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

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The zebra mussel *Dreissena polymorpha* established populations in western Lake Erie in 1986 and achieved densities exceeding 3.4×10^5 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 (*Polarthra* 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.

Les populations de dreissena polymorphe (*Dreissena polymorpha*) déjà établies dans la partie ouest du lac Érié en 1986 atteignaient des densités supérieures à $3,4 \times 10^5$ individus par mètre carré au cours de 1990. Nous avons évalué la prédation du zooplancton du lac Érié et de l'étang Erindale par les dreissenas adultes. Les larves des dreissenas et les petits rotifères (*Polarthra* spp., *Keratella* spp., *Trichocerca*) présentaient une mortalité par prédation variant de moyenne à élevée tandis que les plus gros taxons (*Bosmina*, *Scapholeberis*) résistaient à toute prédation. Les larves de *Dreissena* des lacs européens présentent presque toujours un taux de mortalité supérieur à 99 %. La mortalité a surtout été attribuée à l'absence d'un substrat de fixation adéquat et à des conditions environnementales défavorables, mais elle peut être confondue avec celle découlant de la prédation des larves par les adultes. Nous avons montré, à l'aide d'un modèle STELLA_{md}, que les densités de dreissenas fixées notées en 1990 n'auraient 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 prévues 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 décelées dans les lacs Érié et Ste-Claire et dans certains bassins hydrographiques européens.

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The composition of biological communities in the St. Lawrence Great Lakes has been profoundly altered by the introduction of exotic species. The zebra mussel *Dreissena polymorpha* (Pallas) is one of the most recent and potentially destructive species to invade these ecosystems. *Dreissena* was first observed in North America in Lake St. Clair and western and central Lake Erie during 1988 (Hebert et al. 1989). Based on mussel size distributions in Lake St. Clair, Hebert et al. (1991) suggested that populations first became established during 1986.

Dreissena is unique among North American freshwater bivalves in possessing free-swimming veliger larvae and byssate adults. These unusual life history characteristics have facilitated rapid dispersal and the exploitation of unused solid,

benthic substrates. Hebert et al. (1991) described 1000-fold increases in settled mussel densities in Lake St. Clair between 1986 and 1989. Populations inhabiting reefs in western Lake Erie expanded from a maximum mean density of 3.2×10^4 individuals·m⁻² in May 1989 to 3.42×10^5 individuals·m⁻² in October 1990 (Fig. 1).

Female and male *Dreissena* synchronously release eggs and sperm into the water column where fertilization takes place. Veligers remain free-swimming for periods of 8–45 d, during which time they grow from ~70 to 250 μm. Veligers utilize a ciliated velum for propulsion and food collection. Individuals between 200 and 250 μm body length undergo metamorphosis to become postveligers; in the process the velum is replaced by siphons, the characteristic bivalve foot and shells develop, and

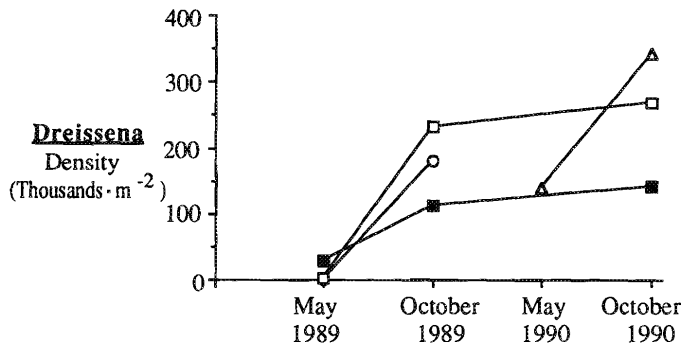


FIG. 1. Mean estimated population densities of *Dreissena polymorpha* inhabiting reefs west (open symbols) and southeast (solid symbols) of Pelee Island, Ontario, in the western basin of Lake Erie. Individuals ranged between 1 and 29 mm in maximum shell length.

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% (Stañczykowska 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 (Stañczykowska 1977; Lewandowski 1982; Lewandowski and Ejsmont-Karabin 1983). Moreover, these sources of mortality may be confounded 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 palps, 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 . Mikheyev (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 Shevtsova 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).

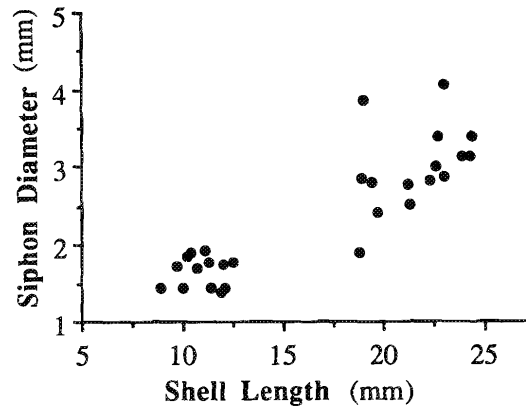


FIG. 2. Relationship between exterior inhalant siphon diameter and *Dreissena* shell length. Pearson's correlation coefficient, $r = 0.87$.

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. Inhalant 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 $\sim 0.8 \mu\text{g}$ *Cryptomonas* sp. mL^{-1} (9×10^3 cells $\cdot \text{mL}^{-1}$). 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 \pm 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 $0.45 \mu\text{g}$ 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 \pm SD = $208 \pm 13 \mu\text{m}$), *Polyarthra remata* ($82 \pm 9 \mu\text{m}$), and *Trichocerca multicornis* ($189 \pm 17 \mu\text{m}$), *Dreissena* veligers ($170 \pm 40 \mu\text{m}$), and the cla-

docerans *Bosmina longirostris* ($312 \pm 62 \mu\text{m}$) and *Scaphloberis kingi* ($647 \pm 124 \mu\text{m}$). 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 (experiment 2). Macrozooplankton 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 \times 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 $\cdot\text{mL}^{-1}$) was added to one *Dreissena* treatment to supplement ambient food resources and reduce exploitation competition between *Dreissena* and *Polyarthra*, the numerically dominant zooplankton 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

$$\text{CR} = V(\ln[E_0/E_t] - \ln[C_0/C_t])/tn$$

$$\text{IR} = \text{CR} \cdot C_0$$

where V was the experimental volume, E_0 and E_t were the initial and final prey densities in the experimental vessels, respectively, C_0 and C_t were the initial and final prey densities in the

controls, respectively, t 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 $\cdot\text{m}^{-2}$ (i.e. 714.3 individuals $\cdot\text{m}^{-3}$) 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 $\cdot\text{predator}^{-1} \cdot\text{d}^{-1}$) for the predation impact calculation. Densities and rotifer-based clearance rates of other predators were derived from the literature.

Population Modelling¹

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 Stańczykowska 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 (Stańczykowska 1977; Hebert et al. 1991). Age-specific fecundity (Appendix 1) was parameterized using European literature values (Stańczykowska 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

¹See Note Added in Proof.

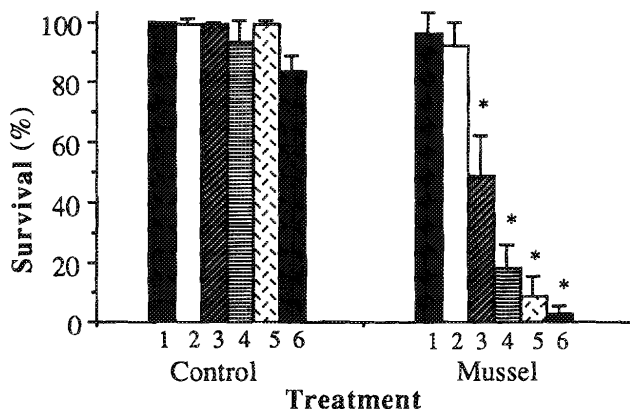


FIG. 3. Mean (+1 SE) densities of the cladocerans *Bosmina longirostris* (1) and *Scapholeberis kingi* (2), *Dreissena veligers* (3), and the rotifers *Trichocerca multicrinis* (4), *Keratella crassa* (5), and *Polyarthra remata* (6) in the absence and presence of one adult *Dreissena* (experiment 1).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

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 (Fr chet te 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 5×10^8 individuals, based on a ballast volume of 10⁷ 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 (Stańczykowska 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

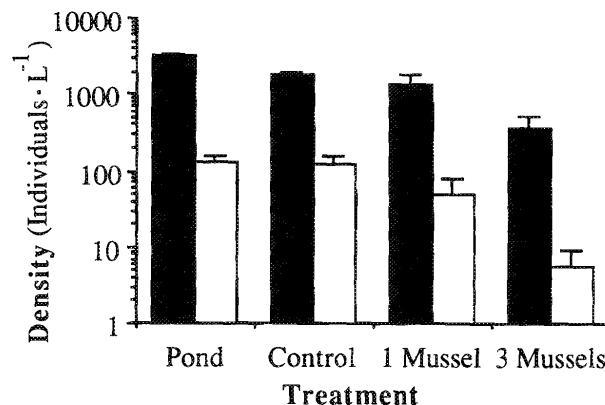


FIG. 4. Population densities (mean +1 SE; $n = 3$) of *Polyarthra remata* (solid) and *Keratella cochlearis* (open) in the presence of zero (control), one, or three adult *Dreissena* (experiment 2). Plankton samples were also preserved prior to the experiment (Pond).

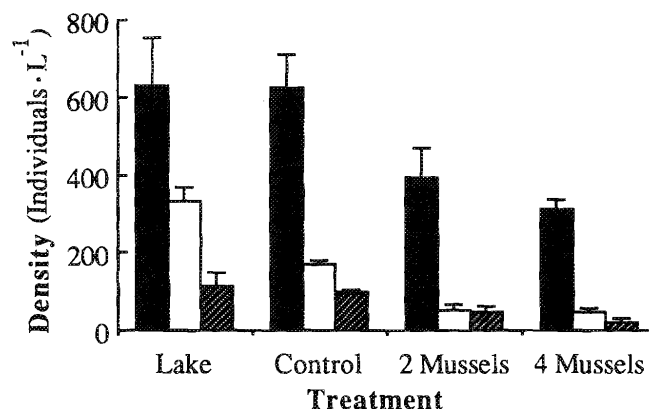


FIG. 5. Population densities of Lake Erie *Dreissena veligers* (solid), *Polyarthra* spp. (open), and *Keratella* spp. (hatched) in samples with zero (control), two, or four adult *Dreissena* (experiment 3). Zooplankton was also preserved prior to the experiment (Lake). Each bar represents the mean (+1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

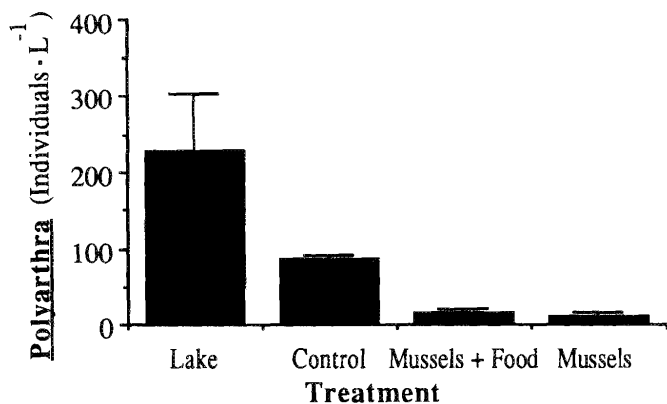


FIG. 6. Densities of Lake Erie *Polyarthra* spp. after 50 h in treatments with zero (control) or six (mussels + food, mussels) adult *Dreissena* (experiment 4). Control samples were also preserved immediately prior to the experiment (lake). Food in the mussels + food treatment was supplemented with $0.63 \mu\text{g}$ *Cryptomonas* sp. mL^{-1} . Each bar is the mean ($+1 \text{ SE}$) of three (lake, control), four (mussels + food), or two (mussels) replicate samples.

populations preserved at the end of the experiment (Scheffe's test, $\alpha = 0.05$).

Field Experiments

The microzooplankton community of Lake Erie near Wheatley, Ontario, was dominated numerically by *Dreissena* veligers, *Polyarthra* spp., and *Keratella* spp. during late August 1990. Each of these taxa experienced graded predatory losses in relation to *Dreissena* density (experiment 3; Fig. 5). Although veliger mortality tended to increase with *Dreissena* density, differences in density were not significant (ANOVA, $0.10 > P > 0.05$) because of low statistical power associated with small sample sizes. *Polyarthra* density was significantly (ANOVA, $p < 0.001$) lower in bottles containing *Dreissena*,

but differences between treatments with two and four mussels were not significant (Scheffe's test, $\alpha = 0.05$). The density of *Keratella* varied in a similar manner, although differences among individual means were not significant (Scheffe's tests, $\alpha = 0.05$).

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* ($>2 \text{ cm}$) had an effective average density of $714 \text{ individuals} \cdot \text{m}^{-3}$ in western Lake Erie and a median rotifer-based clearance rate of $41.2 \text{ mL} \cdot \text{predator}^{-1} \cdot \text{h}^{-1}$ ($0.99 \text{ L} \cdot \text{predator}^{-1} \cdot \text{d}^{-1}$) (Table 2). At these rates, adult *Dreissena* can impose a per capita death rate of up to $0.71 \cdot \text{d}^{-1}$ 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-

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 $\sim 0.62 \mu\text{g}$ *Cryptomonas* sp. dry weight $\cdot \text{mL}^{-1}$.

Experiment	Zooplankton taxon	<i>Dreissena</i> (number $\cdot \text{jar}^{-1}$)	Volume (L)	Time (h)	<i>Dreissena</i>	
					Clearance rate ($\text{mL} \cdot \text{ind.}^{-1} \cdot \text{h}^{-1}$)	Ingestion rate ($\text{prey} \cdot \text{ind.}^{-1} \cdot \text{h}^{-1}$)
1	<i>Bosmina longirostris</i>	1	0.05	24	1.8	0.9
1	<i>Scapholeberis kingi</i>	1	0.05	24	1.0	0.5
1	<i>Dreissena</i> veligers	1	0.05	24	17.7	17.7
1	<i>Trichocerca multirinis</i>	1	0.05	24	41.2	41.2
1	<i>Keratella crassa</i>	1	0.05	24	61.0	61.0
1	<i>Polyarthra remata</i>	1	0.05	24	86.0	86.0
2	<i>Keratella cochlearis</i>	1	3	24	108.7	14.6
2	<i>Keratella cochlearis</i>	3	3	24	126.4	17.0
2	<i>Polyarthra remata</i>	1	3	24	65.6	203.3
2	<i>Polyarthra remata</i>	3	3	24	34.7	107.5
3	<i>Dreissena</i> veligers	2	3.7	24	13.4	11.3
3	<i>Dreissena</i> veligers	4	3.7	24	13.4	8.5
3	<i>Polyarthra</i> spp.	2	3.7	24	45.8	15.2
3	<i>Polyarthra</i> spp.	4	3.7	24	25.6	8.5
3	<i>Keratella</i> spp.	2	3.7	24	30.0	3.4
3	<i>Keratella</i> spp.	4	3.7	24	29.3	3.4
4a	<i>Polyarthra</i> spp.	6	3.7	50	24.5	5.6
4b	<i>Polyarthra</i> spp.	6	3.7	50	20.0	4.6

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⁻² and a mixed water column 7 m deep.

Predator	Predator density (ind.·m ⁻³)	Rotifer-based clearance rate (L·predator ⁻¹ ·d ⁻¹)	Impact (d ⁻¹)	Source
<i>Mysis relicta</i>	4.3	4.3	0.02	1
<i>Limnocalanus macrurus</i>	61	0.16	0.01	1
<i>Bythotrephes cederstroemi</i>	23	0.26	<0.01	2, 3, 4
<i>Senecella calanoides</i>	93	0.44	0.04	1
<i>Dreissena polymorpha</i>	714.3	0.99	0.71	5

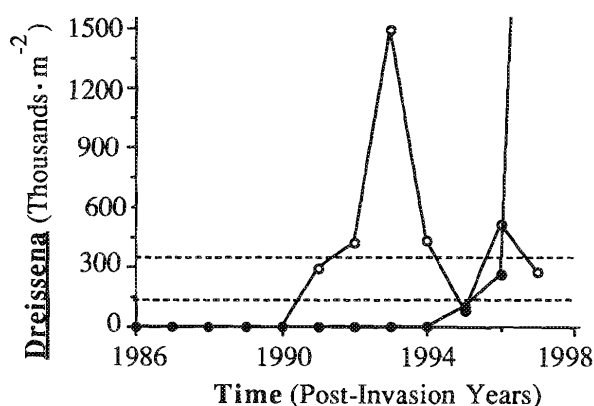


FIG. 7. Projected population abundance of *Dreissena* in western Lake Erie according to composite (open circles) and noncannibalistic (closed circles) models. The range of mean densities observed on reefs during 1990 is denoted by the broken horizontal lines (Fig. 1). Time of invasion is assumed to be 1986. Both models assume fecundity values of 1×10^4 , 2×10^4 , and 3×10^4 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 (5×10^9 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 8×10^4 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 copepodids. 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 siphonal 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

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; Stanczykowska 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 5×10^8 individuals (see Materials and Methods).

Model	Larval mortality rate (% of veligers produced)	Fecundity (eggs·female ⁻¹ ·yr ⁻¹)			Year 1990 mussel density reached	
		Age 1	Age 2	Age 3		
Noncannibalistic	99	10 ⁴	2 × 10 ⁴	3 × 10 ⁴	1996	
	99.5				1998	
	99	10 ⁴	2 × 10 ⁵	10 ⁶	1994	
	99.5				1996	
	Composite	70	10 ⁴	2 × 10 ⁴	3 × 10 ⁴	1990
		80				1991
90					1992	
70		10 ⁴	2 × 10 ⁵	10 ⁶	1990	
80					1991	
90					1991	

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 (Treasurer 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 10⁶ 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 Stanczykowska 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 (Stanczykowska 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.

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 mortality following nonpreferential 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 (Mikheyev 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 Rumian, 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 (Majcz Wielki, Poland) of which we are aware that clearly exhibited a total larval mortality rate lower than 99% is notable in that recruitment occurred primarily on "safe" settling substrates provided by plants (Lewandowski 1982). André and Rosenberg (1991) reported that settlement success of marine bivalve larvae was inversely related to the density of adults and reasoned that predation by adults may limit the recruitment of new individuals.

Dreissena Population Growth

Our noncannibalistic model clearly demonstrates that settled mussel densities observed in western Lake Erie during 1990 could not have been achieved if mortality of veligers to the settled subadult stage totalled 99%, even if optimistic reproductive schedules (Walz 1978b) and veliger inocula are employed (Table 3). Large increases in the fecundity of large mussels had little impact on time-to-current-density because these individuals represent only a small fraction of the total population (Lewandowski 1982; Mackie 1990; Hebert et al. 1991).

The composite model is consistent with population growth patterns in western Lake Erie. Populations in the basin are projected to demonstrate unrestricted growth for only the first few years, after which recruitment declines in relation to the density of predatory mussels. The recruitment decline observed in the lake between 1989 and 1990 (Garton and Haag 1990) can also be explained if exploitative competition between veligers, other herbivorous zooplankton, and benthic adult *Dreissena* resulted in high veliger mortality. This possibility seems unlikely because small-bodied zooplankton, such as rotifers, have low-threshold food levels (the food concentration at which energy intake equals metabolic losses) and should be less affected by declines in ambient food levels than larger species (Stemberger

and Gilbert 1987). Veligers are similar to many herbivorous rotifer species with respect to body size and the manner in which food is collected (ciliated velum versus ciliated corona) and may have similar food requirements. Any increase in veliger mortality associated with low food levels should be preceded or accompanied by a decline in population densities of large herbivorous zooplankton.

It can be argued that current mussel densities in the western basin have resulted, in part, from migration of mussels from unsuitable substrates to adjacent suitable ones. While this possibility exists, on at least a very local scale, mortality to the settled subadult stage would still have to be less than 99% because mussel migration, and higher population densities associated with it, is incorporated into mortality calculations for European lakes (Stańczykowska 1977; Lewandowski 1982; Sprung 1989).

Our models utilized current western basin *Dreissena* population size structure to determine the mortality between age-class compartments. While we have not defined the mechanisms responsible for intercompartment mortality, intraspecific competition is a likely possibility. Hebert et al. (1991) noted that mussel growth was least pronounced in areas where sessile populations were 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* population growth in western Lake Erie is shown in Fig. A.1. *Dreissena* populations consist of veliger, adult 1, adult 2, and adult 3 subpopulations. Total veliger production is determined as $\sum_{i=1}^3 \text{fecundity}_i \times (0.5 \times \text{adult}_i \text{ density})$ where i is age-class. Fecundities were initially set at 10^4 , 2×10^4 , and 3×10^4 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-yr-old mussel densities are shown below the model. Adult 1 age-class recruitment for the non-cannibalistic 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 5×10^8 veligers (see Materials and Methods). Densities of each adult age-class were calculated based on uniform distributions over $3.34 \times 10^8 \cdot \text{m}^{-2}$ 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 noncannibalistic model and between 1989 and 1990 for variants of the composite model.

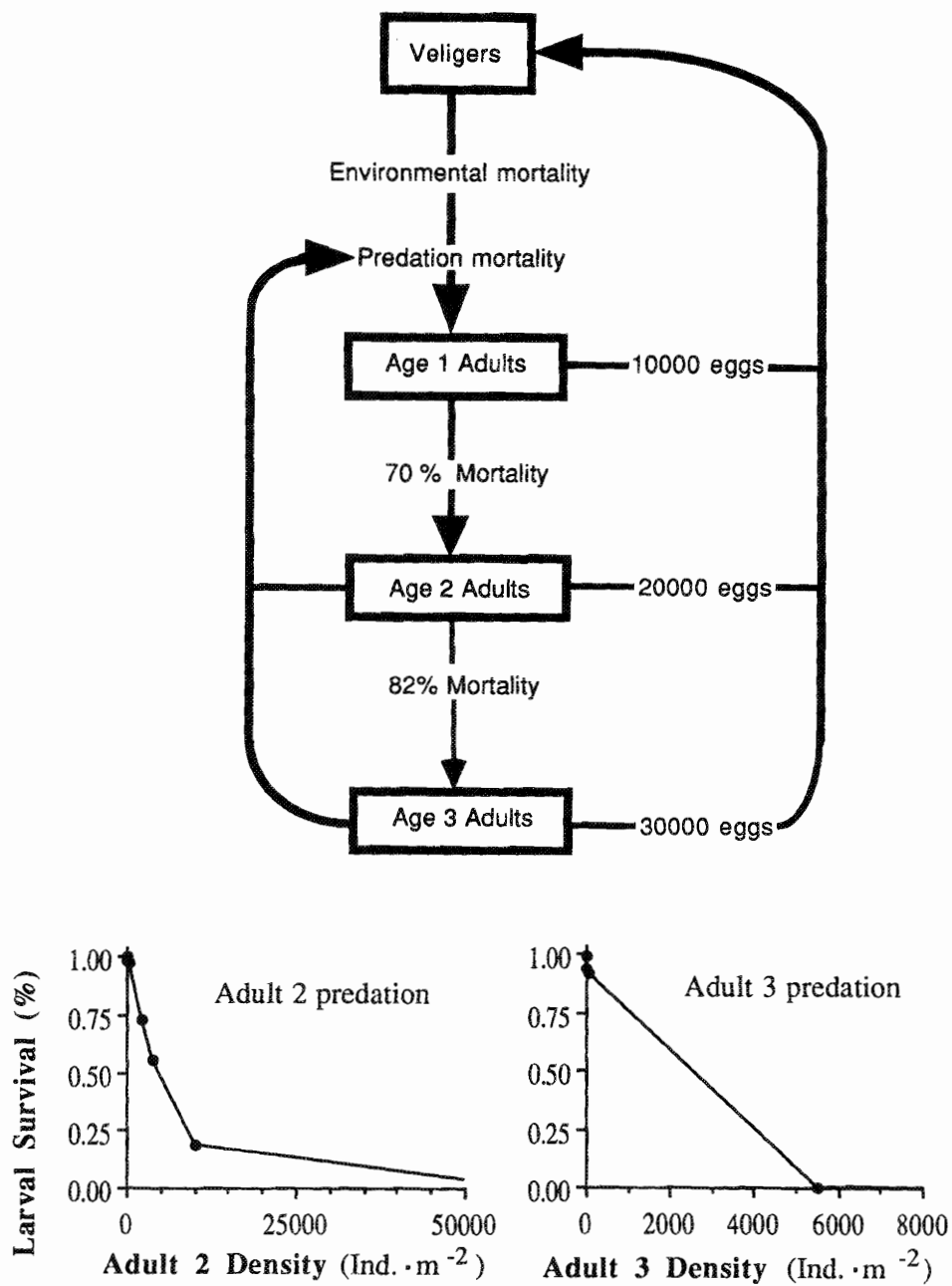


FIG. A.1. Schematic representation of a STELLA[®] composite model.

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