

Long-term food web change in Lake Superior

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Abstract: Restoration and rehabilitation of native species in the Laurentian Great Lakes is a priority for fisheries management agencies. Restoration efforts are increasingly incorporating a perspective that considers species within a broader food web context. We used stable isotope analysis and museum-preserved specimens to describe and quantify 100 years of food web changes in the Lake Superior fish community. We validated stable isotope analysis of museum specimens by showing a positive correlation between isotope- and diet-based estimates of trophic position. While introductions have created a more trophically diverse food web than historically found in Lake Superior, two separate metrics revealed little community-wide change in the food web. Our species-specific analysis revealed trophic niche differences between shortjaw (*Coregonus zenithicus*) and shortnose (*Coregonus reighardi*) ciscoes, two species previously argued to be indistinguishable based on morphological characteristics. By providing a historical context, our findings show the ability of the Lake Superior food web to accommodate non-native species introductions over the last century while still supporting native species populations. This long-term information about food web structure can help guide management and restoration goals in Lake Superior. Furthermore, Lake Superior can serve as a basis for comparing food web changes in other, more highly altered Great Lakes.

Résumé : La restauration et la réhabilitation des espèces indigènes dans les Grands Lacs laurentiens sont une priorité pour les agences de gestion des pêches. Les efforts de restauration incorporent de plus en plus une perspective qui considère les espèces dans le contexte d'un réseau alimentaire élargi. Nous avons utilisé des analyses d'isotopes stables et des spécimens conservés dans des musées pour décrire et mesurer les changements au cours de 100 ans dans les réseaux alimentaires de la communauté de poissons du lac Supérieur. Nous avons validé l'analyse des isotopes stables des spécimens de musée en montrant une corrélation positive entre les estimations de la position trophique basées sur les isotopes et sur le régime alimentaire. Alors que les introductions ont créé un réseau alimentaire de plus grande diversité trophique que dans le passé dans le lac Supérieur, deux métriques différentes révèlent peu de changements à l'échelle de la communauté dans le réseau alimentaire. Notre analyse spécifique à l'espèce montre des différences de niche trophique entre les ciscos à mâchoires égales (*Coregonus zenithicus*) et les ciscos à museau court (*Coregonus reighardi*), deux espèces considérées antérieurement comme impossibles à distinguer par leurs caractères morphologiques. En fournissant ce contexte historique, nos résultats démontrent la capacité du réseau alimentaire du lac Supérieur à s'accommoder des introductions d'espèces non indigènes au cours du dernier siècle, tout en soutenant les populations d'espèces indigènes. Cette information sur une longue période concernant la structure du réseau alimentaire peut servir à guider les objectifs de gestion et de restauration au lac Supérieur. De plus, le lac Supérieur peut servir de point de comparaison pour les changements de réseau alimentaire dans les autres Grands Lacs plus fortement modifiés.

[Traduit par la Rédaction]

Introduction

The combined effects of species introductions and overfishing over the last century have resulted in the extirpation of many native fish species in the Laurentian Great Lakes (Lawrie and Rahrer 1972; Christie 1974; Bronte et al. 2003). Of these, the introductions of non-native species have had the greatest impact on the Great Lakes ecosystems. In the last decade, the rehabilitation of native biotic communities has emerged as a unifying goal of the Great Lakes management community (Horns et al. 2003). Restoration, as defined by the Society of Ecological Restoration International (Society for Ecological Restoration (SER) International Science & Policy Working Group 2004), attempts to

return an ecosystem to its historic trajectory, which may include rehabilitating (i.e., reparation of ecosystem processes, productivity, and services) native communities. Balancing the restoration and rehabilitation of native communities while maintaining existing fisheries based on non-native species will present a major ecosystem management challenge (Kitchell et al. 2000).

Among the Great Lakes, Lake Superior remains the least altered by non-native species and other anthropogenic effects and is unique in that no native fishes have been extirpated from the lake. Additionally, the lake retains naturally reproducing populations of both native lake trout (*Salvelinus namaycush*) and deepwater coregonines (Bronte et al. 2003).

Received 27 January 2009. Accepted 13 August 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 24 November 2009.
J21026

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Nevertheless, the fish community of Lake Superior has undergone some substantial changes in the last century due to the establishment of non-native fishes (Lawrie and Rahrer 1972; Christie 1974; Bronte et al. 2003). The sea lamprey (*Petromyzon marinus*) had the most dramatic effect on the Lake Superior fish community, nearly removing the native lake trout in the mid-1950s (Lawrie and Rahrer 1972). The degree to which rainbow smelt (*Osmerus mordax*) have altered native cisco populations is still uncertain (Anderson and Smith 1971; Selgeby et al. 1978; Bronte et al. 2003); however, rainbow smelt replaced native lake herring (*Coregonus artedii*) as the predominant prey item for lake trout (Dryer et al. 1965; Lawrie and Rahrer 1972; Conner et al. 1993). It has, therefore, become ecologically important to manage rainbow smelt populations that sustain a highly valuable lake trout fishery. The present-day food web of Lake Superior represents a complex network of interactions among native and non-native fish species (Kitchell et al. 2000).

Researchers and managers realize the importance of considering the dynamics of species within their broader food web context (Polis and Winemiller 1996; Kitchell et al. 2000). Therefore, a food web perspective has been increasingly incorporated into environmental management and restoration efforts (Vander Zanden et al. 2006). Stable isotope analyses have proven to be useful for describing food webs (Minagawa and Wada 1984; Peterson and Fry 1987). It is widely documented that there is a 3‰–4‰ increase in $\delta^{15}\text{N}$ from prey to predator, allowing estimation of consumer trophic position (Vander Zanden and Rasmussen 2001). $\delta^{13}\text{C}$ fractionation is small (0‰–1‰), and carbon isotope ratios remain similar through the food chain. Carbon isotope ratios provide information about the organic source at the base of the food web (Hecky and Hesslein 1995; Vander Zanden et al. 1999). Stable isotope analysis has been used to examine trophic overlap among populations (Campbell et al. 2003) and to characterize food web changes due to species invasions (Sierszen et al. 1996; Vander Zanden et al. 1999; Vander Zanden et al. 2003).

Museum-archived fish specimens have recently been used for retrospective food web studies (Vander Zanden et al. 2003). Several studies have shown that isotopic shifts in tissue due to preservation effects are small and correctable (Arrington and Winemiller 2002; Edwards et al. 2002; Sarkinios et al. 2002). Using stable isotopes and museum specimens, Vander Zanden et al. (2003) elucidated 120 years of food web change in Lake Tahoe, California–Nevada, and identified lakes near Lake Tahoe with the least food web alteration. Understanding the degree of food web change in a historical context allowed evaluation of restoration potential of native species in these lakes.

There is surprisingly little historical information about trophic niches of native and non-native species within the Great Lakes, making it difficult to establish benchmark restoration goals. The prospect of using stable isotopes and preserved specimens to assess Great Lakes food web change may have important implications for — and give guidance to — efforts at restoration of native species such as the deepwater coregonines. By providing an historical context, we can gain an understanding of how the ecosystem has

changed due to non-native species introductions over the past century.

The objectives of this paper are threefold. First, we validate stable isotope analysis of museum specimens as a reliable tool for elucidating historical feeding relationships. Previous studies have shown stable isotope analysis to be an effective measure of trophic position using dietary data (Vander Zanden et al. 1997). However, no study has compared historical dietary data with stable isotope data obtained from historical fish specimens. Second, we describe and analyze the historical and contemporary food web structure of the Lake Superior fish community. Finally, we compare niche partitioning among deepwater coregonine species (shortjaw cisco (*Coregonus zenithicus*), shortnose cisco (*Coregonus reighardi*), and blackfin cisco (*Coregonus nigripinnis*)) over the past century. Previous studies have examined these interactions using morphological and genetic data (Todd et al. 1981). Here, we use stable isotope analysis to examine trophic interactions and resource partitioning among these species. Invasive species, overfishing, and other anthropogenic impacts have all played a role in shaping the Lake Superior food web. Elucidating the historical food web will reveal the extent of food web change in Lake Superior over the past century and help guide restoration goals for native fishes in the Great Lakes (Shuter and Mason 2001; White et al. 2004).

Materials and methods

We conducted stable isotope analysis of museum-archived preserved specimens to reconstruct the historical food web of Lake Superior over the last century. For the fish community, we examined native planktivores (lake herring; lake whitefish, *Coregonus clupeaformis*), non-native planktivores (rainbow smelt; alewife, *Alosa pseudoharengus*), native benthic fishes (bloater, *Coregonus hoyi*; kiyi, *Coregonus kiyi*; shortjaw cisco; shortnose cisco; blackfin cisco; deepwater sculpin, *Myoxocephalus thompsoni*), native predators (lake trout), and non-native predators (Chinook salmon, *Oncorhynchus tshawytscha*; coho salmon, *Oncorhynchus kisutch*; sea lamprey). Of the lake trout samples analyzed, all were assumed to be “lean” lake trout based on museum catalog descriptions or personal observations. All specimens were adult fish to reduce any bias in isotope signatures due to ontogenetic diet shifts.

We measured carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios in preserved dorsal muscle tissue of Lake Superior fish specimens. Samples were dried at 60 °C for 24–48 h and then ground into a powder. Approximately 1.0 mg (± 0.3 mg) of tissue was packed into 5 × 8 mm tin capsules for sample analysis. Stable isotope analysis was performed at the University of California – Davis Stable Isotope Facility on a Europa Hydra 20/20 continuous-flow isotope ratio mass spectrometer. Stable isotope ratios are expressed in delta (δ) notation (parts per thousand (‰) deviation from a standard — atmospheric nitrogen or Pee Dee Belemnite carbon):

$$(1) \quad \delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. Replicate samples were ana-

Table 1. Preservation effects on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish muscle tissue.

Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Source
<i>Percina caprodes</i> (logperch)	-0.8	0.5	Edwards et al. 2002
<i>Percina roanoka</i> (Roanoke darter)	-0.8	0.5	
<i>Etheostoma tippecanoe</i> (Tippecanoe darter)	-0.8	0.5	
<i>Pleuronectes americanus</i> (winter flounder)	-2.17	1.41	Bosley and Wainright 1999
<i>Arius felis</i> (hardhead catfish)	-1.12	0.62	Arrington and Winemiller 2002
<i>Cynoscion nebulosus</i> (spotted seatrout)	-1.12	0.62	
<i>Dorosoma cepedianum</i> (gizzard shad)	-1.12	0.62	
<i>Mugil cephalus</i> (striped mullet)	-1.12	0.62	
<i>Hemibarbus barbus</i>		-0.25	Ogawa et al. 2001
<i>Lepomis macrochirus</i> (bluegill)		0	Ogawa et al. 2001
<i>Micropterus salmoides salmoides</i> (largemouth bass)		-0.3	Ogawa et al. 2001
<i>Zacco platypus</i>		0.45	Ogawa et al. 2001
Mean	-1.13	0.44	
SE	0.16	0.13	

Note: Estimation of mean preservation effect was based only on studies analyzing specimens that were fixed in formalin and transferred to ethanol for long-term storage.

lyzed ($n = 32$), resulting in a mean standard error of 0.29‰ for $\delta^{15}\text{N}$ and 0.19‰ for $\delta^{13}\text{C}$.

Museum protocol calls for fish specimens to be formalin-fixed for at least two weeks and then transferred to ethanol for long-term storage (D. Nelson, University of Michigan, Museum of Zoology, 1109 Geddes Avenue, Ann Arbor, MI 48109, USA, personal communication). We assumed that all museums followed this protocol for all specimens sampled. We corrected for preservation effects on stable isotope values based on previously published experimental studies quantifying the effects of tissue preservation on isotope values (see references in Table 1). We used correction factors (0.44‰ for $\delta^{15}\text{N}$ and -1.13‰ $\delta^{13}\text{C}$) that represented the mean preservation effect on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from studies analyzing fish that had been formalin-fixed and then transferred to ethanol for long-term storage (Table 1).

$\delta^{13}\text{C}$ corrections: lipids and Suess effect

Lipids tend to be isotopically depleted in $\delta^{13}\text{C}$ relative to other tissues (DeNiro and Epstein 1977; McConnaughey and McRoy 1979; Post et al. 2007). To account for variability in carbon signature due to lipid content differences, we extracted lipids from and reanalyzed a subset ($n = 29$) of fish tissue samples for $\delta^{13}\text{C}$. Lipids were extracted from dried tissue using a modified Folch method as described by Sweeting et al. (2006). Briefly, tissue was homogenized in a 2:1 chloroform-methanol mixture and sonicated. Samples were then centrifuged to separate the remaining tissue, and the supernatant was removed. Samples were washed with ultra-pure water and sonicated and centrifuged once more. The remaining tissue was oven-dried at 60 °C for 24 h. Lipid content was determined by weight difference and expressed as a proportion of the weight of the original tissue sample.

Lipid-extracted samples were analyzed for $\delta^{13}\text{C}$ and compared with $\delta^{13}\text{C}$ values for bulk tissue samples. The difference (Δ) in $\delta^{13}\text{C}$ was calculated for each sample as $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{lipid-extracted}} - \delta^{13}\text{C}_{\text{bulk}}$. The C-N ratio (C:N) of pre-extracted samples was a significant predictor of $\Delta\delta^{13}\text{C}$ ($P < 0.001$) using the following multiple linear regression equation (adjusted $R^2 = 0.29$, $F_{[1,53]} = 21.14$, $P < 0.001$):

$$(2) \quad \Delta\delta^{13}\text{C} = -0.8868 + (0.3489 \cdot \text{C:N})$$

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

$$(3) \quad \delta^{13}\text{C}_{\text{standardized}} = \delta^{13}\text{C}_{\text{bulk}} + \Delta\delta^{13}\text{C}$$

The burning of fossil fuels has resulted in a 1.4‰ depletion in the $\delta^{13}\text{C}$ of atmospheric carbon dioxide (CO_2) over the last century (Schelske and Hodell 1995). Known as the Suess effect, this phenomenon could potentially influence $\delta^{13}\text{C}$ values for our historical samples collected from Lake Superior. To correct all data for the Suess effect, we employed a new method that uses a 6th-order polynomial fit of previously published sediment core data (Verburg 2007). This correction applies to data from 1700 to 2000 and accurately predicts changes in $\delta^{13}\text{C}$ with time (average absolute standard deviation between predicted values and actual data was 0.06‰, ± 0.05 standard deviation, SD) (Verburg 2007).

$\delta^{15}\text{N}$ corrections: trophic position estimates and baseline corrections

Stable isotope ($\delta^{15}\text{N}$) estimates of trophic position were determined from museum-archived fish specimens collected from Lake Superior. Because the $\delta^{15}\text{N}$ of primary producers can vary widely among and within systems (Cabana and Rasmussen 1996) and are passed up the food web, raw $\delta^{15}\text{N}$ values were converted to trophic position using a $\delta^{15}\text{N}$ baseline correction:

$$(4) \quad \text{TP} = [(\text{fish } \delta^{15}\text{N} - \text{baseline } \delta^{15}\text{N})/3.4] + 2$$

Trophic position (TP) is the difference between the isotopic value of fish and primary consumers (i.e., baseline) divided by one trophic level increment represented by 3.4‰ (Vander Zanden et al. 1997). Unionid mussels are the preferred primary consumer used in baseline corrections (Cabana and Rasmussen 1996; Post 2002) because they are long-lived, meaning that their tissues integrate $\delta^{15}\text{N}$ over a long period of time. Unfortunately, few museum collections of preserved unionids or other primary consumers (i.e., zoo-

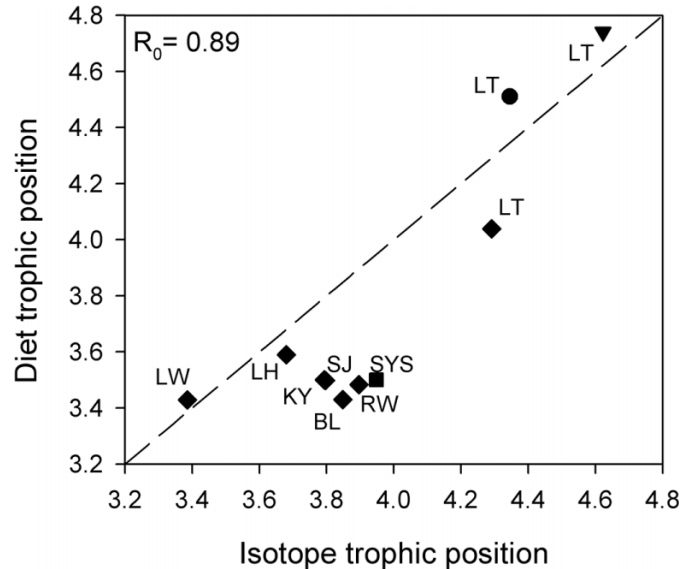
plankton) exist for the Great Lakes. Based on estimates from the small number of museum-preserved Unionid mussels from 1945 that we were able to obtain and present-day values of zooplankton from Lake Superior (Keough et al. 1996; Harvey and Kitchell 2000), the baseline nitrogen isotopic value for Lake Superior was assumed to be 2.86‰. The average $\delta^{15}\text{N}$ value for Unionids in 1945 was 3.29‰, compared with 2.82‰ for present-day average values of zooplankton. We were unable to statistically compare values over time due to small samples sizes; however, the difference is less than 0.5‰, which is considerably smaller than typical trophic fractionation of $\delta^{15}\text{N}$.

Although anthropogenic inputs (i.e., sewage, agricultural fertilizers, etc.) have been shown to increase $\delta^{15}\text{N}$ values (Cabana and Rasmussen 1996; Lake et al. 2001), the watershed of Lake Superior is largely forested and has received the least amount of anthropogenic nutrient loading of all the Great Lakes (Lawrie and Rahrer 1972; Bronte et al. 2003). In fact, Lake Superior is one of the least productive lakes in the world (Hecky 2000), with near pristine water quality conditions (Matheson and Munawar 1978). However, recent studies have noted a marked increase in nitrate concentrations in the lake over the last 100 years (Ostrom et al. 1998; Sterner et al. 2007). Finlay et al. (2007) showed that the increase in nitrate is due to nitrification occurring in the lake, rather than nitrate deposited directly from external sources. Unlike denitrification (Cline and Kaplan 1975; Altabet et al. 1995), nitrification causes small fractionation of $\delta^{15}\text{N}$ isotopes. Furthermore, sediment cores analyzed by Ostrom et al. (1998) from Lake Superior showed low variation in $\delta^{15}\text{N}$ to a depth representing roughly 170 years of deposition and no overall down core trend in $\delta^{15}\text{N}$ values of sedimentary organic matter. For these reasons, we assumed that the baseline $\delta^{15}\text{N}$ value as calculated above did not shift over time and is applicable to all samples throughout time.

To validate our stable isotope estimates of fish trophic position in Lake Superior, we compared stable isotope estimates and diet-based estimates of trophic position (Fig. 1). For diet-based estimates, we compiled stomach content data for fishes of Lake Superior from literature dating from the 1950s through the 1980s. However, we are aware of only six published papers that contain relevant Lake Superior diet data (Dryer and Beil 1964; Dryer et al. 1965; Anderson and Smith 1971; Selgeby 1988; Bronte et al. 1991; Conner et al. 1993), so time periods were divided by decades. In this analysis, we only considered diet data that were presented as percent dry weight, percent wet weight, and percent volume. To calculate diet-based trophic position estimates, these percentage values were expressed as percent diet composition. Identification of prey items was kept to the lowest level of taxonomic resolution presented in the literature. In some studies, prey items were classified to the species level, whereas in other studies, prey items were grouped into broader taxonomic groups. Only fish species for which more than 25 stomachs were examined were included for this analysis.

A diet-based trophic position estimate of fish from a given time period was calculated using the equation below, where TP is diet-based trophic position, V_i is the percent contribution of a prey item i to the diet, and TP_i is the tro-

Fig. 1. Comparison of isotope-calculated trophic positions with trophic positions calculated from diet data reported in the literature ($R_0 = 0.89$, $P < 0.001$). Each symbol represents a fish species from a given time period (circles, 1950–1954; diamonds, 1965–1968; squares, 1971–1972; inverted triangles, 1981–1987). Data labels are as follows: LT, lake trout (*Salvelinus namaycush*); LH, lake herring (*Coregonus artedii*); LW, lake whitefish (*C. clupeaformis*); SJ, shortjaw cisco (*C. zenithicus*); BL, bloater (*C. hoyi*); KY, kiyi (*C. kiyi*); RW, round whitefish (*Prosopium cylindraceum*); SYS, slimy sculpin (*Cottus cognatus*). The 1:1 line is shown for visual comparison. Diet data were compiled from six previous studies (Dryer and Beil 1964; Dryer et al. 1965; Anderson and Smith 1971; Selgeby 1988; Bronte et al. 1991; Conner et al. 1993).



phic position of prey item i (Winemiller 1990; Vander Zanden et al. 1997).

$$(5) \quad TP = \sum (V_i \cdot TP_i) + 1$$

Trophic positions (TP_i) of prey items were assigned based on known feeding ecology (Vander Zanden et al. 1997) or were calculated using the diet data from the literature. Primary producers were trophic level 1, primary consumers were trophic level 2, and so on. Prey items known to be predators were assigned trophic position 3, whereas strict herbivores were assigned trophic position 2. Omnivores such as many zooplankton and aquatic insects were assigned trophic position 2.5. Although most fishes ascend through trophic positions as they increase in size, we assumed that unidentified fish were trophic position 3, regardless of size.

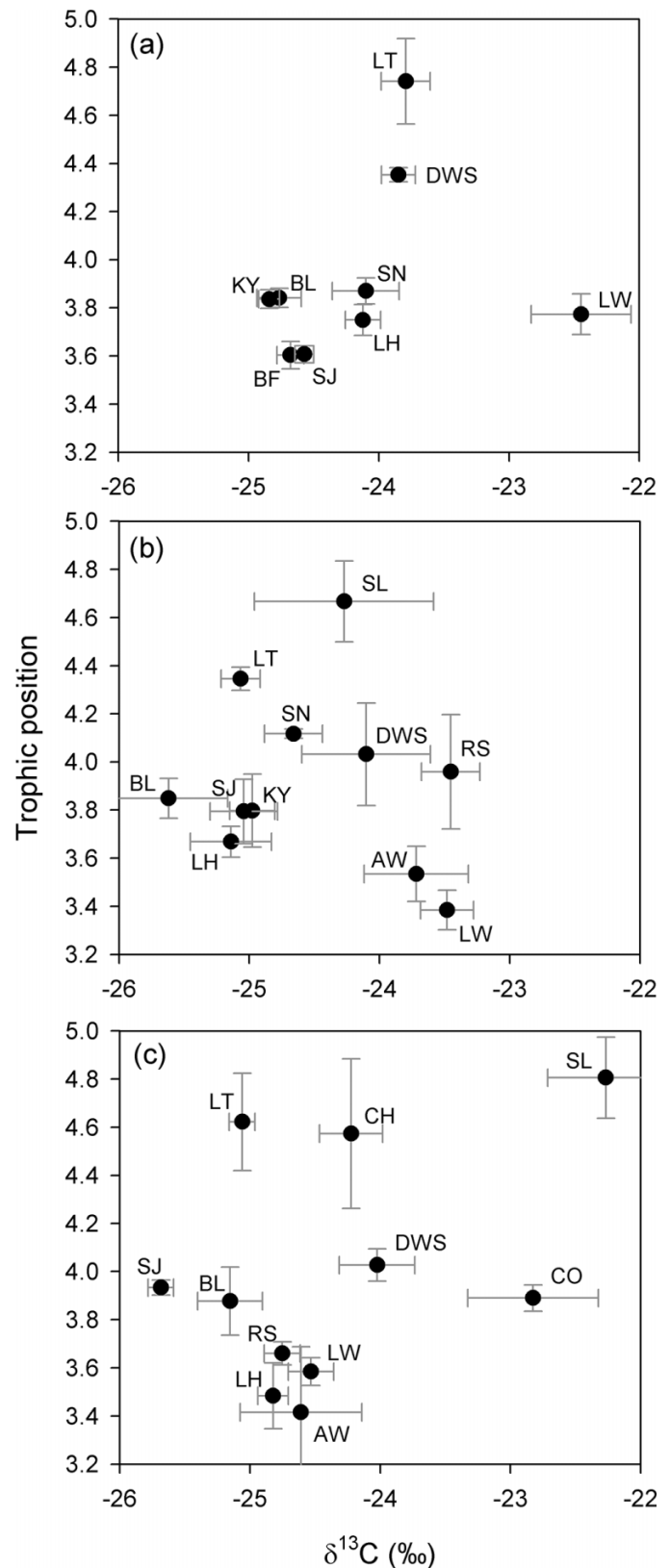
Characterizing food web change

Stable isotope data from museum specimens were broken down into three time periods based on availability of museum specimens and the time line of non-native species introductions. To evaluate food web change over time, we present corrected $\delta^{13}\text{C}$ vs. trophic position biplots from Lake Superior for the following time periods: 1897–1929, 1934–1966, and 1972–1998 ($n = 181, 75,$ and $66,$ respectively). These time periods were chosen based on availability of museum specimens and the timeline of species introductions. We also applied new quantitative methods for

Fig. 2. Stable isotope food web diagrams ($\delta^{13}\text{C}$ vs. trophic position) of the Lake Superior fish community for all time periods: (a) 1897–1929; (b) 1934–1966; (c) 1972–1998. Each point represents the mean $\delta^{13}\text{C}$ and trophic position for a given species. Error bars show ± 1 standard error from the mean. Data labels are as follows: DWS, deepwater sculpin (*Myoxocephalus thompsoni*); LW, lake whitefish (*Coregonus clupeaformis*); LH, lake herring (*C. artedii*); SN, shortnose cisco (*C. reighardi*); SJ, shortjaw cisco (*C. zenithicus*); BL, bloater (*C. hoyi*); KY, kiyi (*C. kiyi*); BF, blackfin cisco (*C. nigrinpinnis*); LT, lake trout (*Salvelinus namaycush*); SL, sea lamprey (*Petromyzon marinus*); RS, rainbow smelt (*Osmerus mordax*); AW, alewife (*Alosa pseudoharengus*); CH, Chinook salmon (*Oncorhynchus tshawytscha*); CO, coho salmon (*Oncorhynchus kisutch*).

comparing stable isotope food web data over time and space (Layman et al. 2007; Schmidt et al. 2007). While the food web diagrams are represented in $\delta^{13}\text{C}$ vs. trophic position, these new quantitative methods require the use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data as these dimensions share the same units of measurement (i.e., delta units). We used community-wide metrics to characterize food web structure as described by Layman et al. (2007). These metrics are used to quantify and compare trophic diversity and trophic redundancy. Trophic diversity (i.e., the total extent of spacing within $\delta^{13}\text{C} - \delta^{15}\text{N}$ biplot space) was compared over time by measuring $\delta^{15}\text{N}$ range (NR), $\delta^{13}\text{C}$ range (CR), total area (TA), and mean distance to the centroid (CD) (Layman et al. 2007). We would expect trophic diversity to increase, for example, with the addition of trophic levels (i.e., increase in NR, TA, and CD). Trophic redundancy (i.e., the position of species relative to each other within niche space) was compared by measuring mean nearest-neighbor distance (NND) and the standard deviation of nearest-neighbor distance (SDNND) (Layman et al. 2007). Low values for NND correspond to an increase in trophic redundancy, i.e., species are packed more closely together in trophic niche space. Low values for SDNND indicate a more even distribution of species' spacing, that is, there tend to be fewer "groupings" or "clusters" of species in trophic niche space.

We also quantified directional food web changes (magnitude and direction) for the Lake Superior fish community using corrected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and circular statistics (Schmidt et al. 2007). This method allows assessment of community-wide patterns of trophic niche shifts through time, that is, whether all species are shifting in similar direction or are shifting in all directions with equal frequency. The direction and magnitude of species shifting is presented in arrow diagrams in which each arrow represents a single species. The direction of the arrow shows the direction in trophic niche space that a species shifted over time, whereas the length of the arrow corresponds to how far the species moved in trophic niche space. A strict shift in carbon space is represented by an angle of 90° (enriched $\delta^{13}\text{C}$) or 270° (depleted $\delta^{13}\text{C}$). A strict shift in nitrogen space is represented by an angle of $0^\circ/360^\circ$ (increased trophic position) or 180° (decreased trophic position). We use a Rayleigh's test to assess whether the distribution of angles of direction for all species in a given food web departs from uniformity (Batschelet 1981). If a community-wide food web response



were occurring, then we would expect all species to shift in the same direction (i.e., all species' arrows to point in the same direction). By taking all species' angles in an arrow diagram, we can calculate the mean angle of change among

Table 2. Directional change (angle (θ ; expressed in degrees) and magnitude) for each species across all time steps in the Lake Superior fish community.

Species	1897–1929 to 1934–1966		1934–1966 to 1972–1998	
	Magnitude	θ ($^\circ$)	Magnitude	θ ($^\circ$)
<i>Coregonus hoyi</i> (bloater)	0.85	271.7	0.48	78.3
<i>C. kiyi</i> (kiyi)	0.19	225.0		
<i>C. zenithicus</i> (shortjaw cisco)	0.79	323.5	0.80	306.4
<i>C. reighardi</i> (shortnose cisco)	1.01	326.4		
<i>C. artedi</i> (lake herring)	1.06	254.8	0.70	153.1
<i>C. clupeaformis</i> (lake whitefish)	1.68	218.1	1.25	302.8
<i>Salvelinus namaycush</i> (lake trout)	1.85	223.4	0.94	0.4
<i>Myoxocephalus thompsoni</i> (deepwater sculpin)	1.12	193.0	0.08	101.9
<i>Alosa pseudoharengus</i> (alewife)			0.98	245.6
<i>Osmerus mordax</i> (rainbow smelt)			1.65	232.0
<i>Petromyzon marinus</i> (sea lamprey)			1.84	51.3

all species (i.e., the community) and test for differences in the mean angle of change for the community over time. This mean angle of change for the community is presented in the arrow diagrams using a straight broken line.

Results

Among all species, there is a significant positive correlation between isotope- and diet-based estimates of trophic positions ($R_0 = 0.89$, $P < 0.001$; Fig. 1). The slope of the best fit regression line was not significantly different than 1 at the 95% confidence interval ($y = -0.99 + 1.20x$, $df = 1,9$, $P < 0.001$, adjusted $R^2 = 0.77$). The intercept was also not significantly different than 0 ($P = 0.28$). Even among lake trout, for which diet data and stable isotope data are available from several time periods, the positive correlation between trophic position estimates holds true.

Food web diagrams of $\delta^{13}\text{C}$ vs. trophic positions were plotted for each time period for the Lake Superior fish community (Fig. 2). By the second time period (1934–1966), sea lamprey had established populations in Lake Superior; sea lamprey ascended to the top of the food web and replaced lake trout as the top predator. Rainbow smelt also became established and occupied a niche that was initially distinct from native deepwater coregonines. However, by the final time period (1972–1998), rainbow smelt shifted to a trophic niche that is more similar to that of the historical deepwater coregonines. Sea lamprey also shifted to considerably more enriched $\delta^{13}\text{C}$ values from 1934–1966 to the final time period. Stocked Chinook salmon occupied a trophic position similar to that of native top predator lake trout in the final time period. The smaller coho salmon had a lower trophic position, similar to that of native deepwater coregonines, bloater and shortjaw cisco. Deepwater sculpin tended to occupy a higher trophic position than expected for a small benthivore. There were no museum specimens available for kiyi or shortnose cisco in the final time period.

There is a general trend towards more negative (i.e., depleted) $\delta^{13}\text{C}$ values through time in the Lake Superior food web (Fig. 2). This trend is further corroborated by quantifying directional change (angle and magnitude) for each species across time periods (Table 2; Fig. 3a). For the first time step (1897–1929 to 1934–1966), there is a significant directionality in species' isotopic signatures shifting in food

web space (Rayleigh's test, $P < 0.05$; Table 3). The mean angle of change for the community is 252° , indicative of an isotopic shift to more negative $\delta^{13}\text{C}$ values (Fig. 3a). If there had been a change in baseline due to biogeochemical shifts in $\delta^{15}\text{N}$, we would expect an increase in $\delta^{15}\text{N}$ in all species over time. Instead, the shifting occurs only along a carbon gradient or is random.

The mean angle of change for the community in the second time step is 350° , though there is no significant directionality for the second time step (Rayleigh's test, $P = 0.93$; Table 3; Fig. 3b). This trend does not differ when comparing only native species in the final time step ($P = 0.72$; Table 3; Fig. 3c). All native species shifts in trophic niche space in the final time step are relatively small (magnitude $< 1.25\%$). At the species level, as noted in the food web diagrams, both rainbow smelt and sea lamprey trophic niches exhibit considerable shifts (Fig. 3b).

Community-wide trophic structure has remained relatively constant over the last century, especially among native species (Table 4). When comparing all species, the range in trophic diversity increased by slightly more than one delta unit along a nitrogen range (NR), whereas the carbon range (CR) increased in only the final time period. However, among native species only, the range in nitrogen remained constant, whereas the carbon range actually decreased slightly. Total area (TA) of the entire food web nearly doubled from the second to the final time period, whereas total area declined slightly over time among native species only. The overall degree of trophic diversity (CD) ranged from 1.19 to 1.69 among all species but did not significantly change over time (analysis of variance, ANOVA, $P = 0.25$). The degree of trophic diversity (CD) remained even more constant among native species only (ANOVA, $P = 0.78$). For all species and native species only, trophic redundancy (NND) did not differ significantly over time (ANOVA, $P = 0.67$ and $P = 0.69$, respectively). Similarly, the evenness of species' distribution in trophic niche space did not differ much across time periods for both analyses (all species or native species only).

In years when data are available, shortnose cisco were always distinct in both trophic position and $\delta^{13}\text{C}$ from blackfin and shortjaw ciscoes (Fig. 4a). Shortnose cisco remained elevated in trophic position relative to shortjaw and blackfin ciscoes over the century. There was no difference between

Fig. 3. Arrow diagrams for angle of change (θ) for the fish community in Lake Superior at each time step. Each diagram shows directional food web changes in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space between consecutive time periods: (a) 1897–1929 to 1934–1966 and (b) 1934–1966 to 1972–1998, all species, and (c) 1934–1966 to 1972–1998, natives only. Each arrow represents a single species and the direction in trophic niche space in which the species moved. The length of the arrow represents the magnitude of change, in delta units (‰, for both ^{13}C and ^{15}N), for that particular species. Concentric circles correspond to magnitude (i.e., distance in delta units) of change. The straight broken line is the mean vector of change (μ) among all species; the curved broken line on the rim indicates the 95% confidence interval around the mean vector of change. Data labels are as follows: DWS, deepwater sculpin (*Myoxocephalus thompsoni*); LW, lake whitefish (*Coregonus clupeaformis*); LH, lake herring (*C. artedii*); SN, shortnose cisco (*C. reighardi*); SJ, shortjaw cisco (*C. zenithicus*); BL, bloater (*C. hoyi*); KY, kiyi (*C. kiyi*); LT, lake trout (*Salvelinus namaycush*); SL, sea lamprey (*Petromyzon marinus*); RS, rainbow smelt (*Osmerus mordax*); AW, alewife (*Alosa pseudoharengus*).

shortjaw cisco and blackfin cisco in the early 1900s (Fig. 4a). In the average across available specimens, species were significantly different from one another in trophic niche space (Fig. 4b; multivariate analysis of variance, MANOVA Wilks' lambda, $df = 4,166$, $F = 8.512$, $P < 0.001$). A pairwise MANOVA revealed a significant difference between shortnose and shortjaw ciscoes (MANOVA, Wilks' lambda, $df = 2,64$, $F = 14.220$, $P < 0.001$). There was no difference in trophic niche space between shortjaw and blackfin ciscoes (MANOVA, Wilks' lambda, $df = 2,66$, $F = 1.782$, $P = 0.18$).

Discussion

Through stable isotope analysis of preserved museum specimens, our analysis spans 100 years and provides important insight into food web changes over a long time scale. This paper is the first to reconstruct the historical food web of Lake Superior prior to species invasions and examine how the food web has changed. We document niche partitioning of native and non-native species throughout the past century. These findings have the potential to guide management objectives aimed at balancing the restoration of native communities while maintaining economically important fisheries supported by non-native species (Kitchell et al. 2000).

Stable isotope analysis of archived fish tissues

A number of contemporary food web studies use gut content analyses to validate stable isotope data (Vander Zanden et al. 1997; Harvey and Kitchell 2000). However, this is the first validation using isotope data from tissues of museum specimens and previously published diet data. Notably, individual specimens from the museums used for isotopic analyses were likely not the same as those examined for gut contents in the published studies. Even though the sampled specimens for the two methods were different, the significant positive correlation between trophic estimates suggests that stable isotope analysis is a valid approach for inferring dietary information and feeding patterns from preserved specimens.

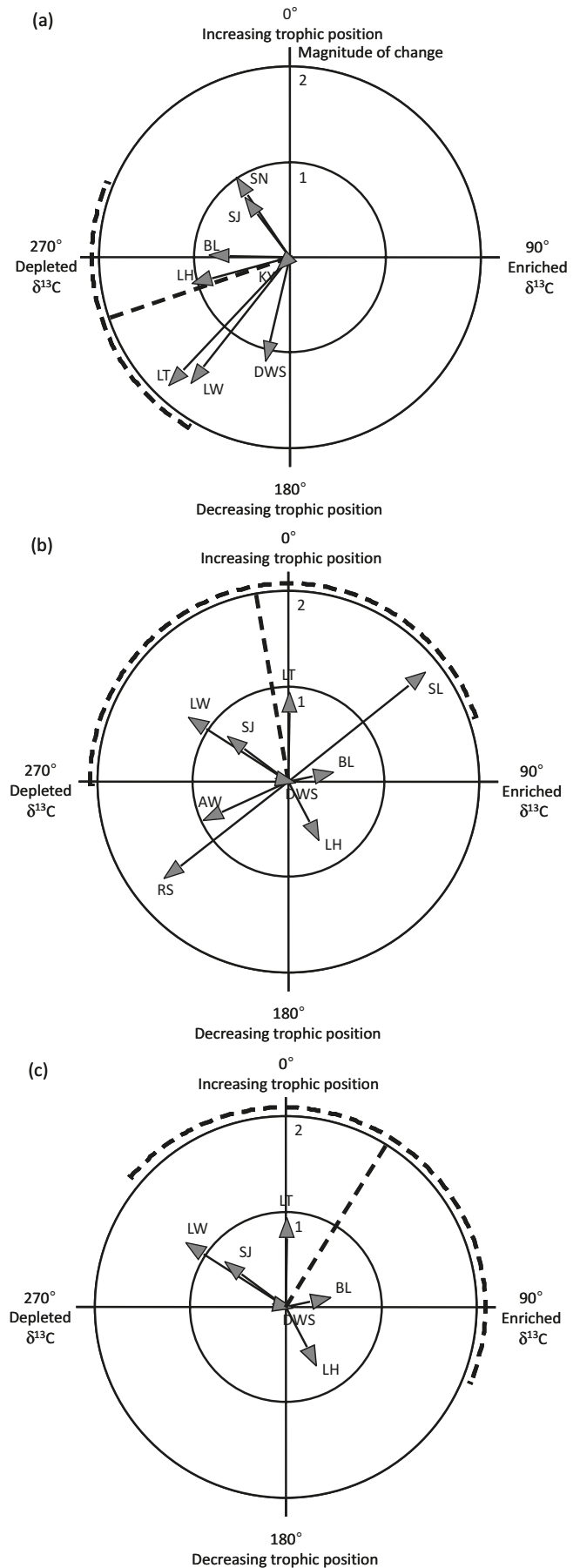


Table 3. Directional statistics quantifying change in isotope niche space for fish communities in Lake Superior over time.

Variable	1897–1929 to 1934– 1966	1934–1966 to 1972–1998 (all species)	1934–1966 to 1972–1998 (natives only)
Number of observations	8	9	6
Mean vector (μ)	251.5	350.0	31.9
Length of mean vector (r)	0.71	0.09	0.24
Angular standard deviation	47.9	124.9	96.3
Rayleigh's test (Z statistic)	3.98	0.08	0.36
Rayleigh's test (P)	0.014	0.927	0.718

Note: Rayleigh's test assesses whether the distribution of mean angles of direction (i.e., angular variance) departs from uniformity. P values in bold are significant at the $\alpha = 0.05$ level. For the first time step (1897–1929 to 1934–1966), native species were the only common species between the two time periods. For the second time step (1934–1966 to 1972–1998), analyses for all species and natives only are provided.

Table 4. Summary of shape dispersion statistics (Layman et al. 2007) for each time period in the Lake Superior fish community.

Time period	$\delta^{15}\text{N}$ range	$\delta^{13}\text{C}$ range	Total area	Centroid distance	Nearest-neighbor distance	SD nearest-neighbor distance
(a) All species						
1897–1929	3.87	2.40	4.75	1.19	0.61	0.64
1934–1966	4.04	2.17	5.88	1.22	0.61	0.40
1972–1998	5.09	3.41	10.05	1.69	0.80	0.60
ANOVA F test ($F_{[2,28]}$)				1.449	0.401	
ANOVA (P)				0.25	0.67	
(b) Natives only						
1897–1929	3.87	2.40	4.75	1.19	0.61	0.64
1934–1966	3.27	2.14	3.25	0.98	0.67	0.62
1972–1998	3.87	1.66	3.38	1.19	0.91	0.73
ANOVA F test ($F_{[2,20]}$)				0.251	0.384	
ANOVA (P)				0.78	0.69	

Note: The analysis for all species (a) included both native and non-native species (rainbow smelt, alewife, sea lamprey, and Pacific salmon). SD, standard deviation.

Stable isotope analysis can be effectively used on preserved specimens to evaluate historical food webs; however, corrections for shifts in carbon signatures due to the effects of storage on lipid content need to be considered (Post et al. 2007). Lipids are known to be isotopically depleted in $\delta^{13}\text{C}$ relative to other tissues (DeNiro and Epstein 1977; McConaughy and McRoy 1979; Post et al. 2007). We extracted lipids from a subset of samples and found that across the subsampled species, the average difference in $\delta^{13}\text{C}$ between bulk tissue and lipid-extracted tissue was relatively small (0.59‰, SD = 0.49). Years of storage in ethanol have probably caused lipids to leach out of muscle tissues, whereas our extraction removed remaining tightly bound membrane lipids. For this reason, previously proposed arithmetic corrections did not apply to our data (see Post et al. 2007). We developed a new arithmetic correction based on lipid-extracted samples to account for lipids that may have remained after preservation and subsequent storage in ethanol.

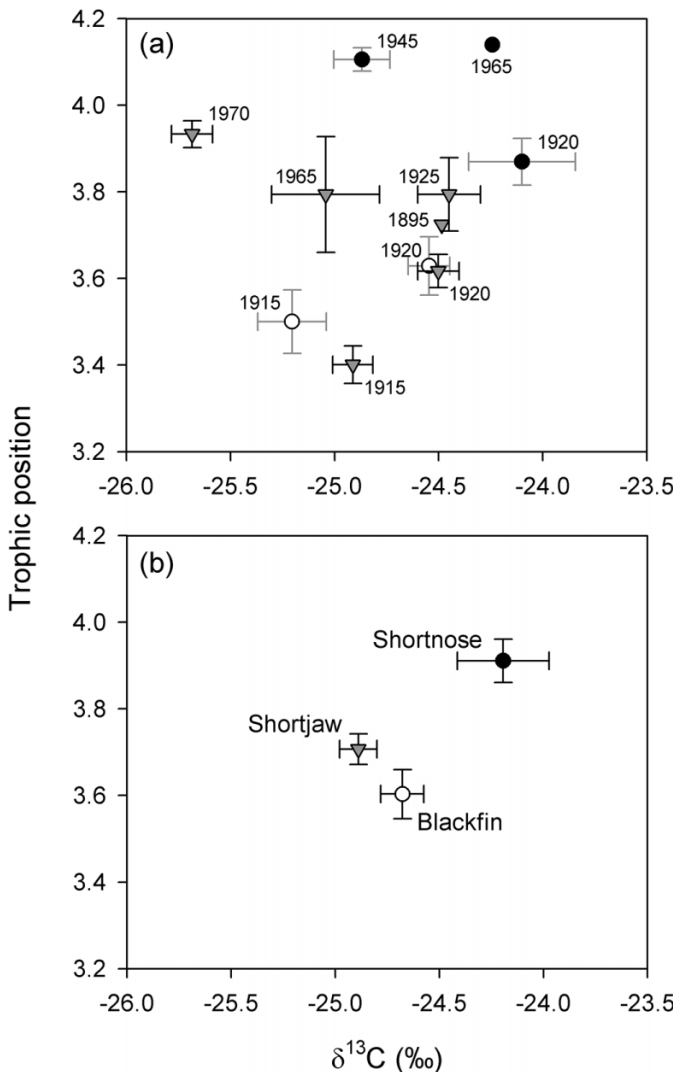
Historical and contemporary food web structure

The food web of Lake Superior has undergone several changes over the last century. Prior to the 1930s, the food

web was comprised of lake trout as the top predator, with native coregonines dominating the forage base. Introduced non-natives Chinook salmon and sea lamprey joined lake trout as a top predator in later time periods. Pacific salmonids were intentionally stocked in the mid-1960s and sea lamprey were first detected in Lake Superior in 1946 (Lawrie 1978). The position of coho salmon in relation to native lake trout in the most recent time period (1972–1998) is similar to that found by Harvey and Kitchell (2000) for contemporary Lake Superior. The modest trophic niche overlap suggests little competitive interaction between these two species. As expected, the trophic position of sea lamprey is higher than that of lake trout. The relative trophic niche positionings of natives lake trout, deepwater coregonines, lake herring, and lake whitefish are similar to those found by Harvey et al. (2008) for three major ecoregions in Lake Superior. Overall, with almost all species introductions, there is remarkably little overlap between natives and non-natives in isotopic food web space.

At the species level, sea lamprey and rainbow smelt trophic niches exhibited the largest shifts (magnitude > 1.25 delta units) that could not be explained by community-wide

Fig. 4. Average $\delta^{13}\text{C}$ vs. trophic position for cisco species (blackfin (open circles), shortjaw (shaded triangles), and shortnose (solid circles)) (a) across five-year incremental periods (i.e., 1925–1929, 1930–1934, etc.) and (b) across all years (i.e., all available specimens). Error bars represent ± 1 standard error. Overall, species are significantly different from one another in trophic niche space (multivariate analysis of variance, MANOVA, Wilks' lambda, $df = 4, 166$, $F = 8.512$, $P < 0.001$).



dynamics. All other trophic niche shifts not explained by community-wide dynamics were considered negligible given the nature of the data. We would expect some small differences in trophic niches when data span over 100 years and multiple locations in Lake Superior. The positioning of sea lamprey in the final time period (1972–1998), however, is potentially a localized spatial effect related to differences in foraging behavior or diet (Harvey et al. 2008), as those samples were collected in the Gravel River, located on the northern shore. The higher $\delta^{13}\text{C}$ values indicate a shift in reliance from lake trout to hosts such as longnose and white suckers (Harvey et al. 2008). Rainbow smelt were initially separated in trophic niche space from native coregonines when first introduced in the 1930s, but they eventually shifted to a trophic niche position similar to that of native

coregonines in the final time period. Rainbow smelt from the final time period were collected prior to the population decline in the early 1980s (Bronte et al. 2003). It is possible that the growing populations of rainbow smelt were taking advantage of resources previously used by declining lake herring populations. However, we acknowledge that we lack depth data for any samples and differences in the depth of sample collection could cause variation in isotope signatures.

Throughout all time periods, deepwater sculpin were unusually elevated in trophic position for a small forage fish. This finding is similar to what Zimmerman et al. (2009) found for deepwater sculpin in Great Slave Lake. Sierszen et al. (2006) found that *Diporeia* became significantly enriched in $\delta^{15}\text{N}$ with increasing depth in Lake Superior and that deepwater sculpin tend to occupy depths ranging from around 70 m to greater than 300 m (Dryer 1966). However, deepwater coregonines such as kiyi and bloater occupy depths similar to that of deepwater sculpin and do not reflect this elevated trend in trophic position. Deepwater sculpin diet consists primarily of *Diporeia*, supplemented by *Mysis* (Selgeby 1988). Therefore, both prey items likely to be consumed by deepwater sculpin are enriched in $\delta^{15}\text{N}$ due to depth-driven isotopic fractionation. On the other hand, coregonines tend to consume a diet high in *Mysis*, supplemented by Copepoda (Anderson and Smith 1971), which are depleted in $\delta^{15}\text{N}$ relative to *Mysis* (Harvey and Kitchell 2000). We would therefore conclude that the elevated trophic position of deepwater sculpins is driven by both diet- and depth-related $\delta^{15}\text{N}$ differences in prey items.

Despite introductions of non-native species, the historical food web structure of the native Lake Superior community has remained largely intact. The trophic extent (i.e., range) of the native community remained stable over time, whereas the trophic extent of the entire community (natives + non-natives) increased slightly in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ due to the introductions of sea lamprey and coho salmon. For both community comparisons (all species or natives only), the overall degree of trophic diversity, represented by centroid distance, did not change significantly over time. Similarly, trophic redundancy did not change significantly over the last 100 years, despite the distant positions of sea lamprey and coho salmon in niche space relative to all other species in the most recent time period. The lack of significant change in any of the community-wide metrics proposed by Layman et al. (2007) suggests little community-wide change in the Lake Superior fish community over the last century. This trend is especially evident when comparing only native species. That is, the general “shape” and “placement” of the native food web in trophic niche space has not changed over time. Rather, changes appeared to have occurred on a species-specific level where species have entered the food web without causing community-wide differences in the native fish community.

The only detectable pattern of community-wide change observed in Lake Superior was the shifting of all species along the $\delta^{13}\text{C}$ axis toward more pelagic-based production, which occurred in the first time step (1897–1929 to 1934–1966). Unfortunately, the lack of historical zooplankton and benthic organisms makes it difficult to determine whether the $\delta^{13}\text{C}$ shift is actually biogeochemical or food web re-

lated. If the shifting were food web related, we might expect some change that has caused all Lake Superior species to rely more on pelagic-based resources (as indicated by a lower $\delta^{13}\text{C}$ signature), e.g., the introduction of a non-native pelagic zooplankton or a decrease in benthic-based resources. However, neither of those scenarios has been documented in Lake Superior during this time period. It is more plausible that the shifting is due to a biogeochemical effect at the base of the Lake Superior food web (Vander Zanden and Rasmussen 2001) as all species' trophic niches responded the same way. Unfortunately, we lack sufficient data and historical information to test this hypothesis and identify the exact biogeochemical effect that would have caused the observed shift in $\delta^{13}\text{C}$. Nonetheless, two different measures of community-wide dynamics (Layman et al. 2007; Schmidt et al. 2007) revealed no significant changes in the Lake Superior community that could be attributed to food web related differences alone.

Niche partitioning

The deepwater coregonines of the Great Lakes are a complex group of species and the subject of debate about taxonomic and ecological differences among the group (Todd and Smith 1980; Todd et al. 1981). This is especially apparent in the consideration of shortnose, shortjaw, and blackfin ciscoes in Lake Superior. Early studies documented and classified the three species as separate and distinct (Christie 1974), but those classifications were challenged and disputed by Todd and Smith (1980) through closer examination of morphometric characters of the three species. Todd and Smith (1980) argue that blackfin ciscoes described by Koelz (1929) were simply larger variants of shortjaw ciscoes and that shortnose ciscoes were populations of shortjaw ciscoes found almost entirely in the northern bays of Lake Superior. The shortnose cisco specimens that we sampled were collected throughout Lake Superior and were not limited to the northern bays. Our stable isotope analysis revealed no difference between shortjaw and blackfin ciscoes in trophic niche space, suggesting that these species were ecologically similar based on niche partitioning. On the other hand, we found significant differences in niche partitioning between shortnose and shortjaw ciscoes, indicating ecological differences. Although these species are perhaps phenotypically very similar, they retained slight, but ecologically distinct, differences over time as revealed by stable isotope analysis. Unfortunately, we can only speculate on the feeding ecology that may cause these small differences; analysis of direct stomach contents of museum specimens proved inconclusive because of empty stomachs or unidentifiable contents. Further studies on diet and habitat preferences of these species in Lake Superior and other lakes in which they co-exist would help resolve what is driving the subtle ecological differences. If the species are ecologically distinct, this result has interesting implications with regards to restoration of native Lake Superior fish assemblages. Efforts to rehabilitate the native deepwater coregonines populations must consider the unique ecology of each species in addition to morphological and genetic differences.

Implications for management

Through stable isotope analysis of preserved museum

specimens, our analysis spans 100 years and provides important insight into food web changes over a long time scale. We document niche partitioning of native and non-native species throughout the past century. Admittedly, our ability to provide an in-depth story of the specific ecology of these fishes over time has been limited by the availability of data and specimens. Instead of species-specific analyses, we provide a community-wide analysis and a food web approach, which are increasingly being used as tools for restoration ecology (Vander Zanden et al. 2006). This paper highlights some ways in which the food web has changed or, rather, not changed. These findings have the potential to guide management objectives aimed at balancing the restoration of native communities while maintaining economically important fisheries supported by non-native species (Kitchell et al. 2000).

The fish community of Lake Superior now includes numerous non-native species; however, the long-term food web structure has largely remained intact, especially among native species. Overall, there is surprisingly little trophic niche overlap among native and non-native species within the same time period. In some cases, introduced species overlap trophic positions with native species (but do not overlap along the $\delta^{13}\text{C}$ axis); however, this trophic position overlap has not resulted in a loss of species diversity. Introductions have not changed the trophic redundancy of the food web. The lack of community-wide changes among native species despite multiple species introductions reflects the resilience of the Lake Superior food web. Noting population recovery of native species such as lake herring, Horns et al. (2003) suggest that the fish community is shifting back to more natural and historical conditions. These findings are good news for (i) restoration of native species and (ii) management of fisheries that depend on non-native species such as rainbow smelt and Pacific salmon. The stable and resilient food web structure allows recovery of native species, while the lack of overlap among natives and non-natives suggests that restoration can proceed without the eradication or mitigation of economically important non-natives.

Gaining long-term perspectives on ecosystem change is essential to guide development of restoration and conservation efforts (Willis and Birks 2006). As the least changed of the Laurentian Great Lakes, Lake Superior can serve as an indicator for the restoration of fish communities in other Great Lakes. Analyses of food web changes in Lakes Michigan, Huron, and Ontario can be compared with the changes in Lake Superior to evaluate the magnitude of food web changes in those lakes. Do the other Great Lakes show a similar, lower, or higher degree of food web change over the last century? Answering this question is especially important in light of the growing need to understand environmental changes at a regional scale (Carpenter et al. 2007).

Acknowledgements

We are greatly indebted to the generosity of Doug Nelson (University of Michigan Museum of Zoology), Sylvie Laframboise (Canadian Museum of Nature), Mary Burrige (Royal Ontario Museum), Tony Gamble (Bell Museum), Randy Mooi (Milwaukee Public Museum), John Lyons (University of Wisconsin), Michael Retzer (Illinois Natural History Survey), and Mary Anne Rogers (Field Museum) for

providing archived specimens. We thank W. Fetzer, J. McCarthy, and L. Richter for help with sample collection and laboratory analyses. We also thank David Harris and the UC–Davis Stable Isotope Facility for isotopic analyses. Comments by O. Jensen, S. Higgins, K. Butkas, J. Fox, M. Diebel, and three anonymous reviewers greatly improved this manuscript. This project was funded by the Great Lakes Fishery Commission (grant awarded to J.V.Z.) and the University of Wisconsin – Sea Grant program (grant No. R/LR-92 awarded to J.V.Z.). S. Schmidt was partially funded by a University of Wisconsin Graduate Engineering Research Scholars fellowship during the preparation of this manuscript.

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