Lake whitefish (Coregonus clupeaformis) energy and nutrient partitioning in lakes Michigan, Erie and Superior

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ABSTRACT

A concurrent decrease in lake whitefish (Coregonus clupeaformis) condition and Diporeia spp. abundance in Lake Michigan has spurred investigations into possible links between the two phenomena. We examined female lake whitefish δ13C and δ15N stable isotopes, growth, reproductive investment, dorsal muscle total lipid and docosahexaenoic acid (DHA) contents from lakes Erie, Michigan and Superior to determine whether differences in food source were correlated with measures of stock success. Stocks with higher somatic growth rates and mean reproductive potential had higher energy stores in terms of percent total lipid. Stocks with low muscle lipid concentration also had smaller egg sizes as egg number increased. Diet varied among stocks as evidenced by δ13C and δ15N stable isotope analyses; however, muscle total lipid and DHA were not correlated to apparent Diporeia spp. prey use. When compared to stocks from lakes Erie and Superior, Lake Michigan stocks had lower growth, reproduction, and lipid stores. While stocks in Lake Michigan with access to declining Diporeia spp. populations may still feed on the amphipod, it appears that they are unable to consume the quantities necessary to maintain historical growth and reproduction. Stable isotope analyses of lakes Erie and Superior stocks, with higher growth rates and lipid values, indicated different feeding strategies with no indication of reliance on Diporeia spp. While differences in prey resources may have an effect on lake whitefish stocks, differences in Diporeia spp. abundance alone cannot explain differences in lake whitefish condition observed among the Great Lakes included in this study.

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Introduction

Lake whitefish (Coregonus clupeaformis) are a key component of the Great Lakes’ commercial and recreational fishery. Commercial lake whitefish harvest has increased annually since 1985 and, by 1995, lake whitefish catches out of lakes Huron and Michigan reached 9 million kg (Ebener, 1997; Madenjian et al., 2002). Diporeia spp. was an important energy-rich prey resource for lake whitefish in the Great Lakes (Hardy, 1994). Both native species play an important role in the benthic food web, connecting pelagic primary productivity to harvestable fish destined for human consumption (Nalepa et al., 2005).

In the early 2000s however, growth and condition of lake whitefish from Lake Michigan declined, creating a concern for the fishery (Madenjian et al., 2002; Pothoven et al., 2001; Pothoven et al., 2006; Pothoven and Nalepa, 2006; Schneeberger et al., 2005). A concurrent decrease in the abundance of Diporeia spp. in Lake Michigan spurred investigations into possible links between the two events (e.g., Fagan et al., 2012; Kratzer et al., 2007; Madenjian et al., 2002; Pothoven et al., 2001). However, as the Great Lakes are a dynamic ecosystem, other factors, such as increases in lake whitefish density (DeBruyne et al., 2008) and/or declines in food availability and/or quality may also be invoked to explain the declines in lake whitefish growth and condition. Kratzer et al. (2007) reported that lake whitefish density increases, in combination with declining abundances of Diporeia spp., affected lake whitefish condition in Lake Michigan (also noted in Schneeberger et al., 2005) through changes in ration because increased fish density tends to

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promote heightened intra-specific competition for prey resources. Similarly, Fagan et al. (2012) reported that, with declines in Diporeia spp. abundance, the use of less energetic, alternative, prey in Lake Michigan by lake whitefish may have contributed to reduced lake whitefish condition. Furthermore, by dreissenid mussels and declines in Diporeia spp. abundance in Lake Huron, lake whitefish diets shifted from Diporeia spp. to dreissenids which led to higher consumption rates, higher activity levels, lower conversion efficiency (Rennie et al., 2012), and slower growth (Gobin et al., 2015). However, in productive lakes such as Lake Erie, changes in lake whitefish abundance (Lumb et al., 2007), or the extirpation of Diporeia spp. (Cook et al., 2005), had no measurable impact on lake whitefish condition because ration was not limited. Similarly, invasion of productive Lake Champlain by dreissenid mussels did not have a measurable effect on lake whitefish condition (Herbst et al., 2013).

The contrasting findings from lakes Huron and Michigan versus lakes Erie and Champlain suggest that effects of ecosystem changes on lake whitefish are lake-specific (Lumb et al., 2007) and likely driven by underlying differences in relative primary productivity rates (trophic status) (Barbiero and Tuchman, 2001). Furthermore, in less productive systems, changes at the base of the food web may more readily cascade through successive trophic levels to affect overall prey availability and the carrying capacity for consumers at upper trophic levels (Downing et al., 1990). This seems to be the case in Lake Huron (Gobin et al., 2015) and could, in turn, lead to the observed differences in energy consumption (Fagan et al., 2012; Rennie et al., 2012).

Differences in ration among lakes are likely important to lake whitefish growth and condition, and may affect population dynamics. As a rule, consumed energy and nutrients are partitioned into growth, reproduction, and/or maintenance, which include foraging costs, metabolism, eggestion and excretion (Elliott, 1994). Surplus available energy and nutrients, after maintenance needs are met, is channeled into growth (somatic growth) and/or reproduction (gonadal development; Roff, 1992) and will vary in response to food availability. For example, basic energy balance considerations predict that a loss in consumed energy leads directly to a reduction in surplus energy, under the assumption that maintenance costs remain constant (e.g., Elliott, 1994). Thus, food availability, foraging costs and intra-specific competition are linked through food use in ways that suggest a complex mosaic of possible trade-offs to maintain either condition or reproductive investment in the face of declining energy intake. For example, Rennie et al. (2012) found that when faced with reduced Diporeia spp. abundances, lake whitefish experience reduced conversion efficiencies, increased activity levels and slower growth rates, and Muir et al. (2014) presented evidence that lake whitefish in the Great Lakes use a reproductive quality control strategy, trading off somatic condition to maintain reproductive investment when faced with energetic constraints.

Here we use published and new data to examine the relationships among lake whitefish δ13C and δ15N stable isotopes, growth, reproductive investment, and physiological condition to determine whether differences in food source, as evidenced by stable isotope analysis, were correlated with measures of stock success. The following hypotheses were tested using data from female lake whitefish sampled from eight different stocks in lakes Erie, Michigan and Superior: [1] observed differences in growth (i.e., length-at-age) and reproduction (i.e., gonadosomatic index and fecundity) of lake whitefish among stocks were related to energy availability and quality (i.e., percent lipid and docosahexaenoic acid [DHA]); [2] lake whitefish with low energy reserves and quality (i.e., percent lipid and DHA) would exhibit trade-offs between egg size and fecundity to maintain reproductive output (e.g., Muir et al., 2014); and, [3] energy reserves and quality (i.e., percent lipid and DHA) in lake whitefish were positively correlated with use of Diporeia spp. as a food source (e.g., Hoyle et al., 1999; Mohr and Ebener, 2005; Pothoven et al., 2001).

Materials and methods

Sampling

Adult female lake whitefish were sampled from six sites around Lake Michigan (Saugatuck, Ludington, Elk Rapids, Naubinway, Big Bay de Noc, and Bailey’s Harbor) and, for comparative purposes, at one site in each of lakes Erie (Point Pelee) and Superior (Whitefish Point) where Diporeia spp. abundances have declined, respectively, either significantly (Cook et al., 2005) or in only a limited manner (Scharold et al., 2004) (Fig. 1). Fish were collected between October and December in both 2004 and 2005 using commercial trap and gill nets. At each site, up to 30 pre-ovulatory females were collected, and each fish was measured for total weight, gonad weight, and total length. Egg diameter was measured for 30 eggs selected from each of the anterior, middle, and posterior sections of the ovary and these data were used to compute an average egg diameter for each fish. Up to 200 eggs were weighed from each section of the ovary to determine average wet weight per egg and the average of all three sections, mean wet weight per egg, was used to calculate fecundity based on total gonad weight. Egg size and fecundity data were previously published by Muir et al., 2014, but have been used in this study to address the relationship between energy reserves and reproductive trade-offs not previously addressed. All fish were aged using scales (as in Muir et al., 2008). Scales were used because, at the time of collection and analysis, scales were the most widely used structure for estimating lake whitefish age and the use of scales facilitated comparisons to the historical literature. Skinless dorsal muscle plugs were also collected from each fish and stored frozen (−85 °C) for stable isotope (SIA) and lipid analyses.

Diporeia spp. were collected with an Ekman dredge or a benthic sled (when densities were low) between mid-June and early-July of 2005 at Bailey’s Harbor (50–70 m depth), Elk Rapids (87–92 m), Ludington (91–98 m), Saugatuck (86 m) and Whitefish Point (86–89 m). Particulate organic matter (POM) was collected in late-June 2007 to supplement the 2005 sampling. Two samples per site (as in Fig. 1) of littoral zone water were filtered through 2.2 μm pore-size quartz fibre filters (Whatman grade QMA) to obtain representative POM samples for use in stable isotope baseline estimation (e.g., Post, 2002). Prior to vacuum filtration, all large particles were removed from water samples using a 20 μm sieve. Filters were immediately frozen for SIA.

Stable isotope analysis

In the laboratory, lake whitefish skinless dorsal muscle tissue, whole Diporeia spp. bodies and POM filters were dried at 50 °C for 48 h. Fish muscle tissue and Diporeia spp. were pulverized to a homogenate with a Retsch MM 301 ball mill grinder (F. Kurt Retsch GmbH Co., Haan, Germany) and was determined by repeat analysis (±0.3‰) of laboratory working standards cross-calibrated to International Atomic Energy Agency standards CH6 for δ13C and N1 and N2 for δ15N. Duplicate analysis of 1 in 10 samples was used to further assess measurement...
precision. Stable isotope data for Lake Michigan fish were previously published in Fagan et al. (2012).

To compare among lakes and account for possible anthropogenically-induced variation in stable isotope signatures at the base of the food web (e.g., Post, 2002), nitrogen isotopic signatures were baseline corrected. With appropriate estimates of basal $\delta^{15}$N, it is possible to determine if observed variation in organism isotope measures occurs because of differences in food web structure or because of variation at the base of the food web (Post, 2002; Vander Zanden and Rasmussen, 1999). For this study, baseline correction was accomplished by subtracting the average POM $\delta^{15}$N signature for each lake from all relevant $\delta^{15}$N signatures. The resulting corrected $\delta^{15}$N measures, therefore, scale fish and Diporeia spp. in terms of trophic distance from the base of the food web and facilitate among lake comparisons (Post, 2002).

**Lipid and DHA analysis**

Total lipid and docosahexaenoic acid (DHA; 22:6n-3) contents in individual adult lake whitefish samples were analyzed at the National Water Research Institute laboratories of Environment and Climate Change Canada, Burlington, Ontario. DHA is an essential omega-3 fatty acid that occurs in high concentrations in membrane phospholipids and is known to have positive effects on teleost egg, neural and eye development (Bell and Dick, 1993; Dalsgaard et al., 2003). Because of the important role that DHA plays in the nutritional health of fish (Arts and Kohler, 2009; Kelly and Kohler, 1999; Snyder and Hennessey, 2003), we used DHA as a proxy for food quality.

Skinless dorsal muscle samples were freeze-dried in preparation for total lipid and DHA analyses. Analysis involved three steps: gravimetric extraction, derivatization, and quantification on an HP6890 gas chromatograph following the methods described in McMeans et al. (2012). Samples were extracted three times by grinding freeze-dried materials in a 2:1 chloroform:methanol solution (Folch et al., 1957). Centrifugation at 4000 rpm was used to remove the majority of non-lipid material, then the supernatant was transferred to acid-washed, 15-ml centrifuge tubes and rinsed with chloroform:methanol. The centrifuging 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 2 ml volume, a 200 µl of sample extract was weighed on a Sartorius ME-5 microbalance (Sartorius AG, Gottingen, Germany) to provide a gravimetric measure of total lipid content. Fatty acids were methylated using sulfuric acid:methanol (1% v/v) overnight at 50 °C.
(Christie, 1989). DHA was identified and quantified with reference to Supelco’s 37 component FAME mix (#47885-U). An internal standard (5 α-cholestan; Sigma-Aldrich; #C8003) was added to the tissue before extraction to estimate percent recovery during the extraction procedure. The mass fractions of DHA are reported as µg FAME/mg dry mass of tissue. Percent lipid and DHA data were previously published in Fagan et al. (2012) and Muir et al. (2014).

Data analysis

Fish used in growth rate estimates ranged in age from 4 to 10, with >95% of all fish occurring in the 4–9 age-range. Age data were used to determine stock growth rates using the slope of length at age linear regressions given the lack of juvenile and lower age-class fish included in the sampling. Resources partitioned to reproduction were estimated using fecundity (F) and the gonadosomatic index (GSI). F was calculated from available prey (Bearhop et al., 2004; Layman et al., 2007). Bartlett’s test for variance homogeneity (Bartlett, 1937a; Bartlett, 1937b) was applied to determine whether there were significant differences in lake whitefish δ13C and baseline corrected δ15N signatures were used, respectively, as a measure of niche breadth diversity at the base of the food web and trophic diversity (Layman et al., 2007). Greater variation reflects greater inter-individual differences in the use of available prey (Bearhop et al., 2004; Layman et al., 2007). Bartlett’s test for variance homogeneity (Bartlett, 1937a; Bartlett, 1937b) was applied to determine whether there were significant differences in lake whitefish δ13C and baseline corrected δ15N variances among stocks and between groups with and without reproductive trade-offs for total lipid and DHA. Welch t-test or Welch-ANOVA was applied when groups had unequal variances (Zar, 2010).

Results

Growth

Estimated growth models for length-at-age did not share a common slope among stocks (F7, 208 = 5.71, P < 0.001; Fig. 2). Point Pelee (Lake Erie) and Whitefish Point (Lake Superior) lake whitefish had similar length-at-age slopes (F1, 50 = 3.47, P = 0.07), and similar intercepts (ANOVA, F1, 51 = 3.32, P = 0.07; Table 1). All Lake Michigan stocks had similar length-at-age slopes (F5, 223 = 0.59, P = 0.71), but differed significantly in intercepts (ANOVA, F5, 227 = 28.55, P < 0.001).

Reproductive investment

GSI varied among stocks of lake whitefish (Fig. 3a; ANOVA, F7, 305 = 16.86, P < 0.001). The GSI calculated for the Point Pelee stock was significantly higher than the GSI for other stocks (Tukey’s post-hoc HSD test, P < 0.05).

A significant positive relationship between log fecundity and log body weight was observed for all lake whitefish spawning stocks (Table 1). Although a common slope model could not be estimated among all stocks (F2, 297 = 2.23, P = 0.032), stocks separated into two groups. Fish caught in Big Bay de Noc, Ludington, Saugatuck, Point Pelee and Whitefish Point composed the first group and possessed a common mean slope (F4, 167 = 0.90, P = 0.47) that was less steep than the common mean slope (F2, 130 = 0.52, P = 0.60) estimated for the second group of lake whitefish from Bailey’s Harbor, Naubinway and Elk Rapids. Both groups displayed heterogeneity with respect to intercept estimates (group 1: ANOVA, F4, 171 = 37.00, P < 0.001; group 2: F2, 132 = 3.49, P = 0.033). Significant negative linear relationships occurred between standardized fecundity and log egg diameter measurements for fish collected from Bailey’s Harbor, Naubinway, Elk Rapids and Saugatuck locations (Fig. 4). All significant models shared a common slope (F2, 166 = 0.83, P = 0.48; Table 1), but differed significantly in regression intercepts (ANOVA, F2, 169 = 9.81, P < 0.001).

Lipid and DHA

Log mean percent total lipid (ANOVA, F7, 306 = 43.17, P < 0.001) and DHA (ANOVA, F7, 306 = 24.08, P < 0.001) differed significantly among stocks (Fig. 3b and c). Point Pelee fish had higher mean total lipid values
Fig. 2. Length (mm) versus mean scale age for each lake whitefish stock with estimated linear regressions included.

Table 1
Estimated length (mm)-at-age, log fecundity-body weight (g) and standardized log fecundity-log egg diameter (mm) model regression estimates for female lake whitefish from each study location. Confidence limits, upper and lower 95%, are given in parentheses. Common slope estimate are denoted with a common superscript (e.g. A, B). Significant linear relationships by site are denoted by *.

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<td>11.65 (3.99, 19.31) B</td>
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<tr>
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<td>7.51 (-2.66, 17.67)</td>
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<td>56</td>
<td>421.55</td>
<td>9.78 (3.17, 16.39) B</td>
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<tr>
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<td>33</td>
<td>398.11</td>
<td>21.26 (12.44, 30.07) A</td>
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compared to all other stocks (Tukey-Kramer post-hoc HSD test, $P < 0.05$). The remaining stocks sorted into overlapping groups within which mean total lipid values did not differ (Tukey’s post-hoc HSD test, $P < 0.05$). The first group (with the highest lipid levels) included Big Bay de Noc, Ludington and Whitefish Point, the second group included Bailey’s Harbor, Ludington, Naubinway, Saugatuck and Whitefish Point, and the last group (with the lowest total lipid values) included Bailey’s Harbor, Elk Rapids, Ludington, Naubinway and Whitefish Point.

Mean dorsal muscle DHA contents of lake whitefish sorted into three groupings based on stock capture location (Tukey’s post-hoc HSD test, $P < 0.05$; Fig. 3c). Bailey’s Harbor, Big Bay de Noc, Elk Rapids, Ludington, Naubinway and Whitefish Point shared the highest mass fractions of DHA. Fish caught near Point Pelee had significantly lower DHA compared to fish caught from the other locations (Tukey’s post-hoc HSD, $P < 0.05$).

### Stable isotope analysis

Carbon stable isotope $\delta^{13}$C variances differed significantly among locations ($\chi = 11.45, P < 0.001$), but baseline adjusted $\delta^{15}$N variances did not differ ($\chi = 1.20, P = 0.30$). Fish collected from Whitefish Point and Naubinway had $\delta^{13}$C coefficient of variations approximately two-fold greater than that observed in the remaining locations (Table 2). Fish from Whitefish Point had the largest coefficient of variation, whereas fish from Point Pelee showed the lowest variability in $\delta^{15}$N.

Significant differences were found among stock mean $\delta^{13}$C (Welch ANOVA, $F_{7, 115.53} = 62.50, P < 0.001$) and baseline corrected $\delta^{15}$N (ANOVA, $F_{7, 301} = 158.42, P < 0.001$) stable isotope values (Table 2). Along the $\delta^{15}$N axis, stocks grouped into five overlapping clusters within which mean baseline corrected $\delta^{15}$N values did not differ (Table 2, Fig. 5). Naubinway and Whitefish Point lake whitefish had significantly lower mean baseline-corrected $\delta^{15}$N than all other stocks (Tukey’s post-hoc HSD test, $P < 0.05$). The next lowest cluster included the Bailey’s Harbor, Big Bay de Noc and Whitefish Point lake whitefish below Ludington. Saugatuck and Elk Rapids formed another grouping, approximately 1‰ above the previous group. Point Pelee lake whitefish had the highest mean baseline corrected $\delta^{15}$N signature (Tukey’s post-hoc HSD test, $P < 0.05$) that was a full trophic level above the lowest mean signature seen in Naubinway.

Four overlapping $\delta^{13}$C clusters are apparent (Table 2, Fig. 5). The first cluster included the Big Bay de Noc, Ludington, Point Pelee and Saugatuck stocks, which had the most negative mean $\delta^{13}$C values (Tukey’s post-hoc HSD test, $P < 0.05$) of all stocks. A second cluster included the Bailey’s Harbor, Big Bay de Noc, Point Pelee and Saugatuck lake whitefish (Tukey’s post-hoc HSD test, $P < 0.05$) with average mean $\delta^{13}$C values in the $-25.2$ to $-24.8$‰ range. The Elk Rapids stock differed significantly from all other stocks (Tukey’s post-hoc HSD test, $P < 0.05$), and was approximately 2‰ lower than mean $\delta^{13}$C values recorded for the Naubinway and Whitefish Point stocks (Tukey’s post-hoc HSD test, $P < 0.05$).

Euclidean distances from mean Diporeia spp. signatures ($\Delta_{WD}$) varied by stock. Bailey’s Harbor, Big Bay de Noc and Elk Rapids had $\Delta_{WD}$ in the 3 to 4‰ range, consistent with high feeding use of Diporeia spp. Low and high $\Delta_{WD}$ values were present for Ludington and Whitefish Point lake whitefish (1.4‰ and 9.2‰ respectively) suggesting low reliance on Diporeia spp. as a food source (Table 2, Fig. 5).

### Trade-offs, growth, lipid and DHA

There was no significant correlation between somatic growth rate and log mean total lipid among all stock estimates (ANOVA, $F_{1, 6} = 1.78, P = 0.23$; Fig. 6a). A significant positive relationship was observed between GSI and log mean total lipid among all stock estimates (ANOVA, $F_{7, 311} = 70.67, P < 0.001$; Fig. 6b).

Stocks displaying reproductive trade-offs between egg size and number (Fig. 4) included: Bailey’s Harbor, Elk Rapids, Naubinway and Saugatuck. The group displaying reproductive trade-offs had significantly lower mean total lipid content in muscle tissue (Welch $t$-test, $t_{1, 153.46} = 7.75, P < 0.001$; Fig. 6c) and significantly higher mass fractions of DHA (Welch $t$-test, $t_{1, 268.19} = 2.88, P = 0.004$) compared to stocks in which there was no trade-off between egg size and number.

No relationship was apparent between log mean total lipid and stocks with $\Delta_{WD}$ suggesting feeding on Diporeia spp. (Fig. 6d). Stocks with $\Delta_{WD}$ suggesting high dependence on Diporeia spp. (e.g., Elk Rapids $\Delta_{WD} = 3.6‰$ and Bailey’s Harbor $\Delta_{WD} = 3.3‰$) had similar log mean total lipid as other stocks in Lake Michigan and at Whitefish Point that had $\Delta_{WD}$ values suggesting no consumption of Diporeia spp. (e.g., Ludington $\Delta_{WD} = 1.4‰$ and Whitefish Point $\Delta_{WD} = 9.2‰$). Additionally, stocks with $\Delta_{WD}$ suggesting high consumption of Diporeia spp. had significantly
lower log mean total lipid than the stock at Point Pelee where no *Diporeia* spp. are available for consumption (Figs. 3b and 6d).

A comparison between GSI and somatic growth rate among stocks (Fig. 7) indicated that the Point Pelee stock had both high growth rates and GSI, whereas the Whitefish Point stock invested more in growth than reproduction. Collectively, the Lake Michigan stocks formed a cluster among which there were no significant differences (ANOVA, $F_{1,4} = 1.62$, $P = 0.27$).

Discussion

As hypothesized, stocks with higher somatic growth rates and higher mean reproductive potential had higher energy stores in terms of percent total lipids, but did not show evidence of any association with mass fractions of DHA. Stocks with low muscle lipid concentrations had smaller egg sizes as egg number increased. While the relationship suggests reproductive trade-offs, the evidence was stock-specific. Stable isotope analysis varied among stocks and none of the results obtained here supported the hypothesis that high energy reserves were associated with a greater use of *Diporeia* spp. as estimated with Euclidean distance or, vice versa, that low energy reserves existed in stocks where use of *Diporeia* spp. was low. Lake Michigan stocks with access to declining *Diporeia* spp. populations may still feed on the amphipod, but due to decreasing *Diporeia* spp. abundances are now unable to consume the quantities necessary to maintain historical growth and reproduction. In contrast stocks from lakes Erie and Superior that had higher growth
Trade-offs, growth, lipid and DHA

Our analyses suggest that lake whitefish from Lake Michigan have less surplus energy available after meeting maintenance requirements than stocks in either lakes Erie or Superior which may explain reproductive trade-offs among these stocks. Reduced surplus energy was manifested in lower somatic growth rates in Lake Michigan fish compared to fish from lakes Erie or Superior. Slower lake whitefish growth has also been documented from similarly scale-aged fish in Lake Michigan (DeBruyne et al., 2008) and Lake Huron (Gobin et al., 2015). Length-at-age for all regions of Lake Michigan in the 1980 (DeBruyne et al., 2008) and Lake Huron (Gobin et al., 2015). Length-at-age for all regions of Lake Michigan in the 1980s (DeBruyne et al., 2008) was higher than observed for lakes Erie and Superior from this study, suggesting a dramatic change in growth for Lake Michigan stocks. Particularly energy-limited investment in growth and reproductive was evident for Bailey’s Harbor, Elk Rapids, Naubinway and Saugatuck, with all stocks displaying slow to no growth at sampled ages as well as reproductive trade-offs between egg size and number. Three of the four stocks (i.e., Naubinway, Elk Rapids and Bailey’s Harbor) that displayed trade-offs also had a steeper common fecundity to body weight slope and low intercept, suggesting rapid reproductive responses to changing feeding conditions.

The low growth and reproductive investment for most Lake Michigan stocks suggests lake whitefish are energetically constrained and have adapted reproductive and growth strategies requiring trade-offs to maximize fitness, especially if egg condition needs to be maintained above a threshold quality (Muir et al., 2014). In Lake Michigan, stocks appear to be maximizing fecundity and egg size using all available energy resources at the cost of growth as reported in Muir et al. (2014). Larger egg sizes tend to be selected for when resource availability is reduced (Hutchings, 1991), with ultimate egg size being limited by maternal size (Bell et al., 1977). In some salmonids, e.g., rainbow trout (Oncorhynchus mykiss), egg size is unaffected by adult food availability and ration limitations are manifested in decreased egg number (Scott, 1962). Altering reproductive frequency is another method adopted by some fishes when faced with ration limitations. For example Atlantic herring (Clupea harengus) were found to skip spawning seasons when energetically limited (Kennedy et al., 2010).

The Point Pelee and Whitefish Point stocks invested more energy in growth and reproduction than Lake Michigan stocks. Both stocks had statistically similar high growth rates, high lipid reserves and provided no evidence of reproductive trade-offs. During the 1990s, lake whitefish in Lake Superior had lower maximum lengths than northern Lake Michigan stocks (Taylor et al., 1992), possibly as a consequence of lower primary productivity, colder water temperatures and the shorter growing season in Lake Superior (Barbiero and Tuchman, 2001). While Lake Superior fish appeared to have invested more energy in somatic growth at each age than Lake Michigan, there were no corresponding differences in GSI values. This may be because energy intake during winter is generally low for freshwater fishes (Næsje et al., 2006), with over-winter survival positively related to fish length (Griffiths and Kirkwood, 1995; Pangle et al., 2004; Heermann et al., 2009). Thus, the lack of evidence for reproductive trade-offs in lake whitefish from Whitefish Point suggests that lake whitefish have adopted an energy partitioning strategy favouring growth over reproduction, possibly as an adaption to the disruption of offshore-to-nearshore energy linkages in winter (e.g., Stockwell et al., 2014) and as a means of optimizing over-wintering survival. In contrast, there has not been a significant change in Lake Erie lake whitefish length-at-age since 1972 (Lumb et al., 2007). The high GSI values suggest that Point Pelee fish invest more energy in reproduction for a given body size compared to other stocks, a trend also observed in a comparative study of Lake Erie and Lake Ontario stocks (Lumb et al., 2007). The combination of growth rate and reproductive investment thus suggests that Lake Erie lake whitefish are not energy limited in comparison to stocks from other regions of the Great Lakes; particularly compared to Lake Michigan stocks.

Overall, stocks with high lipid reserves also tended to have high growth and reproductive investment. For example, the Point Pelee and Whitefish Point stocks had high percent total lipid stored in muscle tissue and comparably higher growth and no reproductive trade-offs. Lake whitefish stocks in Lake Michigan (e.g., Naubinway, Elk Rapids) with lower lipid stores demonstrated reproductive trade-offs and lower investment in growth. Lipids are a primary energy reserve mobilized by teleost fishes for meeting the energetic requirements of reproduction and are an important component of egg yolk (Wiegand, 1996). Endogenous growth of larval lake whitefish has been shown to be positively related to parental female lipid content and total egg lipid (Brown & Taylor, 1992). The importance of lipids extends to maturation schedules, as specific quantities of mesenteric lipid reserves are necessary before salmonids mature sexually (Adams and Huntingford, 1997; Reshetnikov et al., 1970; Thorpe, 1986). Pre-ovulatory female lake whitefish would have previously mobilized muscle lipids to egg yolks, meaning that the remaining lipids measured in muscle may be reflective of the resources necessary, or available, for over-winter survival. For example, an energy reduction of 34 to 57% total lipid over the winter period was measured for juvenile Atlantic salmon (Salmo salar) (Næsje et al., 2006).
Therefore, stocks with a higher investment in reproduction, a higher percent lipid stored in muscle tissue and greater length-at-age should be in better overall condition to deal with over-winter survival. Although DHA is considered an important indicator of fish health (Arts and Kohler, 2009), we did not observe any association between DHA and fish growth and reproductive strategies. DHA is highly conserved through aquatic food webs, being incorporated primarily in phospholipids and preferentially mobilized from muscle tissue for use in ovary development during spawning (Dalsgaard et al., 2003). Nevertheless, there was no relationship between the concentration of DHA stored in muscle tissue and energy investment in growth and reproduction. For example, Point Pelee lake whitefish had the lowest mass fractions of DHA and the highest percent lipid in comparison to all other studied stocks. In contrast, the stock from Elk Rapids had significantly higher DHA, but was at the low end of the lipid reserve range. Thus, DHA does not appear to be directly related to fish growth and reproductive strategies as observed with total lipid levels. Instead, DHA levels in fish muscle tissues may depend on the DHA levels in the diet and the prevailing abiotic environmental conditions (e.g., water temperature) in the study lakes.

Polyunsaturated fatty acids play an important role in homeoviscous adaptation of phospholipid membranes (Arts and Kohler, 2009; Kelly and Kohler, 1999; Snyder and Hennessey, 2003). Specifically, unsaturated fatty acids are crucial for maintaining the fluidity necessary for proper functioning of phospholipid membranes (Arts and Kohler, 2009 and references within). Studies have linked the importance of DHA and other unsaturated fatty acids with fish acclimatization to cold temperatures (Kelly and Kohler, 1999; Snyder and Hennessey, 2003). Colder temperatures require greater amounts of unsaturated fatty acids (e.g., DHA) to maintain functioning membranes. Literature-suggested links between temperature and DHA as described above are consistent with results observed here, with stocks from colder, northern locations (e.g., Whitefish Point to Ludington) tending to have greater tissue DHA than stocks from warmer, southern location (e.g., Point Pelee, Lake Erie).

Stable isotope analysis and overall condition

Niche width varied among stocks as indicated by the significantly different stock carbon stable isotope variances. Within location niche variability (i.e., use of variable prey sources at the base of the food web) was greatest for Whitefish Point and Naubinway. Stocks with large niche widths are termed generalist populations and can be composed of all generalist feeders or many specialists (Bearhop et al., 2004). All other studied stocks had a low δ¹³C variance, suggesting a lower degree of niche diversification and stocks with more specialized diets (Bearhop et al., 2004). In contrast, δ¹⁵N variance was not statistically different among stocks meaning that the degree of omnivory was similar for all studied stocks (Bearhop et al., 2004).

The literature suggests that lake whitefish populations in Lake Michigan were physiologically-stressed, as manifested by declining growth and condition, subsequent to Diporeia spp. abundance declines.
In this study, lake whitefish dependence on Diporeia spp. as estimated using Euclidean distance of mean stable carbon and nitrogen isotope signatures were not related to measures of lipid stores in muscle tissue. The lack of association suggests no strong linkages between feeding on Diporeia spp. and fish condition. For example, Bailey’s Harbor and Elk Rapids stocks in Lake Michigan had average Euclidean distances (\(\Delta d\)) that suggested greater reliance on Diporeia spp. as a food source, but both stocks evidenced poorer growth, reproductive trade-offs and lower lipid stores than other stocks. Fagan et al. (2012) presented stable isotope mixing model data supporting the Euclidean distance findings here. These mixing model results indicated that lake whitefish stocks from Elk Rapids were using Diporeia spp. as the main dietary resource, while lake whitefish from the northwest region of Lake Michigan (Bailey’s Harbor and Big Bay de Noc combined) also consumed Diporeia spp. but to a lesser extent (Fagan et al., 2012). It is possible that Lake Michigan stocks with access to declining Diporeia spp. populations are still feeding on the amphipod but, because of decreasing abundances of Diporeia spp., are unable to consume sufficient quantities necessary for historical growth and reproduction. As a result, these lake whitefish stocks may have increased activity rates due to increased foraging activity in an energetically depleted prey community as concluded in Rennie et al. (2012). Lake Erie and Superior stocks with higher growth rates and lipid values were not linked isotopically with Diporeia spp. Thus, lake whitefish stocks may successfully switch from consuming Diporeia spp. as the primary prey choice by adopting a variety of feeding tactics.

Conclusion

Lake whitefish from Lake Michigan have lower growth and reproduction, and invest less in lipid stores than lake whitefish from lakes Erie and Superior, but our study could not associate differences in condition to prey resources among stocks. Instead, where loss of prey resources promotes increased inter-specific competition for food resources, lake whitefish may be competitively inferior and suffer consequent declines in condition. Where loss of prey resources did not result in increased inter-specific competition (e.g., because of higher local productivity as in Lake Erie), or where lake whitefish themselves are competitively superior (e.g. colder environments in Lake Superior), there was no apparent decline in lake whitefish condition as a result of the loss of Diporeia spp. as a prey resource. Given previous evidence of spatially varied diets (e.g., Harvey et al., 2008), the linkages between diet and declining condition in lake whitefish may be more complex than the lack of availability of a single prey resource.

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