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LIFE CYCLE OF *PERFORATELLA BIDENTATA* (GMELIN, 1791) (GASTROPODA: PULMONATA: HELICIDAE)

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ABSTRACT: Laboratory and field observations made it possible to ascertain the following life cycle parameters of *Perforatella bidentata* (Gmel.): mating includes four phases, the longest being courtship; sperm is transferred in spermatophores. Eggs are laid in winter (November–February) and summer (May–September), in batches of 2–20. They are calcified, slightly oval, ca. 1.5 × 1.8 mm. Incubation takes 8–34 days, hatching is asynchronous. Growth from hatching to maturity lasts from ca. 3 to 9 months. In the wild the youngest age class appears in July. The maximum life span is 3 years. The activity is the greatest in spring and autumn; in all seasons it is greater in the night and early morning; juveniles are more active than adults. The individual mobility is up to 5 m/month.

KEY WORDS: land snails, *Perforatella bidentata*, life cycle

INTRODUCTION

Though very common, *Perforatella bidentata* (Gmelin, 1791) is among the least known snails with respect to its life history. It is an Eastern European species, widespread in Russia where it reaches the Volga River. Northwards its range extends to southern Finland, in the west – to the Vosges in France; it includes all of the Czech Republic, Poland and Slovakia; it has isolated localities in Sweden, Denmark, Austria, Hungary and the former Yugoslavia (WIKTOR 2004). In Poland *P. bidentata* is found in all the lowlands and up to ca. 500 m a.s.l. in the mountains, except the Tatra and the Karkonosze. In some areas, especially submontane and in Wielkopolska, it appears to be receding, being more frequent as subfossil than it is at present (RIEDEL 1988). *P. bidentata* is a hygrophile, most often found in wetlands and wet places in forests. It stays on the ground, under pieces of timber or among plant debris. Our studies aimed at describing its life cycle.

STUDY AREA

The population of *P. bidentata*, selected for field observations because of its high density, was located in Muszkowice near Henryków, at the boundary of the nature reserve Muszkowicki Las Bukowy (for exact location and detailed description of the site see KUŹNIK-KOWALSKA 2006). The study plot was located in a planted alder forest (Fig. 1).

MATERIAL AND METHODS

LABORATORY OBSERVATIONS

The material for the laboratory culture (snails of various ages, eggs) was collected on the 7th of October 2005 in Muszkowice. The observations included the period October 8th 2005–May 31st 2007. The total number of individuals was 492, originating from 86 snails brought from the field. The snails were kept in Petri dishes and in containers of a size depending on the number of inhabitants (dish diameter 5–14

Fig. 1. Study site in Muszkowice (Photo E. KUŹNIK-KOWALSKA)

cm, containers 6 × 7 × 7 cm, 7 × 11.5 × 7 cm and 12 × 15 × 7 cm). Damp tissue paper was used as substratum, with pieces of rotting timber and litter brought from the habitat where the snails were collected. The plant debris provided places for egg-laying, and food (microflora). Additionally the snails were fed lettuce, cabbage, carrot, cucumber and apple. Crushed egg shells were provided as the source of calcium (Fig. 2). The temperature in the room ranged from 17°C (winter) to 25°C (summer). Humidity in the dishes and containers was maintained at a constant level of ca. 80%. The containers were aired at least once a week, and during periods of intense observations – every day or two days; water and food were supplied according to need.

Laboratory observations included growth rate, maturation, longevity, possibility of uniparental reproduction, mating behaviour, fecundity, egg-laying,

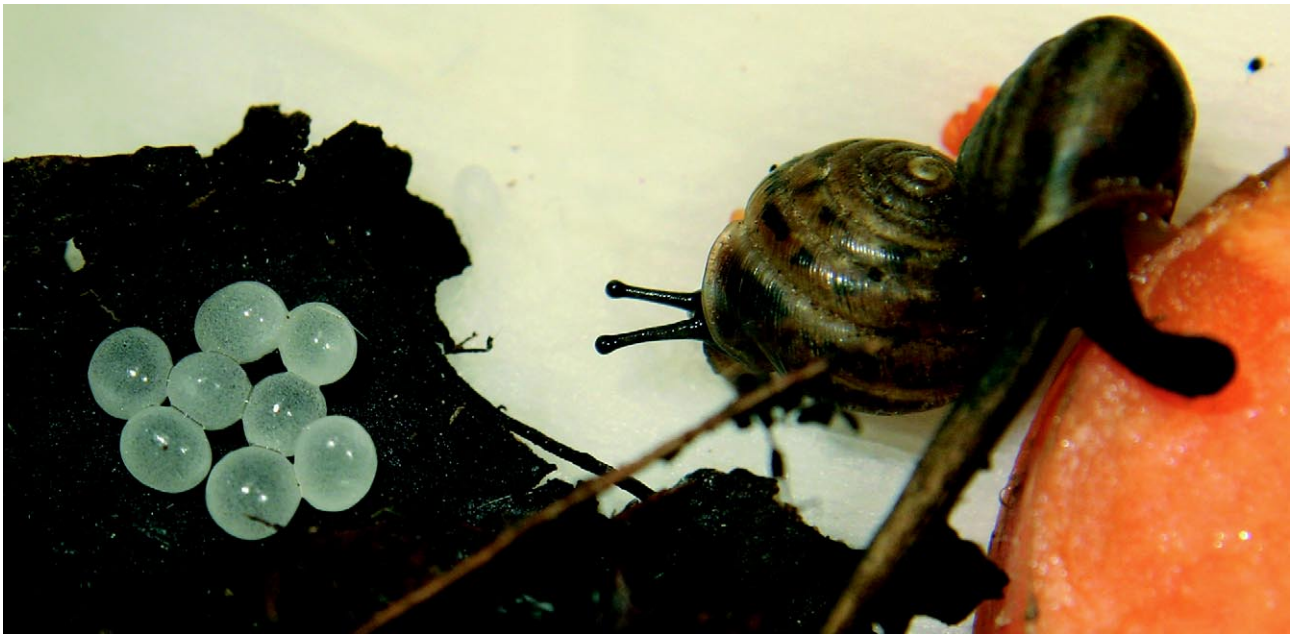

Fig. 2. *P. bidentata* in laboratory culture (Photo E. KUŹNIK-KOWALSKA)

egg morphometrics, incubation, hatching and cannibalism. In order to ascertain the growth rate whorls were counted every 7–30 days with EHRMANN's (1933) method. In order to test the possibility of uniparental reproduction, some individuals were kept singly since the egg stage or early juvenile stages. Observations of mating behaviour required keeping snails in pairs and groups. The numbers of individuals kept in these ways were: 18 isolated snails, 10 kept in pairs (5 pairs) and 464 in groups of 4 to 20 individuals. The maximum of reproduction was estimated through counting the total number of eggs produced within each of 12 consecutive months, starting on November 23rd 2005. Fecundity and reproductive success of snails kept in isolation were recorded from the beginning of their life, through counting eggs and calculating hatching success. For fecundity estimates of individuals which had an opportunity to mate, some snails initially kept in pairs or groups were isolated prior to egg-laying by any member of the group, their eggs were counted and the hatching success calculated. The number of such snails was six. For estimates of incubation duration, newly laid egg batches were placed in separate dishes of 3 cm diameter; the number of such eggs was 427. Eggs of individuals kept singly, in pairs and in groups were measured with calibrated eye-piece to the nearest 0.025 mm (n=84). Observations on cannibalism included 99 snails. Two tests were used to check the possibility of cannibalism: offering conspecific eggs to newly hatched juveniles and offering non-conspecific eggs to adults. Diurnal activity was assessed during every season of the year, through 24 hours of observations of both juvenile and adult individuals, depending on changing day and night temperature. Crawling, feeding, mating or egg-laying snails were regarded as active. Longevity was estimated by adding life time of snails brought from the field (time from lip completion till death) and of the earliest hatched laboratory individuals (time from hatching till lip completion). Statistical analysis of the data used Statistica PL 6.0 and Microsoft Excel 2003.

SEM photos were taken at the Laboratory of Electron Microscopy, Wrocław University of Environmental and Life Sciences.

FIELD OBSERVATIONS

Behaviour of snails in their habitat (shelters, egg-laying places, mating behaviour, mobility) was observed during collecting material for the laboratory culture and quantitative sampling.

In order to make a list of accompanying fauna and estimate the density of *P. bidentata* in the study site, quantitative samples were taken three times during the vegetation season (May 7th, August 9th and October 15th, 2006). The total surface area of the samples was 3 m of litter, herbs and 2–3 cm soil layer taken with Oekland frame of 50 × 50 cm. Each sample was sorted three times: directly after bringing it to the laboratory, and then twice after drying the material and separating it into fractions (for details see CAMERON & POKRYSZKO 2005). Only live snails were considered. Individuals from each sample were placed in a separate, numbered container, drowned in boiled water and preserved in 70–75% ethanol. The accompanying fauna was identified using KERNEY et al. (1983) and WIKTOR (2004); the nomenclature follows RIEDEL (1988).

Seasonal changes in the age structure were traced based on regular samples (visual search) taken monthly from May till October 2006. On each occasion snails were collected during 3 hours, from an area of 10 m. Growth rate and longevity estimates in the field were based on monthly marking with nail varnish (each month a different colour) (Fig. 3). Marking consisted in painting a narrow stripe on the shell, just next to the aperture margin, so that the shell increment could be read on recapture. The following numbers of individuals were marked: May – 62, June – 155 (9 recaptured), July – 145 (3 recaptured), August – 134 (17 recaptured), September – 87 (30 recaptured), October – 84 (32 recaptured). Growth rate was expressed as whorl increment, since because of large differences in the ultimate size, this method is more reliable than expressing growth as size increment (POKRYSZKO 1990b, HELLER et al. 1997). Six age classes were distinguished (Table 1).

Fig. 3. Marked individual of *P. bidentata* in the field (Photo E. KUŹNIK-KOWALSKA)

Table 1. Age classes of *P. bidentata*

Age class	Number of whorls
I	1.2–2.1
II	2.2–3.1
III	3.2–4.1
IV	4.2–5.1
V	5.2–6.1
VI	6.2–7.1

RESULTS

LABORATORY OBSERVATIONS

Mating

In the laboratory mating was observed on four occasions, when individuals previously kept in isolation were joined in pairs: November 10th, 11th and 12th, 2006 and May 9th, 2007, always between 18.00 and 20.00. It included four phases. The initial phase lasted from 3 to 5 minutes; it started with an apparently accidental encounter of two snails which then took positions facing each other, with slightly elevated anterior part of foot and extended tentacles. Courtship was initiated by one of the partners which was then joined by the other snail; both partners made small clockwise circles. After a few minutes they slowed down, while the circles became increasingly smaller; the circle diameter never exceeded 3–4 cm and the total number of circles made was 10–12. Subsequently the snails tilted their heads to the left (right side of the partner) which made possible mutual touching of foot margins and genital atria, now partly everted, with mouths and tentacles. This phase lasted 30 minutes. Full eversion of copulatory organs and spermatophore transfer took place simultaneously in both partners. With the two snails adhering to each other with raised anterior body sections, each spermatophore was introduced into the opening of the partner's spermatheca duct. Subsequently the atria were slowly retracted, with the snails still for a few seconds connected by their spermatophores. Then the separated snails completely retracted their received spermatophores within 5 seconds. Copulation took 20 minutes. Post-copulation phase lasted ca. 10 minutes; the snails remained motionless, with their whole bodies except the heads touching. Then one of the partners left while the other consumed the mucus produced during mating.

Egg-laying, incubation and hatching

The time between copulation and egg laying was 28 days (9.05–6.06.2007). In the laboratory the snails laid eggs in the winter: from the end of November (2+5 eggs found on 23.11.2005) till the beginning of February (19 eggs found on 6.02.2006), and in the summer: from the end of May (3 eggs found on 22.05.2006) till half of September (12 eggs found on 12.09.2006). Outside these periods eggs were laid only on 19.04.2006 (17 eggs). The total number of eggs laid in the laboratory was 947 (including two uniparentally produced eggs) (Fig. 4). The eggs were laid under bark, litter, lettuce leaves or pieces of carrot, often directly on the tissue paper. Egg laying was observed directly on three occasions: 28.07.06 (2 eggs), 30.07.06 (4 eggs) and 12.09.06 (1 egg). Laying one egg took about 20 minutes.

Newly laid eggs were calcified, milky white, with a pearly sheen as a result of the covering mucus (Fig. 5). After 6–7 days they became cream-coloured and matt, after 8–10 days – light brown, and then their envelopes became almost completely translucent (12–16 days) (Fig. 6). The egg size was: minor diameter 1.25–1.94 mm (mean 1.49, SD 0.14, n=84), major diameter 1.42–2.23 mm (mean 1.78, SD 0.19, n=84) (Fig. 7).

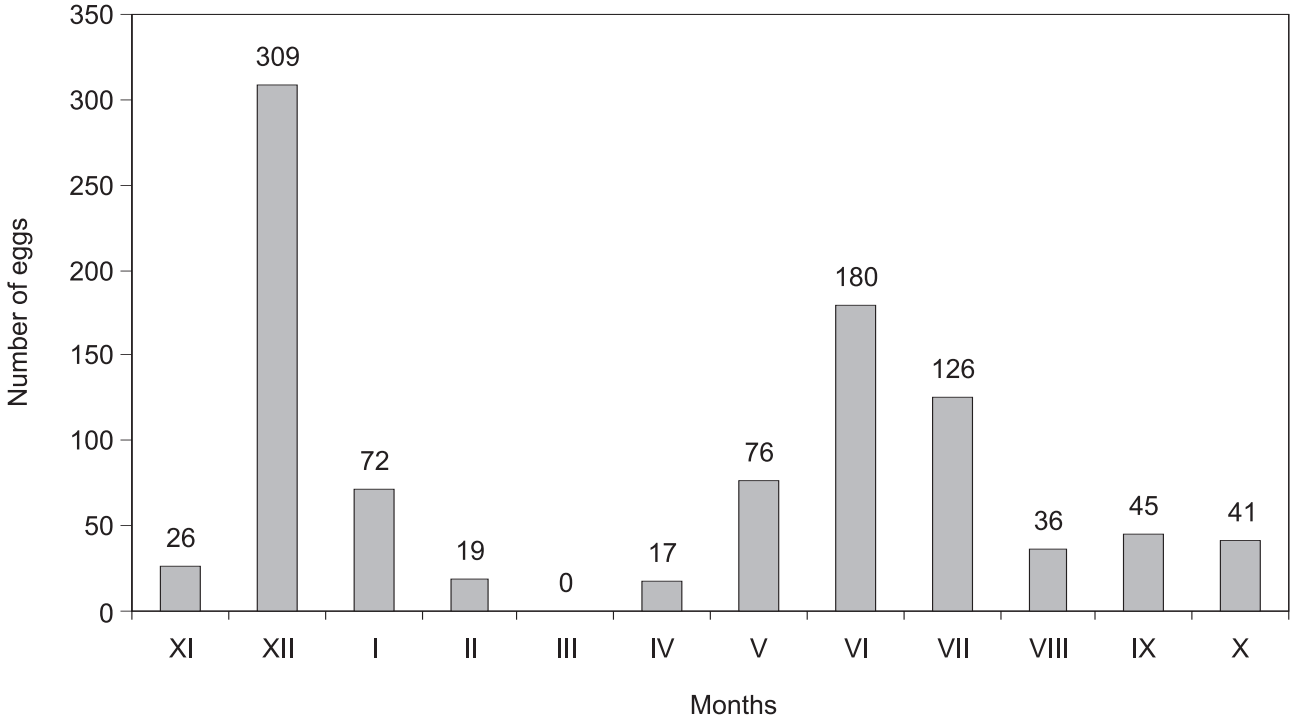

Fig. 4. Reproduction dynamics of *P. bidentata* in laboratory

The eggs were laid singly or in batches in the form of a row or pyramid; their number per batch ranged from 2 to 20 (mean 8.54, SD 4.70, n=100) (Fig. 8).

Incubation lasted from 8 to 34 days (mean 15.37, SD 5.37, n=427) (Fig. 9). Hatching was asynchronous, juveniles of the same batch hatching during one to seven days. The juveniles ate their way through their egg envelopes (Fig. 10). Newly hatched juveniles had translucent shells and bodies; their shells had 1.1–1.7 whorl (mean 1.51, SD 0.12, n=242) (Figs 11, 12). The initial part of the shell (embryonic whorls proper) was smooth, the next part of the whorl bore microsculpture in the form of radially arranged short, periostracal ridges (Figs 13, 14) which in later life were lost. The number of such ridges and the fraction of the whorl occupied by them varied among the hatchlings. Hatching success among the offspring of individuals kept in pairs or groups was 95.25% (n=96), while the two eggs produced uniparentally never hatched. No cannibalism was observed; neither newly hatched juveniles nor adults ate or damaged

Fig. 5. Newly laid eggs of *P. bidentata* (Photo E. KUŹNIK-KOWALSKA)

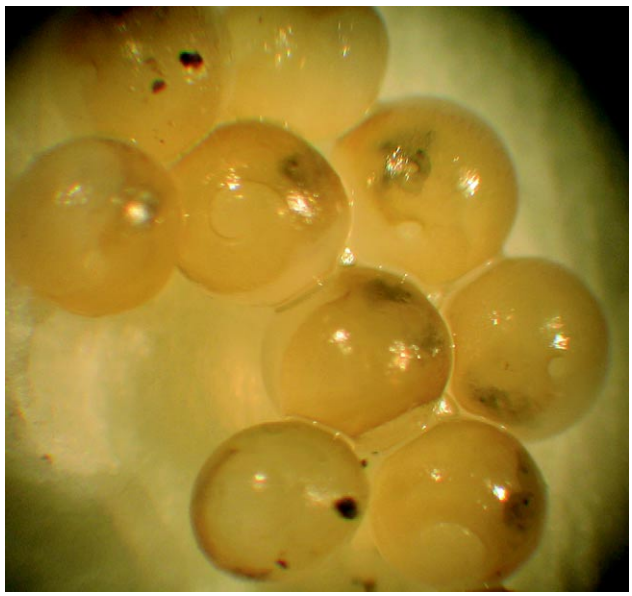

Fig. 6. Eggs of *P. bidentata* on the 14th day of incubation (Photo E. KUŹNIK-KOWALSKA)

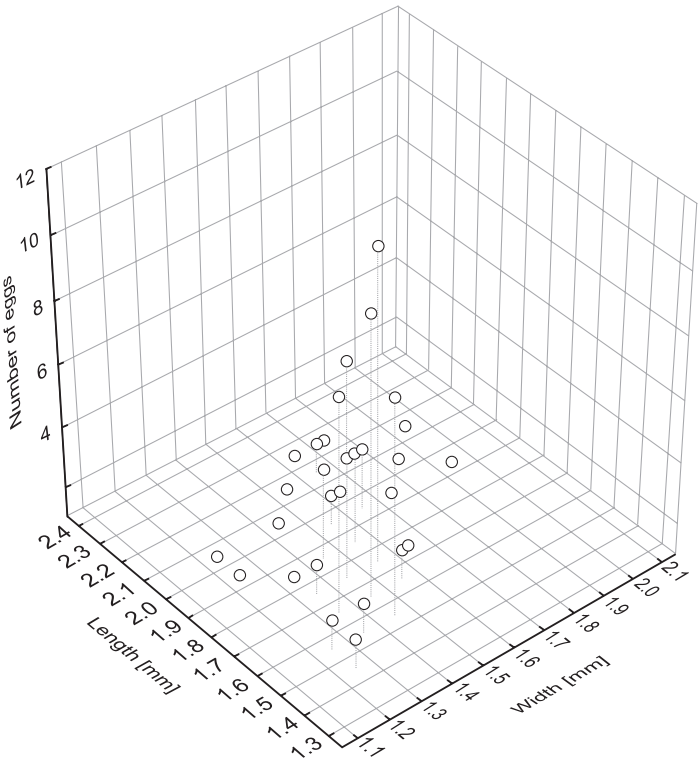

Fig. 7. *P. bidentata*. Variation in egg measurements

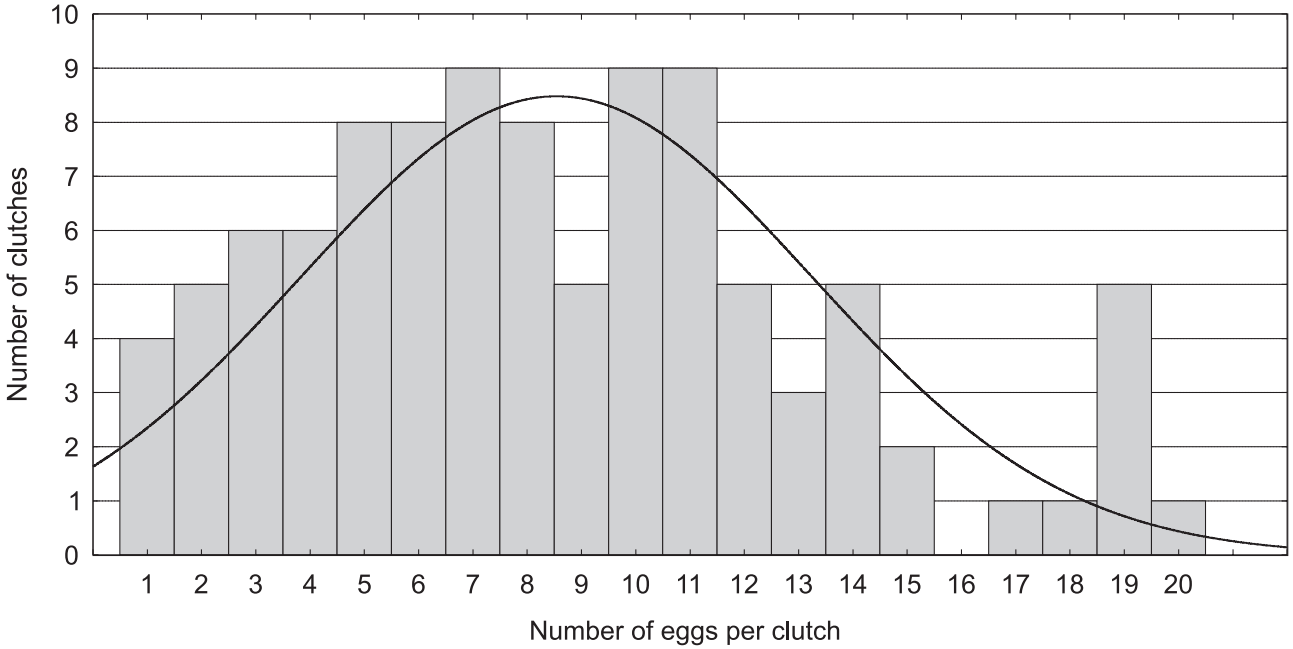

Fig. 8. *P. bidentata*. Number of eggs per batch

conspecific or non-conspecific eggs, even in the absence of other food.

Growth and maturation

The time from hatching to ultimate size (lip formation completed) ranged from 93.3 to 273.9 days. Juveniles hatched in the spring formed lips within 93.3–181.5 days (mean 131.6, SD 42, n=20), those hatched in the winter started lip formation only after 168–273.9 days (mean 205.5, SD 35.32, n=20). The spring individuals formed lips at the earliest at 4.9 and usually at 5.3–5.5 whorls (mean 5.57, SD 0.08, n=20), the winter snails – at 6.1–6.3 whorls (mean 6.16, SD 0.10, n=20). The growth progressed in two phases:

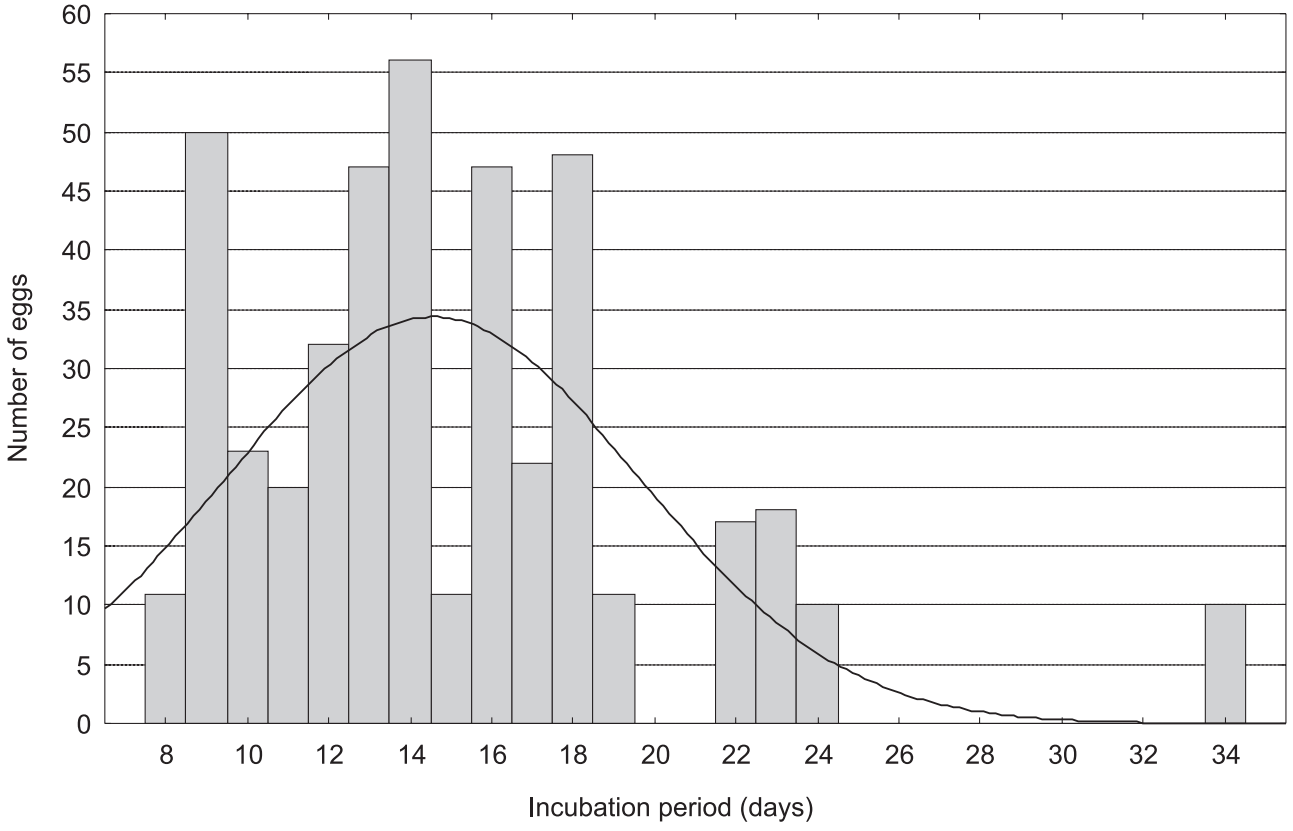

Fig. 9. *P. bidentata*. Duration of incubation

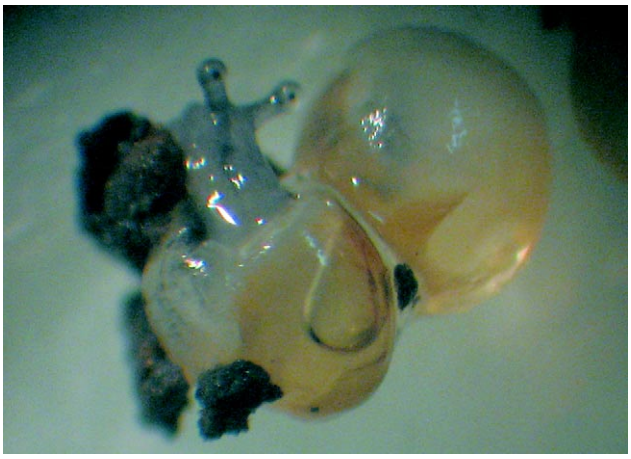

Fig. 10. Hatching juvenile of *P. bidentata* (Photo E. KUŹNIK-KOWALSKA)

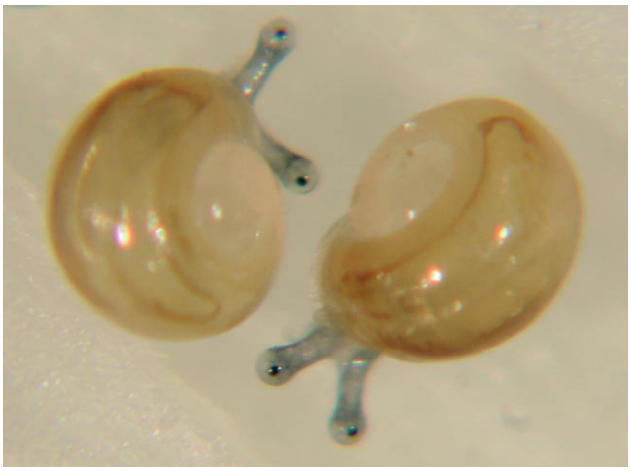

Fig. 11. Hatchlings of *P. bidentata* (Photo E. KUŹNIK-KOWALSKA)

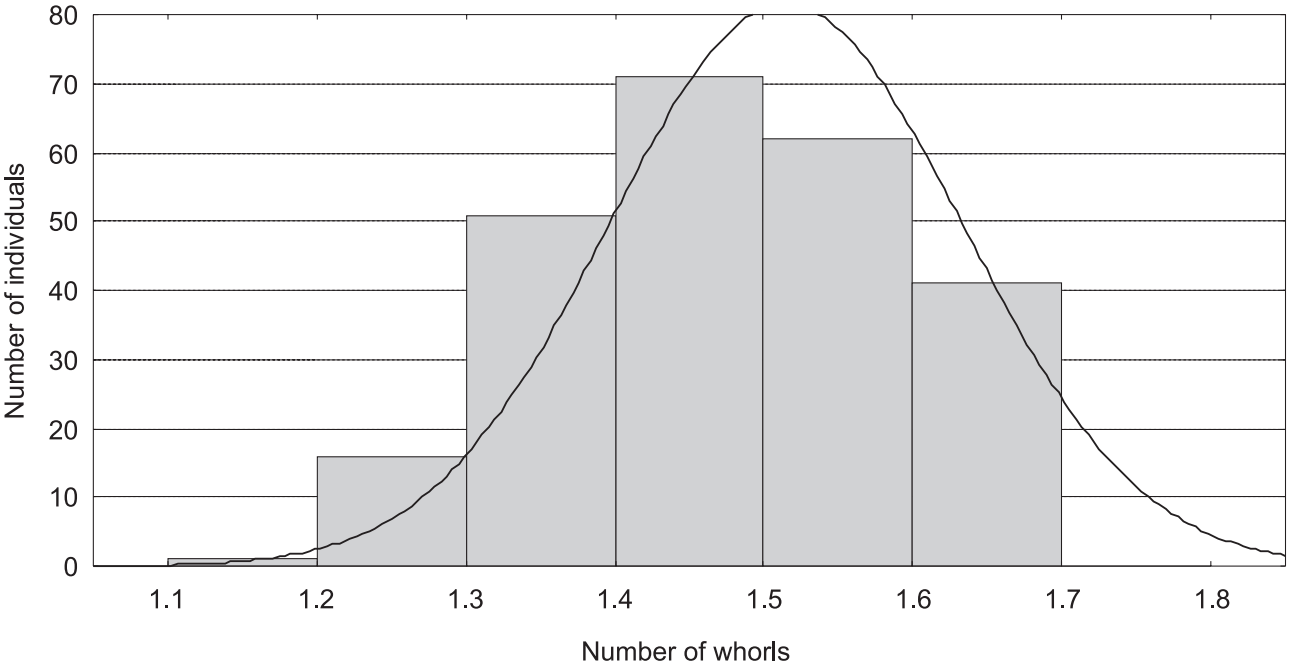

Fig. 12. Number of whorls in hatchlings of *P. bidentata*

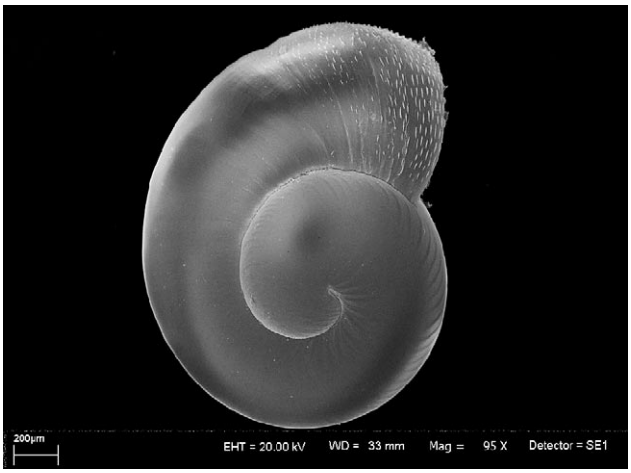

Fig. 13. Embryonic shell of *P. bidentata*. SEM

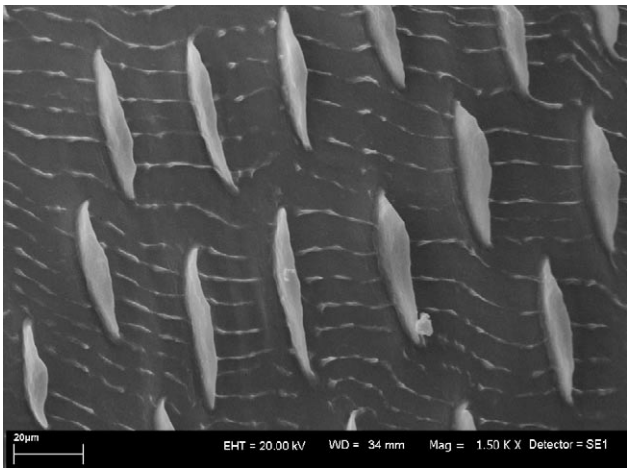

Fig. 14. Ridges on first shell increment of *P. bidentata*. SEM

phase I, fast: from hatching to 4.5–5.0 whorls (30.8–50.2 days/whorl) (mean 40.5, SD 10.89, n=30); phase II, slow: after reaching 5.0 whorls (61–90.7 days/whorl) (mean 74.35, SD 17.49, n=20). After lip formation the shells showed a slight increment during ca. 2 months (forming the fragment of shell which in completely grown individuals protrudes outside the lip). Growth of ten selected individuals is shown in Table 2 and Fig. 15.

Diurnal activity

In the summer and autumn the snails were active in the late evening, night and morning (from 20.00 till 10.00). About 11.00 the activity decreased rapidly and the snails retracted into their shells. The activity depended on the air temperature. In the summer, during the day, when the temperature was 21°C, the snails were less active than in the autumn. In the night juveniles were more often active than adults; in the daytime their activity did not differ. In the winter the snails showed the greatest activity at 7.00 and between 12.00 and 15.00, outside these hours the activity level was constant. At all times juveniles were more active than adults. In the spring their activity was high throughout the day, with a slight decrease between 14.00 and 17.00 (Fig. 16).

Life span

The life span of *P. bidentata* could not be ascertained through direct observations: the culture, started in October, was initially composed mostly of adults (with completed lips) brought from the field, whereas snails hatched in the laboratory did not die before the end of observations (31.05.2007). The

Table 2. Growth of 10 selected individuals of *P. bidentata*, number of whorls at lip formation indicated in bold

Date	Individual number									
	1	2	3	4	5	6	7	8	9	10
19.12.2005	1.50	1.40	1.60	1.40	1.50	1.60	1.40	1.70	1.60	1.50
22.01.2006	2.10	2.10	2.25	2.00	2.15	2.30	2.00	2.15	2.00	2.20
27.02.2006	2.80	2.80	3.00	2.90	3.00	3.20	3.05	2.90	2.80	2.95
26.03.2006	3.20	3.20	3.40	3.25	3.30	3.50	3.45	3.30	3.30	3.40
22.04.2006	3.80	3.85	4.00	3.80	4.00	4.10	4.10	3.90	3.85	3.85
18.05.2006	4.40	4.55	4.60	4.45	4.70	4.70	4.60	4.50	4.50	4.50
16.06.2006	5.00	5.15	5.20	5.10	5.25	5.30	5.10	5.00	5.05	5.00
23.07.2006	5.20	5.40	5.40	5.30	5.50	5.60	5.40	5.25	5.25	5.20
18.08.2006	5.70	**5.85**	5.95	5.70	**5.90**	**6.00**	5.75	5.80	5.70	5.75
25.09.2006	**6.05**	6.00	**6.20**	**6.20**	6.15	6.00	**6.10**	**6.25**	**6.00**	6.00
29.10.2006	6.20	6.05		6.25		6.10		6.40		**6.10**

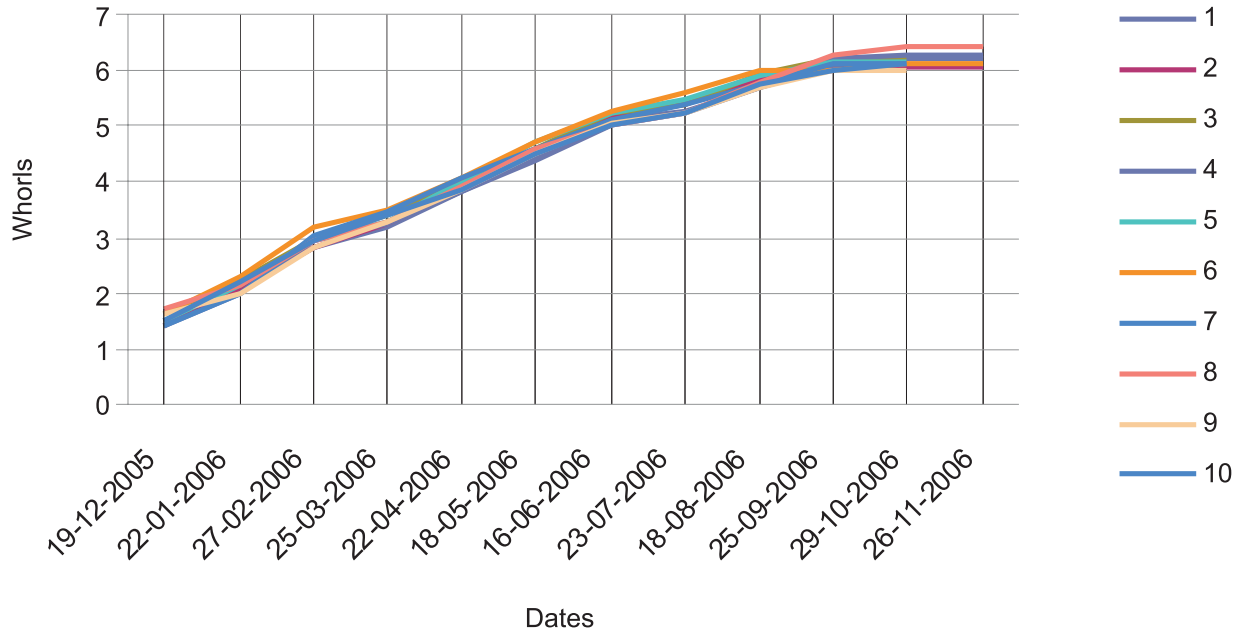

Fig. 15. Growth curves of 10 selected individuals of *P. bidentata*

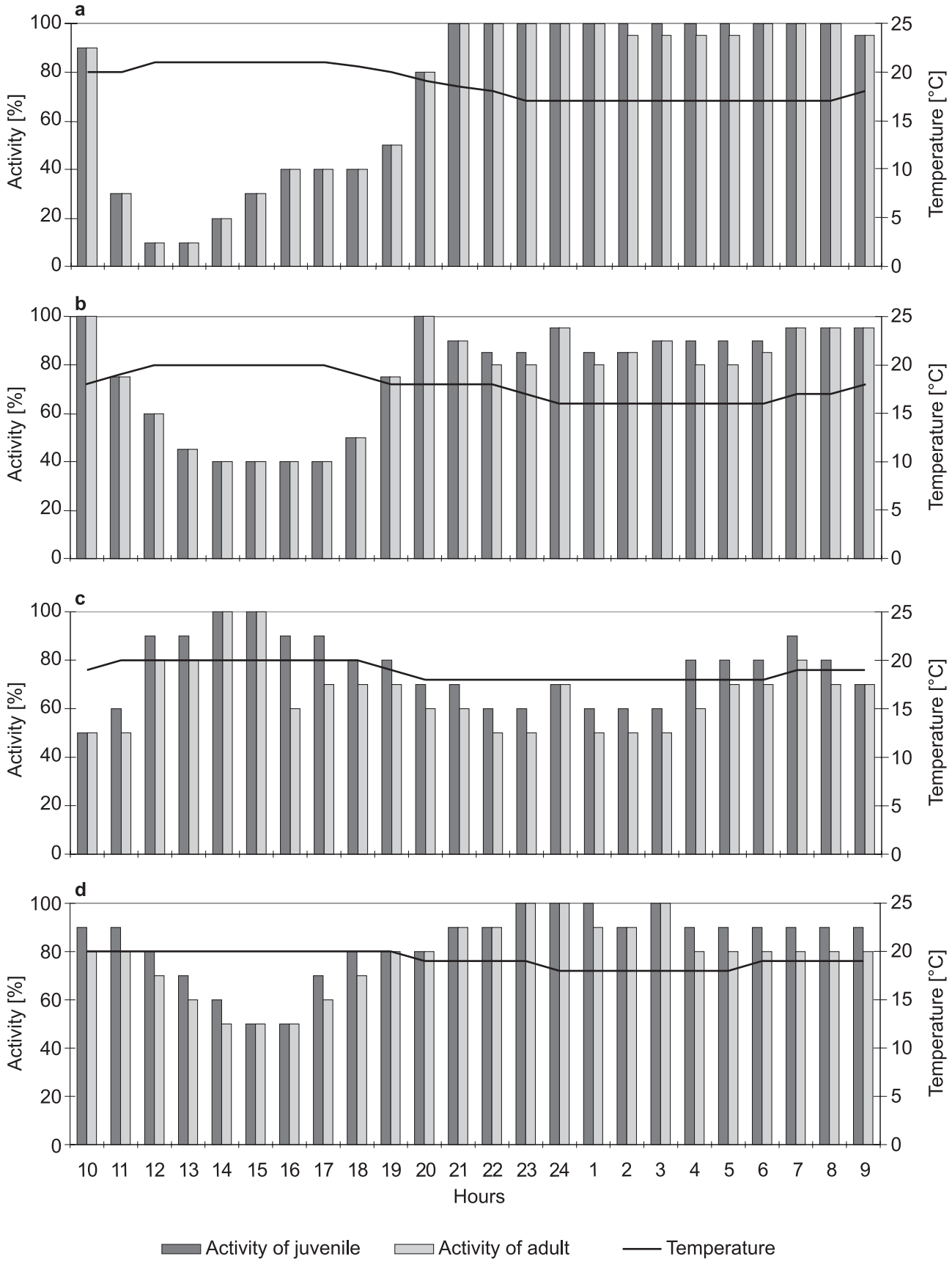

Fig. 16. Diurnal activity of juvenile and adult *P. bidentata*: a – summer, b – autumn, c – winter, d – spring

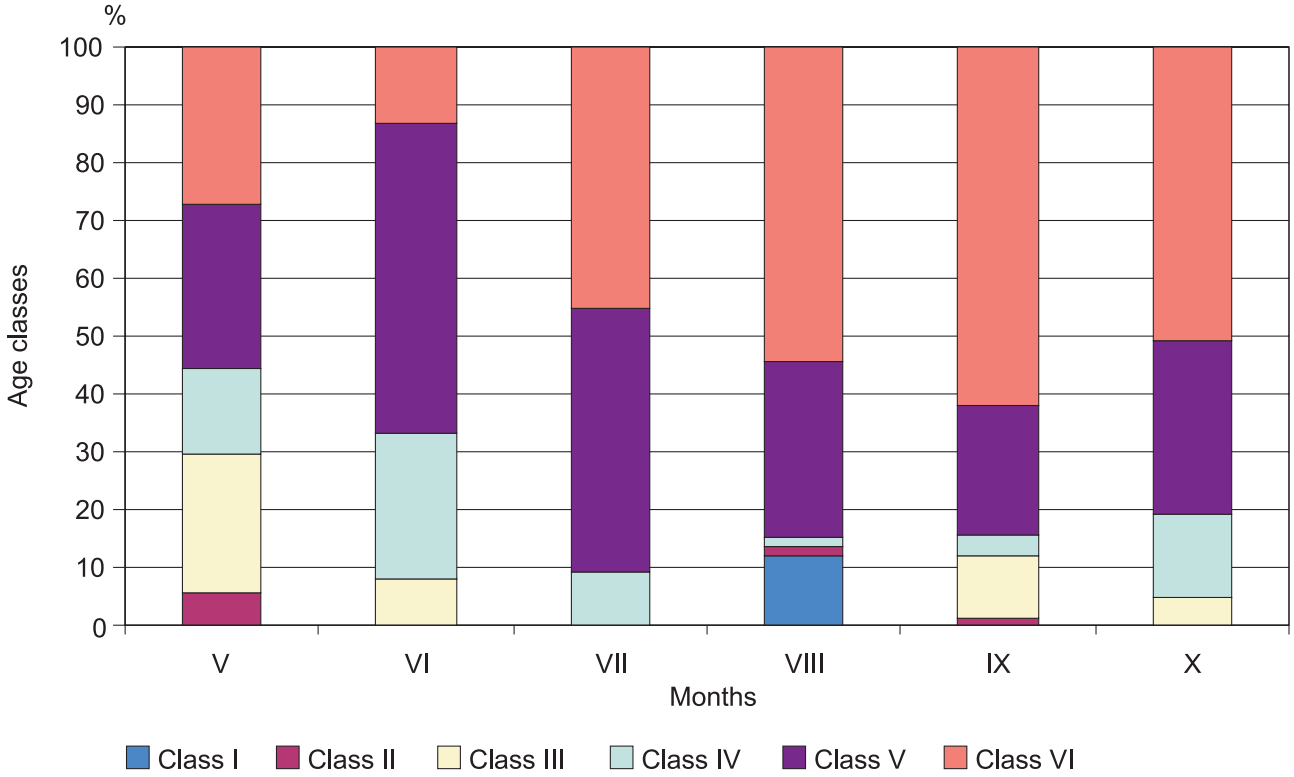

Fig. 17. Population dynamics of *P. bidentata* – division into age classes (see Table 1)

time from hatching to lip completion in the laboratory ranged from 93.3 to 273.9 days. Juveniles hatched in the spring formed their lip after 93.3–181.5 days (mean 131.6, SD 42, n=20), while those hatched in the winter started its formation as late as after 168–273.9 days (mean 205.5, SD 35.32, n=20) (see above: Growth and maturation). Snails brought from the field as adults started dying after 273 days (mean 345.34, SD 47.28, n=70). Thus the mean life span ranged from 476.94 (spring generation) to 550.84 days (winter generation) (16–18 months).

FIELD OBSERVATIONS

In the field *P. bidentata* was found inside curled dry leaves, under litter and sometimes directly on plants,

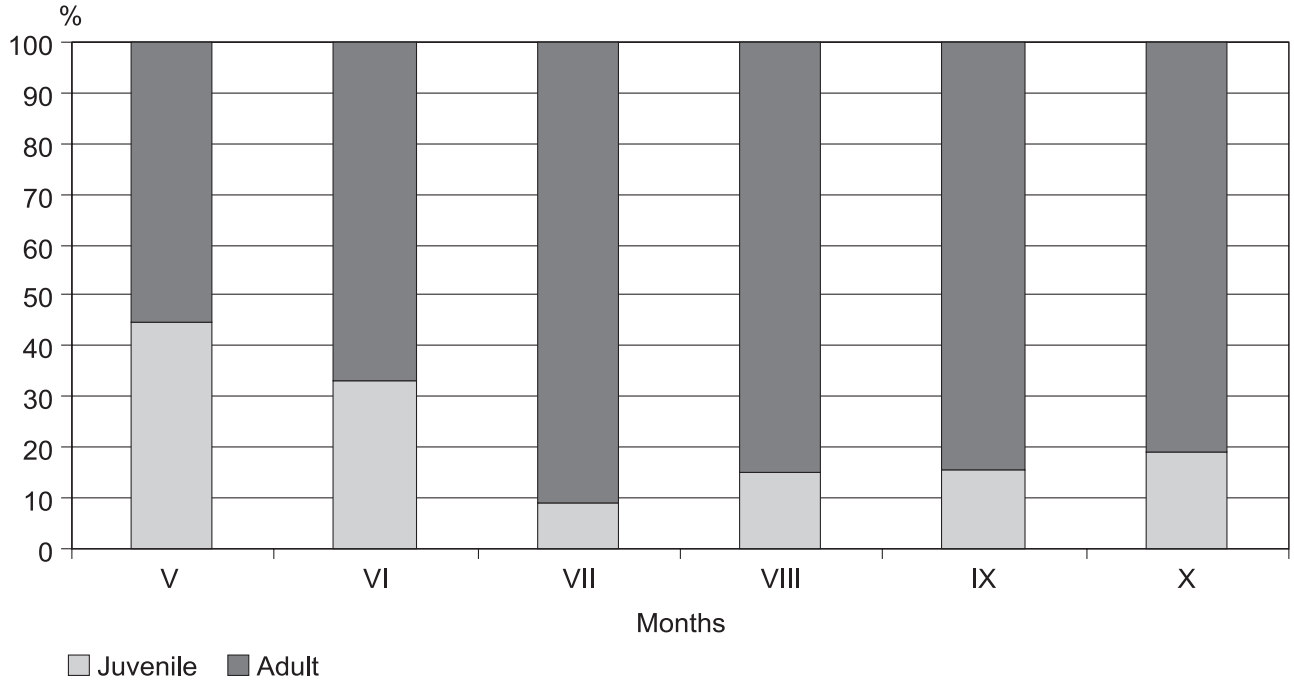

Fig. 18. Populaction dynamics of *P. bidentata* – proportion of juveniles and adults

Table 3. Growth of marked individuals in the field. Individuals found dead indicated in bold.

Individual number	Number of whorls on marking	Number of days	Increment	Number of whorls on recapture	Number of days	Increment	Number of whorls on recapture
1	3.50	35	0.80	4.30			
2	3.95	130	2.20	6.15			
3	4.10	35	0.80	4.90			
4	4.20	93	2.00	6.20			
5	4.25	35	0.80	5.05			
6	4.30	93	1.80	6.10			
7	4.30	35	0.85	5.15			
8	4.50	35	1.15	5.65			
9	4.60	33	0.70	5.30			
10	5.00	31	0.15	5.15			
11	5.10	93	0.30	5.40			
12	5.30	93	0.60	5.90			
13	5.30	95	0.95	6.25			
14	5.50	93	0.25	5.75			
15	5.70	68	0.20	5.90			
16	5.70	35	0.20	5.90			
17	5.75	94	0.20	5.95			
18	5.75	93	0.35	6.10			
19	5.75	93	0.20	5.95	37	0.05	6.00
20	5.90	31	0.00	5.90			
21	5.90	26	0.00	5.95	37	0.00	5.95
22	5.90	63	0.20	6.10	31	0.10	6.20
23	6.00	93	0.00	6.00			
24	6.00	93	0.00	6.00			
25	6.00	48	0.00	6.00			
26	6.00	93	0.10	6.10			
27	6.00	93	0.00	6.00			
28	6.00	37	0.15	6.15			
29	6.00	35	0.00	6.00			
30	6.00	93	0.00	6.00			
31	6.00	130	0.25	6.25			
32	6.00	37	0.15	6.15			
33	6.00	31	0.10	6.10			
34	6.10	93	0.00	6.10			
35	6.10	48	0.05	6.15			
36	6.10	93	0.30	6.40			
37	6.10	63	0.10	6.20			
38	6.10	37	0.00	6.10			
39	6.10	37	0.05	6.15			
40	6.10	94	0.00	6.10			
41	6.10	26	0.10	6.20	37	0.00	**6.20**
42	6.15	48	0.00	**6.15**			
43	6.15	48	0.00	6.15			

Table 2 – continued

Individual number	Number of whorls on marking	Number of days	Increment	Number of whorls on recapture	Number of days	Increment	Number of whorls on recapture
44	6.15	37	0.10	6.25			
45	6.20	31	0.00	6.20			
46	6.20	93	0.00	6.20			
47	6.20	31	0.00	6.20			
48	6.20	93	0.00	6.20			
49	6.20	93	0.00	6.20			
50	6.20	35	0.05	**6.25**			
51	6.20	35	0.00	6.20			
52	6.20	37	0.05	6.25			
53	6.20	48	0.00	6.20			
54	6.20	37	0.00	6.20			
55	6.20	37	0.05	6.25			
56	6.20	31	0.00	6.20			
57	6.20	37	0.05	6.25			
58	6.20	31	0.00	6.20			
59	6.20	26	0.05	6.25	37	0.05	6.30
60	6.25	31	0.00	6.25			
61	6.25	67	0.35	6.60			
62	6.25	93	0.00	6.25			
63	6.30	130	0.05	6.35			
64	6.30	37	0.05	6.35			
65	6.30	26	0.00	6.30	37	0.05	6.35
66	6.35	63	0.00	6.35			
67	6.40	35	0.05	6.45			
68	6.40	48	0.00	6.40			
69	6.40	48	0.00	6.40			
70	6.40	37	0.00	**6.40**			
71	6.40	31	0.00	6.40			
72	6.40	31	0.00	6.40			
73	6.40	31	0.00	**6.40**			
74	6.40	63	0.00	6.40			
75	6.50	67	0.00	6.50			
76	6.50	31	0.00	6.50			
77	6.50	31	0.00	6.50			
78	6.60	33	0.00	6.60			
79	6.70	37	0.05	6.75			
80	6.70	63	0.00	6.70			
81	6.70	63	0.00	6.70			
82	6.75	37	0.00	6.75			
83	6.75	26	0.00	6.75	37	0.00	6.75
84	6.80	48	0.00	6.80			

but never climbing higher than a few centimetres. Its population density was 17–20 individuals/m^2. It laid eggs in shaded places, under litter or in the topmost soil layer. The accompanying fauna in the sampling plot included *Carychium tridentatum* (Risso, 1826), *Succinea putris* (Linnaeus, 1758), *Cochlicopa lubrica* (O. F. Müller, 1774), *Ena montana* (Draparnaud, 1801), *Discus rotundatus* (O. F. Müller, 1774), *D. perspectivus* (Megerle von Mühlfeld, 1818), *Arion rufus* (Linnaeus, 1758), *A. silvaticus* Lohmander, 1937, *Aegopinella epipedostoma* (Fagot, 1879), *Daudebardia rufa* (Draparnaud, 1805), *Clausilia pumila* (C. Pfeiffer, 1828), *Alinda biplicata* (Montagu, 1803), *Bradybaena fruticum* (O. F. Müller, 1774), *Perforatella incarnata* (O. F. Müller, 1774), *P. vicina* (Rossmässler, 1842), *Trichia hispida* (Linnaeus, 1758), *Arianta arbustorum* (Linnaeus, 1758) and *Helix pomatia* Linnaeus, 1758.

Age structure and growth rate

The youngest age class (1.2–2.1 whorl) appeared only in August (Fig. 17). The second class (2.2–3.1) was at its peak in May (juveniles of the previous year); it occurred also in August and September (juveniles of the same year). Class III (3.2–4.1) showed its maximum abundance in May and June, and the minimum in September and October. Class IV (4.2–5.1) was present in all months, reaching its peak abundance in June. Class V (5.2–6.1) had its peak in June and from July its abundance decreased gradually. Class VI (6.2–7.1), with the maximum in July and August, was at its minimum in May and June. The proportion of juveniles (classes I–IV) in the population was the greatest in May (40%), through July (30%) and August (10%) it decreased considerably, and then increased again from September to reach 17% in October (Fig. 18).

Among the 742 marked juveniles and adults, 84 (11.32%) were recaptured, 7 (0.94%) were recaptured twice (Table 3). The growth rate based on recaptures and growth readings was 0.67 whorl/month in the fast phase (to 4.5–5.0 whorls) and 0.06 whorl/month in the slow pase (4.5–5.0 whorls till lip formation).

Mobility

Based on recaptures, the mobility of *P. bidentata* did not exceed 7 m per month; in most cases it was 2–3 m. On each control 10–15 individuals were found in the place of their release or near it (ca. 0.5 m).

DISCUSSION

Depending on their phylogenetic position and probably on some other factors, pulmonates mate in two ways, one of which – with one partner sitting on the other's shell and usually only one partner everting its copulatory organs – is probably more plesiomorphic (MORTON 1954, PURCHON 1977, DOLL 1982, POKRYSZKO 1990b, KUŹNIK-KOWALSKA 1999). *P. bidentata* follows the second pattern, with both partners adopting the same position and both everting their genitalia, characteristic of most pulmonates (WÄCHTLER 1929, WIKTOR 1960, 1981, 1989, HERZBERG 1965, RIEDEL & WIKTOR 1974, BAILEY 1975, DZIABASZEWSKI 1975, KOSIŃSKA 1980, KILIAS 1985, GIUSTI & ANDREINI 1988, BAUR & BAUR 1992, 1997, REISE 1995, KORALEWSKA-BATURA 1999, KOZŁOWSKI 2000, KOZŁOWSKI & SIONEK 2001, MALTZ 2003). It copulates in a horizontal position which is typical for most helicids (GIUSTI & ANDREINI 1988, BAUR & BAUR 1992, MALTZ 2003). Possible significance of this has been discussed by GIUSTI & ANDREINI (1988) and MALTZ (2003).

Likewise, the duration of sperm transfer in *P. bidentata* does not depart from such duration in other helicids (KORALEWSKA-BATURA 1999); the duration of post-copulation phase is relatively short (10 minutes) whereas among other pulmonates it varies widely from none (most slugs) to more than two hours (some members of *Helix*) (WIKTOR 1960, 1989, DZIABASZEWSKI 1975, KOSIŃSKA 1980, GIUSTI & ANDREINI 1988, REISE 1995, KORALEWSKA-BATURA 1999, KOZŁOWSKI & SIONEK 2001, MALTZ 2003). Another typically helicid character displayed by *P. bidentata* is spermatophore formation (TOMPA 1984),

The only form of parental care observed in *P. bidentata* is laying eggs in places which would protect them from drying out and ensure food supply for hatchlings, and covering the eggs with mucus; this is common behaviour in terrestrial pulmonates and its significance has been extensively discussed (WOLDA 1970, 1972, DZIABASZEWSKI 1975, COWIE 1980, TOMPA 1980, 1984, BAUR & BAUR 1986, HELLER & ITTIEL 1990, POKRYSZKO 1990b, KORALEWSKA-BATURA 1999, MALTZ 2003).

The fact that in the field *P. bidentata* laid eggs only in the summer and in the laboratory – in both summer and winter, indicates that its reproduction is regulated by external factors. There is no exact information on either external or internal factors regulating seasonality of snail reproduction; for details on particular species see MORTON (1954), TOMPA (1984), WIKTOR (1989), BAUR (1990), BULMAN (1990), HELLER & ITTIEL (1990), POKRYSZKO (1990a, b), HELLER et al. (1997), KUŹNIK-KOWALSKA (1998, 1999, 2005, 2006), KORALEWSKA-BATURA (1999) and MALTZ (1999).

The relative size of eggs, their number per batch and per lifetime depend largely on the adult size and

– indirectly – longevity (BAUR 1984, 1990, BAUR & RABOUD 1988, BAUR & BAUR 1996, 1997, KUŹNIK-KOWALSKA 1999, 2005, HELLER 2001, MALTZ 2003). These parameteres place *P. bidentata* among medium-sized snails.

The incubation time in *P. bidentata* varies widely, from 8 to 34 days; the difference can not be entirely attributed to temperature, since it pertained to some batches incubated at the same time in the same dish. Similar differences have been observed for *Punctum pygmaeum* (BAUR 1988) or *Helicodonta obvoluta* (MALTZ 2003). Shells of hatchlings vary much in the number of whorls, like in *Discus rotundatus* (KUŹNIK-KOWALSKA 1999). Most hatchlings of these two species have not only embryonic whorls proper, but also a fragment of the first definitive whorl, in *P. bidentata* covered by radial ridges, in *D. rotundatus* – ribbed. Most of their juveniles start feeding already within the egg envelopes, resulting in the hatchling eating its way out of the egg; the differences in the size of the definitive whorl fragment with which the snail hatches may result from different duration of such feeding.

Only two of the individuals of *P. bidentata* kept singly produced eggs which however did not hatch. Most authors regard helicids as incapable of uniparental reproduction (FRETTER & GRAHAM 1964 and references cited therein), though it has been observed in many other pulmonate taxa (WHITNEY 1938, FRETTER & GRAHAM 1964, PIECHOCKI 1979, TOMPA 1984, BAUR 1989, POKRYSZKO 1990b, KUŹNIK-KOWALSKA 1999, 2006, RIEDEL & WIKTOR 1974, TOMPA 1984 and references cited therein, WIKTOR 1989, BAUR & BAUR 1992, JORDAENS et al. 1998).

The growth phases observed in *P. bidentata* (fast phase followed by slow phase) seem to be characteristic of helicids (MALTZ 2003). The slow growth phase in such species is associated with the development of the reproductive system and has been discussed in MALTZ (2003) and MALTZ & SULIKOWSKA-DROZD (2008). Differences in the growth rate between the summer and winter cohorts, like those observed in *P. bidentata*, have also been reported for *Helicodonta obvoluta* (MALTZ 2003). The slow growth of the winter snails could result directly from the distinctly smaller activity in the winter (cf. Fig. 16).

Seasonal changes in the age structure of the studied population, combined with the growth rate, make it possible to reconstruct the life cycle of the species. Juveniles start hatching in July. The earliest hatched snails grow to ca. 4 whorls in their first season. Wintering juveniles have shells of 3.2–4.1 whorls. The growth rate is ca. 0.67 whorl/month. In the next season the snails resume their growth to reach 5.2–6.1 whorls in June. It is not known if they reproduce in the same year. Probably only some of them reproduce in the same year, while others reach maturity only in their third season.

The mobility of *P. bidentata* is not much smaller from that recorded for members of the genus *Cepaea* (LAMOTTE 1951, GOODHART 1962, DENNY 1980, COOK 1998) or for *Helicodonta obvoluta* (O. F. Müller, 1774) (MALTZ 2003), both of a slightly larger shell size.

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