ECOLOGY

Note: This is a condensed version of a recently published article as given below. The article includes more details on methods, statistical procedures, and results of laboratory experiments.

Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation?

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Introduction

The increased spread of aquatic invasive species has led to the growing realization that these invaders, either individually or in concert, can change ecosystems at many levels of organization (Simon and Townsend 2003). A striking example is the Great Lakes ecosystem where, over the past 10-15 years, species invasions have led to the loss of native species, altered pathways of energy and nutrient flux through food webs, and re-defined fundamental understanding of ecosystem function (Nalepa et al. 1996; Vanderploeg et al. 2002; Hecky et al. 2004). When considering imposed changes within the Great Lakes, perhaps the most large-scale, and certainly the most equivocal, has been the disappearance of the deepwater amphipod *Diporeia* spp. Declines in *Diporeia* populations have recently been documented in all the lakes except Lake Superior, and large areas in southeastern Lake Michigan (Nalepa et al. 1998), outer Saginaw Bay, Lake Huron (Nalepa et al. 2003), eastern Lake Erie (Dermott and Kerec 1997), and Lake Ontario (Dermott 2001; Lozano et al. 2001) are now mostly devoid of this organism.

Declines of *Diporeia* populations in the Great Lakes were first noted in the early 1990s and, in all lake areas, these declines were coincident with the introduction and spread of the invading species *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel). A common hypothesis for the decline is that dreissenids are outcompeting *Diporeia* for available food (Nalepa et al. 1998; Dermott 2001). Dreissenids filter feed near the sediment surface, and this hypothesis assumes that settling organic material is intercepted by dreissenids before it becomes available to *Diporeia*, which burrows and feeds in the upper 2 cm of sediment. Deepwater amphipods such as *Diporeia* (neararctic) and the closely related *Monoporeia affinis* (palearctic) are generally food limited, and both short and long term population trends have been attributed to changes in pelagic food inputs to the benthic region (Sarvala 1986; Johnson and Wiederholm 1992; Goedkoop and Johnson 2001). Yet despite the broad negative response of *Diporeia* to *Dreissena*, there are inconsistencies when examining decline patterns relative to the food-limitation hypothesis. For one, *Diporeia* populations have disappeared from several areas in the Great Lakes that were far-removed from dreissenid colonies and where potential food was still present in overlying waters and pre-
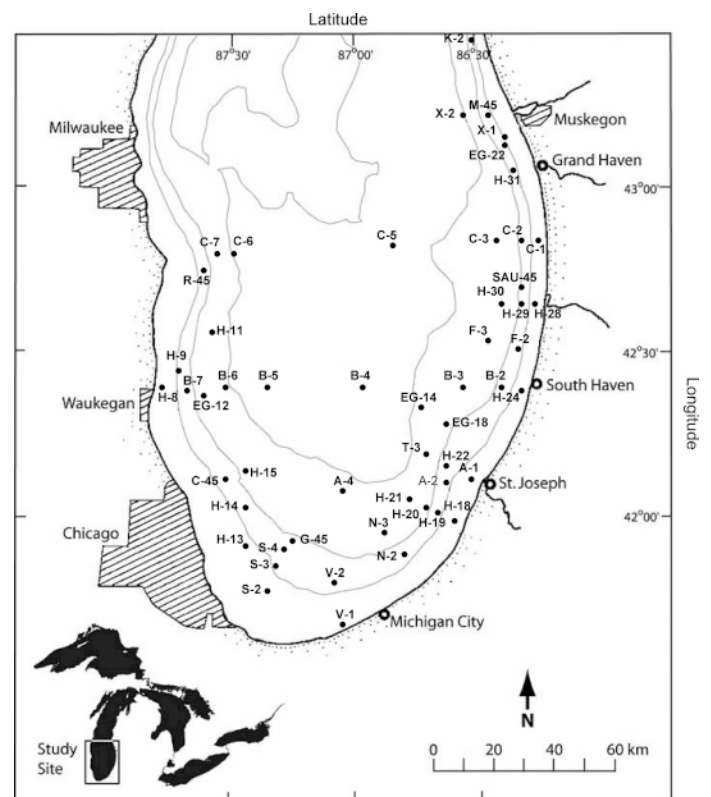

Fig. 1. Sampling sites in southern Lake Michigan. Depth contours are 25, 50, and 100 m.

sumed to be settling to the bottom (Dermott 2001; Nalepa et al. 2003). Also, *Diporeia* are still abundant in some areas despite the presence of dreissenids (Dermott et al. 2005).

In this paper, we document recent spatial and temporal trends of *Diporeia* populations in Lake Michigan relative to expanding numbers of dreissenids. We also examine changes in age structure, physiological well-being, and pelagic food inputs during periods of population loss. These changes were compared to similar observations made prior to the introduction of dreissenids and *Diporeia* declines.

Methods

Spatial and temporal trends in densities

To document long-term spatial and temporal trends in densities of *Diporeia* and *Dreissena* in Lake Michigan, benthic samples were collected over several time periods at sites located in the southern basin, and also at sites located throughout the entire lake. In the southern basin, samples were collected at 40 sites in 1998-2002. These 40 sites are part of a long term monitoring program of the total macroinvertebrate community and have been sampled for two consecutive years every five years between 1980 and 1993 (Nalepa 1987; Nalepa et al. 1998). Consistent with this program, samples were again collected at these sites in 1998-1999. In 2000-2002, samples were collected at the same 40 sites, and at 13 additional sites (Figure 1). Whereas data from all 53 sites were used to better define spatial distributions of *Diporeia* and *Dreissena* in each of the three years, only data from the original 40 sites were used when examining temporal trends. Samples in 1998-1999 were collected in spring (mid-May/early June), summer (late July/early August), and fall (September/October), but in 2000-2002 samples were collected only in fall.

Densities of *Diporeia* and *Dreissena* were determined throughout Lake Michigan by sampling at 158 sites in late summer/fall 2000. Besides the 53 sites sampled in the southern basin, an additional 105 sites were sampled in the central and northern basins, Green Bay, and Grand Traverse Bay. Many of these sites (42 of 105) were sampled previously in 1994/1995 (Nalepa et al. 2000).

Methods of collection and analysis were the same for all sampling periods. Sediment samples were taken in triplicate with a Ponar grab (area = 0.046 m^2) at each site and washed into an elutriation device fitted with a nitex sleeve having 0.5-mm openings. Retained material was immediately preserved in 5% buffered formalin containing rose bengal stain. In the laboratory, all macrobenthic organisms in the 1998-99 samples were picked, counted, and sorted into major taxonomic groups (Amphipoda, Oligochaeta, Chironomidae, *Dreissena*, Sphaeriidae) under a low-power magnifier lamp (1.5 x). Chironomidae densities were low as in previous years and therefore not reported here. Only *Diporeia* and *Dreissena* were enumerated in samples collected in 2000-2002.

Population age structure, physiological condition, and physical variables

Soon after it became apparent that the *Diporeia* population in the southern basin was declining (Nalepa et al. 1998), we initiated a monthly sampling program in 1997 at four sites in the southeastern portion of the lake to document trends in age structure, lipid content, and length-weight, and also to document relative amounts of potential food settling to the benthic region. The sites were located at 45-m water depth off St. Joseph (H-22), Saugatuck (SAU-45), Grand Haven (H-31), and Muskegon (M-45) (Figure 1). Based on sampling prior to 1997, we knew that the status of population at the four sites varied widely, ranging from no longer present at H-22 to still abundant at M-45. In 1997 and 1998, Ponar samples at all four sites were collected monthly from late March/April to late October/November. After 1998, monthly sampling continued at sites where *Diporeia* was still present, and lasted until it was no longer found.

Beginning in 1994 at H-31 and in 1997 at the other 45-m sites, body lengths of *Diporeia* in each of the replicate samples were determined by first tracing individuals (body mid-line) under 12x magnification using a camera lucida, and then measuring tracings with a digitizer (Quigley and Lang 1989). In addition, body lengths were determined on animals in Ponar grabs collected monthly (April to November) at H-31 in 1986-1988. After lengths were determined, animals were placed into three size categories: 0-3 mm (newly recruited young-YOY), 3-5 mm (juveniles), and > 5 mm (adults).

On each sampling date beginning in 1994, extra Ponar grabs were taken at each site for the determination of *Diporeia* lipid content and length-weight. Upon collection, entire grab samples (animals, sediments, and overlying waters) were placed into plastic bags and kept cool during transport back to the laboratory. Within 24 h of collection, 20-25 juveniles and adults were placed individually into pre-weighed mini-test tubes (6 x 50 mm). For YOY, 5-10 individuals were placed into each tube (3-5 replicates). Before animals were placed into the tubes, individual body lengths were traced and later measured. The animals were dried for 48 h (under N_2 at 50-60°C) and then stored frozen under vacuum until lipid extraction. Animals were re-weighed just prior to lipid extraction, and individual animal weights were used to derive length/dry weight relationships. For YOY, mean length and weight were used in derived relationships. Total lipids were extracted using chloroform: methanol (2:1), quantified gravimetrically, and reported as percent dry weight (Gardner et al. 1985a).

Sediment traps were deployed at the 45-m sites in 1997-1999 to measure potential pelagic inputs to the benthic region. The traps were deployed just below the thermocline (30 m water depth) from March/early April to October at SAU-45, H-31, and M-45 in 1997, at all four sites in 1998, and at H-31 and M-45 in 1999.

After collection, trap material was poured through a 50-μm screen to remove benthos and large zooplankton, and then allowed to settle for at least 24 h before the supernatant was decanted. The samples were then freeze-dried and kept frozen until analysis. Total organic carbon (TOC) was analyzed with a Carlos Erba CHN Elemental Analyzer. Prior to analysis, sub-samples for TOC were treated with 2N HCL, shaken for 24 h, and then dried at 60°C to remove mineral carbonates. Chlorophyll a (Chl) was determined according to the method of Hansson (1988). Biogenic silica (BiS) was determined by first using a wet alkaline method for digestion and then measuring concentrations of SiO_2 with a Alpkem FS3000 Analyzer (Krausse et al. 1983).

Interval;	Year						
Taxa	1992	1993	1998	1999	2000	2001	2002
16-30 m							
Diporeia	2618±504	2698±543	236±212	130±125	207±205	223±223	287±287
Oligochaeta	1713±376	1647±434	2367±600	2085±624	-	-	-
Sphaeriidae	1381±384	535±123	340±247	309±142	-	-	-
D. polymorpha	389±253	1929±1698	978±255	2056±1014	617±340	193±74	885±464
D. bugensis	0±0	0±0	0±0	0±0	0±0	3±3	117±63
31-50 m							
Diporeia	8710±759	7021±870	1957±883	892±450	1427±847	1364±798	665±395
Oligochaeta	4487±466	3166±330	4518±1146	6029±2219	-	-	-
Sphaeriidae	2273±303	1068±166	1434±294	707±162	-	-	-
D. polymorpha	7±3	25±12	433±156	1059±414	865±555	1298±858	1112±755
D. bugensis	0±0	0±0	0±0	0±0	0±0	5±5	752±495
51-90 m							
Diporeia	6380±332	5352±373	4593±1007	2380±577	3503±1185	2991±992	2963±959
Oligochaeta	2042±135	1530±97	2245±412	1986±345	-	-	-
Sphaeriidae	801±153	384±72	660±100	578±94	-	-	-
D. polymorpha	1±1	1±1	5±3	3±2	8±5	13±7	20±15
D. bugensis	0±0	0±0	0±0	0±0	0±0	0±0	8±5
> 90 m							
Diporeia	3195±389	3226±515	4833±762	1794±249	2814±570	2608±392	3623±647
Oligochaeta	1179±151	1123±159	1009±176	1034±222	-	-	-
Sphaeriidae	113±30	98±36	197±99	154±84	-	-	-
D. polymorpha	0±0	0±0	4±4	0±0	0±0	0±0	0±0
D. bugensis	0±0	0±0	0±0	0±0	0±0	0±0	0±0

Table 1. Mean (± standard error) densities (no.·m^{-2}) of the major taxa found in southern Lake Michigan in 1992-2002. Oligochaeta and Sphaeriidae were not sampled in 2000-2002. The number of sites (n) in each of the four depth intervals were n = 11 (16-30 m), n = 12 (31-50 m), n = 51-90 m), n = 6 (>90 m).
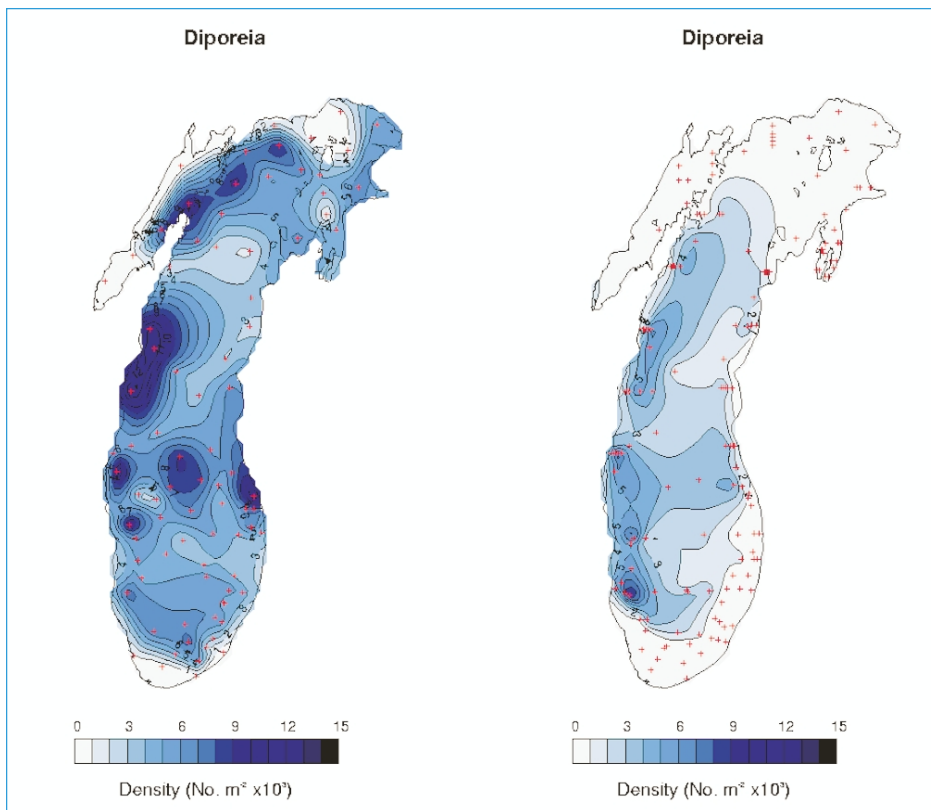
Fig. 2. Mean density (no.•m^{-2} x 10^3) of *Diporeia* spp. throughout Lake Michigan, 1994/1995 and 2000. Small crosses denote sampling sites. (a) = 1994/1995; (b) = 2000.

Results

Density trends of major taxa groups in southern basin, 1992-2002

Declines in *Diporeia* populations in the southern basin, which were initially documented in 1992-1993 (Nalepa et al. 1998), continued through 2002 (Table 1). Over the 1992-2002 period, significant differences in *Diporeia* densities occurred for years (ANOVA, P = 0.0001), intervals (P = 0.0001), and year x interval interaction (P = 0.0001). Annual densities in 1998-2002 were not significantly different from each other but significantly lower than densities found in 1992 and 1993 (P < 0.05, Tukey HSD). Mean densities at the < 30 m, 31-50 m, and 51-90 m intervals decreased by 89.4%, 90.5%, and 44.6%, respectively, between 1992 and 2002. Declines were more pronounced on the east side of the basin than the west side as lower densities, first observed in the southeastern portion of the basin in 1992, extended farther north and offshore over time. By 2002, *Diporeia* were rare or completely gone to depths of at least 50 m in an area from near Chicago to Grand Haven. Of 23 sites sampled in 2002 that were in less than 50 m water depth, *Diporeia* were present only at Stations H-8, B-7, and EG-12, all on the west side of the basin (densities 3155 m^{-2}, 4091 m^{-2}, and 3150 m^{-2}, respectively). Although still present, densities at these three sites in 2002 were lower than densities found in 1993 (declines of 46.2%, 46.2%, and 68.4%, respectively).

Whereas *Diporeia* continued to decline between 1992 and 2002, the dreissenid population became more widespread and abundant (Table 1). Differences in densities of *Dreissena* were significant for years (ANOVA, P = 0.0001), intervals (P = 0.0001), and year x interval interaction (P = 0.0001). Over the 10-year period, dreissenids were mostly confined to depths < 50 m, and greatest increases occurred at the 31-50 m interval (Table 1). Mean density of the dreissenid population at the three west-side sites where *Diporeia* were still present in 2002 (H-8, B-7, and EG-12) were not significantly different from densities at the other 20 sites of similar depth (< 50 m) where *Diporeia* had disappeared (t-test, P = 0.98).

Abundances of oligochaetes and sphaeriids in the southern basin were documented only in 1992-1993 and 1998-1999 (Table 1). Differences in oligochaete densities were significant for years (ANOVA, P = 0.03), intervals (P = 0.0001), and year x interval interaction (P = 0.0001). Densities in 1993 were significantly lower than the other three years (P = 0.03, Tukey HSD), but a consistent temporal trend over the entire 1992-1999 period was not apparent at any of the four intervals (Table 1). Sphaeriid densities were also significantly different for years (ANOVA, P = 0.0001), intervals (P = 0.0001), and year x interval (P = 0.0001). The general trend was for a decline in densities at the two shallowest depth intervals over the period.

Density trends lake-wide, 1994/1995-2000

Comparisons of lake-wide densities in 1994/1995 and 2000 indicated that declines of *Diporeia* occurred not only in the southern basin but also throughout the lake (Figure 2). Mean lake-wide density was 65% lower in 2000 compared to 1994/95 and this difference was significant (ANOVA, P = 0.0001). The decline occurred across all depth intervals as the year x interval interaction was not significant (P = 0.09). Densities at the < 30 m, 31-50 m, 51-90 m, and > 90 m intervals were 77.9%, 73.7%, 53.2%, and 51.6% lower, respectively (Table 2). Further, the extent of the decline was greatest in the northern region; the overall decline was 91.4% in the north compared to 65.0% and 42.4% in the south and central regions. While densities were lower in the north in each of the four depth intervals, a regional difference was only significant only at the > 90 m interval (ANOVA, P = 0.001; Tukey HSD, P < 0.003). Lake-wide densities of *Dreissena* were significantly higher in 2000 compared to 1994/1995 (ANOVA, P = 0.0001). At sites < 50 m, mean dreissenid densities were highest in the northern region in both

Depth Interval;	Diporeia		Dreissena	
Lake Region	1994/1995	2000	1994/1995	2000
<30 m				
South (7,11)	3488 ± 1842	207 ± 205	414 ± 132	617 ± 340
Central (2,16)	2173 ± 2852	1794 ± 655	0 ± 0	2541 ± 848
North (9,20)	2897 ± 1156	77 ± 34	926 ± 921	2025 ± 594
Overall	3124 ± 916	692 ± 252	623 ± 457	1871 ± 399
31-50 m				
South (6,20)	6306 ± 1454	1194 ± 561	48 ± 42	589 ± 338
Central (2,11)	10 477 ± 4088	4702 ± 1210	89 ± 82	629 ± 217
North (5,16)	4462 ± 2150	100 ± 39	528 ± 528	2268 ± 1353
Overall	6249 ± 1243	1642 ± 444	239 ± 201	1170 ± 489
51-90 m				
South (20,15)	5285 ± 423	2742 ± 932	< 1 ± < 1	6 ± 4
Central (5,19)	11 997 ± 1189	4691 ± 487	0 ± 0	32 ± 16
North (6,12)	6262 ± 925	893 ± 414	0 ± 0	7 ± 5
Overall	6550 ± 570	3064 ± 437	< 1 ± < 1	17 ± 7
>90 m				
South (9,6)	4466 ± 335	2814 ± 570	0 ± 0	0 ± 0
Central (9,6)	4443 ± 627	2818 ± 836	0 ± 0	0 ± 0
North (5, 5)	5007 ± 1567	754 ± 459	0 ± 0	0 ± 0
Overall	4567 ± 414	2209 ± 429	0 ± 0	0 ± 0

Table 2. Mean (± standard error) densities (no.·m^{-2}) of *Diporeia* and *Dreissena* at four depth intervals in Lake Michigan in three different regions in 1994/1995 and 2000. See Nalepa et al. (2000) for delineation of regions. Values in parenthesis are numbers of sites sampled in 1994/1995 and 2000, respectively, within each depth interval and lake region. In 1994/1995, all *Dreissena* were *D. polymorpha*; in 2000, 98.3% were *D. polymorpha* and 1.7% were *D. bugensis*.

Fig. 3. Density (no.•m^{-2}) of *Diporeia* spp. at three 45-m sites in southeastern Lake Michigan, 1980-2002. Top = H-31; Middle = SAU-45; Bottom = H-22. The dashed lines at H-31 give the lipid content (percent dry weight.) of *Diporeia* spp. at this site.

sampling periods, which may explain greater declines of *Diporeia* in this portion of the lake.

Annual density trends, 45-m sites

From the long term monitoring program, densities of *Diporeia* were available for three of the 45-m sites (H-22, SAU-45, and H-31) in1980-1981 and 1986-1987, which were the years just prior to the first report of *Dreissena* in Lake Michigan [first reported in 1989; Marsden et al. (1993)]. Mean annual density of *Diporeia* by site and year ranged from 5,347 to 14,044 m^{-2} (Figure 3). Beginning in 1992, the population declined systematically, first at the southern-most site (H-22) and later at the more northern sites. By fall 2002, *Diporeia* had disappeared from all four sites (Figures 3, 4). Whereas *Diporeia* disappeared from each site within a 10-year period, rates and patterns of decline were site-specific. In 1992, densities at H-22 declined from 10,600 m^{-2} in spring to 200 m^{-2} in fall, a 98% decline in just six months. Declines to total loss were more gradual at the other 45-m sites, occurring between 1994 and 1999 at H-31 and between 1997 and 2002 at M-45. Unlike populations at the other 45-m sites, the population at M-45 recovered somewhat after initial declines were
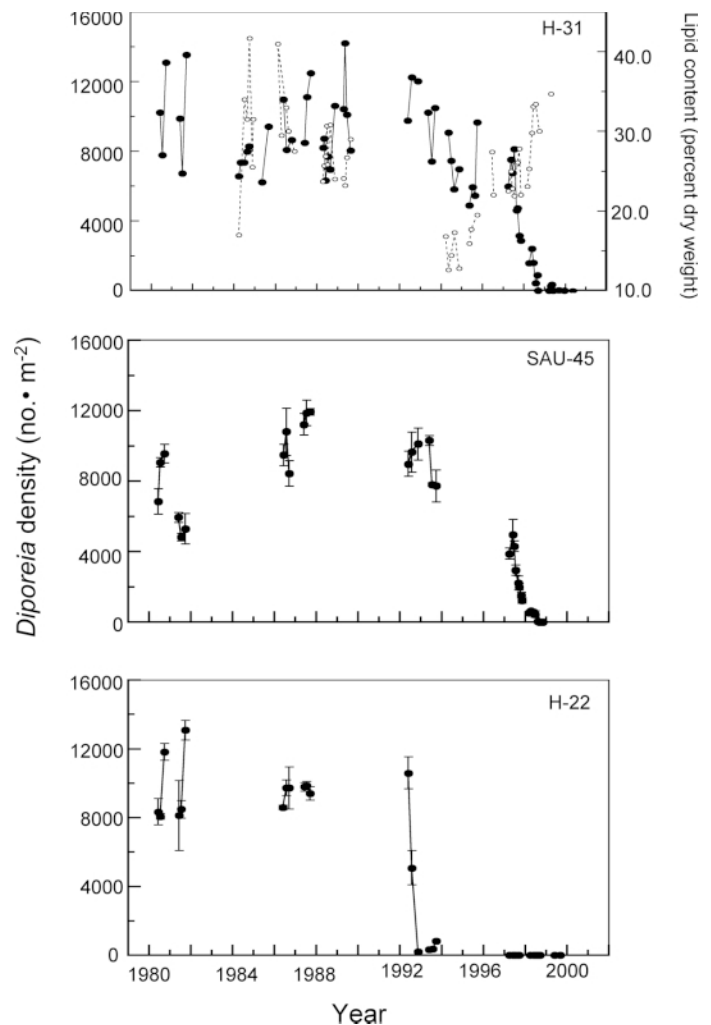
observed. Densities increased throughout 1999 and remained higher into spring 2000; however, densities decreased thereafter (Figure 4). When considering all four 45-m sites, the period of time in which *Diporeia* declined from densities of 5,300-14,000 m^{-2} to < 200 m^{-2} varied from 0.5 to 5 years.

The relationship between annual densities of *Diporeia* and *Dreissena* was examined over the time period between just prior to initial declines and total disappearance. Densities of *Diporeia* and *Dreissena* were not well-correlated at H-22; the population at this site collapsed in 1992 and totally disappeared by 1997, but *Dreissena* was not found at this site until 2000. At H-31 and M-45, there was a strong relationship between mean annual density of *Diporeia* and a 1-year time lag (t-1) in mean annual density of *Dreissena* (linear regression; R^2 = 0.59, P = 0.003).

Recruitment and age classes, 45-m sites

Because of limited availability of seasonal, size-frequency data collected prior to declines at H-22 and SAU-45, meaningful analysis of density trends in the various age classes was only possible for populations at H-31
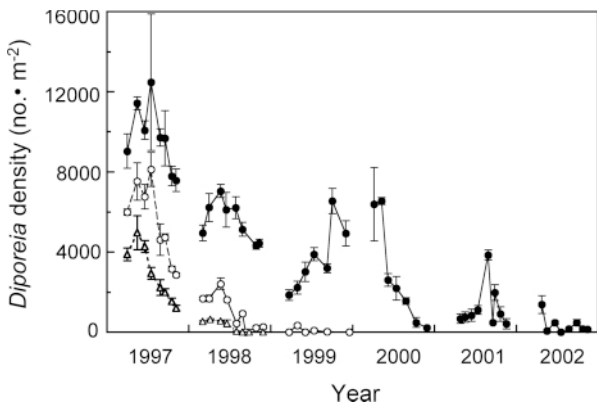
Fig. 4. Mean density (no.•m⁻²) of *Diporeia* spp. on each sampling date at three 45-m sites in 1997-2002. Although not shown, no *Diporeia* were collected at the other 45-m site (H-22) during the sampling period. Error bars denote standard error. SAU-45 = triangle; H-31 = open circle; M-45 = solid circle.

and M-45. As noted, declines in population density at H-31 were initially observed in 1994. Based on relative densities of YOY, juveniles, and adults, lower density in this year was a result of poor recruitment. Mean annual density of YOY in 1994 was only 215 m⁻² compared to a range of 920-2438 m⁻² in 1986-1993. In contrast, mean densities of juveniles and adults in 1994 were within the range found in 1986 to 1993 - juvenile density was 3860 m⁻² in 1994 compared to 2004-4283 m⁻² in 1986-1993, and adult density was 3588 m⁻² in 1994 compared to 3462-7173 m⁻² in 1986-1993. Considering *Diporeia* has a 2-year life cycle at this depth in southeastern Lake Michigan (Winnell and White 1984), the lack of recruitment in 1994 likely accounted for lower juvenile densities observed in 1995 (Figure 5). Recruitment in 1995-1997 was generally similar to recruitment in 1986-1993 as strong peaks in YOY occurred in 1995 (2438 m⁻²) and 1997 (2640 m⁻²) and, although we only sampled on one date in 1996 (July), a relatively high density of YOY (2202 m⁻²) indi-cated recruitment also occurred in that year. Despite good recruitment, juvenile densities in these three years remained lower than found in 1986-1994, indicating poor YOY survival. Juvenile densities at H-31 subsequently collapsed in 1997, declining from 3300 m⁻² in early spring to 150 m⁻² in late fall. Adult densities remained stable in 1997 but declined in 1998, most likely a result of the lack of juveniles the previous year.

At M-45, annual recruitment occurred between 1997 and 2002, and peaks in YOY densities ranged from 1200 m⁻² to 4700 m⁻² (Figure 6). Yet despite recruitment, juvenile densities generally declined each year, again indicating poor YOY survival. The exception to this pattern oc-curred in 1999. YOY survival was high in 1999 as evidenced by an increase in juvenile densities through-out the year, peaking at 3500 m⁻² in November; this accounted for the increase in population density in that year (Figure 4). Juveniles continued to grow and survive through winter 2000 as evidenced by high adult density in spring 2000 (4000 m⁻²). Recruitment occurred in 2000, but as in 1997 and 1998, these recruits did not survive to become juveniles.
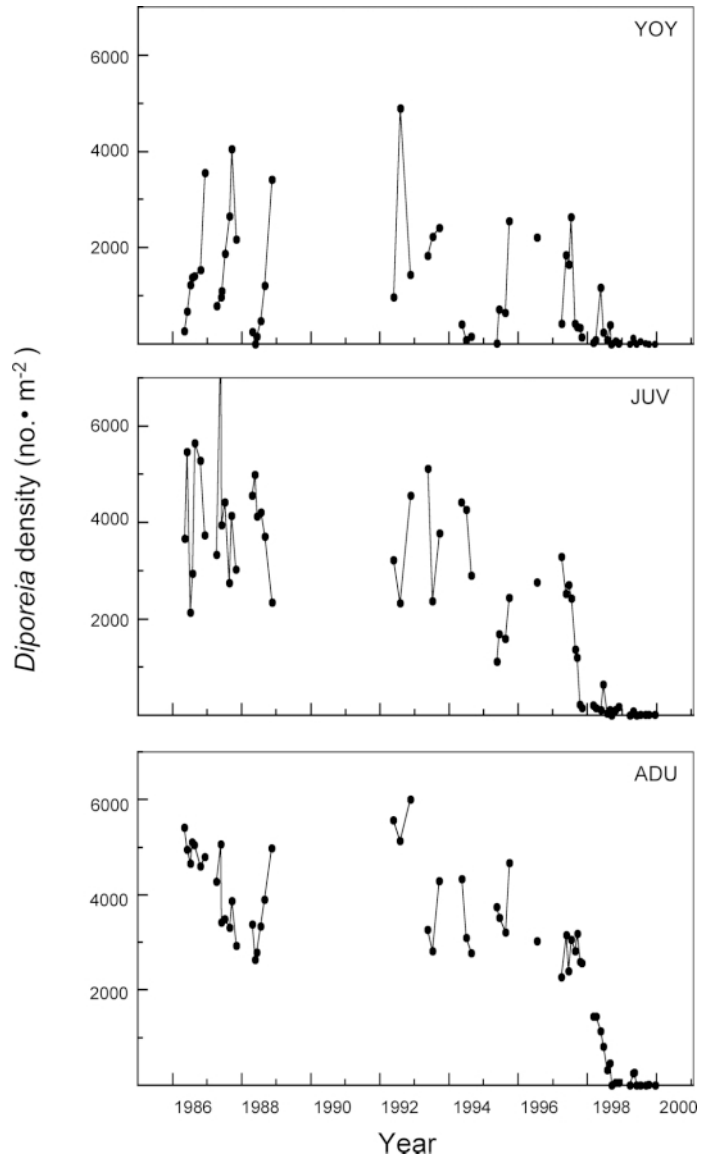

Fig. 5. Density (no.•m⁻²) of three life stages of *Diporeia* spp. at H-31 in 1986-1999. top = young-of-year; middle = juveniles; bottom = adults.

The number of eggs per gravid female was determined in spring 2001 at M-45 to determine if brood size had declined since the 1980s. In a 1981 study at a 42-m site in southeast-ern Lake Michigan, Winnell and White (1984) found that brood size ranged from 10 to 25 eggs per female and was directly related to female size. Brood size in 2001 varied from 21-32 eggs per gravid female (n = 7) and fit the same functional relationship to female size as in 1981.

Lipid content and length-weight, 45-m sites

When densities at the 45-m sites were declining, lipid content of juvenile and adult *Diporeia* tended to increase (Figure 7). Detailed analysis of trends between density and lipid content were restricted to M-45 since densities at the other 45-m sites were already declining prior to 1997. Between 1997 and 2001, there was a significant difference between years (ANOVA, P = 0.0001), age classes (P = 0.0001), and year x age class interaction (P = 0.0001). Yearly means in 1999-2001 were signifi-
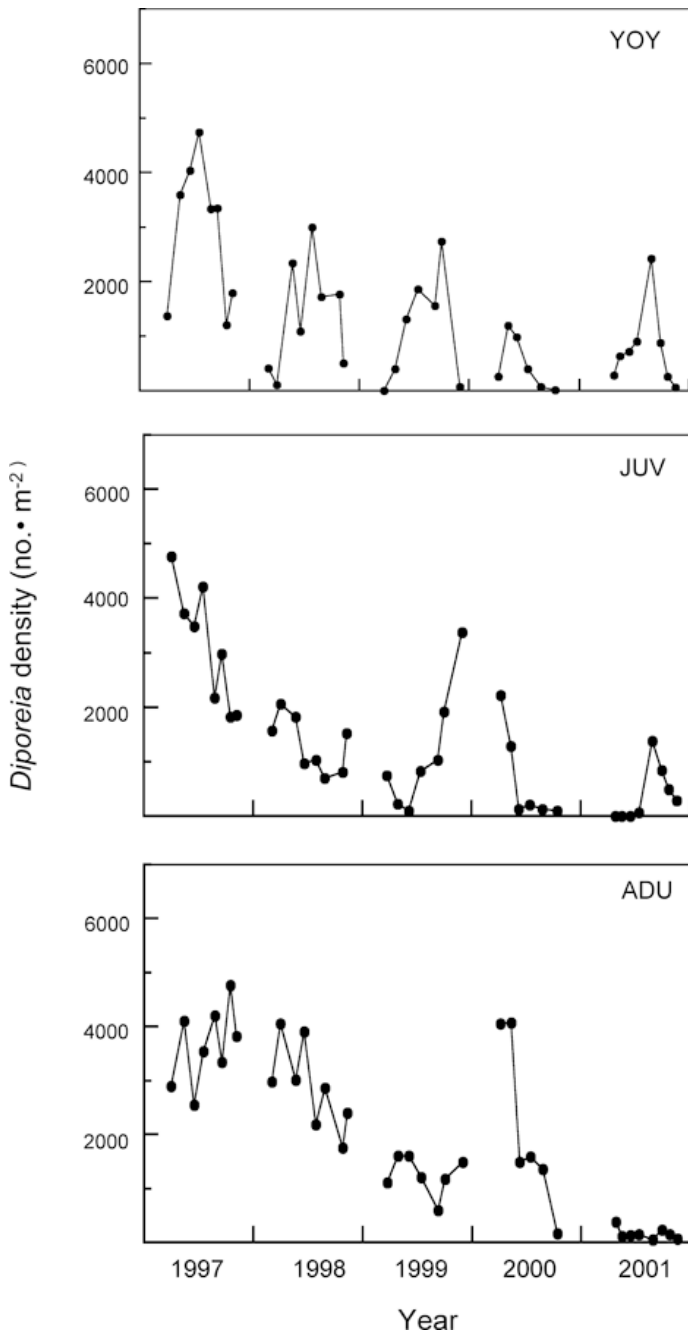
Fig. 6. Density (no.•m⁻²) of three life stages of *Diporeia* spp. at M-45 in 1997-2001. top = young-of-year; middle = juveniles; bottom = adults.

Fig. 7. Mean lipid content (percent dry weight) of young-of-year (+ · · · +), juvenile (o – – o), and adult (● —— ●) *Diporeia* spp. at three 45-m sites in 1997-2001. top = M-45; middle = H-31; bottom = SAU-45.

cantly higher than in 1997-1998 (P = 0.0001, Tukey HSD), and lipid content in juveniles and adults were significantly higher than in YOY (P = 0.0001 Tukey HSD). When just considering juveniles and adults, lipid levels increased from 21.6% ± 0.42% in 1997-1998 to 28.7% ± 0.56% in 1999-2001. Similarly, as densities declined at H-31 between 1997 and 1999, mean adult lipid content increased from 23.9% ± 0.6% in 1997 to 34.7% ± 2.1% in 1999. The relationship between lipid content and density can be put into a more long-term perspective by examining trends at H-31 beginning in the 1980s (Figure 3). Seasonal trends in lipid content of adult *Diporeia* were measured at this site in 1984, 1986, 1988, and 1989 (Cavaletto et al. 1996; Gardner et al. 1985b; Gauvin et al.

1989). Mean annual lipid content in 1984-1989 varied from 26% to 32%. When density declines were first observed in 1994, mean lipid content was only 15%. As densities continued to decline after 1994, lipid content increased each successive year until by 1998-1999 lipid values were as high as found in the 1980s.

Lipid content in juveniles and adults generally peaked in spring or summer and then declined in fall (Figure 7). Seasonal peaks in late spring/summer are consistent with the premise that intensive feeding during the spring diatom bloom results in the storage of energy as lipids (Gardner et al. 1985b; Gardner et al. 1990). To determine if seasonal peaks in 1997-2001 were comparable to those found in 1984-1989 (adults only), the seasonal maximum

Fig. 8. Lipid-free dry weight (mg) of a 5-mm *Diporeia* at each of the 45-m sites in Lake Michigan. Weight calculated from a length-weight regression of individuals collected monthly at each site for a particular year. ● —— ● = SAU-45; ○ – – ○ = H-31; Δ —— Δ = M-45.

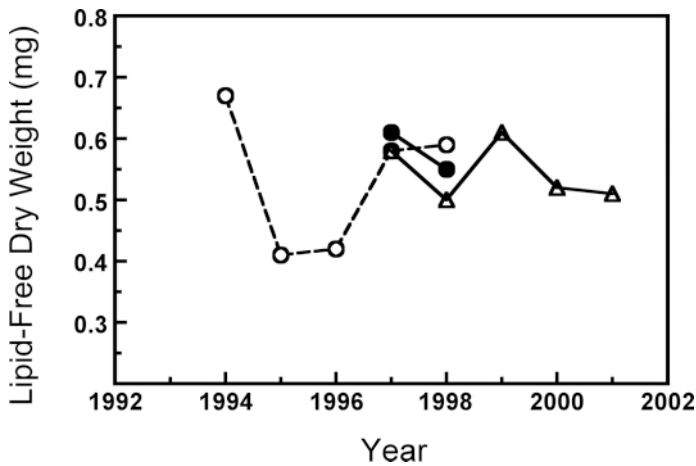was divided by the early spring minimum and the ratio compared between the two periods. For the 1997-2001 period, only those sites and years in which adults were collected throughout the year were included. The mean ratio was 1.31 ± 0.07 (n = 8) in 1997-2001 and 1.58 ± 0.28 (n = 4) in 1984-1989. Although lower in the 1997-2001 period, the difference was not significant (t-test; $P > 0.05$).

In deepwater amphipods, weight per unit length generally declines when animals are food limited (Hill et al. 1992; Lehtonen 1996). The relationship between lipid-free dry weight and length was defined by LFDW= aLb [where LFDW = lipid-free dry weight (mg) and L = length (mm)] and determined annually for each 45-m site over the 1994-2001 period. All regressions were significant (range of R^2: 0.56 - 0.96). When non-lipid dry weight for a standard 5-mm animal was calculated, yearly trends were not apparent within a particular site (Figure 8). Also, when *Diporeia* were present at three of the 45-m sites in 1997 and 1998, weights were generally similar even though populations at the sites were in various stages of decline.

Sedimentation rates

Sediment traps, deployed at the 45-m sites in 1997-1999, documented amounts of organic material settling to the bottom that potentially served as a food source for *Diporeia*. In general, there was a consistent primary peak of TOC, BiS, and Chl in spring, and a secondary peak in fall at each of the sites (Figure 9). Most relevant to *Diporeia* populations were flux rates associated with the spring peaks; these peaks are enriched in organic materials (diatoms) compared to peaks in the fall (Scavia and Fahnenstiel 1987; Gardner et al. 1989). Over the 1997-1999 period, the magnitude of spring peaks at H-31 and M-45 decreased for all constituents (Figure 9). In spring 1997 the spring-average (March-May) flux rates of TOC at these two sites were 434 and 461 mg•m^{-2}•d^{-1}, respectively, and flux rates of BiS were 1176 and 1199 mg•m^{-2}•d^{-1}. In contrast, in spring 1999 flux rates of TOC were only 88 and 57 mg•m^{-2}•d^{-1}, and flux rates of BiS

were 181 and 45 mg•m^{-2}•d^{-1}. Low flux rates in 1999 were mostly related to quantitative changes in inputs as nutrient content of collected material was generally higher in 1999 than in previous years. Further, mean annual C:N ratio (weight) did not show a consistent trend at these two sites over the same period; the ratio tended to increase at M-45 but not at H-31. In 1998 when flux rates were measured at all four 45-m sites, spring-average flux rates of all constituents increased on a spatial gradient from south to north, being lowest at H-22 and highest at M-45 (Figure 9), while the mean C: N ratio also decreased along the same gradient, declining from 12.8 at H-22 to 9.3 at M-45.

Discussion

On a broad scale, the decline of *Diporeia* in Lake Michigan in the 1990s was closely related to the expansion of dreissenid populations within the lake. In the southern basin, greatest declines occurred in the 30-50 m depth interval where dressenid densities increased to the greatest extent. Also, declines lake-wide were most extensive in the northern portion of the lake where dreissenid densities were higher than in more southern portions. Yet on a local scale, inconsistencies were apparent. Whereas *Diporeia* and dreissenids were negatively correlated at several sites, *Diporeia* remained abundant at some sites despite the long-term presence of dreissenids, but yet declined rapidly at a site with no dreissenids. Our field observations failed to establish a clear, direct relationship between the loss of *Diporeia* and indicators of food availability. From our results, several questions pertinent to the food-limitation hypothesis remain enigmatic: 1) why did the *Diporeia* population collapse so completely in an area where there were no mussels and where at least some pelagic food material was still likely settling to the benthic region? and 2) why did lipid content, which is an indicator of energy reserves and directly related to food availability, remain at high levels as the population disappeared?

In areas where dreissenids were not present or found in low numbers, such as at H-22, sediment traps should accurately reflect pelagic inputs to the upper sediments. That is, mussels at the sediment surface would not be intercepting settling organic material prior to becoming available to *Diporeia* feeding in the upper sediments. *Diporeia* at H-22 completely disappeared by 1997, yet based on trap flux rates of TOC, BiS, and Chl in 1998, at least some organic material was still settling to the bottom. Others have also documented a collapse of *Diporeia* populations in areas far removed from *Dreissena* colonies and where potential food was still found in the water column (Dermott 2001; Nalepa et al. 2003). Dermott (2001) theorized that the remote loss of *Diporeia* may be a function of their spatial distributions relative to dreissenid beds and dominant current patterns. Particulate organic material in water flowing over dreissenid beds would be removed by mussel filtration and unavailable to *Diporeia* located in areas downcurrent. With this
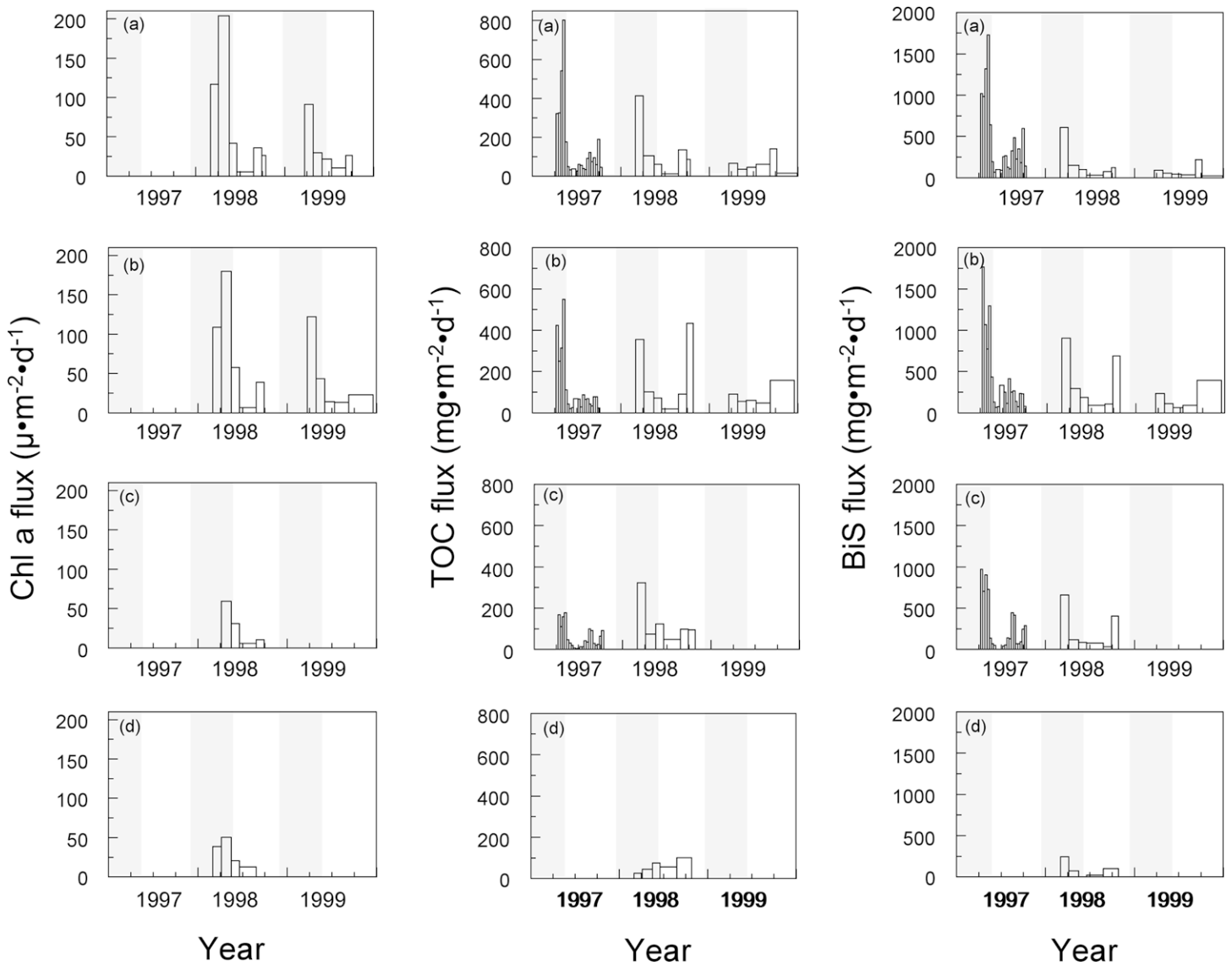
Fig. 9. Flux rates of chlorophyll (left) total organic carbon (middle), and biogenic silica (right), at the 45-m sites (M-45, H-31, SAU-45, H-22 in 1997-1999. Rates were derived from material collected in sediment traps placed at 30 m depth in the water column. The input from local re-suspension was corrected for by subtracting local surface sediment concentrations from trap concentrations, then multiplying by the mass flux. Shaded areas indicate unstratified periods. (a) = M-45; (b) = H-31; (c) = SAU-45; (d) = H-22.

hypothesis, it is difficult to reconcile how the remote removal of potential food by dreissenids in shallow, nearshore regions can so effectively eliminate *Diporeia* populations from deeper depths in southeastern Lake Michigan. In this area of the lake, nearshore-offshore transport of particulate material occurs mainly during storm events in the spring (Eadie et al. 2002). Dreissenid colonies can conceivably affect this transport process by retaining more organic matter in the nearshore zone, and thus reducing deposition in offshore areas (Hecky et al. 2004). The role of nearshore transport compared to local pelagic inputs in supporting offshore *Diporeia* populations is unknown. Yet if nearshore retention of organic material by dreissenids was the reason for the total loss of *Diporeia*, then the population at 45 m must have been far more nutritionally dependent upon inputs from the nearshore than pelagic inputs from the immediate overlying waters. This seems unlikely since ingestion rates,

assimilation rates, and lipid levels were closely linked to water column productivity at 45 m in the years prior to *Dreissena* (Fitzgerald and Gardner 1993; Gardner et al. 1989). In terms of food quality, C:N ratios of trap material at H-22 were 10-13, similar to the ratio of autochthonous matter produced by decomposed plankton (Wetzel 2001). Fresh algal material has a ratio of 6.7 (Redfield ratio). Ratios at H-22 were generally higher than ratios at the other 45-m sites, but below the threshold known to affect growth and development of some benthic detritivores (Soderstrom 1988; Dorgelo and Leonards 2001). While densities of deepwater amphipods are a function of fresh algal inputs (Johnson and Wiederholm 1992), the relationship between food quality and the survival of the population remains unclear. However, *Diporeia* has historically been the dominant benthic macroinvertebrate in the deepest regions of the Great Lakes where benthic food inputs are minimal and highly refractive. Further, the

rapid decline at H-22 was first observed after the spring period, which is inconsistent with the food-limitation hypothesis since this is the period when food availability would be at a seasonal maximum.

The disappearance of *Diporeia* at H-31 and M-45 was more gradual (5 years) than at H-22 and well-correlated to an increase in the *Dreissena* population. Given this close temporal association, food limitation may indeed have played a major role in the loss of *Diporeia* at these sites. Yet flux rates of constituents indicative of food inputs during the period of initial declines were similar to rates reported prior to *Dreissena*. For instance, the population at H-31 began to decline in 1994 and col-lapsed in 1997 and 1998, while the population at M-45 began to decline in 1997. In 1997 and 1998, average spring flux rates of TOC at these two sites varied from 273-461 mg•m^{-2}•d^{-1}, which were comparable to rates of 288 mg•m^{-2}•d^{-1} and 430 mg•m^{-2}•d^{-1} found at H-31 in 1986 and 1990 (BJ Eadie, unpublished data). Mean spring flux rates of BiS in 1997-1998 were 433-1500 mg•m^{-2}•d^{-1}. These rates were generally similar to or greater than a mean spring flux rate of 475 mg•m^{-2}•d^{-1} found at H-31 in 1986 (Gardner et al. 1989). Populations were already declining in 1999 when far lower flux rates of all constitu-ents were observed. Low flux rates in 1999 were likely a result of an uncommon occurrence rather than the beginning of a trend. In most years, water-column chloro-phyll peaks in spring, but in 1999, the peak occurred in early winter (BJ Eadie, unpublished data). Thus, we likely missed the spring diatom peak with our deployment in 1999. As noted, sediment traps do not reflect pelagic inputs to the upper sediments in areas when *Dreissena* densities are high. *Dreissena* densities were > 500 m^{-2} in 1997 at H-31 when the *Diporeia* population collapsed, but < 50 m^{-2} in 1994 when initial declines were observed. Thus, despite high pelagic inputs that were still likely present in 1994, even low densities of *Dreissena* had a negative impact on *Diporeia*.

Laboratory experiments indicated that sediments from H-31 and M-45 did not have an adverse impact on *Diporeia* per se (Nalepa et al. 2006). In these experiments, mortality in animals from M-45 was not observed after a 66-day exposure to sediments from both sites, and the sediments were not actively avoided. Interestingly, whereas there was no mortality during the laboratory experiments, the population of *Diporeia* at M-45 declined by 66% over the same 66-day period (May to July). Thus, conditions that led to the decline at M-45 were not dupli-cated in the laboratory using sediments from the same site and animals from the same population. This may imply that the population was reacting negatively en masse to the physical deposition of organic material in the spring. As noted, the rapid decline at H-22 was similarly observed after the spring period. Sediments from H-31 and M-45 were not acutely toxic to *Diporeia*, the same result found for sediments from H-22 (Landrum et al. 2000).

If food limitation was the primary cause for the loss of *Diporeia*, then the animals should show some physiologi-cal signs of starvation before or during the period of population loss. In deepwater amphipods, lipid levels are a good indicator of food availability; levels increase just after the spring diatom bloom when food is readily available, and decline during periods of low benthic food inputs in late summer and winter (Gardner et al. 1985b; Hill et al. 1992; Lehtonen 1996). When the population began to decline at H-31 in 1994, mean annual lipid content was only 15%, and the spring lipid peak was only 17%. These values indicate severe starvation - similar levels were found in laboratory animals starved for 120 days (Gauvin et al. 1989). Recruitment was poor in 1994, which is consistent with the suggestion that lipid values below 20% leads to reproductive failure (Hill et al. 1992). As densities continued to decline after 1994, lipid content unexpectedly increased and annual recruitment occurred. Possibly lipid content increased because declining densities led to more food for remaining organisms. Yet if this were so, then poor YOY survival should not have occurred, and the population should have stabilized at some reduced level consistent with a diminished food supply. Further, the increase in dreissenids over this period would have further reduced available food and resulted in lower rather than higher lipid values. As *Diporeia* densities approached zero in 1999, lipid levels were over 30% and comparable to levels found at this site in the 1980s just after the spring diatom bloom (Cavaletto et al. 1996; Gardner et al. 1985b).

While the long term decrease and then increase in lipid content found at H-31 has not been previously docu-mented in field populations, such a pattern was found in animals starved in the laboratory (Gauvin et al. 1989). In these experiments, lipid content declined from 30% to 12% after 120 days, and then increased to 18% after 191 days. The increase was attributed to the selective catabo-lism of non-lipid material (tissue components) after storage lipids were utilized. "Weight-specific" lipid content may thus increase even though "absolute" lipid content and total weight may decrease. This possibility seems to be refuted by the consistency in non-lipid weight (relative to length) at the 45-m sites over the time period when lipids increased. Further, "absolute" lipid content re-mained stable or actually increased during this period. Under some circumstances, an increase in lipid content may reflect an interference with lipid degradation or lipid transport processes (Giesy et al. 1988). Accumulated lipids would thus remain un-utilized as an energy source during periods of low food availability. A decline in lipid content and lack of mortality during a 66-d food-depriva-tion experiment indicated, however, that the animals were still able to utilize lipid material as an energy source (Nalepa et al. 2006). The increase and relatively high lipid content at the 45-m sites as populations disappeared suggests that biochemical/physiological changes were occurring in the animals, but the cause and meaning of such changes remain unresolved.

When *Diporeia* were declining, adult fecundity (eggs per brood) was similar to that found in the 1980s when

abundances were high. Except in 1994, these young developed and were recruited into the population. Population declines after 1994 occurred because the YOY were not surviving to become juveniles; that is, annual peaks in YOY were generally not followed by increased numbers of juveniles. Eventually, declines in adults resulted from reduced numbers of juveniles rather than adult-specific mortality. Because of higher metabolic and growth rates, YOY are more sensitive to declines in food levels than adults. In laboratory experiments assessing food competition between YOY and adults, YOY mortality was high at low to medium food regimes, whereas adults were not affected (Hill 1992; Wenngren and Olafsson 2002). Annual fluctuations in *Monoporeia* densities have been attributed to high mortality of YOY because of intraspecific competition for food with adults (Johnson and Wiederholm 1989; Sarvala 1986). Initial declines of juveniles relative to adults at the 45-m sites suggest that food limitation may indeed be a cause of the population decline, at least at these sites. Inconsistent with this premise is that lipid content of juveniles remained high and displayed spring peaks even as numbers decreased.

If food limitation was the cause of declines in *Diporeia*, then dreissenid biodeposits must not be available as a nutrition source. Either biodeposits are too refractive to sustain *Diporeia*, or biodeposits are somehow having a negative impact. In laboratory microcosms, *Diporeia* survival was reduced by 25% when exposed to mussel pseudofeces for 90 d (Dermott et al. 2005), so perhaps there is a direct negative response. In contrast, oligochaete densities remained stable between 1993 and 1999, which may reflect an ability to utilize this material as a food source. Whether oligochaetes will persist at these densities remains unclear. In Lake Ontario, where the dreissenid expansion occurred earlier than in Lake Michigan, oligochaete densities have recently declined (Lozano et al. 2001).

Although the loss of *Diporeia* in the Great Lakes has been extensive since *Dreissena* became established, these two taxa do seem to co-exist in some areas. In some Finger Lakes, NY, *Diporeia* abundances have not decreased despite an increase in dreissenids over the same time period (Dermott et al. 2005). In Lake Michigan, *Diporeia* continues to be present (although in reduced numbers) at a site < 30 m on the western side of the southern basin despite the presence of dreissenids. The persistence of *Diporeia* at this site may be temporary, but it does further illustrate the inconsistency associated with temporal and spatial patterns of decline.

In summary, features of declining *Diporeia* populations in Lake Michigan were highly variable. Depending on the site, declines in abundances were rapid and apparent in all age classes, or declines were more extended and mostly a result of poor juvenile survival. The former suggests mass mortality in response to perhaps a dreissenid toxic agent, whereas the latter suggests possible food limitation from dreissenid filtering activities. Our quantitative and limited qualitative measures of

benthic food inputs, along with observed changes in physiological well-being and laboratory mortality/avoidance experiments, failed to provide conclusive evidence of a cause. Inconsistencies apparent in our results may imply a multitude of causative factors whose relative importance may vary depending on specific environmental conditions. Other studies have shown that pathogens (Messick et al. 2004) or epibionts (Foley et al. 2006) are not likely causes for the decline. If food limitation is the sole cause, then a nutritional problem not evident from our measures of gross food inputs or physiological well-being is a possibility. Given this, detailed studies of cellular or biochemical indicators may prove worthwhile. For instance, profiles of essential fatty acids (Brett and Muller-Navarra 1997) or functional protein groups (Lopez et al. 2001) in areas with declining and stable populations may show differences specific to nutritional deficiencies or to disease/defense mechanisms. Populations from areas subject to upwelling/downwelling and high/low sedimentation would be of particular interest. By better understanding reasons for *Diporeia's* decline relative to increased numbers of dreissenids, we may better predict the eventual extent and ultimate consequences of the population loss.

About the Author

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MONITORING

Bioaccumulation of human waterborne parasites by *Dreissena polymorpha* and *Corbicula fluminea*

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Abstract

Dreissena polymorpha and *Corbicula fluminea* are nonindigenous invasive bivalves present in North America freshwaters that are frequently contaminated with human enteric parasites such as *Cryptosporidium parvum* and *Giardia lamblia*. Six-week laboratory exposure of