

## Comparative Energetics of Two Populations of the Unionid, *Anodonta cataracta* (Say)<sup>1</sup>

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*Abstract.* *Anodonta cataracta* from Layton's Lake are more abundant (24.3/m<sup>2</sup>), have a substantially higher rate of tissue weight accumulation and lower rates of respiration, filtration and fecal production than individuals from Morice Lake (3.9/m<sup>2</sup>). Seston concentrations are only slightly higher in Layton's Lake but concentrations of suspended organic carbon do not differ. In spite of higher seston densities, the lower filtration rate of Layton's Lake *Anodonta* resulted in a lower potential clearance of particles. Possible explanations for the differences in energetics of the two populations are discussed.

Different populations of the same species of bivalve molluscs not uncommonly show differences in growth rate, particularly as measured by dry tissue weight (Haukioja & Hakala 1978; Jorgensen 1976; Negus 1966; Stanczykowska 1976). Jorgensen (1976) has postulated that there are a number of factors responsible for the observed differences but the most important is amount and nature of the food supply. Griffiths and King (1979), Langton *et al.* (1977), Thompson and Bayne (1974) and Waltz (1978a,b,c;1979) have shown experimentally that as food supply increases within usable limits there is an increase in filtration rate, respiration rate, and increased scope for growth.

A number of authors (Aldridge & McMahon 1978; Alimov 1970; Dame 1972; Hibbert 1977; Hughes 1970a,b; Kuenzler 1961) have attempted to establish partial or complete energy budgets for single populations of bivalves. These studies are useful for understanding the ecology of individual populations but there appears to be an underlying assumption that the proportion of the consumed energy that is diverted into the various components of the energetic equation for one population is representative of the energy compartmentalization of other populations of the same species. Bayne and Widdows (1978) and Bayne and Worrall (1980), in a study of two populations of *Mytilus edulis*, showed that one had a higher rate of oxygen consumption, a higher clearance (filtration) rate and a higher growth rate. The complex interactions between seasonal variations in temperature and food supply at the two sites make it difficult to determine if the two populations are responding in a comparable fashion to these environmental variables. Haukioja and Hakala (1978) in a study of thirteen populations of *Anodonta piscinalis* observed differences in growth rate which they partially attributed to variability in resources although this factor was not directly measured.

Preliminary observations on the ecology of two populations of the freshwater bivalve *Anodonta cataracta* (Say) located in the Nova Scotia-New Brunswick border region of eastern Canada revealed differences that could not easily be explained on the basis of environmental characteristics. The populations differed most noticeably in average density. The present study was undertaken as a preliminary examination of the extent and possible causes of differences in the ecological energetics of the two populations.

### MATERIALS AND METHODS

Layton's Lake is an 11.3 ha meromictic lake located in Nova Scotia, 14.5 km southwest of Sackville, New Brunswick. Surface waters have an average conductivity of 472

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$\mu\text{mhos/cm}$  at  $25^\circ\text{C}$ . Surface values for pH range from 7.1 to 8.9 while calcium ion concentrations vary from 47.5 to 61.5 mg/liter. *Anodonta cataracta* (Say), the only bivalve in the lake, is abundant only in the three regions of the littoral zone indicated in Fig. 1. The present study was restricted to the population inhabiting a shallow sand bar on the west side of the lake. Maximum depth of water at the site was 1.0 m.

Morice Lake, which contains populations of *Elliptio complanata* (Lightfoot), *Anodonta cataracta*, *Anodonta implicata* (Say), and *Lampsilis ochracea* (Say), is a  $1.5 \text{ km}^2$ , old (ca. 1765), polymictic, mesotrophic reservoir located 1.5 km north of Sackville, New Brunswick. Collection of *Anodonta cataracta* was restricted to the southwest study arm (Fig. 2). The water near the bottom where *Anodonta* reside has an average conductivity of  $52.8 \mu\text{mhos/cm}$  at  $25^\circ\text{C}$ . The pH range is from 5.5 to 7.4 and the calcium ion concentration varies from 3.0 to 5.0 mg/liter. Because of the close proximity of the lakes, their seasonal temperature regimes are very similar.

Quantitative estimates of *Anodonta* abundance in Layton's Lake were obtained by placing a  $0.25 \text{ m} \times 0.25 \text{ m}$  plexiglass frame on the substrate of the sand bar at 24 randomly selected sites. In Morice Lake, ten  $22.9 \text{ cm} \times 22.9 \text{ cm}$  ( $9 \times 9$  inches) Ekman grab samples ( $522.6 \text{ cm}^2$ ) were taken at each of the ten sampling stations shown in Figure 2. This sampling was repeated on five occasions throughout the ice-free period. Visual observation of the functioning of this sampler at the shallower stations indicates that it is an efficient sampler for bivalves inhabiting the type of substrate found in Morice Lake.

From early May until ice freeze-up, samples of 25 *Anodonta* covering the size range were collected at approximately two to three week intervals from both lakes. At Layton's

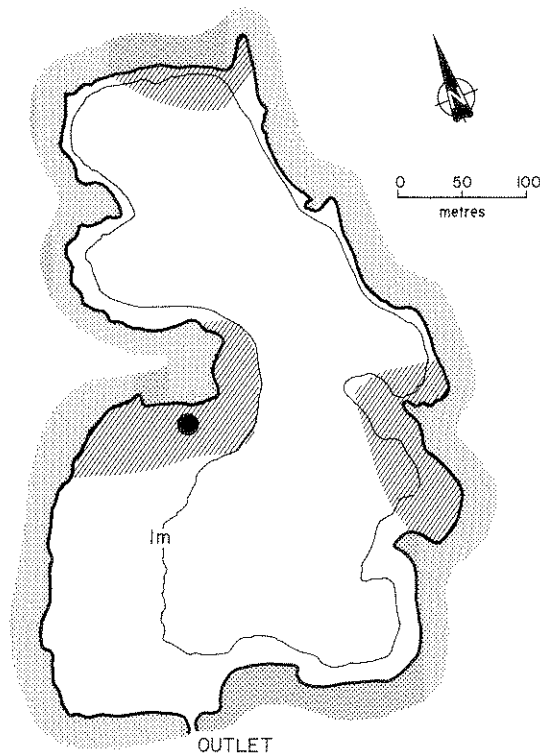


Fig. 1. Layton's Lake, N.S. *Anodonta cataracta* inhabit the areas indicated by diagonal shading. The location of the sub-population used in this study is indicated by a black circle.

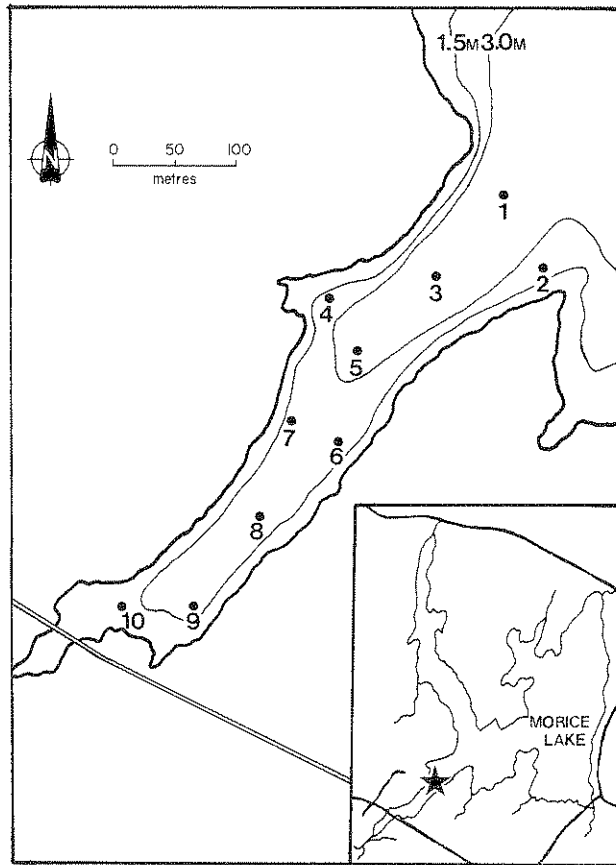


Fig. 2. The south-west study arm of Morice Lake, N.B. Numbers represent the ten quantitative sampling stations.

Lake, specimens were picked by hand from the sand bar, while in Morice Lake they were collected by towing a basket-drag behind a powered boat. Specimens were brushed to remove concretions and maximum length determined to the nearest 0.5 mm using calipers. Each bivalve was opened by cutting the adductor muscles and sexed by observing eggs and/or glochidia in the marsupia or by making wet mounts of gonadal material. Several eggs and/or glochidia from each female were measured to determine average diameter. Wet tissue was scraped into pre-weighed aluminum drying dishes and both tissue and shell dried at 60° C for 48 hours, cooled to room temperature and weighed to the nearest 0.001 g. Samples of tissue from various sizes of male and female specimens collected throughout the summer from both lakes were ground and the energy content determined using a Phillipson microbomb calorimeter.

Growth curves for male and female *Anodonta* from both lakes were constructed by counting the number of visible growth rings on each specimen.

When females were carrying glochidia in the marsupia, collections were made of bivalves from both lakes. For females in which the marsupia appeared to have received full complements of glochidia, the marsupia were excised and stored in separate vials of 10% formalin. Later, the marsupia from each female were placed in one liter of water and vigorously stirred until the marsupia were broken and the glochidia distributed evenly throughout the volume of water. Five 2 ml aliquots were removed and the number of

glochidia in each sample counted. The average number of glochidia in the five samples was used to determine the total number of glochidia.

Comparative respiration rates for specimens from both lakes were determined at 4, 12, and 20°C. Specimens were gently scrubbed and placed in tanks of 45  $\mu\text{m}$  sieved water from the appropriate lake. These tanks were placed in an incubator where they were aerated at the experimental temperature for a minimum period of forty-eight hours. Individual bivalves were then placed in respirometers which were filled with oxygen-saturated lake water filtered through a 45  $\mu\text{m}$  sieve and previously adjusted to the experimental temperature. Respirometers were sealed and placed in an incubator for three to five hours. To compensate for changes in oxygen concentration caused by seston less than 45  $\mu\text{m}$ , controls were run for each experiment. After incubation the contents of each respirometer were fixed to determine oxygen concentration using the sodium azide modification of the Winkler technique (APHA, 1971). Replicate samples were determined for each respirometer. Respirometers were modified wide-mouthed collecting jars. A silicone seal was constructed around the mouth of the jar to prevent leakage and the covers were drilled to accommodate a ground glass stopper from a standard BOD bottle. Three bottle volumes of 137, 269, and 495 ml were used. The bottle used for each bivalve was selected so that the specimen represented less than approximately 25% of the bottle volume. The balance between respirometer volume and bivalve size was such that the dissolved oxygen concentration in the respirometers never dropped below 50% saturation and only rarely below 75%.

To determine comparative filtration rates, bivalves from both lakes with lengths of between 7 and 8 cm were scrubbed to remove matter adhering to the shell and then placed in a tank of aerated water from the appropriate lake which had been filtered through a 45  $\mu\text{m}$  sieve. After being left in the aerating tank for twelve hours to acclimate to experimental conditions, they were re-washed and transferred to 1500 ml of 45  $\mu\text{m}$  filtered, aerated lake water. At the initiation of the experiment and after three and six hours, 50 ml samples were passed through a 100  $\mu\text{m}$  aperture of a Model TA2 Coulter Counter. The 100  $\mu\text{m}$  aperture counts particles between 2 and 40  $\mu\text{m}$  in equivalent spherical diameter. All experiments were conducted at 21°C. Filtration rates were calculated as in Paterson (1984).

To determine rates of fecal production 20 bivalves covering the size range were collected from each lake at approximately three week intervals during the summer. After the shells were gently scrubbed they were placed in an aquarium of lake water that had been filtered through a 1.2  $\mu\text{m}$  Millipore filter. The aquarium was held in an incubator set at lake water temperature as measured at the time of collection. The bivalves were left in the aquarium for 24 hours to clean their shell cavities of pseudofeces, removed from the aquarium, re-washed in water adjusted to lake temperature and placed in 250 ml culture dishes filled with 1.2  $\mu\text{m}$  Millipore filtered, oxygen saturated water at lake temperature. Culture dishes were then held in the incubator for six hours. At the end of this period each bivalve was removed and washed to remove feces adhering to the shell. This wash water plus the contents of each culture dish were filtered through preweighed 1.2  $\mu\text{m}$  Millipore filters which were dried for 24 hours at 60°C and reweighed. Removal of specimens from a natural array of seston 24 hours prior to initiation of experiments allows time for partial gut clearance. However, this procedure was necessary as any appreciably shorter time resulted in production of pseudofeces which could not be separated from fecal material.

At weekly intervals throughout the summer water samples were collected above the sand bar at Layton's Lake or approximately 10 cm above the substrate in Morice Lake. The samples were passed through a Model TA2 Coulter Counter equipped with a 70  $\mu\text{m}$  aperture to determine the quantity of seston. The 70  $\mu\text{m}$  aperture measures particles with equivalent spherical diameters of between 1.4 and 28.0  $\mu\text{m}$ . As it was unknown what

proportion of the sestonic particles might be inorganic, and therefore unsuitable as an energy source for *Anodonta*, samples of unmodified lake water were injected with a 200  $\mu\text{m}$  needle into a Beckman Model 915 Total Organic Carbon Analyser. On five separate occasions samples were filtered through 0.45  $\mu\text{m}$  Millipore filters to estimate what fraction of the total organic carbon would be in a dissolved form. It was found that the dissolved organic carbon contributed only a very small amount of the total organic carbon.

Where regression equations were established for the two populations, they were first compared by using 't' statistics to determine if the slopes were significantly different (Zar, 1974). If they were not different the intercepts were then compared.

## RESULTS

*Abundance and Growth.* Quantitative sampling of *Anodonta cataracta* in Layton's Lake revealed a population density on the sand bar of  $24.32 \pm 4.64 (\bar{x} \pm \text{SE})/\text{m}^2$ . The population density in the study arm of Morice Lake was  $3.87 \pm 0.42/\text{m}^2$ . Size frequency distributions of the bivalves collected in the quantitative samples are shown in Figure 3. The most obvious differences in length frequencies is the dominance of bivalves between 5 cm and 8 cm in Morice Lake, while smaller bivalves dominate in Layton's Lake. It is also noteworthy that in Layton's Lake bivalves with a length greater than 8 cm are relatively common, although rare in Morice Lake. The variations observed between the two populations in factors such as size frequency distributions are thought not to be a product of the different quantitative sampling techniques as values obtained from random qualitative sampling are essentially identical.

Increase in shell length with age for the two populations is shown in Figure 4. Initially growth curves were constructed for both male and female bivalves but these were not significantly different in either lake. Shell length as a function of age for *Anodonta* from Layton's Lake can be adequately described by the equation:  $\log_{10} L (\text{cm}) = 0.399 + 0.539 \log_{10} A (\text{yr})$  ( $r = 0.98$ ,  $p < 0.001$ ). For Morice Lake the regression of shell length on age is described by  $\log_{10} L (\text{cm}) = 0.342 + 0.596 \log_{10} A (\text{yr})$  ( $r = 0.991$ ,  $p < 0.001$ ). The two growth equations do not differ in slope ( $t = 0.83$ ), or elevation ( $t = 0.003$ ).

Because of marked differences in calcium concentrations of the two lakes, it was suspected that, although there was no significant difference in shell length at any given age, there might be differences in shell weight or shell proportions. It was found for both lakes that there was no significant difference in these parameters between male and female bivalves, and that there was no seasonal variation in shell weight for a bivalve of a given length. Shell weight as a function of shell length for bivalves from Layton's Lake was adequately described by the equation:  $\log_{10} W (\text{g}) = -1.92 + 3.12 \log_{10} L (\text{cm})$  ( $r = 0.96$ ,  $p < 0.001$ ). The appropriate equation for Morice Lake *Anodonta* was  $\log_{10} W (\text{g}) = -1.97 + 3.07 \log_{10} L (\text{cm})$  ( $r = 0.98$ ,  $p < 0.001$ ). These equations do not differ in slope ( $t = 0.07$ ) or elevation ( $t = 0.76$ ). In addition, numbers of measurements of shell length, maximum shell height and maximum shell width did not show any differences in proportion between the two populations.

Comparison of the tissue weight for a bivalve of any given length in both lakes showed no difference between males and females. Pooling of all data gave a regression equation of dry tissue weight as a function of shell length of  $\log_{10} W (\text{g}) = 2.915 \log_{10} L (\text{cm}) - 2.597$  for Morice Lake (Fig. 5), and  $\log_{10} W (\text{g}) = 2.701 \log_{10} L (\text{cm}) - 2.131$  for Layton's Lake (Fig. 5). The slopes of these equations are significantly different ( $t = 1.97$ ,  $p < 0.05$ ). For example, a 6 cm bivalve, which would be approximately five years old and sexually mature, would have an average dry tissue weight in Layton's Lake of 0.935 g, while in Morice Lake the dry tissue weight of the same length bivalve would be 0.469 g.

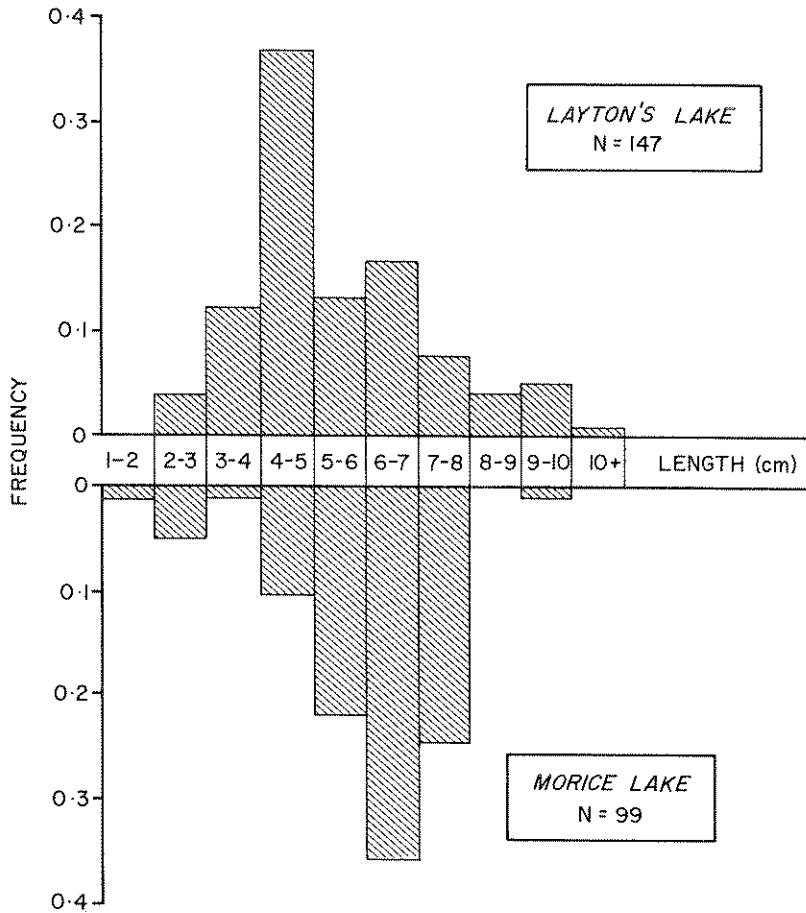


Fig. 3. Size-frequency distributions for *Anodonta cataracta* from Layton's Lake and Morice Lake.

The dry tissue of bivalves from Morice Lake did not show differences in caloric content related to sex and the average value for all bivalves was  $4611.3 \pm 140.5$  calories/g. In contrast, in Layton's Lake, the males and females showed significant differences in caloric content with the males having an average value of  $5162.8 \pm 91.1$  calories/g while females averaged  $4731.6 \pm 90.1$  calories/g.

**Respiration.** The respiration rates of *Anodonta cataracta* from Layton's Lake and Morice Lake at 4, 12, and 10°C as expressed as a function of tissue weight are presented in Table 1. In all cases for bivalves of comparative tissue weight the respiration rate in mg O<sub>2</sub>/g/h was significantly greater for Morice Lake bivalves than those from Layton's Lake.

**Reproduction.** The seasonal pattern of reproductive activity in the two populations of *Anodonta cataracta* was similar. Glochidia with a diameter of approximately 350 μm were released from the marsupia of the female in late April or early May. At this time, the eggs in the ovary had an average diameter of approximately 150 μm. In Layton's Lake, eggs were found in the marsupia in early June at a comparable diameter. These then increased rapidly in size until they reached a diameter of approximately 450 μm in early August. These transformed by mid-August to glochidia of 350 μm diameter, which then remained at the same size until released the following spring. The only observable

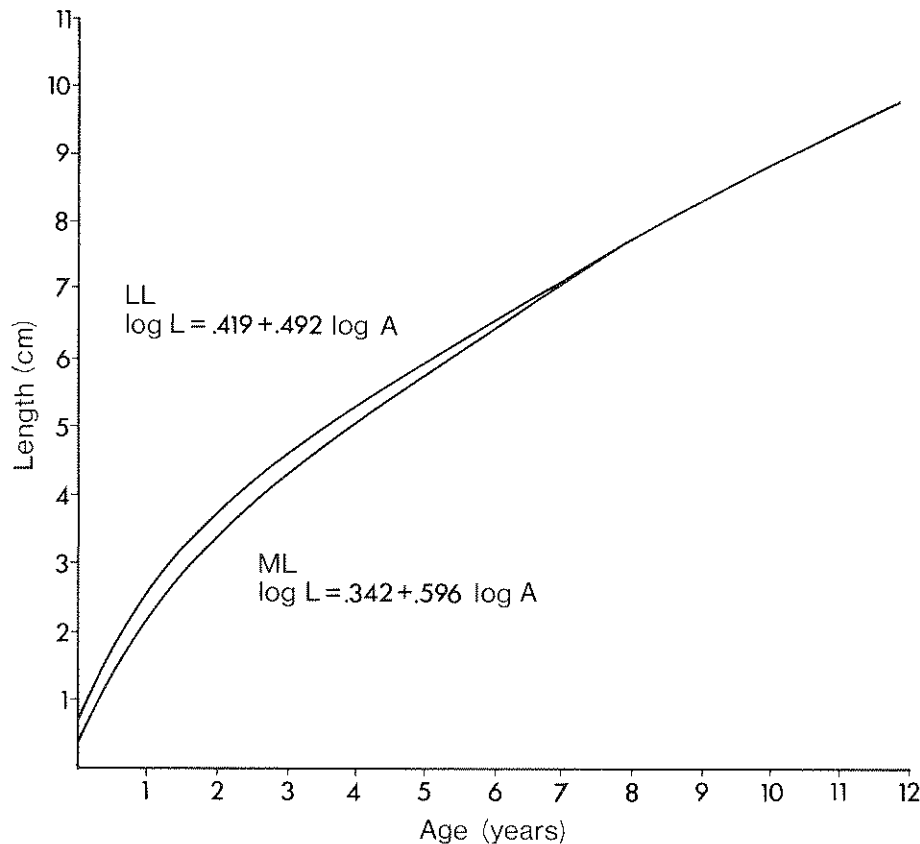


Fig. 4. Shell length as a function of age for *Anodonta cataracta* from Layton's Lake (LL) and Morice Lake (ML).

difference in the pattern in Morice Lake was that, in spite of frequent sampling, eggs were not discovered in the marsupium until mid-July. When the number of glochidia produced was related to shell length for female bivalves from both lakes the following regression equations were obtained: Layton's Lake:  $\log_{10} N = 2.96 + 2.41 \log_{10} L$  ( $r = 0.63$ ,  $n = 21$ ,  $p < 0.01$ ); Morice Lake:  $\log_{10} N = 0.17 + 5.20 \log_{10} L$  ( $r = 0.68$ ,  $n = 27$ ,  $p < 0.01$ ) where  $N$  = number of glochidia and  $L$  is shell length in cm. Thus, a female from Layton's Lake produces more glochidia than a comparable length female from Morice Lake. However, when regression equations were established relating number of glochidia to tissue weight for females from both lakes it was discovered that there is no significant difference ( $t = 0.65$ ).

**Fecal Production.** Most determinations of fecal production rates were conducted at summer temperatures between  $18^{\circ}$  -  $21^{\circ}$  C. Over this temperature range, fecal production rates as expressed in mg/g/h for Layton's Lake individuals could be expressed by the equation:  $\log_{10} F = -0.34 - 0.51 \log_{10} L$  ( $r = 0.76$ ,  $p < 0.001$ ,  $n = 98$ ) where  $L$  is shell length in cm and  $F$  is fecal weight in mg. The equation for Morice Lake specimens was  $\log_{10} F = 0.26 - 0.50 \log_{10} L$  ( $r = 0.84$ ,  $p < 0.001$ ,  $n = 93$ ). There are no differences in the slopes of these equations but there is a significant difference in the Y intercept ( $t = 3.51$ ,  $p < 0.001$ ). For example, a 6 cm bivalve from Layton's Lake would have an average fecal production of 0.183 mg/g/h and based on actual tissue weight would produce feces at the rate of 0.171 mg/h. In contrast, a 6 cm specimen from Morice Lake would have a fecal production rate of 0.743 mg/g/h or an actual production rate of 0.348 mg/h, a rate twice that of a

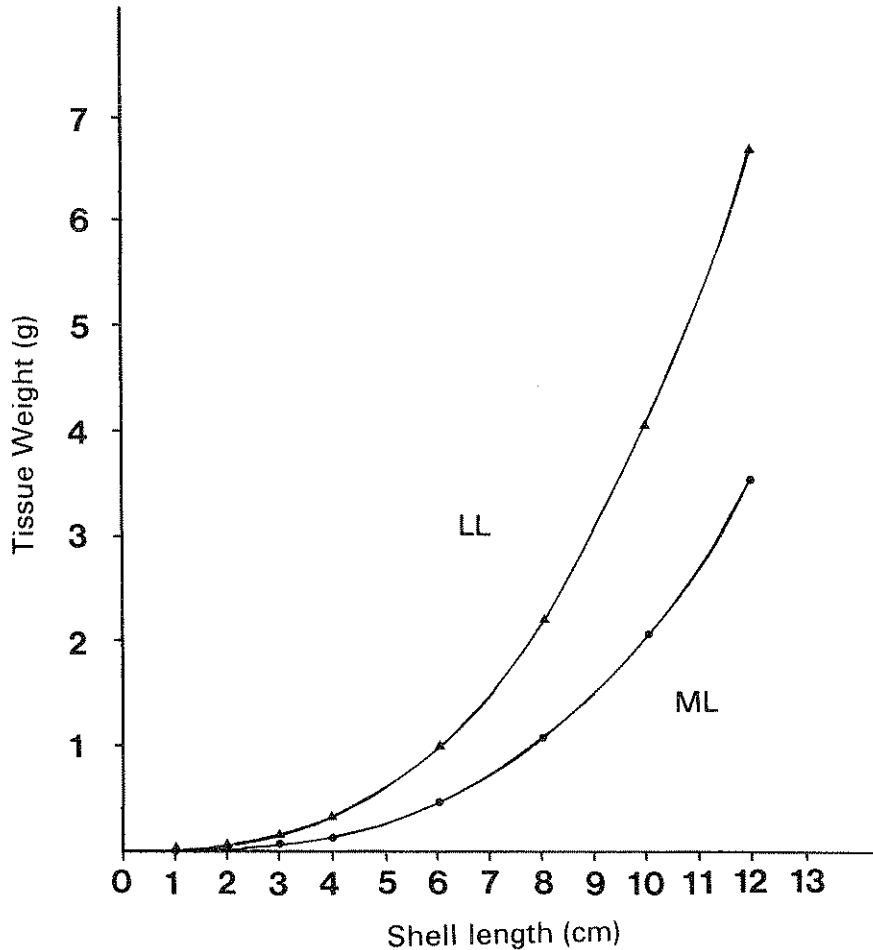


Fig. 5. The relationship between dry tissue weight and shell length for *Anodonta cataracta* from Layton's Lake (LL) and Morice Lake (ML).

specimen from Layton's Lake. Limited observation in the spring and fall at substantially lower temperatures did not show differences in the slopes of the regression equation and again differences between the intercepts.

*Filtration Rate, Seston Abundance and Seston Organic Content.* All experiments concerning comparative filtration rates of the two populations were conducted using bivalves between 7 and 8 cm in maximum length, so that adequate regressions for filtration rate as a function of shell length were not determined. However, it was discovered that the average filtration rate of a bivalve within this size range from Layton's Lake at a temperature of 21°C was  $209 \pm 63.5$  ml/g/h, or expressed on the basis of tissue weight, a rate of 357.0 ml/h. A similar length bivalve from Morice Lake at the same experimental temperature had a filtration rate of  $703 \pm 159$  ml/g/h or an actual filtration rate of 632.0 ml/h. The average values expressed either as ml/g/h or ml/h are significantly different ( $t = 2.56$ ,  $p < 0.05$ ). Expressed in a somewhat different fashion, for bivalves of this length a Layton's Lake individual can support a dry tissue weight approximately 1.9 times that of a Morice Lake specimen with a filtration rate which is only 56.5% that of the Morice Lake individual. However, it is to be expected that a specimen with a lower tissue weight would filter at a higher rate in ml/g/h. In previous



TABLE 1

Respiration rates of *Anodonta cataracta* from Layton's Lake and Morice Lake as measured at 4°, 12°, and 20°C. Rate (R) expressed as mg O<sub>2</sub>/g dry tissue/h.

		r <sub>1</sub>	n <sub>2</sub>	p <sub>3</sub>
Layton's Lake				
4°C	R = 0.080 W(g) <sup>-0.433</sup>	-0.81	20	<0.001
12°C	R = 0.138 W(g) <sup>-0.400</sup>	-0.68	29	<0.001
20°C	R = 0.300 W(g) <sup>-0.466</sup>	-0.71	21	<0.001
Morice Lake				
4°C	R = 0.189 W(g) <sup>-0.460</sup>	-0.47	36	<0.01
12°C	R = 0.253 W(g) <sup>-0.455</sup>	-0.60	27	<0.001
20°C	R = 0.433 W(g) <sup>-0.403</sup>	-0.58	15	<0.05

<sup>1</sup>correlation coefficient

<sup>2</sup>number of determinations

<sup>3</sup>probability

unpublished work, filtration rates of *A. cataracta* from Morice Lake were determined over the size range of the species by measuring the uptake of a neutral red stain. When log<sub>10</sub> filtration rate (ml/g/h) was plotted against log<sub>10</sub> tissue weight (g) a slope of -0.61 was found. Using the assumption that determination of filtration rate of Layton's Lake *Anodonta* by the neutral red also would generate a slope approximating to -0.61, it is possible to calculate that for equivalent tissue weights (1.71 g) the rates in Layton's Lake would be 209 ml/g/h or 357.0 ml/h, while the individual from Morice Lake would have rates of 648.7 ml/g/h or 1109.3 ml/h.

In Layton's Lake the average concentration of sestonic particles between 1.4 μm and 28.0 μm in diameter (692,000 ± 103,660 particles/ml) was significantly greater (t = 2.31, p < 0.05) than the average concentration (453,250 ± 52,732 particles/ml) in Morice Lake.

If the assumption that a bivalve with a tissue weight of 1.71 g would filter 357.0 ml/h in Layton's Lake and 1109.3 ml/h in Morice Lake is correct then the average filtration activity for such a bivalve in Layton's Lake would be 2.470 × 10<sup>8</sup> particles/h while in Morice Lake the value would be 5.020 × 10<sup>8</sup> particles/h. The individual from Morice Lake would have filtered out about twice as many particles but had to use energy to pump 3.1 times as much water.

The organic carbon content of Layton's Lake averaged 11.22 ± 1.75 mg C/liter while that in Morice Lake was 12.49 ± 1.27 mg C/liter. These two values are not significantly different (t = 0.60).

## DISCUSSION

Griffiths and King (1979); Langton *et al.* (1977); Thompson and Bayne (1974) and Waltz (1978a,b,c,d; 1979) have shown that as the food supply for bivalves increases within useable limits there is an increase in filtration rate, respiration and growth. Layton's Lake has a slightly higher seston concentration than is found in Morice Lake but there is no significant difference in the content of organic carbon. *Anodonta* from Layton's Lake had a lower filtration rate and, in spite of somewhat higher seston densities, had a lower potential clearance of seston particles. The lower filtration rate is associated with reduced rates of respiration and fecal production but an increased rate of tissue accumulation when compared to Morice Lake specimens.

It is interesting to note that despite much more rapid tissue growth and much higher calcium concentrations in Layton's Lake, shell growth of the two populations is identical. Shell growth may be under genetic control.

The current study was not designed to provide evidence for the underlying causes of the observed differences in the energetics of the two populations. However, there appears to be several potential explanations for the differences. A possible explanation would be that Layton's Lake *Anodonta* can, with a lower expenditure of energy on filtration, obtain sufficient energy because of a higher assimilation efficiency. Reduced filtration leads to reduced respiration and substantially more assimilated energy can be diverted to tissue growth and reproductive products. The lower rate of fecal production observed in Layton's Lake suggests either a lower ingestion rate, which would not be expected to result in an increased growth rate, or is the result of a higher efficiency of assimilation.

Numbers of authors, including Paterson and Fernando (1971) have shown that benthic invertebrates often have an aggregated distribution. Only in relatively few cases, such as the work of Sephton *et al.* (1980), has it been possible to observe a response of organisms to one or more environmental variables which explain the aggregation. This then raises the question of the ecological significance of such aggregations, particularly as some observed aggregations seem to be brought about by behavioural responses.

Researchers have showed that, within limits, fishes such as rainbow trout (Itazawa *et al.* 1978), medaka (Itazawa *et al.* 1978; Kanda & Itazawa 1978), and catfish eel (Kanda & Itazawa 1981) have increased growth and decreased oxygen consumption when in groups rather than when isolated. In Morice Lake, both the bivalves *Elliptio complanata* and *Anodonta cataraacta* show aggregated distributions, and the effects of such aggregated distributions on the respiration rate of *E. complanata* were determined (Paterson 1983). Respiration rate per individual decreased, within limits, as the number of individuals in the respirometer increased. It was further shown that a single bivalve placed in water which previously contained numbers of bivalves would respire at a rate equal to the average rate of the previous inhabitants, a rate substantially lower than observed when the respiration rate of a single individual was measured in water that had not previously contained bivalves.

Jorgensen (1966) has suggested that the amount of water drawn across the gill mechanisms of bivalves during the process of pumping and filtration provides a potential oxygen supply far in excess of the needs of the organism. Experiments on filtration of *Anodonta* from both Layton's Lake and Morice Lake revealed, on all occasions, extensive production of pseudofeces. Microscopic examination of natural seston and pseudofeces failed to reveal any evidence of selection of particular food types from the natural array. Consequently the filtration activities of individuals from both populations would appear to satisfy food requirements.

In bivalves the increased filtration (pumping) rate and accompanying increase in respiration rate above that necessary to insure adequate supplies of food and oxygen possibly may be related to a sensing of the immediate environment, a sensing which is modified by the presence of numbers of the same species. If this hypothesis is correct then a possible explanation of the results obtained from this study would be that the observed differences are the result of the higher population densities in Layton's Lake. The higher densities in Layton's Lake result in each individual being able to more readily sense the presence of other individuals in proximity. This results in an expenditure of less energy in pumping water for the purpose of sensing the environment. Reduction in such pumping activity decreases metabolic demands on assimilated energy and the energy saving can be diverted to tissue growth and reproductive products. The decrease in filtration and subsequent decrease in ingestion of sestonic particles beyond levels which can be readily assimilated would reduce fecal production. In contrast, in Morice Lake the sparse density results in use of substantial amounts of energy to operate the pumping mechanism for purposes of sensing the environment. Such activity increases respiration rate and subsequently diverts energy from growth and reproduction. The increased filtration also

results in an increased rate of ingestion which would be reflected in an elevated rate of fecal production. However, if food is present in abundances greater than the organism can readily use, increased filtration would not necessarily result in an increase in assimilation.

A further possible explanation for the observed differences between the two *Anodonta* populations lies in the differences in calcium concentrations of the two lakes. Many molluscs must extract substantial amounts of calcium from the water for shell construction. The low levels of calcium in Morice Lake could increase the amount of water that must be pumped above the amount necessary to supply food and oxygen. This then necessitates an increase in respiration rate which decreases the amount of assimilated energy available for growth.

Koehn and Shumway (1982) have reported that in the oyster (*Crassostrea virginica*) the degree of heterozygosity is positively correlated with growth rate and negatively correlated with respiration rate, which provides a possible genetic basis for observed differences in energetics among populations. The increased tissue growth and decreased respiration in Layton's Lake *Anodonta* compared to those in Morice Lake, therefore, could be the result of genetic differences. The relative balance between increased growth and decreased respiration could be such that a higher growth can be achieved in spite of lower rates of filtration and fecal production.

The design of the present study was such that it is not possible to determine if water quality, quality and quantity of food, genetic factors, differences in densities, or possibly a combination of these, are important in determining the observed ecological differences. It does, however, appear that differences in compartmentalization within the energy budget must be considered in comparing populations of a species.

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