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# Vulnerability of *Dreissena polymorpha* Larvae to Predation by Great Lakes Calanoid Copepods: the Importance of the Bivalve Shell

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***ABSTRACT.*** Dreissena polymorpha *larvae were vulnerable to predation by three different species of calanoid copepods,* Diaptomus sicilis, Limnocalanus macrurus, *and* Epischura lacustris, *when presented to these copepods in bottle experiments. The degree of vulnerability was dependent upon the stage of the larva and the type of predator: trochophore larvae (without shells) were much more vulnerable than D-stage larvae (with shells).* D. sicilis *and* L. macrurus *were offered algae as alternate food, and each cleared trochophore larvae at a higher rate than algae. However, the clearance rate for* D. sicilis *feeding on D-stage larvae was not significantly different from zero, suggesting that this suspension-feeding omnivore-herbivore was not able to ingest D-stage larvae. Of the three species, the large cruising predator,* L. macrurus, *had the highest clearance rate for trochophore larvae (55.8 mL • animal$^{-1}$ • d$^{-1}$), but had a significantly lower clearance rate for D-stage larvae, only one eighth of that for trochophores. The smaller predator,* E. lacustris, *was more adept than* L. macrurus *or* D. sicilis *at preying on D-stage larvae: its clearance rate for D-stage larvae (17.9 mL • animal-1 • d$^{-1}$) was about one half of its clearance rate for trochophore larvae. Since bivalve larvae, including* Dreissena, *and copepods co-occur in many aquatic environments, our results suggest that copepod predation may have been a selective force for production of a protective shell early in the larval development of bivalves.*

***INDEX WORDS:*** *Zebra mussel, larvae, predation, zooplankton, Great Lakes.*

## INTRODUCTION

The pelagic larval stage may be the weak link in the life cycle of the zebra mussel, *Dreissena polymorpha.* Mortality is quite variable during the pelagic phase and can be very high (Stanczykowska 1978; Walz 1978; Sprung 1989, 1993). Sprung (1989) observed mortalities greater than 60% from trochophore to D-stage and greater than 99% from D-stage to settling. It is not clear to what extent environmental conditions, starvation, and predation affect this mortality rate. Little information is available on predation, however, there are anecdotal reports of larval fishes and cyclopoid copepods feeding on the larvae (Karabin 1978, Sprung 1989). Pelagic larvae range in size from 70–260 μm, which suggests that they may be vulnerable to calanoid copepods, which prey on a variety of microzooplankton—such as rotifers, ciliates, and nauplii—in this size range (Warren 1985, Schulze and Folt 1990, Burns and Gilbert 1993). The ecology of the larvae, including predation, must be investigated before we can understand the consequences of *Dreissena* invading an ecosystem such as the Great Lakes, and the possibility of their biological control. This study sought to explore the vulnerability of the larvae to calanoid predation, especially because of the recently recognized importance of calanoids, including suspension feeders, as predators of microzooplankton (e.g., Burns and Gilbert 1993).

The vulnerability of the larvae to predation may be strongly dependent on the stage of larval development. At summer temperatures (~20°C), the fertilized benthic eggs of *Dreissena* become pelagic larvae that swim using their cilia within several hours. This marks the beginning of their vulnerability to zooplankton predation. The trochophore larvae develop within 24 h and have a prototroch, or ring of cilia, which facilitates a directed swimming motion. After 2–4 d, veliger larvae develop their first D-stage shell (prodissoconch I), 90–100 μm in

length, and swim by means of a velum (Meisenheimer 1901, Galtsoff 1964, Bayne 1976, Sprung 1989). Depending on their development rate, the larvae may remain in the plankton for 8–30 d (Sprung 1989, 1993), if they survive to settling stage. When disturbed, a bivalve larva can close its shell to protect its soft body parts. Because the shell-like carapaces of certain cladocerans are known to offer protection against predation by predacious zooplankton (Kerfoot *et al.* 1980), we hypothesized that the D-stage shell is an important anti-predator device. We are not aware of any studies that have evaluated the importance of the shell in protecting pelagic bivalve larvae against predation.

To evaluate the vulnerability of *Dreissena polymorpha* larvae to predation and the protective value of the shell, we chose to work with two stages of larvae having the ability for directed swimming: the trochophore, which has no shell, and the early D-stage, which has a D-shaped bivalve shell. We presented the larvae to three calanoid copepods native to the Great lakes: *Diaptomus sicilis, Epischura lacustris,* and *Limnocalanus macrurus.* Each of these copepods was chosen to be representative of a particular type of predator, rather than a species that *D. polymorpha* would necessarily encounter in the field. *Diaptomus sicilis* is a suspension-feeding omnivore-herbivore (Vanderploeg *et al.* 1990). *Epischura lacustris* is a small predator of microzooplankton (Wong 1981, Wong and Sprules 1985, Schulze and Folt 1990). *Limnocalanus macrurus* is a large cruising predator of micro- and mesozooplankton (Warren 1985, Wong and Chow-Fraser 1985, Wong and Sprules 1986).

## METHODS

The zooplankton used in this study were collected by towing a 153-μm mesh plankton net vertically through the water column. *Epischura lacustris* were collected from Whitmore Lake, Michigan, on the day before each experiment. *Diaptomus sicilis* and *Limnocalanus macrurus* were collected from offshore Lake Michigan 1–14 d before each experiment. All were brought back to the Great Lakes Environmental Research Laboratory (GLERL) in Ann Arbor, Michigan, and kept at ambient lake temperature (11–12°C for Whitmore Lake and 4–5°C for Lake Michigan hypolimnion) until the day before an experiment, at which time they were acclimated to 10°C, the experimental temperature. Previous experience with lipid-rich *D. sicilis* and *L. macrurus* showed that they could be held for periods of 1 month or more without negative effects on survival or feeding rate (Vanderploeg *et al.* 1990).

To obtain *Dreissena polymorpha* larvae used in experiments, mussels maintained in our laboratory were induced to spawn using serotonin, after methods modified from Ram *et al.* (1993). Ripe broodstock mussels were captured from western Lake Erie and Thunder Bay (Lake Huron) during June and July, respectively. These stocks were maintained in ripe condition in aerated aquaria at 4–6°C (Bayne 1965) with daily feeding of concentrated *Thalassiosira pseudonana* ('Algae Diet I' from Coast Seafoods Co., South Bend, Washington) until needed for production of larvae. The mussels were gradually warmed to the spawning temperature of 17°C over 4–14 d. Spawning was induced using $10^{-4}$ M serotonin in 0.2-μm filtered water from the Huron River near Ann Arbor, Michigan, and each of the approximately 20 mussels spawned for an experiment was confined to a single 50-mL beaker. After gamete production started, the mussel was rinsed and transferred to a new beaker containing only filtered river water to complete spawning. Males invariably produced sperm before females spawned. Sperm suspension produced by all of the males was collected and about 1 mL added to each beaker containing a female to further encourage egg production and fertilization. The concentrated suspension of fertilized eggs was diluted to 10 eggs • $mL^{-1}$ and held at an appropriate temperature for either rapid or slow development. The trochophore larvae were 1 d old (at 10°C), and the D-stage larvae were 2–3 d old (at 22–25°C) at the start of an experiment. D-stage larvae were gradually acclimated to 10°C a few hours before the experiment.

Experiments were conducted with copepods (*Epischura lacustris, Diaptomus sicilis,* or *Limnocalanus macrurus*) feeding on *Dreissena polymorpha* trochophore or D-stage larvae. Prey concentrations of 1.0 larvae • $mL^{-1}$ (= 0.2 $mm^3$ • $L^{-1}$) *Dreissena* larvae and 265 cells • $mL^{-1}$ (= 0.2 $mm^3$ • $L^{-1}$) *Cryptomonas reflexa* in 0.2 μm filtered lake water were used in experiments with *Diaptomus* and *Limnocalanus. Cryptomonas* was cultured in filter sterilized WC medium (Guillard and Lorenzen 1972) at a light intensity of about 70 μEinst • $m^{-2}$ • $s^{-1}$ at 15°C with a 16:8 L:D cycle. Cells used in the experiment were in exponential phase growth. Initial concentrations and volumes of larval bodies and algal cells were determined with a model TA II Coulter Counter. The 0.2 $mm^3$ • $L^{-1}$ concentration of *Cryptomonas* is below the incipient limiting concentration for *D. sicilis* (Vander-

ploeg *et al.* 1984). This highly desirable algal food served as a check that *Diaptomus* and *Limnocalanus* were feeding well, in case no larvae were eaten. The feeding rate of *Epischura* on algae (Chow-Fraser and Wong 1985) was deemed to be too low to serve as a check, so experiments with *Epischura* were conducted in suspensions of 1.0 larvae • $mL^{-1}$ only in 0.2 μm filtered lake water. The feeding suspension was made and poured among duplicate 600-mL control bottles and triplicate 600-mL experimental bottles just prior to the start of an experiment. To start an experiment, 60 *Diaptomus* females, 40 *Limnocalanus* females, or 30 *Epischura* females were added to the experimental bottles containing the feeding suspension. Then the control and experimental bottles were placed on a rotating wheel at 0.5 rpm at 10°C in dim light (4–8 μEinst • $m^{-2}$ • $s^{-1}$) with a 12:12 L:D cycle. The experiments were ended by pouring the entire bottle contents through a 400-μm screen to remove the copepods. The bottle contents were then filtered (using a very low vacuum pressure to avoid damaging the larvae) through a 25-mm Poretics polycarbonate membrane filter of 18-μm pore size to collect the larvae. A Whatman GF/F glass fiber filter beneath the membrane filter collected the algae for chlorophyll analysis. The membrane filter holding the larvae was placed upside down into a cylindrical 2-mL plankton counting chamber containing water with a few drops of surfactant and formalin for counting on an inverted microscope. The surfactant was used to break the surface tension so the filter would settle to bottom of the chamber. The filter was placed in a counting chamber instead of on a microscope slide because the larvae were often crushed by the slide cover glass.

Clearance rates (F) for the larvae and the fluorometrically determined chlorophyll (Parsons *et al.* 1984) for each experimental bottle were calculated as $F = V[\ln(C/Z)]/tN$; where V is the volume of a bottle, C is the final mean concentration in control bottles, Z is the final concentration in the experimental bottle, t is the duration of the experiment, and N is the number of copepods per bottle (Vanderploeg *et al.* 1984). In some experiments, attacks on D-stage larvae left behind shell fragments that were not ingested, so two different clearance rates were calculated. To determine the clearance rate for which more than 50% of a larva was ingested, those larvae that were 50–100% intact were included in the count for Z; counts of whole larvae only were used to determine the clearance rate for attack on D-stage larvae (Vanderploeg *et al.* 1988).

Controls were used to determine if the larval prey had died or developed to another stage during the experiment. Microscopic examination of trochophore larvae verified that they did not metamorphose into D-stage larvae. Trochophore and D-stage larvae were similar in size at the end of each experiment, 80–110 μm in diameter and 90–110 μm in length, respectively. In preliminary experiments, larval counts in final controls were 96–100% of those in initial controls, indicating that nonpredatory mortality was low or nonexistent.

## RESULTS

All three copepod species fed on trochophore larvae, with *Limnocalanus* exhibiting the highest clearance rate; however, *Epischura* had the highest weight-specific clearance rate (Table 1). Clearance rates for *Dreissena* larvae by all three species were significantly higher (t-test, $P < 0.001$) for trochophores than they were for D-stage veligers. *Diaptomus sicilis* was able to feed very well on trochophore larvae, clearing them at a rate twice that for *Cryptomonas*. As indicated by the very low clearance rate on the D-stage larvae, which was not significantly different from zero, *Diaptomus* did not attack, or was unable to ingest, the larvae with shells. *Limnocalanus macrurus* was able to ingest the D-stage larvae, albeit not efficiently, as shown by a clearance rate for D-stage larvae one-eighth of that for trochophores. Pieces of broken shell found in the bottles and the higher clearance rate for attack than for ingestion for the *Limnocalanus* experiments provided evidence that *Limnocalanus* had difficulty ingesting larvae with shells (Table 1). In contrast, *Epischura lacustris* apparently was more effective at handling and ingesting the D-stage larvae, since it cleared them at a rate of only about one half of the clearance rate for the trochophore larvae. Moreover, no broken or empty shells were found in the *Epischura* experiment, implying that *E. lacustris* was able to ingest the entire larva with shell in one piece or efficiently ingest it in pieces.

## DISCUSSION

The larval bivalve shell may play an important role in providing protection from some predators. Since *Dreissena* larvae are in the water column for 8-30 d (Sprung 1993), predation by copepods is potentially a significant source of mortality. *Dreissena* larvae are not strong swimmers (personal observation) and probably cannot escape most predators by

*TABLE 1. Vulnerability of* **Dreissena** *larvae before and after formation of D-stage shell to three omnivorous calanoid copepods, expressed by clearance rates of the predators on* **Dreissena** *alone* **(Epischura)** *or in mixtures with* **Cryptomonas reflexa (Diaptomus, Limnocalanus).** *Because* **Limnocalanus** *did not always completely ingest all D-stage larvae attacked, clearance rates for larvae ingested and attacked are given. Values in parentheses below numbers are clearance rates normalized per µg dry weight of predator.*[a]

| Predator | | | Clearance rate (mL • animal $^{-1}$ • d$^{-1}$) | | | |
|---|---|---|---|---|---|---|
| | | | Before shell | | After shell | |
| Species | Prosome length (mm) | Dry wt. (µg) | *Cryptomonas* | Trochophore | *Cryptomonas* | D-stage veliger |
| *Diaptomus sicilis* | 1.2 | 17 | 11.64±1.03 (0.68) | 23.26±0.52 (1.37) | 16.26±0.61 (0.96) | 0.47±0.31 (0.03) |
| *Epischura lacustris* | 1.2 | 11 | — | 33.75±0.85 (3.07) | — | 17.86±1.47 (1.62) |
| *Limnocalanus macrurus* | 1.8 | 45 | | | | |
| Ingested | | | 1.64±0.49 (0.04) | 55.80±5.40 (1.24) | 1.52±0.65 (0.03) | 6.99±1.23 (0.16) |
| Attacked | | | | | | 9.78±1.13 (0.22) |

[a]Dry weights are mean values from Hawkins and Evans (1979).

swimming away. Our results suggest that the larval shell foils predation to some degree by at least some copepods. Note that we are primarily interested in relative predation rates on trochophore and D-stage larvae. Due to a higher than optimal density of predators in each experimental bottle in terms of predator interference (Schulze and Folt 1989, Ramcharan and Sprules 1991), our clearance rates on *Dreissena* larvae may have been less than maximal. Nevertheless, trochophore larvae were ingested at a high rate by all three copepod species, and D-stage larvae were ingested at a significantly lower rate in each case. The differential feeding on the two larval stages probably can be attributed solely to the D-stage shell because other factors (e.g., size, swimming ability) were essentially the same for both stages of larvae.

The shell possibly inhibits predation in two ways. First, the larva may escape mechanical detection by closing its shell and falling relatively quietly through the water column as has been described for the akinesis response of *Bosmina* and *Chydorus* (Kerfoot *et al.* 1980). Second, the rigid shell may make handling and ingestion more difficult. The ability of *E. lacustris* to handle D-stage larvae possibly relates to its ability to prey on small cladocerans that have bivalve carapaces (Kerfoot *et al.* 1980). *E. lacustris* (prosome length = 1.2 mm) has well developed predatory mandibles that are about the same size as the larger predator (prosome length = 1.8 mm), *L. macrurus* (Wong 1984). Perhaps L. macrurus was not as successful as *E. lacustris* because *L. macrurus* is adapted to larger soft-bodied prey such as copepods (Wong and Chow-Fraser 1985). Also, because the maxillae and maxillipeds of L. macrurus are larger than those of *E. lacustris* (Wong 1984), *L. macrurus* may not be adept at holding the small hard-bodied D-stage larva for ingestion. All of the mouthparts of *D. sicilis* are much smaller than those of *E. lacustris* and *L. macrurus* (Wong 1984) and may be inadequate for handling and breaking the larval shell. Moreover, *D. sicilis* has a mouth opening of about 35 µm in diameter (Vanderploeg 1981) which is too small for ingesting the rigid D-stage larva whole. Films or videotapes of the handling process for each species would provide further insight.

*Dreissena* larvae are especially vulnerable to predation at the trochophore stage. Each of the copepods tested had high clearance rates for trochophore larvae that were consistant with, but lower than, clearance rates for microzooplankton (Table 2) in other studies (Warren 1985, Burns and Gilbert 1993). The lower rates in these experiments may have been the result of the relatively high density of predators (Schulze and Folt 1989, Ramcharan and Sprules 1991). Temperature may have been another factor, because other studies of *Diaptomus* and *Epischura* were done at higher temperatures (Table 2), which may increase feeding rates. The lower

***TABLE 2. Clearance rates (F) of* Diaptomus *spp.,* Epischura lacustris, *and* Limnocalanus macrurus *on algae and microzooplankton in other studies.***

| Predator | Temp (°C) | Prey | | F |
|---|---|---|---|---|
| | | Item | Size (μm) | (ml • [animal • d]$^{-1}$) |
| *Diaptomus pallidus*[a] | 20 | *Synchaeta* | 140 | 167 |
| *Diaptomus pygmaeus*[b] | 20 | *Strombolidium* | 61 | 73 |
| *Diaptomus sicilis*[c,d] | 10 | *Chlamydomonas* | 14 | 14-25 |
| *Epischura lacustris*[b] | 20 | *Strombolidium* | 61 | 516 |
| *Epischura lacustris*[e] | 10 | *Pediastrum* | 30-40 | 1.8 |
| *Epischura lacustris*[e] | 10 | *Scenedesmus* | 4-5 | 0.05 |
| *Limnocalanus macrurus*[f] | 4 | Copepod nauplii | 260 | 206 |
| *Limnocalanus macrurus*[g] | 0.2 | *Chlamydomonas* | — | 1.0 |

[a]Williamson and Butler 1986; [b]Burns and Gilbert 1993; [c]Vanderploeg *et al.* 1984, [d]1988; [e]Chow-Fraser and Wong 1985; [f]Warren 1985; [g]Kibby and Rigler 1973.

clearance rate for *L. macrurus* preying on trochophores relative to nauplii may imply that trochophores are too small for efficient detection by these large cruising predators. Clearance rates by *D. sicilis* and *L. macrurus* for *Cryptomonas* were in the expected range (Kibby and Rigler 1973, Vanderploeg *et al.* 1984). Since *D. sicilis* is a suspension feeder with strong herbivorous tendencies, its high clearance rate for trochophore larvae, higher than that for *Cryptomonas,* suggests that trochophores are extremely vulnerable to any planktonic copepod that they encounter. The preference of *D. sicilis* for trochophores over *Cryptomonas* is consistant with other recent studies of suspension-feeding calanoid copepods showing a preference for microzooplankton such as rotifers and ciliates over algae (Williamson and Butler 1986, Burns and Gilbert 1993, Hartmann *et al.* 1993). This preference is related to the greater distance at which copepods detect microzooplankton relative to algae (Williamson and Vanderploeg 1988).

The D-stage bivalve shell of *Dreissena* and coastal marine oysters, clams, and mussels develops rapidly in the life of the larva (e.g., Meisenheimer 1901, Galtsoff 1964, Bayne 1976, Sprung 1989). In coastal marine environments, copepods are abundant and, therefore, potential predators of bivalve larvae in those environments. Marine veliger larvae are protected by their bivalve shell when they are captured, but not digested or killed, by the medusa stage of the scyphozoan *Chrysaora quinquecirrha* (Purcell *et al.* 1991). Because of the effectiveness of the larval bivalve shell as an antipredation foil, we speculate that copepod and other invertebrate predation may have been a selective force for shell development early in larval life.

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