Abundance, distribution and identification of the shortjaw cisco (Coregonus zenithicus) in the proposed Lake Superior marine protected area

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ABUNDANCE, DISTRIBUTION AND IDENTIFICATION OF THE SHORTJAW CISCO (*COREGONUS ZENITHICUS*) IN THE PROPOSED LAKE SUPERIOR MARINE PROTECTED AREA

by

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ABSTRACT AND RÉSUMÉ

The shortjaw cisco (*Coregonus zenithicus*) has been extirpated, or undergone dramatic declines in its abundance, throughout much of its' native range. This has led to the shortjaw cisco being listed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Overfishing and changes in fish community structure have likely contributed to the low abundance of shortjaw cisco in Lake Superior. Our understanding of the abundance of shortjaw cisco is further complicated by the difficulty in distinguishing this species from other deepwater ciscoes. In this survey, we aimed to: 1) determine the abundance of shortjaw cisco, and compare the current deepwater fish community, with historic surveys; 2) examine the depth distribution of *Coregonus* spp.; and 3) determine which morphological characteristics best allow for identification of deepwater ciscoes in a portion of Lake Superior that is located within the proposed boundaries of the Lake Superior National Marine Conservation Area. We documented the presence of shortjaw cisco at all our fishing sites and shortjaw cisco made up, on average, 10% of the deepwater cisco assemblage. An average of 5.5 shortjaw cisco per net km were captured. These abundance levels were significantly reduced from surveys performed in the 1920's, but abundance levels were higher than any other area of Lake Superior recently surveyed. Shortjaw ciscoes were captured at similar densities in every depth strata, although the proportion of shortjaw cisco in the deepwater cisco catch increased with increasing depth. We were able to successfully differentiate shortjaw cisco from other coregonines based primarily on an occluded lower jaw and the low number of short gill rakers.

Le cisco à mâchoires égales (*Coregonus zenithicus*) est disparu, ou son peuplement a subi un déclin spectaculaire, dans toute son étendue naturelle, ce qui lui a valu d'être classé comme espèce menacée par le Comité sur la situation des espèces en péril au Canada (COSEPAC). La pêche excessive et les changements dans la structure de la communauté halieutique ont contribué à la faible abondance de ciscos à mâchoires égales dans le lac Supérieur. Il est davantage plus compliqué de comprendre la profusion de ce poisson à cause de la difficulté de distinguer ces espèces des ciscos de profondeur. Dans la présente étude, nous avons pour objectif : 1) de déterminer l'abondance de ciscos à mâchoires égales et de comparer la communauté de poissons de profondeur avec les études historiques, 2) d'examiner la répartition en profondeur des *Coregonus spp.*, et 3) de déterminer les caractéristiques morphologiques qui sont les meilleurs pour l'identification des ciscos de profondeur dans une partie du lac Supérieur, située dans les limites proposées de l'aire marine nationale de conservation du lac Supérieur. Nous avons documenté sur tous nos sites de pêche la présence de ciscos à mâchoires égales, qui correspondait en moyenne à 10 % du groupement de ciscos de profondeur. On a capturé une moyenne de 5,5 de ciscos à mâchoires égales par kilomètre net. Ces niveaux d'abondance ont baissé de manière importante depuis les études réalisées dans les années 1920, mais sont plus élevés que

dans toute autre partie du lac Supérieur récemment observée. Nous avons capturé une quantité similaire de ciscos à mâchoires égales dans chaque couche de profondeur, bien que la proportion de ciscos à mâchoires égales attrapés parmi les ciscos de profondeur augmente au fur et à mesure que la profondeur augmente. Nous avons pu différencier avec succès le cisco à mâchoires égales des autres ciscos, en nous basant principalement sur une mâchoire inférieure occluse et sur la faible quantité de branchicténies courtes.

INTRODUCTION

The shortjaw cisco, *Coregonus zenithicus* (Jordan and Evermann 1909), is one of three recognized deepwater coregonines remaining in Lake Superior. The three extant species are remanants of a taxonomically complicated deepwater cisco flock which characterized the Great Lakes. Shortjaw cisco is widely distributed, ranging from the Laurentian Great Lakes north through Great Slave Lake in the Northwest Territories (Todd 2003). The current status of most shortjaw cisco populations is not known and where known, in many cases the status appears to be some level of risk. The species has been extirpated from some lakes, and has experienced steep declines in others, leading the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to list the shortjaw cisco as Threatened (Houston 1988, Todd 2003). In 2004, Fisheries and Oceans Canada solicited opinions as to whether shortjaw cisco should be added to Schedule 1 list of the Species at Risk Act (SARA), making it legally protected. This would have the potential to greatly impact current commercial and aboriginal fishing practices throughout its range, including Lake Superior.

Deepwater ciscoes were part of a sizeable targeted fishery In Lake Superior from 1894-1950, with almost 11 million metric tonnes harvested (Hoff and Todd 2004). Shortjaw cisco represented more than 90% of the commercial deepwater cisco catch in the 1920s, but recent surveys replicating the methods of the 1920s surveys have documented a shift in the deepwater community. Shortjaw cisco appear to have been replaced by bloater *C. hoyi* and kiyi *C. kiyi* and make up, on average, < 5% of the catch (Petzold 2002, Hoff and Todd 2004). The shortjaw cisco decline has primarily been attributed to commercial overharvest (Lawrie 1978), although invasive species, habitat degradation and inter-specific competition or predation are suggested as factors that may be limiting recovery.

Assessing deepwater cisco populations is challenging due to the spatial overlap and morphological plasticity of the species involved. Shortjaw cisco, bloater, kiyi and cisco (*C. artedi*) share similar physical characteristics and there is no single diagnostic character that separates these species, although gill raker counts and lower jaw position are most important for identifying shortjaw cisco from the other three species (Todd and Smith 1980, Todd 2003). Selgeby and Hoff (1996) presented evidence for differences in inter-specific depth distribution, with shortjaw cisco and kiyi found at depths of 105-145 m, bloater at 65-105 m, and cisco < 65 m.

The research outlined in this manuscript is aimed to: 1) determine the abundance of shortjaw cisco, and compare current catches to Koelz's (1929) assessment of the deepwater fish community; 2) examine the depth distribution of *Coregonus* spp.; and 3) determine which morphological characteristics best allow for identification of deepwater ciscoes, in a portion of Lake Superior that would fall within the proposed Lake Superior National Marine Conservation Area.

METHODS AND MATERIALS

The deepwater cisco assessment was undertaken around the Rossport area of Lake Superior (Figure 1a). The area was chosen as it had relatively close access to deep water, its numerous islands allowed us to sample in windy conditions, the site complemented other recent deepwater cisco surveys (e.g., Petzold 2002), and recent United States Geological Survey surveys found no evidence for shortjaw cisco in the area (Owen Gorman, United States Geological Survey, personal communication, 2006). In addition, these waters are slated to become part of the Lake Superior National Marine Conservation Area (see www.parkscanada.pch.gc.ca/progs/amnc-nmca/proposals/LS_proposal_e.asp), which may open up future research opportunities.

Sampling occurred September 14-23, 2004 in four main areas: the Schreiber and Simpson channels, and inside and outside the protective islands (Figure 1b). Mean fishing depth and management grid data for each location are presented in Table 1. No pre-determined sampling design was used, as one of the study objectives was to sample sites previously identified in Koelz (1929). However, we did endeavour to sample across a wide variety of depths to ensure that the resulting data could address objective 2.

The relative abundance of shortjaw cisco in the Rossport area was assessed using overnight gill net sets except, on one occasion, when a single net was left for two nights due to adverse weather conditions. Our net gangs were composed of four 92 m nylon mesh panels, alternating 64 mm and 70 mm stretch mesh (for a total gang length of 366 m). Mesh size and material were chosen to as closely replicate the nets used in the Koelz (1929) surveys, although Koelz (1929) used cotton or linen nets.

Gill net catches were tallied on-board by mesh size, and a total weight per lift was taken for each species, except for deepwater ciscoes which were weighed together. *Coregonus* spp. were tentatively identified to species based on external morphological characteristics (primarily mouth and fin position and colour) and all putative shortjaw cisco, along with four randomly selected bloater, kiyi and cisco from each net set, were labeled and frozen for later morphometric and biological analyses. Ciscoes were identified with the aid of a variety of unpublished keys provided by Owen Gorman, Tom Todd and Michael Hoff of the United States Geological Service. In the 28 net sets, a total of 57 shortjaw cisco, 66 bloater, 28 kiyi and 66 cisco (all tentative identifications) were kept.

In the laboratory, frozen fish were thawed, photographed (full body and head), weighed and a total length taken. Initial identifications were re-assessed by three biologists, and any potential changes in identification were noted. A number of specimens had characteristics from more than one species; these fish would likely have been classified as hybrids in other studies, but we assigned them to the species for which they most fit the criteria. Stomachs and a tissue sample for potential future genetic analysis were removed and stored in 95% ethanol. A suite of 27 characteristics, 21 morphometric measurements and six meristic counts, were taken (Figure 2; Vuorinen et al. 1993). An additional three characters (colour, mouth position and premaxillary angle) were also added (Clarke 1973). Aging structures (scales and otoliths) were removed, individuals were examined for sex and state of maturity, and gonads were weighed. All fish identified as shortjaw cisco were re-frozen after processing, while the remaining species were discarded.

Fish were aged by mounting scales between glass slides and annuli were interpreted using a 48X magnification microfiche projector. Scales were extensively examined for annulus characteristics, such as changes in circuli spacing and cutting over, prior to counting and measuring annuli. Radii and annuli distances were manually measured along the lateral region of each scale. Forty percent of the scales were interpreted by a second, independent ager.

Measured annuli were applied to the standard Fraser-Lee method (DeVries and Frie 1996) to back-calculate growth rates. This method assumes a linear relationship ($L_c = a + bS_c$) between the total length (L_c) of the fish and the scale radius (S_c). Scale radius was estimated from a minimum of five scales. A separate intercept, *a*, was estimated for each species. The regression line equations were:

Cisco	L_c = 37.6 (mm) + 0.64 (mm)S_c ; r^2 = 0.42
Bloater	L_c = 29.9 (mm) + 0.66 (mm)S_c ; r^2 = 0.44
Kiyi	L_c = 19.9 (mm) + 0.83 (mm)S_c ; r^2 = 0.69
Shortjaw cisco	L_c = 28.3 (mm) + 0.72 (mm)S_c ; r^2 = 0.51

Length-at-age was calculated from the equation:

$$L_i = a + (L_c - a)S_i / S_c$$

where S_i is the difference between the scale foci and annulus i.

Data analysis

The catch for all species was averaged and the proportion of shortjaw cisco in the deepwater cisco fauna calculated for each of the four fishing areas by average depth of each net set (<65m, 66-104m, >104m). Catch from the one net left for two overnight periods was divided by two for the above, and all subsequent, analyses. To determine whether the expected deepwater cisco spatial segregation was evident in the Rossport area, we tested for differences in shortjaw cisco, bloater, kiyi and cisco abundance among sampling areas and depth classes, using Kruskal-Wallis non-parametric analyses of variance (Zar 1999). Non-parametric tests were used as the catch data could not be transformed to meet normality assumptions in all cases. Bonferroni correction factors were applied to alpha values to ensure the question-wise probability remained at alpha = 0.05. When significant among site or depth differences were found, a pair-wise mean rank post-hoc comparison procedure was used to separate sites or depths (Siegel and Castellan 1988). Relative abundance was assessed by combining catches from the 64 and 70 mm meshes, as Koelz (1929) also combined catches from his two mesh sizes.

We compared the historic and current deepwater fish community in the Rossport area by specifically examining three areas that were fished in both the Koelz (1929) and current survey. Any multiple night sets were converted to provide an average catch per one overnight. Our data for the Simpson Channel were restricted to the three deep net sets to allow a more relevant comparison with the Koelz (1929) samples, as those sets were all in the deepest part of the channel.

To provide a lake-wide comparison of the historic and current deepwater fish community, we expanded the above approach to summarize all the recent deepwater cisco surveys that used the replica Koelz (1929) gear. A Wilcoxon matched pairs test, the non-parametric equivalent of a paired t-test, was used to test for differences in historic and current shortjaw cisco catch-per-effort (Zar 1999). Data from Koelz (1929), Petzold (2002), Hoff and Todd (2004) and this survey were included in the analysis.

One-way analyses of variance were used on the back-calculated length-at-age data to determine if there were growth differences among species. Bonferroni corrections were applied to ensure alpha remained at 0.05. Tukey HSD post-hoc tests were used to separate species when significant differences were detected.

To determine whether key morphological characters identified in previous coregonine studies (e.g., Clarke 1973, Todd 2003) differed among deepwater ciscoes, we tested for differences in gill-raker count and length, premaxillary angle, maxillary length and snout length using one-way ANOVA. Morphometric variables were adjusted to remove the effect of body size by standardizing all measurements against standard length. Data were $\ln(x+1)$ transformed to meet normality assumptions. When significant differences were detected, Tukey HSD post-hoc tests were used to separate species.

Prior to multivariate analysis, morphological measurements were $\ln(x+1)$ transformed to meet normality assumptions and the suggestions of Reist (1985, 1986) to adjust for potential body size effects. The values of each morphological variable were first standardized to a mean 0 and a standard deviation of 1 to avoid any confounding effects due to among-site differences. Each character was regressed against $\ln(x + 1)$ transformed standard length, and the resulting residuals were used as the morphometric variables in both principal components and discriminant function analyses to determined whether the suite of morphometric variables could define these closely related species. The classification algorithms from discriminant function analysis were validated using a jackknife routine to test model accuracy (Manly 1994), in which each fish was assigned to its closest assigned species without using that fish in the classification algorithm.

RESULTS

Ten species were captured in our 28 overnight gill net sets. Cisco was the most commonly encountered species across all areas, followed by lake trout (*Salvelinus namaycush*), bloater, lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*). Deepwater ciscoes were most common at the Inner Islands and Simpson Channel sites. Conversely, lake trout were dominant in the Schreiber Channel and Outer Islands sites (Table 2). Similar numbers of shortjaw cisco were captured in all areas, although the percentage of shortjaw cisco in the deepwater cisco fauna ranged from a low of approximately 5% to a high of 13%. Among the deepwater ciscoes and cisco, only cisco catches were found to significantly differ among areas, with higher relative abundance found at the Inner Islands and in the Simpson Channel (Table 3).

Differences among depth strata were more pronounced, as the catches of most species declined precipitously in our deepest sets (> 105 m, Table 4). Only burbot relative abundance increased with increasing depth. The three deepwater ciscoes and cisco also followed this pattern, although only cisco and bloater catches were significantly different among depth classes (Table 3). Cisco were unexpected abundant at medium depths (66-104m). Shortjaw cisco were captured in all three depth bins, and although numerically less abundant at the > 105 m sites, made up a greater percentage of the deepwater cisco fauna in this deepest depth strata (Table 3).

Shortjaw cisco catches have declined precipitously in the Rossport area since the early 20th century (Table 5). Shortjaw cisco dominated the historic catch, with few other species represented in the gill nets of Koelz (1929). Interestingly, the overall catch-per-effort appears to have not changed significantly over the same time period as catches for other coregonines have increased in this area (Table 5). This precipitous decline in shortjaw cisco abundance is apparent in all regions of Lake Superior, as shortjaw cisco catch-per-effort has significantly declined from the 1920s through to present day (Z = 2.4, P = 0.018, Table 6). The Rossport area appears to contain the healthiest shortjaw cisco population of any of the recently surveyed sites, with catches 5 – 10 times higher than other areas (Table 6).

Growth patterns were similar among cisco, bloater, kiyi and shortjaw cisco (Figure 3). Cisco appeared to have the fastest growth, but the only significant differences in growth among species were observed in kiyi, which grew slower than cisco and bloater at ages 1 through 4.

Shortjaw cisco significantly differed from bloater, kiyi and cisco in three of five characters previously identified as being central for separating these similar species. Shortjaw cisco had fewer, shorter gill rakers, and a steeper premaxillary angle (Table 7). We were also able to differentiate cisco, which had a significantly shorter snout, longer premaxillary and more gill rakers than the other species. Bloater and kiyi characters consistently fell in between that of shortjaw cisco and cisco. Consequently gill raker number and length, maxillary length and angle and snout length could not be used to differentiate these latter two species.

Despite among-species differences in the univariate characters, a principal components analysis on the full suite of morphometric and meristic characters was unable to separate the species (Figure 4). Characters were poorly correlated, and individual principal components did not account for much of the variation in the data (Table 8). Few of the characters, previously identified as being important for separating these species, were key contributors to the first few principal component axes. A discriminant function analysis on the same data set was more successful at separating species, and most of the characters identified in the univariate analyses were also important in the discriminant function (Figure 5). The first two canonical variables explained 95% (CV 1 = 60%, CV 2 = 35%) of the variance in the morphometric data (Table 9). The first CV was characterized primarily by a number of gill raker characters, which effectively discriminated shortjaw cisco (and to a lesser degree cisco) from the other species. The second CV was characterized by gill raker, fin and head measurements, and it helped separate bloaters from the other species. The resulting classification algorithm identified approximately 2/3 of the fishes correctly, with shortjaw cisco being correctly classified 70% of the time (Table 10a). The assignment of shortjaw cisco remained relatively similar in the jackknifed discriminant function classification (shortjaw cisco were correctly classified 63% of the time), but the correct assignment of the cisco and kiyi declined dramatically with only 38% and 25% of individuals being correctly assigned, respectively (Table 10b).

DISCUSSION

Shortjaw cisco were captured at every location fished in the Rossport area, however, densities were uniformly low. In the 1920s, shortjaw cisco completely dominated the deepwater fish community, comprising > 99% of the coregonine catch and biomass in most areas (Koelz 1929). Recent surveys have demonstrated a shift in the deepwater community, with shortjaw cisco at now less than 1% of their historic abundance (this study; Petzold 2002, Hoff and Todd

2004). Dramatic shortjaw cisco declines were also apparent in our survey in comparison to the Koelz (1929) survey, but shortjaw cisco catches in the Rossport area were much higher than those in other targeted surveys (Petzold 2002, Hoff and Todd 2004).

There has been a demonstrable long-term decline in Lake Superior shortjaw cisco catches. In the Koelz (1929) survey, shortjaw cisco were dominant across the lake with catch-per-unit-effort > 100 fish / net km in many areas. By 1959, shortjaw cisco and bloater were co-dominant in the deepwater cisco catch (Brown, Jr., unpublished data cited in Hoff and Todd 2004). In the 1970s, shortjaw cisco represented a maximum of 30 % of the deepwater cisco catch in Michigan waters (Peck 1977). Contemporary surveys (Petzold 2002, Hoff and Todd 2004) documented an almost complete loss of the species in many areas. Our survey established the greatest proportion of shortjaw cisco in the deepwater catch (> 10 %) and the highest densities (5.5 / net km) of all the contemporary surveys, but these levels remain well below historic densities. It is believed that shortjaw cisco in Lake Superior declined because of commercial overharvest (Lawrie 1978), and a variety of mechanisms (inter-specific competition, predation by lake trout, habitat loss) are hypothesized for their continued low abundance, even in the absence of most commercial fishing pressure (Petzold 2002). Cisco and bloater were the dominant coregonines in this study and in Hoff and Todd (2004), and bloater was by far the most abundant coregonine in the Petzold (2002) survey. Overall coregonine densities in the Rossport area, if the potential for differences in density due to soak time and net material are minimal (see below), were similar to historic levels (Koelz 1929) as bloaters increased in abundance to make up for losses in other coregonines. This suggests that some community-level factor (e.g. competition or selective predation) is helping to keep shortjaw cisco at their current low abundance.

While the mesh sizes fished in the current survey were selected to match the survey of Koelz (1929), there are important differences in gear construction and use that may have led to gear efficiency differences between the two surveys. The nets used by Koelz (1929) were constructed of cotton and linen, which typically catch less than one-half of the fishes caught by the nylon nets used in this survey (Pycha 1962). In addition, gill nets left more than one overnight period (i.e., soak time) in Lake Superior can ‘fill up’ with fishes, reducing their fishing efficiency (Wilberg et al. 2003). These factors mean that the differences in shortjaw cisco relative abundance observed between the surveys may be even larger than presented above.

The expected separation in the depth distribution of deepwater ciscoes and cisco (i.e. shortjaw cisco and kiyi found at depths of 105-145 m, bloater at 65-105 m, and cisco < 65 m (Selgeby and Hoff (1996)) was not apparent in this survey. Cisco and bloater were common in all depths up to 105 m, and there was no evidence to suggest that kiyi and shortjaw cisco were more common at deeper depths. The deeper gill net sets produced very few deepwater ciscoes or cisco.

In contrast, Petzold (2002) found the deeper (> 105 m) stratum in Michipicoten Harbour contained the same density of coregonines as the shallower stratum, and he found no differences in the depth distribution of any species. Hoff and Todd (2004) determined shortjaw cisco were captured in deeper (mean depth 89 m) versus shallower (mean depth 68 m) gill net sets in their survey, but further depth distribution comparisons with our study are not possible given the way that their data are presented.

Growth of shortjaw cisco in Lake Superior appears to have slowed considerably over the past 80 years. Four-year old shortjaw cisco collected in 1922 averaged 234 mm (Van Oosten 1936), while those captured in this survey averaged 208 mm. Eight-year old fish in the Van Oosten (1936) survey were 325 mm, while shortjaw cisco captured in the Hoff and Todd (2004) and this survey averaged 285 mm and 290 mm, respectively. Fluctuating growth patterns have also been observed for bloater and cisco in Lake Superior, where increased growth was found when lake trout populations collapsed (Dryer and Beil 1968). Siscowets, a deep water lake trout form, are currently at high abundance in Lake Superior (Petzold 2002), and high siscowet predation may have led to the observed lower growth rates.

Our univariate morphometric analysis indicated that characteristics previously identified as useful for identifying coregonines were successful in separating two of the four study species, shortjaw cisco and cisco. These characters include some of the traditional characters used in identifying shortjaw cisco: gill raker counts and length, and premaxillary angle (Todd and Smith 1980, Todd 2003). The same characters were also useful for species identification in the discriminant function analysis. However, four groups, representing the four species, were not apparent in the principal components results. Principal components analyses on other closely related fishes have been found to separate species (i.e., Dynes et al. 1999, Svanbäck and Eklöv 2001), but not in all cases (e.g., Rincón 2000).

The characteristics identified in the univariate and discriminant function analyses provide additional characters to the one character used to identify fishes in the field: a prognathous lower jaw. It is apparent that additional head characteristics, including gill raker number and length, premaxillary angle and maxillary and eye size are important characteristics for identifying deepwater ciscoes. We did have a number of fish that displayed key identification characteristics of more than one species that would likely have been classified as hybrids by others (e.g., Petzold 2002, Hoff and Todd 2004), but we endeavoured to assign a species identity to every specimen. It is quite likely that our multivariate analyses would have been better at distinguishing among species if these fishes had been labelled as hybrids and excluded from the analysis.

The steep decline of shortjaw cisco throughout the Great Lakes has resulted in it currently being ranked as Threatened by COSEWIC, and assessed for inclusion on the Schedule 1 list of the Species at Risk Act (SARA), which would make it legally protected (e.g., prohibitions against killing, capturing or possessing shortjaw cisco). The development of a recovery strategy to protect and rehabilitate shortjaw cisco populations and the discovery of relatively high shortjaw cisco densities remaining in the Rossport area of Lake Superior may provide interesting opportunities for the protection of this species. Commercial fishing has been banned from the Rossport area since the early 1970s (Ken Cullis, Ontario Ministry of Natural Resources, personal communication, 2006). The waters fished during this survey all lie within the proposed boundaries of the Lake Superior National Marine Conservation Area, which may also provide opportunities for the innovative and collaborative management of shortjaw cisco in this region.

Lake Superior likely supports the largest remaining shortjaw cisco population in the world and further research on the biology and population dynamics of this species is required to understand what factors may limit its recovery. While recovery strategies are being developed and implemented, a monitoring program should be initiated to provide an ongoing evaluation of recovery efforts.

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Table 1. Grid location, number of nights fished and mean net depth by fishing area.

Fishing area	Grid locations	Sampling effort (m) and # of sets	Mean depth (m)
Schreiber Channel	458-13, 458-22, 458-24	1098 (3)	94
Inner Islands	457-11, 457-21, 457-23	5856 (15)	74
Simpson Channel	456-12, 456-21, 456-23, 456-24, 456-34	2196 (6)	111
Outer Islands	457-51, 556-24, 557-11, 557-14	1464 (4)	92

Table 2. The mean catch per 366 m gill net gang by area, ± 95 % confidence interval (parentheses under mean), of species captured in deepwater cisco nets near Rossport, Ontario. The percentage that shortjaw cisco (% SJC) comprise of the deepwater cisco fauna (collectively known as chubs, including *C. zenithicus*, *C. hoyi*, and *C. kiyi*) is also identified. An explanation of the species abbreviations used, and their common and scientific names, is located below.

Area	Species[1]										% SJC
	LNS	RBS	CI	LW	BL	KI	SJC	RW	LT	BU	
Schreiber	1.7	0	11.7	1.7	9.7	3.3	0.7	0.7	66.7	3.3	4.9
Channel	(-3.5-6.8)	(0-0)	(10.2-13.1)	(-2.1-5.5)	(0.3-19.1)	(-4.3-10.9)	(-0.8-2.1)	(-2.2-3.5)	(-32.2-165.5)	(-4.3-10.9)	
Inner	0.7	0.4	30.1	9.8	16.7	0.8	2.6	0.9	1.9	7.2	13.0
Islands	(-0.1-1.4)	(-0.1-0.9)	(26.3-33.9)	(7.9-11.6)	(11.9-21.4)	(-0.2-1.8)	(1.5-3.7)	(-0.5-2.2)	(1.0-2.8)	(5.0-9.4)	
Simpson	3.2	0.3	25.5	5.5	21.3	0.2	1.8	0.3	10.3	11.7	7.9
Channel	(-1.6-8.0)	(-0.2-0.9)	(-2.0-53.0)	(1.8-92)	(-8.2-50.8)	(-0.3-0.6)	(-1.4-5.0)	(-0.3-0.6)	(-4.1-24.7)	(2.8-20.5)	
Outer	0.3	0	3.5	3.0	8.0	3.3	1.0	0	39.0	0.8	8.2
Islands	(-0.5-1.0)	(0,0)	(-0.7-7.7)	(-4.6-10.6)	(-1.1-17.1)	(-1.3-7.8)	(1.0-1.0)	(0,0)	(-8.4-86.4)	(0.0-1.5)	
Total	1.3	0.3	23.3	7.0	15.7	1.3	2.0	0.6	15.9	6.8	10.6
	(0.3-2.2)	(0.0-0.5)	(17.2-29.5)	(5.2-8.8)	(10.1-21.3)	(0.4-2.1)	(1.2-2.8)	(-0.1-1.3)	(5.4-26.4)	(4.5-9.1)	

[1] LNS = longnose sucker, *Catostomus catostomus*; RBS = rainbow smelt, *Osmerus mordax*; CI = cisco, *Coregonus artedii*; LW = lake whitefish, *C. clupeaformis*; BL = bloater, *C. hoyi*; KI = kiyi, *C. kiyi*; SJC = shortjaw cisco, *C. zenithicus*; RW = round whitefish, *Prosopium cylindraceum*; LT = lake trout, *Salvelinus namaycush*; BU = burbot, *Lota lota*

Table 3. Summary of Kruskal-Wallis tests of deepwater ciscoes and cisco for location and depth distribution. Probabilities marked with an asterisk indicate significance after the application of a Bonferroni correction factor. Codes for post-hoc multiple comparison procedures are as follows: Spatial Schreiber Channel = a, Inner Islands = b, Simpson Channel = c, Outer Islands = d; Depth < 65 m = shall, 66-104 m = mid, > 105 m = deep.

Species	Location			Depth		
	H (3, n = 28)	*P*	Post-hoc	H (2, n = 28)	*P*	Post-hoc
cisco	10.8	0.012*	b,c > a,d	9.7	0.008*	shall=mid>deep
bloater	3.4	0.34		10.8	0.005*	shall=mid>deep
kiyi	9.1	0.03		4.1	0.13	
shortjaw cisco	5.6	0.13		3.0	0.22	

Table 4. The mean catch per 366 m gill net gang by depth strata, ± 95 % confidence intervals (shown in parentheses under mean), of species captured in deepwater cisco nets near Rossport, Ontario. The percentage that shortjaw cisco (% SJC) comprise of the deepwater cisco fauna (collectively known as chubs, including *C. zenithicus*, *C. hoyi*, and *C. kiyi*) is also identified. See Table 2 for an explanation of species codes.

Depth (m)	Species										% SJC
	LNS	RBS	CI	LW	BL	KI	SJC	RW	LT	BU	
< 65	1.8	0.8	31.6	11.8	13.2	0.2	1.6	0	2.6	9.2	10.7
(n=5)	(-0.7-4.3)	(-0.8-2.4)	(20.5-42.7)	(9.3-14.3)	(1.1-25.3)	(-0.4-0.8)	(-0.7-3.9)	(0-0)	(-0.3-5.5)	(2.4-16.0)	
66-104	1.4	0.2	26.3	7.0	20.2	1.9	2.4	0.9	22.0	5.0	10.0
(n=18)	(-0.1-2.9)	(0.0-0.4)	(18.5-34.0)	(5.0-8.9)	(12.3-27.7)	(0.6-3.2)	(1.3-3.6)	(-0.2-2.0)	(6.0-38.0)	(3.5-6.5)	
>105	0.2	0	4.4	2.4	2.6	0.2	0.8	0	7.4	11.0	22.2
(n=5)	(-0.4-0.8)	(0-0)	(-0.9-9.7)	(-2.5-7.3)	(-1.0-6.2)	(-0.4-0.8)	(0.2-1.4)	(0-0)	(-2.9-17.7)	(-2.85-24.8)	

Table 5. Comparison of coregonine catch-per-effort (CPE, fish per km) from targeted deepwater ciscoes gill net (64 and 70 mm stretch mesh) catches between Koelz (1929) and this study (2004) at individual sites. Three of the four sites for each time period were in similar geographic locations. Multiple night sets are adjusted to reflect an average catch per one overnight period; multiple sets from the same geographic area were averaged. See Table 2 for an explanation of species codes.

Site	Location	Depth (m)	CI	LW	BL	KI	SJC	RW	Total
1	Bread Rock (Koelz)	155	0.8	0.0	1.6	0.0	172.2	0.0	174.7
	Schreiber Channel (2004)	94	31.9	4.5	26.4	9.1	1.8	1.8	75.5
2	Off Salter Island (Koelz)	77	0.0	0.0	1.6	0.0	22.1	0.0	23.8
	Inner Islands (2004)	74	82.1	26.7	45.5	2.2	7.1	2.4	166.0
3	Simpson Channel (Koelz)	135	0.0	0.0	0.0	0.0	13.1	0.0	13.1
	Simpson Channel[a] (2004)	137	8.2	10.9	2.7	0.0	1.8	0.0	8.2

[a] These numbers differ from Table 2 as there were three deep and three shallow sets in the Simpson Channel in the current study, and only the deep sets were used for this comparison to match the Koelz (1929) depths.

Table 6. Comparison of shortjaw cisco catch-per-effort (CUE, fish per km) from targeted deepwater ciscoes gill net (64 and 70 mm stretch mesh) catches through time from across Lake Superior. Multiple night sets are adjusted to reflect an average catch per one overnight period; multiple sets from the same geographic area were averaged. N is the number of nets set in a given location.

Location	Koelz (1929) 1921-23 survey		Recent (1999-2004) surveys	
	N	CUE	N	CUE
Whitefish Bay, MI	1	182.3	2[a]	1.1
Marquette, MI	2	51.3	2[a]	0.6
Ontonagon, MI	2	111.0	2[a]	0.5
Apostle Islands, WI	1	393.7	2[a]	0.0
Grand Marais, MN	1	263.8	2[a]	0.7
Rossport, ON	4	56.0	28[c]	5.5
Michipicoten Island, ON	1	32.8	32[b]	1.2

[a] Hoff and Todd (2004)
[b] Petzold (2002)
[c] This survey

Table 7. Mean gill-raker count and length, premaxillary angle, maxillary length and snout length for *Coregonus* spp. sampled near Rossport, Ontario. Gill-raker, maxillary and snout lengths were standardized as a percent of standard length. Error measurements in brackets are standard deviation

Species	Mean gill-raker count	Standardized middle gill-raker length (%)	Premaxillary angle (degrees)	Standardized maxillary length (%)	Standardized snout length (%)
cisco	43.7 (2.3)	4.1 (0.7)	39.9 (8.1)	8.0 (1.0)	5.9 (0.6)
bloater	42.4 (2.2)	3.8 (0.9)	39.1 (8.3)	9.1 (0.6)	6.6 (0.7)
kiyi	42.9 (2.1)	3.9 (0.8)	38.5 (9.7)	8.7 (0.8)	6.4 (0.7)
shortjaw cisco	40.8 (2.6)	3.4 (0.9)	45.3 (8.1)	8.8 (0.8)	6.4 (0.8)
ANOVA result	$F_{3,208}=16.7$; $P<0.001$	$F_{3,208}=6.8$; $P=0.002$	$F_{3,208}=7.3$; $P=0.001$	$F_{3,208}=23.3$; $P<0.001$	$F_{3,208}=11.7$; $P<0.001$
Post-hoc test	SJC< BL, KI < LH	SJC < BL, KI, LH	SJC < BL, KI, LH	LH < SJC, KI, BL	LH < SJC, KI, BL

Table 8. Character loadings, eigenvalues and the percent variance explained for the first five principal components. Character abbreviations, with the exception of premaxillary angle (PMA), are defined in Figure 2.

Character	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Eigenvalue	3.93	2.65	2.36	1.64	1.45
% Variation	14.56	9.82	8.73	6.08	5.38
POL	0.48	0.54	0.00	-0.30	-0.02
OOL	0.49	-0.52	0.16	-0.07	0.13
PSL	0.45	0.44	-0.13	-0.27	0.01
TTL	0.19	0.38	-0.22	-0.02	0.24
DOL	0.40	0.06	-0.54	0.23	0.01
LUL	-0.15	0.18	0.25	-0.21	-0.17
CPL	-0.29	0.15	-0.20	-0.28	0.13
CPD	-0.05	-0.56	-0.06	0.09	0.17
HDD	0.75	-0.09	0.14	-0.04	0.09
BDD	0.50	-0.26	-0.13	-0.01	0.32
ANL	0.36	-0.12	-0.31	0.49	0.09
IOW	0.26	-0.35	-0.35	-0.13	0.13
MXL	0.69	0.19	-0.09	-0.13	0.20
ADL	0.41	-0.24	0.14	-0.13	-0.25
GRL	-0.26	-0.52	-0.57	-0.27	-0.02
LAL	0.44	-0.23	0.33	-0.09	0.06
DRC	0.46	0.36	0.67	0.20	0.05
ARC	0.59	-0.24	-0.10	-0.23	-0.44
PRC	0.53	-0.23	-0.17	-0.13	-0.51
VRC	-0.07	0.02	-0.31	-0.35	0.50
UGR	0.25	0.26	-0.32	0.35	0.06
LGR	0.18	0.42	-0.35	0.39	-0.21
GRS	-0.05	-0.10	-0.06	0.52	-0.10
PLV	0.10	0.11	-0.34	0.18	0.02
PCL	-0.10	0.09	-0.32	-0.17	-0.45
MXW	-0.25	-0.05	-0.10	0.02	-0.29
PMA	0.10	-0.49	0.33	0.29	0.02

Table 9. Mean standardized canonical coefficients for canonical variables (CV), eigenvalues, percent discrimination and character loadings from a discriminant function analysis on standardized *Coregonus* spp. morphometric and meristic data. Character abbreviations, with the exception of premaxillary angle (PMA), are defined in Figure 2. Characters with an asterisk denote a significant addition to the model.

	Canonical variable		
	CV 1	CV 2	CV 3
Eigenvalue	0.87	0.52	0.08
% Variation	59.5	35.3	5.1
Species	Means of canonical variables		
cisco	-1.07	0.18	0.25
bloater	0.22	-1.05	-0.10
kiyi	-0.58	0.81	-0.60
shortjaw cisco	1.29	0.56	0.12
Character	Standardized coefficients		
POL	0.05	-0.31	-0.16
OOL*	0.26	0.39	-0.49
PSL	0.19	0.10	-0.01
TTL	0.28	-0.08	0.28
DOL	0.14	-0.11	0.21
LUL	-0.12	-0.12	0.10
CPL	-0.35	0.00	-0.04
CPD	0.16	0.12	-0.04
HDD	0.01	0.26	0.03
BDD*	-0.10	-0.82	-0.17
ANL	-0.06	-0.32	0.06
IOW	-0.06	0.03	0.23
MXL*	0.28	-0.30	-0.03
ADL	-0.04	0.10	0.36
GRL	-1.14	0.87	2.05
LAL	0.51	-0.80	-0.76
GRS	-0.80	1.15	1.78
PLV	-0.34	-0.08	-0.01
PCL	0.29	0.05	-0.19
MXW	-0.21	-0.01	-0.01
DRC	-0.01	-0.05	0.03
ARC	-0.10	0.04	0.03
PRC	-0.22	0.10	0.29
VRC	0.05	0.07	-0.10
UGR	-0.17	-0.10	-0.60
LGR*	-0.51	-0.18	-0.08
PMA*	0.38	0.10	0.19

Table 10. The a) standardized and b) jackknifed classification tables from a linear discriminant function analysis calculated on deepwater cisco morphometric and meristic characters. Table entries under the species names show the number of individuals classified to that species.

a) Observed species	Predicted species				% correct
	cisco	bloater	kiyi	shortjaw cisco	
cisco	36	12	14	3	55.4
bloater	9	44	1	9	69.8
kiyi	4	1	21	2	75.0
shortjaw cisco	1	10	6	39	69.6

b) Observed species	Predicted species				% correct
	cisco	bloater	kiyi	shortjaw cisco	
cisco	25	15	21	4	38.5
bloater	11	38	2	12	60.3
kiyi	12	3	7	6	25.0
shortjaw cisco	2	11	8	35	62.5

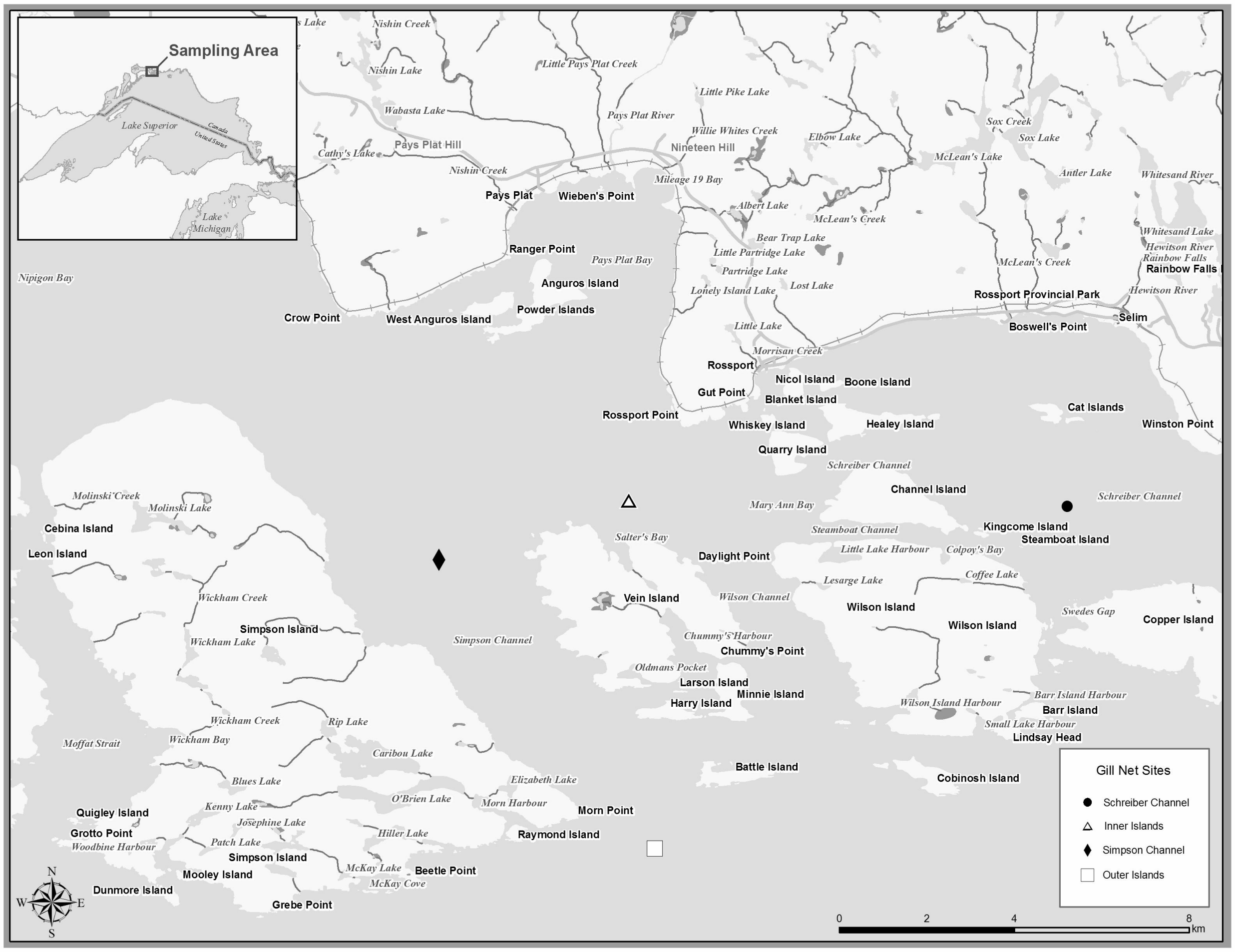

Figure 1. The location of the broad study area and specific gillnet sites for our deepwater cisco survey. ●=Schreiber Channel, Δ=Inner Islands, ♦=Simpson Channel, □=Outer Islands.

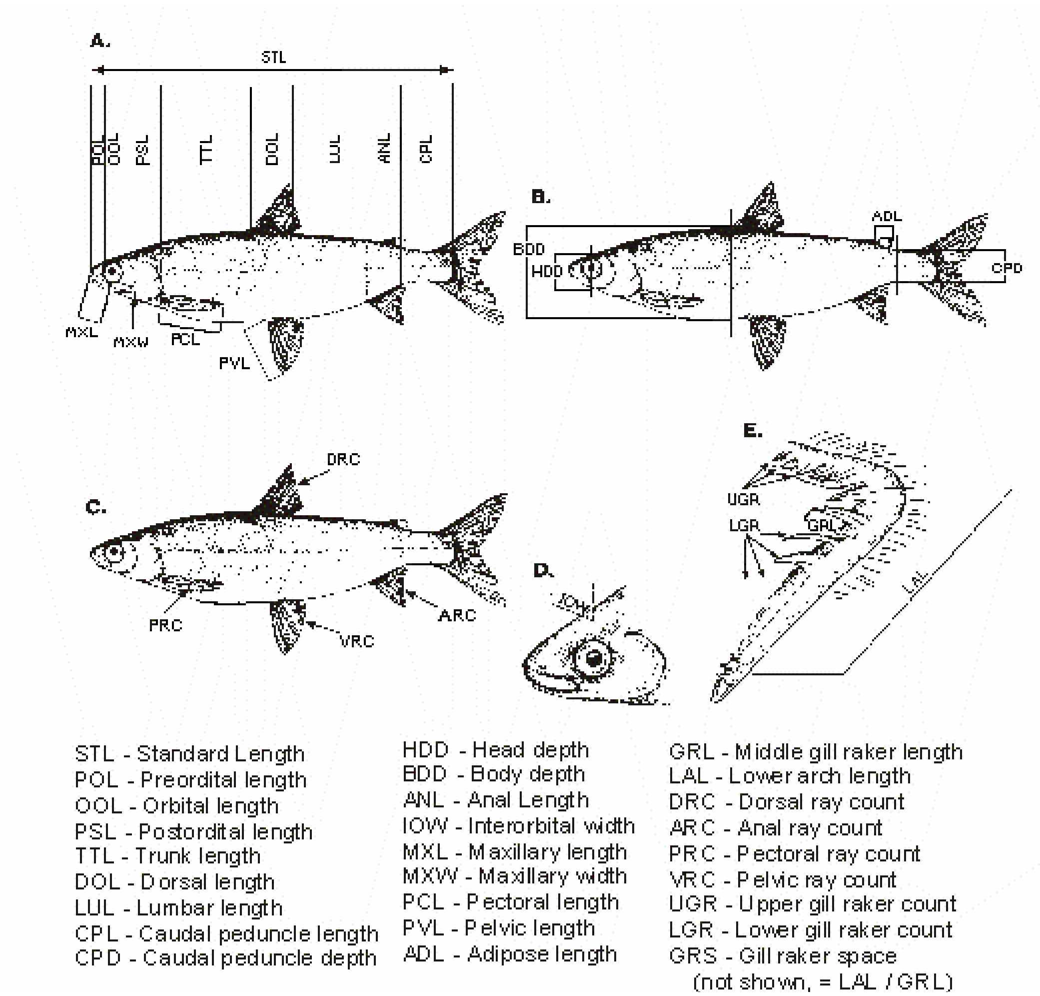

Figure 2. Morphometric measurements and meristic counts taken from deepwater ciscoes captured in the Rossport area of Lake Superior (after Vuorninen et al. 1993).

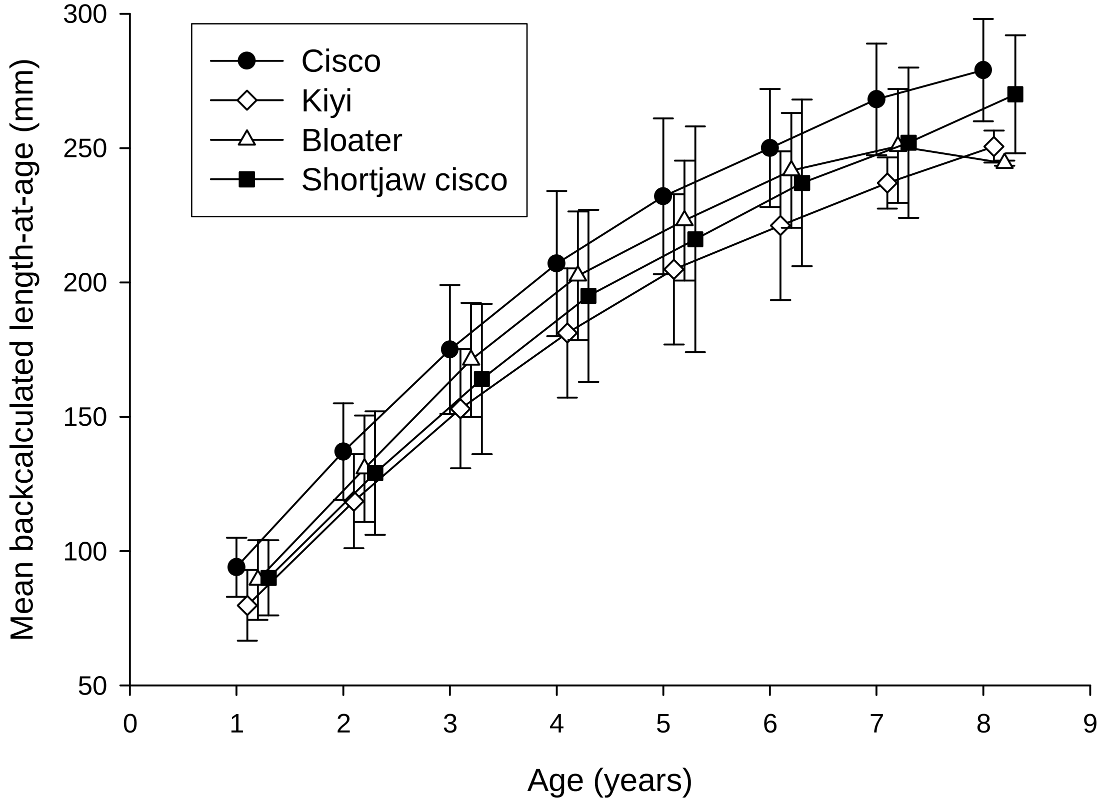

Figure 3. Back-calculated length-at-age data for Lake Superior deepwater ciscoes.

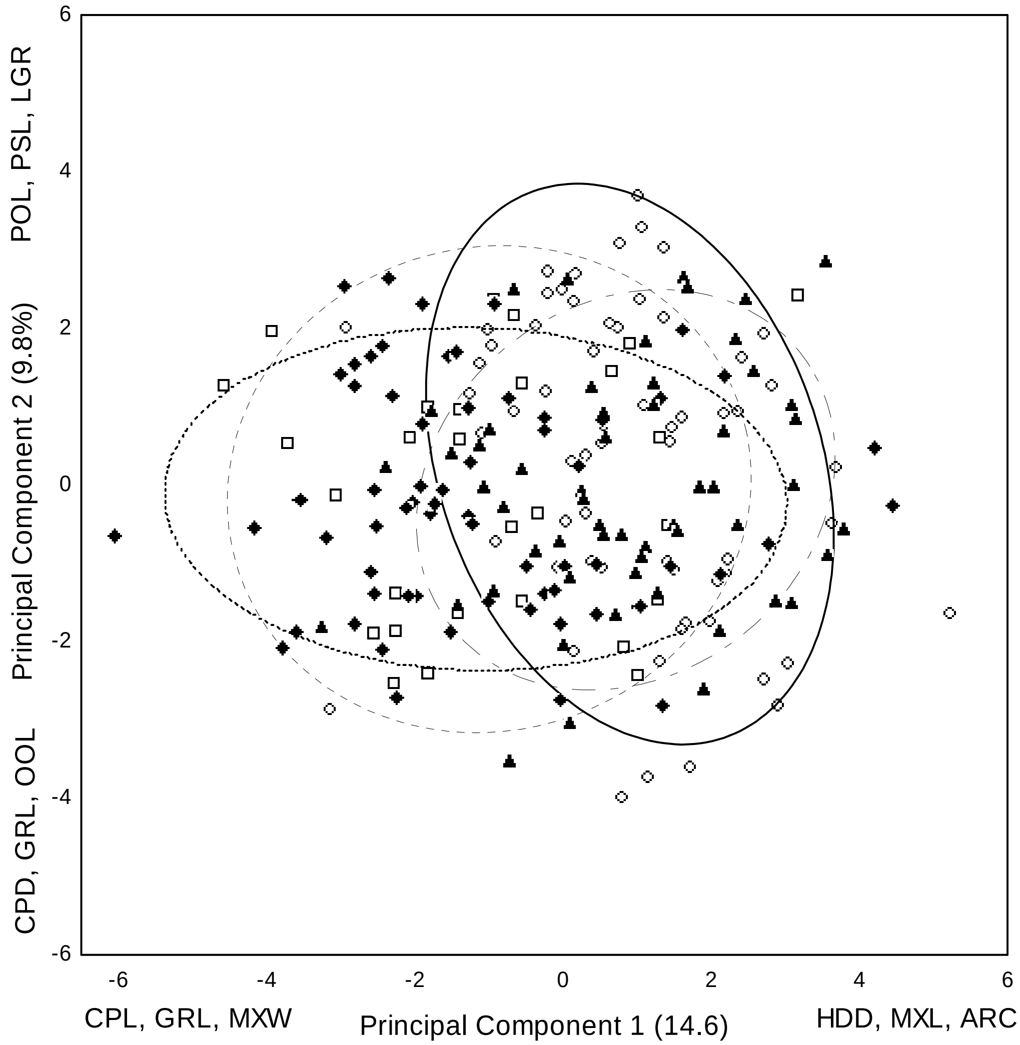

Figure 4. Plot of first and second principal components from Lake Superior deepwater ciscoes based on morphometric and meristic characteristics. Individual points represent scores from individual fish, and ellipses represent the 95% confidence intervals around each species. Symbol and 95% confidence interval abbreviations: cisco = ♦, ··········; bloater = ○, ——; kiyi = □, – – – –; shortjaw cisco =,▲, – · – · – · –. The characteristics identified on each principal component axes had the highest correlations. Character abbreviations are defined in Figure 2.

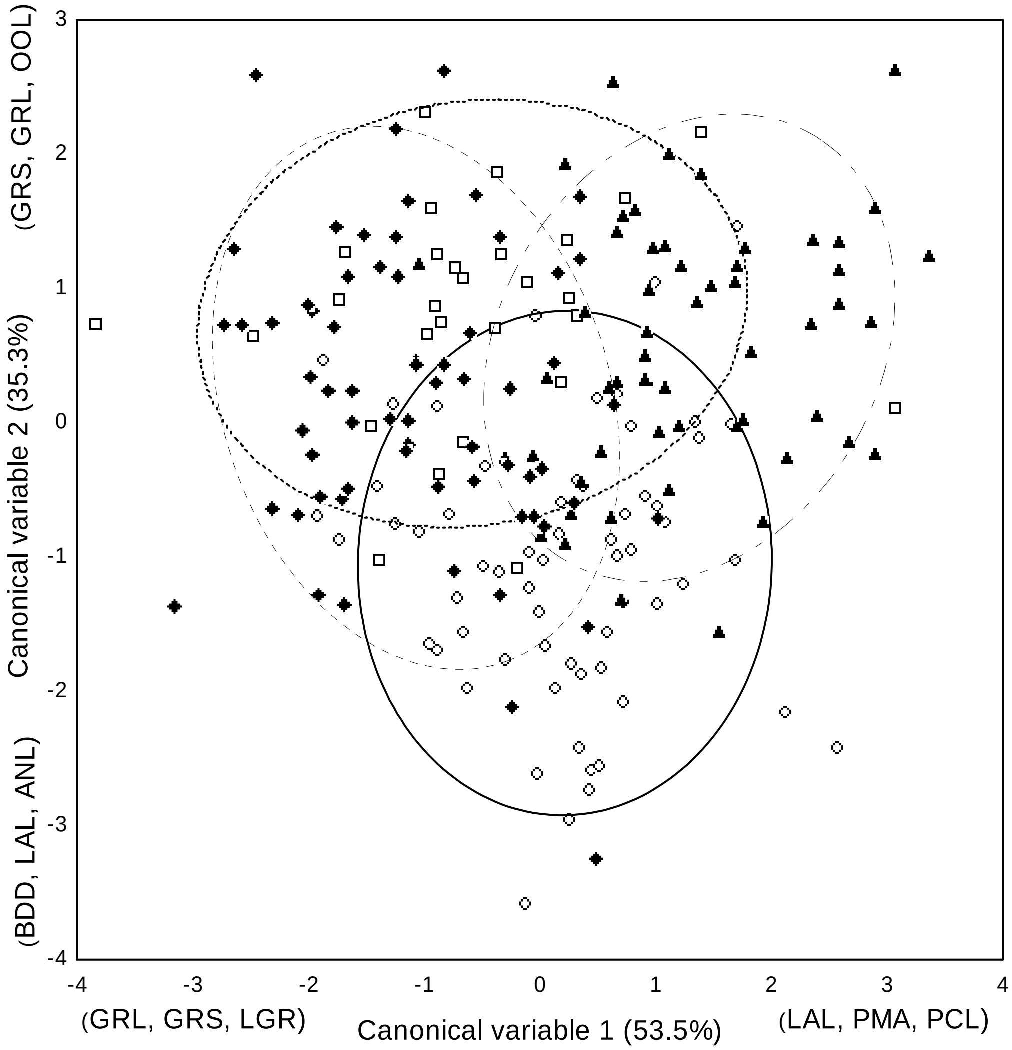

Figure 5. Plot of first and second canonical variables from Lake Superior deepwater ciscoes based on morphometric and meristic characteristics. Individual points represent scores from individual fish, and ellipses represent the 95% confidence intervals around each species. Symbol and 95% confidence interval abbreviations: cisco = ♦, ··········; bloater = ○, ——; kiyi = □, – – – –; shortjaw cisco =,▲, – · – · – · –. The characteristics identified on each principal component axes had the highest correlations. Character abbreviations are defined in Figure 2.