Non-annual external annuli in the freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoidea**

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SUMMARY

1. Two species of freshwater mussels, *Lampsilis radiata siliquoidea* and *Anodonta grandis grandis* were measured and permanently marked with pointed, plastic tape positioned at the postero-lateral edge of the shell. Mussels were returned to original conditions at two sites in an oligotrophic lake, retrieved at yearly intervals, re-measured, and external annuli that had been added since marking were counted.

2. External annuli were formed much less frequently than annually; the overall median number of annuli formed each year was 0.5. In one of the four populations studied, the rate of annulus formation was >1 in small animals and <1 in large ones. Many mussels showed no new external annuli at all, even several years after marking.

3. Ford–Walford plots of shell annuli did not yield consistent indices of shell growth. Repeated measurement of mussels in successive years showed that estimates of growth based on shell annuli consistently overestimated real shell growth.

Introduction

An annulus in the shell of a bivalve is customarily considered to consist of two bands: one wide and light coloured, and one narrow and dark coloured. Concentric rings of light and dark are visible on the outsides of the valves, widest at the shell's posterior end, narrowing ventrally and anteriorly, to nearly zero at the hinge on the dorsal side. Several authors have presented theoretical explanations for their formation (Biedermann, 1902; Isely, 1914; Coker *et al.*, 1922; Chamberlain, 1930; Sebestyen, 1942; Agrell, 1949; Haskin, 1954; Crowley, 1957; Wilbur, 1964; Beedham, 1965; Lutz & Rhoads, 1977; Rhoads & Lutz, 1980; Saleuddin & Petit, 1983; Beukema, Knol & Cadee, 1985). The differently coloured bands are

thought to be due to the different relative content of calcium and organic matter caused by temperature variations or other changes (e.g. Crowley, 1957) and/ or anaerobiosis (e.g. Lutz & Rhoads, 1977).

Annular rings have long been used to determine bivalve age and growth rates, even though data supporting this practice are few. Isely (1914) believed that '...[w]inter rings, especially where environmental conditions are stable, are usually sufficiently regular for use as indicators of age...', although in the same year Crozier (1914) found so much variation in the formation of annuli that he questioned their use in determining age. Chamberlain (1930) reviewed work on freshwater bivalve annuli from 1854 and concluded that the dark rings in shells are caused by the slowing of growth and that, although dark lines could result from almost any disturbance, those caused by winter are especially dark. Haskin (1954) found external annuli 'particularly useful in provid-

ing information rapidly on the age composition of the population'. Recently, Imlay (1982) considered them 'perhaps 95% reliable' in determining the age of individual mussels.

The annual formation of external annuli in freshwater mussels has been assumed by many ecologists (e.g. Coker *et al.*, 1922; Sebastyen, 1942; Crowley, 1957; Negus, 1966; Heard, 1975; Coon, Ekblad & Trygstad, 1977; Haukioja & Hakala, 1978; McCuaig & Green, 1983; Mitchell, 1984; Hinch, Bailey & Green, 1986; Bauer, 1987; Hanson, Mackay & Prepas, 1988; Jansen & Hanson, 1990; Heller, 1990; Huebner, Malley & Donkersloot, 1990). The assumption that external annuli are laid down yearly is only rarely checked, and recent tests yield equivocal results. Negus (1966) marked 575 mussels with a dentist's drill, of which fifty-six were recaptured 1 year later. Of these, forty-three could be 'aged reliably' but of these, six formed no rings, fifteen formed one ring and twenty-two formed two rings. Ghent, Singer & Johnson-Singer (1978) cleaned, dried and spray-painted one valve of each of thirty-eight mussels. Of the fourteen they examined a year later, all of them formed 'one (and only one) continuous dark ring following additional late-summer growth beyond their outlined sizes on the day of painting'. Haukioja & Hakala (1978) carved numbers into the shell of several mussels and counted the number of annuli formed after 1 and 3 years. Although they conclude that '...in most cases the number of new rings coincided with the number of winters that had elapsed', 36% of the mussels surveyed formed an inappropriate number of annuli.

In spite of the weak justification, Tevesz & Carter (1980), in a review of unionid shell growth stated that '...these bands yield absolute age information...'. Most recent studies of growth in freshwater mussels suggest that annuli are formed annually (e.g. Huebner, Malley & Donkersloot, 1990) and their support for this assumption can usually be traced either to Coker *et al.* (1921) or Isely (1914). Coker *et al.* (1921) presented the following evidence:

'Some years ago when collecting mussels in southern Michigan it was observed that the shells of the fat muckets were all marked with several conspicuous rings which were approximately equally spaced on all the mussels of a bed. It seemed a natural inference that these dark rings represented winter periods and thus afforded a means of age determination. At another time, upon examination of

mussels which had been measured and placed in crates in the river 2 years previously, it was observed that there were rings apparently corresponding to the two winters which had elapsed since the date of the original measurement...',

and Isely (1914) concluded:

'...that the concentric rings are by no means dependable as absolute annual rings is well shown in many specimens...'.

Wilbur & Owen (1964) advised: 'Clearly, the use of rings as an indicator of age requires their establishment as annual marks for the species under study'. Marine studies using radio-isotopes (Jones, 1983) suggest that counting annuli overestimates age in some species (e.g. Krantz, Jones & Williams, 1984). We have been unable to find any rigorous tests of the assumption that freshwater mussels form one and only one annulus each year.

The increasing appreciation of the importance of freshwater mussel populations (Downing & Downing, 1992) renders the accurate analysis of age and growth essential. Their unselective feeding and high filtering rates affect phytoplankton populations (Winter, 1978; Price & Schiebe, 1978; Tessier *et al.*, 1984) and stimulate microinvertebrate production (Sephton, Paterson & Fernando, 1980). They can make up much of the benthos biomass in lakes (Magnin & Stanczykowska, 1971; Golightly & Kosinsky, 1981), their juveniles are important food for fish (Negus, 1966) and small mammals (Coker *et al.*, 1922; Cvancara, 1970), and their glochidia can be fatal parasites of fishes (Lefevre & Curtis, 1910; Matteson, 1948). Freshwater mussels also have an expanding role in applied ecological research. They are of increasing importance in pollution monitoring and detection (Day, Metcalfe & Batchelor, 1990; Metcalfe & Charlton, 1990); acidification (Pynnönen, 1990) and alkalinity budgets (Green, 1980); palaeontology (Green, 1972), and archaeology (Kunz, 1893; Hill, 1983). Economically they are the basis of the world's freshwater pearl industry (Coker *et al.*, 1922; Kat, 1982) while the Asian clam (*Corbicula fluminea* Müller; Lauritsen & Mozley, 1989; Leff *et al.*, 1990) and the Zebra mussel (*Dreissena polymorpha* Pallas; Hebert *et al.*, 1991) threaten disaster. Several indigenous species of freshwater mussels are now endangered (Strayer, 1980; DiStephano, 1984; Miller, Payne & Siemsen, 1986).

In the early 1980s we initiated a study to determine the age and growth of unionid mussels in several

temperate lakes. Although some (e.g. Hendelberg, 1960) have advocated more intricate methods of age determination, we chose to use the most commonly used method: the counting of external annuli. The project was discontinued after 3 years' work because we questioned the validity of external annuli as indicators of age. We then set up this study to test the hypothesis that external annuli are formed annually in two common species of unionid mussels under natural lake conditions. If data failed to uphold this hypothesis, we also sought to test the hypothesis that standard Ford–Walford plots, based on the regularity rather than the annularity of growth annuli (see McCuaig & Green, 1983), would yield an unbiased index of growth in these species of unionid mussels.

Study area

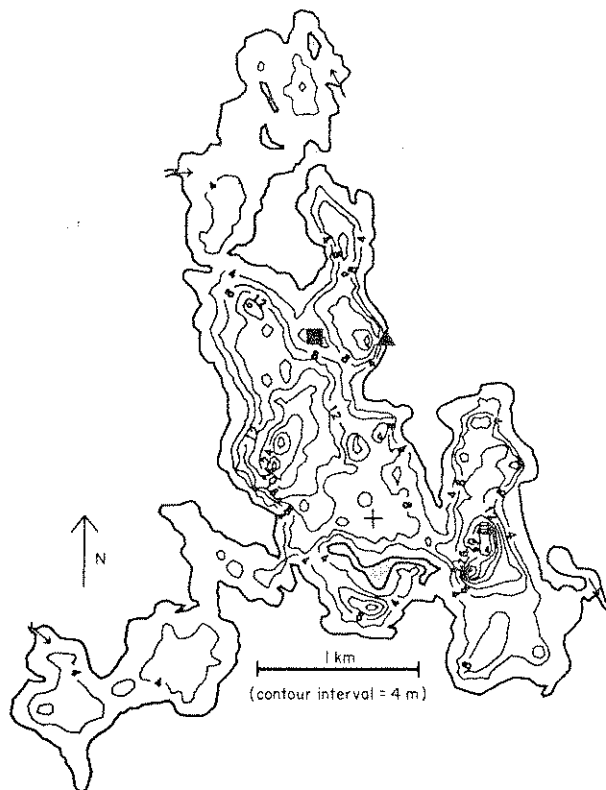This study was performed at two sites in Wabana Lake, Minnesota (Fig. 1), a 863 ha meandered lake

Fig. 1 Morphometric map of Wabana Lake, Minnesota, showing the two sampling sites. The contour interval is 4 m. ■, position of the sand-bar site; ▲, position of the bay site; and +, the position 47°24′N and 93°31′W. Arrows indicate direction of inflowing and outflowing streams.

formed by the stranding of ice blocks in glacial till at the end of the last glaciation ($\approx 12\,000$ yr BP). Wabana Lake is oligotrophic ($11\,\mu g\,l^{-1}$ total P; $2.4\,\mu g\,l^{-1}$ chlorophyll a), well buffered (total alkalinity: $110\,mg\,l^{-1}$), and practically uncoloured (8 Pt-Co units) (Heiskary & Wilson, 1990). The climate is temperate and the lake is ice-covered from December until April. The temperature of the mussels' substrate is near 0°C in winter, increasing to 8°C by the second week of May, a high of 23°C in early August, and falling rapidly beginning in late August (W. Downing, unpublished data).

Nearshore sediments are composed of mixtures of silt, sand, and gravel, depending upon wind exposure. Several shallow sandbars (<3 m depth) are found in open parts of the lake. Indigenous mussel populations are found around >70% of the perimeter and on all sandbars (J. Downing, unpublished data) and consist of primarily *Lampsilis radiata siliquoidea* (Barnes) and *Anodonta grandis grandis* (Say) (voucher specimens are deposited at the Science Museum of Minnesota, St Paul, Minnesota). Populations of both species were present at each of our sampling sites (Fig. 1); one on a sandbar (≈ 2 m depth) and one in a bay on the eastern shore of Wabana Lake (≈ 1.5 m depth). Both sites are exposed to the prevailing west-north-westerly winds. Sediments at the sandbar site were composed of fine sand, gravel and cobble, while sediments at the bay site were uniform sand. Sand at both sites was underlain by hard-packed sand and clay, thus there is little summer endobenthic population at these sites (cf. Amyot & Downing, 1991). There is only moderate recreational development on this lake and there is no evidence of recent chemical or biological change.

Methods

The hypothesis that annuli are formed annually was tested in both species and at both sites by marking the edges of the shells at a recorded time, returning the mussels to their natural habitat, then measuring the dimensions and counting the number of external growth annuli formed after an appropriate growth period. Traditionally, annular growth studies of marine bivalves have marked the shell edge at a known point in time by removing the animal from the water and filing grooves at the shell margin (e.g. Orton, 1926; Stevenson & Dickie, 1954). We used

the gentler procedure of removing the animal from the water briefly, gluing on a pointed plastic label (Dymo[TM]) with the point even with the shell edge at the posterior—ventral margin of one valve of each marked mussel, measuring and photographing, and quickly returning the marked animal to the water. The posterior—ventral margin was chosen for marking because shell growth is greatest at this point (Chamberlain, 1930) and because the label can be seen above the sediment surface when the mussel is in its natural position. The label was glued in place with non-toxic, instant setting, waterproof dental cement (Healthco Fill-It[TM]) and individual animals were recognized in subsequent years using a numerical code embossed on the plastic label.

Twenty-three *Lampsilis* and twenty-one *Anodonta* were marked at the sandbar site in 1988 and fifty *Lampsilis* and thirty-four *Anodonta* were marked at the bay site during August of 1986 and 1988, thus annulus formation was determined in as many as 128 marked mussels as could be relocated, covering between 3 and 6 growth-years. As full a range as possible of mussels was marked (38.8–109.9 mm length). The number of annuli formed since marking was determined by each of two of the authors (W.L.D. and J.S.) in August of 1990 and again in August of 1991. The area where marked mussels were released in previous years was examined by divers and all visible marked mussels were retrieved. Mussels were handled gently, kept at lake temperature in a large bucket of ambient lake water, and were measured, examined and returned to the water within 1 h of collection. One annulus was defined as a paired dark and light ring visible on the outside of the valve. Two annuli were counted if two dark rings and two light rings were visible following the plastic marker, three annuli were counted if three dark rings and three light rings were visible following the marker, etc. Growth of mussels is probably minimal after the month of August, as much of the population becomes endobenthic in September, passing the winter buried in the sand (W. Downing, unpublished data). Fractional numbers of annuli were sometimes found if light and dark rings did not occur in pairs. Annulus counts were made independently by the two readers, and sometimes differed by 0.5 annulus but never by more than one annulus. Where the two readers disagreed, the judgement of one was not chosen over the other, but the data were recorded as the average

of the two readings. Re-examination of shells to reconcile differences was not attempted because differences were infrequent and considered negligible. The number of annuli formed per year was calculated by dividing the apparent number of annuli formed by the number of years since marking. Tests for significance of departures of the number of annuli actually formed from the number that would have been formed if one annulus had been laid down each year were performed using a Wilcoxon signed-rank test (Conover, 1974).

Tests of the accuracy of growth estimates made by the Ford—Walford growth equation applied to external growth annuli were made on the bay site mussels during 1988 and 1989. In 1988, the height of each mussel was measured using an electronic caliper (± 0.1 mm) exactly perpendicular to the hinge at the umbo. The use of the hinge as a reference point increased precision: 95% of measurement errors in 630 repeated trials were ≤ 1 mm. In 1989, the same height measurement was repeated on each marked mussel, except that an additional measurement was made of the distance perpendicular to the hinge at the umbo to the dark band or 'winter ring' closest to the margin of the valve. If annuli are formed annually, then the measured change in shell height perpendicular to the hinge from August 1988 to August 1989, and the difference between the shell height in 1989 and the distance from the hinge to the most recently formed 'winter ring', should be the same. In other words, Ford—Walford plots of actual heights in subsequent years, and Ford—Walford plots of 1989 height against 1988 'height' guessed from external annuli, should not be significantly different. This hypothesis was tested using ANCOVA (Gujarati, 1978).

Results

The number of apparent growth annuli formed was much fewer than the number of years elapsed since marking, but varied widely. Out of 127 assessments of annulus formation, after 2–5 years elapsed since marking, fourteen showed no annulus formation and forty failed to form even one complete annulus. One 65-mm long *Lampsilis* failed to grow at all and thus did not form any dark or light external shell band after 5 years had elapsed since marking. The most rapid annulus formation was found in one small
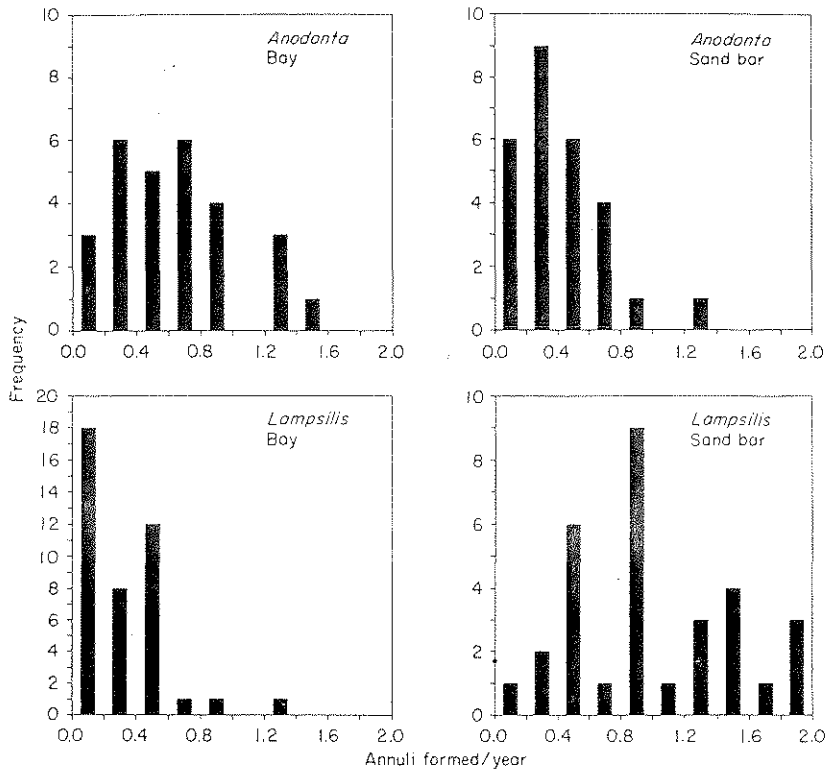
Fig. 2 Frequency of formation of recognizable, external growth annuli of two species of freshwater mussels at two sites in Wabana Lake. For example, the bar between 0 and 0.2 indicates the number of mussels that formed a number of annuli that was ≥ 0 and <0.2. If annuli were formed annually in these populations, then all of the estimates would fall in the range of $1.0-1.2$.

Lampsilis at the sandbar site, that formed four annuli in just 2 years.

The average rate of annulus formation was very low (Fig. 2). Although many authors have based studies on the assumption that freshwater mussels form one distinct external annulus per year, *Anodonta* at both the bay and sandbar sites formed an average 0.65 and 0.42 annulus yr^{-1}, respectively, while *Lampsilis* at the bay site formed an average 0.3 annulus yr^{-1}. Wilcoxon signed-rank tests of the hypothesis that these populations form one external annulus each year firmly reject this hypothesis ($P = 0.0007$, $P < 0.0001$, and $P < 0.0001$, respectively). Only *Lampsilis* at the sandbar site formed a number of annuli that did not differ significantly ($P > 0.05$) from the number of years elapsed since marking (Fig. 2), but this is an artefact resulting from the fact that small *Lampsilis* at this site formed >1 annulus yr^{-1}, while large ones formed <1 annulus yr^{-1} (Fig. 3; $r^2 = 0.33$, $P = 0.0007$).

Fig. 4 compares actual mussel growth, measured in 2 successive years, to that which would be inferred from estimates of the position of external annuli. Fitting the Ford–Walford approximation of the von Bertalanffy growth equation (Ford, 1933; Walford,
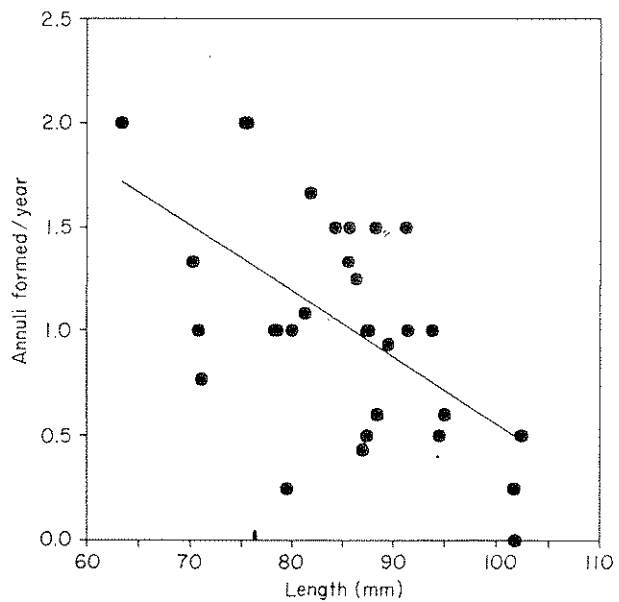

Fig. 3 Relationship of total shell length and the frequency of annulus formation in *L. radiata siliquoidea* at the sand-bar site on Wabana Lake. Length was measured as maximum shell length, on an anterior to posterior axis. The line shown is the least squares regression of the relationship ($r^2 = 0.33$; $n = 31$; $P = 0.0007$). No such relationship was seen in the other three species–site combinations.
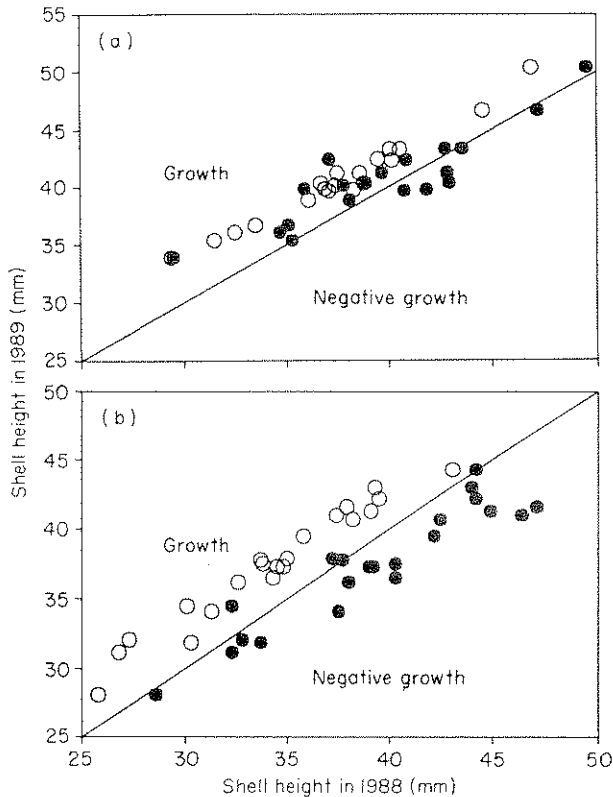
Fig. 4 The Ford–Walford plot of the relationship between the shell height in 2 successive years determined from direct shell measurement (●) or by inference from external annuli (○) in (a) *A. grandis grandis* and (b) *L. radiata siliquoidea* at the bay site (Fig. 1) in Wabana Lake, Minnesota. The straight line indicates the 1:1 relationship that would have been seen if no growth had occurred. Points falling below this line are mussels that were shrinking.

1946) to the data in Fig. 4 shows in both cases that the slopes of the Walford relationships were lower when the real changes in shell height were considered than when changes in height over consecutive years were inferred from annuli. ANCOVA of the data in Fig. 4 shows that the growth inferred from annuli greatly overestimated actual growth in these two populations of mussels (*P* < 0.0005).

Discussion

Counting the number of external annuli in these mussels would not yield a reliable index of age or growth, as mussels at three out of four species–site combinations formed many fewer than one annulus per year. At all sites, mussels are probably much older

than the number of external growth annuli would suggest, and at one site we obtained evidence that the rate of annulus formation is size dependent. Future studies on the age and growth of mussels should rigorously test the assumption that annuli are formed annually, and previous studies of mussel age and growth that have failed to test this assumption should be interpreted with great caution.

Tests of the hypothesis that Ford–Walford plots can yield realistic indices of mussel growth were equally pessimistic. In fact, in many of the mussels, especially *L. radiata siliquoidea*, animals were smaller in successive years. Such animals usually formed no annuli at the posterior–ventral margin of the shell (Fig. 2). Predictions of height at age made by fitting the von Bertalanffy equation to real growth data are nonsensical because they suggest that maximum shell height is attained at about 30 and 40 mm in *Lampsilis* and *Anodonta*, respectively. These figures are less than many of the observed shell heights (Fig. 4). This and other growth algorithms cannot deal with negative growth in animals of advanced size. Other repercussions of negative growth on the interpretation of molluscan growth data will be explored in a future paper. These results warn against the use of annuli in age and growth studies of freshwater mussels. Even if annual rings could be identified reliably, in shrinking mussels the apparent growth found near the current edge of the valve may have been laid down many years ago, depending upon how long the mussel failed to form annuli (Fig. 2) and how many positive growth years have already been removed.

Wilbur & Owen's (1964) caution is well justified. In the populations that we examined, external annuli appear to be formed much less frequently than annually. The rate of formation of these annuli can vary systematically with body size. Finally, the use of Walford plots of shell annuli do not yield reliable indices of actual shell growth. Not only is it unclear what the external annuli represent, but it cannot be assumed that the growth appearing at the edge of the valve, is the most recent shell growth.

Acknowledgments

References

Agrell I. (1949) The shell morphology of some Swedish unionides as affected by ecological conditions. *Arkiv for Zoologi*, **41A**, 1–30.

Amyot J-P. & Downing J.A. (1991) Endo- and epibenthic distribution of the unionid mollusc *Elliptio complanata*. *Journal of the North American Benthological Society*, **10**, 280–285.

Bauer G. (1987) Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology* **56**, 691–704.

Beedham G.E. (1965) Repair of the shell in species of *Anodonta*. *Proceedings of the Zoological Society of London*, **145**, 107–126.

Beukema J.J., Knol E. & Cadee G.C. (1985) Effects of temperature on the length of the annual growing season in the Tellinid bivalve *Macoma balthica* living on tidal flats in the Dutch Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **90**, 129–144.

Biedermann Von W. (1902) Ueber die bedeutung von krystallisationsprozessen bei der bildung der skelette wirbelloser tiere, namentlich der molluskenschalen. *Zeitschrift für Allgemeine Physiologie*, **1**, 154–208.

Chamberlain T.K. (1930) Annual growth in freshwater mussels. *Bulletin of the United States Bureau of Fisheries*, **46**, 713–739.

Coker R.E., Shira A.F., Clark H.W. & Howard A.D. (1922) Natural history and propagation of fresh-water mussels. *Bulletin of the United States Bureau of Fisheries*, **37**, 75–181.

Conover W.J. (1971) *Practical Non-Parametric Statistics*. Wiley, New York, N.Y.

Coon T.G., Eckblad J.W. & Trygstad P.M. (1977) Relative abundance and growth of mussels (Mollusca: Eulamellibranchia) in pools 8, 9 and 10 of the Mississippi River. *Freshwater Biology*, **7**, 279–285.

Crowley T.E. (1957) Age determination in *Anodonta*. *Journal of Conchology*, **24**, 201–207.

Crozier W.J. (1914) The growth of the shell in the lamelli-branch *Dosinia discus* (Reeve). *Zoologische Jahrbucher Abteilung für Anatomie und Ontogenie der Tiere*, **38**, 577–584.

Cvancara A.M. (1970) Mussels (Unionidae) of the Red River Valley in North Dakota and Minnesota, U.S.A. *Malacologia*, **10**, 57–92.

Day K.E., Metcalfe J.L. & Batchelor S.P. (1990) Changes in intracellular free amino acids in tissues of the caged mussel, *Elliptio complanata*, exposed to contaminated environments. *Archives of Environmental Contamination and Toxicology*, **19**, 816–827.

DiStephano R.J. (1984) Freshwater mussels (Bivalvia: Unionidae) of Horse Lick Creek, Rockcastle River, Kentucky. *Nautilus*, **98**, 110–113.

Downing J.A. & Downing W.L. (1992) Spatial aggregation, precision and power in surveys of freshwater mussel populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 985–991.

Ford E. (1933) An account of the herring investigations conducted at Plymouth during the years from 1924–1933. *Journal of the Marine Biological Association of the United Kingdom*, **19**, 305–384.

Ghent A.W., Singer R. & Johnson-Singer L. (1978) Depth distributions determined with SCUBA, and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. *Canadian Journal of Zoology*, **56**, 1654–1663.

Golightly C.G., Jr. & Kosinsky R.J. (1981) Estimating the biomass of freshwater mussels (Bivalvia: Unionidae) from shell dimensions. *Hydrobiologia*, **80**, 263–267.

Green R.H. (1972) Distribution and morphological variation of *Lampsilis radiata* (Pelecypoda, Unionidae) in some central Canadian lakes. *Journal of the Fisheries Research Board of Canada*, **29**, 1565–1570.

Green R.H. (1980) Role of a unionid clam population in the calcium budget of a small arctic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 219–224.

Gujarati D. (1978) *Basic Econometrics*. McGraw-Hill, New York, N.Y., 462 pp.

Hanson J.M., Mackay W.C. & Prepas E.E. (1988) The effects of water depth and density on the growth of a unionid clam. *Freshwater Biology*, **19**, 345–355.

Haskin H.H. (1954) Age determination in molluscs. *Transactions of the New York Academy of Science Series II*, **16**, 300–304.

Haukioja E. & Hakala T. (1978) Measuring growth from shell rings in populations of *Anodonta piscinalis*. *Annali Zoologica Fennici*, **15**, 60–65.

Heard W.H. (1975) Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia*, **15**, 81–103.

Hebert P.D.N., Wilson C.C., Murdoch M.H. & Lazar R. (1991) Demography and ecological impacts of the

invading mollusc *Dreissena polymorpha. Canadian Journal of Zoology*, **69**, 405–409.

Heiskary S.A. & Wilson C.B. (1990) *Minnesota Lake Water Quality Report*, 2nd edn. Minnesota Pollution Control Agency, St Paul, Minnesota.

Heller J. (1990) Longevity in molluscs. *Malacologia*, **31**, 259–295.

Hendelberg J. (1960) The fresh-water pearl mussel, *Margaritifera margaritifera* (L.). *Report of the Institute of Freshwater Research Dröttningholm*, **41**, 141–171.

Hinch S.G., Bailey R.C. & Green R.H. (1986) Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in sand and mud: a reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 548–552.

Hill F.C. (1983) Unexplained occurrence of the mactrid bivalve, *Rangia cuneata*, from the Arrowhead Farms Indian site near Louisville, Kentucky. *Nautilus*, **97**, 79–81.

Huebner J.D., Malley D.F. & Donkersloot K. (1990) Population ecology of the freshwater mussel *Anodonta grandis grandis* in a Precambrian shield lake. *Canadian Journal of Zoology*, **68**, 1931–1941.

Imlay M.J. (1982) Use of shells of freshwater mussels in monitoring heavy metals and environmental stresses. *Malacological Review*, **15**, 1–14.

Isely F.B. (1914) Experimental Study of the Growth and Migration of Fresh-Water Mussels. Appendix III to the *Report of the U.S. Commissioner of Fisheries for 1913*, Bureau of Fisheries Document No. 792, Government Printing Office, Washington, D.C.

Jansen W.A. & Hanson J.M. (1990) Estimates of the number of glochidia produced by clams (*Anodonta grandis simpsoniana* Lea), attaching to the yellow perch (*Perca flavescens*), and surviving to various ages in Narrow Lake, Alberta. *Canadian Journal of Zoology*, **69**, 973–977.

Jones D.S. (1983) Sclerochronology: reading the record of the molluscan shell. *American Scientist*, **71**, 384–391.

Kat P.W. (1982) Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). *Malacological Review*, **15**, 119–127.

Krantz D.E., Jones D.S. & Williams D.F. (1984) Growth rates of the sea scallop, *Placopecten magellanicus*, determined from the $^{18}O/^{16}O$ record in shell calcite. *Biological Bulletin* **167**, 186–199.

Kunz G.F. (1893) On the occurrence of pearls in the United States, and shall we legislate to preserve the fisheries. *Transactions of the American Fisheries Society*, 16–34.

Lauritsen D.D. & Mozley S.C. (1989) Nutrient excretion by the Asiatic clam *Corbicula fluminea. Journal of the North American Benthological Society*, **8**,134–139.

Lefevre G. & Curtis W.C. (1910) Studies on the reproduction and artificial propagation of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries*, **30**, 105–202.

Leff L.G., Burch J.L. & McArthur J.V. (1990) Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal plain stream. *Freshwater Biology*, **24**, 409–416.

Lutz R.A. & Rhoads D.C. (1977) Anaerobiosis and a theory of growth line formation. *Science*, **198**, 1222–1227.

Magnin E. and Stanczykowska A. (1971) Quelques données sur la croissance, la biomasse et la production annuelle de trois mollusques Unionidae de la région de Montréal. *Canadian Journal of Zoology*, **49**, 491–497.

Matteson M.R. (1948) Life history of *Elliptio complanatus* (Dillwyn, 1817). *American Midland Naturalist*, **40**, 690–723.

McCuaig J.M. & Green R.H. (1983) Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 436–442.

Metcalfe J.L. & Charlton M.N. (1990) Freshwater mussels as biomonitors for organic industrial contaminants and pesticides in the St. Lawrence River. *Science of the Total Environment*, **97–8**, 595–615.

Miller A.C., Payne B.F. & Siemsen T. (1986) Description of the habitat of the endangered mussel *Plethobasus cooperianus. Nautilus*, **100**, 14–18.

Mitchell H.M. (1984) *Investigations of the relationship between unionid clam shell parameters (Elliptio complanata) and mean chlorophyll a concentrations in lakes.* M. Sc. thesis, University of Toronto, 91 pp.

Negus C.L. (1966) A quantitative study of growth and production of unionid mussels in the River Thames at Reading. *Journal of Animal Ecology*, **35**, 513–532.

Orton J.H. (1926) On the rate of growth of *Cardium edule*. Part I. Experimental observations. *Journal of the Marine Biological Association of the United Kingdom*, **14**, 239–279.

Price R.E. & Schiebe F.R. (1978) Measurements of velocity from excurrent siphons of freshwater clams. *Nautilus*, **92**, 67–69.

Pynnönen K. (1990) Physiological responses to severe acid stress in four species of freshwater clams (Unionidae). *Archives of Environmental Contamination and Toxicology*, **19**, 471–478.

Rhoads D.C. & Lutz R.A. (eds) (1980) *Skeletal Growth of Aquatic Organisms*. Plenum Press, New York.

Saleuddin A.S.M. & Petit H.P. (1983) The mode of formation and the structure of the periostracum. *The Mollusca* (Eds A.S.M. Saleuddin and K.M.

Wilbur), Vol. 4 Part 1, pp. 199–234. Academic Press, New York, N.Y.

Sebestyen O. (1942) Notes on the growth of Unionidae in Lake Balaton. *Rivista di Biologia*, **33**, 244–253.

Sephton T.W., Paterson C.G. & Fernando C.H. (1980) Spatial interrelationships of bivalves and nonbivalve benthos in a small reservoir in New Brunswick, Canada. *Canadian Journal of Zoology*, **58**, 852–859.

Stevenson J.A. & Dickie L.M. (1954) Annual growth rings and rate of growth of the giant scallop, *Placopecten magellanicus* in the Digby Area of the Bay of Fundy. *Journal of the Fisheries Research Board of Canada*, **11**, 660–671.

Strayer D. (1980) The freshwater mussels (Bivalvia: Unionidae) of the Clinton River, Michigan, with comments on man's impact on the fauna, 1870–1978. *Nautilus*, **94**, 142–149.

Tessier A., Campbell P.G.C., Auclair J.C. & Bisson M. (1984) Relationships between the partitioning of trace metals in sediments and their accumulation in the tissues of the freshwater mollusc *Elliptio complanata* in a mining area. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1463–1472.

Tevesz M.J.S. & Carter J.G. (1980) Environmental relationships of shell formation and structure of unionacean bivalves. *Skeletal Growth of Aquatic Organisms* (Eds D.C. Rhoads and R.A. Lutz), pp. 295–322. Plenum Press, New York.

Walford L.A. (1946) A new graphic method of describing the growth of animals. *Biological Bulletin*, **90**, 141–147.

Wilbur K.M. (1964) Shell formation and regeneration. *Physiology of Mollusca* (Eds K.M. Wilbur and C.M. Yonge), pp. 243–282. Academic Press, New York.

Wilbur K.M. & Owen G. (1964) Growth. *Physiology of Mollusca* (Eds K.M. Wilbur and C.M. Yonge), pp. 211–241. Academic Press, New York.

Winter J.E. (1978) A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture*, **13**, 1–33.