Spatial and Temporal Variation in a Population of Freshwater Mussels in Shell Lake, N.W.T.

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A population of *Anodonta grandis* (Bivalvia; Unionidae) in a small Arctic lake was sampled in 1973 and 1986. In both of the years sampled there were about 14 times more mussels in deep (>1.5 m) water than in shallow water. There was a decline in growth rate, a shift towards an older age structure, and a drop in population density from 2.3 to 0.65 animals per·m⁻² between 1973 and 1986. This pattern is consistent with an hypothesis of anthropogenic impact. The limitations of such an interpretation are discussed.

Une population d'Anodonta grandis (bivalves; Unionidés) d'un petit lac arctique a été échantillonnée en 1973 et 1986. Les deux fois, il y avait environ 14 fois plus de moules en eau profonde (plus de 1,5 m) qu'en eau peu profonde. Les auteurs ont observé une diminution du rythme de croissance, une structure d'âge plus vieille et une baisse de la densité de population de 2,3 à 0,65 moules par m² entre 1973 et 1986. Ces caractéristiques vont dans le sens d'une hypothèse faisant intervenir un impact anthropique. Les auteurs traitent des limites de cette interprétation.

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n 1973, Green (1980) estimated the size distribution and density of a population of Anodonta grandis (Bivalvia; Unionidae) in Shell Lake, Inuvik, Northwest Territories. Of over 1000 individuals sampled, he found no mussels less than 57 mm in length (about 5 yr old). Green proposed three explanations for this result. (i) Collecting bias: young unionids may be difficult to collect using sampling techniques designed for large individuals. Green (1980) sampled with SCUBA, using his bare hands to detect the mussels in the sediment. (ii) Naturally bad years: the years immediately prior to Green's (1980) sampling may have been poor for mussel recruitment due to natural variability in environmental factors. (iii) Anthropogenic impact: Shell Lake has served as an important float plane base since 1968 (i.e. 5 yr before Green's (1980) sampling). By 1973 there were six private bases on this small (84.3 ha) lake, and it continues to be heavily used today. Chang (1975), citing a personal communication from Westlake and Cook, reported high numbers of oleoclastic microorganisms and hydrocarbons in the lakeshore sediment in the early 1970's. Hydrocarbon pollution or other anthropogenically induced changes may have reduced recruitment in the mussel population in the 5 yr prior to Green's (1980) study.

In an attempt to evalute these hypotheses, the A. grandis population in Shell Lake was resampled in 1986. We predicted the following results, depending on which of the hypotheses was correct: (i) collecting bias: we would find the same lack of young mussels as Green (1980), but the density and age structure of the population would be similar to that observed in 1973. (ii) Naturally bad years: we would find mussels born between 1973 and 1985, and particularly young mussels, unless the years just prior to the 1986 sampling were also "naturally bad" for recruitment. The density and age structure of the population

would be similar to that observed in 1973 unless a permanent, natural deterioration of the mussel habitat had occurred. (iii) Anthropogenic impact: if recruitment were severely reduced beginning in 1968, there should be a low density of mussels relative to the numbers observed by Green (1980) in 1973.

These hypotheses are not mutually exclusive. In addition, previous research (e.g. Ghent et al. 1978) has shown that the distribution of A. grandis is strongly correlated with water depth. Thus, we stratified our analyses of the data by depth in order to see if differences between the 1973 and 1986 samples depended on the depth considered, and to see if previously observed patterns of A. grandis distribution occurred in this small, Arctic lake.

Materials and Methods

Sampling was done by hand (using SCUBA) in late July 1986, along the same four transects as used by Green (1980). Mussels were collected and shell length was measured as described in Green (1980). In addition, we cleaned 48 mussels from those collected and measured two consecutive growth rings on their shells for growth rate analysis (see below).

To evaluate the collecting bias hypothesis we compared the proportion of small (<60 mm) mussels found in 1973 and 1986. We used a loglinear model (Fienberg 1980), as programmed in the Systat TABLES module (Wilkinson 1987), to examine differences in the proportion of mussels in the two size classes (<60, ≥60 mm) due to the depth of sampling (≤2, >2 m), the year of sampling (1973, 1986), and any interaction between depth and year. Given that the same collecting technique was used in 1973 and 1986, an increase in the proportion

of small mussels in 1986 would be inconsistent with the "collecting bias" hypothesis.

If the proportion of small mussels was low in both years, biased sampling may be part (but not all) of the explanation. A lack of young mussels may indicate a declining population, which would be evidence for the anthropogenic impact hypothesis. A factorial ANOVA was used to assess the effect of depth (≤1.5, >1.5 m) and year (1973, 1986) on the number of mussels collected from a pair of circular sampling plots at a given site (total area = 4 m²). "Deep" and "shallow" were defined differently in the loglinear (described above) and ANOVA analyses in an effort to balance the number of observations per cell in each of the two analyses. A regression of log, (variance) on log_e (mean) for 20 paired samples indicated that something between a log and a square root transformation of the density data was appropriate prior to using parametric ANOVA (see Green 1979, p. 46-47). Statistical results using these two transformations, as well as the exact, optimal transformation, did not markedly differ. Therefore, we used $\log_e{(x+1)}$ transformations of the data (there were some zero values) in the analysis reported here. We used the Systat MGLH module (Wilkinson 1987) to carry out the analysis.

To further characterize any variation in the density and structure of the A. grandis population in space (deep versus shallow water) and time (1973 versus 1986), we examined variation in the length-frequency distribution of large (≥60 mm) mussels. These mussels were presumably sampled with less of the bias that may have influenced collection of the smaller individuals. As above, we used a loglinear model, this time to examine variation in the relative frequency of mussels in the three large size classes (60-74, 75-89, ≥90 mm) which were due to the depth of sampling (\leq 2, >2 m), the year of sampling (1973, 1986), and the interaction of depth and year. To determine whether or not changes in the length-frequency distribution of the population between 1973 and 1986 reflected variation in age structure or growth rates, we used a Walford plot analysis (McCuaig and Green 1983) of consecutive external growth rings (L1, L2) measured on a group of individuals from each of the two sampling years. The Walford plots from the two years were compared using ANCOVA, as programmed in the Systat MGLH module (Wilkinson 1987).

Results

A loglinear model including depth/year and depth/size interactions (as well as main effects) did not adequately explain variation in the proportion of small (<60 mm) mussels found at each depth in 1973 and 1986 ($X^2 = 35.7$; df = 2; p < 0.001). When a year/size interaction was included in the model (accounting for differences between the years in the proportion of small mussels at a given depth), the fit to the observed data improved significantly ($X^2 = 0.94$; df = 1; p = 0.34). In deep water, 8.3% of the mussels collected in 1986 were less than 60 mm, compared with 1.3% in 1973. In shallow water, 4.0% of the mussels collected in 1986 were "small," compared with 0.6% in 1973. At both depths there was a greater proportion of small mussels in 1986 than in 1973, while in both years sampled there was a greater proportion of small mussels in deep than in shallow water (Fig. 1).

Factorial ANOVA of \log_e (density + 1) indicated no interaction between year and depth (F=0.003; df=1.41; p=0.96). There were independent effects of both year (F=4.25; df=1.44; p=0.046) and depth (F=17.4; df=1.44; p<0.001)

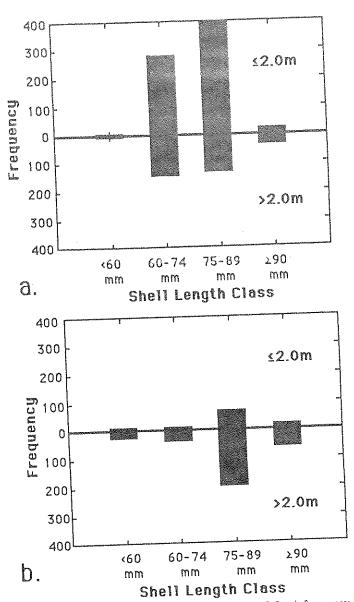


Fig. 1. Depth-specific (upper: ≤2.0 m; lower: >2.0 m) frequency distributions for shell lengths of mussels collected in (a) 1973 and (b) 1986.

on density. The geometric mean densities (per 4 m²) across both deep and shallow areas were 9.2 (95% confidence interval: 4.2, 19) for 1973 and 2.7 (0.75, 6.7) for 1986. The confidence limits are asymmetrical because they have been back-transformed from logarithms. Geometric mean densities across both years were 16.3 (8.2, 31.4) in deep water and 1.2 (0, 3.7) in shallow water.

A loglinear model including all possible two-way interactions between depth, year, and length class was inadequate in explaining variation in the length-frequency distribution of the large (\geq 60 mm) mussels in relation to depth and year ($X^2=13.35; df=2; p=0.001$). Thus, any differences between length-frequency distributions in 1973 and 1986 depended on the depth-examined. The data show a higher proportion of the largest sized shells (i.e. \geq 75 mm) in both deep and shallow areas in 1986, relative to 1973. The three-way interaction of depth, year, and length class was due to different length frequencies in deep and shallow water in the 1973 sample, which

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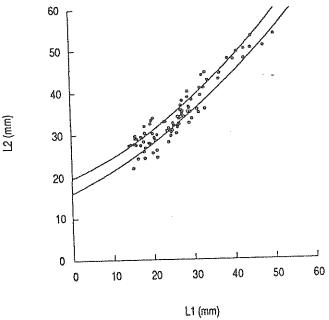


Fig. 2. Walford plot of consecutive annual ring measurements made in 1973 (closed circles) and 1986 (open circles). Quadratic curves of best fit are shown for 1973 (upper) and 1986 (lower) ring data.

appeared to converge to similar distributions in the 1986 sample

(Fig. 1).

Walford plot analysis of the growth ring data showed significantly higher growth rates in the 1973 population (F=72.0; df=1.81; p<0.001). A quadratic ANCOVA model (including L_1^2 as a predictor) was fitted to the ring data (as in Green 1980). There was no significant difference in either the linear or quadratic terms in the Walford plot model between the 1973 and 1986 mussels (linear: F=0.03; df=1.79; p=0.87; quadratic: F=0.08; df=1.79; p=0.78). The difference in the height of the two fitted curves (i.e. their y-intercepts) indicated the higher growth rate in the 1973 population (Fig. 2). This result is evidence that the observed increase in the proportion of large individuals in the 1986 population reflects a changing age structure rather than faster growth.

Discussion

Spatial and Temporal Variation of Anodonta grandis in an Arctic Lake

In a small, central Ontario lake, Ghent et al. (1978) found greater numbers of A. grandis in deep water relative to the depth distribution of Elliptio complanata. They reported finding A. grandis to depths of 14 m, and based on this, and its "floater" shaped shell, speculated that it evolved primarily as a deepwater species. Our results agree with those of Ghent et al. (1978); we found greater numbers of mussels in deep water in both 1973 and 1986. We also found (in both years) a higher proportion of small (<75 mm) mussels in deep water than in shallow. Large piles of empty shells (i.e. muskrat middens) were observed scattered around the littoral zone of the lake. It seems possible that smaller mussels might be easier for muskrats to open and hence smaller individuals may be selectively preyed upon.

Although a greater proportion of small (<60 mm) mussels were found in 1986 than in 1973, there were still far fewer

small, young mussels collected in 1986 than large, old mussels. The size distribution of the mussel population is not a perfect reflection of the age distribution (e.g. there could be many more year classes grouped together in large size categories than in small size categories), but the fact that the smallest size class had the smallest proportion of individuals at both depths in both years strongly suggests either biased sampling, a declining population, or both. The decline in density, aging of the population, and lower individual growth rates between 1973 and 1986 indicate that biased sampling alone cannot account for the lack of young mussels collected.

Green (1980) speculated that the years immediately prior to his sampling in 1973 may have been "naturally bad" for recruitment. The "naturally bad years" hypothesis implies stochastic runs of good and bad years, with a more or less stable population size and age structure. Given our data, it is impossible to classify the decline in density between 1973 and 1986 as either part of any normal fluctuations in numbers or an indication of a long-term decline. The growth ring data, which integrate growth rates over many years up to about 5 or 10 yr before the mussels are measured (recently laid down rings are usually not measured), do support the latter interpretation. The A. grandis population had a lower rate of shell growth in 1986 than in 1973, indicating faster growth from 1960 to 1968 than from 1973 to 1981. Taken together, changes in the lengthfrequency distributions, densities, and growth rates of the population between 1973 and 1986 are consistent with a declining population due to anthropogenic impact (Green's (1980) third hypothesis).

Limitations of the Anthropogenic Impact Interpretation

Green (1980) provided only three hypotheses for the lack of small mussels in his sample from Shell Lake ("biased sampling," "naturally bad years," "anthropogenic impact"), and the data gathered in 1986 are consistent with the "anthropogenic impact" hypothesis. There are, however, several important limitations to interpreting the differences in length-frequency distributions, densities, and growth rates between 1973 and 1986 as an effect of anthropogenic impact. We have a suboptimal design for detecting an impact (sensu Green 1979), because the presumed impact has already occurred, there is no control area, and therefore "the impact must be inferred from temporal change alone" (Green 1979).

We have no "among year" or "among lake" replication, meaning that whatever differences in the A. grandis population that we observed between 1973 and 1986 could have just as easily been present between two consecutive years in one lake or in two similar lakes sampled in a given year. Such "pseudoreplication" (Hurlbert 1984) is impossible to avoid when specific questions and limited data narrow the sampling frame.

Finally, any difference in the techniques used by the two samplers (R. H. Green in 1973; R. C. Bailey in 1986) may have "created" the observed differences in data from the two years of sampling. We tried to minimize any differences by carefully matching the sampling method, but hand sampling with SCUBA is bound to result in some human bias. Such a bias may explain why a greater proportion of small mussels was collected at both depths in the 1986 sample. However, the pronounced differences in length-frequency distributions, growth rates, and densities between 1973 and 1986 seem greater than what can reasonably be attributed to bias.

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