1992

T · H · E
OHIO STATE UNIVERSITY

Department of Entomology

103 Botany and Zoology Building
1735 Neil Avenue
Columbus, OH 43210-1220

Phone 614-292-8209
FAX 614-292-2180

December 17, 1991

Dr. Richard J. Neves
Cooperative Fish and Wildlife Unit
Cheatham Hall
Virginia Tech University
Blacksburg, VA 24061

Dear Dr. Neves:

I very much enjoyed our discussion at the Zebra Mussel Conference in Rochester. As promised, enclosed is the submitted draft of our work on effects of zebra mussel fouling on unionid populations. The project went very well and Wendell did a nice job in taking the lead on the writing of the manuscript.

As I mentioned in Rochester, I will be working (hopefully) in the lab of Sheldon Guttman of the Department of Zoology at Miami University beginning late this summer. We are interested in further pursuing the links between zebra mussels and unionids, especially impacts on genetic structure of unionid populations. I have been in contact with Jerry Ferris regarding submission of proposals to U.S. EPA and Sea Grant.

Please feel free to send along any comments you may have regarding the manuscript. If it is of interest to you, I would like to pursue the possibility of collaborative work between our lab and yours. I believe Ohio Sea Grant may be interested in providing some initial funding (materials, travel, etc.). We would also be interested in showing you the lab and our electrophoretic techniques if you would care to venture up to Ohio.

Sincerely,

Dave

David J. Berg
Postdoctoral Research Associate
(614)292-6306
(614)292-8209 (secretary)

Enclosure

Submitted to CJFAS
12-17-91

Haag et al 1992

Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (Dreissena polymorpha) in western Lake Erie

Wendell R. Haag[1], David J. Berg[1], David W. Garton[1], and Jerry L. Farris[2].

[1] Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, and F.T. Stone Laboratory, P.O. Box 119, Put-in-Bay, OH 43456, USA

[2] Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0321, USA

Haag, W.R., D.J. Berg, D.W. Garton, J.L. Farris. 199X. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (Dreissena polymorpha) in western Lake Erie. Can. J. Fish. Aquat. Sci. XX:XXX-XXX.

Abstract

Fouling by the recently established zebra mussel (Dreissena polymorpha) causes differential effects among species in the Lake Erie bivalve community. In three-month field experiments and field surveys conducted in western Lake Erie, two native bivalves, Lampsilis radiata and Amblema plicata, showed consistent differences in mortality and biochemical indices of fitness in response to fouling by Dreissena. Lampsilis was very sensitive to fouling, experiencing high mortality and reduced fitness in experiments and natural populations. In experiments, female Lampsilis suffered higher mortality and lower fitness than males. Amblema was less sensitive to fouling. Fitness was reduced in fouled Amblema in experiments, but fitness in natural populations and mortality was not affected by fouling. 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 Lampsilis) than the Ambleminae (including Amblema) 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 Dreissena will result in profound changes in bivalve community structure.

Introduction

The sudden arrival of new species into established communities can result in massive restructuring because these communities evolved in the absence of the "foreign" species and have no mechanisms for dealing with novel members. The introduction of non-native aquatic organisms has had dramatic effects on native biota of the North American Great Lakes. Successful establishment of non-native fishes, in particular, has dramatically altered native fish communities (Christie 1974; Smith 1970). 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 $\cdot$ m^{-2} in some areas (Griffiths et al. 1991). The sudden addition of Dreissena as an abundant member of the benthos has raised much concern about possible changes in benthic community structure in the Great Lakes.

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 the biomass of the benthic community (Negus 1966) and serve as an important food resource for fish and other animals (Daiber 1952; Neves 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, Dreissena 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 anti-fouling strategies (Wahl 1989), while most freshwater communities evolved in the absence of fouling. The arrival of Dreissena 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 Dreissena. Individual unionids in Lake St. Clair have been reported to be encrusted with more than 10,000 Dreissena (Hebert et al. 1991). Such heavy encrustations may significantly interfere with normal activities of the unionid, such as filtering and locomotion (Mackie 1991).

Because many populations of unionids have been severely reduced or extirpated due to habitat modification by humans, the recent appearance of Dreissena in North America has raised concern regarding its possible effects on already-stressed unionid populations (Hebert et al. 1989; Schloesser and Kovalak in press). Several researchers have studied the effect of Dreissena on aquatic systems in Europe and North America, and some have speculated on its effects on other bivalves (Sebestyn 1938, Lewandowski 1976, Hebert et al. 1991, Mackie 1991). However the impact of Dreissena fouling on survival and fitness in native unionids has not been thoroughly investigated and documented.

In this study, we examine the effects of fouling by Dreissena on native unionid bivalves. First, we use field experiments to test the hypotheses that i) survival and biochemical indices of fitness in native unionids are reduced by Dreissena encrustation and ii) different species of unionids show different responses to fouling. Then, we extend these hypotheses to natural populations and examine mortality and fitness as a function of the number of encrusting Dreissena in natural populations of the unionid species used in the experiment. Finally, we examine patterns of mortality related to Dreissena fouling among six species in natural unionid populations in Lake Erie.

Methods

The experiment

Adult unionids of two species, Lampsilis radiata and Amblema plicata (55-85 mm length), were collected from large natural populations in Lake Erie at Put-in-Bay and Kelley's Island, OH (Figure 1) in early July, 1990. Dreissena were removed and each unionid was measured and weighed. Each species was randomly divided into two groups of approximately 40 animals. For Lampsilis radiata, which is sexually dimorphic, both groups contained approximately equal numbers of males and females. Amblema plicata is not sexually dimorphic and could not be sexed from external morphology. One group was left cleared of Dreissena for use as a control. Treatment animals were placed in aerated flow-through aquaria, allowed to orient themselves naturally in sand, then covered with Dreissena and left for 24-48 hours to allow Dreissena to attach to the unionids (Figure 2). This process resulted in encrustations that were similar to natural encrustations. Mean number of Dreissena on treatment animals was 199.5 ± 19.0 (SE, n=27), while mean number on naturally encrusted animals was 215.9 ± 14.5 (SE, n=92). Treatment and control animals were marked by scribing shallow grooves in the anterior end of the right or left valve, respectively (Figure 2).

Approximately two weeks after collection, all animals were returned to the lake and placed in 4 m^2 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 insured that water flow was not restricted in the pens and the pens merely served to facilitate recovery of the animals at the end of the experiment. Pens were inspected two weeks after initiation of the experiment to remove dead animals that may have been stressed during holding in the lab. Animals that died during this period were not considered in later data analysis. During this period, 4 control and 2 treatment Lampsilis died; no Amblema died.

In late October, 1990, 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 Dreissena throughout the experiment (mean number of Dreissena on controls at the end of the experiment was 3.3 ± 0.8 (SE)). Survivors were weighed and soft tissues were flash frozen for later biochemical analyses. Soft tissues of unionids were homogenized and divided into 4 measured aliquots for determination of total glycogen and lipid content, cellulase enzyme activity, and dry weight. Cellulase activity has been shown to be negatively correlated with stress in bivalves (Farris et al. 1988). Glycogen, lipids, and cellulase activity were determined using published procedures (MacInnis and Voge 1970; Van Handel 1985; Farris et al. 1988, respectively). Biochemical indices were weight-standardized and expressed as µg · g wet weight^{-1} (glycogen and lipid) or units · µg dry weight^{-1} (cellulase activity). Differences in mortality and biochemical indices of fitness among groups were tested using analysis of variance (ANOVA).

The survey

Lampsilis radiata and A. plicata 55-85 mm in length were collected from natural populations at three sites in western Lake Erie (Figure 1) in October 1990, within two days of termination of the experiments. Amblema was common at all three sites, but Lampsilis was only common at Put-in-Bay and sample sizes at Kelley's Island and LaPlaisance Bay were small. Animals were weighed, measured, and prepared for biochemical assays following the same procedure used for experimental animals. Total number of encrusting Dreissena was determined for each unionid and weight-standardized glycogen and lipid content and cellulase activity were correlated with number of Dreissena using regression and analysis of covariance (ANCOVA).

In October, 1990, native bivalve communities at three sites in western Lake Erie (Figure 1) were surveyed for survivorship of six common species belonging to three subfamilies, Anodonta grandis (subfamily Anodontinae), Lampsilis radiata, Leptodea fragilis and Potamilus alatus (subfamily Lampsilinae), and Quadrula pustulosa and Amblema plicata (subfamily Ambleminae). At each site, only species for which 5 or more individuals were collected were included in data analysis. 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 in order to examine mortality only in animals fouled by Dreissena. Because the nacrous 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 RxC contingency tables or Fisher's exact test if tables had low expected values.

Results

The experiment

Dreissena encrustation produced species-specific and sex-specific mortality in the study species (Figure 3). No mortality was observed among Amblema in either the treatment or control group during the experiment. In Lampsilis, however, encrusted (treatment) females experienced much lower survival (16.7%) than control animals (68.4% for both males and females) or encrusted males (64.3%). There were no differences in survival between male and female control animals or between male treatment and control animals.

Biochemical indices of fitness also differed for the two species in response to Dreissena encrustation. Although encrusted Amblema showed no mortality, glycogen content and cellulase activity were lower in encrusted animals than in controls (Figure 4). Lipid content was not significantly different between the two groups. Surviving Lampsilis showed sex-specific responses to encrustation (Figure 5). Glycogen content and cellulase activity were lower in encrusted animals than controls and females had lower glycogen content and cellulase activity than males. There were no differences in lipid content among treatments or sexes in Lampsilis.

The survey

Mortality in natural populations of Lampsilis and Amblema reflected experimental results. Proportions of live to dead animals were lower for Lampsilis than Amblema at the two sites having sufficient numbers of Lampsilis for analysis (Figure 6). At LaPlaisance Bay, MI, L. radiata was too rare for inclusion in this analysis. Mortality was low for Amblema in the western basin, with greater than 90% of animals alive at all three sites (Figure 6).

Correlations of fitness and number of encrusting Dreissena differed among Amblema and Lampsilis from natural populations. For Amblema at all three sites, there was no significant relationship between glycogen or lipid content, or cellulase activity and total number of encrusting Dreissena (Figure 7). Lampsilis were only collected in sufficient numbers for analysis at Put-in-Bay. There were no differences in any of the three biochemical measures between sexes at Put-in-Bay, so sexes were pooled for further analyses. Glycogen content was negatively correlated with number of encrusting Dreissena (Figure 8). This relationship was curvi-linear, suggesting a threshold level of encrustation above which increasing numbers of encrusting Dreissena have no increasing effect on fitness. Cellulase activity was not correlated with number of Dreissena by simple linear regression. However, analysis of covariance among experimentally encrusted animals and naturally encrusted animals using number of Dreissena as a covariate showed a significant negative correlation between cellulase activity and number of Dreissena. In Lampsilis, lipid content was not correlated with number of encrusting Dreissena.

Biochemical indices of fitness in populations of Amblema and Lampsilis showed strong interpopulation differences that were unrelated to Dreissena encrustation (Table 1). Mean glycogen content and cellulase activity were significantly higher in Amblema and Lampsilis from LaPlaisance Bay than in animals from Put-in-Bay and Kelley's Island. Mean glycogen and enzyme activity did not differ between Put-in-Bay and Kelley's Island for either species except for cellulase activity, which was higher in Put-in-Bay Lampsilis. Lipid content was generally low in both species. Lipids were slightly lower at Kelley's Island for both species, but Put-in-Bay and LaPlaisance Bay animals did not differ.

Patterns of mortality in natural populations of unionids in Lake Erie varied across species, but were taxonomically consistent at the subfamily level. Proportion of live to dead animals differed among subfamilies at all sites (Figure 6). Proportions of live to dead animals were lower for the subfamilies Anodontinae (Anodonta grandis) and Lampsilinae

(Lampsilis radiata, Leptodea fragilis, and Potamilus alatus) than the subfamily Ambleminae (Amblema plicata and Quadrula pustulosa) at all three sites. At Put-in-Bay, proportions of live to dead animals for the Anodontinae were lower than the Lampsilinae, but did not differ at Kelley's Island or LaPlaisance Bay. At all three sites, proportions of live to dead animals was high for the subfamily Ambleminae, indicating 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 Dreissena with which to compare our observations. However, the taxonomic and geographic consistency of our observations suggest that strong, differential mortality in unionid populations has indeed occurred across western Lake Erie within roughly the last year.

Discussion

Effects on individual species

Fouling by Dreissena 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 Dreissena. 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 these experimental results. Lampsilis in natural populations experienced higher mortality in the western basin of Lake Erie in the recent past (after the arrival of Dreissena) than Amblema, which did not experience high mortality. Thus, two common species in the Lake Erie bivalve community are differentially affected by Dreissena, with Amblema being more tolerant of fouling than Lampsilis.

Biochemical indices of fitness were more variable in encrusted animals from natural populations than animals from the experiments, but these data are consistent with the hypothesis that Amblema is more tolerant of fouling than Lampsilis. Concordant with experimental results, Dreissena encrustation in natural populations of Lampsilis was negatively correlated with glycogen content and cellulase activity but not with lipid content. In contrast to experimental results, Amblema suffered no reduction of fitness as a function of Dreissena encrustation. The number of encrusting Dreissena was variable on animals collected from natural populations, but most animals were heavily encrusted. Our experiments, however, consisted of heavily encrusted animals compared to completely cleared individuals. Consequently, a relatively tolerant species such as Amblema may show short-term effects of fouling only in strictly controlled situations. A less tolerant species such as Lampsilis will 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 Dreissena fouling in natural populations of unionids are 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 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 Lampsilis and Amblema. 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 the primary energy store, glycogen, was sensitive to fouling by Dreissena, whereas lipid content did not differ between encrusted and unencrusted animals. Similarly, glycogen content was inversely related to number of encrusting Dreissena in Lampsilis in a natural population, while lipid content was not related to encrustation density. Thus, fouling by Dreissena, an energetic expense for unionids, 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 to these results, Hebert et al. (1991) concluded that fouling by Dreissena causes a reduction in lipids in Lake St. Clair unionids, although no regression statistics were provided to support the assertion. Although it is plausible that encrustation by Dreissena 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 lipid content and cellulase activity in native unionids varied across sites in western Lake Erie, independent of encrustation densities of Dreissena. Glycogen content and cellulase activity for Amblema and Lampsilis were significantly higher at LaPlaisance Bay, MI, than specimens from the other two sites. Lipid content also varied significantly across sites, but the differences were less dramatic. In general, Kelley's Island unionids had lower lipid content than the other two sites. Therefore, local environmental conditions (e.g., temperature regimes, quantity and quality of food, substrate stability, etc.) have strong effects on the nutrient status of native unionids. Preliminary studies of the impact of Dreissena on unionids have pooled samples across sites without considering possible site differences in baseline nutritional status (e.g., Hebert et al. 1991). However, field studies assessing the potential impacts of encrustation by Dreissena on biochemical nutrient status of native unionids must account for geographic variation in environmental conditions.

Effects on bivalve community structure

Experimental and survey data indicate that the introduction of Dreissena into the Great Lakes will alter community structure of unionid bivalves by causing differential mortality and reductions in fitness among 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 non-native freshwater bivalves have become established in North America (notably, Corbicula fluminea; see McMahon 1983), but none have been shown to result in extreme and rapid changes in community composition (Leff et al. 1990). Corbicula 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, Corbicula may be unable to become established in areas with healthy unionid populations because the niche of the infaunal, filter-feeding bivalve is already filled (reviewed in McMahon 1983). Epibiotic Dreissena, however, present a novel challenge to freshwater communities that are naive in dealing with fouling. Thus, Dreissena 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.

The subfamilies Anodontinae and Lampsilinae have experienced widespread mortality during the presence of Dreissena as an abundant member of the benthos in western Lake Erie, while the Ambleminae have not. Consistent taxonomic trends among subfamilies lead to the proposal of hypotheses regarding mechanisms of differential mortality induced by Dreissena fouling. The subfamilies Anodontinae and Lampsilinae share a common life history trait of females brooding glochidia larvae in the gills for long periods, usually 9-12 months (Clarke 1981). The Ambleminae, however, are short-term breeders, brooding young for only a few weeks to 2 months. 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. Consequently, 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 Lampsilis but no difference in mortality between encrusted and unencrusted males, and no mortality for the short-term breeder, Amblema. Thus, a long-term breeding strategy which evolved in a pre-Dreissena environment may now be of disadvantage in an environment with abundant fouling organisms.

The 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 2). 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 Dreissena to the posterior surface of a light shelled anodontine or lampsiline 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 Dreissena on an individual unionid may exceed the weight of the unionid by a factor of four (Schloesser and Kovalak in press). 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 to lampsilines and anodontines. Thus, differences in shell morphology among unionid subfamilies may result in differences in responses to fouling.

The introduction of Dreissena into the Great Lakes may have 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 Dreissena. The lack of any evolutionary experience with fouling in 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 and shell morphology may suddenly be manifested as differences in responses to fouling by Dreissena.

Acknowledgements

This project would not have been possible without the assistance of John R. Hageman, manager of The Ohio State University's F.T. Stone Laboratory at Put-in-Bay, OH. Jack Wade and Paul Buescher and other members of the Ohio Underwater Research Association assisted in the collection of animals from Kelley's Island. We would also like to thank R. Hancock, P. Pappas, T. Cvetnik, P. Berg, L. Hall, B. Ling, D. Jameson, and D. Insley for assistance in the lab and field. D. Stansbery of the Ohio State University Museum of Zoology provided unionid specimens for measurement of shell weight. S. Madon and C. Franz critically reviewed drafts of the manuscript. This project was supported by the Ohio Sea Grant Development Fund and the American Electric Power Company.

Literature cited

Buchanan A.C. 1980. Mussels (Naiades) of the Meramec River Basin, Missouri. Aquatic Series no. 17, Missouri Department Conservation, Jefferson City, MO.

Christie, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Bd. Can. 31:827-854.

Clarke, A.H. 1981. The Freshwater Molluscs of Canada. National Museum of Natural Sciences. Ottawa.

Clarke, A.H. and D.H. Stansbery. 1988. Are some Lake Erie mollusks products of post-Pleistocene evolution? p. 85-91. In J.F. Downhower (ed.) The Biogeography of the Island Region of Western Lake Erie. The Ohio State University Press, Columbus, OH.

Daiber, F.C. 1952. The food and feeding relationships of the freshwater drum, Aplodinotus grunniens Rafinesque, in western Lake Erie. Ohio J. Science. 52:35-46.

Farris, J.L, J.H. Van Hassel, S.E. Belanger, D.S. Cherry, and J. Cairns, Jr. 1988. Application of celluloytic activity of asiatic clams (Corbicula sp.) to in-stream monitoring of power plant effluents. Environ. Toxicol. Chem. 7:701-713.

Griffiths, R.W., D.W. Schloesser, J.H. Leach, and W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (Dreissena polymorpha) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48:1381-1388.

Hebert, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on Dreissena polymorpha (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46:1587-1591.

Hebert, P.D.N., C.C. Wilson, M.H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc Dreissena polymorpha. Can J. Zool. 69:405-409.

Leff, L.G., J.L.Burch, and J. Vaun McArthur. 1990. Spatial distribution, seston removal, and potential competitive interactions of the bivalves Corbicula fluminea and Elliptio complanata, in a coastal plain stream. Freshwater Biol. 24:409-416.

Lewandowski, K. 1975. Unionidae as a substratum for Dreissena polymorpha Pall. Pol. Arch. Hydrobiol. 23:409-420.

McMahon, R.F. 1983. Ecology of an invasive pest bivalve, Corbicula, p. 505-561 In W.D. Russell-Hunter [ed.] The Mollusca vol. 6, Ecology. Academic Press, New York.

MacInnis, A.J. and M. Voge. 1970. Experiments and Techniques in Parasitology. W.H. Freeman, San Francisco, CA.

Mackie, G.L. 1984. Bivalves, p.351-418 In A.S. Tompa, N.H. Verdonk, and J.A.M. van den Biggelaar [eds.] The Mollusca vol. 7, Reproduction. Academic Press, New York.

Mackie, G.L. 1991. Biology of the exotic zebra mussel, Dreissena polymorpha, in relation to native bivalves and its potential impact in Lake St. Clair. Hydrobiol. 219:251-268.

Negus, C.L. 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. J. Anim. Ecol. 35:513-532.

Neves, R.J. and M.C. Odom. 1988. Muskrat predation on endangered freshwater mussels in Virginia. J. Wildl. Manage. 53:934-941.

Nichols, F.H., J.K. Thompson, and L.E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the asian clam Potamocorbula amurensis. II. Displacement of a former community. Mar. Ecol. Prog. Ser. 66:95-101.

Pandian, T.J. 1975. Mechanisms of heterotrophy, p.61-249. In O. Kinne [ed.] Marine Ecology Vol. 2, Physiological Mechanisms. Wiley, London.

Schloesser, D.W. and W. Kovalak. Infestation of unionids by Dreissena polymorpha in a power plant canal in Lake Erie. J. Shellfish Res. (in press).

Sebestyn, O. 1938. Colonization of two new fauna-elements of Pontus-origin (Dreissena polymorpha Pall. and Corophium curvispinum G.O. Sars forma devium Wundsch) in Lake Balaton. Verh. Internat. Verein. Limnol. 8:169-181.

Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99:754-765.

Van Handel, E. 1985. Rapid determination of total lipids in mosquitoes. J. Am. Mosq. Control Assoc. 1:302-304.

Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Mar. Ecol. Prog. Ser. 58:175-189.

Figure Legends

Figure 1. Map of western Lake Erie showing sample sites. Stars representing sample sites are, from west to east; LaPlaisance Bay, MI, Put-in-Bay, OH, and Kelley's Island, OH.

Figure 2. Artificially encrusted treatment (left) and cleared control (right) Amblema plicata. Shallow grooves cut into the shell allowed identification of the group regardless of encrustation density at the end of the experiment.

Figure 3. Percent survival of native bivalves following three month field experiment. Error bars represent one standard error, calculated using a binomial distribution. Sample size equals number of living and dead individuals recovered. Lampsilis females suffered significantly greater mortality when encrusted (G-test, $p<0.010$). There was no significant difference in survival between controls and treatment males. Amblema suffered no mortality in experiments.

Figure 4. Biochemical indices of fitness in encrusted and unencrusted Amblema plicata after a three month field experiment. Error bars represent one standard error of the mean. Encrusted animals had significantly lower glycogen content and cellulase activity (ANOVA, $p<0.050$). Lipid content did not differ between the two groups.

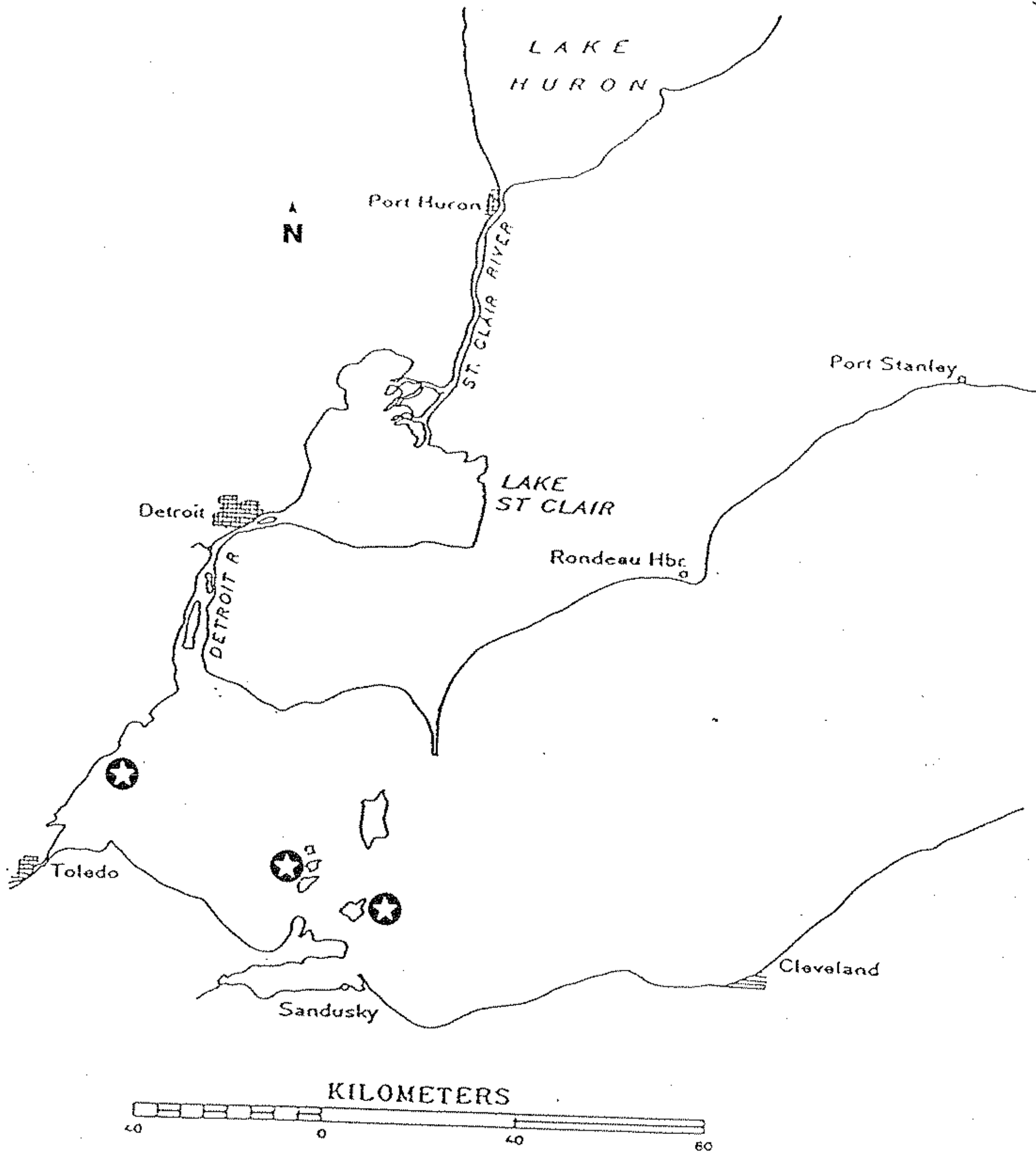
Figure 5. Biochemical indices of fitness in encrusted and unencrusted Lampsilis radiata after a three month field experiment. Error bars represent one standard error of the mean. Glycogen content and cellulase activity differed between controls and treatments and between males and females (ANOVA, $p<0.050$). Lipid content did not differ among treatments or sexes.

Figure 6. Percent of live individuals of native bivalve species from three sites across western Lake Erie. Percent alive represents the ratio of live to recently-dead individuals, with sample size equal to the total number of live and recently-dead individuals recovered. Percent alive for Lampsilis is lower than Amblema at the two sites at which Lampsilis was present in sufficient numbers (Fisher's exact test, $p<0.010$). Anodontinae and Lampsilinae showed lower percentages of live animals than Ambleminae at all three sites (χ^2 test, $p<0.001$). Anodontinae showed a lower percentage than Lampsilinae at Put-in-Bay (Fisher's exact test, $p<0.001$), but did not differ at the other 2 sites.

Figure 7. Biochemical indices of fitness in Amblema plicata from three natural populations in western Lake Erie. Filled circles represent animals from Put-in-Bay, OH, open circles represent Kelley's Island, OH, and triangles represent animals from LaPlaisance Bay, MI. Dashed lines indicate best-fit lines from simple linear regression for which slopes are not significantly different from zero ($p>0.050$).

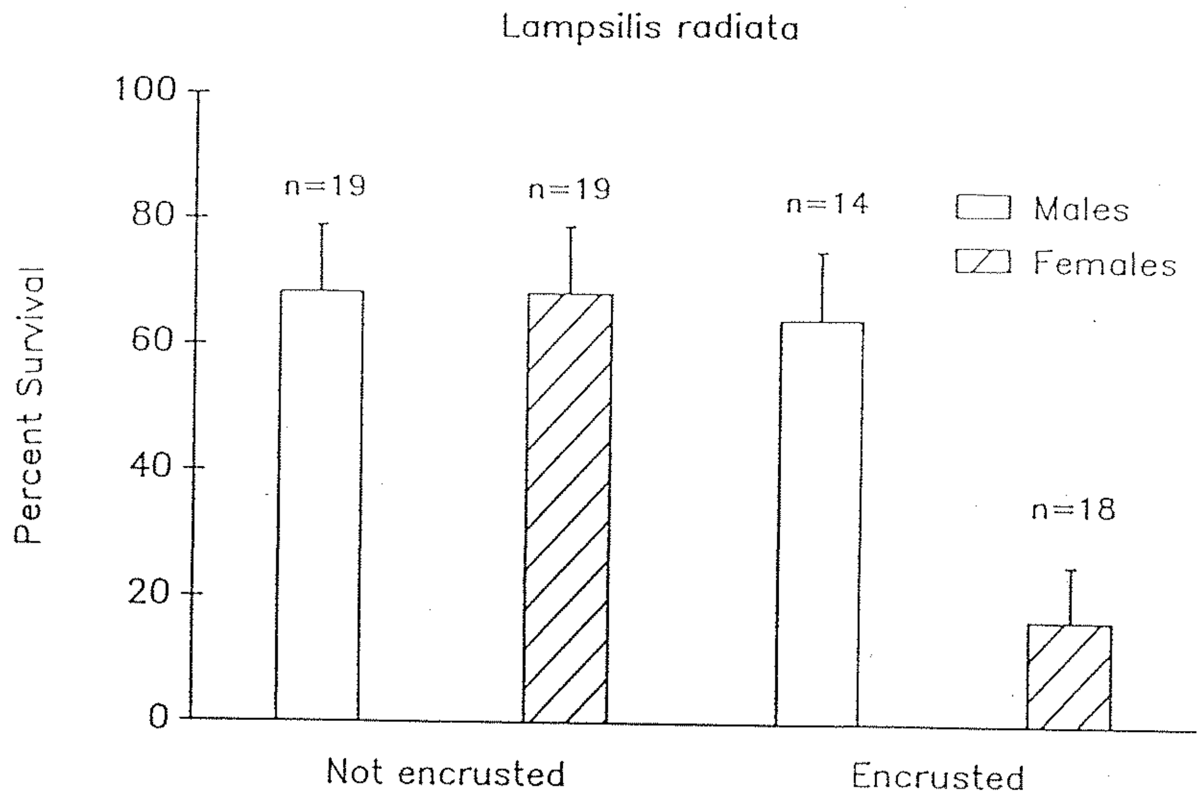
Figure 8. Biochemical indices of fitness in Lampsilis radiata from a natural population in Lake Erie at Put-in-Bay, OH. The solid line for glycogen represents a significant correlation by second-order regression. Cellulase activity (*) was negatively correlated with number of Dreissena (ANCOVA, $p<0.050$). Dashed lines represent best-fit lines from simple linear regression for which slopes are not significantly different from zero ($p>0.050$).

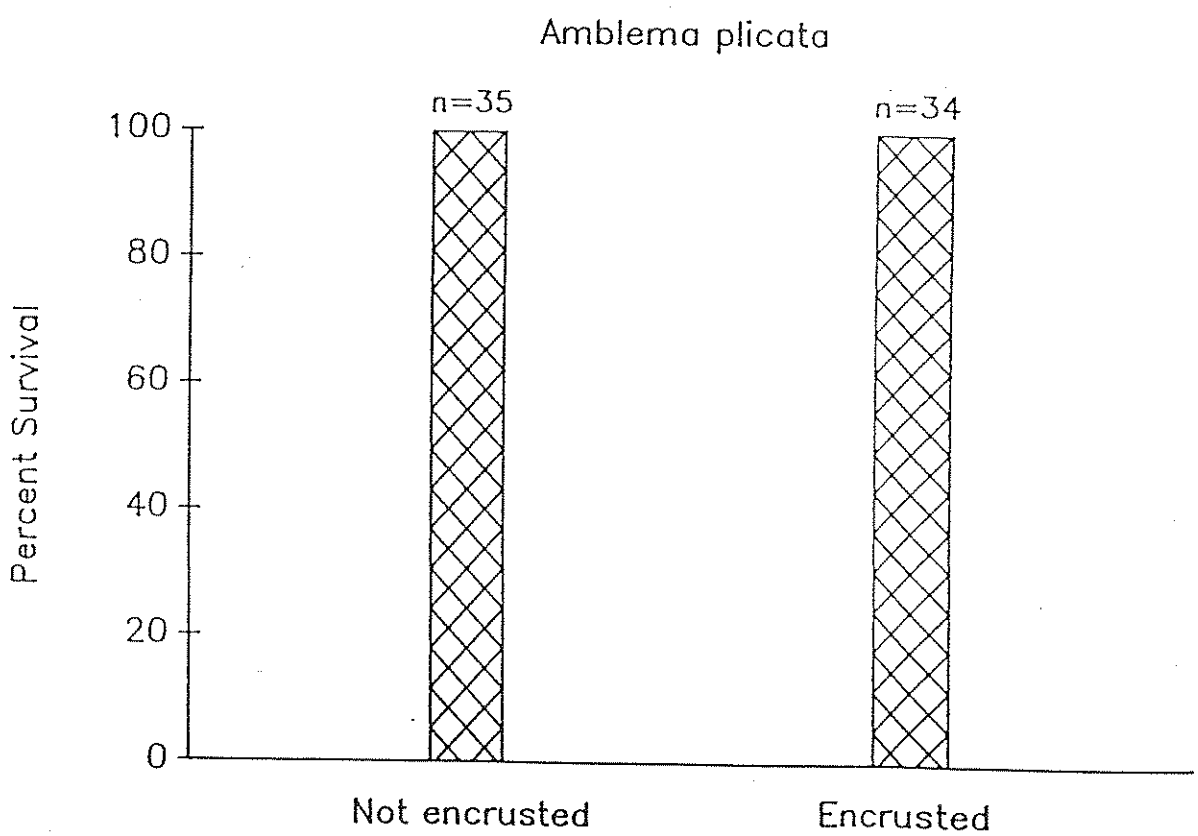
Haag et al.
Fig. 1



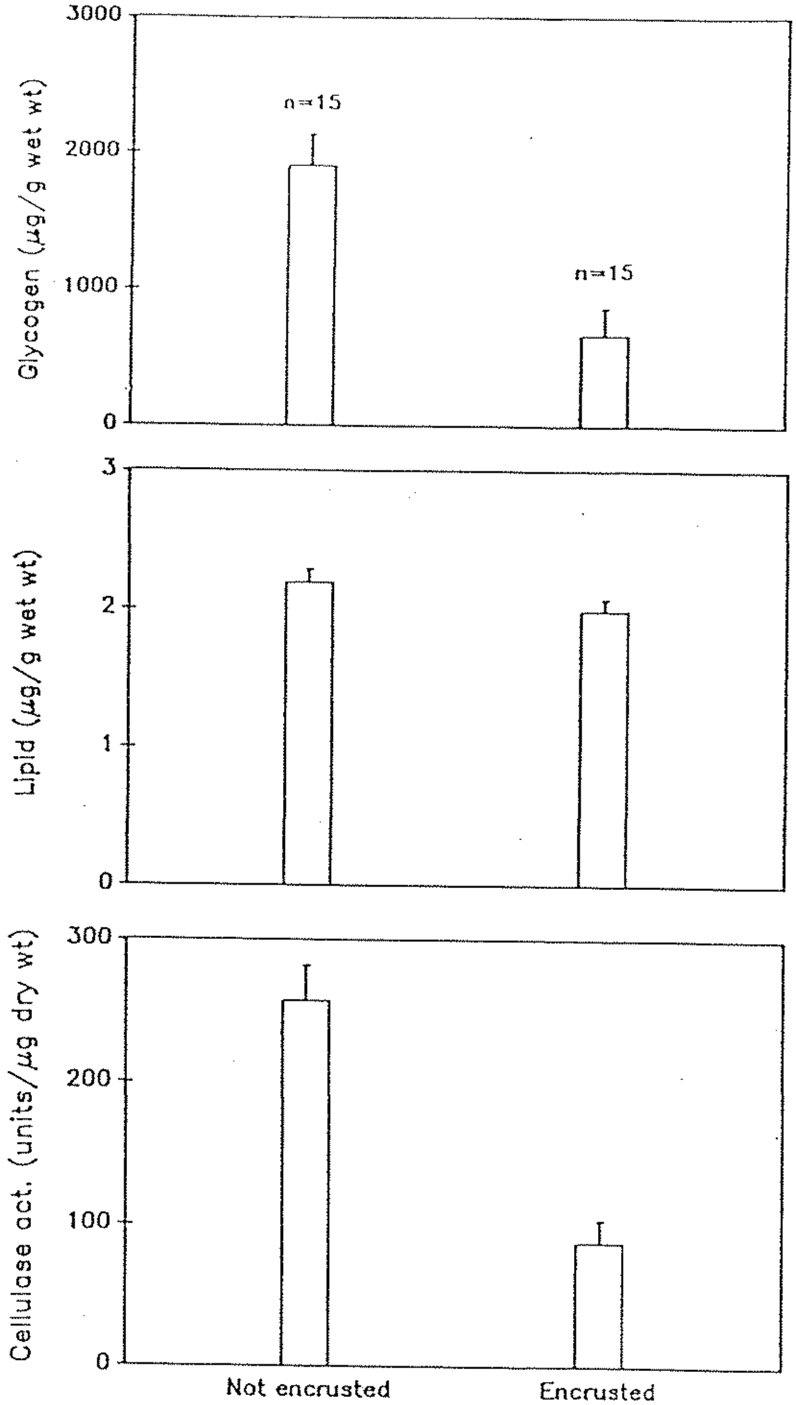
Haag et al.
Fig 2

Haag et al.
Fig. 3

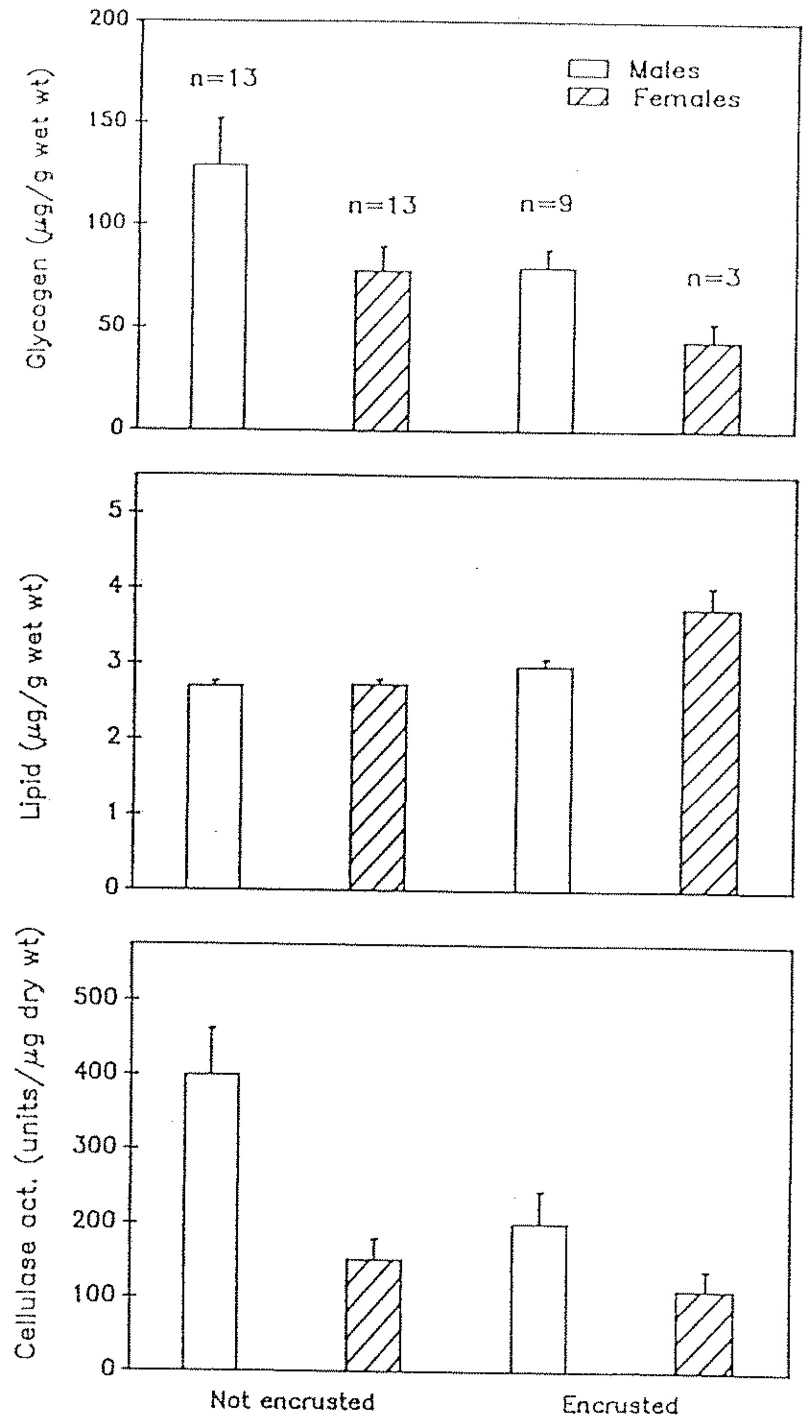




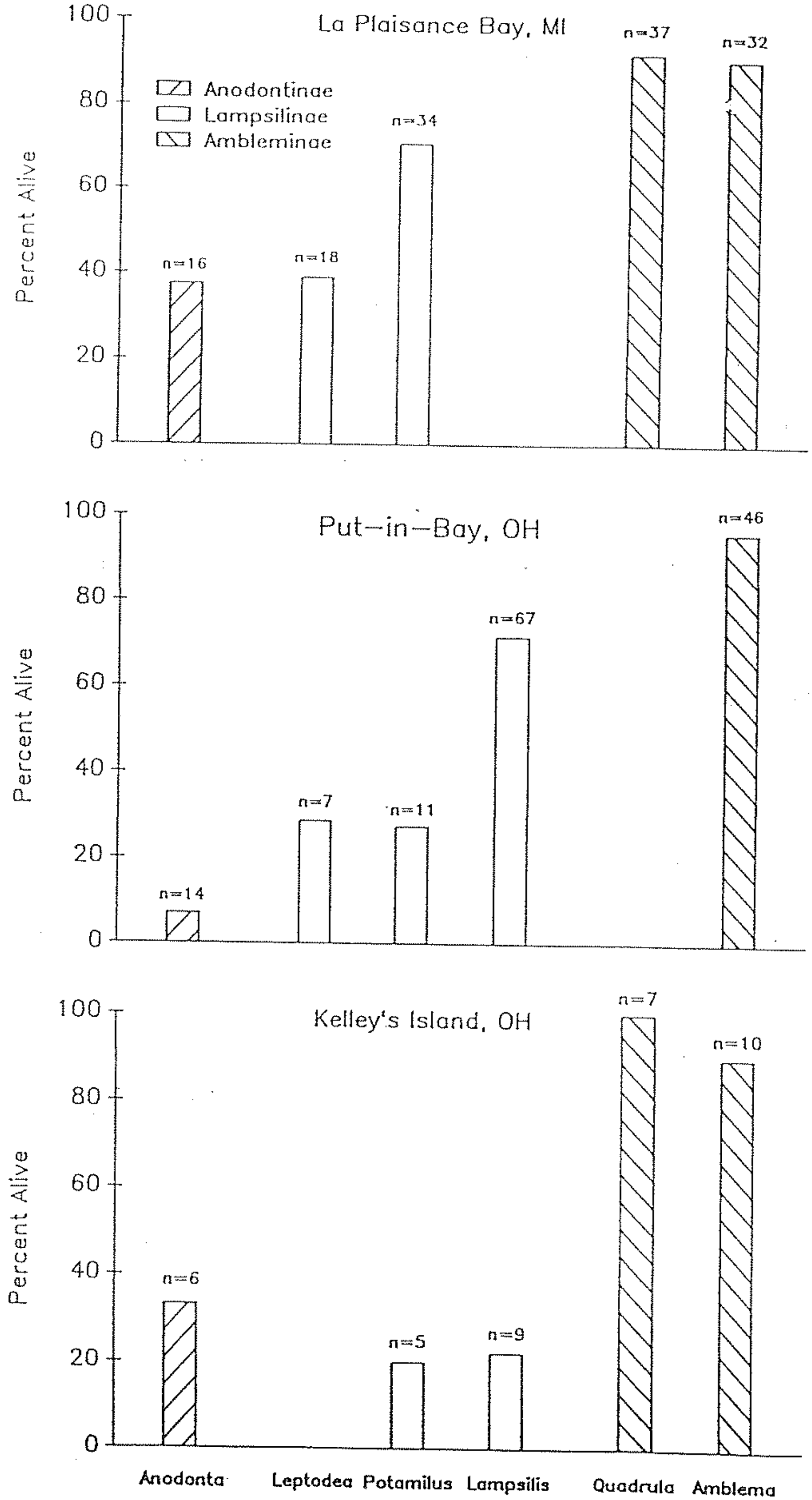
HAAG et al. fig. 4



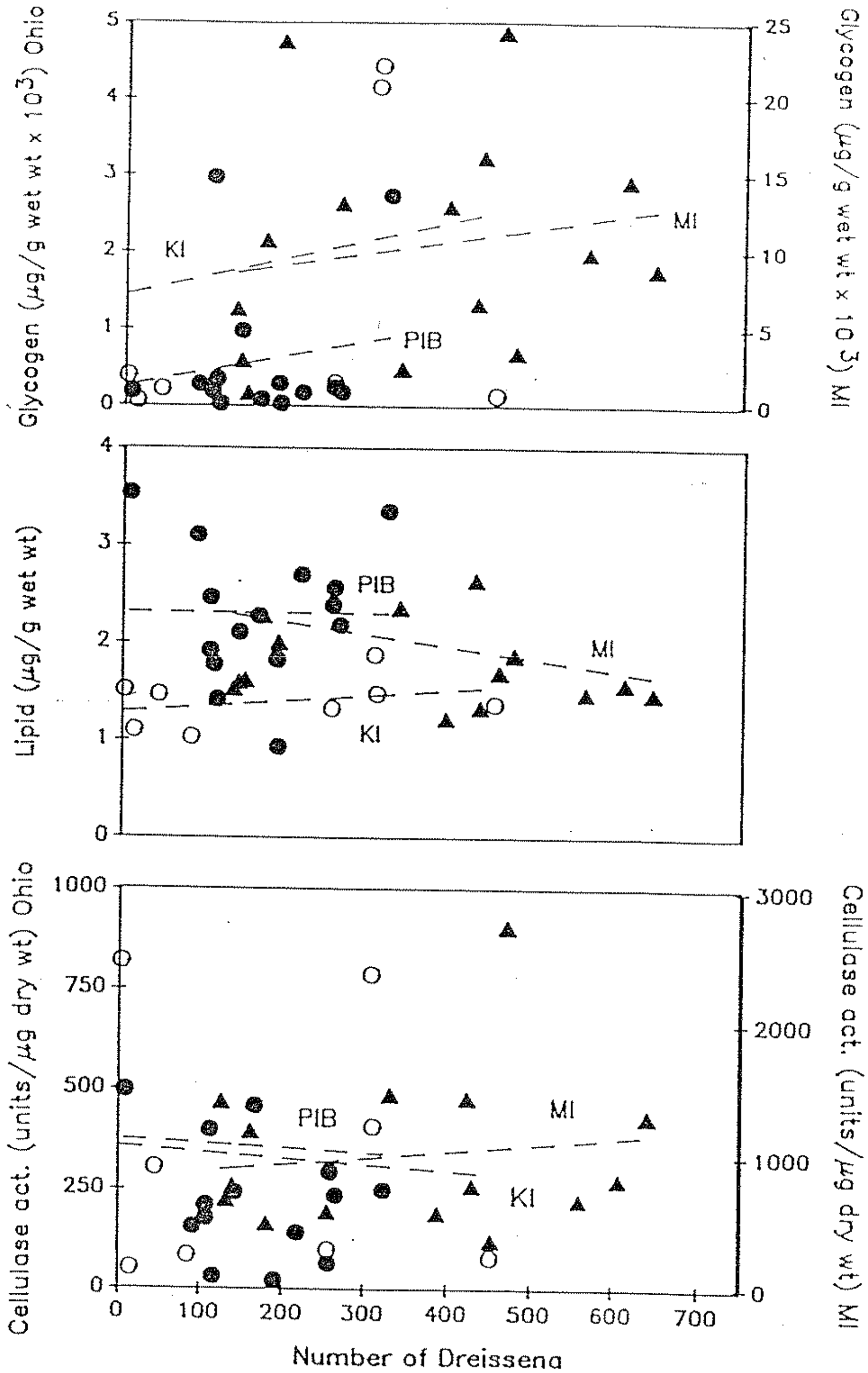
Haag et al. Fig 5



Haag et Al. Fig 6



Haag et al. Fig 7



Haag et al. Fig. 8

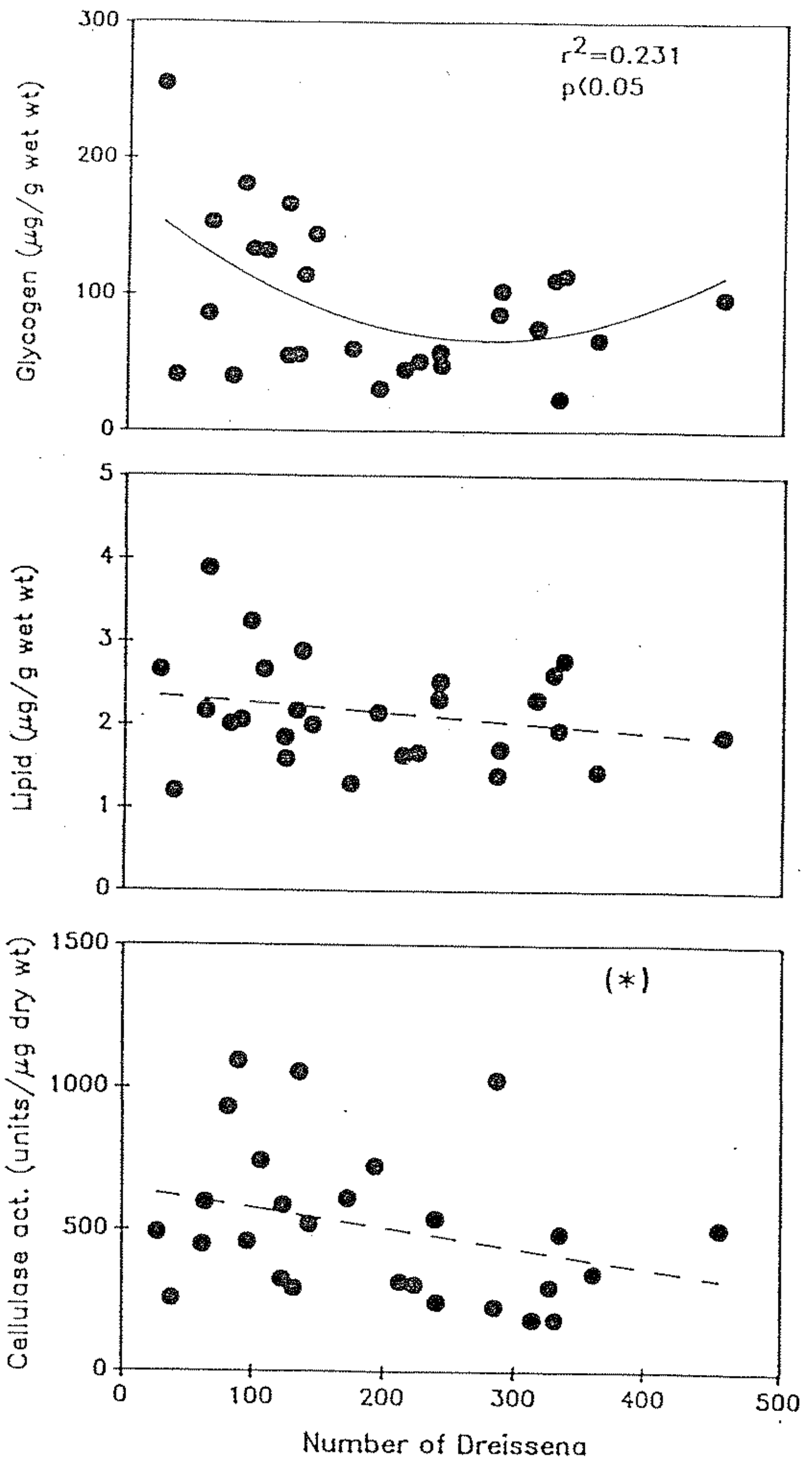


Table 1. Weight-standardized glycogen content, lipid content, and cellulase activity for *Amblema plicata* and *Lampsilis radiata* from three natural populations in western Lake Erie. Site abbreviations are PIB = Put-in-Bay, OH, KEL = Kelley's Island, OH, and MI = LaPlaisance Bay, MI. Values are means $\pm$ SE. Species means within the same column with the same superscript letter are not significantly different, those with different superscripts are significantly different ($p<0.05$, Tukey's multiple comparisons).

Species site	Glycogen cont. (µg/g wet wt.)	Lipid cont. (µg/g wet wt.)	Cellulase act. (units/µg dry wt.)	n
Amblema				
PIB	60.0 ± 244.0^{a}	2.303 ± 0.181^{a}	357.0 ± 135.0^{a}	15
KEL	1711.0 ± 748.0^{a}	1.375 ± 0.085^{b}	328.5 ± 99.2^{a}	9
MI	10360.0 ± 1860.0^{b}	2.005 ± 0.262^{ab}	1010.0 ± 156.0^{b}	15
Lampsilis				
PIB	94.0 ± 10.0^{a}	2.149 ± 0.120^{ab}	512.0 ± 51.6^{a}	27
KEL	48.0 ± 5.0^{a}	1.400 ± 0.213^{b}	72.1 ± 21.7^{b}	4
MI	7620.0 ± 5350.0^{b}	2.762 ± 0.334^{a}	1168.0 ± 347.0^{c}	4

Table 2. 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 *Quadrula pustulosa* which is from the Muskingum River, OH. Values in parentheses are standard errors of the mean, n = sample size.

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