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LIFE CYCLE AND POPULATION DYNAMICS OF *DISCUS ROTUNDATUS* (O. F. MÜLLER, 1774) (GASTROPODA: PULMONATA: ENDODONTIDAE)

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ABSTRACT: The following life history traits of *D. rotundatus* (O. F. Müll.) were established based on field and laboratory observations: fully calcified eggs ca 1 mm in diameter, of a size correlated with the number of parent's whorls; 1–11 eggs per clutch; 1–178 eggs per lifetime, in 1–36 clutches; incubation period 14–36 days; egg cannibalism with a strong preference for conspecific eggs; quick growth (33–35 days per whorl) prior to maturity and slow growth in mature snails, resulting from energy expenditure for egg-laying; sexual maturity at 5.5 whorls (2nd–3rd year of life); life span 2.5–3.5 years. Isolated individuals produce fewer eggs of lower viability than individuals kept in groups, they lay their eggs later and at a larger size. Most eggs in the laboratory are laid in June, in the field the maximum of the reproductive period falls in July/August.

KEY WORDS: Endodontidae, *Discus rotundatus*, life history, cannibalism, growth, uniparental reproduction

INTRODUCTION

Discus rotundatus (O. F. Müller, 1774) is a West and Central European species; it reaches 63°N latitude in Norway and 58°N in Sweden; in the south its distribution includes Mediterranean countries of Europe; its eastern distribution border is not exactly known, but it is absent from the Balkan and southern Carpathian countries. Its upper altitudinal limit is 1200 m a.s.l. in the Carpathians and Sudetes and 2700 m a.s.l. in the Alps. In Poland it is common in entire country, except the Bieszczady Mts (UMIŃSKI 1962, RIEDEL & WIKTOR 1974). Originally a woodland species, it invades also some anthropogenic habitats (parks, ruins etc.). It inhabits leaf-litter, being rather closely associated with rotting wood.

Like other members of the genus *Discus*, except some fragmentary and sometimes unreliable data scattered in the literature, it is very little known with respect to its life history. ANT (1963) pointed to a wide range of pH in its habitats; HAGEN (1952) provided some data on its humidity preferences; FRÖMMING (1954) analysed its food based on the composition of faeces, and gave an approximate egg size; TAYLOR (1903) observed the maximum of reproductive period in the British Isles and provided some information on incubation period and growth, albeit without supporting it with laboratory experiments. WÄREBORN (1982) studied the effect of various forms of bound calcium on snail reproduction, using among others *D. rotundatus* as an example, and BOETTGER (1939) investigated shell variation under the effect of climatic conditions.

This paper is the first of a series dealing with various aspects of life history of members of the genus *Discus*. Its aim is to give an account of life history of *D. rotundatus*, based on four years of laboratory observations and on samples taken in the field. Special attention is paid to differences between uniparentally and normally reproducing individuals, incubation, growth rate and cannibalism. Other problems revealed during this study (shell variation under the effect of laboratory conditions, gametogenesis etc.) will be discussed elsewhere.

MATERIAL AND METHODS

LABORATORY STUDIES

The material for the laboratory culture (individuals of various age, eggs) was collected at intervals from October 5th 1995 in W Sudetes: Kletno (Śnieżnik massif), Bardo Śląskie near Kłodzko and Boboszów near Międzylesie, and in NE Poland: Białowieża. The laboratory observations lasted from October 5th 1995 till January 21st 1999. The total number of individuals was 215, originating from 37 initially collected snails.

The snails were kept in Petri dishes of a size depending on the number of individuals per dish (∅ 5–14 cm), on humid tissue paper, with addition of pieces of decomposing wood as shelter and substratum for egg-laying. The snails feed mainly on microflora growing on decaying wood (FRÖMMING 1954) and were additionally fed with lettuce. Hen egg shells served as a supplementary source of calcium.

The temperature in the room varied from 17°C in winter to 25°C in summer. The relative humidity in the dishes was constant, ca. 100%. The dishes were aired once a week, with water and food supplied when necessary.

In order to study uniparental reproduction, 46 individuals were kept singly from egg stage or early juvenile stages. The remaining 130 individuals were kept in pairs (15 pairs) and groups of 3–20 per dish.

Observations on cannibalism included 59 juveniles, and ca. 500 eggs of *D. rotundatus*, *D. ruderatus* (Fér.), *D. perspectivus* (Mühlf.) and *Trichia hispida* (L.). The following tests were aimed at ascertaining cannibalistic preferences of the snails. Test I. Ten newly hatched *D. rotundatus*, kept together in a dish of ∅ 10 cm, were offered 5 eggs of each of the following species: *T. hispida, D. ruderatus* and *D. perspectivus*. Test II. Twelve juvenile *D. rotundatus*, aged 7 days and kept together in a dish of ∅ 10 cm, were offered 23 eggs of *D. rotundatus*, 10 of each *D. ruderatus* and *D. perspectivus* and 5 of *T. hispida*. Test III. Seven newly hatched *D. rotundatus* were kept singly in dishes of ∅ 5 cm and offered various eggs (see Table 3). Test IV. Twenty juvenile *D. rotundatus* were fed only with eggs of their own species (ca. 300 eggs) and their growth rate was recorded (see Table 4). In all the tests except IV, lettuce was also available in the dish.

Fig. 1. Location of the main sampling localities of *D. rotundatus* in SW Poland (arrows)

Growth rate was recorded for cannibalistic as well as normally fed individuals (20 and 20 individuals, respectively). Whorls were counted according to EHRMANN's (1933) method.

To establish the variability range of egg size, and to find differences between the uniparental and biparental eggs, 63 eggs were measured using calibrated eyepiece, accuracy ±0.025 mm.

Statistical calculations were performed using Statistica, version PL 5.1. Chi square, Spearman correlation and the level of statistical significance of differences between two mean values were calculated as described by STANISZ (1998).

FIELD STUDIES

Seasonal changes in age structure and population density were estimated based on samples of 16–50 individuals taken regularly in Bardo Śląskie (May–October 1996) and Boboszów (May–September 1997) (Fig. 1) at monthly intervals, and sporadically in Kletno, Białowieża and three sites in the Austrian Alps (Tiefbrunau, Ebenau, Mühlball). The individuals obtained from the samples were divided into age classes according to the number of whorls (Table 1).

Table 1. Age classes of *D. rotundatus* according to the number of whorls

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

RESULTS

COURTSHIP AND COPULATION

In spite of numerous attempts, it was impossible to observe the entire courtship and copulation either in the field or in the laboratory. A part of copulation was observed only once, on May 17th 1998 in the nature reserve Muszkowicki Las Bukowy (where the species is by no means abundant). When the copulating pair was noticed, one snail was sitting on its partner's shell. Their penes were everted and stuck together with mucus. After transferring the snails into a place where it was possible to take a photograph, they separated and partly retracted their penes (Fig. 2), and then resumed copulation in a way described above, which lasted another 20 minutes. Following copulation, the partners separated and retracted their genital organs. In the laboratory each was placed in a separate dish. Both snails laid eggs on June 2nd 1998, one 7 eggs (clutches of 3 and 4 eggs), another 5 eggs in one clutch. One laid more eggs on June 9th (2 clutches of 3+4 eggs) and on August 10th (4+3), another on June 10th (2 clutches of 5+3 eggs).

EGG-LAYING

D. rotundatus lays eggs in humid, sheltered places, preferably on a substratum that will later serve as a food source for the hatchlings, e.g. bits of bark and decaying wood, and in the laboratory also on lettuce leaves and tissue paper. In the field eggs are laid mainly in decaying wood.

Freshly laid eggs are calcified, slightly ellipsoidal and flattened, milky white, initially shining because of the covering fresh mucus, and after 5–7 days mat. They are ca. 1 mm in diameter (Fig. 3) (major diameter 0.9–1.3 mm, mean 1.1 mm, SD = 0.1 mm, n = 63). The eggs resulting from uniparental reproduction differ in size from the eggs of individuals kept in pairs and groups. The major diameter of the former is 0.9–1.2 mm (mean 1.06 mm, SD = 0.89 mm, n = 30); that of the latter – 1–1.3 mm (mean 1.14, SD = 0.1, n = 33). The difference is statistically significant (test for two mean values, p = 0.3). The egg size is very strongly correlated with the number of whorls in the parent (Table 2, Fig. 4).

Fig. 2. *D. rotundatus* with their penes partly everted. Photo JERZY MACIĄŻEK

The number of eggs per clutch ranges from 1 to 11 (Fig. 5) (mean 4.27, SD = 2.39, n = 55). Most often there are 3–4 eggs per clutch, arranged in a characteristic pyramid or in a row (Fig. 6). The number of eggs per clutch differs between the isolated individuals and those kept in pairs and groups, the values being 1–8 (mean 3.90, SD = 2.03, n = 24) and 1–11 (mean 4.51, SD = 2.64, n = 31); p = 0.201 (test for two mean values). Sometimes (9 out of 43 observed cases) two clutches were laid per day, one of the clutches being mostly smaller: 2+4, 2+4, 2+3, 4+1, 5+1, 3+1, 3+2, 3+3, 1+2.

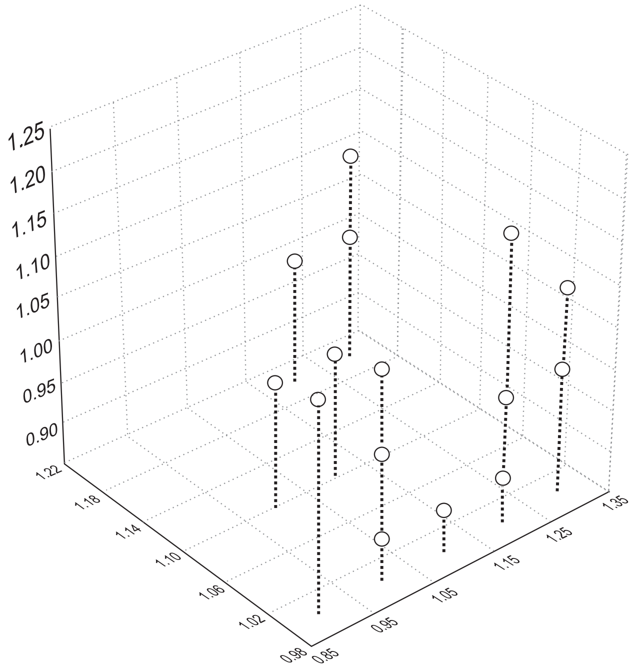


Fig. 3. Egg measurements in *D. rotundatus* – three diameters [mm], n = 63

Since in the laboratory the snails reproduce throughout the year, it is difficult to refer to the number of eggs per season. The number of eggs per individual lifetime varies from 1 to 178 (mean 32.75, SD = 43.23, n = 32), most often being 22–57, the number of clutches being 1–36 (mean 11.43, SD = 10.29, n = 56). Both the number of eggs and the number of clutches produced per lifetime differ between the isolated individuals and those kept in pairs and groups. In the former the number of eggs ranges from 1 to 53, the number of clutches being 1–15 (mean 13.62, SD = 15.3, n = 16; mean 5.7, SD = 4.29, n = 28, respectively), in the latter the respective values are: 6–178 (mean 51.87, SD = 53.36, n = 16) and 6–36 (mean 17.14, SD = 11.37, n = 28). The difference is statistically significant (p = 0.00, test for two means). Both the number of eggs and of clutches, as well as their distribution in time vary very widely (Fig. 7).

Table 2. Number of whorls in parent *D. rotundatus* and egg sizes (three diameters).

Individual number	Shell size (number of whorls)	Egg size (mm)
1	5.7	1.0×1.0×0.9
2	5.9	1.0×1.0×0.9
3	6.15	1.1×1.0×1.0
4	6.75	1.2×1.2×.1.0
5	6.75	1.3×1.2×1.0
6	6.9	1.3×1.2×1.0
7	6.9	1.3×1.2×1.1

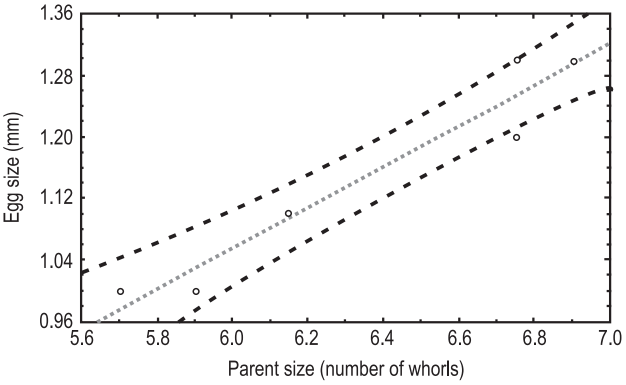


Fig. 4. Egg size (major diameter) in *D. rotundatus* plotted against parent size. Correlation coefficient: r = 0.97, regression equation: y = 0.35x – 1.92, n = 7, confidence limits 95%

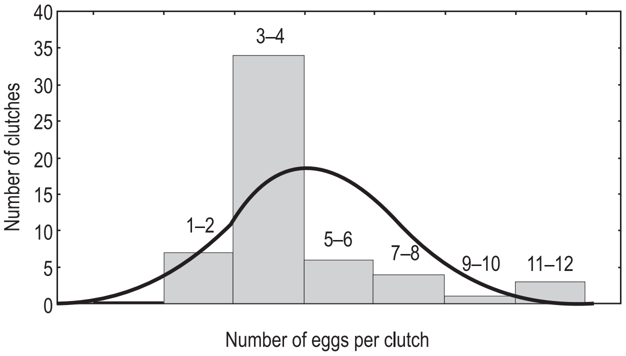


Fig. 5. Distribution of the number of eggs per clutch in *D. rotundatus*

INCUBATION

The incubation period ranges from 14 to 36 days (mean 23.36, SD = 5.4, n = 130) (Fig. 8).

HATCHING

The percentage of hatching eggs laid by individuals kept in pairs or groups is 77.4% (n = 212), of those laid by isolated snails is 35.7% (n = 235). The

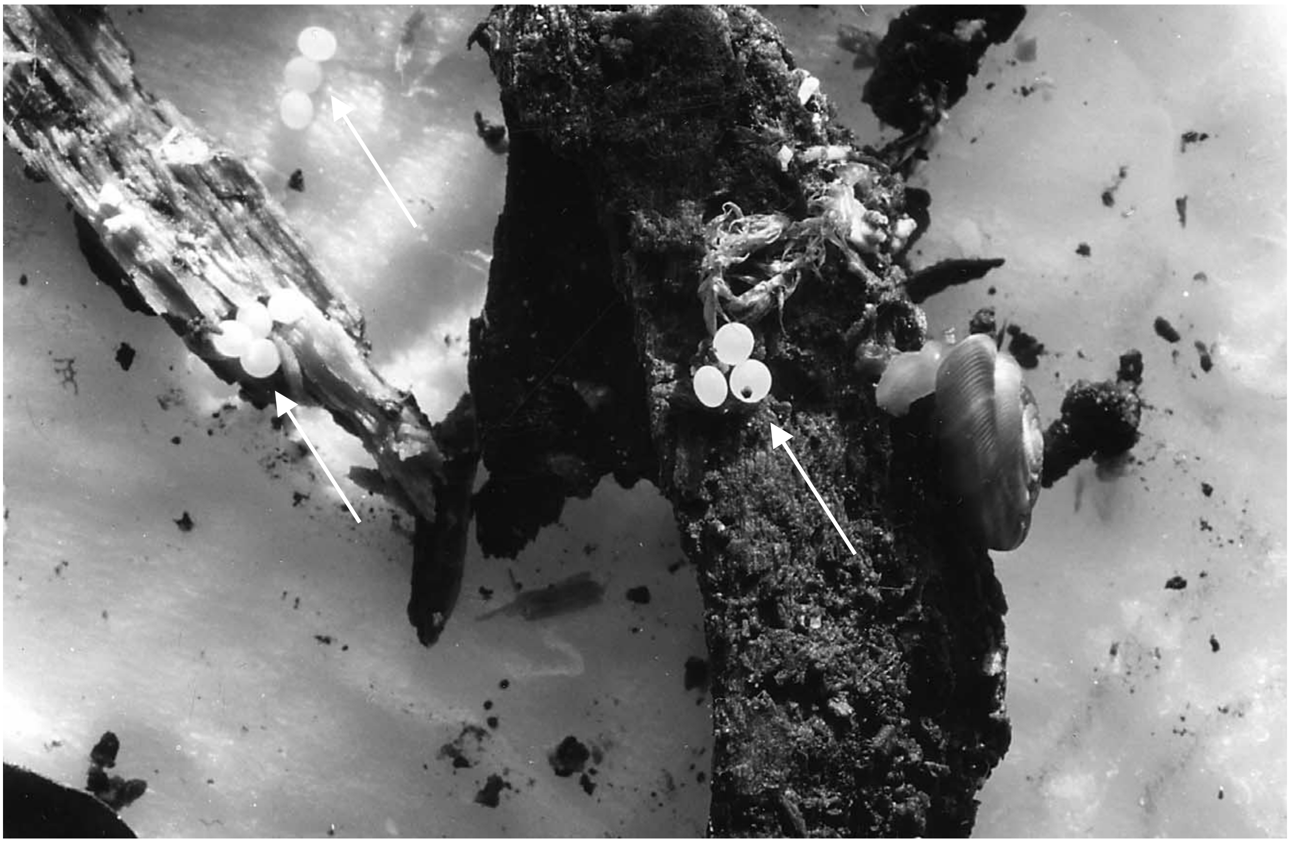


Fig. 6. *D. rotundatus* and its egg clutches (arrows). Photo JERZY MACIĄŻEK

difference is statistically significant (chi square 78.14, p = 0.0).

Hatching lasts 1.5–2 hrs. Since the eggs are not translucent, it is impossible to observe if the baby snail pierces the egg shell with its radula; viewed from the outside, the first symptom of hatching is a fragment of egg shell falling off.

Hatchlings have translucent shells and bodies. In 85% (n = 100) hatchlings the shell margin is brown. The embryonic shell has 1.5–2.4 whorl (Fig. 9), the first 1.5–2.0 whorl being always smooth; the remaining part is formed by the first 1–3 ribs of the first definitive whorl. The young are very active: first they consume at least a part of the egg shell and then look for other food.

CANNIBALISM

Egg cannibalism has been observed. Juveniles consumed conspecific eggs (both of their own clutch and of different clutches). When offered eggs of their own species, of another species of *Discus* (*ruderatus* or *perspectivus*) and of *Trichia hispida*, they selected conspecific eggs (Table 3). When offered eggs of an-

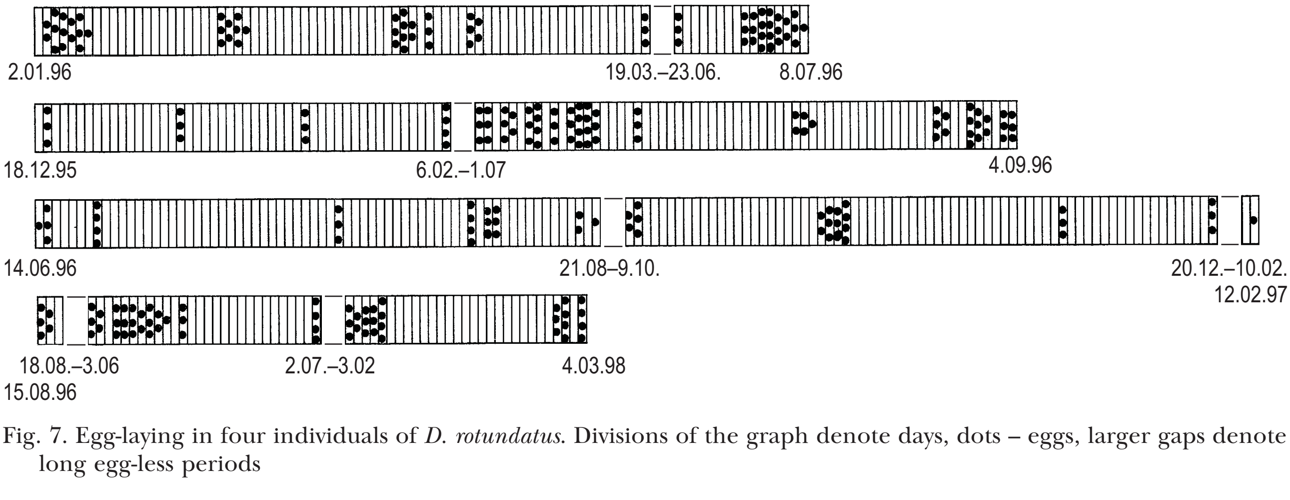


Fig. 7. Egg-laying in four individuals of *D. rotundatus*. Divisions of the graph denote days, dots – eggs, larger gaps denote long egg-less periods

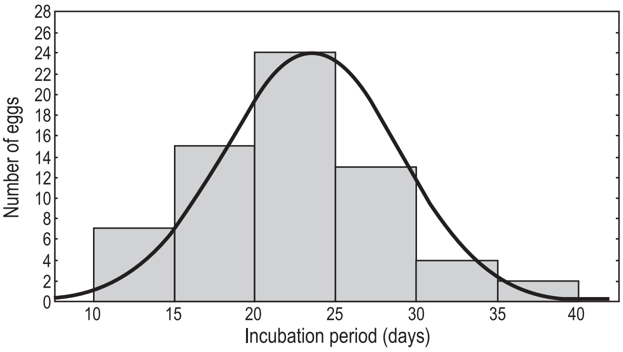


Fig. 8. Distribution of incubation period duration in *D. rotundatus*

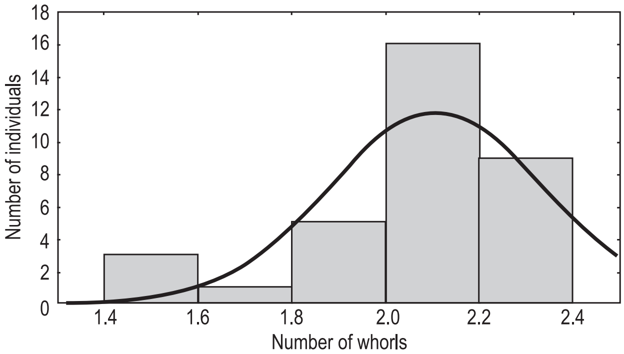


Fig. 9. Distribution of the number of whorls in hatchlings of *D. rotundatus*

other species of *Discus* and of *Trichia*, they consumed only congeneric eggs. During 7 days (cf. Materials and methods, Test II) the young consumed wholly 8 conspecific eggs (35%) and 3 eggs (33%) of *D. ruderatus*; they damaged 13 conspecific eggs (56%), 3 eggs (33%) of *D. ruderatus* and 2 eggs (20%) of *D. perspectivus*. No egg of *T. hispida* was consumed or even damaged.

Adults were observed to consume their own eggs only exceptionally. In one case an isolated adult consumed two of its eggs, though other food was abundant. In dishes where snails were kept in groups, some adults ate eggs (their own or of other individuals?) sporadically when food was abundant and regularly when there was no food on the dish (10 observations). In the same dishes cases were observed of juvenile-juvenile or adult-adult cannibalism, the individual consumed being always smaller. For example, four individuals of 5.0, 5.3, 5.3 and 6.1 whorls devoured their dish-mate of 4.75 whorls, and a juvenile of 3.0 whorls ate another of 2.5 whorls; an individual of 3.6 whorls ate another of 2.2. whorls.

Growth rate in 20 selected individuals fed only with eggs is presented in Table 4. It does not differ from that rate in normally fed individuals (Table 5) in a statistically significant way.

Table 3. Egg selection by cannibalistic juveniles of *D. rotundatus*

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

Table 4. Growth rate of 20 selected *D. rotundatus* fed with conspecific eggs (size at the first egg-laying indicated with bold)

Date	Individual number																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
2.01.1997	2.2	2.0	2.4	2.4	1.8	1.9	1.8	2.0	2.3	2.0	2.0	1.8	2.4	2.4	2.4	2.5	2.4	2.3	2.6	2.6
15.01.1997	2.7	2.5	3.0	3.1	2.1	2.4	2.1	2.15	2.9	2.5	2.5	2.0	3.4	3.1	3.3	3.5	3.4	3.0	3.0	3.25
31.01.1997	3.7	2.9	3.5	3.5	3.0	3.3	3.0	3.3	3.7	3.3	3.3	2.6	4.1	3.7	3.6	3.9	3.6	3.6	3.6	3.7
6.03.1997	5.0	4.75	4.25	4.6	4.6	4.75	4.4	4.4	4.4	4.1	3.75	3.9	5.0	5.0	4.9	4.9	5.0	4.75	4.7	4.9
6.04.1997	5.5	5.3	4.9	5.6	5.4	5.5	5.2	5.3	5.4	5.0	4.4	4.5	5.5	5.25	5.4	5.3	5.5	5.5	5.5	5.8
6.05.1997	**5.7**	5.8	5.4	**5.9**	5.7	5.8	5.7	5.8	5.7	5.3	5.4	5.4	**5.6**	5.6	**5.7**	**5.8**	**5.8**	**5.9**	**5.5**	**5.8**
6.06.1997	5.8	**5.8**	**5.7**	5.9	**5.8**	**5.8**	**5.8**	**5.8**	**5.7**	**5.6**	**5.5**	**5.6**	6.6	**5.7**	5.75	5.8	5.85	5.9	5.55	5.8

Number of whorls is given as a measure of growth

Table 5. Growth rate of 10 selected normally fed *D. rotundatus* (size at the first egg-laying indicated with bold)

Date	Individual number									
	1	2	3	4	5	6	7	8	9	10
1.12.95	1.8	2.1	2.2	2.1	2.0	2.0	2.0	1.8	1.5	2.1
12.12.95	2.2	2.6	2.6	2.6	2.5	2.5	2.4	2.0	1.8	2.6
5.01.96	3.1	3.0	3.4	3.0	3.0	2.9	3.0	2.9	2.6	3.2
15.01.96	3.5	3.5	3.6	3.3	3.25	3.2	3.3	3.15	3.4	3.75
25.01.96	3.8	3.7	3.8	3.7	3.6	3.5	3.5	3.75	3.6	4.3
15.02.96	4.6	4.2	4.7	4.25	4.15	4.1	4.5	4.4	4.4	5.3
13.03.96	5.6	5.1	5.5	5.1	5.1	5.0	5.0	5.2	5.3	5.4
15.04.96	**5.9**	5.5	5.9	**5.8**	5.8	**5.5**	5.25	5.6	5.75	5.6
15.05.96	6.1	**5.7**	**6.1**	6.0	**6.0**	5.9	5.75	**5.85**	5.75	**5.6**
15.06.96	6.1	5.7	6.1	6.1	6.1	5.9	**5.75**	5.9	**5.8**	5.9
15.07.96	6.1	5.75	6.1	6.1	6.1	5.9	6.0	6.0	6.0	6.0
13.08.96	6.1	5.75	6.1	6.1	6.1	5.9	6.0	6.0	6.0	6.0
15.09.96	6.2	5.9	6.1	6.1	6.1	6.0	6.0	6.0	6.1	6.2
15.10.96	6.2	5.9	6.1	6.2	6.2	6.1	6.2	6.0	6.1	6.2
15.11.96	6.25	6.0	6.1	6.3	6.3	6.1	6.2	6.1	6.1	6.2
6.03.97	6.3	6.2	6.25	6.3	6.3	6.1	6.4	6.4	6.25	6.2
20.05.97	6.4	6.25	6.4	6.4	6.3	6.1	6.4	6.5	6.4	6.25
17.12.97		6.25	6.55	6.4	6.3	6.1	6.45	6.5	6.5	6.25
20.01.98		6.25	6.55	6.4	6.3			6.5	6.5	6.25
5.05.98		625	6.55	6.4	6.3			6.5	6.5	6.25
8.07.98				6.5	6.3			6.5	6.5	6.25
10.10.98				6.5	6.3			6.5		6.25
21.01.99				6.5						6.25

Number of whorls is given as a measure of growth

GROWTH AND MATURATION

D. rotundatus reaches sexual maturity, as indicated by the morphological characters of its reproductive system, at a size of 5.5. whorls. However, the first egg is laid at a size of 5.5–6.55 whorls (Tables 4, 5). The time elapsing between hatching and the first egg ranges from 132 to 564 days (mean 272.25, SD = 166.75, n = 20). Formation of one whorl takes on an average from 116.5 to 283.6 days (mean 215.00, SD = 42.96, n = 40).

The graphs in Fig. 10 represent growth curves in selected individuals. Two distinct phases of growth occur: 1. from hatching till maturity the growth is rapid (33.2–55.5 days per whorl, mean 42.81, SD = 6.24, n = 10); 2. from maturity till death the growth is very slow (787.1–2096.6 days per whorl, mean 1038.24, SD = 612.6, n = 10).

The time elapsing between hatching and maturity as indicated by the number of whorls (5.5 whorls) is 92–156 days (mean 114.53, SD = 17.91, n = 40). It does not differ significantly between the isolated individuals and those kept in pairs or groups, the respective values being 95–156 (mean 111.35, SD = 19.38, n = 20) and 92–140 (mean 117.7, SD = 16.16, n = 20).

However, the period between hatching and the first egg laid is much longer in isolated, uniparentally reproducing individuals (Tables 6, 7); it ranged from 166 to 564 days (mean 398.7, SD = 151.63, n = 10), and in individuals kept in pairs or groups it was 132–174 (mean 145.8, SD = 13.33, n = 10). The difference is statistically significant (p = 0.0, test for two mean values). At first egg-laying the isolated individuals were significantly larger in terms of the number of whorls than snails kept in pairs or groups, the repective values being: 5.8–6.9 (mean 6.29, SD = 0.27, n = 20), and 5.5–5.9 (mean 5.63, SD = 0.12, n = 20), p = 0.0 (test for two means) (cf. also Tables 6, 7).

REPRODUCTIVE SEASON

In the laboratory the snails reproduce throughout the year, but most eggs are laid in June (Fig. 11). Seasonal changes in age structure in the population from Boboszów, as well as age structure of single samples

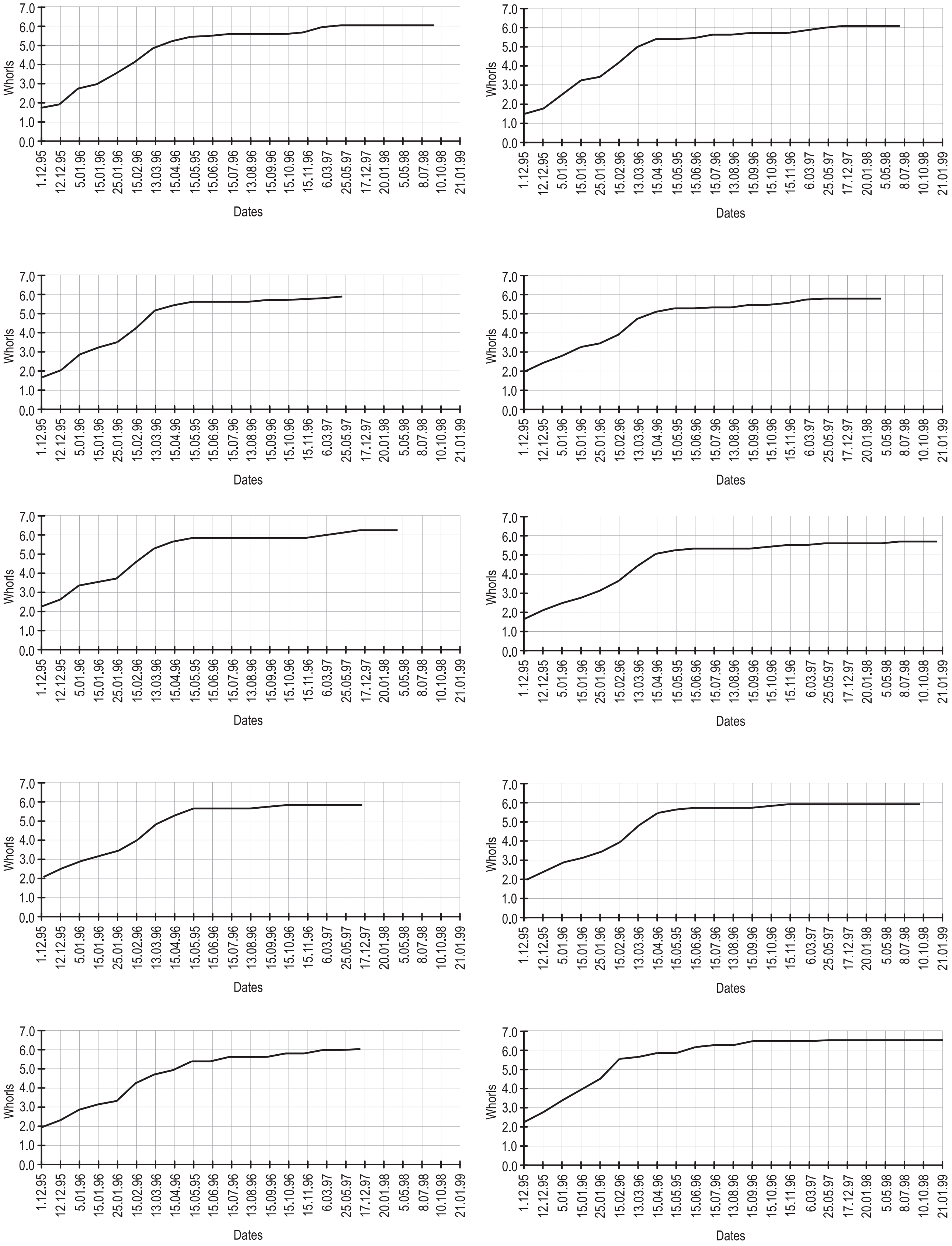


Fig. 10. Growth curves of 10 selected individuals of *D. rotundatus*

Table 6. Life histories of selected isolated individuals of *D. rotundatus*

Individual number	Hatching	First egg	Number of whorls	Last egg	Number of whorls	Total eggs	Death	Number of whorls
1	30.01.1995	4.06.1997	6.4	20.07.1997	6.4	6	12.09.1997	6.4
2	30.11.1995	5.01.1997	6.2	15.01.1997	6.3	7	15.05.1998	6.3
3	1.12.1995	14.06.1996	6.1	6.03.1998	6.55	38	18.07.1998	6.55
4	19.12.1995	15.12.1996	6.4	26.06.1997	6.5	13	10.12.1998	6.4
5	19.12.1995	20.06.1996	5.8	27.05.1997	6.2	12	1.12.1998	6.0
6	18.01.1996	4.06.1997	6.5	12..08.1997	6.6	10	9.10.1998	6.75
7	5.01.1996	20.07.1997	6.4	1.08.1997	6.4	7	5.12.1998	6.75
8	5.01.1996	4.06.1997	6.4	1.08.1997	6.4	3	20.10.1998	6.4
9	5.01.1996	6.09.1996	6.1	30.04.1997	6.4	15	20.10.1998	6.5
10	5.01.1996	26.05.1997	6.5	23.02.1998	6.6	25	15.07.1998	6.6

Table 7. Life histories of selected unisolated individuals of *D. rotundatus*

Individual number	Hatching	First egg	Number of whorls	Last egg	Number of whorls	Death	Number of whorls
1	5.12.1995	15.04.1996	5.8	20.07.1997	6.1	17.12.1997	6.1
2	5.12.1995	20.04.1996	5.8	20.07.1997	6.3	10.10.1998	6.3
3	5.12.1995	22.04.1996	5.5	20.07.1997	6.3	21.01.1999	6.5
4	5.01.1996	15.05.1996	5.7	3.06.1997	6.4	10.10.1998	6.4
5	5.01.1996	22.05.1996	5.7	3.07.1997	6.0	1.12.1997	6.0
6	5.01.1996	26.06.1996	5.6	12.08.1997	6.25	11.10.1998	6.6
7	5.01.1996	14.06.1996	5.9	13.09.1998	6.2	1.12.1997	6.25
8	5.01.1996	28.05.1996	5.7	11.08.1998	6.2	20.10.1998	6.4
9	5.01.1996	26.05.1996	5.6	1.09.1998	6.25	30.10.1998	6.3
10	5.01.1996	4.06.1996	5.5	23.10.1998	6.6	15.01.1999	6.8

from other sites, are presented in Figures 12–17. In the field juveniles hatch from June till October, with a maximum in July/August. The earliest hatched individuals reach 4 whorls in the same season; most wintering young have shells of 2.6–3.5 whorls. The average growth rate is 0.5 whorl per month. Next spring the young resume their growth, reaching ca. 5 whorls; some of them start reproducing, the remaining ones reach sexual maturity in the third year of life.

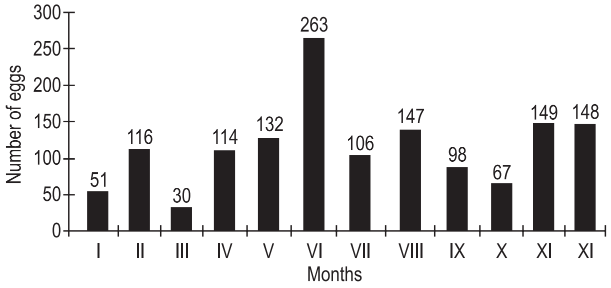


Fig. 11. Total number of eggs laid in 12 consecutive months (Roman numerals) by 50 individuals of *D. rotundatus*

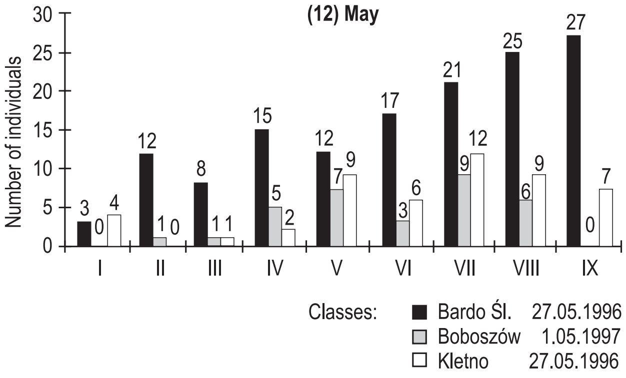
LIFE SPAN

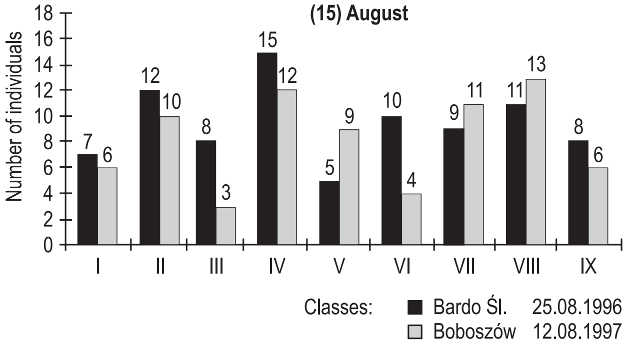
The life span ranges from 653 to 1145 days (mean 954.75, SD = 148.02, n = 20), and the time elapsing between the last egg and death is 50–551 days (mean 332.05, SD = 197.8, n = 20).

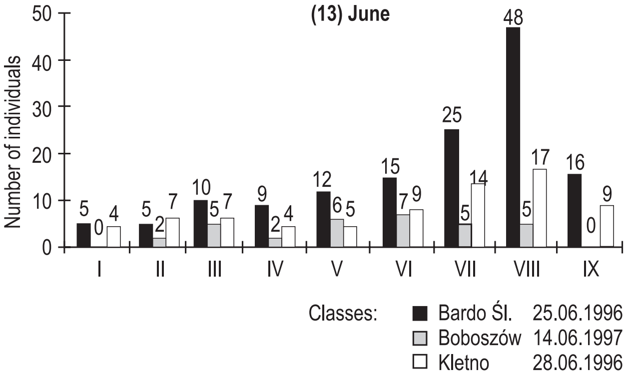
DISCUSSION

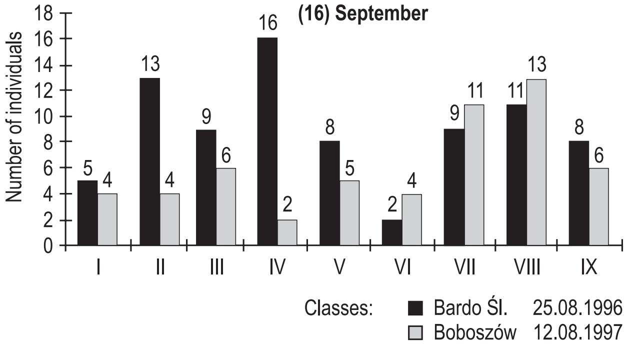
COURTSHIP AND COPULATION

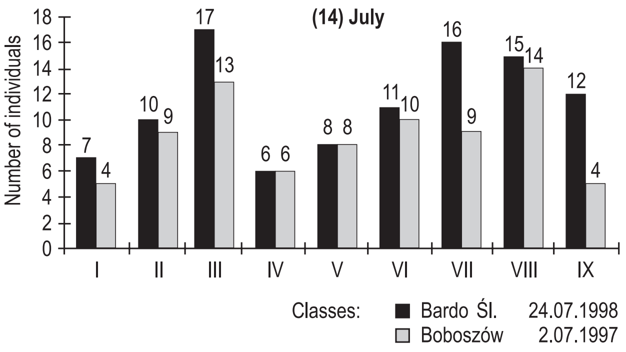
The mode of copulation with one partner sitting on the other`s shell is common among the basommatophorans (lymnaeids, ellobioids) (PURCHON 1977, DOLL 1982) and was observed in a stylommatophoran genus *Vertigo* (POKRYSZKO 1990). Though in the latter genus it may be associated with aphallism

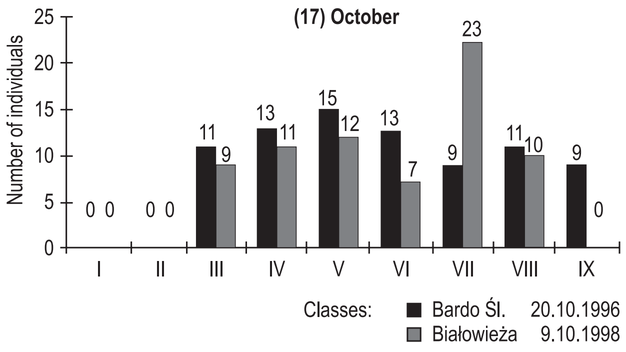


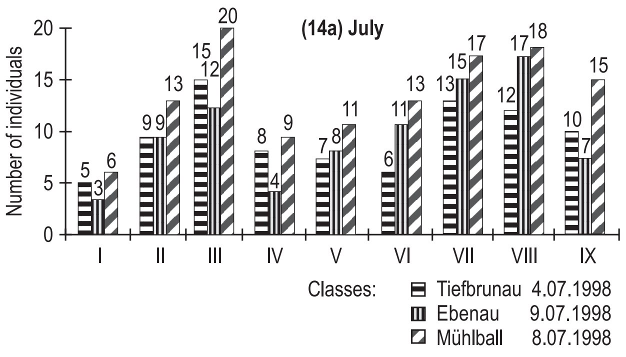












Figs 12–17. Age structure of populations of *D. rotundatus* in six cosecutive months based on field samples

(POKRYSZKO 1990), in the lymnaeids and ellobioids, in which both partners have both male and female copulatory organs, it simply has to be regarded as a more ancestral mode of copulation. The endodontids are thought to be among the most ancestral Stylommatophora; this opinion is based mainly on anatomical characters (SOLEM 1959, 1976, RIEDEL & WIKTOR 1974). Now it is additionally confirmed by their reproductive behaviour.

Although no copulation could be observed in the laboratory, the great differences in the quality and number of eggs between isolated individuals and those kept in pairs and groups indicate that the latter must have copulated.

UNIPARENTAL REPRODUCTION

Individuals of *D. rotundatus* kept in isolation from very early ontogenetic stages (eggs, hatchlings) are able to reproduce. It is unknown whether parthenogeny or self-fertilisation is concerned. Their reproduction differs from that of individuals kept in groups or pairs in several aspects that merit a discussion.

Both isolated and unisolated snails reach the "mature" size of 5.5 whorls at the same time. However, the time elapsing between hatching and first egg laid differs in a statistically significant way – the isolated individuals lay their first eggs much later.

The eggs resulting from uniparental reproduction are significantly smaller than those of unisolated individuals, they are fewer in terms of the number of eggs per clutch, the number of clutches and the number of eggs per lifetime, the result being at least twice (or even thrice) fewer eggs in the case of isolated snails. The percentage of hatching eggs laid by the latter individuals is more than twice lower than in individuals kept in pairs or groups. Combining the egg production with the hatching percentage, it can be said that the reproductive success of uniparentally reproducing snails is on an average three to four times lower than that of individuals kept in pairs or groups.

The only other endodontid known to reproduce uniparentally is *Punctum pygmaeum* (Drap.) (BAUR 1987, 1989). In that species, no difference was found in the number or quality of eggs laid by isolated individuals vs. snails kept in pairs (BAUR 1989). However, since a considerable percentage or even most of individuals of *P. pygmaeum* are aphallic (RIEDEL & WIKTOR 1974), it can not be said if the snails kept in pairs actually copulated. Non-endodontid stylommatophorans known to reproduce uniparentally are some members of the genera *Deroceras, Vertigo, Bradybaena* and *Triodopsis*, and *Rumina decollata* (L.) (DUNCAN 1975, TOMPA 1984, POKRYSZKO 1990). In most studied cases either the authors did not compare the reproductive success of uniparentally and biparentally reproducing individuals, or found it to be equal (e.g. in *Philomycus* – IKEDA & EMURA 1934, in *Rumina decollata* – SELANDER et al. 1974 and in *Vertigo pusilla* O. F. Müll. – POKRYSZKO 1990). However, MCCRACKEN & BRUSSARD (1980) found that isolated *Triodopsis albolabris* (Say), like *D. rotundatus*, reproduced only afer several months of apparent self-sterility, the average reproductive success of paired individuals being 86 times greater than that of isolates. IKEDA & EMURA (1934) noted that the reproduction rate was reduced in self-fertilising *Bradybaena similaris* (Fér.). The ability to reproduce uniparentally, even if less successfully, is one of the many attributes of good colonisers. In their study of 14 land snails, MCCRACKEN & SELANDER (1980) found that self-fertilising species occupied a wider range of habitats and more successfully invaded new areas. Though *D. rotundatus* is not the widest distributed Palaearctic *Discus*, within its distribution range it is the most common, with the widest range of occupied habitats and is the only member of the genus penetrating into some anthropogenic habitats. At the same time, of the three studied species (*D. rotundatus, D. ruderatus, D. perspectivus* – own, unpublished results) only *D. rotundatus* is capable of uniparental reproduction.

INCUBATION AND HATCHING

The incubation period in *D. rotundatus* varies too widely (cf. Fig. 8) to attribute this variation only to temperature, especially that all the laboratory individuals were kept in the same conditions. At the same time the shells of hatchlings vary widely in diameter. A part of this variation is accounted for by the variable size of embryonic shell. Most hatchlings, however, have not only the translucent-white and smooth embryonic shell in strict sense, but also the first few ribs of the first definitive whorl. The very wide variation in duration of development is usually attributed to a variable period of egg-retention (TOMPA 1984). Two endodontids, namely *Helicodiscus* (GUGLER 1972) and *Punctum pygmaeum* (BAUR 1989), are known to retain eggs; in the latter species the eggs are transparent so that the development stage of the embryo upon egg-laying can be easily estimated. No such possibility exists in *Discus*, but in all probability it also retains eggs for a variable period of time. The distribution of incubation period classes in Figure 8 would then indicate that 20–25 days is the normal period when eggs are laid soon after fertilisation. Another peculiarity of the development of *D. rotundatus* is that most of its juveniles start forming their definitive whorls when still inside egg covers. This would indicate that most baby snails start feeding before hatching, and probably do it for a variable period of time which additionally contributes to the variation in shell size of the hatchlings. No similar case was described in the literature. Hatching itself may result simply from wear of the egg shell consumed from the inside.

CANNIBALISM

Juvenile *D. rotundatus* readily consume unhatched eggs, prefering conspecific to congeneric eggs, but refuse to eat eggs of *Trichia*. In laboratory experiments of Baur (1988), *Arianta arbustorum* (L.) and *Helix pomatia* L. ate only conspecific eggs, refusing to consume each other's batches, but in the literature there are no data on the ability to distinguish between congeneric and non-congeneric eggs. The preference for conspecific eggs and also the ability to distinguish them is great, since the juveniles eat on an average ca. 3 conspecific eggs per 1 egg of another species.

Gastropods are known to use chemical cues to discriminate between food types (Baur 1988), and snail species differ in terms of histochemical properties of their egg shell (Bayne 1968). The hatchling's behaviour of eating the remnants of its own egg shell and the egg cannibalism are traits that most often co-occur and are characteristic of a species. As a consequence of eating their own egg shells, hatchlings of such species may be conditioned to the taste of conspecific eggs (Baur 1988). Congeneric eggs are thus accepted due to their similarity to conspecific eggs.

Snail eggs are rich in energy and nutrients (Duncan 1975, Tompa 1984). Newly hatched *A. arbustorum* fed with cannibalistic diet had a higher growth rate and reached maturity earlier than non-cannibalistic individuals (Baur 1990). Cannibalistic *D. rotundatus* had the same growth rate as the individuals fed with normal diet. If cannibalism confers any benefits on juvenile *Discus*, these are not measurable in terms of growth rate and maturity.

GROWTH

Like other endodontids studied (*Punctum pygmaeum*, Baur 1989, *D. ruderatus, D. perspectivus* – own, unpublished results), *D. rotundatus* continues growing after reaching sexual maturity. However, the growth of sexually mature snails is much slower (cf. Fig. 10): compared with ca. 4 definitive whorls formed prior to maturation, hardly a whorl is built during the whole adult life. Similar results were obtained by Baur (1989) who studied growth of *P. pygmaeum*. The slow growth appears to be associated mainly with the great energy (and calcium) expenditure during egg-laying. The egg diameter is ca. 10–15% shell diameter of the parent, and there may be up to five eggs in a clutch. This explanation is confirmed by the larger average size of uniparentally reproducing snails at their first egg-laying. The energy expenditure is also reflected by long "non-reproductive" periods following each egg-laying period in Figure 7.

REPRODUCTIVE PERIOD

In the laboratory the snails reproduce throughout the year, but most eggs are laid in June. In the wild the maximum abundance of small juveniles falls in July and August which would suggest that most eggs are laid by ca. 1 month earlier. According to Frömming (1954) eggs are laid in May and June, but his data on *D. rotundatus* do not seem to be reliable, since he reports for example that this species lays only one clutch in a lifetime. Taylor (1909) found that in the British Isles *D. rotundatus* laid eggs from early spring till late autumn. This is in agreement with my field observations. A comparison of field and laboratory results indicates that the winter cessation of reproduction is an effect of low temperature rather than changes in photoperiod.

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