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*University of Windsor*

W. Gary Sprules  
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Ingestion of Small-Bodied Zooplankton by Zebra Mussels (Dreissena polymorpha): Can Cannibalism on Larvae Influence Population Dynamics?

Hugh J. MacIsaac and W. Gary Sprules

Department of Zoology, University of Toronto, Erindale College, Mississauga, Ont. L5L 1C6, Canada

and J. H. Leach

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


The zebra mussel Dreissena polymorpha established populations in western Lake Erie in 1986 and achieved densities exceeding 3.4 × 10^4 individuals m^-2 during 1990. We assessed apparently incidental predation on Lake Erie and Erindale Pond zooplankton by adult mussels. Dreissena larvae and small rotifers (Polyarthra spp., Keratella spp., Trichocerca) sustained moderate to high predatory mortality whereas larger taxa (Bosmina, Scapholeberis) were invulnerable to predation. Larval Dreissena almost always sustain >99% mortality in European lakes. While mortality has been ascribed primarily to lack of suitable settling substrate and unfavourable environmental conditions, it may be confounded by larval predation by adults. We demonstrate using STELLA®-modelling that with a larval mortality rate of 99%, settled mussel densities observed in western Lake Erie during 1990 would not be achieved until at least 1994. A model that combines a lower rate (70%) of abiotic mortality with larval predation by adult mussels correctly predicts 1990 mussel densities. This model of Dreissena population growth is also consistent with larval settlement patterns in Lakes Erie and St. Clair and some European systems.

L'ingestion de zooplancton de petite taille par les moules à dents (Dreissena polymorpha) a été établie dans les lacs de la partie ouest du lac Érié en 1986 et atteignant des densités de 3.4 × 10^4 individus par mètre carré en 1990. Nous avons évalué la prédation zooplanctonique par les adultes de Dreissena en utilisant un modèle dont nous avons comparé les résultats avec ceux obtenus en utilisant un modèle de prédation par les adultes. Nous avons démontré que les densités de Dreissena fixées en 1990 n’auraient pas été atteintes qu’en 1994 dans le lac Érié si le taux de mortalité avait été de 99 %. Les densités réelles de 1990 n’ont pu être prédites qu’en utilisant un modèle dont le taux de mortalité abiotique par prédation par les adultes était plus faible (70 %). Ce modèle de la croissance des populations de Dreissena est cohérent avec les allures de fixation des larves décélées dans les lacs Érié et Ste-Claire et dans certains bassins hydrographiques européens.

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the animals settle from the plankton and attach to benthic substrates (Lewandowski 1982; Sprung 1989; reviewed in Mackie et al. 1989).

Overall dynamics of settled Dreissena populations appear to be governed primarily by the severity of mortality between planktonic veliger and settled subadult phases. Mortality between these phases almost always exceeds 99% (Stańczykowska 1977; Walz 1978a; Lewandowski 1982; Sprung 1989). Veliger and postveliger mortality has been attributed to a lack of suitable settling substrate, unfavourable oxygen or thermal conditions, and predation by larval fish or invertebrates, but their respective intensities have not been determined (Stańczykowska 1977; Lewandowski 1982; Lewandowski and Ejsmont-Karabin 1983). Moreover, these sources of mortality may be conflated by predation by adult Dreissena. For example, adult marine bivalves have been reported to consume both conspecific and heterospecific larvae (see Bayne 1964; André and Rosenberg 1991).

The ability of adult Dreissena to prey on planktonic veligers and settling postveligers, and thereby influence recruitment dynamics, has received scant attention. Zooplankton has been infrequently reported in Dreissena diets, presumably because of their relatively large size. Large particles irritate tentacles lining the inhalant siphon and are rejected. Other particles may also be sorted and rejected by the labial palp, mouth, and stomach (Morton 1969). Adult Dreissena have been reported to ingest some large food items, nevertheless. Ten Winkel and Davids (1982) indicated that well-fed adult Dreissena preferred algal foods smaller than 50 μm, while starved individuals fed nonselectively and ingested diatoms as large as 750 μm. Mikhayev (1967) reported that particles between 80 and 450 μm, including microzooplankton, were ingested by Dreissena. The clearest evidence of zooplankton predation by Dreissena was provided by Scheytsova et al. (1986) in a series of laboratory and field experiments. They determined that adult Dreissena polymorpha and Dreissena bugensis consumed a wide array of microzooplankton up to 400 μm in body length.

In this study we assess the ability of Dreissena polymorpha to prey on populations of microzooplankton from Lake Erie and Erindale Pond. In addition, we propose a model that relates Dreissena population growth in western Lake Erie to the density of predatory adults. Our purpose in constructing the model was to demonstrate that Dreissena population growth patterns in the lake are inconsistent with predictions based on European experiences (i.e. >99% density-independent larval mortality).

Fig. 1. Mean estimated population densities of Dreissena polymorpha inhabiting reefs west (open symbols) and southeast (solid symbols) of Pelee Island, Ontario, in the western basin of Lake Erie. Individuals ranged between 1 and 29 mm in maximum shell length.

Fig. 2. Relationship between exterior inhalant siphon diameter and Dreissena shell length. Pearson’s correlation coefficient, $r = 0.87$.

**Materials and Methods**

Population densities and size distributions of Dreissena inhabiting reefs in the western basin of Lake Erie were estimated by collecting representative rock samples. Samples were collected from reefs west and southeast of Pelee Island. Six to 12 collections were made per reef for each date. The relationship between Dreissena maximum shell length and exterior inhalant siphon diameter was explored using live animals maintained in laboratory cultures. Shell length and siphon diameter were measured to the nearest 0.01 mm with a Fowler ultra-cal II digital caliper and microcomputer-based caliper measurement system (Sprules et al. 1981), respectively. Inhaling siphon diameter of Dreissena increases with shell length ($r = 0.87, n = 28$; Fig. 2) and can exceed the body size of many species of Great Lakes zooplankton by an order of magnitude (Stemberger 1979).

**Predation Trials**

Vulnerability of individual zooplankton species to predation by adult Dreissena was initially assessed in short-term trials in 50-mL beakers. Dreissena was collected from submerged littoral rocks in Lake Erie near Wheatley, Ontario, and maintained in aerated laboratory aquaria at 20°C in a culture medium of glass-fibre-filtered Whatman 934-AH Erindale Pond (Erindale College, Mississauga, Ontario) water supplemented every 2 d with ~0.8 μg Cryptomonas sp.·mL$^{-1}$ (9 × 10$^3$ cells·mL$^{-1}$). Zooplankton for all experiments was collected from 1-2 m depth with a 30-L Schindler–Patalas trap outfitted with a 41-μm Nitex mesh sock. Lake Erie zooplankton was maintained in Cryptomonas-supplemented laboratory cultures prior to experiments. All experimental adult mussels were of the same approximate size (mean shell length ± SD = 2.25 ± 0.23 cm) and were acclimated in test beakers for 2 h prior to predation trials. Experiments were conducted in 50 mL of culture medium supplemented with 0.45 μg dry weight Cryptomonas sp.·mL$^{-1}$ to simulate natural food conditions. Zooplankton was incubated in beakers, in triplicate, with zero (control) or one adult mussel for 2 h, after which time the mussel was removed and zooplankton survivorship assessed (experiment 1). Experiments were conducted with the rotifers Keratella crassa (mean body length ± SD = 208 ± 13 μm), Polyarthra remata (82 ± 9μm), and Trichocerca multicrins (189 ± 17 μm), Dreissena veligers (170 ± 40 μm), and the clau-
docerans Bosmina longirostris (312 ± 62 μm) and Scapholeberis kingi (647 ± 124 μm). Fifty rotifers or mussel veligers or 25 cladocerans were used to initiate trials. Wastes expelled by, and digestive tracts of, mussels were examined for the presence of zooplankton. The effect of Dreissena on zooplankton survival was assessed for each species using Bonferroni-corrected t-tests on ln(x + 1)-transformed abundance data for control and experimental populations.

A second laboratory experiment was conducted to assess the capability of adult Dreissena to suppress zooplankton from Erindale Pond (experiments 2). Macrozoooplankton was removed to preclude interactions with microzooplankton by straining pond water through 363-μm Nitex mesh. Experiments consisted of placing 3 L of pond water containing microzooplankton, concentrated to 150% of pond density, in 4-L jars with zero (control), one, or three adult Dreissena. These Dreissena densities are well within the range of effective densities found in western basin of Lake Erie during 1990 (Leach 1991). All treatments were replicated three times. Experiments were conducted in a controlled environment chamber at 20°C with photoperiod of 15 h light: 9 h dark. Experiments lasted 24 h, after which time mussels were removed from test containers and zooplankton concentrated and fixed with 4% sucrose–formalin. Zooplankton was subsampled, settled overnight, and counted at 63× magnification. Differences in zooplankton densities between treatments were analyzed with ANOVA and Scheffe’s multiple comparisons tests performed on ln(x + 1)-transformed abundance data (Day and Quinn 1989).

Two similar experiments were conducted in Lake Erie adjacent to Wheatley, Ontario. In an experiment conducted between 22 and 23 August 1990, 3.7 L of lake water was filtered through 363 μm Nitex mesh to remove macrozooplankton, and placed into 4-L bottles with zero, two, or four adult Dreissena (experiment 3). The bottles were sealed and tethered in wire-mesh baskets at 5 m for 24 h, after which time zooplankton and Dreissena were fixed as above. Three control zooplankton samples were fixed at the outset of the experiment to test for the presence of a bottle effect. While all other treatments were replicated four times, strong seas reduced the number of recovered replicates to two for each treatment.

In an otherwise identical experiment conducted in Lake Erie between 9 and 11 July 1990, zooplankton was incubated with zero or six adult Dreissena. Cryptomonas (0.62 μg dry weight·mL⁻¹) was added to one Dreissena treatment to supplement ambient food resources and reduce exploitation competition between Dreissena and Polyarthra, the numerically dominant zooplankter in the lake (experiment 4). The second Dreissena treatment and control zooplankton containers were incubated with ambient food and, as a volume control, an equivalent quantity of algal growth medium as that placed in the treatment with supplemented food. Zooplankton and Dreissena were preserved after 50 h. Polyarthra densities were ln(x + 1)-transformed prior to statistical analysis with an ANOVA test.

Dreissena prey-based clearance rates (CR) and ingestion rates (IR) were calculated for each species for each experiment as

\[
CR = \frac{V[ln(E_0/E_i) - ln(C_i/C)]}{ln(n)}
\]

\[
IR = CR - C_0
\]

where V was the experimental volume, \(E_0\) and \(E_i\) were the initial and final prey densities in the experimental vessels, respectively, \(C_0\) and \(C_i\) were the initial and final prey densities in the controls, respectively, \(n\) was the experimental period, and \(n\) was the predator number (modified from Reeders et al. 1989).

We compared the potential predation impact of Dreissena on rotifers with impacts reported for other invertebrate predators in the Great Lakes. Predation impact refers to the per capita mortality rate imposed on rotifer prey by the predator population in one day and is calculated as the product of predator volume density (predators per cubic metre) and predator clearance rate (litres per predator per day). Settled Dreissena densities (predators per square metre) were converted to volume densities (predators per cubic metre) by assuming that the overlying water column was well mixed and 7 m deep. We conservatively estimate that zooplankton was preyed on only by mussels larger than 2 cm, which averaged 5000 individuals·m⁻² (i.e. 714.3 individuals·m⁻³) on reefs in western Lake Erie during the fall of 1990 (Leach 1991). We used the median rotifer clearance rate from all our experiments (0.99 L·predator⁻¹·d⁻¹) for the predation impact calculation. Densities and rotifer-based clearance rates of other predators were derived from the literature.

Population Modelling

We used STELLA® software (High Performance Systems, Inc. 1988) to construct two models of Dreissena population growth in the western basin of Lake Erie. The models differ only with respect to the sources and intensities of larval mortality. The first model, which for clarity we define as the non-cannibalistic model (see Appendix 1), assumes a constant density-independent mortality rate between veliger and settled adult phases of 99% due to inhospitable settling substrate (e.g. mud, sand), unsuitable chemical (e.g. oxygen) or thermal conditions, and from fish and invertebrate predation (see Stafczykowska 1977; Lewandowski 1982; Sprung 1989). The second model, termed the composite model (Appendix 1), combines a constant density-independent mortality of 70% with density-dependent mortality due to predation by conspecific adults so that the total mortality rate can exceed 99%. Mussel populations in each model consist of four life history stages, individuals within which have characteristic fecundity functions, and, in the composite model, cannibalism functions. The compartments represent subpopulations of (1) veligers, (2) reproductive but nonpredacious 1-yr-old adults, and (3 and 4) reproductive and predacious 2- and 3-yr-old adults. All individuals die by the end of their third year, as apparently occurs in Lake St. Clair (Mackie 1990). Mortality rates between adult compartments were parameterized using the fall 1990 population size structure in western Lake Erie (J. Leach, unpubl. data) (see Appendix 1). Mortality between age-classes is not ascribed to specific agents, but apparently can result from both density-dependent and density-independent factors (Stafczykowska 1977; Hebert et al. 1991). Age-specific fecundity (Appendix 1) was parameterized using European literature values (Stafczykowska 1977; Walz 1978b).

The composite model incorporates separate predation functions for 2- and 3-yr-old adult mussels feeding on veligers and postveligers. Planktonic veligers may be brought into contact with, and be ingested by, 2- and 3-yr-old mussels due to mixing of the water column. Settling postveligers may become entrained in feeding currents of adult mussels and consumed. Predation rates were modelled as negative functions of adult

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1See Note Added in Proof.
density (Appendix 1) because refiltration of water, from which larvae have already been strained, can be appreciable in the benthic boundary layer when sessile mussel densities are high (Fréchet et al. 1989). The exact nature of the predation rate curves is difficult to establish because postveliger susceptibility to cannibalism varies inversely with distance above mussel beds.

Population densities within each compartment were calculated based on a uniform mussel distribution over 334 km² of habitable substrate (gravel and bedrock) in the western basin (derived from Hartman 1973). Our models assume an initial veliger inoculum of $5 \times 10^8$ individuals, based on a ballast volume of $10^7$ L containing 50 veligers L$^{-1}$, dumped entirely into western Lake Erie. Our modelling approach is conservative (i.e. it favours the noncannibalistic model) for a number of reasons. First, it is very unlikely that all of the ballast containing the inoculum was actually dumped into Lake Erie because mussels were first observed in Lake St. Clair. It is also unlikely that the veliger inoculum was as large as modelled because it assumes a large ballast volume and a high density of veligers surviving transit in ballast tanks. Finally, the noncannibalistic model assumes a larval mortality rate (99%) considerably lower than the values commonly estimated for European systems (Stachczynska 1977; Lewandowski 1982; Sprung 1989). We assessed the sensitivity of both noncannibalistic and composite models by varying reproductive schedules and larval mortality rates and observing resultant time required to reach 1990 density from initial density (see Appendix 1). The models iterate once per year (i.e. individuals spend 1 yr in each age-class compartment) using Euler’s integration method.

**Results**

**Laboratory Experiments**

All small zooplankton species incubated with adult *Dreissena* sustained significant ($t$-tests, $p < 0.01$; Fig. 3) mortality in the short-term laboratory experiments whereas densities of large-bodied species were unaffected ($t$-tests, $p > 0.05$). The rotifer *Polyarthra remata* was suppressed most severely (<5% survival) by *Dreissena*. *Keratella crassa* also sustained intense mortality (9% survival). *Dreissena* digestive tracts contained

**Fig. 3.** Mean (+1 se) densities of the cladocers *Bosmina longirostris* (1) and *Scapholeberis kingi* (2), *Dreissena* veligers (3), and the rotifers *Trichocerca multicornis* (4), *Keratella crassa* (5), and *Polyarthra remata* (6) in the absence and presence of one adult *Dreissena* (experiment 1). *Significant* $t$-test ($p < 0.01$) difference between density in control and mussel treatment.

**Fig. 4.** Population densities (mean +1 se; $n = 3$) of *Polyarthra remata* (solid) and *Keratella cochlearis* (open) in the presence of zero (control), one, or three adult *Dreissena* (experiment 2). Plankton samples were also preserved prior to the experiment (Pond).

**Fig. 5.** Population densities of Lake Erie *Dreissena* veligers (solid), *Polyarthra* spp. (open), and *Keratella* spp. (hatched) in samples with zero (control), two, or four adult *Dreissena* (experiment 3). Zooplankton was also preserved prior to the experiment (Lake). Each bar represents the mean (+1 se) of three (lake) or two (control, mussel treatments) replicate samples.

*Keratella* loricae at the end of the experiment, verifying predation as the suppressive mechanism. Survival rates of experimental *Trichocerca similis* and *Dreissena* veligers were 17% and 49%, respectively, while those of the cladocerans *Bosmina longirostris* and *Scapholeberis kingi* were greater than 90% (Fig. 3). Considering the small volume of the experimental vessels, these data are most useful in a broad consideration of differential zooplankton susceptibility to predation. They are, however, corroborated by experiments conducted in the laboratory and field using much larger volumes and realistic *Dreissena* densities.

The late-summer Erindale Pond zooplankton community was dominated numerically by *Polyarthra remata* and *Keratella cochlearis*. Densities of both species were significantly (experiment 2; ANOVA tests, $p < 0.05$) lower in bottles with three mussels than in those lacking mussels (Fig. 4), while densities in bottles with one mussel were not statistically different from controls (Scheffe’s tests, $\alpha = 0.05$). The density of *Polyarthra* was also influenced by the experimental procedure, as mean density of control populations preserved at time 0 ("pond") was significantly greater than that of control
but differences between treatments with two and four mussels were not significant (Scheffe's test, α = 0.05). The density of Keratella varied in a similar manner, although differences among individual means were not significant (Scheffe's tests, α = 0.05).

*Polyarthra* spp. dominated the Lake Erie plankton community numerically earlier in the summer at the same locality (experiment 4). *Polyarthra* densities were significantly lower in bottles with *Dreissena* than in controls (ANOVA, p < 0.005). Food supplementation did not decrease the effect of *Dreissena* (Fig. 6), as *Polyarthra* densities were only slightly lower in containers incubated with ambient food. Exploitation competition appeared to play a minor role, if any, in the suppression of *Polyarthra*.

*Dreissena* clearance and ingestion rates on Lake Erie and Erindale Pond zooplankton were strongly related to prey size (Table 1). Ingestion rates were highest on rotifers, intermediate on *Dreissena* veligers, and lowest on crustaceans. Predation rates on *Polyarthra* were always higher than those on *Keratella* within an experiment. Ingestion rates of *Polyarthra* were also quite variable, reflecting moderate differences among experiments in calculated clearance rates (Table 1) and large differences in initial zooplankton density.

Large *Dreissena* (>2 cm) had an effective average density of 714 individuals m⁻³ in western Lake Erie and a median rotifer-based clearance rate of 41.2 mL·predator⁻¹·h⁻¹ (0.99 L·predator⁻¹·d⁻¹) (Table 2). At these rates, adult *Dreissena* can impose a per capita death rate of up to 0.71 d⁻¹ on vulnerable rotifer prey, assuming complete mixing of the water column. This predatory potential exceeds that of other invertebrate predators by more than an order of magnitude (Table 2).

### Population Modelling

*Dreissena* densities observed during 1990 in western Lake Erie could not have been achieved if total mortality equalled or exceeded 99% (noncannibalistic model), even if high repro-

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**Table 1.** Clearance rates and ingestion of *Dreissena* on Lake Erie and Erindale Pond microzooplankton. Experiment 4a, ambient food level; experiment 4b, ambient food level supplemented with ~0.62 μg *Cryptomonas* sp. dry weight·mL⁻¹.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Zooplankton taxon</th>
<th><em>Dreissena</em> (number·jar⁻¹)</th>
<th>Volume (L)</th>
<th>Time (h)</th>
<th>Clearance rate (mL·ind⁻¹·h⁻¹)</th>
<th>Ingestion rate (prey·ind⁻¹·h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Bosmina longirostris</em></td>
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<td>0.05</td>
<td>24</td>
<td>1.8</td>
<td>0.9</td>
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<tr>
<td>1</td>
<td><em>Scapholeberis kingi</em></td>
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<td>1.0</td>
<td>0.5</td>
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<td><em>Dreissena veligers</em></td>
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<td>0.05</td>
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<td>41.2</td>
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<td>50</td>
<td>24.5</td>
<td>5.6</td>
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<td>4b</td>
<td><em>Polyarthra spp.</em></td>
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<td>3.7</td>
<td>50</td>
<td>20.0</td>
<td>4.6</td>
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</table>
TABLE 2. Potential impacts of Great Lakes invertebrate predators on planktonic rotifers based on typical predator densities and clearance rates. Clearance rate is the volume of water from which an individual predator removes all prey in 1 d. Impact is the per capita prey death rate exerted by the predator population. Source key: 1 = Nero and Sprules (1986); 2 = Grossnickle (1990); 3 = Fero and Riessen (1990); 4 = Vanderploeg et al. (1990); 5 = this study. Dreissena volumetric density was calculated based on 5000 adult mussels m$^{-3}$ and a mixed water column 7 m deep.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Prey density (ind.·m$^{-2}$)</th>
<th>Rotifer-based clearance rate (L·predator$^{-1}$·d$^{-1}$)</th>
<th>Impact (d$^{-1}$)</th>
<th>Source</th>
</tr>
</thead>
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<td>4.3</td>
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<td>1</td>
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<td>Limnocalanus macrurus</td>
<td>61</td>
<td>0.16</td>
<td>0.01</td>
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<tr>
<td>Bythotrephes cedroeimi</td>
<td>23</td>
<td>0.26</td>
<td>&lt;0.01</td>
<td>2, 3, 4</td>
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<tr>
<td>Senecella calanoides</td>
<td>93</td>
<td>0.44</td>
<td>0.04</td>
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<tr>
<td>Dreissena polymorpha</td>
<td>714.3</td>
<td>0.99</td>
<td>0.71</td>
<td>5</td>
</tr>
</tbody>
</table>

Fig. 7. Projected population abundance of Dreissena in western Lake Erie according to composite (open circles) and noncannibalistic (closed circles) models. The range of mean densities observed on reefs during 1990 is denoted by the broken horizontal lines (Fig. 1). Time of invasion is assumed to be 1986. Both models assume fecundity values of $1 \times 10^4$, $2 \times 10^4$, and $3 \times 10^4$ eggs/female$^{-1}$·yr$^{-1}$ for 1-, 2-, and 3-yr-old adults, respectively. Total larval mortality rate = 99% in the noncannibalistic model. Initial larval mortality rate = 80% in the composite model.

ductive schedules are utilized (Fig. 7; Table 3). Indeed, the noncannibalistic model does not predict 1990 densities until at least 1994 when total larval mortality equals or exceeds 99% (Table 3). These results are insensitive to variation in initial veliger inoculum, as the time to 1990 density is decreased by only 1 yr if the inoculum is increased by an order of magnitude ($5 \times 10^4$ individuals). By contrast, the composite model correctly projects 1990 densities if total larval mortality is initially set at 70% (Table 3; Fig. 7). Larval mortality did not exceed 99% in the composite model until the combined densities of 2- and 3-yr-old adults exceeded $8 \times 10^4$ individuals·m$^{-2}$.

**Discussion**

Our study indicates that some species of zooplankton may experience high mortality rates in shallow, well-mixed regions of the Great Lakes which support large populations of adult Dreissena, including western Lake Erie and southern Lake St. Clair. Small-bodied, weak-swimming species of rotifers and Dreissena veligers appear particularly susceptible to entrainment in filtering currents generated by adult Dreissena (Fig. 3; Table 1). Our findings are generally consistent with those of Shevtsova et al. (1986) who reported that adult Dreissena consumed many small zooplankton species including the rotifers Keratella quadrata, Polyarthra vulgaris, and Euchlanis dilatata, Dreissena veligers, protozoans, and cyclopoid copepods. However, whereas we found that relatively large zooplankton (Bosmina, Scapholeberis) were invulnerable to ingestion by Dreissena (Fig. 3), Shevtsova et al. (1986) reported that some large species (Bosmina, Podon) were vulnerable while others (Chydorus, Alona) were not.

Maximum Dreissena prey size may be constrained by the effective diameter of the inhalant siphon. For example, contact between Scapholeberis and tentacles lining the inhalant siphon elicited a rapid response from the mussel in which water intake ceased and the siphon was temporarily withdrawn. Smaller species of zooplankton flowed into the mussel's mantle cavity without stimulating siphalon tentacles. The minimum size of Dreissena capable of ingesting zooplankton has not been determined but is probably correlated with the inner diameter of the inhalant siphon and mussel shell length. Shevtsova et al. (1986) determined that Dreissena as small as 18–20 mm consumed zooplankton. It is also possible that some zooplankton drawn into the mantle cavity may be expelled in pseudofaeces, as has been reported for the marine mussel Mytilus edulis (Bayne 1964).

Prey swimming ability and vertical location in the plankton may also influence predation rates. Polyarthra is capable of escaping from weak flow currents only, such as those generated by feeding Daphnia, by rapidly beating its ventral paddles (Gilbert 1987). This tactic was insufficient to propel some individuals from the inhalant current of adult Dreissena despite repeated escape attempts. By contrast, copepods and other zooplankton capable of strong swimming bursts are unlikely to become trapped in mussel feeding currents (H. J. MacIsaac, pers. obs.). Vertical separation of planktonic zooplankton and benthic Dreissena may also reduce predation rates, particularly when the water column is stratified or poorly mixed. This problem is unlikely to affect predation rates on postveligers because they must sink from the plankton during settlement, and possibly encounter adults in the process (see Bayne 1964).

Settled Dreissena may suppress Lake Erie zooplankton through a combination of exploitative competition and predation. Between 1988 and 1990, water clarity in the western basin almost doubled, settled mussel populations increased from 400 to 341 000 individuals·m$^{-2}$, and chlorophyll a and particulate organic carbon levels declined (Leach 1991). Based on fall 1990 Dreissena size–frequency distributions in western Lake Erie and associated literature-derived clearance rates, H. J. MacIsaac and W. G. Sprules (unpubl. data) calculated that sessile
zebra mussel populations may filter the water column more than 18 times per day. These calculations indicate that the western basin may be experiencing an unprecedented diversion of energy from pelagic to benthic food webs and corroborate the high ingestion rates and predation impacts observed in this study (Tables 1 and 2). Comparative data describing microzooplankton densities before and after Dreissena establishment in European systems are lacking. However, Shevtsova and Kharchenko (1981) commented that low stocks of bacterioplankton, phytoplankton, and zooplankton in the North-Crimean Canal appeared to have been caused by the filtering activities of large populations of Dreissena. Knowledge of these impacts is essential considering the dietary dependence of early life history stages of commercial Lake Erie fishes (e.g. Perca) on microzooplankton (Treasure 1990).

Most of our microzooplankton-based Dreissena clearance rates were less than 100 mL-individual$^{-1}$ h$^{-1}$ (Table 1). These rates are consistent with those from some previous investigations in which natural phytoplankton or other small particles were used as tracers (see Kryger and Riisgård 1988) and indicate that Dreissena may have been feeding relatively nonselectively on microzooplankton. Dreissena had unusually high clearance rates on Keratella in experiment 2 (Table 1); these values resulted from the depletion of Keratella in experimental vessels and from the sensitivity of the clearance rate equation to prey depletion.

Mortality in Dreissena populations is generally most concentrated between the planktonic veliger and settled subadult phases. Because individual females are capable of producing up to $10^7$ eggs per year (Walz 1978b), mortality of larvae must approach 100% in stable or near-stable populations. The determinants of larval mortality have remained elusive despite the practical significance of the problem. While our study clearly implicates intraspecific predation as a regulatory mechanism, European workers have focused primarily on the availability of suitable settling substrate (see Stańczykowska 1977; Lewandowski 1982). The available evidence is not entirely consistent with this hypothesis. However, assuming that veligers have a uniform horizontal distribution in the water column, a mortality rate exceeding 99% implies that less than 1% of benthic habitats are suitable for colonization by Dreissena, an unlikely possibility in most lakes. Indeed, veligers are often concentrated in belts above benthic adults (Stańczykowska 1977) and thus may actually have a higher probability of settling on suitable substrate than if their horizontal distribution were uniform. Lewandowski (1982) calculated that mortality to the settling stage amounted to 99.4% in Lake Kolowin, Poland, despite the abundance of suitable settling substrate (21.8% of surface area). As much as 56.4% of benthic substrate in Lake Majcz Wielki, Poland, was suitable for settlement of postveligers, yet mortality amounted to 95.8% of the initial veliger cohort (Lewandowski 1982). Postveliger densities in western Lake Erie declined by 44% between 1989 and 1990 despite a 75-fold increase in settled mussel density (Garton and Haag 1990) and a threefold increase in the density of planktonic veligers (Leach 1991). If recruitment was determined simply by the amount of total substrate in the basin, 1990 settlement values should have greatly exceeded those for 1989. Each of these studies is consistent with the hypothesis that recruitment is related not to the absolute amount of substrate available, but rather to the amount of suitable substrate not already heavily populated by adult mussels.

Recruitment patterns in Lake St. Clair and some other European systems are also consistent with the intraspecific predation hypothesis. Laval settlement in Lake St. Clair was highest near adults in 1988 when adult densities were low but was most pronounced at population peripheries in 1989, by which time settled mussel densities had increased nearly 1000-fold (Hebert et al. 1991). Hebert and co-workers speculated that these patterns may have resulted from a chemical factor released by adults which triggered larval settlement when adults were present at low density, but which deterred settlement when adults were abundant. Chemical factors induce larval settling in many benthic invertebrates (see review by Burke 1986), but a dual facilitation-inhibition role is difficult to envisage.

Table 3. Variation in predicted time to 1990 Dreissena density for noncannibalistic and composite models in relation to age-specific fecundity and total larval mortality rate. High and low reproductive values were derived from European studies (Walz 1978b; Stańczykowska 1977), as were larval mortality rates (see Discussion). Western Lake Erie fall 1990 population survey data (Leach 1991) were used to establish age structure; populations consisted of 74, 22, and 4% of adult age-classes 1, 2, and 3, respectively. All models assume a veliger inoculum of $5 \times 10^4$ individuals (see Materials and Methods).

<table>
<thead>
<tr>
<th>Model</th>
<th>Larval mortality rate (% of veligers produced)</th>
<th>Fecundity (eggs·female$^{-1}$·yr$^{-1}$)</th>
<th>Year 1990 mussel density reached</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noncannibalistic</td>
<td>99</td>
<td>$10^4$</td>
<td>1990</td>
</tr>
<tr>
<td></td>
<td>99.5</td>
<td>$2 \times 10^4$</td>
<td>1991</td>
</tr>
<tr>
<td></td>
<td>99</td>
<td>$3 \times 10^4$</td>
<td>1991</td>
</tr>
<tr>
<td>Composite</td>
<td>70</td>
<td>$10^4$</td>
<td>1990</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>$2 \times 10^4$</td>
<td>1991</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>$3 \times 10^4$</td>
<td>1991</td>
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<td>70</td>
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<td>80</td>
<td>$2 \times 10^4$</td>
<td>1991</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>$3 \times 10^4$</td>
<td>1991</td>
</tr>
</tbody>
</table>
Lewandowski (1982) reported that submerged Characeae (stoneworts) provided the best substrate for settlement of Dreissena larvae, followed in order by Dreissena colonies, stones, sand, and mud. Lewandowski (1982) suggested that these patterns may have resulted from substrate-specific settlement by postveligers. However, they are also consistent with the hypothesis of substrate-specific settlement following non-preferential settlement. Postsettlement mortality agents and intensities could be substrate specific; for example, postveligers settling on sand or mud may lack sufficient structural support upon which to secure byssal threads or they may experience difficulty in feeding, while those settling on established colonies containing large size-classes may be eaten (Mikeyev 1967; Shevtsova et al. 1986) (Fig. 3 and 5). Lewandowski (1982) also described pronounced differences in age-class strengths among mussel populations residing on plants and in benthic colonies in Lake Ruman, Poland; plant-dwelling mussel distributions were highly skewed toward young (small) age-classes whereas colony-dwelling Dreissena were more equitably distributed among young and old age-classes. While these patterns may have resulted from preferential settling of larvae on plants and mortality of older plants and older mussels thereupon (Lewandowski 1982), they are also consistent with the hypothesis of differential mortality of larvae settling on plants and established Dreissena colonies. Clear differentiation between preferential settling by, and substrate-specific mortality of, postveligers will require carefully designed and executed field experiments. To date, only Sprung (1989) has observed high veliger mortality rates (99%) in the absence of predation. The only lake (Maejc Wielki, Poland) of which we are aware that clearly exhibited a total larval mortality rate lower than 99% is notable in that it was in highest density. Intraspecific competition for food could skew population age structures toward small size-classes because large mussels have higher mass-specific metabolic demands and are more susceptible to food shortages than are smaller individuals (Walz 1978c).

In conclusion, our study demonstrates the predatory capability of adult Dreissena on Great Lakes rotifers and Dreissena larvae. Potential predation rates on rotifers exceed those of other invertebrate Great Lakes predators. Our models of mussel population growth in the western basin of Lake Erie indicate that mortality of larvae to the settled subadult phase could not have been as intense as previously described for European systems. We propose that larval mortality was initially substantially lower than 99% due to a lack of predatory adult mussels.

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Appendix 1.

A schematic representation of a STELLA® (High Performance Systems, Inc. 1988) composite model for predicting Dreissena polymorpha population growth in western Lake Erie is shown in Fig. A.1. Dreissena populations consist of veliger, adult 1, and adult 2, and adult 3 subpopulations. Total veliger production is determined as \[\sum_{i=1}^{3} \text{fecundity}_i \times (0.5 \times \text{adult, density})\] where \(i\) is age-class. Fecundities were initially set at \(10^4, 2 \times 10^4,\) and \(3 \times 10^4\) eggs/female\(^{-1}\) for adult age-classes 1, 2, and 3, respectively. The model assumes an even sex ratio and that all eggs produced are viable and fertilized. Adult 1 age-class recruitment is determined as the product of the number of veligers available to settle (veligers), the environmental survival rate (environmental mortality), and predation survival rates (predation mortality). Composite model larval survival functions in relation to 2- and 3-year-old mussel densities are shown below the model. Adult 1 age-class recruitment for the noncanaliblastic model is identical except that it lacks predation mortality functions. In both models, 30% of age 1 individuals survive to age 2 (70% mortality), and 18% of these individuals survive to age 3 (82% mortality) (Leach 1991). All mussels live a maximum of 3 yr. The inoculum consisted of 5 \(\times 10^6\) veligers (see Materials and Methods). Densities of each adult age-class were calculated based on uniform distributions over 3.34 \(\times 10^4\) m\(^{-2}\) of habitable substrate in the lake’s western basin (Hartman 1973). The models iterate once per year. Fecundity values and environmental mortality rates were varied to determine the model’s sensitivity (see Table 3).

Note added in proof

Our models assume that the initial cohort of veligers introduced to Lake Erie in 1986 were age 1 adults in 1987 and contributed to the veliger subpopulation for the first time in 1988. However, Dreissena populations in Lake Erie appear capable of reproducing in their year of settlement (i.e. individuals entering the age 1 subpopulation during 1987 reproduce and contribute to the veliger subpopulation in 1987). Our results are fairly robust to this modelling alternative. Using the range of larval mortality and adult fecundity values described in Table 3, and the same initial veliger inoculum, mean Dreissena densities observed in western Lake Erie during 1990 are predicted to be achieved between 1992 and 1994 for variants of the noncanaliblastic model and between 1989 and 1990 for variants of the composite model.
Fig. A.1. Schematic representation of a STELLA® composite model.
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