is likely driving morphological diversification. The gill-raker apparatus, in particular, facilitates the use of different dietary niches across an array of trophic levels (Kahilainen et al. 2011). Accordingly, the size of the lake may be an indication of the complexity of trophic structure, and natural selection will favour fish suited for rapid shifts in gill-raker traits to exploit new resources. In Threespine Stickleback (*Gasterosteus aculeatus*), trophic traits such as gill-raker length, gill-raker number, and mouth size are strongly associated with lake size (Lavin and McPhail 1986). Typically, sticklebacks in small, shallow lakes have larger mouths and fewer, shorter gill rakers than those in large, deep lakes (Lavin and McPhail 1986). This interlacustrine variation in trophic morphology and lake size likely reflects an evolutionary response by sticklebacks to the local foraging regime (McPhail 1991). In the present study, the distribution of gill rakers may be associated with lake size and suggests that larger lakes support more trophic forms of cisco. Generally, larger lakes are linked to greater niche diversity and an increased potential for unexploited resources, particularly in northern deglaciated lakes. However, with only four lakes available for comparison, such a generalization is poorly supported at best. Lake Superior, the largest of the four lakes in this study, has the largest array of cisco species/morphotypes present in the lake (cf. Smith and Todd 1984; Scott and Crossman 1998), but for the purposes of this study only a single species (i.e., *C. zenithicus*) is included to make specific taxonomic reference to the type locality. The largest of the Manitoban lakes examined, Reindeer Lake, supports three morphs; Lake Athapapuskow has two morphs; and the smallest lake, George Lake, has a single morph. Gill-raker number and morphology appear to be reliable markers for identifying ecological morphs, however, their utility as taxonomic characters remains unclear.

Molecular tools have been used in an attempt to resolve debates regarding relatedness and to develop an appropriate method to classify North American ciscoes. However, morphological change in ciscoes with time or with distance from putative glacial refugial areas, neither implies nor precludes genetic divergence. Several studies have failed to find a genetic marker that differentiates between closely related *C. zenithicus* and *C. artedi* in North America (Reed et al. 1998; Reist et al. 1998; Steinhilber et al. 2002). Genetic similarity between these two species is likely due to insufficient time for divergence and incomplete lineage sorting. Most recently, Turgeon and Bernatchez (2003) completed a genetic characterization of North American ciscoes with mitochondrial and microsatellite markers. Putative *C. zenithicus* from five locations including Lake Superior and George Lake were not reciprocally monophyletic, and in at least one instance were genetically indistinguishable from *C. artedi* and *C. hoyi*. Often *C. zenithicus* were found to have closer relationships with sympatric or nearby *C. artedi* populations than with putative conspecifics. These data suggest that some populations of taxonomically identified *C. zenithicus* may be polyphyletic and do not share a common genetic origin. The genetic variation was attributed to geography rather than taxonomy, but in Barrow Lake and La Grande

Reservoir, normal and dwarf sympatric morphotypes of *C. artedi*, representing two gene pools, were supported by variation in microsatellite loci (Turgeon and Bernatchez 2003). Furthermore, there has been similar genetic divergence between sympatric morphotypes in Lake Nipigon; one of which morphologically equates to *C. zenithicus* and is genetically distinct among Lake Nipigon cisco morphotypes (Turgeon et al. 1999). The apparent parallel patterns of phenotypic divergence between morphotypes in postglacial lakes are strong evidence that natural selection has favoured the evolution of specialization likely in response to environmentally mediated fitness tradeoffs (Schluter 1996). These parallel events have likely evolved independently and multiple times. However, further direct evidence of reproductive isolation and the genetic basis for key discriminating characters in these lakes as well as those explored in this study, are needed before a formal taxonomic designation.

The evolutionary processes leading to present day morphological diversity in continental ciscoes represents a culmination of historical and contemporary reticulate events beginning at the end of the last glaciation. Shortjaw Cisco is hypothesized to represent one of the cisco lineages that predated the Pleistocene glaciation based on its widespread distribution across North America (Todd and Smith 1992). Additionally, Smith and Todd (1984) suggested that *C. artedi* and *C. zenithicus* were the first colonizing ciscoes in North America. These taxa, like others in post-glacial northern lakes, exhibit considerable morphological, life history, and behavioural plasticity; many of these taxa are rapidly diverging and in some instances form new species (Schluter 1996; Bernatchez and Wilson 1998). The relatively high rate of divergence is poorly understood. Contemporary glacial relict lake environments, however, provide both spatial and temporal variation in ecological conditions that favours functional adaptive responses. Adaptive radiation and a propensity for phenotypic plasticity have led to local diversification of ciscoes mediated by disruptive selection, sometimes in sympatry.

The morphological data presented here provide convincing evidence for distinct assemblages of *Coregonus* spp., both within and among lakes that should be used to corroborate future study concerning the *C. artedi* complex and when re-evaluating the alpha-taxonomy of *C. zenithicus*. Furthermore, this study will hopefully stimulate an interest in wider understanding of the roles of morphological plasticity in the ecology, conservation, and evolution of postglacial fish fauna.

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Table 1. Morphometric and meristic variables evaluated for use in discriminant function analyses.

Variable	Acronym
<i>Morphometric</i>	
1. Standard length	STL
2. Pre-orbital length	POL
3. Orbital length	OOL
4. Post-orbital length	PSL
5. Trunk length	TTL
6. Dorsal length	DOL
7. Lumbar length	LUL
8. Anal length	ANL
9. Caudal peduncle length	CPL
10. Head depth	HDD
11. Body depth	BDD
12. Caudal peduncle depth	CPD
13. Inter-orbital width	IOW
14. Maxillary length	MXL
15. Maxillary width	MXW
16. Pectoral length	PCL
17. Pelvic length	PVL
18. Adipose length	ADL
19. Gill-raker length	GRL
20. Lower arch length	LAL
21. Premaxillary angle	PMA
<i>Meristic</i>	
22. Total gill-raker count ¹	TGR
23. Dorsal ray count	DRC
24. Anal ray count	ARC
25. Pectoral ray count	PRC
26. Pelvic ray count	VRC

¹TGR was used as a grouping variable and was not included in DFA analysis between morphotypes

Table 2. Cross validated classification matrices based on lake and morphotype. Percentages of individuals that correctly classified back to their own lake are shaded.

Lake	Predicted Group Membership (%) ^a				Total
	Athapapuskow	George	Reindeer	Superior	
Athapapuskow	96.9	0.0	3.1	0.0	100
George	0.0	100.0	0.0	0.0	100
Reindeer	0.0	0.0	97.3	2.7	100
Superior	0.0	0.0	1.2	98.8	100

Morph	Predicted Group Membership (%) ^b			Total
	Sparsley-rakered	Moderately-rakered	Densely-rakered	
Sparsley-rakered	91.5	8.1	0.4	100
Moderately-rakered	16.2	78.7	5.1	100
Densely-rakered	8.2	14.3	77.5	100

^a 98.1% of cross-validated grouped cases correctly classified.

^b 86.2% of cross-validated grouped cases correctly classified.

Table 3. The standardized canonical discriminant function coefficient table with 26 morphological variables analysed with two independent discriminant functions analyses (discrimination between lakes, and between morphotypes). The two highest discriminant functions coefficients on the first two axes are shaded. Discriminant function coefficients between lakes includes specimens from Lake Superior and Manitoba lakes. Discriminant function coefficients between morphotypes includes only specimens from Manitoba lakes. Adjusted morphometric variables according to Reist (1986). Acronyms according to Table 1.

Variable	Between lakes			Between morphotypes	
	1	2	3	1	2
<i>Morphometric</i>					
STL	0.568	-0.066	-0.084	-0.252	0.187
Adjusted POL	0.194	-0.223	-0.291	-0.273	-0.180
Adjusted OOL	-0.245	0.055	0.310	0.083	-0.233
Adjusted PSL	0.074	0.061	0.131	-0.033	0.189
Adjusted TTL	-0.111	0.142	0.124	0.113	0.171
Adjusted DOL	0.054	-0.096	-0.124	-0.052	0.019
Adjusted LUL	-0.055	-0.130	0.171	-0.024	-0.023
Adjusted ANL	0.056	-0.357	0.343	0.402	-0.089
Adjusted CPL	0.135	-0.399	0.317	0.134	-0.085
Adjusted HDD	-0.070	0.506	-0.191	0.047	0.246
Adjusted BDD	0.237	0.479	-0.110	-0.529	0.052
Adjusted CPD	-0.107	-0.080	0.109	0.198	-0.079
Adjusted IOW	0.209	0.087	-0.223	0.307	0.182
Adjusted MXL	-0.222	-0.146	0.434	0.282	0.741
Adjusted MXW	-0.107	0.037	-0.096	-0.178	-0.183
Adjusted PCL	0.297	-0.125	0.267	0.377	0.031
Adjusted PVL	0.003	0.456	-0.048	0.129	-0.069
Adjusted ADL	-0.060	0.331	0.117	0.080	0.296
Adjusted GRL	-0.097	-0.254	-0.895	0.739	-0.504
Adjusted LAL	-0.016	-0.387	-0.234	-0.274	0.065
PMA	-0.212	0.053	0.132	-0.355	-0.057
<i>Meristic</i>					
TGR	0.497	-0.077	0.666	N/A	N/A
DRC	-0.333	0.070	0.191	0.126	0.195
ARC	-0.141	0.224	-0.088	-0.025	0.182
PRC	0.160	-0.044	-0.230	-0.182	-0.023
VRC	0.122	0.064	-0.115	-0.091	-0.038

Table 4. Sample size, means \pm standard deviations, and ranges for non-adjusted characters representing the two highest canonical coefficient loadings for each of two axes – between lake and between morphotype comparisons. Morphological characters are measured for each morphotype of *Coregonus* spp. in three Manitoban lakes, and *Coregonus zenithicus* in Lake Superior. All measurements are in mm. All morphological characters differed significantly among groups (ANOVA, $P < 0.001$).

	Sparsley-rakered (≤ 31)			Moderately-rakered ($32 \leq X \leq 38$)			Densely-rakered ($39 \leq$)			Total		
Lake Athapapuskow (<i>Coregonus</i> spp.)												
Standard length ¹	43	152.7 \pm 12.2	132–187	19	154.7 \pm 18.7	127–191	2	134.5 \pm 2.1	133–136	64	152.7 \pm 14.5	127–191
Total gill-raker count ¹	43	26.8 \pm 2.8	20–31	19	33.7 \pm 1.4	32–38	2	41.5 \pm 0.7	41–42	64	29.3 \pm 4.5	20–42
Head depth ¹	43	17.8 \pm 1.8	14.2–22.7	19	18.6 \pm 2.9	14.2–24.8	2	15.5 \pm 1.4	14.5–16.5	64	18 \pm 2.2	14.2–24.8
Gill-raker length ²	43	4.7 \pm 0.8	3.4–6.9	19	5.6 \pm 0.8	4.1–7.0	2	5.1 \pm 0.1	5.0–5.2	64	5.0 \pm 0.9	3.4–7.0
Body depth ^{1,2}	43	37.1 \pm 4.6	26.9–51.5	19	36.3 \pm 6.5	26.4–47.8	2	27.1 \pm 3.9	24.3–29.8	64	36.6 \pm 5.4	24.3–51.5
Maxillary length ²	43	13.1 \pm 1.3	10.6–16.4	19	14.2 \pm 2.1	11.0–18.4	2	10.9 \pm 0.8	10.3–11.5	64	13.3 \pm 1.7	10.3–18.4
George Lake (<i>Coregonus</i> spp.)												
Standard length ¹	3	145.3 \pm 9.1	137–155	51	150.1 \pm 13.0	127–175				54	149.9 \pm 12.8	127–175
Total gill-raker count ¹	3	30.7 \pm 0.6	30–31	51	33.8 \pm 1.5	32–37				54	33.6 \pm 1.7	30–37
Head depth ¹	3	15.9 \pm 1.4	14.3–16.9	51	17.4 \pm 1.4	14.2–19.6				54	17.3 \pm 1.4	14.2–19.6
Gill-raker length ²	3	2.8 \pm 0.7	2.3–3.6	51	3.1 \pm 0.6	2.1–4.6				54	3.1 \pm 0.6	2.1–4.6
Body depth ^{1,2}	3	33.5 \pm 3.6	29.6–36.8	51	35.7 \pm 4.3	26.3–44.5				54	35.6 \pm 4.3	26.3–44.5
Maxillary length ²	3	12.6 \pm 1.4	11.0–13.8	51	13.8 \pm 1.4	11.0–16.7				54	13.7 \pm 1.4	11.0–16.7
Reindeer Lake (<i>Coregonus</i> spp.)												
Standard length ¹	202	164.7 \pm 16.1	129–210	47	164.6 \pm 16.0	135–201	47	155.3 \pm 14.8	130–197	296	163.2 \pm 16.2	129–210
Total gill-raker count ¹	202	28.2 \pm 1.3	23–31	47	35.2 \pm 1.6	32–38	47	42.1 \pm 2.2	39–48	296	31.5 \pm 5.5	23–48
Head depth ¹	202	17.2 \pm 1.8	13.0–22.5	47	19.0 \pm 2.4	14.6–25.4	47	17.3 \pm 1.8	13.0–20.4	296	17.5 \pm 2.0	13.0–25.4
Gill-raker length ²	202	4.1 \pm 0.6	2.9–6.3	47	6.0 \pm 0.9	4.0–7.8	47	6.3 \pm 1.1	4.4–9.8	296	4.8 \pm 1.2	2.9–9.8
Body depth ^{1,2}	202	33.7 \pm 4.3	25.4–46.2	47	33.8 \pm 4.2	26.3–44.9	47	33.2 \pm 5.6	25.1–47.8	296	33.7 \pm 4.5	25.1–47.8

	Sparsley-rakered (≤ 31)			Moderately-rakered ($32 \leq X \leq 38$)			Densely-rakered ($39 \leq$)			Total		
Maxillary length ²	202	14.6 ± 1.4	11.0–18.7	47	16.2 ± 1.9	12.3–19.8	47	13.6 ± 1.6	10.3–17.4	296	14.7 ± 1.7	10.3–19.8
Lake Superior (<i>C. zenithicus</i>)												
Standard length ¹				37	209.4 ± 29.8	147–275	292	218.0 ± 29.0	146–295	329	217.0 ± 29.2	146–295
Total gill-raker count ¹				37	37.1 ± 1.5	32–38	292	41.3 ± 1.6	39–46	329	40.8 ± 2.1	32–46
Head depth ¹				37	22.6 ± 2.7	16.9–28.3	292	23.2 ± 2.9	15.5–33.3	329	23.2 ± 2.9	15.5–33.3
Gill-raker length ²				37	6.5 ± 1.2	4.2–8.9	292	7.2 ± 1.4	3.5–11.6	329	7.1 ± 1.4	3.5–11.6
Body depth ^{1,2}				37	51.6 ± 9.0	34.3–80.4	292	54.9 ± 9.6	29.6–81.5	329	54.5 ± 9.5	29.6–81.5
Maxillary length ²				37	16.9 ± 2.3	11.1–21.3	292	17.5 ± 2.4	11.4–24.7	329	17.5 ± 2.4	11.1–24.7
Total												
Standard length ¹	248	162.3 ± 16.1	129–210	154	169.3 ± 30.4	127–275	341	208.8 ± 35.4	130–295	743	185.1 ± 36.5	127–295
Total gill-raker count ¹	248	28 ± 1.8	20–31	154	35.0 ± 2.0	32–38	341	41.4 ± 1.7	39–48	743	35.6 ± 6.2	20–48
Head depth ¹	248	17.3 ± 1.8	13.0–22.7	154	19.3 ± 3.0	14.2–28.3	341	22.4 ± 3.5	13.0–33.3	743	20.0 ± 3.7	13.0–33.3
Gill-raker length ²	248	4.2 ± 0.6	2.3–6.9	154	5.1 ± 1.7	2.1–8.9	341	7.0 ± 1.4	3.5–11.6	743	5.7 ± 1.8	2.1–11.6
Body depth ^{1,2}	248	34.2 ± 4.5	25.4–51.5	154	39.0 ± 9.3	26.3–80.4	341	51.7 ± 11.9	24.3–81.5	743	43.3 ± 12.4	24.3–81.5
Maxillary length ²	248	14.3 ± 1.5	10.6–18.7	154	15.3 ± 2.3	11–21.3	341	16.9 ± 2.7	10.3–24.7	743	15.7 ± 2.6	10.3–24.7

¹ High canonical discriminant function coefficient between lakes

² High canonical discriminant function coefficient between morphotypes

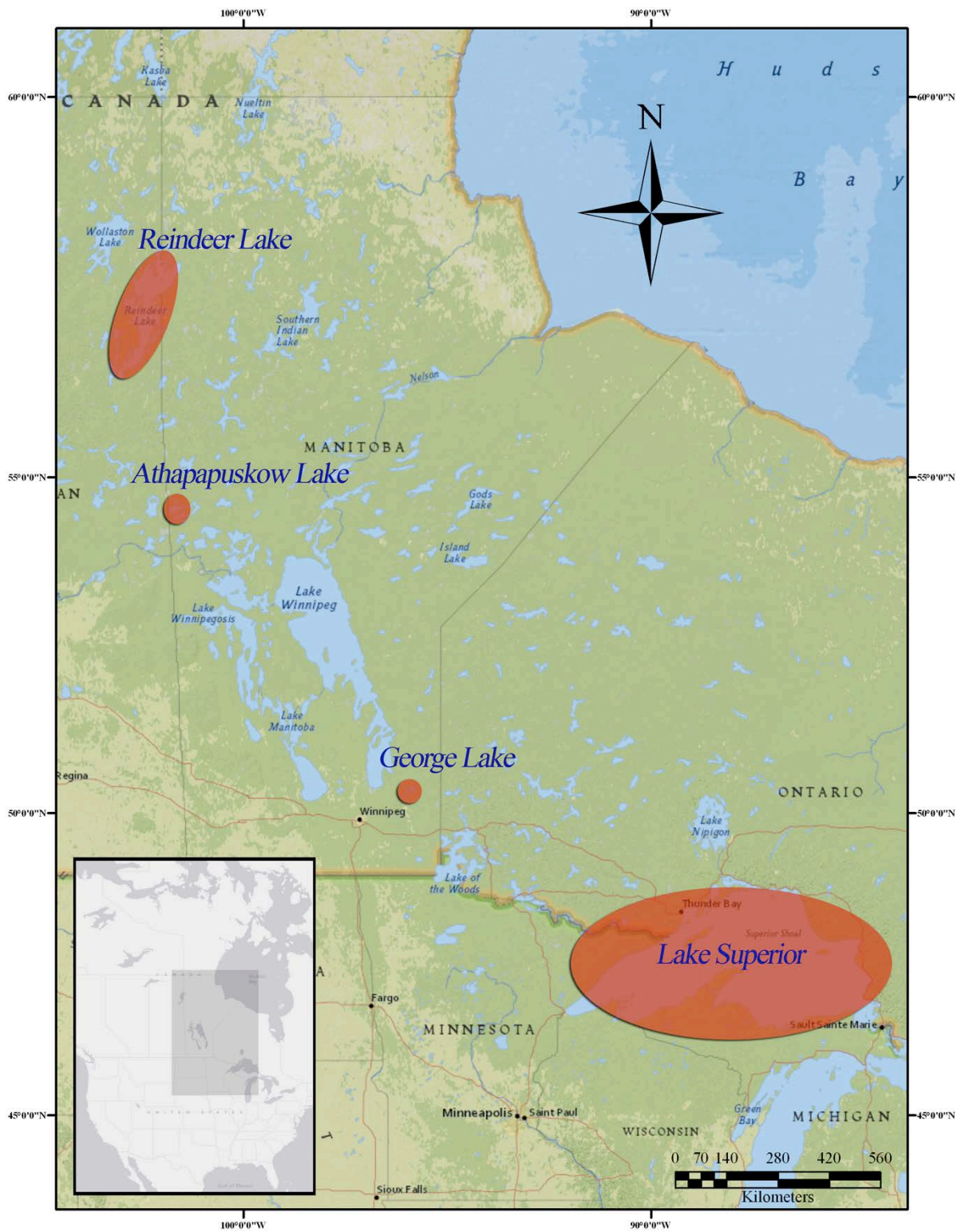


Figure 1. Location of lakes where *C. artemis* and *C. zenithicus* were collected.

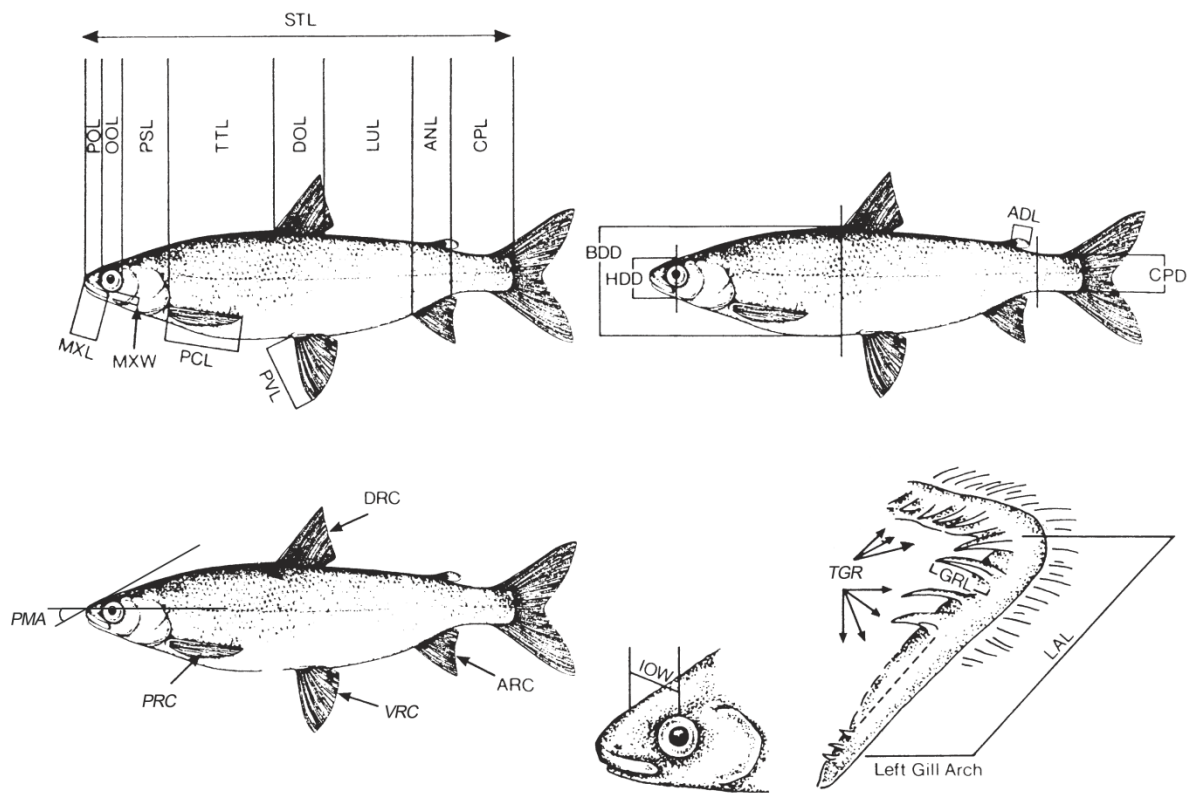


Figure 2. Meristic and morphometric measurements (modified from Vuorinen et al. 1993). See Table 1 for acronyms.

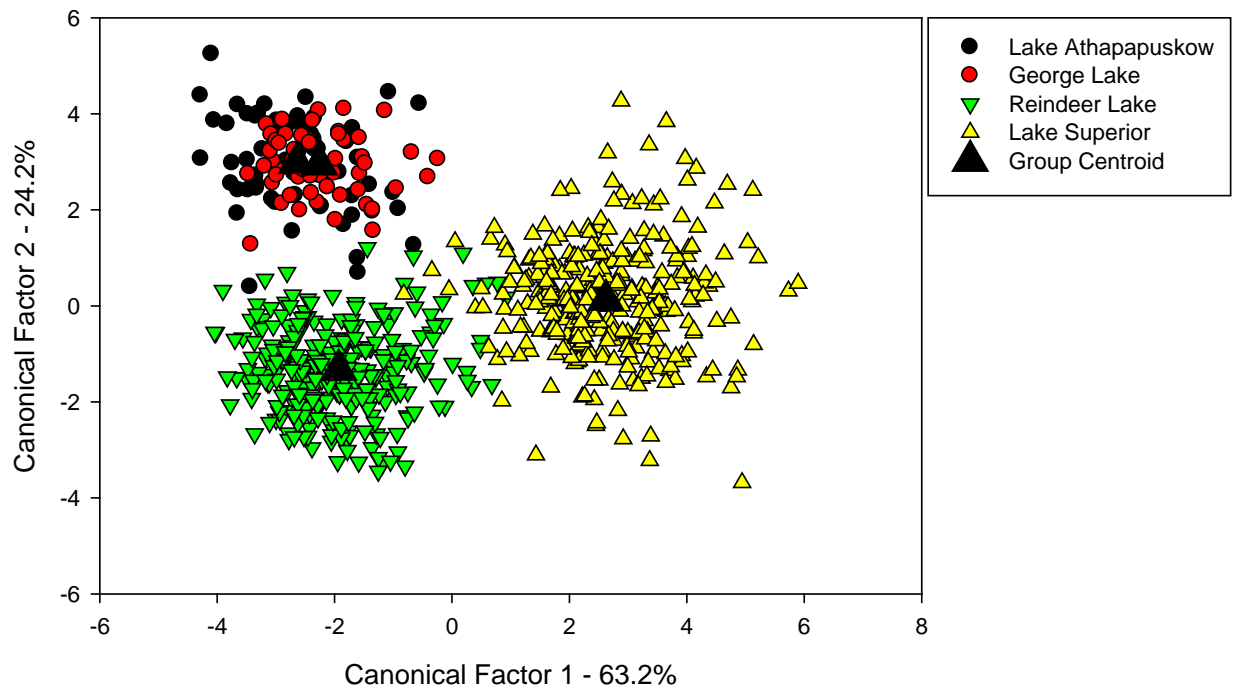


Figure 3. Bivariate plot of discriminant function score by lake.

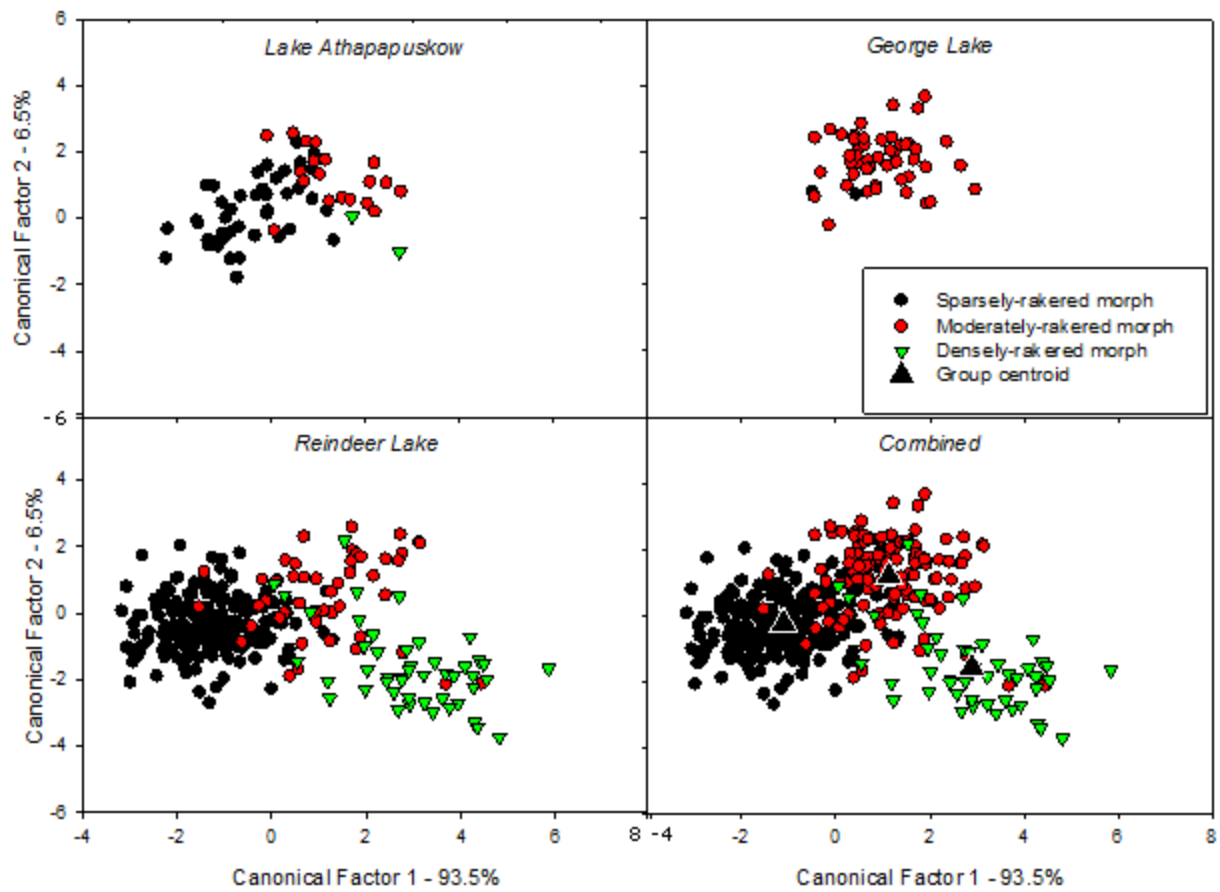


Figure 4. Bivariate plots of discriminant function score by morphotype. The Combined bivariate plot represents the resulting output, while bivariate plots of each lake are illustrated to facilitate interpretations.

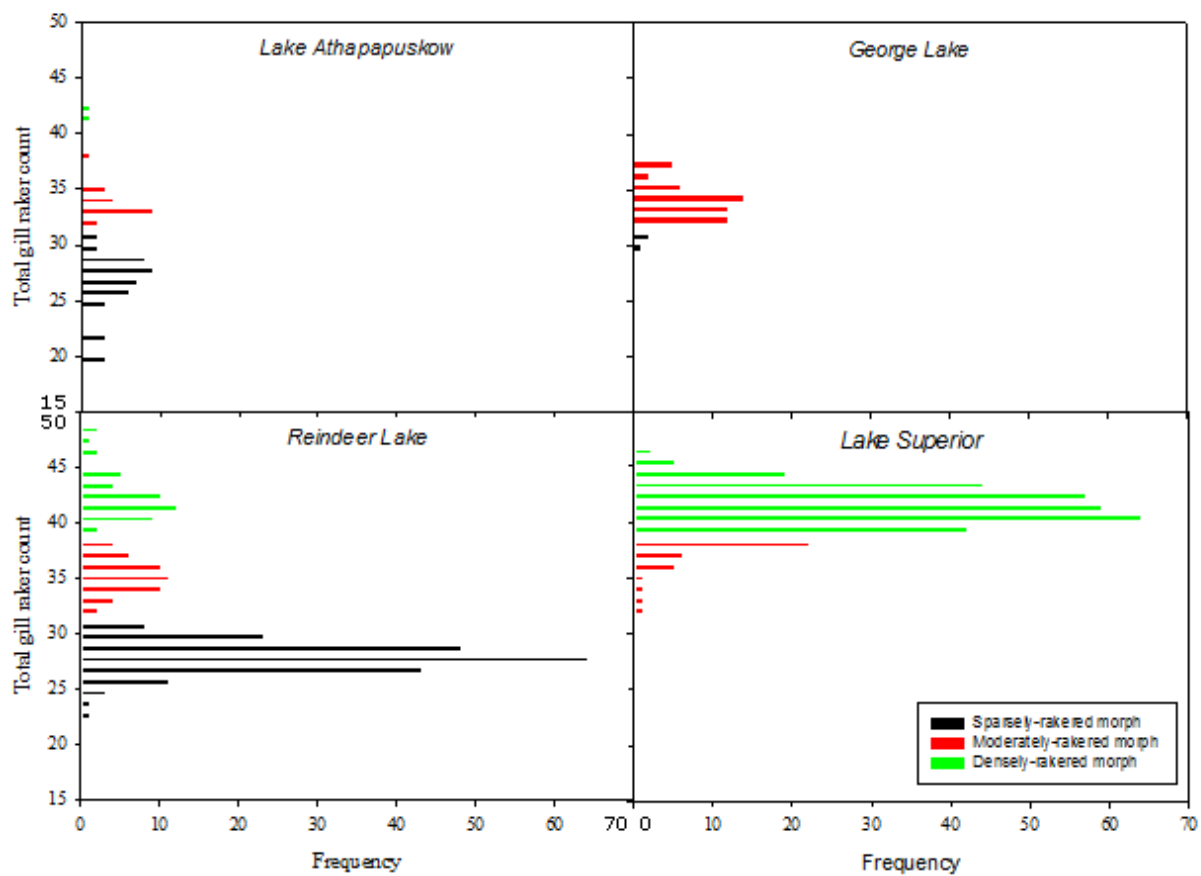


Figure 5. Frequency distribution of sparsely-, moderately-, and densely-rakered morphotypes by lake.