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Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in lakes Huron and Michigan

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Abstract – The deepwater sculpin *Myoxocephalus thompsonii* is a glacial relict in the Laurentian Great Lakes that primarily consumes two glacial relict crustaceans, *Mysis relicta* and *Diporeia* spp. Deepwater sculpin were collected in Lake Michigan off Little Sable Point (in 2001) and Muskegon, Michigan (in 2001 and 2009), and in Lake Huron off Harbor Beach, Michigan (in 2007) for energy density and diet analyses. These sites and years represented differences in available prey. In Lake Michigan, energy densities of deepwater sculpin in 2001 were similar to those reported in 1969–1971. In contrast, energy content declined at least 26% at Muskegon between 2001 and 2009. Overall, energy density was 31–34% higher at a site with abundant *Diporeia* spp. compared with two sites without *Diporeia* spp. Deepwater sculpin diets consisted primarily of *M. relicta* at all sites, but included 10–17% (dry mass) *Diporeia* spp. at sites where this crustacean was still abundant. Food biomass in stomachs was higher at sites with abundant *Diporeia* spp. than at those without *Diporeia* spp. Deepwater sculpin energy density and food biomass in stomachs were similar between two sites without *Diporeia* spp. despite differences in abundance of remaining prey, *M. relicta*. Declines in deepwater sculpin energy density suggest the potential for further effects on other species and changes in the flow of energy through the food web of the Great Lakes.

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Introduction

The deepwater sculpin *Myoxocephalus thompsonii* is a benthic fish found in deep, postglacial lakes of North America, including the Laurentian Great Lakes. It is widely distributed in lakes Superior, Michigan, and Huron and can account for a large proportion of the offshore fish biomass in these lakes. Deepwater sculpin accounted for 30% of the fish biomass caught in a bottom trawl survey in Lake Michigan during 1999–2007 (Bunnell et al. 2009) and historically have been the most abundant fish collected at depths >80 m in the lake (Wells 1968).

Deepwater sculpin are closely related to the four-horn sculpin *Myoxocephalus quadricornis* that is found in the Arctic and northern Europe (Kontula & Väinölä 2003). The origin and distribution of deepwater sculpin within North America was mediated by the advance and retreat of glaciers during the Pleistocene epoch (Dadswell 1972; Kontula & Väinölä 2003; Sheldon et al. 2008). The deepwater sculpin always co-occurs with at least one other glacial-relict fauna such as *Mysis relicta* or *Diporeia* spp. (Dadswell 1972, 1974). *Mysis relicta* and *Diporeia* spp. are generally the two main prey eaten by deepwater sculpin in the Great Lakes (Scott & Crossman 1973;

Wojcik et al. 1986; Selgeby 1998; Hondorp et al. 2005; O'Brien et al. 2009).

Recently, abundances of one of the main prey for the deepwater sculpin, *Diporeia* spp., have undergone dramatic declines in the Laurentian Great Lakes (Nalepa et al. 2007, 2009; Watkins et al. 2007). *Diporeia* spp. have completely disappeared in the southern basin of Lake Michigan at depths <90 m, and densities in the deeper areas (>90 m) declined from 3925 m⁻² in the 1980s to 576 m⁻² in 2007 (Nalepa et al. 2009). Similarly, in depths >90 m in Lake Huron, *Diporeia* spp. declined from 1918 to 900 m⁻² between 2000 and 2003 (Nalepa et al. 2007). The near disappearance of *Diporeia* spp. is expected to have affected deepwater sculpin growth or condition, given their importance as a prey item for this and other profundal fish species. Previous work examining deepwater sculpin diet and condition over a gradient of *Diporeia* spp. densities suggested that *M. relicta* would become a greater component of deepwater sculpin diets as *Diporeia* spp. continued to decline, and that this switch to *M. relicta* would not halt deepwater sculpin condition declines (Hondorp et al. 2005).

The goal of this study was to evaluate the response of deepwater sculpin energy to the collapse of *Diporeia* spp. using two approaches: (i) energy

densities of deepwater sculpin were determined during October at a single site prior to and following the loss of *Diporeia* spp., and (ii) energy densities of deepwater sculpin were determined seasonally at three sites that represented a gradient of *Diporeia* spp. and *M. relicta* biomass. Further, deepwater sculpin stomach content biomass, diet composition and relative population abundance were determined to provide insight into any differences observed in energy density across time or sites.

Methods

Deepwater sculpin were collected as part of various food web studies in 2001, 2007 and 2009. Fish were collected using 7.6-m semi-balloon bottom trawl (13-mm mesh liner) during the day at each of three sites: Little Sable Point and Muskegon in Lake Michigan, and Harbor Beach in Lake Huron (Fig. 1). Trawls were towed for 5–20 min, depending on the conditions. Catch-per-unit-effort (CPUE) was expressed as number of deepwater sculpin caught in a trawl, standardised to a 10-min tow. All fishes, or subsamples of large catches, were frozen in water until they were analysed.

Fish were collected on various dates at the three sites: Little Sable Point in June, August, and October

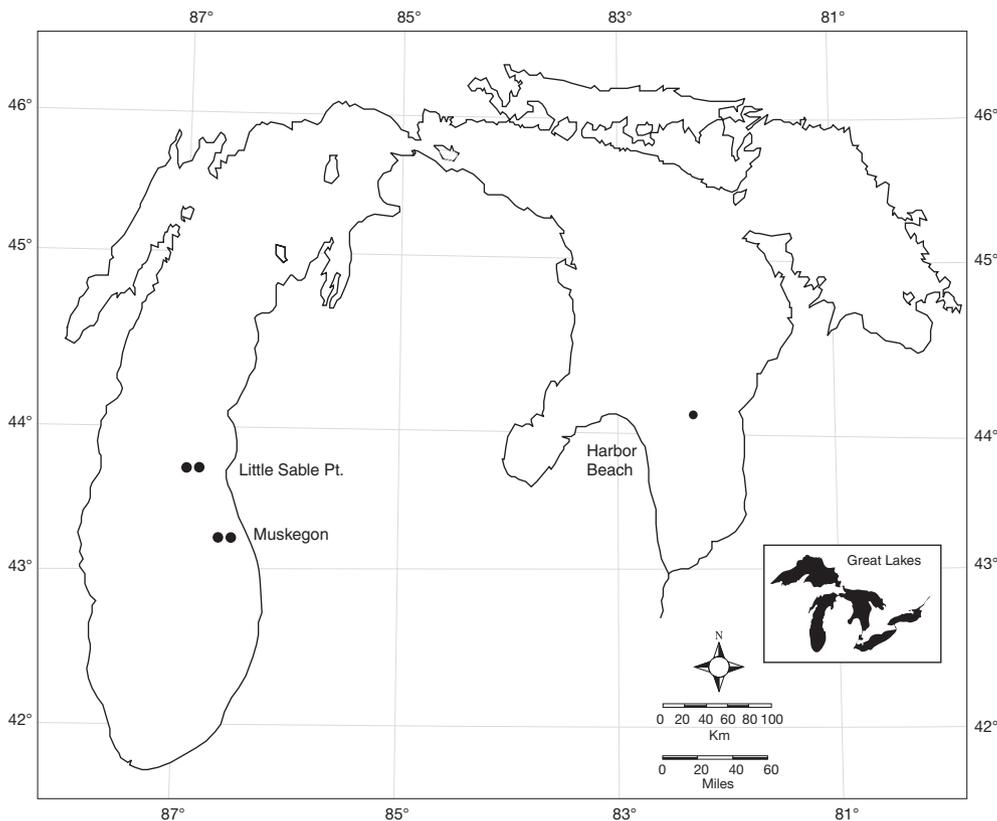


Fig. 1. Map of lakes Michigan and Huron showing locations of sampling sites for deepwater sculpin and their prey within each lake.

2001; Muskegon in June, August, and October 2001 and 2009; and Harbor Beach in June, August, and October 2007. Fish were primarily collected in an area 75–85 m deep at Little Sable Point and Muskegon in 2001, 87–101 m deep at Muskegon in 2009 and 88–93 m deep at Harbor Beach in 2007. *Diporeia* spp., although in decline, were still relatively abundant in 2001 off Muskegon and Little Sable Point (Hondorp et al. 2005), but were below the detectable levels at Muskegon in 2009 and at Harbor Beach in 2007 (see Table 2). In the laboratory, fish were thawed and counted, and a subsample was measured (TL ± 1 mm), weighed (nearest 0.01 g) and their stomach contents removed. Subsequently, individual fish were homogenised, dried at 65–75 °C for 48–60 h and reweighed. No fish from June or August 2001 from Muskegon were dried, and only a small number of fish from June and August 2001 (19 and 20, respectively) from Little Sable Point were dried.

After fish were dried, a subsample of fish from each year and month (except Muskegon 2001) was used for direct energy density determinations (Table 1). After drying, individual fish used for direct energy determinations were further ground with a mortar and pestle. A 1-g subsample of the dried, ground material was combusted in a Parr 1261 isoperibol bomb calorimeter that was standardised with benzoic acid. Energy density for each individual fish was converted to J·g⁻¹ wet mass using the known dry:wet weight ratio for that fish. Energy density for each year (i.e., 2001 or 2009 Lake Michigan, 2007 Lake Huron) was regressed as a function of the dry:wet weight ratio. ANCOVA was used to determine whether there were

differences among the three regression lines after first ensuring slopes were homogenous by confirming there was no significant interaction between the covariate and the factor ($P < 0.05$; SYSTAT 11). In cases where the categorical variable (e.g., year or lake) in the ANCOVA was nonsignificant, data from multiple factors were combined to generate a common regression of fish energy density as a function of dry:wet weight ratio. These regressions were used to estimate energy density for all remaining dried fish whose energy density was not directly determined (Table 1) as done in previous studies (Hartman & Brandt 1995; Lumb et al. 2007).

All prey in each fish stomach were identified and counted. Lengths of whole prey were measured using an image-analysis system. These lengths were converted to dry weights with appropriate weight–length relationships (Culver et al. 1985; Shea & Makarewicz 1989; T. Nalepa, unpublished data). Dry weights of partial prey were assumed to be the same as the mean individual dry weight for the same prey for a given month, year and site. Partial prey were defined by the presence of an intact head. Average dry mass of an individual of each prey type was determined for each site, month, and year and multiplied by the number of each prey type in a stomach to determine dry-biomass contribution of each prey type in an individual stomach. Diet composition was expressed as the percentage of total calculated dry weight of food for all fish in a given month, year or site.

To assess the availability of prey for each year and location, we sampled *Diporeia* spp. and *M. relicta* at sites within the area of the trawl transects in conjunction with all fish collections: 75-m sites at Muskegon and Little Sable Point in 2001, a 100- or 110-m site at Muskegon in 2009, and an 87-m site at Harbor Beach in 2007. Details on sampling are available elsewhere (Hondorp et al. 2005). Briefly, *Diporeia* spp. were collected with triplicate ponars at each site on each date. *Mysis relicta* were collected at night at each site on each date with triplicate vertical net tows. Prey densities were expressed on an areal basis (Pothoven & Vanderploeg 2004) to facilitate comparisons of *Diporeia* spp. and *M. relicta* data. Individual lengths of *Diporeia* spp. and *M. relicta* were measured with an image-analysis system and converted to biomass using weight–length relationships as done for diet analysis.

Differences in deepwater sculpin CPUE among years and sites were evaluated with the nonparametric Kruskal–Wallis test. If overall differences were significant, then a nonparametric post hoc test was used to test differences between specific sites (Zar 1974).

Temporal trends in energy density were examined by comparing values found at Muskegon in October of 2001 and 2009. ANCOVA with fish wet mass as the covariate was used to evaluate whether energy density

Table 1. Number of deepwater sculpin 60–120 mm TL whose energy density was directly determined using bomb calorimetry and number whose energy density was indirectly determined using energy density to dry:wet weight ratio regression equations at three study sites.

Site	Month(s)	Year	Direct	Indirect
Muskegon	October	2001	0	48
Muskegon	October	2009	17	67
Little Sable Point	June, August, October	2001	25	72
Harbor Beach	June, August, October	2007	26	84
Muskegon	June, August, October	2009	58	182

Table 2. Mean annual biomass (mg·m⁻²) ± 1 SE of *Diporeia* spp. and *Mysis relicta* at three sites in lakes Michigan and Huron during June, August and October 2001–2009. *N* = number of dates (three replicates/date) sampled for each year.

Site	Year	<i>Diporeia</i> spp.	<i>N</i>	<i>Mysis relicta</i>	<i>N</i>
Muskegon, MI	2001	8472 ± 2252	3	216 ± 54	3
Muskegon, MI	2009	0	4	202 ± 14	4
Little Sable Point	2001	7367 ± 470	3	201 ± 94	3
Harbor Beach, MI	2007	0	3	15 ± 11	2

differed between the 2 years. ANCOVA with fish wet mass as the covariate was also used to evaluate whether the amount of food (June, August, and October) in stomachs varied between years and among seasons at Muskegon.

To examine relationships between energy density and ecological conditions (i.e., prey biomass and/or deepwater sculpin abundance), we used June, August and October data from Little Sable Point (2001), Muskegon (2009) and Harbor Beach (2007). ANCOVA with fish wet mass as the covariate was used to test whether energy density or the amount of food in stomachs differed among sites and months. If overall differences were significant, a *post hoc* test was used to test differences between specific sites (Quinn & Keough 2002).

For all ANCOVA tests, we first tested whether slopes were homogenous by confirming there was no significant interaction between the covariate and the factor ($P > 0.05$). For ANCOVA, only fish 60–120 mm TL were used for analysis to better meet the assumption of a similar range of covariate values across factors (Quinn & Keough 2002).

Results

A total of 173 deepwater sculpin were used to determine energy density as a function of dry: wet weight (Fig. 2). Predictive equations relating energy density to the dry:wet weight ratio were similar for Lake Michigan fish across years (Muskegon 2009 and Little Sable Point 2001) (ANCOVA: $F_{1,122} = 0.318$, $P = 0.58$), so a single equation was used to predict energy for Lake Michigan as follows: $J \cdot g^{-1} \text{ (wet)} = (33455 \times \text{dry:wet weight ratio}) - 2083.9$, $n = 125$, $R^2 = 0.98$. There was however a significant interaction between the covariate and the factor when comparing the Lake Michigan equation with the Lake Huron equation ($F_{1,169} = 27.8$, $P < 0.001$), indicating that slopes were not homogenous. Therefore, a

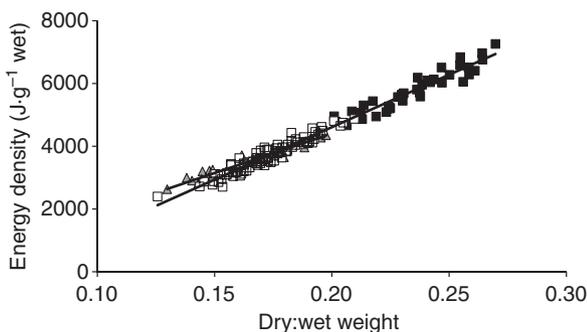


Fig. 2. Energy density of deepwater sculpin as a function of dry:wet weight for Lake Michigan 2001 (shaded squares) and 2009 (open squares) combined and Lake Huron (shaded triangles).

separate equation was used to predict energy density for Lake Huron fish as follows: $J \cdot g^{-1} \text{ (wet)} = (25157 \times \text{dry:wet weight ratio}) - 626.04$, $n = 48$, $R^2 = 0.93$.

For the analysis of trends in energy density, direct calorimetric measurements were made for a total of 126 fish with lengths 60–120 mm TL (Table 1). Energy density was also estimated for an additional 453 fish using the aforementioned lake-specific, dry:wet weight ratio to energy density regression equations.

Muskegon 2001 versus 2009

Diporeia spp. biomass declined dramatically between 2001 and 2009 at the Muskegon site, averaging $8472 \text{ mg} \cdot \text{m}^{-2}$ in 2001 but was below the detectable levels by 2009 (Table 2). *Mysis relicta* biomass varied little between 2001 and 2009 at Muskegon, with average values of 216 and $202 \text{ mg} \cdot \text{m}^{-2}$, respectively.

Mean CPUE of deepwater sculpin (# caught per 10 min) at Muskegon over all 3 months was 305 ± 131 (1 SE, $n = 6$) in 2001 and 77 ± 15 ($n = 6$) in 2009. However, owing to high variability among catches, especially in 2001, CPUE did not differ significantly between the 2 years (KW test, $P = 0.26$).

Energy density increased at a faster rate with fish mass in 2001 than 2009 (Fig. 3a) as revealed by a significant interaction between the covariate (fish

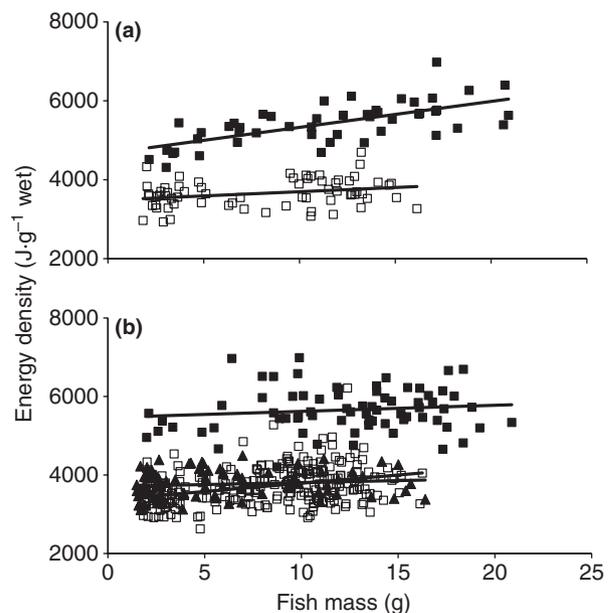


Fig. 3. Energy density of deepwater sculpin as a function of fish mass for: (a) Muskegon in October 2001 (closed) and October 2009 (open), and (b) Little Sable Point in 2001 (shaded square), Muskegon in 2009 (open square) and Harbor Beach in 2007 (shaded triangle).

mass) and factor (year) ($F_{1,111} = 9.9$, $P = 0.002$). Energy density was 26–33% higher in 2001 than in 2009 for a given sized fish across the size range of fish collected in 2009. Mean dry:wet weight ratio was 0.22 in 2001 and 0.17 in 2009.

Deepwater sculpin diet (% dry weight) in 2001 consisted of 17% *Diporeia* spp., 78% *M. relicta* and 5% other prey, but in 2009 the diet consisted of 91% *M. relicta* and 9% other prey (Fig. 4). Fish eggs accounted for the majority of food mass in the ‘other’ category for both years. Mean adjusted food mass, controlling for fish weight, differed between years (ANCOVA: $F_{1,335} = 84.2$, $P < 0.001$). Mean adjusted food mass was 19.3 ± 0.82 mg in 2001, but only 8.8 ± 0.76 mg in 2009. Food mass also varied by season (ANCOVA: $F_{2,335} = 83.6$, $P < 0.001$) and there was a significant year \times month interaction (ANCOVA: $F_{2,335} = 125.6$, $P < 0.001$).

Prey gradient across sites: Little Sable Point, Muskegon, Harbor Beach

During 2001 at Little Sable Point, *Diporeia* spp. biomass averaged $7367 \text{ mg}\cdot\text{m}^{-2}$, but biomass was below the detection levels during 2009 at Muskegon and during 2007 at Harbor Beach. Mean *M. relicta* biomass during 2001 at Little Sable Point and during 2009 at Muskegon was similar (201 and $202 \text{ mg}\cdot\text{m}^{-2}$ respectively), but comparatively lower during 2007 at Harbor Beach (only $15 \text{ mg}\cdot\text{m}^{-2}$) (Table 2). Thus, the sites (and respective years) represented discrete differences in prey availability, that is, abundant *Diporeia* spp. and *M. relicta* (Little Sable Point 2001), relatively abundant *M. relicta* but no *Diporeia* spp. (Muskegon 2009), and no *Diporeia* spp. and few *M. relicta* (Harbor Beach 2007).

Mean deepwater sculpin CPUE (# caught per 10 min) was 426 ± 62 ($n = 6$) at Little Sable Point, 77 ± 15 ($n = 6$) at Muskegon (2009) and 10 ± 3 ($n = 5$) at Harbor Beach; these site differences were significant (KW test, $P < 0.01$). Pairwise comparisons

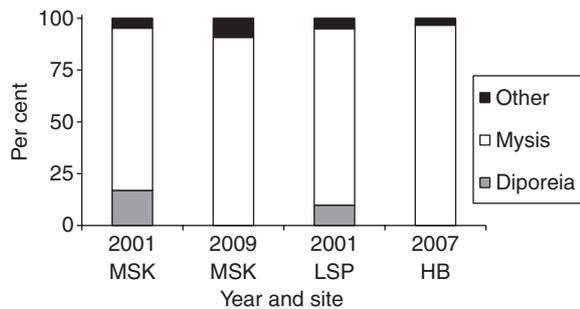


Fig. 4. Diet composition (% dry mass) for deepwater sculpin at three sites in lakes Michigan and Huron during 2001–2009. MSK = Muskegon, LSP = Little Sable Point, HB = Harbor Beach.

indicated that CPUE at the Little Sable Point site was significantly different from that at the Harbor Beach site ($P < 0.05$), but there were no other differences among pairs of sites because of high variation and relatively low sample sizes.

Mean adjusted energy density of deepwater sculpin, controlling for fish weight, differed significantly among sites (ANCOVA: $F_{2,328} = 367.3$, $P < 0.001$) (Fig. 3b). Adjusted energy densities at Muskegon (2009) ($3652 \pm 32 \text{ J}\cdot\text{g}^{-1}$) and Harbor Beach ($3737 \pm 61 \text{ J}\cdot\text{g}^{-1}$) were not significantly different, but adjusted energy density at both sites differed from Little Sable Point ($5577 \pm 64 \text{ J}\cdot\text{g}^{-1}$) ($P < 0.05$). Mean dry:wet weight ratio was 0.23, 0.17 and 0.17 at Little Sable Point, Muskegon (2009) and Harbor Beach, respectively. Energy density also differed among months (ANCOVA: $F_{2,328} = 6.9$, $P = 0.001$) and the site \times month interaction was significant (ANCOVA: $F_{4,328} = 3.9$, $P = 0.004$) (Fig. 5a). Overall, energy density was highest in August, a trend which was apparent at both Little Sable Point and Harbor Beach, but not at Muskegon (2009), where energy content varied little with month.

Deepwater sculpin diet (% dry weight) at Little Sable Point in 2001 was 10% *Diporeia* spp., 85% *M. relicta* and 5% other prey. Diet at Muskegon in

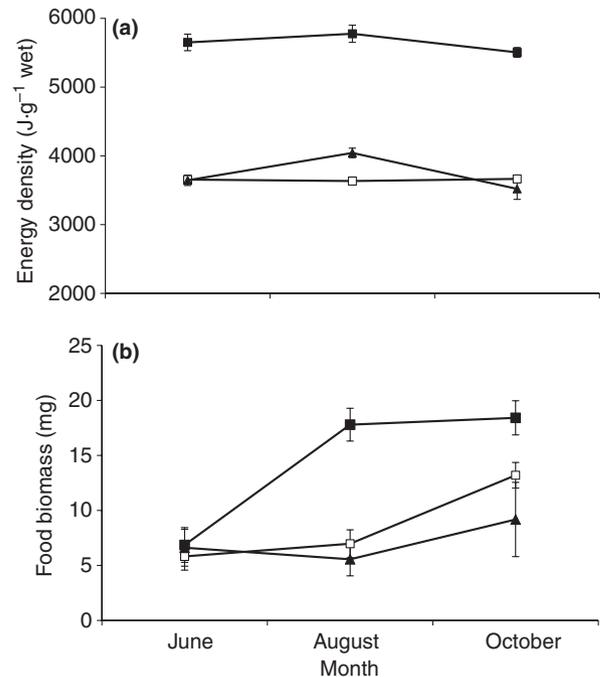


Fig. 5. Deepwater sculpin (a) mean adjusted energy density (± 1 SE) controlling for fish mass (ANCOVA) and (b) mean adjusted food biomass (± 1 SE), controlling for fish mass, at three sites in lakes Michigan and Huron during June, August and October. Little Sable Point in 2001 (shaded square), Muskegon in 2009 (open square) and Harbor Beach in 2007 (shaded triangle).

2009, as noted previously, was 91% *M. relicta* and 9% other prey, whereas diet at Harbor Beach in 2007 was 97% *M. relicta* and 3% other prey (Fig. 4). The category 'other' consisted mainly of fish eggs at Little Sable Point and Muskegon (2009) and large calanoid copepods at Harbor Beach. Mean adjusted food mass, controlling for fish mass, differed among sites (ANCOVA: $F_{2,379} = 11.6$, $P < 0.001$) (Fig. 5b). As with energy density, adjusted food mass was similar at Harbor Beach and Muskegon (2009), but adjusted food mass at both sites differed from that at Little Sable Point ($P < 0.05$). Adjusted food mass also differed among months (ANCOVA: $F_{2,379} = 14.0$, $P < 0.001$), and the site \times month interaction was significant (ANCOVA: $F_{4,379} = 4.8$, $P < 0.001$). At Muskegon (2009) and Harbor Beach, adjusted food masses were similar between June and August, then increased in October. At Little Sable Point, food mass was lowest in June with higher values during August and October (Fig. 5b).

Discussion

Deepwater sculpin energy density declined dramatically off Muskegon in Lake Michigan between 2001 and 2009, decreasing at least 26% over this 8-year period. In a previous study of energy density of deepwater sculpin in Lake Michigan conducted during 1969–1971, Rottiers & Tucker (1982) reported that the energy density of a composite of fish (14.6 g mean weight) was $5421 \text{ J}\cdot\text{g}^{-1}$. Our predicted energy density for a 14.6 g fish in 2001 was $5628 \text{ J}\cdot\text{g}^{-1}$ (4831–6425; 95% CI), similar to the mean value reported in 1969–1971. However, the predicted energy density in 2009 for a 14.6-g fish was $3795 \text{ J}\cdot\text{g}^{-1}$ (3089–4502; 95% CI), a 30% decrease compared to 1969–1971. The decline was similar to data collected as part of a pilot study at Muskegon in July 2008, which predicted an energy density for a 14.6-g deepwater sculpin of $3206 \text{ J}\cdot\text{g}^{-1}$ (S. Pothoven, unpublished data). Declines in energy density have implications for food web dynamics. Energy reserves influence fish survival, reproduction, growth and vulnerability to predators (see Madenjian et al. 2000; Breck 2008). Ultimately, changes in energy density of forage fish such as deepwater sculpin impact energy available to piscivores (Madenjian et al. 2000, 2006).

Deepwater sculpin energy density also varied across sites which had varying biomasses of *Diporeia* spp. Deepwater sculpin had higher energy density at sites with abundant *Diporeia* spp. compared with areas where *Diporeia* spp. had disappeared. An examination of deepwater sculpin energy density across a spatial gradient of *Diporeia* spp. abundance in Lake Michigan in October 2001 indicated that energy density was lowest at a site (St. Joseph) with low *Diporeia* spp.

numbers compared with the two sites also examined in this study (Muskegon and Little Sable Point), where *Diporeia* spp. was in decline but still relatively abundant (Hondorp et al. 2005). Interestingly, at the site with low *Diporeia* spp. numbers in 2001 (St. Joseph) in the Hondorp et al. (2005) study, *Diporeia* spp. were still a substantial component of the diet, and energy density at the site was much higher ($5253 \text{ J}\cdot\text{g}^{-1}$) compared with the sites in this study with no *Diporeia* spp. ($<3800 \text{ J}\cdot\text{g}^{-1}$). These results support predictions that the *Diporeia* spp. decline and concurrent expansion of *Dreissena* spp. populations could lead to declines in fish condition or production (Madenjian et al. 2000; Nalepa et al. 2009).

The decline in deepwater sculpin energy density in conjunction with the disappearance of *Diporeia* spp. is consistent with changes observed for the pelagic alewife *Alosa pseudoharengus* in Lake Michigan. The energy density of alewife in Lake Michigan declined on average 23% between 1979–1981 and 2002–2004, a change that was largely attributed to the decline of *Diporeia* spp. (Madenjian et al. 2006). The disappearance of *Diporeia* spp. is also one of several factors that have contributed to declines in condition and energy density of the lake whitefish *Coregonus clupeaformis* in the Laurentian Great Lakes (Pothoven et al. 2006; Rennie & Verdon 2008).

Diporeia spp. have historically been an important food item for deepwater sculpin throughout their distribution. Although they only accounted for 10–17% of the diet in 2001 at Little Sable Point and Muskegon, the previous year they had accounted for over 50% of the diet at these same sites (Hondorp et al. 2005). Wojcik et al. (1986) found that *Diporeia* spp. accounted for >67% of the diet volume of deepwater sculpin in south-eastern Lake Michigan in 1981–1982. In Lake Huron, despite rapidly declining densities of *Diporeia* spp., they still accounted for 15–25% of deepwater sculpin diets in fall 2003–2005 (O'Brien et al. 2009). Hondorp et al. (2005) suggested that loss of *Diporeia* spp. could limit food availability or increase foraging time required to achieve a given ration. Our results support this observation, where sites without *Diporeia* spp. had lower stomach biomass, suggesting reduced consumption rates compared with sites with higher *Diporeia* spp. biomass.

Although *M. relicta* have historically been a prominent component of deepwater sculpin diets along with *Diporeia* spp. (Wells 1980; Hondorp et al. 2005), it appears deepwater sculpin are unable to maintain their previous level of energy density following the near complete collapse of *Diporeia* spp. populations. One factor might be that *M. relicta* biomass was a fraction of that of *Diporeia* spp. before its decline, which could lead to increased foraging time to achieve the same ration. Although we saw little difference in *M. relicta*

biomass over time at Muskegon, *M. relictus* production may have already been in decline in south-eastern Lake Michigan by 2000 (Pothoven et al. 2010). Therefore, *M. relictus* production might not be adequate to support increased predation pressure by deepwater sculpin with the loss of *Diporeia* spp. It is also possible that *M. relictus* are physically less available to deepwater sculpin as a prey than *Diporeia* spp. would have historically been. *Mysis relictus* undergo diel vertical migrations, making them less available to benthic fishes at night, and they could have a more evasive escape response than *Diporeia* spp. (Hondorp 2006; O'Brien et al. 2009).

In addition to prey density, fish population abundances can affect feeding rates and ultimately energy content (Madenjian et al. 2000; Pothoven et al. 2006; Kratzer et al. 2007). Spatial differences in population abundances have been linked with similar spatial differences in energy content for both deepwater sculpin (Madenjian et al. 2000) and slimy sculpin *Cottus cognatus* (Owens & Noguchi 1998). However, recent declines in deepwater sculpin energy density found during this study were clearly not linked to increased abundance of fish based on lower or unchanged catch rates. Some studies have suggested abundances of deepwater sculpin may be decreasing throughout Lake Michigan (Bunnell et al. 2009) and Lake Huron (O'Brien et al. 2009). However, even if deepwater sculpin abundances are declining, predation pressure on *M. relictus* could be intense as other planktivores in the lake increase utilisation of *M. relictus* following declines of *Diporeia* spp., reducing effective feeding rate. For example, individual alewife consumption of *M. relictus* increased following the decline of *Diporeia* spp. in Lake Michigan (Pothoven & Madenjian 2008).

Energy density of deepwater sculpin at the two sites without *Diporeia* spp. was similar, despite large differences in the availability of remaining important prey, *M. relictus*, (e.g., higher *M. relictus* biomass at Muskegon (2009) than at Harbor Beach). One possible explanation is that energy content is as low as it can physiologically be at Harbor Beach and Muskegon and, if further decreases in food availability occurred at Muskegon, one might expect that deepwater sculpin population abundances would decline. An alternate explanation is that low deepwater sculpin population abundances in the Harbor Beach region were a result of other factors such as greater predation pressure, and that further declines in food availability at Muskegon would not necessarily lead to lower numbers of fish, but to even further declines in energy density. Predation on deepwater sculpin could be higher in Lake Huron than in Lake Michigan given the collapse of the dominant planktivore, alewife, in Lake Huron (Riley et al. 2008). In either case, deepwater sculpin energy density is declining, a change which ultimately

could lead to increased vulnerability to predation and higher probability of death (Breck 2008).

Previous work indicated that predation by alewife on larval fish stages and by burbot *Lota lota* on older stages of deepwater sculpin limited their abundance in Lake Michigan (Madenjian et al. 2005). However, our study indicates that bottom-up constraints have become increasingly important in regulating deepwater sculpin dynamics following the dreissenid mussel-induced changes in the Great Lakes, including declining primary production (Fahnenstiel et al. 2010) and the decline of *Diporeia* spp. (Nalepa et al. 2009). Despite relatively low numbers of deepwater sculpin, their energy density appears to be quite low. If mechanisms that control deepwater sculpin dynamics are changing, it could impact success of efforts to re-establish deepwater sculpin in Lake Ontario, where they were nearly extirpated by the 1960s (Lantry et al. 2007). Deepwater sculpin declines in Lake Ontario were likely caused by alewife predation on larval fish stages (Madenjian et al. 2005) which were also stressed by alewife competition for prey resources (Lantry et al. 2007).

As a glacial relict, the ecology of deepwater sculpin is clearly linked with that of two crustacean glacial relicts, *M. relictus* and *Diporeia* spp. That the decline of the more abundant of these two crustaceans would impact deepwater sculpin should not be surprising. Even though fish can alter diets when faced with changes in their food base, there are still constraints associated with switching prey that might ultimately restrict fish production (Nobriga & Feyrer 2008). Some have suggested that deepwater sculpin may be a relatively vulnerable species given their limited dispersal ability and range (Sheldon et al. 2008). Their vulnerability is evidenced by their decline from nuisance levels in Lake Ontario to near extirpation by the 1960s (Wells & McLain 1973; Lantry et al. 2007). As a potentially vulnerable species, they are often considered an indicator of the well-being of the deepwater ecosystem (COSEWIC 2006). Thus, declines in energy density of a relatively vulnerable species such as deepwater sculpin might be indicative of the potential for further effects on other species and changes in the flow of energy through the food web of the Great Lakes.

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