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The analysis of the reproductive traits of the pulmonate molluscs: a mini-review

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ABSTRACT. The information on reproductive characteristics of more than 100 species of the pulmonate molluscs (clutch size, egg size, hatching success, etc.) is summarized. It is shown that the pulmonates demonstrate a very wide range of reproductive strategies that serve to enhance the survival of species in different (sometimes very unfavorable) environmental conditions.

Introduction

Land snails and slugs demonstrate great variation in life history traits, including such aspects as self-fertilisation, egg and clutch size variation, etc. These have been reviewed in many papers published in past decades of 20th century [Peake, 1978; Cain, 1983; Baur, 1994; Heller, 2001]. The aim of this paper is to synthesize available information on reproductive traits of the pulmonate molluscs accumulated until first decade of 21st century. First of all we are interesting in the interrelations between the clutch size and the egg size as an aspect of these animals reproductive strategy which no consideration has been given earlier.

Material and methods

The numerous published and own data on the various reproductive traits of more than 100 pulmonates were analysed. The median (*Me*) value as for as the first (*Q*1) and the thirds quartile (*Q*3) values were obtained for the basic characteristics as clutch size, egg size, hatching success, etc. The groups both of the snails and slugs were distinguished on the base of the main reproductive peculiarities with using the normal probability paper. All statistical analyses were carried out using of standard procedures [Sokal, Rohlf, 1995].

Results and discussion

The information on reproductive characteristics for more than 100 species of the pulmonates (clutch size, egg size, hatching success and others) is summarized in Table 1. In general, the number of eggs per clutch among land snails and slugs varies from 1 to 205, although the maximum number of eggs in a clutch can reach 400 (for example, for *Achatina fulica*). However, it may be noted the pulmonate molluscs are characterized by a low reproductive capacity since the median values of clutch size in different species only slightly exceed 30 eggs. On the other hand, some species have a very high reproductive capacity and their clutches contain more than one hundred eggs (Fig. 1A). The distribution of the mean clutch size on normal probability paper reveals at least two groups, for which the threshold value is 9-12 eggs per clutch (Fig. 1B).

The egg diameter in different species of land snails and slugs varies from 0.5 to 4-5 mm, and the median value is 1.76 mm (Fig. 2A). However, the egg diameter can reach 10-12 mm and more in some tropical species. Distribution of the mean egg diameter on the normal probability paper reveals at least two groups, for which the threshold value is about 2 mm (Fig. 2B).

Thus in relation to the clutch size and eggs size, four groups of species with different reproductive characteristics can be distinguished among the pulmonate molluscs. The first group is characterized by clutches containing less than 10 eggs (very often containing a single egg), average diameter of which does not exceed 2 mm. Most species of this group are small snails which live in forest and belong to the families Clausiliidae, Discidae, Punctidae, Cochlicopidae and Succineidae.

Group 2 includes the largest tropical species of Africa, Australia and New Zealand; their few clutches contain very large eggs (13-18 mm in diameter) (*Archachatina marginata, Paryphanta busbyi watti, Hedleyella falconeri*).

Group 3 consists mostly of the xerophilous species of snails with medium-sized shells; their numerous clutches contain eggs rarely exceeding 2 mm in diameter. Though, such hygrophilous species of land snails as *Fruticicola fruticum* and *Succinea putris* also fall to this group.

Group 4 mostly contains the achatinid and helicid snails of middle and large size; their numerous

Table 1. The reproductive traits of land snails and slugs.

Таблица 1. Репродуктивные показатели наземных моллюсков и слизней.

Notes. *D*ovo – the average diameter of eggs. *HS* – the hatching success. Self – self-fertilisation. MC – multiple oviposition.

Species	Clutch size (egg)			*D*ovo (mm)	*HS* (%)	Self	MO	Literature
	min	*max*	*mean*					
Achatina achatina (L., 1758)			131.8					Hodasi, 1982
A. achatina	20	40	30.0	9.00				Nisbet, 1974
A. achatina			18.6		72.8			Okon *et al*., 2012
Achatina fulica Bowdich, 1822	10	400					+	Raut, 1978; Raut, Barker, 2002
A. fulica	78	120						Thangavelu, Bijoy, 1983
A. fulica	93	184	139.0					Lange, 1950
A. fulica	50	200	120.0	5.90				Nisbet, 1974
A. fulica	100	200	140.0	4.30				Pawson, Chase, 1984
Achatina panthera Férussac, 1832	20	120	60.0	5.20				Nisbet, 1974
Allogona townsendiana (I. Lea, 1838)	18	54	34.0	3.10				Steensma *et al*., 2009
Anadenus altivagus (Theobald, 1862)	1	50	25.0	6.60	50.0			Gupta, Oli, 1998
Archachatina marginata (Swainson, 1821)	3	16	8.0		70.0		+	Plummer, 1975
A. marginata	1	13	6.3	1.33	70.6			Ibom *et al*., 2012
A. marginata	3	16	9.0	17.80				Nisbet, 1974
Arianta aethiops (Bielz, 1851)			38.3	3.40	58.6			Baur *et al*., 2000
Arianta arbustorum (L., 1758)			48.1					Andreassen, 1981
A. arbustorum			47.6	2.84	74.6		+	Baur, Baur, 1998
A. arbustorum			38.7	3.02	78.7			Baur *et al*., 2000
A. arbustorum	26	111	60.2	2.50				Terhivuo, 1978
A. arbustorum	11	65	40.6					Frömming, 1954
Ariolimax buttoni (Pilsbry et Vanatta, 1896)	12	80	33.3			+	+	Leonard *et al*., 2007
Arion lusitanicus Mabille, 1868	18	225	45.0	3.51				Briner, Frank, 1998
A. lusitanicus	5	185	67.5	3.83			+	Kozlowski, 2007; Kozlowski, Kozlowski, 2000; Kozlowski, Sionek, 2000
Balea perversa (L., 1758)					97.0	+		Baur, Baur, 2000
Balea stabilis (Pfeiffer, 1847)	1	17	6.9	1.58				Maltz, Sulikowska-Drozd, 2008; Sulikowska-Drozd, Maltz, 2012
Bradybaena pellucida Kuroda et Habe, 1953			25.2		91.0		+	Wiwegweaw *et al*., 2009; 2009a
B. pellucida			79.9					Seki, Asami, 1995
Bradybaena similaris (Férussac, 1821)	1	202	60.0					Carvalho *et al*., 2008
B. similaris	1	38	3.5			+	+	Almeida, Bessa, 2001
B. similaris			25.5		92.0		+	Wiwegweaw *et al*., 2009; 2009a
Brephulopsis cylindrica (Menke, 1828)	8	44	18.2	1.73				Vitchalkovskaya, Kramarenko, 2006
Bulimulus tenuissimus (d'Orbigny, 1835)	6	252	58.3		39.0	+		Silva *et al*., 2008; Silva *et al*., 2009
Burtoa nilotica Pfeiffer, 1861	40	50	45.0	4.30				Nisbet, 1974
Catinella rotundata (Gould, 1846)	3	19	12.0					Rundell, Cowie, 2003
Cepaea hortensis (Müller, 1774)			37.9					Andreassen, 1981
Cepaea nemoralis (L., 1758)			72.1		59.0			Wolda, Kreulen, 1973
Cepaea vindobonensis (Férussac, 1821)	31	166	85.8	3.51				Kramarenko, Popov, 1997
C. vindobonensis	29	67	49.2	3.17				Staikou, 1998
Cernuella virgata (daCosta, 1778)	30	60						Real, Real-Testud, 1983
C. virgata	1	257	62.8				+	Baker, 1991
Charpentieria ornata (Rossmässler, 1836)	1	11	4.7	1.49				Maltz, Sulikowska-Drozd, 2008
Clausilia dubia Draparnaud, 1805				1.43				Maltz, Sulikowska-Drozd, 2008
Clausilia parvula Férussac, 1807	1	9	2.4	1.11				Maltz, Sulikowska-Drozd, 2008
Clausilia pumila Pfeiffer, 1828	2	10	7.6	1.38				Maltz, Sulikowska-Drozd, 2008
Cochlicopa lubrica (Müller, 1774)			1.0	1.15			+	Uminski, Focht, 1979
Cochlodina laminata (Montagu, 1803)	1	25		1.50				Bulman, 1995

Table 1. Continued

Таблица 1. Продолжение

Species	Clutch size (egg)			*D*ovo (mm)	*HS* (%)	Self	MO	Literature
	min	*max*	*mean*					
C. laminata	5	17	10.3	1.62				Maltz, Sulikowska-Drozd, 2008
Cochlodina orthostoma (Menke, 1830)				1.73				Maltz, Sulikowska-Drozd, 2008
Columella edentula (Draparnaud, 1805)				0.67				Myzyk, 2005
Cornu aspersum (Müller, 1774)			85.7				+	Madec, Daguzan, 1987
C. aspersum						+		Lucarz, 1991
C. aspersum			95.0					Lazaridou-Dimitriadou, Kattoulas, 1981
C. aspersum	11	96	53.0					Herzberg, Herznerg, 1962
C. aspersum			105.0		78.2			Lazaridou-Dimitriadou *et al*., 1998
C. aspersum			144.0				+	Madec *et al*., 2000
C. aspersum			145.8		83.6		+	Nicolai *et al*., 2010
Cristataria genezarethana (Tristram, 1865)	5	11	7.7	1.00				Heller, Dolev, 1994
Deroceras laeve (Müller, 1774)			18.0		98.0	+		Nicklas, Hoffman, 1981
Deroceras sturanyi (Simroth, 1894)			11.0					Kosinska, 1980
Discus perspectivus (Mühlfeld, 1816)	1	9	3.9	0.95	51.0		+	Kuznik-Kowalska, 2005
Discus rotundatus (Müller, 1774)	2	5	3.0	1.00				Frömming, 1954
D. rotundatus	1	11	4.3	1.00	77.4	+	+	Kuznik-Kowalska, 1999
Discus ruderatus (Hartmann, 1821)	1	6	3.0	1.39	54.0		+	Kuznik-Kowalska, 2006
Drymaeus multilineatus (Say, 1825)	40	99		2.00				Deisler, 1983
Eobania vermiculata (Müller, 1774)	30	50						Lazaridou-Dimitriadou, Kattoulas, 1991
E. vermiculata			70.0					Lazaridou-Dimitriadou, Kattoulas, 1981
E. vermiculata	24	175	84.0	3.56				Kramarenko, Popov, 1999
Fruticicola fruticum (Müller, 1774)	33	55	44.2	1.98				Staikou *et al*., 1990
Habroconus semenlini (Moricand, 1846)						+		Silva *et al*., 2009a
Hedleyella falconeri (Gray, 1834)			3.4	17.00				Murphy, 2002
Helicella pappi Schütt, 1962	42	85	69.0					Lazaridou-Dimitriadou, 1995
Helicodonta obvoluta (Müller, 1774)	9	27	17.2	2.36	60.0			Maltz, 2003
Helix albescens Rossmässler, 1839	7	22	14.5	8.60				Popov, 1995; personal data
Helix lucorum L., 1758	25	82	50.5	4.43				Staikou *et al*., 1988
Helix lutescens Rossmässler, 1837	16	67	35.0	4.30				Koralewska-Batura, 1999
Helix pomatia L., 1758	24	93	50.0	7.10	36.8			Dziabaszewski, 1975
H. pomatia	10	82						Pollard, 1975
H. pomatia				5.90	80.0			Turcek, 1970
H. pomatia	30	50						Vincent *et al*., 1982
H. pomatia			32.0	7.00				Alyakrinskaya, 1979; Andreykevich, 1969
H. pomatia	3	83	45.7	5.17	48.0			Golab, Lipinska, 2009
H. pomatia	5	89	41.7				+	Ligaszewski *et al*., 2007
H. pomatia	21	58	39.4					Nica *et al*., 2012
H. pomatia	23	40	33.8	5.92				personal data
H. pomatia			48.3	6.23				Hatziioannou *et al*., 1989
Helix texta Mousson, 1861			59.3	5.46				Heller, Ittiel, 1990
Indosuccinea semiserica (Gould, 1846)	24	86	54.0					Raut, Ghose, 1984
Lacinaria plicata (Draparnaud, 1801)	1	11	4.7	1.68				Maltz, Sulikowska-Drozd, 2008
Lehmannia valentiana (Férussac, 1822)			2.7		41.0			Udaka *et al*., 2007
Leptinaria unilamellata (d'Orbigny, 1835)	1	22	7.4			+		Almeida, Bessa, 2001a
Liguus fasciatus (Müller 1774)	5	30						Tuskes, 1981
L. fasciatus						+		Hillis, 1989

Table 1. Continued

Таблица 1. Продолжение

Species	Clutch size (egg)			*D*ovo (mm)	*HS* (%)	Self	MO	Literature
	min	*max*	*mean*					
Limax valentianus Férussac, 1822			46.2		30.0	+		Hommay *et al*., 2001
Limicolaria martensiana (Smith, 1880)	8	25	14.8					Owen, 1965
L. martensiana	22	58	35.0			+	+	Owiny, 1974
Macrochlamys indica Godwin-Austen,1832			16.2	2.66	97.0			Jahan *et al*., 2002
Macrochlamys opiparus Godwin-Austin, 1832			49.6	0.91	98.0			Jahan *et al*., 2002
Macrogastra badia (Pfeiffer, 1828)	1	3	2.4	1.45				Maltz, Pokryszko, 2009
Macrogastra latestriata (Schmidt, 1857)	1	8	3.3	1.49				Maltz, Sulikowska-Drozd, 2008
Macrogastra tumida (Rossmässler, 1836)	1	11	6.6	1.70				Maltz, Sulikowska-Drozd, 2008
Macrogastra ventricosa (Draparnaud, 1801)	1	23	8.2	1.75				Maltz, Sulikowska-Drozd, 2008
Mesodon normalis (Pilsbry, 1900)	15	100	35.3		50.0	+	+	Foster, Stiven, 1994; Stiven, Foster, 1996
Microxeromagna armillata (Lowe, 1852)			22.0	1.22	69.0	+	+	Lush, 2007
M. armillata				1.04	90.0			Zhao *et al*., 2004
Monacha cantiana (Montagu, 1803)	60	90	75.0	1.80				Chatfield, 1968
Monacha cartusiana (Müller, 1774)			32.7		75.5			Staikou, Lazaridou-Dimitriadou, 1990
M. cartusiana	40	80	60.0	1.80				Chatfield, 1968
Omalonyx matheroni (Potiez et Michaud, 1838)			14.7	2.10	91.0	+	+	Montresor *et al*., 2012
Ovachlamys fulgens (Gude, 1900)	1	9	4.6	1.75	88.0		+	Barrientos, 1998
Oxychilus atlanticus (Morelet et Drouët, 1857)				1.50				Rodrigues *et al*., 2003
Paryphanta busbyi watti Powell, 1946	1	6	3.7	12.60	83.0		+	Stringer *et al*., 2002; Stringer *et al*., 2003
Perforatella bidentata (Gmelin, 1791)	2	20	8.5	1.63	95.3			Kuznik-Kowalska, Roksela, 2009
Placostylus ambagiosus Suter, 1906	1	70	34.5	4.83				Stringer, Grant, 2007
Placostylus hongii (Lesson, 1830)	8	84	24.5	4.68				Stringer, Grant, 2007
Pontophaedusa funiculum (Mousson, 1856)	1	6	3.4	1.70				Pall-Gergely, 2010; Pall-Gergely, Nemeth, 2008
Punctum pygmaeum (Draparnaud, 1801)			1.0	0.47	67.0	+	+	Baur, 1987; 1989
Rumina decollata (L., 1758)	14	41	32.0		66.0	+		Dundee, 1986; Selander, Kaufman, 1973; Selander *et al*., 1974
Rumina saharica Pallary, 1901	1	28	17.0	2.80	25.5	+		Orstan, 2008
Sphincterochila boissieri (Charpentier, 1847)			21.0					Yom-Tov, 1972
Sphincterochila candidissima (Draparnaud, 1801)	23	50	30.5	4.20				Dominquez, Robles, 1995
Succinea costaricana (Martens, 1898)	2	11	6.8	1.37	95.0		+	Villalobos *et al*., 1995
Succinea putris (L., 1758)	25	65	48.0	1.25				Datkauskiene, 2005
S. putris	1	176	45.3		79.0	+	+	Dillen *et al*., 2009; Dillen *et al*., 2010
Succinea thaanumi Ancey, 1899	1	16	7.0					Brown *et al*., 2003
S. thaanumi	1	16	9.0					Rundell, Cowie, 2003
Testacella scutulum Sowerby, 1821	3	13	7.1	3.50	64.0		+	Stokes, 1958
Theba pisana (Müller, 1774)	60	107	80.0					Heller, 1982
T. pisana	2	225	79.0				+	Baker, 1991
T. pisana	3	269	76.7				+	Cowie, 1982
Triodopsis albolabris (Say, 1816)			33.2		73.2	+	+	McCracken, Brussard, 1980
Trochoidea seetzeni (Pfeiffer, 1846)			33.0	2.30				Yom-Tov, 1972

Table 1. End

Таблица 1. Окончание

Species	Clutch size (egg)			*D*ovo (mm)	*HS* (%)	Self	MO	Literature
	min	*max*	*mean*					
Vertigo angustior Jeffreys, 1830				0.59				Myzyk, 2005
Vertigo antivertigo (Draparnaud, 1801)				0.65				Myzyk, 2005
Vertigo moulinsiana (Dupuy, 1849)				0.74				Myzyk, 2005a
Vertigo pusilla Müller, 1774	1	2		0.54				Pokryszko, 1990
V. pusilla				0.63				Myzyk, 2005
Vertigo pygmaea (Draparnaud, 1801)				0.54				Myzyk, 2005
Vertigo ronnebyensis (Westerlund, 1871)				0.70				Myzyk, 2005
Vertigo substriata (Jeffreys, 1833)				0.64				Myzyk, 2005
Vestia elata (Rossmässler, 1836)	1	6		1.48				Piechocki, 1982
V. elata	2	10	4.4	1.93	80.4		+	Sulikowska-Drozd, 2008
V. elata	2	10	4.5	1.93	85.8			Sulikowska-Drozd, 2009
Vestia gulo (Bielz, 1859)	6	19	9.4	1.75	88.3			Sulikowska-Drozd, 2009
Vestia turgida (Rossmässler, 1836)	1	11	3.9	1.74				Maltz, Sulikowska-Drozd, 2008
V. turgida			3.8	1.77				Sulikowska-Drozd, 2009
Xerolenta obvia (Menke, 1828)	17	95	57	1.00				Lazaridou, Chatziioannou, 2005
Xeropicta arenosa (Ziegler, 1827)	15	51	31.3	1.28				Staikou, Lazaridou-Dimitriadou, 1991
Xeropicta derbentina (Krynicki, 1836)	39	128	87.0					Popov, Dragomoschenko, 1997
X. derbentina	12	168	58.3	1.56				Kramarenko, 2002
Xeropicta krynickii (Krynicki, 1833)	20	152	57.0	1.63				personal data
Zonitoides arboreus (Say, 1817)	3	5	4.0		61.2			Hollingsworth *et al*., 2003
Zonitoides nitidus (Müller, 1774)			5.5					Didier, Rondeland, 1987

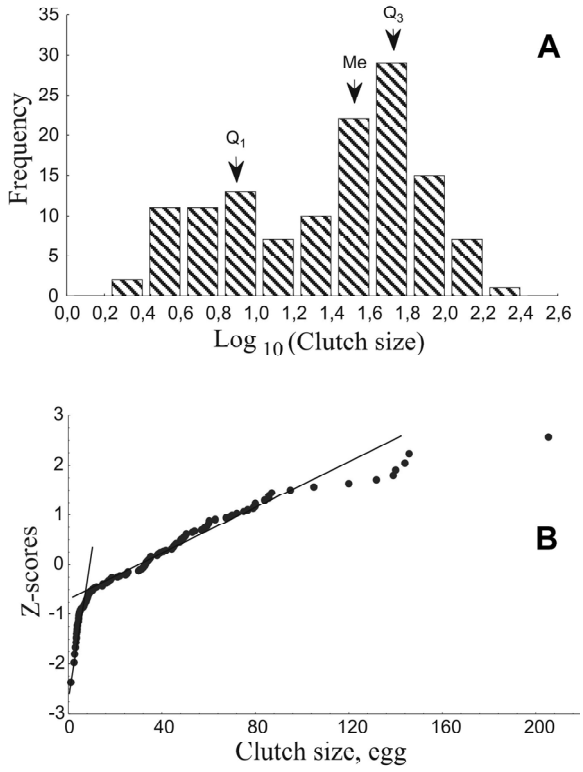

FIG. 1. Variation of the mean clutch size of the different species of the pulmonate molluscs in logarithm scale (A) and in the normal probability paper (B).

РИС. 1. Изменчивость среднего размера кладки у разных видов легочных моллюсков в логарифмическом масштабе (А) и на нормальной вероятностной бумаге (В).

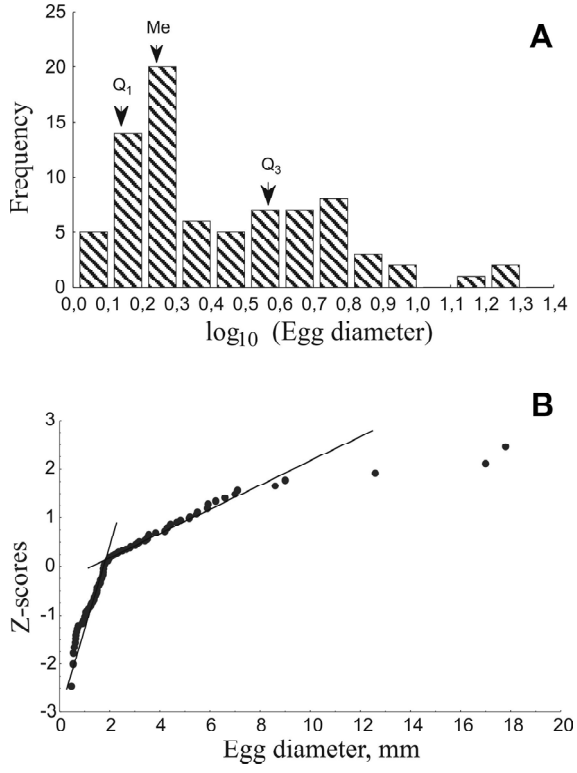

FIG. 2. Variation of the mean egg diameter of the different species of the pulmonate molluscs in logarithm scale (A) and in the normal probability paper (B).

РИС. 2. Изменчивость среднего диаметра яйца у разных видов легочных моллюсков в логарифмическом масштабе (А) и на нормальной вероятностной бумаге (В).

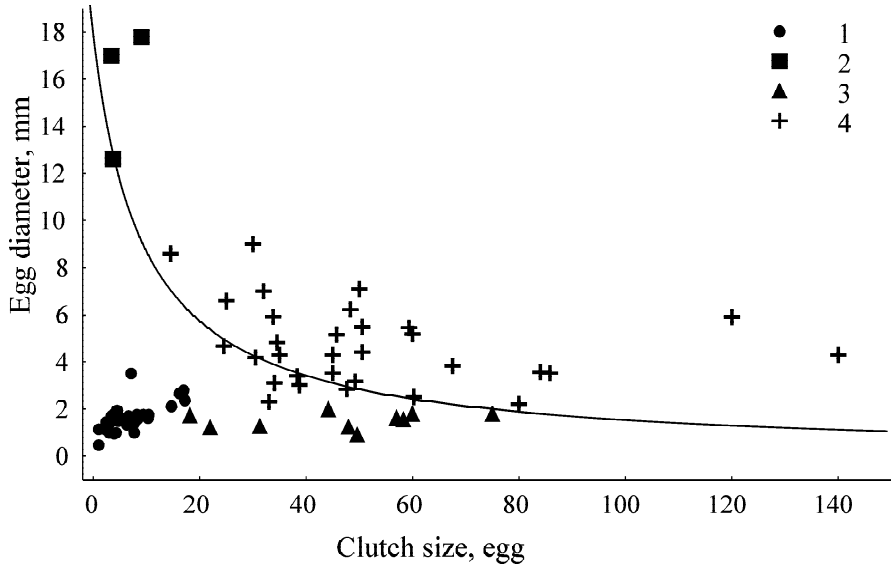

FIG. 3. Distribution of different species of the pulmonate molluscs in relation to mean clutch size and mean egg diameter.

РИС. 3. Распределение различных видов легочных моллюсков в отношении среднего размера кладки и среднего диаметра яйца.

clutches contain relatively large size eggs (*Helix pomatia, H. lucorum, H. lutescens, H. albescens, H. texta, Arianta arbustorum, A. aethiops, Cepaea vindobonensis, Eobania vermiculata, Theba pisana, Achatina fulica, A. panthera*). This group also includes slugs (e.g. *Arion lusitanicus*) as well as tropical snails *Placostylus hongii* and *P. ambagiosus* (Bulimulidae), polygyrid species *Allogona townsendiana*, xerophilous *Trochoidea seetzeni* and *Sphincterochila candidissima*.

As expected, a general inverse relationship between the clutch size and the egg size of land snail (Fig. 3) has been found. Only small-sized species of the first group represent the exception.

The eggs of land snails are characterized by a high hatching success (Fig. 4). The hatching success exceeds 60% for three quarters of the studied species of the pulmonates, 75% for a half of the studied species. The hatching success does not depend on the number of eggs per clutch (Fig. 5A), but the significant trend of decrease in hatching success with increasing egg size was, however, noted (Fig. 5B).

Ability of multiple oviposition of the land snails and slugs is one of the additional mechanisms to increase their reproductive success. Forming of repeated clutches was recorded for 27 analyzed species of snails and slugs. For example, *Theba pisana* was found to laid 11 to 46 clutches per year, and *Cernuella virgata* – 9 to 96 clutches per year. Thus, the total number of eggs that *T. pisana* has laid during the year exceeds 4,500, and for *C. virgata* this parameter exceeds 8,000 [Baker, 1991].

In general, the smaller forms living in the forest litter (both in tropical and temperate latitudes) are reproducing repeatedly and evenly throughout the year, however, they lay a single egg or a few eggs at a time. While xerophilous species, in contrast, have a narrow breeding season but their clutches contain relatively many eggs.

Capability of some snails and slugs to self-fertilization is another mechanism to increase their reproductive success. This ability to self-fertilization has been revealed under laboratory conditions in 20 species of terrestrial mollusks (Table 1). It was also noted that the reproductive characteristics of the self-fertilizing species were smaller than those in the cross-fertilizing ones (for the average clutch size: 25.4 and 40.5 eggs per clutch; for the average egg diameter: 1.52 and 3.07 mm, respectively), although these differences are not statistically significant. On the other hand, the egg size and hatching success for individuals who were kept in isolation proved to be significantly less as compared with those individuals kept in groups (*Succinea putris* [Dillen et al., 2009], *Microxeromagna armillata* [Lush, 2007], *Triodopsis albolabris* [McCracken, Brussard, 1980], *Bulimulis tenuissimus* [Silva et al., 2009], *Discus rotubdatus* [Kuznik, Kowalska, 1999], etc.).

Thus, the pulmonate molluscs demonstrate a very wide range of reproductive strategies that

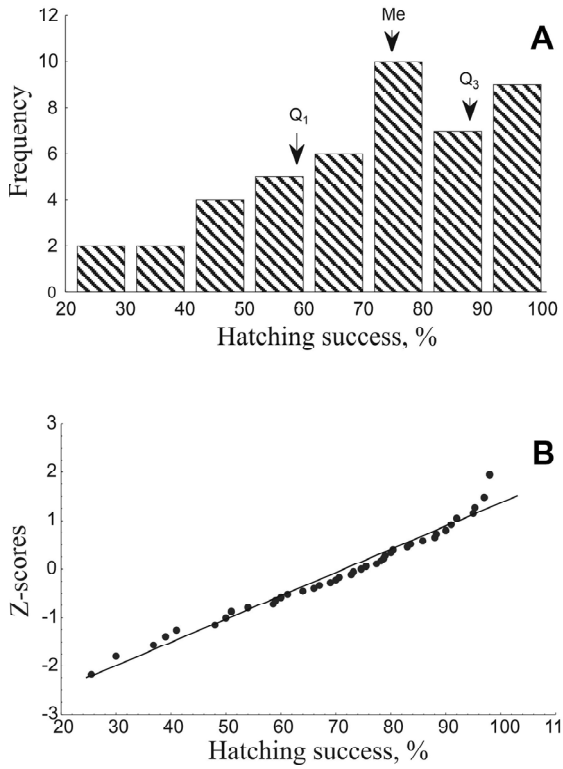

FIG. 4. Variation of the hatching success of different species of the pulmonate molluscs in absolute scale (A) and in the normal probability paper (B).

РИС. 4. Изменчивость вылупляемости у разных видов легочных моллюсков в абсолютном масштабе (А) и на нормальной вероятностной бумаге (В).

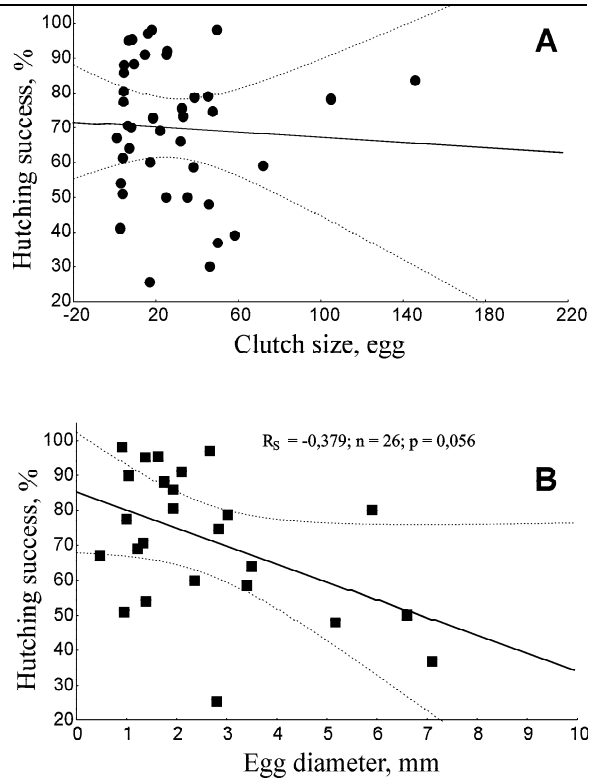

FIG. 5. Relationship between hatching success and the clutch size (A) and between hatching success and-egg diameter (B) of different species of the pulmonate molluscs (95% confidence interval is marked by dotted line).

РИС. 5. График зависимости вылупляемости от размера кладки (А) и диаметра яйца (В) у разных видов легочных моллюсков (95% доверительный интервал отмечен пунктирной линией).

serve to enhance their survival in different (sometimes very unfavorable) environmental conditions.

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Анализ репродуктивных показателей легочных моллюсков: мини-обзор

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РЕЗЮМЕ. В обзоре проанализирована информация о репродуктивных характеристиках (размер кладки, размер яйца, вылупляемость и др.) для более 100 видов наземных легочных моллюсков. Показано, что для них отмечается очень широкий спектр различных репродуктивных стратегий, направленных на повышение выживаемости вида в разных, порой самых неблагоприятных, условиях внешней среды.