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2001

Biology Bulletin, Vol. 28, No. 3, 2001, pp. 273–279. Translated from Izvestiya Akademii Nauk, Seriya Biologicheskaya, No. 3, 2001, pp. 331–338.
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ANIMAL AND HUMAN PHYSIOLOGY

Respiration Rate and Species-Specific Lifespan in Freshwater Bivalves of Margaritiferidae and Unionidae Families

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Received September 5, 2000

Abstract—We studied changes in the respiration rate in five species of freshwater bivalves as a function of animal age and size. The species-specific lifespan was calculated on the basis of the obtained data: Rubner's constant (*Ru*) and lifespan at standard temperature 20°C (T_{20}). The longest and shortest lifespan among the studied mollusks was specific for the pearl mussel *Margaritifera margaritifera* ($Ru = 37$ kJ and $T_{20} = 36$ years) and the freshwater mussel *Anodonta anatina* ($Ru = 8$ kJ and $T_{20} = 8$ years), respectively.

Bivalves are among the animals with the longest lifespan. An age of 50 years is not uncommon for them, and they often live over 100 years (Table 1). Apparently, the most long lived species—*Arctica islandica*, 220 years old according to Jones (1983)—has been found among marine bivalves. Note, however, that Zolotarev (1989) estimates the maximum age of this species in the Barents and White seas populations as low as 28 years. A maximum age variability has been described for other mollusk species as well (Table 1).

The highest lifespan among freshwater bivalves is specific for the pearl mussel *Margaritifera margaritifera* L. (family Margaritiferidae) (Hendelberg, 1960; Bauer, 1991, 1992). According to Bauer (1992), the maximum lifespan of the pearl mussel is 132 years. This is one order of magnitude higher than that in related freshwater mollusks of the Unionidae family, with this value estimated as 10–20 years (Alimov, 1981).

The lifespan of poikilotherms depends to a large extent on environmental conditions and temperature in particular. For instance, Bauer (1992) demonstrated that the top age of *M. margaritifera* ranges from 30 years in southern populations (Spain) to 130 years in northern populations (Sweden). Hence, the environmental conditions should be normalized in order to compare the lifespan of different animal species, or an environment-independent test should be used. Rubner's constant can serve as such a test.

Rubner (1908) demonstrated that the amount of oxygen consumed over the entire lifespan per weight unit is constant for many animal species:

$$Ru = \int_0^T \dot{q}_{O_2} dt, \qquad (1)$$

where *Ru* is Rubner's constant, *T* is lifespan, and $\dot{q}_{O_2}$ is the respiration rate (the rate of oxygen consumption per weight unit).

Rubner's constant is sometimes considered as a test of species-specific lifespan (Zotin and Alekseeva, 1984; Zotin, 1993). Zotin (1993) demonstrated that Rubner's constant can be used to determine the species-specific lifespan in virtually all animal groups (including bivalves).

Here, we measured the rate of respiration in five bivalve species of various age. The species-specific lifespan (Rubner's constant) of these mollusks was calculated from the obtained data.

MATERIALS AND METHODS

Five freshwater bivalves species have been studied: *Margaritifera margaritifera* L., *Dahurinaia laevis* Haas (Margaritiferidae family), *Unio pitorum* L., *U. tumidus* Philipsson, and *Anodonta anatina* L. (Unionidae family). *M. margaritifera* was collected in August 1995 in the Varzuga River (Terskii region, Murmansk oblast). *D. laevis* was collected in June 1995 in the Bryanka River (Anivskii region, Sakhalin oblast). The animals of Unionidae family were collected in summer of 1996 in the Oka River (Kashirskii region, Moscow oblast).

The mollusks were acclimated to the experimental temperature for at least one week: 14 and 20°C for Margaritiferidae and Unionidae families, respectively. The rate of oxygen consumption was determined by the standard technique (Semikhatova and Chulanovskaya, 1965). In the case of Margaritiferidae family, the obtained value was recalculated for 20°C using Krogh's normal curve (Zotin and Zotin, 1999):

$$\dot{Q}_{O_2} = \dot{Q}_{t^0} e^{0.085(t^0-20)} \approx 0.6\dot{Q}_{t^0},$$

where $\dot{Q}_{O_2}$ and $\dot{Q}_{t^0}$ are the rates of oxygen consumption at 20 and 14°C, respectively.

The total weight, as well as weight of soft tissues and the shell, was determined for calculating the mollusks respiration rate (the rate of oxygen consumption

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Table 1. Maximum lifespan (*T*, years) of certain bivalve species

Species	*T*	Habitat	Reference
Family Arcticidae			
Arctica islandica	28	White and Barents seas	Zolotarev, 1989
	220	Middle of Atlantic shelf (USA, New Jersey)	Jones, 1983
Family Mytilidae			
Crenomytilus grayanus	95	Sea of Japan, Lazurnaya Bay	Zolotarev, 1980, 1989
	108	Sea of Japan, Vostok Bay	
	150	Sea of Japan, Vityaz' Bay	
Modiolus modiolus	61	Sea of Japan, Vostok Bay	Zolotarev, 1980, 1989
Family Margaritiferidae			
Margaritifera margaritifera	80	Germany	Rubbel, 1913
	100	Germany	Israel, 1913
	116	Sweden	Hendelberg, 1960
	132	Sweden	Bauer, 1992
Family Hiatellidae			
Panope generosa	120	Pacific Ocean, Puget Sound Bay	Jones, 1983
Family Malletiidae			
Tindaria callistiformis	100	North Atlantics, 3800 m depth	Turekian *et al.*, 1975
Family Veneridae			
Callista brevisiphonata	63	Sea of Japan, Vostok Bay	Zolotarev, 1980, 1989
	76	Sea of Japan, Astaf'ev Bay	
Family Glycymeridae			
Glycymeris yessoensis	64	Sea of Japan, Vostok Bay	Zolotarev, 1980, 1989
Family Tellinidae			
Peronidia zyonoensis	61	Sea of Japan, Vostok Bay	Zolotarev, 1980, 1989
Family Carditidae			
Venericardia crebricostata	58	Sea of Okhotsk, Penzhinskaya Bay	Zolotarev, 1980, 1989
Family Mactridae			
Spisula voji	52	Komandorskie Islands	Zolotarev, 1980, 1989
	16	Pacific Ocean	
S. Sachalinensis	55	Sea of Japan, Vostok Bay	Zolotarev, 1980, 1989

per weight unit). In addition, the shell length—the maximum distance between the anterior and posterior ends—was measured.

The mollusks age was determined by counting annual rings. False annual rings and their number in the corroding area of the shell were accounted for using Bertalanffy's growth equation (Zyuganov *et al.*, 1993).

The calculation of coefficients of allometric equations and statistical processing of the data were carried out as described elsewhere (Zotin, 2000).

The data approximation by Eqs. (5) (below) was carried out by the Newton–Gauss method (Nosach, 1994).

RESULTS AND DISCUSSION

Weight used for calculating respiration rate. The problems of calculating the respiration rate in bivalves is complicated by the fact that most of their weight—the shell and mantle cavity fluid—is not involved in oxygen consumption. This suggests accounting only for the mollusks body weight; however, the shell is built by metabolic processes using the oxygen and, hence, its weight should be accounted for when calculating Rubner's constant from the total respiration rate during the entire lifespan.

Hereafter, we present the values of respiration rate calculated per soft body weight, while in the case of

Table 2. Ratios of shell weight (M_s), soft tissue weight (M_{st}), and mantle cavity fluid (M_{mf}) to total weight (M) in different bivalve species; n is number of mollusks

Species	M_s/M	M_{st}/M	M_{mf}/M
Anodonta anatina	0.295 ± 0.008 ($n = 21$)	0.313 ± 0.008 ($n = 54$)	0.392 ± 0.016 ($n = 21$)
Unio pictorum	0.448 ± 0.006 ($n = 29$)	0.297 ± 0.007 ($n = 34$)	0.255 ± 0.009 ($n = 28$)
U. tumidus	0.445 ± 0.008 ($n = 33$)	0.364 ± 0.019 ($n = 22$)	0.191 ± 0.009 ($n = 32$)
Margaritifera margaritifera	0.491 ± 0.005 ($n = 27$)	0.164 ± 0.004 ($n = 38$)	0.345 ± 0.006 ($n = 27$)
Dahurinaia laevis	0.478 ± 0.007 ($n = 21$)	0.166 ± 0.005 ($n = 28$)	0.356 ± 0.010 ($n = 21$)

Rubner's constant the calculations are given per total weight without the mantle cavity fluid.

Note that the proportions between total weight and weights of the shell, soft tissues, and the mantle cavity fluid do not depend on age. Hence, the presented data on the respiration rate can be recalculated per total mollusk weight using the coefficients presented in Table 2.

Table 2 demonstrates variability of relative shell and soft tissues weight in the studied species. Mollusks of Margaritiferidae family feature the most massive shell (48.5% total weight on the average) and the smallest relative body weight (16.5%), which reliably distinguishes them from those in Unionidae family. The least massive shell is specific for the freshwater mussels *Anodonta anatina* (29.5%), while the highest relative body weight is observed in the pearly mussel *Unio tumidus* (36.4%).

Relationship between respiration rate and mollusk age. Respiration rate in adult specimen decreases with age in most animal species (Zotin and Zotina, 1993). The studied bivalve species constitute no exception to this relationship. The data presented in Table 3 and Fig. 1 demonstrate gradual decrease in respiration rate with age in all five mollusk species.

Let us consider the thermodynamics of nonequilibrium processes in order to determine the nature of the respiration–age relationship. Zotin *et al.* (Zotin, 1984; Zotin and Zotina, 1993; Zotin and Zotin, 1999) demonstrated that in thermodynamical terms the respiration rate can serve as the measure of "specific function of external dissipation" (ψ_d):

$$\psi_d \approx \dot{q}_{O_2}. \tag{2}$$

This function increases with the rate of entropy production and describes the level of thermodynamic system deviation from equilibrium. The system evolves towards equilibrium so that its probability increases. Linear approximation reduces it to (Zotin and Zotina, 1993)

$$\frac{dp}{dt} = \beta(p_{st} - p), \tag{3}$$

where p is probability of the system condition at the current moment, p_{st} is probability of the system at the final stationary condition, and β is a constant.

On the other hand, the specific function of external dissipation varies inversely with the probability of the condition of the system (Zotin and Zotina, 1993):

$$\psi_d = \psi_{st}\frac{p_{st}}{p}, \tag{4}$$

where ψ_{st} is the specific function of external dissipation at the final stationary condition.

Table 3. Dependence of soft tissue weight (M_{st}, g), rate of oxygen consumption ($\dot{Q}_{O_2}$, mW), and respiration rate ($\dot{q}_{O_2}$, mW/g) on the mollusk age (t, years); n is number of mollusks

Species	t	n	M_{st}	$\dot{Q}_{O_2}$	$\dot{q}_{O_2}$
Anodonta anatina	1–2	5	2.6	0.316	0.132
	3–4	37	16.5	0.737	0.043
	5–6	6	25.7	0.918	0.036
	>6	6	34.9	0.739	0.020
Unio tumidus	1–2	16	1.5	0.377	0.329
	3–4	15	4.2	0.547	0.187
	5–6	16	7.4	0.475	0.073
	>6	7	14.2	0.746	0.054
U. pictorum	1–2	28	1.8	0.304	0.231
	3–4	18	6.2	0.630	0.145
	5–6	8	7.7	0.998	0.116
	>6	9	13.9	1.572	0.098
Margaritifera margaritifera	20–26	4	4.4	0.711	0.168
	27–33	14	6.4	0.883	0.138
	34–40	11	8.2	1.010	0.119
	>40	7	11.2	1.179	0.112
D. laevis	7–8	6	3.9	0.750	0.184
	9–13	8	7.8	1.317	0.171
	14–20	5	13.9	1.641	0.121
	>20	4	23.9	2.211	0.090

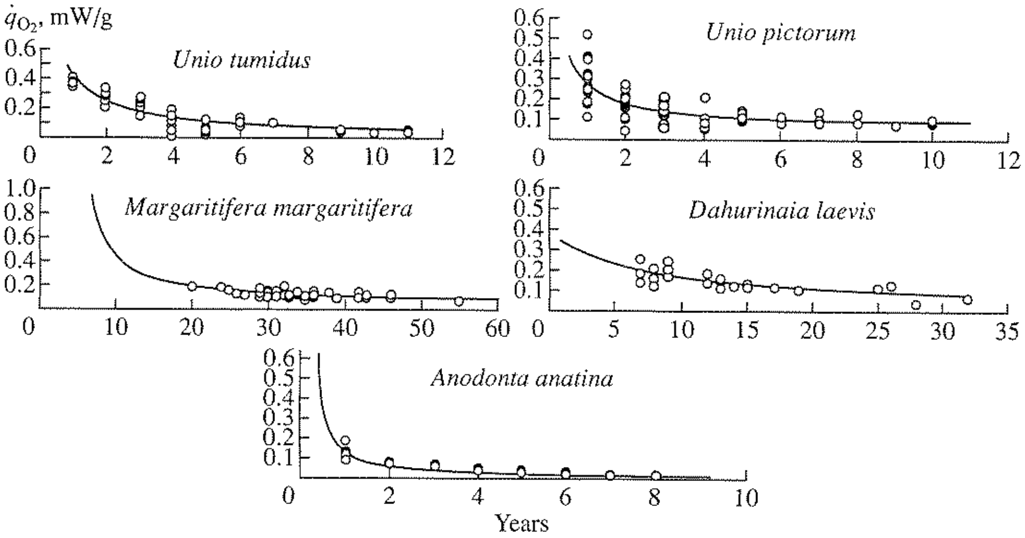

Fig. 1. Respiration rate as a function of age in freshwater bivalves; the data were approximated by equation (5).

Considering Eqs. (2)–(4), one can record the respiration rate:

$$\frac{1}{\dot{q}_{O_2}}\frac{d\dot{q}_{O_2}}{dt} = \alpha(\dot{q}_{st} - \dot{q}_{O_2});$$
$$\dot{q}_{O_2} = \frac{\dot{q}_{st}}{1 - A\exp(-kt)}, \qquad (5)$$

where $\dot{q}_{st}$ is respiration rate at the final stationary condition, $\alpha = \beta p_{st}$, $k = \alpha\dot{q}_{st}$, $A = 1 - \dot{q}_{st}/\dot{q}_0$ is the differentiation constant, and $\dot{q}_0$ is the respiration rate at the initial moment $t = 0$.

Equation (5) satisfactorily approximates the experimental data (Fig. 1). The coefficients of Eqs. (5) for the studied mollusk species are presented in Table 4.

Relationship between respiration rate and mollusk dimensions. Ample experimental data demonstrate that the respiration rate–body weight relationship can be approximated by allometric function (Brody, 1945; Dol'nik, 1968, 1978; Vinberg, 1976; Zotin and Zotin, 1999):

$$\dot{q}_{O_2} = aM^{-b}, \qquad (6)$$

where M is body weight, while a and b are constants.

A similar relationship is specific for bivalves as well (Zyuganov *et al.*, 1993; Zotin and Zotin, 1999).

Coefficient a, also called the relative metabolic rate (Zotin, 1984; Zotin and Zotin, 1999), can be interpreted as the respiration rate provided that the body weight equals unity. This coefficient can be used to compare the respiration rate in animals with different weights as long as the exponential coefficient b from the allometric equation (6) is the same in the compared animals.

Table 4. Rubner's constant (Ru) calculated for total weight and soft tissue weight for freshwater bivalves, the indices required for its calculation from equation (10), and lifespan at 20°C (T_{20}) calculated from equation (11); n is amount of data used for the calculations

Species	k, year^{-1}	r_0	r_T	Calculation per soft tissue weight		Calculation per total weight		T_{20}, years
				$\dot{q}_{st}$, mW/g	Ru, kJ	$\dot{q}_{st}$, mW/g	Ru, kJ	
Anodonta anatina	0.2735 ± 0.0092	0.0060 ± 0.0005	0.895	0.0304 ± 0.0019	25	0.0095 ± 0.0006	8	8
Unio tumidus	0.1448 ± 0.0068	0.0294 ± 0.0019	0.899	0.0675 ± 0.0060	84	0.0200 ± 0.0018	25	16
U. pictorum	0.1930 ± 0.0047	0.0963 ± 0.0013	0.899	0.0703 ± 0.0040	51	0.0256 ± 0.0014	18	11
Margaritifera margaritifera	0.0558 ± 0.0003	0.0900 ± 0.0018	0.879	0.0939 ± 0.0030	228	0.0154 ± 0.0005	37	36
Dahurinaia laevis	0.0536 ± 0.0005	0.0902 ± 0.0013	0.855	0.0775 ± 0.0036	186	0.0129 ± 0.0006	31	34

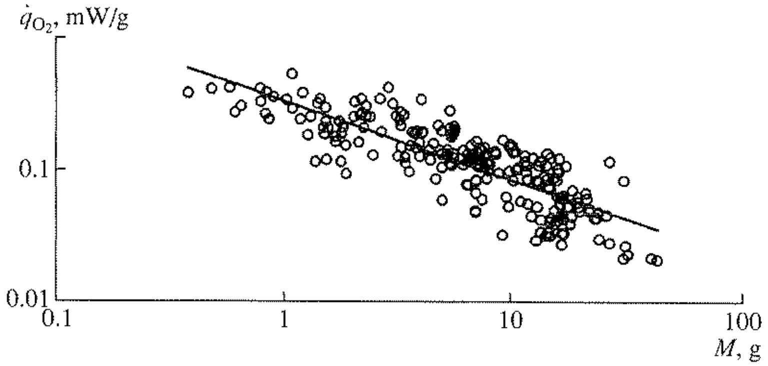

Fig. 2. Respiration rate as a function of soft tissue weight in all studied mollusks; the data were approximated by allometric equation (6).

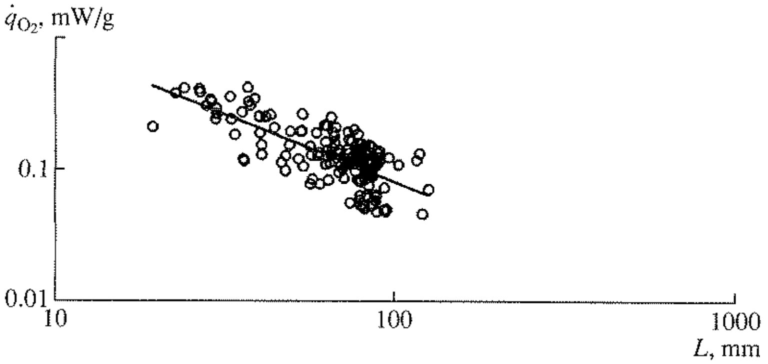

Fig. 3. Respiration rate as a function of shell length in all studied mollusks; the data were approximated the allometric equation (7).

Calculations on the basis of the linearity test (Zotin, 2000) demonstrate that the respiration rate–soft tissue weight relationship in bivalves can be approximated by the universal allometric equation (6) with coefficients $a = 0.318 \pm 0.009$ and $b = 0.567 \pm 0.033$ ($n = 235$) (Fig. 2). Hence, the studied species are indistinguishable by the relative metabolic rate.

The relationship between respiration rate and shell length (L) in bivalves can also be approximated by an allometric equation:

$$\dot{q}_{O_2} = lL^{-c}.$$

In this case, the data for all mollusk species can also be approximated by a universal equation with coefficients $l = 8.73 \pm 0.25$ and $c = 1.02 \pm 0.12$ ($n = 185$) (Fig. 3). Note that constant c does not reliably differ from unity. Hence, the approximate respiration rate grows inversely with the shell length:

$$\dot{q}_{O_2} \approx \frac{8.73}{L}. \quad (7)$$

Equation (7) can be used in particular for the approximate calculation of respiration rate from the shell length of freshwater bivalves.

Note that Eq. (7) can also be derived from the equation of mollusk linear growth. Multiple studies demonstrate that linear growth of the mollusk shell can be approximated by Bertalanffy's equation in the form (Alimov, 1974, 1981; Zyuganov *et al.*, 1993)

$$L = L_\infty(1 - A\exp(-kt)), \quad (8)$$

where L_∞ is the limiting length that L tends to at $t \longrightarrow \infty$, A is the constant of initial conditions, and k is the growth constant.

The allometric relationship is satisfied if constants A and k equal to the corresponding constants of Eq. (5). It follows that the rate of respiration should grow inversely with the shell length. Denoting the ratio between the current respiration rate and that at the final stationery condition as r_t, we have

$$r_t = \frac{\dot{q}_{O_2}}{\dot{q}_{st}} = \frac{L_\infty}{L}. \quad (9)$$

Rubner's constant and species-specific lifespan. As was already noted, Rubner's constant can serve as a test of species-specific lifespan. We will use the integral representation of the respiration rate–age relationship (5) and respiration rate–shell length relationship (9),

$$Ru = \int_0^T \frac{\dot{q}_{st}}{1 - A\exp(-kt)}dt = \frac{\dot{q}_{st}}{k}\ln\frac{\exp(kT) - A}{1 - A},$$

or, expressing Ru from equation (9),

$$Ru = \frac{\dot{q}_{st}}{k}\ln\frac{(1 - r_0)r_T}{(1 - r_T)r_0}, \qquad (10)$$

where r_0 and r_T are relationships (9) at the initial moment $t = 0$ and maximum age T, respectively.

All constants in Eq. (10) except r_T were determined approximately from the data in Eq. (5).

Let us use the conclusions of Alimov (1981) based on freshwater bivalves investigation: (1) bivalves are well protected from external factors and many of them survive to the maximum age; (2) the proportion between the shell length at the maximum age and limiting length (L_T/L_∞) is constant for a given mollusk species.

Hence, r_T value can be determined from the proportion between the shell length of the oldest animals in the population and the limiting length. The limiting length can be determined from Bertalanffy's growth equation (8).

Rubner's constant values and the indices required for its calculation are presented in Table 4. The calculations were carried out for total weight and soft tissues weight. In the both cases, the lowest and highest Rubner's constant was specific for *A. anatina* and *M. margaritifera*, respectively. The obtained values of Rubner's constant are similar to those obtained for other mollusks: 67.3 kJ for *Lymnae* sp. (Gastropoda) and 30.3 kJ for *Ostrea virginica* (Bivalvia) (Zotin, 1993).

In order to express the species-specific lifespan in conventional units, it can be calculated on the basis of synthetic equation of respiration rate (5) with an account of equation (9). Since the respiration rate was calculated for 20°C, the resulting value can be interpreted as the lifespan at 20°C (T_{20}):

$$T_{20} = \frac{1}{k}\ln\frac{(1 - r_0)}{(1 - r_T)}. \qquad (11)$$

Note one more advantage of using T_{20} to determine the species-specific lifespan as compared to Rubner's constant: this value is independent from the accounted weight.

The results of T_{20} calculations are presented in Table 4. The calculated lifespan at 20°C corresponds to the experimental values for Unionidae midlatitude populations (Alimov, 1981) and Margaritiferidae southern populations (Bauer, 1992).

Note in conclusion that, although the species-specific lifespan of the pearl mussel *M. margaritifera* is higher as compared to other studied mollusks, its value for 20°C (36 years) is not maximal for animals.

ACKNOWLEDGMENTS

We are grateful to V.V. Zyuganov and L.P. Nezlin for their help in collecting mollusks of the Margaritiferidae family.

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