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LIFE CYCLE AND POPULATION DYNAMICS OF *DISCUS PERSPECTIVUS* (MEGERLE VON MÜHLFELD, 1818) (GASTROPODA: PULMONATA: ENDODONTIDAE)

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ABSTRACT: Life cycle and population dynamics of *Discus perspectivus* (Mühlf.) were studied in the field and in the laboratory. No courtship, copulation or uniparental reproduction could be observed. The eggs, laid in June, July and August on rotting timber are calcified, ellipsoidal, ca. 1 mm in major diameter; the number of eggs per batch is 1–9 (mostly 3–4), with a total of 17–33 eggs per individual per season. The incubation period is 24–35 days, hatching is nearly synchronous; the proportion of hatching eggs laid by individuals brought from the field is 51% (for eggs brought from the field 38.7%). The hatchlings have shells of 1.8–2.3 whorls; they consume their egg envelopes immediately after hatching. The egg cannibalism is prolonged into adult stage; only conspecific eggs are consumed; juveniles eat eggs of their own and alien batches. The growth rate in the laboratory is 1 whorl per 49–188 days (slower in the field); the growth is faster in juvenile and slower in mature snails. The snails reach maturity at slightly over 5 whorls (mature gametes present in the gonad), the life span is 173–849 days, the reproductive life constituting ca. 7% total life span. In the field juveniles hatch from June till October, with the maximum in August; till their first hibernation they reach 2.6–3.5 whorls and become mature in their second season to reproduce in the same or next year. The population density exceeds 50 m^{-2} in summer, and ranges from 25 to 30 m^{-2} during the remaining seasons. *D. perspectivus* shows aggregated distribution in August and October, in the remaining months the distribution is even. Some laboratory-born individuals have very much elevated spires and their shells become scalariform at the level of 5.3–5.75 whorls.

KEY WORDS: terrestrial pulmonates, *Discus perspectivus*, life cycle, population dynamics, growth, reproduction

INTRODUCTION

Life cycles and population dynamics of most European terrestrial pulmonates still remain unknown (for review see KUŹNIK-KOWALSKA 1999, MALTZ 2003b). On the other hand, such data are of great importance for evolutionary inferences (reproductive strategies), systematics and phylogeny (though life history parameters are only rarely used as characters), or ecology and protection of endangered species and communities of which they form a part.

Apart from *Discus rotundatus* (O. F. Müller, 1774) (KUŹNIK-KOWALSKA 1999), and some fragmentary and sometimes contradictory data on other species of the genus (UMIŃSKI 1962, RIEDEL & WIKTOR 1974), there is no published information on life cycles of members of *Discus*.

The 1993–1995 study (KUŹNIK 1997) on the comparability of the Oekland method and ”volume” method provided preliminary data on the population dynamics and life cycle of *D. perspectivus*. The objective of this paper was to describe its population dynamics and life cyle in more detail.

Discus perspectivus is a Carpathian-Dinaric-E Alpine species of disjunct range. It inhabits almost whole Carpathians, westward reaching the south-western fringe of Bavaria, neighborhood of Munich and Nürnberg, northward – parts of the Czech Republic, Lower Silesia, Cracow-Wieluń Jura and northern parts of the Carpathians. In Poland it is rather rare, known from the Bieszczady Mts, where it reaches up to 1,000 m a.s.l., Pogórze Dynowskie, Beskid Niski Mts, Beskid Sądecki Mts, Beskid Wyspowy Mts and Pieniny Mts (up to 700 m a.s.l.). Outside the Carpathians and the subcarpathian region, it is found in the western range of the Sudetes: Złote Mts, Bardzkie Mts and Sowie Mts. Its insular localities are situated on the Biskupia Kopa mt south of the Nysa River, in the nature reserve Muszkowicki Las Bukowy in Muszkowice near Ząbkowice Śląskie and in the Ślęża massif (UMIŃSKI 1962, RIEDEL & WIKTOR 1974, WIKTOR 2004). The northern border of its distribution range crosses Poland. *D. perspectivus* is a forest-dweller, inhabiting montane and submontane forests, mostly at 300–650 m a.s.l. It prefers shady and humid places where it stays in leaf litter or on rotting timber.

MATERIAL AND METHODS

LABORATORY STUDIES

The material for the laboratory culture (snails of various age and eggs) was collected on various occasions from the 5th of October 1995 till the 30th of October 1998 in the nature reserve Muszkowicki Las Bukowy in Muszkowice near Ząbkowice Śląskie (SW. Poland) and in Ebenau (Austria). The laboratory observations were conducted from October 5th 1995 till November 1999. The total number of individuals in the laboratory culture was 122, originating from 49 snails brought from the field.

The snails were kept in Petri dishes, of a diameter depending on the number of individuals (∅ 5–14 cm), on a humid tissue paper with pieces of rotting wood. The snails ate mainly microflora developing on the rotting timber (FRÖMMING 1954). Their diet was supplemented with lettuce, cabbage, carrot, cucumber and apple. Hen egg shells were placed in the dishes as a source of calcium. The temperature ranged from 17°C in winter to 25°C in summer, the humidity was constant, of ca. 100%. The dishes were aired once a week, food and water being added when necessary.

In order to check the possibility of uniparental reproduction, snails were kept singly from the egg or early juvenile stages; in order to observe mating they were kept in pairs and groups of several individuals: 50 isolated individuals, 72 in pairs (10 pairs) and groups of 3–15.

Observations on egg cannibalism included 17 juvenile snails and, as food, 69 eggs of *D. rotundatus*, *D. ruderatus*, *D. perspectivus* and *T. hispida*. The following food choice tests were used: Test I: 10 newly hatched snails were kept in a dish, ∅ 10 cm, and were offered 10 eggs of *D. perspectivus* and 5 of each of the following species: *T. hispida, D. ruderatus* and *D. rotundatus* (see Table 3). Test II: 7 newly hatched snails were kept singly in dishes, ∅ 5 cm, and given various eggs (see Table 4). As a supplementary food the snails received lettuce.

Growth rate was measured for both cannibalistic and non-cannibalistic individuals; whorls were counted according to EHRMANN's (1933) method. Eggs (n=70) were measured with calibrated eye-piece, to the nearest 0.025 mm.

Standard histological slides were made of gonads of snails collected in Muszkowicki Las Bukowy in order to determine when mature gametes appeared in the gonads. The snails were dissected and their gonads preserved in the Bouin fixative, dehydrated in a graded ethanol series and xylen or toluene, embedded in paraffin, cut into 4 μm sections, deparaffinated in toluene and a graded ethanol series, rinsed in distilled water and stained with Delafield haematoxylin and eosin.

Statistical analysis was performed with Statistica, PL. 5.1, using Chi square test, test for statistical difference between the means and Spearman correlation (STANISZ 1998).

FIELD STUDIES

To estimate seasonal changes in age structure and density, the population from Muszkowicki Las Bukowy (SW. Poland) was sampled monthly from October 1993 to October 1994, and from April till October in 1995–1998). The site was located in the lower part of the slope, where the dominant tree species are ash, alder and hornbeam; the soil there is humid and well shaded by the herb layer (for detailed description see KUŹNIK 1997).

Samples for the estimates of age structure and density (1993–1994) were taken with the Oekland method (KUŹNIK 1997). Leaf litter and the topmost layer of soil (2–3 cm) were removed from squares of 50 × 50 cm (0.25 m^2). The size of the quadrats was dictated by the need to estimate the possible aggregated distribution of the snails; smaller quadrats are used to avoid the effect of such distribution on the results

Table 1. Age classes of *D. perspectivus*

Age class	Number of whorls
I	2.0–2.5
II	2.6–3.0
III	3.1–3.5
IV	3.6–4.0
V	4.1–4.5
VI	4.6–5.0
VII	5.1–5.5
VIII	5.6–6.0
IX	6.1–6.5

(DYDUCH-FALNIOWSKA & TOBIS 1989). Each monthly series of 4 samples equalled 1 m^2. Besides the Oekland samples, from May till October 1994 sieve samples of 10 l unprocessed litter were taken parallelly. Each sample was hand-sorted three times, and only live snails were taken into account. From April 1996 to October 1998 some individuals of *D. perspectivus* in Muszkowicki Las Bukowy were marked monthly in such a way that the growth since last marking could be read on re-capture (a stripe of nail varnish on the body whorl, next to the aperture, each month a different colour).

The division into age classes adopted for the estimates of age structure is presented in Table 1.

RESULTS

No courtship dance or copulation could be observed in the laboratory or in the field, despite numerous attempts.

LABORATORY OBSERVATIONS

Egg-laying, incubation, hatching

In the laboratory *D. perspectivus* laid eggs on pieces of bark and rotting timber, and often also on tissue paper, lettuce leaves or hen egg shells. The eggs were laid only by individuals brought from the field; no egg laying by snails hatched in the laboratory was observed. Newly laid eggs were calcified, ellipsoidal, slightly flattened and milky white. Initially shiny as a result of the coveing mucus layer, after 5–7 days they became matt. Their major diameter was ca. 1 mm (0.7–1.2 mm; mean = 0.95 mm; SD = 0.1 mm; n = 30) (Fig. 1). The egg size was not correlated with the number of whorls of the parents. The number of eggs in a batch ranged from 1 to 9 (mean = 3.88; SD = 1.93; n = 70) (Fig. 2). Most batches consisted of 3–4 eggs arranged in a charactersitic pyramid or row (Fig. 3). Not more than one batch was laid per day.

D. perspectivus laid eggs in June, July and August. No young hatched from the two batches laid outside this period, in December (two batches from two individuals, 2 eggs each). The number of eggs produced by an individual during one season reanged from 17 to 33 (some individuals could have laid eggs before being brought to the laboratory, see above) (mean = 25.25; SD = 6.21; n = 22), in 3–9 batches (mean = 6.33; SD = 1.65; n = 30). The number of eggs and batches, as well as their distribution in time varied between individuals (Table 2).

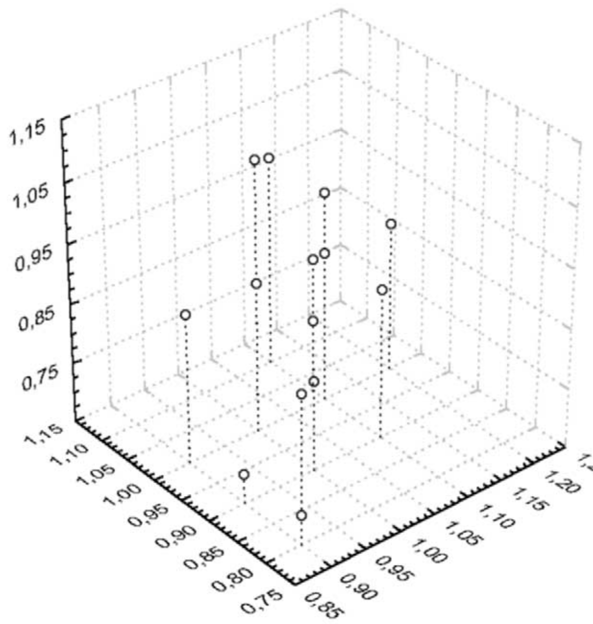

Fig. 1. *D. perspectivus*. Distribution of egg size, three measurements [mm], n = 30

Table 2. *D. perspectivus*. Egg-laying by 10 individuals

No.	Number of whorls at the first and last egg-laying	Date of the first and last egg-laying	Number of batches	Number of eggs
1	6.1	19.06.1996–20.07.1996	6	22
2	5.5	20.06.1996–12.07.1996	5	21
3	5.7–5.8	25.06.1996–1.08.1996	4	18
4	6.0	19.06.1996–29.08.1996	8	30
5	5.5–5.6	9.06.1996–31.08.1996	9	33
6	5.5	21.06.1996–9.08.1996	6	19
7	5.7	15.06.1996–2.08.1996	6	20
8	5.9	9.06.1996–25.07.1996	7	31
9	6.1	16.06.1996–2.07.1996	3	8
10	5.8	8.06.1996–29.06.1996	3	9

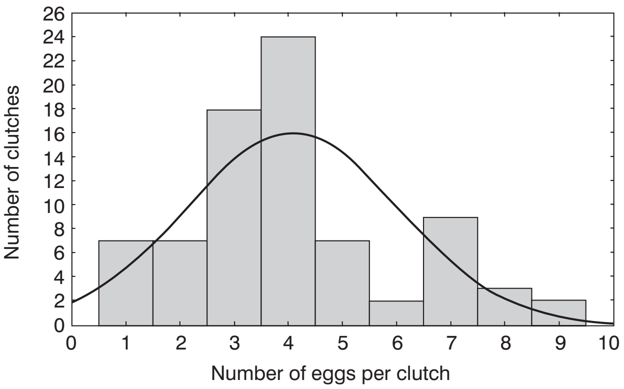

Fig. 2. *D. perspectivus*. Distribution of the number of eggs per batch

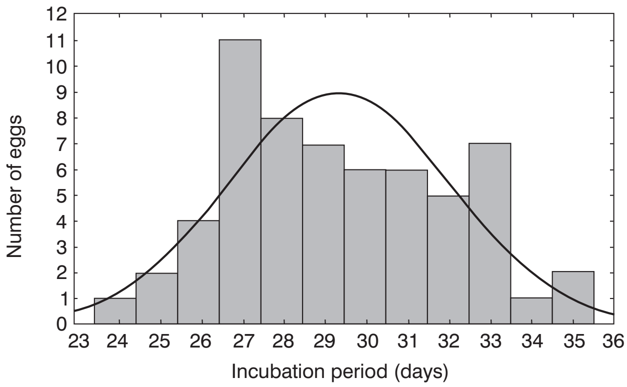

Fig. 4. *D. perspectivus*. Distribution of the duration of incubation period

Fig. 3. *D. perspectivus*. Egg batches

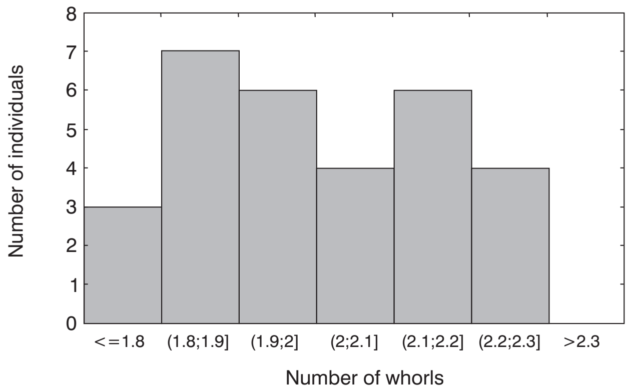

Fig. 5. *D. perspectivus*. Distribution of the number of whorls in hatchlings

The incubation period ranged from 24 to 35 days (mean = 29.38; SD = 2.67; n = 60) (Fig. 4). Hatching within batches was nearly synchronous, i.e. all juveniles from the same batch hatched within a few to about a dozen hours. Hatching took about 1.5–2 hours. Since the eggs are opaque, it was impossible to observe if the young snail used its radula to disrupt the egg envelopes; from the outside the first sign of hatching was a small piece of the egg shell breaking off. The percentage of hatching from eggs laid by individuals brought from the field was 51% (n = 200), and for eggs brought from the field it was 38.7% (n = 62).

The shells and bodies of newly hatched snails were translucent. Their shells had 1.8–2.3 whorl (mean = 2.03; SD = 0.16; n = 30) (Fig. 5). The first 1.8–2.0 whorls were always smooth, the remaining, brown part had a shape of the first 1–3 ribs of definitive whorls. The juveniles were very active, they started feeding immediately, the egg shell being the first to be consumed.

Cannibalism

In the laboratory juvenile *D. perspectivus* consumed eggs of the same or other batches. Sporadically adults were observed to eat their own eggs though other food was available. No juvenile or adult individuals were consumed or attacked by their conspecifics.

Juveniles which were offered various eggs, ate only eggs of their own species, ignoring those of *D. rotundatus* and *D. ruderatus* and also *T. hispida*. Eggs were consumed not only by neonates, but also by oder juveniles, subadults and adults. The results of food preference tests for cannibalistic juveniles of *D. perspectivus* are presented in Tables 3 and 4.

Growth and maturation

Formation of one shell whorl in growing *D. perspectivus* lasted on an average from 49.43 to 187.9 days (mean = 127.28; SD = 40.34; n = 30). Growth of ten selected individuals is presented in Table 5 and Fig. 6. The growth progressed in two phases: I – from hatch-

Table 3. *D. perspectivus*. Egg choice by cannibalistic juveniles (test I)

Number of individuals	Eggs of *D. perspectivus* (proposed/eaten/damaged)	Eggs of *D. ruderatus* (proposed/eaten/damaged)	Eggs of *D. rotundatus* (proposed/eaten/damaged)	Eggs of *T. hispida* (proposed/eaten/damaged)
10	10/4/5	5/0/0	5/0/0	5/0/0

Table 4. *D. perspectivus*. Egg choice by cannibalistic juveniles (test II)

Individual number	Eggs of *D. perspectivus* (proposed/eaten/damaged)	Eggs of *D. ruderatus* (proposed/eaten/damaged)	Eggs of *D. rotundatus* (proposed/eaten/damaged)	Eggs of *T. hispida* (proposed/eaten/damaged)
1	4/0/0	3/0/0	3/0/0	0
2	4/1/0	0	3/0/0	0
3	4/1/0	0	0	3/0/0
4	4/2/0	0	0	2/0/0
5	8/2/0	0	0	0
6	0	4/0/0	4/0/0	2/0/0
7	0	3/0/0	0	3/0/0

ing to maturity it was quicker (73–143 days/whorl; mean = 101.0; SD = 23.24; n = 10); II – from maturity to death it was very slow (60–725 days/whorl; mean = 426.2; SD = 191.99; n = 10).

Shells of some individuals born in the laboratory (10 out of 60 cases) tended to have more elevated spires compared to field-born snails, and the body whorl or its part adjoining the aperture became scalariform. The number of whorls in such individ-

Table 5. *D. perspectivus*. Growth of 10 individuals

Date	No.									
	1	2	3	4	5	6	7	8	9	10
6.08.96	2.7	2.5	2.7	2.75	2.75	2.4	2.5	2.7	2.8	2.7
5.09.96	3.6	3.6	4.0	3.6	3.5	3.5	3.75	3.5	4.0	3.75
9.10.96	4.75	4.75	5.2	4.5	4.6	4.75	4.6	4.7	4.9	4.75
15.11.96	5.1	5.5	6.0	5.0	5.45	5.25	5.1	5.5	5.4	5.55
15.12.96	5.5	5.75	6.2	5.4	5.6	5.6	5.5	5.75	5.8	5.75
14.01.97	5.75	5.75	6.4	5.4	5.9	5.9	5.9	5.8	6.1	6.0
4.03.97	6.3	6.2	6.5		6.0	6.2	5.9	6.0	6.4	6.1
18.04.97	6.3	6.2	6.5		6.2	6.2	6.0	6.2	6.45	6.4
18.05.97	6.4	6.4	6.6		6.4	6.4	6.1	6.4	6.5	6.4
20.09.97	6.4	6.4	6.6		6.4	6.4	6.15	6.4	6.5	6.5
11.12.97		6.4			6.4	6.4	6.15	6.4		6.5
12.07.98		6.6						6.4		6.5
10.10.98		6.6								

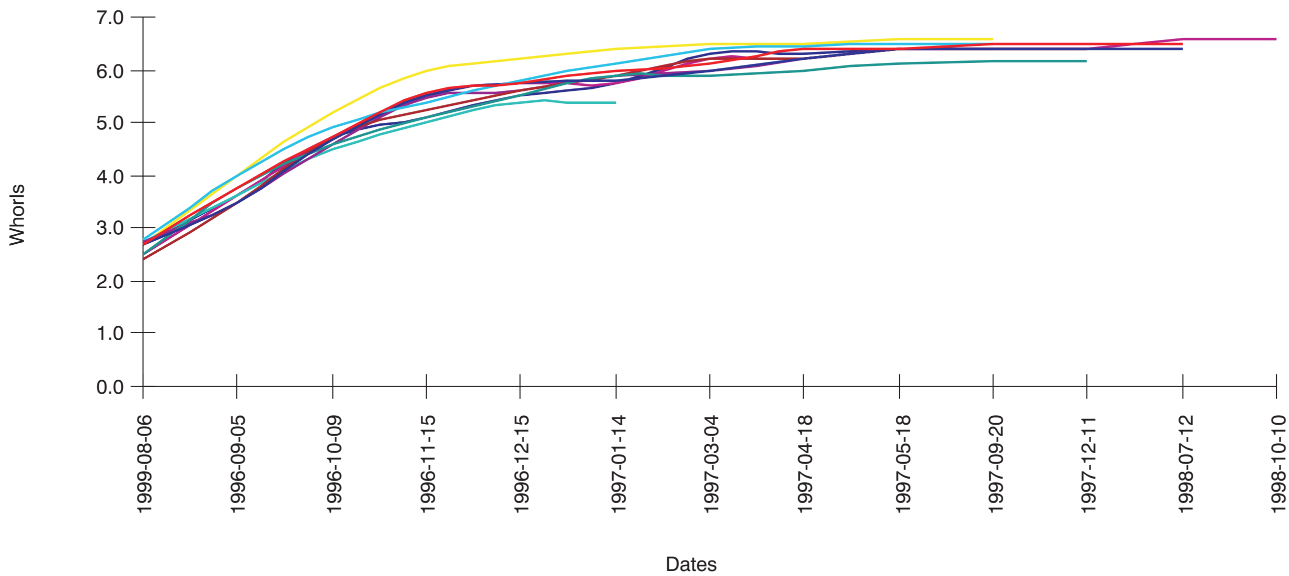

Fig. 6. *D. perspectivus*. Growth curves of 10 individuals

uals ranged from 5.6 to 6.9 (mean = 6.15; SD = 0.47; n = 10). The shells became scalariform at the level of 5.3–5.75 whorls (mean = 5.55; SD = 0.126; n = 10).

Since individuals of *D. perspectivus* hatched in the laboratory did not reproduce, the number of whorls at which the snails reached maturity could be estimated only based on: a. morphological character of their reproductive system, b. the lowest number of whorls in individuals brought from the field and reproducing; c. gamete production (see below). The smallest individuals brought from the field had 5.5 whorls when laying eggs. Among 60 dissected *D. perspectivus* (from 4 to 6.0 whorls) 32 individuals which had morphologically mature reproductive system, had 5 or more whorls (the highest number of whorls in adults was 6.9). Mature gametes appeared at the earliest in gonads of individuals of 5.2–5.3 whorls (Fig. 7); gonads of smaller individuals (4–5 whorls) contained oocytes and spermatocytes at earlier development stages.

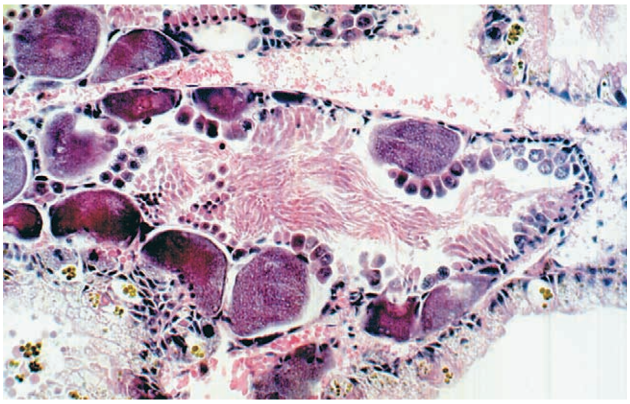

Fig. 7. *D. perspectivus*. Mature gonad of an individual of 5.75 whorls; 100×

Life span

Life span of *D. perspectivus* ranged from 173 to 849 days (mean = 603.3; SD = 171.27; n = 20), the time between the last egg laid and death was 29–698 days (mean = 377; SD =193.5; n = 10). The reproductive life was most probably ca. 7% life span.

FIELD OBSERVATIONS

In the field *D. perspectivus* laid eggs from May till August, with a clear maximum in June, while in August the eggs were much less numerous. The eggs were found in humid, sheltered places, mostly on pieces of bark and rotting timber, on logs and under bark of stumps and also on the soil, under leaf litter.

Seasonal changes of the age structure of the population from Muszkowicki Las Bukowy based on surface and volume samples are presented in Figs 8–11. The results of surface and volume sampling were very similar. Seasonal changes in the age structure of the population of *Discus perspectivus* (Figs 8–11) make it

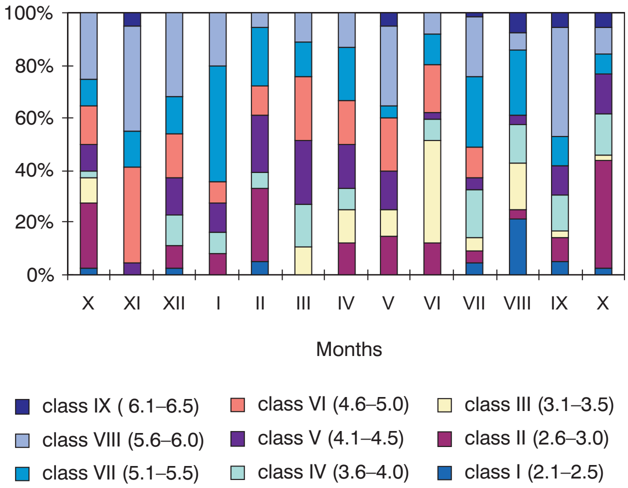

Fig. 8. *D. perspectivus*. Age structure of the population during 13 months in 1993/94 (surface samples), age classes

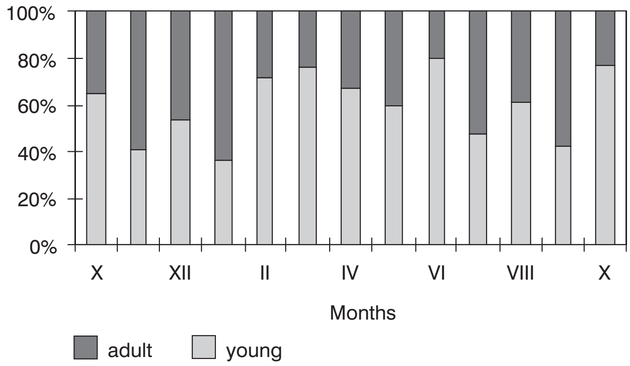

Fig. 9. *D. perspectivus*. Age structure of the population during 13 months in 1993/94 (surface samples), juveniles and adults

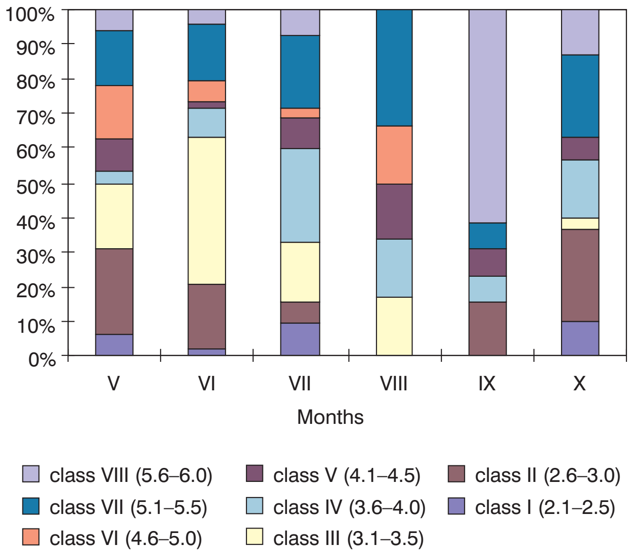

Fig. 10. *D. perspectivus*. Age structure of the population, 1994 (volume samples), age classes

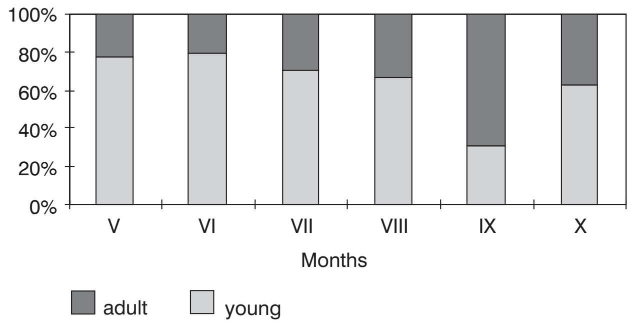

Fig. 11. *D. perspectivus*. Age structure of the population, 1994 (volume samples), juveniles and adults

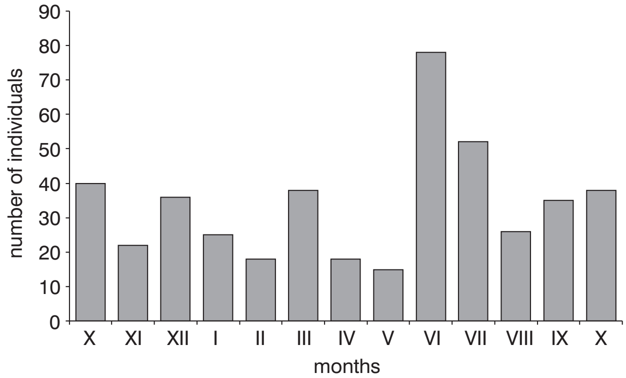

Fig. 12. *D. perspectivus*. Seasonal changes in abundance in a total area of 3 m^2 in 1993/94 (surface samples)

Table 6. *Discus perspectivus*. Distribution in a total area of 3 m^2 in consecutive months in 1993/94

Month	Expected	Observed	Chi^2	df	P
October	10	12/11/1/16	12.200	3	<0.006
November	5.5	6/9/5/2/	4.545	3	<0.208
December	8.75	11/7/8/8	1.057	3	<0.787
January	6.25	7/11/4/3	6.200	3	<0.102
February	4.5	3/5/8/2	4.666	3	<0.198
March	9.25	13/10/9/5	3.540	3	<0.315
April	6	7/4/6/7	1.000	3	<0.801
May	5	7/6/4/3	2.000	3	<0.572
June	19	25/22/18/11	5.789	3	<0.122
July	15.5	18/12/17/15	1.354	3	<0.716
August	7	13/3/11/1	14.857	3	<0.002
September	9	4/10/10/12	4.000	3	<0.261
October	9.75	25/8/4/2	33.718	3	<0.000

possible to reconstruct its life cycle. Juveniles hatch from July till October, with the maximum in August. The earliest hatched snails reach a size of 3.5 whorls in the same season. When wintering, the new generation has shells of 2.6–3.5 whorls. The growth rate is probably about 0.5 whorl per month. In the second season, the snails resume growth to reach 5 whorls in June–July. It is unknown if such snails start reproducing in the same year; probably only some of them do, while the remaining ones reach maturity only in their third season. Mature snails continue growing.

The low abundance of the youngest age class may reult from the difficulty to find the smallest juveniles (*D. perspectivus* lays eggs in rotting timber and the hatching snails have shells of ca. 1 mm diameter). The oldest age class, also poorly represented, most probably includes old individuals which have terminated reproduction. Seasonal changes in the density are presented in Fig. 12. The population density of *D. perspectivus* in spring, autumn and winter was about 25–30 individuals m^{-2}; in summer it exceeded 50 individuals m^{-2}. The proportion of juveniles was the lowest in spring (18.5%), in summer it increased to 47.6%, while in autumn and winter it was similar, and amounted to ca. 30%. The summer increase in population density resulted from the maximum of the reproductive period (cf. age structure), while the autumn decrease in abundance resulted from both mortality of juveniles and that of post-reproductive adults.

A comparison of expected and actual distribution of snails in 12 samples totalling 3 m^2 (Chi^2 test) shows that *D. perspectivus* was unevenly distributed only during two months (August and October), in the remaining months its distribution was even (Table 6).

Out of 737 marked juveniles and adults of *D. perspectivus*, 212 (28.76%) were re-captured once, 135 – twice, 52 – three times, 16 – four times, 6 – five times, 3 – six times (Table 7). The growth rate based on reading shell increments ranged from 56.87 to 4,080.0 days/whorl (mean = 415; SD = 560.4; n = 115), in the first phase from 56.87 to 2,040 days/whorl (mean = 290.28; SD = 323.03; n = 84), in the second phase from 58 to 4,080 days/whorl (mean = 755.496; SD = 861.02; n = 31).

Table 7. *D. perspectivus*. Growth of selected individuals marked in the field. Specimens found dead indicated in bold

No.	Whorls at first marking	Days till first recapture & increment	Days till second recapture & increment	Days till third recapture & increment	Days till fourth recapture & increment	Days till fifth recapture & increment
1	2.9	393 & 2 (4.9)				
2	3.25	29 & 0.65 (3.9)				
3	3.4	91 & 1.6 (5)				
4	3.6	323 & 1.65 (5.25)	272 & 0.95 (6.2)			
5	3.7	62 & 0.7 (4.4)				
6	4.0	33 & 0.4 (4.4)				
7	4.0	29 & 0.4 (4.4)	33 & 0.2 (4.6)	276 & 0.6 (5.2)	30 & 0.1 (5.3)	
8	4.2	29 & 0.4 (4.6)	33 & 0.2 (5)			
9	4.2	38 & 0.2 (4.4)	234 & 0.1 (4.5)	30 & 0.1 (4.6)		
10	4.25	29 & 0.45 (4.7)	33 & 0.3 (5)			
11	4.4	306 & 1 (5.4)	274 & 0.6 (6)			
12	4.4	234 & 0.4 (4.8)	30 & 0.1 (4.9)	272 & 1 (5.9)		
13	4.5	29 & 0.3 (4.8)	105 & 0.3 (5.1)			
14	4.5	29 & 0.3 (4.8)	33 & 0.4 (5.2)	72 & 0.1 (5.3)	204 & 0.3 (5.6)	
15	4.75	268 & 1 (5.75)	89 & 0.25 (6)	272 & 0.1 (6.1)		
16	4.75	29 & 0.25 (5)	33 & 0.25 (5.25)	72 & 0.15 (5.4)	204 & 0.3 (5.7)	30 & 0 (5.7)
17	4.75	62 & 0.45 (5.2)	38 & 0.2 (5.4)	34 & 0.05 (5.45)	204 & 0.05 (5.5)	30 & 0 (5.5)
18	4.75	134 & 0.75 (5.5)	204 & 0 (5.5)	30 & 0 (5.5)		
19	4.8	29 & 0.2 (5)	33 & 0.1 (5.1)			
20	4.9	62 & 0.5 (5.4)	105 & 0.1 (5.5)			
21	4.9	134 & 0.7 (5.6)	30 & 0.3 (5.9)	242 & 0.1 (**6**)		
22	4.9	234 & 0.85 (5.75)	272 & 0.35 (6.1)			
23	5	33 & 0.2 (5.5)	72 & 0.1 (5.6)	204 & 0.45 (6.05)		
24	5	33 & 0.25 (5.25)	72 & 0.15 (5.4)	234 & 0.2 (5.6)		
25	5.1	38 & 0.1 (5.2)	34 & 0.1 (5.3)			
26.	5.1	38 & 0.1 (5.2)	34 & 0 (5.2)			
27	5.1	276 & 0.4 (5.5)	30 & 0.25 (5.75)			
28	5.1	234 & 0.5 (5.6)	272 & 0.6 (6.2)			
29	5.15	32 & 0.25 (5.4)	38 & 0.1 (5.5)	34 & 0 (5.5)	234 & 0.1 (5.6)	
30	5.2	29 & 0.1 (5.3)	33 & 0.2 (5.5)			
31	5.2	38 & 0.2 (5.4)	34 & 0 (5.4)			
32	5.2	89 & 0.5 (5.7)	274 & 0.5 (6.2)			
33	5.25	33 & 0.15 (5.4)	38 & 0 (5.4)	34 & 0 (5.4)		
34	5.25	38 & 0.25 (5.5)	34 & 0 (5.5)			
35	5.25	29 & 0.25 (5.5)	33 & 0.25 (5.75)			
36	5.25	33 & 0.25 (5.5)	38 & 0.25 (5.75)	268 & 0.25 (6)		
37	5.4	204 & 0.1 (5.5)	30 & 0.1 (5.6)			
38	5.45	204 & 0.15 (5.6)	30 & 0.1 (5.7)			
39	5.5	29 & 0.25 (5.75)	33 & 0.25 (6)	38 & 0 (6)	234 & 0.2 (6.2)	30 & 0 (6.2)
40	5.5	29 & 0.2 (5.7)	105 & 0.2 (5.9)	204 & 0.2 (**6.1**)		
41	5.5	238 & 0 (5.5)	30 & 0.05 (5.55)			
42	5.6	71 & 0.1 (5.7)	34 & 0 (5.7)			
43	5.6	204 & 0.1 (5.7)	30 & 0 (5.7)			

Table 7 continued

No.	Whorls at first marking	Days till first recapture & increment	Days till second recapture & increment	Days till third recapture & increment	Days till fourth recapture & increment	Days till fifth recapture & increment
44	5.7	34 & 0 (5.7)	204 & 0.3 (**6**)			
45	5.7	204 & 0.05 (5.75)	30 & 0 (5.75)			
46	5.7	29 & 0 (5.7)	105 & 0 (5.7)			
47	5.8	89 & 0.2 (6)	274 & 0.2 (6.2)			
48	5.9	30 & 0.1 (6)				
49	6	34 & 0 (6)	234 & 0.1 (6.1)			
50	6.2	204 & 0 (**6.2**)				

DISCUSSION

EGG-LYING, INCUBATION, HATCHING

Like *D. rotundatus* (KUŹNIK-KOWALSKA 1999) and *D. ruderatus* (KUŹNIK-KOWALSKA in prep.), in the field *D. perspectivus* lays eggs preferably on or in rotting timber (in the laboratory also on tissue paper, lettuce leaves etc.); adults of all these species are associated with this substratum, and laying eggs in such places prevents them from drying out and ensures a food supply for hatching juveniles, like in e.g. *Vertigo pusilla* O. F. Müll. (POKRYSZKO 1990b). Having laid eggs, the snail covers them with mucus, crawling over the batch. This may be a form of protection against desiccation, microorganisms or the mucus may contain subtances deterring potential egg consumers (TOMPA 1980, 1984).

Contrary to the other two species of *Discus* (KUŹNIK-KOWALSKA 1999 and in prep.) which in the laboratory lay eggs throughout the year, *D. perspectivus*, except for sporadic instances of laying single eggs in winter, reproduces from June till August, both in the field and in the laboratory. Among the snails living in habitats similar to those of *D. perspectivus*, there are forms of very strictly defined reproductive period (*Columella edentula* (Drap.) and *Vertigo pusilla* O. F. Müll., POKRYSZKO 1990a, b; *Arianta arbustorum* (L.), BAUR 1990; *Alinda biplicata* (Mont.), KUŹNIK-KOWALSKA 1999; *Helicodonta obvoluta* (Müll.), MALTZ 2003b) and species reproducing irrespective from the season, though sometimes with varied intensity (e.g. *Carychium tridentatum* (Risso), MORTON 1954, BULMAN 1990). Possible reasons and implications of such differences, as well as mechanisms of regulation of the onset of reproduction have been discussed by MALTZ (2003b).

The egg size and number of eggs per batch in *D. perspectivus* are similar to those observed in the other two species of *Discus* (KUŹNIK-KOWALSKA 1999 and in prep.): the mean relative egg size is ca. 11% (large individuals) adult size. The number of eggs in a batch is low, the number of egg/batches per lifetime is probably also low (maximum 33 per season). It seems that the relative egg size, the number of eggs in a batch and during lifetime depend on the size and longevity (which largely depends on the size; HELLER 1990) of adult snails rather than on the phylogenetic position of the species: *Vertigo pusilla* O. F. Müll. (Vertiginidae), *Vallonia pulchella* (Müll.) (Valloniidae) and *Carychium tridentatum* (Risso) (Ellobiidae), of a size and life span comparable to those of *P. pygmaeum* (Drap.) (data from WHITNEY 1938, BULMAN 1990 and POKRYSZKO 1990b) lay eggs of a relative size of up to 30% largest dimension of adult shell, most often singly, and their mean number produced per lifetime ranges from 8 to 15. The dependence between the size of adult individuals on the one hand, and the relative egg size, number of eggs per batch and the total number of eggs produced in a lifetime on the other, for the three species of *Discus*, as well as its evolutionary and ecological implications, will be discussed elsewhere (KUŹNIK-KOWALSKA in prep.).

The egg size is often correlated with the adult size also within species; such a correlation has been found e.g. in *D. rotundatus* (KUŹNIK-KOWALSKA 1999), or *Arianta arbustorum* (L.) (BAUR 1984, 1990, BAUR & RABOUD 1988). BAUR (1984, 1990), BAUR & BAUR (1997) and BAUR & RABOUD (1988) found size-dependent differences in the content of nutritive materials in eggs, while in their opinion the dependence parent size-egg size is best explained by the greater possibility of energy investment by larger snails. However, no such correlation was found in *D. perspectivus.*

The time of incubation in *D. rotundatus* (KUŹNIK-KOWALSKA 1999) and also in *D. ruderatus* (KUŹNIK-KOWALSKA in prep.) varies very widely. In *D. perspectivus* the range is much narrower, and the mean incubation time is statistically significantly longer. In all three species the range of variation is too long to be attributed to temperature differences alone, especially under fairly stable laboratory conditions; moreover, the observed differences often pertained to batches incubated at the same time and in the same dish. Very wide ranges of incubation period are usually attributed to variable time of egg retention in the reproductive tract of the parental individual (TOMPA 1984). Egg retention has been observed in two members of Endodontidae: a species of *Helicodiscus* (GUGLER 1972) and *Punctum pygmaeum* (Drap.) (BAUR 1989); in the latter species it is possible to asses the development stage of the embryo in the newly laid egg, since the egg envelopes are translucent. In *Discus* this is impossible because of the opaque egg shell, but it is not excluded that the snails may retain eggs for various periods, though never very long, since no eggs were found in the reproductive system upon dissection which would rather indicate laying eggs immediately after they have been formed (TOMPA 1984). Besides, the range of incubation time in the egg-retaining *P. pygmaeum* is 1–34 days (BAUR 1989), and is thus about twice wider than in *Discus*, which suggests longer periods of egg retention. The distribution of the duration of incubation period in figure 4 would indicate a period of 20–30 days (20–25 days for *D. rotundatus*; KUŹNIK-KOWALSKA 1999) as normal when the eggs are laid immediately after they have been formed. However, shells of hatching juveniles vary rather much in the number of whorls (cf. Fig. 5); the probable reasons for these differences have been discussed by KUŹNIK-KOWALSKA (1999).

UNIPARENTAL REPRODUCTION

Contrary to *D. rotundatus* (KUŹNIK-KOWALSKA 1999) and *D. ruderatus* (KUŹNIK-KOWALSKA in prep.), no uniparental reproduction was observed in *D. perspectivus*. This mode of reproduction may be completely absent in this species, or the failure to observe it may result from the fact that only individuals brought from the field as adults during the reproductive season laid eggs in the laboratory.

CANNIBALISM

Juvenile *D. rotundatus* and *D. ruderatus* consume conspecific eggs but, in their absence, would also eat eggs of other species (KUŹNIK-KOWALSKA 1999 and in prep.). *D. perspectivus* consumes only conspecific eggs. The problems of recognising the species identity of eggs by juveniles, possible advantages of cannibalism and the selection significance of the phenomenon have been discussed by BAYNE (1968), BAUR (1987a, b, 1988) and KUŹNIK-KOWALSKA (1999). Since hatching in *D. perspectivus* is almost synchronous within batch, so that the next juvenile hatches most often when the previous one finishes eating the remnants of the egg shell, it is difficult to test preferences for eggs of the same versus alien batches. Sporadic observations, however, indicate that both kinds of eggs are consumed. Similarly, juvenile *A. arbustorum* (L.) cannot distinguish betwen the eggs from sibling and alien batches, and consume both equally readily (BAUR 1987b).

Like *D. rotundatus* (KUŹNIK-KOWALSKA 1999), *D. perspectivus* shows cannibalistic behaviour not only during the first period of its life, but contrary to the former species, the cannibalism is limited to eating eggs.

GROWTH AND MATURATION

The growth rate in *D. perspectivus* was studied both in the laboratory and in the field. Like other members of *Discus*, *D. perspectivus* grows throughout life and does not form a lip. The growth from hatching to maturity, both in the field and in the laboratory, is much faster than in mature individuals. Compared to 4–6 whorls formed prior to maturity, the increment in adult snails is at most one whorl. Similar results were obtained by BAUR (1989) for *P. pygmaeum* (Drap.) and KUŹNIK-KOWALSKA (1999) for *D. rotundatus*. The slow growth in adult, reproducing *D. rotundatus* might be associated with energy and calcium expenditure during egg-laying (KUŹNIK-KOWALSKA 1999). On the other hand, individuals of *D. perspectivus* hatched from eggs produced in the laboratory never reproduced, and their growth curves were similar to those of *D. rotundatus*. Growth rate of terrestrial snails was studied mainly the field, based on the age structure of populations. The studies showed variation in the growth rate of many species, e.g. *Bradybaena fruticum* (O. F. Müll.) (BABA 1985, STAIKOU et al. 1990), *Eobania vermiculata* (O. F. Müll.), *Xeropicta arenosa* (Ziegler) and *Cernuella virgata* (Da Costa) (LAZARIDOU-DIMITRIADOU 1981, LAZARIDOU-DIMITRIADOU & KATTOULAS 1985), and *Helix lucorum* L. (STAIKOU et al. 1988). In all these cases, however, the changes were seasonal, resulting mostly from varied temperatures, humidity or food availability. *Balea perversa* (L.) and *Chondrina clienta* (Westerlund), both forming a lip and terminating their growth when mature, have growth curves much like those of the studied species of *Discus* (cf. BAUR 1991, BAUR & BAUR 1992); their growth becomes much slower just before maturation and the onset of reproduction. The same was found in *Helicodonta obvoluta* (O. F. Müll), also terminating growth when mature, where, based on detail analysis of the gonad development and gametogenesis, MALTZ (2003a, b) explained it by the energy and matter investment into rapidly developing gonad.

The age at which sexual maturity is attained, as expressed by morphological characters of the reproductive system and laying the first egg, varies between species. In two members of *Discus*: *rotundatus* and *ruderatus*, it is similar (KUŹNIK-KOWALSKA 1999 and in prep.), and almost twice greater in *D. perspectivus* (606 days) which attains maturity at slightly over 5 whorls (mature oocytes and spermatozoa in the gonad), like *D. rotundatus* (KUŹNIK-KOWALSKA 1999).

LIFE SPAN

The life span in *D. perspectivus* varies widely, like in the other two members of *Discus* (KUŹNIK-KOWALSKA 1999 and in prep.); the mean life span in the laboratory was 603.3 days, thus being intermediate between *D. rotundatus* and *D. ruderatus*. The highest number of whorls in the laboratory was 6.9, much like in *D. rotundatus* (KUŹNIK-KOWALSKA 1999) and higher than in *D. ruderatus* (5.5–5.7; KUŹNIK-KOWALSKA in prep.). The largest live *D. perspectivus* found in the field had a shell of 6.2 whorls, like *D. rotundatus* and larger than *D. ruderatus* (4.5 whorls). This would indicate a longer life span in the laboratory which probably results from a prolonged senile period of life, i. e. the time elapsing between the last egg and death (KOSIŃSKA 1980).

POPULATION DENSITY AND DISTRIBITION

The maximum density od *D. perspectivus*, observed in June, results from the mass appearance of the youngest age class (cf. Fig. 8). The gradual decrease in the density which continues till October results both from mortality of a part of juveniles, and that of old snails which have terminated reproduction. The low density observed in spring (May), just before the reproductive season, may result from the fact that some of the youngest and oldest individuals die during hibernation.

D. perspectivus shows aggregated distribition only during two months: October and August. The fact that nearly all other component species of the malacocoenosis displayed aggregated distribution in a different period suggests that the distribution is affected by many factors which probably vary between species (KUŹNIK-KOWALSKA 1998a). Apart from the association of some gastropods with certain plant species (DYDUCH-FALNIOWSKA & TOBIS 1989 and literature cited therein) little is known about reasons for aggregated distribution of litter-dwelling snails. The possible factors are reproduction (aggregation of adults in convenient egg-laying places, or of hatchlings from the same batch), feeding (aggregation at unevenly distributed food sources) and seeking shelter during drought or in winter. *D. perspectivus* is strongly associated with rotting timber: there it lays eggs and shelters in winter or during drought. Its aggregated distribution in August 1994 could result from the prolonged drought, and in October – from aggregation in hibernation shelters.

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