

Length-specific growth rates in freshwater mussels (Bivalvia: Unionidae): extreme longevity or generalized growth cessation?

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SUMMARY

1. North American lacustrine freshwater mussels (Bivalvia: Unionidae) are one of the world's most imperilled groups of organisms. Knowledge of their age structure and longevity is needed for the understanding and management of mussels. Current methods for age estimation in freshwater mussels are insufficient and may have resulted in an erroneous view of the ages of lacustrine freshwater mussels.
2. We collected growth data through mark-recapture in Minnesota and Rhode Island, U.S.A., examining four lentic populations of three of the most common species of freshwater mussels, *Elliptio complanata*, *Lampsilis siliquoidea*, and *Pyganodon grandis*. Using an inversion of the von Bertalanffy growth equation, we estimated age at length from length-specific growth relationships.
3. In some populations, lacustrine mussels may be much older than previously predicted. Ages predicted from actual growth rates suggest that individuals in some populations frequently reach ages in excess of a century, placing unionid mussels among the Earth's longest-lived animals. Alternatively, if growth has only recently slowed in these populations, generalized growth cessation may be occurring over a broad distributional range of some common North American lacustrine mussels.

Keywords: annuli, von Bertalanffy, freshwater mussels, longevity, Unionidae

Introduction

North American freshwater mussels (Bivalvia: Unionidae) are an economically and ecologically important fauna. They have been the foundation of several multimillion-dollar industries (Fassler, 1994) and their filter feeding may affect water quality (Green, 1980; Nalepa, Gardner & Malczyk, 1991) and phytoplankton ecology (Winter, 1978). Despite their importance, North American unionid mussels are presently one of the Earth's most imperilled groups of

organisms (Williams *et al.*, 1993). Even as many of these bivalves are at the brink of extinction, however, we are faced with a considerable deficit in our knowledge of such basic biological parameters as their growth and longevity.

Historically, information on the growth rates and ages of freshwater bivalves has been derived by assuming that shell structures such as internal and external rings, or annuli, were produced annually (e.g. Isley, 1914; Chamberlain, 1931; Negus, 1966). Attempts to validate this assumption have frequently failed, however, or have produced conflicting results (e.g. Negus, 1966; Ghent, Singer & Johnson-Singer, 1978; Haukioja & Hakala, 1978; Neves & Moyer, 1988). Moreover, recent studies indicate that the use of

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annuli may substantially underestimate age and overestimate growth in freshwater mussels (Downing, Shostell & Downing, 1992; Kesler & Downing, 1997). Despite the absence of reliable, rigorous data to support the veracity of annulus-based techniques, many studies have employed them to estimate age and growth in unionid mussels, generally yielding longevity estimates of less than 20 years (Table 1; see also Heller, 1990). If annuli are not valid annual markers, however, these studies may have provided a dangerously inaccurate portrayal of mussel age and growth dynamics.

Although several alternative methods of age estimation have been attempted for marine bivalve species, they are unlikely to be suitable for application to freshwater mussels. For example, the use of stable oxygen isotopes is contingent upon significant annual growth increments (Krantz, Jones & Williams, 1984) which are often lacking in freshwater mussels (Downing *et al.*, 1992; Downing & Downing, 1993; Kesler & Downing, 1997). Likewise, uranium-series radioisotope dating (e.g. Turekian *et al.*, 1975; Turekian, Cochran, & Nozaki, 1979) provides insufficient resolution for application to freshwater mussels (J.L. Anthony & J.A. Downing, unpublished observation).

Inversion of the von Bertalanffy growth equation: a potential alternative

The von Bertalanffy growth equation, which has been routinely applied to characterize molluscan growth

Table 1 Longevity estimates inferred from annuli for the freshwater unionid mussels *Elliptio complanata*, *Lampsilis siliquoidea*, and *Pyganodon grandis*

Species	Age (years)	Source
<i>Elliptio complanata</i>	14*	Hinch & Stephenson (1987)
<i>E. complanata</i>	17*	Metcalfe-Smith & Green (1992)
<i>E. complanata</i>	12	Matteson (1948)
<i>E. complanata</i>	18	Strayer <i>et al.</i> (1981)
<i>E. complanata</i>	19	Ghent <i>et al.</i> (1978)
<i>Lampsilis siliquoidea</i>	19	Grier (1922)
<i>L. siliquoidea</i>	13	Chamberlain (1931)
<i>Pyganodon grandis</i>	14	Ghent <i>et al.</i> (1978)
<i>Pyganodon grandis simpsoniana</i>	11	Hanson, Mackay & Prepas (1988)

*Estimates are based on counts of internal annuli while all other estimates are based on external annuli.

(Brousseau, 1979; Bretos, 1980; Hughes & Roberts, 1980; Berg & Alatalo, 1985; Parada *et al.*, 1989; Bauer, 1992), may be an accessible alternative to annulus-based or isotopic age estimation techniques. Described by von Bertalanffy (1938), the model is expressed mathematically as

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

where L_t represents the length of the organism at time t (age), L_∞ (asymptotic length) represents the theoretical maximum length an organism would reach at infinite age, K (Brody's growth constant) depicts the rate at which the organism's size approaches L_∞ , and t_0 (the theoretical time at which $L_t = 0$) positions the growth curve horizontally (Ricker, 1975; see also Fabens, 1965). Although generally used to describe the rate of growth where body size and age are known or can be measured directly, the von Bertalanffy growth equation (eqn 1) can be algebraically rearranged to solve for age (t) at length (L_t) as

$$t = t_0 + \ln\{[1 - (L_t/L_\infty)] / -K\} \quad (2)$$

Optimally, the equation's three parameters, L_∞ , K , and t_0 would be determined by following the growth of organisms through their lives, but data are nearly always incomplete or based upon only a few individuals. The equation's parameters must therefore often be estimated using an alternative method such as linear regression analyses of the Ford-Walford relationship (Ford, 1933; Walford, 1946). This relationship, utilizing mark and recapture growth data from a subset of a population, relates the length or mass of marked organisms at an initial capture with their length or mass after living at large for some known period of time (Ricker, 1975). Using simple mark and recapture techniques, we can estimate L_∞ and K for the population by employing eqns 3 and 4, respectively

$$L_\infty = [a / (1 - \beta)] \quad (3)$$

$$K = -\ln \beta \quad (4)$$

where a is the y intercept and β is the slope of the linear regression of the mark and recapture derived Ford-Walford relationship (Ricker, 1975).

In the absence of a known age-at-length relationship, one is unable to estimate the parameter t_0 (Hampton, 1991) and must frequently assume that

$t_0 = 0$ (Labelle *et al.*, 1993). Alternatively, Southward & Chapman (1965) provide a useful interpretation of the von Bertalanffy growth equation, which uses the parameter L_0 (length at $t = 0$) rather than t_0 in order to position the growth curve horizontally (see also Fabens, 1965):

$$L_t = L_\infty - (L_\infty - L_0)e^{-Kt} \quad (5)$$

Although estimation of L_0 also requires independent estimates of age (Fabens, 1965), published estimates of the size of mussel larvae, or glochidia, provide a plausible approximation of mussel size at $t = 0$, or L_0 . Equation 5 can then be algebraically rearranged to solve for t as

$$t = \ln[(L_t - L_\infty)/(L_0 + L_\infty)] / -K \quad (6)$$

The concept of using the von Bertalanffy growth equation to estimate ages from length-specific growth rates has already been applied to a variety of molluscan species (e.g. Bretos, 1980; Hughes & Roberts, 1980; Narisimham, 1981; Berg & Alatalo, 1985). Unfortunately, when the equation has been used to construct growth curves for unionid mussels, growth rates derived from annuli have generally been used to estimate the equation's parameters (e.g. McCuaig & Green, 1983; Day, 1984; Hinch, Bailey & Green, 1986). If growth rings are not annually formed, these age estimates must be erroneous. Even when actual growth increments have been used to estimate the equation's parameters, however, the application has been inadequate. For example, Parada *et al.*'s (1989) mark and recapture study of a South American unionid species only measured growth in 1 year, is unlikely to accurately reflect annual variability in mussel growth, and might skew the resultant age estimates.

The development of new methods for estimating ages and growth rates of North American freshwater mussels is necessary to ensure effective mussel conservation and management. The proper application of the inversion of the von Bertalanffy growth equation may offer a viable alternative to conventional techniques. The purpose of this study is to use information from mark and recapture growth measurements to evaluate the ability of the von Bertalanffy growth equation to predict age from length-specific growth measurements in four populations of three common lacustrine mussel species in Minnesota and Rhode Island, U.S.A.

Methods

Mussel age estimation

The inversion of the von Bertalanffy growth equation (eqn 6) was applied to freshwater mussels in four lacustrine populations to calculate the most probable ages of animals of differing lengths. Mussel growth was studied in Wabana Lake, MN, U.S.A. (47°24'N, 93°31'W) between 1986 and 1994, in Worden Pond, RI, U.S.A. (41°26'N, 71°43'W) between 1991 and 1999, and in Yawgoo Pond, RI, U.S.A. (41°30'N, 71°34' W) between 1995 and 1999. Wabana Lake is a 863 ha, meandered, oligotrophic lake in north-central Minnesota, U.S.A (Heiskary & Wilson, 1990). Worden Pond is a 430 ha, shallow, eutrophic lake in southern Rhode Island, U.S.A. (Green & Herron, 1994). Yawgoo Pond, located less than 10 km from Worden Pond, is a 59 ha oligotrophic-mesotrophic lake in southern Rhode Island, U.S.A. (Green & Herron, 1996). We followed the growth of 83 fatmuckets, *Lampsilis siliquoidea* (Barnes, 1823), and 55 giant floaters, *Pyganodon grandis* (Say, 1829), in Wabana Lake, 204 eastern elliptios, *Elliptio complanata* (Lightfoot, 1786), in Worden Pond, and 69 eastern elliptios, *E. complanata* (Lightfoot, 1786), in Yawgoo Pond. These Minnesota and Rhode Island populations are separated by more than 2000 km and were chosen to represent good lacustrine mussel habitat in two distinct regions of North America.

In Wabana Lake, plastic tags (Dymo®; Esselte, London, U.K.), each with a lettered code, were attached to the postero-ventral margin of each animal's shell with cyanoacrylate instant-setting, waterproof dental cement. In both Worden and Yawgoo Ponds, mussels were cleaned and marked with fluorescent orange paint (Krylon®; Sherwin-Williams, Cleveland, OH, U.S.A.) in the method described by Ghent *et al.* (1978). Following tagging, each animal was measured for length perpendicular to the hinge at the umbo in Wabana Lake while those in Worden and Yawgoo Ponds were measured postero-anteriorly along the axis of maximum growth, using digital vernier calipers. All animals were subsequently released, recaptured and measured at approximately annual intervals.

The von Bertalanffy parameters L_∞ and K were estimated for each mussel population in each year of the study using the Ford-Walford method (eqns 3 and 4) (Ricker, 1975). Because freshwater mussels

may exhibit apparent 'good' and 'bad' growth-years, we calculated values of L_{∞} and K for each year in each population using that year's mark and recapture-derived growth increments. Published estimates of glochidial lengths for *E. complanata* (0.21 mm, Matteson, 1948), *L. siliquioidea* (0.25 mm, = *Lampsilis luteola*, Lefevre & Curtis, 1910), and *P. grandis* (0.42 mm, Lefevre & Curtis, 1910) were used as approximations of L_0 . Using these parameter estimates in eqn 6, we were able to calculate the probable age of each individual at each recapture. Confidence limits ($\alpha = 0.05$) were calculated as the variation among age estimates made using several years' growth parameter estimates. For one population of *E. complanata* (Worden Pond, RI, U.S.A.), we were also able to directly compare age estimates based on parameters derived from actual growth rates to those made using published estimates of parameters derived from internal annuli (Kesler & Downing, 1997).

Some mussels in each of the three lakes exhibited negative growth during the study period. Although some decreases could have arisen because of measurement error, some have been attributed to actual shell shrinkage (Downing *et al.*, 1992; Downing & Downing, 1993). Preliminary analyses revealed that the inclusion of these negative growth increments in the Ford-Walford framework led to large underestimates of the maximum sizes actually observed in the populations. We therefore set all negative growth values, regardless of causation, to zero growth. Our application of this procedure causes us to overestimate growth rates and underestimate actual mussel ages.

Mortality rate estimation

We further wished to corroborate age estimates by determining whether predicted ages would be potentially attainable given the rates of mortality experienced by these mussel populations. Mortality rates of the mussels in the four marked populations could be provisionally estimated using sequential recaptures of marked animals, assuming that the annual decline in recapture numbers primarily reflected the loss of animals to mortality. This assumption overestimated mortality and underestimated attainable ages because we followed a random assemblage of sizes over several years (few small animals) and, although we

were unable to locate a few animals in some years, most were later found to be living.

The exponential rate of annual mortality for each population was calculated as

$$m = -\ln[s_{(t)}]/t \quad (7)$$

where m is the exponential rate of mortality and $s_{(t)}$ is survivorship over some known time period t (Ricklefs, 1990). Mortality rates for *E. complanata* (Worden and Yawgoo Ponds) were calculated using annual recovery numbers. Because additional *L. siliquioidea* and *P. grandis* (Wabana Lake) were marked at two more locations within the same lake for 2 years in the study, however, the mortality rates for the Wabana Lake populations were calculated as the mean rate of mortality among the three marking locations. These estimates allowed us to extrapolate mortality curves to estimate maximum ages for the mixed-age set of marked animals.

Results

Mussel growth and age estimation

Mussels in Wabana Lake and Worden Pond grew slowly (Table 2). Mean estimates of Brody's growth constant (K) for *L. siliquioidea* (0.055 year⁻¹, Wabana Lake), *P. grandis* (0.032 year⁻¹, Wabana Lake), and *E. complanata* (0.027 year⁻¹, Worden Pond) show that mussels in these three populations were approaching their theoretical maximum lengths (L_{∞}) at very slow rates. These growth coefficients are very similar to those of ocean quahogs (*Arctica islandica*), green sea turtles (*Chelonia mydas*), and American lobsters (*Homarus americanus*), species known to be very long-lived (Campbell, 1983; Frazer & Ehrhart, 1985; Brey *et al.*, 1990). In contrast, *E. complanata* grew more rapidly in Yawgoo Pond yielding a higher mean estimate of K (0.176 year⁻¹).

Estimates of the von Bertalanffy parameters L_{∞} and K for mussel species in all three lakes varied among years reflecting annually variable mussel growth rates. Parameter estimates for *L. siliquioidea* (Wabana Lake, MN, U.S.A.), in particular, exhibited considerable annual variability ($S_{L_{\infty}}^2 = 1293$; $s_K^2 = 0.005$), especially during the first and sixth year of the study (Table 2). It is notable that growth of *L. siliquioidea* in the first year of the study was, however, based upon the examination

Table 2 Annual recapture numbers, estimates of L_{∞} and K from mark and recapture-inferred growth rates, and r^2 values for linear regression analyses of the Ford-Walford relationships for *Elliptio complanata* (Worden and Yawgoo Ponds, RI, U.S.A.), *Lampsilis siliquoides* (Wabana Lake, MN, U.S.A.) and *Pygamodon grandis* (Wabana Lake, MN, U.S.A.). It is notable that recapture numbers for the *L. siliquoides* and *P. grandis* reflect animals marked at three locations in Wabana Lake. Mussels were not always recaptured in all three locations in each year. Because of few recaptures in 1987, von Bertalanffy parameters were not calculated for *P. grandis* until 1989

Year	<i>E. complanata</i> Worden Pond, RI				<i>E. complanata</i> Yawgoo Pond, RI				<i>L. siliquoides</i> Wabana Lake, MN				<i>P. grandis</i> Wabana Lake, MN			
	Number Recaptured	L_{∞}	K	r^2	Number Recaptured	L_{∞}	K	r^2	Number Recaptured	L_{∞}	K	r^2	Number Recaptured	L_{∞}	K	r^2
1986	-	-	-	-	-	-	-	-	35	-	-	-	9	-	-	-
1987	-	-	-	-	-	-	-	-	9	78.3	0.158	0.9474	3	-	-	-
1988	-	-	-	-	-	-	-	-	68	178.7	0.014	0.9751	45	-	-	-
1989	-	-	-	-	-	-	-	-	21	153.9	0.004	0.9982	26	105.5	0.053	0.9661
1990	-	-	-	-	-	-	-	-	35	136.0	0.006	0.9979	31	128.0	0.025	0.9778
1991	204	-	-	-	-	-	-	-	50	133.3	0.007	0.9933	33	102.4	0.018	0.9921
1992	183	62.8	0.014	0.9867	-	-	-	-	15	101.7	0.142	0.9601	-	-	-	-
1993	158	64.9	0.026	0.9976	-	-	-	-	-	-	-	-	-	-	-	-
1994	159	60.5	0.018	0.9984	-	-	-	-	-	-	-	-	-	-	-	-
1995	143	63.2	0.058	0.9943	69	-	-	-	-	-	-	-	-	-	-	-
1996	130	63.0	0.035	0.9963	57	70.5	0.119	0.9867	-	-	-	-	-	-	-	-
1997	131	58.4	0.019	0.9990	44	75.9	0.273	0.9570	-	-	-	-	-	-	-	-
1998	110	62.8	0.036	0.9950	43	78.5	0.236	0.9082	-	-	-	-	-	-	-	-
1999	101	64.6	0.011	0.9982	20	71.1	0.074	0.9790	-	-	-	-	-	-	-	-
Mean	-	62.5	0.027	0.9957	-	74.0	0.176	0.9577	-	130.3	0.055	0.9787	-	112.0	0.032	0.9787

of some small individuals ($n = 9$ recaptures). Observations of the growth of *P. grandis* for the first year of observation in the same lake were also based upon few individuals ($n = 3$ recaptures) and were disregarded. It therefore remains unclear whether this was a simply naturally occurring annual growth variability in *L. siliquoides* or, rather, the result of some larger, atypical environmental phenomenon, which should also have affected *P. grandis*. Regardless of causation, the annual variability of mussel growth rates was manifested in wide confidence limits surrounding mean age estimates for mussels in all three lakes (Fig. 1).

The slow growth rates implied by the von Bertalanffy parameter estimates were reflected in estimates of age-at-length. The inversion of the von Bertalanffy growth equation, using parameters estimated from actual length-specific growth rates, yielded

many ages near or in excess of 100 years for all three species in Wabana Lake and Worden Pond (Table 3). Mean age estimates obtained for marked *L. siliquoides* (73 ± 50 years) and *P. grandis* (45 ± 30 years) from Wabana Lake and *E. complanata* (75 ± 29 years) from Worden Pond, generally exceeded maximum ages predicted for the same species using annuli (Table 1). Although variability was high and increased with mussel size, even the lower bounds of 95% confidence intervals for estimates of maximum observed age in *E. complanata* (Worden Pond), and *L. siliquoides* (61 and 80 years, respectively) were several times the ages previously thought to prevail in freshwater unionid mussels (cf. Table 1). The lower bound of the 95% confidence interval for the observed maximum age in *P. grandis* (17 years) is, however, similar to lifespans estimated for this species using annuli (cf. Table 1).

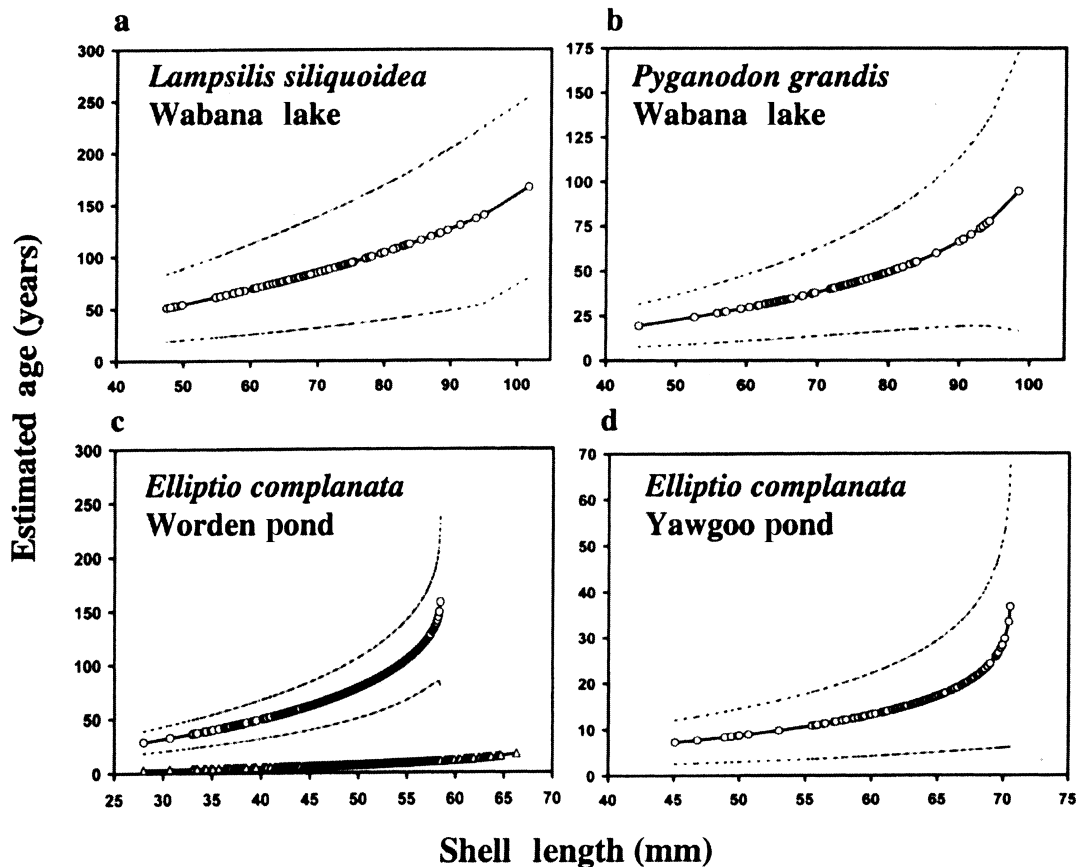


Fig. 1 Mussel ages (O) with 95% confidence intervals (–) estimated using the inversion of the von Bertalanffy growth equation (eqn 6) with parameters derived from mark and recapture-inferred growth rates for (a) *Lampsilis siliquoides* (Wabana Lake), (b) *Pyganodon grandis* (Wabana Lake), (c) *Elliptio complanata* (Worden Pond) and (d) *E. complanata* (Yawgoo Pond). Ages estimated using published estimates of internal annulus-inferred growth rates (Δ) (Kesler & Downing, 1997) were also calculated for (c) *E. complanata* (Worden Pond).

Table 3 Minimum, mean, and maximum age estimates ($\pm 95\%$ confidence limits) for *Elliptio complanata*, *Lampsilis siliquoidea*, and *Pyganodon grandis* using the inversion of the von Bertalanffy growth equation with growth rates inferred from mark and recapture measurements and internal annuli (*E. complanata*, Worden Pond, Kesler & Downing, 1997)

Species	Minimum	Mean	Maximum
<i>E. complanata</i> (Worden Pond)			
Actual growth rates	25 \pm 9	75 \pm 29	149 \pm 88
Internal annuli	3	8	17
<i>E. complanata</i> (Yawgoo Pond)			
Actual growth rates	7 \pm 5	17 \pm 12	37 \pm 31
<i>P. grandis</i> (Wabana Lake)			
Actual growth rates	20 \pm 12	45 \pm 30	95 \pm 78
<i>L. siliquoidea</i> (Wabana Lake)			
Actual growth rates	44 \pm 28	73 \pm 50	167 \pm 87

In all three lacustrine environments, mussel growth decelerated and grew more variable with increasing size (Fig. 1). This decelerating linear growth does not, however, necessarily reflect decelerating volumetric growth. That variability in linear mussel growth and resultant age estimates increased with decelerating growth rates and increasing mussel size is evident in the progressive widening of confidence intervals towards maximum ages in all four populations (Fig. 1). This trend is expected, however, as predictions of age for very large individuals must be highly variable as individual lengths begin to approach the asymptote (L_{∞}). Additionally, it would be overly optimistic to expect any model to describe growth equally well through an entire life span.

Mussel longevity may also vary intraspecifically among locations. Just as estimates of K for *E. complanata* in Yawgoo Pond were consistently higher than those observed for the same species in Worden Pond (Table 2), maximum age estimates for animals in this population were, accordingly, much lower than those estimated for the Worden Pond animals (Table 3). Although mean age estimates for the Yawgoo Pond *E. complanata* were often higher than those previously expected (Table 3), the lower bounds of confidence intervals do not surpass traditional age estimates (cf. Table 1). For *E. complanata* in Worden Pond, however, even the lower bounds of the confidence limits on age estimates across all observed lengths were greater than those predicted using annulus-derived parameters (Fig. 1c). In fact, the maximum observed age predicted for this population using parameters derived from annulus-inferred growth rates (17 years) was several times lower than even the mean observed

age as estimated using actual growth rates (75 \pm 29 years).

Mortality

Recapture of animals in years subsequent to marking declined slowly, reflecting low levels of mortality in the Worden Pond and Wabana Lake mussel populations (Table 2). The exponential rates of mortality (eqn 7) estimated for *L. siliquoidea* ($-0.1295 \text{ year}^{-1}$) and *P. grandis* ($-0.1504 \text{ year}^{-1}$) were slightly higher than that estimated for the Worden Pond population of *E. complanata* ($-0.1004 \text{ year}^{-1}$). A much higher mortality estimate ($-0.3096 \text{ year}^{-1}$) was obtained for *E. complanata* in Yawgoo Pond.

Extrapolation of the exponential mortality curves for *E. complanata* (Worden Pond), *E. complanata* (Yawgoo Pond), *L. siliquoidea* (Wabana Lake), and *P. grandis* (Wabana Lake) reveal that the last of the marked animals should die 53, 13, 34 and 26 years after marking for each population, respectively. Given mean age estimates of 75 \pm 29, 17 \pm 12, 73 \pm 50 and 45 \pm 30 years for *E. complanata* (Worden Pond), *E. complanata* (Yawgoo Pond), *L. siliquoidea* and *P. grandis*, respectively, mortality rates indicate that the last of the marked mussels in each population should reach ages of 128 \pm 29 years (*E. complanata*, Worden Pond), 30 \pm 12 years (*E. complanata*, Yawgoo Pond), 107 \pm 50 years (*L. siliquoidea*), and 71 \pm 30 years (*P. grandis*) before death. Although the calculated mortality rates are probably overestimates because not all animals subsequently unrecovered were actually lost to mortality, the projected ages at death for the last of the marked animals are near to the average maximum ages estimated for each

population using the von Bertalanffy growth equation (cf. Table 3).

Discussion

Mark and recapture growth information suggests that, in some lacustrine populations, freshwater mussel lifespans may surpass, by an order of magnitude, most of the ages indicated by traditional annulus counting methods. Even the lower bounds of the confidence intervals of ages predicted using the inversion of the von Bertalanffy growth equation are often many times those indicated using annuli (cf. Tables 1 and 3, Fig. 3). In addition, by correcting all negative growth to reflect zero growth, we overestimated growth rates and underestimated ages, thereby understating the discrepancy between the two techniques. That the traditional annulus-based methods would yield markedly lower estimates of mussel ages is expected, however, given the recent evidence that both external and internal annuli can be produced over time-spans much greater than a single year (Downing *et al.*, 1992; Kesler & Downing, 1997).

Although the magnitude of mussel life spans we present for animals in Wabana Lake, MN, U.S.A. and Worden Pond, RI, U.S.A. vastly exceed those predicted using traditional methods, similar life spans are not unprecedented in the world's bivalve fauna. The closely related freshwater pearl mussel, *Margaritifera margaritifera* (Hendelberg, 1961; Bauer, 1992), the ocean quahog, *Arctica islandica* (Thompson, Jones & Dreibelbis, 1980), and another marine bivalve, *Tindaria callistiformis* (Turekian *et al.*, 1975), are all thought to reach ages exceeding a century. The advanced ages evident in these bivalve species indicate that life spans in excess of a century are indeed attainable within the Mollusca and are plausible within the freshwater unionid mussels.

The low rates of mortality evident in *E. complanata* (Worden Pond), *L. siliquoides* (Wabana Lake), and *P. grandis* (Wabana Lake) offer additional support for the advanced ages predicted using the inversion of the von Bertalanffy growth equation, although the mortality estimate for *E. complanata* in Yawgoo Pond was relatively high ($-0.3096 \text{ year}^{-1}$), it is consistent with expectations for a shorter-lived population and corroborates the relatively low estimates of age in the Yawgoo Pond animals. That mortality estimates are consistent with age estimates in all populations,

regardless of the magnitude of projected lifespans, suggest that our application of the inversion of the von Bertalanffy growth equation is valid.

The von Bertalanffy growth equation indicates that mussels are not equally long-lived in all populations. Equality of growth rates would not be expected as different systems and habitats do not always manifest conditions that are optimal for mussel growth (Bauer, 1992). It is reasonable that estimates of mussel longevity should vary among ecosystems just as the conditions influencing their growth may vary. The ability of our application of the von Bertalanffy growth equation to predict both relatively short and relatively extended longevity in different systems reflects its versatility. This also suggests that age estimates exceeding a century are realistic approximations of actual mussel ages in some populations.

Our results also demonstrate the considerable inter- and intra-specific plasticity of mussel growth and longevity. While annual variation in mussel growth rates may render the von Bertalanffy growth equation insufficient for the absolute age estimates necessary in some management scenarios, it also means that short-term studies (e.g. Parada *et al.*, 1989) have likely provided a short-sighted view of mussel growth and longevity. Additionally, conservation and management efforts based on traditional methods will likely prove inadequate and potentially dangerous if applied too broadly. Rather, future conservation efforts and inquiries into the growth and longevity of these imperilled mollusks must acknowledge the considerable variability in growth and longevity evident even among populations in relatively close proximity to one another.

Despite strong evidence that traditional longevity estimates for these lacustrine mussel populations have been inaccurate, there remains an alternative interpretation. The more rapid rate of mussel growth and relatively short estimates of longevity for animals in Yawgoo Pond may suggest that mussel growth has only recently slowed dramatically in populations for which mark and recapture growth data have implied longevity estimates near or exceeding a century. If mussel growth has indeed recently slowed to near cessation in the Worden Pond and Wabana Lake populations, our mark and recapture-inferred growth observations would be underestimates of the growth rates expected for individuals in healthy populations. This would have

caused our application of the von Bertalanffy growth equation to overestimate age.

Although generalized growth cessation may be a logically viable interpretation of our results, it does not seem likely as none of the lakes for which mussel growth data were collected should be considered even marginal mussel habitat and conditions do not appear to have recently changed dramatically. In addition, preliminary analyses of mussel growth data from 10 of 12 lakes in Québec, Canada corroborate the slow rates of growth and advanced ages predicted for the Wabana Lake and Worden Pond populations (J.L. Anthony & J.A. Downing, unpublished observation). It is difficult to imagine a force that could simultaneously slow mussel growth at these geographically distant locations. If we further consider that low mortality rates in the Worden Pond and Wabana Lake populations corroborate the extreme ages estimated for these animals, widespread growth cessation seems improbable. Rather, it seems likely that an aberrant cessation of growth, perpetuated through over half of the life span predicted using annuli, would increase the rate of mortality in these populations. It therefore seems doubtful that our extreme longevity estimates reflect generalized growth cessation in these mussel populations.

Our application of the von Bertalanffy growth equation not only seems to be a valid tool for estimating age in freshwater unionid mussels, but has also indicated that our current understanding of mussel age and growth dynamics may be severely flawed. The development of new age estimation techniques like the inversion of the von Bertalanffy growth equation is critical for allowing the re-examination of the life history strategies of these unique organisms and will perhaps lead to a greater understanding of how so many species of the Unionidae are near extinction (Williams *et al.*, 1993). The possibility of regionally generalized growth cessation, although seemingly implausible, should also not be ignored. If dramatic declines in growth rates have originated only recently in these and other freshwater mussel populations, we may expect widespread mass mortality events and further declines in North American lacustrine freshwater mussel populations. If generalized growth cessation is occurring, future mark and recapture growth studies and estimates of von Bertalanffy parameters may allow us to identify these imperilled populations and to gather insight into the

factors that may incite and perpetuate growth cessation and mass mortality. The ancient life-spans predicted for some lacustrine mussel populations using the von Bertalanffy growth equation may have serious implications for how we consider the management, recovery, and commercial harvest potential of these imperilled creatures, which may be among the most ancient living animals on Earth.

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