

Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*

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SUMMARY

1. The native amphipod *Diporeia* spp. was once the dominant benthic organism in Lake Michigan and served as an important pathway of energy flow from lower to upper trophic levels. Lake-wide surveys were conducted in 1994/1995, 2000 and 2005, and abundances of *Diporeia* and the invasive bivalves *Dreissena polymorpha* (zebra mussel) and *Dreissena rostriformis bugensis* (quagga mussel) were assessed. In addition, more frequent surveys were conducted in the southern region of the lake between 1980 and 2007 to augment trend interpretation.

2. Between 1994/1995 and 2005, lake-wide density of *Diporeia* declined from 5365 to 329 m⁻², and biomass (dry weight, DW) declined from 3.9 to 0.4 g DW m⁻². The percentage of all sites with no *Diporeia* increased over time: 1.1% in 1994/1995, 21.7% in 2000 and 66.9% in 2005. On the other hand, total dreissenid density increased from 173 to 8816 m⁻², and total biomass increased from 0.4 to 28.6 g DW m⁻². Over this 10-year time period, *D. r. bugensis* displaced *D. polymorpha* as the dominant dreissenid, comprising 97.7% of the total population in 2005. In 2007, *Diporeia* was rarely found at depths shallower than 90 m and continued to decline at greater depths, whereas densities of *D. r. bugensis* continued to increase at depths greater than 50 m.

3. The decline in *Diporeia* occurred progressively from shallow to deep regions, and was temporally coincident with the expansion of *D. polymorpha* in nearshore waters followed by the expansion of *D. r. bugensis* in offshore waters. In addition, *Diporeia* density was negatively related to dreissenid density within and across depth intervals; the latter result indicated that dreissenids in shallow waters remotely influenced *Diporeia* in deep waters.

4. With the loss of *Diporeia* and increase in *D. r. bugensis*, the benthic community has become a major energy sink rather than a pathway to upper trophic levels. With this replacement of dominant taxa, we estimate that the relative benthic energy pool increased from 17 to 109 kcal m⁻² between 1994/1995 and 2005, and to 342 kcal m⁻² by 2007. We project that previously observed impacts on fish populations will continue and become more pronounced as the *D. r. bugensis* population continues to expand in deeper waters.

Keywords: benthos, food webs, invasive species, lakes, populations

Introduction

Invasive species can cause changes in host aquatic ecosystems at many levels of organization, with perhaps the most common change being the loss of native species and a decline in biodiversity (Moyle & Light, 1996; Simon & Townsend, 2003; J.L. Molnar, R.L. Gamboa, C. Revenga and M.D. Spalding, unpublished data). Invaders negatively impact native species through competition, predation and habitat alteration (Richter *et al.*, 1997). Frequently, invasive species have a phase of rapid population growth and range expansion, and native species can be lost over a short time span (Diamond & Case, 1986; Crooks & Soule, 1999). Such rapid shifts in community dominance have complex implications for ecosystem function. Ultimately, functional impacts depend on food web roles and biological attributes of the species involved, and also on the particular habitat. In theory, if the invader plays a very similar functional role to the native species it has displaced, then ecosystem disruption would be minimal (Dick & Platvoet, 2000; Palmer & Ricciardi, 2005). More often though, because native species are well adapted to local conditions and evolved into an ecological niche over time, displacement will have at least some functional consequences. The displacement of species will be most disruptive where severe environmental conditions preclude the presence of a wide variety of species (Lodge, 1993; Covich, Palmer & Crowl, 1999). Moreover, functional changes are particularly pronounced in large homogeneous environments where strong physicochemical gradients do not exist (Moyle & Light, 1996). Such severe conditions, minimal diversity and lack of strong spatial gradients describes the benthic habitat in the offshore region of the Great Lakes.

In this study, we document a lake-wide replacement of a native species by an invader in Lake Michigan, and present evidence that the ensuing change in the composition of the benthic community will have a large functional impact. The taxa involved in this recent, dramatic transition are the native amphipod *Diporeia* spp., which has virtually disappeared, and the invasive mussel *Dreissena rostriformis bugensis* (Andrusov), which has become dominant. *Diporeia* are part of a fauna that inhabit cold, deep proglaciated lakes, brackish estuaries and coastal margins in the Holarctic region (Bousfield, 1989). Prior to the introduction and spread of two dreissenid species,

Dreissena polymorpha (Pallas) and *D. r. bugensis*, *Diporeia* was the dominant benthic organism in deeper waters (>30 m) of all the Great Lakes, comprising over 70% of benthic biomass in this offshore region (Cook & Johnson, 1974; Nalepa, 1989). It was present but less dominant in open, shallow regions (<30 m), and naturally absent from shallow, warm bays and basins. As a benthic detritivore, *Diporeia* feeds on organic material settled from the water column, being particularly reliant on material deposited during the spring diatom bloom (Gardner *et al.*, 1990). Depending on depth and seasonal period, epilithic algae and detritus/bacteria are also a source of food (Guiguer & Barton, 2002; Sierszen, Peterson & Scharold, 2006). In general though, ingestion rates, growth rates and lipid levels are at a seasonal peak during or just after the spring bloom (Gardner *et al.*, 1985, 1989; Dermott & Corning, 1988). *Diporeia* are fed upon by many fish species (Scott & Crossman, 1973; Wells, 1980), thereby serving as a keystone organism in the cycling of energy between lower and upper trophic levels. *Diporeia* populations began declining soon after *D. polymorpha* and *D. r. bugensis* became established in the Great Lakes in the late 1980s, and large areas in all the Great Lakes except Lake Superior are now completely devoid of this organism (Dermott & Kerec, 1997; Nalepa *et al.*, 2006a, 2007; Watkins *et al.*, 2007). Exact reasons for the negative response of *Diporeia* to dreissenids are not clear, and may be related to a combination of factors (Nalepa *et al.*, 2006a; Nalepa, Rockwell & Schloesser, 2006b).

In Lake Michigan, declines in *Diporeia* were first observed in the southern portion of the lake in the early 1990s, a few years after *D. polymorpha* first colonized that region in 1989 (Nalepa *et al.*, 1998). As *D. polymorpha* continued to spread, declines in *Diporeia* became more extensive, and by 2000 *Diporeia* were gone or rare in the far southern and northern portions of the lake, and along the eastern shoreline to depths of 50 m (Nalepa *et al.*, 2006a). The other dreissenid, *D. r. bugensis*, became established in the lake in 1997 (Nalepa *et al.*, 2001). This species was found in Lake Ontario 7 years prior to being found in Lake Michigan, and studies documented several important aspects of its expansion. First, unlike *D. polymorpha*, *D. r. bugensis* attained relatively high densities in deeper regions (>50 m) and, second, it displaced *D. polymorpha* in shallow regions (Mills *et al.*, 1999). We hypothesized that a similar expansion

pattern into offshore regions would occur in Lake Michigan, and that such an expansion would have strong, additional consequences to remaining *Diporeia* populations.

We here document lake-wide trends in *Diporeia*, *D. r. bugensis* and *D. polymorpha* in Lake Michigan over the period between 1994/1995 and 2005, and also provide more detailed trends in the southern basin of the lake between the early/mid-1980s (before dreissenid invasions) and 2007. While previous studies in Lake Michigan and the other Great Lakes have documented declines in *Diporeia* relative to dreissenids, changes in biomass and energy costs of such a shift in community composition have not been estimated. We show that the *Diporeia* population has declined to levels that make it no longer relevant as a pathway for energy cycling in the Lake Michigan food web, and also show that *D. r. bugensis* has expanded, displaced *D. polymorpha*, and now serves as a major energy sink within the lake.

Methods

Population trends of *Diporeia* and dreissenids in Lake Michigan were derived from lake-wide surveys in 1994/1995, 2000 and 2005. Numbers of sites sampled were 87, 157 and 160 in each of the three periods respectively. Each year, samples were collected in the late summer–early autumn period (August–September). Location of all sampling sites and collection dates are given in Nalepa *et al.* (2008). Of the sites sampled lake wide in 2000 and 2005, a subset of 40 sites in the southern basin was sampled again in 2006 and 2007. These sites were part of a long-term monitoring programme and also sampled in 1980–81, 1986–87, 1992–93 and every year between 1998 and 2007. Samples at these 40 sites were collected in spring, summer and autumn each year prior to 2000, and also in 2004 and 2005. Otherwise, samples were collected in late summer/autumn. Samples at each site were consistently taken in triplicate with a Ponar grab (sampling area = 0.046 m²). Sediments were washed through an elutriation device fitted with a 0.5-mm mesh net, and retained residue preserved in 5% formalin containing rose bengal stain. In the laboratory, all *Diporeia* and dreissenids were picked and counted under a low-power magnifier lamp (1.5×). In replicate samples with high numbers of either taxa, individuals were sub-sampled by using a folsom

plankton splitter (*Diporeia*), or by selecting a random quadrat of individuals that were evenly distributed in a gridded tray (dreissenids).

Dry-weight biomass of *Diporeia* in 1994/1995 was reported in Nalepa *et al.* (2000). In this previous study, biomass was derived from measured length–weight relationships and size–frequencies over various depth intervals and lake regions. To calculate biomass in 2005, mean weight in 1994–95 within each of four depth intervals (≤ 30 , 31–50, 51–90 and >90 m) was multiplied by mean density in that interval in 2005. We assumed that average weight (i.e. biomass divided by density) did not change over the 10-year time period since length–weight relationships and most size frequencies remained stable as densities declined between 1997 and 2002 (Nalepa *et al.*, 2006a). Lake-wide biomass in 1994/1995 was previously reported as the mean of all collected sites (Nalepa *et al.*, 2000). Since greater numbers of sites were sampled in 2005, we calculated 2005 lake-wide biomass and re-calculated 1994/1995 lake-wide biomass by first multiplying mean biomass in each of the four intervals by lake area within that interval, summing the value for all intervals, and then dividing by total lake area. Thus, biomasses were pro-rated as a function of lake area within a given depth interval. The proportion of lake area in the ≤ 30 , 31–50, 51–90 and >90 m intervals was 12.7%, 14.7%, 31.0% and 41.5% respectively. Biomass was not determined for 2000.

Dry-weight biomass of dreissenids in 1994/1995 and 2005 was also estimated from size frequencies and derived length–weight relationships. All dreissenids collected in 1994/1995 were measured (shell length), whereas in 2005 dreissenids were measured at 34 representative sites. The sites chosen in 2005 were considered representative of the lake as a whole; that is, they were located mostly along depth transects on the east and west side of the lake, and in three lake regions (south, central and north; Nalepa *et al.*, 2000). Of the 34 sites, 12 were located in the ≤ 30 m interval, 10 in the 31–50 m interval and 12 in the 51–90 m interval. Shell lengths were binned into 1 mm categories from 1 to 31 mm.

Length–weight relationships for both *D. polymorpha* and *D. r. bugensis* were derived from specimens collected at two sites (25 and 45 m) on the east side of the lake (off Muskegon, Michigan), and at two sites (18 and 45 m) on the west side of the lake (off Waukegan, Illinois) in 2004. These sites represented

conditions above and below the thermocline, which is about 30 m in Lake Michigan. Samples were collected on seven dates at the east sites (20 April, 3 June, 23 June, 21 July, 31 August, 21 September and 27 October) and on four dates at the west sites (27 May, 1 July, 25 August and 20 September). Mussels were collected with a Ponar grab, kept cool and shell-free dry weights (DW) determined within 48 h. For each species, shell lengths of 25 individuals collected on each date were measured (range 9–30 mm), soft tissues placed into pre-weighed aluminum planchets, dried at 60 °C for 48 h, and then re-weighed. A length–weight relationship derived from the 18 and 25 m sites (all dates) was used to determine biomass at all sites ≤ 30 m where mussels were measured ($n = 12$). Similarly, a length–weight relationship derived from the two 45 m sites on all dates was used to determine biomass at sites >30 m where mussels were measured ($n = 22$). The average weight of a mussel in these two intervals was determined and then used to calculate interval-specific biomass at all other sites (i.e. average weight \times density). Lake-wide biomass for dreissenids was determined as previously described for *Diporeia*.

While data from all sites were included in plots of density distributions, only sites in the main basin were included in statistical analysis and calculation of lake-wide biomass. Sites located in two bays, Green Bay and Grand Traverse Bay, were excluded since a greater number of sites were sampled in these two bays in 2000 and 2005 compared to 1994/1995 (29 versus 6). Thus, numbers of sites used in the actual analysis were 82, 128 and 131 in 1994/1995, 2000 and 2005 respectively. The sites were placed into four depth intervals (≤ 30 , 31–50, 51–90 and >90 m), and density differences between years and year \times interval interactions were tested with a two-way ANOVA after $\ln + 1$ transformation to homogenize variances. Station means were treated as the source of variation within intervals. When differences between years were significant ($P < 0.05$), Tukey's *post hoc* multiple range test was used to make pair-wise comparisons. Since some sites ($n = 34$) were sampled in all three periods, we also examined differences using repeated measures ANOVA (Green, 1993). Statistical outcomes were similar to those of the two-way ANOVA; thus, only outcomes of the two-way ANOVA are reported. Since all 40 sites sampled in the southern region in 2005 were re-sampled in 2006 and 2007, differences

between the 3 years were tested with repeated measures ANOVA after $\ln + 1$ transformation.

Results

Over the 10-year period between 1994/1995 and 2005, mean lake-wide density of *Diporeia* declined from 5365 to 329 m^{-2} , and biomass declined from 3.9 to 0.4 g DW m^{-2} . Densities were significantly different between the three sampling periods ($F_{[2, 329]} = 98.13$, $P < 0.001$), with densities significantly lower in 2000 compared to 1994/1995 ($P < 0.001$), and significantly lower in 2005 compared to 2000 ($P < 0.001$) (Table 1). The year \times interval interaction was also significant ($F_{[16, 329]} = 4.67$, $P < 0.001$), indicating declines were not consistent across all depth intervals. Over the 10-year period, declines were 96.9%, 99.6%, 91.6% and 72.8% in the ≤ 30 , 31–50, 51–90 and >90 m depth intervals, respectively. The percentage of all sites with no *Diporeia* increased over time: 1.1% in 1994/1995, 21.7% in 2000 and 66.9% in 2005 (Fig. 1).

Densities continued to decline at the southern basin sites between 2005 and 2007 (Fig. 2). Differences between 2005, 2006 and 2007 were significant ($F_{[2, 78]} = 10.17$, $P \leq 0.001$), with densities significantly lower in 2006 than in 2005 ($P < 0.05$) and densities

Table 1 Mean (\pm SE) density (no. m^{-2}) of *Diporeia* spp., *Dreissena polymorpha* and *Dreissena r. bugensis* in Lake Michigan at each of four depth intervals in 1994/1995, 2000 and 2005

	Year		
	1994/1995	2000	2005
<i>Diporeia</i> (m)			
≤ 30	3489 \pm 995	870 \pm 324	111 \pm 95
31–50	5850 \pm 1283	2001 \pm 534	23 \pm 15
51–90	6557 \pm 570	3422 \pm 460	548 \pm 131
>90	4567 \pm 414	2752 \pm 448	1244 \pm 217
<i>D. polymorpha</i> (m)			
≤ 30	702 \pm 512	1836 \pm 467	223 \pm 84
31–50	259 \pm 218	1366 \pm 584	446 \pm 106
51–90	<1 \pm <1	18 \pm 8	38 \pm 29
>90	0 \pm 0	0 \pm 0	<1 \pm <1
<i>D. bugensis</i> (m)			
≤ 30	0 \pm 0	37 \pm 23	6285 \pm 1450
31–50	0 \pm 0	25 \pm 17	16 415 \pm 2690
51–90	0 \pm 0	0 \pm 0	6472 \pm 1704
>90	0 \pm 0	0 \pm 0	12 \pm 7

The number of sites sampled each year in the ≤ 30 , 31–50, 51–90 and >90 m intervals were respectively: 1994/1995 = 16, 12, 31, 23; 2000 = 36, 38, 41, 13; 2005 = 38, 39, 41, 13.

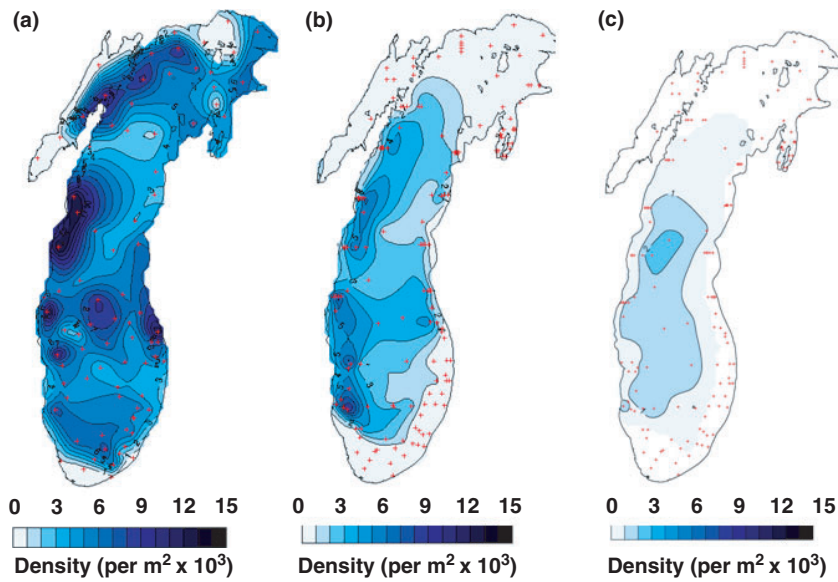


Fig. 1 Mean density (no. m^{-2}) of *Diporeia* in Lake Michigan. Small crosses denote sampling sites. (a) 1994–95, (b) 2000, (c) 2005.

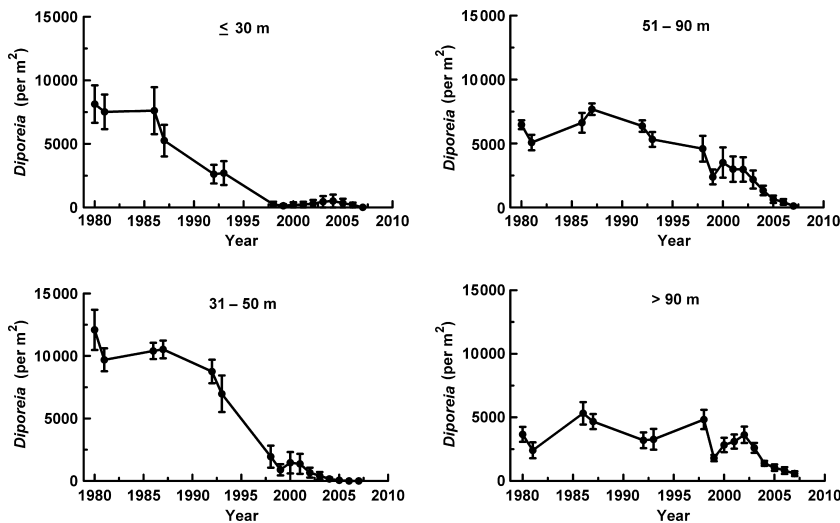


Fig. 2 Mean (\pm SE) density (no. m^{-2}) of *Diporeia* in each of four depth intervals at 40 sites in the southern basin of Lake Michigan between 1980 and 2007. The number of sites in each depth interval was ≤ 30 m = 12, 31–50 m = 10, 51–90 m = 12, > 90 m = 6.

in 2007 significantly lower than 2006 ($P < 0.01$; repeated measures ANOVA, *post hoc*). In the 1980s, prior to the *Diporeia* decline and the establishment of *Dreissena* (i.e. 1980–81, 1986–87), mean densities in the southern basin at the four depth intervals were 7162, 10 687, 6426 and 3925 m^{-2} respectively. In 2007, densities in the same intervals were 13, 1, 112 and 576 m^{-2} . Based on these frequently sampled sites, it was evident that declines occurred progressively from shallow to deep regions. Initial declines occurred in the early/mid-1990s at the ≤ 30 and 31–50 m intervals, in the late 1990s/early 2000s at the 51–90 m interval, and in 2004 at the > 90 m interval (Fig. 2).

While the lake-wide population of *Diporeia* declined between 1994/1995 and 2005, the total dreissenid population increased (Table 1). Mean total density of dreissenids increased from 173 m^{-2} in 1994/1995 to 8816 m^{-2} in 2005, and total biomass increased from 0.4 to 28.6 g DW m^{-2} . Densities were significantly different between the 3 years ($F_{2, 3291} = 97.22$, $P < 0.001$), with densities significantly higher in 2000 compared to 1994/1995 ($P < 0.001$), and significantly higher in 2005 compared to 2000 ($P < 0.001$). The year \times depth interval interaction was also significant ($F_{16, 3291} = 9.87$, $P < 0.001$), likely reflecting the expansion of dreissenids from shallow to deep water

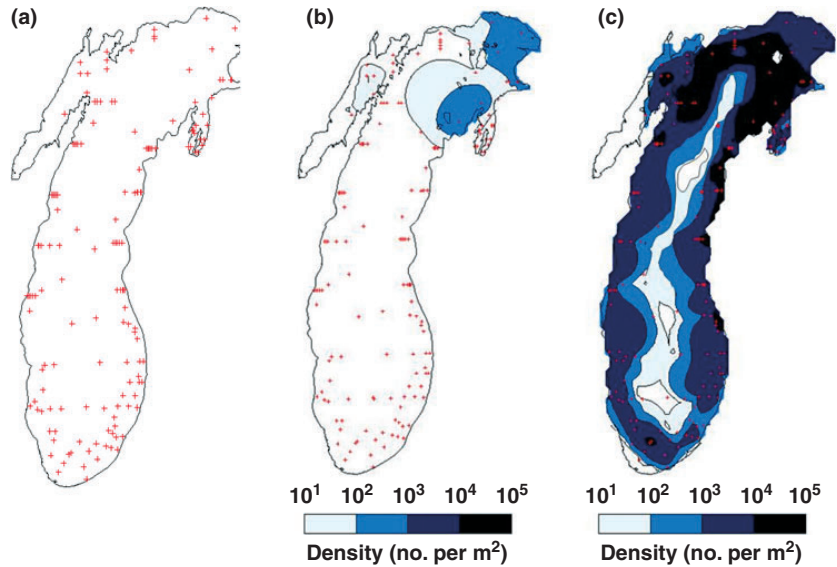


Fig. 3 Mean density (no. m⁻²) of *Dreissena r. bugensis* in Lake Michigan. Small crosses denote sampling sites. (a) 1994–95, (b) 2000, (c) 2005. For 2005, contours were manipulated slightly in the northern, mid-lake region to reflect more realistic patterns. Although not thoroughly sampled, this region would have few mussels because of extreme depths.

over this period (Table 1). Over the 10-year period, *D. r. bugensis* became established in the lake and displaced *D. polymorpha* as the dominant species. *Dreissena r. bugensis* was not found at any of the sites in 1994/1995, comprised only 1.9% of the total dreissenid population in 2000, but comprised 97.7% of the total in 2005 (Table 1). After becoming established in the northern portion of the lake in 1997 (Nalepa *et al.*, 2001), it spread rapidly southward (Fig. 3). Overall densities were significantly greater in 2005 compared to 2000, and the difference was a function of depth ($P < 0.01$, Tukey's *post hoc* test; year \times interval interaction: $P < 0.01$). Mean densities increased from less than 50 m⁻² in 2000 to more than 5000 m⁻² in 2005 at each of the three shallowest depth

intervals, but the increase at the >90 m interval was minimal (Table 1). All individuals collected in both 2000 and 2005 were the profunda or deepwater phenotype (see Dermott & Munawar, 1993).

In the southern basin, *D. r. bugensis* began to increase at the <30 and 31–50 m intervals in 2002, and began to increase at sites in the 51–90 m interval in 2005 (Fig. 4). As of 2007, densities appeared to have stabilized at the two former intervals, were still increasing at the latter, and were beginning to increase at the >90 m interval. Mean maximum density in 2007 was 13 289 m⁻² in the 31–50 m interval.

Over the 10-year sampling period, densities of *D. polymorpha* increased between 1994/1995 and 2000, but then decreased between 2000 and 2005 (Table 1).

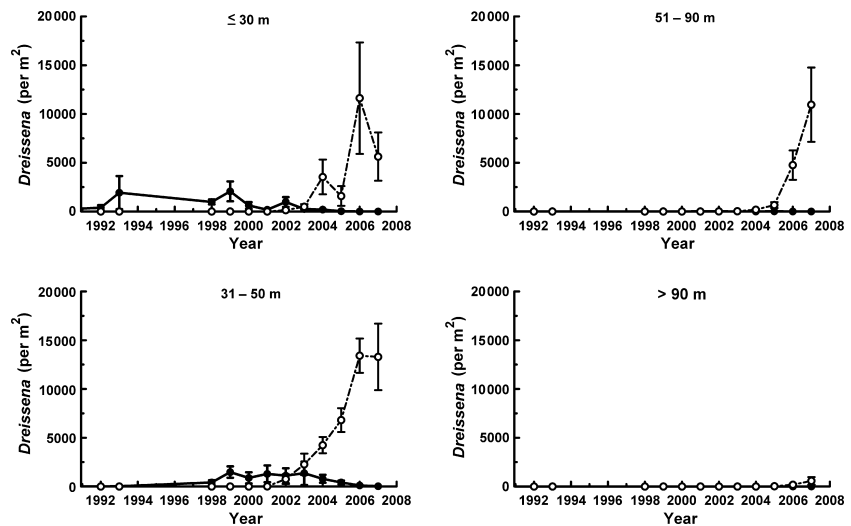


Fig. 4 Mean (\pm SE) density (no. m⁻²) of *Dreissena* in each of four depth intervals at 40 sites in the southern basin of Lake Michigan between 1992 and 2007. The number of sites in each depth interval was ≤ 30 m = 12, 31–50 m = 10, 51–90 m = 12, >90 m = 6. Solid circle, *Dreissena polymorpha*; open circle, *Dreissena r. bugensis*.

Differences between these three periods were significant ($P < 0.01$, Tukey's *post hoc* test; year \times interval interaction: $P < 0.01$). Although *D. polymorpha* was present, densities were minimal in the 51–90 and >90 m intervals over the entire 10-year sampling period. In the southern basin, abundances of *D. polymorpha* continued to decline through 2007 (Fig. 4). As an example, mean maximum density in 2005 was 416 m⁻² in the 31–50 m interval, but only 24 m⁻² in the same interval in 2007.

As noted, the decline of *Diporeia* in the southern basin occurred progressively over time, occurring first at sites within the shallow intervals followed by declines at sites in the deeper intervals. This trend coincided with the increase in *D. polymorpha* to depths of 50 m through the 1990s, and then with increases in *D. r. bugensis* at deeper depths thereafter (Fig. 4). We used correlation analysis to determine if there was a negative relationship between densities of *Diporeia* and dreissenids within and across depth intervals over the time period between 1992 and 2007 (Table 2). Except for the ≤ 30 m interval, there was a strong negative relationship between the two taxa within each depth interval. In addition, there was a similarly strong negative relationship across intervals; that is, *Diporeia* densities at deep intervals were negatively correlated to dreissenid densities at shallower intervals.

Discussion

The offshore benthic community of Lake Michigan has undergone a major transformation over the past

Table 2 Correlation (Pearson's coefficients) between *Diporeia* and *Dreissena* spp. within and across depth intervals for the period between 1992 and 2007 in the southern basin of Lake Michigan

<i>Diporeia</i>	<i>Dreissena</i> spp.			
	≤ 30 m	31–50 m	51–90 m	>90 m
≤ 30 m	-0.361			
31–50 m	-0.758*	-0.823**		
51–90 m	-0.704*	-0.773*	-0.962**	
>90 m	-0.753*	-0.678*	-0.902**	-0.854**

Each yearly depth mean was considered an observation ($n = 12$; no samples for 1994–97). Correlation analysis performed on $\ln + 1$ transformed values.

Significant at * $P < 0.05$; ** $P < 0.01$.

10–12 years. The native amphipod *Diporeia* has been replaced by the invasive mussel *D. r. bugensis* as the dominant benthic organism in the lake, and overall benthic biomass has increased. In general, the decline of *Diporeia* in Lake Michigan is comparable to declines found in Lakes Huron and Ontario over the same general time period (Nalepa *et al.*, 2007; Watkins *et al.*, 2007). At depths of 30–90 m, the *Diporeia* population declined 96% between 1994/1995 and 2005 in Lake Michigan, declined 99% between 1994 and 2003 in Lake Ontario, and declined 93% between 2000 and 2007 in Lake Huron (Fig. 5). On a broad scale, declines in all three lakes coincided with the introduction and expansion of the dreissenid population; decreased densities of *Diporeia* are evident even at dreissenid densities of less than 1000 m⁻² (Fig. 6).

As mentioned previously, reasons for the negative association between *Diporeia* and *Dreissena* are not clear. A common early hypothesis was that *Diporeia* were being out-competed for available food resources (Dermott & Kerec, 1997; Nalepa *et al.*, 1998). Dreissenids are filter-feeders that inhabit the sediment surface, whereas *Diporeia* is a detritivore that feeds in the upper few centimeters of sediment. Dreissenids would thus have access to freshly-settled organic material before *Diporeia*. Assuming that *Diporeia* is dependent on pelagic food inputs in offshore waters, it follows that *Diporeia* could be out-competed for settling food and hence show measurable signs of starvation as the population declined. In *Diporeia* and other deepwater amphipods, lipid levels are a good

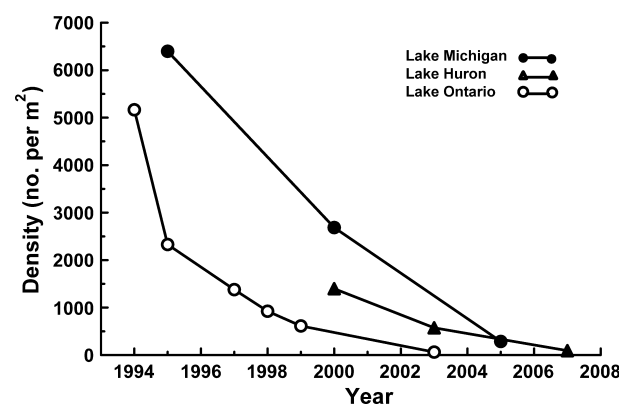


Fig. 5 Trends in mean density (no. m⁻²) of *Diporeia* in Lake Michigan (this study), Lake Ontario (Watkins *et al.*, 2007), and Lake Huron (Nalepa *et al.*, 2007; T.F. Nalepa, unpubl. data) at a depth of 30–90 m between 1994 and 2007. Solid circle, Lake Michigan; open circle, Lake Ontario; solid triangle, Lake Huron.

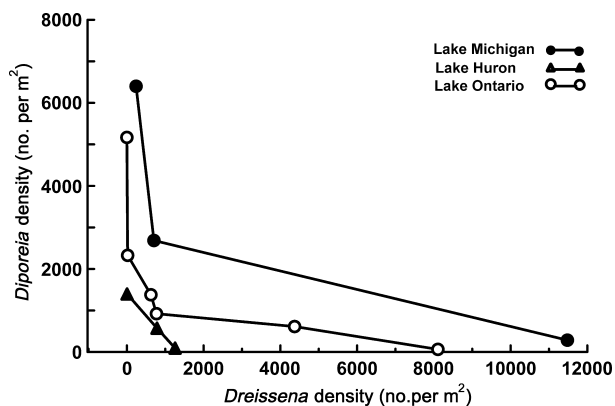


Fig. 6 Relationship between mean densities (no. m⁻²) of *Diporeia* and *Dreissena* in Lake Michigan (this study), Lake Ontario (Watkins *et al.*, 2007) and Lake Huron (Nalepa *et al.*, 2007; T.F. Nalepa unpubl. data) at a depth of 30–90 m between 1994 and 2007. Solid circle, Lake Michigan; open circle, Lake Ontario; solid triangle, Lake Huron.

indicator of available food, increasing in the spring when benthic food inputs are high, and then decreasing later when food inputs are minimal (Gardner *et al.*, 1985; Hill *et al.*, 1992; Lehtonen, 1996). By utilizing lipid stores, *Diporeia* can be highly resistant to food deprivation. In laboratory experiments, *Diporeia* survived for up to 120 days with little or no food as lipid levels declined from 30% to 12% (Gauvin, Gardner & Quigley, 1989). Inconsistent with the food-limitation hypothesis, lipid levels and weight per unit length did not decrease as the population declined at several Lake Michigan sites (Nalepa *et al.*, 2006a). Further, sedimentation traps indicated at least some organic material (including diatoms as indicated by silica flux) was still settling to the bottom in areas where *Diporeia* had disappeared and dreissenids were not present (Nalepa *et al.*, 2006a). Similar declines have been recorded in areas removed from dreissenid populations and with seemingly adequate food resources in the water column (diatoms) (Dermott, 2001; Nalepa *et al.*, 2003). Given this, it would be paradoxical to assume that food-deprivation would be the only cause for the population decline. In this study, there was a strong negative correlation between *Dreissena* densities at shallow sites and *Diporeia* densities at deep sites, and this is consistent with the finding that the progressive decline of *Diporeia* from shallow to deeper waters generally precedes the shallow-to-deep expansion of dreissenids (Nalepa *et al.*, 2007; Watkins *et al.*, 2007). The

remote influence of dreissenids on *Diporeia* suggests that some unknown agent associated with dreissenids is being transported beyond areas colonized by these mussels. *Diporeia* survival was reduced by 25% when exposed to dreissenid pseudofaeces for 90 days in laboratory experiments, giving credence to the alternative hypothesis that an agent associated with dreissenid biodeposits is having a negative influence (Dermott *et al.*, 2005). Since dreissenid biodeposits are loosely aggregated and therefore readily re-suspended (Hecky *et al.*, 2004), this material may be transported beyond mussel beds and remotely affect *Diporeia*. Of course, inconsistent with this hypothesis is the coexistence of *Diporeia* and dreissenids in some locations for extended periods. In this study, *Diporeia* and dreissenids coexisted for 14 years at a 20 m site in the southern basin before the former taxa disappeared in 2007.

In general, deep-water amphipods appear to be highly sensitive to environmental perturbations. In European waters, there are records of rapid and extended declines in populations of the closely-related amphipod *Monoporeia affinis* Lindström. Over a 40-year period, Goedkoop (2006) documented annual density fluctuations between fewer than 10 m⁻² and 10 000 m⁻² in *M. affinis* at sites deeper than 30 m in Swedish lakes. In some lakes, low densities could be related to periodic low oxygen concentrations in the profundal zone, but in other lakes, low annual densities could not be clearly attributed to any environmental stress. In the Baltic Sea, *M. affinis* has a natural population cycle of 6–7 years, with densities periodically declining to near zero only to increase within a few years (Sarvala, 1986). However, recent broad declines of *M. affinis* in the Baltic Sea appear to be unrelated to intrinsic factors (Cederwall, Jermakovs & Lagzdins, 1999; Kotta & Olafsson, 2003) and may reflect a disruption in benthic food inputs because of compositional shifts in phytoplankton. That is, the phytoplankton community has shifted from diatoms to dinoflagellates and, because the latter do not settle to the bottom as readily as the former, less food would be available to *M. affinis* (A.K.E. Wiklund, B. Sundelin & R. Rosa, unpublished data). Although *Diporeia* were generally not present in local areas subject to environmental degradation in the Great Lakes in the 1970s (Nalepa & Thomas, 1976; Vander Wal, 1977; Kraft, 1979), the recent, broad disappearance of this organism in Lake Michigan and

the other Great Lakes is unique to this system and unlike declines of *M. affinis* observed in European waters. For one thing, monitoring of *Diporeia* in offshore waters of Lake Michigan indicated that the population was generally stable from year-to-year in the pre-*Driessena* period (in 1980s; see Fig. 2). Moreover, there has been no indication of a recovery in Lake Michigan or in any of the other Great Lakes once the population has disappeared from a given area.

Prior to its decline, *Diporeia* dominated and thrived in the offshore region of Lake Michigan because it was well-adapted to seasonal variations in benthic food inputs. Most organic material settling to the bottom occurred during the diatom bloom in the spring when cold temperatures hinder decomposition during settlement through the water column, and zooplankton grazers are at a minimum (Scavia & Fahnenstiel, 1987). As noted, *Diporeia* fed intensively during this period and accumulated lipids that reached as high as 50% of its DW by late spring (Gardner *et al.*, 1990). After stratification, benthic food inputs were minimal, and *Diporeia* relied on stored lipids to survive and reproduce. In contrast, lipid levels of *D. r. bugensis* in Lake Michigan are consistently below 20% and levels of glycogen, another pathway of energy storage in mussels, are less than 4% of dry body weight (T.F. Nalepa, unpubl. data). How then can *D. r. bugensis* thrive in an environment characterized by low, intermittent food inputs and continuously cold temperatures? Insights into the suitability of *D. r. bugensis* for this harsh environment can be derived from several studies that compared physiological traits of *D. r. bugensis* and *D. polymorpha* to determine why the former species was displacing the latter in the Great Lakes. In one study, *D. r. bugensis* was found to have a higher assimilation efficiency than *D. polymorpha*, especially at lower food levels (81% versus 63%; Baldwin *et al.*, 2002). Thus, it is able to maintain higher growth and fecundity rates with less available food. In the other study, *D. r. bugensis* had a lower respiration rate under a wide range of temperature regimes compared to *D. polymorpha* (Stoeckmann, 2003). Lower respiration rates decrease metabolic costs and further increase the efficient utilization of assimilated material. At low levels of natural seston (i.e. $1 \mu\text{g L}^{-1}$ Chl), *D. r. bugensis* grew 19 times faster than *D. polymorpha* (Baldwin *et al.*, 2002). These low levels are now generally found in offshore waters of Lake Michigan (Lesht & Wortman, 2007). Moreover,

D. r. bugensis allocates more energy to soft tissue relative to shell compared to *D. polymorpha*, giving it a further advantage (Roe & MacIsaac, 1997).

Conceivably then, because of a relatively high assimilation efficiency and a low respiration rate, *D. r. bugensis* can sustain growth and reproduction at low food levels without relying on energy stores as does *Diporeia*. It should be noted that assimilation efficiency is a function of food quality, and the experimentally-derived assimilation efficiency of 81% reported for *D. r. bugensis* occurred when food quality was high (Baldwin *et al.*, 2002). In comparison, Dermott (1995) found that the maximum assimilation efficiency of *Diporeia* over a seasonal period was 42% (as corrected for selective ingestion). This maximum occurred in June just after the spring bloom when food quality was at a peak. This value is comparable to an assimilation efficiency of 40% for *M. affinis* when feeding on freshly-deposited organic material collected in the spring in the Baltic Sea (Lopez & Elmgren, 1989). Thus, when food quality is high, assimilation efficiency of *D. r. bugensis* appears to be twice that of *Diporeia*.

Another key physiological trait when considering adaptation to low food environments is growth efficiency, or the proportion of assimilated material that is incorporated into production relative to that respired. In offshore waters, growth efficiency for *Diporeia* was 33–35% (Johnson & Brinkhurst, 1971; Fitzgerald & Gardner, 1993). The growth efficiency of *D. r. bugensis* in offshore regions is unknown, but some indication of relative growth efficiencies of these two taxa can be derived by comparing respiration rates. Johannsson *et al.* (1985) determined respiration rates of *Diporeia* at several sites below the thermocline in Lake Ontario and provided a regression equation relating rates to water temperature. From their equation, the respiration rate of *Diporeia* at 4 °C was determined to be $1.29 \mu\text{g O}_2 \text{ mg DW h}^{-1}$. In comparison, the respiration rate of *D. r. bugensis* at 4 °C was determined to be about $0.87 \mu\text{g O}_2 \text{ mg DW h}^{-1}$ (Stoeckmann, 2003), or about 33% lower than *Diporeia*. This is not unexpected since a stationary filter-feeder like *D. r. bugensis* would be less active than a burrowing detritivore like *Diporeia*. As noted earlier, lower respiration rates would allow more assimilated energy to be utilized for growth and reproduction.

The replacement of *Diporeia* by *D. r. bugensis* can be viewed as a process that has caused a major disruption

in the energy flow through the benthic community. That is, energy once efficiently cycled through *Diporeia* to upper trophic levels now resides in dreissenid biomass or is lost to the system, and the benthic community now serves as a major energy sink rather than a pathway. As found in this study, mean lake-wide biomass of *D. r. bugensis* was 28.6 g DW m⁻² in 2005. When the proportion of depth-specific biomass in the southern basin relative to the entire lake was calculated for 2005 and proportionately applied to the entire lake based on the 2007 data, the mean lake-wide biomass in 2007 was estimated to be 80 g DW m⁻². Assuming *Diporeia* has an energy content of 1159 cal g⁻¹ wet weight (WW) (McNickle, Rennie & Sprules, 2006), the biomass of 3.9 g DW m⁻² found in 1994/1995 was equivalent to 14.5 g WW m⁻² (DW = 27% WW; Landrum, 1988) and represented an energy pool of 16.8 kcal m⁻². Assuming *Dreissena* has an energy content of 580 cal g⁻¹ WW (Schneider, 1992), the 28.6 g DW m⁻² biomass of *D. r. bugensis* in 2005 was equivalent to 188 g WW m⁻² (DW = 15% WW, Schneider, 1992) and represented an energy pool of 109 kcal m⁻². Ignoring the low biomass of dreissenids in 1994/95 and the low biomass of *Diporeia* in 2005 and assuming biomass contribution of other taxa is minimal (Nalepa, 1989; Nalepa *et al.*, 1998), this represents a 6.5-fold increase in the lake-wide benthic energy pool in 10 years. When estimated for 2007, this energy pool was 342 kcal m⁻², a 20-fold increase over 1994/1995.

In addition to having a relatively low respiration rate and a high assimilation efficiency compared to *Diporeia*, the high energy pool achieved by *D. r. bugensis* can be partly explained by its feeding mode. An active filter-feeder like *D. r. bugensis* has access to pelagic production during the entire unstratified period, while a passive detritivore like *Diporeia* has access to such production mostly in the spring when conditions favour pelagic deposition.

Of course, the concept of an energy sink is only valid if *D. r. bugensis* is not being fed upon by upper trophic levels, and this is not entirely true. For example, large lake whitefish (*Coregonis clupeaformis* [Mitchill]) are now feeding almost exclusively on *D. r. bugensis*, when previously these fish fed mostly on *Diporeia* (Pothoven & Nalepa, 2006). The problem with switching from *Diporeia* to *D. r. bugensis* lies in the ingestion of the dreissenid shell, which comprises more than 80% of total dry mass in *D. r. bugensis* (Roe

& MacIsaac, 1997). The shell offers little nutritional value, but represents an energetic cost to the fish in terms of handling and digestion. Further, the amount of energy placed into shell growth by dreissenids is unknown, but in marine mussels it is 50% of production (Kuenzler, 1961). In the constantly cold waters of offshore regions, production in all taxa is about equal to biomass (i.e. P/B = 1; Johnson & Brinkhurst, 1971). Therefore, the energy sink represented by *D. r. bugensis* can be 50% greater than represented by standing biomass if the cost of producing the shell is also considered. Energy is lost to the food web when the shell is ingested, and also lost when the shell is produced.

Recent studies suggest that the disappearance of *Diporeia*, an energy-rich, readily-available food source, is having a negative impact on fish communities in Lake Michigan and other Great Lakes (i.e. Lakes Huron and Ontario) (Mohr & Nalepa, 2005). For example, the diet, abundance and energy density of alewife (*Alosa pseudoharengus* [Wilson]), sculpin (*Cottus cognatus* Richardson and *Myoxocephalus thompsonii* [Girard]), and bloater (*Coregonus hoyi* [Gill]), were examined in areas of southeastern Lake Michigan with and without *Diporeia* (Hondorp, Pothoven & Brandt, 2005). These fish species serve as important prey of the larger piscivores within the lake. In the area with no *Diporeia*, fish feeding habits were altered, and abundance and energy density were significantly lower than fish from the area where *Diporeia* was still present. Further, energy density of alewife in the lake has declined 23%, and condition of lake whitefish has decreased 27% since the mid-1990s when *Diporeia* began declining (Pothoven *et al.*, 2001; Madenjian *et al.*, 2006). More recently, total biomass (WW) of prey fish in Lake Michigan has declined from 91 kilotonnes in 2005 to 31 kilotonnes in 2007, which is down from 450 kilotonnes in 1989 (C. Madenjian, pers. comm.). Based on our study, total WW biomass (shell and soft tissue) of *D. r. bugensis* was 36 kilotonnes in 2005 and estimated to have increased to 113 kilotonnes in 2007 (assuming tissue DW is 5% total WW in *D. r. bugensis*, T.F. Nalepa, unpubl. data). Other factors besides a decline in *Diporeia* and an increase in dreissenid biomass may have contributed to the loss of prey fish biomass (Bunnell *et al.*, 2009), but, nevertheless, total dreissenid biomass (tissue and shell) is now estimated to be about 3.8 times greater than prey fish biomass within the lake.

Presently in Lake Michigan, *Diporeia* have disappeared to depths of 90 m, and current trends indicate that populations at depths greater than 90 m are now in a state of decline. Exact reasons for the disappearance of *Diporeia* are not entirely clear but, based on past trends, the expected increase of *D. r. bugensis* at depths greater than 90 m portends a continued loss of *Diporeia* within this deep region. During the initial stages of expansion, most dreissenid populations tend to follow a boom-and-bust scenario, with populations increasing rapidly for a period followed by a decline to more stable, sustainable levels (Strayer & Malcom, 2006). In 2007, the *D. r. bugensis* population in Lake Michigan was still expanding, and we estimate that lake-wide biomass was at least three times greater than found in 2005. Yet even though the population will stabilize and decline at some point, it is unlikely that *Diporeia* will soon recover since extirpation occurs even at low densities of *Dreissena*. As shown, the disappearance of *Diporeia* has progressed from shallow to deep water over time, and its recent rapid decline at 51–90 m coincides with the increase of *D. r. bugensis* at this depth interval. Given evidence that fish prefer to feed on *Diporeia* even when densities are low (Hondorp *et al.*, 2005) and most prey fish are found at depths less than 90 m (Wells, 1980), the recent decline of *Diporeia* at depths of 51–90 m would indicate that further impacts on the fish community are forthcoming.

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