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Trends in benthic macroinvertebrate populations in southern Lake Michigan

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Introduction

Long-term changes in benthic macroinvertebrate populations have long been used to assess trends in environmental conditions and trophic status in the Great Lakes (for summary see Cook & Johnson 1974). Until the late 1960s/early 1970s, although some sensitive forms declined, the general trend was for an increase in numbers of most benthic groups, particularly in the bays and nearshore areas. These increases reflected increasing nutrient loads (phosphorus) and greater system productivity, allowing greater inputs of organic material to the benthic region. This material served as food for the taxa most able to utilize this resource. To reverse eutrophic trends, phosphorus control measures were implemented in the mid-1970s. By the early 1980s, overall productivity declined in many areas and water quality improved as indicated by decreased macroinvertebrate densities and a return of more sensitive taxa (Johnson & McNeil 1986, Schloesser et al. 1995, Krieger & Ross 1993).

Interpretations of trophic trends based on macroinvertebrate populations became confounded in the late 1980s when the zebra mussel, *Dreissena polymorpha*, became established in the Great Lakes. Many benthic taxa increased in density by utilizing *Dreissena* biodeposits as a source of food, or by taking advantage of increased substrate complexity and structure resulting from dense mussel clumps (Griffiths 1993, Stewart & Haynes 1994, Stewart et al. 1998). *Dreissena* negatively affected other taxa through food competition or physical disruption (Nalepa et al. 1996, Dermott & Kerec 1997). Implications of *Dreissena*-induced changes are clear – it can no longer be assumed that changes in benthic macroinvertebrate densities and composition are primarily a function of changes in trophic status. This is true not only for areas with high *Dreissena* abundances, but also for areas without high abundances that are located in well-mixed regions in close proximity to *Dreissena*-infested areas (Nalepa & Fahnenstiel 1995).

In this paper, we summarize trends in densities of the major benthic macroinvertebrate groups in southern Lake Michigan over the period between the mid-1960s and 1993. Changes in densities between the 1960s and 1980–1981 were reported by Nalepa (1987), and changes between 1980–1981 and 1992–1993 were reported by Nalepa et al. (1998). Our purposes here are to summarize trends over the entire period, and to closely examine potential reasons for the changes observed.

Methods

Sample collection and processing

We sampled at 40 sites in the spring, summer, and fall of 1980–1981, 1986–1987, and 1992–1993 (Fig. 1). These sites were originally chosen because each was sampled in the 1960s or earlier by various investigators (Nalepa 1987). Water depth at these sites ranged from 16 to 154 m. The exact location, water depth, and substrate type of each station is given in Nalepa et al. (1985). Samples were collected in triplicate with a Ponar grab (area 0.046 m^2) and washed through an elutriation device fitted with a nitex screen with 0.5-mm mesh openings. The material retained was immediately preserved in 10% buffered formalin containing rose bengal stain.

In the laboratory, the material was placed into a white enamel pan and organisms were picked, counted, and sorted into major benthic groups. The dominant groups were *Diporeia* (Amphipoda), Oligochaeta, Sphaeriidae, Chironomidae, Gastropoda, and *Dreissena polymorpha*. Organisms were identified to the lowest practical taxonomic level. Trends in individual species were presented in earlier papers (Nalepa 1987, Nalepa et al. 1998) and will not be discussed here.

Data analysis

While we sampled at all 40 sites between 1980 and 1993, not all of these sites were sampled quantitatively for all major benthic groups in the 1960s.

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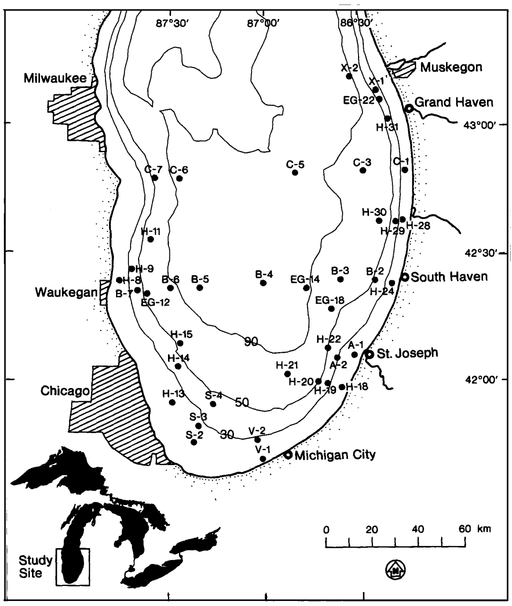

Fig. 1. Location of sampling sites in southern Lake Michigan. Depth contours are 30 m, 50 m, and 90 m.

Therefore, so as not to bias our examination of density trends over the entire period, we restricted our analysis to 31 sites, with the following sites not included in the present analysis: EG-12, EG-14, EG-18, EG-22, H-22, H-28, H-29, H-30, and H-31. The 1960s data were taken from Beeton (unpublished data), who sampled in 1962, and from Alley & Mozley (1975), who sampled in 1964–1967. Since samples were collected at different seasonal and annual frequencies in these two studies, only annual station means were used in the analysis of all data collected between the 1960s and 1993. To facilitate comparisons, sites were divided into four depth categories: 16–30 m (n = 10), 31–50 m (n = 8), 51–90 m (n = 8), and >90 m (n = 5). These depth categories are consistent with prior characterization of depth–macroinvertebrate relationships in Lake Michigan (Alley & Mozley 1975, Nalepa 1987). Analyses of density trends were limited to the three dominant benthic groups, *Diporeia*, Oligochaeta, and Sphaeriidae. These groups are the most abundant and widely distributed in Lake Michigan, and their abundance has been reported in all previous surveys.

Results and discussion

The extent of density changes in the three major macroinvertebrate groups between the 1960s and 1992–1993 depended upon the depth interval. At sites with a water depth of less than 50 m, total densities of all three groups increased between the 1960s and 1980, and then declined from 1980 to 1993 (Fig. 2a). The extent of these temporal changes was greatest at the shallowest interval (16–30 m). At this interval, total densities increased from 7,011 m^{-2} in the 1960s to a peak of 16,895 m^{-2} in 1980, and then declined to a low of 4,265 m^{-2} in 1993. Total densities followed a similar pattern at the 31- to 50-m interval. Densities increased from 13,316 m^{-2} in the 1960s to a peak of 21,422 m^{-2} in 1980, and then declined to 9,654 m^{-2} in 1993. At these two depth intervals, all three macroinvertebrate groups increased 2- to 5-fold between the 1960s and 1980, and then declined 2- to 4-fold between 1980 and 1993. A comparison of mean densities between the 1960s and 1993 for each group and depth interval indicated that differences between the two time periods were not significantly different with the exception of sphaeriids; this group had significantly (matched-pairs signed rank test, $P < 0.05$) lower densities at the 31- to 50-m interval in 1993 compared to the 1960s (Nalepa et al. 1998).

Trends in total densities at sites with a water depth greater than 50 m were not as consistent as at the shallower sites (Fig. 2b). Densities tended to be greatest in 1986–1987 at both the 51- to 90-m and >90-m intervals, with mean annual densities varying from 6,400 m^{-2} (in the 1960s) to 10,453 m^{-2} (in 1987) at the 51- to 90-m interval, and from 3,300 m^{-2} (in 1981) to 6,800 m^{-2} (in 1986) at the >90-m interval. A comparison of *Diporeia* and oligochaete densities in the 1960s and 1993 at these two deeper intervals indicated no significant differences ($P > 0.05$) between the two periods; however, densities of sphaeriids were significantly lower in 1993 than in the 1960s at both intervals (Nalepa et al. 1998).

Temporal trends in total densities at depths <50 m basically followed temporal patterns of

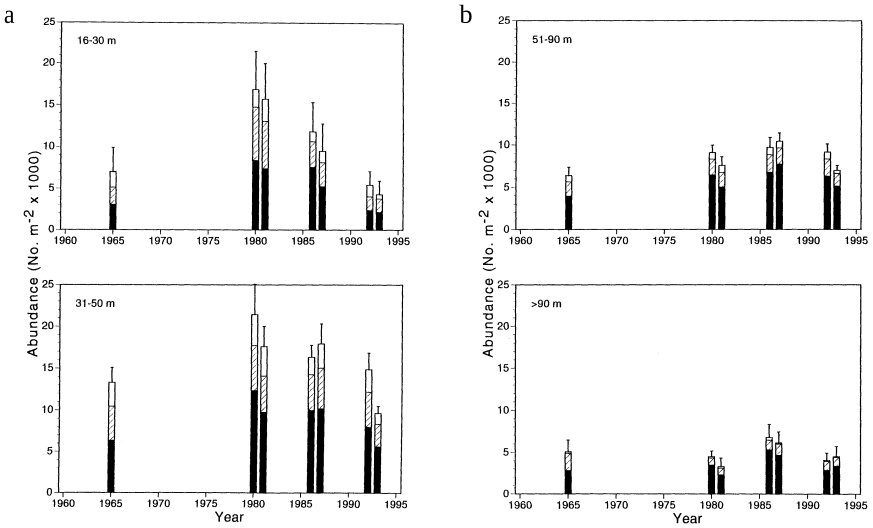

Fig. 2. (a) Total annual densities (ind. m^{-2}, x ± S.E.) of the dominant macroinvertebrate groups in southern Lake Michigan over the period between the 1960s and 1993. Upper: sites in the 16- to 30-m depth interval; lower: sites in the 31- to 50-m depth interval; solid: *Diporeia*, stripped: Oligochaeta, clear: Sphaeriidae. (b) Total annual densities (ind. m^{-2}, x ± S.E.) of the dominant macroinvertebrate groups in southern Lake Michigan over the period between the 1960s and 1993. Upper: sites in the 51- to 90-m depth interval; lower: sites in the >90-m depth interval; solid: *Diporeia*; stripped: Oligochaeta; clear: Sphaeriidae.

phosphorus loads and pelagic productivity over the same time period. Phosphorus loads to the lake increased up to the mid-1970s, and then declined after control measures were implemented (Fig. 3). Pelagic productivity showed similar temporal patterns. Phytoplankton abundance in 1977 was typically 1.5–3.0 times greater than that in 1962–1963, and the intensity of the spring diatom bloom increased until about the mid-1970s (ROCKWELL et al. 1980, VANDERCASTLE 1985). After the mid-1970s, total spring phosphorus, the intensity of the spring diatom bloom, and summer chlorophyll all declined (VANDERCASTLE 1985, SCAVIA et al. 1986, CHANG & ROSSMAN 1988). Based on our surveys, total densities at depths <50 m peaked in 1980, or 5–10 years after peak loads occurred. This may have been because of a time lag before benthic populations responded to productivity declines, or perhaps peak densities actually occurred in the late 1970s when samples were not collected. Total densities at depths >50 m peaked later (in 1986–1987) than at shallower depths, and changes were not as pronounced. Pelagic productivity in offshore areas of Lake Michigan is not as great, and not as well coupled to nutrient inputs, compared to nearshore areas (SCHELSKE et al. 1980). At any rate, the close relationship between trends in nutrient loads, pelagic productivity, and abundance of *Diporeia*, oligochaetes, and sphaeriids is typical for large, deep lakes like Lake Michigan where the hypolimnion is much greater than the epilimnion, and oxygen concentrations never become limiting (SAETHER 1980).

Besides changes in system productivity, two other factors probably impacted macroinvertebrate densities: fish predation and *Dreissena polymorpha*. Of the three dominant benthic groups, *Diporeia* increased the most at depths <50 m between the 1960s and 1980–1981 (NALEPA 1987). This increase was attributed to not only increased nutrient loads, but also to a decline in fish predation. Many of the fish species that feed heavily on *Diporeia* in nearshore areas, including yellow perch (*Perca flavescens*), slimy sculpin (*Cottus cognatus*), and alewife (*Alosa pseudoharengus*), declined over this

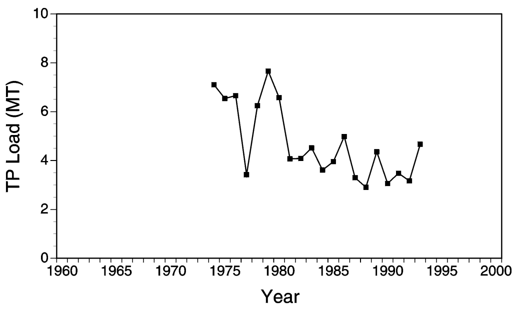

Fig. 3. Annual phosphorus loads (metric tonnes) into Lake Michigan in the period between the 1970s and early 1990s. Loads in the late 1960s/early 1970s were taken from estimates provided by SCHELSKE (1978). Loads between 1974 and 1993 were from JOHENGEN et al. (1994) and the International Joint Commission (unpublished data).

period. In the Great Lakes, changes in *Diporeia* densities have been linked to changes in fish predation pressure (JOHNSON & MCNEIL 1986, MCDONALD et al. 1990).

Another factor that had an impact on macroinvertebrate populations, at least in the later portion of our study period, was the introduction and rapid spread of *Dreissena polymorpha*. This species became established in the southern end of Lake Michigan in 1989, and by 1993 had reached densities of up to 268,00 m^{-2} in some nearshore areas (MARSDEN et al. 1993). Because of the filtering activity of *Dreissena* and the removal of organic material from the water column, water clarity increased by over 50% in the south/southwestern portion of the lake (MARSDEN et al. 1993). Thus, at least some of the macroinvertebrate declines in the later portion of our study period at depths <50 m may have been due to reduced food availability caused by *Dreissena*. Since the 1986–1987 survey was conducted just prior to the establishment of *Dreissena*, we compared relative declines between the 1980/1981–1986/1987 period and the 1986/1987–1992/1993 period (NALEPA et al. 1998). Rates of decline were calculated (percent decline per year) for the two time periods for each of the three macroinvertebrate groups. At the 16- to 30-m interval, yearly rates of decline were greater in the 1980/1981–1986/1987 period than in the 1986/1987–1992/1993 period for oligochaetes (8.2% and 7.4% for the two time periods, respectively) and sphaeriids (7.5% and 4.5%), but greater in the 1986/1987–1992/1993 period for *Diporeia* (2.6% and 10.0%). This suggests that, at least at this shallowest interval, oligochaetes and sphaeriids responded more rapidly to nutrient reductions than did *Diporeia*, and/or that *Diporeia* may have been more influenced by *Dreissena* than the other two groups. For the 31- to 50-m interval, rates of decline were greater in the later time period for all three groups.

Further evidence for the potential impact of *Dreissena* on *Diporeia* was the spatial patterns of density declines in the three groups. All sites less than 50 m in water depth (23 total) were ranked by relative mean density in both 1980–1981 and 1992–1993, and rank differences between the two 2-year surveys were tested for each group using Chi Square. For oligochaetes and sphaeriids, rank differences were not significantly different ($P > 0.05$), indicating that relative declines in these two benthic groups were consistent for all sites at these depths. However, there was a significant difference in ranks for *Diporeia* ($P < 0.01$), indicating that some sites declined more than others. An examination of changes in spatial densities indicated that *Diporeia* declined to the greatest extent at sites in the south/southeastern portion of the study area. Of the 11 sites where *Diporeia* declined more than 60% between 1980–1981 and 1992–1993, all were located in the south/southeastern portion of the lake (Table 1). The mean decline at these sites was 82%. Of the other 12 sites at these depths, *Diporeia* declined an average of only 26% at eight sites, and did not decline at four sites. The area of greatest *Diporeia* decline corresponded to the area where *Dreissena* was most abundant, or had the most impact on available food (MARSDEN et al. 1993, NALEPA et al. 1998). We suspect that food competition between *Diporeia* and *Dreissena* may have led to accelerated declines in the former species. *Diporeia* is a surface-feeding detritivore that relies on material freshly settled from the water column, while *Dreissena* filters this mate-

Table 1. Mean annual density (ind. m^{-2}) of the amphipod *Diporeia* at select sites in the far south/southeastern portion of the study area in southern Lake Michigan.

Station	Depth (m)	Year					
		1980	1981	1986	1987	1992	1993
V–1	16	4,988	4,254	5,923	6,357	64	9
S–2	17	4,857	1,304	8,367	3,046	497	92
A–1	18	9,688	7,751	8,749	6,990	1,970	9
H–13	19	18,247	8,063	5,965	4,335	380	2,201
H–18	19	5,587	2,128	3,372	2,437	449	26
H–24	19	8,836	3,070	1,624	895	652	778
S–3	25	6,476	8,321	1,801	369	2,851	764
V–2	29	13,396	14,421	17,517	10,759	5,740	6,497
A–2	35	19,273	11,150	10,947	11,403	8,801	380
H–19	37	15,157	11,058	9,456	9,262	5,092	2,525
H–22	46	9,408	9,896	9,347	9,685	5,285	492

rial before it reaches the sediment surface. A similar decline in *Diporeia* was noted in eastern Lake Erie after *Dreissena* became established (DERMOTT & KEREC 1997). In our study area, fish predation was dismissed as a potential factor in causing the spatially-focused declines in *Diporeia* because predation pressure did not change over the later portion of our study period and, also, fish species that prey on *Diporeia* were distributed over the entire southern basin and not concentrated in the south/southeastern end where *Diporeia* declined (NALEPA et al. 1998).

In comparison, declines in oligochaetes and sphaeriids at sites <50 m occurred consistently over the 1980/1981–1986/1987 and 1986/1987–1992/1993 periods, and occurred uniformly over the entire study area. This implies that declines in these two groups were more related to nutrient reductions than to *Dreissena* filtering activities. In eastern Lake Erie, oligochaetes did not decline in the presence of *Dreissena* but, in contrast to our findings, sphaeriid densities did decline (DERMOTT & KEREC 1997). Oligochaetes are infaunal detritivores, while the dominant sphaeriid genus in our study area, *Pisidium*, feeds by filtering suspended microorganisms from interstitial waters (LOPEZ & HOLOPAINEN 1987). Thus, both groups are not as dependent upon material freshly settled from the water column as is *Diporeia*, and actually may be utilizing *Dreissena* biodeposits directly or indirectly (through bacteria) as a food source.

In summary, densities of the three major macroinvertebrate groups in southern Lake Michigan, the amphipod *Diporeia*, Oligochaeta, and Sphaeridae, increased at depths <50 m between the 1960s and 1980, but then declined from 1980 to 1993. Densities in 1993 were not different from densities in the 1960s with the exception of sphaeriids, which were lower. Trends were not as discernible at depths >50 m; but total densities appeared to peak in 1986–1987. At the deeper depths, only sphaeriid densities were significantly lower in 1993 compared to the 1960s. Density increases between the 1960s and 1980–1981 at depths <50 m can be mainly attributed to increased nutrient loads and system productivity over most of this period, but a decrease in fish predation pressure may have also accounted for the increase in *Diporeia*. Declines in *Diporeia*, oligochaetes, and sphaeriids after 1980 can be attributed to continued declines in nutrient loads. However, accelerated declines in *Diporeia* after 1986–87 were most likely related to the introduction and spread of the zebra mussel, *Dreissena polymorpha*, which may outcompete *Diporeia* for available food.

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