

## Population size, growth, and production of a unionid clam, *Anodonta grandis simpsoniana*, in a small, deep Boreal Forest lake in central Alberta<sup>1</sup>

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Unionid clams were sampled quantitatively by divers searching quadrats and by dredging in Narrow Lake, central Alberta. The mean density and biomass of *Anodonta grandis simpsoniana* Lea (aged  $\geq 2$  years) on the area of the littoral zone available to clams (80%) were 15/m<sup>2</sup> and 132 g/m<sup>2</sup> (live weight), respectively. The mean length at 5 years of age was 49 mm and only increased to 69 mm by 11 years of age. Variation in length at annulus was high. Years of small growth increments (1982 and 1983) coincided with years of poor juvenile recruitment. Production/biomass ratios were highest for clams of 2 and 3 years of age, but the amount of biomass produced was greatest for clams of 5–8 years of age. The overall production/biomass ratio (live weight) was 0.25 and varied with annual differences in growth.

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Le dénombrement par plongée dans des grilles échantillons et des prélèvements par dragage ont permis de faire un échantillonnage quantitatif des moules d'eau douce dans le lac Narrow, dans le centre de l'Alberta. La densité moyenne des *Anodonta grandis simpsoniana* Lea (âge  $\geq 2$ ) était de 15/m<sup>2</sup> et la biomasse moyenne, de 132 g/m<sup>2</sup> (masse fraîche), dans la partie disponible (80%) de la zone littorale. La longueur moyenne à l'âge de 5 ans était de 49 mm et cette longueur n'atteignait que 69 mm à l'âge de 11 ans. D'après les stries d'accroissement, la croissance en longueur fluctuait beaucoup. Les années de croissance faible (1982 et 1983) étaient des années où le recrutement des jeunes moules était faible. Le rapport production/biomasse était maximal chez les moules d'âge 2 et 3, mais c'est chez les moules âgées de 5 à 8 ans que la quantité de biomasse produite s'est avérée la plus forte. Le rapport production/biomasse calculé sur l'ensemble des moules (masse fraîche) a été évalué à 0.25 et variait en fonction des fluctuations annuelles de croissance.

[Traduit par la revue]

### Introduction

Unionid clams often dominate the biomass of benthic fauna in rivers and lakes (Okland 1963; Negus 1966; Fisher and Tevesz 1976), yet they are seldom studied for any other purpose than to document geographic and depth distribution. Clams eat the same food as organisms eaten by fish, but represent a loss of energy potentially available to fish because clams are largely immune from fish predation because of their large size and thick shell. It is impossible to estimate how much energy is contained in clams and how the amount of energy varies among lakes because unionid clams are usually omitted from quantitative estimates of bottom fauna. Consequently, estimates of population size, age structure, growth, and production are rare. Calculation of the amount of energy contained in unionid clam populations and the rate of turnover of this energy should be relatively simple because clams live in shallow water (Okland 1963; Cvangara 1972; Lewandowski and Stanczykowska 1975), are largely immobile, and age can usually be determined from annuli (Negus 1966; Ghent et al. 1978; McCuaig and Green 1983).

*Anodonta grandis simpsoniana* Lea is typically found in lakes of the Boreal forest zone of Canada, where it reaches a maximum length of 125 mm (Clarke 1981). There is almost no published information on the biology of this subspecies. Much of the information on the more southern subspecies (*Anodonta grandis grandis* Say) deals with geographic or depth distribution (Headlee 1906; Van Cleave 1940; Reigle 1967; Cvangara 1972), although a limited amount of data exist on growth (Ghent et al. 1978; McCuaig and Green 1983) and reproduction (Lewis 1985).

This study was part of a larger study to estimate the biomass and size structure of macroinvertebrate populations in a small, deep, Boreal Forest lake in central Alberta. The goals of the present study were to estimate the population size, age structure, growth, and production of unionid clams in the lake.

### Materials and methods

We quantitatively sampled unionid clams in Narrow Lake (54°35' N; 113°37' W), a small (1.14 km<sup>2</sup>), deep (mean depth 14.2 m), unproductive (mean summer total phosphorus 12.9 mg/m<sup>3</sup>) lake in the Boreal Forest zone of central Alberta. The morphometry and water chemistry of Narrow Lake have been described in Prepas and Trew (1983) and Prepas and Vickery (1984). The lower limit of the littoral zone, defined as the maximum depth of colonization of macrophytes, occurs between 5 and 6 m. We used 6 m as the lower limit, hence the littoral zone comprises 20.5% (23.4 ha) of the surface area. Six of the 24 sites we sampled (Fig. 1) supported extensive beds of the macroalga *Chara* > 10 cm tall, and clams were absent. *Chara* > 10 cm tall forms a thick mat of plants over foul-smelling, flocculent sediments. We concluded that clams were excluded from *Chara* beds because of the almost liquid nature of the sediments and because of low-oxygen conditions under the mat of plants and associated debris. Therefore, we visually surveyed the littoral zone of the lake, plotted the location and approximate size of the *Chara* beds on a bathymetric map, and estimated the percentage of the littoral zone dominated by *Chara*. The littoral zone area (18.7 ha) used in the analyses of population size represents 80% of the total. No correction was needed for the area of the upper part (10.1 ha) of the sublittoral zone (6–8 m) because clams were found on sites dominated by *Chara* and on sites where *Chara* was absent or rare. We assume that samples collected at 1, 3, and 5 m represent the littoral zone and that samples collected at 7 m represent the upper part of the sublittoral zone.

Two methods were used to collect specimens of *A. grandis simpsoniana* in Narrow Lake: divers searching quadrats, and dredging. Divers using scuba collected clams from six sites in Narrow Lake

<sup>1</sup>A contribution from the Meanook Biological Research Station, University of Alberta.

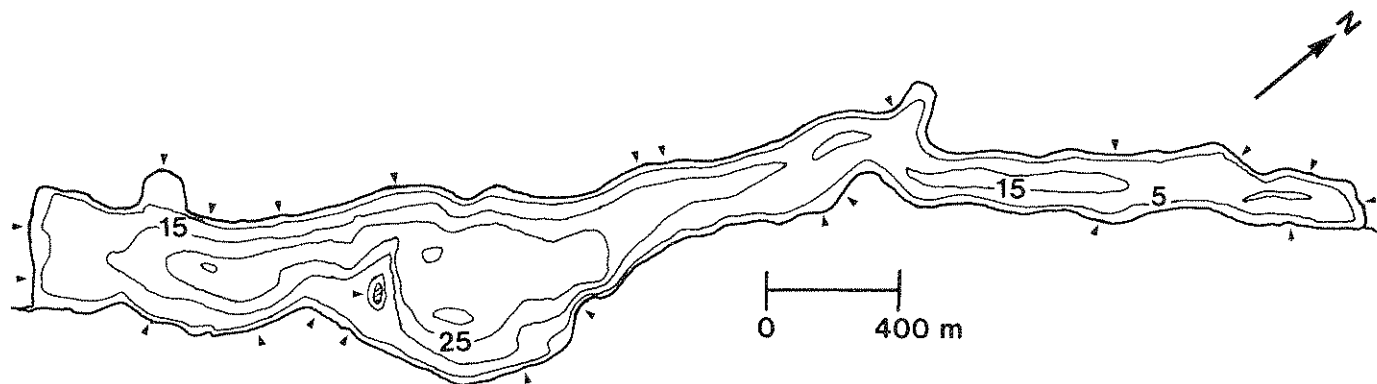


FIG. 1. Bathymetric map of Narrow Lake. Depth contours are at 10-m intervals beginning at 5 m. Sample sites are indicated by arrows.

during August 1985. One site on each side of the lake was chosen at random in the north, central, and south basins of the lake. Four  $0.5 \times 0.5$  m quadrats were searched at depths of 1, 3, 5, and 7 m at each site. An additional four quadrats were searched at a depth of 9 m at one site in each basin. No clams were recovered from the 12 quadrats ( $3 \text{ m}^2$ ) searched at 9 m, and this depth was not sampled for the rest of the study. The second sampling method involved taking 12 samples with a  $23 \times 23 \times 23$  cm Ekman dredge at each of the 1, 3, 5, and 7 m depths on 18 randomly chosen sites. We were able to sample two or three sites every 2 weeks from May 16 to August 9, 1986. The sediments collected with the dredge were washed gently on a 6 mm mesh screen and the unionid clams were removed. The screen retained all clams  $>8$ –10 mm in length, representing ages of 2 years and older. When we compared the size distributions of clams collected by divers with those collected by dredging, it was clear that divers had been unable to sample effectively clams  $<30$  mm in length ( $G$ -test,  $P < 0.001$ ). We estimated that samples collected by divers could underestimate clam density by about 23%, but because the clams were small, the samples would only underestimate the biomass by about 1.5%. Therefore, clams collected by divers were only used in estimating biomass and growth. The population means and 95% confidence intervals (CI) were based on  $\log_{10}$ -transformed data for biomass estimates and on square root transformed data  $((x + 0.5)^{1/2})$  for density estimates (Steel and Torrie 1980; Sokal and Rohlf 1981).

We collected additional clams  $<10$  mm long as part of our routine sampling of benthic macroinvertebrates. Sediments were collected with a  $15 \times 15 \times 15$  cm Ekman dredge, washed on a 0.5-mm sieve, and examined for small unionid clams before preservation with formaldehyde. This method was not quantitative, and the samples were only used to obtain specimens for the weight-length regressions and to confirm the position of the first annulus.

All 588 clams collected in 1985 and 1986 were taken alive to the laboratory, where the debris encrusting the outside of the shell was removed and live weight (to the nearest 1 mg), total length (maximum anterior-posterior length to the nearest 0.1 mm), age, and length at annulus were recorded. The use of annuli to age clams is generally considered valid for clams of the genus *Anodonta* because they show clear growth rings and false annuli are usually easy to differentiate from true annuli (Negus 1966; Ghent et al. 1978; Haukioja and Hakala 1978; McCuaig and Green 1983). The annuli of all clams were counted independently twice and on clams showing a discrepancy they were counted a third time. A subsample of 100 clams was aged by two people and the results were compared. Discrepancies were uncommon and were usually due to the less experienced reader missing the first annulus. We consider errors in aging to be minimal throughout this study. The geometric mean lengths at annulus were calculated for all data combined and for each year class separately. The annual growth increment was calculated for each clam, the mean increment calculated for each year class, and the annual increment at age tested for significant differences in growth among years. This analysis used mean increment for ages 1–7 from 1981 to 1984, testing for significant differences in growth among age-classes and

among years (two-way ANOVA).

Dry weight of shell and wet and dry weight of the viscera were recorded for a subsample of 170 individuals. All weights were measured to an accuracy of 0.1 mg. Wet weight of viscera was determined by removing the body from the shell, blotting excess water from the mantle, mantle cavity, gills, and foot, and weighing the body. The clam body was then dried to a constant weight at  $60^\circ\text{C}$  (24–36 h). The shells were air-dried for 24 h, weighed, and then sprayed with clear acrylic resin to prevent cracking. These data were used to calculate weight-length regressions.

Production was calculated by methods similar to those of Magnin and Stanczykowska (1971), Lewandowski and Stanczykowska (1975), and Strayer et al. (1981). The number of clams of age  $n$  was calculated by multiplying the mean number of clams  $\geq 2$  years of age in the population by the proportion of clams of age  $n$ . The geometric mean weight of clams of age  $n$  was estimated from the weight at annulus  $n$  for each clam (calculated from the appropriate weight-length relationship). The mean weight increment for clams of age  $n$  was determined as mean weight of clams in the population at age  $n$  minus mean weight at age  $n - 1$ . This differs from the method used by Magnin and Stanczykowska (1971) and Strayer et al. (1981) in that they calculated the mean weight increment of clams of age  $n$  as mean weight at age  $n + 1$  minus weight at age  $n$ . The latter method estimates the biomass the present population will produce over the current year and assumes there will be no mortality. This method is therefore an overestimate. Our method estimates the biomass produced over the past year by the present population and is an underestimate because mortality is not accounted for. Neither method accounts for reproductive products.

## Results

Only *Anodonta grandis simpsoniana* was collected from Narrow Lake. The mean density of *A. grandis simpsoniana*  $\geq 2$  years of age on the littoral zone (0–6 m) was 14.9 clams/ $\text{m}^2$  (95% CI = 10.2–20.4 clams/ $\text{m}^2$ ,  $n = 13$ ), which represents  $2.79 \times 10^6$  clams. Clams were only present in 4 of 24 samples collected from the 6–8 m depth zone. The mean density in this depth zone was 0.9 clams/ $\text{m}^2$  (95% CI = 0.03–2.3 clams/ $\text{m}^2$ ,  $n = 24$ ) which represents  $0.1 \times 10^6$  clams. The mean biomass (live weight) of clams on the littoral zone was 131.8 g/ $\text{m}^2$  (95% CI = 92.6–186.6 g/ $\text{m}^2$ ,  $n = 18$ ) or 24.7 t. The mean biomass of clams in the 6–8 m depth zone was 1.4 g/ $\text{m}^2$  (95% CI = 0.03–4.4 g/ $\text{m}^2$ ,  $n = 24$ ) or 0.14 t. Overall, we estimate that there were  $2.89 \times 10^6$  clams weighing 24.8 t (live weight) in Narrow Lake (about 8.18 t wet viscera weight, 0.83 t dry viscera weight, and 3.69 t shell weight).

The weight-length regression analyses indicated that live weight essentially increased in proportion to the cube of

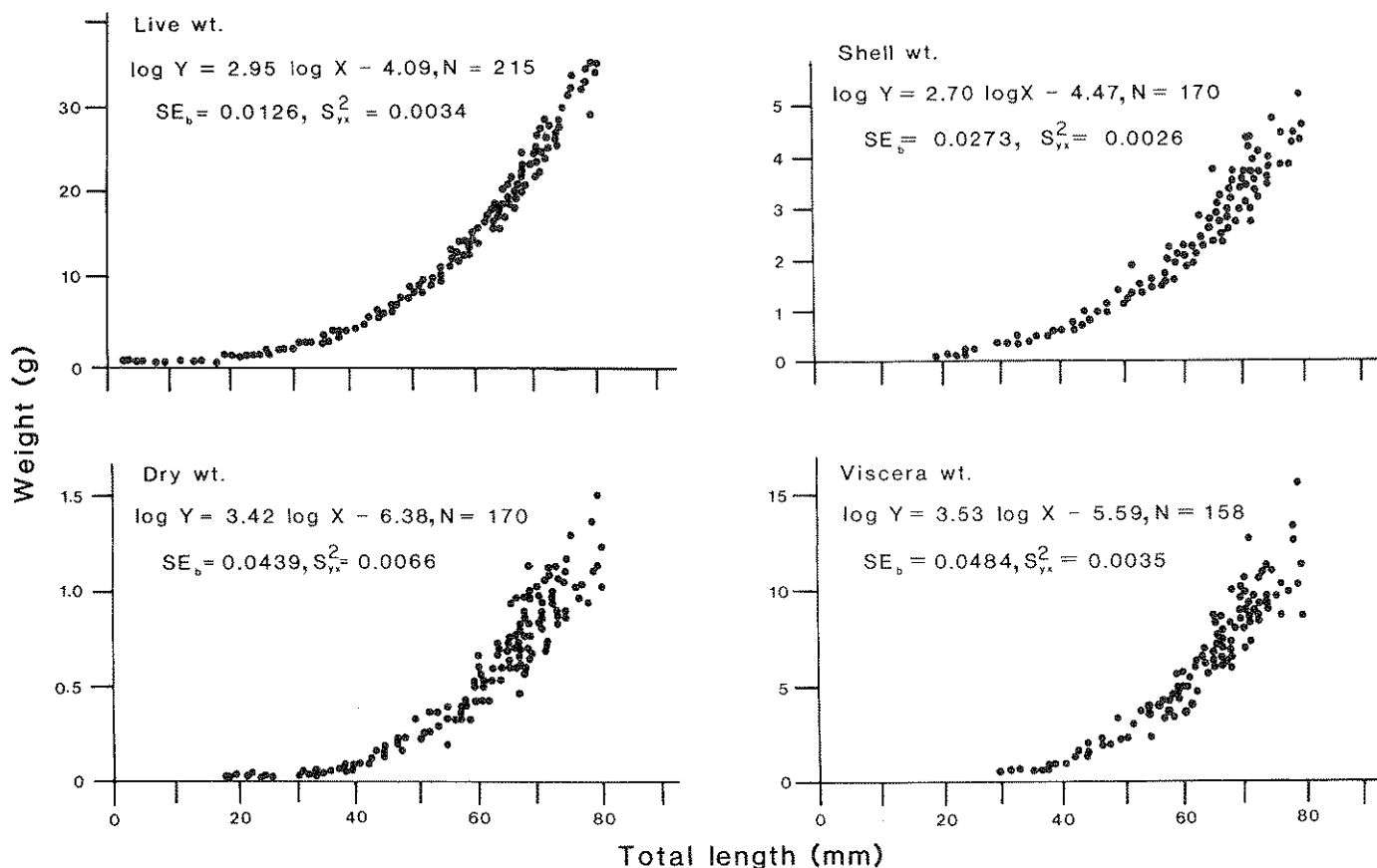


FIG. 2. Regression of live weight, shell weight, dry viscera weight, and blotted viscera weight on total length for *A. grandis simpsoniana* in Narrow Lake.

length, whereas shell weight, dry viscera weight, and blotted viscera weight did not (Fig. 2). The exponent of the live weight – length relationship (2.95) was significantly different from 3.00 ( $t = 4.127$ ,  $df = 213$ ,  $P < 0.001$ ), but this difference is very small. The exponent of the shell weight – length relationship (2.70) was  $\ll 3.00$  ( $t = 11.06$ ,  $df = 168$ ,  $P < 0.001$ ), which indicates that the shell weight is a smaller fraction of the live weight of larger clams. As expected from the preceding data, viscera weight was a larger fraction of the weight of larger clams, as shown by the exponents of the weight – length relationships being  $\geq 3.00$  (dry weight: exponent = 3.42,  $t = 9.50$ ,  $df = 168$ ,  $P < 0.001$ ; wet weight: exponent = 3.53,  $t = 10.91$ ,  $df = 156$ ,  $P < 0.001$ ).

The length – frequency histogram indicates that the lengths of clams in Narrow Lake were not evenly distributed. About 55% of the clams were  $> 50$  mm long while only 17% were 25–45 mm long (Fig. 3A). The age – frequency histogram suggests that there was considerable variation in year-class strength (Fig. 3B). Clams born in 1981 (age 5) and 1984 (age 2) were markedly more abundant than clams born in 1982 (age 4) and 1983 (age 3). The relatively small numbers of clams aged 3 and 4 years corresponds with the low proportion of clams in the 25–45 mm size class.

*Anodonta grandis simpsoniana* in Narrow Lake attained a mean length of 49.1 mm by 5 years of age but only increased 13 mm in length between 6 and 11 years of age (Fig. 4). The large number of clams examined resulted in very narrow 95% confidence intervals around the means, yet the variation in length at annulus was quite large, e.g., a range of 36 mm for clams aged 4 and 5 years. This variation decreased quite

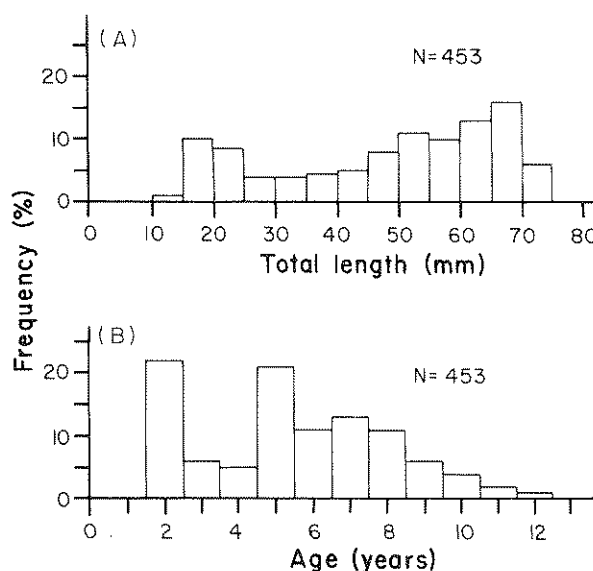


FIG. 3. Length–frequency (A) and age–frequency (B) distributions of *Anodonta grandis simpsoniana* in Narrow Lake in 1986.

markedly after 7 years of age, with few clams exceeding 75 mm in length, whereas the lower range of lengths moved upwards as the clams grew.

A possible source of the wide variation in length at annulus is annual variation in growth. The age – frequency histogram (Fig. 3B) suggests that 1982 and 1983 were poor years for clam recruitment. If clam recruitment were environmentally

TABLE 1. Comparison of methods for calculating production (live weight) of clams in Narrow Lake

| Age (yr) | No./m <sup>2</sup> | WT (g) | -95% CI | +95% CI | Method A |                        |  |      | Method B |                        |  |      |
|----------|--------------------|--------|---------|---------|----------|------------------------|--|------|----------|------------------------|--|------|
|          |                    |        |         |         | dWT      | B (g·m <sup>-2</sup> ) | P (g·m <sup>-2</sup> ·yr <sup>-1</sup> ) | P/B  | dWT      | B (g·m <sup>-2</sup> ) | P (g·m <sup>-2</sup> ·yr <sup>-1</sup> ) | P/B  |
| 1        | —                  | 0.008  | 0.007   | 0.009   | —        | —                      | —  | —    | —        | —                      | —  | —    |
| 2        | 3.41               | 0.25   | 0.23    | 0.27    | 0.24     | 0.85                   | 0.82                                     | 0.96 | 1.12     | 0.85                   | 3.82                                     | 4.49 |
| 3        | 0.92               | 1.37   | 1.29    | 1.45    | 1.12     | 1.26                   | 1.03                                     | 0.82 | 2.72     | 1.26                   | 2.50                                     | 1.98 |
| 4        | 0.76               | 4.09   | 3.88    | 4.54    | 2.72     | 3.11                   | 2.07                                     | 0.67 | 3.91     | 3.11                   | 5.14                                     | 1.65 |
| 5        | 3.13               | 8.00   | 7.68    | 8.33    | 3.91     | 25.05                  | 12.25                                    | 0.49 | 3.65     | 25.05                  | 11.42                                    | 0.46 |
| 6        | 1.65               | 11.65  | 11.19   | 12.12   | 3.65     | 19.22                  | 6.01                                     | 0.31 | 3.26     | 19.22                  | 5.38                                     | 0.28 |
| 7        | 1.86               | 14.91  | 14.38   | 15.46   | 3.26     | 27.73                  | 6.07                                     | 0.22 | 1.79     | 27.73                  | 3.33                                     | 0.12 |
| 8        | 1.58               | 16.70  | 16.08   | 17.35   | 1.79     | 26.39                  | 2.83                                     | 0.11 | 1.79     | 26.39                  | 2.83                                     | 0.11 |
| 9        | 0.82               | 18.49  | 17.76   | 19.24   | 1.79     | 15.16                  | 1.46                                     | 0.10 | 1.76     | 15.16                  | 1.44                                     | 0.09 |
| 10       | 0.55               | 20.25  | 19.31   | 21.22   | 1.76     | 11.14                  | 0.97                                     | 0.09 | 1.99     | 11.14                  | 1.09                                     | 0.10 |
| 11       | 0.21               | 22.24  | 19.87   | 24.90   | 1.99     | 4.67                   | 0.42                                     | 0.09 | 1.38     | 4.67                   | 0.29                                     | 0.06 |
| Total    | 14.89              |        |         |         |          | 134.58                 | 33.93                                    | 0.25 |          | 134.58                 | 37.24                                    | 0.28 |

NOTE: Method A (this study) calculates changes in weight as  $dWT = WT_n - WT_{n-1}$ ; method B (Magnin and Stanczykowska 1971) uses  $dWT = WT_{n+1} - WT_n$ . WT, mean weight at annulus; B, biomass; P, production; P/B, production:biomass ratio.

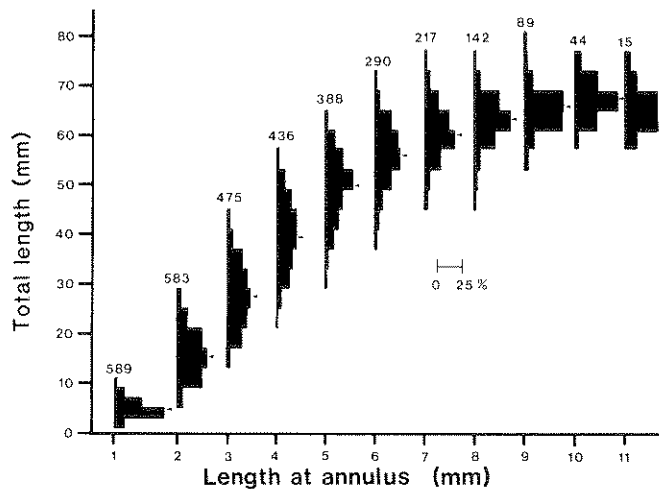


FIG. 4. Frequency distribution of length at annulus for *Anodonta grandis simpsoniana* in Narrow Lake. The 95% confidence intervals around the mean length at annulus (arrow) were too narrow to plot. The limits were 0.14 mm for age 1, 0.6–0.9 mm for ages 3–9, and 2.72 mm for age 12.

controlled, then 1982 and 1983 should have been years of poor clam growth and 1981 and 1984 should have been years of good growth. We tested this hypothesis by examining the mean increment at age for clams 1–7 years old from 1981 to 1984 (Fig. 5). For all years, the maximum growth increment occurred between 2 and 3 years of age and then declined to about 5 mm between 6 and 7 years of age. As predicted, clam growth in 1982 (ANOVA,  $F_{1, 18} = 26.5$ ;  $P < 0.001$ ) and 1983 (ANOVA,  $F_{1, 18} = 45.3$ ;  $P < 0.001$ ) was significantly slower than during 1981 and 1984, with differences as great as 4 mm/year observed. There were no significant differences in growth increments between 1981 and 1984 (ANOVA,  $F_{1, 18} = 2.6$ ;  $P < 0.001$ ). It therefore appears that between-year differences in growth can contribute significantly to the observed variation in length at annulus (Fig. 4).

We compared our method (A) of calculating production to the methods (B) of Magnin and Stanczykowska (1971) and Strayer et al. (1981) using our live weight data. The latter method yielded much higher estimates of production for clams

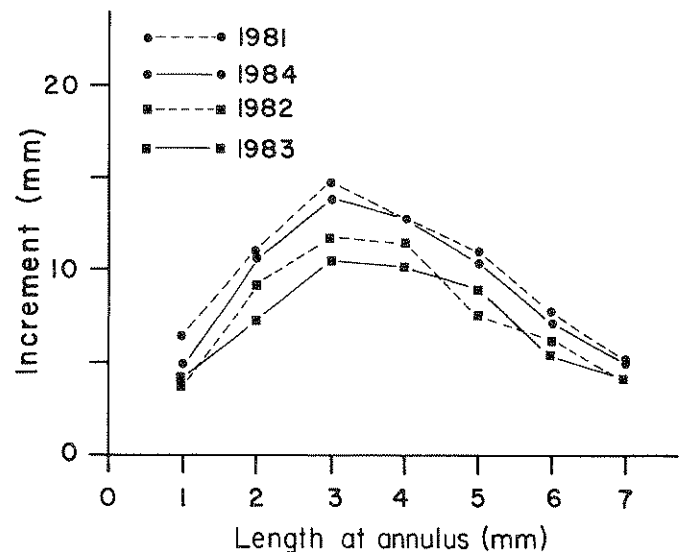


FIG. 5. Mean growth increments for *Anodonta grandis simpsoniana* of 1–7 years of age in Narrow Lake during 1981–1984. The 95% confidence intervals around each mean were too narrow to plot, ranging from 0.25 to 1.00 mm, depending on sample size (22–106 clams per observation).

aged 2–4 years and lower production for those aged 5–7 years (Table 1). Total production calculated by method B was higher by  $3.31 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  (9.8%) than estimates based on our more conservative method (A). Both methods show that the production/biomass ratio was highest for clams aged 2–4 years, that the maximum biomass was produced by clams 5 years of age, and that the production of new tissue by clams aged 8–11 years was low (about 10% per year).

*Anodonta grandis simpsoniana* in Narrow Lake produced a total of  $4.86 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  as shell,  $12.05 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-2}$  as blotted viscera, and  $1.22 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  as dry viscera (Table 2). For all three measures, the production/biomass ratio (P/B) was highest for clams aged 2–4 years and the maximum biomass was produced by 5-year-old clams. The P/B ratio at each age and the overall P/B ratio were higher for the two measures of viscera, as expected from the weight – length relationships, which showed shell weight to comprise propor-

TABLE 2. Calculation of production as shell, blotted viscera, and dry viscera for clams in Narrow Lake

| Age<br>(yr) | No./m <sup>2</sup> | Shell     |                             |   |      | Blotted viscera |                             |   |      | Dry viscera |                             |   |      |
|-------------|--------------------|-----------|-----------------------------|---|------|-----------------|-----------------------------|---|------|-------------|-----------------------------|---|------|
|             |                    | WT<br>(g) | B<br>(g · m <sup>-2</sup> ) | P<br>(g · m <sup>-2</sup> ·<br>yr <sup>-1</sup> ) | P/B  | WT<br>(g)       | B<br>(g · m <sup>-2</sup> ) | P<br>(g · m <sup>-2</sup> ·<br>yr <sup>-1</sup> ) | P/B  | WT<br>(g)   | B<br>(g · m <sup>-2</sup> ) | P<br>(g · m <sup>-2</sup> ·<br>yr <sup>-1</sup> ) | P/B  |
| 1           | —                  | —         | —                           | —   | —    | —               | —                           | —   | —    | —           | —                           | —   | —    |
| 2           | 3.41               | 0.052     | 0.18                        | 0.17  | 0.96 | 0.038           | 0.13                        | 0.13  | 0.98 | 0.004       | 0.015                       | 0.015   | 0.98 |
| 3           | 0.92               | 0.246     | 0.23                        | 0.18  | 0.79 | 0.289           | 0.27                        | 0.23  | 0.87 | 0.032       | 0.030                       | 0.026   | 0.87 |
| 4           | 0.76               | 0.670     | 0.51                        | 0.32  | 0.63 | 1.071           | 0.81                        | 0.59  | 0.73 | 0.114       | 0.087                       | 0.062   | 0.72 |
| 5           | 3.13               | 1.238     | 3.88                        | 1.78  | 0.46 | 2.388           | 7.48                        | 4.12  | 0.55 | 0.249       | 0.778                       | 0.420   | 0.54 |
| 6           | 1.65               | 1.744     | 2.88                        | 0.84  | 0.29 | 3.740           | 6.17                        | 2.22  | 0.36 | 0.384       | 0.633                       | 0.223   | 0.35 |
| 7           | 1.86               | 2.186     | 4.07                        | 0.82  | 0.20 | 5.025           | 9.35                        | 2.39  | 0.26 | 0.511       | 0.950                       | 0.236   | 0.25 |
| 8           | 1.58               | 2.426     | 3.83                        | 0.38  | 0.10 | 5.756           | 9.09                        | 1.16  | 0.13 | 0.583       | 0.921                       | 0.113   | 0.12 |
| 9           | 0.82               | 2.661     | 2.18                        | 0.19  | 0.09 | 6.497           | 5.33                        | 0.61  | 0.11 | 0.655       | 0.537                       | 0.060   | 0.11 |
| 10          | 0.55               | 2.893     | 1.59                        | 0.13  | 0.08 | 7.244           | 3.98                        | 0.41  | 0.10 | 0.728       | 0.400                       | 0.040   | 0.10 |
| 11          | 0.21               | 3.152     | 0.66                        | 0.05  | 0.08 | 8.105           | 1.70                        | 0.18  | 0.11 | 0.812       | 0.171                       | 0.017   | 0.10 |
| Total       | 14.89              |           | 19.91                       | 4.86  | 0.24 |                 | 44.31                       | 12.05   | 0.27 |             | 4.52                        | 1.21  | 0.27 |

NOTE: WT, mean weight at annulus; B, biomass; P, production; P/B, production:biomass ratio.

tionately less of the live weight as clams increased in length (Fig. 2).

### Discussion

Divers in our study were unable to collect clams <35 mm, whereas the minimum size of clams collected by dredging depended on the mesh size of the screen used to wash the sediments. It is notable that studies in which clams are collected by divers using SCUBA or by hand picking usually report an absence of small clams (e.g., Magnin and Stanczykowska 1971; Cvancara 1972; Green 1980; Strayer et al. 1981; Samad and Stanley 1986), whereas studies in which clams are collected by dredging usually report small clams to be present (e.g., Okland 1963; Negus 1966; Tudorancea 1972; Kasprzak 1986). However, small dredges (e.g., the 15 × 15 × 15 cm Ekman dredge) do not always sample the larger clams effectively (Haukioja and Hakala 1974; J. M. Hanson, personal observation). It is clearly inappropriate to collect clams only by divers using SCUBA if the goal of the study is to estimate the size and age structure of a clam population, but it is also important that a dredge be sufficiently large and heavy to collect the large clams.

*Anodonta grandis simpsoniana* was rare in the upper sublittoral zone (6–8 m) of Narrow Lake. Clams were only present in 4 of 24 samples. The mean biomass was 1.4 g/m<sup>2</sup> and the mean density was 0.9 clams/m<sup>2</sup>. The apparent mean size would be 1.6 g/clam (or a length of 28 mm). This is a statistical artifact. No clams <40 mm were collected at this depth (J. M. Hanson, unpublished data). We are currently examining the effects of water depth on the distribution and growth of clams in Narrow Lake.

*Anodonta grandis simpsoniana* dominated the biomass of the bottom fauna in Narrow Lake. The mean biomass of unionid clams on the littoral zone was 131.8 g/m<sup>2</sup> or 24.7 t. The mean biomass (live weight) of other macroinvertebrates was 27.4 g/m<sup>2</sup> or 6.42 t (J. M. Hanson, unpublished data). On a whole-lake basis, there were 24.8 t of *A. grandis simpsoniana*, which represents 69% of the total area-weighted biomass of macroinvertebrates. These results are consistent with those from studies on the River Thames (Negus 1966), Lake Borrevann (Okland 1963), and Lake Pocotopaug (Fisher

and Tevesz 1976). In Mirror Lake, however, unionid clams only comprise about 25% of the biomass of bottom fauna (Strayer et al. 1981).

Our estimates of unionid clam biomass for Narrow Lake are much lower than the maximum density of 161/m<sup>2</sup> and 9.0 kg/m<sup>2</sup> reported for one site in Lake Matikko (Haukioja and Hakala 1974). We calculated the mean unionid clam density on the littoral zone of Lake Matikko to be 41/m<sup>2</sup> or 2.1 kg/m<sup>2</sup> (Table 3). In contrast, the unionid clam densities in Mirror Lake and Lake Mikolajskie were <5% of those in Narrow Lake. Much more work is required to determine whether clam population size varies in some systematic fashion.

Individuals of *A. grandis simpsoniana* in Narrow Lake grew slowly. They only attained a mean length of 49 mm by 5 years and 69 mm by 11 years of age. In an adjacent lake, Long Lake, *A. grandis simpsoniana* attained a mean length of 70 mm by 5 and 86 mm by 11 years of age (J. M. Hanson, unpublished data). Since the two lakes are connected by a stream (about 600 m long), the two populations are unlikely to differ genetically. Green (1980) reports that specimens of *A. grandis* (almost certainly *A. grandis simpsoniana*) attain a length of 110 mm and an age of 20 years in Shell Lake, near the MacKenzie River delta. Despite being a more northern population (68°19' N), these clams grow slightly faster than clams in Narrow Lake. They attain mean lengths of 52 and 85 mm at 5 and 11 years of age, respectively. It is unclear why clam growth is markedly slower in Narrow Lake. The southern subspecies, *A. grandis grandis*, reaches a mean length of 69 mm at 5 years and 133 mm by 16 years of age in Lake Erie (McCuaig and Green 1983). Ghent et al. (1978) report wide variation in mean length of *A. grandis grandis* collected at five different depths in Bernard Lake, Ontario. These clams were 25–30 mm long at 5 years of age in the 11–12 m depth zone and 50–55 mm long at the same age in the 0.5–2.0 m depth zone. Clams older than 9 years were not reported from Bernard Lake. However, only one site was sampled and few clams were collected (*N* = 51). These comparisons of growth in length between the two subspecies are not strictly valid because the two subspecies differ in shape, *A. grandis simpsoniana* being more elongate (Clarke 1981).

We observed wide variation in length at annulus (Fig. 3) and identified significant differences in annual growth as one

TABLE 3. Comparison of density, biomass, and production estimates for unionid clams (biomass is expressed as live weight or blotted viscera weight; production and production : biomass ratios are based on blotted viscera weight)

| Waterbody                          | No./m <sup>2</sup> | LWT<br>(g·m <sup>-2</sup> ) | VWT<br>(g·m <sup>-2</sup> ) | P    | P/B  | Taxon  |
|------------------------------------|--------------------|-----------------------------|-----------------------------|------|------|--|
| Narrow L. <sup>a</sup>             | 14.9               | 131.8                       | 44.9                        | 12.1 | 0.27 | <i>Anodonta grandis simpsoniana</i>  |
| L. des Deux Montagnes <sup>b</sup> | 25.0               | —                           | 85.9                        | 16.6 | 0.20 | <i>Elliptio complanata</i> , <i>E. dilatatus</i> , <i>Lampsilis radiata</i>                      |
| Mirror L. <sup>c</sup>             | 0.03               | —                           | 0.52                        | 0.06 | 0.12 | <i>E. complanata</i>   |
| L. Pocotopaug <sup>d</sup>         | 32–60              | —                           | 33.7–70.4<br>(dry wt.)      | —    | —    | <i>E. complanata</i>   |
| R. Thames <sup>e</sup>             | 24.1               | 292.2                       | 120.8                       | 20.5 | 0.17 | <i>A. anatina</i> , <i>Unio pictorum</i> , <i>U. tumidus</i>                                     |
| L. Mikolajskie <sup>f</sup>        | 0.6                | 11.0                        | 6.6                         | 2.2  | 0.35 | <i>A. piscinalis</i> , <i>U. tumidus</i>   |
| Crapina Pool <sup>g</sup>          | 12.3               | 152.0                       | 47.6                        | 10.6 | 0.22 | <i>A. piscinalis</i> , <i>U. tumidus</i> , <i>U. pictorum</i>                                    |
| L. Borrevann <sup>h</sup>          | 19.0               | 248.2                       | —                           | —    | —    | <i>A. piscinalis</i>   |
| L. Matikko <sup>i</sup>            | 40.9               | 2110.6                      | —                           | —    | —    | <i>U. tumidus</i> , <i>U. pictorum</i> , <i>A. piscinalis</i> , <i>Pseudoanodonta complanata</i> |
| Paimionjoki R. <sup>i</sup>        | 61.4               | 1929.8                      | —                           | —    | —    | <i>U. tumidus</i> , <i>U. pictorum</i> , <i>A. piscinalis</i> , <i>P. complanata</i>             |

NOTE: LWT, live weight; VWT, blotted viscera weight; P, production; B, biomass; P/B, production:biomass ratio.

<sup>a</sup>This study.

<sup>b</sup>Magnin and Stanczykowska 1971.

<sup>c</sup>Strayer et al. 1981.

<sup>d</sup>Fisher and Tevesz 1976.

<sup>e</sup>Negus 1966.

<sup>f</sup>Lewandowski and Stanczykowska 1975.

<sup>g</sup>Tudorancea 1972.

<sup>h</sup>Okland 1963.

<sup>i</sup>Haukioja and Hakala 1974.

source of this variation (Fig. 4). The faster growth of clams in 1984 compared with 1983 corresponds with the observed differences in water temperature between the 2 years. The cumulative degree-days (>0°C) at a depth of 1 m from May 9 to August 26 were 1968 and 1853 for 1984 and 1983, respectively (E. E. Prepas, unpublished data). Negus (1966) and Haukioja and Hakala (1978) also report that clams grow faster in warm years. Factors that may affect growth within a single growing season include water depth (Ghent et al. 1978), substrate type (Haukioja and Hakala 1978; Kat 1982; Hinch et al. 1986), and clam density (Kat 1982). Unfortunately, it is usually impossible to distinguish between the effects of water temperature, clam density and substrate type in the field because clams are not evenly distributed among depths (Cvanara 1972; Haukioja and Hakala 1974; Strayer et al. 1981), and unionid clams, particularly those in the genus *Anodonta*, are capable of dispersals covering tens of metres (Van Cleave 1940; Negus 1966; Tudorancea 1972; Kat 1982). A dispersal of 10–20 m would be sufficient to move a clam from 1 to 5 m in depth (and vice versa) in most of Narrow Lake, and could minimize the effect of water depth on clam growth. Manipulative field experiments are needed to assess and separate the effects of the different factors affecting clam growth. We are currently conducting *in situ* experiments to test the effects of clam density and water depth on clam growth.

*Anodonta grandis simpsoniana* produced a minimum of 12.1 g·m<sup>-2</sup>·year<sup>-1</sup> of wet viscera weight on the littoral zone of Narrow Lake in 1985. This is substantially less than the production of unionids in the River Thames and Lac des Deux Montagnes, although the P/B ratio for Narrow Lake was higher (Table 3). Only Lake Mikolajskie has a higher P/B ratio.

A number of factors can influence production estimates. The age structure of the population is clearly important because small clams grow faster than large clams. The biomass of young clams is usually low, however, and most production occurs from 5 to 8 years of age (Magnin and Stanczykowska

1971; Lewandowski and Stanczykowska 1975; this study). Most unionid clam populations appear to be dominated (in terms of biomass) by larger animals, presumably because large clams have few predators and indeterminate growth. The variation in recruitment that we observed (Fig. 2B) is expected to affect the annual production in future years as the strong, or poor, year classes move through the most productive ages. The size of the clam population will largely determine the actual amount of biomass produced but the production rate will be controlled by all of the factors which influence clam growth. Among-year differences in water temperature appear to affect growth rates and, therefore, could affect production. For example, if we start with the same clam density and age structure as shown in Table 1 and apply the growth increments for 1–9 years of age in 1983 and 1984, we obtain different estimates of production. Clams in 1984 would have produced 36.4 g/m<sup>2</sup> (live weight) compared with 28.8 g/m<sup>2</sup> for 1983, a difference of 20%. The wide variation in published production rates (Table 3) could be due to the independent or combined effects of annual differences in water temperature, variation in clam density, effects of substrate type, and water depth. In addition, many species are represented in the summary table, and it is unknown whether species differ in how they allocate energy to growth and reproduction. Clearly, there is a need for further research into factors influencing clam production because clams represent a large mass of energy not available to fish.

Clams may have an important role in energy flow in lakes because they feed by filtering suspended material from the water. Estimates of unionid clam filtration rates are scarce. Lewandowski and Stanczykowska (1975) estimate that *Anodonta piscinalis* 60–64 mm in length filter an average of 14.3 mL·g<sup>-1</sup>·h<sup>-1</sup> (live weight; range 2.9–23.3). If we use this value, the 24.7 t of *Anodonta* on the littoral zone of Narrow Lake could filter 8447 m<sup>3</sup> of water each day. If we assume that clams filter actively over 5 months (150 days), then *Anodonta* could filter about 1 267 000 m<sup>3</sup> or 24% of the epilimnetic water

(0–5 m) in one season. This is less than the estimate of 79% for unionids in Lake Zbechy (Kasprzak 1986) but much greater than the estimates of <1% for *Elliptio complanata* in Mirror Lake (Strayer et al. 1981) and <3% for *Anodonta* in Lake Mikolajskie (Lewandowski and Stanczykowska 1975). The amount of water filtered by clams in a water body will depend on the species and size-specific filtration rates, biomass of clams, and quality of food in the water (Stanczykowska et al. 1976; Paterson 1986).

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