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Growth parameters of endangered freshwater pearl mussel (*Margaritifera laevis*, Unionoida)

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With 3 figures and 3 tables

Abstract: We observed periodic increments of the annuli to verify the annual growth-age relationship in two populations of a freshwater pearl mussel, *Margaritifera laevis* (Bivalvia, Unionoida), in northern Japan and confirmed that one annulus is added each year. The relationship between yearly shell growth and age was regarded as a unimodal distribution. We fitted several growth models to the shell length-age relationships of these two populations, which had different densities and age distributions. The Gompertz function showed the best fit, in terms of both RSS (residual sum of squares) and the difference between the observed maximum shell length and the asymptotic shell length. The life span of *M. laevis* was shorter than that reported for *Margaritifera margaritifera* populations at higher latitudes ($\geq 50^\circ\text{N}$), which have been widely recognized as threatened. Margaritiferid mussels living at lower latitudes tend to have shorter life spans and smaller maximum size. These results suggest that margaritiferid mussels in southern regions such as *M. laevis* in Japan and *M. margaritifera* in Spain may be particularly vulnerable when conditions are unsuitable for juvenile mussels for prolonged periods.

Key words: growth models, Gompertz function, annuli, maximum shell length, life-span, conservation.

Introduction

Environmental characteristics greatly affect the metabolic rates of ectothermic animals such as bivalves. Many ectothermic species display metabolic acclimation to their environment; thus, even in these same species, growth rate, body size, and life span, all of which relate to metabolic rate, vary in relation to the environment. Variations in these life-history parameters influence the population dynamics of ectothermic species living in different habitats.

The freshwater pearl mussel, *Margaritifera laevis* (Haas) is found in Japan, the Kurile Islands and Sakhalin Island (Kohmoto 1928, Taki 1930, Kuroda 1931, Miyadi 1938, Kondo 2008). The species is declining in Japan and is therefore listed as endangered by the Ministry of the Environment of Japan (Ministry

of the Environment 2007), and conservation measures for these mussels are required. Another margaritiferid species, *Margaritifera margaritifera* (Linnaeus) living in Europe and North America is also declining (Bespalaya et al. 2007, Frank & Gerstmann 2007) and is also recognized as a threatened species (Young et al. 2001).

According to Comfort (1957), Awakura (1969) and Heller (1990), mussels are the longest-lived invertebrates. The life span and maximum size of *M. laevis* differ among populations. In five Japanese populations, the maximum age varies between 36 to 67 years, and the maximum shell length from 111 to 133 mm (Awakura & Sugiwaka 1988). For both these life-history traits, a parameter of the exponential growth is a major determinant (Bauer 1992). This parameter determines the curvature of the growth curve, that is,

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the rate at which the size approaches the maximum shell length (Bertalanffy 1938). Maximum size and life span are inversely related to the magnitude of this growth constant (Bauer 1992).

The number of eggs in marsupia of a female *M. laevis* mussel tends to increase as the mussel size increases (Awakura 1968). Margaritiferid mussels probably do not have a post-reproductive period, because it has been shown that *M. laevis* can reproduce even at 57 years of age (Awakura 1969) and *M. margaritifera* at over 100 years (Bauer 1987). Thus, a population of *M. laevis* with a longer life span can provide recruitment for a longer period. Since the reproductive success which depend on exogenous factors, such as the dynamics of host (larvae in Unionoida spend part of their life cycle attached to fish and/or amphibian) may vary over time, longevity decreases the vulnerability of the population. Several mathematical functions have been proposed to describe animal growth with time (Chicharo & Chicharo 2000, Pouvreau et al. 2000, Millstein & O'Clair 2001). Such models include a parameter for growth rate, theoretical maximum size and maximum age. These growth-model parameters have been used to assess the conservation status of *M. margaritifera* populations (Beasley & Roberts 1999). In this species, life span and shell size are associated with productivity and various environmental factors such as water temperature and the concentration of nitrate in the water (Bauer 1992, Hastie et al. 2000a). Accurate estimation of these parameters in growth models based on age and body length helps the understanding of the life-history of *M. laevis*. It may be also be helpful for their conservation. However, no morphological trait indicating age has been identified in *M. laevis*, so an optimal growth model has not yet been developed.

The aims of the present study were (1) to confirm that growth bands are incremented annually; (2) to qualitatively verify the assumptions required for selecting the appropriate growth model from the relationship between age and the annual increment in shell length (i.e., to verify the age at which this mussel attains its annual growth peak and to determine whether the annual growth versus age curve is symmetric); and (3) to find the best descriptor of mussel growth by fitting four non linear growth models (i.e., hyperbolic saturation function, Gompertz function, logistic function, and Bertalanffy growth function), to the *M. laevis* length-at-age data sets and comparing their fit and performance.

Methods

Sampling sites

We obtained *M. laevis* specimens from one site in the Shiribetsu River in Rankoshi town and Chitose Rivers in Chitose city, Hokkaido, Japan, respectively. The Shiribetsu River is 126 km long and the Chitose River is 108 km long. Mussels, including adults and juveniles, are distributed abundantly in the lower reaches of the Shiribetsu River and in the middle reaches of the Chitose River. Such populations including abundant juvenile mussels are not common in Japan (Akiyama 2007). Thus, by using specimens from these rivers with abundant juveniles, we could ascertain the true growth model for *M. laevis*, allowing us to accurately understand the growth pattern not only during the adult stage but also during the juvenile stage. The number of mussels used for the present study was 186 individuals from the Shiribetsu River and 229 individuals from the Chitose River. In these specimens, 79 individuals in the Shiribetsu River and 229 individuals in the Chitose River were sacrificed (Table 1). License for mussel collection was obtained from the Chitose city government and Shiribetsu fisheries cooperative association in advance.

Table 1. Outline of methods for respective rivers.

	year	Purpose	The main method	The number of collected data / samples used / sacrificed per act
Shiribetsu River	2004	Verification of ring increments	Observation of shell surface	107 / 107 / 0
	2003	Verification of growth pattern	Boiling shell, length measurement and ring count	298 / 53 / 53*
	2003	Growth model fitting	Length measurement and ring count	79 / 79 / 79
Chitose River	2003	Verification of growth pattern	Boiling shell, length measurement and ring count	378 / 96 / 96*
	2003	Growth model fitting	Length measurement and ring count	229 / 229 / 229

* All of these mussels consist of a part of specimens for growth model fitting for each population.

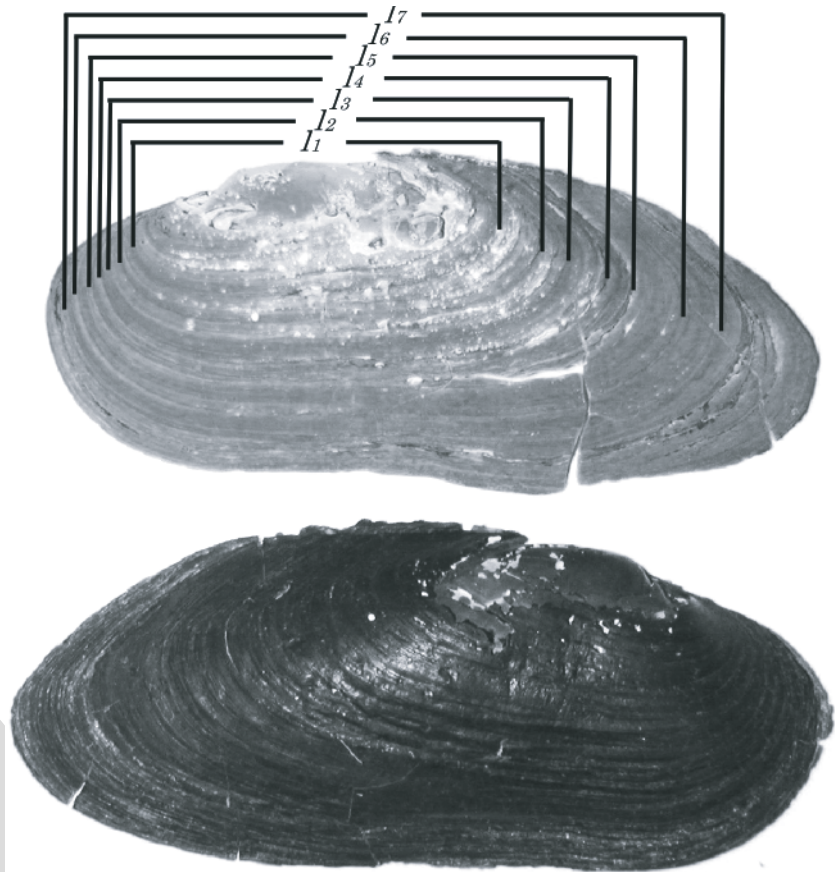


Fig. 1. Photographs of *Margaritifera laevis* shells: boiled in a 1 N NaOH solution (top), and an untreated shell (bottom). l_i , long axis length of the i th observable annulus.

Observation of annual growth ring increments on the mussel shell surface

We hypothesized that the growth ring of *M. laevis* is formed in winter and yearly individual growth can be estimated from length between consecutive growth rings because the growth rings of three mussel species, *Anodonta anatina*, *Unio tumidus* and *Unio pictorum* belonging to the same order as *M. laevis*, are known to form in winter (Negus 1966). In August 2004, 107 mussels were collected randomly from the Shiribetsu River, and, after measurement of their shell lengths with a vernier caliper to within 0.01 mm, their shell surfaces were abraded with a label by using a miniature electric drill. Immediately thereafter, the mussels were released to their original river habitats. A year later, the labeled mussels were collected again and the number of growth rings on the marginal parts of the mussel shells that had grown during the previous year was counted. The result showed that growth rings of *M. laevis* in the Chitose River increased by one each year (Akiyama 2004).

Change in annual growth with age

To verify the characteristic of the growth pattern of *M. laevis*, 53 mussels were collected from the Shiribetsu River, and 96 from the Chitose River, in 2003. The length axes of the growth rings (annuli) on the shell surface were measured with a digital caliper to within 0.01 mm and the differences in the long axis lengths (Fig. 1) between consecutive growth rings were ascertained. Shells with obscure growth rings were boiled in

1 N NaOH solution for about 10 minutes to carefully remove the periostracum and render these growth rings clearly visible. To estimate the age of the specimen, the number of growth rings was counted and recorded. We obtained these data from all specimens and combined them per river ($N = 298$ for the Shiribetsu River and $N = 378$ for the Chitose River) to examine the relationship between annual shell growth and age for each river. A problem arose with old specimens, because in these specimens fairly large areas around the umbo are often badly abraded, thus hampering observation of several of the earliest annuli. To avoid the problem caused by this absence of data, we corrected the ages of these specimens by using data from juvenile specimens with less erosion. A complete shell (8.6 mm in shell length) without erosion from the Chitose River had growth rings that could be observed clearly. We measured the length axis of the first annulus (0.52 mm) of this specimen with a digital caliper to within 0.01 mm under a binocular microscope with 25 \times magnification. Kobayashi & Kondo (2005) reported that the mean shell length of *M. laevis* juveniles in the Chubu-nogu River, Japan, shortly after detachment from their host fish was 470 μm . In addition, shell growth of juvenile *M. margaritifera* from different rivers is known to be rather uniform until the end of their first winter (Buddensiek 1995). These findings suggest that the first-annulus of our specimen formed in the first winter after the juvenile mussel detached from its host fish. The length-axis length of the second annulus, which formed in the next winter when the mussel was one year old was 1.33 mm. Thus, we estimated the number of growth rings on the abraded part of the shell around the umbo on the basis of the relationship

between shell length and the number of growth rings obtained from less eroded juvenile shells.

Fitting growth models to shell length-age relationships and comparison of growth parameters between the two populations

To investigate the growth characteristics of each population, we fitted four nonlinear growth models to the shell length-at-age relationships. In 2003, 79 and 229 mussels, including the specimens used to verify the growth pattern, were collected from the Shiribetsu River and the Chitose River, respectively. We especially tried to catch the mussel with maximum size in each river for about an hour. The shell length of each individual was measured with a vernier caliper to within 0.01 mm. The age of each shell was estimated according to Hendelberg's (1961) method, by which a mussel's age is determined from the number of annual layers on cut surface of its ligament. This method is suitable for the age determination of long lived mussels with thickly developed ligament and could be carried out with low cost and short labor hour, and thereby the method has often been used for Margaritiferidae (Bauer 1983, Hruska 1992, Hastie & Toy 2008). The age estimated by the method in Hendelberg (1961) tends to be several years younger than that estimated by the method of counting annuli on the shell surface of *M. laevis* in the Chubu-Nougu River in central Japan due to obscure rings (Kobayashi & Kondo, 2008). However, average air temperature in our sampling sites lying in northern Japan, are lower than in the study site of Kobayashi & Kondo (2008) (Rankoshi town: 7.5 °C, Chitose city: 7.1 °C, Omachi city which is sampling site in Kobayashi & Kondo (2008): 9.3 °C, these temperatures were calculated based on the data between 1979 to 2008 provided by Japan Meteorological Agency) with long winter (i.e., land is covered with snow for about five months in a year), and thus mussels in our sampling sites had clear and thick rings and these lines could be easily counted. Another method recommended by Neves & Moyer (1988), which is thin-sectioning of a shell, is the most effective techniques for many mussel species, whereas, the method in Hendelberg (1961) is suitable for several species including Margaritiferidae. This is because the latter only applies to mussels with thickly developed ligament, and consequently, the method is unsuitable for genera with thin shells, e.g. Anodonta. Since the method in Hendelberg (1961) can be easily done at low cost, it is very convenient for at least some margaritiferid populations including *M. laevis* in northern Japan. After considering these facts, we eventually decided that the age estimation according to Hendelberg (1961) is a suitable method for *M. laevis* in our study because our specimens had distinct growth lines in well developed ligament.

In the present study, we fitted the following four growth functions to the shell length and age data. The hyperbolic saturation function, or Michaelis-Menten equation, is commonly used by ecologists (Li 1983, Kluth & Bruelheide 2004). San Miguel et al. (2004) modified this function by adding two parameters to apply the function to a mussel population after a certain age. In the present study, we applied a three-parameter function with one additional age parameter (eq. 1). The Gompertz function (eq. 2, Gompertz 1825) is asymmetrical in relation to the inflection point, whereas the logistic function (eq. 3, Verhulst 1845, 1847) is symmetrical. The Bertalanffy growth function (eq. 4, Bertalanffy 1938) does not incorporate an inflection point and is commonly used to describe growth after the initial exponential growth phase in the first year of life (Ricker 1975). Both the Gompertz function and the logistic function have been used for marine bivalves (Dean 1993, Devillers et al. 1998, Ohnishi & Akamine 2006). The Bertalanffy growth function has been

widely used for freshwater mussel species, including *M. margaritifera* (Hastie et al. 2000a, King 2000). The four models are expressed by the following functions:

Hyperbolic saturation function

$$L_t = \frac{L_\infty k(t-t_0)}{1+k(t-t_0)} \quad (1)$$

Gompertz function

$$L_t = L_\infty e^{-ae^{-kt}} \quad (2)$$

Logistic function

$$L_t = \frac{L_\infty}{1+e^{-k(t-b)}} \quad (3)$$

Bertalanffy growth function

$$L_t = L_\infty (1-e^{-k(t-t_0)}) \quad (4)$$

where L_∞ is the theoretical maximum length (or asymptotic length, mm), k is the growth coefficient (year^{-1}), t_0 is the theoretical age at zero length (years), and a and b (year) are constants. The parameter values of each function were estimated by the Gauss-Newton algorithm, which is the most common algorithm for solving nonlinear regressions (Myers 1990). The best-fitting model was selected by comparing RSS (residual sum of squares). Computer programs for all tasks were built with R version 2.4.1 (R Development Core Team 2006).

Results

Yearly increment of growth rings on the mussel shell surface

Forty-nine labeled mussels were collected again a year after their release. In 38 of these mussels, the shell surface had been incremented by one ring during the previous year. These 38 mussels were all less than 93.9 mm in shell length. In mussels larger than 98.4 mm, and in a few mussels less than 93.9 mm long, the growth band increment could not be precisely confirmed because their growth rate was low and the shell surface was a dark color. Moreover, false rings had formed in 17 mussels as a result of stress caused by the mini-drill. These false rings, however, could be clearly distinguished from true growth rings because the false rings were narrow and discontinuous, especially on the anterior part of the shell.

Change in annual growth with age

Annual shell growth, as indicated by the difference in the length of the length-axis of adjacent annuli, was unimodal against age, with maximum growth reached at 5 years in the Shiribetsu River. In contrast, in the Chitose River, the relationship appeared bimodal, with

a small peak at 3 years and a broad peak and maximum growth at 7 years. In both rivers, shell growth was gradual during the early juvenile phase, and after the mussels attained their maximum annual growth increment at the age of 5 to 7 years, it decreased gradually with age (Fig. 2).

Determination of a suitable growth model

In both populations of *M. laevis*, the growth curve was an asymmetric sigmoid curve (Fig. 3). Among the collected specimens, the maximum age and the maximum shell length were 21 years and 118.3 mm, respectively, for the Shiribetsu River population, and 55 years and 118.4 mm for the Chitose River population. For both populations, the best-fitting and the second-best-fitting models were the Gompertz function and the Bertalanffy growth function (Table 2). Fitting of the Gompertz function resulted in an L_{∞} (95 % confidence intervals) value of 113.4 mm (110.0–116.7 mm) for the Shiribetsu River population and 106.7 mm (98.1–115.3 mm) for the Chitose River population (Table 2). These values were significantly lower than the observed maximum shell lengths. The L_{∞} values calculated for the hyperbolic function and the logistic function were significantly higher and lower than the observed values, respectively. The L_{∞} value for the population in the Shiribetsu River calculated with the Bertalanffy growth function was not significantly different from the observed value, whereas that for the population in the Chitose River was significantly higher than the observed value.

Discussion

We confirmed that the number of annuli of *M. laevis* increased by one each year, and that we could distinguish false rings from genuine rings. These findings indicate that the age and annual growth rate of these mussels can be estimated from the annuli on their shell surfaces. However, in the present study, we did not estimate the ages of *M. laevis* from the number of annuli but from the number of annual layers in the ligament because the former permit age estimation for mussels up to 30–40 years old, whereas the latter can be applied to mussels over 100 years (Hendelberg 1961). Even if age estimation errors (Kobayashi & Kondo 2008) are taken into account, growth layers are incremented in the ligament roughly synchronously with the annual ring increment on the shell surface (Akiyama 2007). Accordingly, increases in annual rings and in annual layers approximately coincide, and the method of age

Table 2. Parameter estimates of four growth models for two Japanese *Margaritifera laevis* populations. Values in parentheses indicate 95 % confidence intervals.

	Shiribetsu R.				Chitose R.			
	Hyperbolic function	Gompertz function	Logistic function	von Bertalanffy growth function	Hyperbolic function	Gompertz function	Logistic function	Von Bertalanffy growth function
L_{∞} (mm)	166.8 (153.2 to 180.3)	113.4 (110.0 to 116.7)	109.2 (106.5 to 112.0)	123.7 (117.6 to 129.7)	243.1 (190.6 to 295.6)	106.7 (98.1 to 115.3)	91.4 (85.4 to 97.3)	150.8 (125.7 to 175.9)
K (year ⁻¹)	0.135 (0.107 to 0.164)	0.278 (0.251 to 0.305)	0.415 (0.374 to 0.455)	0.150 (0.130 to 0.170)	0.018 (0.012 to 0.024)	0.087 (0.077 to 0.097)	0.159 (0.143 to 0.175)	0.028 (0.021 to 0.035)
a		4.32 (3.71 to 4.92)				2.92 (2.72 to 3.11)		
b			6.63 (6.36 to 6.89)				14.33 (13.30 to 15.35)	
T_0 (years)	2.28 (2.04 to 2.51)			2.13 (1.90 to 2.37)	1.14 (0.51 to 1.78)			1.05 (0.45 to 1.65)
RSS	2314	2018	2378	2088	10495	10105	11139	10352
Residual error*	48.5	-4.9	-9.1	5.4	124.7	-11.7	-27.0	32.4

* Residual error: L_{∞} – observed maximum shell length

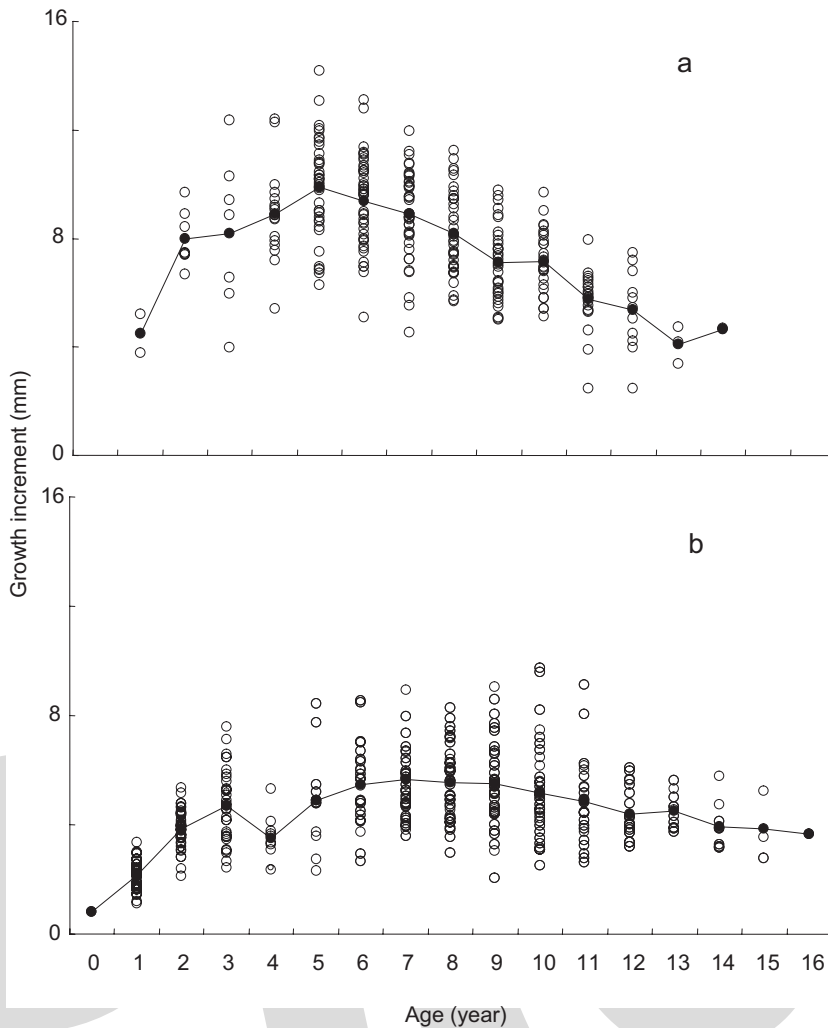


Fig. 2. Variation of yearly incremental growth with age in *Margaritifera laevis* populations in the Shiribetsu (a) and Chitose (b) Rivers. s and d represent individual growth and mean incremental growth per year of age, respectively.

estimation from annual layers in the ligament used for *M. margaritifera* (Bauer 1988, Hastie et al. 2000a, 2000b) is also applicable to *M. laevis*.

The annual growth increment of these mussels increased gradually with age until they reached 5 to 7 years of age, and then yearly incremental shell growth gradually decreased (Fig. 2). In the Chitose River population, the annual growth at 4 years of age was lower than that at ages 3 or 5 years. This result might reflect the small sample size of 4-year-old mussels ($n = 10$). The unimodal distribution of growth rate against age implied that the best-fitting model for the growth of *M. laevis* should have an inflection point. Therefore, although the Bertalanffy growth function is often used for describing margaritiferid growth (Hastie et al. 2000a, San Miguel et al. 2004, Outeiro et al. 2008), this model is unsuitable for *M. laevis* because it has no left-hand 'tail'. Moreover, the maximum age that mussels in the Shiribetsu and Chitose Rivers attained

was 21 and 55 years, respectively. Therefore, the peak growth rate of *M. laevis* is not in the middle of its life span. These growth patterns and life spans indicate that the shape of the growth-model curve for *M. laevis* is asymmetrical. These facts suggest that the Gompertz function is most suitable for describing the growth of *M. laevis*, and, in fact, the Gompertz growth function was the best-fitting function as indicated by the lowest RSS. The Gompertz function family, which includes the Laird-Gompertz function (Laird et al. 1965), has been used as a suitable growth model for a wide range of organisms, including mammals (Bergmann et al. 2006, Mattson et al. 2006), reptiles (Hailey & Coulson 1999), fish (Matic-Skoko et al. 2007), crustaceans (Piscart et al. 2003), echinodermata (Skold et al. 2001), and molluscs (Blanchard & Feder 2000). However, only a few studies have used the Gompertz function for freshwater mussels (e.g., Nakagawa et al. 1998), whereas the Bertalanffy growth function is more com-

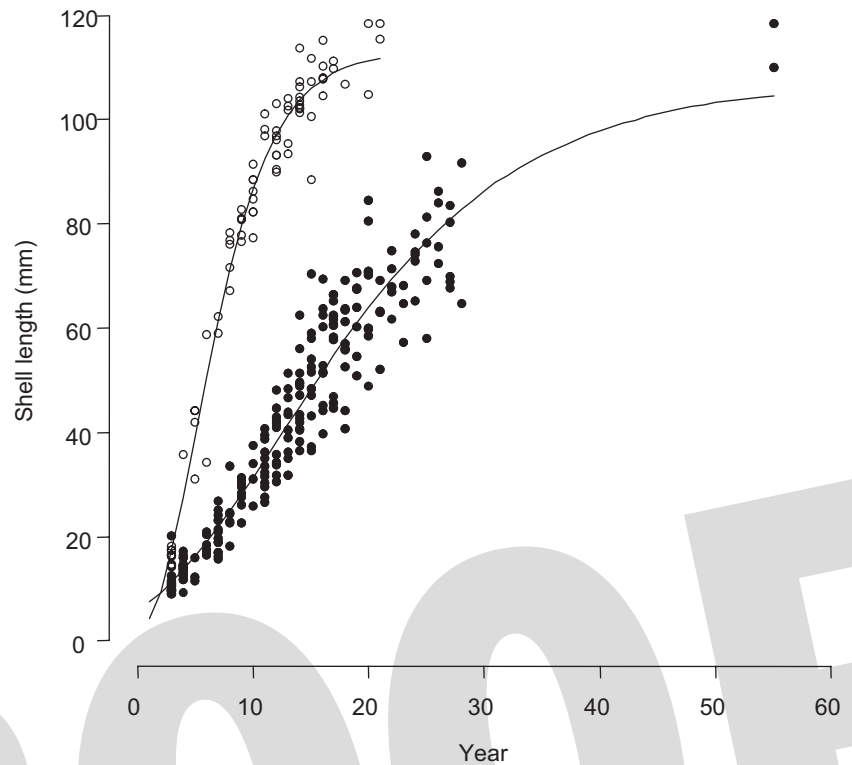


Fig. 3. Estimated Gompertz growth curves for *Margaritifera laevis* populations in the Shiribetsu River (s) and the Chitose River (d).

monly used (Hastie et al. 2000a, King 2000, Czarnoleski et al. 2003, Helama & Valovirta 2007). San Miguel et al. (2004) demonstrated that the yearly incremental growth of *M. margaritifera* is highest between 4 and 7 years of age. Although mussels younger than 3 years were not included in their study, the relationship between shell growth and age showed a unimodal distribution. This result suggests that the Gompertz function might also be a more suitable growth function for a population of *M. margaritifera* with juveniles, a suggestion supported by Buddensiek (1995), who found that the yearly growth of caged *M. margaritifera* increases with age between 1 and 4 years. Yearly growth increment decreases with age after 12 years of age (Helama & Valovirta 2007)

In the present study, the growth coefficient (k) in the Shiribetsu River population was higher than that in the Chitose River population. This result implies that the population in the Shiribetsu River consisted of mussels with smaller maximum size and lower maximum age. Indeed, the maximum observed age in the Shiribetsu River was less than that in the Chitose River in the present study. Moreover, Awakura & Sugiwaka (1988) reported that the maximum age attained is 36 years in the Shiribetsu River and 47 years in the Chitose River. Maximum sizes were approximately the same in both rivers in the present study, and Awakura

& Sugiwaka (1988) found maximum sizes of 133 mm in the Shiribetsu River and 130 mm in the Chitose River. Thus, our findings are consistent with those of Awakura & Sugiwaka (1988) in terms of the maximum age and maximum sizes relationships between the two rivers. The different results obtained by Bauer (1992) from our results and those of Awakura & Sugiwaka (1988) might reflect differences in species, number of sampling sites, or spatial sampling scale. The maximum ages and maximum sizes of mussels from the Shiribetsu and Chitose Rivers were different between the present study and that by Awakura & Sugiwaka (1988): maximum size of mussels was lower in the present study than in the study of Awakura & Sugiwaka (1988). Maximum age of mussels was lower than the maximum age reported by Awakura & Sugiwaka (1988) for mussels from the Chitose River, whereas the opposite was true for animals from the Shiribetsu River. It is known that *M. margaritifera* mussels living in the lower reaches of rivers grow faster than those living in the upper reaches and that the maximum size and maximum age differ among sampling sites along the same river (Hastie et al. 2000a). The difference in results between Awakura & Sugiwaka (1988) and the present study even for the same rivers might thus have been caused by differences in the sampling locations or by sampling time.

Table 3. Comparison of maximum age (A_{\max}) and maximum shell length (L_{\max}) among *Margaritifera laevis* and *Margaritifera margaritifera* populations. Numeric value in parenthesis is the result of the present study.

Species	Country	River	A_{\max} (years)	L_{\max} (mm)	n
<i>M. laevis</i>	Far east Russia	Brianka	32 ¹	123 ¹	23 ¹
	Far east Russia	Rikardo	28 ¹	136 ¹	13 ¹
	Japan	Shiribetsu	36 ² (21)	133 ² (118.3)	94 ²
	Japan	Chitose	47 ² (55)	130 ² (118.4)	351 ²
	Japan	Shibetsu	54 ²	121 ²	237 ²
	Japan	Masuhoro	58 ²	113 ²	127 ²
	Japan	Shokan-betsu	67 ²	111 ²	120 ²
<i>M. margaritifera</i>	Northwest Russia	Varzuga	190 ¹	120 ¹	44 ¹
	Northwest Russia	Thorma	155 ¹	152 ¹	13 ¹
	Northwest Russia	Keret	114 ¹	162 ¹	16 ¹
	United Kingdom	–	95 ³	132 ³	37 ³
	United Kingdom	–	73 ³	105 ³	52 ³
	United Kingdom	–	69 ³	150 ³	68 ³
	United Kingdom	–	84 ³	118 ³	87 ³
	United Kingdom	–	110 ³	139 ³	160 ³
	United Kingdom	–	123 ³	150 ³	82 ³
	United Kingdom	–	102 ³	125 ³	48 ³
	United Kingdom	–	52 ³	144 ³	65 ³
	United Kingdom	–	48 ³	140 ³	81 ³
	United Kingdom	–	112 ³	129 ³	31 ³
	Spain	Eo	50 ⁴	111.24 ⁴	157 ^{1,4}
	Spain	Landro	44 ⁴	117.32 ⁴	53 ^{1,4}
	Spain	Masma	45 ⁴	98.37 ⁴	90 ^{1,4}
	Spain	Mera	49 ⁴	96.77 ⁴	69 ^{1,4}
	Spain	Ouro	64 ⁴	103.13 ⁴	84 ^{1,4}
	Spain	Ulla	45 ⁴	99.9 ¹	52 ^{1,4}
	Spain	Arnego	48 ⁴	90.5 ⁴	22 ⁴
	Spain	Mandeo	38 ⁴	111.24 ⁴	38 ⁴
	Spain	Narcea	35 ⁴	99.76 ⁴	12 ⁴
	Spain	Narla	53 ⁴	101.65 ⁴	30 ⁴
Spain	Tambre	65 ⁴	106.67 ⁴	27 ⁴	
Spain	Trimaz	52 ⁴	90.56 ⁴	22 ⁴	

Sources: ¹ Ziuganov et al. (2000); ² Awakura & Sugiwaka (1988); ³ Hastie et al. (2000a); ⁴ San Miguel et al. (2004)

Although the growth coefficients (k) calculated for the four growth functions were all higher in the Shiribetsu River population, the theoretical maximum size (L_{∞}) associated with fecundity was larger in the Shiribetsu River when the Gompertz and logistic functions were fitted. However, L_{∞} was larger in the Chitose River population when the hyperbolic saturation and Bertalanffy growth functions were fitted (Table 2). Thus, the comparative assessment of the two populations based on the growth-model parameters depended on the specific growth model used. Differences between the observed maximum shell length and L_{∞} were smallest when L_{∞} was estimated with the Gompertz function (Table 2). Therefore, we considered L_{∞} estimated with the Gompertz function to be optimal, even though this function underestimated L_{∞} somewhat (Table 2). In *M.*

margaritifera, the L_{∞} value calculated with the Bertalanffy growth function was also underestimated except in a population with a short life span (i.e., maximum age of 35 years; San Miguel et al. 2004). In contrast, the L_{∞} value for the same population calculated with the hyperbolic growth function was overestimated (San Miguel et al. 2004). Therefore, these errors should be taken into account when using L_{∞} to assess fecundity in Margaritiferidae.

A_{\max} and L_{\max} in margaritiferid mussels differ among species, and variation within species across countries and populations can also be observed (Table 3). In terms of A_{\max} , no old mussel with the age over one hundred year has been reported in *M. laevis*. However, such old mussels have often been found in populations of *M. margaritifera*, especially in high latitude areas,

i.e. northwest Russia and UK, consistent with the fact that lifespan of *M. margaritifera* tend to be longer at higher latitude (Bauer 1992). Mussels in populations of *M. margaritifera* in Spain, the southernmost distribution area for the species in Europe (Young et al. 2001), have a lifespan similar to that of *M. laevis* (Table 3). Margaritiferid mussels probably do not have a post-reproductive period (Awakura 1969, Bauer 1987), and *M. laevis* and *M. margaritifera* reach sexual maturity when they are about 13 (Akiyama 2007) and 12–13 years old in Scotland (Young & Williams 1984), respectively. These results suggest that the reproductive period in *M. laevis* is shorter than that of *M. margaritifera* in higher latitudinal areas. Populations without juveniles are often observed in both margaritiferid species (Lucey 1993, Beasley et al. 1998, Alvarez et al. 2000, Cosgrove et al. 2000, Akiyama 2007) due to higher survival rate in adult mussels (Bauer 2001). These facts indicate that long-lived adults contribute to persistence of a population even when recruitment fails continually for several decades. If unsuitable environment prevents juvenile recruitment for a long period, population persistence will be dependent upon survival of adult mussels. Accordingly, under unsuitable habitat for juveniles, a *M. laevis* population is more vulnerable than a *M. margaritifera* population at high latitude because of its shorter lifespan.

L_{\max} in *M. laevis* was generally larger than that in *M. margaritifera* in Spain, but not larger than that in other countries. Although the fecundity of *M. laevis* may be correlated with shell length (Awakura 1968), the relationship is not common in *M. margaritifera* (Bauer 1998). Several causes should be considered to explain the result. If a mature mussel spends much energy for reproduction, growth rate may be reduced due to energy trade-off between reproduction and growth. Moreover, in this species, the value of immediate self-preservation of energy is high in relation to immediate reproduction (Sibly & Calow 1986). Thus, if environment factors that affect growth rate of mussels change rapidly on a very small spatial scales during several years, fecundities of individual mussels will not be correlated with their shell lengths. In the present study, mussel fecundity showed a clear correlation with shell length; however shell length might reflect effects of some endogenous factors such as variation in metabolism and reproductive effort depending on environmental changes.

At lower latitudes such as in Japan and Spain, extinction of populations in *M. laevis* and *M. margaritifera* may occur more rapidly under unfavorable environmental conditions due to the shorter lifespan

of the organisms after detachment from the host and free-living phase of larvae in high water temperature (Bauer 1992, Buddensiek 1995, Zimmerman & Neves 2002, Akiyama & Iwakuma 2007). Monitoring of margaritiferid populations is necessary to detect changes in vulnerable populations earlier and to take prompt action for conservation, especially for low-latitude populations.

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