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Population ecology of the freshwater mussel *Anodonta grandis grandis* in a Precambrian Shield lake

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Anodonta grandis grandis is found in about half of 50 Experimental Lakes Area lakes surveyed but is abundant in only some of these lakes, including lake 377. Lake 377 is a typical small Precambrian Shield lake, 27.7 ha in area and 17.9 m in maximum depth, with $[Ca^{2+}]$ of $\simeq 2.2\ mg \cdot L^{-1}$, conductivity of $25\ \mu mho \cdot cm^{-1}$ (1 mho = 1 S), and alkalinity of $\simeq 110\ \mu equiv. \cdot L^{-1}$. The water renewal time of approximately 187 days is shorter than that of most Precambrian Shield lakes. Bottom sediments in the sublittoral zone ranged from fine sand through granules to cobbles and boulders. Several species of possible glochidial host fish including yellow perch were collected from lake 377. The size of the mussel population, estimated by depth-stratified random sampling, was 36 800 ± 12 000 (±95% confidence interval). Mean density was 0.133 mussels/m^2 lake surface, and maximum density was 4.3 mussels/m^2. Mussels were most abundant in the 1.5- to 3.1-m depth stratum. Mean lengths and weights in collections ranged from 77 to 87 mm and from 43 to 56 g, respectively. Maximum length and weight were 117.9 mm and 109.6 g, respectively. Based on external annuli, mussels live to 15+ years in lake 377. Flesh and shell averaged 25.1 and 23.2% of live weight, respectively. Calcium constituted 44.7% of the ash weight of shell. We estimated a standing dry weight biomass of mussels of $330–390\ mg \cdot m^{-2}$ and dry weight production of $60\ mg \cdot m^{-2} \cdot year^{-1}$. This is ≃0.13% of the estimated annual dry weight algal production. The shells of live mussels contain ≃2.3% of the total calcium in lake 377. Despite oligotrophic conditions and low $[Ca^{2+}]$, lake 377 supports a substantial population of *A. g. grandis* growing at a moderate rate. Lake 377 may be a favourable habitat for this species because of its short water-turnover time.

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Anodonta grandis grandis vit dans environ la moitié des 50 lacs recensés dans une zone expérimentale (Experimental Lakes Area), mais son abondance n'est considérable que dans certains de ces lacs, en particulier le lac 377. Ce lac, un petit lac typique du Bouclier précambrien, a 27,7 ha de surface, une profondeur maximale de 17,9 m, une concentration de $[Ca^{2+}]$ d'environ $2,2\ mg \cdot L^{-1}$, une conductivité de $25\ \mu mho \cdot cm^{-1}$ et une alcalinité d'environ $110\ \mu equiv. \cdot L^{-1}$. Le temps nécessaire au renouvellement complet des eaux est d'environ 187 jours, moins que dans la plupart des lacs du Bouclier. Les sédiments de la zone sublittorale contiennent du sable fin, des granules, des cailloux et de grosses pierres. Plusieurs espèces de poissons qui peuvent abriter la glochidie, y compris la Perchaude, ont été capturés dans le lac 377. L'abondance de la population de moules, estimée par un échantillonnage aléatoire stratifié en fonction de la profondeur, est de 36 800 ± 12 000 moules (intervalle de confiance de ±95%). La densité moyenne est de 0,133 moules/m^2 de surface et la densité maximale est de 4,3 moules/m^2. Les moules sont abondantes surtout dans la strate 1,5–3,1 m. Les longueurs et les masses moyennes des échantillons vont de 77 à 87 mm et de 43 à 56 g. La longueur maximale est de 117,9 mm et la masse maximale, de 109,6 g. D'après le nombre d'anneaux sur la coquille, les moules vivent jusqu'à l'âge de 15+ ans dans le lac 377. La chair constitue en moyenne 25,1% de la masse totale des moules vivantes, la coquille, 23,2%. Le calcium constitue 44,7% de la masse de cendres de la coquille. Nous avons estimé la biomasse sèche des moules à $330–390\ mg \cdot m^{-2}$ et la production annuelle (masse sèche) à $60\ mg \cdot m^{-2}$. Cette valeur représente environ 0,13% de la production annuelle estimée d'algues (masse sèche). Les coquilles des animaux vivants contiennent environ 2,3% du calcium total du lac 377. Malgré les conditions oligotrophes et le contenu faible en $[Ca^{2+}]$, le lac 377 supporte une population importante d'*A. g. grandis* à taux de croissance moyen. Le lac 377 constitue probablement un habitat favorable à l'espèce à cause de son taux de renouvellement d'eau plutôt rapide.

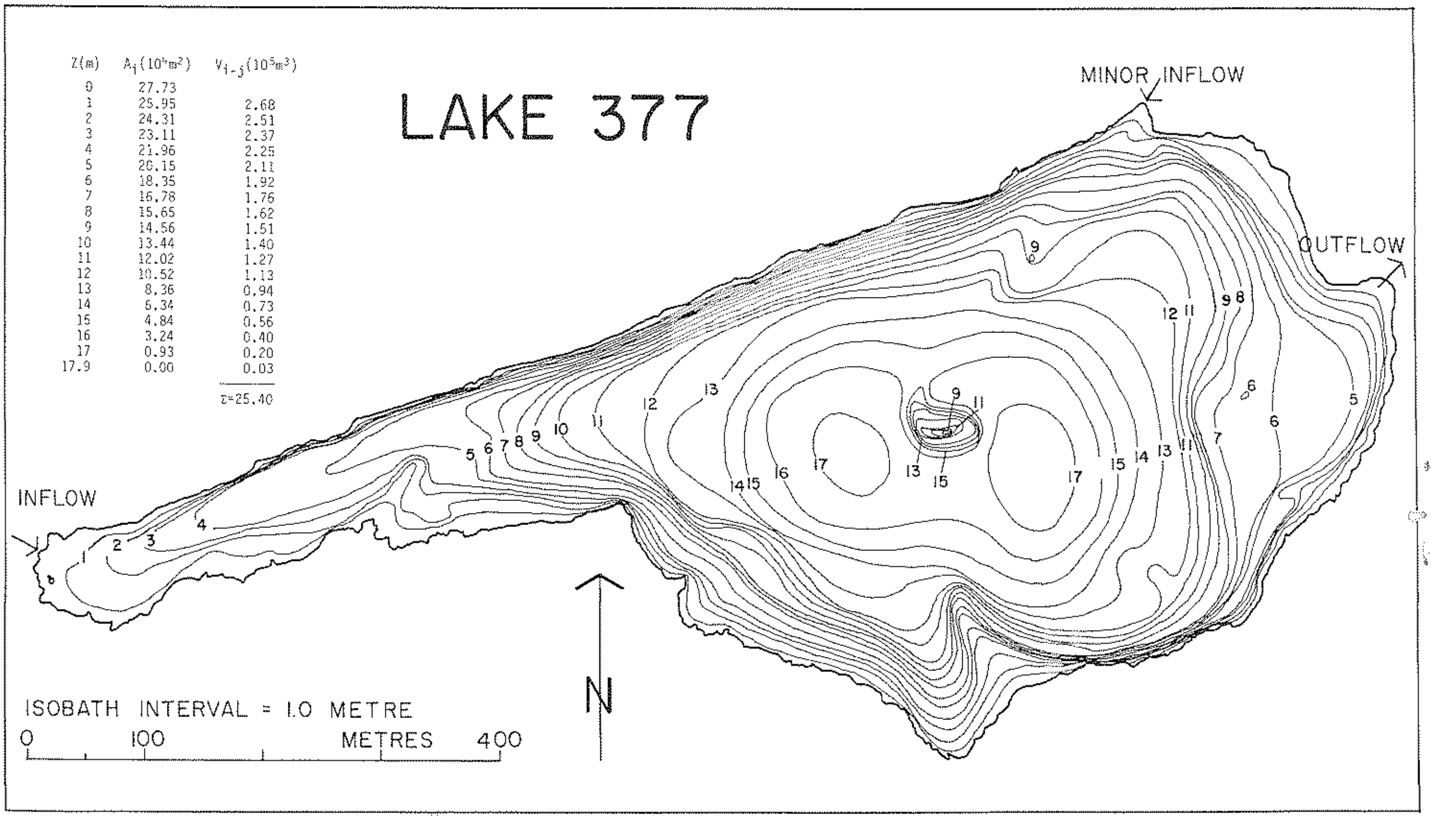
[Traduit par la revue]

Introduction

Within North America, the floater mussel *Anodonta grandis grandis* is broadly distributed throughout the Canadian interior basin from central Ontario to central Alberta, in the Great Lakes – St. Lawrence system east to near Montréal, and into the United States (Clarke 1981). It can be found in waters of widely varying ionic strength and productivity, although it prefers Precambrian Shield lakes to high-alkalinity, high-NaCl lakes (Green 1972). It occurs in permanent ponds and in lakes and rivers of various sizes (Clarke 1981).

The lakes at the Experimental Lakes Area (ELA) in northwestern Ontario are among the softest in the world in which molluscs occur. These small Precambrian Shield lakes are especially prone to acidification and contamination from metals and organic pollutants (Schindler 1988). Recently, unionid mussels have been used as indicators of environmental change at ELA, since they are acid sensitive (Okland and Okland 1986; Eilers et al. 1984; Malley et al. 1988) and accumulate metals (Hinch and Stephenson 1987; Green et al. 1986; Carell et al. 1987; Malley et al. 1989) and organic contaminants (Pugsley et al. 1985). Little is known of the ecological roles of unionid mussels in the soft-water, low-productivity aquatic ecosystems at ELA.

This study describes the population ecology of *A. g. grandis* in a representative lake where it maintains a relatively large population. We describe population size, abundance, depth distribution, length–weight and length–age distributions, standing biomass, and annual production. Sediment characteristics,



Z(m)	$A_i(10^4 m^2)$	$V_{i-j}(10^5 m^3)$
0	27.73	
1	25.95	2.68
2	24.31	2.51
3	23.11	2.37
4	21.96	2.25
5	20.15	2.11
6	18.35	1.92
7	16.78	1.76
8	15.65	1.62
9	14.56	1.51
10	13.44	1.40
11	12.02	1.27
12	10.52	1.13
13	8.36	0.94
14	6.34	0.73
15	4.84	0.56
16	3.24	0.40
17	0.93	0.20
17.9	0.00	0.03
		Σ=25.40

FIG. 1. Bathymetric map of lake 377, reproduced from Campbell et al. (1990).

water chemistry, and lake water renewal time are also described. Lastly, we compare annual mussel production with annual primary production of the lake and estimate the proportion of the lake's total calcium bound up in this population.

Materials and methods

Site, water chemistry, and hydrology of lake 377

The Experimental Lakes Area is underlain by Precambrian acid granites thinly covered in some areas by glacial drift composed largely of sands and gravels. Principal vegetation in the area is jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) (Brunskill and Schindler 1971). Lake 377 is situated within ELA at longitude 93°48′W and latitude 49°43′N. The lake has a surface area of 27.73 ha, a watershed area of 83.87 ha, and a total drainage basin area of 2030 ha (G. McCullough, Freshwater Institute, unpublished data). Its volume is 25.40×10^5 m^3 (Fig. 1). Lake 377 has two inlet streams, at the northeast and west ends of the lake, and one outlet at the east end of the lake (Fig. 1). Cleugh and Hauser (1971) reported that lake 377 has a Secchi disc visibility of 4.5 m, total dissolved solids of 10 mg·L^{-1}, and conductivity of 23 μmho·cm^{-1} (1 mho = 1 S) at 25°C.

Samples of epilimnetic water had been taken for water chemistry during three helicopter surveys during 1982. For the present study, the epilimnion and hypolimnion were sampled on 27 June and 25 July 1984, using a Van Dorn water sampler at 0 and 11 m, respectively. On 4 September 1985, only epilimnetic water was sampled. Water analyses were performed at ELA or at the Freshwater Institute analytical laboratory, using methods described by Stainton et al. (1977).

Average annual renewal time was calculated from the total drainage basin area (2030 ha), lake volume, and mean annual precipitation of 70 cm, using the method of Newbury and Beaty (1980). Stream velocity and volume of both inlet and outlet streams were measured on 15 June 1984. Measurements of flow rate were taken across the streams by means of an Ott type C-1 small current meter. Values were converted to mean velocity with the use of standard stream-metering calculations, to obtain a single direct estimate of lake water renewal time.

Sampling and analysis of sediments

Sediments of lake 377 were sampled by SCUBA divers on 25 June 1984 (Fig. 2). Twenty-six cores were obtained by inserting a Plexiglas tube (8 cm diameter × 30 cm height) into the sediment to a depth of ≥10 cm where substrate type permitted. The upper end of the tube was sealed with a rubber stopper. The tube was then removed from the sediment and the lower end sealed with a stopper to prevent loss of sediment. Cores were taken in pairs within 30 cm of each other. An attempt was made to sample representative bottom types over a range of depths in areas with and without mussels.

Sediments were dried at 150°C for 24 h, then weighed to the nearest 0.1 g. For cores longer than 10 cm, only the upper 10 cm was analyzed. For cores shorter than 10 cm, the entire core was analyzed. A Taylor horizontal and vertical shaker with sieves of Taylor standard sieve numbers of 4 (4.76 mm opening), 10 (2.00 mm), 18 (1.00 mm), 35 (0.500 mm), 60 (0.250 mm), 120 (0.125 mm), and 200 (0.075 mm) was used to size-fractionate each sample. A grain-size distribution diagram was prepared for each sediment sample, expressing cumulative percent finer by weight as a function of grain size in millimetres. For each sediment sample, five parameters were calculated as defined by Inman (1952). The use of these five parameters allows one to compute five significant points on the grain size distribution diagram. These are mean diameter in phi (ϕ) units, ϕ standard deviation (sorting), kurtosis (peakedness), ϕ skewness measure, and second ϕ skewness measure.

The ϕ diameter is the negative logarithm to the base 2 of the particle diameter in millimetres. Phi–millimetre equivalents are given by Inman (1952): −1.0 on the ϕ scale, the division between very coarse sand and granules, is equivalent to 2.00 mm; 0 ϕ units, the division

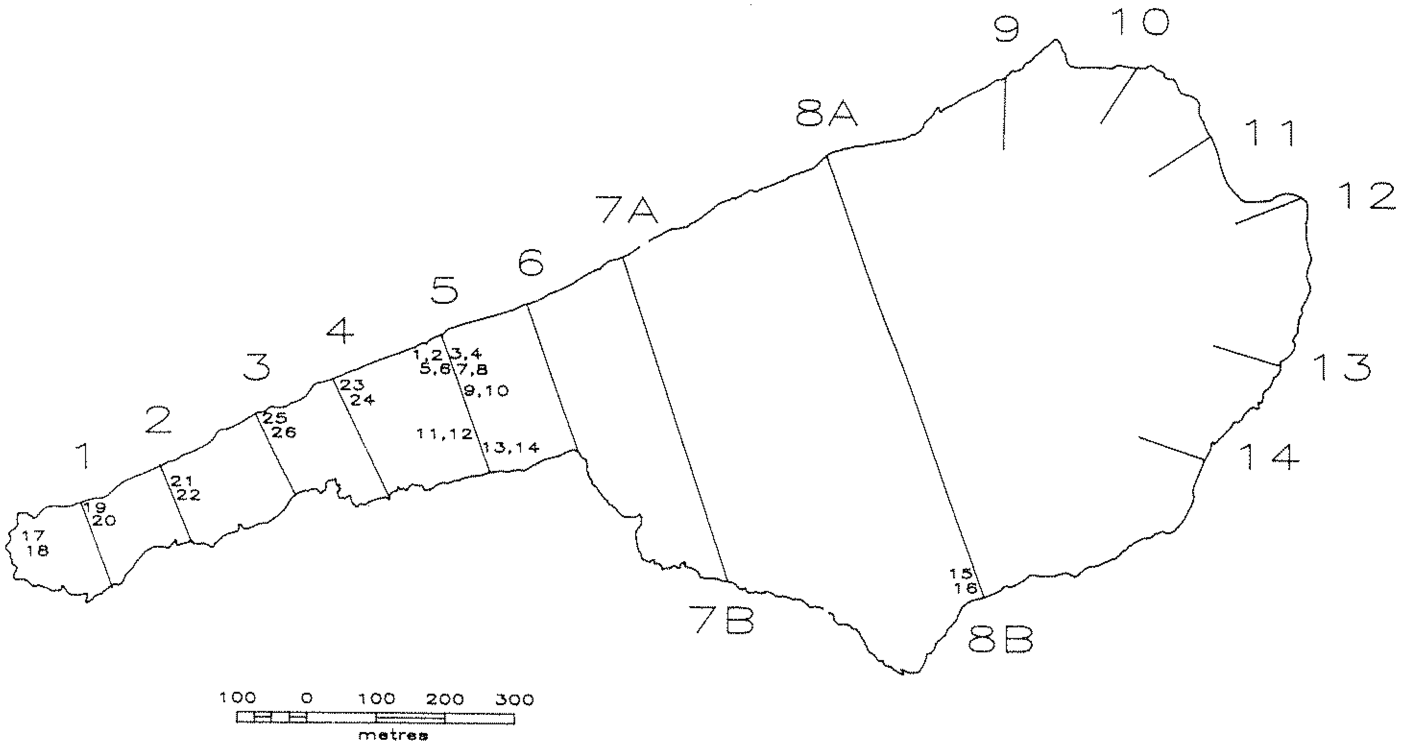


FIG. 2. Outline of lake 377, showing 14 line transects (numbers outside lake outline) used for population estimate of mussels and 26 sites where sediments were sampled (numbers inside lake outline).

between coarse sand and very coarse sand, is equivalent to 1.00 mm; 1.0 ϕ units is equivalent to 0.5 mm; and 2.5 ϕ units (fine sand) is equivalent to 0.177 mm.

Mussel population estimate in lake 377

Sampling was done using SCUBA during a 3-week period in June 1984, according to a method devised by I. J. Davies (Freshwater Institute, personal communication). Sixteen transects were set up to sample all possible substrates (Fig. 2). Each transect line consisted of a 5-mm nylon rope anchored to the shore, with lead weights, one every 5 m along the rope, to serve as both weights and markers. One diver, using a metre stick attached to a writing tablet, counted all the mussels within 50 cm of each side of the line and recorded the substrate type and vegetation in each depth stratum. The second diver informed the first of the boundaries of the depth strata. Depth information was provided by a calibrated digital gauge worn by a diver. Strata were sampled along a 10 × 1 m segment perpendicular to the shoreline, resulting in a sample area of 10 m^2 per stratum. There were five depth strata for each transect, 0–1.6, 1.6–3.1, 3.1–4.7, 4.7–6.1, and 6.1–7.6 m. In areas where the bottom gradient was too steep to sample 10 m perpendicular to the shore, a 10-m nylon rope was set out parallel to the shore in the appropriate depth stratum.

Population estimates were made using stratified random sampling methods (Elliott 1971; Prepas 1984) and weighted degrees of freedom, as in the method of Sampford (1962), to reduce the variance per stratum. The mean number of mussels and standard error of the mean were calculated for each transect. Then the total number of mussels and standard error were calculated for each stratum and for the combined strata, using weighted degrees of freedom.

For clarity, the calculation method of Sampford (1962) is summarized below. The total number of mussels is

$$[1]\quad x = \sum_{0}^{i} y_i \cdot g_i$$

where x is the total number of mussels in the lake, i is the number of strata, y_i is the sample total (total number of organisms encountered in all the n_i sampling units), and g_i is the raising factor ($g_i = 1/f_i$, where f_i is the fraction sampled, and is defined by n_i/N_i, with n_i being the number of sampling units counted in the ith stratum, and N_i the total potential number of sampling units in the ith stratum).

The 95% confidence interval (CI) around the total number of mussels in the lake is given by

$$[2]\quad (x \pm t)\cdot\sqrt{\sum_{0}^{i}\frac{(N_i^2\cdot S_{y_i}^2\cdot(1-f_i)}{n_i}}$$

where $S_{y_i}^2$ is the sample variance computed from raw counts in the n_i sampling units in the ith stratum, and t is Student's t for the effective degrees of freedom.

The effective degrees of freedom are given by

$$[3]\quad \frac{1}{\sum_{0}^{i}\frac{(L_i^2)}{\mathrm{df}}}$$

where

$$L_i = \frac{\dfrac{N_i^2\cdot S_{y_i}^2\cdot(1-f_i)}{n_i}}{\sum_{0}^{i}\dfrac{N_i^2\cdot S_{y_i}^2\cdot(1-f_i)}{n_i}}$$

Morphometrics, age, and dry and ash weights

Two hundred and three mussels were collected from lake 377 by SCUBA divers on 13, 14, and 20 June 1984 between 1 and 3 m depth in the shallower west bay of the lake. All individuals seen were collected. On 5 September 1985, an additional 61 mussels were collected in the same manner at the east end of lake 377 near the outlet stream.

A third collection of mussels for physiological study was made on 13 and 25 July 1985 by snorkelling in about 1.5 m water depth in the west bay. On this date, 162 of the largest individuals seen were selected.

TABLE 1. Chemical composition of the epilimnion and hypolimnion of ELA lake 377

	Epilimnion			Hypolimnion	
	Mean	Range	N	Range	N
Na^{+} (mg·L^{-1})	1.20	1.04–1.52	5	—	—
K^{+} (mg·L^{-1})	0.50	0.48–0.54	5	—	—
Ca^{2+} (mg·L^{-1})	2.26	2.16–2.50	5	—	—
Mg^{2+} (mg·L^{-1})	0.60	0.57–0.64	5	—	—
Fe (mg·L^{-1})	0.037	0.03–0.04	4	—	—
Mn (mg·L^{-1})	—	<0.01–0.03	4	—	—
Cl^{-} (mg·L^{-1})	0.5	0.2–0.7	5	—	—
SO$_4^{2-}$ (mg·L^{-1})	3.48	3.0–3.8	5	—	—
Suspended P (μg·L^{-1})	2.8	2–5	4	—	—
TDP (μg·L^{-1})	2.75	1–4	4	11–27	2
Suspended N (μg·L^{-1})	51	23–114	4	—	—
TDN (μg·L^{-1})	227	177–274	5	208–307	2
Suspended C (μg·L^{-1})	440	270–850	4	—	—
SRSi (mg·L^{-1})	0.90	0.79–0.97	3	—	—
DOC (μequiv.·L^{-1})	693	500–1200	4	—	—
pH	—	6.90–7.09	5	6.24–6.35	2
Alkalinity (μequiv.·L^{-1})	109	104–113	3	—	—
Chlorophyll *a* (μg·L^{-1})	1.7	0.1–2.5	4	0.2	1
DIC (μmol·L^{-1})	96	40–122	5	97–204	2
Conductivity (μmho·cm^{-1} at 25°C)	28	25–34	3	27–35	2

NOTE: The epilimnion was sampled on six occasions: 8 July, 17 August, and 29 September 1982, 27 June and 25 July 1984, and 4 September 1985. The hypolimnion was sampled twice: on 27 June and 25 July 1984. Data for 1982 were supplied by G. Linsey. TDP, total dissolved phosphorus; TDN, total dissolved nitrogen; SRSi, soluble reactive silicon; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon.

In the laboratory, mussels were cleaned with a plastic scrub pad to remove adhering algae, blotted with paper towel, and weighed to the nearest 0.01 g. Length was measured along the longest anterior–posterior axis of the animal. Height was measured dorsoventrally, perpendicular to the anterior–posterior axis at the umbo. Width was the side-to-side measurement perpendicular to the anterior–posterior axis at the widest part of the mussel. In addition, the length of the valve at each identifiable growth ring was measured. All measurements were made with vernier calipers to the nearest 0.1 mm.

Mussels were aged by counting the complete rings visible on the outside of the shells. These are generally considered to be annual rings (Negus 1966; Ghent et al. 1978; Haukioja and Hakala 1978; McCuaig and Green 1983).

Fifteen mussels collected on 23 July 1983 from the west bay of lake 377 were weighed, measured, and dissected. The mussels were opened by cutting the adductor muscles. The flesh was removed from the valves, blotted with paper towels, and placed on preweighed aluminum foil dishes for drying. The valves were separated by cutting the ligament. The valves and body were dried to constant weight at 80°C, the valves for 20 h and the body for 43 h. Weights were measured to the nearest milligram. Valves were ashed at 550°C in a muffle furnace for 20–24 h. Ashed samples were weighed to the nearest milligram, then dissolved in 12 M HCl and diluted to a final volume of 25 or 100 mL with deionized water. These samples were analyzed for Ca^{2+}, Na^{+}, K^{+}, and Mg^{2+} by atomic absorption spectrophotometry at the Freshwater Institute analytical laboratory (Stainton et al. 1977).

Anodonta *biomass, production estimates, and role as a calcium store*

Total live and shell-less dry weight biomass of *A. g. grandis* in lake 377 were estimated by apportioning the total population size across 20 weight categories (Fig. 3B). The mussels in each category were assumed to have a live weight equivalent to the midpoint of the category, and shell-less dry weight as a proportion of live weight as determined from the drying of shell-less bodies. Dry weight biomass, including the organic component of shell, and annual production were estimated according to the method of Magnin and Stanczykowska (1977). The age distribution was estimated from the decline in numbers with increasing age shown in Table 5 and apportioned to the total population estimated to be present in lake 377. Mean live weight at each age was calculated from the mean length at each age shown in Table 5 by means of the weight–length relationships for 1984 from Table 4. The mean dry weight per individual was determined by drying and weighing shell-less bodies. To this was added the proportion of live weight contributed by organic matter in the shell.

The total amount of Ca^{2+} in the lake sequestered in shells of live *Anodonta* was estimated by apportioning the total population size across 20 weight categories (Fig. 3B). The weight of Ca^{2+} in the shell in each category was calculated from the percentage of Ca^{2+} in shell, determined from ashed shells. The sum of these weights was compared with estimated total dissolved Ca^{2+} in the lake.

Results

Water chemistry and preliminary hydrology of lake 377

Water chemistry of lake 377 (Table 1) is typical of small unmanipulated Precambrian Shield lakes at ELA (Prokopowich 1979). The [Ca^{2+}] of about 2.2 mg·L^{-1}, conductivity of 25 μmho·cm^{-1}, and alkalinity of 110 μequiv.·L^{-1} place this lake among the most dilute in the world (Armstrong and Schindler 1971).

The estimate of water renewal time was 195% per year, or 187 days. This was calculated from the general nomogram of Newbury and Beaty (1980), using a total drainage basin area of 2030 ha, lake volume of 254.0 × 10^{4} m^{3}, and mean annual precipitation of 70 cm. Water flow into the lake on 15 June 1984 was 0.0228 m^{3}·s^{-1} at the northeast inlet and 0.242 m^{3}·s^{-1} at the northwest inlet (i.e., two culverts). Water outflow measured at the east end of the lake was 0.415 m^{3}·s^{-1}. Recognizing that measurements at a single point in time are influenced by immediate past precipitation history and are, therefore, very rough, we estimated lake water renewal time from the inflow and outflow values. If the inflows represented mean annual flow through the lake, lake water renewal time would be (254 × 10^{4} m^{3})/(0.2648 m^{3}·s^{-1}), or 111.0 d. Lake water renewal time, similarly estimated from the outflow values, was 70.7 d. A very

TABLE 2. Description of sediment sampled at 26 sites in lake 377

Sample No.	Water depth (m)	Sediment surface	Length of core (m)	Graphic mean particle size (φ units)	Sorting (inclusive graphic standard deviation)	Kurtosis	φ skewness measure	Second φ skewness measure	Occurrence of mussels
1	1.5	Coarse sand, silt, and floc; vegetation	5.0	Too much organic matter to permit analysis					Absent
2			9.5	−1.32	−3.01	0.27	−0.03	0.04	
3	2.75	Coarse sand, floc, cobbles 8–18 cm in diameter	9.2	−0.91	−2.55	0.36	−0.13	0.02	Present
4			10.0	0.57	−3.27	0.24	−0.03	−0.02	
5	3	Fine sand	8.5	1.51	−1.44	0.44	−0.20	0.15	Absent
6			8.6	2.11	−0.89	1.88	−0.24	0.20	
7	5.2	Floc	9.5	0.57	−1.83	0.52	−0.08	−0.05	Absent
8			10.0	0.74	−1.42	0.76	−0.17	−0.10	
9	6.1	Floc above coarse sand	10.0	0.61	−3.04	0.24	−0.15	−0.21	Absent
10			8.0	−0.29	−2.76	0.37	−0.16	−0.10	
11	4.4	Coarse sand, cobbles	8.7	0.47	−2.47	0.52	−0.49	0.66	Present
12			10.0	1.04	−2.60	0.51	−0.46	0.73	
13	1.8	Coarse sand, boulders >0.3 m	9.6	−1.54	−2.28	0.39	−0.07	−0.02	Present
14			9.2	−0.40	−1.65	0.41	−0.01	−0.21	
15	0.6	Silt, vegetation	8.2	Too much organic matter to permit analysis					Absent
16			7.2						
17	0.75	Coarse sand, cobbles	4.8	2.38	1.16	1.03	−0.22	−0.67	Present
18			9.4	2.15	−0.97	1.20	−0.26	−0.54	
19	1.1	Boulders, thin layer of coarse sand over bedrock	7.3	Too much organic matter to permit analysis					Present
20			5.5						
21	2.4	Coarse sand, boulders >0.6 m	10.0	1.28	−1.66	0.56	−0.05	−0.14	Present
22			8.7	0.38	−1.52	0.79	−0.02	0.18	
23	3.05	Coarse sand	7.8	1.23	−1.37	0.65	−0.24	−0.25	Present
24			9.3	0.94	−1.62	0.56	−0.30	−0.56	
25	2.1	Fine sand, cobbles 8–30 cm	5.0	−0.85	−2.97	0.24	−0.14	−0.07	Present
26			4.9	0.16	−1.79	0.49	−0.08	−0.12	

NOTE: Sample numbers correspond to locations shown in Fig. 2.

small proportion of the flowthrough occurs during the ice-on season, thus if these estimates are applied to two-thirds of the year, the annual water renewal times become 166.5 and 106.2 d, respectively. The direct and indirect measurements of water renewal time are, thus, in general agreement.

Although lakes at ELA of similar size to lake 377 have water turnover times ranging from a few weeks to 12 years, this lake turns over more rapidly than most other lakes at ELA.

Bottom sediments of lake 377

On the Wentworth size scale, the sediments sampled at 26 locations in lake 377 ranged between granules (−1.2 φ units) and fine sand (2.5–3.0 φ units) (Table 2). There was some variability in graphic mean particle size between members of the pairs of cores. There was no obvious relationship between presence or absence of mussels and sediment particle size (Table 2).

Density and distribution of mussels in lake 377

The depth-stratified random sampling method gave a total population estimate of mussels in lake 377 of 36 800 ± 12 000 (95% CI). Whole lake mean density was 0.133 mussels/m^2 lake surface. Mussels were found distributed around the lake but were most abundant in the 1.5- to 3.1-m depth stratum, reaching a maximum density of 4.3 individuals/m^2 at this depth on transect 3 (Table 3). Density calculated for the 0- to 5-m depth stratum was 0.49 mussels/m^2.

The greatest densities of mussels were found associated with coarse sandy substrates (1.08 individuals/m^2 at 1.5–3.1 m; 0.44 individuals/m^2 at 3.1–4.7 m), with most of the remaining mussels found in areas with small rocks (cobbles) (0.93 individuals/m^2 at 1.5–3.1 m; 0.22 individuals/m^2 at 3.1–4.7 m; Table 3). There is little vegetation in lake 377. Mussels were not observed in the areas where macrophytes were present. Overall, mussels were most abundant in the shallow bay in the western part of the lake and near the outflow at the eastern end of the lake. With the exception of transect 9, mussels were not found at depths below 4.7 m, regardless of substrate type. In areas between transects, mussels were collected at depths as shallow as 0.7 m on nonrocky substrates.

Morphometrics and age of mussels

The 203 mussels collected from the west bay in June 1984 were 34.9–109 mm long, with most animals between 65 and 95 mm long (Fig. 3A, Table 4). Shells of many of the mussels were partially devoid of periostracum, and some were eroded to the point of perforation, especially in the region of the umbo. Mean length, height, width, and weight and their relationships are given in Table 4. Most of the mussels weighed less than 65 g (Fig. 3B).

TABLE 3. Qualitative surface sediment type and density of mussels (individuals/m^2) along 14 transects in lake 377

	Depth stratum (m)					
Transect	0–1.5*	1.5–3.1	3.1–4.7	4.7–6.1	6.1–7.6	>7.6
1	B	C, F, 0.3	—	—	—	—
2	B	C, 0.63	—	—	—	—
3	B	C, 4.3	F, 0.3	—	—	—
4	B	C, 0.9	C, 0.1	—	—	—
5	B	C, 1.1	F, 0.1	—	—	—
6	B	B, 0	R, 0	R, 0	—	—
7A	B	B, 0	R, 0.1	R, 0	0	—
7B	B	R, C, 0.5	R, 0.4	C, 0	0	—
8A	B	C, 0.7	R, 0.4	R, 0	0	0
8B	B	C, 0.9	C, 0.1	C, 0	0	0
9	B	C, 0.15	C, 0.4	C, 0.1	—	—
10	B	C, 0.9	C, 0.6	C, 0	—	—
11	B	C, R, 0.35	C, 0.4	C, 0	C, 0	—
12	B	R, C, 1.75	C, R, 0.73	C, 0	—	—
13	B	C, R, 1.9	R, 0.7	C, 0	—	—
14	B	Cliff	R, B, 0.1	C, 0	R, C, 0	—

NOTE: B, boulders; C, coarse sand; F, fine sand; R, rocks (cobbles).
*There were no mussels at any station.

TABLE 4. Morphometrics of *A. g. grandis* collected from lake 377

	West bay, June 1984	West bay, July 1985	East end, Sept. 1985	*P*
N	203	162	61	
Length (mm)	77.3±1.1 (34.9–109.5)	87.1±0.7 (62.1–108.5)	84.5±2.2 (48.0–117.9)	
Height (mm)	41.3±0.6 (19.8–56.2)	45.2±0.4 (30.6–57.6)	44.7±1.1 (25.9–59.4)	
Width (mm)	26.6±0.4 (11.2–38.0)	29.3±0.3 (20.1–37.3)	29.6±0.7 (16.7–41.2)	
Weight (g)	43.4±1.5 (3.74–98.1)	54.6±1.2 (18.5–92.2)	56.1±3.4 (10.1–109.6)	
Regression				
Log weight (*Y*) vs. log length (*X*)	$Y = -3.78 + 2.85X$, $r^2 = 0.98$	$Y = -3.40 + 2.64X$, $r^2 = 0.94$	$Y = -3.43 + 2.67X$, $r^2 = 0.98$	<0.001
Log height vs. log length	$Y = -0.09 + 0.90X$, $r^2 = 0.90$	$Y = -0.09 + 0.90X$, $r^2 = 0.98$	$Y = -0.15 + 0.93X$, $r^2 = 0.95$	0.700
Log width vs. log length	$Y = -0.43 + 0.98X$, $r^2 = 0.91$	$Y = -0.20 + 0.86X$, $r^2 = 0.69$	$Y = -0.15 + 0.84X$, $r^2 = 0.90$	0.0014

NOTE: Values are given as mean ± SE, with range in parentheses. *P* is the probability that the regression coefficients are not different.

Measurements from the 61 mussels collected in 1985 from the east end of the lake near the outflow are summarized in Figs. 3C and 3D and Table 4. Mussels in this collection were significantly ($P < 0.05$) longer, higher, wider, and heavier than those from the 1984 west bay collection. The weight–length and width–length relationships were significantly different in slope (Table 4).

The weight–length and height–length relationships for 162 mussels collected in 1985 from the west bay were virtually identical to those of the east end mussels (Table 4). Although the slopes of the width–length relationships were not different, the east end mussels were slightly wider than the west bay mussels. There were differences in the morphometric relationships between the 1984 and 1985 west bay collections, but these may be due to the smaller mean lengths in the 1984 collection rather than to real year-to-year differences.

The smallest mussels observed in these collections in 1983, 1984, and summer 1985 were about 3 years old. It was not until September 1985 that mussels in their first and second years were collected. Three mussels in their first year (mean 14.2 ± 0.7 (SE) mm long, 7.9 ± 0.4 mm high, and 4.6 ± 0.3 mm deep), and three mussels in their second year (19.6 ± 1.7 mm long, 12.7 ± 2.3 mm high, and 6.5 ± 0.6 mm deep) were collected. The juveniles were collected among older mussels near the outflow to lake 377. Even though several cubic metres of sediment from the west bay was sieved in the fall of 1987 through a 5-mm^2 mesh, no young mussels were obtained.

Up to 14 annual growth rings could be discerned in some

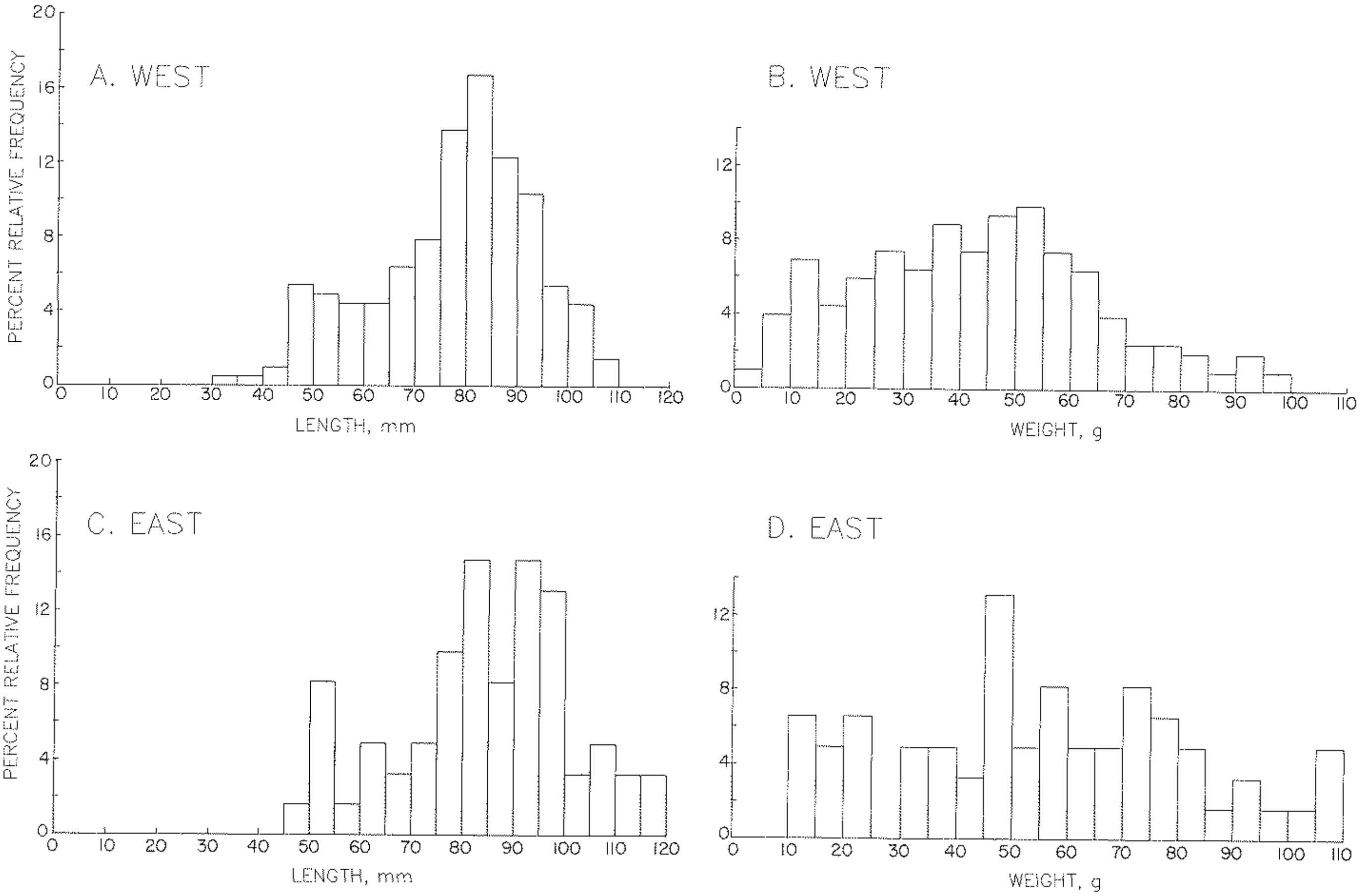


FIG. 3. Frequency distributions of length and weight for 203 specimens of *A. g. grandis* collected in the west end of lake 377 in 1984 (A and B) and for 61 specimens collected in the east end in 1985 (C and D).

TABLE 5. Lengths of annual growth rings in 47 *A. g. grandis* from lake 377 in July 1985

Year growth	No. of measurements	Length (mm)	
		Mean ± SE	Range
1*	31	20.1±0.6	15.3–29.7
2*	45	30.8±0.7	22.1–43.1
3	47	40.9±0.9	28.8–56.9
4	46	50.3±1.1	35.4–67.9
5	46	59.9±1.1	38.6–74.0
6	41	67.1±1.2	47.9–80.7
7	39	73.7±1.1	54.9–88.1
8	34	79.7±1.2	59.6–93.3
9	26	83.8±1.2	68.0–95.7
10	15	87.4±1.8	73.6–98.7
11	5	90.0±2.1	84.6–95.8
12	3	92.3±3.3	89.0–98.9
13	2	96.5±5.0	91.5–101.5
14	1	103.9	—

*These rings could not be measured in some individuals because of shell erosion.

individuals from the west bay of lake 377 (Table 5). In most larger individuals the last annual rings could not be distinguished from one another by our method. Therefore, it is likely that mussels in lake 377 can live for at least 15 years. There was a great deal of overlap between the ranges of lengths of adjacent annuli. For example, a mussel 60 mm long may have been 4, 5, 6, 7, or 8 years old. Thus, growth rate among mussels was highly variable, and length is not a reliable measure of age. Most of the mussels removed from the lake were found to be 9–10 years old. This is reflected in Table 5: there are few mussels with more than 10 annuli.

Anodonta *standing biomass, production, and role as a calcium store*

Assuming a total population size of 36 800 mussels in lake 377, with a distribution of live weights as shown in Fig. 3B, standing live biomass is estimated to be 1587.6 kg for the lake, 5.73 $g \cdot m^{-2}$ over the whole lake surface and 20.94 $g \cdot m^{-2}$ in the 0- to 5-m depth stratum. Of this, 410.4 kg (1.48 $g \cdot m^{-2}$ for the whole lake; 5.41 $g \cdot m^{-2}$ in the 0- to 5-m stratum) was flesh and 368.3 kg (1.33 $g \cdot m^{-2}$ for the whole lake; 4.86 $g \cdot m^{-2}$ in the 0- to 5-m stratum) was shell.

Dry weight biomass was calculated from determinations on 15 mussels collected from the west bay on 23 July 1893. Mean live weights and lengths of the 15 mussels were 88.06 ± 1.48 (SE) mm and 55.30 ± 2.48 g, respectively. Upon dissection the flesh weighed 13.88 ± 0.54 g (25.1% of live weight) and the shell weighed 12.92 ± 0.77 g (23.2% of live weight). The weight lost upon dissection (51.7%) was largely water from the mantle cavity. Within the size range of the 15 mussels (75.25–97.75 mm), dry weight / wet weight did not vary as a function of body size, as shown by analysis of covariance of log-transformed live weight and flesh dry weight against length (probability of difference between regression coefficients, $P = 0.35$, not significant). Shell-less dry weight biomass of *A. g.*

TABLE 6. Estimates of biomass and annual production of *A. g. grandis* in lake 377

Age (years)	No./m^2	Mean dry weight/ individual (mg)	Dry weight/ individual per annum (mg)	Biomass, B ($mg \cdot m^{-2}$)	Production, P ($mg \cdot m^{-2} \cdot year^{-1}$)	P/B
4	0.0029	677	437	1.99	1.28	0.643
5	0.0117	1114	425	13.07	4.99	0.382
6	0.0059	1539	472	9.03	2.77	0.307
7	0.0117	2011	502	23.60	5.90	0.250
8	0.0176	2513	386	44.25	6.80	0.154
9	0.0352	2899	369	102.11	13.00	0.127
10	0.0235	3269	285	76.74	6.69	0.087
11	0.0088	3553	265	31.29	2.33	0.075
12	0.0088	3818	516	33.62	4.55	0.135
13	0.0088	4335	1016	38.16	8.95	0.235
14	0.0029	5351	1016	15.70	2.98	0.190
Total				389.56	60.24	
Mean						0.155

grandis, therefore, was estimated to be 40.5 kg for the lake or 146 $mg \cdot m^{-2}$ for the whole lake surface.

Shell dry weight in the 15 mussels averaged 12.06 ± 0.72 g, or 93.4 ± 0.4% of their wet weight. Dry weight biomass of shell of live mussels in the lake was estimated as 344 kg (1.24 $g \cdot m^{-2}$ of lake surface). Shell ash weight was 10.28 ± 0.53 g, or 85.2% of shell dry weight. Conversely, organic content (loss on ignition) of shell was 14.8% of its dry weight or 50.9 kg for the lake (184 $mg \cdot m^{-2}$).

We extrapolated from the proportions of ages seen in 47 mussels (Table 5) to calculate the number per square metre in each age group and converted the mean length in each age group to weight. This gave a standing dry biomass of 390 $mg \cdot m^{-2}$ (Table 6). This is close to the sum of the standing dry biomass of flesh and organic component of shell, 330 $mg \cdot m^{-2}$, calculated from the size rather than the age distribution. Production of the mussels for the whole lake was estimated to be 60 $mg \cdot m^{-2} \cdot year^{-1}$ (Table 6), or 219 $mg \cdot m^{-2}$ for the 0- to 5-m depth stratum. The production/biomass (P/B) ratio was highest in the youngest mussels, lowest for age 11 years, and then rose with age. One gram of dry weight biomass was produced from 1.55–13.41 g of standing dry biomass, depending upon the age of the mussel.

Mean daily phytoplankton primary production in the euphotic zone of lake 377 was 190 $mg\,C \cdot m^{-2}$ for 1987, based on measurements conducted from 1 May through 31 August 1987. A nearby lake, lake 373, exhibiting productivity values similar to those in lake 377 in 1987, was used to estimate mean annual production in lake 377 because of its longer-term primary productivity record. Mean values for daily productivity in lake 373 were 143, 104, 190, and 207 $mg\,C \cdot m^{-2}$, in 1987, 1986, 1985, and 1984, respectively. The actual total annual ice-free season productivity values in lake 373 were 24.1, 15.0, 26.8, and 29.0 $g\,C \cdot m^{-2}$, respectively, for those years (E. DeBruyn, Freshwater Institute, unpublished data). We assume that the mean production of 23.7 $g\,C \cdot m^{-2} \cdot year^{-1}$ measured in lake 373 is a good estimate for lake 377. Approximately 50% of the dry weight of algae is carbon (P. Healey, Freshwater Institute, personal communication). Therefore, the estimated mean annual primary production of 23.7 $g\,C \cdot m^{-2}$ yields 47.5 $g \cdot m^{-2}$ dry algal biomass. Dry weight annual production of *A. g. grandis* of 60 $mg \cdot m^{-2} \cdot year^{-1}$ is thus calculated to be 0.13% of the estimated algal dry weight annual production in lake 377.

Ashed shells were 44.68 ± 0.80% Ca^{2+}, 0.213 ± 0.003% Na^+, 0.0025 ± 0.0001% Mg^{2+}, and 0.00066 ± 0.00003% K^+. The mussel population in lake 377 thus contained a total of 130.95 kg Ca^{2+}. Assuming lake water contained 2.2 g $Ca^{2+} \cdot m^{-3}$ (Table 1) throughout its volume of 25.40 × 10^5 m^3, the amount of dissolved Ca^{2+} in the lake would be 5588 kg. The shells of live mussels contained 2.3% of the total Ca^{2+} in lake 377.

Discussion

Despite its very soft, low-productivity water, lake 377 maintains an abundant population of *A. g. grandis*. The water is softer and of lower alkalinity than in most other localities where the species is found (Green 1972; Paterson and Cameron 1985; Hanson et al. 1988*b*). Mackie and Flippance (1983) found *A. g. grandis* only in lakes with pH >7.0, alkalinity >35 $mg \cdot L^{-1}$, and [Ca^{2+}] 5–60 $mg \cdot L^{-1}$. Green (1980) found the species in Shell Lake, Northwest Territories, at pH 6.3–7.2 and [Ca^{2+}] 10.02 $mg \cdot L^{-1}$. Nevertheless, waters containing only 2–3 mg $Ca^{2+} \cdot L^{-1}$ have been reported to support *A. grandis* (Ghent et al. 1978) and another unionid mussel, *Elliptio complanata* (Strayer et al. 1981). We agree with Strayer et al. (1981) that [Ca^{2+}] of 2–3 $mg \cdot L^{-1}$ is not limiting to mussel populations, although it is likely close to the lower limit.

Low lake productivity, low alkalinity, and low [Ca^{2+}] tend to co-occur, and their influences on mussel populations are difficult to separate. These conditions in lake 377 produced relatively slow-growing, stunted mussels. The largest *A. g. grandis* collected from lake 377 was 118 mm long, whereas maximum lengths were 148 mm from Lake Minnedosa (Huebner 1980), about 130 mm from Lake Bernard (Ghent et al. 1978), and 156 mm from the Sheyenne River near Lake Ashtabula (Cvancara and Freeman 1978). Although the largest mussel collected in Lake Ashtabula itself was only 84 mm long (Cvancara and Freeman 1978), the small size appeared to be the result of youth rather than of stunted growth. The maximum length and size-frequency distribution of mussels in lake 377 are most similar to those of mussels (probably *Anodonta grandis simpsoniana*, based on the geographic distribution described by Clarke 1981) in Shell Lake, Northwest Territories (Green 1980). The [Ca^{2+}] and productivity of Shell Lake are similar to those of lake 377, suggesting that environment has a significant influence on growth.

The range of depth distribution of *A. g. grandis* in lake 377

(0.7–4.7 m) is similar to that reported by other authors (Green 1980; Cvancara and Freeman 1978). In Lake McConaughy, western Nebraska, Baxa (1981) found *A.g. grandis* between 3 and 5 m. Ghent et al. (1978) and Cvancara (1972) found this subspecies substantially deeper in Lake Bernard, Ontario, and Long Lake, Minnesota, respectively. Abundance of mussels changed with depth in lake 377, being higher in the 1.5- to 3.1-m depth stratum than in the 3.1- to 4.7-m stratum. Abundance of *A.g. grandis* in Lake Bernard was also depth related, but less sharply than in lake 377. Abundance was about 0.04–0.05/m^2 between 2.5 and 10 m, decreasing upward to 1 m depth and downward to 12 m depth (Ghent et al. 1978). In Long Lake, mean density in the littoral zone was 14.9 m^2 but only 0.9 m^2 in the 6- to 8-m depth stratum. In southwestern Finland, abundance of *Anodonta piscinalis* was highest at 0–1 m depth; few mussels were found below 5 m (Haukioja and Hakala 1974). Hanson et al. (1988*b*) reported *A.g. simpsoniana* in Narrow Lake, Alberta, to be most abundant at 1, 3, and 5 m depths and much rarer at 7 m depth. Suitable substrate is found in lake 377 down to depths of 8–9 m. We did not find a relationship between grain size (in the range of fine sand to very coarse sand) and the abundance of mussels in lake 377. Thus, *A.g. grandis* in lake 377 appears to be depth limited by factors other than substrate. Ghent et al. (1978) and Cvancara (1972) indicated that *A.g. grandis* appears particularly well adapted to the softer substrates that often prevail in deeper areas. Cvancara (1972) commented that the depth distribution of mussels may be related to thermal stratification in lakes, with slower metabolism, reproduction, and growth occurring in the metalimnion.

Hanson et al. (1988*b*), found no difference in growth in mussels in Narrow Lake collected at 1, 3, 5, and 7 m depth, but mussels caged and unable to migrate showed growth rates at 1 and 3 > 5 > 7 m. They attributed all the difference in growth between depths to temperature differences. Nevertheless, other factors, such as less water movement providing slower transport of food to mussels, may make the metalimnion less favourable to growth than the epilimnion. Food may also be of lower quantity and (or) quality.

Unionids achieve greatest species diversity and abundance in rivers (Pennak 1953), although the phenomenon has not been adequately explained. We suggest that the success of *A.g. grandis* in lake 377 is related to the relatively high water turnover rate of this lake. Preliminary surveys of about 50 ELA lakes indicate that *A.g. grandis* is more likely to occur in lakes with high water turnover rate (unpublished data). High water turnover rate in lakes may produce some of the favourable habitat conditions found in rivers.

Anodonta grandis grandis, like other unionids, passes through a larval stage, the glochidium, which is obligately parasitic on fish. Lake 377 contained cisco (*Coregonus artedii*), yellow perch (*Perca flavescens*), burbot (*Lota lota lacustris*), white sucker (*Catastomus commersoni commersoni*), and lake trout (*Salvelinus namaycush namaycush*), based on the results of gill netting on 12 July 1984 in approximately 8 m of water (unpublished data). The Ontario Ministry of Natural Resources (G. J. Gibbard, personal communication) reported that lake 377 also contains longnose dace (*Rhinichthys cataractae*), pearl dace (*Semotilus margarita*), and spottail shiner (*Notropis hudsonius*). The number of known fish hosts of *A. grandis* exceeds 30 mostly warm-water species (Trdan and Hoeh 1982). Of the fish species in lake 377, yellow perch is a known host, and congeneric species of *Rhinichthys*, *Notropis*, and *Semotilus* have been reported as hosts (Trdan and Hoeh 1982). Thus, several fish species in lake 377 probably act as hosts. Glochidia are normally released by the mussels in April or May (Clarke 1973; Huebner 1980), remain on fish for only a few days (Trdan and Hoeh 1982), and were not expected to be infecting fish caught in lake 377 in July. Until infected fish are obtained from lake 377, likely in April or May, we will not know how many of the fish species in the lake are capable of acting as hosts.

It is extremely common in studies of unionids to find young mussels of 0–3 years to be absent from the samples or at least greatly underrepresented (Hunter 1964). The smallest mussel in the general collection from lake 377 was 34.9 mm, from Shell Lake, 57 mm and 5 years old (Green 1980), from Lake Bernard, about 31 mm (Ghent et al. 1978), from Long Lake, 33 mm (Cvancara 1972), from Lake Ashtabula and the Sheyenne river, 38 and 60 mm, respectively (Cvancara and Freeman 1978), and from Lake McConaughy, 80 mm (Baxa 1981). Small mussels, about 30 mm long, were collected from Lake Minnedosa (Huebner 1980), but even these were already in their second or third growing season. Since the virtual absence of year 1, 2, and 3 mussels from collections is so widespread a phenomenon, it is difficult to attribute it to pollution, as did Green (1980), or to one or two years of poor recruitment. A more likely explanation in uncontaminated lakes is that the usual sampling methods do not capture the young. Hanson et al. (1988*a*) pointed out that studies in which mussels are collected by SCUBA usually miss individuals <35 mm in length. On the other hand, studies in which mussels are collected by dredging usually report small mussels present. Using a dredge and a 6 mm mesh screen to wash samples, Hanson et al. (1988*b*) collected about 50% of year 1 *A.g. simpsoniana* and all mussels of age 2 or older.

Hanson et al. (1988*b*) reviewed published values of density, biomass, and production of unionid mussels. In Narrow Lake, Alberta, *A.g. simpsoniana* ≥2 years were found in the littoral zone (0–6 m), at 14.9 mussels/m^2. Our density of 0.49 mussels/m^2 in the 0- to 5-m stratum is considerably lower, but not as low as the density of 0.03/m^2 of *E. complanata* in Mirror Lake (Strayer et al. 1981). The live biomass of *A.g. grandis* in the 0- to 5-m stratum of lake 377, 20.94 $\text{g}\cdot\text{m}^{-2}$, is also lower than that of *A.g. simpsoniana* in Narrow Lake, 131.8 $\text{g}\cdot\text{m}^{-2}$, and is among the lowest in the literature. Although we include the organic component of the shell in our estimate of production, the production of 2.20 g wet weight$\cdot\text{m}^{-2}$ in the 0- to 5-m stratum of lake 377 is at the lower end of the range in lakes, 0.6–20.5 g visceral wet weight$\cdot\text{m}^{-2}$, summarized by Hanson et al. 1988*b*. The P/B ratio of 0.16 for lake 377 is also at the lower end of the range of 0.12–0.35 given by Hanson et al. (1988*b*).

Green (1980) made one of the few other attempts to estimate the role of a unionid mussel, *A.g. simpsoniana*, in the calcium budget of a lake. Shell Lake is 84.2 ha in surface area, 20.6×10^5 m^3 in volume, and contained a total mass of dissolved Ca^{2+} of 20 600 kg. In comparison, lake 377 is deeper, is 27.7 ha in area and 25.4×10^5 m^3 in volume, and contains 5588 kg Ca^{2+}. Green estimated that the live mussels in Shell Lake contain 10 100 kg Ca^{2+}, or about one-third of the lake's total Ca^{2+}, whereas we estimate that the mussels in lake 377 contain 131 kg, or only 2.3% of the lake's Ca^{2+}. Green did not report the population size of mussels in Shell Lake, but presumably it is much larger than that in lake 377. The estimates in neither lake include the young year classes of mussels. In Shell Lake, mussels less than 5 years of age were not collected.

In conclusion, the population of mussels in lake 377 lives at or near the lower limits of [Ca^{2+}] for freshwater molluscs. The population is relatively small, slow-growing, and long-lived compared with populations of unionids in more favourable environments. The secondary production of mussels is equivalent to a very small proportion, <1%, of the ice-free season primary production. The population ties up a small but measurable portion of the lake's total Ca^{2+}, possibly as much as 5%, when shells of dead mussels are included.

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