

## Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake

DAVID L. STRAYER, JONATHAN J. COLE, GENE E. LIKENS and  
DONALD C. BUSO Section of Ecology and Systematics, Cornell University, Ithaca,  
New York, U.S.A.

**SUMMARY.** An extensive survey of Mirror Lake, New Hampshire, was carried out by divers with SCUBA to assess the importance of the freshwater mussel *Elliptio complanata* in this softwater lake ecosystem. Density (0.032 adults m<sup>-2</sup>), biomass (52 mg m<sup>-2</sup> as dry organic matter) and annual production (6.4 mg m<sup>-2</sup> as dry organic matter) of the mussel population are low when compared with results from other studies, corresponding with the general observation that mussels are scarce in soft, oligotrophic waters. We reject the traditional view that the low mussel density is a result of low calcium concentrations in Mirror Lake, and propose that mussel populations may be regulated by a scarcity of appropriate fish hosts in unproductive lakes. *Elliptio complanata* is probably not important in the metabolism or biochemistry of the Mirror Lake ecosystem.

### Introduction

Although unionid mussels have been the subject of a great many studies, relatively few workers have been concerned with their role in the structure and function of freshwater ecosystems (see especially Negus, 1966; Tudorancea, 1972; Lewandowski & Stanczykowska, 1975). In this paper, we present data on the distribution and abundance of a freshwater mussel in Mirror Lake, New Hampshire, with particular reference to its importance in the lake ecosystem.

Mirror Lake is a small (surface area 15 ha, mean depth 5.75 m) oligotrophic lake in the White Mountains of New Hampshire. Its water is clear and soft; typical midsummer epilimnetic water chemistry values include: pH 6.5-7.0, alkalinity 0.06-0.08 mequiv l<sup>-1</sup>, calcium 2-3 mg

l<sup>-1</sup>, dissolved organic carbon 2.0-2.5 mg l<sup>-1</sup>, and Secchi disc 5-9 m. The lake has been the subject of numerous ecological investigations (Likens, 1981) and is one of the few lakes for which an organic carbon budget has been constructed (Jordan & Likens, 1975, 1980). Information on the macrobenthos of Mirror Lake is available in Walter (1976, 1981). *Elliptio complanata* (Lightfoot), which is common and widespread in the streams and lakes of north-eastern North America, is the only unionid in the lake.

### Methods

During July-September 1978 and 1979, divers with SCUBA swam transects at 80-m intervals around the entire lake, and at 40-m intervals in regions of high clam population density. Each transect was 1 m wide, and extended from the shore toward the centre of the lake, ending at

Correspondence: David L. Strayer, Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850, U.S.A.

the 7-m depth contour (beyond 7 m depth, the lake bottom is soft gyttja and lacks mussels). We marked off 1-m depth contours along the transects so that specimens could be segregated by depth of occurrence. All individuals encountered were collected. Because the lake water is clear, and because specimens of *E. complanata* in Mirror Lake do not bury themselves deeply, we believe that very few clams greater than 4 years of age were missed. In total, we searched 1399 m<sup>2</sup> of the lake bottom in this fashion.

In the laboratory, we measured length and air-dry weight of the shells. In addition, we dried the bodies of 39 individuals to constant weight at 60°C, and used these data to develop a shell weight to body weight regression.

We aged the mussels by counting the growth rings on the shells, and measured shell length at each ring to reconstruct growth curves. Because *E. complanata* is difficult to age (cf. Ghent *et al.*, 1978), each shell was read by two observers

and ambiguous data were discarded. Although growth rings are not always produced annually, workers have verified their annual nature in several environments (Isely, 1914; Sebestyen, 1942; Negus, 1966; Haukioja & Hakala, 1978) and there is no reason to doubt that they are annual in Mirror Lake.

Calculations of biomass and annual production follow Magnin & Stanczykowska (1971). Dry body weight was found from our measurements to be about 8.2% of shell weight, and we assumed, following the work of Cameron *et al.* (1979), that 2.79% of the shell of *E. complanata* is organic matter.

We estimated biomass and annual production of 'young clams', which were less than 5 years old, by assuming the population densities and weights shown in Figs 1 and 2B. Shell weights (*W*, g) for the young clams were estimated from shell length (mm) using the power-law relationship:

$$W = 4.83 L^{3.47} \times 10^{-6} \quad (1)$$

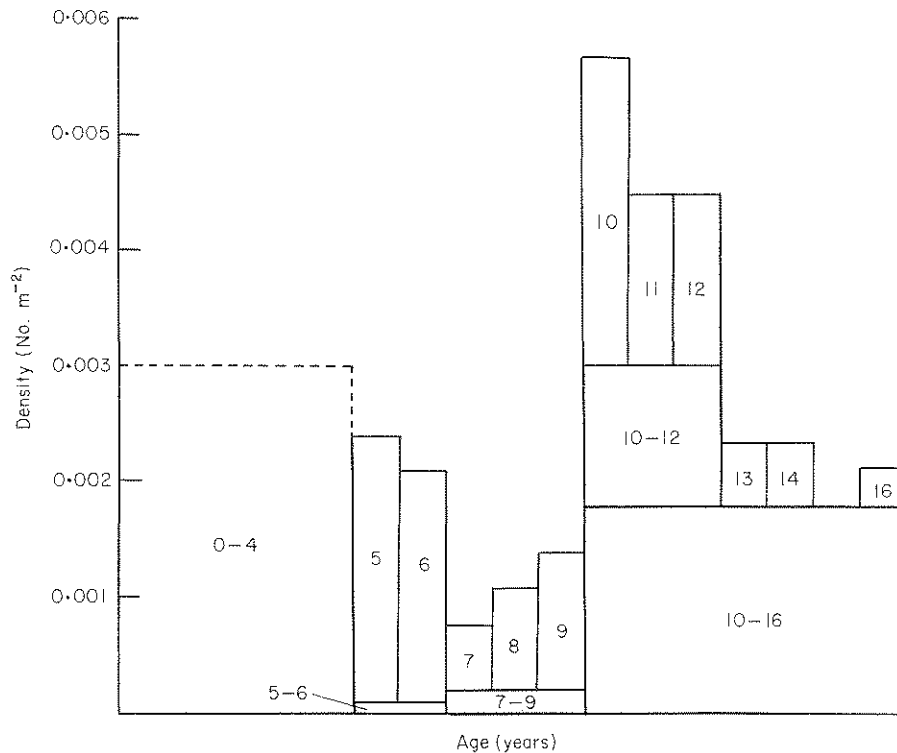


FIG. 1. Age structure of the *E. complanata* population in Mirror Lake. The large blocks (e.g., '10-16') represent clams for which no exact age could be determined; these individuals were assigned evenly to the appropriate composite age-class. Densities for 0-4 year olds were estimated by using the approximate mean density of older age-classes.

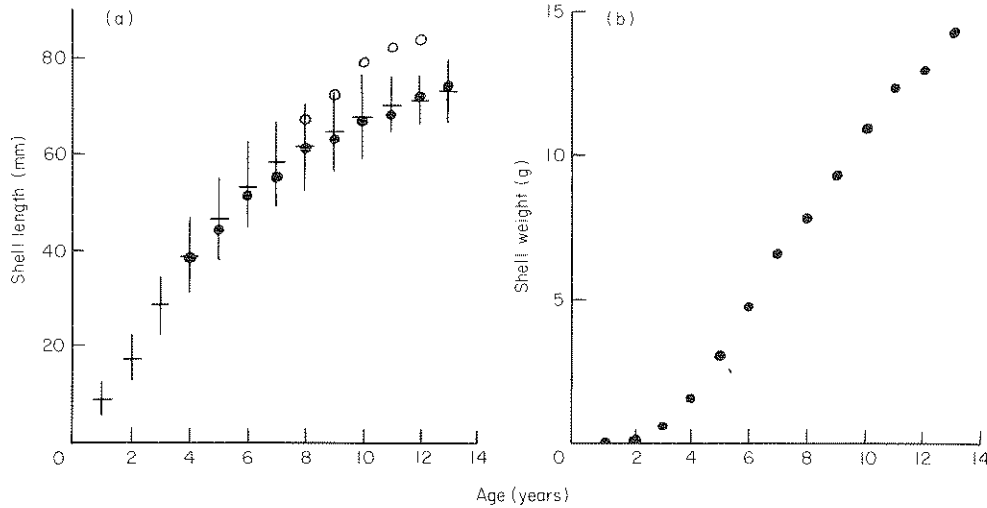


FIG. 2. (a) Growth of *E. complanata* from Mirror Lake (—), Lac des Deux Montagnes (O) and Lac Saint-Louis (●), expressed as shell length. For Mirror Lake, horizontal lines are means and vertical lines are 95% confidence intervals on individuals. Calcium concentrations ( $\text{mg l}^{-1}$ ) for the three lakes are: 2.3 (ML), 9.6 (LSL), and 38.9 (LdDM). Data for the latter two lakes from Magnin (1970) and Magnin & Stanczykowska (1971). (b) Growth of *E. complanata* in Mirror Lake expressed as shell weight. Values derived by combining data shown in Figure 2a with our shell length to weight relationship (eqn 1).

Unless otherwise noted, the results presented below include contributions of young age-classes estimated using these assumptions.

Shells remain intact for some period of time after the deaths of the animals and form a substantial portion of the biomass associated with mussel populations ('dead biomass'). To determine the length of time that shell material persists in Mirror Lake, we set out 40 pre-weighed shells in varying degrees of dissolution and decay at 0.5 m depth in the lake and measured the loss in air-dry weight after 1 year.

**Results**

*E. complanata* is not abundant in Mirror Lake (0.032 individuals per  $\text{m}^2$  excluding young clams). It reaches its maximum density between 2 and 3 m depth (0.17 individuals per  $\text{m}^2$  excluding young clams) and is most common in gently sloping sandy areas. It is scarce on steep rocky slopes and was never found on the soft gyttja.

The age structure of the population (Fig. 1) is similar to those reported for unionids in other freshwater ecosystems (Negus, 1966; Magnin & Stanczykowska, 1971; Tudorancea, 1972;

Lewandowski & Stanczykowska, 1975; Haukioja & Hakala, 1978) and suggests low adult mortality and considerable year-to-year variation in recruitment. Only 3% of biomass and 16% of annual production are in the younger age-classes, according to our estimates (see above). It appears that *E. complanata* may live to be 16–18 years old in Mirror Lake.

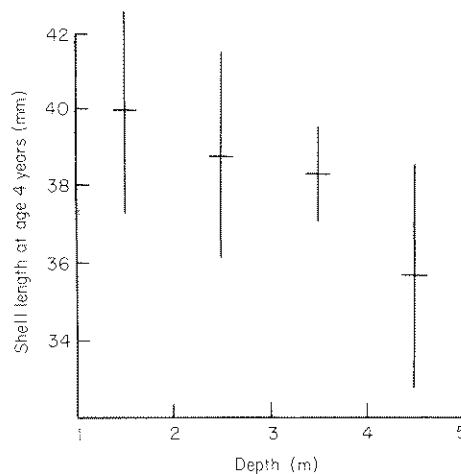


FIG. 3. Growth of *E. complanata* in Mirror Lake as a function of depth of collection. Horizontal lines are means and vertical lines are 95% confidence intervals on the means. For the means,  $r = -0.95$ ,  $P = 0.05$ .

Although most of the growth in shell length is attained in the first 6–8 years, shell weight increases at a nearly constant rate after year 4 (Fig. 2). There is a trend toward slower growth rates at depth (Fig. 3) which, as Cvcancara (1972) has proposed, is probably due to lower temperatures there.

We found that dead shells lose about 16% of their weight in a year, although there was considerable variability (range = 6.9–29.6%). At this rate, the dead shell biomass pool would be about 60% of that in the shells of living clams.

### Discussion

Although the *E. complanata* population forms a considerable portion of benthic biomass between 1 and 4 m depth (Fig. 4), it appears to play a trivial role in the functioning of the Mirror Lake ecosystem. Its annual production is

only *c.* 0.1% of total macrobenthic production (Walter, 1976) and, if published filtering rates are applicable (DeBruin & Davids, 1970; Lewandowski & Stanczykowska, 1975), it filters about 1% of the epilimnetic volume annually. In other lakes, unionids may be important in the calcium cycle (Green, 1980), but in Mirror Lake the standing stock of calcium in unionid shells is only *c.* 2% of that dissolved in the water column. Movements of unionids may be important in mixing lake sediments (McCall *et al.*, 1979), but this is probably unimportant at the low population densities in Mirror Lake.

The population density, biomass, and annual production of unionids in Mirror Lake are low when compared to other ecosystems (Table 1). Nonetheless, Mirror Lake is probably typical of many softwater oligotrophic lakes in north-eastern North America (*cf.* Ghent *et al.*, 1978).

Two factors are probably responsible for the low population densities in Mirror Lake. First, the lake has large areas of soft gyttja, but

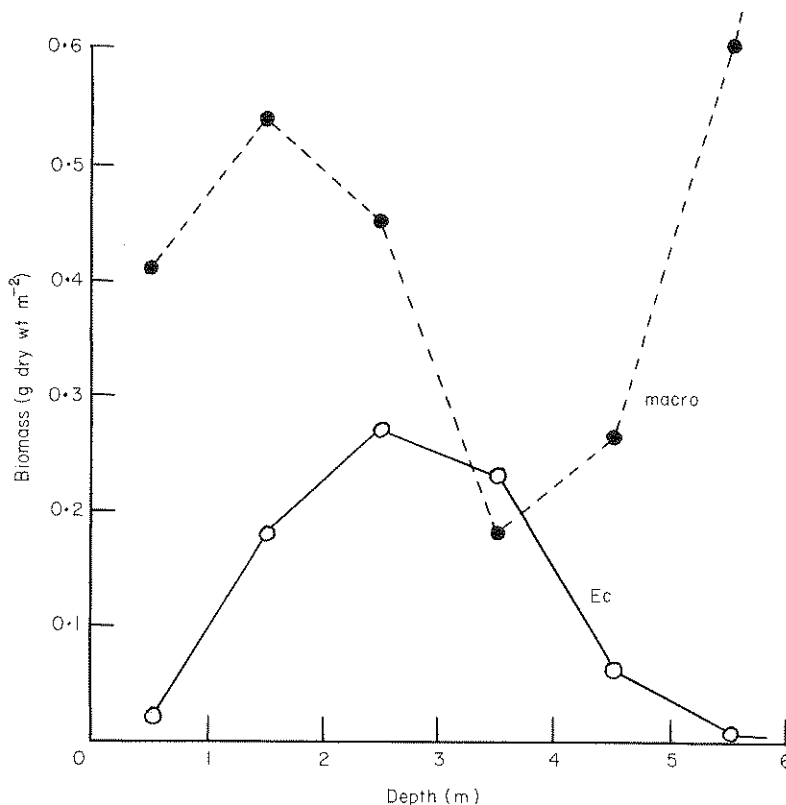


FIG. 4. Biomass of *E. complanata* (Ec) and all other macrobenthos (macro) from the littoral and sublittoral zones of Mirror Lake, expressed as dry organic matter. Macrobenthos data from Walter (1981).

TABLE 1. Biomass and annual production of unionid mussels in several freshwater ecosystems. Data for shells from Mirror Lake given in  $\text{g m}^{-2} \text{CaCO}_3$ ; all other values as  $\text{g m}^{-2}$  dry organic matter

Ecosystem	Biomass	Production	Source
Mirror Lake (shells)	0.74*	0.057	This study
Mirror Lake	0.05	0.006	This study
Mikolajskie Lake	0.20†	0.07†	Lewandowski & Stanczykowska (1975)
Lac Saint-Louis	0.71†	—‡	Magnin & Stanczykowska (1971)
Crapina pool (Danube River)	4.8†	1.1†	Tudorancea (1972)
Lac des Deux Montagnes	8.6†	1.7†	Magnin & Stanczykowska (1971)
Thames River	12.1†	2.1†	Negus (1966)

\*Includes estimated contribution of dead biomass.

†Original data in terms of wet weight; converted to dry weight by multiplying by 0.1, except for Mikolajskie Lake, for which a factor of 0.04 was used (see Lewandowski & Stanczykowska, 1975).

‡The value given in the original paper (0.07) appears to be incorrect.

contains no unionid species able to tolerate such a substratum (e.g., *Anodonta*; see Ghent *et al.*, 1978).

Second, most of the other studies were conducted in hard, productive waters. It has often been observed that soft, unproductive waters such as Mirror Lake support few mussels (e.g., Agrell, 1949; Pennak, 1978). Although this is often assumed to be the result of low calcium concentrations, which render difficult the maintenance of a calcareous shell, other mechanisms are possible. Larval unionid mussels are obligate parasites of fish (Pennak, 1978), so their populations may be regulated in the parasitic stage by the number of available fish hosts. Because soft waters are often oligotrophic, both food and fish hosts are likely to be scarce. Mussels, therefore, may be rare in soft waters because of low densities of fish hosts rather than because of low calcium concentrations.

It should be possible to distinguish between these two types of limitation. If calcium (or food) is limiting, we should find slower growth rates, as well as lower population densities, in soft waters, whereas a shortage of fish hosts should not affect the growth rates of individual mussels. Although data bearing on this question are scarce and imperfect, we can make some tentative statements about calcium limitation. In comparing the growth rates of *Anodonta* from two lakes in Canada, Green (1980) found slower growth in the lake with lower calcium concentrations, which he took as evidence of calcium limitation. However, the growth rate of *E. complanata* in Mirror Lake is very similar to the rates reported for Lac Saint-Louis and Lac des Deux Montagnes (Fig. 2a), both of which

have much higher calcium concentrations than Mirror Lake. Furthermore, although several features of shell geometry vary with water hardness, Green (1972) found that the inside volume of the shell was relatively unresponsive to changes in water chemistry. [We are treating here changes in body weight or its presumed correlates only, so decreases in shell thickness with decreasing ambient calcium concentrations (Green, 1972, 1980) are not relevant.] It would be desirable to have more information on the role of fish-mussel relations in mussel population dynamics.

#### Acknowledgments

We thank Nina Caraco, Rob Edwards, Robert Moeller, Steve Nodvin, Cathy Weiler, and Jim Wetterer for useful discussions and technical assistance. This is a contribution to the Hubbard Brook Ecosystem Study. Financial support was provided through grants by the National Science Foundation. D. L. Strayer was supported by a National Science Foundation Graduate Fellowship.

#### References

- Agrell J. (1949) The shell morphology of some Swedish unionids as affected by ecological conditions. *Arkiv für Zoologi*, **41A**, 1–30.
- Cameron C.J., Cameron I.F. & Paterson C.G. (1979) Contribution of shell organic matter to biomass estimates of unionid bivalves. *Canadian Journal of Zoology*, **57**, 1666–1669.
- Cvancara, A.M. (1972) Lake mussel distribution as determined by SCUBA. *Ecology*, **53**, 154–157.

- DeBruin J.P.C. & Davids C. (1970) Observations on the rate of water pumping of the freshwater mussel *Anodonta cygnea zellensis* (Gmelin). *Netherlands Journal of Zoology*, **20**, 380–391.
- Ghent A.W., Singer R. & Johnson-Singer L. (1978) Depth distributions determined with SCUBA, and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. *Canadian Journal of Zoology*, **56**, 1654–1663.
- 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. (1980) Role of a unionid clam population in the calcium budget of a small Arctic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 219–224.
- Haukioja E. & Hakala T. (1978) Measuring growth from shell rings in populations of *Anodonta piscinalis* (Pelecypoda: Unionidae). *Annales Zoologici Fennici*, **15**, 60–65.
- Isely F.B. (1914) Experimental study on the growth and migration of freshwater mussels. *United States Bureau of Fisheries Document*, **792**, 1–27.
- Jordan M.J. & Likens G.E. (1975) An organic carbon budget for an oligotrophic lake in New Hampshire, U.S.A. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **19**, 994–1003.
- Jordan M.J. & Likens G.E. (1980) measurement of planktonic bacterial production in an oligotrophic lake. *Limnology and Oceanography*, **25**, 721–734.
- Lewandowski K. & Stanczykowska A. (1975) Occurrence and role of bivalves of the family Unionidae in Mikolajskie Lake. *Ekologia Polska*, **23**, 317–334.
- Likens G.E. (1981) *Air–Land–Water Interactions: A Case Study in Aquatic Ecology*. Springer-Verlag New York Inc. (in press).
- Magnin E. (1970) Faune benthique littorale du lac Saint-Louis. *Annales d'Hydrobiologie*, **1**, 179–193.
- Magnin E. & Stanczykowska A. (1971) Quelques données sur la croissance, la biomasse, et la production annuelle de trois mollusques Unionidae de la région de Montréal. *Canadian Journal of Zoology*, **49**, 491–497.
- McCall P.I., Tevesz M.J.S. & Schwegien S.F. (1979) Sediment mixing by *Lampsilis radiata siliquoidea* (Mollusca) from western Lake Erie. *Journal of Great Lakes Research*, **5**, 105–111.
- Negus C.L. (1966) A quantitative study of growth and production of unionid mussels in the River Thames at Reading. *Journal of Animal Ecology*, **35**, 513–532.
- Pennak R.W. (1978) *Freshwater Invertebrates of the United States*. Second Edition. Wiley-Interscience, New York, 803 pp.
- Sebestyen O. (1942) Notes on the growth of Unionidae in Lake Balaton. *Rivista di Biologia*, **33**, 244–253.
- Tudorancea C. (1972) Studies on Unionidae populations from the Crapina and Jujila complex of pools (Danube zone liable to inundation). *Hydrobiologia*, **39**, 527–561.
- Walter R.A. (1976) The role of the benthic macrofauna in the structure and function of the Mirror Lake ecosystem. Unpublished M.S. Thesis, Cornell University.
- Walter R.A. (1981) Benthic invertebrates. IN: *Air–Land–Water Interactions: A Case Study in Aquatic Ecology* (Ed. G. E. Likens). Springer-Verlag New York Inc. (in press).

(Manuscript accepted 8 September 1980)