

Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels

Charles P. Madenjian, Steven A. Pothoven, John M. Dettmers, and Jeffrey D. Holuszko

Abstract: The dreissenid mussel invasion of Lake Michigan during the 1990s has been linked to a concomitant decrease in the abundance of the amphipod *Diporeia*. We tracked the seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan during 2002–2004 and compared our findings with previously published results for years 1979–1981. Adult alewife energy density exhibited a pronounced seasonal cycle during both the pre-invasion and post-invasion periods, with energy density in October or November nearly twice as high as that in early summer. However, on average, adult alewife energy density was 23% lower during the post-invasion period compared with the pre-invasion period. This significant decline in energy density was attributable to decreased importance of *Diporeia* in adult alewife diet. In contrast, energy density of juvenile alewives did not significantly differ between the pre-invasion and post-invasion periods. To attain a weight of 8 kg by age 4, bioenergetics modeling indicated that a Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan would have to consume 22.1% more alewives during the post-invasion period compared with the pre-invasion period.

Résumé : On a relié l'invasion du lac Michigan par les bivalves dreissenidés durant les années 1990 au déclin simultané de l'abondance de l'amphipode *Diporeia*. Nous avons suivi la dynamique énergétique saisonnière des gaspareaux (*Alosa pseudoharengus*) au lac Michigan en 2002–2004 et comparé nos résultats à ceux des années 1979–1981 dans la littérature scientifique. La densité énergétique des gaspareaux adultes suit un cycle saisonnier bien marqué, tant dans les périodes qui précèdent que celles qui suivent l'invasion; la densité énergétique en octobre ou novembre est presque deux fois plus grande qu'en début d'été. Cependant, en moyenne, la densité énergétique moyenne des gaspareaux adultes est de 23 % plus basse durant la période qui suit l'invasion que durant la période qui la précède. Ce déclin significatif de la densité énergétique s'explique par la diminution considérable des *Diporeia* dans le régime alimentaire des gaspareaux adultes. En revanche, la densité énergétique des jeunes gaspareaux après l'invasion ne diffère pas significativement de celle d'avant l'invasion. Les modèles bioénergétiques indiquent que, pour atteindre une masse de 8 kg à l'âge de 4 ans, les saumons quinnat (*Oncorhynchus tshawytscha*) du lac Michigan doivent consommer 22,1 % plus de gaspareaux durant la période qui suit l'invasion que durant la période qui la précède.

[Traduit par la Rédaction]

Introduction

Although the invasion of lakes and rivers by dreissenid mussels has been shown to have strong influences on the lower food web, soundly demonstrating effects of dreissenid mussel invasions on fish populations has proven to be difficult (Strayer et al. 2004). Few studies have documented clear effects of dreissenid invaders on fish abundance or fish growth. Barriers impeding the detection of dreissenid invader impacts on fish included (i) lack of long-term observations on the lower food web, (ii) lack of sufficiently long

time series of observations on fish abundances or fish growth to discern changes, and (iii) complications from changes in other factors during the post-invasion period (Strayer et al. 2004). Moreover, changes in fish growth need to be interpreted in light of changes in fish density (Walters and Post 1993). Fish growth often can be characterized as density-dependent, with growth being inversely related to fish density. For example, the decline in lake whitefish (*Coregonus clupeaformis*) growth and condition in Lake Michigan during the 1990s has been attributed to both a decline in the abundance of the amphipod *Diporeia* and a concomitant in-

Received 8 August 2005. Accepted 22 December 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 4 March 2006.
J18831

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crease in lake whitefish abundance (Pothoven et al. 2001; Madenjian et al. 2002).

To date, effects of dreissenid invasions on the energy dynamics of fish have not been investigated. Yet, a long-term decrease in the energy density of prey fish could result in increased predation on prey fish by piscivorous fish, because the piscivorous fish would need to increase its consumption rate to maintain its growth rate (Rand et al. 1994). Thus, by altering the energy dynamics of a prey fish, a dreissenid invasion could eventually lead to increased consumption of prey fish by piscivorous fish. In aquatic ecosystems where sport fisheries are sustained through stocking of piscivorous fish, substantial increases in consumption of prey fish by piscivorous fish would have management ramifications, including an impetus to reduce stocking rate of the predator (Stewart et al. 1981; Hansen and Holey 2002). Hence, a dreissenid mussel invasion may have potential to perturb aquatic ecosystems all the way to the top-predator level.

Alewife (*Alosa pseudoharengus*) invaded Lake Michigan during the 1940s (Wells and McLain 1973). A major salmonine stocking program was initiated in 1965 to control the alewife population and to establish a sport fishery (Tody and Tanner 1966; Madenjian et al. 2002). The five species of salmonines stocked into the lake included Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), lake trout (*Salvelinus namaycush*), and brown trout (*Salmo trutta*). The predominant predator on alewives in Lake Michigan has been Chinook salmon (Madenjian et al. 2002). Based on observations during 1979–1981, Flath and Diana (1985) concluded that adult alewives experience a pronounced seasonal cycle in their energy density, which fluctuated from about $5100 \text{ J}\cdot\text{g}^{-1}$ (wet weight basis) in June to nearly $9700 \text{ J}\cdot\text{g}^{-1}$ in late October. During the 1960s and 1970s, *Diporeia* constituted nearly 30% of adult alewife diet in Lake Michigan (Hewett and Stewart 1989). Alewives in Lake Michigan typically do not begin feeding on *Diporeia* until the fall of the second year in the lake (Stewart and Binkowski 1986).

The zebra mussel (*Dreissena polymorpha*) was first observed in Lake Michigan in 1989, and the invader was established in the lake by 1993 (Marsden et al. 1993; Nalepa et al. 1998). The quagga mussel (*Dreissena bugensis*) was first noticed in Lake Michigan in 1997, and this invader was abundant in the lake by 2002 (Nalepa et al. 2001, 2006). Nalepa et al. (2006) documented a decline in *Diporeia* abundance in Lake Michigan during the 1990s and early 2000s, and these researchers have attributed this decline to the dreissenid mussel invasion. Although the mechanisms by which dreissenid mussels negatively affect *Diporeia* remain unidentified, the decrease in *Diporeia* abundance coincided with the dreissenid mussel invasion not only in Lake Michigan, but also in Lakes Huron, Erie, and Ontario (Nalepa et al. 2005, 2006; T. Nalepa, National Oceanic and Atmospheric Administration (NOAA) Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA, personal communication).

Quantifying the effects of the dreissenid mussel invasion on alewife energy dynamics would be better facilitated in Lake Michigan compared with most other lakes because (i) the benthic macroinvertebrate community has been regularly surveyed in Lake Michigan since 1980 (Nalepa et al.

2006), (ii) the seasonal energy dynamics of alewives in Lake Michigan prior to the dreissenid mussel invasion has been well characterized (Flath 1982; Flath and Diana 1985; Stewart and Binkowski 1986), (iii) abundance, growth, and condition of alewives in Lake Michigan have been regularly tracked since 1973 (Madenjian et al. 2003, 2005a, 2005b), and (iv) diet of alewives in Lake Michigan has been documented both before and after the dreissenid mussel invasion (Hewett and Stewart 1989; Davis et al. 1997; Hondorp et al. 2005). Because a substantial portion of the food web dynamics in the lake has been explored, the task of isolating effects of the dreissenid mussel invasion on alewives is tractable.

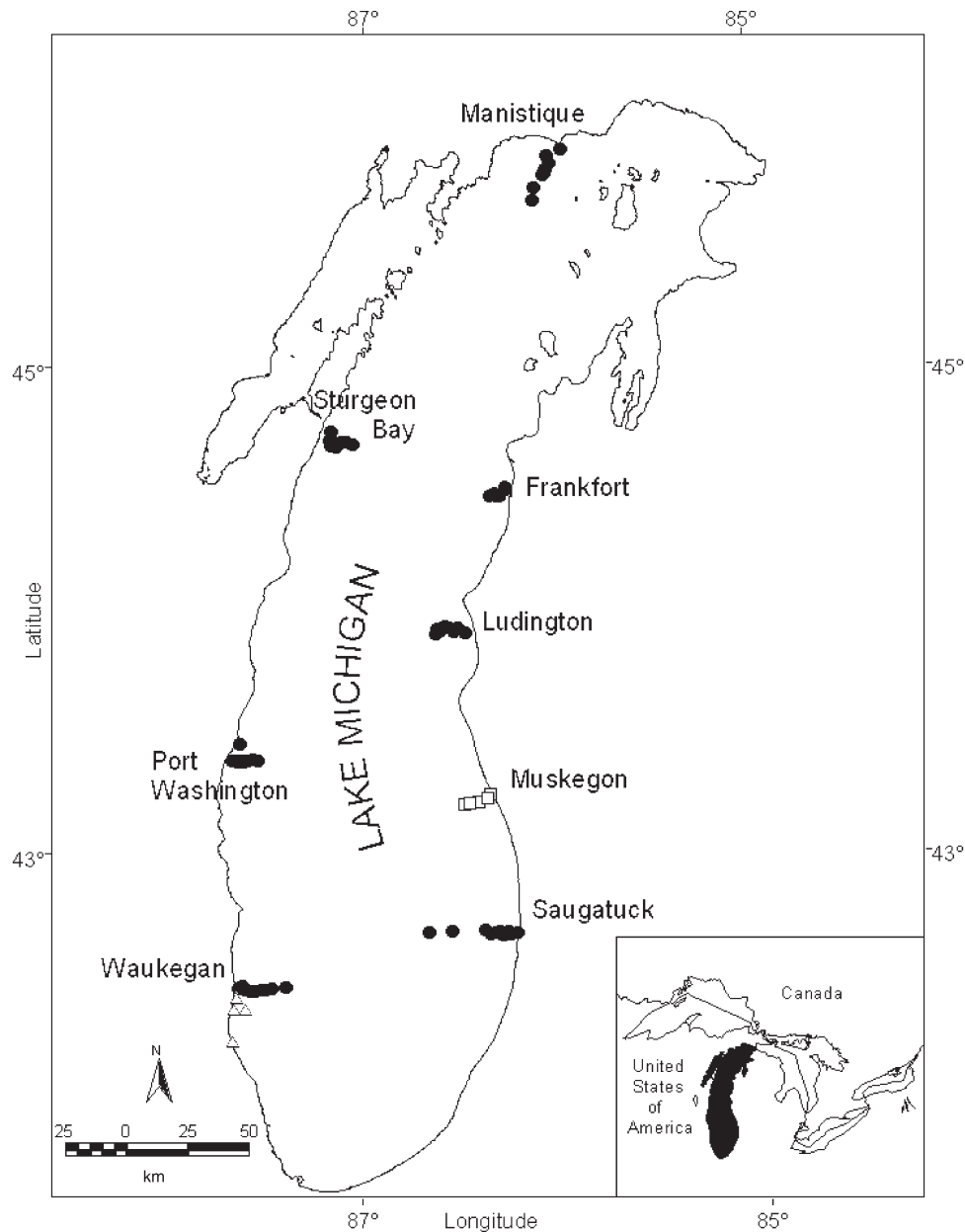
Herein, we measure changes in seasonal energy dynamics of alewives from Lake Michigan following the dreissenid mussel invasion and the accompanying decline in *Diporeia* abundance. To accomplish this primary objective, we characterize the seasonal cycle in alewife energy density during the post-invasion period and then compare the seasonal cycle during the post-invasion period with the seasonal cycle during the pre-invasion period, as determined by Flath and Diana (1985). Secondary objectives of our study include (i) measuring the change in alewife lipid content between the pre- and post-invasion periods, (ii) determining whether any change in adult alewife energy density between the pre- and post-invasion periods is attributable to density-dependent effects, (iii) quantifying the effect of changes in alewife energy density between the pre- and post-invasion periods on food consumption by Chinook salmon, (iv) determining the predictability of alewife energy density based on water content, lipid content, and condition, and (v) determining whether alewife energy density during 2002–2004 significantly increased as alewife total length increased beyond 90 mm.

Materials and methods

Field sampling

During 2002–2004, alewives were caught in bottom trawls and gill nets from a variety of locations in Lake Michigan. During September and October 2002–2003, alewives were captured during the lakewide survey of the Lake Michigan fish community conducted by the Great Lakes Science Center (GLSC). This GLSC lakewide survey has been performed each fall since 1973. The basic unit of sampling for the GLSC survey was a 10 min tow using a bottom trawl (12 m headrope and 13 mm stretched-mesh liner) dragged on depth contour during daylight hours (Hatch et al. 1981; Madenjian et al. 2005a, 2005b). Sampling depths ranged from 9 to 110 m. The complete survey included transects off these seven ports: Manistique (Michigan), Frankfort (Michigan), Ludington (Michigan), Saugatuck (Michigan), Waukegan (Illinois), Port Washington (Wisconsin), and Sturgeon Bay (Wisconsin) (Fig. 1). Owing to mechanical problems aboard the vessel and time constraints, tows at Manistique were not performed in 2002. For each combination of port and year, an attempt was made to collect 100 large ($>120 \text{ mm}$ in total length (TL)) and 100 small ($\leq 120 \text{ mm}$ TL) alewives. A cutoff length of 120 mm TL was employed to match the classification system used by Stewart et al. (1981, 1983) to develop bioenergetics models for Lake Michigan salmonines. Fish were separated by size category, bagged with water, frozen, and transported to the GLSC laboratory in Ann

Fig. 1. Map of Lake Michigan, including locations of sampling sites. Solid circles denote locations of sampling sites for the US Geological Survey Great Lakes Science Center bottom trawl survey. Open squares denote locations of sites sampled by the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory researchers. Open triangles denote locations of sites sampled by Illinois Natural History Survey and Illinois Department of Natural Resources researchers.



Arbor (Michigan), where they were stored in a freezer at -30°C until processing.

In Lake Michigan in the vicinity of Muskegon (Michigan) (Fig. 1), alewives were caught during April through November 2003–2004 using a semi-balloon bottom trawl (7.8 m headrope with 13 mm stretch mesh liner). Trawl tows were conducted during daylight hours at depths ranging from 10 to 90 m, depending on seasonal inshore–offshore movements of alewives. All sampling was performed by NOAA Great Lakes Environmental Research Laboratory researchers. For each combination of year and month, an attempt was made to collect 100 large and 100 small alewives. Again, fish were

separated by size class, bagged with water, frozen, and transported to the GLSC laboratory.

From the Illinois waters of Lake Michigan near Waukegan (Fig. 1), alewives were caught during April through October 2003–2004 by Illinois Department of Natural Resources and Illinois Natural History Survey personnel. During April and May, graded-mesh gillnets were fished overnight at various depths between 10 and 100 m. During June through October, alewives were captured monthly using a bottom trawl (4.9 m headrope with 13 mm stretched-mesh liner) fished during daylight hours at depths ranging from 3 to 10 m. All alewives were sorted by size class and immediately placed on

ice. Upon return to the laboratory in Zion (Illinois), up to 100 large and 100 small individuals were frozen in water each month and then transported to the GLSC laboratory.

Laboratory processing of samples

After thawing in the laboratory, each alewife's TL was measured to the nearest millimetre, and each alewife was weighed to the nearest 0.1 g. Up to five 20-fish composites were formed for each combination of year, month, port, and size class. Each composite was then homogenized in a blender, and between 40 and 120 g of the homogenate was placed in a glass jar. Each jar was sealed with aluminum foil, capped, and kept frozen at -30°C until time of energy density or lipid content determinations.

To determine energy density, about 35 g of the homogenate was dried to a constant weight in a drying oven at 70°C ; drying typically required about 3 days. The dried tissue was ground using a mortar and pestle, and then 1 g of the dried sample was combusted in a Parr 1261 isoperibol calorimeter. All energy densities were reported on a wet weight basis.

To estimate the variability in our energy density determinations from an alewife composite sample, we determined energy density of three replicates from each of 10 samples. The coefficient of variation averaged 1.03% over the 10 samples. Flath (1982) reported an average coefficient of variation of 1.05% for his replicate values of energy density determinations. Thus, precision in the estimates of alewife energy density was very similar between our study and that of Flath and Diana (1985).

For large alewives, Flath and Diana (1985) removed the contents of the stomachs before determining energy density, whereas we included the stomach contents in our energy density determinations. However, this difference in processing had a practically negligible effect on comparability of energy density between the two studies, because stomach contents of large alewives from Lake Michigan represent only about 1% of their body weight (Davis et al. 1997; S.A. Pothoven, unpublished data). For example, the food found in the stomachs of large alewives caught near Muskegon during August 2004 comprised 1.36% of their total body weight on average. Coupling our estimate of large alewife energy density (at Muskegon during August 2004) with published values for the energy density of the prey found in the stomachs, we estimated a factor of 1.008 to correct our energy density estimate for direct comparison with an energy density estimate by Flath and Diana (1985). Given the extremely low value of this correction factor, we opted not to apply it to our estimates of energy density.

To determine lipid content, the procedure outlined by Schmidt and Hesselberg (1992) was followed. Lipids were extracted from the homogenate using petroleum ether and ethyl acetate as solvents. Percent extractable lipid was determined by evaporating 1 mL of extract and weighing the residue (Hesselberg et al. 1990). All lipid contents were reported on a wet weight basis.

Data analysis

To compare alewife energy density during 2002–2004 with alewife energy density during 1979–1981, we first calculated mean energy density during the 2002–2004 period for each

combination of month and alewife size category. Data from all years (2002–2004) and all ports were pooled for these calculations. For each combination of month and alewife size category, we also calculated the average day of capture during the month. We assigned mean energy density to the average day of capture for the month. In addition, the 95% confidence interval was calculated for each mean energy density. Next, we plotted the mean energy densities, with corresponding 95% confidence intervals, from the 2002–2004 period together with the alewife energy density schedules developed by Stewart and Binkowski (1986) and Hewett and Johnson (1992), largely based on 1979–1981 data from Flath and Diana (1985). For both small and large alewives, we paired monthly means of energy density from the 2002–2004 period with corresponding values from the energy density schedule based on 1979–1981 data and then performed a *t* test for paired comparisons to determine if mean energy density significantly changed between the 1979–1981 and 2002–2004 periods. Stewart and Binkowski (1986) developed their energy density schedule for small alewives by using data for only young-of-the-year alewives during the fall months. However, an age-length key, presented in Madenjian et al. (2005b), indicated that the alewives used to form five composite samples from November 2004 were most likely yearlings. Therefore, to better compare the energy densities from 2002–2004 with the energy density schedule developed by Stewart and Binkowski (1986), these five samples were not included in this analysis.

We were justified in pooling data across years 2002–2004 and across all ports sampled during 2002–2004 because (i) energy density did not vary significantly across the years, and (ii) Stewart and Binkowski (1986) also pooled data across years and ports in developing their energy density schedules for alewives. For both small and large alewives, mean energy density of fish caught during GLSC fall surveys did not significantly differ between 2002 and 2003 (two-sample *t* tests, $P > 0.05$). Similarly, neither alewives from Muskegon nor alewives from Waukegan (caught by State of Illinois researchers) differed significantly in energy content between years 2003 and 2004 (two-sample *t* tests, $P > 0.05$). In addition, alewife energy density at Muskegon and Waukegan appeared to be representative of the lake, because mean energy density of alewives at Muskegon and Waukegan during September and October of 2003 did not significantly differ from mean energy density of alewives caught in the GLSC lakewide survey during 2003 (two-sample *t* tests, $P > 0.05$). Alewives used in the Flath and Diana (1985) study were caught near Saugatuck, Port Sheldon (Michigan), and Grand Haven (Michigan) during 1979–1981. Stewart and Binkowski (1986) believed that their energy density schedules were representative of the lake, because their energy density schedules were very similar to ones derived from observations by Yeo (1978) for alewives caught in Wisconsin waters of Lake Michigan during the 1970s.

To compare alewife lipid content during 2002–2004 with alewife lipid content during 1979–1981, we first calculated mean lipid content and its corresponding 95% confidence interval of large alewives by month during 2002–2004. Data were pooled across years and ports in calculating these monthly means. We then plotted monthly means with 95% confidence intervals together with the monthly means for

alewife lipid content presented by Flath and Diana (1985) from observations during 1979–1981. In addition, a *t* test for paired comparisons was performed to determine if lipid content of large alewives significantly changed between the 1979–1981 and 2002–2004 periods. Comparison of lipid content of small alewives between the two time periods was not conducted, because lipid content data for small alewives during 1979–1981 were not reported by Flath and Diana (1985).

To compare the diet composition of adult alewives of Lake Michigan between the pre-invasion and post-invasion periods, we surveyed the literature. Hewett and Stewart (1989) integrated the data from several diet studies on Lake Michigan alewives performed during the 1960s and 1970s to arrive at an annual diet schedule for Lake Michigan adult alewives; this diet schedule was then used in their bioenergetics model applications. Their diet schedule represented data from both the eastern and western sides of the lake. Using the Hewett and Stewart (1989) diet schedule, we averaged the proportion of each of the various components in the diet across all seasons to compute an annual average diet composition for adult alewives in Lake Michigan during the pre-invasion period. Davis et al. (1997) characterized the diet of adult alewives caught in Lake Michigan near Saugatuck, Port Washington, and Sturgeon Bay during spring and fall 1995. Similarly, Hondorp et al. (2005) characterized the diet of adult alewives caught in Lake Michigan near Muskegon and St. Joseph (Michigan) during spring, summer, and fall 2000–2001. Using data from these two studies, we averaged the proportion of each of the components in the diet across seasons and locations to calculate an annual average diet composition for adult alewives in Lake Michigan during the post-invasion period. We calculated diet compositions on a wet weight basis. Using these calculated annual average diet compositions, we compared the proportion of *Diporeia* in adult alewife diet during the pre-invasion with that during the post-invasion period. In addition, we used the calculated annual average diet compositions, as well as the energy densities for each of the diet components as reported by Hewett and Stewart (1989), to estimate the energy density of the food of Lake Michigan adult alewives during both the pre-invasion and post-invasion periods.

To determine the reliability of predicting alewife energy density based on a correlate, we conducted simple linear regression analyses of alewife energy density as a function of percent water, lipid content, and condition. To use condition in the regression analysis, we calculated Fulton's condition *K* (equal to $(\text{weight} \times 10^5) \times \text{TL}^{-3}$) for each of the 20 alewives in the composite sample and then calculated the average *K* for the sample; weight is expressed in grams and TL is expressed in millimetres. The percent variation in alewife energy density explained by the predictor was calculated for each of the three regressions. Data from all 220 alewife composites were included in our first set of regression analyses. In our second set of regression analyses, we divided the data into one set for small alewives and one set for large alewives. We then performed a simple linear regression of energy density as a function of each of the three predictor variables for both small and large alewives.

To corroborate our assessment of the effect of the dreissenid mussel invasion on energy density of adult alewives in

Lake Michigan, we first calculated the decrease in adult alewife *K* between the 1979–1994 and 1995–2004 periods using the long-term data from the GLSC fall lakewide surveys. For this analysis, we considered adult alewives to be those of spawner size ($\text{TL} \geq 150$ mm) (O'Gorman et al. 2004; Madenjian et al. 2005a). Condition of age-2 and older alewives in Lake Michigan decreased by 14% between the 1984–1994 and 1995–2001 periods (Madenjian et al. 2003). We added data from years 1979–1983 and 2002–2004 to the data used in their study to bracket all of the years encompassed by our comparison, calculated mean condition of adult alewives for each year during 1979–2004, and then averaged annual means to generate grand means for the 1979–1994 and 1995–2004 periods. Next, we substituted these two grand means into the regression equation for energy density of large alewives as a function of condition to estimate mean energy density of adult alewives in the fall during the 1979–1994 and 1995–2004 periods. The percent change in energy density between the two time periods was then calculated. This calculated percent change in energy density was then compared with the percent change in energy density calculated by direct comparison of the energy density schedule for large alewives developed by Stewart and Binkowski (1986) and our energy density schedule for large alewives from 2002–2004 data. More specifically, we averaged the eight monthly means for energy density of large alewives to arrive at an overall mean energy density for large alewives during 2002–2004. We also averaged the eight corresponding values on the Stewart and Binkowski (1986) energy density schedule for large alewives to generate an overall mean energy density for large alewives during the 1979–1981 period. Then, the percent change in mean energy density between the two time periods was calculated. Madenjian et al. (2003) used change-point regression analysis to show that a stepwise decline in alewife condition occurred in 1995. We applied change-point regression analysis to the extended time series, including years 1979–2004, for mean condition of adult alewives to confirm that the drop in alewife condition did occur in 1995.

To determine whether a change in adult alewife energy density was attributable to density-dependent effects, we compared mean abundance (expressed as $\text{kg}\cdot\text{ha}^{-1}$) of adult alewives in Lake Michigan during 1979–1981 with that during 2002–2004, using the long-term data from the GLSC bottom trawl survey (Madenjian et al. 2005b). In addition, we computed the correlation coefficient between mean *K* for adult alewives and adult alewife annual abundance, using the 1979–2004 data. Then, we determined whether the correlation coefficient was significantly different from zero ($P > 0.05$). This test was performed to ascertain whether adult alewife condition showed a significant density-dependent response over the range of densities observed during 1979–2004.

Flath (1982) observed neither an increasing nor decreasing trend in alewife energy density as alewife TL increased beyond 90 mm during 1979–1981. To determine whether this same pattern was present during 2002–2004, we performed a simple linear regression of alewife energy density as a function of alewife $\text{TL} \geq 90$ mm. Based largely on the Flath (1982) and Flath and Diana (1985) data, Stewart and Binkowski (1986) concluded that energy density showed no

further increase as alewife age increased beyond 2 years. Thus, to characterize the seasonal energy dynamics of large alewives from Lake Michigan, Stewart and Binkowski (1986) relied on determinations of energy density for age-2 and older alewives only. To estimate the percentage of age-2 and older alewives in the set of large alewives used in our study, we applied an age-length key, taken from Madenjian et al. (2005b), to the length-frequency distribution of large alewives used in our study.

Bioenergetics modeling

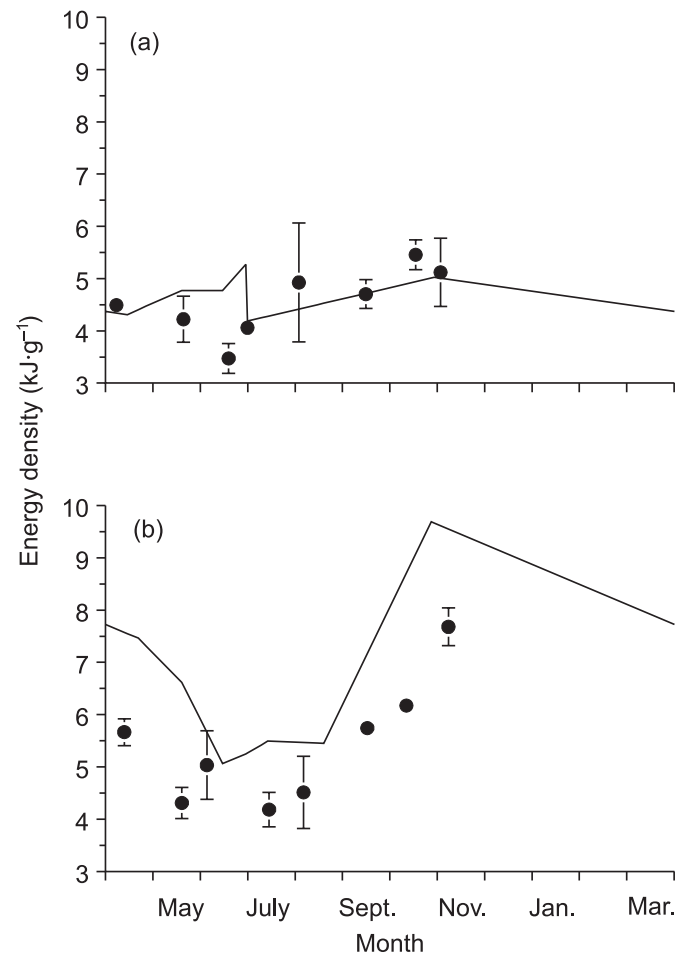
We used the bioenergetics model for Chinook salmon originally formulated by Stewart (1980) and Stewart et al. (1981), and later refined by Stewart and Ibarra (1991), to determine the effect of long-term changes in alewife energy density on consumption of alewives by Chinook salmon. The same water temperature regime and diet composition schedules used by Stewart and Ibarra (1991) were used in our simulations. Chinook salmon weight at age in Lake Michigan trended neither upward nor downward during 1983–2003 (Peeters and Royseck 2004). The growth trajectory based on weight-at-age data for 1983 represented a typical growth trajectory for Chinook salmon in Lake Michigan during the post-1982 period (Szalai 2003); we used this trajectory as inputs to the bioenergetics model for our simulations. According to this trajectory, weights at time of stocking, age 1, age 2, age 3, and age 4 were 4.5 g, 586 g, 2.557 kg, 5.463 kg, and 7.865 kg, respectively. Using the bioenergetics modeling software by Hanson et al. (1997), Chinook salmon growth and consumption was simulated from time of stocking to age 4 both under the alewife energy density schedules developed by Stewart and Binkowski (1986) and under the alewife energy density schedules from our 2002–2004 data. To generate our schedules, we assigned the mean monthly energy density to the average day of capture for the month and then linearly interpolated among the eight monthly means.

Results

Energy density of small (≤ 120 mm TL) alewives in April, August, October, and November was higher during the post-invasion period than during the pre-invasion period (Fig. 2a). In May, June, July, and September, energy density of small alewives during 1979–1981 was higher than the corresponding value from the 2002–2004 schedule. Confidence intervals about the monthly means for 2002–2004 overlapped the corresponding values from the 1979–1981 schedule in April, August, September, and November (Fig. 2a). Averaging the eight monthly means from 2002–2004 yielded a grand mean of $4.556 \text{ kJ}\cdot\text{g}^{-1}$, and averaging the eight corresponding points from the 1979–1981 schedule yielded a grand mean of $4.661 \text{ kJ}\cdot\text{g}^{-1}$. Mean energy density of small alewives during post-invasion period was not significantly different from mean energy density of small alewives during the pre-invasion period (mean difference = $0.104 \text{ kJ}\cdot\text{g}^{-1}$; $t = 0.46$, $df = 7$, $P = 0.6587$).

Energy density of large (>120 mm TL) alewives during the pre-invasion period exceeded large alewife energy density during post-invasion period over all months between April and November (Fig. 2b). Only in June did the confidence interval about the monthly mean from the 2002–2004

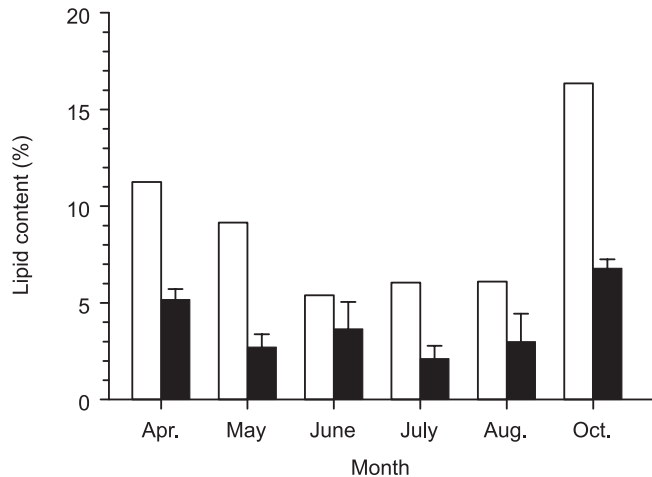
Fig. 2. Energy density of (a) small (≤ 120 mm total length, TL) and (b) large (>120 mm TL) alewives (*Alosa pseudoharengus*) in Lake Michigan during 1979–1981 (solid line) and during 2002–2004 (solid circles). Energy density schedule during 1979–1981 was taken from Stewart and Binkowski (1986) and Hewett and Johnson (1992). Bars about each point represent the 95% confidence interval about the mean. Energy density is expressed on a wet weight basis.



schedule overlap with the corresponding value from the 1979–1981 schedule. The average of the eight monthly means for 2002–2004 was $5.413 \text{ kJ}\cdot\text{g}^{-1}$, whereas the average of the eight corresponding points from the 1979–1981 schedule was $7.030 \text{ kJ}\cdot\text{g}^{-1}$. Thus, large alewife energy density was 23.0% lower during the post-invasion period compared with the pre-invasion period. Mean energy density of large alewives was significantly higher during the pre-invasion period than during the post-invasion period (mean difference = $1.617 \text{ kJ}\cdot\text{g}^{-1}$; $t = 6.95$, $df = 7$, $P = 0.0002$).

Lipid content of large alewives was higher during the pre-invasion period than during the post-invasion period in each of the 6 months for which data from 1979–1981 were available (Fig. 3). Moreover, 95% confidence intervals about the monthly means for 2002–2004 did not overlap with the corresponding monthly means for 1979–1981 in any of the 6 months. Mean lipid content over the 6 months (depicted in Fig. 3) was 9.1% during 1979–1981, but only 3.9% during 2002–2004; this difference was significant (mean difference =

Fig. 3. Mean lipid content of large (>120 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan during 1979–1981 (open bars) and during 2002–2004 (solid bars). Lipid content during 1979–1981 was taken from Flath and Diana (1985). Error bars represent 95% confidence interval. Lipid content is expressed on a wet weight basis.



5.1%; $t = 4.49$, $df = 5$, $P = 0.0064$). It should be pointed out that mean lipid content of large alewives in November during 2002–2004 was 10.7% (Table 1). However, even considering the relatively high lipid content observed during November 2002–2004, lipid content of large alewives in Lake Michigan decreased by roughly 50% between the two time periods.

Lipid content of small alewives ranged from 1.7% in June to 5.6% in November during the post-invasion period (Table 1). In general, both lipid content and energy density of large alewives were higher than lipid content and energy density of small alewives.

Proportions of cladocerans, copepods, *Mysis*, and *Diporeia* in Lake Michigan adult alewife diet during the pre-invasion period were 0.26, 0.34, 0.11, and 0.29, respectively. Proportions of cladocerans, copepods, *Mysis*, and *Diporeia* in Lake Michigan adult alewife diet during the post-invasion period were 0.35, 0.36, 0.17, and 0.12, respectively. Energy densities of cladocerans, copepods, *Mysis*, and *Diporeia* have been reported as 1.674, 2.300, 4.604, and 4.185 $\text{kJ}\cdot\text{g}^{-1}$, respectively, on a wet weight basis (Hewett and Stewart 1989). Thus, the energy densities of the food of adult alewives in Lake Michigan during the pre-invasion and post-invasion periods were 2.939 and 2.699 $\text{kJ}\cdot\text{g}^{-1}$, respectively.

Percent water was better correlated with energy density than with either lipid content or condition (Table 2; Fig. 4). Percent water and lipid content were very good to excellent predictors of alewife energy density. Percent water accounted for 94%, 97%, and 95% of the variation in energy density for small alewives, large alewives, and alewives of both sizes, respectively (Table 2). Lipid content explained 86%, 96%, and 91% of the variation in energy density for small alewives, large alewives, and alewives of both sizes, respectively. Condition was a fairly reliable indicator of energy density of large alewives, as condition explained 75% of the variation in energy density (Table 2; Fig. 4). However, the

reliability of condition as a predictor of energy density was lower for small alewives or for alewives of both sizes.

Examination of the GLSC long-term series of observations on condition of adult alewives in Lake Michigan corroborated results from our direct comparison of energy density of large alewives between the pre- and post-invasion periods. Change-point regression analysis applied to this long-term series identified 1995 as a change-point year (Fig. 5). Further, mean condition did not show a significant trend during 1979–1994 (t test; $t = 1.89$, $df = 13$, $P = 0.0809$) or during 1995–2004 (t test; $t = 0.81$, $df = 8$, $P = 0.4393$). Mean condition of adult alewives was significantly higher during 1979–1994 than during 1995–2004 (t test; $t = 6.87$, $df = 23$, $P < 0.0001$). Residuals from these statistical analyses were not significantly autocorrelated (portmanteau test from Box and Jenkins (1976); $P > 0.05$). Mean condition decreased from 0.83 during 1979–1994 to 0.73 during 1995–2004 (Fig. 5). Substitution of these two means into the regression equation for large alewives from Table 2 yielded predictions of alewife energy density of 7.215 and 5.650 $\text{kJ}\cdot\text{g}^{-1}$ during the pre- and post-invasion periods, respectively. Thus, energy density of large alewives was predicted to decrease 21.7% between the two time periods, based on long-term series of observations on adult alewife condition and use of the regression equation to predict energy density from condition. Results from our direct comparison showed that energy density of large alewives decreased 23.0% between the pre- and post-invasion periods. Given the amount of variability about the regression line for energy density as a function of condition (Fig. 4c), this prediction of changes in energy density based on long-term trends in adult alewife condition was reasonably close to the change in large alewife energy density estimated by our direct comparison of observations on energy density between the two time periods.

The decline in energy density of large alewives between 1979–1981 and 2002–2004 was not due to higher abundance of alewives during the 2002–2004 period. Based on the GLSC lakewide fall surveys, average adult density of alewives was 11.8 $\text{kg}\cdot\text{ha}^{-1}$ during 1979–1981 and 9.1 $\text{kg}\cdot\text{ha}^{-1}$ during 2002–2004. Additionally, the correlation coefficient between mean K of adult alewives and adult alewife abundance was not significantly different from zero ($r = -0.36$; $t = -1.76$; $df = 21$; $P = 0.0935$).

Alewife energy density during the post-invasion period did not significantly change as alewife TL increased beyond 90 mm (slope = 0.0054 $\text{kJ}\cdot\text{mm}^{-1}$; $t = 1.04$, $df = 160$, $P = 0.2998$). Based on application of the age–length key to the length–frequency distribution, 99.5% of the large alewives used in our study were age 2 or older.

According to the results of the bioenergetics modeling, long-term changes in the energy density schedule for alewives could have a substantial effect on the amount of alewives consumed by a Chinook salmon in Lake Michigan. Based on the energy density schedules for alewives during the pre-invasion period (as depicted in Fig. 2), a Chinook salmon would consume 38.523 kg of alewives to attain a size of 7.865 kg after spending 4 years in the lake. Based on the post-invasion energy density schedule (also depicted in Fig. 2), a Chinook salmon would consume 47.028 kg of alewives to attain the same size while spending 4 years in the

Table 1. Mean energy density and mean lipid content of small (≤ 120 mm total length, TL) and large (>120 mm TL) alewives (*Alosa pseudoharengus*) from Lake Michigan, by month, during 2002–2004.

Month	Small alewives			Large alewives				
	<i>N</i>	Mean capture day	Mean energy density (kJ·g ⁻¹)	Mean lipid content (%)	<i>N</i>	Mean capture day	Mean energy density (kJ·g ⁻¹)	Mean lipid content (%)
April	6	8	4.493 (0.062)	4.0 (0.2)	7	13	5.665 (0.105)	5.2 (0.2)
May	16	21	4.223 (0.208)	3.3 (0.4)	17	20	4.312 (0.140)	2.7 (0.3)
June	4	19	3.471 (0.090)	1.7 (0.3)	7	5	5.035 (0.267)	3.7 (0.6)
July	6	1	4.059 (0.065)	2.5 (0.1)	11	15	4.184 (0.149)	2.1 (0.3)
August	3	3	4.926 (0.265)	4.4 (0.3)	7	6	4.514 (0.282)	3.0 (0.6)
September	11	15	4.703 (0.124)	3.3 (0.2)	57	16	5.741 (0.083)	5.5 (0.2)
October	12	17	5.458 (0.129)	5.1 (0.2)	32	11	6.172 (0.080)	6.8 (0.2)
November	7	2	5.120 (0.266)	5.6 (0.5)	12	7	7.680 (0.164)	10.7 (0.4)

Note: Standard error is shown in parentheses. *N* is the number of observations; each observation represents a determination from a 20-fish composite. Mean capture day refers to the average day of capture for the month. Energy density and lipid content are expressed on a wet-weight basis.

Table 2. Simple linear regression coefficients for energy density (kJ·g⁻¹) as a function of percent water, lipid content, and Fulton's condition.

Predictor	Grouping	α	β	r^2
Percent water (%)	Small alewife	30.4602	-0.3243	0.94
	Large alewife	33.7474	-0.3705	0.97
	Both sizes	31.0678	-0.3342	0.95
Lipid content (%)	Small alewife	3.1482	0.3797	0.86
	Large alewife	3.4249	0.4062	0.96
	Both sizes	3.2795	0.4101	0.91
Fulton's condition (<i>K</i>)	Small alewife	-1.0077	8.6944	0.39
	Large alewife	-5.8073	15.6554	0.75
	Both sizes	-3.7265	12.7857	0.64

Note: Small (≤ 120 mm total length, TL) alewife (*Alosa pseudoharengus*) regressions are based on 70 samples and large (>120 mm TL) alewife regressions are based on 150 samples. Energy density and lipid content are expressed on a wet weight basis. α , regression line intercept; β , regression line slope; r^2 , proportion of variation in energy density explained by the predictor variable.

lake. Thus, alewife consumption by Chinook salmon would have to increase 22.1% to compensate for the decrease in alewife energy density between the pre- and post-invasion periods while maintaining the same growth.

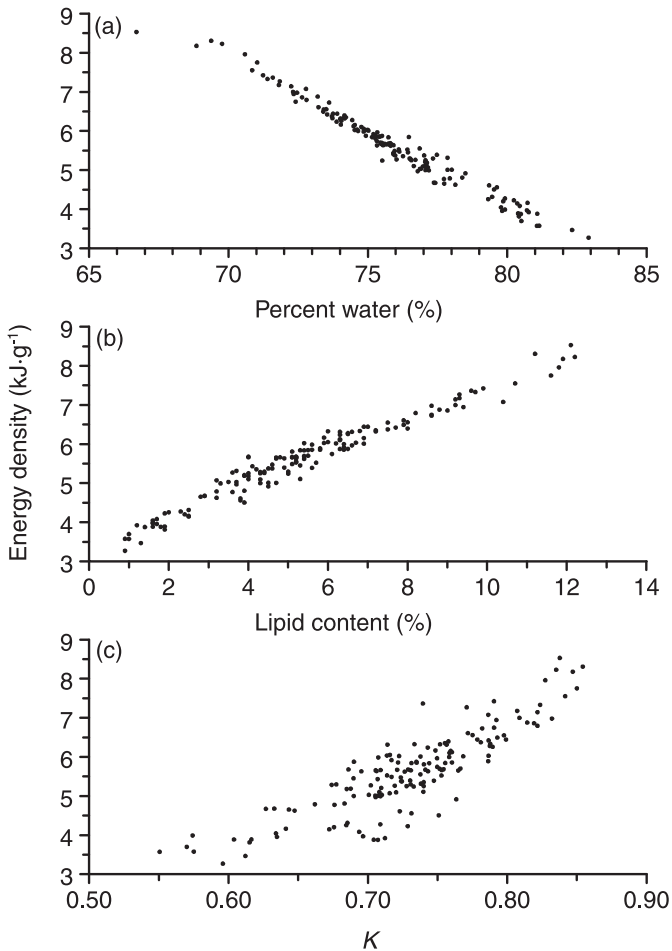
Discussion

In conjunction with alewife diet studies, our analyses indicated that energy density of large alewives in Lake Michigan has decreased by more than 20% as a consequence of the dreissenid mussel invasion and the accompanying decrease in *Diporeia* abundance. Our direct comparison of data from the pre-invasion period with that from the post-invasion period showed that energy density of large alewives in the lake decreased by 23% between the two time periods. Furthermore, our analysis of the long-term trends in condition of adult alewives from the lake suggested that the decrease in energy density occurred during the mid 1990s, just after establishment of a zebra mussel population throughout Lake Michigan. Diet data for alewives in Lake Michigan also supported the contention that the dreissenid mussel invasion led to the decline in large alewife energy density. *Diporeia* accounted for 29% of the adult alewife diet in Lake Michigan during the pre-invasion period, whereas *Diporeia* represented only 12% of the adult alewife diet in Lake Michigan

during the post-invasion period. Therefore, the importance of *Diporeia* in alewife diet in Lake Michigan decreased substantially between the 1960–1994 and 1995–2004 periods. Moreover, large alewife energy density at Muskegon was higher than that at St. Joseph, and Hondorp et al. (2005) attributed the difference to a greater proportion of *Diporeia* in the alewife diet at Muskegon. *Diporeia* is relatively high in lipid content compared with other invertebrates, and a decrease in its importance in the diet of large alewives would be expected to lead to decreases in both lipid content and energy density (Madenjian et al. 2000a). Furthermore, based on our analyses, the hypothesis that density-dependent effects were responsible for the decrease in adult alewife energy density between the pre- and post-invasion periods could be soundly dismissed. Finally, as previously mentioned, the substantial decline in *Diporeia* abundance in Lake Michigan during the 1990s has been attributed to the dreissenid mussel invasion (Nalepa et al. 2005, 2006).

Our finding that energy density of small alewives did not substantially change between the pre- and post-invasion periods further supported the contention that the dreissenid mussel invasion, along with the accompanying decline in *Diporeia* abundance, were responsible for decreased energy density of large alewives. Alewives in Lake Michigan typically do not begin to feed on *Diporeia* at a substantial rate

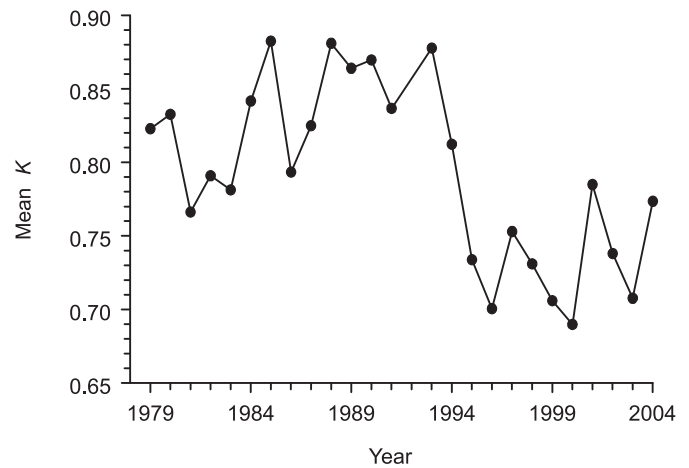
Fig. 4. Scatter plots of energy density of large (>120 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan during 2002–2004 as a function of their percent water, lipid content, and condition (Fulton's K). Each point represents a determination from a 20-fish composite sample. Condition was averaged over the 20 fish forming the composite. Energy density and lipid content are expressed on a wet weight basis.



until the fall of their second year in the lake (Stewart and Binkowski 1986). Because small alewives do not utilize *Diporeia* as a food source to any sizeable degree, a decrease in the abundance of *Diporeia* would not be expected to affect the energy density of small alewives.

Large alewives appeared to exhibit a threshold response to decreasing levels of *Diporeia* abundance, because the importance of *Diporeia* in adult alewife diet and adult alewife condition appeared to rapidly drop once abundance of *Diporeia* fell below a certain level. Also, alewife condition remained at a low level as *Diporeia* abundance continued to decline following 1995. *Diporeia* density in southern Lake Michigan decreased from 5175 individuals·m⁻² in 1992–1993 to 1936 individuals·m⁻² in 1997–1998 and then further decreased to 1438 individuals·m⁻² in 2002–2003 (Nalepa et al. 2006); the threshold level would be between the 1992–1993 and 1997–1998 values. In an analogous case, once white perch (*Morone americana*) attained a certain level of abundance in Lake Erie, recruitment of white bass (*Morone chrysops*) immediately dropped and recruitment has remained low since 1982

Fig. 5. Mean condition (Fulton's K) of spawner-size (≥ 150 mm total length) alewives (*Alosa pseudoharengus*) in Lake Michigan, 1979–2004. Data from the US Geological Survey Great Lakes Science Center bottom trawl survey.



(Madenjian et al. 2000b). White perch invaded Lake Erie during the 1970s, became well established in the lake by 1982, and their abundance continued to increase from 1982 to 1991. As the impacts of invaders are further explored in the upcoming years, we would expect more documented examples of a threshold response on the part of the native or naturalized population to the invasion. Because these threshold responses are highly nonlinear, the problem of determining the effects of an invasion on the fish community is rendered more complex by having to consider both linear and threshold responses.

Apparently, both the proportion of *Diporeia* in the diet and the feeding rate of adult alewives in Lake Michigan declined between the pre- and post-invasion periods. As previously mentioned, the proportion of *Diporeia* in adult alewife diet declined from 0.29 to 0.12 between the two time periods. We calculated that the energy density of the food of adult alewives in Lake Michigan declined from 2.939 to 2.699 kJ·g⁻¹ between the two time periods; this decline represented an 8% drop in food energy density. In addition, average weight at age of adult alewives decreased approximately 20% between the 1984–1994 and 1995–2001 periods (Madenjian et al. 2003). A reduction in growth is typically caused by a reduction in feeding rate (Stewart and Binkowski 1986). Lipid content is directly proportional to energy density, and lipid content is dependent on both the lipid content of the food and feeding rate (Madenjian et al. 2000a). Therefore, the decline in adult alewife energy density between the pre- and post-invasion periods was likely due to both the decreased proportion of *Diporeia* in adult alewife diet and an overall reduction in feeding rate of adult alewives.

Although the simplest and most obvious explanation for the reduced importance of *Diporeia* in adult alewife diet in Lake Michigan was the decrease in *Diporeia* abundance during the 1990s, the possibility that other factors were involved with the reduced importance of *Diporeia* in adult alewife diet cannot be completely ruled out. Mean depth of alewives caught in GLSC bottom trawls from the annual fall survey trended neither upward nor downward during the

1990s (C. Madenjian, unpublished data), so alewife spatial distribution apparently did not change during the 1990s. Similarly, based on sampling with Ponar grabs, no apparent changes in *Diporeia* behavior during the 1990s were evident (T. Nalepa, NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA, personal communication). Nevertheless, perhaps changes in some aspects of alewife or *Diporeia* behavior, which were undetected by surveys in the lake, resulted in reduced availability of *Diporeia* to alewives. However, the most parsimonious explanation for decreased importance of *Diporeia* in adult alewife diet during the late 1990s remains decreased *Diporeia* abundance.

Despite the overall decrease in energy density of large alewives in Lake Michigan between the pre- and post-invasion periods, energy density of large alewives exhibited a pronounced seasonal cycle during both time periods. The trough of the cycle occurred during early summer and the peak of the cycle was during the fall, when energy density was nearly twice as high as the summer minimum value. Stewart and Binkowski (1986) attributed the seasonal cycle in large alewife energy density to the highest feeding rates occurring during the fall, low feeding rates during the winter, increased feeding rates during the spring, and then a decrease in feeding rates in early summer prior to spawning. The dreissenid mussel invasion, and its subsequent negative effect on *Diporeia* abundance, did not appear to disrupt this seasonal pattern in feeding rate. The last sampling date of the calendar year included in the Flath and Diana (1985) study was 27 October, and Stewart and Binkowski (1986) speculated that the peak energy density of large alewives may occur in November or December rather than in late October. Our study results suggested that energy density of large alewives may continue to increase into November. Additional sampling will be required to determine the precise time of the year at which peak energy density of large alewives occurs.

Although the average TL of large alewives used in energy density determinations by Flath and Diana (1985) slightly exceeded the average TL of large alewives used in our study (165 vs. 155 mm), the contribution of this size difference toward explaining the observed difference in energy density between the pre- and post-invasion periods was negligible. We found that alewife energy density did not significantly increase as alewife TL exceeded 90 mm. Moreover, practically all of the large alewives used in our study were age 2 or older, and so our results were directly comparable with the results from Flath and Diana (1985). We also point out that even if adult alewife energy density did continue to increase with increasing alewife size, the observed difference in energy density between the pre- and post-invasion periods would still be attributable to the dreissenid mussel invasion. Madenjian et al. (2003) documented a decrease in mean length at age and mean weight at age in alewives from Lake Michigan during the 1990s, and they ascribed this decrease in growth to decreased abundance of *Diporeia*. Therefore, the presence of smaller adult alewives in Lake Michigan during 2002–2004 compared with 1979–1981 was probably due to the dreissenid mussel invasion.

Because Chinook salmon size at age in Lake Michigan has remained relatively stable over the past 20 years (Peeters and Royseck 2004), our bioenergetics modeling results indi-

cated that Lake Michigan Chinook salmon have compensated for the decrease in adult alewife energy density during the 1990s by increasing their consumption rates so that growth rate has not changed. Our model simulations were based on the assumption that Chinook salmon activity did not change between the pre- and post-invasion periods. Such an assumption may be reasonable, given that Chinook salmon appear to be an accomplished predator on clupeids (Healey 1991).

To better manage the salmonine fisheries of Lake Michigan and to better understand the role of alewives within the Lake Michigan ecosystem, our results will need to be incorporated into future bioenergetics modeling efforts. Bioenergetics modeling has already made an important contribution toward managing the salmon and trout populations in Lake Michigan, as management decisions to reduce Chinook salmon stocking rates have been partially based on results from bioenergetics models applied to salmon and trout populations to estimate annual consumption of alewives (Stewart et al. 1981; Stewart and Ibarra 1991; Hansen et al. 1993). More recently, a decision model, including a salmonine bioenergetics modeling component, has been developed to assist fishery managers in optimizing stocking rates of Chinook salmon (Szalai 2003). Most of these bioenergetics model applications to Lake Michigan salmonines have utilized the alewife energy density schedules developed by Stewart and Binkowski (1986). Our study has shown that use of the Stewart and Binkowski (1986) energy density schedules could result in underestimation of alewife consumption by 22.1% when bioenergetics modeling is applied to salmonine populations in Lake Michigan after 1994. More accurate estimation of alewife consumption by salmonines should lead to better decisions on salmon stocking rates. Therefore, we recommend that the energy density schedules presented in Table 1 be used when applying bioenergetics models to salmon and trout populations in Lake Michigan after 1994. Additionally, accuracy of annual estimates of consumption of invertebrates by the alewife population in Lake Michigan after 1994 would be improved by using the energy density schedules in Table 1 rather than the schedules presented in Stewart and Binkowski (1986). Hewett and Stewart (1989) have used the alewife bioenergetics model developed by Stewart and Binkowski (1986) to relate the degree of zooplanktivory by the alewife population to zooplankton abundance in Lake Michigan. Finally, we conclude that identifying the effects of an aquatic invader on the fish community is best facilitated by the availability of long-term observations on the various components of the food web. We relied on long-term time series for alewife abundance, alewife condition, and abundance of *Diporeia* in Lake Michigan to examine the effect of the dreissenid mussel invasion on alewife energy dynamics. Even though the objective of the study was focused on quantifying the effects of the dreissenid mussel invasion on alewife energy density, availability of data from the GLSC long-term survey of prey fish abundances in Lake Michigan allowed us to rule out the possibility that the decrease in energy density during the 1990s was due to an increase in alewife abundance. Further, the long-term series for alewife condition in Lake Michigan dropped abruptly in 1995 and condition remained at a relatively low level during 1995–2004, suggesting a dreissenid mussel ef-

fect. Analogously, Madenjian et al. (2000b) relied on long-term time series for abundances of age-0 white bass and white perch, for abundances of adult white perch and white bass, and for phosphorus loading to Lake Erie to show that the reduction in white bass recruitment in Lake Erie was most likely due to the white perch invasion. Because the rate of invasions of freshwater fishes and invertebrates into aquatic ecosystems has increased in many areas around the world over the past three decades (Mills et al. 1993; Rahel 2000; Kolar and Lodge 2002), maintaining the long-term surveys of biota becomes even more critical in understanding and managing important aquatic ecosystems.

Acknowledgements

L. Begnoche and K. Smith conducted the lipid analysis of the alewife samples, and J. Hickey facilitated the procurement of solvents used in the lipid analysis. D. Makauskas and S. Robillard assisted with the field collections. S. Wootke entered data into computer files and performed a preliminary analysis of the alewife length–weight data. T. Desorcie provided the map of Lake Michigan. D. Bunnell, J. Diana, L. Flath, D. Hondorp, T. Nalepa, J. Savino, T. Todd, and D. Warner reviewed the manuscript and made helpful suggestions for its improvement. This article is Contribution 1356 of the USGS Great Lakes Science Center and Contribution No. 1379 of the NOAA Great Lakes Environmental Research Laboratory.

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