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Changes in Consumption by Alewives and Lake Whitefish after Dreissenid Mussel Invasions in Lakes Michigan and Huron

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Abstract.—Growth of alewives *Alosa pseudoharengus* and lake whitefish *Coregonus clupeaformis* has declined since the arrival and spread of dreissenid mussels in Lakes Michigan and Huron. Alewives are the main forage for the salmonids in Lake Michigan, and lake whitefish are the most important commercial species in both lakes. Bioenergetics modeling was used to determine consumption by the average individual fish before and after the dreissenid invasion and to provide insight into the invasion's effects on fish growth and food web dynamics. Alewives feed on both zooplankton and benthic macroinvertebrates, and lake whitefish are benthivores. Annual consumption of zooplankton by an average alewife in Lake Michigan was 37% lower and consumption of benthic macroinvertebrates (amphipods *Diporeia* spp., opossum shrimp *Mysis relicta*, and Chironomidae) was 19% lower during the postinvasion period (1995–2005) than during the preinvasion period (1983–1994). Reduced consumption by alewives corresponded with reduced alewife growth. In Lakes Michigan and Huron, consumption of nonmollusk macroinvertebrates (*Diporeia* spp., opossum shrimp, Chironomidae) by the average lake whitefish was 46–96% lower and consumption of mollusks (mainly dreissenids and gastropods) was 2–5 times greater during the postinvasion period than during the preinvasion period. Even though total food consumption by lake whitefish did not differ between the two periods in Lake Huron or the Southern Management Unit in Lake Michigan, postinvasion weight at age was at least 38% lower than preinvasion weight at age. Under the current postinvasion diet regime, consumption by lake whitefish would have to increase by up to 122% to achieve preinvasion growth rates.

The energy flow and availability of lower food web resources for fish production in aquatic systems including the Laurentian Great Lakes have been altered by dreissenid mussels (Vanderploeg et al. 2002). Phytoplankton and zooplankton community structure can be affected directly and indirectly by dreissenids (Fahnenstiel et al. 1995; MacIsaac et al. 1995; Caraco et al. 1997; Johannsson et al. 2000); thus, fish that depend on pelagic food pathways may be negatively affected by dreissenid invasions (Fahnenstiel et al. 1995; Johannsson et al. 2000; Strayer et al. 2004). Zoobenthos that depend directly on pelagic pathways are also negatively affected by dreissenids; therefore, zooplanktivorous and benthivorous fishes could be indirectly affected (Strayer et al. 2004). On the other hand, dreissenid invasions can lead to increased benthic primary and secondary production (Stewart and Haynes 1994; Fahnenstiel et al. 1995), which may benefit fish that depend on benthic food pathways or that directly consume dreissenids (Karatayev et al. 1997; Johannsson et al. 2000).

Management strategies for both recreational and commercial fisheries in the Great Lakes should be evaluated relative to ongoing changes in the food web. However, relating changes in fish populations to dreissenid mussel invasions has been difficult due to the lack of long-term data sets and complications from other environmental disturbances (Strayer et al. 2004). Strayer et al. (2004) proposed that a balance between three indirect pathways that link fish and dreissenids define a system's response to dreissenid invasion: (1) dreissenids may reduce phytoplankton, leading to decreases in zooplankton or zoobenthos, (2) dreissenids may provide food and shelter, leading to increased production for some benthic macroinvertebrates, and (3) dreissenid filtering may lead to increased light penetration, resulting in higher benthic primary production or macrophyte abundance. These mechanisms are complex, however, and disparate results have been noted in field and laboratory studies (Mayer et al. 2000; Strayer et al. 2004). For example, while dreissenid invasions may lead to increases for other benthic macroinvertebrates, the structural complexity of mussel beds may inhibit fish foraging ability (Mayer et al. 2000, 2001). The ability to forage in dreissenid clusters may also vary with fish species or age (Gonzales and

Downing 1999; Mayer et al. 2000). Additionally, some fish can directly consume dreissenids (Strayer et al. 2004).

Recent work has shown that growth, condition, and diet composition of several fish species, including the alewife *Alosa pseudoharengus* and lake whitefish *Coregonus clupeaformis*, have been altered since the dreissenid invasion of Lakes Michigan and Huron (Pothoven et al. 2001; Madenjian et al. 2003, 2006b; Hondorp et al. 2005; Mohr and Ebener 2005; Pothoven and Nalepa 2006). Alewives are pelagic planktivores that invaded Lake Michigan in the 1940s (Wells and McLain 1973) and currently account for over 70% of the diet of stocked salmonines (Madenjian et al. 2002). Lake whitefish are benthivores and constitute the most important commercial fish species in Lakes Michigan and Huron, accounting for 65% and 85% of the commercial harvest in each respective lake, for a total value of US$15.7 million (Baldwin et al. 2002).

Although changes in fish growth and diet composition for both alewives and lake whitefish have been correlated with the dreissenid invasion, such studies have not used a bioenergetics component to examine actual feeding rates. Without knowing consumption (amount of food eaten per year), it is difficult to know whether changes in diet composition really reflect differences in the amount of a particular prey that is eaten. For fishes like alewives that feed on zooplankton and benthic macroinvertebrates other than mollusks, a reasonable hypothesis is that the dreissenid invasion will lead to decreased consumption, which would be consistent with the observed declines in growth (Madenjian et al. 2003). For benthivorous fishes like lake whitefish, a reasonable hypothesis is that fish consumption of nonmollusk macroinvertebrates that depend on pelagic inputs of energy will decline, whereas consumption of mollusks, particularly dreissenids, will increase. This change would be consistent with the observed declines in lake whitefish growth because dreissenids are lower in energy content than most nonmollusk macroinvertebrates (Pothoven and Nalepa 2006).

The objective of this study was to examine consumption (food eaten per year) before and after dreissenid invasion for (1) alewives, which feed on both zooplankton and benthic macroinvertebrates other than mollusks and (2) lake whitefish, which are benthivorous fish that are also capable of feeding directly on dreissenid mussels. Bioenergetics modeling was used to (1) estimate rates of consumption by an average individual alewife before and after the dreissenid invasion of Lake Michigan and (2) estimate rates of consumption by an average individual lake

whitefish before and after the dreissenid invasions of Lakes Michigan and Huron.

Methods

Consumption by individual alewives and lake whitefish was examined during two time intervals: 1983–1994 (preinvasion) and 1995–2005 (postinvasion). During 1995–2005, abundance and distribution of dreissenid mussels (zebra mussel *Dreissena polymorpha* and quagga mussel *D. bugensis*) expanded throughout Lakes Michigan and Huron (Nalepa et al. 2006, 2007). Consumption was determined using the Wisconsin Fish Bioenergetics 3.1 model with species parameters for alewives and generalized coregonids (Hanson et al. 1997). Fish growth, water temperature, fish diet composition, and fish and prey energy densities are required model inputs. For lake whitefish, the respiration component in the bioenergetics model was lowered from 0.00180 to 0.00085 g $O_2 \cdot g^{-1}$ fish $\cdot d^{-1}$ as indicated in Madenjian et al. (2006a). Consumption by individual fish was examined over the course of a year for each fish age-class. The model was used to determine annual consumption rates during pre- and postinvasion periods. We also determined the consumption rate needed for a single fish to grow at the preinvasion rate based on the postinvasion diet composition.

Alewives.—Patterns of consumption by alewives were examined throughout Lake Michigan. Data were pooled over the entire lake for consistency with previous studies that examined alewife bioenergetics (Stewart and Binkowski 1986; Hewett and Stewart 1989), growth (Madenjian et al. 2003), and energy density (ED; Madenjian et al. 2006b). Unless otherwise noted, data for intervening days between sample dates were estimated by linear interpolation.

Growth was input as the mean weight at age for each time period (Table 1). Weight at age was determined for alewives that were collected in bottom trawls along seven transects throughout Lake Michigan as part of the Great Lakes Science Center's (U.S. Geological Survey) annual fall lakewide surveys following protocols outlined in Madenjian et al. (2003). The average collection date was 12 October for 1984–1994 and 30 September for 1995–2004.

Alewife ED during the preinvasion period was taken from a monthly schedule (April–October) of adult ED in Lake Michigan (Stewart and Binkowski 1986), which was based largely on data from 1979 to 1981 (Flath and Diana 1985). For the postinvasion period, monthly (April–November) ED of adult alewives in Lake Michigan collected during 2002–2004 was used (Madenjian et al. 2006b).

Seasonal diet data summarized and presented in

TABLE 1.—Mean weight at age (g) of alewives and lake whitefish before (pre) and after (post) dreissenid mussel invasion of Lakes Michigan and Huron.

			Lake whitefish											
			Lake Michigan						Lake Huron					
	Alewife in Lake Michigan		North		Central		South		North		Central		South	
Age	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
1	15.9	12.2												
2	31.5	22.5	167	185			376	180			196	100	366	145
3	41.1	28.9	651	506	731	488	833	529	401	161	537	183	671	264
4	48.2	36.1	824	824	1076	702	1,327	813	669	253	870	366	844	516
5	55.5	41.0	1,109	1,105	1,431	1,034	1,578	1,019	935	607	1,241	669	1,373	962
6	60.4	47.6	1,301	1,357	1,757	1,174	1,904	1,112	1,156	883	1,440	992	1,793	1,218
7			1,613	1,446	2,047	1,352	2,270	1,424	1,412	1,073	1,860	1,145	1,947	1,410
8			1,726	1,551	2,269	1,602	2,495	1,851	1,745	1,155				

Hewett and Stewart (1989) were used for the preinvasion diet composition (Table 2). To model consumption by fish between ages 1 and 2, the yearling diet schedule was used for October–July and the adult schedule was used for the remainder of the year. This was necessary because the Hewett and Stewart (1989) simulations began on 1 July instead of during the fall. Postinvasion diet composition for adults was taken from 1,632 fish with nonempty stomachs (32–690 fish/month), which were collected in bottom trawls during May–November 1998–2004 from several sites in Lake Michigan. Prey in stomachs were counted, and prey numbers were converted to dry weights (Pothoven and Vanderploeg 2004; Hondorp et al. 2005; S.A.P., unpublished data) and then to wet-weight composition (Hanson et al. 1997). For yearling diet composition, diets of yearlings were analyzed for October–July and the adult diet composition was used for the remainder of the year. Adult diet composition was used for all other age-class simulations.

Some model inputs remained constant for the pre- and postinvasion periods. The water temperature schedule for adult alewives was taken from Stewart and Binkowski (1986). Although water temperatures may have changed over time, we believe using the same water temperature cycle for both periods is valid (1) given the relatively small amplitude of any climate-induced changes over such a relatively short period of time (McCormick and Fahnenstiel 1999) and (2) because adult alewives are generally not found in the epilimnion, where climate-induced warming would be most pronounced. Fish spawned in mid-June at ages 3 and older, and 6.9% of body mass was shed as gametes (Stewart and Binkowski 1986). Wet-weight prey energy densities for cladocerans (1,674 J/g), copepods (2,300 J/g), amphipods *Diporeia* spp. (4,185 J/g), and opossum shrimp (4,604 J/g) were taken from Stewart and Binkowski (1986) as derived from Cummins and Wuycheck (1971). Most of the "other" prey category during the postinvasion period consisted of Chironomidae, so the ED (3,138 J/g) reported by Lantry and Stewart (1993) for this category was used. Spiny water fleas were assigned the same energy value as cladocerans.

Lake whitefish.—Consumption by lake whitefish was determined for fish from three management units in Lake Michigan (northern: WFM-05; central: WFM-06; southern: WFM-08) and three management units in Lake Huron (northern: WFH-04; central: OH-3; southern: OH-4/5; Figure 1). Consumption was modeled separately for each management unit because of growth and diet differences among areas (Mohr and Ebener 2005; Pothoven 2005; Pothoven and Nalepa 2006).

Data from lake whitefish collected in commercial trap nets and gill nets and research gill nets by the Michigan Department of Natural Resources, Ontario Ministry of Natural Resources, Chippewa Ottawa Resource Authority, and Grand Traverse Band of Chippewa and Ottawa Indians were used to determine weight at age for growth inputs (Table 1). Analyses were restricted to ages 2–8 because few data were available for fish younger than age 2 and because accurate aging of lake whitefish older than age 8 can be difficult during periods of slow growth.

Energy density for lake whitefish increases as fish weight approaches 800 g and then remains fairly constant for larger fish (Madenjian et al. 2006a; Pothoven et al. 2006). There is little seasonal variation in lake whitefish ED (Pothoven et al. 2006), so energy was modeled as a function of fish size (Rudstam et al. 1994). For the postinvasion period, ED from Lakes Michigan and Huron during 2002–2004 was used (Madenjian et al. 2006a; Pothoven et al. 2006). Energy density was not directly available for the preinvasion period. We determined the relationship between

TABLE 2.—Taxonomic composition (proportion of total wet weight) of prey consumed by yearling and adult alewives before (pre) and after (post) dreissenid mussel invasion of Lake Michigan. Preinvasion diet composition was derived from Hewett and Stewart (1989). Other prey are primarily Chironomidae.

Life stage and period	Date	Prey taxon					
		Cladocera	Bythotrephes[a]	Copepoda	Diporeia[b]	Mysis[c]	Other
Yearling							
Pre	12 Oct	0.68	0.00	0.28	0.04	0.00	0.00
	1 Dec	0.68	0.00	0.28	0.04	0.00	0.00
	1 Feb	0.07	0.00	0.87	0.06	0.00	0.00
	1 Apr	0.06	0.00	0.86	0.08	0.00	0.00
	1 Jun	0.15	0.00	0.75	0.10	0.00	0.00
	30 Jun	0.30	0.00	0.45	0.20	0.05	0.00
	1 Oct	0.40	0.00	0.30	0.20	0.10	0.00
	11 Oct	0.40	0.00	0.29	0.21	0.10	0.00
Post	30 Sep	0.16	0.30	0.54	0.00	0.00	0.00
	2 Oct	0.16	0.30	0.54	0.00	0.00	0.00
	5 Jun	0.20	0.00	0.64	0.12	0.01	0.03
	25 Jul	0.07	0.12	0.20	0.10	0.51	0.00
	7 Aug	0.68	0.14	0.06	0.01	0.07	0.04
	4 Sep	0.27	0.02	0.22	0.01	0.48	0.00
	29 Sep	0.41	0.04	0.13	0.00	0.40	0.02
Adult							
Pre	12 Oct	0.40	0.00	0.28	0.22	0.10	0.00
	1 Jan	0.35	0.00	0.20	0.30	0.15	0.00
	1 Feb	0.10	0.00	0.35	0.40	0.15	0.00
	1 Apr	0.10	0.00	0.35	0.40	0.15	0.00
	1 Jun	0.10	0.00	0.45	0.35	0.10	0.00
	1 Jul	0.30	0.00	0.45	0.20	0.05	0.00
	1 Oct	0.40	0.00	0.30	0.20	0.10	0.00
	11 Oct	0.40	0.00	0.29	0.21	0.10	0.00
Post	30 Sept	0.40	0.04	0.14	0.00	0.41	0.01
	10 Oct	0.46	0.06	0.12	0.00	0.36	0.00
	5 Nov	0.68	0.05	0.25	0.00	0.02	0.00
	5 May	0.00	0.00	0.04	0.55	0.37	0.04
	16 Jun	0.06	0.00	0.59	0.12	0.18	0.05
	25 Jul	0.07	0.12	0.20	0.10	0.51	0.00
	7 Aug	0.68	0.14	0.06	0.01	0.07	0.04
	4 Sep	0.27	0.02	0.22	0.01	0.48	0.00
	29 Sep	0.41	0.04	0.13	0.00	0.40	0.02

[a] Spiny water flea *B. longimanus*.
[b] Benthic amphipods.
[c] Opossum shrimp *M. relicta*.

Fulton's condition factor (K) and ED from the postinvasion period to estimate preinvasion ED, and we adjusted the preinvasion size-based regressions accordingly. The relationship between ED and K was ED = 11,420K − 3,101 (r^2 = 0.77, n = 40) for Lake Michigan and ED = 4,216K − 1,673 (r^2 = 0.41, n = 242) for Lake Huron. The regressions were applied, and we determined the average percent change in ED between pre- and postinvasion periods. In Lake Michigan, postinvasion ED was 3% higher in the northern unit, 20% lower in the central unit, and 14% lower in the southern unit than preinvasion ED for fish smaller than 800 g; postinvasion ED was 5% lower in the northern unit, 15% lower in the central unit, and 24% lower in the southern unit than preinvasion ED for fish larger than 800 g. In Lake Huron, postinvasion ED was 11% lower in the northern unit, 5% lower in the central unit, and 9% lower in the southern unit than

preinvasion ED for fish smaller than 800 g; postinvasion values were 7, 5, and 7% lower, respectively, than preinvasion values for fish larger than 800 g. The y-intercepts of the regression lines relating ED with fish size were adjusted accordingly for the preinvasion period.

Diet data from Lakes Huron and Ontario (Ihssen et al. 1981) and Lake Michigan (Ward 1896) were combined to form the preinvasion diet composition (Table 3). Although based on relatively few fish (n = 51), these data are consistent with more recent diet composition results (52% *Diporeia*, 7% opossum shrimp, 13% Chironomidae, and 17% Mollusca) from an area in Lake Michigan that had not experienced drastic declines in *Diporeia* (Pothoven et al. 2001). Diets for postinvasion periods were based on data from 1,309 lake whitefish collected between 1998 and 2004 (62–790 fish/management area; Pothoven et al. 2001;
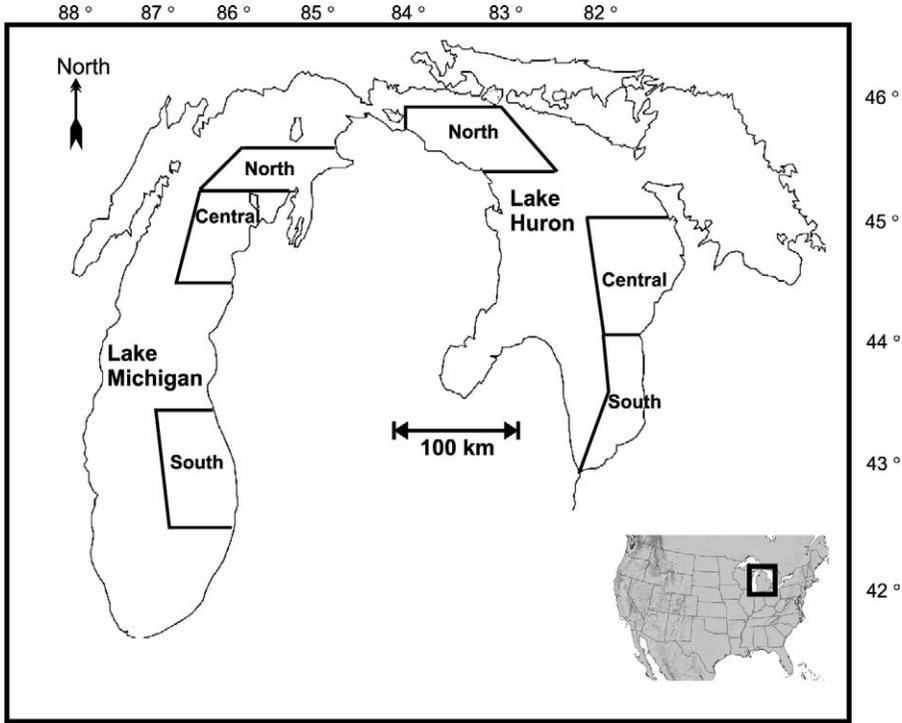
FIGURE 1.—Map of lake whitefish sampling areas within the northern, central, and southern management units of Lakes Michigan and Huron. Alewives were also sampled in Lake Michigan.

Pothoven 2005; Pothoven and Nalepa 2006). Lake whitefish stomachs were processed in the same manner as for alewives to determine wet-weight diet composition. Shell weights were included in wet weights of mollusks.

Some input values were assumed constant between the pre- and postinvasion periods and between lakes. The temperature schedule based on archival tag data from lake whitefish in Lake Huron was used (Madenjian et al. 2006a). The same prey energy densities for *Diporeia*, opossum shrimp, and Chironomidae that were used for the alewife model were used for the lake whitefish analysis. Fish and *Dreissena* were assigned ED values of 4,435 and 1,703 J/g, respectively (Lantry and Stewart 1993; Madenjian et al. 2006a); other mollusks (clams, snails) were assigned the same ED value as *Dreissena*. The prey category "other" was mainly various macroinvertebrates and

TABLE 3.—Taxonomic composition (proportion of total wet weight) of prey consumed by lake whitefish in northern, central, and southern management units of Lakes Michigan and Huron before (pre) and after (post) dreissenid mussel invasion. Mollusca includes only non-dreissenid molluscs (Gastropoda and Sphaeriidae). In Lake Michigan, other prey are primarily spiny water fleas, fish eggs, isopods, amphipods *Gammarus* spp., and ostracods. In Lake Huron, other prey are primarily isopods and spiny water fleas. Preinvasion diet is combined for the two lakes and was derived from Ward (1896) and Ihssen et al. (1981).

| Lake	Period	Unit	Prey taxon						
			Diporeia	*Mysis*[a]	*Dreissena*	Mollusca	Chironomidae	Fish	Other
Combined	Pre	All	0.47	0.32	0.00	0.16	0.04	0.00	0.01
Michigan	Post	North	0.00	0.00	0.32	0.02	0.05	0.46	0.15
	Post	Central	0.15	0.04	0.26	0.17	0.24	0.04	0.01
	Post	South	0.13	0.14	0.42	0.17	0.06	0.03	0.05
Huron	Post	North	0.00	0.01	0.33	0.49	0.01	0.15	0.01
	Post	Central	0.01	0.00	0.09	0.77	0.10	0.03	0.00
	Post	South	0.06	0.00	0.75	0.01	0.08	0.09	0.01

[a] Opossum shrimp.
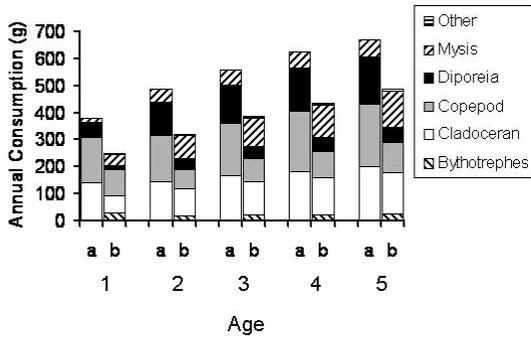
FIGURE 2.—Annual consumption (g) of various prey taxa by alewives in Lake Michigan (a) prior to dreissenid mussel invasion and (b) after invasion (age = starting age for bioenergetics simulations).

FIGURE 3.—Specific consumption (g food·g^{-1} fish·d^{-1}) by alewives as a function of fish weight, as observed before (pre) and after (post) dreissenid mussel invasion of Lake Michigan.

was assigned a value of 3,138 J/g for all areas except northern Lake Michigan, where other prey were mainly zooplankton (1,987 J/g; Lantry and Stewart 1993). Lake whitefish first spawned at age 4 on 15 November, and 5.2% of body weight was shed as gametes (Mohr and Ebener 2005; Madenjian et al. 2006a).

Annual consumption by the average individual fish, proportion of maximum consumption (pC_{max}), and gross conversion efficiency (GCE; change in fish weight per amount of food eaten) were paired by time period for each age-class of alewives in Lake Michigan or lake whitefish in each management area, and paired t-tests were used to determine differences between pre- and postinvasion periods across age-groups. The average change in consumption (if any) across age-groups was determined. Proportional values (pC_{max}, GCE) were arcsine-transformed before statistical testing. For statistical tests, P-values less than 0.05 were considered significant. The average daily specific consumption (g food·g^{-1} fish·d^{-1}) was plotted as a function of the average fish weight over the year to

evaluate feeding rate for a given size of fish between the pre- and postinvasion periods.

Results

Alewives

Based on averages across alewife age-groups, annual consumption of zooplankton (cladocerans, spiny water fleas, copepods) declined by 37% on average (paired t-test: $t = -25.6$, df = 4, $P < 0.001$) and annual consumption of benthic macroinvertebrates (*Diporeia*, opossum shrimp, and chironomids combined) declined by 19% on average ($t = -5.5$, df = 4, $P < 0.01$) between pre- and postinvasion periods, despite increases in opossum shrimp consumption (Figure 2). Total annual consumption by an average alewife declined 31% between the pre- and postinvasion periods ($t = -15.6$, df = 4, $P < 0.001$). For an alewife to achieve preinvasion growth based on the postinvasion diet composition, total consumption would have to increase by 30% on average over the observed postinvasion consumption.

The GCE was about 4.1% between ages 1 and 2, then decreased with age to less than 2% (Table 4). There was no change in GCE between the two time periods (paired t-test: $t = 1.5$, df = 4, $P > 0.05$). The pC_{max} decreased with age from 0.26 to 0.22 during the preinvasion period and from 0.23 to 0.20 during the postinvasion period (Table 4). On average, pC_{max} was 10% lower during the postinvasion period than during the preinvasion period ($t = -9.7$, df = 4, $P < 0.001$). Specific consumption was lower for a given-sized alewife during the postinvasion period than during the preinvasion period (Figure 3).

Lake Whitefish in Lake Michigan

Annual consumption of nonmollusk benthic macroinvertebrates (*Diporeia*, opossum shrimp chironomids) averaged across lake whitefish age-groups decreased between pre- and postinvasion periods in all areas of

TABLE 4.—Gross conversion efficiency (GCE; %) and proportion of maximum consumption (pC_{max}) determined for alewives in Lake Michigan before (pre) and after (post) dreissenid mussel invasion.

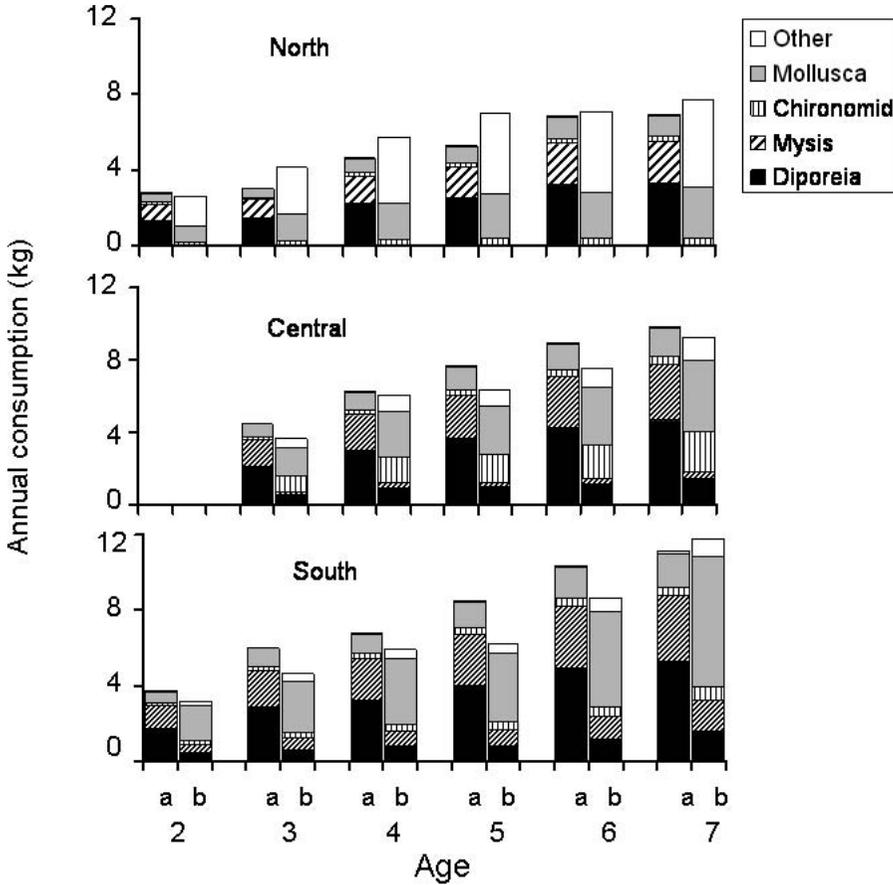| Period	Age	GCE	pC_{max}
Pre	1–2	4.1	0.26
	2–3	2.0	0.22
	3–4	1.3	0.22
	4–5	1.2	0.22
	5–6	0.7	0.22
Post	1–2	4.1	0.23
	2–3	2.0	0.20
	3–4	1.9	0.20
	4–5	1.1	0.20
	5–6	1.4	0.20

FIGURE 4.—Annual consumption (kg) of various prey taxa by lake whitefish in three management units of Lake Michigan (a) prior to dreissenid mussel invasion and (b) after invasion (age = starting age for bioenergetics simulations). Mollusca includes dreissenid and nondreissenid mollusks; other prey include fish, other macroinvertebrates, and zooplankton.

Lake Michigan (paired t-test: $t = -6.5$ to -8.0, df = 4 or 5, $P < 0.05$; Figure 4). Consumption of nonmollusk benthic macroinvertebrates in the lake declined across age-groups by an average of 93% in the northern unit, 45% in the central unit, and 61% in the southern unit between the pre- and postinvasion periods. However, annual consumption of mollusks, including dreissenids, increased 2.3–3.1 times across units ($t = 4.7$–6.7, df = 4 or 5, $P < 0.05$). The increased consumption of shelled prey was mainly due to postinvasion consumption of *Dreissena*. Relative to preinvasion total consumption, postinvasion consumption (all prey groups combined) by an average lake whitefish decreased in the central unit ($t = -4.0$, df = 4, $P < 0.05$), was unchanged in the southern unit ($t = -2.4$, df = 5, $P > 0.05$), and increased in the northern unit ($t = 2.9$, df = 5, $P < 0.05$); the latter result was largely due to the greater consumption of fish during the postinvasion period. For a lake whitefish to achieve preinvasion growth

based on the postinvasion diet composition, total postinvasion consumption would have to increase by 10% on average in the northern unit, 61% in the central unit, and 73% in the southern unit.

Average GCE (paired t-test: $t = -0.8$ to -1.7, df = 4 or 5, $P > 0.05$) did not change over time in Lake Michigan, but pC_{max} increased by 13–22% ($t = 3.1$–3.9, df = 4 or 5, $P < 0.05$; Table 5). Specific consumption by a given-sized lake whitefish in Lake Michigan was generally either similar between time periods or higher during the postinvasion period (Figure 5).

Lake Whitefish in Lake Huron

In Lake Huron, annual consumption of nonmollusk benthic macroinvertebrates (*Diporeia*, opossum shrimp, chironomids) averaged across age-groups for lake whitefish decreased by 82–96% between pre- and postinvasion periods across management units (paired

TABLE 5.—Gross conversion efficiency (GCE; %) and proportion of maximum consumption (pC_{max}) determined for lake whitefish in management units of Lakes Michigan and Huron before (pre) and after (post) dreissenid mussel invasion.

Lake	Unit	Age	GCE		pC_{max}	
			Pre	Post	Pre	Post
Michigan	North	2–3	17.7	12.5	0.25	0.26
		3–4	5.7	7.7	0.18	0.26
		4–5	6.2	4.9	0.23	0.28
		5–6	3.6	3.6	0.22	0.29
		6–7	4.5	1.2	0.26	0.27
		7–8	1.6	1.4	0.24	0.28
	Central	3–4	7.7	5.8	0.24	0.25
		4–5	5.6	5.5	0.26	0.32
		5–6	4.2	2.2	0.27	0.29
		6–7	3.2	2.4	0.28	0.31
		7–8	2.2	2.7	0.28	0.34
	South	2–3	12.5	11.1	0.25	0.31
		3–4	8.2	6.2	0.28	0.29
		4–5	3.7	3.5	0.26	0.30
		5–6	3.8	1.5	0.28	0.28
		6–7	3.5	3.6	0.31	0.35
		7–8	2.0	3.6	0.30	0.40
Huron	North	3–4	10.3	6.0	0.19	0.21
		4–5	6.9	8.2	0.21	0.36
		5–6	4.7	4.5	0.22	0.36
		6–7	4.4	2.6	0.24	0.36
		7–8	4.4	1.0	0.26	0.34
	Central	2–3	16.4	6.7	0.20	0.22
		3–4	9.9	7.0	0.20	0.30
		4–5	7.2	5.8	0.24	0.39
		5–6	3.4	4.1	0.23	0.42
		6–7	5.2	1.7	0.27	0.40
	South	2–3	11.9	7.5	0.19	0.22
		3–4	5.7	7.7	0.18	0.30
		4–5	8.9	6.5	0.27	0.40
		5–6	5.5	3.0	0.27	0.38
		6–7	1.9	2.0	0.25	0.38

t-test: $t = -5.0$ to -5.9, df $= 4$, $P < 0.05$; Figure 6). On the other hand, consumption of mollusks, including dreissenids, was about five times higher during the postinvasion period than during the preinvasion period ($t = 3.3$–4.5, df $= 4$, $P < 0.05$). Overall, there was no significant change in total consumption by the average lake whitefish ($t = 0.45$–1.14, df $= 4$, $P > 0.05$; Figure 6). For a lake whitefish in Lake Huron to achieve preinvasion growth rates with the postinvasion diet composition, total consumption would have to increase by 78–122% on average over observed postinvasion consumption.

The GCE in Lake Huron increased for some lake whitefish age-classes and decreased for others; overall, GCE was not different between pre- and postinvasion periods (paired t-test: $t = -1.92$ to 1.29, df $= 4$, $P > 0.05$; Table 5). The pC_{max} increased slightly for age 2–3 or 3–4, then increased by 53–60% for older fish ($t = 4.03$–5.42, df $= 4$, $P < 0.05$; Table 5). Specific consumption for a given-sized lake whitefish was higher during the postinvasion period than during the preinvasion period (Figure 5).

Discussion

Alewives

Alewife consumption of both benthic macroinvertebrates and zooplankton declined after the dreissenid invasion. Lower consumption of benthic macroinvertebrates was related mainly to decreased consumption of the benthic amphipod *Diporeia*. *Diporeia* was historically the dominant benthic macroinvertebrate in the offshore waters of the Great Lakes (Nalepa 1989) and served as an important pathway between pelagic primary production and fish production. *Diporeia* feed primarily on pelagic inputs of organic material to the benthic region (Dermott and Corning 1988) and, in turn, are eaten by most offshore fish species (Wells 1980). Declines of *Diporeia* have been documented in all the Laurentian Great Lakes except Lake Superior. Currently, vast areas of Lakes Michigan, Huron, Erie, and Ontario are now devoid of this macroinvertebrate (Dermott and Kerec 1997; Nalepa et al. 1998, 2003, 2006; Dermott 2001). Declines in *Diporeia* have been attributed to the spread of dreissenid mussels, but the exact mechanism is uncertain (Nalepa et al. 2006). Alewives also ate less zooplankton in Lake Michigan after dreissenid invasion even though cladoceran abundance increased over the same period (Barbiero et al. 2005). Therefore, alewives did not fully substitute other prey for *Diporeia*; rather, overall food consumption simply declined. Although alewives are versatile feeders and selectively prey on large-bodied zooplankton (Wells 1970; Janssen 1976; Pothoven and Vanderploeg 2004), temporal changes in zooplankton species composition, spatial distribution, or behavior may have been more important than zooplankton abundance in limiting alewife consumption (Makarewicz et al. 1995; Pangle and Peacor 2006).

Alewife consumption of opossum shrimp did increase after *Diporeia* declined, but alewives apparently could not consume enough opossum shrimp to substitute for lower zooplankton and *Diporeia* consumption. Opossum shrimp numbers in 1998 and 2000 were generally similar to those observed during the 1970s and 1980s (Pothoven et al. 2000, 2004), so opossum shrimp abundance may not have been the main factor limiting consumption of this prey. The ability to find, capture, and consume opossum shrimp could have also affected alewives' ability to attain greater consumption than was observed during the postinvasion period. Opossum shrimp can be distributed in patches, are larger than *Diporeia*, and are eaten mainly at night, when both alewives and opossum shrimp migrate vertically to the base of the thermocline (Janssen and Brandt 1980; Pothoven et al. 2004).
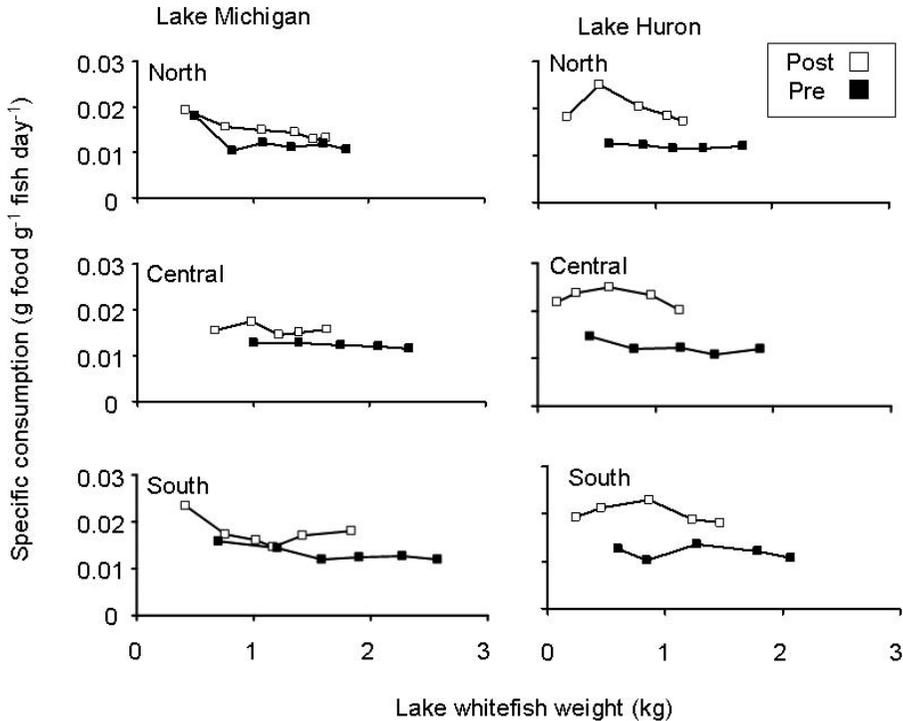
The reduction in consumption after dreissenid

FIGURE 5.—Specific consumption (g food·g^{-1} fish·d^{-1}) by lake whitefish as a function of fish weight, as observed in northern, central, and southern management areas of Lakes Michigan and Huron before (pre) and after (post) dreissenid mussel invasion.

invasion corresponded to declines in alewife growth between pre- and postinvasion periods. Alewife weight at age during the postinvasion period was on average 26% lower than that during the preinvasion period; to achieve preinvasion growth under the postinvasion diet regime, an average alewife would have to increase total consumption by 30%. The most likely cause of reduced alewife growth during the postinvasion period was the reduced abundance of *Diporeia* (Madenjian et al. 2003). Fish growth may become limited when the availability of suitable prey sizes is low (Werner 1974; Hayward and Margraf 1987; Madenjian et al. 1998). *Diporeia* are relatively large, high-energy prey for alewives, and apparently *Diporeia* abundance must be relatively high to ensure rapid alewife growth during ages 1–6 (Madenjian et al. 2003). The reduction in alewife growth during the postinvasion period was not due to density-dependent effects because alewife abundance in Lake Michigan has trended neither upward nor downward since 1982 (Madenjian et al. 2003).

Previous studies have shown that alewife growth, condition, and energy content declined after the dreissenid invasion in Lake Michigan (Madenjian et al. 2003, 2006b). Madenjian et al. (2006b) suggested that a 23% decline in energy content of adult alewives

in Lake Michigan was probably due to a decrease in feeding rate and the loss of *Diporeia*. Bioenergetics analysis confirmed the expectation that postinvasion consumption by alewives was lower than preinvasion consumption.

Lake Whitefish

In Lakes Michigan and Huron, the average lake whitefish ate a dramatically lower amount of non-mollusk macroinvertebrates and a greater amount of mollusks during the postinvasion period than during the preinvasion period. In the northern area, lake whitefish also exhibited greater consumption of fish prey, and growth declined little (4%) between the two time periods. Even though few large-bodied crustaceans, such as *Diporeia* or opossum shrimp, were eaten during the postinvasion period throughout Lake Huron or southern Lake Michigan, consumption of shelled prey (mostly dreissenids and gastropods) by lake whitefish was high enough that postinvasion total consumption did not differ from preinvasion levels. Even though total consumption was unchanged and pC_{max} increased, lake whitefish weight at age was at least 38% lower during the postinvasion period than during the preinvasion period; furthermore, a lake whitefish would have to
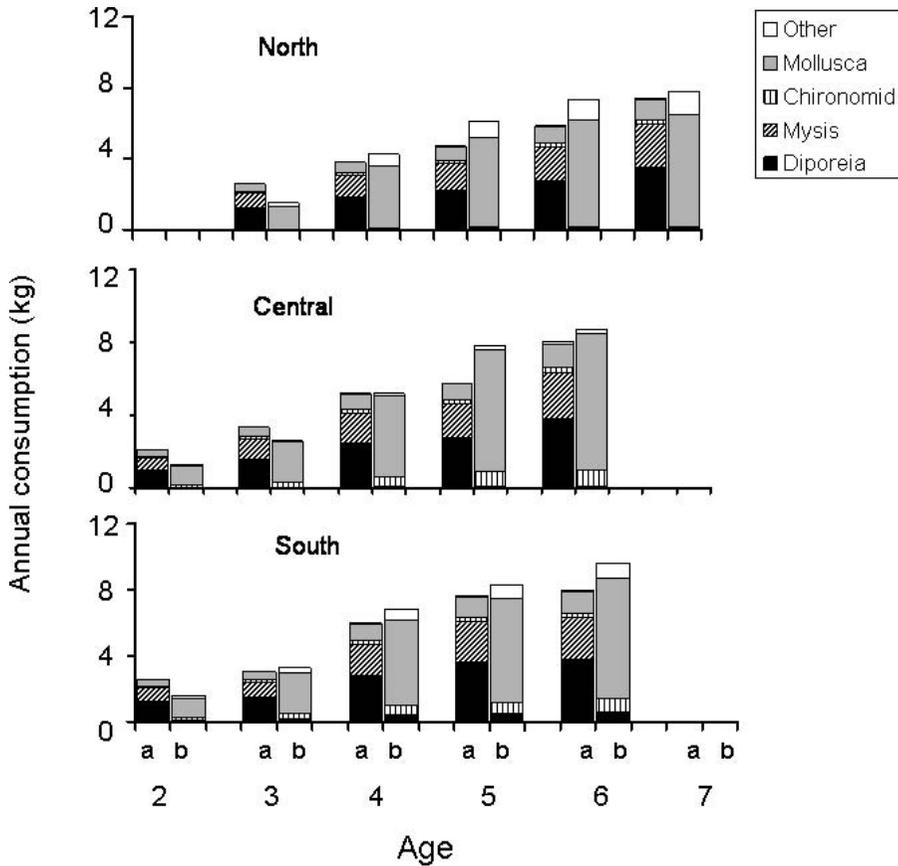
FIGURE 6.—Annual consumption (kg) of various prey taxa by lake whitefish in three management units of Lake Huron (a) prior to dreissenid mussel invasion and (b) after invasion (age = starting age for bioenergetics simulations). Mollusca includes dreissenid and nondreissenid mollusks; other prey include fish, other macroinvertebrates, and zooplankton.

increase consumption by up to 122% to achieve preinvasion growth rates under the postinvasion diet regime. Therefore, even though lake whitefish were able to consume enough mussels to maintain preinvasion consumption rates, they apparently could not consume enough food to maintain preinvasion growth rates. The ED of opossum shrimp and *Diporeia* is about 2.5 times higher than that of dreissenids (Madenjian et al. 2006a), and indigestible shell material accounts for about 50% of a mussel (Dermott et al. 1993). Smaller lake whitefish may not be able to consume the number of dreissenids necessary to utilize them effectively, and the small fish obtain much less energy from mussels because they cannot consume larger, more energetically profitable mussels (Pothoven and Nalepa 2006). Roach *Rutilus rutilus*, which might have benefited from dreissenid invasions in Europe (Karatayev et al. 1997), also cannot feed on mussels in a cost-effective manner until the fish reaches a minimum size (Prejs et al. 1990).

The frequency and (in some instances) proportional biomass of opossum shrimp have increased in lake whitefish diets during the postinvasion period in the Great Lakes (Pothoven et al. 2001; Owens and Dittman 2003). However, the total amount of opossum shrimp eaten by an average lake whitefish was generally lower in each area during the postinvasion period than during the preinvasion period. Opossum shrimp might not be suitable for replacing *Diporeia* in lake whitefish diets because opossum shrimp have a patchy distribution, migrate vertically at night out of the benthic region, and are typically most abundant at depths greater than those occupied by lake whitefish (Janssen and Brandt 1980; Pothoven et al. 2004).

In contrast to alewives, density cannot be dismissed as a factor affecting annual rates of consumption by lake whitefish. In central Lake Michigan during the postinvasion period, lake whitefish catch per unit effort (CPUE; kg/net-lift) in the trap-net fishery increased by 53% (P. Schneeberger, Michigan Department of Natural Resources, unpublished data) and there was a corre-

sponding decrease in total consumption by an average lake whitefish between the pre- and postinvasion periods. In contrast, in southern areas of Lakes Michigan and Huron, trap-net CPUE increased substantially (Mohr and Ebener 2005; P. Schneeberger, unpublished data), but total consumption by an average lake whitefish did not change. In northern areas of Lakes Michigan and Huron, trap-net CPUE was relatively constant over time (Mohr and Ebener 2005; E. Olsen, Grand Traverse Band of Ottawa and Chippewa Indians, personal communication) and total consumption by an average lake whitefish either increased or did not change. Therefore, it is possible that a high abundance of lake whitefish may have exacerbated dreissenid-related changes in consumption rates.

Management Implications

Some ecologists have proposed that the *Diporeia* decline in the Laurentian Great Lakes may cause alewives to substantially increase their rate of zooplanktivory (Hondorp et al. 2005). A sudden zooplanktivory increase could potentially have adverse effects on other zooplanktivorous fishes, including commercially valuable bloaters *Coregonus hoyi*, rainbow smelt *Osmerus mordax*, and yellow perch *Perca flavescens*. However, our bioenergetics modeling results have shown that the rate of zooplankton consumption by an average alewife actually decreased after the invasion of dreissenid mussels. Therefore, alewives might not necessarily place additional predation pressure on zooplankton resources after such invasions.

Decreases in alewife consumption, growth, condition, and ED have been linked to declines in *Diporeia* (Madenjian et al. 2003, 2006b). Alewives in Lake Michigan appear to be unable to eat enough zooplankton or opossum shrimp to offset the loss of *Diporeia* in their diets, so continued low growth, condition, and ED are expected. Madenjian et al. (2006b) suggested that the postinvasion decreases in energy content of alewives should be taken into account when fishery managers decide upon salmonine stocking rates. For example, due to postinvasion declines in alewife ED, a Chinook salmon *Oncorhynchus tshawytscha* must eat 22% more alewives than preinvasion levels to attain 7.865 kg within 4 years (Madenjian et al. 2006b). As long as *Diporeia* abundance remains relatively low, fishery managers should continue to assume a relatively low ED of alewives when determining salmonine stocking rates.

Heretofore published descriptions and models of the role of dreissenid mussels in Great Lakes food webs have not included a strong trophic link between lake whitefish and dreissenids (see Haynes et al. 1999; Hecky et al. 2004). Hecky et al. (2004) proposed a nearshore phosphorus shunt engineered by dreissenid mussels that incorporated a substantial amount of biomass, energy, and nutrients from the benthic macroinvertebrate and benthic algal communities. Our bioenergetics modeling has revealed a strong trophic link between lake whitefish and dreissenid mussels in Lakes Michigan and Huron; an average adult lake whitefish consumes dreissenids at a rate of about 2.5 kg/year in Lake Michigan and 3.0 kg/year in Lake Huron. Therefore, fishery managers' concerns that dreissenids represent a "dead end" do not appear completely warranted.

Although lake whitefish are able to eat dreissenids, a highly abundant food source, there appear to be consequences for growth even if fish maintain preinvasion consumption rates. In Lake Huron and southern Lake Michigan, where enough mollusks were eaten so that total annual consumption was unchanged after dreissenid invasion, growth of lake whitefish still declined dramatically. If the current near-historical high abundance of lake whitefish declines, alternative energy-rich prey such as opossum shrimp might be relatively more available for the remaining fish, but it is still unclear how much fish production can actually be supported by opossum shrimp in the absence of *Diporeia*. Therefore, regardless of lake whitefish abundance, it is likely that the commercial catch of lake whitefish in areas where *Diporeia* are disappearing will continue to mainly consist of slow-growing fish in relatively poor condition.

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