

Characteristics and Potential Causes of Declining *Diporeia* spp. Populations in Southern Lake Michigan and Saginaw Bay, Lake Huron

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Abstract

Populations of the amphipods *Diporeia* spp. are declining in all of the Great Lakes except Lake Superior. We examine characteristics and potential causes of declines in southern Lake Michigan and outer Saginaw Bay, Lake Huron. Amphipod populations began to decline within 3-4 years after zebra mussels (*Dreissena polymorpha*) colonized both areas. In Lake Michigan, which was better studied, the decline occurred first in shallow waters (<30 m) and then progressed deeper (51-90 m). Between 1980-1981 (pre-*Dreissena*) and 1998-1999 (post-*Dreissena*), densities at sites in these two depth intervals declined 92%

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and 58%, respectively. At a 45-m site in southeastern Lake Michigan, densities of *Diporeia* spp. declined to near zero within six months even though mussels were never collected at the site itself. At a nearby 45-m site, densities declined gradually to zero over a six-year period and correlated with increased mussel densities. Although mussels are likely outcompeting *Diporeia* spp. populations for food, and food limitation is probably a contributing factor to population declines, populations show no physiological signs of starvation; lipid content is at a maximum as densities approach zero. Pathogens, fish predation, contaminants, and low dissolved oxygen do not appear to be the sole causes of population declines. The decline of *Diporeia* spp. is likely to continue as dreissenid populations expand.

Introduction

The benthic amphipod *Diporeia* spp. (hereafter diporeia as a common name) is part of a deepwater fauna that inhabit cold, proglaciated lakes, brackish estuaries, and coastal margins in the Holarctic region. This organism was the most abundant benthic macroinvertebrate in the deeper regions of the Great Lakes, comprising >70% of all benthic biomass at depths >30 m (Cook and Johnson 1974; Nalepa 1989). *Diporeia* populations are present but less dominant in open, nearshore regions and naturally absent from shallow, warm bays and basins (i.e., inner Green Bay, inner Saginaw Bay, and western and central Lake Erie). As a detritivore, the amphipod burrows in the upper 1-2 cm of sediment and feeds on organic material settled from the water column. In turn, diporeia populations are fed upon by many fish species, including yellow perch (*Perca flavescens*), alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), deepwater sculpin (*Myoxocephalus thompsoni*), and lake whitefish (*Coregonus clupeaformis*, hereafter whitefish) (Anderson and Smith 1971; Scott and Crossman 1973; Wells 1980). As an important diet item, the amphipod plays a key role in the cycling of energy between lower and upper trophic levels in the offshore region. Because the amphipod has a high lipid content and is rich in calories, it assumes a greater role in the trophic transfer of energy than might be assumed strictly from biomass or production estimates alone.

Diporeia populations are currently in a state of decline in portions of all the Great Lakes except Lake Superior (Dermott and Kerec 1997; Nalepa et al. 1998; Dermott 2001; Lozano et al. 2001; Nalepa et al. 2003). While population declines are evident over wide areas, the amphipod is rare or completely gone from the southeastern and far northern portions of Lake Michigan, outer Saginaw Bay, the eastern basin of Lake Erie, and the eastern portion of Lake Ontario. In each of these areas, diporeia populations have disappeared to water depths of at least 50 m. Population declines were first noted in the late 1980s and early 1990s and coincided with the introduction and spread of the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*D. bugensis*). In each lake area where diporeia populations are no longer found, populations disappeared within six years after mussels were first reported. Diporeia populations appear to be negatively impacted by dreissenids but resolving the exact mechanism for the negative response is difficult. Regardless of cause, however, the population declines are having an adverse impact on fish species that feed heavily on *Diporeia* spp., particularly the commercially important whitefish (Hoyle et al. 1999, Pothoven et al. 2001). In this paper, we examine characteristics of the declines in diporeia populations based on our studies in Lake Michigan and outer Saginaw Bay and explore various hypotheses for these declines. A better understanding of potential causes for the loss of diporeia populations may indicate what other lake areas are at risk and what the potential is for recovery.

Characteristics of Declining Populations in Southern Lake Michigan and Outer Saginaw Bay

As part of a long-term monitoring program of benthic macroinvertebrate populations in southern Lake Michigan, benthic samples have been collected at 40 sites in the southern basin since 1980 (Nalepa 1987; Nalepa et al. 1998) (Fig. 1). At each of the sites, samples were taken in triplicate with a Ponar grab in spring, summer, and fall in 1980-1981, 1986-1987, 1992-1993, and 1998-1999. Bottom substrates at these sites range from coarse sand and gravel to silt, and sampling depths range from 16-154 m. Further details of the sampling design and procedures are given in Nalepa et al. (1985).

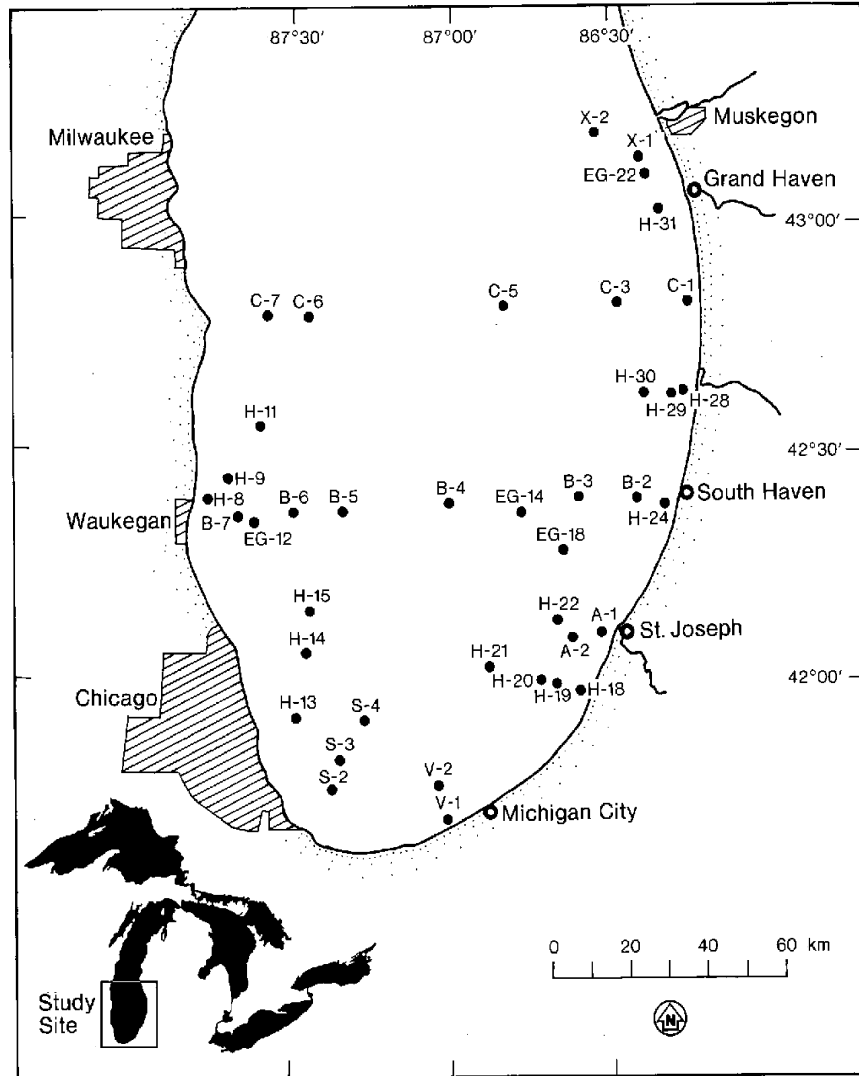


Fig. 1. Location of sampling sites in southern Lake Michigan.

For analysis, the sites were divided into four depth intervals: <30 m, 31-50 m, 51-90 m, and >90 m. These depth intervals are consistent with prior depth-macroinvertebrate associations in Lake Michigan (Alley and Mozley 1975). Over the 20-year sampling period (1980-1999), there were significant declines ($\ln + 1$ transformed; ANOVA; $P < 0.05$) in diporeia population densities at sites at the three shallowest depth intervals (>90 m). Mean densities declined from 7,821 m^{-2} in 1980-1981 to 659 m^{-2} in 1998-1999 at the <30-m interval, from 10,892 m^{-2} to 2,184 m^{-2} at the 31- to 50-m interval, and from 5,769 m^{-2} to 3,405 m^{-2} at the 51- to 90-m interval (Fig. 2). These changes represent declines of 92%, 80%, and 58%, respectively. These population declines occurred mostly after 1986-1987 and showed two distinct spatial patterns: densities declined progressively from shallow to deep water, and declines were more marked on the east side of the basin as compared to the west side. Declines in population density first became evident at sites in the <30-m interval in 1992-1993; mean densities in these two years were significantly lower compared to mean densities in 1986-1987 (ANOVA, Tukey's HSD; $P < 0.05$). Significant declines were not apparent at sites in the 31-50-m and 51-90-m intervals until 1998-1999 (ANOVA, Tukey's HSD; $P < 0.05$). When sites were divided into east and west within the three shallowest depth intervals, declines were more apparent on the east side of the lake than the west for the 31-50-m and 51-90-m intervals (Table 1).

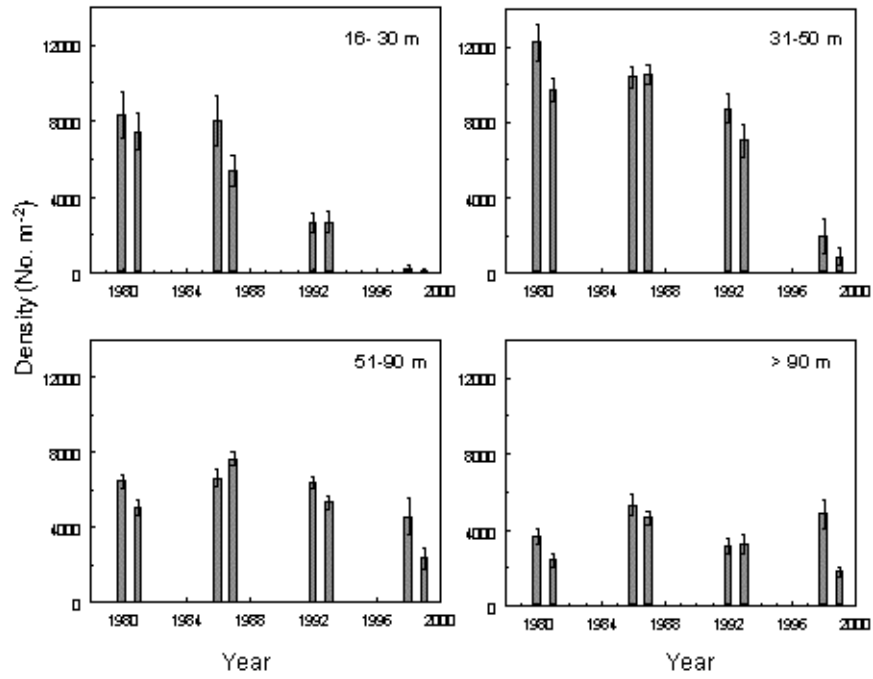


Fig. 2. Mean (\pm SE) density of diporeia populations at each of four depth intervals in southern Lake Michigan between 1980 and 1999: <30 m; 31-50 m; 51-90 m; >90 m. The number of stations in each depth interval were 11, 12, 11, and 6, respectively.

Table 1. Percent decline (mean \pm SE) of diporeia populations on the east and west sides of the southern basin of Lake Michigan between 1980-1981 and 1998-1999. The number of stations is given in parentheses. West Side Stations: B-6, B-7, C-7, EG-12, H-8, H-9, H-11, H-13, H-14, and H-15; East Side Stations: A-1, A-2, B-2, B-3, C-1, C-3, EG-18, H-18, H-19, H-20, H-21, H-22, H-24, H-28, H-29, and H-30 (for locations, see Fig. 1).

Depth Interval (m)	East Side	West Side
< 30	84.4 \pm 13.5 (5)	87.0 \pm 13.0 (2)
31-50	87.4 \pm 7.0 (5)	66.1 \pm 17.9 (3)
51-90	78.5 \pm 12.2 (6)	30.0 \pm 11.1 (5)

Although patterns of decline appeared gradual and systematic on a broad spatial scale, rates of decline were often highly variable even at sites of similar depth along the same side of the lake. For example, at Station H-22, located at a 45-m depth off St. Joseph, MI, diporeia populations declined from a mean density of 10,595 m⁻² in spring 1992 to 193 m⁻² in fall 1992, a decline of 98% in just six months. Diporeia samples were not collected at this site in 1997, 1998, or 1999. In contrast, at Station H-31, located at a 45-m depth off Grand Haven, MI, the decline took longer; mean density declined gradually from 11,340 m⁻² in 1992 to 98 m⁻² in 1999 (Fig. 3).

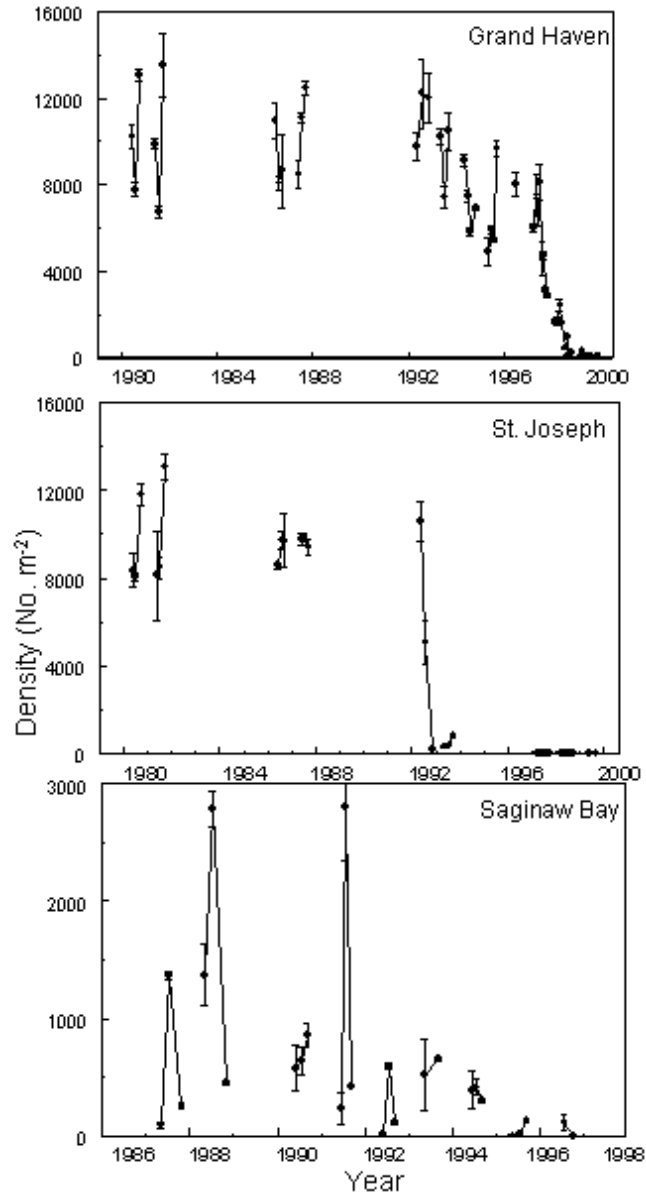


Fig 3. Mean (\pm SE) density of diporeia populations at two 45-m stations in southern Lake Michigan (Grand Haven: H-31; St. Joseph: H-22) between 1980 and 1999 and at a 23-m station in outer Saginaw Bay between 1987 and 1996.

Declines in diporeia populations appear to coincide with the introduction and spread of dreissenids. In southern Lake Michigan, dreissenids were first reported in 1989 along shallow reef areas off Chicago (Marsden et al. 1993). Mussels rapidly spread eastward and then northward along the eastern shore most likely because their veligers were carried by the counterclockwise current patterns typically found in this region (Beletsky et al. 1999). During 1992-1993, the greatest densities of dreissenids and the most dramatic and consistent declines in diporeia populations were found at shallow-water sites (<30 m) in the southeastern portion of the lake (Nalepa et al. 1998). Despite the high correlation between declines in diporeia populations and increased numbers of dreissenids in this area, the rapid decline of diporeia populations at Station H-22 in 1992 (Fig. 3) occurred even though no mussels were collected at this site in 1992. The lack of mussels at this site and in the immediate surrounding area was confirmed in film footage taken with an ROV in 1998. Although mussels were present at depths <30 m, no mussels were observed in deeper water. In contrast, the decline of diporeia populations at Station H-31 was closely related to an increase in dreissenids over a period of six years (Table 2). Hence, population declines at these two 45-m sites are paradoxical.

Table 2. Mean (\pm SE) lipid content (% dry weight) of diporeia at a 45-m site (Station H-31) in Lake Michigan near Grand Haven, MI. The number of individuals is given in parentheses. Also given are mean annual population densities (no. m⁻²) of diporeia and dreissenids.

Year	Lipid Content	Mean Density	
		Diporeia	Dreissenids
1980	-	10,363	0
1981	-	10,048	0
1984	31.6 (67) ¹	-	-
1986	32.2 (30) ²	9,355	0
1987	-	10,687	0
1988	26.8 (\approx 70) ³	-	-
1989	25.8 (\approx 40) ³	-	-
1992	-	11,340	2
1993	-	9,375	14
1994	15.2 \pm 1.0 (59)	7,349	39
1995	17.8 \pm 0.9 (42)	6,484	50
1996	24.9 \pm 1.3 (43)	7,996	143
1997	23.9 \pm 0.6 (121)	6,285	669
1998	30.2 \pm 0.7 (123)	1,154	2561
1999	34.7 \pm 2.1 (5)	98	258

¹ Data from Gardner et al. (1985)

² Data from Gauvin et al. (1989)

³ Data from Cavaletto et al. (1996)

Population trends in Saginaw Bay provide another example of diporeia declines that were spatially distant from dreissenids. Dreissenids were first found in Saginaw Bay in 1991, peaked in shallow-water areas in 1992, and then declined to stable levels during 1993-1996 (Nalepa et al. 2003). At a 23-m site in the outer bay, diporeia populations began to decline in 1992 and by 1996 had fallen 93% compared to 1987-1990 (Fig. 3). Although mussels were found at shallower sites in the outer bay, no mussels were ever collected at the 23-m site itself. Neither amphipods nor mussels were collected in subsequent sampling at this site in 2000 (TFN, unpubl. data).

Historical and Geographical Perspective

A sufficient number of benthic surveys have been conducted in the Great Lakes over the past 70 years to conclude that the current large-scale disappearance of diporeia populations appears to be unprecedented. Studies of temporal changes have documented long-term (decades) (Robertson and Alley 1966; Johnson and McNeil 1986; Nalepa et al. 1987; Nalepa et al. 1998; Dermott 2001) and short-term (seasonal, year-to-year) (Alley and Mozley 1975; Winnell 1984) population trends. Although studies of spatial distributions have documented local areas lacking diporeia because of anthropogenic inputs (Nalepa and Thomas 1976; Vander Wal 1977; Kraft 1979), the systematic loss of a population over widely separated areas over such short time periods is unique. One record exists of an apparent diporeia population die-off from unknown causes near the St. Joseph site (H-22) in 1971, but many individuals survived, and the population soon recovered (Mozley and Howmiller 1977). Outside of the Great Lakes region, there are records of rapid and extended population declines of another deepwater amphipod, *Monoporeia affinis*. This species is closely related to diporeia and is endemic to the Palearctic region of Europe. In the Baltic Sea, the *M. affinis* population declined from 7,000-8,000 m⁻² to 88 m⁻² from 1929 to 1933 and then recovered to 500 m⁻² two years later (Segarstrale 1960). No reason for the sudden decline was given although a pathogenic disease was suspected. A 30-year record of *M. affinis* at several deep sites (47-50 m) in Lake Malaren, Sweden, showed that the population declined to near zero for extended periods on several occasions (Goedkoop and Johnson 2001). Densities exceeded 15,000 m⁻² in 1971 and 1980 but were less than 100 m⁻² in 1973-1976 and 1992-1997. The authors suggested reduced dissolved oxygen (DO) concentrations as a plausible explanation for low densities.

The total disappearance of *M. affinis* in other European lakes over several decades has been attributed to increased eutrophication and reduced DO (Kansanen and Aho 1981; Zmudzinski 1995), and declines in the Baltic Sea in the 1990s have been attributed to both reduced DO and food competition with the invading polychaete *Marenzelleria viridis* (Cederwall et al. 1999; Kotta and Olafsson 2003).

Although dreissenids have just recently become established in North America, they have been naturalized in European waters for nearly a century. Unfortunately, there are no studies that examine temporal trends in deepwater amphipods relative to population expansions of dreissenids. Perhaps the best data set is from Lake Malaren, Sweden. Dreissenids became established in this lake in the 1920s, and the highest densities occurred in the 1960s (Josefsson and Andersson 2001). Dreissenids are presently found in the littoral and sublittoral regions of the deeper, oligotrophic basins but quantitative estimates are lacking (W. Goedkoop, Swedish University of Agricultural Sciences, SE-750 07, Uppsala, Sweden, pers. commun.). *M. affinis* is still present and quite abundant in these basins, although, as indicated earlier, populations fluctuate widely. Of relevance here is that the two species seem to co-occur in the deeper basins of the lake.

Potential Reasons for the Decline of Diporeia Populations in the Great Lakes

Were declines in diporeia populations caused by decreased food availability resulting from the filtering activities of dreissenids? Diporeia populations feed in the upper sediments layers, whereas dreissenids filter-feed at the sediment surface. Thus, food settling to the bottom is likely intercepted and utilized by dreissenids before it actually reaches the upper sediments and becomes available to diporeia. Similar to other benthic organisms found in deep lakes, diporeia abundance is directly related to water-column productivity and the amount of food settling to the bottom (Saether 1980; Siegfried 1985; Johnson 1988). A similar strong relationship has also been found for *M. affinis* in European lakes (Johnson and Wiederholm 1992) and in the Baltic Sea (Andersin et al. 1978). In southern Lake Michigan, mean abundances of diporeia increased 1.5-fold between the mid-1930s and the mid-1960s (Robertson and Alley 1966) and 2- to 5-fold between the 1960s and 1980-1981 (Nalepa 1987). These increases were attributed to increased phosphorus loads and higher water-column productivity. With dreissenids

now present and filtering at the sediment-water interface, food materials settling from the water column are diverted, and a direct relationship between water-column productivity and standing stocks of diporeia can no longer be assumed. In nearshore southeastern Lake Michigan, phytoplankton biomass (as measured by chlorophyll) has declined 50% since the 1970s (Madenjian et al. 2002); in eastern Lake Ontario, diatom biomass declined by 80% (Dermott 2001). Under previous assumptions and with other factors being equal, diporeia populations should have declined by 50% and 80%, respectively. Yet, in both lake areas, diporeia populations have completely disappeared at depths <50 m.

The food-limitation hypothesis is most convincing in areas where mussel populations co-occur directly with diporeia because mussels can severely deplete food resources just above the bottom (Ackerman et al. 2001). In the eastern basin of Lake Erie, quagga mussels became widespread and abundant to the basin's maximum depth of 60 m, and diporeia populations were extirpated within three years (Dermott and Kerec 1997). Over this period, there was a direct inverse relationship in individual grab samples between densities of diporeia and mussels. The food-limitation hypothesis is less convincing in areas such as Station H-22 in Lake Michigan where, as noted, mussels did not spatially overlap with diporeia and yet diporeia population densities declined 98% in six months. At Station H-22, biogenic silica was present in material collected in sedimentation traps in spring 1997 indicating at least some food material (i.e., diatoms) was still settling to the bottom (TFN, unpubl. data). At the previously mentioned outer Saginaw Bay site, water-column chlorophyll and diatom biovolumes did not change during the period when the diporeia population declined (Johengen et al. 2000; H. A. Vanderploeg, NOAA, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105-2945, unpubl. data).

If food limitation is the major cause of the decline in diporeia populations, individuals should logically show physiological signs of starvation before and/or during the period in which populations decrease. In diporeia and *M. affinis*, lipid levels are a good indicator of food availability; levels increase during seasonal periods of high benthic-food inputs and decline when food is scarce (Gardner et al. 1985; Gauvin et al. 1989; Hill et al. 1992; Lehtonen 1995, 1996). In Lake Michigan, lipid levels generally peak in late spring/early summer just after the spring diatom bloom (Gardner et al.

1985). During this event, large diatoms such as *Aulacoseira* spp. (*Melosira*), which typically dominate the unstratified spring period, sink rapidly from the water column and reach the sediments virtually intact. Also, diatom decomposition during settlement is minimized in the spring because of cold water temperatures and the lack of zooplankton grazers. Diporeia populations feed most intensively in the spring, likely in response to this fresh food source (Dermott and Corning 1988; Quigley 1988). A recent study using stable isotopes has confirmed that diporeia uses freshly settled material during the nonstratified period in the spring (Leggett et al. 1999).

Just as lipid levels in diporeia increase after periods of high food availability, lipid levels decrease during periods of food deprivation, as during summer stratification when less algal food settles to the bottom (Scavia and Fahnenstiel 1987). During these periods, diporeia utilizes accumulated lipid reserves as a source of energy. Gauvin et al. (1989) showed that diporeia can live without food for 217 days and that lipid levels gradually decreased over this period. For diporeia, rapid accumulation of lipids during periods of high food availability and use of lipids during periods of food shortage are considered a life-history strategy for survival in cold, deep lakes where benthic food inputs are highly seasonal.

At Station H-31 (Grand Haven, Lake Michigan), mean annual lipid levels for April to November varied from 26% to 32% in larger animals (>5-mm body length (BL)) in the 1980s prior to colonization by dreissenids populations (Table 2). In 1994, after mussels had become widespread in the southern basin, mean lipid level was only 15.2% (Table 2), which is near the low of 12% found in animals starved in the laboratory for 120 days (Gauvin et al. 1989). Levels of at least 20% are considered necessary for successful reproduction in deepwater amphipods (Hill et al. 1992). Densities at Station H-31 began to decline in 1994 (Fig. 3). After 1994-1995, lipid levels increased unexpectedly, and by 1998-1999 were as high as or higher than levels found in the 1980s prior to dreissenid colonization. Reasons for these lipid increases remain unclear. Declining densities may have resulted in greater amounts of food for the remaining diporeia leading to an increase in lipids. Yet, if higher lipids reflect greater amounts of food, then food would not be limiting, and densities should have stabilized rather than continuing to decline in 1998-1999 (Table 2). Also, the increase in mussel densities after 1994-1995 (Table 2) would likely have led to declines in available food, regardless of changes in diporeia densities.

Because lipids are reported on a weight-specific basis, an increase in lipids may be related to selective catabolism of non-lipid materials during periods of severe starvation. Gauvin et al. (1989) attributed an increase in lipid content of diporeia after 191 days without food to the catabolism of non-lipid material. To explore this possibility, we examined the relationship between BL and non-lipid dry weight (NLDW) at Station H-31 from 1994 and 1998. The relationship was described by $NLDW = aBL^b$, and each year's linear regression (based on log-transformed values) was significant ($P < 0.05$). The calculated weight of a standard 5-mm animal from 1994 to 1998 was 0.69, 0.41, 0.45, 0.58, and 0.60, respectively. Thus, non-lipid dry weight did not appear to decrease but tended to increase along with lipid levels, a finding that seems to refute the possibility that lipid increases resulted from selective catabolism of non-lipid material. To examine further the possibility that diporeia were no longer able to metabolize lipids, individuals collected from Station H-31 were placed in filtered lake water and kept without food for 66 days (TFN, unpubl. data). Lipid content gradually decreased over this time period indicating that the animals were still able to use lipids as a source of energy. If the food-limitation hypothesis is correct, the reason why lipids increased as diporeia populations disappeared remains unresolved.

When examining the food-limitation hypothesis, food quality as well as food quantity must be considered. Most food settling to the benthic region occurs during the spring diatom bloom (Scavia and Fahnenstiel 1987). Diatoms are high in long-chain polyunsaturated fatty acids (PUFAs) that serve as precursors to a number of hormones critical to a host of physiological processes in invertebrates including maturation, egg production, egg development, and immunological responses to infection (Brett and Muller-Navarra 1997). Invertebrates can only obtain PUFA from the algal component of their diet, so the PUFA content of settled algal material likely plays a key role in diporeia growth, development, and physiological well being. The amount of PUFA available to diporeia populations may have decreased not only because of lowered numbers of diatoms resulting from filtering activities of dreissenids, but also because of reduced PUFA content of those diatoms remaining. In southern Lake Michigan, water clarity has increased 2-fold since mussels became established (Marsden et al. 1993), allowing for greater light penetration and increased exposure of phytoplankton to ultraviolet radiation. The latter leads to a number of biochemical and physiological changes in phytoplankton, including a reduction in PUFA content (Hessen et al. 1997). The rapid decline of

diporeia populations at Station H-22 likely was not caused by changes in algal PUFA. However, the unexplained increase in lipid content of diporeia at Station H-31 during the gradual decline in population density indicated that physiological/biochemical changes were occurring that potentially could have been related to shifts in food quality.

Members of diporeia populations may be actively avoiding areas influenced by mussels either because of lack of food or because of a negative response to mussel biodeposits (i.e., bacteria/mucus in feces and pseudofeces). Diporeia reside in the upper sediments but are not confined to the benthic region. Nocturnal migrations into the water column have been well documented (Marzolf 1965a; McNaught and Hasler 1966; Wells 1968; Mozley 1974). Most movement into the water column likely is related to mating behavior, but juveniles are also commonly found in the water column at night indicating that swimming behavior may also be a response to changing environmental conditions. Mass horizontal migrations to and from inshore areas in response to seasonal changes in water temperatures have frequently been reported or suspected (Winnell and White 1984, Siegfried 1985, Johnson 1988). In addition, diporeia can be selective in their choice of habitat. When offered a choice of different sediments in laboratory experiments, diporeia overwhelmingly selected sediments from offshore, open-lake areas for burrowing as compared to sediments from harbors and river mouths (Gannon and Beeton 1969). In similar experiments, Marzolf (1965b) found that diporeia burrowed more frequently in sediments where algal food was presented as a light layer over the sediment surface rather than as mixed into the sediment.

Given its swimming behavior and propensity for substrate selection, diporeia were subjected to preference/avoidance experiments to determine their response to sediments collected from sites where populations had disappeared (i.e., Station H-22) and were still present (Landrum et al. 2000). There were significantly fewer animals burrowed in sediments from the site where diporeia had disappeared. When the experiments were repeated with diatoms added to the sediments, there were no significant differences in burrowing between the two types of sediments. This finding suggests that the animals likely were responding to food availability and not to some component of dreissenid biodeposits.

Could diporeia populations be actively swimming away from mussel colonies in search of better food? If so, field collections should show a negative relationship between the two organisms. Ponar grabs at Station H-31 in 1997-1998 did not show a negative relationship between diporeia and dreissenid densities on this small spatial scale (Fig. 4). Most grab samples contained few if any mussels because of patchy dreissenid distributions, but samples with large numbers of dreissenids also contained diporeia, indicating that diporeia did not appear to be actively avoiding mussel clusters.

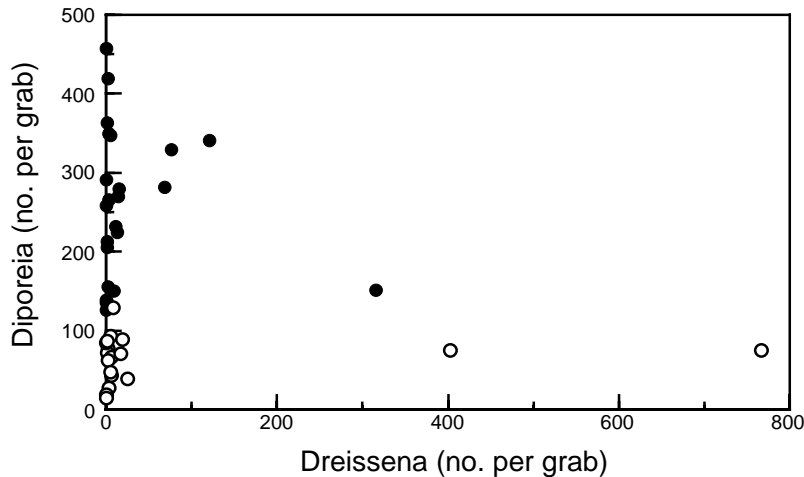


Fig. 4. Numbers of diporeia and dreissenids collected in individual grab samples at Station H-31 in Lake Michigan off Grand Haven, MI. Three replicate samples were taken monthly from April to November (solid circle, 1997; open circle, 1998).

Diporeia are fed upon by many fish species, and some population declines have been attributed to increased predation pressure. For instance, in Lake Michigan, declines in diporeia populations over a four-year period were attributed to increased numbers of yellow perch and bloaters (McDonald et al. 1990). In the Bay of Quinte, Lake Ontario, low abundance of diporeia was attributed to a large population of stunted white perch (*Morona americana*), and abundances increased after the white perch population crashed (Johnson and McNeil 1986). While predation pressure may play a role in population fluctuations, it is unlikely that such pressure would systematically lead to a loss of all diporeia. In southern Lake Michigan, trends in populations of fish that feed heavily on diporeia (such as sculpins, yellow perch, and bloater) could not account for observed decreases in diporeia populations in the early 1990s (Nalepa et al. 1998). While not the sole cause, fish predation may still play some role in population declines. Animals subjected to food declines become more active in search of food and more susceptible to predation (Lomnicki 1978).

Pathogens and diseases are common in amphipods and are known to reduce or limit populations (Pixell-Goodrich 1929; Johnson 1985). A dramatic decline of the amphipod *Corophium volutator* in nearshore waters of the Baltic Sea in 1928-1930 was attributed to the yeast pathogen *Micrococcus* (Segarstrale 1960). The previously mentioned decline in *M. affinis* in the Baltic Sea occurred over the same period but in deeper waters. Given these observations, a pathogen introduced with dreissenids could be affecting diporeia. Alternatively, new stressors related to the establishment of dreissenids (i.e., decrease in quantity and quality of available food) may have made diporeia more susceptible to endemic pathogens. A wide survey of parasites and diseases in diporeia throughout Lakes Michigan and Huron indicated that individuals were infected with various pathogens, including virus-like infections, rickettsia-like organisms, fungi, haplosporidian-like organisms, microsporidian-like organisms, putative epibiotic ciliates, gregarines, cestodes, and acanthocephalan worms (Messick et al. 2004). Incidence rates at 12 sites in southern Lake Michigan, however, were uniformly low (Table 3). Diporeia populations at these sites were in various stages of decline from 1992-1993 to 1998-1999 likely suggesting that pathogens were not a direct cause of decreased populations.

Table 3. The incidence rate (%) of disease and pathogens found in diporeia populations from sites in southern Lake Michigan in 2000. Station locations are given in Fig. 1. Decline is given as the percent decrease in density from 1992-1993 to 1998-1999; *n* = number of animals examined.

Station	Depth Interval	Decline	n	nod	cil	mic	gre	hap	ric	yea	fun	vir
C-5	>90	0.0	20	0.0	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C-6	>90	9.8	15	6.7	26.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B-5	>90	10.9	16	0.0	43.8	6.3	0.0	0.0	0.0	0.0	0.0	0.0
B-6	51-90	13.0	17	0.0	17.7	29.4	0.0	0.0	0.0	0.0	0.0	0.0
B-7	30-50	25.1	23	8.7	17.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C-7	51-90	23.2	19	15.8	31.6	5.3	0.0	0.0	5.3	0.0	5.3	0.0
H-15	51-90	31.9	14	7.1	28.6	0.0	0.0	7.1	0.0	0.0	0.0	0.0
H-9	30-50	33.5	19	5.3	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EG-12	51-90	40.8	19	5.3	42.1	0.0	0.0	0.0	5.3	0.0	0.0	0.0
H-21	51-90	62.8	19	5.3	63.2	0.0	5.3	0.0	0.0	0.0	0.0	0.0
EG-14	>90	63.5	18	0.0	55.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
H-30	51-90	80.2	17	17.7	32.3	0.0	5.9	5.9	0.0	0.0	0.0	0.0

nod = nodules; hemocyte encapsulation of tissue debris, injurious agent, or foreign material

cil = ciliates (externally attached symbionts not considered harmful)

mic = microsporidians (intracellular parasite)

gre = gregarines (sporozoan parasite)

hap = haplosporidia (parasitic protist)

ric = rickettsia-like organism (intracellular, prokaryotic parasite)

yea = yeast

fun = fungus

vir = virus

Diporeia are considered pollution-sensitive and are generally not present or occur in low numbers in areas influenced heavily by contaminants (Nalepa and Thomas 1976; Vander Wal 1977; Kraft 1979). The sensitivity of diporeia was confirmed in laboratory assays with contaminated sediments from various harbors around the Great Lakes; after 48-h exposures, mortality was 70% in diporeia but only 9% in the more tolerant amphipod *Gammarus* (Gannon and Beeton 1969). Could dreissenid biodeposits have an acute toxic effect on diporeia populations, or could dreissenids modify sediment-associated contaminants to increase their toxicity to diporeia populations? Landrum et al. (2000) examined these possibilities by exposing diporeia to sediments from several 45-m sites in southeastern Lake Michigan, including Stations H-22 and H-31. After a 28-d exposure, no mortality was observed in any of the sediments indicating that acute toxicity was not the likely reason for population declines. The bioassays were later repeated with a 66-d exposure, and, again, significant mortality was not observed (TFN, unpubl. data).

Deepwater amphipods such as diporeia and *M. affinis* are generally sensitive to low DO concentrations. As noted earlier, the elimination of *M. affinis* from European lakes and extended periods of low densities in Lake Malaren, Sweden, were attributed to reduced DO. In laboratory experiments, DO concentrations of 2-5 mg·L⁻¹ affected the swimming behavior of *M. affinis* (Johansson 1997), and similar concentrations led to a higher frequency of unfertilized females and a greater number of females carrying dead broods (Ericksson-Wiklund and Sundelin 2001). Although most regions in the Great Lakes with hypoxia (i.e., central basin of Lake Erie) are too warm and shallow for diporeia to be present naturally, diporeia distribution seems to be related to the oxidative state of the sediment surface (Sly and Christie 1992). Could dreissenids have reduced DO at the sediment-water interface to the point of adversely affecting diporeia populations? Within mussel beds, microbial decomposition of mussel biodeposits and/or dead mussel tissue may lead to areas of reduced DO. This reduced DO would mostly be a local effect and not likely in deep, hypolimnetic areas where mussels are not abundant, such as at Station H-22. On the other hand, dreissenid biodeposits from shallow, nearshore regions may resuspend during spring storm events; settle into offshore, depositional zones; and create periods of reduced DO. In nearshore areas with large numbers of mussels, sediment particle-size distributions decreased from 125-200 µm to 4-7 µm because of mussel biodeposits (Howell et al. 1996). Over 80% of mussel pseudofeces can be

<10 μm in size (Reeders and Bij de Vaate 1992). These fine particles are easily resuspended and have a high DO demand when re-deposited. Depositional areas may experience brief periods of reduced DO after sedimentation events (Graf 1987; Hansen and Leppanen 1994). Station H-22 is located in the area of highest sedimentation in Lake Michigan, and most sediment deposition occurs in the spring (Eadie et al. 2002). The decline of diporeia populations at this site was first observed after spring.

Summary and Conclusions

The complete loss of diporeia populations from large areas in Lakes Michigan, Huron, Erie, and Ontario appears to be unprecedented and caused either directly or indirectly by the establishment and spread of zebra and quagga mussels. The only feature common to these areas is that initial declines occurred within 3-4 years after mussels established. Declines typically occur first in shallow waters and then progress deeper. Although several theories have been suggested, field observations and laboratory studies have not established a clear, causative mechanism for the population declines. Inconsistencies in the commonly suggested food-limitation hypothesis are apparent and cannot be readily explained. Diporeia populations declined to near zero very rapidly (months to several years) in areas where mussels were far removed and food was seemingly available. Diporeia lipid levels were low when populations initially began their decline, which is consistent with a food-limitation hypothesis. Yet, as the population decline continued, lipid levels increased and were near maximum levels as numbers approached zero. Increased lipids suggest that physiological changes are occurring, but the cause and meaning of such changes are not clear. Future investigations should examine other indicators of physiological well being, such as respiration rates and nutrient excretion. Investigations at the biochemical or cellular level also may prove informative. Conceivably, a decline in food had an indirect impact on abundances by making the animals more susceptible to other factors, such as lowered DO or predation by fish. Although diporeia are active in the water column, animals from areas where they are still present are not recolonizing areas from which they have long disappeared, indicating that conditions that led to the declines are still present and/or are re-occurring.

The loss of diporeia from extensive areas is having an impact on the food web, particularly on fish that rely heavily on diporeia as a food source. The

loss of diporeia populations has been implicated in the decline of rainbow smelt in eastern Lake Erie (Dermott and Munawar 1993), the decline of sculpins in Lake Ontario (Lozano et al. 2001), and the decline in condition of whitefish (Pothoven et al. 2001) and alewife in Lake Michigan (Madenjian et al. 2003). Moreover, simulation models predict cascading impacts across several trophic levels (Kitchell et al. 2000). For whitefish, specifically, the loss of diporeia has led to increased consumption of dreissenid mussels, which provide less nutrition than diporeia, and to shifts in distribution patterns as fish search for alternate food (Owens et al. 2000; Hoyle 2005).

As dreissenid populations expand (Fleischer et al. 2001; Nalepa et al. 2001), the continued decline of diporeia populations seems inevitable. Long-term field studies should examine changes in diporeia recruitment, growth, and survival before and after the invasion of dreissenids, and laboratory studies should further explore the negative relationship between these two organisms (Dermott et al. 2005). Without fully understanding the cause, predicting the eventual extent of the population loss and the potential for recovery cannot be meaningfully attempted.

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