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1993**Density and ecomorphology of a freshwater mussel (*Elliptio complanata*, Bivalvia:Unionidae) in a Rhode Island lake**

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Abstract. Densities of freshwater mussel species in a small (430 ha), shallow ($z_{\max} = 1.8$ m) lake in Rhode Island were determined by a SCUBA survey. The three dominant mussel species included *Elliptio complanata* ($\bar{x} = 25.7/\text{m}^2 \pm 12.6$ SD), *Lampsilis radiata* (1.1 ± 0.9) and *Ligumia nasuta* (0.5 ± 0.6). *Anodonta cataracta* was found rarely in shallow, sandy areas. A morphological analysis of *E. complanata* showed that individuals living in silt substratum were larger, older, and narrower relative to those in sand. Growth rates, calculated using data on size (length, height, and width of shell) and age (determined by thin section), showed faster growth in the silt substratum. These results conflict with other ecomorphological analyses of *E. complanata* and other unionid species. The sand habitat may be worse and/or the silt habitat better for mussel growth, relative to similar contrasts made previously.

Key words: ecomorphology, Unionidae, *Elliptio*, *Lampsilis*, *Ligumia*, growth and density estimation, Rhode Island.

Although relationships between the habitat of freshwater mussels and their shell growth and morphology are commonly observed (e.g., Tevesz and Carter 1980, Bailey and Green 1988, Hinch and Bailey 1988), few studies have combined population density estimates with careful analysis of morphological variability in mussel shells of a given species within a single basin. The objective of our study was to describe the distribution and shell characteristics of mussels in a Rhode Island lake, Worden Pond. Mussels are an important component of the benthic community in this lake, and no baseline studies of population numbers exist. Estimates of the recent mean and variance in density will provide a benchmark for future studies and an indication of the sampling effort needed to detect changes in population density of the mussels (Downing and Downing 1992). This is particularly important given the likelihood of encroaching urbanization and the invasion of exotic species like the zebra mussel (Strayer 1991). Additionally, substratum variability within the lake allowed us to compare the patterns of growth and morphological variation of these mussels that might be predicted from other studies of unionid ecomorphology (e.g., Hinch

et al. 1986, Bailey and Green 1988, Hinch and Bailey 1988).

Methods

Worden Pond covers 430 ha and has an average depth of 1.2 m and a maximum depth of 1.8 m. Based on chlorophyll concentrations, the lake is mesotrophic to eutrophic, with an alkalinity of 140 $\mu\text{eq/L}$ (Green et al. 1991). Sediment type was categorized as "sand" or "silt". "Silt" substratum did not feel gritty when rolled between the fingers and was dark in color. Mussels were collected by hand, using SCUBA, from 48 stations evenly distributed throughout Worden Pond. Of the 48 stations, 28 were classified as having sediment composed mostly of sand and 20 had sediment composed mostly of silt. All mussels were removed to a depth of at least 10 cm from ten 0.25-m² quadrats at each station. Sampling was performed from 14 June to 1 August 1990. All mussels collected were identified to species using Smith (1986), and voucher specimens were deposited in the Zoology Department, University of Rhode Island.

Shell measurements of length, height, and width were made with dial calipers according

TABLE 1. Standardized and structure coefficients from MANOVA comparing *Elliptio complanata* from sand and silt substrata in Worden Pond (Wilks' lambda = 0.52, $F = 35.2$, $df = 4,152$, $p < 0.001$).

Variable	Structure coefficient	Standardized coefficient	Univariate ANOVA p-level
ln(age)	-0.29	-1.66	0.010
ln(length)	0.34	0.91	0.003
ln(height)	0.34	2.59	0.002
ln(width)	0.17	-1.77	0.137

to Hinch et al. (1989). Additionally, age was estimated for a subset of mussels from both habitats ($n_{\text{sand}} = 65$, $n_{\text{silt}} = 92$) using internal growth lines examined as thin sections (Neves and Moyer 1988). Shell morphology and age were compared between substratum types using multivariate analysis of variance of \log_e -transformed (for allometric linearity) shell descriptors (MANOVA, PROC GLM, SAS Institute Inc., 1985). The "size at age" data were also used to calculate von Bertalanffy growth curves for mussels from each of the two substratum types with the software of Saila et al. (1988). Shell weight was determined from the right valve after air drying. The shell weight of a mussel with a given length was compared between sand and silt substratum areas using analysis of covariance (ANCOVA), with "shell weight" as the dependent variable, "shell length" as the covariate, and "substratum type" as the grouping variable. Wet weight of the soft parts was determined by patting dry on a paper towel and weighing to the nearest 0.01 g. It was used as the response variable in a similar ANCOVA analysis. The dependent variable and the covariate were \log_e -transformed before both analyses to linearize allometric relationships.

External shell erosion was quantified and compared between substratum types by digitizing photocopies of virtually the same subset of

shells ($n_{\text{sand}} = 64$, $n_{\text{silt}} = 93$). With these high contrast copies, any eroded white shell surface contrasted clearly with the intact, black periostracum. Bias from projection of the three-dimensional shells onto a two-dimensional photocopy should have been similar for shells from the two substratum types. The area of shell eroded was compared between sand and silt substratum areas by ANCOVA, with "area eroded" as the dependent variable, "age" and "area not eroded" as the covariates, and "substratum type" as the grouping variable. Both the dependent variable and the covariate were \log_e -transformed before analysis.

Results

The three dominant mussel species found in Worden Pond included *Elliptio complanata* ($\bar{x} = 25.7 \pm 12.6$, mean number/m² ± 1 SD), *Lampsilis radiata* (1.1 ± 0.9) and *Ligumia nasuta* (0.5 ± 0.6). *Anodonta cataracta* was found rarely in shallow, sandy areas. There were no significant differences ($p \geq 0.05$) in the density of each species between sand and silt substrata. Subsequent morphological and growth analyses were limited to the dominant *E. complanata*.

MANOVA revealed that mussels from sand and silt substrata differed with respect to age, shell length, height, and width. Mussels from silt substrata had a higher mean score ($\bar{x} = 0.80$) on the single discriminant axis than those from sand substrata ($\bar{x} = -1.14$). Therefore, canonical structure and standardized coefficients (Table 1) may be interpreted as showing that mussels from silt substrata were longer, narrower, and younger than individuals from sand substrata (Fig. 1). The difference between silt-substratum and sand-substratum mussels was relatively subtle; if mussels were classified as either sand or silt substratum dwellers on the basis of their age and shell measurements only, 14% would be incorrectly categorized. However, indepen-

TABLE 2. Growth curve parameters for length, height, and width of *Elliptio complanata* aged by thin sectioning. L_{max} is estimated maximum size, k is relative growth rate, a measure of the rate a mussel approaches L_{max} . Standard errors are given in parentheses.

Variable	Sand L_{max}	Silt L_{max}	Sand k	Silt k
Length	70.5 (2.4)	83.6 (3.6)	0.163 (0.027)	0.123 (0.021)
Height	37.0 (1.2)	45.5 (1.9)	0.165 (0.027)	0.139 (0.021)
Width	10.4 (0.5)	12.3 (0.7)	0.133 (0.026)	0.122 (0.021)

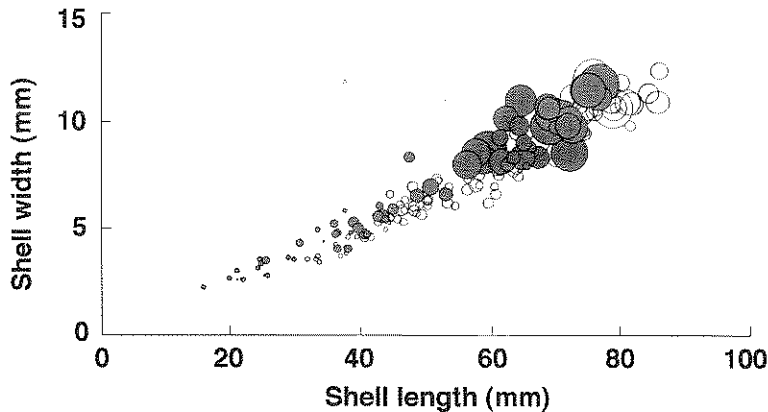


FIG. 1. Variation in shell morphology between *Elliptio complanata* from sand (filled circles) and silt (open circles) substrata. Size of the plotting circle reflects the age of the mussel, which ranged from 3 to 33 years.

dently calculated growth rate analyses showed that *E. complanata* from silt substrata grew to greater maximum lengths, heights, and widths than individuals from sand substrata (Fig. 2, Table 2).

The relationship between shell weight and shell length was similar for mussels from both substratum types (Fig. 3a):

sand:

$$\begin{aligned} \ln(\text{shell weight}) \\ = -12.445 + 3.513 \ln(\text{shell length}) \end{aligned}$$

silt:

$$\begin{aligned} \ln(\text{shell weight}) \\ = -12.515 + 3.516 \ln(\text{shell length}) \end{aligned}$$

The R^2 for the "total model" (including habitat, shell length, and habitat \times length interaction as predictors) was 0.94. No significant difference was detected between the slopes ($p > 0.97$) and intercepts ($p > 0.84$) of the regression lines for each habitat. Because the common slope was significantly greater than 3 (t -test, $p < 0.001$), we concluded that shell weight relative to length increases faster than one would expect if shell thickness or density remained constant with increasing shell size. Shell thickness or density increased with increased shell size.

The relationship between wet weight of the soft parts and shell length was similar for mussels from both substratum types (Fig. 3b):

sand:

$$\begin{aligned} \ln(\text{wet weight}) \\ = -10.499 + 2.881 \ln(\text{shell length}) \end{aligned}$$

silt:

$$\begin{aligned} \ln(\text{wet weight}) \\ = -10.978 + 3.001 \ln(\text{shell length}) \end{aligned}$$

The total model R^2 was 0.98. Once again, no differences were seen between slopes ($p > 0.20$) or intercepts ($p > 0.20$) of these regression lines. The common slope was not significantly greater than 3 (t -test, $p > 0.5$), so we concluded that wet weight relative to length increases at a rate one would expect if the density of soft tissue remained constant in larger mussels.

Age and non-eroded area of the shell were correlated ($r = 0.73$, $p < 0.001$), therefore interpretation of the results of the ANCOVA on eroded area of the shell must be made with caution. The equations predicting eroded area of the shell from non-eroded area and age for the two substrata were as follows:

sand:

$$\begin{aligned} \ln(\text{eroded area}) \\ = 4.283 - 2.074 \ln(\text{age}) \\ - 0.453 \ln(\text{non-eroded area}) \\ + 0.489 (\ln(\text{age}) \times \ln(\text{non-eroded area})) \end{aligned}$$

silt:

$$\begin{aligned} \ln(\text{eroded area}) \\ = 2.497 - 2.601 \ln(\text{age}) \\ - 0.082 \ln(\text{non-eroded area}) \\ + 0.489 (\ln(\text{age}) \times \ln(\text{non-eroded area})) \end{aligned}$$

The total model R^2 was 0.86. There was no three-way interaction of age, non-eroded area, and habitat ($p > 0.33$), therefore the coefficients for

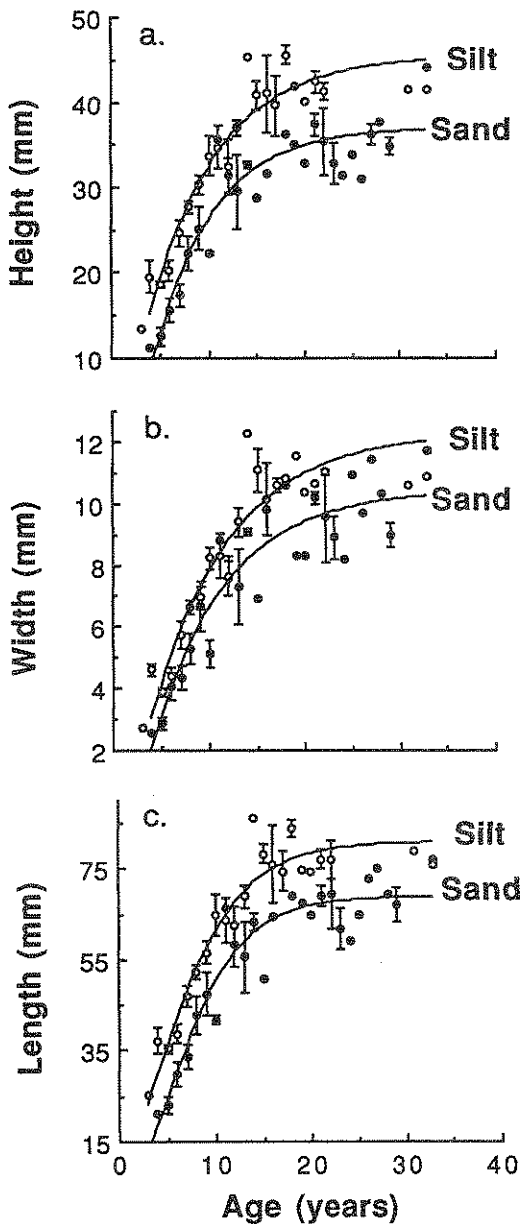


FIG. 2. Fitted von Bertalanffy growth curves for *Elliptio complanata* shell height (a), width (b), and length (c) calculated using individuals collected from sand (filled circles) and silt (open circles) substrata. Error bars are standard errors. Points without error bars represent single individuals.

the significant ($p < 0.001$) two-way interaction of age and non-eroded area are identical (i.e., 0.489) for both substrata. The difference between habitats in the effect of age on eroded area (i.e., -2.074 for sand, -2.601 for silt) was

significant ($p = 0.04$), as was the independent effect of age ($p = 0.02$). This result showed that the increase with age in the proportion of external shell eroded was significantly greater in mussels from the sand substratum than those from the silt substratum. Other interactions and main effects were only marginally significant ($p = 0.07$ for the interaction of non-eroded area and habitat as well as main effect of habitat) or non-significant ($p = 0.30$ for the independent effect of non-eroded area).

Discussion

The densities of *Elliptio complanata* and *Lampsilis radiata* were within the range found for these species by Downing and Downing (1992) in their compilation of quantitative surveys. They reported *E. complanata* ranging from 1.4/m² to 89/m² ($n = 31$), and *L. radiata* ranging from 0.1/m² to 29/m² ($n = 15$). Downing and Downing (1992) predicted, based on an empirical relationship derived from 76 surveys of unionid populations and work on other aquatic taxa, that the variance of a mussel population should relate to the mean as $s^2 = m^{1.5}$, where s^2 = the predicted variance and m = the observed mean density. Thus, for Worden Pond we would predict a variance of $25.7^{1.5} = 130.3$ for *E. complanata* and $1.1^{1.5} = 1.15$ for *L. radiata*, which are reasonably close to the observed values of 158.8 and 0.81, respectively. According to Downing and Downing's (1992) simulation, we would require only about 10 to 20 quadrat counts in the future to detect a 50% decline in the *E. complanata* population from 26 to 13 individuals/m². On the other hand, a more subtle drop of 25% in density would require several hundred samples. Increased sensitivity to density change could be achieved by re-visiting sampling sites within the lake (i.e., blocking) through time (e.g., Bailey and Green 1989).

Morphological and growth differences between *E. complanata* from sand and silt substrata were contrary to previous observations (Kat 1982, Hinch and Bailey 1988, Hinch and Green 1988, Hinch et al. 1989). Individuals from silt substrata had faster growing, narrower shells than those from sandy substrata. This may reflect either "extreme" turbulence in sandy areas of the lake, detrimental to feeding and growth (Green 1972), or a richer food supply in silty areas. A mark-recapture study has verified the difference in mean growth rates between the

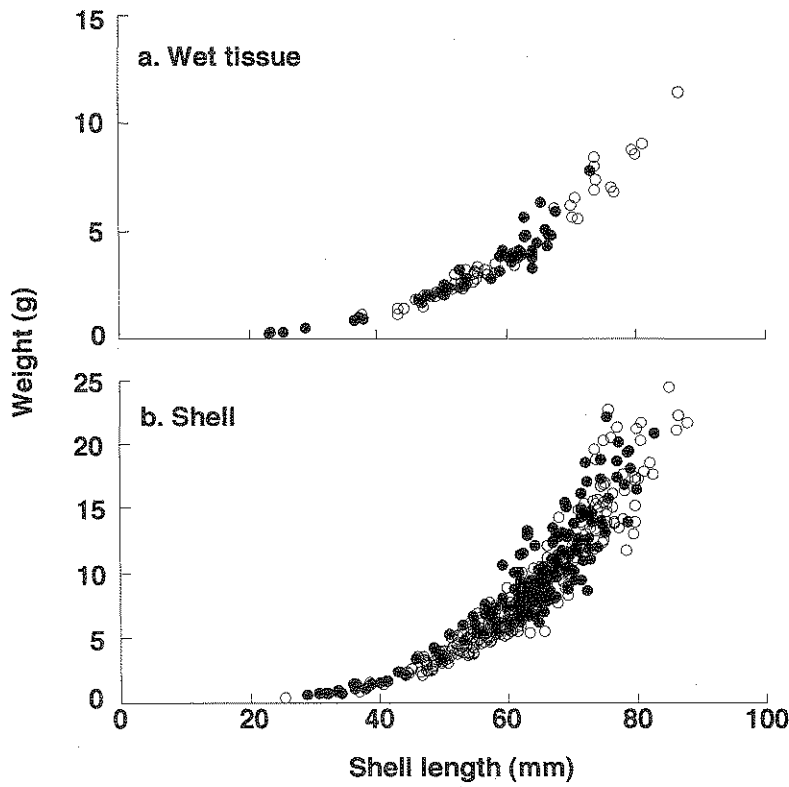


FIG. 3. Wet tissue weight (a) and shell weight (b) vs. shell length for *Elliptio complanata* from sand (filled circles) and silt (open circles) substrata.

two habitats ($t = 10.01$; $df = 354$; $p < 0.0001$) inferred in the present study from internal growth-line counts and shell dimensions (Kessler, unpublished data).

Increase in the area of shell eroded over time was greater in sand than in silt substrata. This conforms to Green et al. (1989), who found greater erosion in coarser, more turbulent bottom habitats. We have been able to assess variability in shell erosion more accurately by statistically separating the effects of habitat, size of the mussel (i.e., non-eroded area), and age. The most striking determinant on the area of eroded shell is the age of the mussel. Older individuals have a greater shell area eroded. But our results show that a mussel of a given size spending one year in silt substratum has significantly less shell erosion than if it spent the year in sand. This conclusion depends on our estimate of mussel age being accurate, or at least similarly biased in both habitats. Downing et al. (1992) have found that external "annuli" on *Lampsilis radiata* and *Anodonta grandis* may be in

fact non-annual. Although we estimated age with the more dependable internal growth lines, the annularity of even these lines needs to be confirmed with an experiment.

The assessment of potential impacts on a population requires careful characterization of the organisms before disturbance by humans or exotic species. We have established the present status of the Worden Pond population of *Elliptio complanata* with respect to density, and determined the sampling effort needed to detect a future change in the density in response to natural or human-influenced changes in environmental conditions. We have also found that "typically" observed relationships between the benthic environment and the relatively plastic shell morphology and growth rate of Unionidae may vary more than previously suspected.

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Literature Cited

- BAILEY, R. C., AND R. H. GREEN. 1988. Within-basin variation in the shell morphology and growth rate of a freshwater mussel. *Canadian Journal of Zoology* 66:1704-1708.
- BAILEY, R. C., AND R. H. GREEN. 1989. Spatial and temporal variation in a population of freshwater mussels in Shell Lake, N. W. T. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1392-1395.
- DOWNING, J. A., AND W. L. DOWNING. 1992. Spatial aggregation, precision, and power in surveys of freshwater mussel populations. *Canadian Journal of Fisheries and Aquatic Sciences* 49:985-991.
- DOWNING, W. L., J. SHOSTELL, AND J. A. DOWNING. 1992. Non-annual external annuli in the freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoidea*. *Freshwater Biology* 28:309-317.
- GREEN, L. T., A. J. GOLD, AND A. LEHRER. 1991. 1990 Rhode Island Watershed Watch. Natural Resources Science Technical Report 91-1. The University of Rhode Island.
- GREEN, R. H. 1972. Distribution and morphological variation of *Lampsilis radiata* (Pelecypoda:Unionidae) in some central Canadian lakes: a multivariate statistical approach. *Journal of the Fisheries Research Board of Canada* 29:1565-1570.
- GREEN, R. H., R. C. BAILEY, S. G. HINCH, J. L. METCALFE, AND V. H. YOUNG. 1989. Use of freshwater mussels (Bivalvia:Unionidae) to monitor the near-shore environment of lakes. *Journal of Great Lakes Research* 15:635-644.
- HINCH, S. G., AND R. C. BAILEY. 1988. Within- and among-lake variation in shell morphology of the freshwater clam *Elliptio complanata* (Bivalvia:Unionidae). *Hydrobiologia* 157:27-33.
- HINCH, S. G., AND R. H. GREEN. 1988. Shell etching on clams from low-alkalinity Ontario lakes: a physical or chemical process? *Canadian Journal of Fisheries and Aquatic Sciences* 45:2110-2113.
- HINCH, S. G., R. C. BAILEY, AND R. H. GREEN. 1986. Growth of *Lampsilis radiata* (Bivalvia:Unionidae) in sand and mud: a reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 43:548-552.
- HINCH, S. G., L. J. KELLY, AND R. H. GREEN. 1989. Morphological variation of *Elliptio complanata* (Bivalvia:Unionidae) in differing substrata of soft-water lakes exposed to acidic deposition. *Canadian Journal of Zoology* 67:1895-1899.
- KAT, P. W. 1982. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia:Unionidae). *Malacological Reviews* 15:119-127.
- NEVES, R. J., AND S. N. MOYER. 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). *Bulletin of the American Malacological Union* 6:179-188.
- SAILA, S. B., C. W. RECKSIEK, AND M. H. PRAGER. 1988. Basic fishery science programs: a compendium of microcomputer programs and manual of operation. Elsevier Scientific Press, Amsterdam.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics. 5th edition. SAS Institute Inc., Cary, North Carolina.
- SMITH, D. G. 1986. Keys to the freshwater macroinvertebrates of Massachusetts (No. 1): Mollusca, Pelecypoda (clams, mussels). Massachusetts Department of Environmental Quality Engineering, Division of Water Pollution Control.
- STRAYER, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1389-1395.
- TEVESZ, M. J. S., AND J. G. CARTER. 1980. Environmental relationships of shell form and structure of unionacean bivalves. Pages 295-322 in D. C. Rhoades and R. A. Lutz (editors). *Skeletal growth of aquatic organisms: biological records of environmental change*. Plenum Press, New York.

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