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Energy density of lake whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan

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Abstract We collected lake whitefish *Coregonus clupeaformis* off Alpena and Tawas City, Michigan, USA in Lake Huron and off Muskegon, Michigan USA in Lake Michigan during 2002–2004. We determined energy density and percent dry weight for lake whitefish from both lakes and lipid content for Lake Michigan fish. Energy density increased with increasing fish weight up to 800 g, and then remained relatively constant with further increases in fish weight. Energy density, adjusted for weight, was lower in Lake Huron than in Lake Michigan for both small (≤800 g) and large fish (>800 g). Energy density did not differ seasonally for small or large lake whitefish or between adult male and female fish. Energy density was strongly correlated with percent dry weight and percent lipid content. Based on data from commercially caught lake whitefish, body condition was lower in Lake Huron than Lake Michigan during 1981–2003, indicating that the dissimilarity in body condition between the lakes could be long standing. Energy density and lipid content in 2002–2004 in Lake Michigan were lower than data for comparable sized fish collected in 1969–1971. Differences in energy density between lakes were attributed to variation in diet and prey energy content as well as factors that affect feeding rates such as lake whitefish density and prey abundance.

Keywords Calorimetry · Condition · Great Lakes · Lake whitefish

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Introduction

Lake whitefish *Coregonus clupeaformis* has long been one of the most economically important commercial fish species in the Laurentian Great Lakes (Ebener 1997). Lake whitefish is also a key component in the benthic food web of the Great Lakes. Historically, lake whitefish relied largely on the benthic amphipod *Diporeia* as a high-energy food source (Ihssen et al. 1981; Jude et al. 1981). Until the early 1990s, *Diporeia* was the dominant benthic macroinvertebrate in the upper Great Lakes and provided a key link between primary production and fish production (Gardner et al. 1990). Lake whitefish now consume prey such as dreissenid mussels following recent declines of *Diporeia* populations in lake Michigan and Ontario; this in part has resulted in lower lake whitefish condition and growth (Hoyle et al. 1999; Pothoven et al. 2001; Owens and Dittman 2003).

Determining energy densities in food web components is an important tool for quantifying trophic dynamics and assessing how ecosystem changes affect lake resources such as fish production. Despite the economic importance of lake whitefish, little work has been published on the energy density or lipid content of this fish species in the Great Lakes. Rand et al. (1994) suggested that energy content of a fish is the most direct measure of fish condition. Energy density, which is directly related to lipid content, provides information on the ability of fish to grow, reproduce, and overwinter (Rottiers and Tucker 1982). Energy content of a fish is also a measure of prey quality and quantity, a useful tool to evaluate ecosystem changes such as the decline of *Diporeia*, and a necessary input for bioenergetic models (Madenjian et al. 2000).

The goals of this study were to: (1) determine the relationships between energy density, total lipid content, and percent dry weight for lake whitefish; (2) evaluate seasonal, size, and sex related trends in energy density for lake whitefish in lakes Huron and Michigan; (3) compare energy density of lake whitefish in lakes Huron and Michigan and examine potential reasons (diet, prey abundance, lake whitefish density) for any differences; and (4) compare historical trends in body condition (length–weight) between lakes Huron and Michigan.

Methods

We conducted sampling off Alpena and Tawas City, Michigan in northwest Lake Huron and off Muskegon, Michigan in southeast Lake Michigan (Fig. 1). Alpena and Tawas City are located with in the WFH-06 and WFH-07 lake whitefish management zones respectively and Muskegon is located within the WFM-08 lake whitefish management zone (Fig. 1). We collected lake whitefish from water depths of 20–55 m using monofilament gill nets (5.1–11.4 cm stretch mesh) set overnight and with a 7.6 m semi-balloon bottom trawl (13 mm stretch mesh liner). We collected fish as part of a benthic food web study in Lake Huron and a bioenergetics study in Lake Michigan. Sampling took place May to September 2002–2004 in Lake Huron and April to November 2002–2003 in Lake Michigan. Sample periods were defined as spring (April–June), summer (July–August) and fall (September–November). We recorded total length (nearest mm) and weight (nearest gram) for each fish. After the stomach contents were removed, we double wrapped fish in foil, bagged, and froze them.

In the laboratory, we grouped lake whitefish from Lake Michigan into 5-fish composites based on 25.4 mm size intervals for each season. We used individual fish for analysis for Lake Huron. We processed fish in a Hobart 4822 grinder and homogenized them with a blender. To determine energy density, we dried a 20–30 g subsample at 70°C to a constant weight (approximately 2 days) (Hartman and Brandt 1995), ground it with a mortar and pestle, and then combusted a 1 g subsample in a (Parr 1261 isoperibol) bomb calorimeter that was standardized with benzoic acid. We determined three energy density estimates from six individual fish initially to estimate within-sample variability. Mean coefficient of variation within a sample was 1.19% so only one subsample was measured for each fish or composite thereafter. Energy density is reported on a wet weight basis.

We plotted energy density against fish weight to investigate the effects of fish size on energy density. We plotted energy density of lake whitefish from composites against the mean weight of the five fish used to form the composite. We used an analysis of covariance (ANCOVA) with fish weight as the covariate to examine differences in energy density between lakes, seasons, and sex.

We determined lipid content for composite samples from Lake Michigan only. Lipids were solvent extracted and analyzed gravimetrically according to a

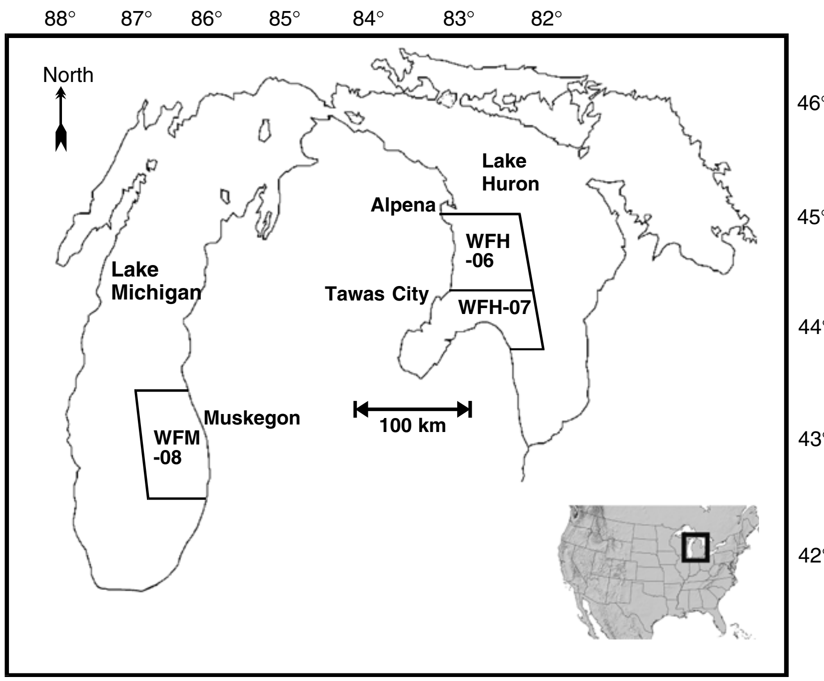

Fig. 1 Map of lakes Michigan and Huron showing field sampling sites and associated whitefish management zones

modified method described by Schmidt (1995). We dried 20 g of tissue homogenate with anhydrous sodium sulfate and Soxhlet extracted for 18 h with a 50:50 mixture of dichloromethane and hexane. The extract was then passed through a sodium sulfate drying column and evaporated under nitrogen with a Zymark Turbovap concentrator to a 10 ml final volume. An aliquot of the concentrate was evaporated under static conditions in a fume hood and analyzed gravimetrically for percent lipids. We expressed percent lipid on a wet weight basis. We determined the relationships between energy density, percent dry weight, and percent lipids using simple linear regression models. We compared the slope relating percent dry weight to energy density between lakes or sites with a *t*-test (Zar 1974).

To evaluate body condition, we used length–weight data of lake whitefish collected during monitoring of the commercial fishery in each respective management zone. We collected data every year between 1985 and 2003 in Lake Michigan and intermittently between 1981 and 2003 in Lake Huron. Length and weight were natural log transformed. We defined body condition as the transformed weight adjusted for differences in transformed total length among years and lakes using ANCOVA (Pothoven et al. 2001; Hoyle 2005). We pooled data over the entire 1981–2003 period and compared condition between lakes Huron and Michigan using ANCOVA. We used catch rates (kg per lift) of lake whitefish from commercial large mesh trap nets to evaluate fish density in each sampling area during 2002–2003. We also used catch rates (number per hour) from our fishery independent bottom trawl collections to corroborate densities calculated from commercial harvest catch data.

We identified all prey contents from each individual lake whitefish, counted, and weighed (wet) them to determine diet composition. We grouped prey into the broad categories of *Diporeia*, *Mysis*, zooplankton, Mollusca, and other. We report diets as percent of the total summed wet weight of prey across all fish because this measure is correlated with total caloric consumption (Pope et al. 2001).

To determine *Diporeia* abundance at each site, we collected benthic invertebrates in May to September 2002–2003 at 30- and 45-m stations in Lake Huron, and in April–October 2002–2003 at a 45-m station in Lake Michigan. Samples were taken in triplicate at each station with a Ponar grab and washed through a 0.5 mm nitex mesh net. Retained material was preserved in 5% formalin containing rose bengal stain and counted in the laboratory. Data are reported as the mean density of *Diporeia* for each station for 2002–2003.

Results

We analyzed a total of 240 individual fish for Lake Huron and 43 composites for Lake Michigan. Energy density increased with lake whitefish weight up to 800 g and then remained relatively constant with further increases in weight (Fig. 2). Therefore, we fitted separate regressions relating energy density to weight for lake whitefish ≤800 g (small) and for fish >800 g (large) for both lakes Michigan and Huron (Table 1). Energy density did not differ between Alpena and Tawas City for small (ANCOVA: $F = 2.96$; df = 1, 196; $P = 0.09$) or large lake whitefish (ANCOVA: $F = 0.43$; df = 1, 38; $P = 0.52$), so data were combined for all further Lake Huron analyses. For small lake whitefish, energy density (adjusted for weight) was significantly higher in Lake Michigan than Lake Huron (5,851 vs. 4,871 J g^{-1}) (ANCOVA: $F = 83.31$; df = 1, 217; $P < 0.01$). For large lake whitefish, adjusted energy density was also higher in Lake Michigan than Lake Huron (7,591 vs. 5,855 J g^{-1}) (ANCOVA: $F = 80.54$; df = 1, 60; $P < 0.01$). Energy density did not differ among seasons for small or large lake whitefish in either Lake Michigan or Lake Huron or between adult male and female fish.

Similar to energy density, lipid content and percent dry weight increased with weight for small lake whitefish, but did not change with weight for larger fish (Fig. 3). Lipids ranged from 3.1% to 9.2% for small lake whitefish and from 6.9% to 12.1% for large fish from Lake Michigan. Percent dry weight ranged from 20% to 28% for small fish from Lake Huron and 23% to 29% in Lake Michigan. For large lake whitefish, percent dry weight ranged from 22% to 32% in Lake Huron and 28% to 32% in Lake Michigan. Energy density was strongly correlated with percent dry weight and percent lipid content (Table 2). Energy density of lake whitefish from Lake Michigan increased at a significantly faster rate with increasing percent dry weight than that for lake whitefish from Lake Huron ($t = 5.40$; df = 279; $P < 0.001$) (Table 2). Lake whitefish energy density increased at similar rates with increasing percent dry weight at the two Lake Huron sites ($t = 0.60$; df = 236; $P > 0.50$).

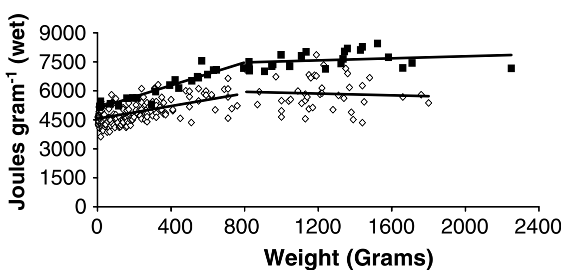

Fig. 2 Lake whitefish energy density (J g^{-1} wet) as a function of fish weight (g) for Lake Michigan (solid) and Lake Huron (open) during 2002–2004. Lake Michigan data are based on 5-fish composites, and Lake Huron data are based on individual fish. Separate regressions were fit for fish ≤800 g and >800 g for each lake

Lake whitefish transformed weight adjusted for transformed length (ANCOVA) differed significantly between Lakes Huron and Michigan during 1981–2003 (ANCOVA: $F = 7{,}084$; df = 1, 20,734; $P < 0.01$) (Fig. 4). Body condition began to decline in Lake Michigan after 1992. Long-term trends are more difficult to detect for fish in Lake Huron because of missing data, but lake whitefish condition has generally declined since the 1980s. Commercial catches in large mesh trap nets averaged 669 and 601 kg $lift^{-1}$ in WFH 06 and 07 (Lake Huron) respectively and 185 kg $lift^{-1}$ in WFM-08 (Lake Michigan) in 2002–2003. Bottom trawl catches in 2002–2004 corroborated the higher density of lake whitefish in Lake Huron, with catch rates of 40 fish h^{-1} in Lake Huron compared to 9 fish h^{-1} in Lake Michigan.

In Lake Michigan, small and large lake whitefish ate mainly a combination of molluscs and *Mysis*. In Lake Huron, small lake whitefish ate mainly zooplankton and molluscs and large fish ate mainly molluscs (Table 3). The vast majority of molluscs (96%) in the diet of small and large lake whitefish were quagga mussels *Dreissena bugensis*. *Diporeia* accounted for only a small portion of the diet of small and large lake whitefish in both lakes (<9%).

The small percentage of *Diporeia* in the diet corresponds to low *Diporeia* densities found in both lakes. At the 45-m site in Lake Michigan, the mean density of *Diporeia* in 2002–2003 was only 204 m^{-2}, a decrease from a mean density of 9,718 m^{-2} in 1997. Similar low densities were found in Lake Huron in 2002–2003. *Diporeia* were not found at either a 30-m

Table 1 Simple linear regression coefficients for energy density (J g^{-1} wet) as a function of lake whitefish weight (g) in lakes Huron and Michigan during 2002–2004

	≤800 g				>800 g			
	α	β	r^2	P	α	β	r^2	P
Lake Huron	4556	1.639	0.32	< 0.01	6130	−0.225	0.004	0.71
Lake Michigan	5094	2.962	0.87	< 0.01	7258	0.265	0.04	0.34

Lake Michigan data are based on 5-fish composites, whereas Lake Huron data are based on individual fish. α = Regression line intercept, β = regression line slope

site off Tawas City, whereas the mean density at 30-m and 45-m sites off Alpena was only 179 m^{-2}.

Discussion

Energy density of both small and large lake whitefish differed between southeast Lake Michigan and northwest Lake Huron. Energy density was 17 and 23% higher in Lake Michigan for small and large lake whitefish respectively during 2002–2004. Energy density, which is directly related to lipid content, is controlled by two factors, (1) energy content of a fishes diet and (2) feeding rate (Madenjian et al. 2000).

There are large differences in energy density of potential prey of lake whitefish, and dissimilar diets could explain at least some of the difference in energy density of fish from lakes Michigan and Huron. Based on data from southeast Lake Michigan, wet weight energy density of *Mysis* and *Diporeia* is 3,924 and 3,625 J g^{-1} respectively, whereas energy density of dreissenid mussels (including shell) is 1,331 J g^{-1}, although tissue energy density is much higher (3,500 J g^{-1}) (Pothoven, unpublished data). Energy density of zooplankton is also low (1,987 J g^{-1}) (Lantry and Stewart 1993) relative to *Diporeia*. The energy-rich *Mysis* and *Diporeia* accounted for about 28 and 40% of the diet of small and large fish respectively, in Lake Michigan during 2002–2003. In contrast, in Lake Huron, *Mysis* and *Diporeia* accounted for < 7% of the diet of both small and large fish. Fish in Lake Huron ate mainly zooplankton and molluscs. The consumption of shelled prey such as dreissenid mussels and small prey such as zooplankton is associated with lower lake whitefish growth (Ihssen et al. 1981; Pothoven et al. 2001). Although lake whitefish crush molluscs in the posterior region of their stomach (Owens and Lewis 2002), there are probably additional energetic costs associated with consuming large quantities of shelled prey (French and Bur 1996; Pothoven et al. 2001; Magoulick and Lewis 2002; Owens and Dittman 2003).

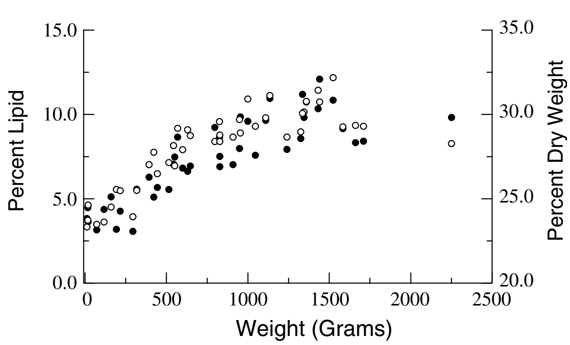

Fig. 3 Lipid content (% wet weight) (solid) and percent dry weight (open) of lake whitefish as a function of fish weight (g) for 5-fish composite samples from Lake Michigan during 2002–2003

In addition to prey energy density, factors that affect lake whitefish feeding rates such as fish abundance could affect their energy density. Growth of lake whitefish in Lake Huron and inland Canadian lakes decreased as abundance increased (Healey 1980; Spangler and Collins 1980; Henderson et al. 1983). Based on commercial large mesh trap net catches and our bottom trawl catches, whitefish density was much higher at our sites in Lake Huron than Lake Michigan in 2002–2003. Lower feeding rates and lipid content were associated with higher densities of a small benthivorous fish, slimy sculpin *Cottus cognatus*, in lakes Michigan and Ontario (Owens and Noguchi 1998; Madenjian et al. 2000). Therefore, increased competition for an increasingly limited food supply could be limiting feeding rates of lake whitefish in Lake Huron.

The 14% difference in body condition (length–weight) between lakes Huron and Michigan (1981–2003) corroborates differences observed for energy density. The data also indicates that the difference in

Table 2 Simple linear regression coefficients for lake whitefish energy density (J g^{-1} wet) as a function of percent dry weight and lipid content (% wet weight) in lakes Huron and Michigan during 2002–2004

	% Dry weight				Lipids (%)			
	α	β	r^2	P	α	β	r^2	P
Lake Huron	−2330	310	0.90	< 0.01	—	—	—	—
Lake Michigan	−4110	392	0.97	< 0.01	4177	365	0.90	< 0.01

Lake Michigan data are based on 5-fish composites, whereas Lake Huron data are based on individual fish. α = Regression line intercept, β = regression line slope

condition between the lakes is long standing. Lake whitefish in Lake Huron as well as Lake Michigan both relied on *Diporeia* during the period preceding the drastic decline of *Diporeia* in both lakes (Ihssen et al. 1981; Jude et al. 1981). Therefore, the present differences in prey energy content and whitefish abundance alone cannot fully explain the variation in energy density between the lakes. Spatial differences in energy densities between lakes Superior and Michigan for another coregonid species, bloater *Coregonus hoyi*, were attributed in part to variations in lake productivity (Vondracek et al. 1996). Maximum standing stocks of benthic prey, including *Diporeia*, were historically lower in Lake Huron than Lake Michigan even prior to the recent declines of *Diporeia* in both lakes (Alley and Powers 1970). Lake Huron had lower phosphorous concentrations and lower crustacean zooplankton biomass than Michigan at offshore sites in 1993–1995, which also suggests the lake may be overall less productive than Lake Michigan (Fahnenstiel et al. 1998).

There is little published historical data for lake whitefish energy density or lipid content in the Great Lakes. In 1969–1971 in Lake Michigan, a small sample of lake whitefish averaging 564 mm in length had energy densities of 12,219 J g^{-1} and lipid content of 22.4% (Rottiers and Tucker 1982). Energy densities of lake whitefish of a similar length from Lake Michigan in 2002–2003 ranged between 7,100 and 7,400 J g^{-1} and lipid contents ranged between 8.3% and 8.4%. The decrease in energy density over time is consistent with the decrease in body condition observed over the 1985–2003 period. Declines in lake whitefish condition in Lake Michigan have been attributed to the arrival of zebra mussels and subsequent decline of *Diporeia* as well as increases in lake whitefish abundance over the same period (Pothoven et al. 2001).

Lake whitefish energy density did not differ seasonally in either Lake Michigan or Lake Huron. Similarly, lipid content of bloater also did not differ seasonally in Lake Michigan (Madenjian et al 2000). Some studies suggest that energy reallocation and decreased feeding prior to spawning can influence fish energy content (Flath and Diana 1985; Vondracek et al. 1996). In Lake Superior, energy density of bloater increased in the fall prior to spawning, whereas that of another coregonid, lake herring *Coregonus artedi*, did not (Vondracek et al. 1996). The authors suggested that bloaters shifted energy toward gonad development or storage for over wintering, whereas lake herring gonad development

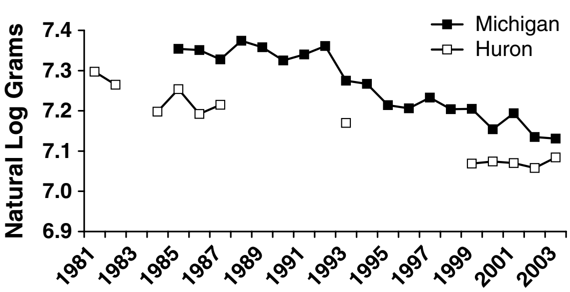

Fig. 4 Natural log transformed weight (g), adjusted for differences in natural log transformed total length (mm) among years and lakes (ANCOVA) for lake whitefish from commercial trap nets in Lake Michigan (WFM-08) and Lake Huron (WFH-06 and WFH-07) during 1981–2003

Table 3 Diet composition (percent total wet weight) for two size classes of lake whitefish in lakes Michigan and Huron during 2002–2004

	≤800 g		>800 g	
	Michigan	Huron	Michigan	Huron
Diporeia	3	<1	9	3
Mysis relicta	25	6	31	<1
Mollusca	56	30	46	93
Zooplankton	<1	51	<1	2
Other	16	13	14	2
N	112	348	200	37

N = number of fish examined that had food in their stomachs occurred through the mobilization of energy from other components of the fish and not as a result of increased feeding (Vondracek et al. 1996). Lake whitefish energy content did not change prior to spawning in the fall in this study.

Energy density was correlated with lake whitefish weight for smaller fish (≤800 g), but did not change with increasing weight for larger fish in either lake. The accumulation of lipids decreases with fish age, corresponding with maturity and slower growth (Rottiers and Tucker 1982). As expected, there also was a strong correlation between percent dry weight and energy density. However, the slopes of the relationship between percent dry weight and energy density differed for fish between lakes Michigan and Huron. There was no difference in the relationship for fish from the two sites on Lake Huron. Percent dry weight versus energy density relationships differed among lakes for several fish species in another study as well (Vondracek et al. 1996).

Energy density is an important variable to consider when evaluating condition or health of a fish stock (Rottiers and Tucker 1982; Rand et al. 1994). This study provides evidence for spatial variation in lake whitefish energy density between southeastern Lake Michigan and northwestern Lake Huron. Both differences in prey energy content as well as factors affecting fish feeding rate appear to influence energy content across the two lakes. Accounting for spatial variation in energy content could be an important factor for bioenergetics modeling of lake whitefish populations, as well as for evaluating changes in fish health in the future.

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References

Alley WP, Powers CF (1970) Dry weight of the macrobenthos as an indicator of eutrophication of the Great Lakes. Proceedings, Thirteenth Conference of Great Lakes Research. International Association of Great Lakes Research, Ann Arbor, Michigan, pp 595–600

Ebener MP (1997) Recovery of lake whitefish populations in the Great Lakes. Fisheries (Bethesda) 22(7):18–22

Fahnenstiel GL, Krause AE, McCormick MJ, Carrick HJ, Schelske CL (1998) The structure of the planktonic food-web in the St. Lawrence Great Lakes. J Great Lake Res 24:531–554

Flath LE, Diana JS (1985) Seasonal dynamics of the alewife in southeastern Lake Michigan. Trans Am Fish Soc 114:328–337

French JRP, Bur MT (1996) The effect of zebra mussel consumption on growth of freshwater drum in Lake Erie. J Freshwater Ecol 11:283–289

Gardner WS, Quigley MA, Fahnenstiel GL, Scavia D, Frez WA (1990) *Pontoporeia hoyi*—a direct trophic link between spring diatoms and fish in Lake Michigan. In: MM Tilzer, C Serruya (eds) Large lakes: ecological structures and functions. Springer-Verlag, Berlin, Germany, pp 632–644

Hartman KJ, Brandt SB (1995) Estimating energy density of fish. Trans Am Fish Soc 124:347–355

Healey MC (1980) Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can J Fish Aquat Sci 37:255–267

Henderson BA, Collins JJ, Reckahn JA (1983) Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. Can J Fish Aquat Sci 40:1556–1567

Hoyle JA (2005) Status of lake whitefish (*Coregonus clupeaformis*) in Lake Ontario and the response to the disappearance of *Diporeia* spp. In: Mohr LC, Nalepa TF (eds) Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fisheries Commission Technical Report 66, Ann Arbor, Michigan, pp 47–66

Hoyle JA, Schaner T, Casselman JM, Dermott R (1999) Changes in lake whitefish (*Coregonus clupeaformis*) stocks in eastern Lake Ontario following *Dreissena* mussel invasion. Great Lake Res Rev 4:5–10

Ihssen PE, Evans DO, Christie WJ, Reckahn JA, DesJardine RL (1981) Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Can J Fish Aquat Sci 38:1790–1807

Jude DJ, Heang TT, Heufelder GR, Schneeberger PJ, Madenjian CP, Rutecki TL, Mansfield PJ, Auer NA, Noguchi GE (1981) Adult, Juvenile and larval fish populations in the vicinity of the J. H. Cambell power plant, eastern Lake Michigan, 1977–1980. University of Michigan, Great Lakes Research Division, Special Report No. 86, Ann Arbor, Michigan, 364 pp

Lantry BF, Stewart DJ (1993) Ecological energetics of rainbow smelt in the Laurentian Great Lakes: An interlake comparison. Trans Am Fish Soc 122:951–976

Madenjian CP, Elliot RF, DeSorcie TJ, Stedman RM, O'Connor DV, Rottiers DV (2000) Lipid concentrations in Lake Michigan fishes: seasonal, spatial, ontogenetic, and long-term trends. J Great Lake Res 26:427–444

Magoulick DD, Lewis LC (2002) Predation on exotic zebra mussels by native fishes: effects on predator and prey. Freshwater Biol 47:1908–1918

Owens RW, Noguchi GE (1998) Intra-lake variation in maturity, fecundity, and spawning of slimy sculpins (*Cottus cognatus*) southern Lake Ontario. J Great Lake Res 24:383–391

Owens RW, Dittman DE (2003) Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. Aquat Ecosyst Health Manage 6:311–323

Pope KL, Brown WG, Duffy WG, Michaletz PH (2001) A caloric based evaluation of diet indices for largemouth bass. Environ Biol Fishe 61:329–339

Pothoven SA, Nalepa TF, Schneeberger PJ, Brandt SB (2001) Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. N AmJ Fish Manage 21:876–883

Rand PS, Lantry BF, R O'Gorman, Owens RW, Stewart DS (1994) Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. Trans Am Fish Soc 123:519–534

Rottiers DV, Tucker RM (1982) Proximate composition and caloric content of eight Lake Michigan fishes. U. S. Fish and Wildlife Service Technical Paper 108. Washington, DC, 8 pp

Schmidt LJ (1995) Extraction and lipid separation of fish samples for contaminant analysis and lipid determination. United States Geological Survey Standard Operation Procedure SOP NO. HC521A

Spangler GR, Collins JJ (1980) Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can J Fish Aquat Sci 37:2039–2046

Vondracek B, Giese BD, Henry MG (1996) Energy density of three fishes from Minnesota waters of Lake Superior. J Great Lake Res 22:757–764

Zar JH (1974) Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New York, 620 pp