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Lake whitefish feeding habits and condition in Lake Michigan

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with 3 figures and 5 tables

Abstract: Lake whitefish (*Coregonus clupeaformis*) have experienced declines in condition in some areas of the Great Lakes. The hypothesis tested was that condition—in terms of relative weight, percent lipid and docosahexaenoic acid (DHA)—was greater in regions where larger proportions of high quality prey (e.g., *Diporeia*) were included in the diet. Samples of spawning lake whitefish from four regions around Lake Michigan (northwest, Naubinway, Elk Rapids and southeast) had distinct mean carbon and nitrogen stable isotope signatures. Lake whitefish may be using a variety of prey items, especially the Naubinway population where fish occupy the largest stable isotopic niche space. However, trophic niche width inferred from stable isotopes did not vary among regions. Relative weight was highest in the southeast and lowest for all northern regions. The mean measured lipid from lake whitefish dorsal, skinless, muscle biopsies were highest for northwest fish. DHA was significantly different among regions, with high mean values in Elk Rapids and the northwest. No correlations were found between stable isotope measures and condition metrics. The results suggest that lake whitefish are coping with declining *Diporeia* abundances by feeding on alternate prey. Overall results do not substantiate the hypothesis of a relationship between condition and prey use, although lake whitefish from Elk Rapids and the northwest had high quality prey and good condition.

Keywords: Lake Michigan, whitefish.

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Introduction

Lake whitefish (*Coregonus clupeaformis*) has a significant position in the Great Lakes fishery, as both fillets and roe are prized for recreational and commercial harvest. An evolutionarily young species (McPahil & Lindsey 1970), lake whitefish in the Great Lakes have experienced fluctuations in population abundance due to pollution, over-fishing, predation by sea lamprey (*Petromyzon marinus*) and interspecific competition with alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*) and white perch (*Morone Americana*, Ebener 1997). More recently, increasing overall abundance and localized declines in the growth and condition of lake whitefish have been reported and hold potentially serious implications for local fisheries (Pothoven et al. 2001, Schneeberger et al. 2005, Pothoven & Nalepa 2006, Pothoven et al. 2006). One suggested cause of the localized declines has been the simultaneous decline in the abundance of the amphipod *Diporeia hoyi* (Dermott & Kerec 1997, Nalepa et al. 1998, Nalepa et al. 2000, Nalepa et al. 2009).

Diporeia is a glacial marine-relict amphipod, and similar to lake whitefish, prefers cold temperatures in deep-water lake habitats below the thermocline (Dadswell 1974). *Diporeia* are rich in energy, i.e., high total lipid concentrations (Cavaletto et al. 1997) and have high concentrations of essential fatty acids (Kainz et al. 2010, including docosahexaenoic acid = DHA; 22:6n-3) that are known to promote fish health, overall condition, and enhance reproductive success (Arts & Kohler 2009, Tocher 2003). Marine fish, including salmonines have, in general, only a poor ability to desaturate and elongate dietary alpha-linolenic acid (18:3n-3) to DHA *de novo* (Tocher 2003). The efficiency at which most freshwater fish species, including lake whitefish, are able to perform these conversions is largely untested although freshwater species in general are presumed to have higher conversion efficiencies than marine fish (Tocher 2003). However, environmental conditions (diet) clearly play a role because lake whitefish exhibit a high degree of temporal plasticity, with respect to DHA concentrations, in Lake Michigan (Wagner et al. 2010). This suggests that this species is dependant, at least to some extent, on obtaining pre-formed DHA in the diet. DHA occurs in high concentrations in membrane phospholipids and is known to have positive effects on teleost egg, neural and eye development (Bell & Dick 1993, Dalsgaard et al. 2003). For example, DHA is a major component of the ocular phospholipids in herring (*Clupea harengus*; Bell & Dick 1993). Thus, we speculate that reductions in *Diporeia* consumption by lake whitefish may result in low DHA uptake, which could lead to reduced individual foraging success as a result of the importance of DHA for the maintenance of ocular health.

In regions of observed *Diporeia* declines, lake whitefish foraging efficiency appears to have fallen as fish switched to lower quality prey. For example, shelled prey such as zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*, respectively) are much more difficult for fish to process and engender longer handling times (Pothoven et al. 2001, Pothoven et al. 2006, Pothoven & Nalepa 2006, Pothoven & Madenjian 2008). *Bythotrephes longimanus*, like other cladocerans, has very low-to-no DHA in its tissues (Arts unpublished). Other prey sources rich in DHA (Schlechtriem et al. 2008) and high in caloric value, such as *Mysis relicta*, exist in Lake Michigan. However, low relative abundance, patchy distributions and vertical migration cycles seem to preclude their wide use as a forage resource by lake whitefish (Bowers 1988, Levy 1991, Cavaletto & Gardner 1998, Pothoven et al. 2004).

To date, a broad spatial examination of the proposed link between observed changes in prey choices and lake whitefish growth and condition have not been investigated explicitly. Lake Michigan provides a gradient of *Diporeia* abundances with which to test these suggested links. Accordingly, the objectives of this study were to determine [1] whether lake whitefish have regionally distinct dietary habits within Lake Michigan, and [2] if lake whitefish prey choices are correlated with measures of fish condition. Our central hypothesis was that Lake Michigan whitefish from regions where *Diporeia* were in low abundance, or absent, would exhibit poorer condition compared to lake whitefish from regions where *Diporeia* were in high abundance. Based on known *Diporeia* densities within Lake Michigan (Nalepa et al. 2009), lake whitefish condition was expected to be best in the northwest and southeast regions, intermediate at Elk Rapids and poorest at Naubinway.

Materials and methods

Adult lake whitefish were sampled at six sites around Lake Michigan including Saugatuck, Ludington, Elk Rapids, Naubinway, Big Bay de Noc, and Bailey's Harbor (Fig. 1). All sites were known to have varying densities of *Diporeia* (Nalepa et al. 2009). Fish were collected between October and December in 2004 and 2005 using either commercial trap nets with 40 cm stretch mesh, with a pot comprised of 11.4 cm stretch mesh, or gillnets with varying mesh grading ranging from 4 to 15 cm. At each site, up to 30 pre-ovulatory females and 30 ripe males were collected. Each fish was measured for total weight (g) and total length (mm). Stomach content analysis was completed on a total of 630 lake whitefish. Stomachs were removed, separated, dried and weighed to determine the proportional contribution by dry weight of each prey item in all non-empty stomachs. Skinless dorsal muscle plugs were collected from each fish and stored frozen (-85 °C) for stable isotope and lipid analyses.

Potential prey sources were collected between mid-June and early-July of 2005 and included dreissenid mussels, zooplankton, *Mysis relicta* and *Diporeia*. Particulate organic matter (POM) and various benthic invertebrates were collected late-June 2007 to supplement the 2005 sampling. Benthic invertebrates were collected from rocky littoral zones, separated and held alive in filtered water overnight for gut clearance (Hamilton et al. 1992) prior to freezing (-10 °C). Benthos were identified to order or family under a dissecting microscope in the lab and included Chironomidae, Trichoptera, Ephemeroptera, Isopoda and Amphipoda. Amphipods collected from littoral zones were distinct and distinguished from *Diporeia* collected offshore. Benthos were separated into replicates ($n = 3$) for stable isotope analysis (SIA).

Tagging studies during 2003–2004 noted movement of lake whitefish away from areas of low *Diporeia* abundance. Surveys in 2005 indicated the absence of Diporeia in the immediate vicinity of Big Bay de Noc, however at depths of 70–90 m, mean Diporeia densities were estimated at 1,055 m^{-2} (Nalepa et al. 2009). Lake whitefish individuals from the Big Bay de Noc site migrate south to the east side of the Door Peninsula, Wisconsin, between spawning seasons (Ebener et al. 2010). Such regional migratory movements suggest foraging can occur over wide areas. Accordingly, for analysis Big Bay de Noc and Bailey's Harbor, data were grouped as a single northwest region. Similarly, due to geographical proximity, Ludington and Saugatuck were grouped as the southeast region, where regional mean *Diporeia* densities were estimated at 454 m^{-2}, at a depth of 86–98 m (Nalepa et al. 2009). Of the lake whitefish tagged in the Naubinway management unit, 87% were recaptured in the same management unit, suggesting that the Naubinway population is sedentary (Ebener et al. 2010). Therefore, Naubinway and Elk Rapids were treated as separate feeding populations, having estimated mean *Diporeia* densities of 0 m^{-2} at depths of 31–46 m and 1,110 m^{-2} at depths of 87–93 m respectively (Nalepa et al. 2009).

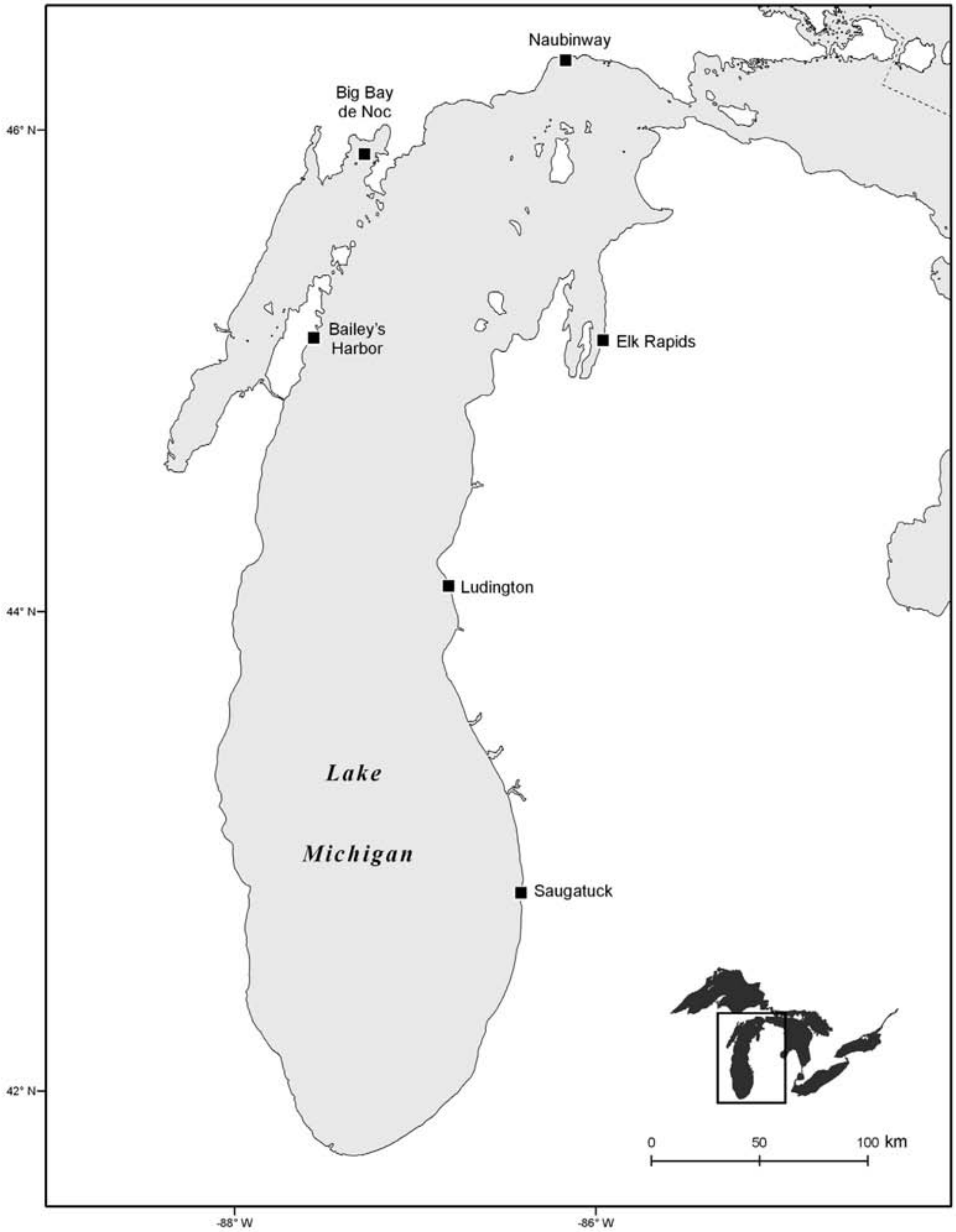

Fig. 1: Lake whitefish and prey source sampling sites in Lake Michigan. Fish were collected between October and December of 2004 and 2005. Potential prey sources were collected June 2005 and 2007.

Stable isotope analysis

Fish skinless dorsal muscle tissue and whole prey bodies were dried at 50 °C for 48 h, pulverized to a homogenate with a Retsch MM 301 ball mill grinder or by hand, and approximately 0.3 mg of the homogenate was weighed out for SIA. Weighed material was inserted into combustible tin cups (SerCon 5 x 3.5 mm). Stable isotope values for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were determined using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer coupled to a Carlo Erba Elemental Analyzer at the Environmental Isotope Laboratory, University of Waterloo, Ontario. Resulting measurements were expressed using standard delta notation (δ) as parts per thousand differences with respect to the international reference standards, which were carbonate rock from the Peedee Belemnite formation $\delta^{13}C$ (Craig 1957) and nitrogen gas in the atmosphere for $\delta^{15}N$ (Mariotti 1983). Machine analytical precision, respectively, for $\delta^{13}C$ and $\delta^{15}N$ was ±0.2 ‰ and ±0.3 ‰ and was determined by repeat analysis ($n = 25$) of laboratory working standards cross-calibrated to International Atomic Energy Agency standards CH6 for $\delta^{13}C$ and N1 and N2 for $\delta^{15}N$.

To compare among regions and account for possible anthropogenic variation in the stable isotope signatures at the base of regional food webs (e.g., Post 2002), nitrogen isotope signatures were baseline corrected. With appropriate estimates of base $\delta^{15}N$, it is possible to determine if observed variation in an organism's isotope signature occurs because of differences in food web structure and carbon flow or because of variation at the base of the food web (Vander Zanden & Rasmussen 1999, Post 2002). Here, baseline correction was accomplished by subtracting the average POM $\delta^{15}N$ signature for each region from all fish and prey $\delta^{15}N$ signatures in the respective region. The resulting corrected $\delta^{15}N$ measure, therefore, functions to scale fish and prey in terms of trophic distance from the base of the food web and facilitates region-to-region comparisons.

Lipid and DHA analysis

Total lipid and DHA concentrations of individual adult lake whitefish samples were analyzed at The National Water Research Institute laboratories of Environment Canada, Burlington, Ontario. Skinless dorsal muscle samples were freeze-dried in preparation for total lipid and DHA analyses. Analysis involved three steps: gravimetric extraction, derivitization, and quantification on a HP6890 gas chromatograph following the methods described in Zellmer et al. (2004). Samples were extracted three times by grinding freeze-dried materials in a 2:1 chloroform:methanol solution (Folch et al. 1957). After centrifugation at 4,000 rpm to remove the majority of non-lipid material, the supernatant was transferred to acid-washed, 15-ml centrifuge tubes and rinsed with chloroform:methanol. This procedure was followed by a salt wash (0.9% aqueous NaCl solution) to remove lipophilic proteins before samples were evaporated to 2 ml. From this volume, 200 μL of sample extract was weighed on a Sartorious ME-5 microbalance to provide an accurate measure of total lipid content. DHA was identified and quantified with a reference to Supelco's 37 component FAME mix (#47885-U). An internal standard (5 α-cholestane; Sigma-Aldrich; #C8003) was added to the tissue before extraction to estimate percent recovery during the extraction procedure. The DHA concentrations are reported as μg FAME/mg dry mass of tissue.

Data analysis

Polygons encompassing fish and prey item stable isotope signatures in $\delta^{13}C$–$\delta^{15}N$ space were defined following Layman et al. (2007) and Cornwell et al. (2006). For lake whitefish, the resulting enclosed area measures the total amount of dietary niche space occupied by a given population in a given region. For prey items, the polygon represents the total amount of dietary niche space occupied by the regional forage base upon which the fish rely and, therefore, is a suitable proxy for the extent of trophic diversity within each regional forage base (Layman et al. 2007). Studies have shown that convex hull polygons, as defined here, provide useful quantitative measures of ecological trait space suitable for use in testing for the effect of trait filtering, e.g., choice of dietary resources (CORNWELL et al. 2006). To avoid biasing estimates of niche central tendency as a result of individual outliers by using the geometric center, the arthimetic mean of all signatures was used to characterize the centre of the polygon-defined niche space. The variance in δ^{13}C and baseline corrected δ^{15}N signatures were used as a second measure of niche width, with greater variation reflecting wider use of available prey resources (BEARHOP et al. 2004). Bartlett's test for variance homogeneity (BARTLETT 1937a, 1937b) was applied to determine whether there were significant differences in lake whitefish δ^{13}C and δ^{15}N variances among Lake Michigan study regions.

To estimate possible proportions of lake whitefish diets accounted for by each sampled prey type, we used ISOSOURCE, a computer program that uses information on prey and consumer stable isotope signatures to determine all possible combinations of varying prey source contributions (0–100%) that sum to the observed isotope signature of the consumer (PHILLIPS & GREGG 2001, PHILLIPS & GREGG 2003). Total energy density of the suggested diet was then calculated as a weighted average using energy densities for each prey source and dietary proportions as determined by ISOSOURCE. A similar calculation was performed for comparative purposes using dietary proportions determined from stomach content analysis. Energy density values for each prey source were obtained from a compilation of sources (i.e., CUMMINS & WUYCHECK 1971, DRIVER et al. 1974, LANTRY & STEWART 1993, EGGLETON & SCHRAMM 2004, STORCH 2005, JOHNSON et al. 2006, MADENJIAN et al. 2006) as reported in RENNIE et al. (2009b). When multiple energy density estimates were found, the average was used.

Stomach content data were used to compute the dietary niche overlap index proposed by HORN (1966) as a means of assessing short-term differences in feeding patterns among studied regions as follows:

$$(1) \qquad R_O = \frac{\sum_{i=1}^{n} (p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \sum_{i=1}^{n} p_{ij} \log p_{ij} - \sum_{i=1}^{n} p_{ik} \log p_{ik}}{2 \log 2}$$

where R_O is the index of dietary overlap between lake whitefish captured in regions *j* and *k*, p_{ij} is the proportion of prey resource *i* in the total of prey resources used by lake whitefish in region *j*, p_{ik} is the proportion of prey resource *i* in the total of prey resources used by lake whitefish in region *k*, and *n* is the total number of prey resource categories. The index varies between 0 and 1, indicating no dietary overlap and complete overlap respectively. The index has been found in simulation studies to minimize bias even under conditions of a changing number of prey resource categories, sample size and resource evenness (RICKLEFS & LAU 1980, SMITH & ZARET 1982). Results were further compared to dietary data reported in the literature (MADENJIAN et al. 2006) for fish captured in the southeast region in the autumns of 1998–2001.

Relative weight (W_r), the ratio of observed individual fish weight (W) to the length specific standardized weight (W_s), was used as the quantitative measure of condition calculated using RENNIE & VERDON's (2008) regression length percentile W_s equations estimated for mature male and female lake whitefish from 385 populations in North America. Specifically,

$$(2) \qquad W_r = \frac{weight}{W_s} \times 100 \quad ,$$

where

Female: $\log W_s = 3.19 \log L – 5.47$

Male: $\log W_s = 3.13 \log L - 5.33$

Statistical analyses were performed using JMP, Version 7 (SAS Institute Inc., Cary, NC). Maximal type I error rates were set at $\alpha = 0.05$. Normality and homogeneity of variance assumptions were checked using plots of regression residuals or with appropriate *F*-tests. Significant analysis of variance (ANOVA) results for stable isotope signatures, mean total lipids, DHA and W_r were followed by a multiple comparison of means using the conservative Tukey-Kramer post-hoc HSD test (ZAR 1999) to determine if there were significant differences in lake whitefish condition metrics among study regions.

Results

Lake whitefish carbon and baseline corrected nitrogen stable isotope signatures varied among regions in Lake Michigan (δ^{13}C ANOVA, $F_{3, 608} = 277.64$, $P < 0.001$; δ^{15}N ANOVA, $F_{3, 608} = 260.48$, $P < 0.001$). Individuals from Naubinway had the most positive δ^{13}C signature (Tukey-Kramer post-hoc HSD test, $P < 0.05$; Table 1). Individuals from the southeast had the lowest δ^{13}C and δ^{15}N values (Tukey-Kramer post hoc HSD test, $P < 0.05$). Elk Rapids had the highest δ^{15}N signatures (Tukey-Kramer post-hoc HSD test, $P < 0.05$). Proximity to the prey resource base also varied among regions, with lake whitefish in the southeast being more closely associated with their putative prey resources than lake whitefish from the other regions (Fig. 2). Available stable isotope signatures for randomly sampled mature male and female fish indicated the most restricted niche space in the southeast and the widest niche space at Naubinway. There was no significant difference in δ^{15}N variation among regions (Bartlett's test, $\chi^2 = 0.24$, df = 3, $P = 0.867$), indicating no variability in trophic niche width within the lake. Regional δ^{13}C variances were heterogeneous (Bartlett's test, $\chi^2 = 50.45$, df = 3, $P < 0.001$).

Stomach content analyses indicated that prior to spawning, lake whitefish in Lake Michigan fed differently depending on location (Table 2). Large proportions of the diet in the northwest consisted of dreissenid mussels and Isopoda, Naubinway lake whitefish fed mainly on Ephemeroptera and Gastropoda, while individuals from Elk Rapids ate high proportions of *Bythotrephes*. Lake whitefish stomachs in the southeast mainly contained dreissenid mussels and *Bythotrephes*.

ISOSOURCE-determined proportional contributions to diet suggest that *Diporeia* are the main dietary resource for individuals from Elk Rapids (Table 3). Both Naubinway and the northwest region fish heavily relied on *Mysis relicta* and Chironomidae and evidenced a high ISOSOURCE-predicted dietary overlap. Diets in the southeast consisted almost exclusively on Isopoda.

Dietary overlap between regions based on autumn stomach contents varied, with high overlap (0.776) between the southeast and northwest and minimum overlap between Elk Rapids and the northwest region of the lake (Table 4). Comparison of literature-reported autumn diets (Madenjian et al. 2006) with diets reported in this study indicated moderately high overlap for the northwest and southeast, but poor overlap with Elk Rapids and Naubinway. In contrast to the short-term feeding comparison based on stomach content data,

Table 1. Number of lake whitefish, their δ^{13}C signatures, POM corrected δ^{15}N signatures and isotope niche space by region. Superscript letters (e.g., A, B, C) describe Tukey-Kramer post-hoc HSD groups of similarity defined using a significant difference standard of $P < 0.05$.

		d^{13}C (‰)		d^{15}N (‰)		d^{13}C and d^{15}N
Region	***n***	**Mean**	**Std Dev.**	**Mean**	**Std Dev.**	**Polygon Area (‰^{2})**
Northwest	229	-24.82^{C}	1.10	7.31^{B}	0.55	15.23
Southeast	148	-25.26^{D}	1.04	6.16^{C}	0.56	10.53
Elk Rapids	117	-22.82^{B}	1.06	8.34^{A}	0.52	12.21
Naubinway	119	-20.89^{A}	2.35	7.44^{B}	0.56	17.64

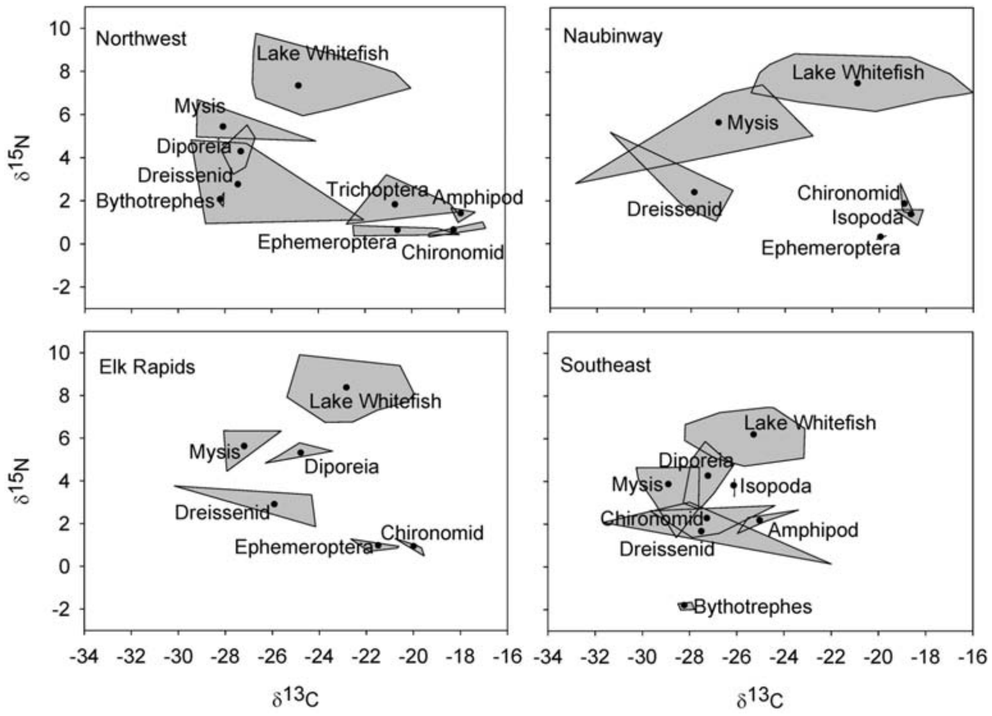

Fig. 2: Isotope niche space polygons for lake whitefish and associated prey resource base for the Lake Michigan study regions. All polygons are baseline adjusted. Dots plot the mean of all signatures for each taxon-specific polygon.

ISOSOURCE analysis suggested a different feeding regime (Table 4) marked by high overlap (0.902) between Naubinway and the northwest regions and low overlap between all other combinations of regions.

Conversion of ISOSOURCE diets to caloric content (J/g) indicated that lake whitefish from Naubinway have the highest apparent caloric intake (3,700 J/g), followed by fish from Elk Rapids (3,650 J/g), fish from the northwest (3,420 J/g) and fish from the southeast (2,820 J/g). A similar pattern was observed when stomach content data were converted to caloric content, with values for Naubinway (2,460 J/g), followed by the northwest (2,130 J/g) and Elk Rapids (2,060 J/g) all exceeding those of the southeast region (1,860 J/g). Comparatively, the caloric content of the diet calculated for lake whitefish in the southeast region during 1998–2001 (Madenjian et al. 2006) was approximately 3,020 J/g, a net decline in the southeast region of 1,160 J/g from 1998–2001 to 2004–2005.

Concentrations of DHA in lake whitefish dorsal muscle tissues varied significantly among regions (ANOVA, $F_{3,614} = 8.41$, $P < 0.001$), ranging from a high of 11.5 µg/mg dry weight of tissue for lake whitefish from Elk Rapids to a low of 10.2 µg/mg dry weight of tissue for individuals from Naubinway (Fig. 3). Percent total dorsal lipid and W_r varied significantly among regions (dorsal lipid % ANOVA, $F_{3,614} = 14.62$, $P < 0.001$; W_r ANOVA, $F_{3,613} = 33.49$, $P < 0.001$). Percent total dorsal muscle lipid was significantly higher (Tukey-Kramer post-hoc

Table 2. Stomach content percent contribution, by dry weight, of sampled lake whitefish in each region from the fall of 2004 and 2005. For comparison purposes, values reported by MADENJIAN et al. (2006) for Fall 1998–2001 captured at Muskegon, in the southeast region, are given. Trace refers to items that make up less than 0.1% by weight of the diet.

Diet item and number of stomachs examined	**North-west**	**South-east**	**Elk Rapids**	**Naubinway**	**Muskegon 1998–2001 (MADENJIAN et al. 2006)**
Diet Item					
Amphipoda	0.3	Trace	–	–	32 (*Diporeia*)
Mysis	–	–	–	–	23
Bythotrephes	9.3	34.9	97.6	16.5	3
Chironomidae	trace	–	–	0.8	9
Dreissenidae	42.9	60.7	0.8	11.7	32
Isopoda	36.7	4.2	0.2	trace	–
Ephemeroptera	–	-	–	37.0	–
Gastropoda	10.8	0.2	–	29.9	–
Unionidae	trace	Trace	–	3.9	–
Alewives (age-0)	–	–	–	–	1
Johnny Darter	–	–	1.4	–	–
Stomachs examined					
Non-empty stomachs	19	52	66	89	46
Empty stomachs	212	106	54	31	38

Table 3. ISOSOURCE mean percentage ± standard deviation of feasible diet scenarios. The 1st and 99th percentile values are given in parenthesis below mean entries.

	Northwest	**Southeast**	**Elk Rapids**	**Naubinway**
Diporeia	1.6 ± 1.9 (0–5)	2.2 ± 2.2 (0–9)	73.3 ± 1.3 (70–76)	–
Mysis	65.5 ± 1.5 (59–68)	0.7 ± 0.9 (0–4)	0.9 ± 1.1 (0–4)	36 ± 0.6 (35–37)
Bythotrephes	0.2 ± 0.5 (0–2)	1.2 ± 1.3 (0–5)	–	–
Chironomidae	31.1 ± 1.1 (28–33)	2.5 ± 2.4 (0–10)	23.8 ± 1.7 (19–26)	58.2 ± 5.5 (45–65)
Dreissenidae	0.4 ± 0.7 (0–2)	2.0 ± 2.0 (0–8)	0.3 ± 0.6 (0–2)	0.1 ± 0.3 (0–1)
Ephemeroptera	1.1 ± 1.3 (0–5)	–	1.7 ± 1.8 (0–7)	0.6 ± 0.8 (0–3)
Isopoda	–	91.3 ± 2.3 (87–97)	–	5.2 ± 5.3 (0–18)

HSD test, $P < 0.05$) in the northwest (12.3%) than in other regions. W_r was significantly higher in the southeast (Tukey-Kramer post-hoc HSD test, $P < 0.05$) and at a minimum for individuals from Naubinway. Although there were some significant linear relationships between $\delta^{13}C$ or $\delta^{15}N$ and measured condition metrics (e.g. W_r, % lipid, and DHA) by region, when regions were grouped, the obtained r^2 values were very poor (Table 5), ranging from 0 to 0.06.

Table 4. Summary of Horn (1966) dietary overlap indices based on the stomachs of pre-spawning lake whitefish by region compared to literature reported values and indices implied by ISOSOURCE percent dietary contributions based on measured stable isotope values. A value of 0 indicates no dietary overlap, whereas 1 infers complete overlap.

	Naubinway	Elk Rapids	Southeast	Madenjian et al. (2006)
Northwest				
Stomachs	0.505	0.266	0.776	0.430
ISOSOURCE	0.902	0.378	0.123	
Naubinway				
Stomachs		0.364	0.478	0.264
ISOSOURCE		0.398	0.247	
Elk Rapids				
Stomachs			0.588	0.124
ISOSOURCE			0.146	
Southeast				
Stomachs				0.507

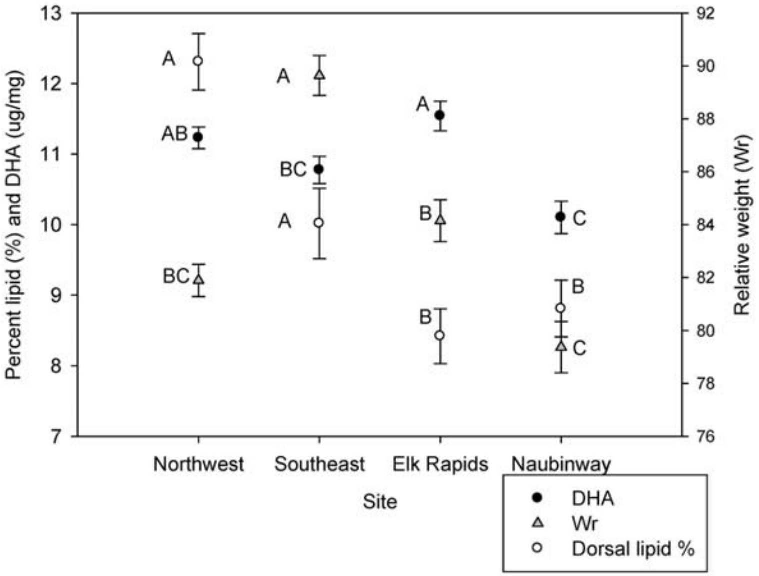

Fig. 3: Mean ± standard error of measured lake whitefish condition metrics by region. DHA defines the measured concentration of docosahexaenoic acid (μg/mg), W_r defines the relative weight metric and dorsal lipid defines the percent of total lipids in dorsal muscle tissue. Letters (e.g., A, B, C) represent homogenous groupings as determined using the Tukey-Kramer post-hoc HSD test.

Table 5. Linear regressions of δ^{13}C and baseline corrected δ^{15}N on measured condition parameters: DHA, W_r and mean total dorsal lipid. DHA defines the essential fatty acid docosahexaenoic acid, W_r defines relative weight and dorsal lipid gives the percent of total lipids in dorsal muscle tissue. F defines the regression F-statistic. Statistical significance ($P < 0.05$) is denoted with * and relationships with no significance are denoted with ^{ns}.

	d^{13}C				**d^{15}N**			
	Intercept	**Slope**	r^2	F	**Intercept**	**Slope**	r^2	F
Pooled data (df = 1, 611)								
DHA	–22.70	–0.10	0.01	7.15*	6.72	0.05	0.01	8.54*
Wr	–19.51	–0.05	0.05	33.79*	8.41	–0.01	0.02	11.46*
Dorsal lipid (%)	–23.13	–0.06	0.03	21.11*	7.42	–0.02	0.01	6.82*
Northwest (df = 1, 227)								
DHA	–24.92	0.01	0.00	0.09^{ns}	6.86	0.04	0.03	7.04*
Wr	–24.42	0.00	0.00	0.39^{ns}	7.28	0.00	0.00	0.01^{ns}
Dorsal lipid (%)	–24.70	–0.01	0.00	1.13^{ns}	7.41	–0.01	0.01	3.28*
Southeast (df = 1, 147)								
DHA	–24.12	–0.11	0.05	7.12*	6.56	–0.04	0.02	2.94^{ns}
Wr	–22.28	–0.03	0.06	9.13*	5.75	0.00	0.00	0.56^{ns}
Dorsal lipid (%)	–24.81	–0.04	0.05	7.59*	6.30	–0.01	0.02	2.34^{ns}
Elk Rapids (df = 1, 115)								
DHA	–23.18	0.03	0.00	0.52^{ns}	11.94	–0.02	0.01	0.76^{ns}
Wr	–23.75	0.01	0.01	0.88^{ns}	11.31	0.00	0.01	0.72^{ns}
Dorsal lipid (%)	–22.70	–0.01	0.00	0.42^{ns}	11.78	–0.01	0.00	0.30^{ns}
Naubinway (df = 1, 118)								
DHA	–19.90	–0.10	0.01	1.26^{ns}	10.02	0.01	0.00	0.38^{ns}
Wr	–18.56	–0.03	0.02	2.12^{ns}	10.38	–0.00	0.00	0.36^{ns}
Dorsal lipid (%)	–20.70	–0.02	0.00	0.18^{ns}	10.18	–0.00	0.00	0.10^{ns}

Discussion

Distinct mean δ^{13}C and baseline corrected δ^{15}N signatures, the variable proximity of lake whitefish signatures to the identified prey resource base, and differences in niche space by region in Lake Michigan suggest that lake whitefish have different feeding habits among regions. However, trophic niche width did not vary by region. With the exception of Elk Rapids, regional dietary overlap was moderately high in the autumn, suggesting short-term seasonal convergence in regional lake whitefish diets. Dietary overlap based on long-term stable isotope signatures, as inferred by ISOSOURCE, was low when comparing northern regions to the southern one. Thus, over the longer term, distinct evidence of regional dietary differences exists. Differences in prey choices, however, did not correlate with measures of fish condition, as indicated by weak relationships between stable isotope signatures and the various condition measures. There was no consistent evidence for the hypothesis that lake whitefish exhibited poor condition in areas of low *Diporeia* abundance.

Lake whitefish in the northwest region, comprised of Bailey's Harbor and Big Bay de Noc, were predicted to have a high caloric intake using diet analysis and the isotope mixing model approach. The main sources of food, as determined by ISOSOURCE, were *Mysis* and Chironomids, both of which have high energy densities, but different concentrations of DHA (Dalsgaard et al. 2003, Sushchik et al. 2006). Fish in the northwest also had significantly higher lipid and DHA concentration, suggesting high individual condition and use of high quality food sources. However, relative weight metrics for the northwest did not reflect lipid and DHA trends. All northern regions, including Naubinway, Elk Rapids and the northwest region, had significantly lower relative weights, a trend also evident in the DeBruyne et al. (2008) study, where it was reported that lake whitefish in the northern region of Lake Michigan consistently had the lowest length-at-age. Relative weight metrics do not differentiate between whether high water or lipid content contributes to total fish weight, a fact that can be problematic given the inverse relationship between the two (Love 1980). Differences in the trends among relative weight, % lipid and DHA found in the studied Lake Michigan populations suggest that relative weight estimated using the Regression-length percentile method for this species does not accurately describe fish condition in all cases.

Lake whitefish from the northwest have *Mysis* and *Diporeia* available to them as prey, the latter being present in high densities in the Bailey's Harbor area (Nalepa et al. 2009). *Diporeia* densities have historically been higher on the western side of Lake Michigan as a result of the prevalence of coldwater upwelling events and higher productivity (Mortimer 1975). Tagging studies have shown that lake whitefish from Big Bay de Noc migrate from poorer prey resource areas towards more resource rich areas like Bailey's Harbor (Ebener et al. 2010). Spatial feeding patterns and relative lengths of time spent in high and low density *Diporeia* areas, however, are essentially unknown. Thus, increased foraging range may serve to break direct linkages between prey density and fish condition.

Although the southeast region had the highest relative weight metric, diet energy density, percent lipid content, and DHA concentration measures were all low compared to the northwest region. The generally lower condition of lake whitefish in the southeast compared to the northwest may be related to the reported declines in the abundance of *Diporeia* at the southeast location. Mean *Diporeia* densities in 2005 were 454 m^{-2} at a depth of 86–98 m in the southeast region, a drop of approximately 4,000 m^{-2} since 1994–95 and 3,000 m^{-2} since 2000 (Nalepa et al. 2000, Nalepa et al. 2009). Decreasing densities of *Diporeia* since 2000 have had an apparent impact on lake whitefish condition, probably as a result of increased foraging costs and the consumption of lower quality food as noted in this study. The lake whitefish populations in the southeast region had the smallest niche space in Lake Michigan, and a very distinct diet consisting mainly of isopods as determined by ISOSOURCE. Autumn feeding data for this population included mainly Dreissenid mussels and *Bythotrephes*, prey with low energy densities (1,703 and 2,027 J/g respectively). Caloric intake in the southeast region has declined by approximately 116,000 J/g since Madenjian et al. (2006), as *Diporeia* densities have declined (Nalepa et al. 2009). Lake whitefish abundances in southern Lake Michigan have been simultaneously increasing (Kratzer et al. 2007, DeBruyne et al. 2008), possibly creating greater intraspecific competition for a less abundant, energy rich prey source. Therefore, lake whitefish may be required to forage over greater distances for lower quality prey. For example, Ihssen et al. (1981) found that lake whitefish populations eating zooplankton and small molluscs, prey sources with low energy content, exhibited slower growth than those feeding on larger bodied *Diporeia* and *Mysis*. After declines in *Diporeia* abundances off Muskegon (1998 to 2000), a site within the southeast region, the contribution of *Diporeia* to lake whitefish diets by weight fell from 61% to 18% (Pothoven et al. 2001). Pothoven et al. (2001) attributed observed declines in lake whitefish condition to reduced use of *Diporeia* and increased use of lower caloric zebra mussels and sphaeriids.

Elk Rapids lake whitefish had a mid-range isotopic niche space, the highest $\delta^{15}N$ signature and, as predicted by isotopic analysis, a large portion of the diet consisted of *Diporeia*. However, in the autumn, this population of lake whitefish fed heavily on *Bythotrephes*, a small and relatively energy poor zooplankton. The Elk Rapids population had the highest concentration of DHA, but mid-level condition in terms of % lipids, relative weight and energy density. The accessibility of *Diporeia* to the Elk Rapids population (Nalepa et al. 2009) and the predicted high reliance of this population on *Diporeia* may explain their significantly higher measured DHA concentration.

The relatively large niche space of Naubinway lake whitefish in comparison to other regions and the variety of prey items eaten in the autumn suggest that this population was feeding on a variety of prey items from multiple trophic levels. It was apparent from the ISOSOURCE analysis that there were two main prey sources, Chironomids and *Mysis*, the same main diet scenarios as the northwest region, with a small contribution from isopods. In contrast to the northwest, Naubinway lake whitefish appear to depend more on Chironomids than *Mysis*. These findings are evidence that the population has adjusted to using other food sources as an alternative to energy rich *Diporeia*. The high energy density calculated for the Naubinway populations was, therefore, related to the high proportions of Chironomids, Ephemeroptera and *Mysis* in the diet, which have high energy densities of 3,730, 3,791 and 3,783 J/g respectively (Cummins & Wuycheck 1971, Driver et al. 1974, Eggleton & Schramm 2004, Madenjian et al. 2006).

Lake whitefish in the northern regions of Lake Michigan do not appear to be regulated by stock density (DeBruyne et al. 2008), which suggests that food web changes are influencing observed stock levels. Optimal foraging theory, which assumes that caloric intake is maximized per unit time, predicts that lake whitefish will feed on prey possessing the greatest amount of energy acquired with the least amount of foraging and handling time (Stephens & Krebs 1986). Although Chironomids and Ephemeroptera have high energy densities, they are small bodied and lack the high concentration of DHA, which is a good indicator of condition and highly conserved through aquatic food webs (Dalsgaard et al. 2003). Ephemeroptera have high eicosapentaenoic acid (EPA, 20:5n-3) levels, however, the biosynthetic capability of lake whitefish to elongate and desaturate EPA to DHA is not known. Reliance on these prey items may explain the observed low DHA concentrations and low percent lipid and relative weights in Naubinway, with high energy intake per prey item consumed being offset by high search costs because of target prey size.

The proportional contribution of each prey source to the diet of lake whitefish was not the same for the stomach content data and the SIA mixing model analysis. Differences may be attributed to the time scale represented by each analysis. Stomach content analysis is a snapshot of recent feeding, whereas isotope signatures represent the product of diet assimilation over months. Differences may, therefore, indicate seasonal variability in feeding patterns, which will not be evident in other measures developed from feeding over long periods of time such as lipids, DHA and/or relative weight. Combining both short- and long-term measures of feeding patterns may, therefore, provide the best insights into condition metric dynamics. Specifically, a snapshot at spawning would not be a good representation of diets based on isotopic signatures because the fish are near shore in shallower waters preparing to spawn. This suggests seasonal variation in food sources due to migration to the spawning grounds.

Although mixing models facilitate inferences about the importance of prey resources to a predator, predictions depend critically on knowledge of the actual prey resources used. A prey resource not considered in the feasible set of consumption items cannot contribute to the calculations used to construct possible diet scenarios on the basis of actual stable isotope signatures. Conversely, a prey resource mistakenly included in the feasible set will contribute to the model calculations. Both scenarios will result in poor predictions and mixing-model results should be ground-truthed against detailed gut content analysis. Thus, while data here suggest significant differences in short- and long-term prey resource use, and differences among regions, results may be an artifact of the prey resources used in the study.

There is some evidence that lake whitefish in some regions of Lake Michigan, such as Naubinway and the southeast, are coping with declining *Diporeia* abundances by feeding on alternate energy rich food sources lacking in high concentrations of DHA, such as Chironomidae and Ephemeroptera. Such lake whitefish tend to have a lower condition as measured by percent lipid and DHA. Furthermore, where relationships between condition and $\delta^{13}C$ were significant, $\delta^{13}C$ tended to relate negatively to the available condition measures, whereas relationships with baseline-corrected $\delta^{15}N$ were inconsistent. If more positive $\delta^{13}C$ estimates relate to increased reliance on nearshore resources (see Fig. 2), then the pattern of results suggests that condition is lower for fish with isotope signatures, reflective of a greater reliance on nearshore prey resources. This interpretation is consistent with other work that indicates declines in condition and associated changes in feeding behavior associated with declines in *Diporeia* (Rennie et al. 2009a). Nevertheless, while there is evidence that lake whitefish feed differently throughout Lake Michigan, our data indicate there is no consistent link between prey choices and the measures of condition used to infer individual or population status.

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