GROWTH OF THE FRESHWATER MUSSEL *PYGANODON GRANDIS* (UNIONIDAE) IN TWO WEST TENNESSEE BORROW PITŚ

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ABSTRACT—We determined the annual growth of the Giant Floater, *Pyganodon grandis* (Say, 1829), in two-west Tennessee borrow pits between April, 1998 and April, 1999. Individuals were collected from one borrow pit (Grandis Canyon), measured for length, numbered, and either returned to Grandis Canyon or transplanted into another, nearby borrow pit (Humphreys Pit). Growth was measured by the change in length of marked individuals. Growth was significantly greater in Humphreys Pit (ANCOVA F = 33.3; d.f. = 1,109; P < 0.001). Ford-Walford plots gave L_{∞} values for Grandis Canyon and Humphreys Pit mussels of 125.6 mm and 209.0 mm, respectively. Values of k were 0.361 for mussels in Grandis Canyon and 0.137 for those in Humphreys Pit. We also determined the length-age relationship of individuals from Grandis Canyon by examining shell internal annuli. This was done to test the reliability of mathematically predicted growth rates, derived from "annuli," for P. grandis in our area. The mean \pm SE values for L_{∞} and k from these data were 169.0 \pm 16.93 mm and 0.184 \pm 0.059, respectively. These values gave predicted length changes significantly greater (t = 6.39; d.f. = 35; P < 0.001) than length changes we observed from remeasurement of P. grandis individuals in Grandis Canyon, but significantly less (t = 2.93; d.f. = 71; P < 0.002) than length changes observed in P. grandis individuals moved to Humphreys Pit. These results demonstrated that growth rate determinations from annuli measurements are unreliable unless environmental conditions remain static.

The giant floater, *Pyganodon grandis* (Say, 1829), (formerly *Anodonta grandis grandis*) is a freshwater mussel widely distributed in North America, being found from the Gulf of Mexico drainage in Louisiana and Texas to throughout the Canadian interior basin from central Ontario to central Alberta (Clarke, 1981; Parmalee and Bogan, 1998). *Pyganodon grandis* also has been recently introduced in New Mexico (Lang, 1996). We have found this species to be more common in lentic-like than lotic habitats of the Wolf River, Tennessee. According to Parmalee and Bogan (1998), *P. grandis* reaches its greatest abundance and size in reservoirs, lakes, and ponds having a mud bottom with little or no current. Likewise, Ghent et al. (1978) found *P. grandis* in a Canadian lake to depths of 13–14 m in very soft sediment. These observations are consistent with the finding that *P. grandis* has a clear preference for finer substrates (Huehner, 1987).

The giant floater has been used to monitor heavy metal concentrations in aquatic environments (Couillard, 1993: Couillard et al., 1995; Malley et al., 1996; Stewart, 1999). It is a common, rapidly growing species with a relatively thin shell, and Downing et al. (1992) used this species to test the assumption that external shell annuli are formed yearly. While not an economically important species in Tennessee, *P. grandis* is a food source for muskrat and otter (Bailey and Green, 1989; Hanson et al., 1989).

The objective of our study was to determine the growth rate of *P. grandis* in two west Tennessee borrow pits (areas excavated for road construction) along the Wolf River, which we named Humphreys Pit and Grandis Canyon. Prior to this study we had observed that individuals seemed to grow faster in Humphreys Pit. To test the hypothesis of faster growth in Humphreys Pit, we

transplanted mussels from Grandis Canyon and compared growth to the source population. We also wanted to compare growth of *P. grandis*, determined from remeasurement to growth predicted from internal growth rings.

MATERIALS AND METHODS

The borrow pits used in this study are located in Shelby County, Tennessee along the Wolf River. The older of these pits, which we called Humphreys Pit (35°07'33.1"N, 89°51'0.7"W), was constructed in 1986 to provide fill for a nearby road. Humphreys Pit is connected to the Wolf River through a narrow channel. It has a surface area of approximately 0.73 ha and a maximum depth of 2.8 m. The newer pit, which we named Grandis Canyon (35°06'58.3"N, 89°50'7.3"W), was constructed in 1988 and has a surface area of 0.35 ha and a maximum depth of 4.9 m. Grandis Canyon receives Wolf River water only during floods. Both of these borrow pits have a soft mud sediment and are extremely turbid.

On April 5, 1998, we collected 88 P. grandis from Grandis Canyon. These were marked with Krylon paint, uniquely numbered, measured to the nearest 0.1 mm for maximum length (Hinche et al., 1989), and returned to Grandis Canyon. On April 26, 1998 103 P. grandis were collected from Grandis Canyon, marked and measured as before, and transplanted to nearby Humphreys Pit. The mean \pm SE length of marked mussels in Grandis Canyon was 108.0 ± 1.4 mm. The mean \pm SE length of marked mussels placed into Humphreys pit was 108.1 ± 1.2 mm. The length-frequency distributions of these two samples did not differ

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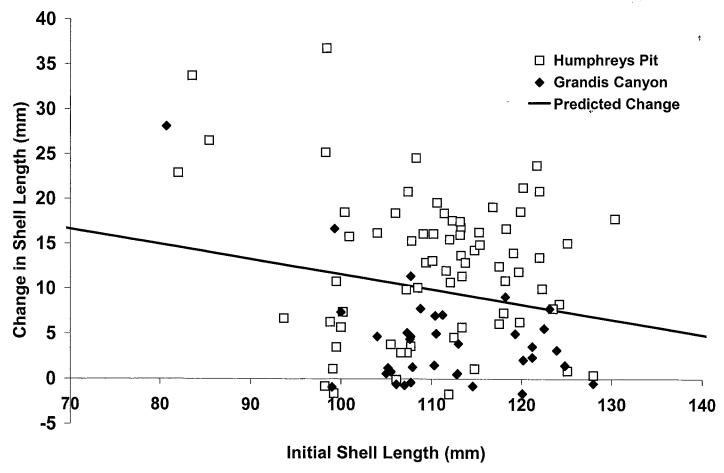


FIG. 1. The annual length change versus initial length of *Pyganodon grandis* from Grandis Canyon and Humphreys Pit, Shelby County, Tennessee. Predicted change line is derived from annuli analysis and the resulting von Bertalanffy equation.

(Komogorov-Smirnov test, $n_1 = 103$, $n_2 = 88$; z = 0.587; P = 0.881).

Every attempt was made to minimize the time spent out of the water during marking, measuring, and transport. According to Chen et al. (1995) *P. grandis* is tolerant of handling stress.

We recollected the marked mussels in Grandis Canyon and Humphreys Pit again six months later in October, 1998, and one year later in April, 1999. Lengths were remeasured to determine growth. No attempt was made to distinguish any individuals with the corpulenta form. Length at remeasurement in April 1999 was plotted against initial length in April 1998. The slope of this line was e^{-k} , from which the growth coefficient k was obtained (Walford, 1946; Everhart et al, 1975). The ultimate length (L_{∞}) was either taken as the point where the growth line intersects a 45° line drawn through the origin, or was computed as

$$L_{\infty} = \frac{\text{intercept}}{1 - e^{-k}}$$

In addition to the remeasurment of the two populations after 12 months, we estimated the age of 22 *P. grandis* from Grandis Canyon by microscopically examining internal growth lines as thin sections (Neves & Moyer, 1988). An additional five large individuals from a nearby tributary feeding into the Wolf River also were aged. Inclusion of these larger individuals did not significantly change the resulting predicted age-length relationship. Internal growth annuli were defined as areas of discontinuity of

the prismatic layer that extended from the nacreous layer to the periostracum (Fig. 9 of Day, 1984). The "size-at-age" data were used to calculate von Bertalanffy growth curves using the software of Saila et al. (1988). The von Bertalanffy growth equation is:

$$L_{t} = L_{\infty}(1 - e^{-k(t-to)}) \tag{1}$$

(Ricker, 1975) where L_t is the shell length at a given age (t; years) measured in mm, t_0 is the extrapolated age at which theoretical length is zero, L_{∞} is the theoretical shell length at infinite age, k is a fitted constant reflecting the rate of approach of L_t toward L_{∞} with increasing age, and e is the base of natural logarithms.

Based on these parameters, the relationship between the predicted rate of annual shell growth $(\Delta \hat{L}_t)$ and shell size (L_t) can be calculated:

$$\Delta \hat{L}_{t} = L_{\infty}(1 - e^{-k}) + L_{t}(e^{-k} - 1)$$
 (2)

(Gulland, 1964). This equation gives the relationship between the predicted incremental growth rates ($\Delta \hat{L}_i$; mm/year) of animals of a given size (L_i). These annual growth rates can then be compared with actual, field-measured growth rates of animals of given sizes using a paired t-test.

The von Bertalanffy equation has been used to describe unionid growth in a variety of conditions and species (McCuaig and Green, 1983; Day, 1984; Hinch, et al., 1986; Parada, et al., 1989). Given the variability in growth rates among individuals,

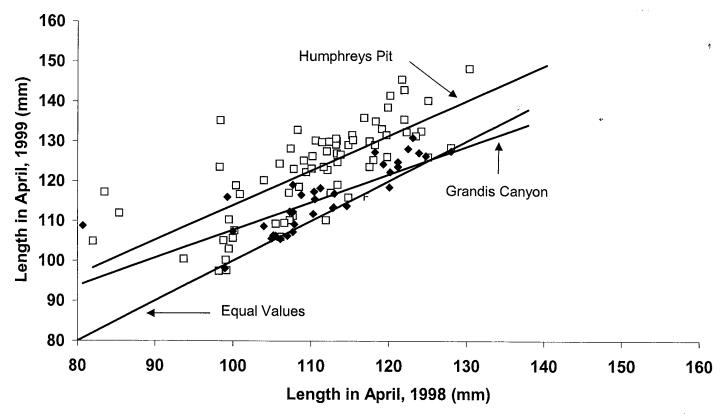


FIG. 2. Ford-Walford plot of *Pyganodon grandis* shell length at time t+1 versus length at time t for individuals from Grandis Canyon and Humphreys Pit, Shelby County, Tennessee.

any small biases the von Bertalanffy equation may introduce, e.g., inaccurate description of very young individual growth (Kaufman, 1981), become trivial.

RESULTS AND DISCUSSION

Of the 88 *P. grandis* marked in Grandis Canyon in April, 1998, 58 (66%) were retrieved in October, 1998, and 36 (41%) were retrieved in April, 1999. This low retrieval rate was due in part to high predation. We observed numerous broken shells along the shore with markings indicating vertebrate predation. We do not feel that our marking technique increased predation rate by visual predators because of the very high turbidity of the water and because marked shells were not overly represented among the broken shells. Of the 103 *P. grandis* placed in Humphreys Pit in April 1998, 82 (80%) were retrieved in October

TABLE 1. Values of L_{∞} and k from remeasurement data (Ford-Walford plots) and annuli or internal rings (von Bertalanffy equation).

Source	L_{∞}	k
Remeasurement Data		
Grandis Canyon	125.6 mm	0.361
Humphreys Pit	209.0 mm	0.137
Von Bertalanffy equation		
Grandis Canyon	169.0 mm	0.184

1998 and 72 (70%) were retrieved in April 1999. This high retrieval rate demonstrates that our marking technique, while inexpensive and quickly applied, is an appropriate method.

The annual length change of P. grandis in Grandis Canyon and Humphreys Pit versus initial length is plotted in Fig. 1. The mean \pm SE length change for P. grandis from Humphreys Pit and Grandis Canyon was 12.6 ± 1.0 mm and 4.3 ± 1.0 mm, respectively. An analysis of covariance (ANCOVA), after a test for homogeneity of slope, revealed that growth was significantly greater in Humphreys Pit (F = 30.5; d.f. = 1,106; P < 0.001). Obvious possibilities for faster growth in Humphreys Pit include a difference in food quantity or quality, and/or a temperature difference. Since all of the mussels in this study came from the same source population, and had identical size-frequency distributions, these data point out the environmentally induced differences possible in mussel growth. They also demonstrate how mussel growth can differ in closely spaced water bodies.

When shell length at time t+1 was plotted against length at time t, the resulting Ford-Walford plot (Fig. 2) was used to determine L_{∞} and the growth coefficient k. These values are given in Table 1. The maximum length (L_{∞}) expected of mussels in Humphreys Pit was 209 mm, while only 125 mm in Grandis Canyon. Given the plasticity in growth shown in this study, these maximum lengths would only be expected if environmental conditions remain constant, which is an unlikely situation.

Another way to determine growth rate is to examine the agelength relationship. While the assumption that growth rings (annuli) are formed annually needs to be rigorously tested (Downing et al., 1992; Kesler and Downing, 1997), we determined the agelength relationship, as described by the von Bertalanffy equation,

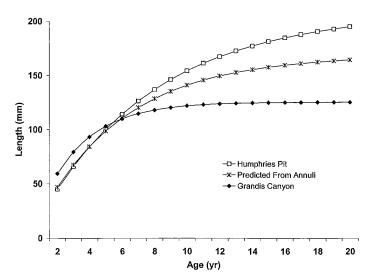


FIG. 3. Age-length relationship for *Pyganodon grandis* determined from annuli and from remeasurement of individuals from Grandis Canyon and Humphreys Pit, Shelby County, Tennessee, as described by von Bertalanffy equations.

for *P. grandis* from Grandis Canyon (and five individuals from a nearby tributary to the Wolf River) (Fig. 3). Growth of *P. grandis*, as determined from annuli in this study, was much faster than reported by others from Canada and Minnesota (McCuaig and Green, 1983; Hanson et al., 1988; Malley et al., 1989; and Huebner et al., 1990; Downing et al., 1992), but similar to that found by M. Havlik (pers. comm.) for a Minnesota population three miles downstream from a sewage treatment plant. These data demonstrate the growth plasticity of this species.

Values for L_{∞} and k from the von Bertalanffy equation for age-length relationship are given in Table 1. These values were intermediate between those derived from remeasurement of Grandis Canyon and Humphreys Pit individuals. Using growth rings to determine the age-length relationship, growth described by the von Bertalanffy equation in Fig. 3 overestimates the growth seen in Grandis Canyon P. grandis between 1998 and 1999. Downing et al. (1992) also observed a higher predicted growth, derived from annuli, than from remeasurement data in P. grandis. They attribute this discrepancy to shell annuli not being formed annually.

Using equation 2 above, predicted changes in lengths were generated for Grandis Canyon mussels. Values for the mean \pm SE of the predicted and observed length changes were 9.7 ± 0.3 mm and 4.3 ± 1.0 mm, respectively. The predicted length change was significantly greater than the observed length change (paired *t*-test, t = 6.39; d.f. = 35; P < 0.001).

The age-length relationship is based on growth by individuals many years ago, as recorded in shell growth. If growth is sensitive to environmental differences, as seen here between individuals placed in closely spaced Humphreys Pit and Grandis Canyon, then we would expect discrepancies between current growth and that predicted from shell annuli. Predicted growth from shell annuli is thus an unreliable method unless environmental conditions remain static. If shell annuli are not formed annually by most of the population, these discrepancies would be augmented. Without demonstrating environmental conditions to have remained constant, and the annual formation of shell

annuli by most individuals, use of shell annuli are likely to yield inaccurate predictions about future mussel growth.

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