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Changes in Diet and Body Condition of Lake Whitefish in Southern Lake Michigan Associated with Changes in Benthos

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Abstract.—We evaluated the long-term trends of the benthic macroinvertebrate community (1980–1999) and biological attributes of lake whitefish *Coregonus clupeaformis* (1985–1999) in southeastern Lake Michigan. We also determined what food types were important to lake whitefish in an area where the amphipod *Diporeia* had not yet declined in 1998 and how the diet of lake whitefish changed as *Diporeia* declined during 1999–2000. Zebra mussels *Dreissena polymorpha* invaded the study area in 1992; *Diporeia* began to decline in 1993 and was nearly absent by 1999. The body condition of lake whitefish decreased after 1993 and remained low thereafter. The length at age and weight at age of lake whitefish was lower in 1992–1999 than in 1985–1991. After declines of *Diporeia* off the city of Muskegon, Michigan, between 1998 and 1999–2000, the proportion of *Diporeia* in the diet by weight fell from 70% to 25% and the percent occurrence decreased from 81% to 45%. In contrast, the proportion of lake whitefish that ate other prey, such as *Mysis relicta* (an opossum shrimp), ostracods, oligochaetes, and zooplankton, increased in the same period. At sites south of Muskegon, where the density of *Diporeia* has been low since 1998, chironomids, zebra mussels, and fingernail clams (Shaeriidae family) were the most important diet items of lake whitefish. Decreases in body condition and growth are associated with the loss of the high-energy prey resource *Diporeia*, the consumption of prey with lower energy content, such as zebra mussels, and possible density-dependence. Commercial harvests of lake whitefish will probably decrease because of low body condition and growth. Future management may require changes in harvest quotas, size restrictions, and depth restrictions as zebra mussel-related impacts spread northward in Lake Michigan.

Historically, lake whitefish *Coregonus clupeaformis* were a mainstay of the commercial fishery in Lake Michigan and other Laurentian Great Lakes (Fleischer 1992). A fishery collapse in Lake Michigan in the 1950s was attributed to pollution, overfishing, and pressure from sea lampreys *Petromyzon marinus* (Wells and McLain 1973). Lake whitefish stocks began to recover in Lake Michigan in the 1970s, and catches currently equal or exceed past levels (Baldwin et al. 2000). During 1990–1998, the average annual commercial harvest of lake whitefish from Lake Michigan was 3,305 metric tons, which accounted for nearly 40% of the total commercial catch in Lake Michigan (P. Schneeberger, Michigan Department of Natural Resources,unpublished data; Baldwin et al. 2000).

Zebra mussels *Dreissena polymorpha* invaded Lake Michigan in 1989 (Marsden et al. 1993) and quickly spread throughout nearshore areas of the southern basin (Nalepa et al. 1998). The benthic amphipod *Diporeia* began to decline in 1993 in southern Lake Michigan, perhaps because zebra

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mussels filtering limited food availability (Nalepa et al. 1998; 2000). *Diporeia* also declined after invasions by zebra mussels and quagga mussels *Dreissena bugensis* in Lake Ontario (Hoyle et al. 1999) and Lake Erie (Dermott and Kerec 1997). *Diporeia* are a trophic link between pelagic primary production and fish production in Lake Michigan (Gardner et al. 1985). Many fish species, including lake whitefish, that historically ate *Diporeia* could be adversely affected if this prey becomes scarce (Ihssen et al. 1981; Jude et al. 1981; Hoyle et al. 1999).

Our first objective was to quantify long-term trends in the benthic macroinvertebrate community (1980–1999) and biological attributes of lake whitefish (1985–1999) in southeastern Lake Michigan. We expected that body condition, length at age, and weight at age of lake whitefish would decrease in association with changes in the benthos related to *Dreissena* invasion (Hoyle et al. 1999). Our second objective was to quantify the diet of lake whitefish relative to the abundance of *Diporeia* in southeastern Lake Michigan in 1998–2000. We expected that *Diporeia* would be an important component of the diet of lake whitefish and that, as *Diporeia* decreased, alternative prey (e.g., mollusks) would be eaten (Hoyle et al. 1999).

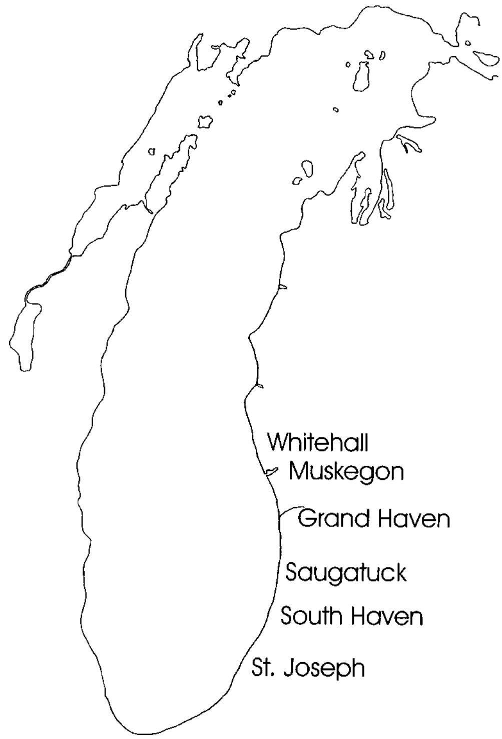

FIGURE 1.—Map of Lake Michigan showing sampling locations for lake whitefish and macroinvertebrates in 1985–2000.

Methods

Benthic macroinvertebrates were collected from a site (H-31) located at a depth of 45 m off the city of Grand Haven, Michigan (Nalepa et al. 1998; Figure 1). Sampling occurred three times each year (spring, summer, autumn) in 1980–1981, 1986–1987, and 1992–1993 and one to six times each year in 1994–1999. Samples were taken in triplicate 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. Macroinvertebrates were identified and counted using a low-power magnifier lamp (1.5×), and were measured using a computer image analysis system. Mean annual densities for the site were calculated.

Long-term biological attributes of lake whitefish were determined from fish that were collected by the Michigan Department of Natural Resources from commercial trap nets in southeastern Lake Michigan. The management zone for lake whitefish in southeastern Lake Michigan extends from the cities of Saugatuck, Michigan, northward to Whitehall, Michigan (Figure 1). Lake whitefish were collected three times each year (spring, summer, autumn) from 1985 to 1999. Fish were measured (total length), weighed, and scales were removed for estimating age. To evaluate condition for ages 2–16, we used an analysis of covariance (ANCOVA) with fish weight as the response, total length as the covariate, and two periods (1985–1991 and 1992–1999) as the treatment. Fish length and weight were $\log_e$-transformed to meet assumptions of linearity and parallelism. The mean length at age and weight at age of lake whitefish were compared between 1985 and 1991 and 1992–1998 with separate *t*-tests for ages 2–13. Older fish were excluded because of small sample size. Length and weight were not transformed because the large sample sizes conformed to the central limit theorem (Zar 1974). The two periods were chosen because zebra mussels were first found in the study area in 1992. We used SYSTAT for all statistical analyses ($\alpha = 0.05$).

Lake whitefish and benthic invertebrates were collected during 1998–2000 off the city of Muskegon, Michigan (Figure 1). Muskegon was chosen for short-term diet analyses because *Diporeia* had not declined there in early spring 1998 but were expected to do so in the near future (Nalepa

TABLE 1.—Date, depth, gear type, number of lake whitefish examined, and number of lake whitefish that contained food off five ports in southeastern Lake Michigan in 1998–2000; GN = gill net, BT = bottom trawl.

				Number of fish	
Port	Date	Depth (m)	Gear	Examined	With food
Muskegon	18 Jun 1998	19–29	GN	59	40
	21 Jun 1998	21	GN	24	21
	10 Oct 1998	20	GN	19	10
	19 Oct 1998	25–35	BT	12	8
	8 Jun 1999	25	BT	4	4
	10 Jun 1999	25	GN	7	5
	24 Jul 1999	15	BT	41	40
	25 May 2000	27	GN	25	17
	7 Aug 2000	45	BT	12	12
	25 Sept 2000	45	BT	3	3
	11 Oct 2000	45	BT	3	3
	24 Oct 2000	45	GN	20	19
Grand Haven	28 Apr 1999	18	GN	20	15
	24 Apr 2000	18	GN	7	7
Saugatuck	29 Apr 1999	18	GN	4	2
	4 May 1999	18	GN	3	2
	27 Apr 2000	18	GN	25	20
	1 May 2000	18	GN	9	6
South Haven	6 May 1999	18	GN	16	4
St. Joseph	11 May 1999	19	GN	19	12
	4 Aug 1999	34	GN	2	1
	31 May 2000	18	GN	39	31
	5 Jun 2000	18	GN	1	1

et al. 1998). Fish were collected from depths of 15–45 m using gill nets (6.4–17.8-cm stretch mesh) and a 7.6-m semiballoon bottom trawl (13-mm stretch-mesh cod liner; Table 1). Benthic invertebrates were collected three to eight times each year off Muskegon in conjunction with fish collections using the same sampling protocol described for the long-term study at Grand Haven. *Mysis relicta* (an opossum shrimp) were collected monthly at night at a 45-m-deep station using a 1-m diameter plankton net (1,000-μm mesh). Lake whitefish were also collected from depths of 18–34 m using gill nets off Grand Haven, Saugatuck, South Haven, and St. Joseph, Michigan in 1999–2000. These sites were chosen because *Diporeia* had declined to negligible levels at each location by 1998 (T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication).

All fish were weighed and measured, and their stomachs were removed and frozen. In the laboratory, stomachs were dissected (esophogus to pyloric caeca), and prey items were identified and counted. Prey lengths of whole organisms were measured using a computer image analysis system (Image-Pro 3.0). Prey length was converted to dry mass using length–weight regressions or species-specific mean weights (Johnson and Brinkhurst 1971; Nalepa and Quigley 1980; Smock 1980; Shea and Makarewicz 1989; Makarewicz and Jones 1990; Prejs et al. 1990; T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication). The dry weight of partially digested organisms was assumed to be equal to the mean weight of measured organisms. Micro-zooplankton (e.g., copepods, cladocerans) from stomachs were added to a known volume of water and subsampled with a Hensen–Stemple pipette. Total counts were multiplied by representative mean weights (Hawkins and Evans 1979) and summed to obtain the biomass of microzooplankton in the diet.

Diet was characterized by the percent of the total calculated dry weight for all fish combined and the frequency of occurrence (percent of fish containing a given prey type) as follows: Muskegon 1998; Muskegon 1999–2000; and Grand Haven, Saugatuck, South Haven, and St Joseph 1999–2000. These three groupings were chosen to represent conditions before, during, and after declines of *Diporeia*, respectively.

Results

Macroinvertebrate Community (1980–1999)

The density of *Diporeia* at station H31 off Grand Haven exceeded 10,000/m^2 during most of the 1980s and early 1990s (Figure 2). After 1992, density declined gradually to 110/m in 1999. Zebra

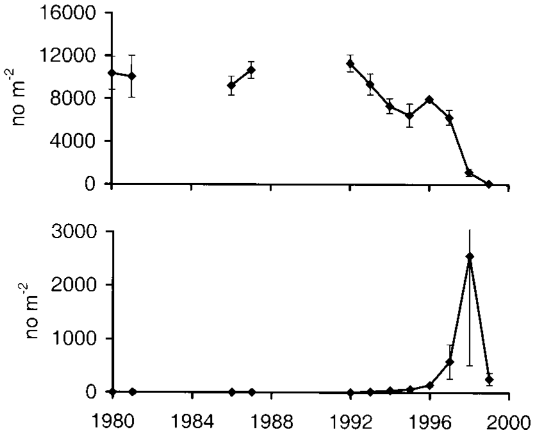

FIGURE 2.—Mean annual density (±1 SE) of *Diporeia* (upper panel) and zebra mussels (lower panel) at a 45-m-deep station offshore of Grand Haven, Michigan, during 1980–1999. Zebra mussels were first found in 1992 at a density of 2/m².

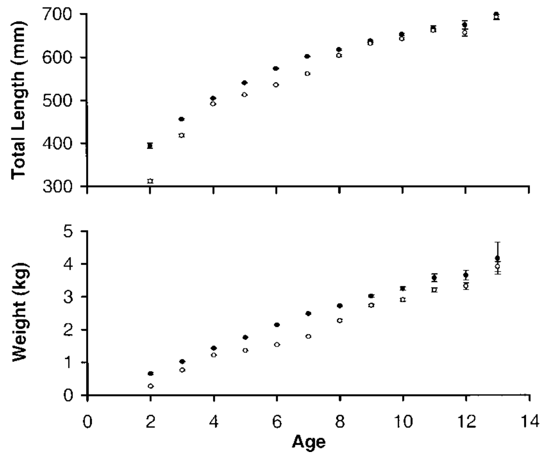

FIGURE 4.—Mean length at age (top panel) and weight at age (bottom panel) ± 1 SE of lake whitefish in southeastern Lake Michigan for 1985–1991 (solid circles) and 1992–1999 (clear circles).

mussels were first observed at Grand Haven in 1992 and increased rapidly from densities of 2–2,561/m² in 1998 and 258/m² in 1999 (Figure 2).

Condition and Growth of Lake Whitefish (1985–1999)

Compared with the 1985–1991 period, mean weight of lake whitefish adjusted for length declined significantly in 1992–1999 (F = 1,344, df = 1, 9,555, $P < 0.01$; Figure 3). The mean adjusted weight of lake whitefish began to decline in 1993 and remained low thereafter. Compared with the 1985–1991 period, mean length at age for ages 2–10 declined in 1992–1999, but this was not observed for ages 11–13; mean weight at age for ages 2–11 declined in 1992–1999, compared with 1985–1991, but did not change for ages 12–13 (Figure 4; Table 2).

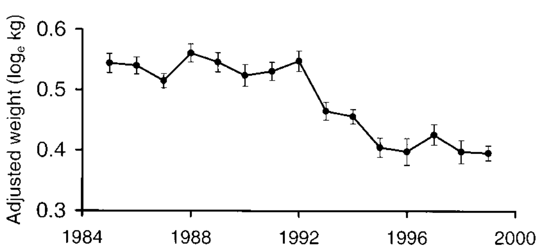

FIGURE 3.—Log$_e$-transformed mean weight (kg); ±1 SE, adjusted for log$_e$-transformed total length (mm), for lake whitefish (ages 2–16) from commercial trap nets in southeastern Lake Michigan in 1985–1999.

Prey Abundance and Lake Whitefish Diet (1998–2000)

The mean density of *Diporeia* off Muskegon (15–45 m) declined from 5,569/m² in 1998 to 1,422/m² in 1999–2000. The respective mean densities of other food types—chironomids, zebra mussels, and *M. relicta*—were 123, 1,058, and 121/m² in 1998 and 129, 633, and 48/m² in 1999–2000. In 1999–2000, *Diporeia* was rare or absent off Grand Haven, Saugatuck, South Haven, and St Joseph out to depths of 70 m (T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication).

A total of 79 (1988) and 103 (1999–2000) lake whitefish off Muskegon contained food (Table 1).

TABLE 2.—Results of t-tests (pooled variance) comparing two periods (1985–1991 and 1992–1999) for differences in lake whitefish (Lake Michigan) length at age and weight at age by age-class; $P < 0.05$.*

	Test statistic (t-value)		
Age	Length	Weight	df
2	−11.78*	−12.08*	98
3	−11.47*	−11.93*	811
4	−6.97*	−13.13*	1,585
5	−21.48*	−28.75*	2,416
6	−38.74*	−33.59*	1,951
7	−20.38*	−27.02*	1,183
8	−4.99*	−11.22*	666
9	−6.68*	−5.34*	405
10	−2.70*	−4.86*	271
11	−0.73	−2.87*	123
12	−1.17	−1.65	55
13	−0.58	−0.65	32

TABLE 3.—Percent of total dry weight and frequency of occurrence for diet items of lake whitefish collected from Lake Michigan off Muskegon, Michigan (number of lake whitefish used for analyses, *N*, = 79 in 1998 and 103 in 1999–2000), and four ports south of Muskegon (Grand Haven, Saugatuck, South Haven, and St. Joseph, Michigan, *N* = 101 in 1999–2000).

	Percent by weight			Frequency of occurrence (%)		
Prey item	Muskegon 1998	Muskegon 1999–2000	South 1999–2000	Muskegon 1998	Muskegon 1999–2000	South 1999–2000
Diporeia	70	25	<1	81	45	2
Chironomidae	22	27	57	87	68	70
D. polymorpha	8	2	22	67	23	58
Mysis relicta	4	31	6	6	16	12
Sphaeriidae	5	4	7	95	60	78
Gastropoda	5	<1	2	26	13	23
Oligochaeta	0	<1	<1	0	37	24
Ostracoda	0	1	1	0	36	19
Isopoda	<1	<1	0	2	3	0
Gammarus spp.	2	<1	4	5	1	3
Zooplankton	<1	5	<1	6	55	7
Insecta	<1	<1	<1	1	1	2
Fish	0	3	0	0	1	0

The length of fish used for diet analyses ranged from 154 to 432 mm (mean = 355 mm) in 1998 and from 165 to 514 mm (mean = 358 mm) in 1999–2000. *Diporeia* accounted for 70% of the diet by weight in 1998, but only 25% in 1998–1999 (Table 3). In contrast, the contribution of *M. relicta*, chironomid larvae and pupae, and zooplankton (mostly *Eurycerus lamellatus* and *B. cederstroemii*) increased in the same period. The contribution of zebra mussels (soft tissue only) to the diet by weight was 8% in 1998 and 2% in 1999–2000. Lake whitefish ate only relatively small Zebra mussels (<10 mm shell length). Other prey items included sphaeriids, gastropods, *Gammarus* spp. (amphipod), isopods, oligochaetes, ostracods, fish, and insects.

The proportion of lake whitefish from Muskegon that ate *Diporeia* decreased from 81% in 1998 to 45% in 1999–2000 (Table 3). The proportion of lake whitefish that consumed zebra mussels also decreased in the same period from 67% to 23%. The proportion of lake whitefish that ate chironomids and sphaeriids also decreased between 1998 and 1999–2000, but they were still eaten by a majority (>60%) of fish in both periods. In contrast, the proportion of lake whitefish that ate other prey such, as *M. relicta*, ostracods, oligochaetes, and zooplankton, increased between 1998 and 1999–2000.

A total of 101 lake whitefish off Grand Haven, Saugatuck, South Haven, and St. Joseph contained food in 1999–2000 (Table 1). The length of fish used for diet analyses ranged from 184 to 564 mm (mean = 418 mm). Chironomids and zebra mussels accounted for 79% of the diet by weight at these sites (Table 3). Most lake whitefish (>58%) ate chironomids, zebra mussels, and sphaeriids at these sites; approximately 20% consumed ostracods, gastropods, and oligochaetes, although these prey were a small part of the diet by weight. *Diporeia* accounted for less than 1% of the diet by weight and were eaten by only 2% of lake whitefish.

Discussion

Body condition, length at age (age 2–10), and weight at age (age 2–11) of lake whitefish decreased in southeastern Lake Michigan following the arrival of zebra mussels in 1992. The density of *Diporeia* also decreased after the proliferation of zebra mussels. The diet of lake whitefish off Muskegon reflected the decline of *Diporeia* between 1998 and 1999–2000 (i.e., *Diporeia* was still available but at reduced numbers). A decline in condition after a decline or loss of a high-energy prey item such as *Diporeia* is consistent with bioenergetic principles (Hanson et al. 1997). Alternative prey such as zebra mussels, chironomids, and *M. relicta* that are now important in lake whitefish diets, are energetically lower quality food than *Diporeia*. The caloric content of *Diporeia* (4,429 J/g wet mass) is higher than that of chironomids (2,428 J/g), zebra mussels (soft tissue) (1,047–2,478 J/g), and *M. relicta* (2,972–4,312 J/g; Schneider 1992; Hanson et al. 1997). Reduced densities of *Diporeia* could increase the foraging time needed to maintain the same ration that a lake whitefish obtains at higher *Diporeia* densities. Important alternative prey such as chironomids appear to be relatively uncommon in southeastern Lake Michigan, and use of this prey could result in increased search times.

The changes in diet composition of lake whitefish in southeast Lake Michigan are generally consistent with observations from Lakes Ontario and Erie, where diet consisted mainly of *Dreissena* spp. and other peleycypods after *Diporeia* disappeared (Hoyle et al. 1999; Cornelius 2000). Lake whitefish off Muskegon consumed zebra mussels before the significant *Diporeia* declines. Zebra mussels could reduce lake whitefish growth if indigestible shell material reduces the overall ration of a fish. Shell material accounts for 67–94% of the total dry weight of zebra mussels (French and Bur 1993). Shell material does not contribute to a fish's diet energetically but takes space in the digestive tract. Condition of lake whitefish in Lake Ontario decreased with the consumption of *Dreissena* spp. (Hoyle et al. 1999). In Lake Erie, freshwater drum *Aplodinotus grunniens* that supplemented their diet with zebra mussels grew slower than they did before the arrival of zebra mussels (French and Bur 1996). Other prey types, such as gastropods and sphaeriids, also contain a high percentage of indigestible shell material and may further contribute to decreases in energy intake in the absence of the high-energy prey *Diporeia*.

A high percentage of lake whitefish ate small-bodied prey such as zooplankton, ostracods, and oligochaetes after *Diporeia* declined off both Muskegon and ports further south. Consumption of small-bodied prey could reduce energy intake for lake whitefish. Populations of lake whitefish in Lake Huron, Lake Ontario, and inland Canadian lakes that ate large macroinvertebrates such as *Diporeia* grew faster than those that ate smaller prey such as zooplankton and small mollusks (Ihssen et al. 1981). This difference may be due to the increased energy expenditure required to locate, capture, handle, and process smaller prey (Ihssen et al. 1981).

Body condition and growth of lake whitefish could also decrease because of density-dependence. In southeastern Lake Michigan, mean catch per effort of lake whitefish in commercial trap nets increased from 118 kg/lift in 1985–1991 to 192 kg/lift in 1992–1998 (P. Schneeberger, Michigan Department of Natural Resources,unpublished data). Length at age of lake whitefish decreased with increased abundance in inland Canadian lakes and in Lake Huron (Healey 1980; Spangler and Collins 1980; Henderson et al. 1983). Weight at age of lake whitefish also decreased with abundance, but the trend was more variable (Healey 1980); however, Henderson et al. (1983) reported reduced growth mainly affected ages 2–3. In contrast, we found decreases in length at age for ages 2–10 and weight at age for ages 2–11. Density-dependent growth reductions are attributed to competition for food (Henderson et al. 1983), so the changes we found in food quality and quantity will exacerbate any effects of higher densities of lake whitefish.

In the future, zebra mussel-related effects are expected to worsen and spread throughout Lake Michigan. Quagga mussels were recently found in Lake Michigan and could cause a rapid acceleration of *Dreissena*-related impacts in the lake (Nalepa et al. 2001). Body condition and growth of lake whitefish are already decreasing in northern areas of Lake Michigan (P. Peeters, Wisconsin Department of Natural Resources, personal communication), and *Diporeia* began to decrease in northern Lake Michigan in 1999–2000 (T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication). Commercial harvest of lake whitefish will probably decrease because of poor growth and body condition, so fishery managers may need to adjust minimum length limits if the age at which fish are recruited to the fishery increases. Fishery managers could also increase harvest quotas to reduce density-dependant competition. If recruitment declines with lower condition, abundance of lake whitefish may also decrease, unless management successfully intervenes. Recruitment of lake whitefish decreased in Lake Ontario in association with *Dreissena* invasion and *Diporeia* declines (Hoyle et al. 1999).

Lake whitefish might move to deeper waters where *Diporeia* (Nalepa et al. 2000) and other large prey such as *Mysis relicta* are more abundant (Reynolds and DeGraeve 1972). Alewives *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, and juvenile lake trout *Salvelinus namaycush* moved to deeper water in Lake Ontario following *Dreissena* invasion (O'Gorman et al. 2000). Although food is more abundant in deeper water, there are energetic costs associated with feeding in colder water (O'Gorman et al. 2000). If lake whitefish move further offshore, they may become unavailable to trap nets, which are legislatively restricted to depths less than 27 m in Michigan.

Our results generate further questions about the ecology of lake whitefish for future studies. First, laboratory studies need to address how the feeding efficiency of lake whitefish depends on prey type, size, and density. Second, the energy density of native and introduced macroinvertebrates in the Great Lakes needs to be evaluated. Most energy density data on invertebrates was determined in studies that occurred outside the Great Lakes region (Schneider 1992; Hanson et al. 1997), and the energy content of native macroinvertebrates may be changing in response to *Dreissena* invasion (Nalepa et al. 2000). Finally, an index of the recruitment and abundance of lake whitefish, independent of the commercial fishery, is needed.

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