Lake Whitefish Diet, Condition, and Energy Density in Lake Champlain and the Lower Four Great Lakes following Dreissenid Invasions

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ARTICLE

Lake Whitefish Diet, Condition, and Energy Density in Lake Champlain and the Lower Four Great Lakes following Dreissenid Invasions

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Abstract
Lake Whitefish Coregonus clupeaformis support some of the most valuable commercial freshwater fisheries in North America. Recent growth and condition decreases in Lake Whitefish populations in the Great Lakes have been attributed to the invasion of the dreissenid mussels, zebra mussels Dreissena polymorpha and quagga mussels D. bugensis, and the subsequent collapse of the amphipod, Diporeia, a once-abundant high energy prey source. Since 1993, Lake Champlain has also experienced the invasion and proliferation of zebra mussels, but in contrast to the Great Lakes, Diporeia were not historically abundant. We compared the diet, condition, and energy density of Lake Whitefish from Lake Champlain after the dreissenid mussel invasion to values for those of Lake Whitefish from Lakes Michigan, Huron, Erie, and Ontario. Lake Whitefish were collected using gill nets and bottom trawls, and their diets were quantified seasonally. Condition was estimated using Fulton's condition factor (K) and by determining energy density. In contrast to Lake Whitefish from some of the Great Lakes, those from Lake Champlain Lake Whitefish did not show a dietary shift towards dreissenid mussels, but instead fed primarily on fish eggs in spring, Mysis diluviana in summer, and gastropods and sphaeriids in fall and winter. Along with these dietary differences, the condition and energy density of Lake Whitefish from Lake Champlain were high compared with those of Lake Whitefish from Lakes Michigan, Huron, and Ontario after the dreissenid invasion, and were similar to Lake Whitefish from Lake Erie; fish from Lakes Michigan, Huron, and Ontario consumed dreissenids, whereas fish from Lake Erie did not. Our comparisons of Lake Whitefish populations in Lake Champlain to those in the Great Lakes indicate that diet and condition of Lake Champlain Lake Whitefish were not negatively affected by the dreissenid mussel invasion.

Lake Whitefish Coregonus clupeaformis continues to be one of the most commercially valuable freshwater species in the United States and the majority of the harvest comes from the Laurentian Great Lakes (NMFS 2008). In 2008, 4.33 million kg of Lake Whitefish, valued at US$8.1 million, were harvested from the U.S. waters of the Great Lakes (NMFS 2008). Lake Whitefish were also of historic importance to the Lake Champlain commercial fishery, and overall harvest and license sales peaked during 1895–1912 when the average annual yield was 18,537 kg/year (Halnon 1963). The commercial fishery closed in 1913, and since then harvest of Lake Whitefish in Lake Champlain has been limited to recreational angling, which has been consistently low (Anderson 1978).

Declines of Lake Whitefish populations in the Great Lakes were associated with the introductions of invasive species including Rainbow Smelt Osmerus mordax, Alewife Alosa

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pseudoharengus, Sea Lamprey Petromyzon marinus, and the dreissenid mussels, zebra mussel Dreissena polymorpha and quagga mussel D. bugensis (Ehener 1997; Nalepa et al. 2005). Lake Champlain also experienced invasions of Alewives and zebra mussels, and incidents of Sea Lamprey wounding on Lake Trout Salvelinus namaycush and Lake Whitefish has been high (Marsden and Hauser 2009; Marsden et al. 2010). The effects of these species on Lake Champlain Lake Whitefish, however, are difficult to interpret because of an absence of historical information.

Dreissenid mussels were first observed in the Great Lakes in the late 1980s in Lake St. Clair and were established throughout all of the lakes by the early 1990s (Hebert et al. 1989; Johnson and Carlton 1996). The expansion of dreissenid mussels was associated with major declines in offshore native benthic invertebrate communities as well as declines in lakewide productivity and increases in water clarity (Dermott et al. 1993; Dermott and Kerec 1997; Dermott 2001; McNickel et al. 2006; Bunnell et al. 2009; Fahrenstiel et al. 2010). In Lakes Michigan, Huron, and Ontario, dreissenid mussels are believed to have played a role in lakewide collapses of the once abundant native amphipod, Diporeia (Nalepa et al. 1998, 2005; Dermott 2001, 2006; Bunnell et al. 2009). In contrast to the collapse in the upper Great Lakes, Diporeia declines in Lake Erie were much less severe (Dermott and Kerec 1997), and Diporeia were never abundant in Lake Champlain’s native benthic community. Potential Lake Whitefish prey in Lake Champlain include gastropods, sphaeriids, amphipods (Gammarus sp.), insect larvae (mostly Diptera and Trichoptera), and Mysis diluviana (Myer and Gruendling 1979; Levey and Fiske 1996). Zebra mussels were first observed in Lake Champlain in 1993 and, because of their negative effects on Great Lakes benthic communities, were expected to negatively affect the benthos of Lake Champlain. Beekey et al. (2004), however, documented that the expansion of zebra mussels on soft sediments led to increased abundance and richness of benthic invertebrates in at least two shallow bays (<7 m) in Lake Champlain, as had been seen elsewhere (e.g., Stewart et al. 1998).

In Lakes Michigan, Huron, and Ontario, declines in Lake Whitefish growth, condition, and energy density were attributed to benthic community shifts, including the loss of Diporeia, that were associated with dreissenid mussel colonization (Pothoven et al. 2001, 2006; Mohr and Nalepa 2005; Madenjian et al. 2006; Lumb et al. 2007). In those studies, changes in condition were evaluated by estimating energy density, an indicator of growth potential, which is influenced by prey availability and energy density (Madenjian et al. 2000). After the proliferation of dreissenids, Lake Whitefish diets from the Great Lakes transitioned from one that predominantly consisted of the energy-rich Diporeia to a diet supplemented by comparatively low-energy dreissenid mussels (Pothoven et al. 2001, 2006; Mohr and Nalepa 2005; Lumb et al. 2007). Energy density estimates for Diporeia and Mysis (3,625 and 3,924 J/g, respectively) exceed that for dreissenid mussels (1,703 J/g) by over twofold (Madenjian et al. 2006). Because of this diet shift, Pothoven and Madenjian (2008) suggested that for Lake Whitefish in Lake Huron to achieve preinvasion growth rates with the postinvasion diet composition, total consumption would have to increase by 78–122%. In contrast to what happened in the Great Lakes, the effects of the zebra mussel invasion on Lake Whitefish in Lake Champlain are unknown.

We hypothesized that because zebra mussels now dominate the benthic biomass in Lake Champlain (Beekey et al. 2004; authors’ personal observations), Lake Whitefish would begin to incorporate zebra mussels into their diets and their condition and energy density would be similar to the Lake Whitefish in the Great Lakes that experienced the negative effects of these invasive mussels. Alternatively, because Lake Champlain’s native benthic community is relatively intact and did not experience a massive loss of a major prey item (e.g., Diporeia, which was never highly abundant; Myer and Gruendling 1979; Beekey et al. 2004), Lake Whitefish may not change their diet to include the new exotic mussel and their condition and energy density would be robust and similar to those fish in Lake Erie. In the absence of Lake Whitefish data from Lake Champlain before the dreissenid mussel invasion, we were limited to comparing current Lake Champlain observations with pre- and postcolonization data from the Great Lakes where Lake Whitefish have either changed their diets after the dreissenid mussel invasions (Lakes Michigan, Huron, and Ontario) or have not (Lake Erie). Our objectives were to (1) quantify Lake Champlain Lake Whitefish diets and compare those with diet information from the Great Lakes, (2) contrast condition indexed with Fulton’s condition factor (K) for the postdreissenid-invasion time period in Lake Champlain with K-values for the Great Lakes before and after dreissenid invasion, and (3) contrast energy density measures of Lake Whitefish from Lake Champlain with estimates from studies conducted in the Great Lakes after the colonization of dreissenid mussels.

METHODS

Study Area

Lake Champlain is a long (~200 km), deep (19.5 m average, 122 m maximum depth), and relatively narrow (~12 km at its widest point) lake with a surface area of 1,130 km². The lake is bordered on the east by Vermont, the west by New York, and the north by the Province of Quebec. Lake Champlain is composed of four basins, separated by geographic and artificial barriers that partially restrict interbasin movement and has varying watershed land uses (agricultural to forested) and trophic status (eutrophic to oligotrophic). Our study focused on the oligotrophic main lake basin near Proctor Shoal and Shelburne Bay (Figure 1). This area has a maximum depth of 43 m and contains a coldwater fish community dominated by Lake Trout, Lake Whitefish, Atlantic Salmon Salmo salar, Rainbow Smelt, and since the mid-2000s, Alewife. Zebra mussels were first observed in Lake Champlain in 1993 and have since expanded throughout the main lake, covering most areas of hard substrate in depths to at least 10 m;
many areas of soft sediment are also carpeted by zebra mussel colonies (Beekey et al. 2004; Marsden and Hauser 2009).

Fish Collections
Lake Whitefish were sampled during the fall from 2006 to 2008 and year-round from 2009 to 2010 in the main basin of Lake Champlain near Proctor Shoal and Shelburne Bay (Figure 1), at depths between 10 and 40 m. Fish were captured using a 7.6-m semiballoon otter trawl (6.4-mm-stretched-mesh cod end liner) with a chain sweep attached to the footrope, which primarily targeted juveniles, and using short-term (3–4 h) bottom-set gill nets focused at dawn and dusk to collect adults. Gill nets
were 1.8 m deep and 70.6–152.4 m long and had panels of 7.6-, 8.9-, 10.2-, 11.4-, 12.7-, 14-, and 15.2-cm stretch mesh. Upon removal from nets, Lake Whitefish weights (nearest gram) and total lengths (TL; ± 1 mm) were recorded, and digestive tracts (esophagus to the posterior end of the intestine) were removed and frozen individually for dissection in the laboratory.

Lake Whitefish from Lake Michigan (management units WFM-01, WFM-02, and WFM-03) and Lake Huron (U.S. waters of main basin) were sampled year-round from commercial nets (gill and trap) and from fishery-independent gill-net surveys during 1986–2008 (M. P. Ebener, Chippewa Ottawa Resource Authority, unpublished data). The commercial gill nets consisted primarily of 11.4- and 11.6-cm stretch mesh and the commercial trap nets used 11.4-cm stretch mesh for the enclosure bag. The fishery-independent surveys captured Lake Whitefish using graded gill nets that had panels of mesh ranging in size from 6.4 cm to 15.2 cm (stretch) in 11.3-cm increments.

**Stomach Dissection**

In the laboratory, stomachs were dissected and all contents were removed, identified to the broad categories of molluscs (gastropods, sphaeriids, and dreissenids), insects, mysids, fish, and fish eggs, and counted. Stomach samples were separated into four seasonal categories, based on changes in the dominant prey items found in the stomachs and on a prior study of year-round diets (M. J. Seider and S. T. Schram, Wisconsin Department of Natural Resources, unpublished report) spring (April, May, and June), summer (July and August), fall (September and October), and winter (November through March). Changes in diet concurrent with these seasonal categories are probably related to the set-up and break-down of the thermocline. Only stomachs containing prey were used for analyses.

**Data Analysis**

**Diet.**—We reported Lake Champlain Lake Whitefish diet for small (<800 g) and large (>800 g) fish in terms of percent composition by wet weight and by number and by frequency of occurrence (Bowen 1996). Wet weights were calculated as the mean weight (in grams) of individual prey items times the number of prey items found in Lake Whitefish stomachs. We compared only the postdreissenid-invasion diet of Lake Whitefish in Lake Champlain with the diets of Lake Whitefish from the Great Lakes because Lake Whitefish diet information before the dreissenid invasion were not available for Lake Champlain. Postinvasion diet information from Lakes Michigan and Huron were derived from 1,309 Lake Whitefish collected from 1998 to 2004 (Pothoven and Madenjian 2008) and diet information for Lakes Erie and Ontario was obtained from seasonal sampling in 2003 (Lumb et al. 2007).

**Condition.**—Fish condition was estimated from age-4 and older Lake Whitefish from Lakes Champlain, Michigan, and Huron using Fulton’s K (Ricker 1975; Nash et al. 2006); comparable data were not available from Lakes Ontario and Erie. Fulton’s K (hereafter K) is strongly correlated with physiological estimates of body condition (e.g., energy density); however, caution is necessary in applying this index to assess population condition because it is related to length for Lake Whitefish (Rennie and Verdon 2008). To examine whether size-related changes in K affected our ability to compare condition across years and lakes we used ANCOVA with length as the covariate and a term that was specific for lake and year (e.g., lake–year group = Champlain 2009) as the independent variable. If the assumption of homogeneity of slopes was not met we then examined restricted length ranges based on inspection of plots of the length–K relationship and areas of the size range where slopes approached zero. After selection of appropriate size ranges, ANCOVA with length as the covariate and lake–year group as the independent variable was used to examine differences among groups. To compare fish condition before and after dreissenid invasion, data were grouped over 1986–1993 and 1998–2008, respectively, for Lakes Michigan and Huron and over the postdreissenid period 2009–2010 for Lake Champlain. An ANCOVA with length as the covariate and lake–period group (where period refers to pre- versus postdreissenid invasion) as the independent variable was then used to compare least-squares mean (LSM) K-values between groups employing the Bonferroni adjustment for multiple comparisons.

**Energy density.**—Energy density was measured for individual Lake Whitefish from a sample of 52 fish, ranging in size from 188 to 566 mm TL, collected from Lake Champlain during March to May 2010. Whole individual Lake Whitefish (≥250 mm) with their stomach and intestine removed, but other viscera intact, were ground to an even homogenate using a Hobart 4822 meat grinder. Small individual Lake Whitefish (<250 mm TL) were ground to an even homogenate with a kitchen blender. A 25–50-g subsample from each homogenate was dried at 65–70°C to a stable weight (approximately 3 d) to determine percentage wet weight. The dried homogenate from each fish was then cooled with dry ice and ground to a fine powder using a Magic Bullet blender and pressed into 3–4 pellets of approximately 1 g each. Pellets were ignited in a Parr Model 1241 Adiabatic bomb calorimeter previously standardized using benzoic acid and the energy content of each pellet was recorded. Energy density values for the 3–4 pellets per fish were averaged and within-sample variability was estimated. Individual fish that had high within-sample variability (i.e., variability among pellets: CV [100 × SD/mean] ≥ 5%), which was thought to be caused by incomplete burning of the pellets, were excluded from the analysis (n = 3). The mean dry weight energy density (J/g) for each fish was converted to wet-weight values using the percentage dry weight determined from drying the homogenate samples.

Energy density estimates for Lake Whitefish from Lakes Michigan, Huron, Erie, and Ontario were acquired directly from the authors of previous studies (Pothoven et al. 2006; Lumb et al. 2007). Lake Michigan fish were collected from April to November from 2002 to 2003 and were processed as five-fish composites based on 25.4-mm size intervals (Pothoven et al. 2006).
Table 1. Seasonal diet composition (% wet weight and % by number) and percentage frequency of occurrence for small (≤800 g) and large (>800 g) Lake Whitefish from Lake Champlain, 2006–2010. Spring = April–June; summer = July–August; fall = September–October; winter = November–March. n is the number of stomachs that contained prey items.

<table>
<thead>
<tr>
<th>Season</th>
<th>Gastropods small/large</th>
<th>Sphaeriids small/large</th>
<th>Zebra mussels small/large</th>
<th>Insects small/large</th>
<th>Fish eggs small/large</th>
<th>Fish small/large</th>
<th>Mysids small/large</th>
<th>n</th>
<th>% empty small/large</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>2.6/42.1</td>
<td>13.6/3.3</td>
<td>0.0/0.05</td>
<td>31.2/50.0</td>
<td>41.9/0.6</td>
<td>10.5/3.5</td>
<td>0.3/0.5</td>
<td>96/53</td>
<td>25.0/24.5</td>
</tr>
<tr>
<td>Summer</td>
<td>9.4/17.5</td>
<td>21.6/6.7</td>
<td>0.5/0.4</td>
<td>1.6/3.3</td>
<td>0.0/0.0</td>
<td>47.9/43.6</td>
<td>19.0/28.6</td>
<td>32/164</td>
<td>25.0/23.8</td>
</tr>
<tr>
<td>Fall</td>
<td>11.5/50.0</td>
<td>38.5/1.2</td>
<td>1.7/0.2</td>
<td>0.0/0.9</td>
<td>0.0/0.0</td>
<td>35.4/42.3</td>
<td>12.9/5.3</td>
<td>9/83</td>
<td>22.2/47.0</td>
</tr>
<tr>
<td>Winter</td>
<td>16.8/86.0</td>
<td>8.4/0.2</td>
<td>0.0/0.5</td>
<td>0.0/3.9</td>
<td>0.1/0.6</td>
<td>74.7/8.9</td>
<td>0.0/0.02</td>
<td>12/62</td>
<td>58.3/22.6</td>
</tr>
</tbody>
</table>

Composition (%) by number

<table>
<thead>
<tr>
<th>Season</th>
<th>Gastropods small/large</th>
<th>Sphaeriids small/large</th>
<th>Zebra mussels small/large</th>
<th>Insects small/large</th>
<th>Fish eggs small/large</th>
<th>Fish small/large</th>
<th>Mysids small/large</th>
<th>n</th>
<th>% empty small/large</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>0.2/46.3</td>
<td>1.6/7.3</td>
<td>0.0/0.0</td>
<td>0.6/18.3</td>
<td>97.6/26.9</td>
<td>0.0/0.1</td>
<td>0.0/1.0</td>
<td>96/53</td>
<td>25.0/24.5</td>
</tr>
<tr>
<td>Summer</td>
<td>10.1/19.3</td>
<td>46.4/14.7</td>
<td>0.1/0.1</td>
<td>0.6/1.2</td>
<td>0.0/0.0</td>
<td>1.3/1.2</td>
<td>40.7/63.2</td>
<td>32/164</td>
<td>25.0/23.8</td>
</tr>
<tr>
<td>Fall</td>
<td>10.0/77.5</td>
<td>66.7/3.8</td>
<td>0.4/0.1</td>
<td>0.0/0.5</td>
<td>0.0/0.0</td>
<td>0.8/1.6</td>
<td>22.2/16.5</td>
<td>9/83</td>
<td>22.2/47.0</td>
</tr>
<tr>
<td>Winter</td>
<td>39.1/77.8</td>
<td>39.1/0.3</td>
<td>0.0/0.1</td>
<td>0.0/1.2</td>
<td>13.0/20.4</td>
<td>4.3/0.2</td>
<td>0.0/0.1</td>
<td>12/62</td>
<td>58.3/22.6</td>
</tr>
</tbody>
</table>

Frequency of occurrence (%)

<table>
<thead>
<tr>
<th>Season</th>
<th>Gastropods small/large</th>
<th>Sphaeriids small/large</th>
<th>Zebra mussels small/large</th>
<th>Insects small/large</th>
<th>Fish eggs small/large</th>
<th>Fish small/large</th>
<th>Mysids small/large</th>
<th>n</th>
<th>% empty small/large</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>33.3/82.5</td>
<td>79.2/67.5</td>
<td>0.2/2.5</td>
<td>19.4/50.0</td>
<td>56.9/15.0</td>
<td>2.8/7.5</td>
<td>5.6/10.0</td>
<td>96/53</td>
<td>25.0/24.5</td>
</tr>
<tr>
<td>Summer</td>
<td>41.7/71.2</td>
<td>83.3/56.0</td>
<td>4.2/1.6</td>
<td>4.2/12.8</td>
<td>0.0/0.0</td>
<td>16.7/25.6</td>
<td>70.8/54.4</td>
<td>32/164</td>
<td>25.0/23.8</td>
</tr>
<tr>
<td>Fall</td>
<td>42.9/68.2</td>
<td>71.4/22.7</td>
<td>14.3/4.5</td>
<td>0.0/15.9</td>
<td>0.0/0.0</td>
<td>28.6/38.6</td>
<td>42.9/15.9</td>
<td>9/83</td>
<td>22.2/47.0</td>
</tr>
<tr>
<td>Winter</td>
<td>20.0/87.5</td>
<td>60.0/4.2</td>
<td>0.0/10.4</td>
<td>0.0/12.5</td>
<td>40.0/14.6</td>
<td>20.0/8.3</td>
<td>0.0/2.1</td>
<td>12/62</td>
<td>58.3/22.6</td>
</tr>
</tbody>
</table>

Lake Huron fish were collected from May to September from 2002 to 2004 and were processed individually (Pothoven et al. 2006). Lake Erie and Lake Ontario fish were collected throughout the year during 2003 and were processed individually. To increase the sample size of fish with energy density estimates in Lakes Erie and Ontario, the relationship between water content (WC, % mass) and energy density (ED, J/g wet weight) was used for individuals with known water content (Lumb et al. 2007). Similar processing and calorimetry techniques were used when determining energy density for fish in all lakes, which allowed for direct comparison of data among all studies (Pothoven et al. 2006; Lumb et al. 2007).

We examined differences in mean energy density within two size categories of Lake Whitefish, small (≤800 g) and large (>800 g), among the five lakes. Separate weight categories were used because previous studies in Lakes Michigan and Huron found energy density increased linearly with body weight up to approximately 800 g and was not related to weight for larger individuals (Pothoven et al. 2006). This split between small and large Lake Whitefish was also consistent with the weight at maturity for all study lakes, probably representing the difference in energy allocation for immature and mature Lake Whitefish for Lakes Michigan and Huron (M. Ebener, Chippewa Ottawa Resource Authority, Sault Ste. Marie, Michigan, unpublished data) and for Lake Ontario (J. Hoyle, Ontario Ministry of Natural Resources, Glenora Fisheries Research Station, Picton, Ontario, personal communication). Because Lumb et al. (2007) observed that Lake Whitefish energy density continued to increase with wet weight beyond 800 g, we used ANCOVA with weight and lake as the covariates to examine size-based relationships for small and large size-classes of Lake Whitefish for all five lakes. Where slopes were not different among groups of lakes, we compared energy density predictions for LSM weight values. For comparisons between all lakes (because slopes differed in some cases) we used the average weight of samples for each lake to calculate a grand average for all five lakes, rounded that to the nearest 25-g increment (1,300 g), checked that against each data scatter point to ensure that this value was within an area near the center of the scatter of measurements, and examined the confidence limits for each lake’s regression line at that point for overlap with those from the other lakes.

RESULTS

Diet

Of the 511 (149 small and 362 large) Lake Whitefish from Lake Champlain that were sampled, 365 had stomach contents, and these were examined for diet. Small and large Lake Whitefish diets were similar among seasons, and the only difference was that the diet of small Lake Whitefish was dominated by fish eggs in the spring whereas the diet of large Lake Whitefish by weight was predominately insects (Table 1). Overall, the diet of Lake Whitefish differed among seasons during 2006–2010, but seasonal patterns were consistent over the 2 years that were sampled in all four seasons (2009 and 2010). In spring, Lake Whitefish fed primarily on large numbers of fish eggs...
were not homogenous (indicated that length was significantly related to condition (F<sub>47,10915</sub> = 1.14, P < 0.24) and not significantly different from zero (P > 0.05) for 44 out of 48 groups. The ANCOVA of pre- and postdreissenid-invasion lake–period groups indicated that length-related slopes were homogenous among groups (F<sub>4,9631</sub> = 0.07, P = 0.99) and length was a significant component of the overall model (P < 0.01); however, the slopes of the relationship between length and K for none of the groups were significantly different from zero. Pairwise comparisons indicated that there were significant differences in condition among lakes and periods (P < 0.0001) except that K was not different (P = 1.0) for fish in Lakes Michigan or Huron after the dreissenid invasion (Table 2). Those comparisons indicated that the 2009–2010 mean K for Lake Champlain Lake Whitefish was 9–13% greater than K-values measured for Lake Michigan and Lake Huron Lake Whitefish during the predreissenid-invasion period and 24% greater than for Lake Whitefish from either lake during the postdreissenid-invasion period. In general, Lake Whitefish K declined in both Lakes Michigan and Huron from the mid-1980s through 2008 (Figure 3).

**Condition**

Using the entire size range of data available for each year from Lakes Champlain, Michigan, and Huron, ANCOVA indicated that length was significantly related to condition (P < 0.0001), but that lake- and year-specific regression line slopes were not homogenous (F<sub>47,107258</sub> = 39.66, P < 0.0001). Plots of those relationships for each lake–year group indicated that the length-related increase in K approached zero at about 540 mm for Lake Whitefish from Lake Champlain, the lake with the greatest slope, and was nearly zero in that size range for fish from Lakes Michigan and Huron. Because most fish sampled from all three lakes were <600 mm (>96%) we examined differences in K between lake–year groups for Lake Whitefish between 540 and 600 mm. Regression line slopes of length-related K for Lake Whitefish in this size range were homogenous between lake–year groups (ANCOVA: F<sub>4,1921</sub> = 1.921) and not significantly different from zero (P > 0.05) for 44 out of 48 groups. The ANCOVA of pre- and postdreissenid-invasion lake–period groups indicated that length-related slopes were homogenous among groups (F<sub>4,5435</sub> = 0.07, P = 0.99) and length was a significant component of the overall model (P < 0.01); however, the slopes of the relationship between length and K for none of the groups were significantly different from zero. Pairwise comparisons indicated that there were significant differences in condition among lakes and periods (P < 0.0001) except that K was not different (P = 1.0) for fish in Lakes Michigan or Huron after the dreissenid invasion (Table 2). Those comparisons indicated that the 2009–2010 mean K for Lake Champlain Lake Whitefish was 9–13% greater than K-values measured for Lake Michigan and Lake Huron Lake Whitefish during the predreissenid-invasion period and 24% greater than for Lake Whitefish from either lake during the postdreissenid-invasion period. In general, Lake Whitefish K declined in both Lakes Michigan and Huron from the mid-1980s through 2008 (Figure 3).

**Energy Density**

Energy density (ED)–weight (W) relationships estimated for small and large Lake Whitefish from Lake Champlain were

\[
ED_{\text{small}} = 2.6197W + 6610.9, \quad r^2 = 0.465
\]

\( (n = 31, P < 0.0001; \text{weight range: 55–780 g}) \)
and
\[ ED_{\text{large}} = -0.3693W + 8722.2, \quad r^2 = 0.026 \]
\( (n = 18, \ P = 0.5258; \ \text{weight range:} \ 810-1750 \ g). \)

Weight-related slopes for the energy density of Lake Whitefish > 800 g were not different from zero for Lakes Champlain, Michigan, or Huron (Lakes Michigan and Huron data from Pothoven et al. 2006) but were significantly greater than zero for Lakes Erie (\( n = 47, \ P < 0.0001 \)) and Ontario (\( n = 18, \ P = 0.0030 \)) (Lakes Erie and Ontario data from Lumb et al. 2007; Table 3). Slopes of weight-related energy density relationships for small individuals were not different between Lakes Champlain, Erie, and Michigan, nor were they different among Lakes Erie, Huron, and Ontario. Mean energy density values for small Lake Whitefish were greater for Lake Champlain than for Lake Erie, and Lake Erie values were greater than those for the other three lakes. Energy density values for fish from Lake Huron and Ontario were not significantly different, and although slopes were different in plots of energy density relationships, Lake Michigan whitefish energy densities appeared greater and the LSM value (6,211.4 J/g) was more than 1,330 J/g higher than in the other two lakes (4,865.8 in Lake Huron and 4,877.0 J/g in Lake Ontario). For large individual Lake Whitefish, slopes were not different among Lakes Champlain, Huron, and Michigan and between Lakes Erie and Ontario. The LSM energy density for whitefish was significantly different among Lakes Champlain, Michigan, and Huron, and Lake Champlain (8,276.2 J/g) was the highest, followed by Lake Michigan (7,594.2 J/g) and then Lake Huron (5,853.7 J/g). The Lake Whitefish LSM energy density for Lake Erie (9,550.8 J/g) was greater than that for Lake Ontario (7,162.4 J/g). The energy densities and associated confidence intervals (CIs) for a 1,300-g Lake Whitefish estimated from each lake-specific regression relationship were different (i.e., the CIs did not overlap), and Lake Erie had the highest value and Lakes Champlain, Michigan, Ontario, and Huron had progressively lower values.

**DISCUSSION**

Despite the fact that zebra mussels have been established in Lake Champlain since 1993, we found little evidence that they were becoming important components of Lake Whitefish diets in this lake and no support for our first hypothesis that Lake Whitefish would incorporate zebra mussels into their diet. Condition and energy density of Lake Whitefish in Lake Champlain during 2009–2010 were high relative to areas of the Great Lakes where Lake Whitefish diets changed after dreissenid mussels became abundant in the mid-1990s (Pothoven et al. 2006; Lumb et al. 2007). Condition of Lake Whitefish in the main lake section of Lake Champlain in this study was similar to condition of Lake Whitefish from the southern lake collection in 1931 and higher than that for fish from Missisquoi Bay collected in 1930 (Van Oosten and Deason 1939; Herbst et al. 2011). These results indicate that Lake Champlain whitefish continue to attain sufficient

### TABLE 3. Energy density (ED; J/g wet weight) in relation to individual fish size of small (<800 g) and large (>800 g) Lake Whitefish in Lakes Champlain, Erie, and Ontario from the raw data summarized in Lumb et al. (2007). Different letters associated with ED values represent significant differences in energy density (\( P < 0.05 \)) determined using a Student’s \( t \)-test.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Mean ED</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Slope</th>
<th>Intercept</th>
<th>( P )-value</th>
<th>Mean ED</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Slope</th>
<th>Intercept</th>
<th>( P )-value</th>
<th>( P ) (slope 1 = slope 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Champlain</td>
<td>7,798 y</td>
<td>7,570</td>
<td>8,027</td>
<td>2.43</td>
<td>6,660</td>
<td>&lt;0.0001</td>
<td>8,278 y</td>
<td>7,854</td>
<td>8,702</td>
<td>&lt;0.66</td>
<td>0.149</td>
<td>0.0002</td>
<td>0.0002</td>
</tr>
<tr>
<td>Erie</td>
<td>6,787 y</td>
<td>6,419</td>
<td>7,155</td>
<td>3.54</td>
<td>5,834</td>
<td>&lt;0.0001</td>
<td>9,483 z</td>
<td>9,221</td>
<td>9,745</td>
<td>1.40</td>
<td>&lt;0.0001</td>
<td>0.0032</td>
<td>0.0001</td>
</tr>
<tr>
<td>Michigan</td>
<td>6,148 x</td>
<td>5,876</td>
<td>6,419</td>
<td>2.77</td>
<td>5,159</td>
<td>&lt;0.0001</td>
<td>7,593 x</td>
<td>7,209</td>
<td>7,976</td>
<td>0.40</td>
<td>0.080</td>
<td>&lt;0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>Ontario</td>
<td>5,438 w</td>
<td>4,957</td>
<td>5,919</td>
<td>1.56</td>
<td>4,783</td>
<td>&lt;0.0226</td>
<td>7,256 x</td>
<td>6,948</td>
<td>7,565</td>
<td>1.74</td>
<td>0.0002</td>
<td>0.905</td>
<td>0.0005</td>
</tr>
<tr>
<td>Huron</td>
<td>4,837 v</td>
<td>4,474</td>
<td>4,927</td>
<td>1.70</td>
<td>4,542</td>
<td>&lt;0.0001</td>
<td>5,854 w</td>
<td>5,573</td>
<td>6,135</td>
<td>&lt;0.13</td>
<td>0.624</td>
<td>&lt;0.0001</td>
<td>0.905</td>
</tr>
</tbody>
</table>
energy to maintain good condition from a diet consisting primarily of fish eggs, mysids, gastropods, and sphaeriids. After the invasion of dreissenid mussels, condition of Lake Whitefish in Lakes Huron and Michigan declined significantly, whereas fish condition in Lake Champlain is higher than the predreon invasion condition in both lakes. Condition of Lake Whitefish from Lake Champlain appears similar to that of age-4 and older Lake Whitefish in both summer and fall in Lake Erie, where fish condition has remained stable throughout the dreissenid colonization period (Cook and Kayle 2011), and substantially greater than fish condition in the other lakes (data herein for Lakes Michigan and Huron; mean $K_i = 0.81$ for Lake Ontario, 1998–2008, J. Hoyle, Ontario Ministry of Natural resources, personal communication). Energy density followed a similar pattern and was greatest for both Lakes Champlain and Erie Lake Whitefish in both small (< 800 mm) and large (> 800 mm) size categories. Overall, compared with Lake Whitefish from Lakes Huron, Michigan, and Ontario, Lake Whitefish from Lake Erie do not appear to have been negatively affected by dreissenid mussel colonization. Because Lake Whitefish from Lake Champlain are similar in condition and energy density to those from Lake Erie and have not transitioned to a diet rich in zebra mussels, they do not appear to have been strongly affected by dreissenids.

The diets of Lake Whitefish from Lake Champlain changed seasonally and were dominated numerically by fish eggs in the spring, mysids in the summer, and gastropods and sphaeriids in the fall and winter. With the exception of fish eggs, these taxa are commonly observed in Lake Whitefish diets from the Great Lakes (Owens and Dittman 2003; Pothoven and Nalepa 2006; Lumb et al. 2007; Pothoven and Madenjian 2008). Experience from this study, however, indicates that fish eggs may only be seasonally available in the coldwater habitats occupied by Lake Whitefish, and thus were missed in diet studies that tended to focus on the warmerweather seasons. Similar to our results, Seider and Schram (unpublished report) found that fish eggs occurred in 66% of stomachs of Lake Whitefish captured during the winter in Lake Superior.

Other studies have documented variations in Lake Whitefish diet among different lakes, seasons, and depths that are consistent with prey availability, suggesting that Lake Whitefish are nonselective feeders (Hart 1931; Pothoven 2005; Pothoven and Nalepa 2006; Pothoven and Madenjian 2008). In the Great Lakes, before the invasion of the dreissenid mussels, Diporeia was highly abundant and comprised a substantial proportion of Lake Whitefish diets. When dreissenid mussels began to dominate the benthic biomass, they became abundant in Lake Whitefish diets in Lakes Huron, Michigan, and Ontario (Ihssen et al. 1981; Pothoven and Nalepa 2006; Pothoven and Madenjian 2008). Lake Whitefish stomachs from Lake Champlain, however, contained few zebra mussels (18 zebra mussels in 365 fish that had stomach contents), even though the exotic mussels are now the most abundant species in the lake’s nearshore benthic community (Beekey et al. 2004; J. E. Marsden, personal observation), suggesting that Lake Whitefish in Lake Champlain are ignoring the abundant zebra mussels and instead consuming less abundant prey. Diporeia were never an abundant food source available to Lake Whitefish in Lake Champlain (Levey and Fiske 1996). Therefore, the change in the benthic community after the addition of dreissenid mussels and loss of Diporeia in the Great Lakes has resulted in foraging responses that do not appear to have occurred in Lake Champlain.

Some Lake Champlain Lake Whitefish appear to specialize on certain prey types on a given day, and individual fish can consume hundreds of individuals of a single prey type that was not necessarily the dominant prey item for the season. Gastropods, fish eggs, and Mysis often appeared as dominant prey items in individual stomachs; however, zebra mussels were only seen singly in any stomach. Pothoven and Nalepa (2006) also documented flexibility in the diet of individual Lake Whitefish from Lake Huron, with some individuals specializing on prey types that were not necessarily consistent with the overall diet composition for the population. Thus, as generalist feeders Lake Whitefish demonstrate individual feeding strategies that appear to be flexible and heterogeneous within populations (e.g., Warburton et al. 1998).

Lake Whitefish diet studies that used Ponar grabs in the Great Lakes have focused on characterizing potential prey items in soft sediments (e.g., Pothoven et al. 2001; Owens and Dittman 2003); however, at least in Lake Champlain, Lake Whitefish may forage partially on hard substrates as indicated by the abundance of gastropods and fish eggs seen in their stomachs. Studies before the invasion of zebra mussels indicated that the most abundant soft-sediment benthic taxa in the main lake were oligochaetes (59–90% of the total fauna) and sphaerid clams, whereas gastropods were the dominant taxon on hard substrates (Myer and Gruenling 1979; Levey and Fiske 1996). Of the fish species the eggs of which were most abundant in Lake Whitefish stomachs, Rainbow Smelt deposit eggs on soft sediments in the main lake at depths of at least 17 m in Lake Champlain (J. E. Marsden, unpublished data), whereas coregonids and Lake Trout deposit eggs on rocky or gravely substrate. Thus, in order to characterize selectivity of prey in Lake Whitefish diets, quantitative sampling of hard substrate benthos is probably needed, but to date, studies have generally focused on soft sediment sampling (e.g., Pothoven et al. 2001; Owens and Dittman 2003; Pothoven and Nalepa 2006).

Lake Whitefish condition in Lakes Huron, Michigan, and Ontario has changed dramatically with ecosystem shifts that resulted in the loss of an energetically valuable prey source (Pothoven et al. 2006; Lumb et al. 2007). These shifts were reflected in decreases in the overall energy content of Lake Whitefish diets. Pothoven and Nalepa (2006) found that energy in Lake Whitefish stomachs was lowest for fish that ate shelled prey (bivalves and gastropods); their results were supported by the low energy densities of Lake Whitefish preying upon large quantities of dreissenids in Lakes Michigan, Huron, and Ontario (Pothoven et al. 2006; Lumb et al. 2007) relative to Lakes Erie.
and Champlain. Lake Whitefish populations in some areas of Lakes Michigan, Huron, and Ontario were unable to find sufficient numbers of alternate prey after the dreissenid invasions and transitioned to foraging on dreissenid mussels, which contributed to decreased energy intake and negative consequences on growth and condition (Hoyle 2005; Mohr and Ebener 2005). In contrast, Lake Erie Lake Whitefish condition did not decrease significantly after the dreissenid invasion, and both Cook et al. (2005) and Lumb et al. (2007) concluded that the invasion of dreissenid mussels in Lake Erie was not associated with reductions in growth or condition because Lake Whitefish were able to locate high quality prey within the diverse assortment of other prey remaining in the benthos. The diet of Lake Champlain Lake Whitefish consisted of prey items with high energy content such as fish eggs (6,243 J/g, Cummins and Wuycheck 1971) and mysids and, as a result, these fish, similar to Lake Erie Lake Whitefish, had high condition values relative to those from Lakes Michigan, Huron, and Ontario.

Because changes in body condition associated with decreases in energy intake may be masked by increased water content in fish, determination of energy density (J/g) yields a clearer view of physiological condition (Love 1980). Energy densities of Lake Champlain Lake Whitefish were higher than those from the Great Lakes affected by dreissenids (i.e., Lakes Michigan, Huron, and Ontario) and was exceeded only by large Lake Whitefish from Lake Erie. Energy densities in Lake Champlain Lake Whitefish were most similar to Lake Whitefish in Lake Michigan; this may be due to the proportion of mysids (30% by weight) in the diet of Lake Whitefish from Lake Michigan (Pothoven et al. 2006), which is similar to the proportion found in Lake Champlain. Despite having similar Diporeia declines, Lake Michigan Lake Whitefish had significantly greater energy densities after the dreissenid invasion than did those from Lake Huron (Pothoven et al. 2006), which implicates factors beyond the colonization by dreissenid. These differences may also be attributed to differences in prey energy density, dissimilar diets, spatial variation, and the productivity of the lakes (Pothoven et al. 2006).

Changes in Lake Whitefish growth and condition may be attributed to density-dependent factors, as has been proposed for Lake Whitefish populations in Lake Michigan (DeBruyne et al. 2008); however, Lumb et al. (2007) did not see density-dependent effects in Lakes Erie or Ontario. Unfortunately, in the absence of historic data on Lake Whitefish populations in Lake Champlain, we cannot draw any conclusions about the influence of density-dependence.

In Lakes Michigan, Huron, and Ontario, where Lake Whitefish condition has declined and Diporeia, an important native prey item, was lost, dreissenids became the principal food resource. Following the zebra mussel colonization of Lake Champlain in 1993, Lake Whitefish diets contained few mussels and their condition and energy density was relatively high and similar to fish from Lake Erie, where Lake Whitefish did not appear to have been negatively affected by the dreissenid colonization. As suggested by Cook et al. (2005) for Lake Erie Lake Whitefish, those in Lake Champlain have access to a diverse diet, which may buffer them against changes in the benthic community. Thus, it appears that the Lake Whitefish populations in Lake Champlain have not yet experienced substantial negative effects as a result of the dreissenid colonization.

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