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LIFE CYCLE OF *ANISUS VORTICULUS* (TROSCHEL, 1834) (GASTROPODA: PULMONATA: PLANORBIDAE) IN THE LABORATORY

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ABSTRACT: Laboratory culture of 2004–2007 provided the following data on the life cycle of *Anisus vorticulus* (Troschel). Snails hatched in May–June and kept in pairs usually started reproducing 42–114 days after hatching, at the shell width of 3.0–5.2 mm and 3.75–5.1 whorls. Some of them continued reproduction next spring. Snails hatched in July-August and kept in pairs produced their first cocoons next year. In the year of hatching the snails produced their last cocoons till October, next year – usually till August. During their lifetime snails kept in pairs produced a maximum of 122 cocoons with a total of 511 eggs (per snail), and the number of eggs per cocoon ranged from 0 to 9. Snails kept in isolation produced a maximum of 10 cocoons (most without eggs, the remaining ones with eggs devoid of oocytes). The life span was 68–776 days (mean 423).

KEY WORDS: Gastropoda, Planorbidae, *Anisus*, life cycle, reproduction

INTRODUCTION

Shells of *Anisus vorticulus* (Troschel, 1834) are planispiral, with a blunt keel usually situated roughly at half height of the body whorl. Some shells bear a delicate conchiolin ridge of variable width along the keel. In the wild the shells reach the width of ca. 5–6 mm, and their height does not exceed 1 mm. Distinct wrinkles on the dorsal side of foot are a rather characteristic morphological character.

A. vorticulus is regarded as threatened and included in Annex II to the EU Habitats Directive. In the region of Sąpolno (NW. Poland) it was found twice: in 1991 a dead snail among the vegetation pulled out of a small lake, and in the same site in 2004 – a live adult on a floating leaf of *Typha latifolia*.

The first information on the biology of the species was provided by PIECHOCKI (1975, 1979). TERRIER et al. (2006), summarising the existing data, stated that the biology and ecology were still insufficiently known. It was only recent studies near Hamburg and Karlsruhe (GLÖER & GROH 2007) that provided new information, among other things on the life span, population structure changes and ecology of *A. vorticulus*.

MATERIAL AND METHODS

All the snails in the laboratory culture originated from one adult found on the 29th of June 2004. Six snails of its offspring (F1) were kept in the culture (2 pairs and 2 individuals kept singly), as well as 12 snails of F2 (2 pairs and 8 singles), 9 snails of F3 (4 pairs and 1 single), 10 snails of F4 (5 pairs) and 2 snails of F5 (kept singly). The total number of snails in the culture was 39, 26 kept in pairs and 13 singly.

Fragments of dead leaves of *Typha latifolia* and sedges (*Carex* sp.), covered in a thick periphyton layer, or less often fragments of live submerged *Typha* leaves were added to the containers as food source. From the beginning of spring till late autumn food was provided every 2–3 weeks, in winter – only when the ice cover on the lakes disappeared.

Just after hatching juveniles were kept in containers 25 mm in diameter, filled with water to 30 mm; when larger (ca. 2 mm), they were transferred to containers of 60 mm diameter, filled with water to ca. 40 mm. The temperature in the culture from April till October mostly ranged within 17–25°C. In the winter some snails were kept at 10–13°C, others at 15–18°C.

Measurements were taken with a calibrated eye-piece, to the nearest 0.01 mm (range 0.1–1.0 mm) or 0.05 mm (above 2.3 mm). Shell width was measured excluding the ridge which was present on some shells; maximum height of the body whorl was adopted as the shell height.

RESULTS AND DISCUSSION

REPRODUCTION TIMING AND DURATION

Cocoon deposition was distinctly seasonal (Figs 1–3) in spite of the fact that in the winter some snails were kept at a high temperature, compared to natural conditions (15–18°C). In the case of wintering snails the spring onset of reproduction was preceded by a period of rather intense feeding of at least a few days (sometimes more than 3 weeks).

Snails hatched between half of May and half of June in most cases (7 pairs) started reproduction in the summer of the same year (end of July or August, one pair in September). The time elapsing between hatching and the first cocoon deposition ranged from 42 to 114 days (mean 66, SD=26, n=7). After wintering two pairs resumed reproduction (17 April and 5 May), while another four pairs produced few cocoons with eggs devoid of oocytes. Among the remaining snails hatched in the spring (inbred F4), two pairs produced their first cocoons only after wintering (all eggs devoid of oocytes), and one pair produced no cocoons. Snails hatched in July–August (3 pairs) started reproducing in the spring next year (April – beginning of June). The time between hatching and producing the first cocoon for such snails was 240–315 days (mean 265).

In the year of hatching the last cocoon was deposited in September, and only rarely as late as in October. The mean duration of reproduction in the year of hatching was 51 days (SD=25, n=7, range 5–90). In the next year after hatching the last cocoons were usually deposited in August, and the two cocoons produced in September contained no eggs. The mean duration of reproduction in the next year was 124 days (SD=24, n=5, range 82–152). Three snails which survived longer and wintered over twice, produced no cocoons in their second year after hatching.

Snails kept singly produced cocoons from April till August. Among the 13 snails kept singly, six produced no cocoons, four produced one cocoon each and only three deposited cocoons repeatedly (maximum during 90 days). The time from hatching to the first cocoon deposition was 89–435 days (mean 243, SD=122, n=7).

The mean time between the last cocoon deposition and death of the longest-surviving snail in the container was: for snails kept in pairs 145 days (SD=103, n=11, range 17–376), for snails kept singly 86 days (SD=78, n=7, range 1–234).

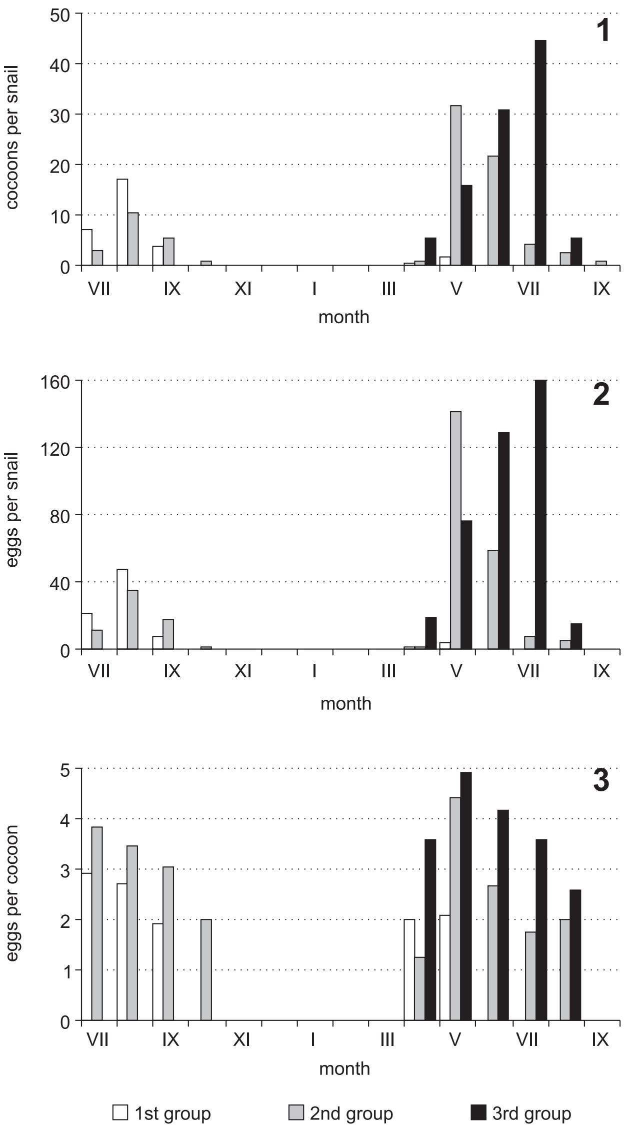
The original adult brought from the lake (found on 29th June 2004) started cocoon deposition after a few days in the laboratory and produced the last cocoon in the first half of August.

FECUNDITY

Within 24 hours usually 1–2 cocoons were produced per pair, but during the period of intense reproduction the number of deposited cocoons was higher (2–4, rarely 5) and they contained a total of up to 27 eggs. A snail left after its partner died and then kept singly produced within 24 hours a maximum of four cocoons with up to 14 eggs.

Figures 1–2 show mean numbers of cocoons and eggs produced during consecutive months and years of life, converted to one snail, and Fig. 3 – changes in the mean number of eggs per cocoon. Because of the differences in the course of reproduction the snails were divided in three groups: group 1 – reproduction only in the year of hatching, dead or producing eggs without oocytes in the next year; group 2 – reproduction in the year of hatching and after wintering, group 3 – reproduction only in the next year after hatching. Three pairs which did not reproduce: two producing only eggs without oocytes and one which produced no cocoons, were omitted from the analysis. Snails included in group 1 produced the most numerous cocoons within a short time after reproduction started (e.g. in August up to 27 cocoons/68 eggs per snail), but already in September the reproduction intensity decreased rapidly (maximum 7 cocoons/16 eggs). The total number of cocoons produced in the year of hatching was 3–50 with 6–128 eggs (mean 24 cocoons/65 eggs), and in the spring next year it was 0–9 with 0–20 eggs without oocytes (mean 2 cocoons with 3 eggs). In the year of hatching the course of reproduction of snails of group 2 was similar as in group 1. In the first season they produced a total of 2–48 cocoons with 4–176 eggs (mean 23 cocoons/80 eggs). After wintering reproduction was the most intense in May (maximum 37 cocoons/181 eggs per snail). The last cocoons with oocyte-containing eggs were deposited at the beginning of July, and those produced later (sometimes till September) contained no eggs or only eggs devoid of oocytes. During the whole spring season the number of produced cocoons was 46–74, with 140–283 eggs (mean 61 cocoons/211 eggs). Reproduction of group 3 snails was rather varied. One pair produced the most numerous cocoons (40) and eggs (213) in May, while another at that time had not even started to reproduce. In June and July reproduction of all such pairs was rather intense (27–46 cocoons with 100–167 eggs per month per snail). In August the number of produced cocoons/eggs became distinctly smaller and the reproduction ceased.

The number of cocoons/eggs produced during lifetime by snails of group 1 (reproduction in the year of hatching) was 3–51 cocoons (mean 26, SD=14,



Figs 1–3. Cocoons laid in consecutive months (year of hatching and next year) by snails kept in pairs; mean number of cocoons (1) and eggs (2) converted to one snail living in a given month, and mean number of eggs in cocoon (3)

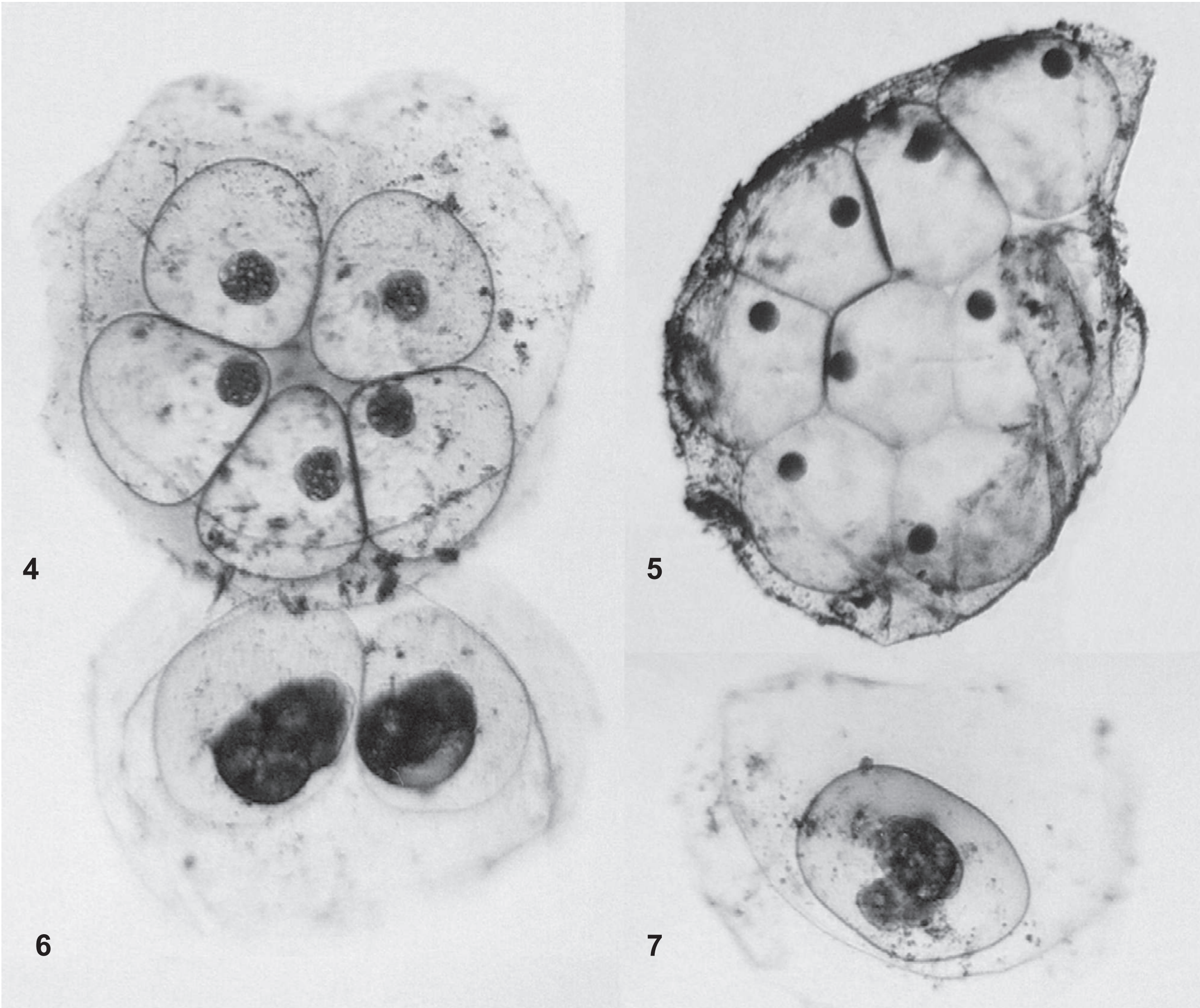
n=10) with 6–129 eggs (mean 68, SD=36), and the mean number of eggs per cocoon was 2.6 (range 2.0–3.2). Snails of group 2 (repeated reproduction) produced 68–122 cocoons (mean 84, SD=22, n=4) with 210–459 eggs (mean 291, SD=102) in their lifetime, and the mean number of eggs per cocoon was 3.5 (range 3.0–3.8). Snails of group 3 (reproduction only next year after hatching) produced 48–114 cocoons (mean 94, SD=23, n=6) containing 168–511 eggs (mean 370, SD=118), the mean number of eggs per cocoon being 3.9 (range 3.3–4.5).

Three of the single snails produced 2–10 cocoons with a total of 2–9 eggs devoid of oocytes.

COCOON AND EGG STRUCTURE

Cocoons fixed to leaves or container walls were much flattened (somewhat more convex only in their cental part), usually rounded in outline (rarely heart-shaped or irregular) (Figs 4–7). Cocoons deposited below the surface film (very rarely) had a shape of an elongated sac. A few cocoons were composed of two capsules connected laterally and arranged in one plane (number of eggs e.g. 2+1 or 2+0). Three cocoons found in one of the containers were composed of 2–4 capsules partly connected with their bases which indicates forming of the connection while still within the parent's body. The cocoon capsule was composed of two parts, with the connecting suture always on the upper side of the cocoon. The cocoon was fixed to the substratum with a thin layer of cementing substance (sometimes its excess was visible on the substratum around the capsule). The upper side of the cocoon was always covered in fine spherical granules (diameter 0.002–0.005 mm), while the underside was smooth (even in cocoons deposited below the surface film). The interior of the cocoon between the eggs was filled with a gelatinous substance which at a higher magnification usually had a granular structure. Measurements of cocoons deposited on leaves or container walls are presented in Table 1. The mean cocoon size depended mainly on the number of contained eggs, and the Pearson correlation coefficients were (n=90): cocoon length/number of eggs r=0.84; cocoon width/number of eggs r=0.86; cocoon length/width r=0.92. The mean cocoon length/width ratio was 1.19 (SD=0.16, n=90, range 1.00–2.17). Among the measured cocoons the smallest was one without eggs (0.67 × 0.45 mm), the largest – one with nine eggs (2.15 × 1.98 mm). Compared to cocoons deposited on hard substratum, those located below the surface film (sac-shaped cocoons) were rather narrow (eg. cocoon with 7 eggs was 1.43 mm long and 0.92 mm wide).

The eggs were usually arranged in one layer and occupied the central part of the cocoon (Figs 4, 6–7). In some cocoons the eggs filled nearly the whole capsule (Fig. 5). Free-laying eggs were roughly oval and flattened. However, in most cocoons they were irregu-

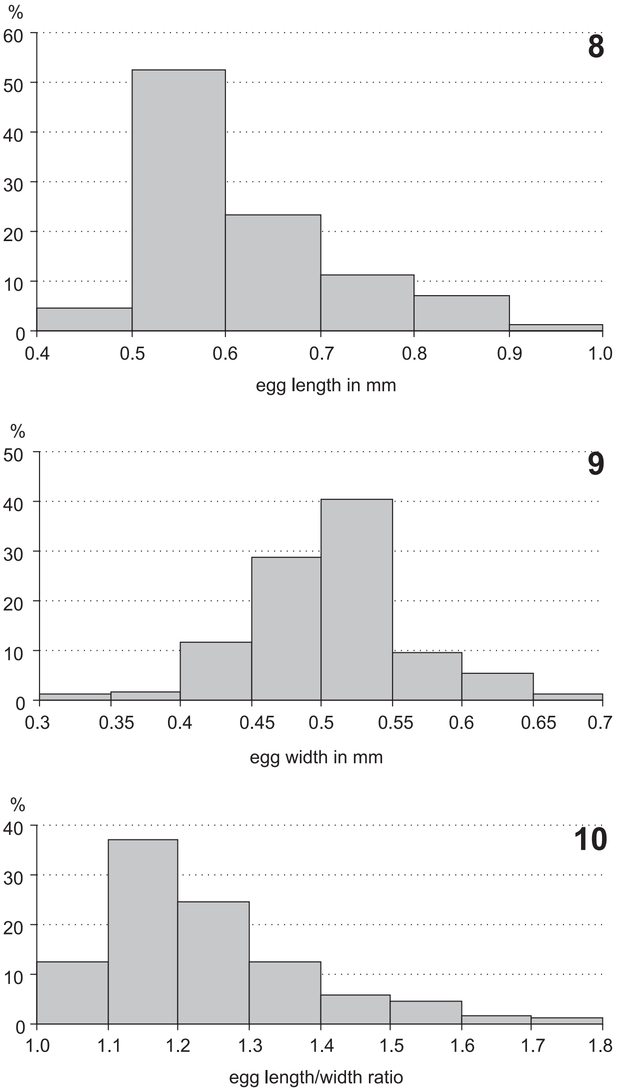


Figs 4–7. Light microscope, examples of *Anisus vorticulus* cocoons, 50×. 4 and 6 – A cocoon with 5 eggs partly glued to a cocoon with 2 eggs

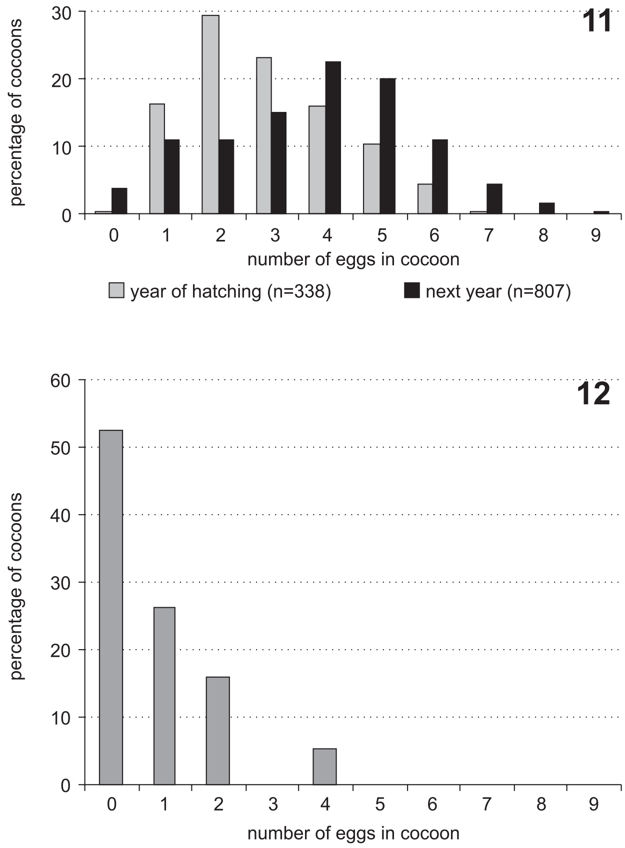
lar. Very rarely eggs were distorted already in the reproductive tracts (e.g. with a constriction or a small swelling at one pole). The eggs were surrounded by a single, colourless, translucent and rather thin envelope. The light yellow oocyte was 0.08–0.10 mm in diameter. Sporadically (0.1%) one envelope contained

Table 1. *Anisus vorticulus,* cocoon size [mm]

Number of eggs in cocoon	n	Length of cocoon		Width of cocoon	
		mean	range	mean	range
0	3	1.05	0.67–1.30	0.57	0.45–0.67
1	21	1.09	0.80–1.38	0.94	0.62–1.36
2	11	1.28	0.94–1.60	1.04	0.73–1.22
3	3	1.47	1.29–1.59	1.25	1.17–1.36
4	13	1.44	1.03–1.66	1.28	0.90–1.56
5	13	1.52	1.26–1.65	1.34	1.15–1.50
6	16	1.69	1.45–1.84	1.44	1.20–1.61
7	5	1.75	1.63–1.89	1.60	1.45–1.70
8	3	1.85	1.70–2.05	1.66	1.54–1.75
9	2	2.00	1.86–2.15	1.80	1.63–1.98



Figs 8–10. Variation in egg size and length/width ratio (n=170)



Figs 11–12. Variation in the number of eggs in cocoon: 11 – Cocoons laid by snails kept in pairs (number of cocoons in parentheses); 12 – Cocoons laid by snails kept singly (n=19)

two oocytes. More often (2.7% of the total) the eggs contined no oocyte which agrees with PIECHOCKI's (1975, 1979) observations. In the laboratory eggs without oocytes were laid by snails kept singly (100% of eggs) and some kept in pairs (mean 2.4% of eggs – mainly at the beginning and end of reproduction in the next year after hatching).

The measurements of free-laying eggs (oval) were (n=170): length 0.42–0.99 mm (mean 0.62, SD=0.11), width 0.30–0.69 mm (mean 0.50, SD=0.06) (Figs 8–9). The measurements of irregularly shaped eggs were within the above range. The egg length/width ratio was 1.02–1.80 (mean 1.24, SD=0.15, n=170) (Fig. 10), and the length/width Pearson correlation coefficient was r=0.70, n=170 (larger eggs were usually more elongate).

Cocoons of *A. vorticulus* contained from 0 to 9 eggs (Figs 11–12). Snails kept in pairs in the year of hatching usually produced cocoons with 2–3 eggs, and in the next year usually 4–5 eggs (Fig. 11). Cocoons without eggs were produced mainly in the next year after hatching and formed on average 3.3% of all produced by snails kept in pairs (range for individual pairs 0.4–11.5%). Among cocoons laid by snails kept singly as many as 52.6% contained no eggs, but e.g. coiled egg envelopes instead; the remaining cocoons contained not more than four eggs (none of them containing oocytes) (Fig. 12). Cocoons of snails kept in pairs, which in the season deposited only eggs devoid of oocytes, had a range of variation similar to that for snails kept singly (33.3% devoid of eggs, the remainder with at most four eggs).

EMBRYONIC DEVELOPMENT

Immediately after cocoon deposition the eggs were usually at early development stages (oocyte I or II). Only in cocoons composed of a few capsules the advancement of embryonic development was sometimes distinctly varied (e.g. in one capsule embryos after several divisions, in another at veliger stage with a 0.2 whorl shell). The duration of embryonic development distinctly depended on the incubation temperature (Fig. 13), and the Pearson correlation coefficient was r=–0.88, n=98. At ca. 26°C hatching usually took place in 8–9 days, at ca. 21°C in 12–14 days, at 17°C as late as in 24 days. At 12.6°C even after 40 days of incubation all embryos were still within their egg envelopes and most showed osmotic disturbances (swelling), while the remaining ones had shells which covered only a part of the body.

The typical course of embryonic development at ca. 21°C was: day 4 – embryo nearly spherical, rotating rather fast; day 7 – embryo sickle-like bent, beginning of shell formation; day 8 – shell of ca. 0.1–0.2 whorl, anterior body part not fitting into the shell, eye spots visible; day 10 – shell of ca. 0.5–0.6 whorl, body when contracted can be accomodated by the shell, small mantle cavity and heart beat visible; day 12 – shell of ca. 1.0 whorl; day 13 – shell of 1.0–1.2 whorl, embryo moves its radula and rasps the envelope till it breaks. The embryonic shell size was usually smaller than the egg size which made it difficult for the juvenile to break the envelope and hatch (some normally developed juveniles died within the egg envelope). Also embryos with distinct osmotic disturbances (swelling of the whole body) usually died within egg envelopes. Eggs containing two embryos developed normally but the shells of such embryos (width, number of whorls) were much smaller than in eggs with one embryo.

The embryonic shells were covered in sparse, very delicate and not very regular spiral riblets (under small magnification visible as thin lines). The upper side of the whorl usually bore 10–13 such riblets. Starting with about 0.5 whorl slightly arcuate fold-like thickenings (radial striae) appeared between the riblets. The embryonic shell measurements were (n=117): width 0.35–0.55 mm (mean 0.467, SD=0.031), number of whorls 0.8–1.25 (mean 1.05, SD=0.10) (Figs 14–15). The shell width/number of whorls correlation coefficient was r=0.81 (n=117). The shell height depended mainly on its size (width, number of whorls) and was usually 0.24–0.29 mm.

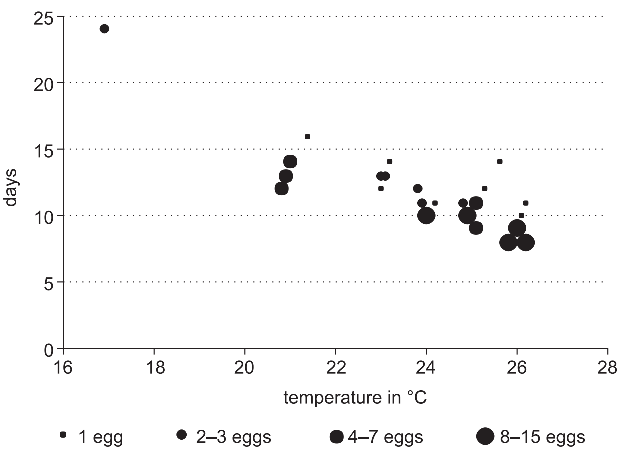
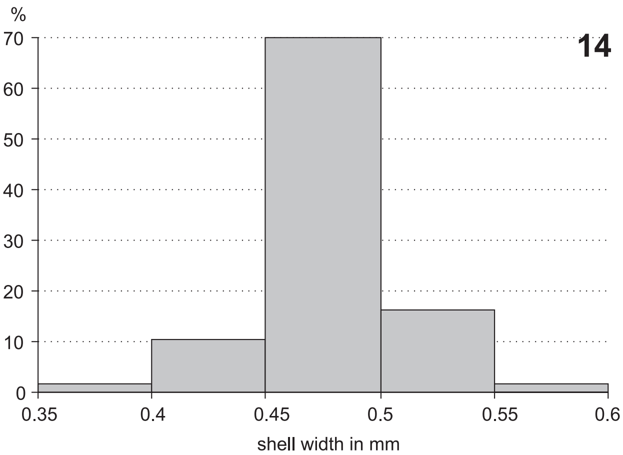
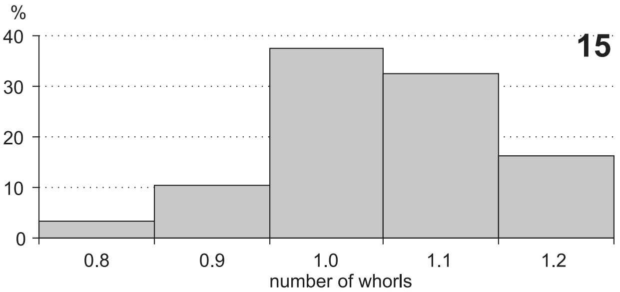


Fig. 13. Duration of embryonic development dependent on the mean temperature (n=98)



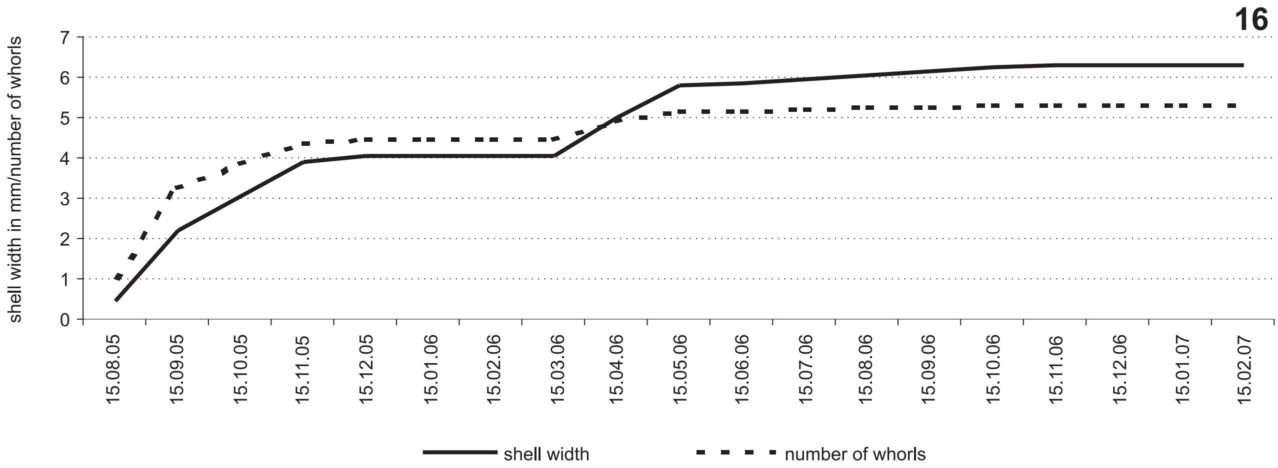


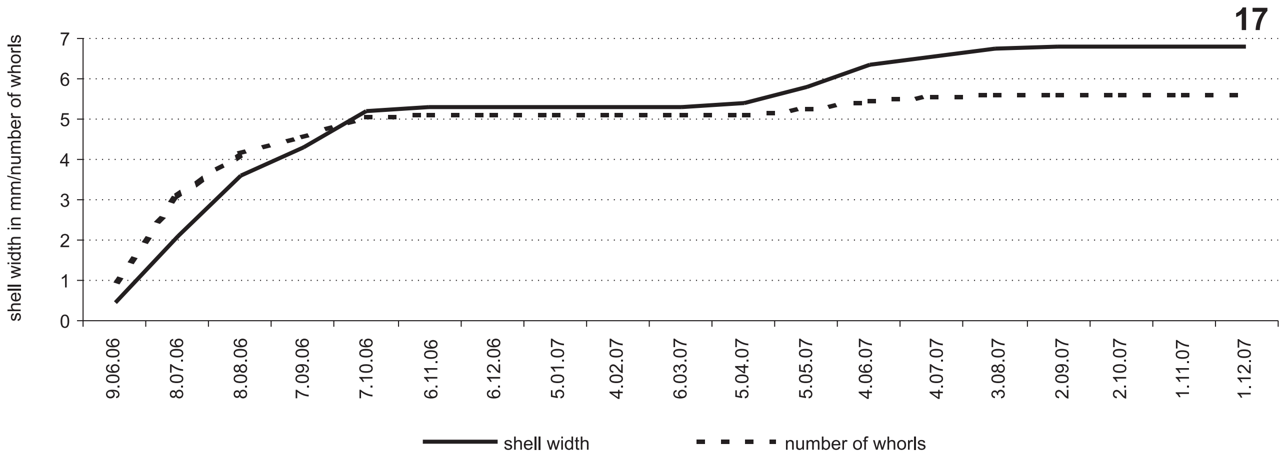
Figs 14–15. Size variation of embryonic shells (n=117)

POST-EMBRYONIC DEVELOPMENT AND MATURATION

The boundary of embryonic shell was rather often marked as a distinct stria. The spiral lines on the embryonic shell rarely passed onto post-embryonic increments. They were replaced by wide spiral striae of nearly smooth surface, with rather regular, radial thickenings inbetween. Not very favourable feeding conditions were among the reasons for numerous instances of death among very young snails. Slightly larger snails (above 2 whorls) were more resistant to starvation and longer periods of growth inhibition were marked as distinct, radial stripes on the shell (sometimes also narrowing of the whorl diameter). Though the two snails coming from the lake had shells with a ridge running along the margin of the body whorl, only some of the offspring in the laboratory had such ridges which were formed only periodically. The ridge width varied, the maximum was 0.11 mm (shells 4.8–5.0 mm wide).

According to TERRIER et al. (2006) the smallest copulating snails had shells 2.5 mm wide. In the laboratory mating was observed only once, at the end of July, and the snails had shells: I – width 3.15 mm/3.85 whorl, II – width 3.45 mm/4.0 whorls. The copulation took place 75 days after hatching, and the first cocoons were deposited three weeks later. In the next year after hatching copulation probably took place only in early spring (end of March – beginning of





Figs 16–17. Mean growth curves of two groups of snails hatched in different periods: 16 – hatched on August 15th 2005 (n=3); 17 – hatched on June 9th 2006 (n=14)

May), since mating in a later period had no effect on the reproduction, like in *Valvata* (MYZYK 2002, 2004, 2007). Most of the snails kept in pairs, which reached large shell size before wintering (width more than 5 mm), in the spring deposited cocoons with eggs devoid of oocytes, like the snails kept singly (no copulation?).

The shell size at the first cocoon deposition among snails kept in pairs varied with the time of beginning of reproduction: in the year of hatching – width 3.0–4.3 mm/3.75–4.5 whorl (rarely more, up to 5.2 mm/5.1 whorl), and in the next year – width 4.4–5.5 mm/4.4–5.1 whorl.

GROWTH

The growth of snails in the first month of life was very fast irrespective of the season of the year in which they hatched. In 30 days from hatching their shells reached the width of 1.82–2.41 mm (mean 2.09, SD=0.16, n=25) and the number of whorls 2.9–3.4 (mean 3.12, SD=0.15). The mean shell increment in the first months of life was 0.054 mm width per day (range 0.044–0.063 mm/day). The maximum growth rate of 0.112 mm/day was observed between the 15th and the 20th day from hatching. In the second month of life the mean growth rate was not much smaller – 0.044 mm/day, but the variation range was much wider (0.007–0.065 mm/day). Sixty days after hatching the shells reached 2.14–4.02 mm in width (mean 3.41, SD=0.47, n=25) and 3.1–4.35 whorls (mean 4.04, SD=0.30). Later the growth rate was usually even smaller and in the third month of life it was on average 0.025 mm/day, but the variation range remained more or less the same (0.009–0.050 mm/day). In the year of hatching the shell growth continued usually till October-November and only shells of small snails (hatched in late summer or autumn) grew slightly also in the winter. In the remaining snails the shell growth ceased completely in the winter (Figs 16–17). The shell size of wintering snails was much varied and depended, among other factors, on the month of hatching and intensity of feeding (range: width 3.08–6.0 mm, number of whorls 3.85–5.3). The next stage of shell growth started usually at the end of March or beginning of April, after fresh food was supplied. The growth rate varied much among individuals, even those kept in the same container. In

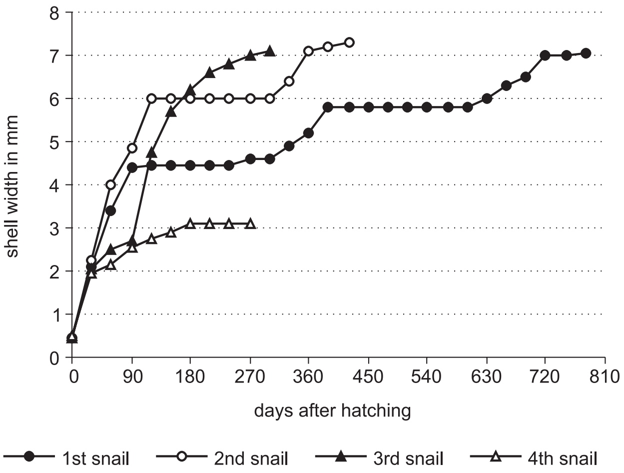
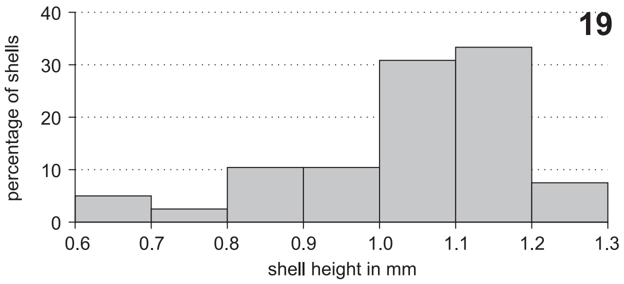
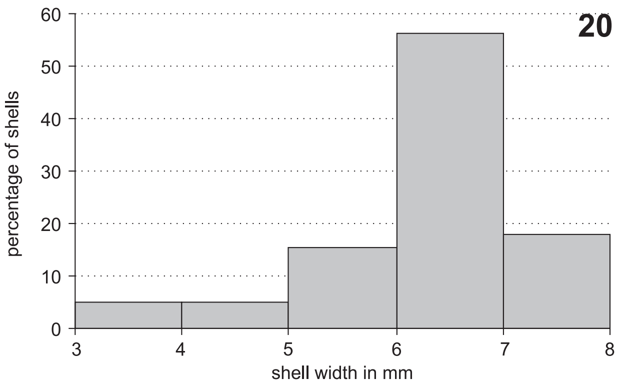
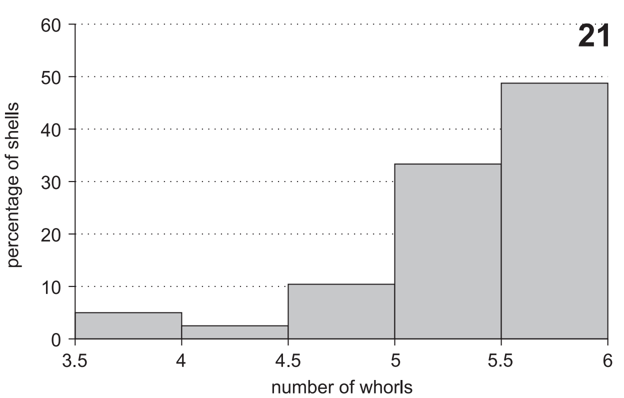


Fig. 18. Examples of individual growth curves for the shell width: 1st snail – the longest-lived in the culture, hatched on July 20th 2004; 2nd snail – hatched on June 9th 2006; 3rd snail – hatched on November 6th 2006; 4th snail – hatched on June 17th 2005







Figs 19–21. Variation in the shell size reached in the laboratory (n=39)

some snails the growth was fastest in April (range 0.005–0.057 mm/day), in others in May (range 0.003–0.040 mm/day). Then some snails ceased growing, while others continued growth till the end of life. Snails which lived longer (ca. 2 years), after the summer growth inhibition, resumed their growth (third stage) in the autumn or after next wintering. Examples of individual variation in growth curves are shown in Fig. 18.

The single stripe resulting from growth inhibition (wintering) in the two snails found in the lake was located at the level of ca. 3.6 whorl (width 2.7 and 3.0 mm). This corresponds to the maximum of population structure curve for January given by GLÖER & GROH (2007: Fig. 3). Laboratory conditions were more favourable than those in the wild, as indicated by the shell size (71.8% of the shells more than 6.0 mm wide). The maximum size of shells from the laboratory was (n=39): height 0.60–1.26 mm (mean 1.04, SD=0.15), width 3.08–7.3 mm (mean 6.21, SD=1.04), number of whorls 3.7–5.75 (mean 5.3, SD=0.5) (Figs 19–21). The Pearson correlation coefficients for pairs of shell parameters were (n=39): shell height/width r=0.93, shell height/number of whorls r=0.88, shell width/number of whorls r=0.99. The body whorl width (measured at the aperture) was 0.71–1.56 mm (mean 1.33, SD=0.20, n=39). The maximum width of body whorl constituted 19.9–24.7% of the shell width (mean 21.5%) and the index decreased with increasing shell size. The aperture height/width ratio was 0.676–0.882 (mean 0.785, SD=0.042) and was not correlated with the number of whorls (r=–0.37) or shell width (r=–0.31, n=39). The shells collected in the wild were: I – width 4.78 mm/4.5 whorl (snail found dead on 21.07.1991); II – width 5.2 mm/5.0 whorls (live snail found on 29.06.2004 – in the laboratory grew to width 6.23 mm/5.4 whorl).

LIFE SPAN AND MORTALITY

The life span varied widely (Fig. 22). For snails kept singly it was 91–459 days (mean 338, SD=103,

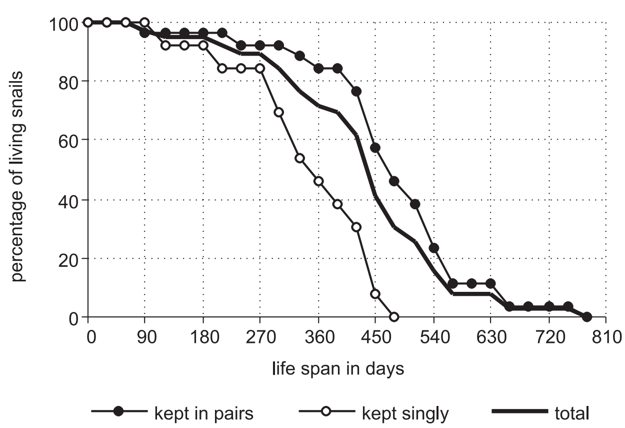


Fig. 22. Mortality of snails in the laboratory

Table 2. Mortality of adult *Anisus vorticulus* in the laboratory: 0 – year of hatching; 1, 2 – consecutive years

Year	Month of death												Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
0	–	–	–	–	–	–	–	1	–	–	1	–	2
1	1	1	1	3	–	2	4	6	5	3	4	3	33
2	–	1	–	–	2	–	–	–	1	–	–	–	4
Σ	1	2	1	3	2	2	4	7	6	3	5	3	39

n=13), for those kept in pairs – 68–776 days (mean 465, SD=133, n=26). The mean life span for all the snails in the laboratory was 423 days (SD=137, n=39). A more intense feeding caused a slight decrease in the life span, as was the case of snails of the genus *Valvata* (MYZYK 2002, 2004, 2007). Most laboratory snails wintered once only, only three (hatched in July–August) wintered twice. The original snail caught in the lake wintered for the first time in the lake (growth inhibition stripe at 3.6 whorl) and again in the laboratory (died on April 15 2005). Dead of adults took place throughout the year, with a slight maximum of mortality in August and September (Table 2).

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