J. Great Lakes Res. 32:489–501
Internat. Assoc. Great Lakes Res., 2006

Feeding Ecology of Lake Whitefish in Lake Huron

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ABSTRACT. *We determined diet composition, feeding strategy, prey size, and effects of prey type on food weight and energy in stomachs for lake whitefish* Coregonus clupeaformis *in Lake Huron during 2002–04. Age-0 lake whitefish (73–149 mm TL) ate mainly large-bodied cladoceran zooplankton in the summer (July–mid September). Medium lake whitefish (≤ 350 mm TL excluding age-0) generally ate soft-bodied macroinvertebrates, especially Chironomidae larvae and pupae, in the spring (mid May-June). Zooplankton, if eaten, were generally most important in the summer. Molluscs were generally a minor part of medium lake whitefish diets. Large lake whitefish (> 350 mm) mainly ate molluscs, particularly quagga mussels* (Dreissena bugensis)*, despite geographic differences in mussel abundance. Large-bodied crustaceans (*Diporeia *spp.,* Mysis relicta, *Isopoda) were a minor part of large lake whitefish diets. Lake whitefish demonstrated a flexible feeding strategy, with individual specialization on some prey and generalized feeding on others. The size of benthic prey (*Diporeia *spp., Chironomidae, and* Dreissena *spp.) eaten increased with fish size and influenced the energetic value of prey for medium and large lake whitefish. The type of prey eaten affected the food and energy intake differently for each size class of lake whitefish. Age-0 lake whitefish that ate mainly zooplankton had more food and energy in stomachs than fish eating shelled prey or other macroinvertebrates. On the other hand, food weight in stomachs did not differ across prey groups for medium fish, but energy in stomachs was lowest for fish that ate shelled prey. For large lake whitefish, there was no difference in food weight or energy in stomachs for different prey groups.*

INDEX WORDS: *Lake whitefish, Lake Huron, diet, feeding ecology.*

INTRODUCTION

Lake whitefish *Coregonus clupeaformis* have long been a mainstay of the commercial fishery in the Laurentian Great Lakes (Ebener 1997) including Lake Huron, where annual harvests have averaged 4.2 million kg since 1993 and accounted for over 70% of the commercial catch (Mohr and Ebener 2005). Past population fluctuations were attributed to over-exploitation, predation and competition from invasive species, and habitat and water quality degradation (Ebener 1997). Recently lake whitefish growth and condition declined markedly in Lakes Huron, Michigan, and Ontario (Hoyle 2005, Mohr and Ebener 2005, Schneeberger *et al.* 2005). Changes in the food web, diet, density dependent growth, and climatic factors were all proposed explanations for decreased growth and condition (Hoyle *et al.* 1999, Pothoven *et al.* 2001, Owens and Dittman 2003, Nalepa *et al.* 2005).

Over the last 20 years, major changes have occurred in the benthos of the Great Lakes that appear to affect lake whitefish (Hoyle *et al.* 1999, Pothoven *et al.* 2001). Zebra mussels *Dreissena polymorpha* and quagga mussels *Dreissena bugensis* were introduced into the Great Lakes in the 1980s (Griffiths *et al.* 1991, Mills *et al.* 1993). The proliferation of *Dreissena* spp. has been implicated in a dramatic decline of the amphipod *Diporeia*

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spp., formerly the dominant benthic invertebrate in offshore waters of the Great Lakes and a key link between primary production and fish production (Gardner *et al.* 1990, Dermott and Kerec 1997, Nalepa *et al.* 1998, Lozano *et al.* 2001). Lake whitefish presumably ate *Diporeia* spp., which would provide a high-energy food source and an efficient pathway between the lower and upper foodwebs (Ihssen *et al.* 1981, Nalepa *et al.* 2005).

Whereas changes in lake whitefish diet following shifts in the benthic community have been well documented in Lake Michigan and Ontario (Hoyle *et al.* 1999, Pothoven *et al.* 2001, Hoyle 2005, Pothoven 2005), the diet and feeding ecology of lake whitefish in Lake Huron is relatively unknown despite the species economic and ecological importance. The objectives of this study were to 1) determine the current seasonal diet of lake whitefish throughout Lake Huron relative to regional differences in benthic invertebrate communities, 2) evaluate feeding strategies of lake whitefish in Lake Huron, 3) determine size structure of prey eaten by lake whitefish, and 4) quantify potential energetic consequences of different diets by examining a) the amount of food and energy in stomachs of lake whitefish that fed predominantly on different prey types and b) the amount of energy available from an individual prey for selected prey types.

METHODS

Lake whitefish were collected from eight Lake Huron management zones during 2002–04 (Fig. 1). Sampling occurred during two time periods, spring (mid May–June) and summer (July–mid September). No fish were collected in WFH-01 in the summer or in QMA 5-8 in the spring. Lake whitefish were collected in each management zone with overnight bottom gill nets sets. Gill nets used in United States waters were 823 m long × 1.83 m deep with nine panels of 5.1–15.2 cm stretch mesh in 1.27 cm increments. Gill nets used in Canadian waters were 400 m long × 1.83 m deep with 2–25 m panels of 3.2 and 3.8 cm stretch mesh and 7–50 m panels of 5.1–12.7 cm mesh in 1.27 cm increments. Gill net collections were part of assessment efforts by the Michigan Department of Natural Resources, United States Fish and Wildlife Service, and the Ontario Ministry of Natural Resources. Additional collections were made in WFH–06 and 07 at night using a 7.6-m semi-balloon 4-seam Skate model bottom trawl (13-mm stretched-mesh cod-liner). All fish were collected in water depths of 11–61 m.

All fish were weighed (nearest g) and measured (total length ± 1 mm) and stomachs (esophagus to pyloric caeca) were removed and frozen. In the laboratory, stomachs were dissected and prey items were separated, identified, counted, and weighed by prey group (wet weight). Measured weights of molluscs that were found in the stomachs included shells. Of the 1,122 stomachs that were examined, 24% were empty and not included in subsequent analyses unless otherwise noted. Diet analysis was done separately for age-0, medium (≤ 350 mm excluding age-0) and large (350–688 mm) lake whitefish. Age-0 fish ranged in length from 73–149 mm and were separated from older fish by aging scales and examining size frequency distributions. The size designation for medium and large fish was chosen because lake whitefish in the main basin of Lake Huron begin maturing around age-4 (Mohr and Ebener 2005) and the average total length of age-4 fish in our study was about 350 mm. Diet is reported as the percentage each prey item comprised of the total measured wet weight of all prey items summed across all fish for each respective size class, season and management zone. Lengths of whole prey were measured using a computer image-analysis system. Prey length (natural log transformed) was examined as a function of natural log transformed lake whitefish length using linear regression. Although multiple prey were measured for some whitefish, each prey length was treated as a separate data point for regression analysis.

To evaluate feeding strategy of lake whitefish, we used an approach proposed by Amundsen *et al.* (1996) where the prey specific abundance (P_i) is plotted against the frequency of occurrence. Prey specific abundance is the percentage a prey type comprises of all prey types in only those fish where that particular prey occurs (Amundsen *et al.* 1996). The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and unimportant prey in the lower left. The vertical axis represents the feeding strategy of the fish in terms of specialization (upper part of plot) and generalization (lower part of plot). Prey points in the upper left indicate specialization by individuals whereas points in the upper right indicate a dominant prey of the overall population (Amundsen *et al.* 1996).

To determine the role of diet composition on food and energy intake, we evaluated the total weight of food and corresponding energy in stomachs for lake whitefish that fed predominantly on different prey categories. Prey were placed in one of three cate-

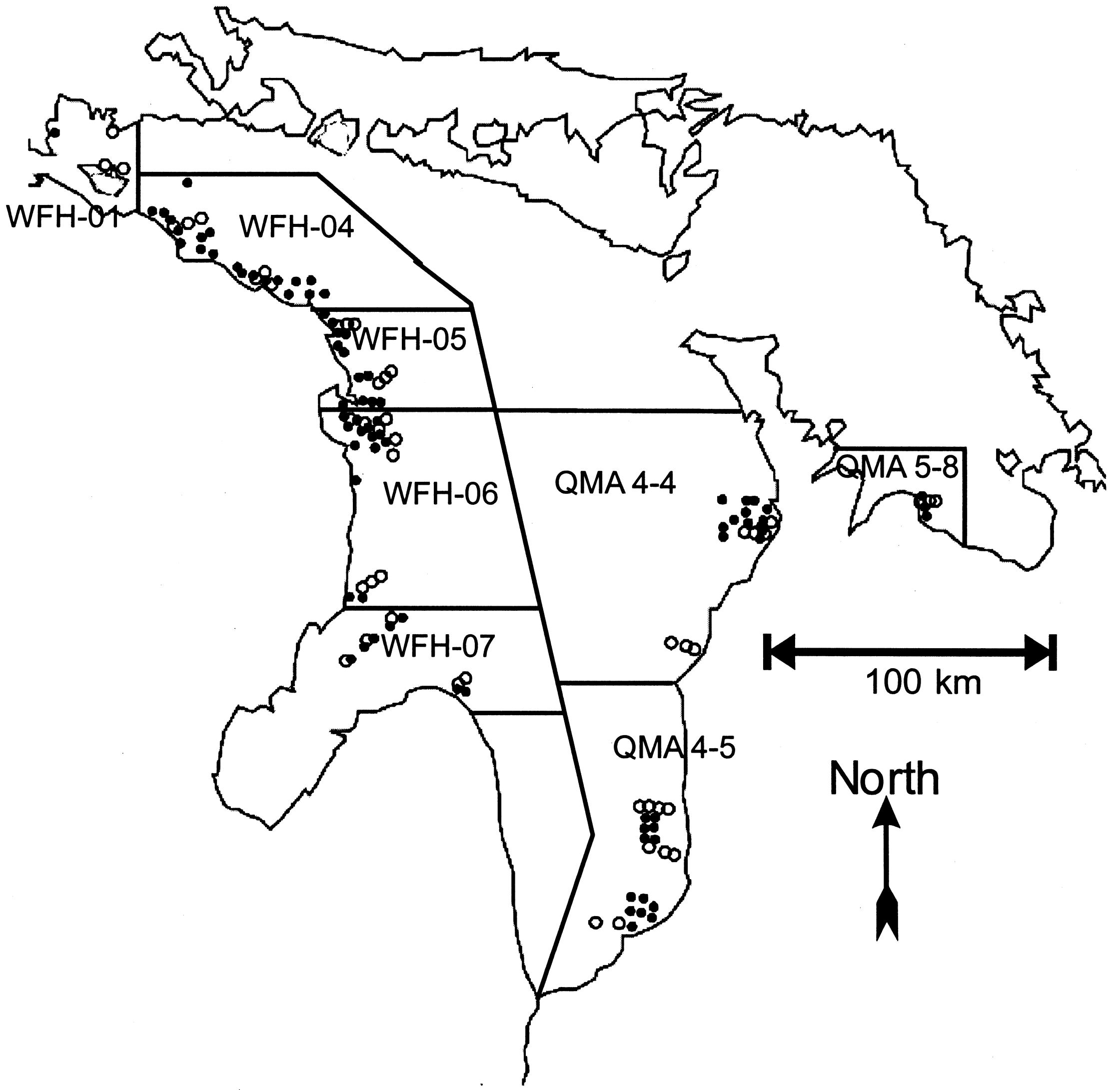

FIG. 1. Map of Lake Huron showing locations of management zones and sites where lake whitefish (closed circles) and benthos (open circles) were collected in 2002–04.

gories: zooplankton (Cladocera, Copepoda, and *Bythotrephes longimanus*), soft-bodied macroinvertebrates (Chironomidae larvae and pupae, *Diporeia* spp., Isopoda, *Mysis relicta*, Ephemeroptera nymphs), and shelled macroinvertebrates (*Dreissena* spp., Gastropoda, Sphaeriidae, Ostracoda). Although Ostracoda are crustaceans, they were included with shelled prey for this analysis due to their benthic nature and shell-like carapace. Individual fish were categorized as specializing on one of the three prey group categories if over 50% of the individual's diet was accounted for by one of the prey groups. Prey weights were converted into energy (Joules) using taxon-specific values of energy density (Lantry and Stewart 1993, Madenjian *et al.* 2006). The amount of food (mg food/g fish) or energy (J food/g fish) in stomachs was compared among (1) prey types and (2) between seasons for each of the three size classes of lake whitefish using Kruskal-Wallis (KW) tests with Chi-square as the test statistic. A nonparametric Tukey-type multiple comparisons test was used to examine pair-wise differences (Zar 1984). Only the fish collected in bottom trawls (WFH-06 and -07) were used for this analysis to minimize bias associated with digestion of stomach contents that could have occurred for fish that spent differing amounts of time in gill nets.

TABLE 1. Mean (± 1 SE) density (per m²) of select macroinvertebrate taxa in each of eight lake whitefish management zones in Lake Huron in water depths of 10–60 m in August 2003. Value in parenthesis is the number of sites sampled in each zone. Other includes Ephemeroptera and Isopoda. P-value gives results of Kruskal-Wallis test of differences between zones for each taxon assuming a Chi-square distribution; values that share a common letter were not significantly different (nonparametric Tukey-type multiple comparisons test).

	Diporeia spp.	Chironomidae	Sphaeriidae	Gastropoda	Zebra mussels	Quagga mussels	Other
WFH-01 (3)	457 ± 262[ab]	19 ± 16	29 ± 14	0 ± 0	17 ± 17[ab]	6,583 ± 6561[b]	0 ± 0
WFH-04 (6)	788 ± 500[ab]	92 ± 23	56 ± 38	0 ± 0	857 ± 547[b]	1,945 ± 625[b]	5 ± 5
WFH-05 (6)	553 ± 187[b]	43 ± 10	86 ± 26	0 ± 0	0 ± 0[a]	1,504 ± 935[b]	1 ± 1
WFH-06 (9)	234 ± 109[ab]	129 ± 31	86 ± 19	< 1 ± < 1	1 ± 1[a]	255 ± 173[ab]	0 ± 0
WFH-07 (6)	324 ± 317[ab]	70 ± 28	48 ± 29	0 ± 0	0 ± 0[a]	46 ± 28[ab]	0 ± 0
QMA 4-4 (7)	51 ± 46[ab]	130 ± 44	42 ± 15	0 ± 0	3 ± 3[a]	374 ± 367[ab]	0 ± 0
QMA 4-5 (9)	0 ± 0[a]	148 ± 95	36 ± 18	0 ± 0	1 ± 1[a]	0 ± 0[a]	0 ± 0
QMA 5-8 (3)	165 ± 165[ab]	277 ± 177	232 ± 189	0 ± 0	178 ± 178[ab]	32 ± 32[ab]	175 ± 175
K-W test	14.67	10.03	9.42	4.44	15.42	23.05	8.47
df	7	7	7	7	7	7	7
P-value	0.041	0.187	0.224	0.727	0.031	0.002	0.293

Seasonal values of food weight and energy included empty stomachs.

To determine the energetic contribution of an individual prey, prey lengths were converted to wet weights using species-specific weight-length relationships (Shea and Makarewicz 1989, Makarewicz and Jones 1990, Prejs *et al.* 1990, Cavaletto *et al.* 1996) and wet to dry weight relationships (Hewett and Johnson 1992). Individual prey weights were then converted to total Joules per individual using prey specific energy densities (Schneider 1992, Lantry and Stewart 1993, Madenjian *et al.* 2006). The energy available in an individual prey was compared using 2-factor ANOVA with fish size class (medium and large) and prey type as the two factors. Tukey's HSD test was used to examine pair-wise differences (Zar 1984).

Since lake whitefish are generally considered benthivores, we quantified potential benthic prey by taking triplicate Ponar grab samples at three to nine sites in each management zone in water depths of 10 to 60 m during August 2003. Samples were washed through a 0.5 mm Nitex mesh net and retained material was preserved in 5% formalin containing rose bengal stain. Macroinvertebrates were identified and counted using a low-power magnifier lamp (1.5X). Mean density of each major taxon was calculated for each management zone and differences among zones were determined using KW with Chi-square as the test statistic. A nonparametric Tukey-type multiple comparisons test was used to examine pair-wise differences (Zar 1984). Prey such as *Mysis relicta*, Ostracoda, and Oligochaeta were excluded from analysis because collection methods were not quantitative for the former two taxa and lake whitefish did not feed to any degree on the latter.

RESULTS

Benthos

Mean densities of major macroinvertebrate taxa in each management zone are given in Table 1. There was a significant difference among zones for *Diporeia* spp., quagga mussels, and zebra mussels. Average densities of *Diporei*a spp. ranged from 0 (QMA 4-5) to 788/m² (WFH-04). Quagga mussel density ranged from 0 (QMA 4-5) to 6,583/m² (WFH-01), but high within zone variability resulted in few pair-wise differences among zones. Zebra mussels were absent or uncommon in all zones except WFH-04 and QMA 5-8. Densities of Chironomidae, Sphaeriidae, Gastropoda, and other benthos did not differ significantly across management zones.

Age-0 Lake Whitefish

Age-0 lake whitefish were only collected in the summer and in the two management zones where bottom trawling occurred (WFH-06 and 07). Zooplankton accounted for the majority of age-0 lake whitefish diets in the summer, but Chironomidae larvae and pupae, *M. relicta*, and Ostracoda also ac-

TABLE 2. Age-0 lake whitefish diet expressed as percent of total measured wet weight of various prey items in two management zones in Lake Huron during summer 2002–2004. N = total number of fish with food in stomachs. Prey within each category are listed in order of decreasing overall importance. T = trace.

	Prey	WFH-06	WFH-07
Zooplankton	Zooplankton	53	98
	B. longimanus	T	0
Soft-Bodied	Chironomidae	26	2
	M. relicta	10	0
	Ephemeroptera	T	0
Shelled	Ostracoda	10	T
	Sphaeriidae	0	T
	N	67	104

counted for at least 10% of the diet in WFH-06 (Table 2). *Daphnia* spp. accounted for 98% of the zooplankton that were eaten.

Zooplankton were the dominant prey for age-0 lake whitefish, i.e. they were eaten by most fish and accounted for most of the diet weight in those fish (Fig. 2). However, some individuals also specialized on *M. relicta*, Ephemeroptera nymphs, and *B. longimanus*.

Food weight (KW test, $\chi^2 = 15.4$, df = 2, $p < 0.001$) and energy (KW test, $\chi^2 = 10.8$, df = 2, $p = 0.004$) depended on prey type for age-0 fish (Table 3). Stomachs of fish that fed mainly on zooplankton contained the highest amounts of food and energy (Table 3).

Medium Lake Whitefish

Overall, the main prey for medium lake whitefish were quagga mussels (24%), zooplankton (20%), Chironomidae larvae and pupae (17%), and *B. longimanus* (13%), but diet differed between seasons and across management zones (Table 4). Chironomidae larvae and pupae were a major prey for medium lake whitefish in the northwestern and west-central part of the lake (WFH-01, 04, 05, 06), especially during spring. The importance of Chironomidae decreased or remained constant in the summer, whereas contributions of *M. relicta*, quagga mussels, and *B. longimanus* generally increased. The highest proportions of *Diporeia* spp. in the diet for any management zone were in WFH-04 in summer (12%) and WFH-05 in spring (32%). The highest contributions of quagga mussels were

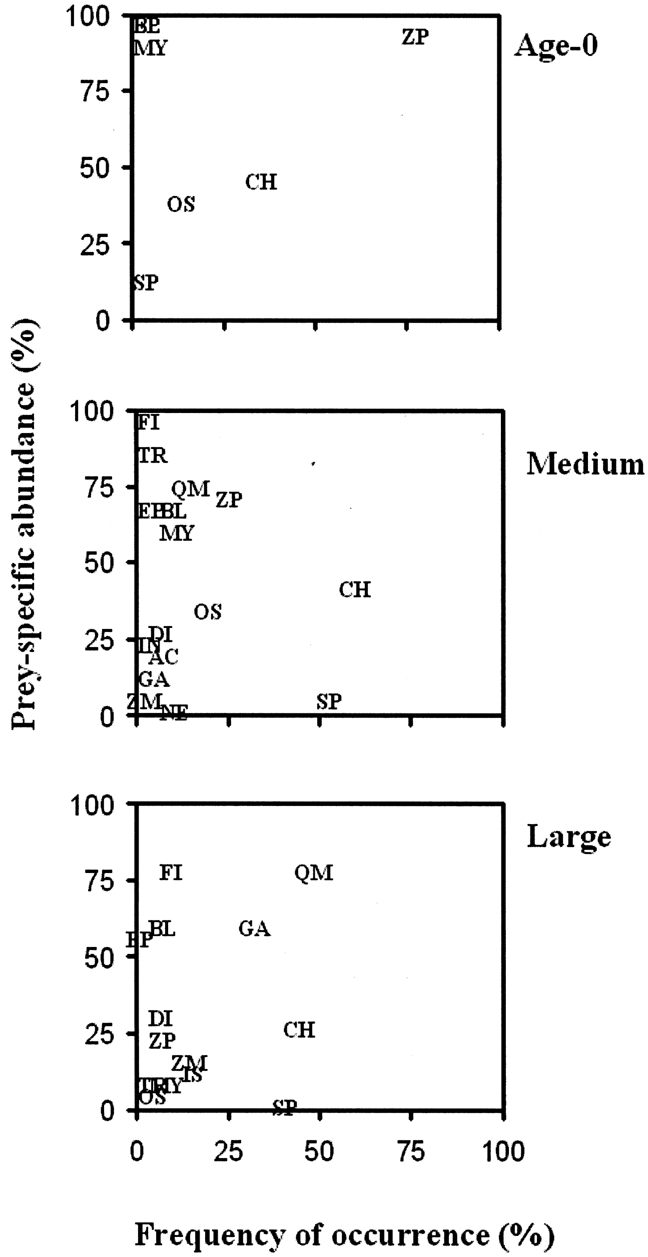

FIG. 2. Feeding strategy plot (prey specific abundance plotted against frequency of occurrence) for age-0, medium (≤ 350 mm excluding age-0) and large (> 350 mm) lake whitefish during summer 2002–2004 for two management zones in Lake Huron. AC = Acarina, BL = B. longimanus, CH = Chironomidae, DI = Diporeia spp., EP = Ephemeroptera, FI = fish, GA = Gastropoda, IN = terrestrial insect, IS = Isopoda, MY = M. relicta, NE = Nematoda, OS = Ostracoda, QM = quagga mussels, SP = Sphaeriidae, TR = Trichoptera, ZM = zebra mussels, ZP = zooplankton.

TABLE 3 Mean food weight (mg food/g fish, wet) and energy (Joules food/g fish, wet) (± 1 SE) in stomachs for three size classes of lake whitefish in Lake Huron during 1) spring and summer and 2) across prey groups for fish that fed predominantly on one type of prey (> 50% of diet weight). Values for food weight and energy during spring and summer include fish with empty stomachs. N = number of fish in each grouping. An asterisk denotes differences in food weight or energy in stomachs between seasons or across prey groups for each size class of fish (Kruskal-Wallis test p < 0.05); values that share a common letter were not significantly different (nonparametric Tukey-type multiple comparisons test).

	Age-0			< 350 mm			> 350 mm		
	Weight	Energy	N	Weight	Energy	N	Weight	Energy	N
Spring	-	-	-	2.31 (0.53)	6.77 (1.78)	32	2.18 (0.89)	3.44 (1.17)0	10
Summer	5.17 (0.43)	11.14 (0.91)	186	2.05 (0.35)	5.01 (1.18)	142	1.92 (0.60)	2.90 (0.80)	64
Soft-bodied	3.17 (0.53)* a	10.33 (1.81)* ab	40	2.99 (0.79)	10.71 (3.05)*a	54	0.34 (0.11)	1.13 (0.40)	18
Shelled	2.92 (0.82) ab	4.08 (1.18) b	11	2.28 (0.77)	3.22 (1.09) b	34	3.69 (1.13)	5.00 (1.50)	33
Zooplankton	6.73 (0.59) b	13.55 (1.19) a	119	2.22 (0.23)	4.21 (0.43) a	57	1.24 (0.25)	2.30 (0.44)	12

TABLE 4. Medium lake whitefish (< 350 mm TL excluding age-0) diet expressed as percent of total measured wet weight of various prey items in eight management zones in Lake Huron during spring (SP) and summer (SU) 2002–2004. N = total number of fish with food in stomachs. Prey within each category are listed in order of decreasing overall importance. T = trace.

		WFH 01	WFH 04		WFH 05	WFH 06		WFH 07		QMA 4-4		QMA 4-5		QMA 5-8
	Prey	SP	SP	SU	SP	SP	SU	SP	SU	SP	SU	SP	SU	SU
Zooplankton	Zooplankton	0	T	0	0	6	6	74	68	4	30	0	5	29
	Bythotrephes longimanus	0	0	8	0	0	41	0	6	0	0	0	3	9
Soft-Bodied	Chironomidae larvae/pupa	49	24	20	38	91	2	1	6	60	20	61	9	T
	Mysis relicta	0	0	36	21	0	19	10	5	2	21	0	0	0
	Ephemeroptera nymphs	0	0	0	0	0	0	0	0	0	0	0	0	58
	Trichoptera larvae	30	12	0	T	0	0	0	0	0	0	0	0	0
	Acarina	T	0	T	0	0	T	T	T	T	0	27	0	T
	Diporeia spp.	0	1	12	32	0	T	T	T	T	0	0	0	0
	Terrestrial insect adult	0	1	3	0	0	0	T	T	T	0	9	0	0
	Isopoda	1	1	0	0	0	0	0	T	0	0	0	0	0
	Nematoda	T	0	T	0	0	0	0	T	T	0	0	0	0
	Oligochaeta	0	T	0	0	0	0	0	0	1	0	T	T	0
	Gammarus spp.	0	0	0	0	0	0	0	0	T	0	0	0	0
Shelled	*Quagga mussels*	14	T	T	0	0	7	0	2	0	23	T	82	0
	Ostracoda	2	0	12	0	0	20	T	8	13	0	0	0	0
	Sphaeriidae	2	25	9	8	3	2	15	4	18	5	3	1	1
	Gastropoda	1	0	0	0	0	2	0	0	2	0	0	T	2
	Zebra mussels	T	0	0	0	0	0	0	1	T	0	T	T	0
Other	Fish	0	35	0	0	0	0	0	0	0	0	0	0	0
	N	11	11	20	12	14	54	13	64	34	7	15	30	18

in the summer in QMA 4-4 (23%) and QMA 4-5 (82%), but mussels accounted for < 7% of the diet in all other zones. In WFH-07, zooplankton accounted for most of the diet in both spring and summer. The zooplankton eaten were mainly copepods (100%) in the spring and a combination of copepods (58%) and *Daphnia* spp. (34%) in the summer. Zooplankton (100% *Daphnia* spp.) also accounted for about 30% of the summer diet in QMA 4-4 and QMA 5-8.

Medium lake whitefish generally had a mixed feeding strategy, with varying degrees of specialization and generalization on different prey (Fig. 2). Chironomidae and Sphaeridae were fed on generally, i.e., they were eaten by over half the fish, but did not account for over half the diet weight in those same fish. Some individual medium lake whitefish specialized on other prey including quagga mussels, zooplankton, *M. relicta*, *B. longimanus* Trichoptera larvae, fish, and Ephemeroptera nymphs.

Food weight (Mann Whitney U test, $\chi^2 = 0.46$, df = 1, p = 0.50) and energy (Mann Whitney U test, $\chi^2 = 0.67$, df = 1, p = 0.41) in stomachs did not differ by season for medium lake whitefish (Table 3). Food weight in stomachs did not differ by prey type (KW test, $\chi^2 = 5.04$, df = 2, p = 0.08), but food energy analysis indicated significant differences (KW test, $\chi^2 = 8.06$, df = 2, p = 0.018). Energy in stomachs was lowest for fish that ate shelled prey (Table 3).

Large Lake Whitefish

Overall, quagga mussels accounted for most (54%) of the diet of large lake whitefish along with Gastropoda (27%). Generally, these two prey types combined for the bulk of the diet in most management zones and seasons (Table 5). Instances where

TABLE 5. Large lake whitefish (> 350 mm TL) diet expressed as percent of total measured wet weight of various prey items in eight management zones in Lake Huron during spring (SP) and summer (SU) 2002–2004. N = total number of fish with food in stomachs. Prey within each category are listed in order of decreasing overall importance. T= trace.

		WFH 01	WFH 04		WFH 05		WFH 06		WFH 07		QMA 4-4		QMA 4-5		QMA 5-8
	Prey	SP	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SP	SU	SU
Zooplankton	*Bythotrephes longimanus*	0	0	1	0	6	0	2	0	5	0	32	0	33	0
	Zooplankton	0	0	1	0	2	0	1	0	15	T	0	0	T	67
Soft-Bodied	Chironomidae larvae/pupa	34	1	1	1	T	5	T	T	7	3	T	2	0	T
	Isopoda	T	6	0	T	T	T	0	0	0	T	0	0	0	0
	Diporeia spp.	0	0	6	T	0	T	2	5	T	T	1	0	0	0
	Mysis relicta	0	0	6	T	T	T	T	0	1	T	0	0	T	0
	Terrestrial insect adult	0	0	0	0	0	0	0	1	T	T	0	0	0	0
	Trichoptera larvae	2		0	0	0	T	0	0	0	T	0	0	0	0
	Ephemeroptera nymphs	0	0	0	0	0	0	0	0	0	0	0	0	0	22
	Oligochaeta	T	0	0	0	0	T	0	0	0	T	0	T	0	0
	Gammarus spp.	T	T	0	0	0	T	0	0	0	0	0	0	0	0
	Acarina	T	T	T	0	0	0	0	T	0	T	0	0	0	0
	Nematoda	0	0	0	0	0	0	0	0	T	T	0	0	0	0
Shelled	Quagga mussels	48	40	83	87	71	62	92	61	58	19	T	T	66	0
	Gastropoda	15	47	1	6	T	19	0	2	T	63	23	0	T	8
	Zebra mussels	T	T	0	T	T	8	1	7	0	13	T	0	T	2
	Sphaeriidae	T	T	1	T	T	3	T	1	6	1	1	0	T	1
	Ostracoda	0	0	0	0	T	0	T	T	T	T	0	0	0	0
Other	Fish	0	6	0	6	20	3	0	23	8	0	43	98	0	0
	N	27	57	15	40	34	30	18	10	38	62	10	4	11	5

quagga mussels or Gastropoda did not dominate the diet included QMA 4-4 (summer) where fish and *B. longimanus* combined with Gastropoda for most of the diet, QMA 4-5 (spring) where mostly fish were eaten, and QMA 5-8 where zooplankton and Ephemeroptera nymphs were eaten. The large crustacean macroinvertebrates *Diporeia* spp. and *M. relicta* never accounted for more than 6% of the diet in any management zone. Zooplankton (71% *Daphnia* spp.) and *B. longimanus* combined for 20% of the diet in WFH-07 in the summer. Fish were eaten by large lake whitefish in all management zones during at least one season except for WFH-01 and QMA 5-8. Fish eaten were mainly nine-spine sticklebacks *Pungitius pungitius* (43%) and round gobies *Neogobius melanostomus* (27%).

For large lake whitefish, quagga mussels were the most dominant prey, i.e., they were eaten by 50% of the fish and accounted for 78% of the diet weight in those fish (Fig. 2). Chironomidae were fed on generally, and other prey such as Gastropoda, fish, *B. longimanus*, and Ephemeroptera nymphs were specialized on by a few lake whitefish.

For large lake whitefish, food weight (Mann Whitney U test, $\chi^2 = 1.03$, df = 1, p = 0.31) and energy (Mann Whitney U test, $\chi^2 = 1.98$, df = 1, p = 0.16) in stomachs did not differ between seasons (Table 3). Food weight (KW test, $\chi^2 = 6.03$, df = 2, p = 0.05) and energy (KW test, $\chi^2 = 2.28$, df = 2, p = 0.319) in stomachs did not differ across prey groups (Table 3).

Prey Size

The length of quagga mussels (F = 541; df = 1, 711; p < 0.001; R^2 = 0.43), zebra mussels (F = 20; df = 1, 67; p < 0.001; R^2 = 0.23), *Diporeia* spp. (F = 126; df = 1, 112; p < 0.001; R^2 = 0.53), and Chironomidae larvae (F = 138; df = 1, 152; p < 0.001; R^2 = 0.48) in stomachs increased significantly with lake whitefish length, but the length of *M. relicta* (F = 1.2 df = 1, 38; p = 0.28; R^2 = 0.03) and *B. longimanus* (F = 0.04; df = 1, 48; p = 0.85; R^2 = 0.001) did not (Fig. 3).

For the statistical analysis of energy content of an individual prey, as derived from measured prey lengths, the interaction term between prey type and lake whitefish size class was significant (F = 5; df = 4, 1061; p < 0.001) so the significance of the main effects was not tested. Zebra mussels and other prey were not used for this analysis because of small numbers of measured prey from stomachs. An individual *M. relicta* contained the most energy of any prey eaten by medium lake whitefish. *Mysis relicta* and quagga mussels each contained more energy than individual *Diporeia* spp. or *B. longimanus* for large lake whitefish (Table 6). The average quagga mussel eaten by a large lake whitefish contained over 8 times as much energy as one eaten by a medium fish.

TABLE 6. Average measured length (mm) and calculated total energy (Joules) of selected prey items for medium (≤ 350 mm TL excluding age-0) and large (> 350 mm TL) lake whitefish. N = number of measured prey. Energy values across all individual cell means for medium and large lake whitefish that share a common letter were not significantly different (Tukey's HSD test).

Whitefish size	Prey	N	Length (mm)	Energy (Joules)
Medium	*Diporeia*	24	4.7	12.7 ad
	Mysis relicta	28	11.8	73.5 b
	Quagga mussels	131	3.7	6.9 a
	Chironomidae	137	6.1	13.2 ad
	B. longimanus	15	10.2	1.7 ac
Large	*Diporeia*	90	7.6	23.2 ad
	Mysis relicta	12	13.2	89.6 b
	Quagga mussels	582	8.1	57.9 b
	Chironomidae	17	10.4	48.1 bcd
	B. longimanus	35	10.0	1.6 a

DISCUSSION

Lake whitefish diets in Lake Huron changed with fish size, season, and geographic location. Age-0 lake whitefish, which were only collected in the west-central region of the lake, ate mainly large zooplankton in the summer. Large-bodied zooplankton including *Daphnia* spp. tend to be most abundant in the summer in Lake Huron (Barbiero *et al.* 2001). Medium lake whitefish generally ate soft-bodied macroinvertebrates, especially Chironomidae larvae and pupae, in the spring. Zooplankton, if eaten, were generally most important in the summer. Molluscs were generally a minor part of medium lake whitefish diets. Large lake whitefish mainly ate *Dreissena* spp. and Gastropoda but fish and zooplankton were also eaten. Large crustaceans (*M. relicta*, *Diporeia* spp., Isopoda) and Chironomidae larvae and pupae were generally a minor part of the diet of large lake whitefish in Lake Huron.

Geographic differences in lake whitefish diets did not necessarily reflect corresponding differences in

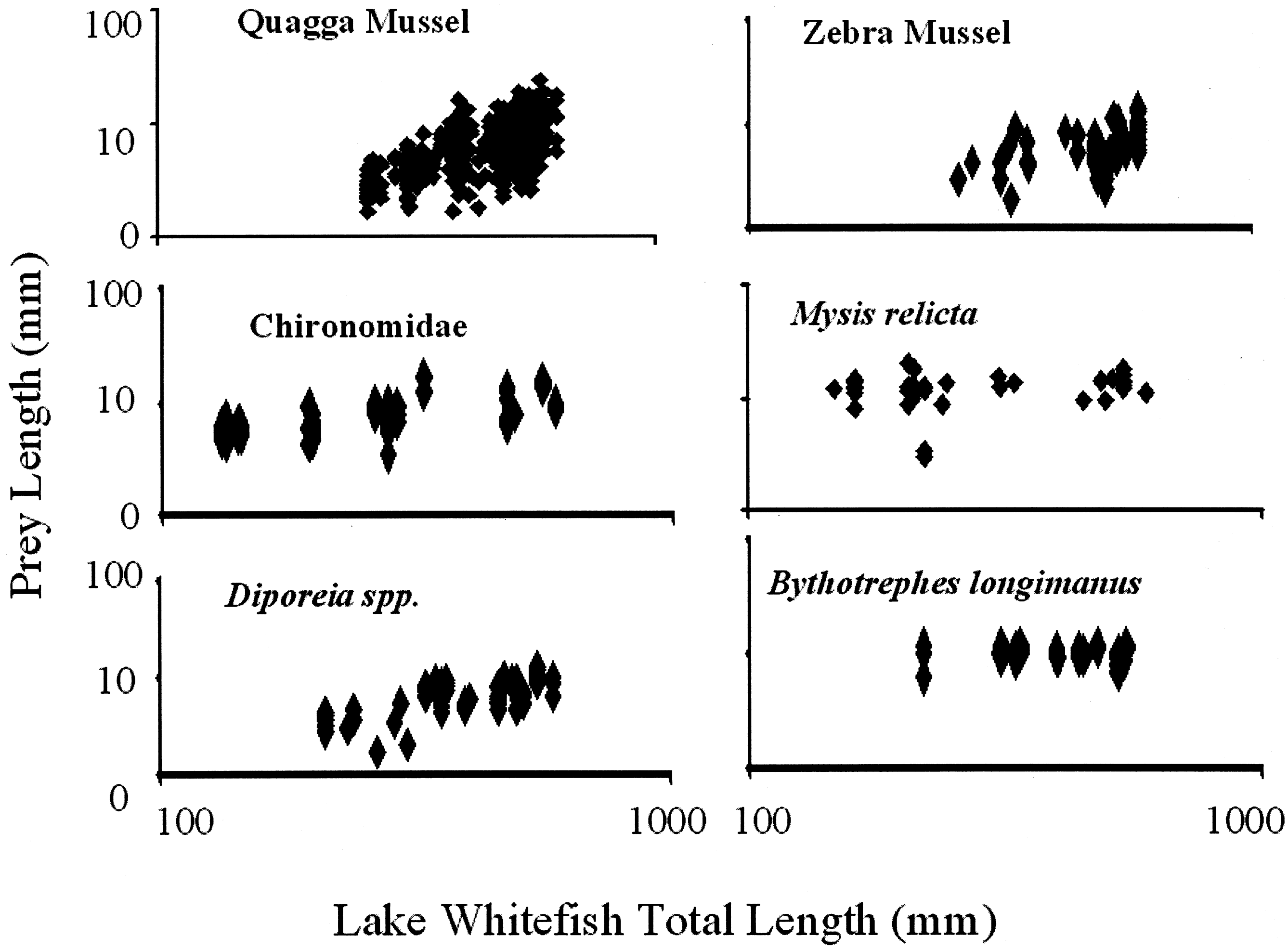

FIG. 3. Prey length plotted as a function of lake whitefish length in Lake Huron.

prey abundances as derived from the benthos samples. For example, although the highest contribution of *Diporeia* spp. to medium lake whitefish diets was in WFH-04 and 05 where *Diporeia* spp. was most abundant, almost no *Diporeia* spp. were eaten by large lake whitefish in the same area. Similarly, quagga mussels comprised most of the food eaten by large lake whitefish at nearly all sites although there were geographic differences in mussel abundance. Also, the highest contribution of quagga mussels to medium lake whitefish diets came from the eastern side of the lake where this prey was least abundant. These discrepancies suggest that prey selection may occur at much smaller scales than we were able to examine with this study which focused on diets and prey abundance at large regional scales and across a range of depths.

Most studies of the feeding ecology of lake whitefish indicate that there are ontogenetic changes in diet. In Lake Michigan, the importance of zebra mussels and Gastropoda increased as fish grew, but other macroinvertebrates such as *Diporeia* spp., *M. relicta*, Chironomidae, or Isopoda were still eaten in most areas of the lake (Pothoven 2005). In Flathead Lake, Montana, less zooplankton and more large bodied macroinvertebrates (*M. relicta*, Diptera), Pelecypoda, and fish were eaten as lake whitefish grew (Tohtz 1993). Similarly, common whitefish *Coregonus lavaretus* in Finland and Europe tended to eat less zooplankton and more benthic prey such as molluscs as well as amphipods, Diptera, Trichoptera, and Ephemeroptera as they grew (Sandlund *et al.* 1992, Tolonen 1999, Heikinheimo *et al.* 2000, Kahilainen *et al.* 2003). Thus, the low importance of non-mollusc macroinvertebrates in the diet of large lake whitefish in our Lake Huron study is a noticeable difference from lake and common whitefish diet studies in other lakes. Based on limited historical data, large lake whitefish in Lake Huron formerly utilized non-mollusc macroinvertebrates, particularly *Diporeia* spp. as a major food source (Ihssen *et al.* 1981). However, in 2002–2004, non-mollusc macroinvertebrates accounted for < 25% of the large lake whitefish diet in all but one management zone, and almost no *Diporeia* spp. were eaten. *Diporeia* spp. were still present in most areas of the lake but densities were much lower than those reported historically (approximately 5,000/m^2, T. Nalepa, unpublished data), suggesting they may no longer be abundant enough to be a profitable food source for large lake whitefish.

Quagga mussels were an important and consistent part of large lake whitefish diets throughout Lake Huron despite geographic differences in abundance and high within zone variability, but they were only a minor prey for medium lake whitefish. Quagga mussels were rare in Lake Huron in 2000 (T. Nalepa, unpublished data), but increased to densities over 1,000/m^2 in some of our sampling areas by 2003. Although large lake whitefish in the Great Lakes and common whitefish in Europe have typically included molluscs in their diet (Ihssen *et al.* 1981, Tolonen 1999, Kahilainen *et al.* 2003), the importance of shelled prey in the diet of lake whitefish in the Great Lakes appears to be increasing following the invasion of *Dreissena* spp. and subsequent decline of *Diporeia* spp. (Hoyle *et al.* 1999, Pothoven *et al.* 2001, Owens and Dittman 2003, Mohr and Ebener 2005).

Lake whitefish diets changed with season as well as fish size. The most notable seasonal trend was the consumption of zooplankton in the summer, when large bodied cladocerans and *B. longimanus* are available (Barbiero *et al.* 2001). The increased proportion of large zooplankton in the diet in the summer also generally coincides with decreases in Chironomidae larvae and pupae abundance, which tend to be most abundant during spring (T. Nalepa, unpublished data). Most diet studies indicate that all sizes of lake and common whitefish will take advantage of zooplankton as a food resource in the summer (Tohtz 1993, Tolonen 1999, Eckmann *et al.* 2002, Kahilainen *et al.* 2003). However, some studies indicate that both lake and common whitefish that eat benthic macroinvertebrates grow faster than those that eat smaller prey like zooplankton (Ihssen *et al.* 1981, Kahilainen *et al.* 2003). Common whitefish that usually feed on benthic prey might eat more zooplankton in periods of benthic food limitation and high intraspecific competition (Knudsen *et al.* 2003). Competition for the limited amounts of non-mollusc prey might be most severe for medium lake whitefish because they were less likely than larger fish to utilize abundant dreissenid mussels for food.

Eating zooplankton could have important life history consequences for lake whitefish. Lake whitefish stocks that ate large amounts of zooplankton have fewer pyloric caeca, more gill rakers and grew more slowly than fish that ate larger prey (Ihssen *et al.* 1981). Changes in morphological characteristics can occur relatively quickly when diets change (Bernatchez 2005). For example, few adult lake whitefish in Lake Huron specialized on pelagic prey, but if for some reason this feeding strategy was highly successful following changes in benthic prey (i.e., *Diporeia* spp. loss), then changes could occur in the morphology of lake whitefish stocks over a few generations (Bernatchez 2005). On the other hand, eating pelagic prey may simply reflect the flexible nature of lake whitefish feeding patterns and their ability to use locally abundant prey. A study in Finland found that planktonic crustaceans were the most important prey for several stocks of common whitefish irrespective of gill raker number (Heikinheimo *et al.* 2000).

The analysis of feeding strategy indicated the flexible nature of lake whitefish feeding. Even if a prey type was eaten by over half the fish and accounted for a large part of the diet weight, there were still some individual fish specializing on other prey types or feeding generally on others. A study in Finland indicated that common whitefish stocks that were flexible in habitat use and feeding habits were most likely to succeed (Heikinheimo *et al.* 2000). Adaptive flexibility in feeding is an important behavior especially when habitat is not productive (Mookerji *et al.* 1998). The individual specialization could also reflect individuals utilizing locally abundant prey at much smaller scales than our benthos sampling occurred (Mookerji *et al.* 1998, Pothoven *et al.* 2004).

The type of prey eaten affected the food and energy intake differently for each size class of lake whitefish. Age-0 lake whitefish appeared well adapted to consuming zooplankton because fish that ate mainly zooplankton had more food and energy in stomachs than fish eating macroinvertebrates or molluscs. Conversely, food weight in stomachs did not differ across prey groups for medium fish, but energy in stomachs was lowest for fish that ate molluscs. This suggests that medium fish eating molluscs might not be compensating for the lower energy in these prey relative to more energy rich non-mollusc macroinvertebrates. Zooplankton are generally digested faster than the other prey which might increase their food value to lake whitefish (Jobling 1987). For large lake whitefish, there was no difference in food weight or energy in stomachs for different prey groups. Lake whitefish appear to crush mussels (Owens and Dittman 2003), which would enable them to get low amounts of high-energy food from the mussel tissue (Magoulick and Lewis 2002). On the other hand, mussels are digested at a relatively slow rate so that, despite the similarity in food and energy intake across prey groups, net energy intake could still be higher for more rapidly digested prey (Andersen 2001, Kahilainen *et al.* 2003).

Prey size appears to affect lake whitefish feeding ecology. The size of benthic prey (*Diporeia* spp., Chironomidae, and *Dreissena* spp.) eaten increased with fish size. On the other hand, the size of pelagic prey (*M. relicta* and *B. longimanus*) eaten was not related to fish size. This could indicate different feeding habits for fish feeding on benthos than in the water column. Also, the increase in mussel size eaten relative to fish size affects the energetic value of this food for different size groups of fish. Large lake whitefish obtain over eight times more energy than medium lake whitefish from the average quagga mussel eaten. A study on roach *Rutilus rutilus* in Poland found that fish needed to reach a minimum size before they are able to eat mussels large enough to have any energetic benefits (Prejs *et al.* 1990). Therefore, it appears that quagga mussels are a relatively unprofitable food source for medium lake whitefish and the loss of *Diporeia* spp. could have a disproportionate impact on medium fish. Large lake whitefish may be able to use mussels more effectively by eating larger individuals, although we know little about the potential digestive costs for mussels relative to other prey.

The changes in lake whitefish diets in Lake Huron following changes in the benthic prey community are similar to what has been observed in Lakes Michigan and Ontario (Hoyle *et al.* 1999, Pothoven *et al.* 2001, Owens and Dittman 2003). Invasive species such as *Dreissena* spp. are now a major component of the benthos and lake whitefish diets. Ontogenetic differences in use of prey such as *Dreissena* spp. along with loss of high-energy prey such as *Diporeia* spp. may influence lake whitefish production in the future. Medium lake whitefish appear more reliant on non-mollusc macroinvertebrates and eat fewer and smaller mussels than larger fish. Lake whitefish age at maturity is inversely related to pre-reproductive growth rates (Beauchamp *et al.* 2004), so changes in diet quality and quantity might be one contributing factor affecting age at maturation in the main basin of Lake Huron (Mohr and Ebener 2005). Laboratory studies that take feeding expenses (search time; energy to attack, capture, and ingest prey; evacuation rates) as well as benefits (energy gained) of different prey into account (Mittelbach 1981) are needed to better understand how the changes in the benthos community of the Great Lakes is affecting lake whitefish diets, growth and ultimately production.

ACKNOWLEDGMENTS

The authors thank the Michigan Department of Natural Resources Alpena Research Station, United States Fish and Wildlife Service Alpena Office, and Ontario Ministry of Natural Resources for providing stomach samples, especially J. Johnson, A. Woldt, and L. Mohr, the crews of the R/V *Shenehon* and R/V *Laurentian*, and all those who provided assistance in the field. M. Ebener and I. Winfield provided helpful comments for this manuscript. This project was supported by funds from the National Oceanic and Atmospheric Administration and Michigan Great Lakes Protection Fund. GLERL contribution number 1391.

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Submitted: 19 January 2006
Accepted: 9 May 2006
Editorial handling: John Janssen