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ON THE POPULATION DYNAMICS, REPRODUCTIVE BIOLOGY AND GROWTH OF *SUCCINEA PUTRIS* (LINNAEUS, 1758) (GASTROPODA: PULMONATA: SUCCINEIDAE)

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ABSTRACT: Selected life-cycle and population parameters of a common Euro-Siberian wetland snail – *Succinea putris* (L.) – were studied in the field and in the laboratory. In the field the snails reproduced at least from April till September, with April–May and August–September peaks; only one such peak (April) was observed in the laboratory, though the snails reproduced throughout the year. The changes in population size structure in the field and the laboratory results (life span 210–420 days, mean 309) indicated semelparity. Growth in the laboratory included two phases: slow (November–March) and fast (June–October); which phase came first during the life cycle depended on the date of hatching. The growth rate in the field corresponded closely with the fast-phase growth in the laboratory. The smallest reproducing individual was slightly over 2.8 whorls; snails of 3.0 whorls were regularly observed to produce eggs (maximum number of whorls in adults: 4.0). Sexual maturity was attained in ca. 160 days. The eggs (non-calcified, translucent, spherical, 1.7–2.0 mm in diameter) were laid in batches, 5–64 per batch; the eggs within a batch were glued together. The batch dimensions were 3.5–25.7×2.2–24.7 mm. The time to lay a batch was 20–35 minutes. Forty-eight snails produced 74 batches within 12 months. The duration of the egg phase was 11–28 days, which might indicate egg retention of varied duration; hatching was asynchronous, spanning 1–12 days within a batch. The hatchlings had shells of 1.1–1.2 whorls; hatching success was 95%. Neither uniparental reproduction, nor egg or juvenile cannibalism were observed. When compared to data in the literature, our results imply that *Succinea putris* displays substantial local variation in life-cycle traits. We also provide an overview table to discuss similarities and adaptive radiation in the European succineid species.

KEY WORDS: population dynamics, reproduction, growth, terrestrial snails, *Succinea putris*

INTRODUCTION

Succinea putris (Linnaeus, 1758) is a Euro-Siberian species; it inhabits the whole of Europe except its northern fringes and the Mediterranean (RIEDEL 1988, WIKTOR 2004). It is a hygrophile, very common and abundant in wetlands, such as: marshes, wet meadows, alder carrs, as well as shores of lakes, ponds and rivers; it is found climbing wetland vegetation or on the ground (RIEDEL 1988).

Earlier studies have dealt with the histology and functional morphology of the alimentary and reproductive system in *S. putris* (RIGBY 1965), and with its mating behaviour (DILLEN et al. 2008, 2010). Some life-cyle parameters of the species have been ascertained based on laboratory studies or on fragmentary field observations (FRÖMMING 1954, HECKER 1965, JACKIEWICZ 1980, ĐATKAUSKIENĖ 2005, JORDAENS et al. 2005), but the seasonal dynamics of its age structure has never been studied. This paper presents more data on the population dynamics and life cycle of *S. putris*.

MATERIAL AND METHODS

FIELD OBSERVATIONS

The observations were conducted in a complex of fish ponds near the town of Milicz (SW Poland: 51°31'08.7"N; 17°14'43.5"E), from April till September 2010. The studied population lived beside a canal supplying water to one of the ponds. Since *S. putris* may co-occur with *S. elegans*, and they are not easy species to distinguish reliably, prior to the study we dissected ten dubious individuals. All of them appeared to be *S. putris*.

Changes in age structure were estimated based on monthly samples: each month the snails were collected from the same 2 × 5 m plot for 60 minutes. The standing vegetation, soil and plant debris were searched carefully so as not to disturb habitat too much. Growth rate was estimated using a mark-release-recapture method. Each month the snails were marked with a different colour of nail varnish: a narrow stripe was painted on the upper surface of the body whorl, along the aperture margin, so that the increment could be read on recapture. Recaptured snails were marked again, in the same way. Growth rate was expressed as whorl increment rather than size increment (Pokryszko 1990, Heller et al. 1997). Three age classes were distinguished: class I – 1.2–2.1 whorls, class II – 2.2–3.1 whorls and class III – 3.2–4.0 whorls. The total number of marked snails was 497.

LABORATORY STUDIES

Material for the laboratory culture was collected on October 14th 2009 near Milicz (the site of field observations). Laboratory observations were conducted from October 19th 2009 till April 28th 2011. The total number of individuals in the laboratory culture was 494, originating from the initial 54 snails collected in the field (those died after egg-laying). The snails were kept in Petri dishes of 6–10 cm diameter, or plastic containers of 15.5×12.5×5 cm, 6×7.5×5 cm and 12×7.5×5 cm, depending on the number of inhabitants. Ten individuals were kept singly since the earliest growth stages, the remaining ones were kept in pairs (8 pairs) and groups (5 groups of 5 individuals, 10 groups of 10 individuals, 10 groups of 20 individuals, 1 group of 23 individuals and 4 groups of 30 individuals each).

Egg batches and hatchlings were transferred to separate dishes. Damp tissue paper with some soil and plant fragments from the original habitat served as a substratum. All the containers were kept in a climate chamber, with a day temperature of 18°C, a night temperature of 12°C, 80% relative humidity, and 12:12 lighting regime. The snails were fed with lettuce and cabbage, occasionally also with cucumber, apple and carrot. Calcium was supplied as dolomite tablets or as crushed chicken egg shells. Food and water were supplied as needed, the containers were aired and cleaned at least once a week.

Laboratory observations included growth rate and maturity, possible uniparental reproduction, mating behaviour, fecundity, egg-laying, egg morphometrics, incubation and hatching. Growth was assessed by counting whorls every 30 days using Ehrmann's method (1933). The maximum of reproduction was assessed by counting the total number of batches produced each month from November 2009 till December 2010. Fecundity and hatching success were estimated based on the number of eggs and hatching percentage. Duration of the egg stage was assessed for 30 batches. The eggs (n = 50) and batches (n = 50) were measured with electronic calipers to the nearest 0.025 mm. The snails were checked for cannibalistic behaviour (offering them conspecific eggs and hatchlings) over 3 months. They were fed normally, but not provided with alternative sources of calcium during the experiment. Spearman's rank correlation coefficient was used to calculate the correlation between the initial whorl numbers of the snails marked and their increment, read during recapture. The differences in the life span between the snails kept in isolation and pairs/groups were specified using Mann-Whitney U test which evaluates differences in medians. Results were statistically analysed with Microsoft Excel 2007 and Statistica 10.

RESULTS

AGE STRUCTURE

In the field, individuals of all size classes were present in the population every month from April to September (Fig. 1); reproduction (egg-laying) continued from April to September. The population density was greatest in April and smallest in September. The smallest size class (1.2–2.1 whorls, n = 50) was present from April till September, with the maximum – in terms of both absolute and relative abundance – in April and the minimum in July. The proportion of class I individuals was 16% in April and 1.5% in July. The generally low density of the youngest age class may have resulted from the difficulty of finding the smallest juveniles (maximum dimension ca. 1 mm; mean = 1.17 whorls). The two peaks of abundance of class I, in April–May and August–September, may either reflect peaks of reproductive activity or they may result from the weather (mainly humidity) conditions making these small snails easier to find. It is also possible that the August and April peaks could be a part of a single overwinter peak. The second age class (2.2–3.1 whorls; n = 200) was the most abundant in May (perhaps derived from hatchlings of the previous year and of the current year's early spring) when it constituted 57.3% of the caught and marked snails; such snails were also numerous in April and August (probably the current year's hatchlings) when they constituted 50% and 52.7%, respectively. The third class, subadult and adult snails (3.2–4.0 whorls; n = 247) reached its maximum abundance in June, when it formed 85.6% of all snails, and its minimum – in May and September.

In the laboratory (see below) the greatest number of egg batches was produced in April. The maximum abundance of the oldest age class in June was a result of growth of the individuals which in April and May were still in class II. Individuals of class III died having reproduced, and the abundance of this class declined from June till September.

GROWTH, MATURITY AND LIFE SPAN

Out of the 497 marked juvenile and adult *S. putris*, 18 (3.62%) were recaptured. Their growth rate ranged from 0.13 to 1.00 whorl per month (mean = 0.44; SD = 0.23). The number of whorls on their first capture varied from 2.1 to 3.8 (classes II and III) but most (12) were in class II. The number of whorls on recapture was 2.5–4.0. The Spearman's rank correlation coefficient indicated that there was a positive relationship between initial whorl number and the increment, read during recapture ($r_S = 0.77$, $P < 0.001$). The mean growth rate in the field corresponded closely with the fast-phase growth observed in the laboratory (see below); the field study included only months when the laboratory culture was showing fast growth.

The growth of ten randomly selected individuals which survived till adulthood in the laboratory is presented in Fig. 2. The growth of snails hatched in November was very slow during the first five months (November-March) of life. Their growth rate from hatching (1.1–1.2 whorls) to 1.5 whorls was 0.04–0.11 whorl/month (mean = 0.09; n = 5). During the next five months (April-October: 1.5–4.0 whorls) the monthly increment was much higher, 0.33–0.48 whorls (mean = 0.41; n = 5) (Fig. 2). The growth pattern was reversed in snails hatched in June: the growth was fast during the first five months of life (June-October; from hatching to 3.4 whorls, i.e. well into adulthood), with the monthly increment of 0.46–0.62 whorl (mean = 0.53; n = 5). The fast phase was followed by a slow phase (November-April:

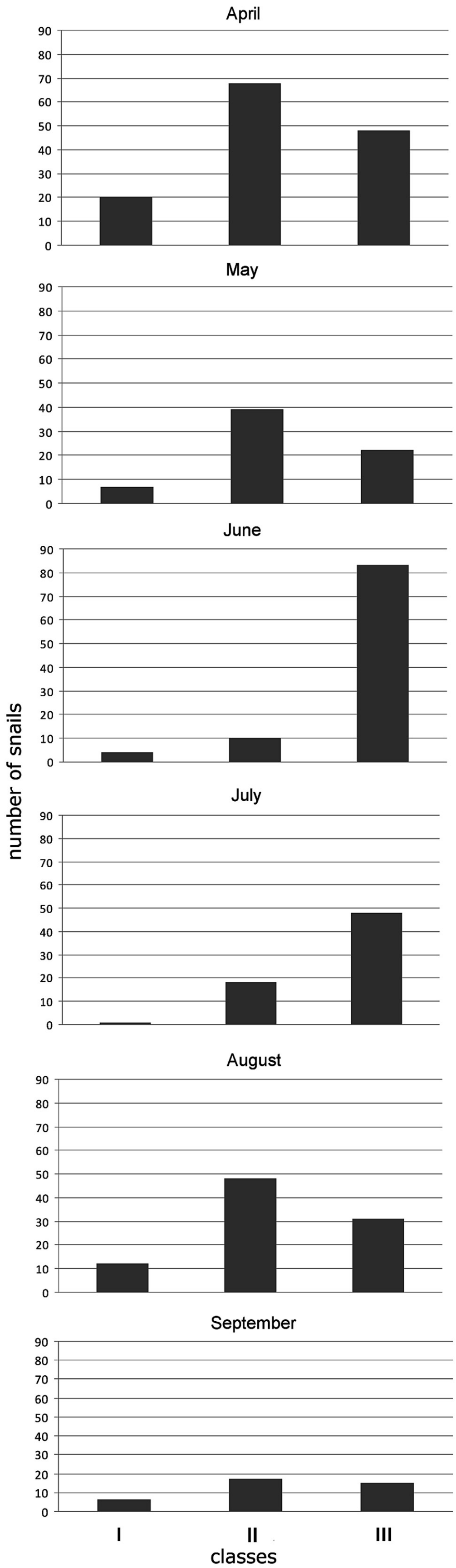

Fig. 1. *Succinea putris*: size structure of the studied population over six consecutive months of 2010. Age classes: I – 1.2–2.1 whorls, II – 2.2.–3.1 whorls and III – 3.2–4.0 whorls

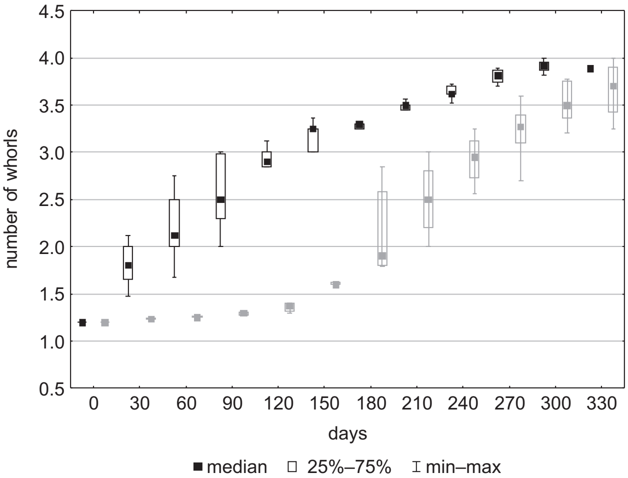

Fig. 2. *Succinea putris*: growth of 10 selected individuals hatched in the laboratory in November 2009 (grey) and in June 2010 (black)

Fig. 3. Two mating pairs of *Succinea putris* (03.03.2010; photo: M. OCZKOWSKA)

3.4–4.0 whorls), with growth rate of 0.07–0.18 whorl/month (mean = 0.14; n = 5) (Fig. 2).

The smallest individual observed to copulate and lay eggs was slightly over 2.8 whorls; snails of 3.0 whorls were regularly observed to produce eggs and this was therefore assumed to be the size of maturation. In the laboratory, sexual maturity (laying the first batch of eggs) was attained about 160 days after hatching (SD = 14; n = 25).

The life span of *S. putris* in the laboratory was 210 to 420 days (mean = 309; SD = 64; n = 40); it was slightly longer for snails kept singly – 270–390 days (mean = 345; SD = 45; n = 10) than for those kept in pairs and groups – 210–420 days (mean = 297; SD = 66; n = 30). The differences were statistically significant (Mann-Whitney U test, $P < 0.05$).

REPRODUCTION

Mating behaviour was partly (only copulation) observed on two occasions in the laboratory (on 03.03.2010, with two couples copulating at the same time, and 20.08.2010), at 12:36–13:12 (36 minutes) and 14:13–14:38 (25 minutes) (Fig. 3). The copulation was anatomically reciprocal: the snails were connected by their copulatory organs. During the copulation they made no movement, except extending their tentacles from time to time. Following the copulation, one of the partners remained motionless for about 15 minutes, while the other snail left and started feeding. Afterwards, each of these snails was placed in a separate container; the date of egg-laying and the number of eggs per batch were recorded (Table 1).

In the field, egg batches were found under leaves of *Typha latifolia* and *Phragmites australis*. In the laboratory, *S. putris* laid eggs on the underside of leaves of lettuce and other plants, and directly on the soil surface. The time to lay a batch ranged from 20 to 35 minutes (mean = 27; SD = 6; n = 4). The number of eggs in a batch ranged from 5 to 64 (mean = 24; SD = 16; n = 50) (Fig. 4). The number of batches produced within 12 months by 48 individuals, all of which produced some egg batches, was 74 (Fig. 5; the isolated individuals are excluded). In the laboratory the snails laid eggs throughout the year: the first batch was produced on 18.11.2009, the last one on 18.04.2011.

The spherical eggs had a diameter of 1.68–2.00 mm (mean = 1.9; SD = 0.07; n = 50), were transparent, lacked any calcium inclusions, were glued together and enveloped with a jelly-like substance. The width of a batch was 2.2–24.7 mm (mean = 9.5; SD = 4.5; n = 50), the length was 3.5–25.7 mm (mean = 9.5; SD = 4.5; n = 50). At first, the batch was translucent, with barely visible embryos; after about four days it assumed a yellowish colour.

Batches took 11 to 28 days to start to hatch (mean = 18; SD = 4; n = 30). The hatching was asynchronous, varying by 1 to 12 days within a batch. The hatchlings

Table 1. *S. putris*: copulation, egg-laying and number of eggs

Individual	Number of whorls	Days from copulation to egg-laying	Eggs per batch	Hatching success [%]
A1	3.00	19	6	100.0
A2	3.25	15	42	90.5
B1	3.56	12	28	96.4
B2	3.00	–	–	–
C1	2.84	15	16	93.8
C2	3.16	–	–	–

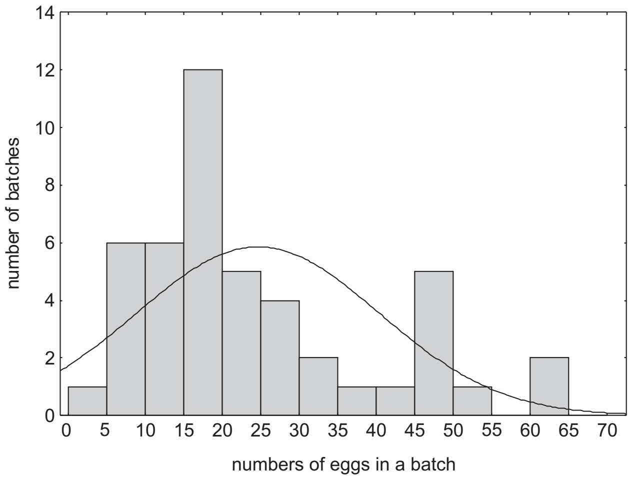

Fig. 4. *Succinea putris*: number of eggs per batch

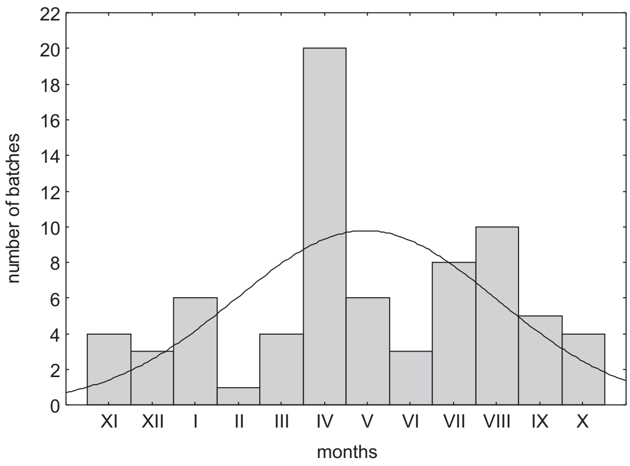

Fig. 5. *Succinea putris*: total number of batches produced during 12 consecutive months by 48 individuals

were glassy-translucent, with the number of whorls ranging from 1.1 to 1.2 (n = 50). The hatching success among the eggs laid by snails kept in pairs and groups was 94.6% (n = 500). None of the ten snails kept singly produced eggs. No egg or juvenile cannibalism was observed.

DISCUSSION

Although some details of the life cycle of *S. putris* still remain unknown, the existing information makes it possible to place its life strategy in the context of other pulmonates and, especially, other succineids.

The mating of *S. putris* is anatomically reciprocal with mostly reciprocal but also unilateral sperm exchange (Jordaens et al. 2005). Though shell-mounting has been observed in *S. putris* and other succineid species such as *S. oblonga*, *S. elegans*, *S. costaricana*, *S. thaanumi* or *Oxyloma retusum* (Hecker 1965, Villalobos et al. 1995, Rundell & Cowie 2003, Örstan 2010), we observed no shell-mounting by our mating snails (see Fig. 3). It is thus possible that the mating position in *S. putris* varies, and perhaps it depends on the kind of substratum on which the mating takes place (horizontal soil versus vertical vegetation). It may be also suspected that in the very beginning the smaller snail was on top of the shell of the larger snail and that it gradually slipped and fell down to the position seen in the photo (Fig. 3). Such a phenomenon was observed during the mating of *Chondrus tournefortianus* (Férussac, 1821), a shell-mounting species from Turkey (Örstan 2009). For the significance of mating position see Giusti & Andreini (1988), Asami et al. (1998), and Davison et al. (2005).

In the laboratory *S. putris* reproduced throughout the year, and in the field at least from April till September; thus its reproduction in the wild is regulated mainly by the external factors such as photoperiod or temperature (Wayne 2001). The latter, for example, has a significant effect on the growth of the snails forcing them to aestivate (Proćków et al. 2012) and thus also prevents the reproduction. *S. putris* is oviparous, although – as indicated by the wide variation of the time between copulation and egg-laying, and of the egg stage – it may possibly retain eggs for some time. Its growth is indeterminate, and sexual maturity precedes the attainment of maximum size. The growth is fast and the life span short, which conforms to the pattern observed by Heller (2001) for semelparous species with annual life cycles and fits into general knowledge of the life cycles in the species of similar size and habitat requirements, e.g. *Vitrina pellucida* (O. F. Müller, 1774) (Umiński 1975) or *Trochulus hispidus* (L., 1758) (Proćków et al. 2013). In contrast, *Discus rotundatus* (O. F. Müller, 1774) or *Aegopinella nitidula* (Draparnaud, 1805) are iteroparous and biennial species, respectively (Mordan 1978, Cameron 1982, Kuźnik-Kowalska 1999). Hecker (1965) and Jackiewicz (2003), however, have reported a life span of *S. putris* of up to three years, with only a five-month period to reach maturity, which may suggest iteroparity.

The succineids as a family are rather uniform in their morphology, habitat preferences and life style (Hecker 1965, Jackiewicz 2003), and they might be expected to have similar life cycles. Fragmentary data on various aspects on life cycles of various members of Succineidae, including *S. putris*, are found in Frömming (1954), Hecker (1965), Patterson (1970), Jackiewicz (2003) and Đatkauskienë (2005); for *S. putris* various authors report different values of life cycle parameters (Table 2).

Table 2. Life history traits of *Succinea* species

	S. putris	*S. oblonga*	*S. elegans*	*S. sarsi*
		mating period		
this study	at least March–September			
ĐATKAUSKIENĖ 2005	March–September or October			
JACKIEWICZ 1980, 2003	May–September	early spring–late summer	May–July or August	mid April–August
HECKER 1965	April–September or October	early spring–late summer	April–August	mid April–August
FRÖMMING 1954	April–October	April, June	May–August	
		time from copulation to egg-laying [days]		
this study	12–19 (lab)			
ĐATKAUSKIENĖ 2005	2–6 (lab)			
JACKIEWICZ 2003	5–10	5–10	5–25	
HECKER 1965	ca.5–10 (also up to 30–40)	ca. 5–10 (4–28)	5–25 (28)	
		number of eggs per batch		
this study	5–64			
ĐATKAUSKIENĖ 2005	25–65 (field), 6–25 (lab)			
JACKIEWICZ 2003	20–100	3–5 (15)	up to 210 per snail	5–10 (older snails: 30–40)
HECKER 1965	ca. 20 (max. 163)	1–15	ca. 7–50 (2–169)	2–95
FRÖMMING 1954	50–100 and more		4–161	
		egg size [mm]		
this study	1.68–2.0			
ĐATKAUSKIENĖ 2005	1.11–1.3			
JACKIEWICZ 2003	2	0.9	0.8–1.3	0.7–1.2
HECKER 1965	1–1.9	0.8–1.1	0.8–1.3	0.7–1.2
FRÖMMING 1954	1.0–1.8	0.5	0.6–1.1	
		duration of egg stage [days] and hatching synchrony		
this study	11–28, asynchronous			
ĐATKAUSKIENĖ 2005	10–20 (F1), 30 (F2)			
JACKIEWICZ 2003	10–13 at 25°C	synchronous	synchronous (in large batches one-day difference)	synchronous
HECKER 1965	11–42	9–34	8–48	7–38
FRÖMMING 1954	11–22	14–15	8–16, asynchronous	

Table 2 continued

	S. putris	*S. oblonga*	*S. elegans*	*S. sarsi*
	hatchling shell size			
this study	1.1–1.2 whorls			
ĐATKAUSKIENĖ 2005	0.95–1.2 mm (embryos just before hatching)			
JACKIEWICZ 2003	1.5 mm	1 mm	1–1.2 mm	0.9–1.2 mm (shell 0.6–0.7 mm)
HECKER 1965	1.1–1.5 mm	1 mm	1–1.2 mm	0.9–1.2 mm (shell 0.6–0.7 mm)
	time to reach maturity [months] (snail size when mature)			
this study	ca. 5.3 (2.8–4 whorls)			
ĐATKAUSKIENĖ 2005	10 (12 mm) (lab), before 10th month (11.3 mm) (field)			
JACKIEWICZ 2003	5–5.5 (10–12 mm)	5–6 (5–6 mm)	3–4.5 (7 mm)	3–3.5 (6.5 mm)
HECKER 1965	5–5.5 (10–12 mm)	5–6 (5–6 mm)	3–4.5 (7 mm)	3–3.5 (6.5 mm)
	life span			
this study	7–17 months (in groups), 9–13 months (singly)			
ĐATKAUSKIENĖ 2005	13–17 months (lab), 15–29 months (field)			
JACKIEWICZ 2003	up to 3 years	1.5–2 years	up to 17 months	up to 16 months
HECKER 1965	up to 3 years	1.5–2 years	up to 17 months, 21 (lab)	up to 16 months
FRÖMMING 1954		1.5–1.75 years	2 years	

The mating period is roughly similar in all four species which have been studied in this respect. The average time elapsing from copulation to egg-laying is roughly similar in *S. putris*, *S. oblonga* and *S. elegans*, from about 5 to 19 days. The batch structure in *S. oblonga* differs from that of the remaining species studied: the batches include 3–5 eggs, not glued together with mucus; the eggs are laid in the soil, and not in the litter (JACKIEWICZ 2003). The batch size is much smaller in *S. oblonga* and much greater in *S. elegans* than in *S. putris*. The eggs of *S. putris* are the largest, up to 2 mm diameter, whereas those of the other species are 1.1–1.3 mm. The duration of the egg stage is similar in *S. putris*, *S. oblonga*, *S. elegans* and *S. sarsi*, as is the number of whorls at hatching. The time required to reach maturity is similar in *S. putris* and *S. oblonga*, and is shorter in *S. elegans* and *S. sarsi*. The life span of all the studied species is roughly similar.

Based on this comparison, it is difficult to generalise about the succineid life cycle, apart from the mating period, time elapsing between mating and egg-laying, duration of egg stage, hatchling size and life span. As a family, the succineids are by no means exceptional in the variety of their life strategies; equal or even greater diversity has been observed for example among clausiliids, even within groups of very closely related species (MALTZ & SULIKOWSKA-DROZD 2008), or helicoids (e.g. LAZARIDOU-DIMITRIADOU 1981, BAUR 1984, BABA 1985, LAZARIDOU-DIMITRIADOU & KATTOULAS 1985, BAUR & RABOUD 1988, STAIKOU et al. 1988, 1990, KORALEWSKA-BATURA 1999, ALMEIDA & BESSA 2001, KUŹNIK-KOWALSKA & ROKSELA 2009; for review see MALTZ 2003).

The number of days elapsing between mating and egg-laying in *S. putris* reported by different authors (see Table 2) varies from 5 to 40 days. This fact may be associated either with the ability to retain sperm, or with the ability to retain eggs for varied periods of time – phenomena not uncommon among pulmonates (TOMPA 1984, HELLER 2001). In our observations the maximum number of eggs per batch for *S. putris* was 64, and greater numbers were reported by other authors (see Table 2). The differences may be age-related, since according to JACKIEWICZ (2003) young adults lay ca. 5–10 eggs, and older adults from 30 to 40 eggs in a batch. The duration of the egg stage, which in *S. putris* varies from 10 to 42 days (11–28 days in our studies), is known to depend on the temperature and on the egg's position in the batch (JACKIEWICZ 2003). In our studies, conducted at constant temperature, temperature-dependent differences can be excluded.

The growth from hatching to maturity takes 5 to 10 months (in our studies ca. 5 months); the differences in growth rate may result both from different external conditions and from individual variation (MALTZ & SULIKOWSKA-DROZD 2008). However, despite the constant food, temperature, humidity and lighting conditions in the laboratory, it seems that the growth was slow or even negligible from November till March and fast from April till October (Fig. 2). It thus appears that the growth rate was not dictated by the external conditions or the age of the juveniles, but purely by the time of year. This observation requires further, more detailed, investigation in the future.

According to JACKIEWICZ (2003) the life span of *S. putris* in the wild is up to three years. ĐATKAUSKIENĖ (2005) points to differences in the life span: 13–17 months in the laboratory and 15–29 months in the wild. In our studies the mean life span in the laboratory was ca. 10 months: 11 months for individuals kept singly and 9 months for those kept in pairs and groups. The differences in life span of laboratory-kept snails and those in the wild often result from the absence of hibernation periods and constant reproduction in the laboratory (MYZYK 2011).

Though we failed to observe uniparental reproduction, it has been recorded for *S. putris* (DILLEN et al. 2009) and many other succineids such as *S. grosvenori, S. unicolor, S. campestris, Omalonyx feline, Oxyloma retusa, O. salleana* and *Quickia purca* (PATTERSON 1970). However, *S. putris* is a predominant outcrosser and its (occasional) self-fertilisation does not seem to account for the high variation observed in many life-history parameters (DILLEN et al. 2009).

The differences in life cycle of *S. putris* reported by various authors indicate inter-population differences in various life cycle parameters.

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