



Declines in the energy content of yearling non-native alewife associated with lower food web changes in Lake Michigan

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Abstract Juveniles of non-native alewife, *Alosa pseudoharengus* (Wilson), were collected in Lake Michigan in 1998, 1999, 2010, 2011 and 2013 to evaluate changes in energy content during a period of major ecosystem changes. Consistent with historical data, energy content of yearling alewife declined from late winter into late spring and was at its lowest point in June. Energy density and length-adjusted, entire-body energy were lower in 2010, 2011 and 2013 than in 1998 and 1999. Energy losses over the first winter in the lake were more severe for the 2010 year class (56% decrease) than for the 1998 year class (28% decrease). Alewife diets in late spring of 2010–2013 reflected the loss of major prey such as *Diporeia* spp. and a shift towards lower energy prey. The recent decline in energy content of yearling alewife can be linked to recent changes in productivity and abundance of key components of the lower food web of Lake Michigan following the dreissenid invasion.

KEY WORDS: *Alosa*, *Diporeia*, *Dreissena*, energy density, overwinter, trophic level.

Introduction

Knowledge about the energy content of fish is important to understand the relationship between fish and their prey. Decreases in energy density of fish have been associated with both altered feeding rates and changes in the energy content of their prey (Madenjian *et al.* 2000, 2006; Pothoven *et al.* 2011). Energy content is often associated with the health of fish (Rottiers & Tucker 1982; Madenjian *et al.* 2000), and it is particularly important for fish to have adequate energy reserves during the winter – a period of reduced growth and food availability, as seen for example in yellow perch, *Perca flavescens* (Mitchill) (Post & Evans 1989), Atlantic silversides, *Menidia menidia* L. (Schultz & Conover 1997), striped bass, *Morone saxatilis* (Walbaum) (Hurst & Conover 2003) and lake herring, *Coregonus artedii* (Lesueur) (Pangle *et al.* 2004). Inadequate energy stores are thought to contribute to higher overwinter mortality directly through starvation or by enhancing vulnerability to predation (Garvey *et al.* 2004;

Pangle *et al.* 2004; Hurst 2007) or stressful thermal conditions (Bergstedt & O’Gorman 1989). To ensure adequate energy stores are available for overwinter, many fish have adapted seasonal patterns that favour allocating energy towards storage prior to winter, with larger fish having more capacity to store energy than smaller fish (Schultz & Conover 1997; Hurst & Conover 2003; Heermann *et al.* 2009).

The alewife, *Alosa pseudoharengus* (Wilson), a non-native fish that is now the dominant planktivore and a key component of the ecosystem in Lake Michigan, is responsible for restructuring zooplankton (Wells 1970) and native planktivore populations (Bunnell *et al.* 2006; Madenjian *et al.* 2008). The alewife now also represents the primary forage fish of salmonines (Jacobs *et al.* 2013). Young alewife deplete a large amount of their body energy over their first winter in Lake Michigan, and age-0 alewife in an inundated river mouth of Lake Michigan did not shift towards energy storage in autumn, suggesting that young alewife might not have an optimal energy

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allocation strategy for survival in the Great Lakes (Höök & Pothoven 2009). Overwinter mortality of alewife is thought to be more severe in populations with low energy reserves (Brown 1972; Flath & Diana 1985; O’Gorman & Schneider 1986; Bergstedt & O’Gorman 1989), although the direct mechanisms are unclear (Lepak & Kraft 2008; Snyder & Murray 2009; Dunlop & Riley 2013). Furthermore, mass mortalities of alewife (die-offs) frequently occur during late spring (Brown 1968; Brown 1972; Flath & Diana 1985), so yearling alewife that survive their first winter into March–May might not necessarily survive until summer (Höök & Pothoven 2009). One factor that could contribute to alewife die-offs in the spring is continued loss of energy by yearling alewife into June (Madenjian *et al.* 2006; Höök & Pothoven 2009).

The Lake Michigan food web has been altered dramatically since the 1990s, following the proliferation of dreissenid mussels and subsequent decline of the spring phytoplankton bloom (Fahnenstiel *et al.* 2010) and summer deep chlorophyll layer (Pothoven & Fahnenstiel 2013). Other notable changes in the food web include the nearly complete disappearance of the amphipod *Diporeia* spp. (Nalepa *et al.* 2009), shifts in zooplankton assemblages (Vanderploeg *et al.* 2012), and declines in alewife abundance (Bunnell *et al.* 2006). The first objective for this study was to document seasonal patterns of energy content for yearling alewife during this period of ecosystem change. To accomplish this objective, alewife were collected in 1998, 1999, 2010, 2011 and 2013, with an emphasis on June, when energy content was expected to be at its lowest point (Madenjian *et al.* 2006; Höök & Pothoven 2009). Energy content was expected to be lower in the later years owing to decreasing productivity in the lake (Fahnenstiel *et al.* 2010) and declines in major food groups following dreissenid invasions (Nalepa *et al.* 2009; Pothoven *et al.* 2010). Overwinter energy losses were also determined for two large year classes of alewife (1998 and 2010 year classes; C. Madenjian, U.S. Geological Survey, personal communication; Warner *et al.* 2013). Overwinter energy losses were expected to be more severe for the 2010 year class than for the 1998 year class related to declines in prey availability (Nalepa *et al.* 2009; Pothoven *et al.* 2010). Finally, interannual patterns in energy content between 1998–1999 and 2010–2013 were evaluated in the context of environmental factors, including prey availability, alewife diets and thermal regimes.

Material and methods

Alewife were collected as part of various projects in Lake Michigan along a 10-km transect in water depths

of 7–45 m in the vicinity of Muskegon, Michigan, USA. Fish were collected during the day using a 7.6-m skate bottom trawl with a 6.4-mm square-mesh cod liner. Alewife were collected during June in 1998, 1999, 2010, 2011 and 2013 to determine late spring energy content of yearling alewife (i.e. fish that had survived one winter). To determine overwinter energy losses during their first winter in the lake, alewife were collected in October 1998, June 1999 (1998 cohort), September 2010 and June 2011 (2010 cohort). To determine seasonal energy patterns for yearling alewife, alewife were collected in March, June, July, August, September and December 2010 and April, May, June, July and August 2013.

Upon capture, alewife were frozen in water to prevent freezer burn. After thawing, total length and weight of individual alewife were measured, and stomach contents were removed for diet analysis. A subsample of alewife specimens was selected for energy density analysis. Individual alewife were homogenised and dried to a constant weight for about three days at 70 °C, and after drying, ground with a mortar and pestle. Entire homogenised fish (or a 1 g subsample for fish >1 g dry weight) from each sampling were individually combusted in a Parr 1261 isoperibol calorimeter that had been standardised with benzoic acid. The mean CV for three replicate samples from an individual fish was determined to be 1.03% ($n = 10$), so only one sample was combusted for all subsequent fish. Mean CV for benzoic acid standardisations was 0.13%. Each individual fish’s proportional dry to wet weight, energy density (based on wet weight) and total body energy content (J g^{-1} wet weight \times total wet weight) were determined.

Although individual young alewife were not aged, length-at-age information (e.g. Madenjian *et al.* 2003) and length-frequency distributions were used to classify individuals caught in June as age-1 (i.e. yearling) if their total length (L_T) was ≤ 120 mm. Similarly, fish ≤ 110 mm in autumn were assumed to be age-0 fish, and nearly, all fish in that size group were <100 mm. While the 120-mm cut-off for June-caught age-1 alewife is fairly conservative, it is remotely feasible that some age-2 fish could be <120 mm. Nonetheless, this size range should largely encompass age-1 fish.

To evaluate temporal patterns of energy dynamics, the allometric relationship (i.e. $E = aL_T^b$) between L_T (in mm) and total body energy (E) in J was used to compare energy across years or months. Length-specific total body energy content is a particularly useful index of condition because it encapsulates both length-specific tissue composition and weight (both of which influence condition). Previous studies indicate that both allometric slopes and constants provide insight into seasonal and

ontogenetic patterns of energy allocation (e.g. Hurst & Conover 2003).

A general linear model was used to evaluate the homogeneity of slopes relating $\log_e E$ to $\log_e L_T$ by determining whether there was a significant interaction between the covariate ($\log_e L_T$) and the factor (year or month). If slopes were homogenous, then an ANCOVA was used to compare mean energy content (adjusted to mean length) between years or months. Energy density (J g^{-1} wet weight) was compared among years or months using ANOVA followed by pairwise comparisons using a Tukey's HSD test. All statistical comparisons were performed using SYSTAT 11 (Systat Software Inc, San Jose CA, USA), with $P < 0.05$ considered significant.

As part of a long-term NOAA research project in the area, water temperature was recorded at a 110-m deep site off Muskegon each month from March/April through November/December with a Sea-Bird CTD. Water temperature in March was used as an index of late winter temperature and in June as an index of late spring water temperature. Zooplankton abundance collected as part of the long-term NOAA research programme at a 45-m and a 110-m deep site off Muskegon was used as an index of zooplankton prey abundance. Zooplankton was collected with entire water-column tows using a 0.5-m-diameter, 153- μm mesh net. Mean zooplankton abundance (i.e. copepods excluding nauplii + herbivorous cladocerans) was calculated from all tows from both sites across March–June as an index of late winter to early summer zooplankton availability for each year. Details on zooplankton collections and processing are available in Vanderploeg *et al.* (2012). Annual abundance of two other potential prey of alewife, *Mysis diluviana* (Loven) and *Diporeia* spp., was also available from the 45 m site off Muskegon. *Mysis diluviana* were collected at night with entire water-column tows using a 1-m-diameter, 1000- μm mesh net. *Diporeia* spp. were collected using a Ponar grab. Details on sampling for *M. diluviana* are available in Pothoven *et al.* (2010), and details on *Diporeia* spp. sampling are available in Nalepa *et al.* (2009). To evaluate which prey were eaten by alewife during June each year, stomachs were dissected, and prey were identified and measured. Published weight-length regressions were used to convert prey lengths to dry weights. Prey weights for each prey group were summed across all individual fish, and diet composition was determined as the percent of the total calculated dry weight for each year. Further details on diet analysis are available in Hondorp *et al.* (2005) and Pothoven and Vanderploeg (2004).

Results

In 2010, length-adjusted, entire-body energy of yearling alewife differed among months (ANCOVA; $F_{4, 144} = 15.82$,

$P < 0.001$) for March–September, with June having the lowest energy (Fig. 1a). In 2010, energy density was also lowest among months in June (Fig. 1c). In 2013, there was a significant interaction between the covariate (L_T) and the factor (month) confounding analysis of L_T -adjusted, entire-body energy (Fig. 1b). However, an inspection of the regression lines indicated that energy was generally lowest in June or May for 2013. The May 2013 sampling took place on May 30, so it was essentially a June sample. Similarly, energy density of yearling alewife during April–August 2013 was lowest for fish collected in May–June, but remained low into July before increasing in August (Fig. 1d).

Length-adjusted, entire-body energy of yearling alewife in June differed among years (ANCOVA; $F_{4, 142} = 335$, $P < 0.001$), decreasing from a high in 1998 to its lowest point in 2013 (Fig. 2). Energy density of yearling alewife in June also differed significantly among years, with the highest values in 1998–1999 and the lowest values in 2010–2013 (Table 1).

The L_T -adjusted, entire-body energy content of age-0 alewife declined overwinter between autumn (October or September) and June of the following year for both the 1998 (ANCOVA; $F_{1, 24} = 14.37$, $P < 0.001$) and 2010 (ANCOVA; $F_{1, 46} = 51.11$, $P < 0.001$) year classes (Fig. 3). However, the percent decline in energy content was more severe for the 2010 year class (56%) than for the 1998 year class (28%). Length-adjusted, entire-body energy content of age-0 alewife in autumn did not differ between 1998 and 2010 (ANCOVA; $F_{1, 39} = 0.46$, $P = 0.50$), despite some variation between sampling date in autumn (19 October 1998 vs 20 September 2010). By contrast, energy content for these same cohorts of alewife the following June as yearlings (in 1999 and 2011) was lower for the 2010 year class than for the 1998 year class (ANCOVA; $F_{1, 31} = 9.1$, $P = 0.005$). Although age-0 fish were collected in October in 1998 and September in 2010, this was probably not an important factor in the results because energy content did not differ for fish caught in September and December 2010 (ANCOVA; $F_{1, 55} = 1.6$, $P = 0.21$).

The coldest water temperatures in late winter (March) and in late spring (June) at the 110 m site were in 2011 (Table 2). By contrast, the warmest late winter temperatures were found in 1998 and 2013, and the warmest late spring temperatures were in 1998 and 2010.

Spring (March–June) zooplankton densities were by far highest in 1998 (45 and 110 m sites combined) (Table 2). Zooplankton densities in 1999 were slightly higher than in 2010–2013. Copepods were the dominant zooplankton group each year (>93%). Similar to zooplankton abundance, annual abundances of *M. diluviana* and *Diporeia* spp. were higher in 1998–1999 than in

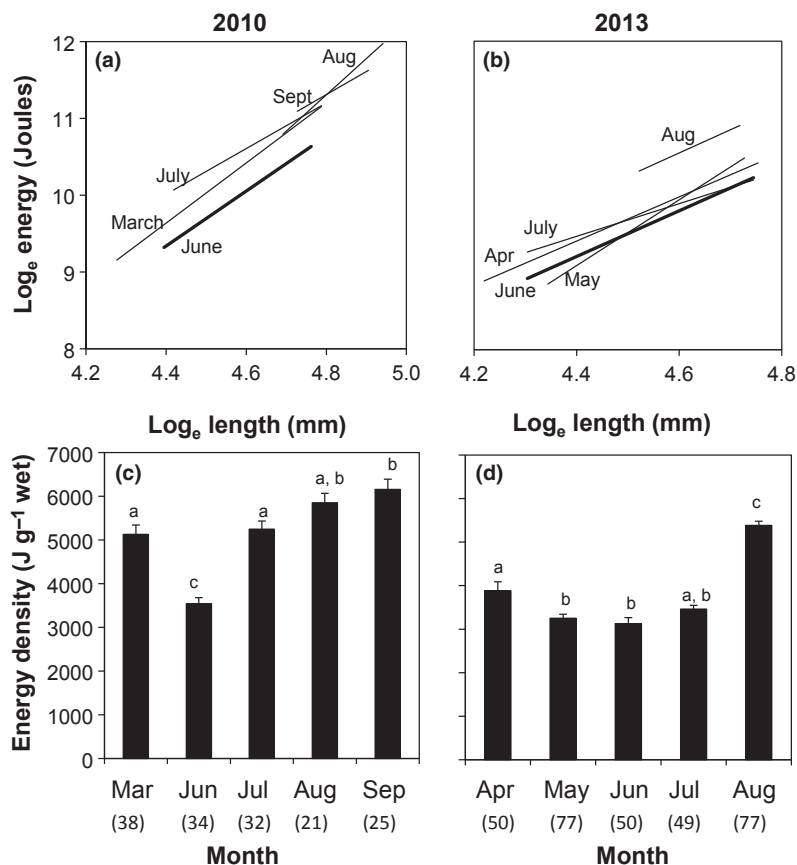


Figure 1. Energy content as a function of total length (a, b) and mean \pm SE energy density (c, d) for yearling alewife from late winter to late summer in Lake Michigan in 2010 and 2013. For energy density, months within a year that share a common superscript letter were not significantly different (Turkey's HSD). Sample sizes for each month given in parentheses.

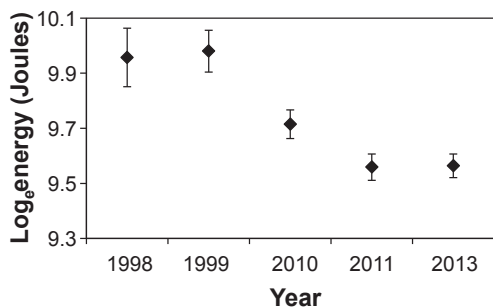


Figure 2. Mean \pm SE \log_{10} energy adjusted to mean \log_{10} total length (i.e. 4.52 mm) for yearling alewife in June 1998, 1999, 2010, 2011 and 2013.

2010–2013 (Table 2). *Diporeia* spp. were not found in the sampling region during 2010–2013.

The diet composition (% dry weight) of yearling alewife in June exhibited notable variation among years (Fig. 4). Even with the interannual variation, large differences were noted between 1998–1999 and 2010–2013.

In 1998 and 1999, *Diporeia* spp. along with *M. diluviana* or copepods were the main components of the diet. By contrast, in 2010–2013, immature chironomids (larvae and pupae) along with copepods or small cladocerans, *Bosmina longirostris* (Müller), were the main prey eaten.

Discussion

Large differences in alewife condition were measured between the study periods of 1998–1999 and 2010–2013. These changes were reflective of more severe energy losses for fish over their first winter and lower post-winter energy content during June for yearling fish. Depleted energy reserves and poor condition have been associated with heightened overwinter mortality for fish (Pangle *et al.* 2004; Shoup & Wahl 2011), including alewife (Brown 1972; Flath & Diana 1985; O’Gorman *et al.* 1987). Although low energy reserves could directly lead to starvation (Adams *et al.* 1985; Hurst 2007), poor condition in fishes most likely combines

Table 1. Mean \pm SE energy density ($J g^{-1}$), dry:wet weight (%), total length (L_T , mm), wet weight (g), sample size (n), equation relating total energy (E , Joules) to L_T and r^2 of equation for alewife caught during June in 1998, 1999, 2010, 2011 and 2013

Year	Energy density	Dry:Wet	L_T	Weight	n	Equation	r^2
1998	5523 \pm 528 ^a	25 \pm 1.4	92 \pm 6	4.8 \pm 1.2	8	$\ln E = 3.73 \times \ln L_T - 6.84$	0.79
1999	4921 \pm 260 ^a	23 \pm 0.8	87 \pm 4	4.5 \pm 0.7	16	$\ln E = 3.70 \times \ln L_T - 6.67$	0.89
2010	3544 \pm 137 ^b	17 \pm 0.4	94 \pm 2	5.7 \pm 0.3	34	$\ln E = 3.59 \times \ln L_T - 6.43$	0.57
2011	3292 \pm 108 ^b	16 \pm 0.4	96 \pm 2	5.8 \pm 0.4	40	$\ln E = 3.84 \times \ln L_T - 7.75$	0.84
2013	3128 \pm 139 ^b	15 \pm 0.4	90 \pm 2	4.7 \pm 0.3	50	$\ln E = 2.97 \times \ln L_T - 3.85$	0.51

Energy density values that share a common superscript letter were not significantly different between years (Turkey's HSD).

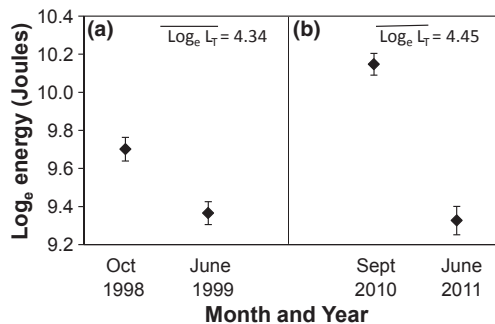


Figure 3. Mean \pm SE \log_e energy adjusted to mean \log_e total length (i.e. 4.34 mm for 1998 year class, 4.45 mm for 2010 year class) for alewife from the (a) 1998 and (b) 2010 year classes in the fall and the following June.

Table 2. Water temperature (in $^{\circ}C$) at a 110-m site offshore of Muskegon during late winter (March) and late spring (June), mean crustacean zooplankton density (number m^{-3}) from 45-m and 110-m sites offshore of Muskegon during March–June, and mean annual density of *Mysis diluviana* and *Diporeia* spp. (number m^{-2}) at a 45 m site offshore of Muskegon

Year	March Temp.	June Temp.	Zooplankton	<i>Mysis</i>	<i>Diporeia</i>
1998	3.1	18.0	14421	123	5569
1999	2.0	10.8	6499	40	1423
2010	1.8	16.2	4612	14	0
2011	1.0	6.5	3917	21	0
2013	3.1	11.8	5312	9	0

with other factors that result in death, such as increased susceptibility to thermal stress (Bergstedt & O'Gorman 1989; Hurst 2007) or increased vulnerability to predation (McCollum *et al.* 2003; Garvey *et al.* 2004).

Overwinter energy losses for two relatively large year classes of alewife, the 1998 year class and the 2010 year class, were observed in this study. Based on these data, overwinter energy losses were considerably more severe for the 2010 year class than for the 1998 year class, even though energy content of age-0 fish did not differ

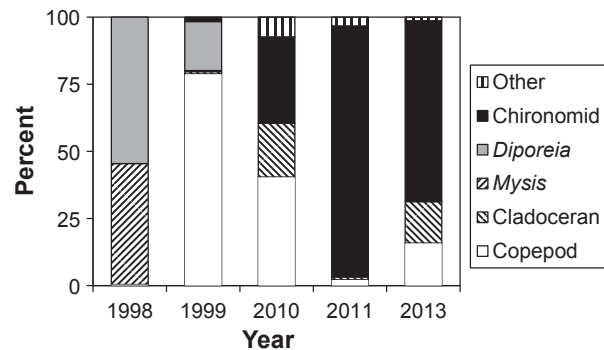


Figure 4. Diet composition (percent of total dry weight) for yearling alewife collected in June each year.

between these two year classes in autumn, indicating that the change in energy loss was due to factors between the autumn and June the following year. Overwinter energy losses are a well-documented occurrence for fish (Schultz & Conover 1997; Hurst & Conover 2003), including alewife (Flath & Diana 1985; Höök & Pothoven 2009), due to factors such as scarcity of resources and low feeding rates.

The lower energy content in June in 2010–2013 provides further support that overwinter energy declines have become more severe and yearling alewife are entering summer in poorer condition than in the late 1990s. Previous data indicated that energy depletion for small alewife continues into the early summer, reaching a low point around June (Madenjian *et al.* 2006; Höök & Pothoven 2009). This study confirmed that yearling alewife still continue to lose energy through the spring into June. Furthermore, the yearling alewife from the 2012 year class demonstrated relatively low energy content over the entire late May to mid-July 2013 period before increasing in August. The continued depletion of energy into the early summer is consistent with observations from the 1960s that found that alewife that had survived the winter into April did not necessarily survive into the summer (Brown 1972).

The recent decline in energy content of yearling alewife can be linked to recent changes in productivity and abundance of key components of the lower food web of Lake Michigan. Large decreases in primary productivity and phytoplankton abundance (Fahnenstiel *et al.* 2010), zooplankton abundance (Vanderploeg *et al.* 2012), the spring diatom bloom (Fahnenstiel *et al.* 2010), deep chlorophyll maximum (Pothoven & Fahnenstiel 2013), *Diporeia* spp. abundance (Nalepa *et al.* 2009) and *M. diluviana* abundance (Pothoven *et al.* 2010) have been documented in Lake Michigan since the late 1990s. These have been attributed directly and indirectly to the colonisation of the lake by dreissenid mussels. Energy content of fish is driven primarily by feeding rate and food quality (Madenjian *et al.* 2000). A decline in specific consumption ($\text{g food g fish}^{-1} \text{d}^{-1}$) and the proportion of maximum consumption for alewife in Lake Michigan after the dreissenid invasion (Pothoven & Madenjian 2008) indicate that alewife feeding rate has declined, which is consistent with declines in most major food types of young alewife (i.e. *Diporeia*, *Mysis* and zooplankton).

A major shift in the diet of young alewife observed in the current study reflects changes in abundance of key prey items in Lake Michigan. Diet composition of yearling alewife in June reflected the nearly complete loss of *Diporeia* spp. (see Nalepa *et al.* 2009) and declines of *M. diluviana* (Pothoven *et al.* 2010) in Lake Michigan, indicating that changes in food quality have taken place since 1998 as well. Most notably, the diet shifted from one that included energy-rich *Diporeia* spp. (4185 J g^{-1}) to a diet composed almost entirely of lower energy prey including chironomids (3185 J g^{-1}) and copepod zooplankton (2300 J g^{-1}) (energy content values from Stewart & Binkowski 1986; Lantry & Stewart 1993). It is also possible that *Diporeia* spp. contained essential fatty acids that were important for overwinter survival of alewife (Kainz *et al.* 2010). Shifts in diet can also lead to situations where essential nutrients for overwinter survival are not obtained (Snyder & Murray 2009). Although *Diporeia* spp. did not appear to be an important diet component for young alewife in some studies (Hewett & Stewart 1989; Hondorp *et al.* 2005), data from Rand *et al.* (1995) and this study both indicated that *Diporeia* spp. were an important prey for small alewife, especially in the spring. The loss of *Diporeia* spp. from the environment and diets is consistent with lower energy content in late spring as this important prey is no longer available to alewife at a time when their energy reserves are low. Nalepa *et al.* (2009) indicated that the shift in the benthic community from one dominated by *Diporeia* spp. to one dominated by dreissenids represents a shift from a benthic community that provided an

efficient pathway to higher trophic levels to one that represents an energy sink.

Changes in prey availability were not simply related to *Diporeia* spp. as declines in *M. diluviana* also appeared to have affected diet composition. Pothoven and Madenjian (2008) found that alternative energy-rich prey such as *M. diluviana* might not be available in sufficient quantities or densities to replace *Diporeia* spp. This appears to be the case, as *M. diluviana* declined in abundance in the environment and was absent from recent alewife diets. Another factor that could have contributed to decreased occurrence of *M. diluviana* in diets was that fewer alewife were collected at the deeper end of the sampling transect in 2010–2013 than in 1998–1999 (S. Pothoven, unpublished data). Although data on chironomid densities for the more recent years were not available, their densities are believed to have been relatively low for the duration of this study and largely unaffected by dreissenid mussels (T. Nalepa, University of Michigan, personal communication). Food web shifts, including loss of *Diporeia* and proliferation of *Dreissena* spp. in Lake Michigan, have been associated with declines in condition and energy content for other fish, including deepwater sculpin, *Myoxocephalus thompsonii* (Girard) (Hondorp *et al.* 2005; Pothoven *et al.* 2011), adult alewife (Hondorp *et al.* 2005; Madenjian *et al.* 2006) and lake whitefish, *Coregonus clupeaformis* (Mitchill) (Pothoven *et al.* 2001; Pothoven & Madenjian 2008).

Other factors such as water temperatures and alewife abundance certainly affect feeding rates and therefore energy content. Abundance of yearling alewife likely varied among years owing to large differences in year-class strength of age-0 alewife the preceding autumn, that is the 1997 and 2009 year classes were considered poor, the 1998 and 2010 year classes were considered large, and 2012 year class was considered average (C. Madenjian, U.S. Geological Survey, personal communication; Warner *et al.* 2013). However, interannual differences in water temperatures or alewife abundance do not appear to be driving the dramatic declines in energy as much as food web changes. For example, energy content of yearling alewife in June 1998 and June 1999 was similar, despite much warmer late winter and spring water temperatures in 1998 along with much lower yearling alewife abundance. Furthermore, a relatively small cohort of yearling alewife in 2010 had experienced a relatively warm spring, but had much lower energy than yearling alewife in either 1998 or 1999. Finally, despite the yearling alewife caught in June 2013 experiencing a relatively mild winter and being part of an average year class, energy content was similar to that of yearling alewife caught in June 2011, which were part of a large

year class that had experienced harsh overwinter conditions and a much colder spring.

The dramatic declines in yearling alewife energy content have implications for the management of the Lake Michigan and other systems impacted by dreissenid invasions. Sport fishing is a multibillion dollar industry in the Great Lakes, and a large component of the fishery is based on stocked Pacific salmonines that rely heavily on alewife as forage (Jacobs *et al.* 2013). Young alewife (this study) and older alewife (Madenjian *et al.* 2006) have lower energy in the post-dreissenid Lake Michigan environment. Alewife populations in poor condition are now potentially more vulnerable to severe conditions (Hurst 2007), which provides additional uncertainty into management strategies. Furthermore, evidence from Lake Huron, which suffered a catastrophic decline of alewife in 2003 due to a number of factors, suggests that poor food web conditions will decrease the resiliency of alewife populations after populations' declines (Dunlop & Riley 2013).

Decreases in adult alewife energy density in Lake Michigan have led to increased consumption demands by Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), which need to eat more alewife to maintain growth rates and ration (Madenjian *et al.* 2006). Despite population declines, the importance of alewife in Chinook salmon diets has actually increased with small alewife accounting for a larger percentage of the diet and being consumed by a higher proportion of salmon (Jacobs *et al.* 2013). If low numbers of alewife prevent salmon from compensating for lower prey energy content, then they will experience lower growth, condition and possibly have higher incidences of disease (Rand *et al.* 1994). Late spring/early summer is a period of rapid growth for salmon (Stewart & Ibarra 1991) and coincides with the timing of the lowest energy content for yearling alewife, placing additional pressures on alewife populations and providing salmon with foraging challenges to meet consumptive demands with alewife populations at historic low levels. Thus, ongoing lower food web changes present continued challenges to managers of forage fish and stocked salmonines in the Great Lakes and other dreissenid invaded systems.

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