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The effects of water depth and density on the growth of a unionid clam*

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SUMMARY. 1. Unionid clams from Narrow Lake, Alberta, were collected to quantify the natural variation in growth, to assess the natural variation in abundance, age and size distribution, and growth with water depth in the lake, and to conduct *in situ* experiments to directly test the effects of water depth (temperature) and clam abundance on clam growth.

2. The unionid clam, *Anodonta grandis simpsoniana,* showed wide variation in length at a given age. There were no significant differences in growth between clams collected at 1, 3, 5, and 7 m depths in the lake despite marked differences in water temperature. The wide variation in clam biomass within each depth zone may have masked possible effects of water depth.

3. The effect of water depth and variation in clam density on clam growth was tested directly by stocking clams into small enclosures at densities equivalent to 50, 150, 250, 350 and 450 g m^{-2} (live weight) at each of 1, 3, 5 and 7 m depths in Narrow Lake (each depth and abundance treatment in triplicate). A uniform sandy substrate was used in all enclosures to eliminate any possible effect of substrate type on growth.

4. Mortality was negligible (0.9%) during the experiment. Clam density had no significant effect on clam growth which suggests that clam growth was not food limited in the lake.

5. Clams reared at 7 m grew more slowly than clams reared at 1, 3 and 5 m. Clams reared at 5 m grew more slowly than clams reared at 1 and 3 m. Growth of clams reared at 1 and 3 m did not differ. These differences in growth were strongly correlated with the measured differences in water temperature between depths.

6. Migration between depths probably accounts for the lack of a depth effect on clams growing in the natural habitat.

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Introduction

A number of recent studies suggest that variation in the growth of bivalves can be used as an indicator of environmental change (Freeman & Dickie, 1979; Jones, 1981; McCuaig & Green, 1983). However, individuals of the same age in clam populations frequently exhibit a wide range in length around the mean length (Lewandowski & Stanczykowska, 1975; Haukioja & Hakala, 1978; Hanson, Mackay & Prepas, 1988). It is important to understand the sources of natural variation in length within an age class before attributing deviations from a baseline model (e.g. McCuaig & Green, 1983) to an artificial pertubation of the environment. In addition, variation in growth will affect the precision of estimates of clam production rates. This can be an important problem because unionid clams often dominate the benthic fauna in lakes and rivers (Negus, 1966; Fisher & Tevesz, 1976; Hanson *et al.*, 1988) yet represent a resource largely unavailable to fish because clams are generally immune from fish predation due to their large size and thick shell.

Between year differences in annual growth increments, which result from annual temperature differences, are one known source of natural variation in length within an age class of unionid clams (Negus, 1966; Haukioja & Hakala, 1978; Hanson *et al.*, 1988). Differences in water depth (probably a temperature effect) (Cvancara, 1972; Ghent, Singer & Johnson-Singer, 1978; Strayer *et al.*, 1981), abundance (Kat, 1982) and substrate (Kat, 1982; Dickie, Boudreau & Freeman, 1984; Hinch, Bailey & Green, 1986) are possible factors responsible for the wide variation in growth observed within a given year. It is very difficult to separate the effects of these last three factors on the basis of samples collected from undisturbed populations. Confirmation of the independent or combined effects of substrate, clam abundance, and water depth on clam growth is probably best accomplished by means of *in situ* experiments.

A small number of workers have conducted *in situ* experiments on the effects of a number of abiotic and biotic factors on the growth of bivalves. Transplant experiments have been used to show that differences in substrate can affect both clam growth rate and body form (Kat, 1982; Dickie *et al.*, 1984; Hinch *et al.*, 1986). However, the underlying mechanism is still poorly understood. Freeman & Dickie (1979) examined the effects of study site and water depth on the growth of four size classes of a marine mussel (*Mytilus edulis*) suspended at three depths in the Bedford Basin and at one depth in St Margaret's Bay, Nova Scotia. There were no significant differences in growth between depths but the results of the study are difficult to interpret because of a number of problems with the methods: it is not known whether water temperature differed between the various water depths, mortality was high and varied widely between experimental treatments, and the mussels used in the various depth treatments were of different sizes. To our knowledge, no experiments have been conducted which directly test for the effects of differences in water depth and clam abundance on the growth of unionid clams.

The goals of this study were threefold: (1) to quantify the natural variation in length of a unionid clam during a single growing season; (2) to assess the natural variation in clam density, age and size distribution, and growth with water depth in a deep Boreal lake; and (3) to conduct *in situ* experiments to test for significant effects of water depth and clam abundance on clam growth.

Materials and Methods

This study was conducted in Narrow Lake (54° 35′ N; 113° 37′ W), a small (1.14 km^2), deep (mean depth 14.2 m), moderately productive (mean summer total phosphorus 12.9 mg m^{-3}) lake in the Boreal forest zone of central Alberta. The morphometry and water chemistry of Narrow Lake are described in Prepas & Trew (1983) and Prepas & Vickery (1984). *Anodonta grandis simpsoniana* Lea (1861) is the only unionid clam in the lake (Hanson *et al.*, 1988).

Field measurements

Water temperature data were collected routinely from the central station on Narrow Lake at 7–14 day intervals during May to the end of August, 1983–86. Water temperatures were recorded at 1 m intervals from the surface

to 30 m depth with a Montedoro Whitney thermistor accurate to 0.1°C, calibrated before each use. The degree-days for a specific depth stratum over a time interval were calculated as the mean water temperature (greater than 0°C) times the number of days in the interval. We calculated the cumulative degree-days for the 1, 3, 5 and 7 m depths from 9 May to 26 August for all four years.

Unionid clams were collected and densities determined by divers searching quadrats and by dredging. Divers collected clams from six sites in Narrow Lake during August 1985. At each site the divers carefully searched four 0.5×0.5 m quadrats which had been placed at random at each of 1, 3, 5 and 7 m depths at each site. One site was chosen at random on the east and west sides of the north, central and south basins of the lake. A total of 24 m^2 of substrate was examined by divers. In addition, we collected twelve samples with a 23×23×23 cm Ekman dredge at each of 1, 3, 5 and 7 m depths from eighteen randomly chosen sites in the lake. We sampled two or three sites every 2 weeks from 16 May to 9 August 1986. A total of 46 m^2 of substrate was sampled by dredging. The sediments collected with the dredge were washed gently on a 6 mm mesh screen and all unionid clams were removed. The screen retained all clams larger than 8–10 mm in length, which corresponded to about 50% of clams of age 1 and virtually all clams of age 2 and older. Clams less than age 2 were omitted from this study. Comparison of the size distributions of clams collected by dredging and by divers (over the same water depths) showed that divers missed a substantial fraction of the clams less than 30 mm long (*G*-test; χ^2=38.5, df=7, P<0.001). The samples collected by divers underestimated the abundance of clams by about 23% but, because the missed clams were small, underestimated the biomass only by about 1.5%. Therefore, clams collected by divers were only used to estimate clam biomass.

All clams were taken, alive, to the laboratory (155 clams in 1985 and 618 clams in 1986) where the debris encrusting the shell was removed carefully and live weight, total length, age, and total length at each annulus were recorded. In addition, we calculated the annual growth increments (total length) for each clam. The use of annuli to age clams generally is considered valid for 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 & Hakala, 1978; McCuaig & Green, 1983).

The natural within-year variation in length within each age class was quantified, for the 1985 growing season, by plotting length–frequency distributions. To do this, the length at last annulus (formed in June 1986) was plotted for each age class of the clams collected during 1986. The clams collected in 1985 were not used in this analysis. We then attempted to determine the role of differences in clam abundance and water depth as sources of this variation.

The natural variation in clam density, age and size distributions, and growth with water depth was determined by partitioning the data by depth of collection. The geometric mean biomass (live weight, g m^{-2}), age and size frequency distributions, geometric mean length at annulus, and mean annual growth increments were then determined for each depth zone. In this analysis only, the calculations of mean length at annulus and mean annual growth increment used all of the back-calculated lengths at annulus. Our use of all of the back-calculated data assumes the clams remain in one depth zone for their entire life; this assumption is addressed in the discussion. We then tested for significant differences in clam biomass (one-way ANOVA), age and size–frequency distributions (*G*-test), and mean annual growth increments (two-way ANOVA) among depths.

Field experiments

The effects of water depth and clam density on clam growth were tested directly by manipulating the numbers of *Anodonta grandis simpsoniana* stocked into small enclosures placed at 1, 3, 5 and 7 m depths at a site in the central basin of Narrow Lake in 1986. The experimental enclosures consisted of small (0.144 m^2), shallow (11 cm deep), plastic trays filled to a depth of 5–6 cm with a uniform sandy silt which was obtained on the study site. The use of a uniform substrate eliminated any possible confounding effect of variation in substrate with depth which occurs in the natu-

ral habitat. All sixty enclosures were covered with chicken wire to prevent mammalian predation. There were three replicates for each density and water depth treatment.

All clams used in the experiment were collected by a diver in the 1–2 m depth zone on the study site. About 1000 clams were transported to the laboratory and held for 1 week in a large, aerated, aquarium. No clams died during this time. We attempted to mimimize the range in size of clams used in this experiment but were limited by the availability of clams of the appropriate size on the study site. The range in lengths of clams used in the experiments was 29–48 mm (11.5–7.5 g) of which 80% were 35–45 mm long (3.0–7.0 g). About 81% of the clams were age 5, 8% were age 4, 8% were age 6 and 3% were age 3. No clams became sexually mature during the experiment. Clams were carefully washed, blotted dry, weighed (to 1 mg), and the total length and length at the last annulus measured (to permit identification of individuals) before placing the clams in uniquely labelled plastic bags at densities equivalent to 50, 150, 250, 350 and 450 g m^{-2}. These densities cover the extremes measured in the littoral zone of Narrow Lake. The geometric mean biomass in the 0–6 m depth zone was 132 g m^{-2} (live weight; 95% CI=93–187 g m^{-2}, n=18). The clams were transported to the study site, stocked into the appropriate enclosures, lowered into the lake, and the depths were checked and adjusted (if necessary) by divers. The experiments were begun on 25 June 1986, which corresponds with the time when clams in the natural environment began to grow. We recovered the enclosures on 16 September 1986, and transported the clams to the laboratory. Individual clams from each enclosure were identified by their unique lengths at the last two annuli, cleaned, blotted live weight and total length measured, and the percentage increase in live weight and total length were calculated. The mean percentage increase in live weight and total length were calculated for each enclosure. Mean percentage increase in weight was used as our principal measure of growth to avoid a possible source of variation in growth in length which may arise as a result of differences in body form of clams collected from different substrates (e.g. Hinch *et al.*, 1986). This could occur in our study because clams were collected from a variety of substrates and then transferred to a uniform substrate in trays. Furthermore, percentage increase in weight also reduces the potential bias caused by the range (6 g) in the initial weights of the clams which occurred despite the narrow range (19 mm) of lengths of clams collected for our experiments.

The data from the field experiments were transformed (arcsin $\sqrt{x}$; Steel & Torrie, 1980; Sokal & Rohlf, 1981) to stabilize the variance

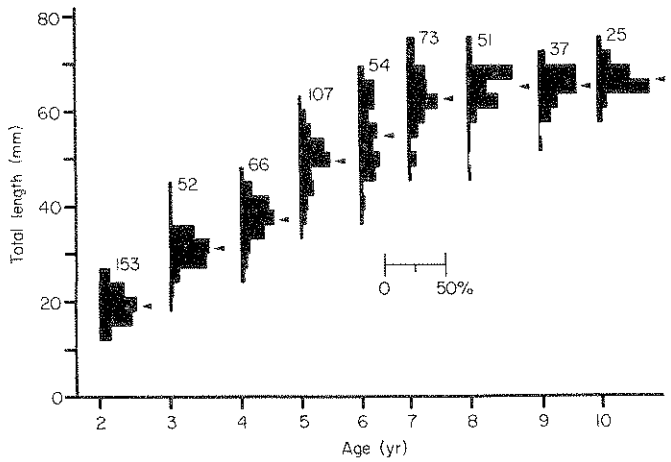

FIG. 1. Frequency distribution of length at last annulus for *Anodonta* in Narrow Lake during 1986. The 95% confidence intervals around the mean length at annulus (solid arrow) were 0.51, 1.12, 1.13, 1.09, 2.20, 1.46, 1.38, 1.31 and 1.35 mm for clams of ages 2, 3, 4, 5, 6, 7, 8, 9 and 10 respectively.

and a two-way ANOVA was used to test for significant effects of water depth, clam density, and water depth×clam density interaction on the mean percentage increase in live weight. We predicted there would be a significant effect of water depth on clam growth and therefore used orthogonal contrasts to test for differences in growth among the four water depth treatments. (For comparative purposes, the same analyses were performed on the percentage increase in total length data. They were identical and are not included in this paper.)

Results

Field measurements

The *Anodonta* in Narrow Lake grew slowly (Fig. 1), attaining a mean length of 49 mm by age 5 but only increasing to 66 mm by age 10. The mean length at age 11 (n=8) and age 12 (n=4) was 69.2 and 69.0 mm, respectively. The data for length of clams at ages 11 and 12 were not included in Fig. 1 because of the very small sample size. The variation in length at annulus was high, with standard deviations of 3.2, 4.0, 4.6, 5.7, 7.4, 6.2, 4.9, 4.0 and 3.3 mm for clams of ages 2, 3, 4, 5, 6, 7, 8, 9 and 10, respectively. The variation in length at annulus decreased markedly after age 7, with no clams exceeding 75 mm in length while the lower range in lengths moved upwards as the clams grew.

Clams at the 5 and 7 mm depths received 12.5% and 33.5% fewer degree-days, respectively, than clams at the 1 m depth from 1983 to 1986 (Table 1). These data indicate that there should be significant differences in growth of clams between depths due to differences in water temperature provided clams remain at one depth. Between-year differences in water temperature were less pronounced than between-depth differences. Over the 1–5 m depths, the maximum between year differences in cumulative degree-days was 6.3% between 1984 and 1986. The between year difference was only 1.5% between 1985 and 1986. Between year variation in water temperature was greater at 7 m. The maximum difference in cumulative degree-days was 22% between 1984 and 1986 and the minimum was 2.5% between 1983 and 1985.

The biomass of *Anodonta* was not evenly distributed among the depths sampled in Narrow Lake (Fig. 2; ANOVA, $F_{3,68}$=29.7, P<0.001) nor was it evenly distributed within a depth as shown by the wide confidence intervals around the means. There was significantly less clam biomass at 7 m (ANOVA, $F_{1,68}$=

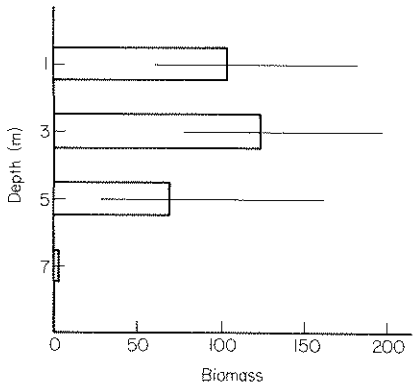

FIG. 2. Biomass (g m^{-2}, live weight) of *Anodonta* at 1, 3, 5 and 7 m depths in Narrow Lake. Means ±95% confidence intervals are presented.

TABLE 1. Degree-days (DD>0°C) for the 1–7 m depths of Narrow Lake from 9 May until 26 August, 1983–86. The number of sampling dates is in parentheses.

	1983 (16)		1984 (15)		1985 (12)		1986 (17)		
Depth (m)	DD	% 1 m	DD	% 1 m	DD	% 1 m	DD	% 1 m	Mean % 1 m
1	1853	100.0	1968	100.0	1841	100.0	1828	100.0	100.0
2	1833	98.9	1878	95.4	1811	98.4	1813	99.2	98.0
3	1820	98.2	1848	93.9	1785	97.0	1764	96.5	96.4
4	1791	96.6	1800	91.5	1725	93.7	1692	92.6	93.6
5	1635	88.2	1715	87.2	1630	88.6	1572	86.0	87.5
6	1441	77.7	1605	81.6	1552	84.3	1372	75.1	79.7
7	1175	63.4	1456	74.0	1216	66.1	1140	62.4	66.5

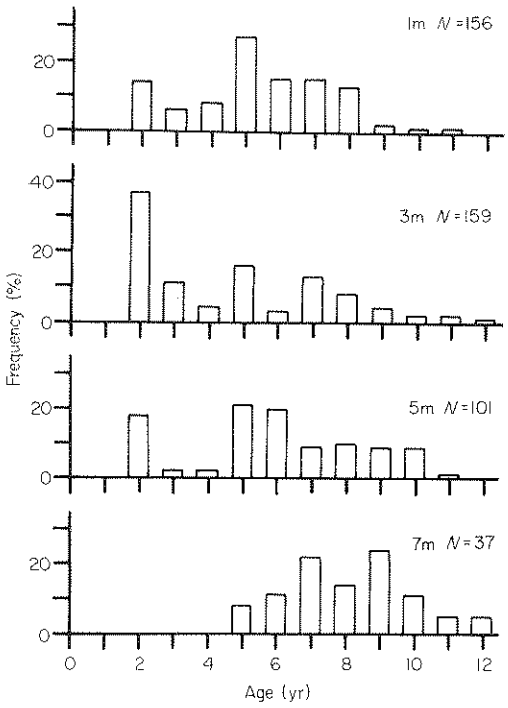

FIG. 3. Age–frequency histograms for *Anodonta* age 2 or older at 1, 3, 5 and 7 m depths in Narrow Lake.

87.5, $P<0.001$) than at the other three depths. The biomass of unionids at 5 m did not differ significantly from that at 1 and 3 m (ANOVA, $F_{1,68}=1.4$, $P>0{\cdot}05$) which also did not differ (ANOVA, $F_{1,68}=0.1$, $P>0.05$).

The age distribution of clams differed between depths (Fig. 3). The 7 m depth clearly differed from the other depths in that very few clams were collected and there were no clams less than age 5. The data we present represent all of the clams collected at 7 m depth with both sampling methods, and therefore were not included in the statistical analyses because the data were collected over 2 years and represent a larger sampling area. The data for the 1, 3 and 5 m depths were all collected by dredging and are, therefore, comparable. At all three depths, clams of age 2 and 5 were proportionately more abundant and clams of age 3 and 4 were rare. Clams greater than age 8 were notably rare in the 1 m depth zone. The age distributions differed significantly between the three depths (*G*-test, $\chi^2=78.7$, df=18, $P<0.001$), which suggests that recruitment varied between depths and/or clams of some size groups migrate more than others.

Given the uneven age distributions, it was not surprising that the size distributions differed between depths. Again, the 7 m depth zone was most different, with few clams less than 55 mm in length present (Fig. 4). The length–frequency distributions differed significantly between the 1, 3 and 5 m depths (*G*-test, $\chi^2=80.8$, $P<0.001$). The high frequency of clams 15–25 mm long in the 3 m depth corresponds to the large number of age 2 clams at this depth (Fig. 3) and the small number of clams 30–40 mm long in the 5 m depth corresponds to the small number of age 3 and age 4 at this depth. Although there were few clams greater than age 8 in the 1 m depth, there were still a large proportion of the clams greater than 50 mm long (Fig. 4), which indicated growth might be faster in the 1 m depth zone.

There was little difference in the mean length of age 1 clams between depths (Fig. 5). After age 1, the clams in the 1 and 3 m depths appeared to grow slightly faster than clams at 5 and 7 m. The mean length at any given age for clams collected from a depth of 1 m was consistently greater than that of clams collected from a depth of 7 m, but the differences were small. At age 4 the mean length of clams

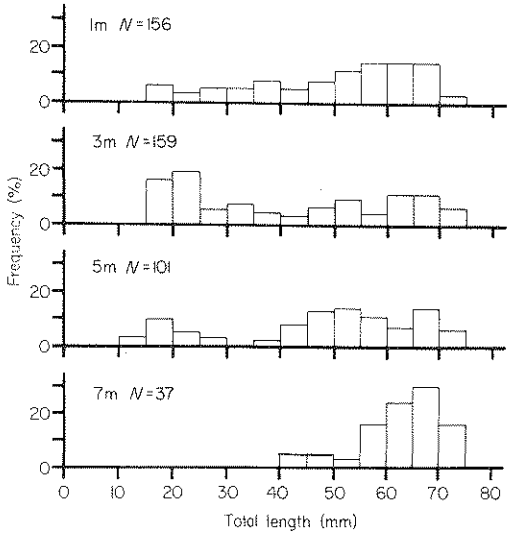

FIG. 4. Length–frequency histograms for *Anodonta* age 2 or older at 1, 3, 5 and 7 m depths in Narrow Lake.

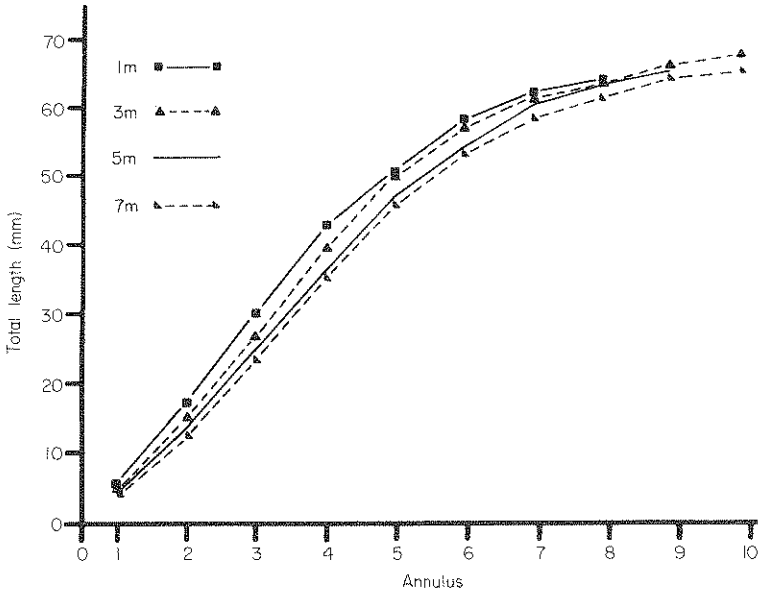

FIG. 5. Mean length at annulus for clams collected at 1, 3, 5 and 7 m depths in Narrow Lake.

at 1 m was about 7 mm greater than that of clams in 5 and 7 m of water. Rather than increasing, the differences decreased such that by age 7 the differences had disappeared. Overall, there were no significant differences in annual growth increments among depths for clams of ages 1–9 (ANOVA, $F_{3,24}=0.2$, $P>0.05$).

Field experiments

Mortality was negligible in the field experiments. Only four clams (0.9%) died, never two in any treatment. Mortality was therefore ignored.

All clams gained weight during the experiment (Fig. 6). There was no significant effect of stocking abundance over the range tested (ANOVA, $F_{4,40}=0.1$, $P>0.05$) nor was the abundance×depth interaction significant (ANOVA, $F_{12,40}=0.8$, $P>0.05$). Clams reared at 7 m grew more slowly than clams at other depths (ANOVA, $F_{1,40}=55.0$, $P<0.001$). Clams reared at 5 m depth grew more slowly (ANOVA, $F_{1,40}=7.4$, $P<0.01$) than clams reared at 1 and 3 m. The growth of clams reared at 1 and 3 m did not differ (ANOVA, $F_{1,40}=0.9$, $P>0.05$). The mean percentage increase in weight was strongly correlated

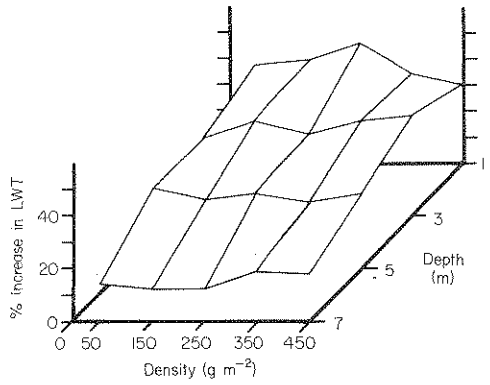

FIG. 6. Mean % increase in live weight (LWT) for *Anodonta* reared at 50, 150, 250, 350 and 450 g m^{-2} at each of 1, 3, 5 and 7 m depths in Narrow Lake from 23 June until 16 September 1986.

TABLE 2. Mean percentage weight gain (%WT), cumulative degree-days (DD greater than 0°C) for the period 23 June to 24 August 1986, and mean difference in water temperature from 1 m (dT) experienced by clams reared at 1, 3, 5 and 7 m in Narrow Lake

Depth (m)	%WT	DD	dT
1	36.9	1165	0.0
3	33.7	1152	0.2
5	27.7	1083	1.2
7	14.8	780	6.0

(r=0.985, df=3, P<0.01) with the degree-days measured at the 1, 3, 5 and 7 m depths during the experiment (Table 2). On average, the water at 7 m depth was 6°C cooler than water at 1 m.

Discussion

No significant difference was detected in growth among clams in the natural population collected from the 1, 3, 5 and 7 m depths in Narrow Lake. In contrast, water depth had a strong effect on growth in both weight and length of clams in our field experiments. We attribute this difference in growth to the decline in water temperatures with increasing depth rather than to differences in food supply because there was no significant effect of stocking abundance on growth. Furthermore, algal biomass (as indicated by chlorophyll *a* fluorescence) was relatively even over the 1–7 m depths in Narrow Lake during our experiments or even increased slightly with depth (A. Trimbee and E. E. Prepas, Department of Zoology, University of Alberta, unpublished data), indicating that food availability was uniform over the range of the clam depth distribution.

The lack of a detectable difference in growth rate among clams collected at various depths in Narrow Lake could arise from a number of factors including migration, selective predation, or differences in substrate. Unionid clams are capable of making migrations of tens of metres which could move them through favourable and unfavourable microhabitats or depths (Tudorancea, 1972; Ghent *et al.*, 1978; Kat, 1982; Samad & Stanley, 1986). A migration of 10–15 m would be sufficient to move a clam from 1 to 5 m depth (or vice versa) in most of Narrow Lake and allow extensive mixing between depths. However, a major assumption of all analyses for differences in growth of clams collected from various depths of water is that clams remain within one depth zone throughout their lives. We attempted to reduce the importance of this assumption by testing for significant differences in growth of clams between depths for the 1985 growing season alone. This analysis only assumed that clams remained within one depth zone from late June 1985 until 9 August 1986. We only tested for significant differences in growth increments for clams of ages 2–9 collected at 1, 3 and 5 m because too few clams were collected at 7 m. Again, there were no significant differences in growth increments between the three sampling depths (ANOVA, $F_{2,14}$=0.09, P>0.05). This result indicates that migration between depths (if it occurred) took place on a scale of less than one growing season in Narrow Lake.

Our observation of a lack of depth effect on the growth of clams collected in Narrow Lake contrasts sharply with the study of Ghent *et al.* (1978) in Lake Bernard, Ontario, where length at annulus differed markedly between depths. Although the number of clams examined from Lake Bernard was small (seven to twelve individuals per depth) the differences reported appear to be too large to be a sampling artefact (e.g. clams averaged 60 mm long at age 6 at 1 m but only 34 mm long at age 6 at 7 m). It is not clear whether water temperature differed between depths because the authors only measured temperatures on one date and there was little difference between 1 and 11 m. In addition, the possible effects of temperature cannot be separated from those of differences in substrate with depth in the lake. A more likely explanation for the difference in clam growth in Narrow Lake versus Lake Bernard is that the slope on the sampling zone in Narrow Lake was between 1 in 4 and 1 in 5 whereas the slope on the sampling zone in Lake Bernard was 1 in 200. A clam need only migrate about 15 m to move from 1 to 5 m in Narrow Lake but would have to cover at least 200 m to move from 1 to 3 m depth in Lake Bernard. One consequence of the lack of a difference in growth rate or biomass of clams with depth in Narrow Lake (this study) is that it is not necessary to partition the data by depth when calculating production. However, it is still necessary to collect reasonably large samples because variation around the mean length at annulus was wide (Fig. 1) and variation around the mean weight at a given age and annual weight increments will also be wide.

Our *in situ* experiments allowed us to test directly for the effects of variation in water temperature and clam abundance on clam growth while preventing migration, mammalian predation, and effects of different substrates. Variation in clam abundance had no

significant effect on clam growth (over the range of densities tested). This was not a surprising result. Clams fed by filtering suspended materials from the water. Lewandowski & Stanczykowska (1975) estimate that *Anodonta piscinalis,* 60–64 mm long, filter at a rate of 14.3 ml g^{-1} h^{-1} (live weight; range 2.9–23.3 ml g^{-1} h^{-1}). If we apply this value, then the estimated 24.7 t of clams (live weight) in the littoral zone of Narrow Lake could filter about 8447 m^3 of water per day. Thus the clam population in the 0–6 m depth zone of Narrow Lake would require about 4 years to filter the volume of the epilimnion once. Even at our highest stocking level (450 g m^{-2}), it would require more than one ice-free season to filter a volume equal to the epilimnion once. These results indicate food was not limiting to clams in Narrow Lake and we think it is unlikely that food is limiting in other lakes because the filtration rates of freshwater clams, while highly variable, are low (de Bruin & Davids, 1970; Lewandowski & Stanczykowska, 1975; Paterson, 1986) and the rate of removal of the small plankton would be several orders of magnitude slower than the turnover rate of the plankton. Kat (1982) suggested that increased clam abundance could lead to increased rates of migration. Unfortunately, it is impossible to determine whether the increased migration rates of clams in Kat's study were due to differences in clam abundance or to variation in substrate. We cannot evaluate whether increased clam abundance resulted in increased migration rates in the present study because the trays in our experiments prevented migration.

The results of our enclosure experiments suggest that production and biomass should be much higher at the 1 and 3 m depths than at 5 and 7 m. However, *Anodonta* biomass did not differ significantly between the 1, 3 and 5 m depths in Narrow Lake despite the 12% fewer degree-days experienced by clams at 5 m. The mean biomass was only lower at 7 m where the water temperatures averaged 6°C less than at 1 m. This pattern of biomass distribution differs from the majority of studies which show marked differences in clam biomass with depth even over the 1–5 m range (Cvancara, 1972; Haukioja & Hakala, 1974; Strayer *et al.*, 1981). The authors do not describe how water temperature varied with depth in these preceding studies nor whether the slopes of the sampling zones were similar.

The low density of clams at 7 m in Narrow Lake probably reflects an active response of clams to avoid the lower temperature and/or some characteristic of the substrate at this depth rather than as inability to survive because all clams maintained at the 7 m depth survived and grew over the 82 day period of our experiment. In addition, we seldom collected empty shells from the 7 m depth during our sampling programme. It appears that the few clams which move into the 7 m depth return quickly to the 1–5 m depth. Also, the absence of clams less than age 5 indicates there was no recruitment of younger (and smaller) clams to the 7 m depth and is also consistent with the hypothesis that larger clams migrate greater distances than small clams. However, the partitioning of time spent among the various depths is not known. If clams do respond to differences in temperature among water depths then the maximum depth of colonization of clams in lakes could be predicted from some measure of mixing depth or from other variables such as wind direction and fetch, and lake morphometry. To our knowledge, the data do not exist to test this hypothesis.

The range of clam biomasses within a sampling depth was quite wide in Narrow Lake, possibly as a response to differences in substrate (Headlee, 1906; Cvancara, 1972; Haukioja & Hakala, 1974). We did not assess the variation in habitat parameters (e.g. substrate characteristics or type and abundance of macrophytes) between sample sites in Narrow Lake, and therefore cannot resolve the question of whether differences in clam biomass within a sample depth correspond to variation in the microhabitat. Further experiments are needed to address the problem of the effect of different substrates on clam growth and biomass and the interaction with water temperature.

The age and size distributions of clams differed between the sampling depths in Narrow Lake. The length–frequency distribution for clams collected from the 1 m depth showed a large proportion of clams in the 55–70 mm range despite the scarcity of clams greater than age 8. The proportionately small numbers of clams greater than age 8 and abrupt truncation

of the size distribution at 70 mm for clams collected at the 1 m depth suggests that some form of size dependent mortality was occurring. We did not observe many empty shells at this depth but muskrats (*Ondatra zebithicus*) are common in the lake and are known to be a major predator of clams (Headlee, 1906; Van Cleave, 1940).

The strong depth effects observed in this study have important implications for attempts to use deviations from a baseline growth model as evidence of environmental perturbation. Our results suggest that differences in water temperature with depth are an important source of natural variation in growth of clams. In addition, substrate type may also affect clam growth in the field (Kat, 1982; Hinch *et al.*, 1986). It is not clear how differences in water depth and substrate interact on clam growth. Any study which uses deviation from a baseline model as evidence of environmental perturbation will have to be designed carefully to account for natural variation in growth due to effects of water depth and substrate type. The ability of clams to migrate among water depths and across different substrates almost necessitates the use of field enclosures.

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