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DEVELOPMENTAL BIOLOGY OF INVERTEBRATES

# Individual Growth of *Anodonta beringiana* (Unionidae, Bivalvia) in Postlarval Ontogenesis

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**Abstract**—Individual linear growth in 26 specimens of *Anodonta beringiana* is studied by measuring the successive annual rings on the surface of the shells. It is shown that the growth of mollusks is well described by the von Bertalanffy growth equation. The coefficients of this equation do not significantly differ between individuals, averaging $k = 0.062 \pm 0.011$ year$^{-1}$ and $L_\infty = 155.8 \pm 19.5$ mm. Species lifespan, calculated as a product of the growth constant $k$ and the maximum longevity of mussels in the population, is 1.7. This value is close to the average species lifespan of other bivalve species.

*Keywords:* growth, bivalves, Bivalvia, *Anodonta beringiana*, species lifespan

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## INTRODUCTION

Studies of individual growth make it necessary to simultaneously identify the age and size of animals at different stages of ontogenesis. This causes certain difficulties for conducting this kind of research in the natural habitat. These can be avoided in the case of bivalve mollusks. Measurement of annual-ring length on the surface of the shell provides data on mollusk sizes at different ages so that an individual growth curve can be constructed. Ring length is regarded as the distance between edges of the ring closest to the anterior and posterior edges of the shell.

In most cases, the von Bertalanffy equation is used to describe the growth of mollusks (Bertalanffy, 1960):

$$L_t = L_\infty[1 - \exp(-k(t + t_0))], \qquad (1)$$

where $t$ is the number of the measured annual ring when counting from the umbo of the shell, $t_0$ is age of the mollusk for the annual ring $t = 0$, $L_t$ is length of the annual ring at the age $t + t_0$, $L_\infty$ is asymptotic length of the shell, and $k$ is the growth constant.

The use of the coefficients of equation (1) allows for comparative intrapopulation, interpopulation, and interspecific studies on the growth of animals.

It was shown that the growth constant is inversely related to the maximum lifespan of the animals, $T_{max}$ (Bauer, 1992). This is also evidenced by the data of Alimov (1981), according to which the ratio of maximum and asymptotic sizes is approximately constant for bivalve mollusks. It, therefore, follows from equation (1) that the product $\tau = kT_{max}$ is also constant. This product could be considered the species lifespan.

The purpose of the present study is to determine the coefficients of the von Bertalanffy growth equation (1) and the species lifespan for the individual linear growth of freshwater bivalve mollusk *A. beringiana*.

## MATERIALS AND METHODS

There are conflicting data on the specific and generic identification of the mollusks under study. Graf and Cummings (2018) place them into the genus *Sinanodonta*, while Starobogatov et al. (2004) into the genus *Beringiana*. In the ITIS database, *Anodonta* (ITIS..., 2018) is considered the valid genus. As a result of revision, all species of freshwater mussels described for northeastern Russia and northwestern North America are combined into one species, *Anodonta beringiana* Middendorff, 1851 (*Osobo*..., 2018a; ITIS..., 2018). We will use this name in the present study. *A. beringiana* is included in the *Red Book of Magadan Oblast* (*Osobo*..., 2018b), and synonymous species are included in the *Red Books of Chukotka Autonomous Okrug* (*Osobo*..., 2018c) and *Sakhalin Oblast* (*Osobo*..., 2018d).

Shells of dead *A. beringiana* mollusks were collected in northeastern Yakutia in the lower reaches of Kolyma River, 30 km from the settlement of Chersky (68°30.73' N 161°30.21' E). A characteristic feature of this area is a large number of oxbow lakes. During the spring flood, they form a single body of water with the

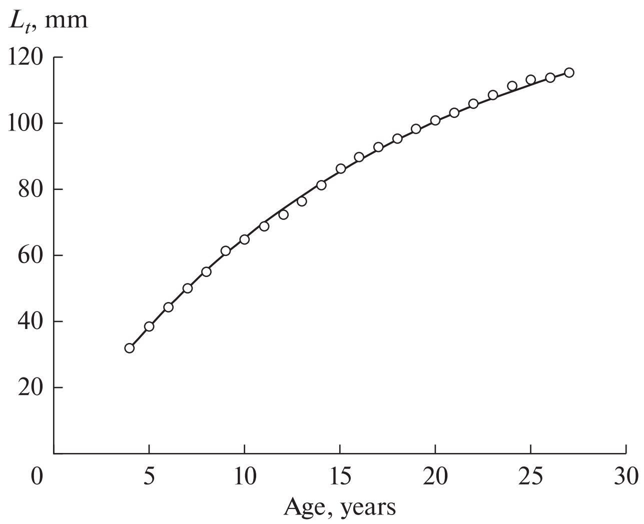


**Fig. 1.** Dependence of annual ring length ($L_t$) on its age on the example of mollusk no. 8 (Table 1). Circles denote measurements. The line is the approximation using von Bertalanffy growth equation (1).

Kolyma River and some of its tributaries. As the water level then decreases, lakes are formed in the floodplain; they are isolated from the river bed to some extent. The lake isolation is frequently disrupted by the breaches in barriers, and the water from the lakes flows into the river. A large number of freshwater mussels were found in one of these dry lakes in 2018. Only 26 of them were sufficiently preserved for the planned study.

It should be noted here that the bivalves from Kolyma River apparently have not been included in scientific collections or studied to date. We at least could not find any references to them in the scientific literature. It is possible that they demonstrate the northern limit for the distribution of naiads in northeastern Russia. The nature of their distribution in the Kolyma basin remains unstudied, but we have been able to determine that they occasionally occur almost to the river mouth: a small number of damaged shells have been found in the nets of local fishermen in the settlement of Chersky.

The shells were photographed with a scale. The images were loaded into Excel. The lengths of the shell and of each intact annual ring were measured with an accuracy of 0.1 mm using the image of each mollusk.

The data were approximated using the recursive form of equation (1):

$$L_{t+1} = cL_t + d, \quad (2)$$

where $L_t$ is the length of the annual ring of age $t$, $L_{t+1}$ is length of the annual ring of age $t + 1$, $c = \exp(-k)$ is the coefficient determining the growth slowdown rate, and $d = L_\infty/(1 - c)$. The approximation was performed using Excel.

The coefficients of equation (2) in different specimens were compared using regression analysis. The applicability of the equation was tested using the nonlinearity criterion (Zotin, 2000).

Age of a given mollusk was calculated as the age sum of the first measured annual ring ($T_1$) and the number of identifiable annual rings on the surface of the shell. The age of the first measured annual ring was calculated using equation (1):

$$T_1 = \log_c\left[1 - L_1/\left(d\left(1 - c\right)\right)\right],$$

where $L_1$ is length of the first measured annual ring. This method of age identification is necessary due to the fact that the umbo zone of the shell is corroded in many mollusks and some annual rings cannot be detected.

The coefficients of equation (2) were compared using regression analysis methods (Hald, 1956).

## RESULTS

Linear growth of *A. beringiana* individuals is accurately described by the equation (1). An example for the approximation of the obtained data using this equation is shown in the figure. Values of the coefficients of equations (1) and (2) and ages of the studied mollusks are given in Table 1.

The coefficients $c$ and $d$ of equation (2) do not differ significantly in different individuals. For the studied population as a whole, $c = 0.940 \pm 0.010$ year$^{-1}$ and $d = 9.3 \pm 0.2$ mm. Therefore, the coefficients of equation (1) are $k = 0.062 \pm 0.011$ year$^{-1}$ and $L_\infty = 155.8 \pm 19.5$ mm. These values can be used for characterization in comparative interpopulation and interspecific studies.

Maximum age ($T_{max}$) for the studied shells was 28 years. If this value is regarded as the maximum age for the entire population, then the species lifespan of *A. beringiana* is $\tau = kT_{max} \approx 1.7$.

## DISCUSSION

The so-called growth constant $k$ from the von Bertalanffy equation is commonly used to characterize the growth of bivalves (Alimov, 1981; Bauer, 1992; Zyuganov et al., 1993). We prefer to use another constant instead, which we call the growth slowdown coefficient ($c$); its relation with the growth constant can be described by equation $c = \exp(-k)$. Note that if $k$ is close to 0, then $k \approx 1 - c$. The coefficient $c$ is preferable to the growth constant since it has near-normal statistical distribution and is included in the recursive form of (2) as regression coefficient and can, therefore, be used for comparison using standard methods of regression analysis.

For the studied mollusks, the mean $c = 0.940$ and, therefore, $k = 0.062$ year$^{-1}$. According to the literature

**Table 1.** Coefficients of equations (1) and (2) for total mass growth in the individual postlarval ontogenesis of *A. beringiana*

| No. of the mollusk | $n$ | Equation (2) | | Equation (1) | | $T$, year | $\tau$ |
|---|---|---|---|---|---|---|---|
| | | $c$ | $d$, mm | $k$, year$^{-1}$ | $L_\infty$, mm | | |
| 1 | 14 | 0.932 ± 0.014 | 11.0 ± 1.0 | 0.071 ± 0.015 | 161.0 ± 14.1 | 17 | 1.2 |
| 2 | 19 | 0.947 ± 0.010 | 7.4 ± 0.7 | 0.054 ± 0.011 | 139.8 ± 10.7 | 25 | 1.3 |
| 3 | 15 | 0.934 ± 0.011 | 8.7 ± 0.7 | 0.068 ± 0.012 | 132.0 ± 8.5 | 20 | 1.4 |
| 4 | 14 | 0.940 ± 0.014 | 10.1 ± 1.1 | 0.062 ± 0.015 | 168.4 ± 17.1 | 18 | 1.1 |
| 5 | 18 | 0.946 ± 0.010 | 8.4 ± 0.8 | 0.055 ± 0.011 | 155.5 ± 12.1 | 24 | 1.3 |
| 6 | 15 | 0.941 ± 0.013 | 7.5 ± 0.8 | 0.061 ± 0.014 | 127.9 ± 12.0 | 19 | 1.2 |
| 7 | 12 | 0.942 ± 0.008 | 10.2 ± 0.6 | 0.060 ± 0.008 | 175.4 ± 12.1 | 16 | 1.0 |
| 8 | 23 | 0.943 ± 0.006 | 8.2 ± 0.5 | 0.058 ± 0.006 | 145.1 ± 5.5 | 28 | 1.6 |
| 9 | 14 | 0.946 ± 0.007 | 10.3 ± 0.5 | 0.055 ± 0.007 | 192.6 ± 12.2 | 18 | 1.0 |
| 10 | 11 | 0.936 ± 0.012 | 11.4 ± 0.9 | 0.067 ± 0.013 | 176.4 ± 16.5 | 15 | 1.0 |
| 11 | 12 | 0.946 ± 0.014 | 9.6 ± 1.0 | 0.055 ± 0.014 | 178.5 ± 20.7 | 17 | 1.0 |
| 12 | 21 | 0.946 ± 0.006 | 8.4 ± 0.4 | 0.056 ± 0.006 | 154.3 ± 6.8 | 26 | 1.5 |
| 13 | 12 | 0.945 ± 0.012 | 10.3 ± 0.9 | 0.057 ± 0.013 | 186.8 ± 20.4 | 16 | 0.9 |
| 14 | 16 | 0.929 ± 0.006 | 11.0 ± 0.5 | 0.074 ± 0.006 | 155.5 ± 5.5 | 20 | 1.4 |
| 15 | 14 | 0.939 ± 0.013 | 10.4 ± 1.1 | 0.063 ± 0.014 | 169.9 ± 16.6 | 18 | 1.2 |
| 16 | 14 | 0.948 ± 0.014 | 9.2 ± 1.0 | 0.053 ± 0.015 | 178.3 ± 22.1 | 18 | 1.0 |
| 17 | 16 | 0.943 ± 0.008 | 9.1 ± 0.6 | 0.058 ± 0.009 | 160.2 ± 11.6 | 19 | 1.1 |
| 18 | 12 | 0.945 ± 0.015 | 8.7 ± 1.0 | 0.057 ± 0.016 | 156.8 ± 18.8 | 18 | 1.0 |
| 19 | 16 | 0.927 ± 0.010 | 10.8 ± 0.8 | 0.076 ± 0.011 | 148.2 ± 8.4 | 19 | 1.5 |
| 20 | 15 | 0.934 ± 0.012 | 10.0 ± 0.9 | 0.068 ± 0.013 | 152.2 ± 12.3 | 19 | 1.3 |
| 21 | 14 | 0.936 ± 0.009 | 9.6 ± 0.6 | 0.066 ± 0.010 | 150.9 ± 9.9 | 18 | 1.2 |
| 22 | 12 | 0.932 ± 0.016 | 10.4 ± 1.1 | 0.071 ± 0.017 | 152.2 ± 15.8 | 16 | 1.1 |
| 23 | 19 | 0.948 ± 0.011 | 7.5 ± 0.8 | 0.053 ± 0.011 | 144.3 ± 12.1 | 25 | 1.3 |
| 24 | 9 | 0.933 ± 0.015 | 8.0 ± 0.9 | 0.069 ± 0.016 | 119.8 ± 10.8 | 16 | 1.1 |
| 25 | 11 | 0.940 ± 0.014 | 9.0 ± 0.9 | 0.061 ± 0.015 | 151.1 ± 16.8 | 15 | 0.9 |
| 26 | 8 | 0.936 ± 0.019 | 8.2 ± 1.1 | 0.066 ± 0.021 | 127.9 ± 16.6 | 14 | 0.9 |
| Mean value | 377 | 0.940 ± 0.010 | 9.3 ± 0.2 | 0.062 ± 0.011 | 155.8 ± 19.5 | – | – |

$n$, number of pairs $L_t - L_{t+1}$; $T$, age of the mollusk; $\tau = kT$; "–", not calculated.

data, the growth constant $k$ ranges 0.127–0.315 year$^{-1}$ for different species in subfamily Anodontinae (Alimov, 1981). Thus, the value of growth constant in *A. beringiana* is lower than in other species of freshwater mussels and is the closest to the value of $k$ in *Margaritifera* (Table 2). It is known that the growth constant for *Margaritifera margaritifera* is inversely related to the latitude and, consequently, to the temperature of the mollusk's habitat (Zotin and Yeshko, 2017). Therefore, it can be assumed that the lower value of $k$ in *A. beringiana* is due to the fact that the studied population lives in a relatively cold waterbody.

A negative correlation between the growth constant and the maximum lifespan is shown for the animals whose the growth can be described by the von Bertalanffy equation (Alimov, 1981; Bauer, 1992); i.e., $\tau = kT_{max}$ can be used as index of species lifespan for these species. The values of $\tau$ for bivalve mollusks are given in Table 2. It is evident from this table that the species lifespan for different mollusk species varies insignificantly from 1.7 to 2.9 (2.2 ± 0.1 on average). The value of $\tau$ obtained for *A. beringiana* corresponds to the lower limit of the range. However, if we consider the small size of the dataset of studied mollusks, it can be hypothesized that the maximum lifespan is actually more than 28 years, and, accordingly, the species lifespan is longer. If we assume that $\tau$ for *A. beringiana* corresponds to the average value for bivalve mollusks, then the estimated maximum lifespan of mollusks in the studied population is 35 years.

This value is relevant to the discussion on the longevity of mollusks inhabiting northern rivers. Freshwater pearl mussels frequently attract attention in this regard, since they can live for a very long time: up to

**Table 2.** Species lifespan in bivalves

| Family | Species | $k$, year$^{-1}$ | $T_{max}$, year | $\tau = kT$ | References |
|---|---|---|---|---|---|
| Mytilidae | *Mytilus edulis* | 0.165 | 13 | 2.1 | 1 |
| Unionidae | *Anodonta anatina* | 0.185 | 12 | 2.2 | 2, 3 |
| (Anodontinae) | *A. seisanensis* | 0.315 | 6.8 | 2.1 | 2 |
| | *A. piscinalis* | 0.350 | 5.8 | 2.0 | 2 |
| | *Cristaria plicata* | 0.127 | 22 | 2.8 | 2 |
| Unionidae | *Lanceolaria cylindrica* | 0.230 | 8.6 | 2.0 | 2 |
| | *Unio pictorum* | 0.336 | 6.7 | 2.3 | 2, 3 |
| | *U. tumidus* | 0.343 | 6.5 | 2.2 | 2, 3 |
| | *U. crassus* | 0.187 | 12 | 2.2 | 2 |
| Margaritiferidae | *Margaritifera dahurica* | 0.122 | 14 | 1.7 | 2 |
| | *M. laevis* | 0.063 | 45 | 2.8 | 2 |
| | *M. margaritifera* | 0.021 | 105 | 2.2 | 2,3 |
| Dreissenidae | *Dreissena polymorpha* | 0.492 | 4.2 | 1.7 | 2 |
| Cyrenidae | *Corbicula purpurea* | 0.336 | 5.7 | 1.9 | 2 |
| | *C. tibetensis* | 0.580 | 4.1 | 2.4 | 2 |
| | *C. fluminalis* | 0.320 | 6.4 | 2.0 | 2 |
| Astartidae | *Astarte borealis* | 0.411 | 7 | 2.9 | 4 |
| | *A. arctica* | 0.485 | 6 | 2.9 | 4 |
| Solecurtidae | *Tagelus plebeius* | 0.173 | 14 | 2.4 | 5 |
| Vesicomyidae | *Calyptogena kilmeri* | 0.25 | 7 | 1.8 | 6 |

$k$, constant of growth from equation (1); $T_{max}$, maximum lifespan; $\tau$, species lifespan. References: 1, Zotin and Ozernyuk, 2004; 2, Alimov, 1981; 3, Zotin, 2009; 4, Celine, 2007; 5, Lomovasky, 2003; 6, Barry et al., 2007.

180 years (Helama and Valovirta, 2008). The highest records are noted in the north of the distribution range (Bolotov et al., 2018). Freshwater pearl mussels are common in the less cold climate than the mollusks we have found. However, the age of the latter is relatively low. This is largely due to the habitat differences: *Anodonta* inhabit more productive, warmer water bodies. In our case, they inhabit the lake that is enriched and heated by the full-flowing river running from the south (these mollusks are not found in the closed cold lakes of the surrounding tundra and forest-tundra). Despite this, however, the climate in the lower reaches of the Kolyma River is apparently close to the extreme for large bivalve mollusks. This means that the special features of the species determine the lifespan range to a greater degree than the habitat conditions.

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