

Influence of *Diporeia* Density on Diet Composition, Relative Abundance, and Energy Density of Planktivorous Fishes in Southeast Lake Michigan

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Abstract.—The benthic amphipod *Diporeia* spp. is an important prey for many fish in offshore areas of the Great Lakes, but its abundance has been rapidly decreasing. To assess the influence of *Diporeia* availability on the food habits, relative abundance, and energetics of planktivorous fish, the diet composition, catch per unit effort (CPUE), and energy density of planktivorous fish in southeast Lake Michigan during 2000–2001 were compared among locations with different *Diporeia* densities. *Diporeia* densities at St. Joseph, Michigan, were near 0/m² over much of the bottom but averaged more than 3,800/m² at Muskegon and Little Sable Point, Michigan. Consistent with these differences in *Diporeia* density, fish diet composition, CPUE, and energy density varied spatially. For example, alternative prey types comprised a larger fraction of the diets of bloater *Coregonus hoyi*, large (>100 mm total length) alewife *Alosa pseudoharengus*, and slimy sculpin *Cottus cognatus* at St. Joseph than at Muskegon and Little Sable Point. This pattern was seasonally dependent for alewives and bloaters because *Diporeia* were eaten mainly in June. Food biomass per stomach was not lower at St. Joseph than elsewhere, suggesting that the spatial variation in diet composition was due to greater consumption of alternative prey by fish at St. Joseph. Although slimy sculpin and bloaters were able to feed on alternative prey, the CPUE of these species at certain depths was considerably lower at St. Joseph than at Muskegon or Little Sable Point, indicating that *Diporeia* availability may also influence fish abundance and distribution. Finally, a link between *Diporeia* density and fish energetics was suggested by the comparatively low energy density of deepwater sculpin *Myoxocephalus thompsonii* and large alewives at St. Joseph, a result that may reflect the low energy content of other prey relative to *Diporeia*.

The fish community of the Great Lakes has been shaped by numerous stressors and perturbations. For example, pollution and eutrophication degraded spawning and nursery habitats for shallow-water and potadromous species, leading to declines in their abundance (Christie 1972, 1974; Wells and McLain 1972; Regier and Hartman 1973). Overfishing and predation by sea lampreys *Petromyzon marinus* reduced native piscivore populations, allowing alewife *Alosa pseudoharengus* and other ex-

otic species to proliferate (Smith 1970; Christie 1972, 1974; Wells and McLain 1972; Regier and Hartman 1973). Competition with or predation by alewives negatively impacted many native planktivores such as emerald shiner *Notropis atherinoides* and yellow perch *Perca flavescens* (Wells and McLain 1972, 1973; Christie 1974; Wells 1977; Eck and Wells 1987). Management actions to limit nutrient inputs and to control alewife and sea lamprey populations have led to the restoration of some native species, but not others (Koonce et al. 1996; Madenjian et al. 2002; Bronte et al. 2003; Mills et al. 2003).

A new threat to fishes in the Great Lakes is the disappearance of an important invertebrate prey,

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the burrowing amphipod *Diporeia* spp. (Dermott and Kerec 1997; Nalepa et al. 1998, 2000, 2003; Dermott 2001; Lozano et al. 2001). Declines in the abundance of *Diporeia* have been rapid and coincidental with the arrival and establishment of dreissenid mussels (*Dreissena* spp.), although a direct relationship has not yet been shown (Nalepa et al. 1998, 2000). *Diporeia* are the dominant members of the offshore macrobenthos community and are preyed upon by many species of planktivorous fish (Wells and Beeton 1963; Wells 1980; Crowder et al. 1981; Lantry and Stewart 1993). Due to their high lipid content, *Diporeia* are a more energy-rich food source than other potential prey and thus represent a critical link between primary production and fish production in the Great Lakes (Gardner et al. 1985, 1990).

The disappearance of *Diporeia* is a concern because it may affect the prey selection and food consumption of planktivorous fishes, with unknown consequences for fishery production and food web dynamics (Madenjian et al. 2002). In fact, certain benthic fishes may already be responding to declines of this invertebrate. In eastern Lake Ontario, for example, the abundance and condition of lake whitefish *Coregonus clupeaformis* declined following the disappearance of *Diporeia* (Hoyle et al. 2003; Mills et al. 2003), and major changes in the diets of lake whitefish and slimy sculpin *Cottus cognatus* were observed (Owens and Dittman 2003). Similar changes in lake whitefish condition and diet composition have occurred in southeast Lake Michigan where *Diporeia* have decreased in abundance (Pothoven et al. 2001).

To assess how other fishes in the Great Lakes may respond to the disappearance of *Diporeia*, we examined the influence of *Diporeia* density on the food habits, relative abundance, and energy content of alewife, bloater *Coregonus hoyi*, rainbow smelt *Osmerus mordax*, slimy sculpin, and deep-water sculpin *Myoxocephalus thompsonii* in southeast Lake Michigan. These fishes are the most abundant planktivores in Lake Michigan and represent the primary prey for Pacific salmonids (*Oncorhynchus* spp.) and lake trout *Salvelinus namaycush* (Stewart et al. 1981; Brandt 1986a; Diana 1990; Madenjian et al. 1998). Southeast Lake Michigan was an ideal setting for this study due to the nearly complete loss of *Diporeia* from some areas of the study region (Nalepa et al. 1998). This allowed the comparison of fish diet composition, catch per unit effort (CPUE), and energy density among locations with significantly different *Diporeia* densities. Given the presumed importance

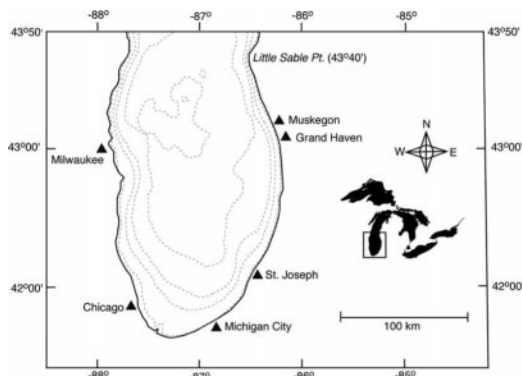


FIGURE 1.—Map of southeast Lake Michigan study locations sampled during 2000–2001.

of *Diporeia* as a food resource for planktivorous fish, we expected these metrics to vary spatially with the availability of *Diporeia*. Thus, it was anticipated that the importance of alternative prey in fish diets would be inversely related to *Diporeia* density at a given sampling location. In the absence of suitable alternative prey, fish would be expected to move or to suffer negative consequences resulting from reduced food intake (e.g., increased mortality, decreased growth or condition). These responses might be reflected in spatial variation in fish catch per unit effort and energy content, with smaller catches and lower energy density at locations with scarce *Diporeia*.

Methods

Study sites.—Sampling occurred in southeast Lake Michigan near St. Joseph, Muskegon, and Little Sable Point, Michigan, during 2000–2001 (Figure 1). These sampling locations were chosen to exploit geographical variation in *Diporeia* abundance in southeast Lake Michigan. Historically, *Diporeia* were abundant throughout this region, with the highest densities occurring at depths between 30 and 50 m (Nalepa 1987, 1989). *Diporeia* at St. Joseph declined dramatically in the early 1990s, and by 1993, densities at depths below 50 m were estimated to be less than 100/m², down from 3,000 to 8,000/m² in 1980–1987 (Nalepa et al. 1998, 2000). In contrast, *Diporeia* densities at 45-m sites near Muskegon and Little Sable Point prior to this study (1997–1999) ranged from 3,600 to 9,700/m² and 3,200 to 7,300/m², respectively (T. F. Nalepa, National Oceanographic and Atmospheric Administration, unpublished data).

Fish sampling and diet analysis.—Fish were sampled at each location during June, August, and

October of 2000 and 2001 from within two depth zones, 35–55 m and 65–85 m. Herein, we refer to these depth ranges as the “transitional” and the “offshore” zones, respectively. Fish were collected during the day using a 7.6-m semiballoon bottom trawl (13-mm stretch mesh cod liner). Trawl tows were made along bottom depth contours at 10-m intervals between 35 m and 85 m at each location (one tow per contour; six tows per location at each sampling). All fish, or subsamples of larger catches, were immediately frozen upon capture. Catch per unit effort for each species (number of fish/km) was compared among locations using the Kruskal–Wallis test followed by nonparametric multiple contrasts (Zar 1984). This nonparametric procedure was used because the distribution of CPUE data were positively skewed.

In the laboratory, fish total length (TL) was measured (to the nearest ± 1 mm) and stomachs were removed and dissected. All macroinvertebrates (e.g., *Mysis* spp., *Diporeia*, chironomids) in stomachs were identified and counted. Zooplankton from stomachs were added to a known volume of water and subsampled with a Hensen-Stempel pipette. Lengths of whole macroinvertebrates were measured using an image-analysis system. These lengths were then converted to dry mass using published weight–length regressions for each species (see Pothoven et al. 2000a, 2001; Pothoven and Vanderploeg 2004 and references therein). The dry weights of partially digested organisms were assumed equal to the mean individual weight of measured organisms. Total counts of invertebrates from fish stomachs were multiplied by the representative mean weight for that invertebrate and then summed to obtain the total biomass of each invertebrate group in the diet. Diet composition was expressed as percent of total dry food mass. To control for ontogenetic variation in alewife diets, alewives were separated by TL into small (TL < 100 mm) and large (TL \geq 100 mm) individuals. Due to low catches of small bloaters and small deepwater sculpin, diet analyses for bloaters and deepwater sculpin were restricted to larger individuals with TL greater than 120 mm and TL greater than 70 mm, respectively.

To assess the influence of *Diporeia* density on overall food consumption by fish, the total weight of food in the stomachs was estimated by summing the biomass of each invertebrate group in the diet. Average food biomass per stomach was then compared among locations, seasons, and years using a mixed-model analysis of variance (ANOVA), with fish length as a covariate and trawl as a ran-

dom effect. The mixed-model ANOVA permitted the use of individual fish as samples and corrected model results for the lack of independence among individuals from the same trawl. The interactions location \times season and location \times year were also included in the model to determine if seasonal and annual trends were similar among locations.

Invertebrate sampling and enumeration.—To assess prey availability in the region, we sampled benthic invertebrates (*Diporeia*, chironomids), *Mysis relicta*, and zooplankton in conjunction with fish collections. Invertebrates were sampled at 45- and 75-m sites at each location during each season. Invertebrate densities at these depths were assumed to be representative of each depth zone (transitional or offshore). Benthic invertebrates were collected using a ponar grab sampler (sampling area = 0.046 m²). Each of three replicate samples was washed through a 0.5-mm nitex screen, and retained material was stored in a solution of 5% sugar-buffered formalin containing rose-bengal stain (Nalepa 1987). Triplicate samples of *Mysis* were collected at night using a 1-m-diameter plankton net (1,000- μ m mesh) towed vertically from 2 m above the bottom to the surface (Pothoven et al. 2000b). Zooplankton were collected with triplicate vertical net tows taken from just above the bottom to the surface using a 0.5-m-diameter plankton net (153- μ m mesh). Both *Mysis* and zooplankton were anesthetized with carbonated water and preserved in a 10% solution of sugar-buffered formalin. In the laboratory, zooplankton were added to a known volume of water, subsampled with a Hensen-Stempel pipette, and at least 200 organisms per subsample were counted. All invertebrates were identified to the lowest possible level.

Replicate samples of invertebrates from a given depth were averaged, providing a set of 12 density measurements for each location (2 depths \times 3 seasons \times 2 years). These densities were transformed (natural log + 1) and compared among locations, depths, seasons, and years using a general linear modeling (GLM ANOVA) procedure. Only main effects (location, depth, season, and year) were included in the model.

Fish energy density.—Whole-body energy density was used as an index of fish condition. This condition metric was selected because energy density is related to lipid content (Rottiers and Tucker 1982), which is reflective of the quantity and quality of food available to a fish (Phillips and Brockway 1959; Flath and Diana 1985; Madenjian and O'Connor 1999). Energy density is an alternative

TABLE 1.—Linear regression coefficients \pm SEs for the relationship of fish wet-weight energy density (J/g) to percent dry weight for fishes sampled in southeast Lake Michigan during 1998–1999. (N = sample size). (A fish that is 25% dry matter (75% water) enters the equation as 25). All regression relationships and parameter estimates were significant ($P < 0.001$).

Species	y-intercept	Slope	N	r^2
Alewife	$-1,782.1 \pm 185.6$	300.3 ± 7.4	272	0.86
Bloater	$-2,379.3 \pm 206.0$	333.2 ± 7.8	180	0.91
Deepwater sculpin ^a	$-2,033.6 \pm 434.9$	332.7 ± 18.5	39	0.90
Slimy sculpin	-778.8 ± 198.3	256.3 ± 8.5	180	0.84

^a Relationship based on fish collected in 2001.

to traditional weight-based condition indices, which can be difficult to interpret (Cone 1989; Springer and Murphy 1990), and is an important parameter in fish bioenergetics models (Hartman and Brandt 1995). Energy density was measured in October, which is near the peak in the seasonal energy cycle in many Great Lakes fishes (Flath and Diana 1985; Vondracek et al. 1996). Energy content at this time is indicative of prior feeding conditions as well as the energy stores available for use over the winter when some fish cease feeding (e.g., alewife).

Fish energy density was estimated from percent dry weight as suggested by Hartman and Brandt (1995). This procedure has been shown to be a reliable method to determine energy density in Great Lakes fish (Flath and Diana 1985; Vondracek et al. 1996). Individuals of each fish species were dried at 75°C for 48 h, after which percent dry weight was calculated as

$$100 \times \text{sample dry weight/sample wet weight.}$$

Whole-body energy density for individuals of each species was then predicted from percent dry weight using the regression equations in Table 1. The regression equations relating percent dry weight to energy density were developed using bomb calorimetry on samples of fish collected from southeastern Lake Michigan during 1998–1999. Mean percent dry weight and energy density (years pooled) were compared among locations us-

ing ANOVA followed by Tukey's honestly significant difference tests.

Results

Invertebrate Density

Sampling location was the most important source of variability in *Diporeia* density in southeastern Lake Michigan during 2000–2001 (Table 2). Consistent with expectations, *Diporeia* density was significantly lower at St. Joseph than at Muskegon and Little Sable Point (Figure 2). The only exception occurred in October 2000 when densities at 75-m sites were similar among locations. At St. Joseph, *Diporeia* were effectively absent from 45-m sites and rare at 75-m sites (0–645/m²). In contrast, *Diporeia* densities at Little Sable Point and Muskegon averaged greater than 3,800/m² (depths, seasons, and years pooled).

Sampling location was not a significant source of variability in the densities of other invertebrate taxa. *Mysis* densities were mainly influenced by sampling depth, season, and year (Table 2). *Mysis* were more abundant at 75-m versus 45-m sites, and more abundant in 2001 than in 2000 (Figure 2). *Mysis* densities also tended to be higher in June and August than in October (Figure 2). Chironomid densities were highly variable, and trends in their abundance were not adequately explained by sampling location, depth, season, or year (Table 2). Season generally had the greatest impact on zooplankton densities (Table 3). For example, the

TABLE 2.—Summary of general linear model results for the effects of location, depth, season, and year on macroinvertebrate densities in southeast Lake Michigan in 2000–2001. Density data (number/m²) were transformed ($\log_e [x] + 1$) prior to analysis; MS = mean square.

Effect	df	<i>Diporeia</i>		<i>Mysis</i>		Chironomids	
		MS	P	MS	P	MS	P
Location	2	135.498	<0.001	1.772	0.052	5.762	0.212
Depth	1	7.562	0.063	2.614	0.036	0.321	0.765
Season	2	1.778	0.426	2.669	0.014	9.968	0.075
Year	1	1.174	0.452	3.062	0.024	6.934	0.171
Error	29	2.022		0.542		3.518	

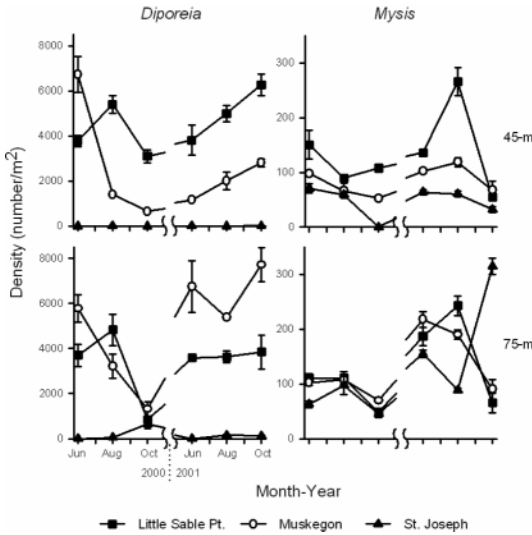


FIGURE 2.—Mean densities (\pm SE) of *Diporeia* and *Mysis* in southeast Lake Michigan during 2000–2001. LSP = Little Sable Point; MSK = Muskegon; STJ = St. Joseph.

highest densities of *Daphnia* spp., *Bosmina* spp., and *Bythotrephes longimanus* typically occurred during August and/or October (Appendix Table A.1). In addition, densities of *Daphnia* and *Bosmina* exhibited significant interannual variation. Copepod abundance was not significantly influenced by sampling location, depth, season, or year (Table 3). Thus, the scarcity of *Diporeia* at St. Joseph represented the only consistent difference among the invertebrate communities of the three sampling locations.

Fish Relative Abundance

Catch per unit effort (CPUE) of small alewives, large alewives, bloaters, and slimy sculpin differed among sampling locations and depth zones (Table 4). Within the transitional zone, CPUE of slimy sculpin was lowest at St. Joseph, the location

where *Diporeia* densities also were lowest. Catches of bloaters in the transitional zone followed a similar pattern, but differences in CPUE among locations were not quite significant ($P = 0.051$). Small alewife CPUE within the transitional zone was higher at Little Sable Point than at Muskegon, although *Diporeia* were relatively abundant at both locations. In the offshore zone, CPUE of bloater was significantly lower at St. Joseph than at Muskegon and Little Sable Point. Slimy sculpin CPUE at offshore sites was lower at St. Joseph than at Little Sable Point, but similar at St. Joseph and Muskegon. Large alewife CPUE within both depth zones was higher at Little Sable Point than at St. Joseph, but CPUE of large alewives at St. Joseph and Muskegon was similar.

Fish Diet

The diets of slimy sculpin, bloaters, and large alewives differed among locations (Figures 3, 4). In general, *Diporeia* represented a greater percentage of the food consumed by fish at Muskegon and Little Sable Point than at St. Joseph, the location with the lowest *Diporeia* density. At St. Joseph, *Diporeia* were essentially absent from the diets of fish within the transitional zone, but low numbers were present in the diets of fish within the offshore zone. The alternative prey consumed by fish at St. Joseph were not more abundant at St. Joseph than at the other sampling locations (Tables 2, 3; Appendix).

These dietary trends were dependent on season for large alewives given that *Diporeia* were eaten by these fish mainly in June (Figure 3). At this time, *Diporeia* were absent from the diet of large alewives from transitional sites of St. Joseph, whereas it formed 30–90% of the diet (by mass) of large alewives collected from similar depths at Muskegon and Little Sable Point. Similarly, at offshore sites, *Diporeia* tended to be less important in the diets of large alewives from St. Joseph than

TABLE 3.—Summary of general linear model results for the effects of location, depth, season, and year on zooplankton densities in southeast Lake Michigan in 2000–2001. Density data (number/m²) were transformed ($\log_e [x] + 1$) prior to analysis; MS = mean square.

Effect	df	<i>Daphnia</i> spp.		<i>Bosmina</i> spp.		Copepods		<i>Bythotrephes longimanus</i>	
		MS	P	MS	P	MS	P	MS	P
Location	2	1.333	0.730	1.170	0.294	0.709	0.065	2.054	0.146
Depth	1	3.987	0.337	0.010	0.919	0.228	0.333	0.687	0.414
Season	2	44.188	<0.001	15.270	<0.001	0.322	0.271	27.214	<0.001
Year	1	23.388	0.025	15.404	<0.001	0.087	0.547	1.157	0.291
Error	29	4.185		0.917		0.236			

TABLE 4.—Catch per unit effort (number/km) \pm SE of planktivorous fish at locations in southeast Lake Michigan in 2000–2001. Within a species, values with different letters are significantly different ($P < 0.05$); H = Kruskal–Wallis test statistic; N = 18 for each cell. Abbreviations are as follows: LSP = Little Sable Point; MSK = Muskegon; STJ = St. Joseph.

Species	LSP	MSK	STJ	H	P
Transitional zone (35–55 m)					
Small alewife	188.2 \pm 90.4 y	6.8 \pm 4.2 z	5.1 \pm 4.2 yz	7.1	0.029
Large alewife	149.6 \pm 68.6 y	42.3 \pm 25.0 yz	10.8 \pm 7.9 z	6.9	0.032
Bloater	18.3 \pm 7.5	8.0 \pm 2.9	0.5 \pm 0.2	5.9	0.051
Rainbow smelt	6.0 \pm 2.8	1.6 \pm 0.7	3.3 \pm 1.8	1.6	0.444
Slimy sculpin	29.2 \pm 10.4 y	5.8 \pm 1.8 y	1.0 \pm 0.4 z	13.2	0.001
Offshore zone (65–85 m)					
Small alewife	9.1 \pm 4.0	5.8 \pm 2.7	1.4 \pm 1.1	5.7	0.057
Large alewife	245.9 \pm 135.5 y	40.9 \pm 12.7 yz	15.3 \pm 6.9 z	15.2	<0.001
Bloater	30.1 \pm 11.7 y	19.3 \pm 4.1 y	5.7 \pm 2.0 z	11.7	0.003
Deepwater sculpin	516.1 \pm 135.6	583.7 \pm 201.8	277.5 \pm 90.7	1.9	0.378
Rainbow smelt	0.3 \pm 0.2	0.2 \pm 0.1	0.6 \pm 0.4	0.2	0.928
Slimy sculpin	58.6 \pm 13.3 y	75.5 \pm 23.4 yz	18.9 \pm 5.9 z	8.5	0.015

from Muskegon or Little Sable Point. Zooplankton (mainly copepods) were the primary prey of large alewives from St. Joseph in June, except at offshore sites in June 2001. Later in the year, during August and October, the diets of large alewives from all locations and depth zones consisted of zooplankton or *Mysis*.

The importance of *Diporeia* in the diets of bloaters also varied among locations in June, but patterns at other times were difficult to discern (Figure 3). In June, *Diporeia* were an important food for bloaters at Little Sable Point and Muskegon, but were less important at St. Joseph. Bloaters at St. Joseph fed mainly on *Mysis* and other alternative prey (mainly chironomids) during June. In August, patterns in bloater diet composition among locations were unclear because bloaters were rare at St. Joseph. In October, bloaters from offshore sites consumed mainly *Mysis* at all locations, but low catches of bloater at St. Joseph precluded diet comparisons for transitional sites.

Consistent with the differences in *Diporeia* density among locations, *Diporeia* was the predominant prey of slimy sculpin from Muskegon and Little Sable Point, whereas *Mysis*, fish eggs, and other alternative prey were the primary foods of slimy sculpin from St. Joseph (Figure 4). These spatial trends were similar across seasons and depth zones, although very low numbers of slimy sculpin were collected at transitional sites of St. Joseph. *Diporeia* were essentially absent from the diets of the few slimy sculpin collected from these sites, but represented 20–40% of the diets of individuals from offshore areas. Fish eggs were found only in slimy sculpin collected from off-

shore sites and represented a large fraction of the diet of slimy sculpin from St. Joseph in October.

In contrast to slimy sculpin, the importance of *Diporeia* in the diet of deepwater sculpin was similar among locations. Diet composition for this species consisted of varying proportions of *Mysis*, *Diporeia*, and fish eggs at all locations (Figure 4). *Diporeia* was a significant component of the diet of deepwater sculpin from St. Joseph despite the low density of this invertebrate.

Numerous gaps in the data sets for rainbow smelt and small alewife necessitated pooling samples of these fish across locations, seasons, years, and depth zones. Diets of rainbow smelt ($n = 231$) were completely dominated by *Mysis*, whereas small alewives ($n = 183$) ate mainly zooplankton. *Diporeia* were rarely eaten by either species.

Mixed-model ANOVA results suggested that food biomass in fish stomachs was similar among locations for most species, as evidenced by the absence of a significant location effect for bloater ($F = 1.00$; $df = 2, 1119$; $P = 0.367$), slimy sculpin ($F = 1.37$; $df = 2, 1185$; $P = 0.255$), and deepwater sculpin ($F = 1.63$; $df = 2, 1170$; $P = 0.196$). A consistent effect of sampling location on food biomass was observed only for large alewife ($F = 7.04$; $df = 2, 915$; $P = 0.001$), but food biomass for this species was lowest at Little Sable Point. These spatial trends were unaffected by year, and season had a significant effect on food biomass only for slimy sculpin (location \times season: $F = 3.86$; $df = 4, 1185$; $P = 0.004$). This interaction was the result of high food biomass at St. Joseph relative to other locations in October.

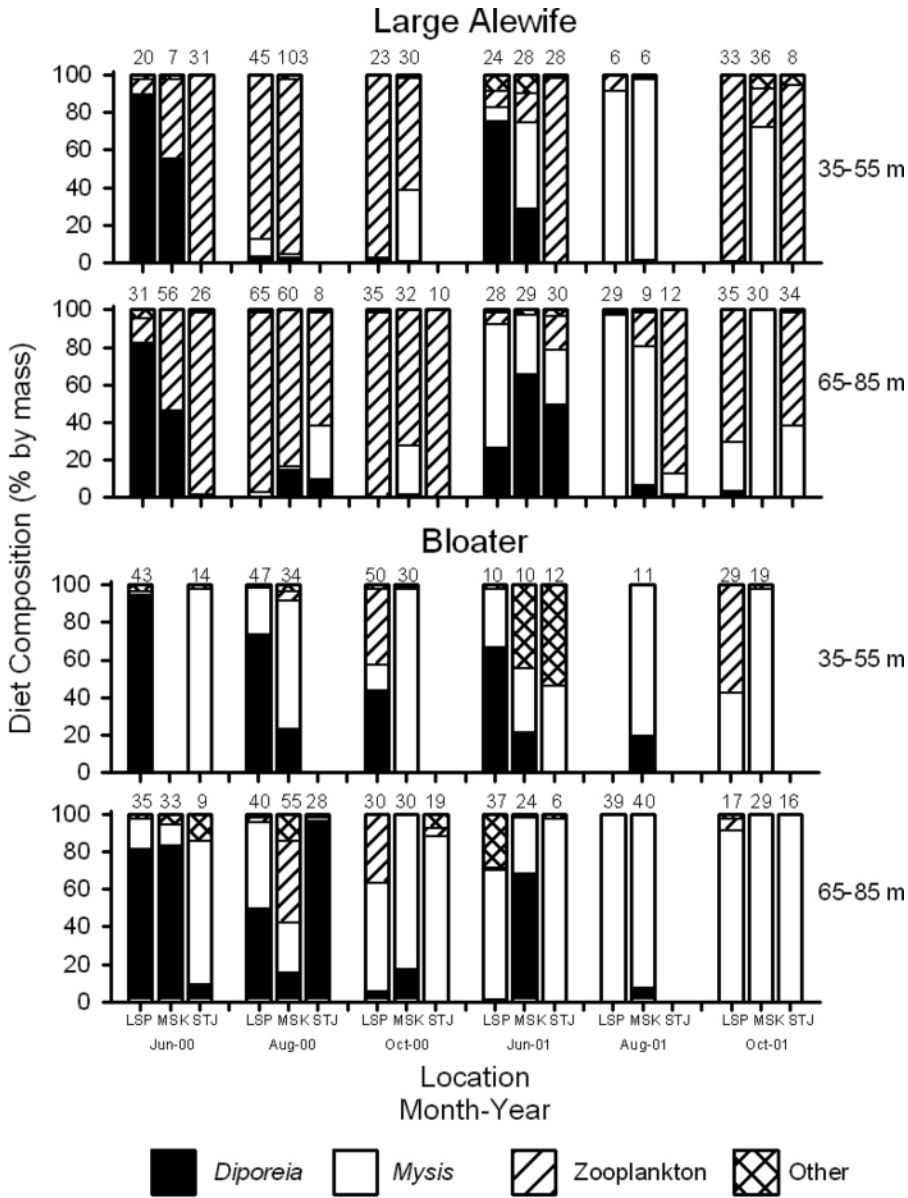


FIGURE 3.—Dry weight diet composition of large (total length ≥ 100 mm) alewives and bloaters in southeast Lake Michigan during 2000–2001. The upper and lower panels for each species represent the diet composition of individuals from the transitional (35–55 m) and offshore (65–85 m) zones, respectively. The number of stomachs containing identifiable food remains is indicated over each bar. LSP = Little Sable Point; MSK = Muskegon; STJ = St. Joseph.

Percent Dry Weight and Energy Density

Percent dry weight and estimated whole-body energy density of large alewife and deepwater sculpin differed among locations (Table 5). Percent dry weight in these species was about 2% lower at St. Joseph than at Muskegon and Little Sable Point, which translated into energy density esti-

mates that were 600–800 J/g lower at St. Joseph than elsewhere (Table 5). Percent dry weight and estimated whole-body energy density did not differ among locations for slimy sculpin, bloater, or small alewife. Too few rainbow smelt were collected in October to estimate percent dry weight and energy density.

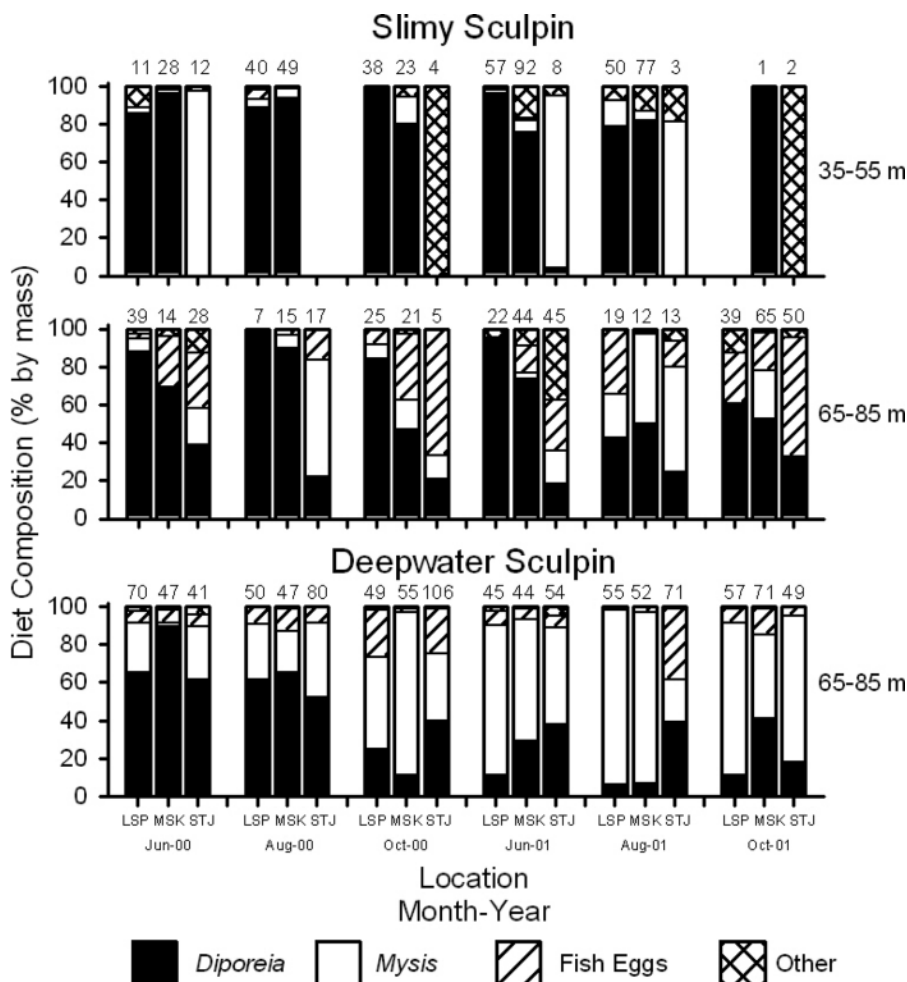


FIGURE 4.—Dry weight diet composition of slimy sculpin and deepwater sculpin in southeast Lake Michigan during 2000–2001. The upper and lower panels for slimy sculpin represent the diet composition of individuals from the transitional (35–55 m) and offshore (65–85 m) zones, respectively. The number of stomachs containing identifiable food remains is indicated over each bar. LSP = Little Sable Point; MSK = Muskegon; STJ = St. Joseph.

Discussion

The benthic amphipod *Diporeia* is an important food resource for planktivorous fish in offshore areas of the Great Lakes, but its abundance has been rapidly decreasing (Dermott and Kerec 1997; Nalepa et al. 1998, 2000, 2003; Dermott 2001; Lozano et al. 2001). It is speculated that *Diporeia* declines will have a significant impact on Great Lakes fish communities, but there have not been any comprehensive studies of the effects of *Diporeia* density on the ecology of the lakes' dominant planktivorous fish species. In this study, the food habits, relative abundance, and energy density of several species of planktivorous fishes were

found to vary spatially with the availability of *Diporeia*, providing some of the first evidence that fish may respond to changes in the density of this invertebrate.

In southeast Lake Michigan, *Diporeia* were significantly less abundant at St. Joseph than at Muskegon and Little Sable Point, but consistent among-location differences in the densities of other invertebrates were not detected. Historically, *Diporeia* were abundant throughout the southern basin, including at St. Joseph; however, *Diporeia* at this location declined rapidly in the early 1990s, nearly disappearing from depths less than 50 m by 1993 (Nalepa et al. 1998, 2000). Our results in-

TABLE 5.—Mean percent dry weight \pm SE and wet-weight energy density (J/g) \pm SE of fishes sampled at locations in southeast Lake Michigan during October 2000–2001. Within a species, values with different letters are significantly different (Tukey's honestly significant difference test, $P < 0.05$). Sample sizes given in parentheses. Abbreviations are defined in Table 4.

Fish species and variable	LSP	MSK	STJ	<i>P</i>
Small alewife				
Dry weight (%)	25.2 \pm 0.5 (39)	25.9 \pm 0.7 (28)	25.3 \pm 0.6 (13)	0.689
Energy density	5,778 \pm 164	5,983 \pm 199	5,811 \pm 180	0.667
Large alewife				
Dry weight (%)	28.3 \pm 0.3 y (55)	27.6 \pm 0.4 y (53)	26.2 \pm 0.4 z (48)	<0.001
Energy density	6,726 \pm 103 y	6,516 \pm 126 y	6,079 \pm 71 z	<0.001
Bloater				
Dry weight (%)	27.3 \pm 0.7 (82)	26.3 \pm 0.5 (94)	26.9 \pm 0.8 (41)	0.478
Energy density	6,724 \pm 218	6,387 \pm 155	6,593 \pm 276	0.639
Deepwater sculpin				
Dry weight (%)	23.7 \pm 0.2 y (104)	24.2 \pm 0.2 y (99)	21.9 \pm 0.2 z (100)	<0.001
Energy density	5,835 \pm 59 y	6,021 \pm 72 y	5,253 \pm 69 z	<0.001
Slimy sculpin				
Dry weight (%)	22.8 \pm 0.2 (39)	22.6 \pm 0.3 (77)	22.2 \pm 0.3 (57)	0.395
Energy density	5,069 \pm 63	5,022 \pm 67	4,922 \pm 86	0.426

dicate that these populations have not recovered. In fact, *Diporeia* at this location may now be entirely absent from depths below 50 m, and only low numbers are present at depths of 75 m and above.

At St. Joseph, alternative prey represented a greater percentage of the diets of fish than at Muskegon and Little Sable Point. This is consistent with studies that have documented shifts in fish diet composition following declines of invertebrate prey (Robertson 1987; Pothoven et al. 2001; Feyrer et al. 2003; Owens and Dittman 2003) and supports the idea that planktivorous fish possess a great deal of trophic adaptability (Gerking 1994). Mechanistically, the increased dietary importance of alternative prey could reflect increased consumption of alternative prey by fish at St. Joseph or lower food biomass in the stomachs of fish from this location. However, because the amount of food in the stomachs of fish from St. Joseph was not lower than that of fish at Muskegon and Little Sable Point, our data indicate that consumption of alternative prey is greater at St. Joseph than at the other locations. This suggests that availability of *Diporeia* influences the consumption of other prey.

Slimy sculpin at St. Joseph fed mainly on *Mysis*, fish eggs, and small benthic invertebrates, whereas slimy sculpin at Little Sable Point and Muskegon ate mostly *Diporeia*. The *Diporeia*-dominated diets of slimy sculpin at these latter locations are more consistent with historical data for this species in the Great Lakes (Wells 1980; Brandt 1986b; Kraft

and Kitchell 1986; Selgeby 1988). It has been suggested that slimy sculpin have difficulty capturing *Mysis* (Kraft and Kitchell 1986), but in southeast Michigan and in eastern Lake Ontario, *Mysis* was found to be an important prey for slimy sculpin where *Diporeia* are scarce (Owens and Weber 1995; Owens and Dittman 2003). Fish eggs, which were also an important alternative prey for slimy sculpin in southeast Lake Michigan, were not eaten by slimy sculpin from *Diporeia*-depleted areas of Lake Ontario (Owens and Weber 1995; Owens and Dittman 2003). Thus, the eggs in the diets of slimy sculpin at St. Joseph may be those of deepwater sculpin or bloater since these species are abundant in offshore areas of Lake Michigan, but have been extirpated from Lake Ontario (Christie 1972). Experiments have shown that slimy sculpin are efficient egg predators and can locate fish eggs non-visually (Dittman et al. 1998; Mirza and Chivers 2002). The opportunistic use of foods such as fish eggs could help protect Lake Michigan slimy sculpin from declines in growth or condition resulting from the disappearance of *Diporeia*, as evidenced by the absence of interlocation differences in energy density for this species.

The diets of other fish may be influenced by *Diporeia* availability only during certain periods of the year. For example, the diets of large alewives and bloaters from St. Joseph also included a larger percentage of alternative prey than at other locations, but in contrast to slimy sculpin, this pattern was observed only in the spring. Large alewives

and bloaters have seasonally variable diets, and *Diporeia* is an important prey for both species in the spring (Wells and Beeton 1963; Hewett and Stewart 1989; Rand et al. 1995; Pothoven and Vanderploeg 2004). The alternative prey used by large alewives and bloaters at St. Joseph appeared to reflect differences in the feeding ecology of these species. Alewives are pelagic planktivores and probably prey only on large macroinvertebrates such as *Diporeia* and *Mysis* that migrate off the bottom (Janssen 1980; Janssen and Brandt 1980; Crowder and Binkowski 1983; Mills et al. 1992). In contrast, bloaters are able to feed on a variety of benthic prey that are unavailable to alewives (Crowder and Binkowski 1983). Accordingly, at St. Joseph, where *Diporeia* were largely unavailable, large alewives fed on pelagic zooplankton in the spring while bloaters fed on semibenthic and benthic prey such as *Mysis* and midge larvae (mainly chironomids).

Although fish at St. Joseph are able to consume other prey, these prey may not fill the same functional role as *Diporeia* in the food web. *Diporeia* are benthic detritivores, whereas zooplankton feed on primary producers or other pelagic zooplankton (Balcer et al. 1984), and *Mysis* are opportunistic omnivores, feeding near bottom on algae and benthos during the day and on zooplankton and algae in the pelagia at night (Grossnickle 1982; Johannsson et al. 2001). Greater reliance on zooplankton and *Mysis* as prey could make fish production in Lake Michigan increasingly dependent upon pelagic pathways, particularly as more and more energy becomes tied up in Dreissenid biomass. Chironomids and ostracods, small benthic invertebrates with a similar ecological role as *Diporeia*, are probably not sufficiently abundant to support an increase in fish predation. Chironomid biomass in southern Lake Michigan, for example, is typically less than 0.5% the average biomass of *Diporeia* (Nalepa 1989).

Variation in *Diporeia* density could also influence fish abundance and distribution. Historical data from locations near St. Joseph suggest that slimy sculpin and bloaters were common at transitional and offshore sites of this location prior to declines in *Diporeia* (Wells 1968). However, in this study, slimy sculpin were essentially absent from the transitional zone of St. Joseph, and bloaters in offshore areas were found to be considerably less abundant at St. Joseph than at Muskegon and Little Sable Point. These fish may be moving to habitats with greater *Diporeia* availability given the historical importance of this invertebrate in their diets

and the fact that their energy densities did not vary spatially with *Diporeia* density. However, we cannot rule out the possibility that the population sizes of slimy sculpin and bloaters are smaller at St. Joseph as result of greater mortality or lower reproductive success, both of which could also be associated with the absence of *Diporeia* at this location.

A link between *Diporeia* abundance and the energetics of certain planktivorous fish was suggested by the comparatively low energy density of deepwater sculpin and large alewives at St. Joseph. Several mechanisms involving *Diporeia* abundance could be responsible for this pattern. First, *Diporeia* availability could limit the amount of food consumed by these fish, although estimates of total food biomass in stomach samples did not support this hypothesis. Secondly, low *Diporeia* availability could increase the foraging effort necessary to acquire a given ration. The low energy density of deepwater sculpin at St. Joseph may be explained by the preceding mechanism since deepwater sculpin at St. Joseph continued to feed on *Diporeia* despite its low availability. Alternatively, the absence of *Diporeia* could lead to a decrease in the average energy content of fish diets because this invertebrate is more energy rich than other prey (Pothoven et al. 2001). For instance, the average energy content of *Diporeia* (4,429 J/g) is more than twice that of zooplankton (1,987 J/g; Stewart and Binkowski 1986). This mechanism has been suggested as the explanation for decreases in the growth and condition of lake whitefish following *Diporeia* declines in Lakes Michigan and Ontario (Pothoven et al. 2001; Hoyle et al. 2003; Mills et al. 2003; Owens and Dittman 2003). It may also explain the variation in alewife energy density observed in this study given that large alewives from St. Joseph fed mainly on zooplankton in the spring. Alewife energy density may be particularly sensitive to changes in diet quality at this time, since adults can experience somatic energy losses up to 27% in the winter and spawning-related losses up to 45% in the spring (Flath and Diana 1985). Recent reports of decreased growth and condition in Lake Michigan alewives also have been attributed to *Diporeia* declines (Madenjian et al. 2003).

The disappearance of *Diporeia* is potentially the latest in a series of community-transforming events facing fish in the Great Lakes. This study clearly demonstrates that diet composition, catch per unit effort, and energy density of several planktivorous fish vary spatially with the availability of

Diporeia. These results imply that continued *Diporeia* declines in the Great Lakes may lead to diet switching by many fish. Detecting changes in the food consumption patterns of some fish species may require seasonal sampling because *Diporeia* may be a primary prey only at specific times of the year. Our data for large alewife showed that *Diporeia* are eaten by this species almost exclusively in the spring. The types of alternative prey utilized by fish where *Diporeia* are rare seem to depend on the feeding ecology of individual species, but will probably include *Mysis* because this invertebrate is available to both benthic and pelagic predators. The abundance and distribution of certain fish species also may be impacted by declines in *Diporeia* density, as evidenced by low relative abundance of slimy sculpin and bloaters at a location where *Diporeia* were rare. This study further indicates that *Diporeia* availability may influence the energetics of some fish, particularly those that switch to foods with low energy content relative to *Diporeia*. Fish that make opportunistic use of other prey without a concomitant reduction in diet quality or feeding efficiency could potentially avoid these losses. It is likely that the responses of fish to future changes in *Diporeia* availability will be species dependent, and thus forecasting the consequences of *Diporeia* declines for Great Lakes fish communities may require a more complete understanding of the feeding behaviors and physiology of the planktivorous fish that depend on *Diporeia*.

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Appendix: Zooplankton Densities

TABLE A.1.—Zooplankton densities (1,000 s/m²) ± SEs in southeast Lake Michigan during 2000–2001. Abbreviations are as follows: LSP = Little Sable Point; MSK = Muskegon; STJ = St. Joseph.

Date	Location	<i>Daphnia</i> spp.	<i>Bosmina</i> spp.	Copepods ^a	<i>Bythotrephes longimanus</i>
45-m sites					
Jun 2000	LSP	0.85 ± 0.85	143.87 ± 4.59	1,152.71 ± 140.48	0.00 ± 0.00
	MSK	2.55 ± 0.00	42.44 ± 3.06	992.28 ± 258.79	0.00 ± 0.00
	STJ	0.00 ± 0.00	26.43 ± 5.29	260.48 ± 17.28	0.00 ± 0.00
Aug 2000	LSP	5.09 ± 2.55	687.55 ± 46.05	551.31 ± 8.35	0.00 ± 0.00
	MSK	14.01 ± 3.37	1,027.93 ± 54.54	474.49 ± 2.97	0.03 ± 0.01
	STJ	5.43 ± 2.65	211.87 ± 68.00	244.46 ± 85.87	0.02 ± 0.01
Oct 2000	LSP	0.64 ± 0.46	19.10 ± 9.99	337.41 ± 150.29	0.82 ± 0.05
	MSK	12.05 ± 2.50	53.65 ± 2.72	365.34 ± 23.36	0.14 ± 0.01
	STJ	5.94 ± 0.85	84.03 ± 5.30	549.19 ± 24.26	0.60 ± 0.05
Jun 2001	LSP	3.57 ± 2.22	16.30 ± 6.39	938.63 ± 54.35	0.00 ± 0.00
	MSK	2.29 ± 1.17	12.14 ± 4.78	979.63 ± 35.79	0.05 ± 0.03
	STJ	7.13 ± 4.07	15.28 ± 3.05	680.42 ± 88.57	0.00 ± 0.00
Aug 2001	LSP	13.75 ± 3.18	130.38 ± 11.20	791.11 ± 37.95	0.00 ± 0.00
	MSK	49.23 ± 6.95	51.78 ± 9.34	423.56 ± 23.81	0.02 ± 0.01
	STJ	43.80 ± 8.88	79.45 ± 17.64	374.84 ± 40.59	0.02 ± 0.01
Oct 2001	LSP	1.70 ± 0.85	72.15 ± 4.24	914.87 ± 26.67	0.17 ± 0.04
	MSK	29.11 ± 3.15	168.15 ± 27.95	421.87 ± 25.22	0.01 ± 0.00
	STJ	50.59 ± 4.56	24.61 ± 2.40	218.49 ± 9.54	0.12 ± 0.01
75-m sites					
Jun 2000	LSP	3.39 ± 1.70	219.00 ± 30.70	2,241.75 ± 172.35	0.00 ± 0.00
	MSK	0.00 ± 0.00	40.74 ± 6.54	542.82 ± 17.93	0.00 ± 0.00
	STJ	0.42 ± 0.42	13.16 ± 4.90	311.95 ± 10.42	0.00 ± 0.00
Aug 2000	LSP	42.44 ± 4.49	1,140.82 ± 73.69	631.52 ± 76.28	0.01 ± 0.01
	MSK	31.92 ± 3.73	865.46 ± 28.15	488.92 ± 13.48	0.21 ± 0.04
	STJ	3.82 ± 2.21	467.79 ± 43.61	666.67 ± 18.59	0.07 ± 0.02
Oct 2000	LSP	26.97 ± 3.91	27.77 ± 4.85	392.24 ± 5.16	0.70 ± 0.01
	MSK	108.56 ± 3.42	391.73 ± 19.96	948.06 ± 101.79	0.14 ± 0.03
	STJ	39.47 ± 7.28	62.39 ± 13.12	413.29 ± 21.91	1.24 ± 0.09
Jun 2001	LSP	1.78 ± 1.03	2.97 ± 1.57	458.71 ± 15.48	0.00 ± 0.00
	MSK	4.67 ± 2.97	7.22 ± 1.85	613.70 ± 78.42	0.00 ± 0.00
	STJ	3.06 ± 0.00	6.11 ± 3.53	535.78 ± 29.11	0.03 ± 0.03
Aug 2001	LSP	2.04 ± 2.04	45.50 ± 14.38	339.36 ± 34.21	0.00 ± 0.00
	MSK	87.94 ± 5.80	44.40 ± 4.90	434.51 ± 7.57	0.05 ± 0.01
	STJ	75.12 ± 20.01	72.57 ± 5.83	1,038.97 ± 47.14	0.08 ± 0.01
Oct 2001	LSP	16.55 ± 3.37	68.75 ± 11.67	1,312.71 ± 52.30	0.11 ± 0.02
	MSK	66.21 ± 19.45	156.18 ± 20.86	807.23 ± 29.40	0.02 ± 0.00
	STJ	81.49 ± 7.78	62.39 ± 13.12	535.61 ± 30.61	0.20 ± 0.03

^a Excludes nauplii.