

APPLIED ISSUES

Suppression of microzooplankton by zebra mussels: importance of mussel size

HUGH J. MACISAAC,*† CHRISTOPHER J. LONNEE* AND J.H. LEACH‡

*Department of Biological Sciences, University of Windsor, Windsor, ON Canada N9B 3P4

†Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON Canada N9B 3P4

‡Ontario Ministry of Natural Resources, Lake Erie Fisheries Station, R.R. #2, Wheatley, ON Canada N0P 2P0

SUMMARY

1. The zebra mussel (*Dreissena polymorpha*) is amongst the most recent species to invade the Great Lakes. We explored the suppressive capabilities of mussels 6–22-mm in size on Lake St Clair microzooplankton (< 240 µm) in laboratory experiments.
2. Absolute suppression of rotifers and *Dreissena* veliger larvae was proportional to mussel shell length for individuals larger than 10 mm; larger zooplankton, mainly copepod nauplii and Cladocera, were not affected. Mussel clearance rates on rotifers generally exceeded those on veligers, although rates for both increased with increasing mussel size. Rotifer-based clearance rates of large (22 mm) mussels approached published values for phytoplankton food.
3. Most zooplankton taxa, particularly rotifers, declined significantly in western Lake Erie during the late 1980s concomitant with the establishment and population growth of zebra mussels in the basin. Densities of some taxa subsequently increased, although rotifers and copepod nauplii densities remained suppressed through 1993. Available evidence indicates that direct suppression by *Dreissena* coupled with food limitation provides the most parsimonious explanation for these patterns.

Introduction

Human activities have facilitated the introduction of non-indigenous species in ecosystems throughout the world. Most species introductions occur with little economic or ecological impact, although a small percentage of invaders become economic or ecological pests (Mills *et al.*, 1993). Molluscs are well represented among introduced species that have achieved pest status (e.g. McMahon, 1983; Kinzie, 1992; Kimmerer, Gartside & Orsi, 1994). Few species introductions to the Great Lakes have caused greater ecological change and economic damage than those associated with establishment of zebra mussels (*Dreissena polymorpha* Pallas) and, more recently, quagga mussels (*Dreissena bugensis* Andrusov). The zebra mussel dispersed rapidly throughout the Great Lakes following its introduction to Lake St Clair in 1986, and has since established populations in numerous river systems and

inland lakes in temperate eastern North America. Prolific growth of *Dreissena* in the Great Lakes has fostered concern that food webs might be adversely affected, including reductions of zooplankton populations upon which commercial and sport fish depend (e.g. see MacIsaac, Sprules & Leach, 1991; Parrish & Margraf, 1994; Wu & Culver, 1994).

Dreissena feeds selectively on particles between 5 and 45 µm (Ten Winkel & Davids, 1982; Sprung & Rose, 1988). Ten Winkel & Davids (1982) reported that stomach contents of previously starved zebra mussels closely resembled the composition of a natural phytoplankton community to which the individuals were exposed, including *Ankistrodesmus longissimus* cells up to 750 µm in length. While particles of this size easily exceed the body length of many small zooplankton taxa, zooplankton has only rarely been reported as a

component of *Dreissena* diet (Shevtsova *et al.*, 1986). MacIsaac *et al.* (1991) demonstrated that adult *D. polymorpha* (> 20 mm) could ingest microzooplankton, and argued that zooplankton community size structure and mussel recruitment could be affected in consequence. However, the competence of small *Dreissena* to suppress microzooplankton has not been addressed. Small *Dreissena* have the potential to exert strong effects on plankton communities because of the high densities they achieve in some regions of the Great Lakes (Bunt, MacIsaac & Sprules, 1993). Many earlier studies have demonstrated that the effects of invertebrate predators (e.g. *Chaoborus*) on zooplankton communities depend on predator and prey sizes (e.g. Yan *et al.*, 1991).

In this study we explore the suppressive capabilities of a wide range of *D. polymorpha* size classes on Great Lakes' microzooplankton. We then relate suppressive capabilities of *Dreissena* to recent changes in the western Lake Erie zooplankton community. *Dreissena* effects are expected to be most pronounced in shallow, non-stratified basins including western Lake Erie (see MacIsaac *et al.*, 1991; MacIsaac *et al.*, 1992).

Materials and methods

Inhalant siphon diameter

The relationship between right valve length and exterior inhalant siphon diameter was determined for zebra mussels. *Dreissena* was collected from Lake St Clair and maintained in the laboratory (described below). Individual mussels between 2 and 20 mm were placed in a small Petri plate filled with filtered lake water. The exterior diameter of fully extended inhalant siphons was measured to the nearest 95 µm using a dissecting microscope with an ocular micrometer.

Predation experiments

Two laboratory experiments were conducted to assess predatory capabilities of different size classes of zebra mussels on microzooplankton, and to determine whether predation rates are affected by mussel hunger level. *Dreissena* was collected on 8 June 1993 in a littoral area of south-west Lake St Clair, Ontario, near the confluence of the Detroit River. Mussels were taken to the laboratory and maintained at ≈ 21 °C in 40-l aquaria with glass-fibre filtered (0.8 µm pore size)

Lake St Clair water. Mussel stocks were provided with 60 mg powdered *Chlorella* tank⁻¹ day⁻¹ (Nichols, 1992). This food level is below the concentration (≈ 2 mg C l⁻¹; 4 mg dry mass l⁻¹) at which *D. polymorpha* increases the production of pseudofaeces to reject excess food (i.e. the incipient limiting concentration) (Walz, 1978).

Zooplankton for all experiments was collected from 1.5 m depth in Lake St Clair with an 18-l modified Schindler-Patalas trap. In each experiment, an initial sample was filtered through 240-µm Nitex mesh to remove large zooplankton. Filtered water was collected in a 20-l carboy. Each additional sample was filtered through 240-µm mesh, the filtrate from which was poured through a 0.5-l container with 41-µm Nitex mesh. This procedure concentrated 41–240 µm microzooplankton to between four and six times lake density, while maintaining phytoplankton < 41 µm at near-lake density. Microzooplankton was concentrated prior to experiments because lake densities were low.

The relationship between *D. polymorpha* size and predation capability was examined in two experiments conducted between 12–17 July and 23–31 July 1993. Experimental mussels were acclimated for at least 4 days in a constant environment chamber at 16 °C under a 15 : 9 (L : D) photoperiod in 4-l containers. The acclimation medium consisted of glass-fibre-filtered (0.8 µm retention) Lake St Clair water supplemented with 8 mg powdered *Chlorella* l⁻¹. This suspension was processed through a qualitative filter (20–25 µm retention) to remove clumped particles, resulting in a final concentration of 4.9 mg *Chlorella* l⁻¹. Mussels were transferred to containers with fresh medium each day during the acclimation period. Experiments consisted of placing zero, two (22 mm), three (18 mm), five (14 mm), ten (10 mm) or thirty-one (6 mm) *Dreissena* into 4-l glass containers which had been filled with 3 l of lake water containing microzooplankton concentrated to either six times lake density (experiment 1) or four times lake density (experiment 2). Mussel number varied inversely with mussel size to equilibrate total clearance rate across different treatments. Clearance rates of different *Dreissena* size classes were based on the clearance rate–shell length relationship established by Kryger & Riisgård (1988). Mussels were measured to the nearest 0.5 mm with vernier calipers.

Lake water was mixed thoroughly and added haphazardly in 1-l increments to each container. Three replicates were conducted for each treatment; one 14-

mm mussel treatment replicate in experiment 1 was accidentally destroyed. Containers were placed in the 16 °C constant-environment chamber for a period of 24 h, following which samples were filtered through 41- μ m mesh and preserved in 5% sugar formalin. An additional set of samples lacking mussels was preserved at the outset of each experiment to test for container effects. Replicate zooplankton subsamples, with replacement, were settled using the Utermöhl technique and identified at 100 magnifications using a compound microscope. Zooplankton was classified into three groups: rotifers, of which the genera *Polysartha* and *Synchaeta* comprised $\geq 85\%$ total abundance; *D. polymorpha* veligers and post-veligers (hereafter referred to as veligers); or other zooplankton, of which $> 80\%$ were calanoid and cyclopoid copepodids and nauplii.

Bonferroni adjusted *t*-tests were used to examine container effects by comparing zooplankton densities in separate 'control' containers preserved at the outset and termination of each experiment. Effects of different *Dreissena* size classes on densities of rotifers, veligers and other zooplankton were assessed by comparing plankton densities using ANOVA and, subsequently, by contrasting densities in treatments with different mussel size classes against those for containers lacking mussels preserved at the same time using one-tailed Dunnett's tests (Day & Quinn, 1989). Scheffé's multiple comparisons tests were used to explore differences among mean plankton densities in different mussel treatments. All zooplankton densities were $\ln(x + 1)$ transformed prior to statistical analysis.

Clearance rates were calculated for mussels feeding on each zooplankton group as:

$$CR = V \frac{\left[\ln \left(\frac{C_0}{E_{24}} \right) - \ln \left(\frac{C_0}{C_{24}} \right) \right]}{nt}$$

where CR is clearance rate (ml mussel⁻¹ h⁻¹), C_0 , C_{24} and E_{24} are mean zooplankton densities (ind. l⁻¹) in control jars at times 0 and 24 h and in treatments at time 24 h, V is experimental volume (l), n is number of experimental mussels, and t is experimental period (h) (Reeders, Bij de Vaate & Slim, 1989). Mass-specific clearance rates were also calculated using the shell length – dry mass (shell included) relationship for *D. polymorpha* from western Lake Erie (dry mass =

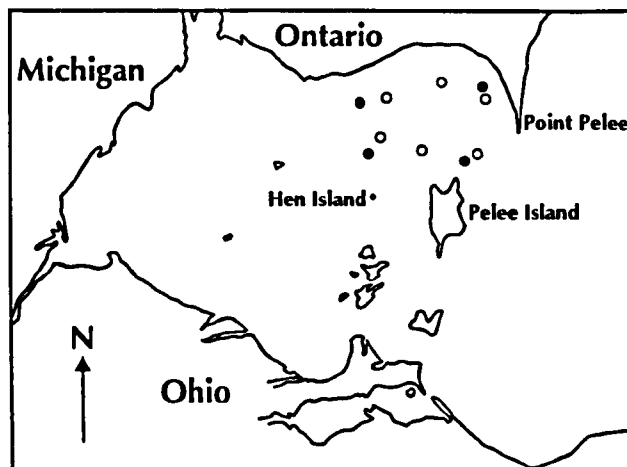


Fig. 1 Location of zooplankton sampling sites in western Lake Erie during 1971 and 1972 (O) and 1988 through 1993 (●). Mussels occupy most hard substrates as well as some sand and mud substrates in deep water throughout the western basin of the lake.

$e^{2.62 + 0.17 \times \text{shell length}}$ (H.J. MacIsaac, unpublished data).

Lake Erie zooplankton

As part of a long-term fisheries and plankton assessment programme, zooplankton samples were collected in western Lake Erie during 1971 and 1972 and between 1988 and 1993 by Ontario Ministry of Natural Resources personnel (e.g. see Leach, 1975). The latter sampling interval encompasses the period of geometric *Dreissena* population growth in the basin. These samples were used to assess temporal changes in plankton abundance and community composition. Vertical-haul plankton samples were collected weekly between May and November during each year using a 50-cm-diameter (76- μ m mesh size) plankton net. Six stations were sampled during 1971 and 1972, whereas four nearby stations were sampled between 1988 and 1993 (Fig. 1). Zooplankton was preserved in 4% sugar-formalin. Densities of rotifers, cladocerans and copepods were compared for the years before (1988) and after (1989–93) *Dreissena* became abundant using Bonferroni-adjusted *t*-tests ($\alpha = 0.05$).

Results

Exterior inhalant siphon diameter was positively correlated with mussel size (Fig. 2). Inhalant siphon diameter of all mussels exceeded body sizes of all veligers

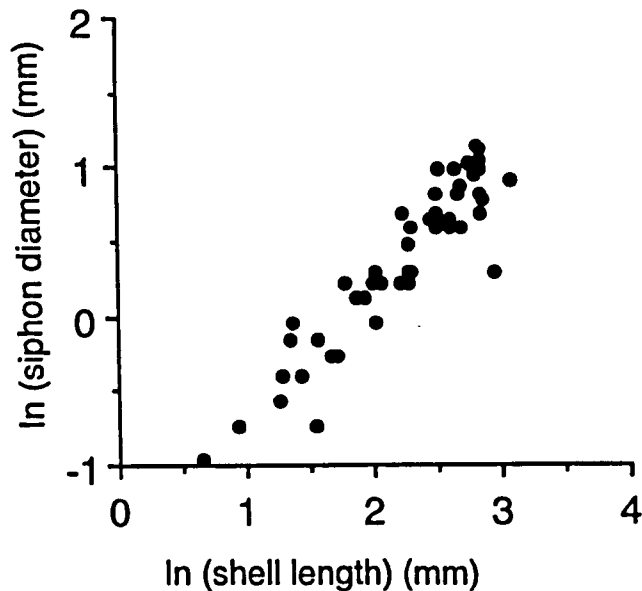


Fig. 2 Relationship between $\ln(\text{inhalant siphon diameter})$ (mm) and $\ln(\text{right valve shell length})$ (mm) for *Dreissena polymorpha* ($y = -1.50 + 0.84x$, $r^2 = 0.86$).

and most species of rotifers found in Lake St Clair and western Lake Erie.

Densities of rotifers, veligers and other zooplankton in control containers (i.e. lacking zebra mussels) preserved at the outset of each experiment were slightly but insignificantly higher than those preserved at the termination of each experiment (t -tests, $P > 0.05$), indicating only a mild container effect.

Dreissena veligers and rotifers together accounted for > 85% of the Lake St Clair microzooplankton during summer 1992 and 1993 (unpublished data); veligers were also numerically dominant in these experiments (Fig. 3). Rotifer density varied significantly among different mussel size-class treatments in both experiments 1 (ANOVA, $F = 5.2$, d.f. = 5, 11, $P = 0.01$) and 2 (ANOVA, $F = 6.4$, d.f. = 5, 12, $P = 0.004$; Fig. 3). Relative to controls lacking *Dreissena*, suppression of rotifers occurred in all mussel treatments in experiment 2 (Fig. 3b; Dunnett's means test, $P < 0.01$), and in all but the 6-mm mussel treatment in experiment 1 (Fig. 3a; Dunnett's means test, $P < 0.05$). Results for *Dreissena* veligers were less consistent between experiments. Veliger density was suppressed in all mussel treatments except that conducted with 14-mm individuals in experiment 2 (Fig. 3b; Dunnett's means test, $P < 0.05$). In experiment 1, however, veligers were not suppressed (ANOVA, $F = 1.3$, d.f. = 5, 11, $P = 0.34$; Fig. 3a). Larger and stronger-swimming

zooplankton were suppressed in neither experiment 1 (ANOVA, $F = 0.8$, d.f. = 5, 11, $P = 0.56$) nor in experiment 2 (ANOVA, $F = 1.8$, d.f. = 5, 12, $P = 0.18$; Fig. 3).

Clearance rates on rotifers and veligers were directly proportional to *Dreissena* size for individuals ≥ 10 mm (Fig. 4a). Clearance rates on rotifers were very similar in experiments 1 and 2 except for 22-mm *Dreissena*. Rotifer-based clearance rates were generally higher than those for veligers (Fig. 4a,b). Clearance rates on other zooplankton were zero. Mass-specific clearance rate on rotifers and veligers was almost invariant for mussels ≥ 10 mm (Fig. 4b).

The composition of the Lake Erie zooplankton community has changed significantly since invasion of the zebra mussel (Fig. 5). Mean total zooplankton density was significantly ($P < 0.05$) lower (55–71%) between 1989 and 1993 relative to 1988. Most of the decline was attributable to a sharp reduction in rotifer abundance, primarily members of the genera *Keratella*, *Polyarthra* and *Synchaeta*. Mean total rotifer density was relatively high during the early 1970s (≈ 300 ind. l^{-1}) and during 1988 (> 400 ind. l^{-1}). However, while rotifer density did not vary significantly ($P > 0.05$) between 1989 and 1993 (78–145 ind. l^{-1}), densities in each of these years were significantly lower than in 1988 ($P < 0.05$). These declines occurred coincident with rapid growth of *Dreissena* populations in western Lake Erie between 1988 and 1989 (Fig. 5). By May 1989 *Dreissena* had colonized only 5% of Hen Island Reef, at a mean density of 3500 ind. m^{-2} , but it was very abundant thereafter (Leach, 1993).

Cladoceran abundance, comprised mainly *Bosmina longirostris* (O.F. Mueller), *Eubosmina coregoni* (Biard), *Daphnia galeata mendotae* Birge and *D. retrocurva* Forbes, declined significantly between 1988 and 1989 ($P < 0.05$; Fig. 5). However, cladoceran density recovered between 1990 and 1993 to values not significantly different from that in 1988 ($P > 0.05$). Densities of copepods, mainly nauplii, also declined between the 1971–88 (122–148 ind. l^{-1}) and 1989–93 (38–74 ind. l^{-1}) periods. Densities of nauplii, cyclopoid and calanoid copepodids, and calanoid copepods declined significantly between 1988 and 1989 ($P < 0.05$). Nauplii density remained suppressed between 1990 and 1993 relative to 1988, although cyclopoid and calanoid copepodids and calanoid copepods increased between 1990 and 1992 to values insignificantly different from 1988 densities ($P > 0.05$). Abundance of cyclopoid copepods, mainly *Diacyclops thomasi* (S.A. Forbes), did

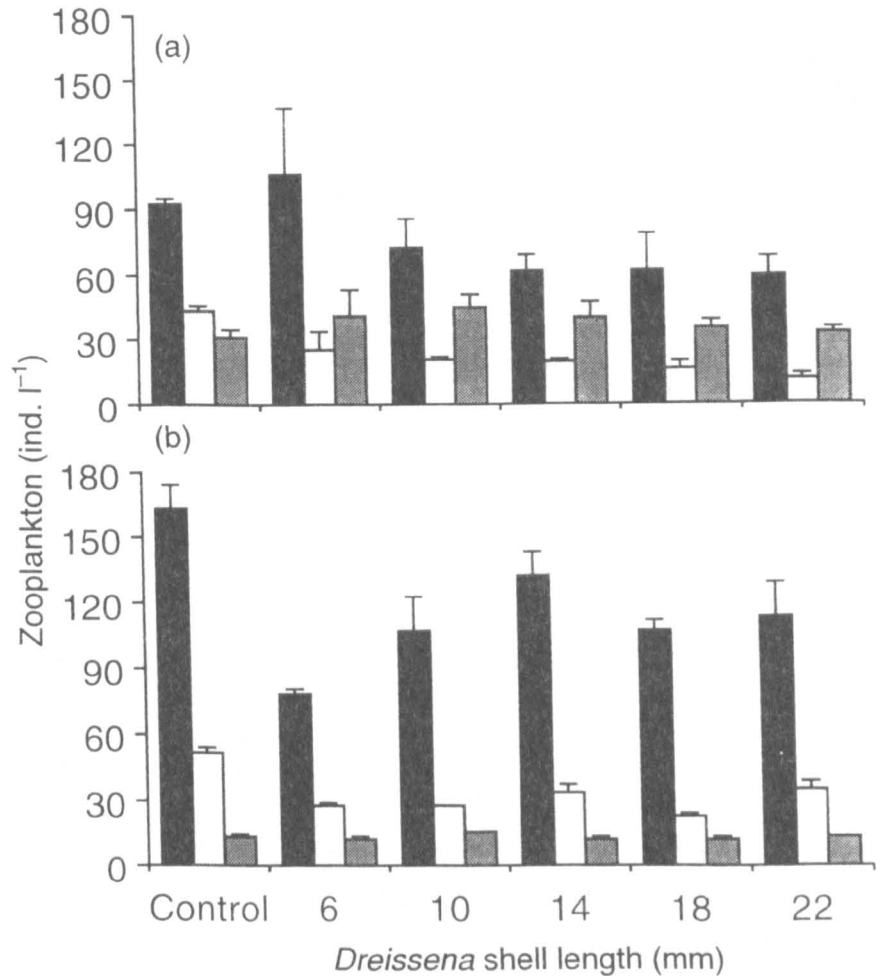


Fig. 3 Mean density (± 1 SE) of veligers (solid), rotifers (light stippled) or other zooplankton (dark stippled) in experiments conducted with zooplankton concentrated to $6\times$ (a) or $4\times$ (b) lake density in treatments lacking *Dreissena* (control) or incubated with 6-, 10-, 14-, 18- or 22-mm mussels.

not differ significantly between 1988 and later years ($P > 0.05$).

Discussion

In an earlier study, MacIsaac *et al.* (1991) demonstrated that large (> 20 mm) *D. polymorpha* were capable of suppressing microzooplankton. Results from this study indicate that the capability to suppress microzooplankton extends to *Dreissena* as small as 10 mm (Figs 3 and 4). Although the mechanism of suppression was not explored in this study, rotifer loricae have been observed in digestive tracts of large (> 20 mm) *Dreissena* collected from Lake Erie and in experiments designed to explore suppression mechanisms (see MacIsaac *et al.*, 1991). Suppression via predation could be augmented by exploitative competition for food resources or by incorporation of microzooplankton in mucus used to form pseudofaeces. Pseudofaeces ejected from the inhalant siphon typically settle on the adjacent lake bed.

Absolute clearance rates on zooplankton were directly proportional to mussel size (Fig. 4a). A threshold size may exist between 6 and 10 mm, below which

Dreissena has a very limited capability to ingest zooplankton. The basis for this limitation is not known, although it could result from a greater probability of siphonal tentacle irritation by microzooplankton entrained in the feeding current. If rejection of entrained zooplankton is based primarily on respective mussel and zooplankton sizes, then different zooplankton taxa may be differentially vulnerable to ingestion by different mussel size classes. We detected no difference in relative suppression of the two most common rotifer genera *Polyarthra* and *Synchaeta*.

Dreissena clearance rates on rotifers tended to be higher than those on veligers (Fig. 4a, b). The nature of the differences in rotifer and veliger clearance rates is not clear, although it may be owing to the smaller size of most rotifers. For example, mean body length of the most common rotifer *Polyarthra* spp. was less ($89 \mu\text{m}$; $n = 25$) than that of both veligers ($144 \mu\text{m}$; $n =$

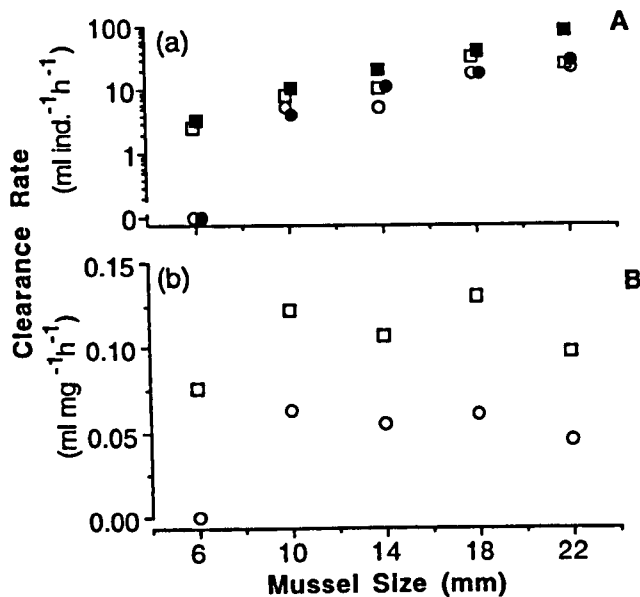


Fig. 4 *Dreissena* clearance rates on rotifers (squares) and veligers (circles) in (a) experiments 1 (solid) and 2 (open) in relation to mussel size. Overlapping values have been slightly offset. Clearance rates on other zooplankton were zero in both experiments and are not shown. (b) Mass-specific clearance rates of *Dreissena*, averaged for both experiments, on rotifers and veligers in relation to mussel shell length.

25) and nauplii (173 μm ; $n = 25$). Copepod nauplii were not suppressed in these experiments, perhaps because they are both larger and more capable swimmers than most rotifers. Consumption by benthic mussels of microzooplankton, including bivalve larvae, represents a potentially important route for energy flow in aquatic ecosystems. Ingestion of invertebrate larvae and zooplankton by benthic invertebrates is not limited to *D. polymorpha*. Previous studies reported nauplii predation by 15–20 mm *D. bugensis* (Shevtsova *et al.*, 1986) and by *Potamocorbula amurensis* (Schrenck), an exotic clam in San Francisco Bay that is similar in size to *Dreissena* (Kimmerer *et al.*, 1994). In addition, André and colleagues observed declines of up to 40% in settlement of the cockle *Cerastoderma edule* (L.) in the presence of high densities of adult conspecifics or softshell clams (*Mya arenaria* L.), and suggested that collective impacts of benthic suspension feeders could effect significant reductions in settlement of bivalve larvae on large scales (see André, Jonsson & Lindgarth, 1993).

Comparative analysis of *Dreissena* clearance rates indicates that rotifers were cleared from suspension at approximately the same rate as natural phytoplankton. For example, 22- and 18-mm *D. polymorpha* cleared

phytoplankton from suspension in Lake Wolderwijd, Netherlands, at 49 and 42 ml ind.⁻¹ h.⁻¹, respectively (Reeders & Bij de Vaate, 1990). By comparison, rotifer-based clearance rate estimates for 22-mm mussels were 87 and 25 ml ind.⁻¹ h.⁻¹, whereas those of 18-mm mussels were 42 and 34 ml ind.⁻¹ h.⁻¹ (Fig. 4a).

The western Lake Erie ecosystem is presently experiencing a plethora of changes, including a decline in nutrient loading (Dolan, 1993), invasion of the predaceous cladoceran *Bythotrephes cederstroemi* Schoedler, and declining recruitment and yield of the important planktivorous fishes yellow perch *Perca flavescens* (Mitchill) and white perch *Morone americana* (Gmelin) (Parrish & Margraf, 1994; Ontario Ministry of Natural Resources, 1994). Historically, the plankton community in the western basin has been dominated numerically by the rotifers *Keratella* spp. and *Polyarthra* spp., cladocerans *D. galeata mendotae*, *D. retrocurva* and *B. longirostris*, cyclopoid copepods *D. thomasi* and *Tropocyclops prasinus mexicanus* Kiefer, and the calanoid copepods *Leptodiaptomus ashlandi* Marsh, *L. minutus* Lilljeborg, and *Skistodiaptomus oregonensis* Lilljeborg (Davis, 1969; Makarewicz, 1993). Available evidence indicates a marked change in the community in recent years, particularly with respect to rotifer abundance. Mean spring and summer rotifer density, measured using a 63- μm -mesh net, ranged between 241 and 443 ind. l.⁻¹ between 1983 and 1987 (Makarewicz, 1993). These values compare favourably to the 1988 mean density of 415 ind. l.⁻¹, measured using a 76- μm net, but are much higher than the mean of 107 ind. l.⁻¹ for the 1989–93 period when zebra mussels were abundant (Fig. 5). Copepod and cladoceran densities have also declined since 1988, although reductions were not as marked or consistent as for rotifers. While seasonal and interannual variation in zooplankton abundance is characteristic of most lentic systems, the sustained and dramatic nature of the decline in rotifer abundance indicates that strong suppression is likely occurring. *Dreissena* has the potential to suppress zooplankton either indirectly through the depletion of essential food resources, or directly by preying on vulnerable species or life stages. An assessment of the respective roles of these mechanisms requires consideration of numerous factors including interannual variation in zooplankton abundances, ambient food concentration, zooplankton threshold food levels (i.e. the food level required to maintain a population growth rate of zero), water column mixing characteristics, and *Dreissena*

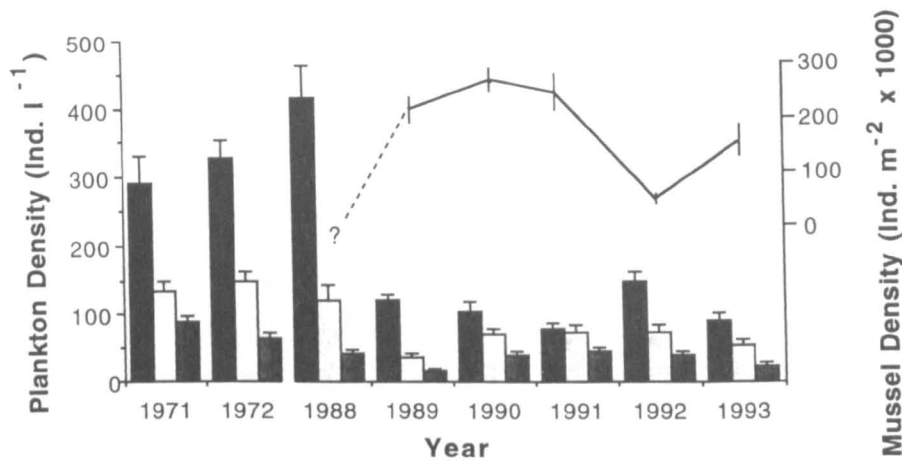


Fig. 5 Mean densities (± 1 SE) of rotifers (solid), copepods (light stipples) and cladocerans (dark stipples) for the May through November period in western Lake Erie between 1971 and 1993 (see Fig. 1 for location of sampling sites). Also shown is autumn mean density (± 1 SE) of *D. polymorpha* at Hen Island Reef, located south-west of plankton sampling sites. *D. polymorpha* colonized the basin in 1986 and was present at low density ($< 4 \times 10^3$ ind. m^{-2} ; Leach, 1992) in spring 1989.

size-frequency distributions and size-dependent predation capabilities.

Some evidence indicates that food limitation may be partially responsible for observed changes in zooplankton abundance. Holland (1993) reported an 82–91% decline in diatom abundance in the Bass Island region of the basin since establishment of zebra mussels. These findings were corroborated by Nicholls & Hopkins (1993), who observed $> 90\%$ diminution in phytoplankton abundance since 1988 for samples collected from a water-intake pipeline adjacent to our plankton collection sites. Chlorophyll *a* concentration averaged between 1 and $4 \mu\text{g l}^{-1}$ in the north-east section of the basin during 1990 (MacIsaac *et al.*, 1992; Leach, 1993), values considerably lower than those ($10\text{--}14 \mu\text{g l}^{-1}$) observed during the decade prior to *Dreissena* invasion (see Nicholls & Hopkins, 1993). Phytoplankton biomass increased dramatically during 1994, but consisted primarily of inedible cyanobacteria (J. Leach, unpublished data). Diatoms, particularly chain-forming *Fragilaria* and *Tabellaria*, dominated the phytoplankton assemblage throughout the 1985–90 period (Nicholls & Hopkins, 1993). Wu & Culver (1994) reported that 'edible' phytoplankton averaged between 1 and $10 \text{ g wet mass m}^{-3}$ ($\approx 220\text{--}2220 \mu\text{g dry mass l}^{-1}$) during 1989 in western Lake Erie. Edible food concentration is greater than threshold food levels of *Polyarthra remata* ($100 \mu\text{g dry mass l}^{-1}$), *Keratella cochlearis* ($60 \mu\text{g dry mass l}^{-1}$), *Daphnia galeata* ($\approx 60 \mu\text{g dry mass l}^{-1}$) and *Diaptomus oregonensis* ($51 \mu\text{g dry mass l}^{-1}$), but was probably low enough at some times during summer 1989 that food limitation affected zooplankton fecundity rates (Stemberger & Gilbert, 1985; Gliwicz, 1990; MacIsaac & Gilbert, 1991; Schulze, Zagarese & Williamson, 1995). Indeed, the significant

decline in abundance between 1988 and 1989 of taxa considered invulnerable to *Dreissena* ingestion (e.g. cladocerans and calanoid copepods) is consistent with the food limitation hypothesis. Wu & Culver (1994) attributed midsummer declines of *D. galeata mendotae* and *D. retrocurva* in western Lake Erie to combined effects of food limitation and yellow perch predation.

It seems unlikely that observed changes in rotifer abundance in western Lake Erie are related to changes in herbivore (*Daphnia*) or predator (*Morone*, *Perca*, *Bythotrephes*) density. Declines in abundances of the primary herbivores *D. galeata mendotae* and *D. retrocurva* would, if anything, benefit microzooplankton owing to a relaxation of exploitative or interference competition (MacIsaac & Gilbert, 1991). Similarly, catch-per-unit-effort estimates of planktivorous young-of-year yellow perch and white perch declined between 1989 and 1993 in western Lake Erie, indicating potential relaxation of predation pressure on vulnerable zooplankton (Ontario Ministry of Natural Resources, 1994). *Bythotrephes*, present since 1985, prefers a variety of cladocerans (*Ceriodaphnia*, *Eubosmina*, *Bosmina*, *D. retrocurva*) over the rotifer *Asplanchna*, copepod nauplii and other small prey (Vanderploeg, Liebig & Omaid, 1993; H. Vanderploeg, personal communication). Furthermore, assuming an *Asplanchna*-based clearance rate of $0.81 \text{ predator}^{-1} \text{ day}^{-1}$ (Vanderploeg *et al.*, 1993) and the maximum observed abundance of *Bythotrephes* in western Lake Erie (126 ind. m^{-3} ; Berg & Garton, 1990), respective maximum population growth rates of *Polyarthra remata* (Skorikov) and *Keratella cochlearis* (Gosse) would only be reduced to 0.29 and 0.18 day^{-1} from 0.39 and 0.28 day^{-1} (Stemberger & Gilbert, 1985). Thus available evidence, while limited, is inconsistent with hypo-

theses regarding suppression of rotifers by changes in herbivore or predator densities.

In conclusion, a combination of food limitation and size-selective predation by zebra mussels provides the most parsimonious explanation for recent changes in the zooplankton community in western Lake Erie.

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