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In an association of the bivalves *Elliptio complanata*, *Anodonta cataracta*, and *Lampsilis ochracea* in a New Brunswick lake, the distribution of standing stock biomass is among tissue (64.6%), shells of living individuals (19.4%), and empty shells and shell fragments (16.0%). Failure to consider the latter two energy compartments would result in serious underestimates of standing stock biomass.

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Chez les populations des bivalves *Elliptio complanata*, *Anodonta cataracta* et *Lampsilis ochracea* dans un lac du Nouveau-Brunswick, la biomasse se répartit entre les tissus (64,6%), les coquilles des individus vivants (19,4%), les coquilles vides et les fragments de coquilles (16%). L'omission de ces deux derniers paramètres entraînerait une sérieuse sous-estimation de la biomasse.

[Traduit par le journal]

Introduction

Cameron et al. (1979) found that for the three unionid bivalves Lampsilis ochracea (Say), Elliptio complanata (Solander), and Anodonta cataracta (Say) the amount of acid extractable organic matter, collectively termed conchiolins (Beedham 1958), in the shell varied from 2.26 to 3.75% of the total shell weight. They calculated that the organic content of the shell contributed between 4.6 and about 30% of the total energy content of the bivalves, depending upon species and size. Failure to take this energy pool into account can result in serious underestimation of the standing stock biomass of living bivalves.

It is a common observation that quantitative samples obtained to estimate standing stocks of bivalves frequently contain substantial quantities of empty shells and shell fragments. It would then follow that any organic material in these bivalve remains also should be included in accurate standing stock estimates. The current study was undertaken to determine if there is a differential rate of loss of organic matter during dissolution of shell material and also to determine the role of such shell fragments in standing stock estimates of three species of unionid bivalves in a New Brunswick lake.

Methods

This study was conducted in the southwest arm of Morice Lake, a relatively old (ca. 1765) polymictic, mesotrophic reservoir, located approximately 3 km north of Sackville, N.B. The area of the study arm is 1.1×10^5 m², while the area with a water depth greater than approximately 1.0 m, where quantitative sampling was conducted, has an area of 2.0×10^4 m². On five occasions between early May and mid-August, 10

samples were obtained at each of 10 stations (Fig. 1) with a standard 9 in. \times 9 in. Ekman grab (522.6 cm²). Grab contents were poured into a bucket with a square mesh (0.5-cm) bottom and swirled in lake water, and the bivalves were removed. All bivalves were identified and maximum shell length was measured to the nearest 0.05 mm with calipers.

Numerous bivalves from the quantitative samples, plus other individuals collected at regular intervals throughout the ice-free period at similar depths by qualitative techniques, were used to establish correlations between dry tissue weight and shell length, and dry shell weight and shell length. Individuals were gently scrubbed to remove shell concretions, opened by severing the adductor muscles, and then sexed by examining wet mounts of gonadal material or observing the presence of eggs or glochidia in the marsupia. Tissue was placed in a preweighed aluminum drying dish and both shell and tissue were dried at 60°C for 48 h before weighing. Concentration of organic shell material (OSM) was determined as outlined below. Energy content of tissue and extracted shell organic material were determined with a Phillipson microbomb calorimeter.

Shells from freshly collected specimens of *Elliptio complanata*, *Anodonta cataracta*, and *Lampsilis ochracea* were cleaned and air dried. A small (<5 cm), medium (5.5–6.5 cm), and large (>6.5 cm) valve of the same species were enclosed in a nylon mesh bag. The nylon bags were then attached to a length of nylon rope which was placed at a depth of about 1 m in Morice Lake on June 20. Enough bags were placed in the lake to allow sampling at 3-week intervals for a period of 1 year. At 3-week intervals, for a total of 18 weeks, two bags were removed from the line for each species. Shells were washed, crushed, and passed through a soil grinder with a 60-mesh screen. Between 0.25 and 0.50 g of the ground shell were dissolved in excess 0.1 N HCl. The HCl solution was then filtered through a preweighed 0.45-µm Millipore filter which was dried at 60°C for 48 h and reweighed. As the results

Table 1. Dry weight and energy content of tissue and organic shell material for three species of unionid bivalves in Morice Lake, N.B. Results are expressed as the average \pm one standard error for an area of 1 m²

Species	Tissue		Shell		
	Dry weight (g)	Energy (J)	Total weight (g)	OSM* weight (g)	Energy (J)
Elliptio complanata	8.037±0.670	149999.4±12526.8	94.953±8.075	2.641±0.230	50643.0±4317.8
Anodonta cataracta		41600.1 ± 5098.4	12.017 ± 1.493	0.459 ± 0.057	9106.4±1138.2
Lampsilis ochracea	0.042 ± 0.115	7737.1 ± 2439.3	2.756 ± 0.899	0.057 ± 0.019	1182.2±394.0
Totals	10.601	199336.6	109.726	3.157	60931.6

^{*}OSM, organic shell material.

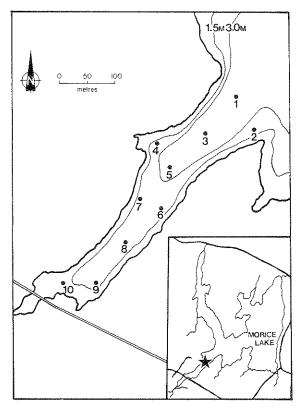


Fig. 1. Distribution of quantitative sampling stations in the southwest arm of Morice Lake, New Brunswick.

obtained after 18 weeks did not show any significant change in the concentration of organic shell material (OSM) as a percentage of shell weight, the lines were left undisturbed until a period of 60 weeks had passed, and further samples were then treated in the manner outlined above.

In June, two standard 6 in. \times 6 in. Ekman grab samples (232.3 cm²) were obtained at each of the 10 stations (Fig. 1) on two separate occasions. Grab contents were gently washed through a 1-mm sieve and all shell fragments that could be detected under a dissecting microscope at $10\times$ were removed. Attempts were made to clean the shell fragments, although this proved difficult with smaller fragments. The shell material was then dried at 60° C for 48 h. Subsamples of the shell

material were used for determining the concentration of OSM as a percentage of dry weight.

Results

As has been observed by Huebner (1980) and others, some fluctuations in the relationship between tissue weight and shell length, and in tissue energy content, were found which might relate to sex and season. However, for purposes of this study the various values were averaged. The regression equations relating tissue weight and length and shell weight and length are given in Cameron et al. (1979).

The standing stocks of tissue and OSM for the three abundant species in Morice Lake are given in Table 1. Failure to consider OSM in a natural population of *E. complanata* would result in an underestimate of the standing stock by approximately 25%, the precise value depending on whether results are expressed as dry weight or energy. Although *A. cataracta* has a higher OSM content (3.82%) than *E. complanata*, its shell is much lighter relative to tissue weight so that the underestimate of standing stock would amount to approximately 17.7%. *L. ochracea* also has a relatively low shell weight/tissue weight ratio and, in addition, the lowest OSM content of the three species. Failure to include OSM in standing stock estimates would result in an error of approximately 13.4%.

Shell valves held in the lake for 60 weeks showed clear evidence of partial dissolution and breakage but their contents of organic matter, expressed as a percentage of shell weight, were not significantly different from initial values ($E.\ complanata$, $2.79 \pm 0.04\%$; $A.\ cataracta$, $3.82 \pm 0.10\%$; $L.\ ochracea$, $2.26 \pm 0.15\%$). Although there is no differential loss of organic matter over 60 weeks, the results obtained for shell fragments collected in Ekman grab samples are more difficult to interpret. Larger fragments, which were easier to clean, produced values comparable to those of freshly collected $E.\ complanata$, the dominant species (77.9%) in the study site. Smaller fragments produced an average value of $5.23 \pm 0.41\%$. However, microscopic examination of these smaller fragments revealed organic concretions

PATERSON 2755

and when particular care was taken in cleaning certain samples the average OSM value dropped to levels close to that found for larger fragments. The most reasonable explanation of the results is that there is no differential rate of loss of OSM as a shell dissolves. Consequently, all shell fragments are considered to have an OSM content of 2.79% by weight, the value obtained for *E. complanata*, the dominant bivalve in the lake.

When the abundance of shell fragments was prorated to an area of 1 m^2 it was found that the average abundance was $94.127 \pm 27.810 \, \text{g}$ which contained an average of $2.625 \pm 0.775 \, \text{g}$ of OSM (47164.50 \pm 13922.40 J).

In the study area of Morice Lake the numerical standing stocks per square metre of the three abundant unionids were: $E.\ complanata$, 15.92 ± 1.22 ; $A.\ cataracta$, 3.87 ± 0.42 ; and $L.\ ochracea$, 0.50 ± 0.15 . These living bivalves contributed $13.758\ g$ (260268 J) to the standing stock biomass. Tissue organics were responsible for 77% of the weight while the remaining 23% came from organic shell material. When the OSM from empty shells and shell fragments is taken into account the average dry weight biomass per square metre increased by $2.625\ g$ to a total of $16.383\ g$, an increase of 19.1%.

Discussion

Although there have been numerous estimates of standing stock biomass for a variety of bivalve species (cf. Dame 1972, 1976; Dare 1976; Hughes 1970; Kuenzler 1961; Lewandowski and Stanczykowska 1975; Magnin and Stanczykowska 1971; Münch-Petersen 1973; Negus 1966; Wolff et al. 1975), few authors have considered the role of organic material contained in the shell of living specimens and in shell fragments.

Dare (1976) used a value for organic shell material of 3.4% in a study of *Mytilus edulis*. He concluded that organic shell material was equal to between 32 and 34% of the total ash-free tissue weight over 3 years in one population and 30 and 71% during 2 years in a second population. Similar calculations from the results of the present study revealed that the importance of organic shell material, expressed as a percentage of tissue weight, varied in the three species: *E. complanata*, 32.9%; *A. cataracta*, 21.3%; and *L. ochracea*, 16.3%.

Hughes (1970) included organic shell material in calculation of an energy budget for *Scrobicularia plana*, but did not present data on the amount of organic material in the shell.

Kuenzler (1961) included conchiolin in determining annual net production and energy flow within a population of *Modiolus demissus* and determined that almost 66% of the dry organic standing stock was in the form of shell organics. However, he determined, by loss on ignition, that the content of organic matter was 10.6% of shell weight, a value substantially higher than the range

of 4.63–6.16% determined by Price et al. (1976) for five populations of the same species. In addition, Kuenzler (1961) assumed that the ratio of shell weight to tissue weight remained constant over the size range of the species.

In a study of *Mytilus edulis*, Nixon et al. (1971) collected empty shells and shell fragments in addition to living individuals, and concluded that dry tissue weight was only 7.14% of total shell weight. If it is assumed that there is no differential rate of loss of organic matter as the shell dissolves, as suggested by the present study of three freshwater unionids, and that the value for shell organics of 3.4% of shell weight used by Daniel (1921) and Dare (1976) for *M. edulis* applies to the population studied by Nixon et al. (1971), then these results can be recalculated. Such calculations show that in this *M. edulis* bed the organic matter was distributed among tissue (67.7%), shells of living specimens (18.0%), and empty shells and shell fragments (14.3%).

In the bivalve community in Morice Lake the distribution of dry weight standing stock of organic matter is among tissue (64.6%), shells of living individuals (19.4%) and empty shells and shell fragments (16.0%). It will be interesting to learn if the marked similarity in energy compartmentalization found in these two studies of quite different species in very different habitats is coincidental or is perhaps a characteristic of other bivalve populations and communities.

The results of the present study, coupled with previously reported findings, clearly underline the necessity of including organic shell material in biomass estimates. Organic material in both shells of living specimens and empty shells and shell fragments must be taken into account. The energy content of all three compartments are part of a dynamic energy pool. The most obvious differences are in the rates at which the energy within the compartments cycle in their environment. Predation or other mortality factors will cause the tissue energy to be transformed rapidly, while the energy pool contained in the shell may well be essentially intact even after a period of 1 year as shown in this study.

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