

# Historical and contemporary trophic niche partitioning among Laurentian Great Lakes coregonines

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**Abstract.** Anthropogenic activities have significantly altered freshwater fish communities. Extirpations of deepwater coregonines (*Coregonus* spp.), a diverse group of fish species, have left vast areas of the Laurentian Great Lakes devoid of a deepwater fish community. Currently, fisheries managers are considering restoring populations by reintroducing deepwater coregonines from Lake Superior and Lake Nipigon. However, little is known about the historical ecology of deepwater coregonines, and species characterization has proved difficult. We used stable isotope analysis of museum-preserved and contemporary specimens to investigate if (1) coregonine species historically occupied distinct niches and (2) the pattern of trophic niche partitioning has changed over the last century. Across all lakes, individual species occupied distinct trophic niches, confirming that these species were ecologically distinct. Understanding trophic niche partitioning helps resolve uncertainty about distinctness of species within and across lakes and may provide a better ecological basis for rehabilitation of Great Lakes food webs and ecosystems.

**Key words:** ciscoes; deepwater coregonines; food webs; Great Lakes; preserved specimens; stable isotopes; trophic niche.

## INTRODUCTION

The Great Lakes of the world are centers of endemism and host a disproportionately large fraction of global biodiversity (Cohen 1995). Great Lakes have been dramatically impacted by anthropogenic activities (Cohen et al. 1996), and the Laurentian Great Lakes of North America are no exception (Christie 1974, Madenjian et al. 2002, Bronte et al. 2003, Dobiesz et al. 2005). By the 1960s, exotic species introductions, overfishing, habitat destruction, cultural eutrophication, and toxic discharges produced a virtual food web collapse in each of the Laurentian Great Lakes (Madenjian et al. 2002, Bronte et al. 2003, Dobiesz et al. 2005). This collapse manifested itself most strongly in the endemic deepwater fish assemblage of the genus *Coregonus*. Historically, the Laurentian Great Lakes supported seven species and 25 separate populations (lake–species combinations) of deepwater coregonines (Table 1). Studies of the historical feeding ecology of these species are limited to Lake Huron and revealed that all species fed on *Mysis* and *Diporeia* (Koelz 1929). Netting surveys that sampled different depth strata led Koelz (1929) to suggest that depth partitioning reduced competition among species. Between the 1940s and the

1960s, overfishing and invasive sea lamprey (*Petromyzon marinus*) caused the extirpation of 15 *Coregonus* populations; the extirpations of *C. johanna*e and *C. alpinea* represented global extinctions (Table 1; Phillips and Ehlinger 1995). Extirpations of these and other native fishes have left vast areas of the Laurentian Great Lakes nearly devoid of a deepwater fish community (Eshenroder and Burnham-Curtis 1999). Only Lake Superior and adjacent Lake Nipigon maintain a semblance of the historical deepwater fish community.

Environmental management efforts during the past few decades have produced substantial improvements in water quality, and the recovery of some fisheries (Madenjian et al. 2002, Bronte et al. 2003, Mills et al. 2003). This has led to a growing interest in rehabilitation of native deepwater fish communities. Fisheries managers have identified four species of deepwater coregonines for reintroduction—*C. hoyi*, *C. kiyi*, *C. zenithicus*, and *C. nigripinnis*—with Lake Superior and Lake Nipigon serving as potential source lakes (Eshenroder and Krueger 2002, Zimmerman and Krueger 2009) (see Plate 1). Unfortunately, virtually nothing is known about the trophic relationships, habitat use, and niche partitioning in historical deepwater food webs, and how this may have changed during the ecological disruption of the last century. It is currently unknown whether these coregonine species historically occupied distinct trophic niches, if a species' trophic niche was similar across lakes, and how niche partitioning among species changed during the dramatic food web changes of the 20th century. A better understanding of both historical

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TABLE 1. Historical and contemporary occurrence of deepwater coregonines in Lakes Superior, Michigan, Ontario, Huron, and Nipigon.

Species	Superior	Michigan	Ontario	Huron	Nipigon
Blackfin cisco, <i>Coregonus nigripinnis</i>	+	X		X	+
Deepwater cisco, <i>Coregonus johanna</i>		X		X	
Shortjaw cisco, <i>Coregonus zenithicus</i>	+	X		X	+
Longjaw cisco, <i>Coregonus alpenae</i>		X		X	
Shortnose cisco, <i>Coregonus reighardi</i>	+	X	X	X	
Kiyi, <i>Coregonus kiyi</i>	+	X	X	X	
Bloater, <i>Coregonus hoyi</i>	+	+	X	+	+

Note: "X" indicates extirpated populations; "+" indicates a present-day population.

and contemporary niche partitioning will be essential for guiding restoration and reintroduction efforts, particularly in light of the trend toward ecosystem-based management of the Laurentian Great Lakes (Madenjian et al. 2002, Bronte et al. 2003, Mills et al. 2003).

Several studies have demonstrated the use of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes to document food web changes (Hebert et al. 1999, Perga and Gerdeaux 2003, Vander Zanden et al. 2003, Gratton and Denno 2006) and evaluate trophic niche partitioning (Bearhop et al. 2004, Newsome et al. 2007). Nitrogen ( $\delta^{15}\text{N}$ ) isotopes allow for estimation of consumer trophic position due to a widely documented 3–4‰ increase in  $\delta^{15}\text{N}$  from resource to consumer (Cabana and Rasmussen 1994, Vander Zanden and Rasmussen 2001). Carbon ( $\delta^{13}\text{C}$ ) isotope fractionation is minimal (0–1‰) from resource to consumer, but is a useful indicator of the primary production source at the base of the food web (Hecky and Hesslein 1995, Vander Zanden et al. 1999).

In this study, we use stable isotope analysis of archived and contemporary samples for four Laurentian Great Lakes to address the following questions: (1) Is there evidence for ecological niche partitioning among historical and contemporary Great Lakes coregonines? (2) Is the pattern of niche partitioning among species the same across lakes? (3) Is the pattern of niche partitioning among these species maintained throughout the major ecological disruption of the 20th century? Understanding the intra-lake and temporal aspects of niche partitioning among Great Lakes coregonines may have important implications for ongoing food web and ecosystem rehabilitation efforts.

## METHODS

### Sample collection and analysis

Museum-archived specimens ( $n = 487$ ) from Lakes Michigan, Superior, Huron, and Nipigon and present-day specimens from Lake Nipigon ( $n = 184$ ) and Superior ( $n = 274$ ) were analyzed for stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) ratios. The species sampled included *Coregonus hoyi* (bloater), *C. nigripinnis* (blackfin cisco), *C. alpenae* (deepwater cisco), *C. kiyi* (kiyi), *C. artedii* (lake herring), *C. clupeaformis* (lake whitefish), *C.*

*johanna* (longjaw cisco), *C. reighardi* (shortnose cisco), and *C. zenithicus* (shortjaw cisco). Contemporary samples from Lake Nipigon were obtained during a gill-netting survey with the Ontario Ministry of Natural Resources Lake Nipigon Fisheries Assessment Unit during the summer of 2005. All samples were taken near the Caribou Island region on Lake Nipigon. Contemporary (1997–2003) isotope data for Lake Superior were provided by C. Harvey (NOAA). These samples were collected in U.S. waters of the western basin of Lake Superior during May–September 1997, 2002, and 2003 in routine annual surveys conducted cooperatively by federal, state, and tribal fisheries agencies (Harvey and Kitchell 2000, Harvey et al. 2008). All samples of dorsal muscle tissue were dried at 60–65°C for 24–48 hours and ground into a powder. Approximately 1.0 mg ( $\pm 0.3$  mg) of tissue was packed into 5 × 8 mm tin capsules for sample analysis. Stable isotope analysis for museum-archived samples was performed at the University of California–Davis Stable Isotope Facility on a Europa Hydra 20/20 continuous-flow isotope ratio mass spectrometer (Europa Scientific Ltd., Crewe, UK). Contemporary samples were analyzed at the University of Wisconsin–Madison on a Europa 20/20 (1997 samples) and at the Northwest Fisheries Science Center (NOAA, Seattle) on a Finnigan Delta Plus (2002–2003 samples). Stable isotope ratios are expressed in delta ( $\delta$ ) notation (parts per thousand deviation from a standard [atmospheric nitrogen or Pee Dee Belemnite carbon]):

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} (\text{‰}) = [(R_{\text{sam}} - R_{\text{std}}/R_{\text{std}})] \times 1000$$

where  $R = {}^{15}\text{N}/{}^{14}\text{N}$  or  ${}^{13}\text{C}/{}^{12}\text{C}$ , sam stands for sample, and std stands for standard.

We corrected for preservation effects on stable isotope values based on previously published experimental studies quantifying the effects of tissue preservation on isotope values (Bosley and Wainright 1999, Ogawa et al. 2001, Arrington and Winemiller 2002, Edwards et al. 2002). Correction factors (0.44‰ for  $\delta^{15}\text{N}$  and –1.13‰ for  $\delta^{13}\text{C}$ ) were estimated using the mean preservation effect on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from studies analyzing fish that had been preserved according to standard museum protocol (formalin-fixed and then transferred to ethanol for long-term storage; Schmidt et al. 2009).

*Lipid correction*

Lipids tend to have lower  $\delta^{13}\text{C}$  values relative to other tissues (DeNiro and Epstein 1977, McConnaughey and McRoy 1979, Post et al. 2007) and variation in lipid content could bias interpretation of carbon isotope data. For contemporary specimens, we used an arithmetic correction based on the C:N values of sample tissue to correct for potential lipid effects (see Kiljunen et al. 2006). The approach of Kiljunen et al. (2006) was chosen since it is a modification of a widely used correction (McConnaughey and McRoy 1979) and can be applied to fish tissues with high C:N. Because lipids can leach out during years of sitting in ethanol and the Kiljunen correction is based on fresh samples, we used a different arithmetic correction for preserved specimens (see Schmidt et al. 2009). Briefly, lipid-extracted samples were reanalyzed for  $\delta^{13}\text{C}$  and the difference ( $\Delta$ ) in  $\delta^{13}\text{C}$  was calculated for each sample as  $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{post-ext}} - \delta^{13}\text{C}_{\text{pre-ext}}$ . The C:N ratio of pre-extracted samples was a significant predictor of  $\Delta\delta^{13}\text{C}$  using the following multiple linear regression equation (adjusted  $R^2 = 0.29$ ,  $F_{1,53} = 21.14$ ,  $P < 0.001$ ):

$$\Delta\delta^{13}\text{C} = -0.8868 + (0.3489 \times [\text{C:N}]). \quad (1)$$

We then standardized (stdzd) all samples for lipids based on the calculated  $\Delta\delta^{13}\text{C}$ , where the value for  $\delta^{13}\text{C}_{\text{stdzd}}$  corresponds to the  $\delta^{13}\text{C}$  after lipid extraction:

$$\delta^{13}\text{C}_{\text{stdzd}} = \delta^{13}\text{C}_{\text{pre-ext}} + \Delta\delta^{13}\text{C}. \quad (2)$$

*Statistical analysis*

Stable isotope data were divided into three time periods for each lake: historical, middle and contemporary. The historical time period was the 1920s for all lakes, which generally represents conditions prior to the major ecological changes in the Great Lakes. The middle time period was slightly different for each lake (Michigan, 1949–1981; Huron, 1951–1985; and Superior, 1946–1975), and is based on the timing of coregonine population collapse and the availability of museum specimens for each lake.

Comparative studies may require correction for spatial or temporal variation in baseline isotope values (Cabana and Rasmussen 1996). One common approach is to reference consumer  $\delta^{15}\text{N}$  values to that of primary consumers (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999, Post 2002). In our study, adequate numbers of archived primary consumers spanning multiple lakes and time periods were not available. Without accurate baseline information, we are unable to compare niche partitioning in  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  space. Other studies have expressed isotopic values relative to a food web centroid as a way to compare isotopic niche differences across systems (Layman et al. 2007, Martínez del Rio et al. 2009). Here, we control for isotopic baseline differences among lakes by standardizing each species'  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  relative to the food

web centroid. For each lake–time period combination, the food web centroid was calculated as the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all species' means. Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from the centroid were calculated for each individual, and averaged across individuals for each species. Hereafter, we refer to these recalculated differences as “relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ,” and use this as a means of characterizing species' trophic niche. This food web centroid approach adjusts for differences in basal isotopic signatures and evaluates niche partitioning by comparing relative positioning of species to one another.

To determine whether coregonine trophic niches differed among species, among lakes, and among time periods, we examined relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  jointly in MANOVA models and as separate response variables in ANOVA models. We tested for a species effect in each lake–time-period separately to determine whether species were isotopically distinct. Using data from each lake separately and species and time period as factors, we examined whether the pattern of trophic niche partitioning was consistent over time in a given lake. To determine whether the pattern of trophic niche partitioning was similar among lakes for a given time period, we used species and lake as factors and examined the data from each time period separately. All factors were modeled as fixed effects, using PROC GLM in SAS (SAS Institute 2004). Significance for MANOVA was assessed based on the Wilks'–Lambda statistic.

## RESULTS

Bi-plots of relative  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  were used to depict niche partitioning of coregonines for the historical time period (1920s, Fig. 1). Coregonines exhibited significant differences in relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for all lake–time-period combinations (Table 2; single-factor MANOVA,  $P < 0.05$ ). In most cases, the species effect was significant when considering  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  separately, and was generally stronger for  $\delta^{13}\text{C}$  than for  $\delta^{15}\text{N}$  (Table 2). In addition, coregonine  $\delta^{13}\text{C}$  decreased significantly with the species' preferred depth (as reported by Koelz 1929) in three of the four lakes (Fig. 2;  $P < 0.05$  for all lakes except Lake Superior). There was no relationship between preferred depth and coregonine  $\delta^{15}\text{N}$ .

Examining each lake separately with time period as a factor reveals a strong species effect, little or no time effect, and a significant species  $\times$  time interaction for three of the four lakes (Table 3; two-factor MANOVAs,  $P < 0.001$  except for Lake Michigan). This indicates that individual species maintained distinct ecological niches throughout this period of major ecological change. The significant species  $\times$  time interaction in three of four lakes indicates that the specific pattern of niche partitioning among species was dynamic within a given lake, with the relative position of species changing across the three major time periods.

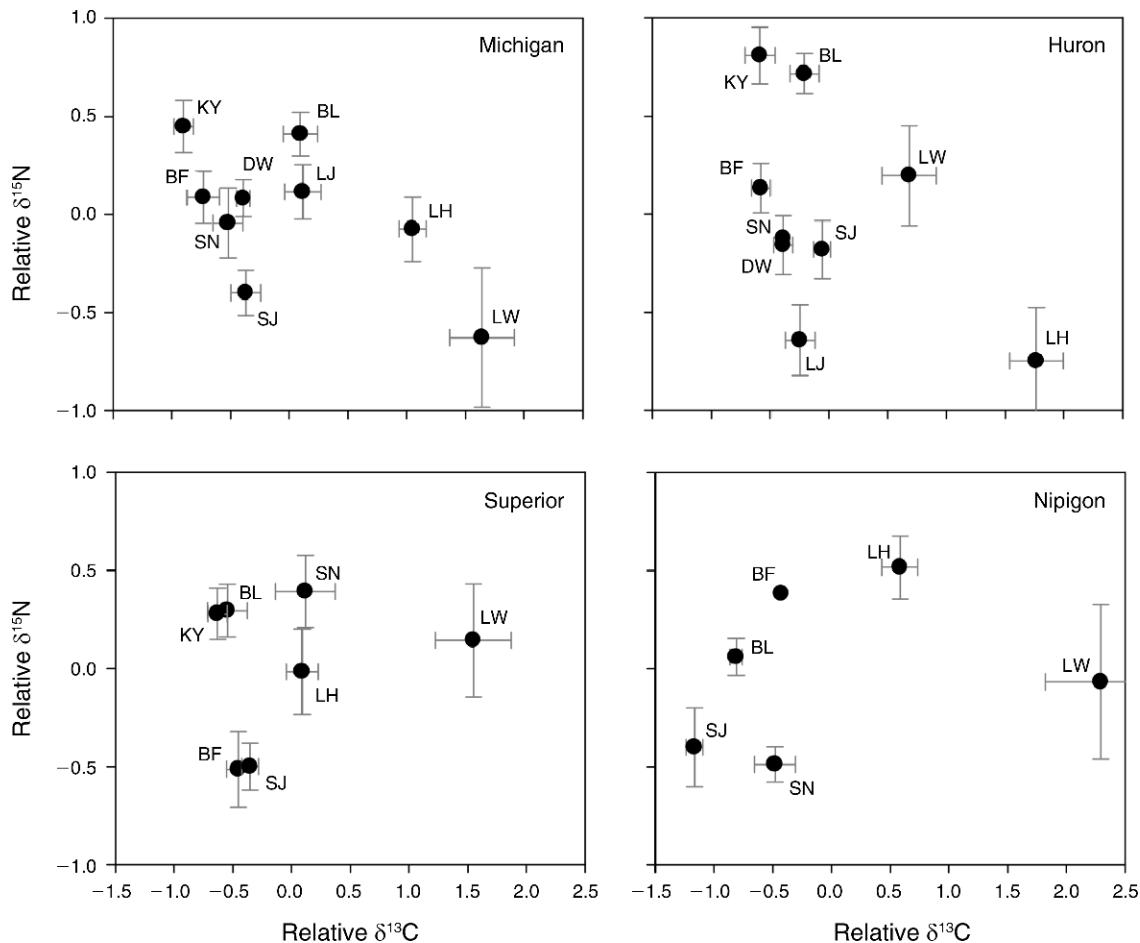


FIG. 1. Historical relative trophic niche partitioning of deepwater coregonines in Lakes Michigan, Huron, Superior, and Nipigon. Each symbol is the mean for a given species within a lake (BF, blackfin cisco; BL, bloater; DW, deepwater cisco; KY, kiyi; LH, lake herring; LJ, longjaw cisco; LW, lake whitefish; SJ, shortjaw cisco; SN, shortnose cisco). Error bars represent ±SE.

TABLE 2. Results of ANOVA and MANOVA assessing trophic niche partitioning among coregonines for each lake–time–period combination.

Lake	df	ANOVA				df	MANOVA	
		Relative δ <sup>13</sup> C		Relative δ <sup>15</sup> N			F	P
		F	P	F	P			
<b>Historical</b>								
Michigan	8, 164	30.24	<0.001	4.24	<0.001	16, 326	14.48	<0.001
Huron	8, 112	26.49	<0.001	8.37	<0.001	16, 222	14.36	<0.001
Superior	6, 144	15.97	<0.001	3.75	<b>0.002</b>	12, 286	9.66	<0.001
Nipigon	5, 35	24.58	<0.001	2.41	0.056	10, 68	11.11	<0.001
<b>Middle</b>								
Michigan	7, 46	1.67	0.140	1.90	0.091	14, 90	1.97	<b>0.029</b>
Huron	7, 54	5.82	<0.001	7.15	<0.001	14, 106	6.05	<0.001
Superior	6, 41	10.41	<0.001	4.94	<0.001	12, 80	6.39	<0.001
<b>Present</b>								
Superior	3, 270	45.21	<0.001	15.96	<0.001	6, 538	30.10	<0.001
Nipigon	4, 179	6.79	<0.001	4.08	<b>0.003</b>	8, 356	4.44	<0.001

Note: P values in boldface type are significant at the α = 0.05 level.

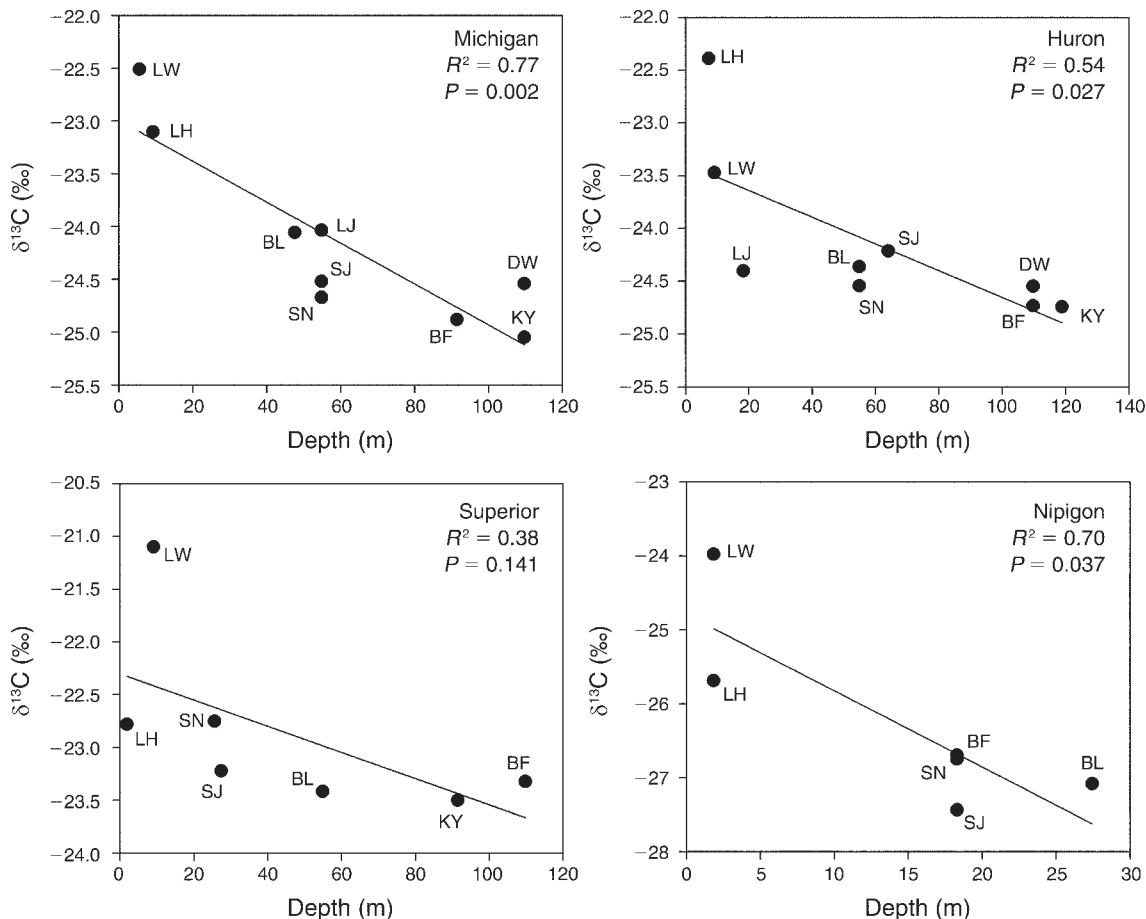


FIG. 2. Carbon partitioning by deepwater coregonines along a depth gradient for historical samples from Lakes Michigan, Huron, Superior, and Nipigon. Each symbol represents the mean  $\delta^{13}\text{C}$  and preferred minimum depth (as reported by Koelz [1929]) for a given species in each lake. Best-fit linear regressions are shown for each lake.  $R^2$  and  $P$  values are reported for each regression. Species labels are the same as in Fig. 1.

A comparison of each time period (historical, middle, and present) with lake as a factor again reveals a strong species effect (three of three periods,  $P < 0.001$ ), a relatively minor lake effect (one of three periods,  $P < 0.001$ ), and a significant species  $\times$  lake interaction for historical and contemporary time periods (Table 3; two-factor MANOVAs,  $P < 0.001$ ). The significant species  $\times$  lake interaction for two of the three periods indicates that for a given time period, the actual pattern of niche partitioning among this group of coregonines was distinct in each of the four lakes.

Coregonine species of conservation concern (those classified as either extirpated or critical/vulnerable) tended to be located closer to other species in food web space (as measured by nearest neighbor Euclidean distance) compared to species that were not listed (Fig. 3; ANOVA,  $F_{2,26} = 9.563$ ,  $P < 0.001$ ). The trend was also evident when lake herring and whitefish were excluded (i.e., deepwater coregonines only), though the results were not statistically significant (ANOVA,  $F_{2,18} = 0.829$ ,  $P = 0.452$ ).

## DISCUSSION

We demonstrate the ability of stable isotopes to provide insight into spatial and temporal patterns of niche partitioning in a historically important and highly impacted fish community. We found individual species' niches within each lake remained significantly different from one another over time. Our analysis further revealed that coregonine trophic niches differed in relative  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  space through time in a given lake, and among lakes for any given time period. The ability for coregonine species to maintain distinctness, even during major ecological disturbances of the 20th century, suggests that coregonine species are somewhat resilient to changes in food web structure.

Great Lakes fisheries managers have called for research that investigates the possibility of reintroducing deepwater coregonines into Lakes Michigan and Huron (Eshenroder and Krueger 2002, Zimmerman and Krueger 2009). Our results indicate that deepwater coregonines were able to maintain some degree of niche separation, even in the face of dramatic ecosystem

TABLE 3. Results of MANOVA on the effects of trophic niche partitioning among coregonines in the Laurentian Great Lakes.

Lake or time period	df	F	P
<b>Superior</b>			
Species	4, 526	11.78	< <b>0.001</b>
Time	4, 526	2.86	<b>0.023</b>
Species × time	8, 526	3.49	< <b>0.001</b>
<b>Nipigon</b>			
Species	8, 422	14.82	< <b>0.001</b>
Time	2, 211	0.21	0.813
Species × time	8, 422	8.79	< <b>0.001</b>
<b>Michigan</b>			
Species	14, 392	8.48	< <b>0.001</b>
Time	2, 196	0.28	0.756
Species × time	14, 392	1.33	0.186
<b>Huron</b>			
Species	14, 288	6.42	< <b>0.001</b>
Time	2, 144	0.09	0.917
Species × time	14, 288	6.11	< <b>0.001</b>
<b>Historical</b>			
Species	10, 708	30.14	< <b>0.001</b>
Lake	6, 708	0.54	0.774
Species × lake	30, 708	5.19	< <b>0.001</b>
<b>Middle</b>			
Species	10, 272	9.70	< <b>0.001</b>
Lake	4, 272	0.20	0.936
Species × lake	20, 272	1.32	0.168
<b>Contemporary</b>			
Species	6, 832	20.73	< <b>0.001</b>
Lake	2, 416	11.24	< <b>0.001</b>
Species × lake	4, 832	14.96	< <b>0.001</b>

Note: P values in boldface type are significant at the  $\alpha = 0.05$  level.

changes. While encouraging, we also recognize that this ability to maintain niche separation was not enough to keep several of the species from being extirpated. Some have suggested that extirpations were driven by top-down forces such as overfishing or nonnative sea lamprey (Smith 1964, 1972). If true, then our analysis would suggest that reintroductions are feasible provided that top-down impacts are managed properly, and that the new benthic communities (increasingly impacted by dreissenid mussels) are hospitable to these species. The reappearance of deepwater sculpins (*Myoxocephalus thompsoni*) and the successful natural spawning of lake trout (*Salvelinus namaycush*) in parts of the Great Lakes does suggest that rehabilitation is possible (Janssen et al. 2006, Riley et al. 2007). However, if the extirpations were driven by resource competition among these species, and possibly exacerbated by nonnative forage fishes such as alewife (*Alosa pseudoharengus*), then reestablishing deepwater coregonines in Lakes Michigan and Huron may be difficult.

Our findings add to the current understanding of deepwater coregonines and contribute to a long-standing debate about species characterization. Because the *Coregonus* species complex is genetically similar (Todd et al. 1981, Turgeon and Bernatchez

2003), morphological characteristics have been primarily used to identify species. However, morphology varies within and across lakes, creating uncertainty about species characterization that inhibits our ability to identify target populations for reintroduction. Despite their genetic similarity and confusing morphology (Todd et al. 1981, Turgeon and Bernatchez 2003), our stable isotope analysis revealed clear and significant ecological differentiation among the Laurentian Great Lakes coregonines, confirming that these often-debated “species” were ecologically distinct.

The degree of trophic redundancy appears to have influenced species persistence during the 20th century (Fig. 3). Threatened or extirpated coregonine species tended to have the least distinct trophic niches. For these species, the elevated trophic overlap with other species may have made it more difficult to persist in the face of a changing ecosystem. Species with the most distinct trophic niches such as lake herring and lake whitefish (and to some extent, kiyi, bloater, and shortjaw) have persisted. This suggests that species with more distinct trophic niches are more able to maintain populations through periods of drastic ecosystem change. Fisheries managers should consider the relatively large degree of separation (Fig. 1) between species like kiyi and blackfin cisco or kiyi and shortjaw cisco as useful indicators of reintroduction potential.

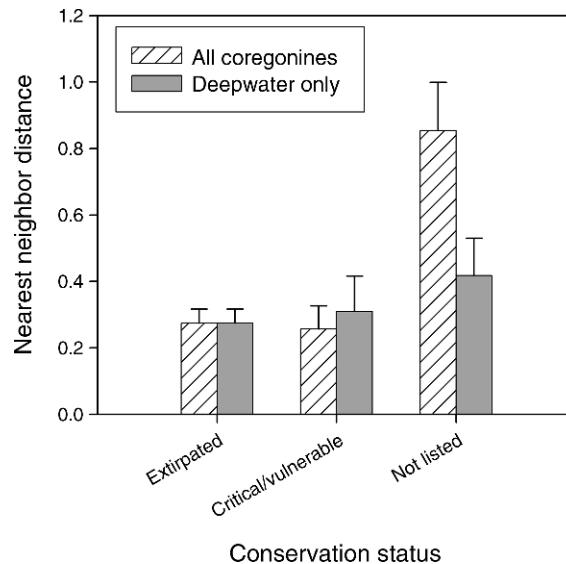


FIG. 3. Historical mean nearest neighbor distance (Euclidean) based on species' conservation status. Each pair of bars shows the mean for all lake–species combinations from the historical time period for all coregonines and for deepwater coregonines only. Conservation status for each species–lake combination was determined from a combination of sources: IUCN red list (International Union for Conservation of Nature and Natural Resources 2010), COSEWIC (Committee on the Status of Endangered Wildlife in Canada 2008), and Ontario NHIC (Natural Heritage Information Centre 2009). Error bars represent +SE.



PLATE 1. Blackfin cisco (*C. nigripinnis*) caught using gillnets on Lake Nipigon (USA) in the summer of 2005 as part of a sampling effort in collaboration with the Ontario Ministry of Natural Resources Lake Nipigon Fisheries Assessment Unit. Photo credit: S. N. Schmidt.

Trophic niche partitioning occurred within a relatively narrow isotopic space; separation among deepwater species (lake herring and lake whitefish excluded) occurs within a range of 1‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Fig. 1). This isotopic space constitutes a small fraction of the resource and habitat breadth of the Laurentian Great Lakes. Yet, even within this narrow range, deepwater coregonines occupy distinct trophic niches. One would expect somewhat similar isotopic values for the deepwater coregonines, since these species have recently diverged and are very similar to each other. Despite their close evolutionary relationship and ecological similarities, we found statistically significant isotopic differences. Additionally, sample sizes for most of our deepwater species tended to be small ( $n < 5$ ). Thus, isotopic differences were observed, in spite of limited statistical power. Historical diet data are limited, but indicate that deepwater coregonines consumed *Mysis* and *Diporeia* (Koelz 1929). This suggests that factors other than diet may drive the fine-scale trophic niche separation among deepwater coregonines.

Our approach considers “niche” in the broad sense, as not only trophic or feeding niche, but also habitat niche (sensu Hutchinson’s  $N$ -dimensional hypervolume; Hutchinson 1957). A study in Lake Superior documented a decrease in *Diporeia*  $\delta^{13}\text{C}$  with depth within the first 40 m, and stabilization beyond 80 m (Sierszen et al. 2006). Similarly, our analysis suggests that carbon

partitioning likely occurs due to depth segregation among the coregonine species in each lake. Depth partitioning by coregonines has been previously reported through gill-netting surveys (Koelz 1929). The reflection of this depth partitioning in our isotopic analysis validates the utility of stable isotopes for characterizing species’ niche partitioning.

By applying the centroid-based correction, we were able to account for baseline differences and compare trophic niche partitioning across multiple food webs. This approach involves referencing each species to the center (centroid) of the food web (in isotopic space). Such a correction is needed because one cannot simply compare raw isotopic values over space and time due to baseline effects that arise from biogeochemical differences/changes in ecosystems. Some sort of method is needed to “line up” food webs for comparison. We lacked sufficient baseline specimens and data to correct raw isotopic values for our Great Lakes data. However, fish assemblage composition could affect the location of the centroid, which in turn, determines the calculated relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. There could be situations where centroid position (and thus, the relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) is quite sensitive to assemblage composition (cases where mean isotopic values of fish species within a system differ widely). In these situations, the centroid-based correction should be used carefully.

The ecological information gained from our analysis can lend insight into historical food web change, as well as the future management of Great Lakes ecosystems. Uncertainty about Great Lakes coregonine diagnostic characteristics has hindered the identification of appropriate target populations for restoration (Turgeon and Bernatchez 2003). Our results highlight how ecological information can supplement morphological data, improving our ability to characterize coregonine species within and across lakes (Todd and Smith 1992). Our desire is that our ecological perspective on Great Lakes coregonines during a period of ecosystem change helps to inform the broader management efforts to rehabilitate the Great Lakes ecosystems and fish communities. Based on our stable isotope analysis, it is clear the Great Lakes coregonines were an ecologically important and diverse fish assemblage. Efforts to restore coregonines would help reestablish this unique, endemic ecological diversity in lakes where deepwater coregonines have been absent for nearly 50 years.

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