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1999**Endo- and epibenthic distribution of the
unionid mollusc *Elliptio complanata***

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Abstract. 18% of a population of *Elliptio complanata* was found living completely buried in the sediments of a Québec lake during mid-summer. This population was found to descend into the sandy sediment as winter approached, and emerged in the spring. More than 60% of the population was endobenthic during late autumn. Endobenthic mussels were significantly smaller than epibenthic mussels (50–60% of average length) and most mussels that were endobenthic during mid-summer were juveniles. Shell morphology did not vary significantly between epi- and endobenthic mussels. Failure to count endobenthic *E. complanata* in population surveys could result in severe underestimates of actual population densities. A sampling program based strictly on epibenthic mussels would underestimate the contribution of young mussels to the biomass and production of this population.

Key words: distribution, sediment, sampling, morphology, Unionidae, Pelecypoda, Mollusca.

Freshwater bivalve molluscs can represent as much as 90% of the standing biomass of benthic invertebrates (Ökland 1963, Mann 1964, Negus 1966). Filter feeding bivalves can play a significant role in removing particulate matter from lake water (DeBruins and Davids 1970, Lewandowski and Stanczykowska 1975, Price and Schiebe 1978, Libois 1988). The sensitivity of large freshwater bivalves to pollutants (e.g., Matteson 1955) makes them useful in monitoring and evaluating polluted ecosystems (Foster and Bates 1978, McCuaig and Green 1983, Green et al. 1989, Hinch and Green 1989). In addition, they are one of the most widely distributed groups of organisms found in the sediments of ancient lakes, and their species composition and shell characteristics can therefore be used to infer long-term variations in abiotic factors (Tolstikova 1978, McCuaig and Green 1983, Green et al. 1989).

Several details of the life history of unionid bivalve molluscs remain poorly understood (Kat 1982). A long-standing mystery of unionid ecology is the fact that juveniles are rarely found (Isely 1910). The most frequently cited explanation for the absence of young mussels in population samples is that recruitment is irregular among years (Matteson 1948; Ökland 1963, Negus 1966, Norelius 1967, Fisher and Tevesz 1976, Green 1980, Hanson et al. 1988a, 1988b, Libois 1988). Others have suggested that the absence of juvenile mussels is coincident (Lewandowski and Stanczykowska 1975); or they are eaten by

fish (Mann 1964, Negus 1966, Fisher and Tevesz 1976, Libois 1988); or their habitats differ from those of adults (Magnin and Stanczykowska 1971, Lewandowski and Stanczykowska 1975, Kat 1982); or they are too sparse to be sampled efficiently by large quadrats (Lewandowski and Stanczykowska 1975, Green 1980); or they are killed by pollution (Green 1980). If recruitment failure were frequent, or fish predation prevalent, we would expect adult populations to fluctuate widely over time. Recent observations (Amyot, unpublished data) suggest a simpler explanation for the absence of juvenile mussels from population samples. In a recent study, we exhaustively marked 557 individuals of *E. complanata* and recorded their movement over time. We found, curiously, that several adult mussels disappeared from the surface of the sediment, then reappeared in about the same place several days or weeks later. Further, during the first and second week of July, we observed that many unmarked young mussels, mostly about 6 yr old, appeared suddenly and unexpectedly at the sediment surface, among the marked adult population. These observations suggested to us that a fraction of the mussel population might be endobenthic.

Epi- and endobenthic mussels would be subject to very different forces and therefore may differ in shell morphology. Green et al. (1989), for example, found evidence of intraspecific variation in shell form when mussels were subjected to different levels of water turbulence. It

is well established that *E. complanata* has a heavy shell and thus is rarely found on soft substrata in deep water. We therefore investigated possible morphological adaptation of the shell between epibenthic and endobenthic mussels found on hard and soft substrata. For example, obesity, which is the width of the shell relative to its length, may indicate an adaptation to soft sediment conditions (Ghent et al. 1978).

The purpose of this study was to find whether a significant fraction of a population of *E. complanata* in a north temperate lake was endobenthic. We also tested the hypotheses that the fraction of the population found to be endobenthic varied with water depth, between sites, or among seasons. Finally we tested the hypothesis that there were morphological differences between endobenthic and epibenthic mussels.

Methods

Tests of the hypotheses were performed at two sites in Lac de l'Achigan (Fig. 1), situated 60 km north of Montréal, Québec. Lac de l'Achigan is a soft-water, oligotrophic lake with a mean annual total phosphorus concentration of 6.4 $\mu\text{g/L}$, and an average alkalinity of 11.5 mg CaCO_3/L (Lamontagne and Gauthier 1974). The littoral zone of the north shore is composed mostly of sandy beaches of low slope. *Elliptio complanata* is the most abundant mussel found in this lake and it reaches maximum densities of 70 individuals/ m^2 (Downing et al. 1989). The most common fishes in this lake are *Lepomis gibbosus*, *Perca flavescens*, *Micropterus salmoides* and *Catostomus catostomus*.

Samples at each site were taken by divers with a 1 \times 1-m Plexiglas® open box that was pushed into the sediment to a depth of 30 cm which corresponds to the average thickness of loose sediment in the littoral zone of this area of the lake. Beyond that sediment depth, sediment was too compact to be easily removed by hand or penetrated by mussels. First we collected all the epibenthic mussels enclosed within each open box, then all the endobenthic mussels were collected quantitatively by passing all the sediment enclosed within the box through a 5-mm mesh plastic sieve until compacted sediment was reached. Epibenthic and endobenthic mussels were held in two separate Nytex® bags. Length (L), height (H), and width (W) of each mussel were measured using a digital cal-

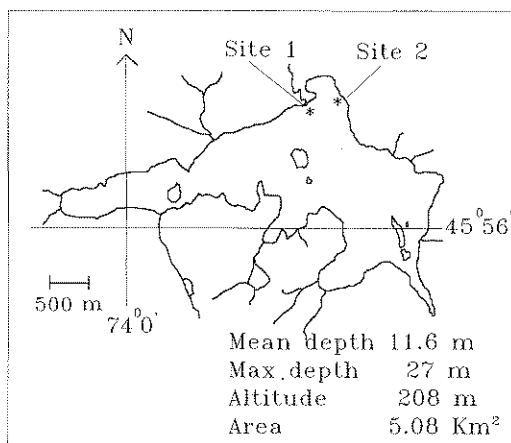


FIG. 1. Study sites in Lac de l'Achigan, Québec.

iper (± 0.01 mm). Annual rings of adult *E. complanata* are sometimes difficult to distinguish (Strayer et al. 1981), therefore we did not determine the age of mussels in our study. Tests for differences in shell morphology between endo- and epibenthic mussels followed the protocol of Bailey and Green (1988) and considered three morphological variables: length, relative height, and obesity. Relative height is H/L and obesity is W/L . All measurements were transformed to their logarithms to equalize the variances (Legendre and Legendre 1984).

The fraction of the population found beneath the sediment surface was determined during July 1989 at six different water depths (0.5, 1.0, 1.5, 2.0, 2.5, 3.0 m) at site 1 by collecting five replicate samples at each depth. The observations were repeated at site 2 during August 1989 by taking 10 replicate samples at each of three depths (1.0, 2.0, 3.0 m). A lateral distance of at least 1 m was left between quadrat samples to avoid sampling disturbed sites. The average sediment organic content was determined by drying (50°C for 52 h) and burning (550°C for 5 h) sediments. At both sites, sediments were similar and were composed almost entirely of sand with only 0.9% ($n = 10$, $SD = 0.14$) of organic matter at 1 m depth. The organic matter content increased with water depth to 2.4% ($n = 10$, $SD = 1.37$) at 2 m, and reached 3.8% ($n = 10$, $SD = 0.90$) at 3 m.

Seasonal variation in the proportion of endobenthic mussels was followed by marking, in mid-June 1988, all the sediment surface-dwell-

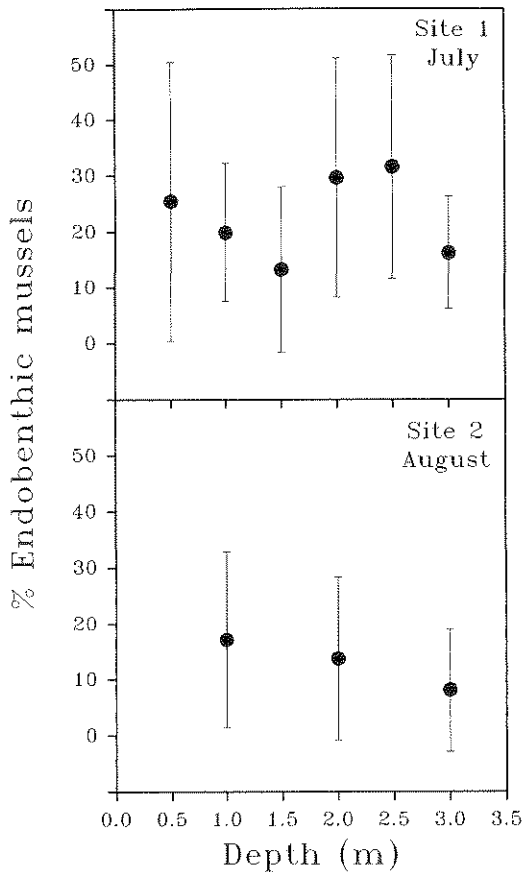


FIG. 2. The average fraction (± 1 SD) of *Elliptio complanata* found beneath the sediment surface at site 1 in July and site 2 in August. Each mean is the result of five replicate samples at site 1 and ten replicate samples at site 2.

ing mussels ($n = 557$) found at a water depth of 1.5–2 m within a 5×8 -m area. This area was situated close to site 1 and had similar sediment composition. Each of 40 1-m^2 contiguous "quadrats" was delimited by four corner stakes, allowing free mussel movement. All mussels were carefully marked underwater, by attaching Dymo® plastic labels to the posterior margin of the valves with underwater glue (Devcon® Wet Surface Repair Putty), limiting disturbance to a few light touches with the divers' fingers. The position of each mussel was later determined by triangulation using rulers attached to each corner stake. A 5.5×1 -m movable plastic frame was used to keep divers at 40 cm above the sediment surface, avoiding direct contact with

organisms. This procedure was performed to measure mussel locomotion (Amyot, in preparation) but also allowed us to measure the proportion of marked mussels found at the sediment surface each week during each of two summers and at 2-wk intervals during autumn and spring. Because sampling of the surface-dwelling mussels was exhaustive, and few mussels attained the rate of locomotion necessary to leave our 5×8 -m area, these measurements allowed us to estimate the fraction of the marked mussels found to be epibenthic at our study site at different times of the year. Although unmarked mussels appearing within our study area were subsequently marked, only the 557 originally marked surface mussels were considered in testing for seasonal variation in the proportion of epibenthic mussels.

The effect of depth and sampling site on the relative abundance of endobenthic mussels was tested using multiple regression analysis, entering water depth (Z), sites (S), and a depth \times site [$Z \times S$] interaction term as independent variables. Multiple regression analysis was also used to determine whether shell morphology was different in endo- and epibenthic mussels or in mussels found at different water depths or sites. The hypothesis that epibenthic mussels were longer than endobenthic ones was tested by regressing shell length on water depth, sites, the dummy variable E (epibenthic: $E = 0$; endobenthic: $E = 1$), and their interaction terms, as independent variables. Finally, the effect of water depth, sites, shell length, and endobenthic habit on shell relative height and obesity was tested similarly using multiple regression analysis.

Results and Discussion

The fraction of the 855 mussels found at sites 1 and 2 that were endobenthic varied from 0% to 62.5% in the 60 samples. Overall, an average of 23% of mussels at site 1, and 13% at site 2 were found beneath the sediment surface (Fig. 2). The fraction of the mussels that were endobenthic did not vary significantly among water depths ($p = 0.925$) or sites ($p = 1.000$) (Fig. 2). *Elliptio complanata* is rarely found in water deeper than about 3 m in this and other North American lakes (Fisher and Tevesz 1976, Ghent et al. 1978). Thus, according to our data, it appears that a fairly constant proportion of this

population is endobenthic during mid-summer, regardless of water depths or sites. Our data, collected using both sediment-surface hand picking and sediment sieving methods, show that a significant fraction of the mussel population in Lac de l'Achigan was found beneath the sediment, rarely deeper than about 20 cm. A study of this same population considering only epibenthic mussels would have underestimated the population of *E. complanata* by an average of 18%. Our results suggest why Hanson et al. (1988b) found that hand-picking sampling alone underestimated the density of *Anodonta grandis simpsoniana* in Narrow Lake, Alberta, by 23%, and why Haukioja and Hakala (1974) found that hand picking at the surface underestimated the population of several unionid species by an average of 14.5% in Mätkkõ Lake, Finland.

Elliptio complanata changes seasonally from an epi- to endobenthic habit. Although 100% of our labelled mussels were visible at the surface at the end of June 1988, they gradually disappeared into the sediments as the season progressed (Fig. 3). At the end of October, only 39% of the 557 labelled mussels were still found at the sediment surface. The following spring (end of May 1989), 96% ($n = 532$) of the original marked population was again found at the sediment surface at the same site. The same seasonal vertical migration was found in 1989 with only 38% of the initial population remaining at the sediment surface in late October 1989 (Fig. 3). Our data demonstrate that most of this population undergoes a seasonal vertical migration. To our knowledge, this is the first demonstration of a seasonal vertical migration in unionid molluscs. A sampling program based solely on the epibenthic fauna could seriously underestimate the density and biomass of a mussel population, and this bias would be most serious if sampling were performed during late summer, autumn or winter.

Endobenthic mussels were smaller than epibenthic ones, and shell length varied among water depths and sites (Table 1A). The average length of endobenthic mussels was only 69% (site 1) and 55% (site 2) of the average length of epibenthic mussels. Because the shell length and age of mussels are closely correlated in this lake (Downing et al. 1989) and others (Hanson et al. 1988b), we think it is likely that mussels found to be endobenthic in mid-summer were

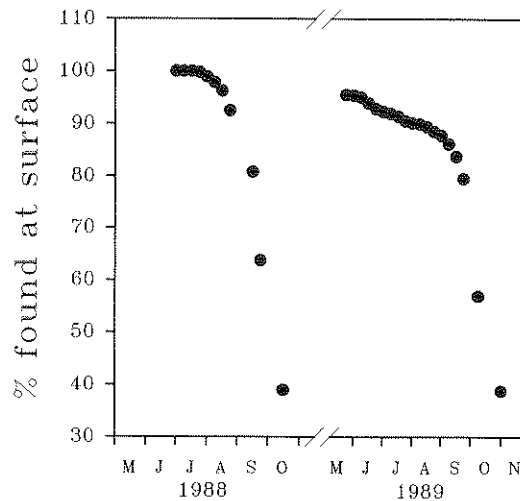


FIG. 3. Seasonal vertical migration of *Elliptio complanata* in Lac de l'Achigan. Dots represent the percentage of marked mussels observed on the surface of the sediment bed in a 40-m² area. Measurements were made each week during the summers of 1988 and 1989. The initial population (100%) was composed of 557 mussels marked at the end of June 1988.

the younger members of the population. This finding perhaps explains why small or young mussels are only rarely found in studies of mussel populations when samples are hand-collected at the sediment surface (Cvancara 1972, Haukioja and Hakala 1974, Fisher and Tevesz 1976, Ghent et al. 1978, Green 1980, Strayer et al. 1981, McCuaig and Green 1983, Hanson et al. 1988a, 1988b, Libois 1988, Bailey and Green 1989). Young mussels are, however, frequently found when mussels are collected with dredges or grabs (e.g., Matteson 1955, Ökland 1963, Mann 1964, Negus 1966, Lewandowski and Stanczykowska 1975, Hanson et al. 1989). The significant [Z × S] interaction (Table 1A) suggests that shell length decreased significantly with depth at site 2. This may be either because juveniles tend to settle in deeper waters and migrate into the shallows as they age or simply because mussels grow more slowly in colder, deeper waters (Cvancara 1972, Strayer et al. 1981). The significant effects of sampling sites ($p = 0.0008$), the [E × S] interaction ($p < 0.0001$), and the [Z × S] interaction ($p = 0.0159$) show that epibenthic mussels were slightly larger at site 2 than at site 1 but that the smallest average length of mussels was found in the deepest water samples at site

TABLE 1. A) The relationship of shell length of *Elliptio complanata* to endobenthic habit, site and depth. The regression model was: $\log_{10} \text{ length} = f(Z, S, E, [Z \times S], [E \times S], [Z \times E])$. Intercept = 1.839. B) The relationship of relative height to endobenthic habit, site and depth. The regression model was: $\log_{10} \text{ height} = f(Z, S, E, [Z \times S], [E \times S], [Z \times E], L)$. Intercept = -0.324. C) The relationship of obesity to endobenthic habit, site and depth. The regression model was: $\log_{10} \text{ width} = f(Z, S, E, [Z \times S], [E \times S], [Z \times E], L)$. Intercept = -0.820. E = 0 = epibenthic; E = 1 = endobenthic, S = 0 = site 1; S = 1 = site 2, Z = depth in m and L = \log_{10} length in mm. $n = 855$. Only the significant variables ($p < 0.05$) are shown.

Independent variables	Effect	p	Coefficient
A) Shell length			
E	-	0.0000	-0.1611
S	+	0.0008	0.0627
[E × S]	-	0.0001	-0.1003
[Z × S]	-	0.0159	-0.0202
B) Relative height: shell height/shell length			
Z	-	0.0004	-0.0038
L	+	0.0000	1.0214
[Z × S]	+	0.0000	0.0033
C) Obesity: shell width/shell length			
S	+	0.0000	0.0234
Z	-	0.0000	-0.0095
L	+	0.0000	1.1290

2. The single term depth (Z) in this regression was not significant.

Endobenthic mussels were not significantly different from epibenthic mussels in body form, but both relative height and obesity varied significantly among mussels found at different water depths and sites. *Elliptio complanata* found at greatest water depths had a significantly ($p = 0.0004$) smaller relative height (Table 1B) and were significantly ($p < 0.0001$) less obese than those found in shallow water (Table 1C). Like Cvancara (1972) and Hinch et al. (1989), we found a significant decrease in obesity (of both epi- and endobenthic mussels) with increasing water depth. According to Hinch et al. (1989), a smaller relative height of the shell would facilitate burrowing into the sediment in turbulent areas and therefore could be an adaptation making mussels less easily dislodged by wave action. Our results show that both epi- and endobenthic mussels in Lac de l'Achigan had low-

er relative heights at greater water depth even though substrates were softest at depths. Our results were contrary to our expectation that variations in shell morphology are linked to adaptations against sinking in soft sediments. If this were true, we would expect mussels at greater water depth to be more obese and have higher relative height (cf. Tables 1A-C). But because regression coefficients associated with obesity and relative height are small, it would be unwise to conclude that epi- and endobenthic *E. complanata* are morphologically adapted to depth or substrate types in Lac de l'Achigan.

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