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## 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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. Following invasion 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, egestion and excretion (Elliot, 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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 ( $-85\text{ }^{\circ}\text{C}$ ) 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  $\mu\text{m}$  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  $\mu\text{m}$  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  $50\text{ }^{\circ}\text{C}$  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) or by hand with mortar and pestle. Approximately 0.3 mg of homogenate was weighed on a Mettler Ultra micro balance with a readability of 0.1  $\mu\text{g}$  (Mettler-Toledo model XP2U, Mettler-Toledo GmbH, Greifensee, Switzerland) and inserted into combustible tin cups (SerCon  $5 \times 3.5\text{ mm}$ ) for SIA. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values were determined using a Delta Plus continuous flow stable isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) at the Environmental Isotope Laboratory, University of Waterloo, Ontario. The resulting measurements were expressed using standard delta notation ( $\delta$ ) as parts per thousand differences with respect to the international reference standards of carbonate rock from the Peedee Belemnite formation for  $\delta^{13}\text{C}$  (Craig, 1957) and atmospheric nitrogen gas for  $\delta^{15}\text{N}$  (Mariotti, 1983). Machine analytical accuracy, respectively, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was  $\pm 0.2\%$  and  $\pm 0.3\%$  and was determined by repeat analysis ( $n = 25$ ) of laboratory working standards cross-calibrated to International Atomic Energy Agency standards CH6 for  $\delta^{13}\text{C}$  and N1 and N2 for  $\delta^{15}\text{N}$ . Duplicate analysis of 1 in 10 samples was used to further assess measurement

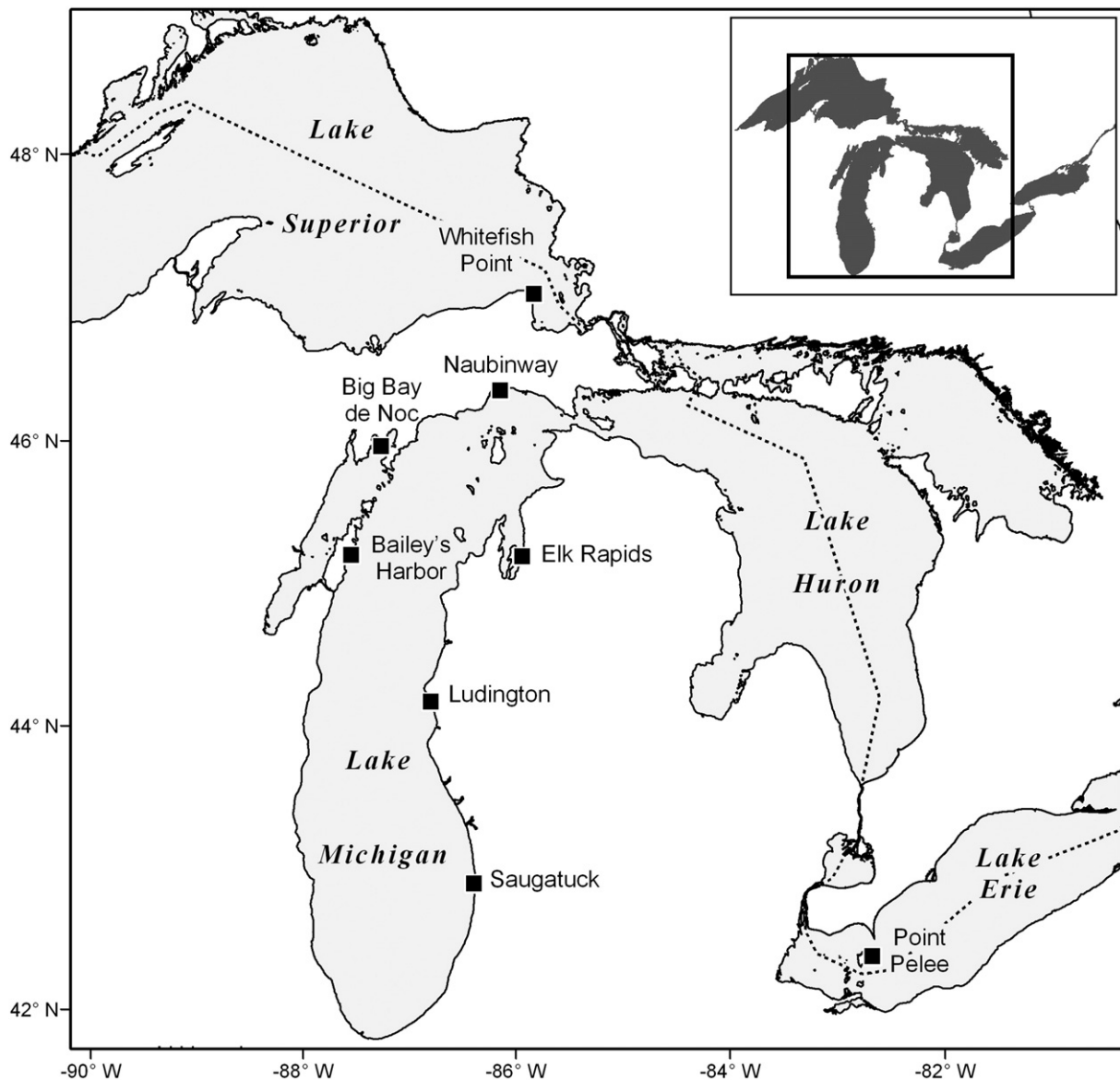


Fig. 1. Sampling locations for the eight stocks of lake whitefish (*Coregonus clupeaformis*) used in this study.

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  $\delta^{15}\text{N}$ , 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  $\delta^{15}\text{N}$  signature for each lake from all relevant  $\delta^{15}\text{N}$  signatures. The resulting corrected  $\delta^{15}\text{N}$  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  $\mu\text{l}$  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  $\alpha$ -cholestane; 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  $\mu\text{g}$  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 using total gonad weight ( $g_w$ ) and estimated mean wet weight per egg ( $e_w$ ):

$$F = g_w/e_w \quad (1)$$

GSI was computed as the ratio of gonad weight to total fish wet weight ( $t_w$ ) adjusted for reproductive tissue (i.e., gonad weight; Roff, 1992) as:

$$\text{GSI} = (g_w/t_w - g_w) \times 100\%. \quad (2)$$

GSI was calculated for all lake whitefish with the exception of identified spent individuals.

Stable isotope values for lake whitefish and *Diporeia* spp. were used to determine the Euclidean distance ( $\Delta_{WD}$ ; Krebs, 1999) between the two taxa in terms of their respective isotopic signatures. Euclidean distances for lake whitefish in Lake Michigan were determined using mean signatures of *Diporeia* spp. sampled from geographically similar regions. *Diporeia* spp. samples were not available for Big Bay de Noc or Naubinway. Therefore, *Diporeia* spp. isotopic signatures from Bailey's Harbor and Elk Rapids were, respectively, used in the calculation of  $\Delta_{WD}$  for Big Bay de Noc and Naubinway as Fig. 1 suggests they are geographically closest. Furthermore,  $\Delta_{WD}$  was not calculated for the Point Pelee stock as *Diporeia* spp. are no longer found in Lake Erie.  $\Delta_{WD}$  was computed as:

$$\Delta_{WD} = \sqrt{(\delta^{13}C_W - \delta^{13}C_D)^2 + (\delta^{15}N_W - \delta^{15}N_D)^2}, \quad (3)$$

where the subscript W denotes the mean  $\delta^{13}C$  and baseline corrected  $\delta^{15}N$  signatures of lake whitefish and the subscript D denotes the mean  $\delta^{13}C$  and baseline corrected  $\delta^{15}N$  signatures of *Diporeia* spp. Taking into consideration the commonly assumed fractionation values of 0.1 for  $\delta^{13}C$  and 3.4 for  $\delta^{15}N$  (Post, 2002), a  $\Delta_{WD}$  of 3.4 would be consistent with high reliance on *Diporeia* spp. as a food source assuming  $\delta^{15}N_W > \delta^{15}N_D$ . Because it is possible to achieve similar  $\Delta_{WD}$  values from different combinations of  $\delta^{13}C$  and  $\delta^{15}N$ , we use corroborating literature studies (Fagan et al., 2012) to avoid potential misinterpretation of the results and interpret the  $\Delta_{WD}$  values as a metric of relative *Diporeia* spp. use.

#### Statistical analysis

Statistical analyses were performed using JMP, Version 7 (SAS Institute Inc., Cary, NC). Maximal Type I error rates were set at  $\alpha = 0.05$  in all analyses. Analysis of covariance (ANCOVA) was used to assess homogeneity of intercepts if the homogeneity of slopes assumption was met (Sokal and Rohlf, 1995; Zar, 2010) in estimated length-at-age, log fecundity-log body weight and standardized fecundity-log egg diameter regression models. If slopes were different and a visual inspection of the

plots suggested that similar slope groups were present, stocks were separated into those groups and tested for homogeneity of slopes and ANCOVA if appropriate. Significant analysis of variance (ANOVA) results were followed by multiple comparisons of means testing using the conservative Tukey's HSD post hoc test (Zar, 2010) to determine whether differences among stocks were significant.

Body weight was a better predictor of fecundity than length for this study. Therefore, individual fecundity estimates were adjusted for fish body weight (Roff, 1992) using the residuals from the log fecundity – log body weight linear regression for each stock. Residuals from the log fecundity – log body weight regression (hereafter referred to as standardized fecundity) were then plotted against individual log egg diameter to determine if trade-offs existed between egg number and size.

The variance in lake whitefish  $\delta^{13}C$  and baseline corrected  $\delta^{15}N$  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  $\delta^{13}C$  and baseline corrected  $\delta^{15}N$  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 ( $F_{7, 290} = 5.71, P < 0.001$ ; Fig. 2). Point Pelee (Lake Erie) and Whitefish Point (Lake Superior) lake whitefish had similar length-at-age slopes ( $F_{1, 50} = 3.47, P = 0.07$ ), and similar intercepts (ANCOVA,  $F_{1, 51} = 3.32, P = 0.07$ ; Table 1). All Lake Michigan stocks had similar length-at-age slope ( $F_{5, 232} = 0.59, P = 0.71$ ), but differed significantly in intercepts (ANCOVA,  $F_{5, 237} = 28.55, P < 0.001$ ).

### Reproductive investment

GSI varied among stocks of lake whitefish (Fig. 3a; ANOVA,  $F_{7, 305} = 16.86, P < 0.001$ ). 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 ( $F_{7, 297} = 2.23, P = 0.032$ ), 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 ( $F_{4, 167} = 0.90, P = 0.47$ ) that was less steep than the common mean slope ( $F_{2, 130} = 0.52, P = 0.60$ ) 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: ANCOVA,  $F_{4, 171} = 37.00, P < 0.001$ ; group 2:  $F_{2, 132} = 3.49, P = 0.033$ ). 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 ( $F_{3, 166} = 0.83, P = 0.48$ ; Table 1), but differed significantly in regression intercepts (ANCOVA,  $F_{3, 169} = 9.81, P < 0.001$ ).

### Lipid and DHA

Log mean percent total lipid (ANOVA,  $F_{7, 306} = 43.17, P < 0.001$ ) and DHA (ANOVA,  $F_{7, 306} = 24.08, P < 0.001$ ) differed significantly among stocks (Fig. 3b and c). Point Pelee fish had higher mean total lipid values

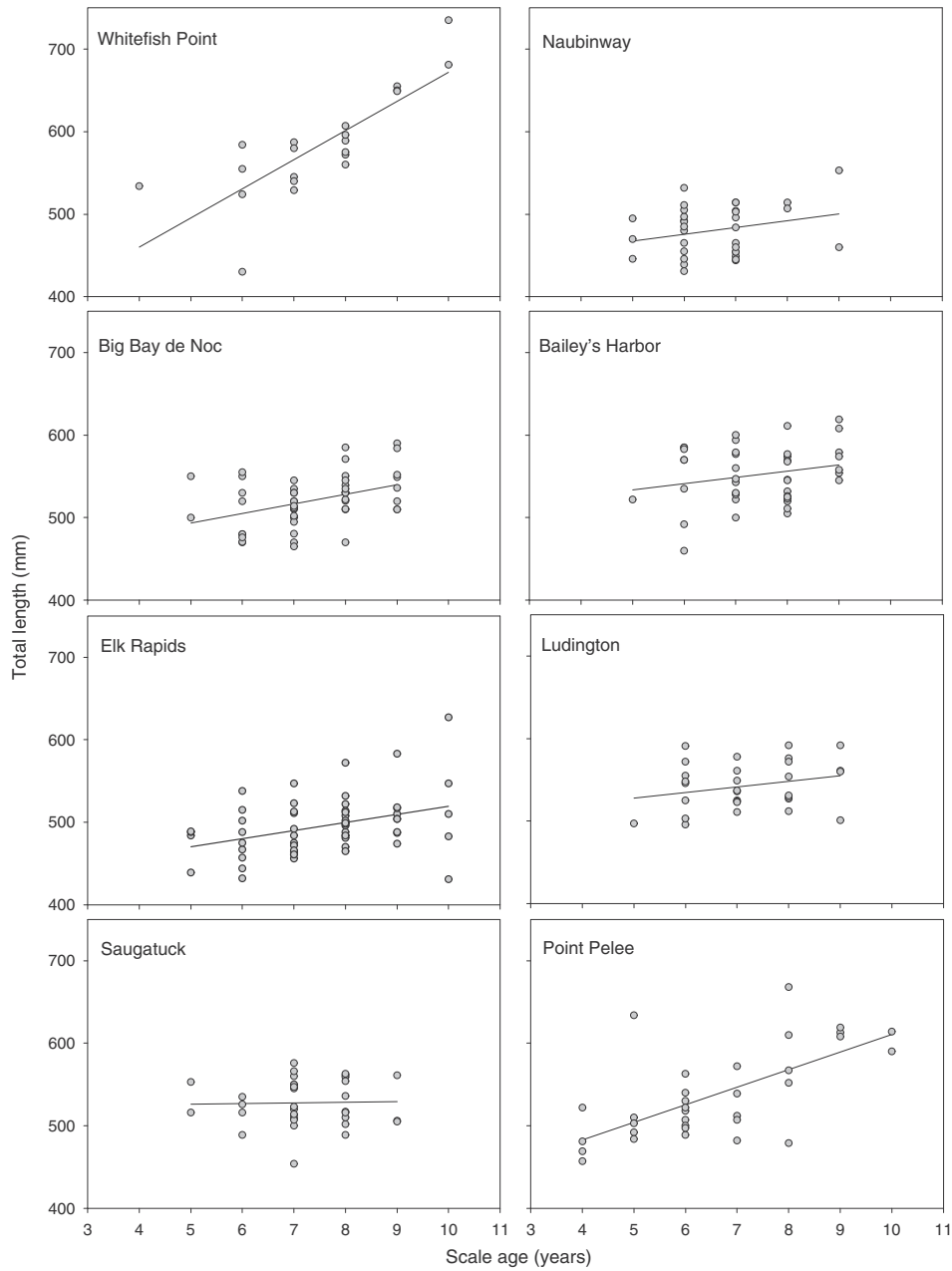
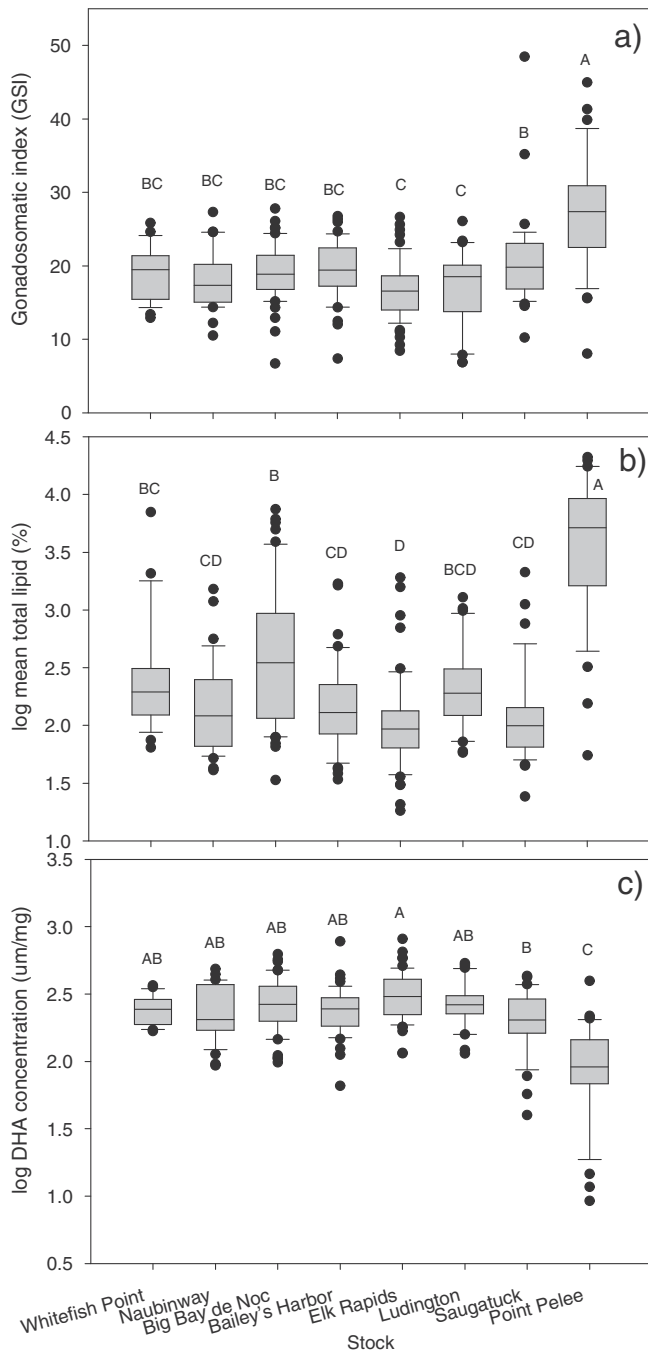


Fig. 2. Length (mm) versus mean scale age for each lake whitefish stock with estimated linear regressions included.

**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 \*.

Site	Growth			Reproduction				
	n	Length-at-age		n	Log fecundity - log body weight		Standard. fecundity - log egg diam.	
		Intercept	Slope (95% CI)		Intercept	Slope (95% CI)	Intercept	Slope (95% CI)
Whitefish Point	21	318.53	35.37 (22.63, 48.10) * A	26	1.65	1.18 (1.05, 1.32)* B	0.98	-1.29 (-2.57, -0.02)
Naubinway	33	426.69	8.16 (-2.89, 19.21)	34	-0.88	1.60 (1.30, 1.90)* A	1.63	-2.36 (-3.31, -1.41)* A
Big Bay de Noc	49	435.24	11.65 (3.99, 19.31)* B	50	2.10	1.15 (0.90, 1.41)* B	0.43	-0.58 (-1.73, 0.58)
Bailey's Harbor	42	496.10	7.51 (-2.66, 17.67)	44	0.97	1.31 (0.89, 1.74)* A	2.04	-2.91 (-4.10, -1.71)* A
Elk Rapids	56	421.55	9.78 (3.17, 16.39)* B	58	-0.22	1.48 (1.18, 1.78)* A	1.79	-2.41 (-2.88, -1.93)* A
Ludington	30	494.34	6.73 (-3.13, 16.59)	30	4.31	0.88 (0.62, 1.15)* B	0.04	-0.07 (-0.50, 0.36)
Saugatuck	34	522.49	0.75 (-9.37, 10.86)	38	4.09	0.86 (0.32, 1.41)* B	1.55	-1.94 (-2.77, -1.11)* A
Point Pelee	33	398.11	21.26 (12.44, 30.07)* A	33	3.54	1.01 (0.71, 1.30)* B	0.90	-1.28 (-3.48, 0.91)



**Fig. 3.** Lake whitefish stock a) gonadosomatic index, b) log mean percent total muscle lipid, and c) log concentration of muscle docosahexaenoic acid (DHA). Letters (A, B, C, D) denote stocks with statistically similar means as determined using the Tukey's *post-hoc* HSD test.

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 Saugatuck.

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  $\delta^{13}\text{C}$  variances differed significantly among locations ( $\chi = 11.45$ ,  $P < 0.001$ ), but baseline adjusted  $\delta^{15}\text{N}$  variances did not differ ( $\chi = 1.20$ ,  $P = 0.30$ ). Fish collected from Whitefish Point and Naubinway had  $\delta^{13}\text{C}$  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  $\delta^{15}\text{N}$ .

Significant differences were found among stock mean  $\delta^{13}\text{C}$  (Welch ANOVA,  $F_{7, 115.53} = 62.50$ ,  $P < 0.001$ ) and baseline corrected  $\delta^{15}\text{N}$  (ANOVA,  $F_{7, 301} = 158.42$ ,  $P < 0.001$ ) stable isotope values (Table 2). Along the  $\delta^{15}\text{N}$  axis, stocks grouped into five overlapping clusters within which mean baseline corrected  $\delta^{15}\text{N}$  values did not differ (Table 2, Fig. 5). Naubinway and Whitefish Point lake whitefish had significantly lower mean baseline-corrected  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  values recorded for the Naubinway and Whitefish Point stocks (Tukey's *post-hoc* HSD test,  $P < 0.05$ ).

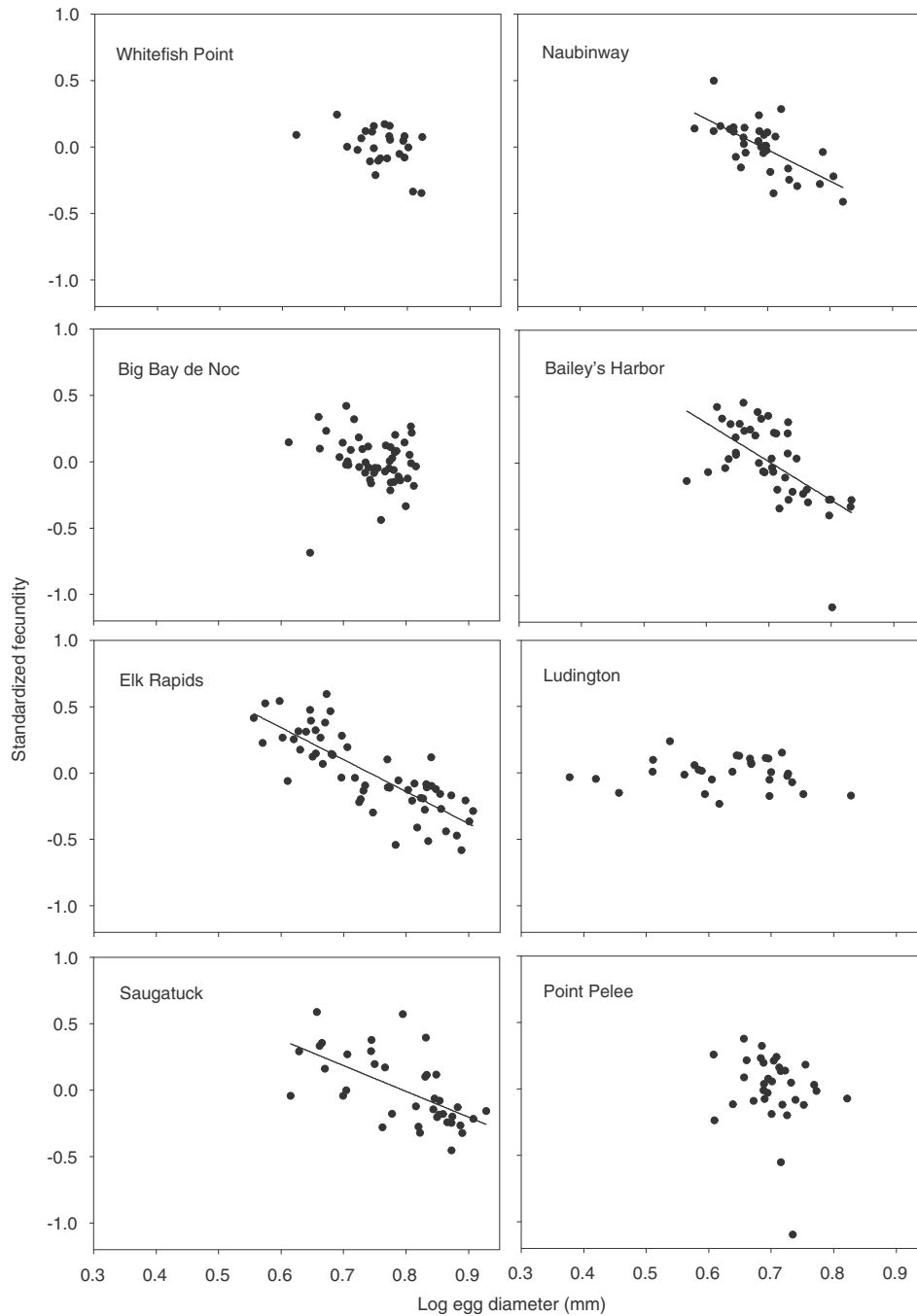
Euclidean distances from mean *Diporeia* spp. signatures ( $\Delta_{\text{WD}}$ ) varied by stock. Bailey's Harbor, Big Bay de Noc and Elk Rapids had  $\Delta_{\text{WD}}$  in the 3 to 4‰ range, consistent with high feeding use of *Diporeia* spp. Low and high  $\Delta_{\text{WD}}$  values were present 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 using all individuals from all stocks (ANOVA,  $F_{1, 311} = 70.67$ ,  $P < 0.001$ ; Fig. 6b).

Stocks displaying reproductive tradeoffs 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  $\Delta_{\text{WD}}$  suggesting feeding on *Diporeia* spp. (Fig. 6d). Stocks with  $\Delta_{\text{WD}}$  suggesting high dependence on *Diporeia* spp. (e.g., Elk Rapids  $\Delta_{\text{WD}} = 3.6\%$  and Bailey's Harbor  $\Delta_{\text{WD}} = 3.3\%$ ) had similar log mean total lipid as other stocks in Lake Michigan and at Whitefish Point that had  $\Delta_{\text{WD}}$  values suggesting no consumption of *Diporeia* spp. (e.g., Ludington  $\Delta_{\text{WD}} = 1.4\%$  and Whitefish Point  $\Delta_{\text{WD}} = 9.2\%$ ). Additionally, stocks with  $\Delta_{\text{WD}}$  suggesting high consumption of *Diporeia* spp. had significantly



**Fig. 4.** Standardized fecundity versus log egg diameter (mm) measurements for each lake whitefish stock. Stocks with significant linear regressions ( $P < 0.05$ ) include the estimated model. This figure is modified and reprinted from Muir et al. (2014).

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

**Table 2**

Female lake whitefish stable carbon ( $\delta^{13}\text{C}$ ) and baseline corrected nitrogen ( $\delta^{15}\text{N}$ ) isotope mean with Tukey *post-hoc* HSD test in superscript and the coefficient of variation in parentheses. Euclidean distance ( $\Delta_{\text{WD}}$ ) between mean lake whitefish and *Diporeia* spp.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  by region.

Population	$\delta^{13}\text{C}$ (CV)	$\delta^{15}\text{N}$ (CV)	$\Delta_{\text{WD}}$
Whitefish Point	−20.45 A (0.09)	6.38 DE (0.11)	9.16
Naubinway	−20.77 A (0.12)	6.06 E (0.08)	4.20
Big Bay de Noc	−25.07 CD (0.04)	6.58 D (0.08)	3.07
Bailey's Harbor	−24.84C (0.04)	6.70 D (0.07)	3.31
Elk Rapids	−22.78 B (0.05)	7.76 B (0.07)	3.59
Ludington	−25.81 D (0.04)	7.37C (0.06)	1.36
Saugatuck	−24.97 CD (0.03)	7.83 B (0.07)	4.02
Point Pelee	−25.24 CD (0.04)	9.57 A (0.05)	n/a

rates and lipid values, displayed different feeding strategies as suggested by heavier and lighter  $\delta^{13}\text{C}$  respectively. Therefore, while differences in prey resources may have an effect on lake whitefish stocks, declining *Diporeia* spp. abundances alone cannot explain differences in lake whitefish condition observed across the Great Lakes basin since our data suggest that some stocks have successfully adopted a variety of feeding strategies.

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

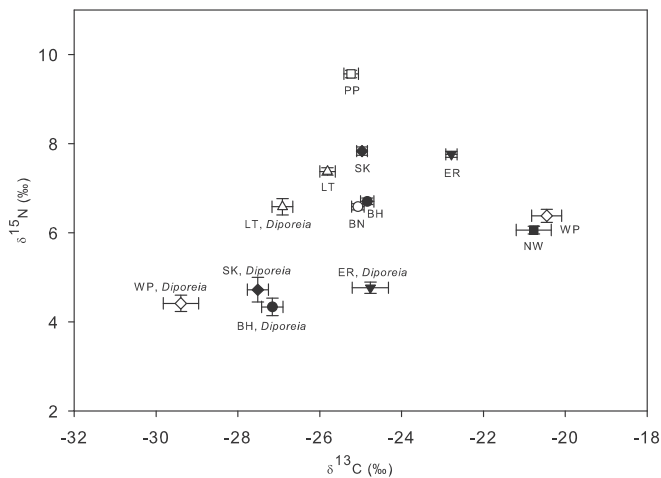
Our analyses suggests that lake whitefish from Lake Michigan have less surplus energy available after meeting maintenance requirements than stocks in either lakes Erie or Superior which may explain reproductive trade-offs among these stocks. Reduced surplus energy was manifested in lower somatic growth 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 1980–1990s (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 reproduction 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).

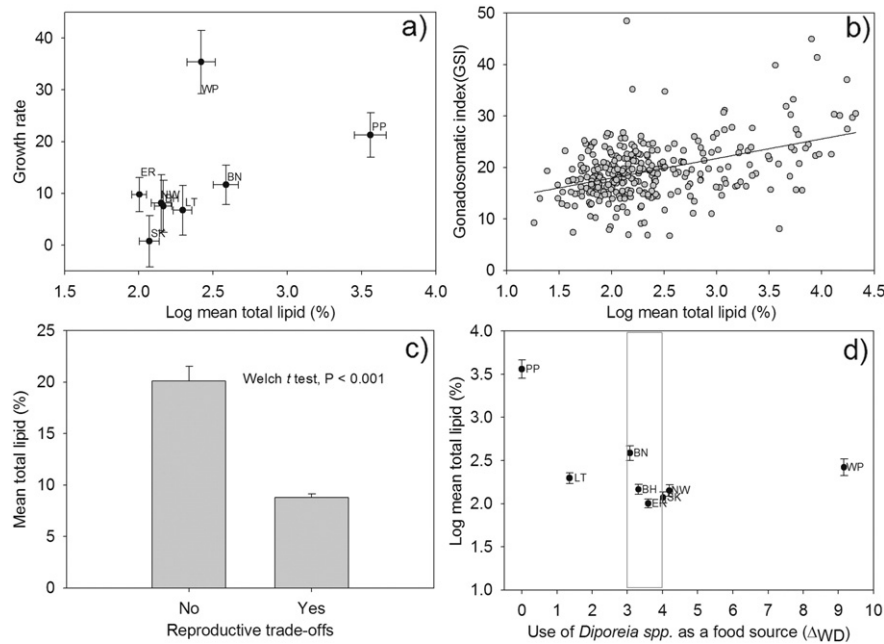
The Point Pelee and Whitefish Point stocks invested more energy in growth and reproduction than Lake Michigan stocks. Both stocks had statistically similar high growth rates, high lipid reserves and provided no evidence of reproductive trade-offs. During the 1990s, lake whitefish in Lake Superior had lower maximum lengths than northern Lake Michigan stocks (Taylor et al., 1992), possibly as a consequence of low 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 adaptation 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



**Fig. 5.** Carbon and nitrogen stable isotope signatures ( $\pm$  standard error) for each stock of lake whitefish and the corresponding *Diporeia* spp. (labelled) signatures from sampled locations. Stocks are identified with labels and symbols as follows: Whitefish Point (WP,  $\diamond$ ), Point Pelee (PP,  $\square$ ), Saugatuck (SK,  $\triangle$ ), Ludington (LT,  $\nabla$ ), Elk Rapids (ER,  $\circ$ ), Naubinway (NW,  $\blacksquare$ ), Big Bay de Noc (BN,  $\circ$ ) and Bailey's Harbor (BH,  $\blacklozenge$ ).





**Fig. 6.** Lake Whitefish a) stock growth rates and log mean total muscle lipid, b) gonadosomatic index (GSI) and log mean total muscle lipid of all individuals, c) mean total percent muscle lipid of grouped stocks: those with significant trade-offs between egg size and number ( $n = 4$ ) and those without trade-offs ( $n = 4$ ), and d) stock log mean total muscle lipid and use of *Diporeia* spp. as a food source in terms of Euclidean distance ( $\Delta_{WD}$ ). The grey box highlights stocks with high probability of feeding on *Diporeia* spp. The Point Pelee stock was assigned a  $\Delta_{WD}$  value of 0 as there are no *Diporeia* spp. in Lake Erie. Where possible the value  $\pm$  standard error was plotted. Stocks were identified with labels as follows: Whitefish Point (WP), Point Pelee (PP), Saugatuck (SK), Ludington (LT), Elk Rapids (ER), Naubinway (NW), Big Bay de Noc (BN) and Bailey's Harbor (BH).

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

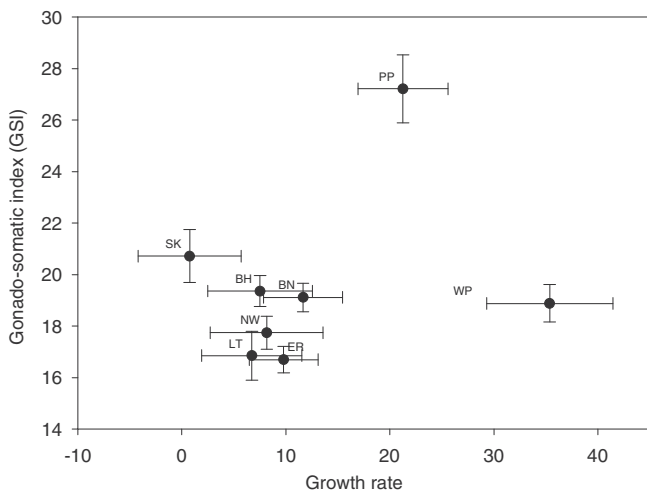
higher DHA, but was at the low end of the lipid reserve range. Thus, DHA does not appear to be directly related to fish growth and reproductive strategies as observed with total lipid levels. Instead, DHA levels in fish muscle tissues may depend on the DHA levels in the diet and the prevailing abiotic 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  $\delta^{13}\text{C}$  variance, suggesting a lower degree of niche diversification and stocks with more specialized diets (Bearhop et al., 2004). In contrast,  $\delta^{15}\text{N}$  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



**Fig. 7.** Mean gonadosomatic index (GSI) and growth rate for each lake whitefish stock ( $\pm$  standard error). Stocks were identified with labels as follows: Whitefish Point (WP), Point Pelee (PP), Saugatuck (SK), Ludington (LT), Elk Rapids (ER), Naubinway (NW), Big Bay de Noc (BN) and Bailey's Harbor (BH).

(Madenjian et al., 2002; Pothoven et al., 2001). 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 ( $\Delta_{WD}$ ) 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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