Spatial patterns in population trends of the amphipod *Diporeia* spp. and *Dreissena* mussels in Lake Michigan

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Introduction

Until the late 1980s, the benthic amphipod Diporeia spp. was the dominant benthic macroinvertebrate in offshore waters of the Laurentian Great Lakes and was considered a keystone species in the lakes' trophic structure (COOK & JOHNSON 1974). In Lake Michigan, it comprised over 70% of macrobenthic biomass at depths >30 m in the 1980s (NALEPA 1989). As a benthic detritivore, Diporeia feeds mainly upon material freshly settled from the water column (i.e. diatoms) and, in turn, is fed upon by many fish species including yellow perch, lake whitefish, bloater, alewife, and sculpin (WELLS 1980, CROWDER et al. 1981, KRAFT & KITCHELL 1986).

Declines in Diporeia populations have been documented in the Great Lakes since the zebra mussel (Dreissena polymorpha) and the quagga mussel (Dreissena *bugensis*) became established in the late 1980s. Large areas of Lakes Michigan, Huron, Erie, and Ontario are now completely devoid of this organism (DERMOTT & KEREC 1997, NALEPA et al. 1998, LOZANO et al. 2001). A common hypothesis for the decline is that Diporeia is being outcompeted for available food resources by Dreissena. Diporeia feeds in the upper few cm of sediment, whereas Dreissena occurs at the sediment surface and filters settling material before it becomes available to *Diporeia*. Spatial and temporal patterns of the Diporeia decline, however, are often inconsistent with this food-limitation hypothesis (NALEPA et al. 2004). In this paper, we examine trends in Diporeia and *Dreissena* populations in different areas of Lake Michigan. By comparing spatial patterns of population trends in these two organisms, we may better define causes of declines and thus better predict the eventual extent of Diporeia losses.

Key words: zebra mussels, quagga mussels, benthic community, Great Lakes

Study design and rationale

Sampling sites were chosen to maximize spatial differences in environmental conditions within the lake. Of consideration were water depth, longitude (east vs. west side), and latitude (south-north gradient). Sites were located at various depths along six transects (Fig. 1). Transects were paired, one on the east and the other on the west side of the lake at about the same latitude, and each pair was at a different latitude

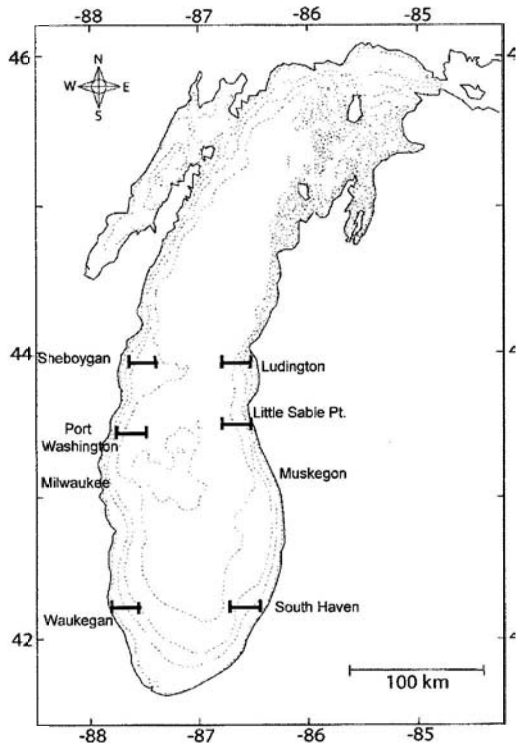

Fig. 1. Location of sampling transects in Lake Michigan in 2000 and 2002. Sites were located at various depths along each transect.

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extending south to north. Transects were located off Waukegon (WAU), Port Washington (PW), and Sheboygan (SY) on the west side, and off South Haven (SH), Little Sable Point (LSP), and Ludington (LU) on the east side (Fig. 1).

Depth plays a major role in defining composition and abundance of the benthic macroinvertebrate community in Lake Michigan (MOZLEY & HOWMILLER 1977, NALEPA 1989). For *Diporeia*, standing stocks are minimal in shallow-water areas, tend to increase with water depth to a peak just below the thermocline at 30–50 m, and then gradually decline. In general, warm, unstable temperatures limit populations of this cold-water stenotherm at depths above the thermocline (≤30 m), and reduced food supplies limit populations at deeper depths (>50 m). In this study, sampling sites at transects PW, SY, LSP, and LU were located at 20, 30, 45, 60, and 80 m. At Transect WAU, sites were located at 20, 45, 56, and 83 m, and at Transect SH sites were located at 20, 45, and 68 m. Sites at these latter two transects are Dart of a larger, ongoing monitoring program that began in 1980 (NALEPA 1987, NALEPA et al. 1998). These sites were also sampled by others in the 1960s (ALLEY & MOZLEY 1975, A. M. BEETON, unpubl.).

Diporeia tends to be more abundant on the west side of the lake than on the east (ALLEY 1968, NALEPA et al. 2000). During summer stratification, dominant southwesterly winds lead to downwelling along the eastern shoreline and upwelling along the western shoreline (MORTIMER 1975). The colder, more enriched waters in the west provide more favorable conditions for *Diporeia* and, hence, greater abundances. Finally, conditions in the southern basin of the lake (defined as the area south of a mid-lake plateau between Milwaukee and Muskegon, see Fig. 1) vary from areas farther north. Most major tributaries are found in the southeastern portion of the basin, resulting in lower water transparency, greater productivity, and higher total deposition of particulate mass and organic carbon (BARTONE & SCHELSKE 1982, MEYERS & EADIE 1993). *Diporeia* densities tend to be lower in the southern basin compared to areas farther north (ALLEY 1968).

Methods

Benthic samples were collected at sites along each transect in July/August 2000 and 2002. Sampling techniques were the same as in the monitoring program (NALEPA 1987). Samples were collected in triplicate with a Ponar grab (0.046 m^2) and washed through an elutriation device fitted with a 0.5-mm mesh net. All retained residue was preserved in 5 % formalin containing rose bengal stain. In the laboratory, all *Diporeia* and *Dreissena* were picked and counted in a white enamel pan under a low-power magnifier lamp (1.5 X).

Results

Declines in the *Diporeia* population of Lake Michigan, first observed in the southeast region of the lake in 1992 (NALEPA et al. 1998), clearly continued between 2000 and 2002 (Fig. 2). Over all sites, densities were significantly lower in 2002 compared to 2000 (Wilcoxon paired rank test; $P < 0.05$). Declines were evident at all transects except SH. At this transect, *Diporeia* densities had declined to zero prior to 2000 (Fig. 3; NALEPA, unpubl. data). For the five other transects, declines between 2000 and 2002 varied by water depth. At depths above the thermocline (≤ 30 m), densities at transects on the east side of the lake were zero at 20 m in 2000, and declined to zero at 30 m in 2002. In contrast, *Diporeia* was still present at 20 and 30 m at transects on the west side of the lake in both years. For transects on the west-side, densities did not decline at 20 m over the 2-year period, but declines did occur at 30 m. For transects on both sides of the lake, greatest declines occurred at the 45 m depth. In 2000, mean (± SE) density at this depth was $9216 \pm 725/m^2$ (n = 5; excluding Transect SH), which was within the density range found at this depth prior to dreissenids (NALEPA et al. 1998). By 2002, mean density had declined to $3171 \pm 836/m^2$. Although mean percent decline at 45 m was greater in the east (73.0%) than in the west (51.7%), the difference was not significant (t-test, arc-sine transformed, $P > 0.05$). At 60 m, declines were minimal at all transects (range: 7.2% to 16.1%) except WAU where the decline was 34.2%. At 80 m, declines were not apparent at any transects (Fig. 2).

As noted, sites along transects WAU and SH are part of a long-term sampling program, so densities in 2000 and 2002 can be put into a more historic perspective. Both transects had sites at 20 and 45 m, so these depths can be compared directly for both sides of the lake. *Diporeia* disappeared at both depths on the east side (Transect SH) in the late 1990s (Fig. 3). On the west side, recent densities at 20 m, although lower than found in the 1960s through the 1990s, have actually increased since 1999.

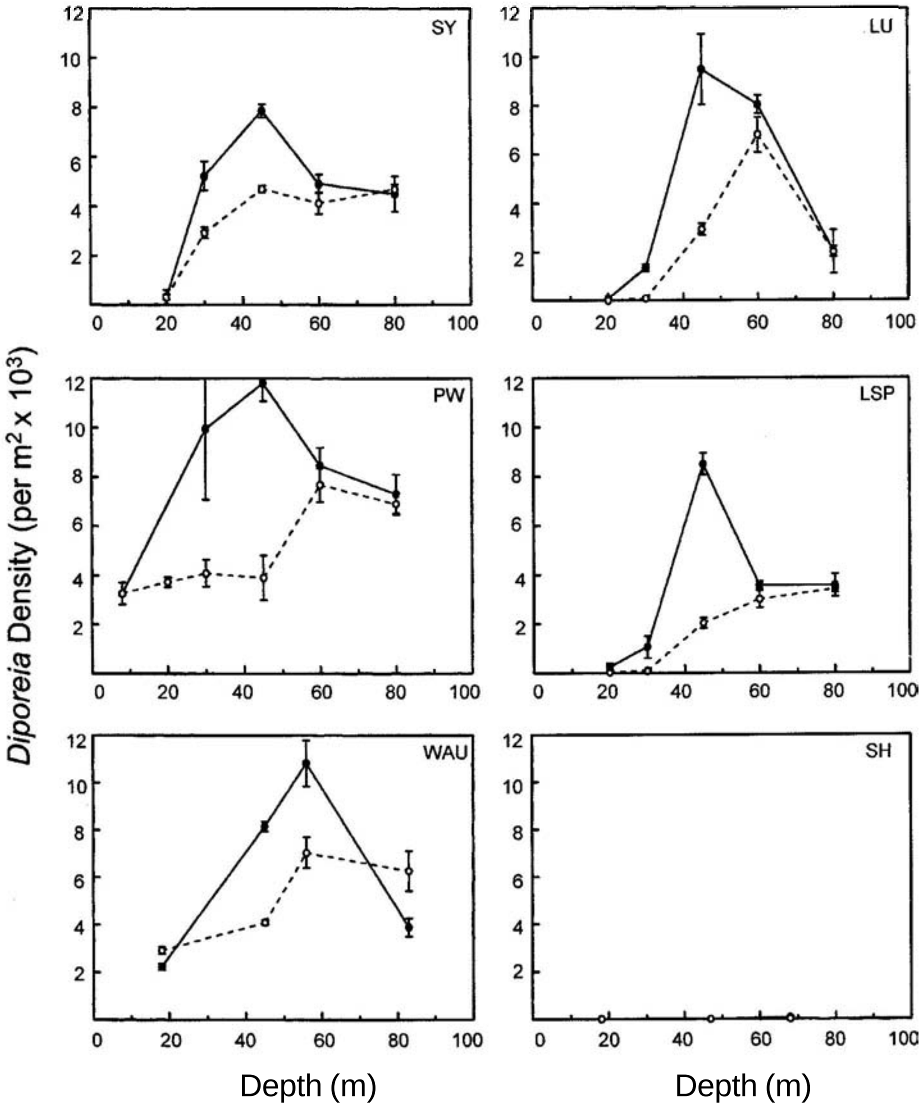

Fig. 2. Mean (± SE) density (per m^2) of *Diporeia* spp. at various depths along each of the six transects in 2000 (●—●) and in 2002 (O– – O). See text for transect designations.

Densities at 45 m declined between 2000 and 2002, but it is not clear if this is the continuation of a downward trend or merely year-to-year variation within a stable population (Fig. 3).

While the overall ***Diporeia*** population declined, the dreissenid population increased (Fig. 4). Total density was significantly higher in 2002 compared to 2000 (Wilcoxon paired rank test; $P < 0.05$). Densities increased at all transects except at SH; at this transect mussel densities were minimal in both years (maximum density: $542/m^2$ in 2000 and $93m^2$ in 2002). In 2000, mean densities at the other five transects were 825, 4782, 416, 64, and $1/m^2$ at 20, 30, 45, 60, and 80 m, respectively, whereas in 2002 densities were 4080, 5308, 1442, 662, and $15/m^2$. Thus, greatest increases (on a per-

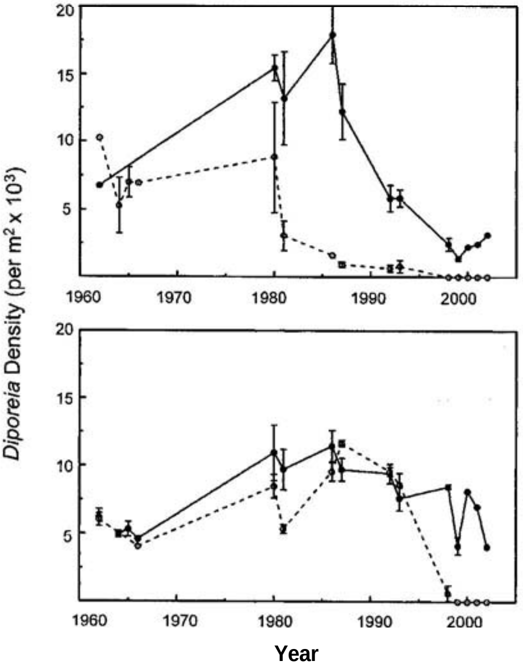

Fig. 3. Mean (± SE) density (per m^2) of *Diporeia* spp. between the mid-1960s and 2002. Upper: 20m site on the west side (●—●) and east side (0 – – 0) of the lake; Lower: 45 m site on the west side (●—●) and east side (0 – – O) of the lake.

centage basis) occurred at deeper depths. The overall increase can be solely attributed to the expansion of the quagga mussel. In 2000, quagga mussels were not collected at any of the sites, but in 2002 they comprised 52% of the total dreissenid population. At depths >50 m, quagga mussels comprised 81% of all dreissenids. In contrast, there was no significant difference in zebra mussel densities between 2000 and 2002 (Wilcoxon paired rank test; $P > 0.05$). The increase in dreissenids was similar on both east and west sides of the lake (Fig. 4), except in the southern basin where dreissenids increased at transect WAU but not SH.

Discussion

In all areas of the Great Lakes where *Diporeia* has declined, decreases have been coincident with the introduction and spread of dreissenids (Dermott & Kerec 1997, Nalepa et al. 1998, Lozano et al. 2001). Despite the broad negative relationship between *Diporeia* and *Dreissena*, local spatial inconsistencies between the extent of *Diporeia* declines and dreissenid abundances present difficulties in defining an exact cause for *Diporeia's* negative response. For instance, *Diporeia* densities rapidly declined in some areas of the Great Lakes where there were no mussels in the immediate vicinity and where food was still apparently available (Dermott 2001, Nalepa et al. 2003). In the present study, greatest declines in *Diporeia* occurred at deeper depths where the dreissenid population increased most over the 2-year time period. On the other hand, the complete absence of *Diporeia* at Transect *SH* despite low relative abundances of dreissenids, provides an example of this inconsistency. Further, at a 45-m site in southeast Lake Michigan just south of Transect SH, *Diporeia* densities declined from $10{,}000/m^2$ to near $0/m^2$ in just 6 months in the early 1990s, even though no mussels were present at the site itself (Nalepa et al. 2004). One hypothesis for this enigma is that *Diporeia* populations located down current from dreissenids are being deprived of food by the filtering activity of mussels (Dermott 2001). Spatial distributions of the two organisms thus do not need to overlap for *Diporeia* to be negatively affected. This may indeed be true, but at 45-m in the southeast portion of Lake Michigan where the *Diporeia* population so rapidly declined, enough food material was still settling to the bottom such that a minimal *Diporeia* population might be sustained (Nalepa, unpubl. data).

In general, the complete loss of *Diporeia* was first evident in shallow-water areas and then extended to deeper areas over time (Nalepa et al. 1998, 2004). This pattern was apparent at shallow water sites (≤30 m) at the two most northern transects along the east side of the lake (Transects LSP, LU). In contrast, despite similar densities of dreissenids on both sides of the lake, *Diporeia* was still relatively abundant at shallow-water sites at 2 of 3 west-side transects. In particular, at the 20-m site along the WAU transect, *Diporeia* did not decline between 2000 and 2002 despite dreissenids increasing from 190 to $4800/m^2$. Whether *Diporeia* will persist at some shallow water locations on the west side remains unclear, but persist-

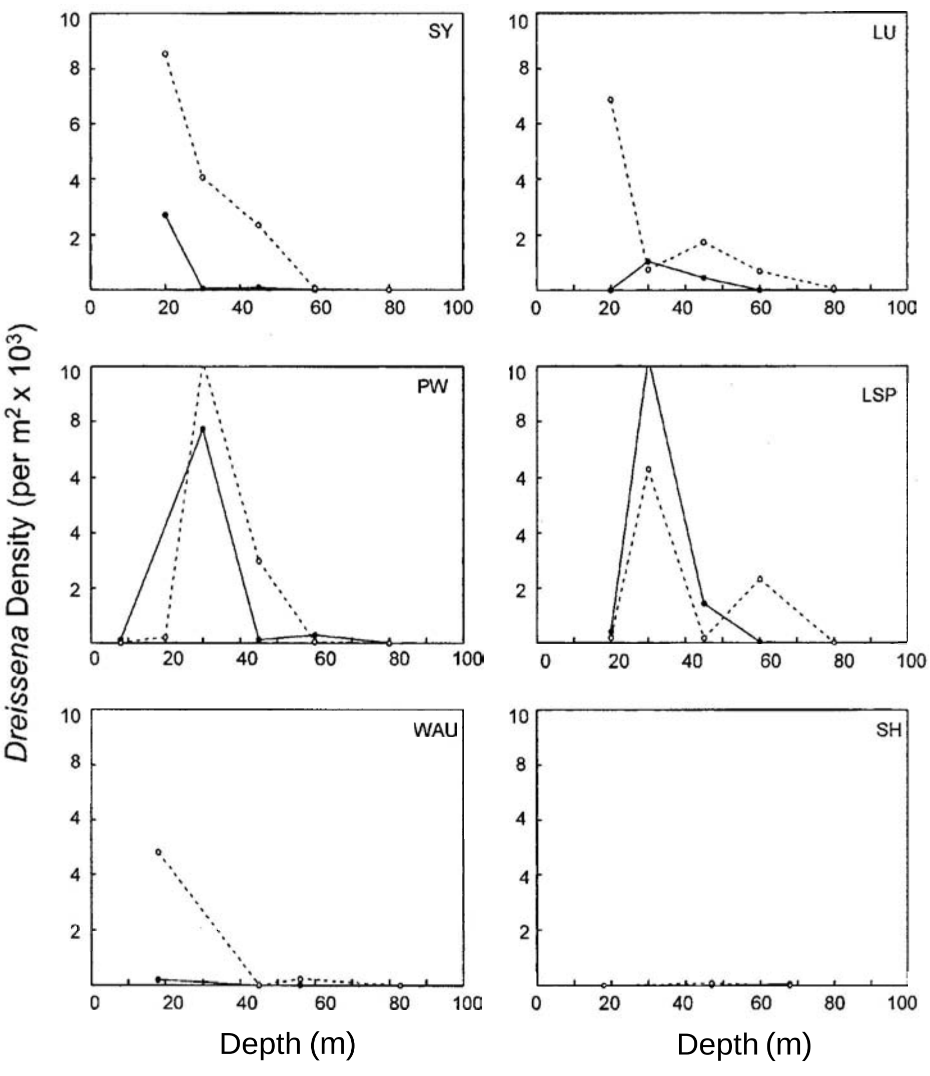

Fig. 4. Mean density (per m^2) of the total *Dreissena* population at various depths along each of the six transects in 2000 (0 — 0) and in 2002 (0 – – 0). See text for transect designations.

ence of *Diporeia* to date is uncharacteristic of trends found in shallow water areas of the other lakes (DERMOTT & KEREC 1997, LOZANO et al. 2001). Further studies are planned to define potential factors that may be sustaining populations in these areas and whether upwelling events may be playing a role.

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