

Susceptibility of larval dragonflies to zebra mussel colonization and its effect on larval movement and survivorship

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Received: 11 April 2008 / Revised: 19 November 2008 / Accepted: 4 December 2008 / Published online: 24 December 2008
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Abstract Colonization by the zebra mussel, *Dreissena polymorpha*, was quantified for five dragonfly species that differed in size and larval habits in a Michigan lake. Both larger size and a non-burrowing habit independently increased susceptibility to colonization. In 2005, over 50% of the final instars of the sprawlers *Didymops transversa* and *Hagenius brevistylus* were colonized, as well as younger instars. Rarely colonized were *Progomphus obscurus* and *Dromogomphus spinosus*, whose larvae burrow under sand, and the sprawler *Epitheca princeps*, whose final instars were lightly covered with sand. *Hagenius* larvae that had been preyed upon carried more mussels than those dying of other causes. More generally, mussel attachment decreased the probability that sprawlers left the water to emerge, the distance that some species traveled before emerging, and the ability of an overturned sprawler to right itself. On average, final instars of *Didymops* and *Hagenius* remaining in the water carried three times as many mussels as individuals known to emerge.

Compared to uncolonized individuals, *Epitheca* and *Progomphus* with mussels emerged closer to the water line. Among colonized *Didymops*, the distance traveled on land before emerging decreased with increasing mussel load. Of the colonized *Didymops* that could right themselves, righting time increased with mussel load. Because the two common species of sprawlers were disproportionately colonized, and mussel attachment decreased their chances of emerging, our results suggest that *D. polymorpha* has the potential to affect the community structure of this guild of aquatic and terrestrial predators.

Keywords *Hagenius* · *Didymops* · *Epitheca* · *Progomphus* · *Dromogomphus* · *Dreissena* · Invasive species · Mobility · Dragonfly community structure

Introduction

Since its introduction to the Great Lakes in the mid-1980s, the zebra mussel, *Dreissena polymorpha*, has devastated native unionid mussel populations (Haag et al., 1993; Nalepa, 1994; Schloessner & Nalepa, 1994; Lauer & McComish, 2001), and has affected ecosystems more generally (e.g. Greenwood et al., 2001; Haynes et al., 2005). Although zebra mussel attachment on dragonflies has been documented, their impact on these important aquatic predators remains unknown. In a review of the occurrence of zebra

Handling editor: R. Bailey

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mussels on final instar larvae from the families Gomphidae, Corduliidae, and Libellulidae in Europe, Canada, and the US, Weihrauch & Borchering (2002) mentioned only incidental sightings of zebra mussels on a few larvae per site.

In sandy bottom habitats that provide relatively few nonliving substrates for zebra mussel attachment, a decline in large-shelled unionids may increase the colonization risk other living substrates such as benthic odonate larvae. For example, in Douglas Lake, a mesotrophic kettle lake in northern Michigan, *D. polymorpha*, was first recorded in 2001. The initial rise in the zebra mussel population was followed by a decrease in unionid mussels (R. Vande Kopple, pers. comm.). At this site, zebra mussels were first observed on dragonfly larvae in the lake in 2003 (B. Scholtens, pers. comm.). In May 2005, McCauley & Wehrly (2007) quantified high rates of colonization on final instars of the dragonflies *Hagenius brevistylus* and *Didymops transversa*. However, their one-day study did not address any fitness consequence of mussel attachment.

The aim of the current study was two-fold. First, we asked whether some species in the Douglas Lake odonate community were more susceptible than others to colonization by zebra mussels. Secondly, we asked how zebra mussels affected larval growth, survivorship, and mobility. Our study species were five common dragonflies from three families that differed in final instar size and larval behavior. Of the five, *Hagenius brevistylus* (Gomphidae), *Didymops transversa* (Micromiidae), and *Epitheca princeps* (Corduliidae), are classified as ‘sprawlers’ because their larvae rest on top of the substrate (Needham et al., 2000). The largest of the five species, *H. brevistylus*, is unique in having a discoid abdomen, which may make it more susceptible to mussel colonization, despite the fact that its larvae hide under debris (Walker, 1958). In contrast to the sprawlers, the larvae of *Dromogomphus spinosus* and *Progomphus obscurus* (Gomphidae) burrow 1–2 in. into the sand, hiding from predators and potential prey (Walker, 1958). We predicted that dragonflies with a sprawling lifestyle and relatively large final instar size were at increased risk of colonization by zebra mussels.

We hypothesized that zebra mussels negatively affect larval fitness by decreasing larval mobility, and thereby indirectly decreasing growth rate and/or survivorship to emergence. Of course, by covering the mouthparts (Fig. 1A) or the area of the dorsal

thorax through which the adult dragonfly emerges (Fig. 1B), zebra mussels can prevent feeding or eclosion directly. If larval mobility interferes more generally with foraging ability and/or predator avoidance, then final instars with mussels should be smaller than those without mussels, and/or more likely to exhibit evidence of predation (Fig. 1C). And because all final instars of the study species must crawl out of the water to emerge, another fitness cost of zebra mussel attachment may be to prevent a larva from reaching shore, or, once there, from traveling a sufficiently safe distance from water before emerging. The burrowers’ *Progomphus obscurus* and *Dromogomphus spinosus* typically emerge on the beach, although the latter can also emerge on trees adjacent to shore. Larvae that emerge at the water’s edge risk getting doused by waves before their wings have fully extended, making subsequent flight impossible. *Hagenius brevistylus* often emerges on the beach but can occasionally be found as high as a meter up on trees in the forest. *D. transeversa* larvae travel far from shore, climbing as high as 9 m before emerging on a tree (O. M. Fincke, unpubl. data). In addition to impeding travel on land, its mussel load may hamper the ability of a larva to right itself when overturned, as sometimes occurs if it encounters wave action while crawling or swimming to shore, or falls while crawling up a vertical surface (O. M. Fincke, unpubl. data). We predicted that increasing mussel load: (1) is negatively correlated with distance traveled on land before emergence, and (2) decreases the ability of a larva to right itself.

Materials and methods

The study site was the eastern portion of Douglas Lake and its shoreline at the University of Michigan Biological Station (UMBS, 45°35’N, 84°42’W) near Pellston, MI, USA. The study species can take up to 4 years to develop (Corbet, 1999). At this site, *Didymops transversa* emerges from late May to early August. *Epitheca princeps*, *Dromogomphus spinosus*, *Progomphus obscura*, and *Hagenius brevistylus* emerge from late May or early June to mid July (O. M. Fincke, unpubl. data). For simplicity, the study species are hereafter referred to by genus only.

Between 28 June and 5 August 2005, larvae found in the water and on the beach were collected along a

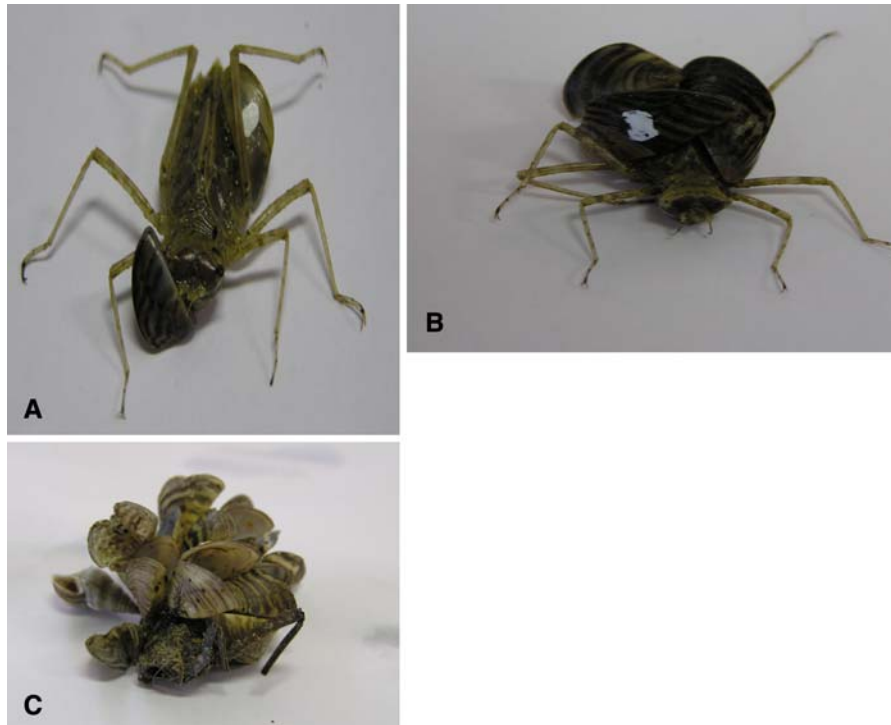


Fig. 1 Effects of zebra mussels on dragonfly fitness: **A** *D. transversa* with zebra mussel attachment that impedes prey capture, **B** zebra mussels positioned such that they prevent

emergence in *D. transversa*, **C** evidence of predation on a heavily colonized *H. brevistylus*, which is missing its head

transect that ran from the eastern end of South Fishtail Bay to Pine Point. In areas of shallow water, larva were collected as far out as 12 m but were more regularly collected 5–7 m from the water line, which was marked off in 1 m sections with flagging. Most sampling in the water was done between 06:00 and 10:00 h when the water was calm and larvae could be detected most easily. Species identity of larvae and exuvia and their distance from the water line were recorded. Although on a daily basis, the width of beach was stable at a given location (i.e. tidal effect was minimal), the water line receded seasonally. To avoid recounts of the same individual, all exuvia were collected. Unless marked with paint and released (see Fig. 1B), live individuals found in the water were held in tanks of lake water at Lakeside Lab for observations, and returned to the lake at the end of the study.

To assess whether mussel attachment increased the probability of predation or premature death of a final instar larvae, the state of a collected larva was scored as living, dead, or ‘exuvia’ (cast skins). Exuvia were

considered evidence of a successful emergence. An intact, dead larva with mussels blocking the central portion of the thorax where the larva emerges was considered a failed emergence due to mussels. Dead larvae that were lacking the head or part of the body were considered to have died from a predation event. The cause of mortality was otherwise undetermined. For each live individual or exuvia, the number of attached zebra mussels was noted.

To determine the effect of larval size on the probability of colonization across species, and to assess indirect effects of zebra mussel load on the growth of final instars, for a subset of dragonflies head width, body length, and abdominal width at the widest part, and the length of all attached mussels were measured with calipers. Body area was estimated as the product of body length and width. A few live individuals of similar size with and without zebra mussels were patted dry and weighed to estimate variation in mussel loads. Additionally, we used a power function (mussel mass = $9.1 \times 10^{-5} \times$ mussel length^{3.09}) determined by McCauley & Wehrly (2007)

to calculate a comparative measure of load as mussel mass/body area of the larval dragonfly.

To determine the extent to which larvae younger than final instars were colonized, on 24 and 25 July and 1 August, 2007, *Hagenius* and *Didymops* larvae were collected from water <1 m deep in a 222 m² area near the drop-off of by East Point in North Fishtail bay, and by the boat-well of UMBS. These larvae were not visible from the surface, and were caught by using a D-shaped net to scoop up sandy substrate near vegetation and debris. The number of attached zebra mussels and the size of the dragonflies were quantified as above. In the lab, each larva was kept individually in a 10.2 cm diameter cup with a sand substrate and filled with lake water. Any molting that occurred over the 2-week holding period was noted and the larva subsequently re-measured. These data allowed us to estimate the size range of final instars, penultimate (i.e. next to last instar, F-1) and younger instars of *Hagenius* and *Didymops*.

To test the effect of mussel attachment on the ability of a larva to right itself, a lab experiment using the above field-collected individuals was conducted between July and August 2007. Two *Hagenius* larvae, with two and three attached mussels, respectively, were unable to right themselves after a period of 2 h. Hence, further righting trials were done only using *Didymops*. In a pan of water with a sand substrate, a larva was placed upside down with its abdominal dorsum touching the sand and then released. The time required for the larva to flip back to its natural resting position, rounded to the nearest second, was recorded. Failure to right within 20 s was scored as 'no flip'. The mean of three trials per individual per day was used for comparisons. To control for variation in condition among individuals, each larva was used as its own control. After recording the righting time without mussels attached, we induced mussel colonization by covering each larva with zebra mussels overnight. This procedure was repeated for 6 days during which time one or more zebra mussels usually attached to a larva. Righting trials were then conducted on larvae with one or more mussels attached. Afterward, the larva and its mussels were patted dry and weighed. The mussels were then removed and the larva reweighed to calculate mussel load in terms of proportion of larval weight. Three final trials were run on the larvae without mussels to serve as a control for any possible

loss of condition while in the lab. All of the dragonfly larvae were then released back into the lake.

Distance and morphological data were log transformed for analyses (i.e. GLM, *t*-tests, correlations) using SAS 9.1 (SAS Institute, Cary, NC). The probit function (i.e. logistical regression on binomial data) was used to determine the independent effects of life history and size on the probability of mussel colonization. Throughout, means are reported as \pm SEM.

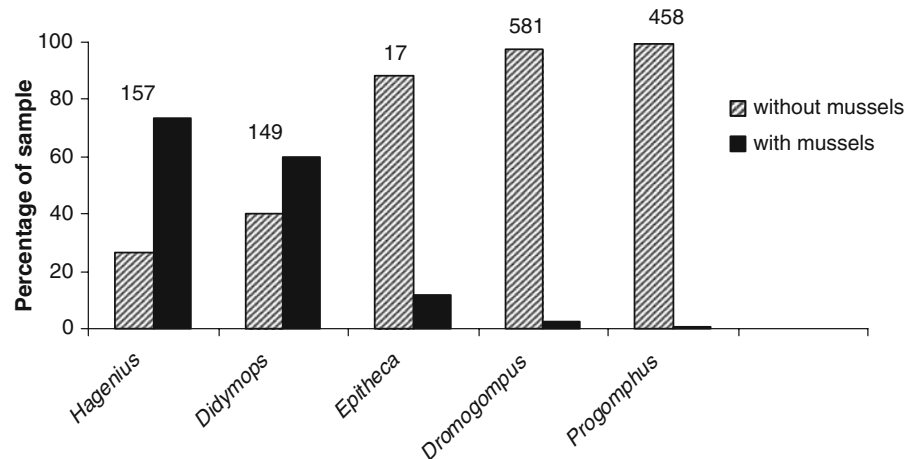
Results

Colonization rates across species, years, and instars

The five study species differed significantly in the body area of final instars ($F_{4,435} = 770.8, P < 0.001$). *Hagenius* was the largest species, with a mean body area of $628.3 \pm 18.8 \text{ mm}^2$ ($n = 42$). *Didymops* did not differ in size ($\bar{x} = 262.7 \pm 5.8 \text{ mm}^2, n = 46$) from *Epitheca* ($\bar{x} = 276.9 \pm 8.9 \text{ mm}^2, n = 8$, Bonferroni test, $P > 0.05$). Final instars of those two species were larger than those of *Dromogomphus* ($\bar{x} = 176.8 \pm 2.6 \text{ mm}^2, n = 223$), which in turn were larger than those of *Progomphus* ($\bar{x} = 146.6 \pm 2.8 \text{ mm}^2, n = 121$, Bonferroni test, $P < 0.05$). In 2005, all of the *Epitheca* (range = 21–25 mm in body length), and *Progomphus* (23–36 mm) and 97% of the *Dromogomphus* (28–29 mm) were collected as exuvia, compared to 75% of the *Hagenius* (22–40 mm) and 67% of *Didymops* (19–30 mm).

Dragonflies were colonized non-randomly with respect to species (Fig. 2). The highest percentage of colonization by zebra mussels in the 2005 sample were on the sprawlers *Hagenius* (74%) and *Didymops* (60%), which did not differ in the proportion of individuals colonized (Fisher exact test, $N = 285, P = 0.25$). Although similar to *Didymops* in size, *Epitheca* was less likely to be colonized ($X^2 = 11.8, \text{df} = 1, P < 0.001$). Nevertheless, as a group, sprawlers were still more likely than the two burrowing species to be colonized by one or more zebra mussels ($F_{1,1359} = 578.0, P < 0.001$). However, compared with the burrowers, the three sprawlers also had a greater surface area available for colonization ($F_{1,448} = 479.2, P < 0.001$). Considering only the subset of individuals that were in the same size class as the burrowers that were colonized (i.e. 140–225 mm²),

Fig. 2 Frequency of dragonfly larvae that were colonized (i.e. ≥ 1 mussel) in 2005. Numbers above the bars are the total samples of live and dead larvae plus exuvia



sprawlers were still more likely than burrowers to be colonized ($X^2 = 212$, $df = 1$, $P < 0.001$). Hence, the probability of being colonized increased both with larval size (logistic regression, Wald $X^2 = 5.0$, $P = 0.025$) and with sprawling behavior by larvae (Wald $X^2 = 180.6$, $P < 0.001$). Although they did not burrow into the sand, final instars of *Epiteca* and less frequently, *Didymops*, were found with their bodies (but not the legs) covered lightly with sand.

Of the 26, exuvia of *Hagenius* found on the beach at Pine Point in late July and early August of 2007, 38% had zebra mussels attached. Of the 21 *Didymops* found, 14% had been colonized, significantly fewer than were colonized in our 2005 sample (Fisher exact test, $P < 0.001$ for each group, $N = 170$ *Didymops*, $N = 183$ *Hagenius*). The only individual found on the beach that did not successfully emerge was a *Hagenius* larva with five zebra mussels attached.

The larval density in the littoral zone off of East Point was 0.19 m^{-2} for *Didymops* and 0.05 m^{-2} for *Hagenius*. One of the 48 *Didymops* (2%) and one of the 11 *Hagenius* (18%) found in the water were colonized by one and two mussels, respectively. Most of the larvae collected were smaller than final instars; the mean length of *Didymops* was 21.72 mm and that of *Hagenius* was 21.98 mm. Nine *Didymops* and one *Hagenius* molted to a subsequent instar while in the lab. None of the molted larvae had any mussels attached. The average growth ratio between molts for *Didymops* was 1.18, as measured by changes in head width. Based on the size gaps among the collected larvae, we conservatively estimated that final instars of *Didymops* were ≥ 23 mm in length and for

Hagenius, ≥ 27 mm in length. This indicated that in the 2005 sample, four of the *Didymops* and five of the *Hagenius* larvae found were younger than final instars. Of those, one *Didymops* and three *Hagenius* were colonized by 1–2 zebra mussels. Pooling across the two study years, we estimated that 3% of the penultimate instars of *Didymops* (20–22.7 mm) and 27% of penultimate instars of *Hagenius* (22.5–26.4 mm in length) were colonized by one or more zebra mussels.

Effects of mussel attachment on survivorship, growth, and movement

In our 2005 sample, all of the *Progomphus* and *Epiteca*, and 97% *Dromogomphus* that were colonized carried only a single zebra mussel; 3% of the *Dromogomphus* carried 2–3 mussels. In contrast, of the colonized *Didymops*, 27% carried 2–6 mussels and 46% of the colonized *Hagenius* carried from 3 to 15 mussels. However, the number of attached mussels did not increase with the area available for colonization (*Didymops*: $r = 0.16$, $N = 48$, $P = 0.28$; *Hagenius*: $r = 0.12$, $N = 47$, $P = 0.40$). Attached zebra mussels varied considerably in size and, hence, weight. For example, one *Didymops* individual with one zebra mussel weighed 1.221 g, $\sim 97\%$ more than a *Didymops* of similar size without mussels (0.617 g). A similar-sized *Didymops* with two zebra mussels had an additional 92% more weight to carry, and one with three zebra mussels carried 302% more weight than an individual of similar size that lacked mussels. One *Hagenius* without mussels weighed 1.254 g, whereas another of similar size with one small zebra mussel

weighed 1.343 g, a gain of only 7%. In addition to mussels, six *Didymops* also carried from 1 to 4 small stones that were caught in the byssal threads of the mussels.

Dead larvae were smaller than those that successfully emerged for *Hagenius* ($t = -2.36$, $P = 0.03$) and *Dromogomphus* ($t = -9.21$, $P = 0.0002$), but not for *Didymops* ($t = -1.26$, $P = 0.22$). Although dead larvae were not more likely to have been colonized (i.e. by at least one mussel) than live larvae or exuvia (Fisher Exact tests, $P > 0.05$ for all three species), the number of mussels attached did have an indirect effect on *Hagenius* survivorship. The 38 dead *Hagenius* larvae had more mussels ($\bar{x} = 4.1 \pm 0.70$) than live *Hagenius* and exuvia ($\bar{x} = 2.07 \pm 0.18$ mussels, $t = 2.83$, $P = 0.007$). Furthermore, the 13 *Hagenius* larvae that had been preyed upon had more mussels attached ($\bar{x} = 7.31 \pm 0.58$) than the 25 that died of other causes ($\bar{x} = 2.44 \pm 1.3$ mussels, $t = -3.37$, $P = 0.004$). In contrast, live *Didymops* and exuvia did not carry fewer mussels than dead individuals ($t = -0.54$, $P = 0.60$). Although the five *Didymops* larvae that were preyed upon had fewer mussels attached ($\bar{x} = 0.2 \pm 0.2$ mussels) than the 30 dead ones ($\bar{x} = 1.17 \pm 0.30$ mussels), this difference was not significant ($t = 2.68$, $P = 0.13$).

For two of the sprawlers, mussel load decreased the probability that a final instar left the lake to emerge. Final instars of *Hagenius* and *Didymops* that were known to have emerged by late July carried fewer mussels than the final instars found in the water ($t = -3.17$, $P = 0.01$ and $t = -3.71$, $P = 0.0004$ for *Hagenius* and *Didymops*, respectively, Fig. 3). Similarly, the estimated total mass of mussels on final instars of *Hagenius* in the water ($\bar{x} = 0.56 \pm 0.34$ g) was greater than the mass of mussels on larvae that had emerged on shore ($\bar{x} = 0.22 \pm 0.04$ g, $t = -2.63$, $P = 0.01$). This comparison for *Didymops* was precluded due to the lack of data on the size of attached mussels on *Didymops* collected from the water.

Of the five study species, uncolonized final instars of *Epitheca* and *Progomphus* traveled farther on land than those with mussels attached ($t = 2.6$, $P < 0.01$, $t = 3.62$, $P < 0.002$, *Epitheca* and *Progomphus*, respectively, Fig. 4). The correlation between the distance traveled and the number of mussels attached was not significant for *Didymops* ($r = -0.08$, $P = 0.41$, $N = 108$) or *Hagenius* ($r = -0.05$,

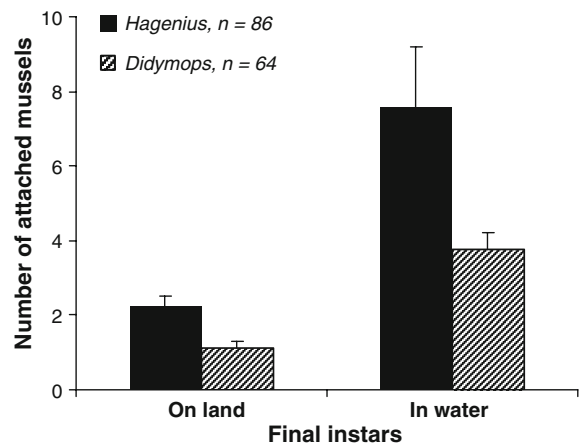


Fig. 3 Mean (\pm SE) number of mussels attached on final instars found on the beach and in the water

$P = 0.53$, $N = 138$). The farthest distance recorded for a *Didymops* on land was 7 m by a larva with two mussels attached, and for *Hagenius*, it was 6 m by a larva with seven mussels attached. When total mussel mass was considered, there was a significant negative correlation between the load of mussels attached and the distance traveled by colonized *Didymops* ($r = -0.64$, $N = 21$, $P = 0.002$, Fig. 5). The trend for *Hagenius* was not significant ($r = -0.23$, $N = 16$, $P = 0.39$). Of the seven exuvia (all *Didymops*) that were found on the vertical surface of cabins or trees (as high as 3 m), none had mussels attached (Fisher exact test, using as expected the percentage of colonized and uncolonized *Didymops*, $N = 115$, $P = 0.002$).

In the 2007 righting experiment, 11 (37%) of the *Didymops* larvae remained uncolonized after multiple attempts to induce mussel attachment. There was no significant relationship between larval area of *Didymops* and the 5–7 zebra mussels that attached after inducement ($r = 0.26$, $P = 0.09$). Nine of the 22 *Didymops* never righted themselves after zebra mussels attached, whereas all of them did so before mussel attachment ($P < 0.001$, Fisher exact test). Of the remaining individuals that could right themselves, righting times were significantly longer with zebra mussels attached (paired $t = 3.34$, $P = 0.006$, $N = 13$, Fig. 6). Righting time also increased with the proportion of total weight that were mussels ($r = 0.43$, $P = 0.04$). In the final trials, righting times for larvae without zebra mussels was no different from the first trials (paired $t = 3.12$,

Fig. 4 Mean (\pm SE) distance traveled from the water line by species with and without mussels. * $P < 0.01$, ** $P < 0.002$

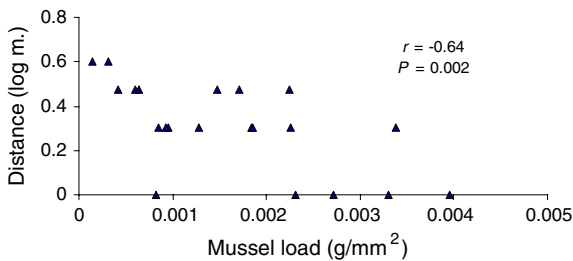
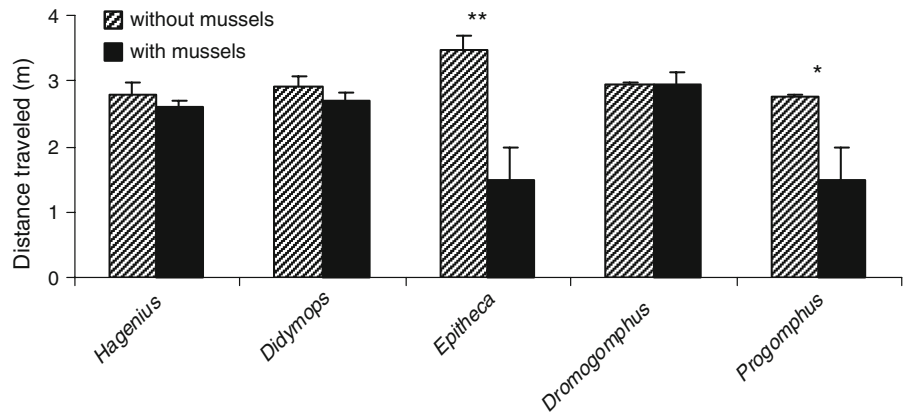


Fig. 5 Distance from the water traveled by *D. transversa* as a function of mussel load

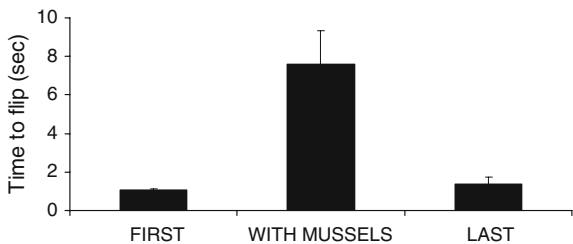


Fig. 6 Mean (\pm SE) righting times of 13 *D. transversa* larvae. In the first and last trials, the larvae had no mussels attached (see text)

$P = 0.01$), indicating that larval performance with mussels attached was not result of a decrease in larval condition caused by lab conditions.

Discussion

Among the five study species, the sprawlers *Didymops* and *Hagenius* were the most susceptible to colonization by zebra mussels, with more than half of the final instars colonized in our 2005 sample. One important result of our study that has not been

documented previously is that for both *Didymops* and *Hagenius*, penultimate instars were also colonized, albeit at lower rates than final instars. Our 2005 colonization rates did not differ from those reported from a sample of 43 larvae collected on a single day in late May of the same year by McCauley & Wehrly (2007) (Fisher exact test, $P = 0.82$, $N = 187$ *Hagenius*; $P = 0.57$, $N = 162$ *Didymops*). However, colonization rates were significantly lower for our 2007 sample when only 38% of *Hagenius* and 14% of *Didymops* were colonized. This trend continued into 2008 (Fincke, unpubl. data) when, based on casual observations, there appeared to be many fewer *Dressina polymorpha* in the lake than were seen in 2005.

The size and behavior of dragonfly larvae had independent effects on the probability that a species was colonized by zebra mussels. The larger size and lack of burrowing behavior of *Didymops* and *Hagenius* made these species more susceptible to colonization than the smaller, slimmer burrowing larvae of *Progomphus* or *Dromogomphus*. Indeed, although similar in size to *Didymops*, *Epitheca*, whose final instars acted more like shallow burrowers, were rarely colonized, and then only by 1–2 mussels. Similarly, *Campeloma decisum* snails that one finds buried in sand in Douglas Lake are less likely to have attached zebra mussels than those found on the surface (O. M. Fincke pers. observation; see also Van Appledorn et al., 2007).

Increasing zebra mussel loads decreased larval survivorship and mobility, particularly in the two most susceptible species. Both *Hagenius* and *Didymops* collected from the lake carried more mussels than individuals known to emerge. And for *Hagenius*, the

species that carried the greatest number of mussels, zebra mussels appeared to increase a larva's susceptibility to predation. Prior to emergence, colonization by *Dreissena polymorpha* decreased larval mobility by making it impossible for some and more difficult for other individuals to right themselves. Although we stopped the righting trials after 20 s, it is possible that some larvae would have eventually righted themselves. However, permitting a longer time to elapse would only have increased the difference reported (Fig. 6).

The larvae of *Epitheca*, *Dromogomphus*, and *Progomphus* rarely carried more than a single mussel. Nevertheless, colonized individuals of the latter two species traveled a shorter distance before emerging on the beach or lake bank than did uncolonized individuals. In contrast, *Didymops* and *Hagenius* carried as many as 6 and 15 mussels, respectively. *Didymops*, which typically travels far from the water to emerge on vertical surfaces, traveled a shorter distance as its mussel load increased. We failed to find a similar effect on *Hagenius*. By focusing primarily on exuvia and larvae on the beach, we likely underestimated the cost of mussel loads on dragonfly mobility for both species. For example, all of the *Didymops* that we occasionally found farther inland were free of mussels. And in a subsequent study, few of the *Hagenius* and *Didymops* that emerged in the forest carried mussels, and those that did never had more than two (O. M. Fincke, unpubl. data).

Although zebra mussels that obstruct a dragonfly's vision or use of its labium would likely interfere with feeding (Fig. 1A), we found no evidence that mussel colonization indirectly hampered the feeding rate of *Hagenius* and *Didymops*. Colonized final instars were not smaller than uncolonized ones. Because both species are sit and wait predators, this result may not be surprising. Indeed, the presence of zebra mussels can attract prey such as chironomids and other small invertebrates (Botts et al., 1996; Greenwood et al., 2001; Beekey et al., 2004), which might mitigate any negative effect of zebra mussel load on feeding rates. In contrast with our results, Van Appledorn et al. (2007) found that zebra mussels in Douglas Lake decreased growth rates of the gastropod snail, *Campelema decisum*.

Our finding that zebra mussels reduced the probability of emergence for two common sprawler

species suggests a greater potential impact on the odonate community than would be inferred solely from the direct effects of zebra mussels on emergence (e.g. Weihrauch & Borcherding, 2002). Because they are the top invertebrate predators in the shallow littoral zone of lakes and streams (Smith & Smock, 1992; Burcher & Smock, 2002; Worthen, 2002), a decrease in the abundance of this dragonfly guild could affect lower trophic levels and alter lake dynamics (e.g. Dodds, 2002). Moreover, the concomitant demise in adult dragonflies, which are major generalist predators on flying prey, could affect a trophic cascade across ecosystems as the odonate move from water to land (e.g. Knight et al., 2005). Populations of *Dreissena polymorpha* fluctuate over time (Strayer & Malcom, 2006). Hence, long-term studies of their rate of colonization on larval dragonflies, coupled with censuses of adult dragonflies, are needed to determine whether the potential impact of the invasive mussels on the odonate community is realized.

Acknowledgments We thank B. Scholtens for help with larval identification, O. M. Fincke's Bio 390 class for help in collecting larvae, and UMBS for logistical support. This work was supported in part by NSF REU site grant DEB-0453328.

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