

# Reduced Survival and Fitness in Native Bivalves in Response to Fouling by the Introduced Zebra Mussel (*Dreissena polymorpha*) in Western Lake Erie

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Fouling by the recently established zebra mussel (*Dreissena polymorpha*) causes differential effects among bivalve communities. In 3-mo experiments and surveys conducted in western Lake Erie during 1990, two native bivalves, *Lampsilis radiata* and *Amblema plicata*, showed consistent differences in mortality and biochemical indices of fitness in response to fouling by *D. polymorpha*. *Lampsilis radiata* was very sensitive to fouling, experiencing high mortality and reduced fitness in experiments and natural populations. In field experiments, female *L. radiata* suffered higher mortality and lower fitness than males. *Amblema plicata* was less sensitive to fouling; fitness was reduced in experimentally fouled *A. plicata*, but mortality and fitness in natural populations were not affected by *D. polymorpha*. Six species of native bivalves showed marked differences in mortality rates at three sites surveyed in western Lake Erie. Mortality was higher in the subfamilies Anodontinae and Lampsilinae (including *L. radiata*) than in Ambleminae (including *A. plicata*) at all three sites, suggesting that differences in life history strategy and shell morphology among subfamilies may be responsible for differential responses to fouling. These data suggest that fouling by *D. polymorpha* will result in profound changes in native bivalve community structure.

L'envahissement par des populations récemment établies de la dreissena polymorphe (*Dreissena polymorpha*) exerce différents effets sur les communautés indigènes de bivalves. Lors de relevés dans la partie ouest du lac Érie et d'expérience d'une durée de 3 mo, en 1990, on a montré que deux bivalves indigènes, *Lampsilis radiata* et *Amblema plicata*, manifestaient constamment des différences dans le taux de mortalité et dans les indicateurs biochimiques de santé par suite de l'envahissement par *D. polymorpha*. *Lampsilis radiata* était très sensible à cet envahissement : au cours d'expériences et dans des populations naturelles, la mortalité était élevée et la santé moins bonne. Au cours des expériences sur le terrain, la mortalité était plus élevée et la santé moins bonne chez les femelles que chez les mâles de *L. radiata*. *Amblema plicata* s'est révélé être moins sensible à l'envahissement : la santé était moins bonne chez les sujets de *A. plicata* expérimentalement soumis à un envahissement, mais la mortalité et la santé des populations naturelles n'ont pas été affectées par *D. polymorpha*. On a observé des différences marquées dans les taux de mortalité chez six espèces de bivalves indigènes à trois stations de la partie ouest du lac Érie. La mortalité était supérieure dans les sous-familles des Anodontinae et des Lampsilinae (y compris *L. radiata*) que chez les Ambleminae (y compris *A. plicata*) aux trois stations; cela pourrait signifier que des différences, entre les sous-familles, dans le cycle biologique ainsi que dans la morphologie des coquilles peuvent être à l'origine de réponses différentes à l'envahissement par *D. polymorpha*. Ces résultats indiquent que l'envahissement par *D. polymorpha* conduira à de profonds changements dans la structure de la communauté des organismes bivalves indigènes.

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The sudden arrival of new species into established communities can result in massive restructuring because these communities evolved in the absence of, and hence have no mechanisms for dealing with, novel members. The introduction of nonnative aquatic organisms has had dramatic effects on native biota of the North American Great Lakes. Successful

establishments of nonnative fishes, in particular, has dramatically altered native fish communities (Smith 1970; Christie 1974). The Eurasian zebra mussel (*Dreissena polymorpha*) has rapidly colonized the Great Lakes since its introduction in the mid-1980s, becoming a dominant member of the benthic fauna with densities exceeding 30 000 animals/m<sup>2</sup> in some areas (Griffiths et al. 1991). The sudden addition of *D. polymorpha* as an abundant member of the benthos has raised much concern about possible changes in benthic community structure in the Great Lakes.

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Bivalves of the family Unionidae are a diverse and conspicuous element of the benthic fauna of Lake Erie, with approximately 36 species native to the lake (Clarke and Stansbery 1988). Where common, unionids account for a large proportion of benthic biomass (Negus 1966) and serve as an important food resource for fish and other animals (Daiber 1952; Neves and Odum 1988). Unionids are infaunal filter-feeders, orienting themselves with the anterior end buried in the substrate and the posterior end (including the siphons) exposed to the water column. In contrast, *D. polymorpha* is a fouling epibiont, attaching to hard substrates with byssal threads much like marine fouling bivalves. Fouling is ecologically important in marine ecosystems, and many benthic marine organisms have developed elaborate antifouling strategies (Wahl 1989). In contrast, most freshwater communities have evolved in the absence of significant fouling organisms. The arrival of *D. polymorpha* in the Great Lakes represents the introduction of an important fouler into a community that has no evolutionary experience with, and therefore, no defensive mechanisms against, fouling. As a result, unionids and other benthic invertebrates often become heavily encrusted with aggregations of *D. polymorpha*. Individual unionids in Lake St. Clair have been reported to be encrusted with more than 10 000 *D. polymorpha* (Hebert et al. 1991). Such heavy encrustations may significantly interfere with the normal activities of unionids, such as filtering and locomotion (reviewed in Mackie 1991).

Because many populations of unionids have been severely reduced or extirpated due to habitat modification by humans, the appearance of *D. polymorpha* in North America has raised concern regarding its possible effects on already-stressed unionid populations (Hebert et al. 1989; Mackie 1991; Schloesser and Kovalak 1991). Several researchers have studied the effect of *D. polymorpha* on aquatic systems in Europe and North America, and some have speculated on its effects on other bivalves (Sebestyn 1938; Lewandowski 1975; Hebert et al. 1991; Mackie 1991). However, the impact of *D. polymorpha* fouling on survival and fitness in native unionids has not been thoroughly investigated and documented.

In this study, we examined the effects of fouling by *D. polymorpha* on native unionid bivalves. First, we used field experiments to test the hypotheses that (i) survival and biochemical indices of fitness in native unionids are reduced by *D. polymorpha* encrustation and (ii) different species of unionids show different responses to fouling. Then, we examined mortality and fitness as a function of the number of encrusting *D. polymorpha* in natural populations of the two unionid species used in the field experiment. Finally, we surveyed patterns of recent mortality among six unionid species in natural populations in western Lake Erie.

## Methods

### Experiment

Adult unionids of two species, *Lampsilis radiata* and *Amblema plicata* (55–85 mm in length), were collected from large natural populations in Lake Erie at Put-in-Bay and Kelleys Island, OH (approximately 41°38'N, 82°50'W and 41°34'N, 82°42'W, respectively), in early July 1990. Attached *D. polymorpha* were removed from every unionid, and each unionid was measured and weighed. Each species was randomly divided into two groups (experimental and control) of approximately 40 animals. For *L. radiata*, both groups contained approximately equal numbers of males and females, as this species can be sexed externally. Female specimens of

*L. radiata* have inflated and elongated valves accommodating gills with enlarged marsupia during the brooding of glochidia; male specimens lack this characteristic. *Amblema plicata* is not sexually dimorphic and cannot be sexed from external shell morphology. Therefore, sex ratio was not controlled for *A. plicata*. For both unionid species, the control group was left cleared of *D. polymorpha*. Experimental (i.e. encrusted) animals were placed in aerated flow-through aquaria, allowed to orient themselves naturally in sand, and then covered with a layer of *D. polymorpha* scraped from rocks collected nearby. Zebra mussels were allowed 24–48 h to attach to the unionids. This technique resulted in dense encrustations similar to natural conditions. Mean number of *D. polymorpha* on experimental animals was  $199.5 \pm 19.0$  (SE,  $n = 27$ ), while mean number on naturally encrusted animals was  $215.9 \pm 14.5$  (SE,  $n = 92$ ). Although the size range of encrusting *D. polymorpha* on each experimental animal could not be controlled, the zebra mussel mass on reencrusted unionids appeared very similar to field-collected encrusted unionids. To aid identification and recovery, experimental and control animals were marked by scribing shallow grooves in the anterior end of the right or left valve, respectively.

Approximately 2 wk after collection, all animals were returned to the lake and placed in 4-m<sup>2</sup> open-topped chicken-wire pens at a depth of 1.75 m at Put-in-Bay, OH. The large diameter of the chicken wire (25 mm) and the open top of the pens ensured that water flow was not restricted in the pens, which merely served to facilitate recovery of the animals at the end of the experiment. Pens were inspected 2 wk after initiation of the experiment to remove dead animals that may have been stressed during holding in the laboratory. Animals that died during this period were not considered in later data analyses. During this period, four control and two experimental specimens of *L. radiata* died; no specimens of *A. plicata* died.

In late October 1990, all animals were retrieved and mortality was recorded. Over 80% of marked animals for each species-treatment combination were recovered. Control animals remained relatively free of *D. polymorpha* throughout the experiment (mean number of *D. polymorpha* on controls at the end of the experiment was  $3.3 \pm 0.8$  (SE)). Survivors were wet weighed and soft tissues were flash frozen for later biochemical analyses. Soft tissues of unionids were homogenized and divided into four measured aliquots for determination of total glycogen and lipid content, cellulase enzyme activity, and estimated dry weight. Glycogen content was determined using a phenol – sulfuric acid method (MacInnis and Voge 1970) and total lipid content using a vanillin – phosphoric acid technique (Van Handel 1985). Cellulase activity, which has been shown to be negatively correlated with stress in bivalves, was determined using an assay described by Farris et al. (1988). Biochemical indices were weight standardized using the general form  $V_x = aW^b$ , where  $V_x$  is total glycogen, lipid, or enzyme activity for the unionid,  $W$  is total wet or dry weight, and  $a$  and  $b$  are fitted constants. The constants  $a$  and  $b$  are calculated from the linear regressions of the log  $V_x$  on the log of body mass;  $a$  represents the intercept and  $b$  the slope of the regression equation. Weight-specific rate variables were finally calculated as  $\dot{V}_x = V_x/W^b$  where  $\dot{V}_x$  is the weight-specific biochemical index and expressed as milligrams and micrograms per gram wet weight (glycogen and lipid) or units per microgram dry weight (cellulase activity) per standard animal (in this case, the average wet or dry weight for all specimens of that species). Statistical differences in mortality and weight-specific

biochemical indices of fitness among groups were tested using analysis of variance (ANOVA).

## Survey

*Lampsilis radiata* and *A. plicata* 55–85 mm in length were collected from natural populations at Put-in-Bay, Kelleys Island, and LaPlaisance Bay, MI (approximately 41°50'N, 83°22'W), in October 1990, within 2 d of termination of the field experiments. Unionid specimens were hand-collected randomly using SCUBA. *Amblema plicata* was common at all three sites, but *L. radiata* was common only at Put-in-Bay, and sample sizes for Kelleys Island and LaPlaisance Bay were small. Animals were weighed, and prepared for biochemical assays following the same procedure used for experimental animals. Total number of encrusting *D. polymorpha* was determined for each unionid, and weight-specific glycogen and lipid content and cellulase activity were correlated with number of *D. polymorpha* using regression and analysis of covariance (ANCOVA).

In October 1990, native bivalve communities at the three sites in western Lake Erie described above were surveyed for survivorship of six common species belonging to three subfamilies, *Anodonta grandis* (Anodontinae), *L. radiata*, *Leptodea fragilis*, and *Potamilus alatus* (Lampsilinae), and *Quadrula pustulosa* and *A. plicata* (Ambleminae). Specimens of live and dead unionids were hand-collected using SCUBA. All six species were present at each site, but only species for which five or more individuals were collected were included in data analyses. All living and recently dead unionids were collected, enumerated, and scored as either encrusted or not encrusted. Only encrusted animals were included in mortality data analysis. Because the nacreous layer of bivalve shells remains lustrous for several months after death, animals that have died recently can be identified (Buchanan 1980). A high proportion of live to recently dead animals for a given species was interpreted as a low mortality rate within the past year, while a low proportion of live animals was interpreted as high mortality. Differences in proportion of live to dead animals among subfamilies and species were tested by calculating chi-square statistics from R × C contingency tables or Fisher's exact test if tables had low expected values.

## Results

### Experiment

*Dreissena polymorpha* encrustation produced species-specific and sex-specific mortality in the study species (Table 1). No mortality was observed among *A. plicata* in either the experimental or control group. In *L. radiata*, however, encrusted females experienced much lower survival (16.7%) than control animals (68.4% for both males and females) or encrusted males (64.3%) ( $G$ -test,  $p < 0.01$ ). There were no differences in survival between male and female control animals or between male experimental and control animals. Biochemical indices of fitness also differed for the two species in response to *D. polymorpha* encrustation. Although encrusted specimens of *A. plicata* experienced no mortality, mean glycogen content and cellulase activity was significantly lower in encrusted animals than in controls (Table 1). Lipid content was not significantly different between the two groups. Surviving specimens of *L. radiata* showed sex-specific responses to encrustation (Table 1). Mean glycogen content and cellulase activity were significantly lower in encrusted animals

than in controls, and females had lower glycogen content and cellulase activity than males. There were no differences in lipid content among treatment or sexes in specimens of *L. radiata*.

### Survey

Mortality in natural populations of *L. radiata* and *A. plicata* reflected experimental results. Proportions of live to dead animals were lower for *L. radiata* than for *A. plicata* at the two sites having sufficient numbers of *Lampsilis* for analysis (Table 2). At LaPlaisance Bay, MI, *L. radiata* was too rare for inclusion in this analysis. Mortality was low for *A. plicata* in the western basin, with greater than 90% of animals alive at all three sites, whereas 66% of *L. radiata* were collected live (Table 2).

Correlations of fitness and number of encrusting *D. polymorpha* differed among specimens of *A. plicata* and *L. radiata* from natural populations. For *A. plicata* at all three sites, there were no significant relationships between glycogen, lipid content, or cellulase activity and total number of encrusting *D. polymorpha* (Fig. 1). Sufficient specimens of *L. radiata* for biochemical analyses were collected only at Put-in-Bay. There were no between-sex differences in the three biochemical measures, so sexes were pooled for further analyses. Glycogen content was negatively correlated with number of encrusting *D. polymorpha* (Fig. 2). Lipid content and cellulase activity were not correlated with number of *D. polymorpha* by simple linear regression. However, combining data sets from experimentally and naturally encrusted animals in an ANCOVA (with experimental group and field population as the treatment variables) and using number of *D. polymorpha* as a covariate revealed a significant negative correlation between cellulase activity and number of encrusting zebra mussels.

Biochemical indices of fitness in populations of *A. plicata* and *L. radiata* showed large interpopulation differences unrelated to the density of encrusting *D. polymorpha* (Table 3). Although within-sample variances were high, sample sizes were adequate for parametric analyses for *A. plicata* ( $n = 15$  for Put-in-Bay and LaPlaisance Bay and  $n = 9$  for Kelleys Island). However, sample sizes of specimens of *L. radiata* were less balanced, with  $n = 4$  for LaPlaisance Bay and Kelleys Island and  $n = 27$  for Put-in-Bay. Therefore, a nonparametric analysis was used for final analysis of biochemical indices for populations of *L. radiata*, which successfully equalized within-sample variance for all populations. Identical results were obtained for parametric ANOVA and nonparametric Kruskal-Wallis  $k$ -sample tests for all three biochemical indices for specimens of *A. plicata* and differed only for cellulase activity for specimens of *L. radiata*. Mean glycogen content did not differ between specimens from Put-in-Bay and Kelleys Island for both species. Mean cellulase activity was higher in specimens of *L. radiata* from Put-in-Bay than in those from Kelleys Island. Lipid content was generally low in both species. Lipids were slightly lower in specimens from Kelleys Island for both species, with significant differences between populations at Kelleys Island and Put-in-Bay for *A. plicata* and between those at Kelleys Island and LaPlaisance Bay for *L. radiata*.

Patterns of mortality in natural populations of unionids in Lake Erie varied across species, but were taxonomically consistent at the subfamily level. Proportions of live to dead animals were lower for the subfamilies Anodontinae (*A. grandis*) and Lampsilinae (*L. radiata*, *L. fragilis*, and *P. alatus*) than for Ambleminae (*A. plicata* and *Q. pustulosa*) at all three sites (Table 2). At Put-in-Bay, proportions of live to dead animals for the Anodontinae were lower than for Lampsilinae, but did

TABLE 1. Survival, glycogen and lipid content, and cellulase enzyme activity for specimens of *A. plicata* and *L. radiata* in the field experiment. Values in parentheses represent standard errors of the means. Glycogen and lipid content are based on tissue wet weights, while enzyme activity is based on tissue dry weights.

Species	Treatment	<i>n</i> <sup>a</sup>	% Survival	Glycogen content (mg/g)	Lipid content (μg/g)	Enzyme activity (units/μg)	<i>n</i> <sup>b</sup>	
<i>Amblema plicata</i>	Control	34	100 (—)	1.90 (0.23)	2.2 (0.1)	257.4 (24.9)	15	
	Encrusted	35	100 (—)	0.67 (0.20)	2.0 (0.1)	87.8 (16.0)	15	
<i>Lampsilis radiata</i>	Male	Control	19	68 (11)	0.13 (0.02)	2.7 (0.1)	399.6 (62.3)	13
		Encrusted	14	64 (11)	0.08 (0.01)	2.7 (0.1)	151.6 (28.4)	9
	Female	Control	19	68 (11)	0.08 (0.01)	3.0 (0.1)	200.5 (44.3)	13
		Encrusted	18	17 (9)	0.04 (0.01)	3.7 (0.3)	111.5 (27.2)	3

<sup>a</sup>Number of individuals placed in field enclosures at start of experiment.

<sup>b</sup>Number of animals used for biochemical analyses.

TABLE 2. Ratio of live individuals to dead individuals of unionid species from three sites across western Lake Erie. Proportion alive for *L. radiata* is significantly lower than for *A. plicata* (Fisher's exact test,  $p < 0.01$ ). Proportion alive for Anodontinae and Lampsilinae is significantly less than for Ambleminae for all sites pooled (goodness of fit test,  $p < 0.001$ ).

Subfamily and species	Location			Total	Proportion alive
	LaPlaisance Bay	Put-in-Bay	Kelleys Island		
Anodontinae					
<i>Anodonta grandis</i>	6:10	1:13	2:4	9:27	0.25
Lampsilinae					
<i>Leptodea fragilis</i>	7:11	2:5	— <sup>a</sup>	9:16	0.36
<i>Potamilus alatus</i>	24:10	3:8	1:4	28:22	0.56
<i>Lampsilis radiata</i>	— <sup>a</sup>	48:19	2:7	50:26	0.66
Ambleminae					
<i>Quadrula pustulosa</i>	34:3	— <sup>a</sup>	7:0	41:3	0.87
<i>Amblema plicata</i>	29:3	44:2	9:1	82:6	0.93

<sup>a</sup>Insufficient number of individuals ( $n < 5$ ) collected for inclusion in analyses.

not differ at Kelleys Island or LaPlaisance Bay. At all three sites, proportions of live to dead animals were high for the subfamily Ambleminae, indicating that these species had not suffered recent mortality. It must be noted that there are no similar data from Lake Erie prior to the introduction of *D. polymorpha* with which to compare our observations. However, the taxonomic and geographic consistency of our observations suggest that strong, differential mortality in unionid populations had occurred across western Lake Erie within the previous year.

## Discussion

### Effects on Individual Species

Fouling by *D. polymorpha* has profound but variable effects on unionid species in western Lake Erie. Some species (e.g. *L. radiata*) may suffer dramatic reductions in fitness and increased mortality due to fouling by *D. polymorpha*. Other species (e.g. *A. plicata*) are not significantly affected in the short term, but fouling significantly reduces long-term fitness by decreasing glycogen content and increasing stress. Survey results corroborate experimental results. Natural populations of *L. radiata* experienced higher mortality in the western basin of Lake Erie in the recent past, following the arrival of *D. polymorpha*, than *A. plicata*. Thus, two common species in the Lake Erie bivalve community are differentially affected by the presence of *D. polymorpha*, with *A. plicata* being more tolerant of fouling than *L. radiata*.

Biochemical indices of fitness were more variable in encrusted animals from natural populations than in animals from the experiments, but these data are consistent with the hypothesis that *A. plicata* is more tolerant of fouling than *L. radiata*. Concordant with experimental results, glycogen content and cellulase activity, but not lipid content, were negatively correlated with *D. polymorpha* encrustation in natural populations of *L. radiata*. In contrast with experimental results, specimens of *A. plicata* collected in the field survey suffered no detectable reduction of biochemical fitness as a function of *D. polymorpha* encrustation. The number of encrusting *D. polymorpha* was variable on animals collected from natural populations, but most animals were heavily encrusted. Our experiments, however, consisted of heavily encrusted animals compared with completely cleared individuals. Consequently, a relatively tolerant species such as *A. plicata* may show short-term effects of fouling only in strictly controlled situations, while a less tolerant species such as *L. radiata* could show high mortality and observable reductions in fitness in response to fouling despite the confounding variables of an uncontrolled field situation. Thus, although significant effects can be induced in controlled experiments, the effects of *D. polymorpha* fouling in natural populations of unionids are likely to be more subtle and variable.

In bivalves, glycogen is the primary energy storage molecule (often present in excess of 30% of total body dry weight) and

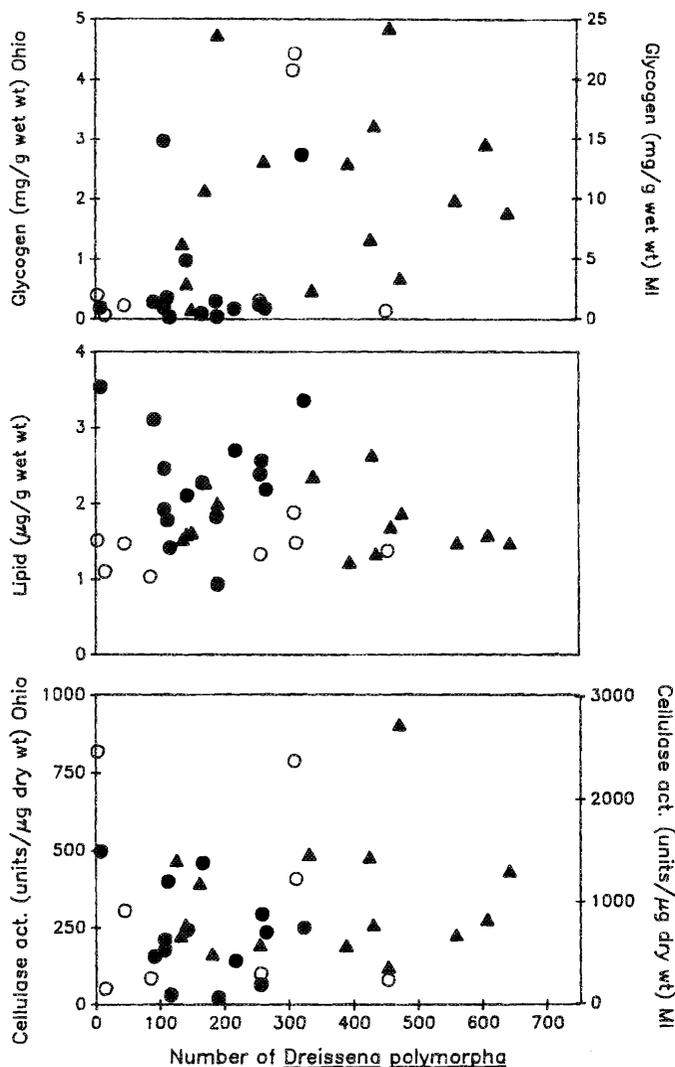


FIG. 1. Biochemical indices of fitness in *A. plicata* from three natural populations in western Lake Erie. Filled circles represent animals from Put-in-Bay, OH, open circles represent animals from Kelleys Island, OH, and triangles represent animals from LaPlaisance Bay, MI. Horizontal axes represent the number of encrusting *D. polymorpha*. There were no significant correlations between biochemical indices of fitness and number of encrusting *D. polymorpha*.

lipid reserves are generally low (reviewed in Pandian 1975). In this study, glycogen content was 1–2 orders of magnitude higher than lipid content for both *L. radiata* and *A. plicata*. Lipid content was less than 1.29% of body weight (not reported whether based on wet or dry weight) for Lake St. Clair unionids (Hebert et al. 1991). Our field experiments revealed that glycogen content was sensitive to fouling by *D. polymorpha* whereas lipid content did not differ between encrusted and unencrusted animals. Similarly, glycogen content was inversely related to number of encrusting *D. polymorpha* for specimens of *L. radiata* from a natural population, while lipid content was not related to encrustation density. Thus, fouling by *D. polymorpha* results in reductions in energy storage (reduced glycogen content) and higher stress (lower cellulase activity), but not necessarily in reduced content of primarily structural molecules such as lipids. In contrast with these results, Hebert et al. (1991) concluded that fouling by *D. polymorpha* causes a reduction in lipids in Lake St. Clair unionids, although no regression statistics were provided to support the assertion.

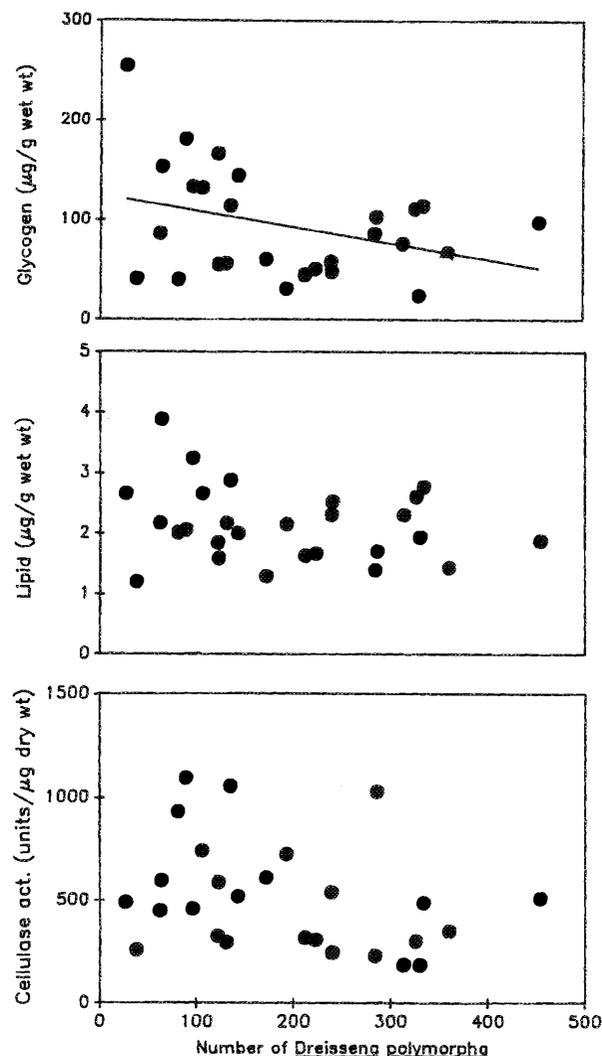


FIG. 2. Biochemical indices of fitness in *L. radiata* from a natural population in Lake Erie at Put-in-Bay, OH. Glycogen content was negatively correlated with number of encrusting *D. polymorpha* ( $r^2 = 0.23$ ,  $n = 27$ ,  $p < 0.03$ ).

Although it is plausible that encrustation by *D. polymorpha* may ultimately reduce lipid content, significant reductions in the primary energy store, glycogen, will have more serious and immediate effects on survival and reproduction of native unionids.

Mean glycogen and cellulase activity in native unionids varied across sites in western Lake Erie, independent of encrustation densities of *D. polymorpha*. Lipid content also varied significantly across sites, but the differences were less dramatic. In general, unionids collected at Kelleys Island had lower lipid content than those at the other two sites. Local environmental conditions (e.g. temperature regimes, quantity and quality of food, substrate stability, etc.) may have strong effects on the nutrient status of native unionids. Although parameters of environmental quality at the three collecting sites were not measured in this study, consistent patterns of biochemical indices among sites suggest significant differences in habitat quality across western Lake Erie. Preliminary studies of the impact of *D. polymorpha* on unionids have pooled samples across sites without considering possible site differences in baseline nutritional status (e.g. Hebert et al.

TABLE 3. Weight-standardized glycogen content, lipid content, and enzyme activity for *A. plicata* and *L. radiata* from three natural populations in western Lake Erie. Site abbreviations: PIB = Put-in-Bay, OH; KEL = Kelleys Island, OH; MI = LaPlaisance Bay, MI. Values are means with standard errors in parentheses. Species means within the same column with the same superscript letter are not significantly different; those with different superscripts are significantly different (Tukey's multiple comparison for *A. plicata*; Kruskal-Wallis *k*-sample test for *L. radiata*). Glycogen and lipid contents are based on tissue wet weights, while enzyme activity is based on tissue dry weights.

Species and site	Glycogen content (mg/g)	Lipid content (μg/g)	Enzyme activity (units/μg)	<i>n</i>
<i>Amblema plicata</i>				
PIB	0.06 (0.24) <sup>a</sup>	2.30 (0.18) <sup>a</sup>	357.0 (135.0) <sup>a</sup>	15
KEL	1.71 (0.75) <sup>a</sup>	1.38 (0.09) <sup>b</sup>	328.5 (99.2) <sup>a</sup>	9
MI	10.36 (1.86) <sup>b</sup>	2.01 (0.26) <sup>a,b</sup>	1010.0 (156.0) <sup>b</sup>	15
<i>Lampsilis radiata</i>				
PIB	0.09 (0.01) <sup>a</sup>	2.15 (0.12) <sup>a,b</sup>	512.0 (51.6) <sup>a</sup>	27
KEL	0.05 (0.01) <sup>a</sup>	1.40 (0.21) <sup>b</sup>	72.1 (21.7) <sup>b</sup>	4
MI	7.62 (5.35) <sup>b</sup>	2.76 (0.33) <sup>a</sup>	1168.0 (347.0) <sup>a</sup>	4

TABLE 4. Standardized left valve weight for six native bivalve species. Adjusted weight is calculated for a standard 78.2-mm valve from linear length-weight regressions of nontransformed data for each species. Increasing slopes of regression equations indicate thicker shells. Regressions were determined for samples from western Lake Erie, except for *Q. pustulosa* which is from the Muskingum River, OH. Values in parentheses are standard errors of the means.

Subfamily	Species	<i>n</i>	Shell length (range, mm)	Slope	Adjusted left valve weight (g)
Ambleminae	<i>Quadrula pustulosa</i>	7	23.5–69.9	1.19	59.55 (1.52)
	<i>Amblema plicata</i>	8	62.9–74.0	0.84	34.22 (1.85)
Lampsilinae	<i>Lampsilis radiata</i>	8	60.2–81.7	0.63	20.85 (1.10)
	<i>Potamilus alatus</i>	8	68.0–109.4	0.64	14.36 (0.83)
	<i>Leptodea fragilis</i>	7	88.7–111.3	0.42	7.83 (2.09)
Anodontinae	<i>Anodonta grandis</i>	8	72.6–131.0	0.51	4.63 (0.81)

1991). Clearly, field studies assessing the potential impacts of encrustation by *D. polymorpha* on biochemical nutrient status of native unionids must account for potential geographic variation in environmental quality.

Unionids feed by filtering small particles from the water column or water-sediment surface interface. Feeding by unionids may be impaired by encrustation and/or loss of suspended particles to grazing *D. polymorpha*. Species and sex-dependent behavioral and morphological differences may have contributed to differential responses to fouling by *D. polymorpha*. Individual unionids which position the posterior margin of the shell further above the substrate, or which have longer siphons, may have better access to available food in the water column. However, differences in feeding behavior and siphonal morphology among species or between sexes have not been studied, and in general, the feeding biology of many species of unionids is not well known (Clarke 1981).

#### Effects on Bivalve Community Structure

Experimental and survey data indicate that the introduction of *D. polymorpha* into the Great Lakes will alter the community structure of unionid bivalves by causing differential mortality and reductions in fitness among some unionid species. Similarly, the introduction of the marine bivalve *Potamocorbula amurensis* into San Francisco Bay resulted in the displacement of the native bivalve community (Nichols et al. 1990). Other nonnative freshwater bivalves have become established in North America (notably *C. fluminea*; see McMahon 1983), but none has been shown to result in extreme and rapid changes

in community composition (Leff et al. 1990). *Corbicula fluminea* is similar to native bivalves in its habit of burrowing into the substrate and thus becomes simply another species in an already species-rich community. Accordingly, *C. fluminea* may be unable to become established in areas with healthy unionid populations because the niche of infaunal, filter-feeding bivalve is already filled (reviewed in McMahon 1983). Epibiotic *D. polymorpha*, however, present a novel challenge to freshwater communities that are naive to fouling. Thus, *D. polymorpha* is easily able to fill the previously empty niche of the epibiont, and effects of fouling are variable among different species of unionids which evolved different life histories, habitat preferences, and other traits in the absence of fouling organisms.

Potential mechanisms for the negative effects of *D. polymorpha* on native unionids have been proposed (Mackie 1991): (i) encrusting biomass hinders locomotion and burrowing, (ii) encrusting biomass concentrated at posterior end disrupts balance and equilibrium, (iii) invasive growth by zebra mussels prevents normal closure and/or opening of valves, (iv) interference of normal functioning of siphons, (v) filter feeding by zebra mussels strips water of available food, (vi) deformation of unionid valves, and (vii) complete valve occlusion leads to suffocation. Any combination of these mechanisms may contribute to unionid mortality or reduction in biochemical fitness.

Most of the above hypotheses have yet to be tested directly, but consistent results within subfamilies in response to fouling by *D. polymorpha* suggest likely mechanisms responsible for differential mortality and reduction in fitness in Lake Erie

unionids. The Anodontinae and Lampsilinae have experienced widespread mortality as *D. polymorpha* has become an abundant member of the benthos in western Lake Erie, while the Ambleminae have not. The Anodontinae and Lampsilinae share a common trait of females brooding glochidia larvae in the gills for long periods, usually 9–12 mo (Clarke 1981). Ambleminae, however, are short-term breeders, brooding young for only a few weeks to 2 mo. Therefore, female anodontines and lampsilines invest considerably more time, and presumably energy, into brooding of larvae (Mackie 1984) and in this way may be more sensitive to fouling than amblemines; also, male lampsilines and anodontines are expected to be less sensitive than females to fouling because they do not brood larvae. As predicted by this hypothesis, our data show severe mortality for fouled female *L. radiata* but no difference in mortality between encrusted and unencrusted males, and no mortality for the short-term breeder, *A. plicata*. Thus, a long-term strategy which evolved in a pre-*D. polymorpha* environment may now be disadvantageous in an environment with abundant fouling organisms.

Anodontinae and Lampsilinae also differ from the Ambleminae in shell morphology. Amblemines are characterized by solid, heavy shells whereas anodontines and lampsilines typically have much lighter shells (Table 4). Like many bivalves, unionids must maintain specific orientation in the substrate for efficient filter feeding and waste excretion. The addition of a large mass of *D. polymorpha* to the posterior surface of a light-shelled anodontine or lampsilinae will change the center of gravity for the animal and make it more energetically expensive to maintain proper posture in the substrate. For lampsilines and anodontines in western Lake Erie, the weight of fouling *D. polymorpha* on an individual unionid may exceed the weight of the unionid by a factor of 4 (Schloesser and Kovalak 1991). In contrast, the center of gravity of a heavy-shelled amblemine would be less affected by additional weight on the shell. Again, as predicted by this hypothesis, heavy-shelled amblemines show low mortality rates as compared with lampsilines and anodontines. Heavy-shelled species may also have stronger adductor muscles and hence be less vulnerable to invasive growth by *D. polymorpha* within the gape. Thus, differences in shell morphology among unionid subfamilies may result in variable responses to fouling by *D. polymorpha*.

The introduction of *D. polymorpha* into the Great Lakes has had profound and rapid effects on the structure of native bivalve communities. The community in Lake Erie can be expected to move increasingly towards domination by thick-shelled amblemines as lampsilines and anodontines are removed by short-term mortality and reductions in fitness. However, amblemines may also experience an overall decline in abundance in the long term because these species are more slowly and subtly affected by heavy fouling by *D. polymorpha*. The lack of any evolutionary experience with fouling in North American unionids means that suites of characters that have arisen in a freshwater environment will suddenly be subject to entirely new selection regimes. In Lake Erie bivalve populations, differences in reproductive strategy, shell morphology, and other factors may suddenly be manifested as differences in responses to fouling by *D. polymorpha*.

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