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CONTRIBUTION TO THE BIOLOGY OF TEN VERTIGINID SPECIES

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ABSTRACT: Laboratory and field observations on *Vertigo angustior* Jeffreys, *V. antivertigo* (Draparnaud), *V. moulinsiana* (Dupuy), *V. pusilla* O. F. Müller, *V. pygmaea* (Draparnaud), *V. ronnebyensis* (Westerlund), *V. substriata* (Jeffreys), *Truncatellina cylindrica* (Férussac), *Columella aspera* Waldén and *C. edentula* (Draparnaud) provided new information on their life cycle. Genus *Vertigo*: the life span is 1–3 years, with most snails dying in the next year after hatching. The reproductive season lasts from half of May till the beginning of September; depending on the life span eggs are laid during 1–3 seasons. The number of eggs per lifetime varies widely, the maximum numbers are 55–79 in *V. moulinsiana*, *pygmaea* and *ronnebyensis*, 102–120 in *V. angustior*, *pusilla* and *substriata* and 218 in *V. antivertigo*. Most eggs are laid at the stage of one cell (even oocyte II), but in some the advancement of development indicates retention of 1–3 days. Hatching usually starts in the second half of June and lasts till the second half of September. Only some of the snails reach maturity in the year of hatching, usually after the reproductive season. Genus *Truncatellina*: in the wild the life span of most individuals is about one year, some live till the age of about two years. Eggs are laid from half of June till the end of August (in laboratory maximum 11 eggs); hatching takes place from July till the end of September. Genus *Columella*: in the laboratory *C. aspera* lays eggs from half of May till the beginning of September (maximum 5 eggs); hatching starts at half of June and continues till the end of September. *C. edentula* in the laboratory lays eggs at half of April, and juveniles hatch at the end of May and beginning of June.

KEY WORDS: land snails, Vertiginidae, reproduction, shell variation

INTRODUCTION

Vertiginid biology is still little known (POKRYSZKO 2003). The best known species is *V. pusilla* (POKRYSZKO 1990a, MAZURKIEWICZ & POKRYSZKO 2005); there exists fragmentary information on a few other species (POKRYSZKO 1990b, 2003, CAMERON 2003, CAMERON et al. 2003, KILLEEN 2003, MYZYK 2005a, b). Most literature information pertains to species identification, shell variation, habitats and distribution (KERNEY et al. 1983, RIEDEL 1988, POKRYSZKO 1990b, FALKNER et al. 2001, PROSCHWITZ 2003, WIKTOR 2004 and others).

My studies were carried out in the environs of the village of Sąpolno (NW. Poland), where a small area holds ten vertiginid species: *Vertigo angustior* Jeffreys, 1830, *V. antivertigo* (Draparnaud, 1801), *V. moulinsiana* (Dupuy, 1849), *V. pusilla* O. F. Müller, 1774, *V. pygmaea* (Draparnaud, 1801), *V. ronnebyensis* (Westerlund, 1871), *V. substriata* (Jeffreys, 1833), *Truncatellina cylindrica* (Férussac, 1807), *Columella aspera* Waldén, 1966 and *C. edentula* (Draparnaud, 1805). *V. angustior* and *V. moulinsiana* are regarded as endangered and included in Annex II, EU Habitats Directive (CAMERON et al. 2003).

MATERIAL AND METHODS

The studied vertiginids were identified using the monograph of POKRYSZKO (1990b). Observations were conducted both in the field (e.g. population age structure) and in the laboratory (e.g. number of eggs and their structure, embryonic development, life span). Snails of the genus *Vertigo* were kept singly in plastic containers of 57 × 22 × 10 mm (sometimes slightly larger). Specimens of the genera *Truncatellina* and *Columella* were kept in groups of a few individuals (usually 3–5) in containers of 45 mm diameter and 60 mm height. Several layers of decomposing leaves were placed in the containers as food (mainly *Populus* sp., *Quercus* sp., *Betula* sp.); the leaves were collected where the vertiginids occurred. To prevent accidental transport of eggs and juveniles into the laboratory, only leaves that could be throughly examined and cleaned were used. The leaves were exchanged every few weeks (except winter), and the relative humidity in the containers was maintained at high level. The temperature from the beginning of April till the end of October was usually 18–25°C (rarely slightly lower or higher), and in winter 8–12°C. During wintering the contents of the containers were examined every few weeks, mould-covered leaves were removed and water supplied when needed. From April till October these operations were performed every few days (in rare periods daily) and the eggs were removed. Degree of advancement of embryonic development was used to ascertain the sequence (date) of egg-laying. Eggs with embryos at initial development stages (not more than a few divisions) were used to trace the dependence between the temperature and duration of incubation. The eggs were incubated on damp, decomposing leaves of trees (mainly poplar, less often birch or oak).

Field observations were carried out near the village of Sąpolno (NW. Poland – Fig. 1). Samples were taken through shaking the snails out of leaf litter and grass tussocks, collecting from dead timber or tall plants (depending on the species) and sorting a small quantity of damp litter under magnifying glass. Eggs brought from the field were identified based on characteristic features of their envelopes (*V. angustior*, *V. moulinsiana*, *V. pygmaea* – for details see MYZYK 2005b), structure of the embryonic shell (*V. pusilla*) or after hatching (*V. antivertigo*, *V. ronnebyensis*, *V. substriata*).

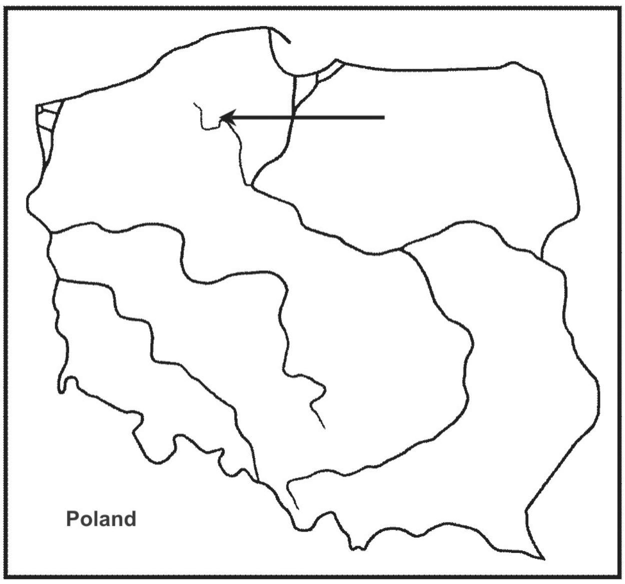


Fig. 1. Location of the study area

Age determination. Observations of several years made it possible to ascertain an aproximate relation between the shell surface appearance and the life span in natural conditions. A characteristic light stria almost always forms around the aperture during wintering of juveniles. In a typical stria the saturation of white colour increases towards the aperture and then the colour suddenly disappears, followed by a growth disturbance (visible also on shells devoid of periostracum). Some adult shells bear two or three such striae; when closely spaced, they probably originated during unstable weather during hibernation. Periods of arrested growth during summer drought are usually poorly marked on the shells. The first damage to periostracum (spots) usually appears after a few months (sporadically after a few weeks), and their size and number increases rather slowly. In the autumn samples separation into age classes is very clear: juveniles and adults with no periostracum damage are individuals hatched earlier in the same year; shells with a stria and damage/lesions on the apex (to the stria) and shells without stria but with small periostracal lesions on the whole surface down to the mouth – hatched in the previous year; shells with a stria and small periostracal lesions on the whole shell surface down to the aperture, and shells with no stria but periostracum much damaged on the whole surface (whitened) – hatched two years previously; shells with a stria and much damaged periostracum on the whole surface (whitened) – hatched three years before. The double criteria for the age classes result from the varied time of maturation (some snails become mature in the year of hatching, others after hibernation). Separation of age classes in the spring samples is more difficult and burdened with a greater error because of uneven formation of new lesions during winter (e.g. some hibernating juveniles show traces of periostracal lesions, others had no such lecions).

Measurements were taken with calibrated eye-piece to the nearest 0.01 mm (range 0.1–1 mm) or 0.025 mm (more than 1 mm). Eggs were measured in a large drop of water. The width of embryonic shell inside the egg envelopes (just before hatching) and after hatching showed that the envelopes acted as a magnifying lens (magnification 3–5%). Consequently, the egg chamber measurements given below are slightly overestimated, and the envelope thickness – underestimated.

RESULTS AND DISCUSSION

Vertigo angustior Jeffreys, 1830

Habitats. Near Sąpolno the species occurs in three distinctly separate localities: on the right bank of the Brda River (narrow valley perpendicular to the river) and at the northern and southern end of Lake Sosnowe (Fig. 2).

The locality on the Brda is located on the bottom of the valley, 100–200 m away from the river, on a damp, unmeliorated meadow (grasses, mosses, herbs). Only subfossil shells were found in the mid part of the valley, on a small hillock. About ten years earlier a small fish pond was built on the meadow; its shores are now covered by trees (mainly birch and willow). The population of *V. angustior* occupies a fairly large area, but reaches a high density only in places (e.g. in tussocks of grass and moss on the margins of the meadow). In some years the species was found in fairly high numbers in mown and drying grass; in the figures the site is referred to as meadow.

The locality at the northern end of Lake Sosnowe is located on the edge of the terrace surrounding the lake (1–1.5 m above the water table). Till half of the 20th c. both the terrace and the lower-situated terrain directly adjoining the water were in agricultural use, and at present are becoming overgrown with trees (*Populus tremula*, *Quercus robur, Alnus glutinosa*). *V. angustior* occurs in a few separate patches, of one to about ten square metres in area. The sandy substratum of the patches is covered by a thick layer of dead and growing grass, moss and decomposing tree leaves. Besides, they are much shaded by the young trees, favouring long-lasting dew. The snails do not occur in drier places and in the wet depression towards the lake. In the figures the site is referred to as lakeshore. Outside the terrace, a small population occurs on grassy edges of a small deciduous forest (mainly *Populus tremula*), ca. 50 m north of the lake. At the southern end of Lake Sosnowe *V. angustior* occurs among grasses and moss at the base of the railway embankment, on its northern side (1–3 m above the water table).

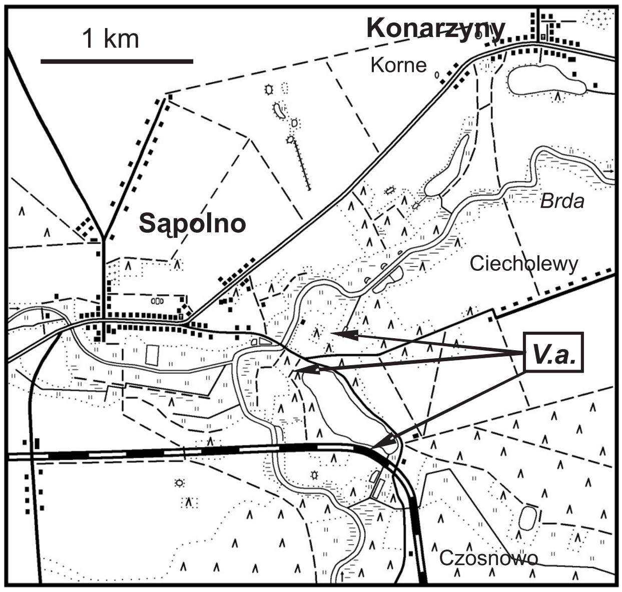


Fig. 2. Map of the neighbourhood of Sąpolno. Localities of *Vertigo angustior* (*V.a.*) indicated with arrows

Reproduction. Adult snails collected in the field (end of March – beginning of June) started to reproduce after 10–23 days (e.g. snails collected on March 29th laid eggs at half of April). In the spring (April–June) most snails laid eggs every day (sometimes two eggs within 24 hours) or at short intervals of 2–3 days (up to 30 eggs per month). Usually at the end of the season these eggless periods became longer (5–15 days, rarely more). The last egg of the season was usually laid in the period June-August. Only the snails which would live till next year continued laying eggs till the end of September, or sporadically later (even in winter). Usually the reproductive period lasted 40–138 days (except single eggs produced in late autumn and winter). Depending on the life span, eggs were laid during one, two or three seasons.

The number of eggs per season ranged from 8 to 77 (mean 38, SD=20, n=21). Adults collected in the field in the spring and reproducing during only one season laid 19–56 eggs (mean 41, SD=13, n=11). Most snails collected in August died after having laid 0–3 eggs. Snails reproducing during two or three seasons showed a higher fecundity: one, collected on 4.08.2004, laid 111 eggs (17+77+17), the second, collected on 3.06.2004, produced 84 eggs (61+23) (Table 1), the third, collected on 4.08.2004, laid 82 eggs (9+65+8). Of two snails hatched and raised in the laboratory, one produced 49 eggs (between April 24th and June 22nd), the second failed to reproduce.

In the wild (lakeshore) eggs were laid on grasses and tree leaves lying on the grass. The earliest-laid egg was found on 24.05.2007 (a slightly bent embryo with no shell). In May and at the beginning of June eggs were found only after heavy rains and were few. Most eggs were laid in July and August, and in some years a fairly intensive reproduction continued till the beginning of September (e.g. some embryos in the sample of 5.09.2006 had shells of 1.2 whorl, others had a few blastomeres).

Egg. Eggs of *V. angustior* were gelatinous, nearly colourless, and usually in the form of a slightly flattened sphere (rarely flattened oval). The egg chamber was covered by three envelopes: internal (thin, parchment-like), gelatinous (the thickest envelope, of a layered structure) and internal (relatively thin). The surface of the external envelope was always covered by distinct granular nodules. The average total envelope thickness was 13.0% of egg diameter. The

Table 1. Egg-laying in the laboratory. Number of eggs deposited in consecutive months and years by two most fecund snails of the genus *Vertigo*

Year	Month	*V. angustior* I	*V. angustior* II	*V.muolinsiana* I	*V. moulinsiana* II	*V. pygmaea* I	*V. pygmaea* II	*V. antivertigo* I	*V. antivertigo* II	*V. pusilla* I	*V. pusilla* II	*V. ronnebyensis* I	*V. ronnebyensis* II	*V. substriata* I	*V. substriata* II
1st	April	–	–	–	8	3	–	10	7	–	–	13	–	–	–
	May	–	–	7	2	20	–	46	31	–	10	16	–	–	–
	June	–	18	15	–	10	–	28	19	–	13	13	14	–	15
	July	–	24	12	1	22	8	45	30	–	13	4	16	–	26
	August	12	15	–	4	14	15	31	39	18	15	9	8	14	20
	September	4	3	–	–	1	2	21	9	10	–	–	–	17	3
	October	1	–	–	–	–	–	3	–	–	–	–	–	2	5
	November	–	1	–	–	–	–	–	–	–	1	–	–	–	2
	December	–	–	–	–	–	–	–	–	–	–	–	–	5	4
2nd	January	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	February	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	March	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	April	6	1	2	8	1	–	2	14	8	7	–	4	16	9
	May	28	22	2	2	8	–	25	27	28	26	–	10	32	17
	June	21	–	–	4	–	11	7	15	13	4	–	–	21	8
	July	12	–	1	–	–	3	–	1	12	–	–	–	13	–
	August	8	–	1	8	–	12	–	–	13	–	–	–	–	–
	September	1	–	3	–	–	1	–	–	–	–	–	–	–	–
	October	1	–	2	–	–	–	–	–	–	–	–	–	–	–
	November	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	December	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3rd	January	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	February	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	March	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	April	7	–	3	–	–	–	–	–	–	–	–	–	–	–
	May	8	–	2	–	–	–	–	–	–	–	–	–	–	–
	June	2	–	2	–	–	–	–	–	–	–	–	–	–	–
	July	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	August	–	–	8	–	–	–	–	–	–	–	–	–	–	–
Total		111	84	60	37	79	52	218	192	102	89	55	52	120	110

egg size (n=721) was: diameter 0.48–0.66 mm (mean 0.591 mm, SD=0.024), chamber diameter 0.40–0.57 mm (mean 0.514 mm, SD=0.022) (for details of structure and variation range see MYZYK 2005b).

Embryonic development. Most eggs were laid at the stage of one cell (some as oocytes II). Polocytes I and II were fairly often seen in the egg chamber, which would indicate fertilisation inside the formed egg. Some embryos in newly laid eggs were distinctly advanced, indicating a retention of 1–3 days. At low air humidity the eggs were very susceptible to dessication. Following a major dehydration, embryos at early development stages usually died. In the case of embryos with formed shells, the shrunk egg envelopes covered the aperture and distinctly inhibited further water loss. In some eggs found in the field such shrunk envelopes tightly adhered to the shell but the embryos were alive.

The duration of embryonic development depended on the incubation temperature. At the temperature of 23°C hatching took place usually after 11 days, at 21°C – after 13 days, at 19°C – after 16 days

(Fig. 3). Pearson's correlation between the temperature and the incubation duration was r=–0.97, n=24. The duration of one egg division (first to second division) at 20°C was ca. 2.4 hours.

At the temperature of ca. 21°C embryonic development was usually as follows: day 1–2 – immobile embryo, spherical (Fig. 4) or irregularly shaped; day 3 – rotating irregular lump (Fig. 5); day 4 – embryo slightly bent, in its middle part conical aggregation of large cells, on one side short foot and thick tentacles, on the opposite side shell apex (initially completely covered, then an orifice in the external layer of cells, gradually increasing and uncovering the shell) (Fig. 6); day 5 – embryo partly covered by shell of 0.2–0.25 whorl, foot elongated and pulsating (Fig. 7); day 6 – shell of 0.5–0.8 whorl, contracted body fits into the shell, heartbeat visible (Fig. 8); day 9 – shell of 1.2–1.25 whorl (Fig. 9). In the following days the shell increment was small (not more than 0.1 whorl) or none. At that time internal organs developed: e.g. rectum and radula. The maximum embryonic shell width was usually somewhat larger than the egg chamber diameter, and the egg before hatching became approximately oval. On day 13 the embryo crawled along the internal envelope and scraped it with the radula, with the head hidden inside the shell, and only the mouthparts protruding. From the moment of breaking of the internal envelope, usually 3–4 hours elapsed before the snail bit a hole in the middle and external envelope and emerged from the egg. In the laboratory, the embryos rarely died inside their egg envelopes; most often the reason was inadequate substratum, less ofen parasitic fungi or drying out.

Growth. The embryonic shells were mostly composed of 1.2–1.3 whorl (mean 1.25, SD=0.07, n=97, range 1.0–1.4) (Fig. 10). The width of the 40 measured shells was 0.47–0.55 mm (mean 0.504 mm, SD=0.021), but for larger samples the range would be wider and close to that of the egg chamber diameter. The surface of embryonic shell was covered by fine irregular nodules, and its boundary was often distinctly marked as a narrow stria of growth disturbance.

The growth of snails hatched in the laboratory was almost continuous (high humidity was maintained in the containers all the time) and rather fast (Fig. 11). Initially, a fragment of leaf on which the snail had hatched was kept as food, then new leaves were added (poplar or birch). From 40 to 55 days after hatching the shells reached their ultimate size and the lip became reflexed. In adult life the reflexed lip grew slightly, and the apertural barriers were gradually thickened and enlarged (especially columellar and parietal teeth).

In the lakeshore site hatchlings were usually found in the first half of July (in eggs laid in May and at the beginning of June most embryos probably died as a result of dessication). The hatching period ended at about half of September, rarely somewhat later. The growth of juveniles was somewhat slower than in the laboratory (no activity at low air humidity). Feeding and growth often terminated at the beginning of October, even though later weather conditions seemed still favourable (temperature above 5°C and high humidity). In the lakeshore locality, on average 25% of the snails reached maturity in the year of hatching (though in some years the proportion could exceed 50%), while on the meadow the percentage was 53% (in some years up to 65%). After hibernation the juveniles almost always had a distinct light stria around their aperture. Two or three such striae were visible on some adult shells, and the distance between them usually did not exceed 0.6 whorl (rarely more, up to ca. 1 whorl). The average size of shells of hibernating juveniles, determined based on the single light stria, was: for lakeshore snails 2.44 whorls (SD=0.49, n=192, range 1.5–4.6), for meadow snails 2.04 whorls (SD=0.36, n=62, range 1.5–3.0) (Fig. 12). In early spring (April-beginning of May) the lakeshore site was usually rather dry and only the growth of young grasses caused an increase in the litter dampness to the level enabling snail activity (at least periodically). When the spring was rainy, the hibernating juveniles resumed their growth already at about half of May, and at the beginning of June fresh increments of up to ca. 0.6 whorl, rarely more, up to 1.4 whorl, were visible on most shells (75%). Shell growth termination varied and depended, among other factors, on the size during hibernation (number of whorls). Mostly, maturity was reached in the period June-August, but sporadically juveniles with the light stria and periostracal damage on the apex were still found at the beginning of October.

Longevity. In the laboratory the life span was 202 and 50 days (both individuals died at the end of June). Adult snails collected in the field usually died after 2–4 months spent in the laboratory (sometimes earlier). Only three individuals survived much longer. One, collected on 3.06.2004 (shell with no stria and no periostracum damage, hatched and adult in 2003), lived till 13.06.2005 (life span ca. 23 months). Two other individuals, collected on 4.08.2004 (shells with a stria and small periostracal damage on apex, hatched in 2003 and adult in 2004), survived till the

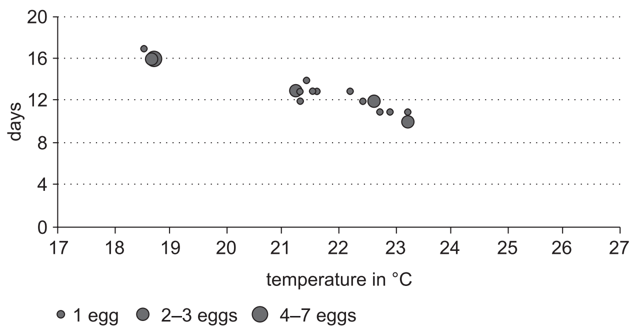
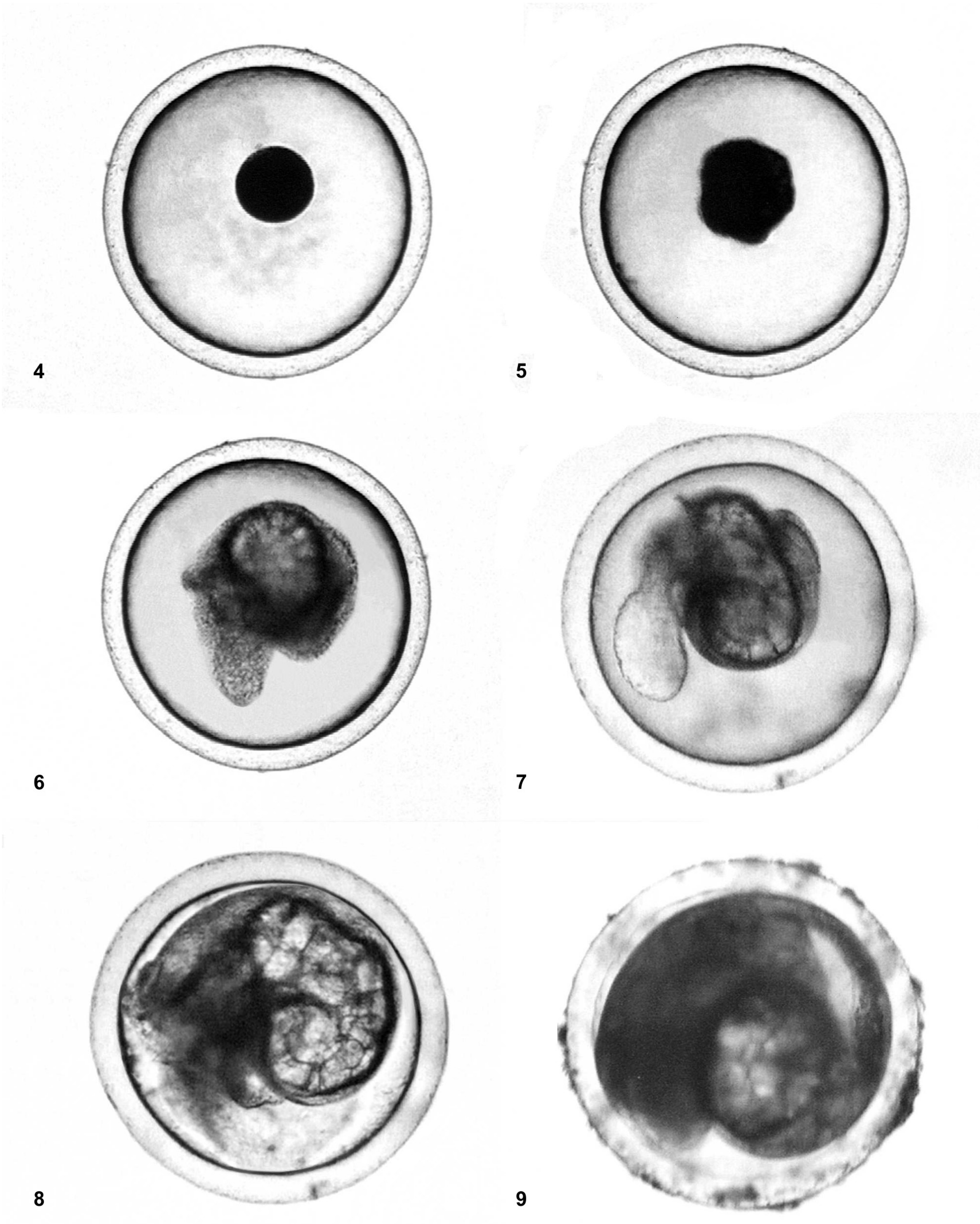


Fig. 3. *Vertigo angustior*: duration of embryonic development dependent on the mean temperature (n=24)

beginning of July 2006 (life span ca. 34 months). Dying out of the snails was distinctly seasonal (June–August) and took place 5–16 days after laying of the last egg (only once later: after 44 days).



Figs 4–9. *Vertigo angustior*: a typical course of embryonic development at ca. 21°C, light microscope, 100×; 4 – newly deposited egg; 5 – third day; 6 – fourth day; 7 – fifth day; 8 – sixth day; 9 – ninth day

Population structure. In the lakeshore site both juveniles and adults were present during all year (the proportion of very small snails was underestimated because of the sampling method adopted). In the spring the number of snails in the samples was small, and apparently adults dominated (proportion of juveniles 10–15%). In June the average proportion of juveniles rapidly increased to 43.2% (in some years even up to 60%), and all the shells bore the light stria near aperture or, rarely, only periostracum damage (hibernation). In July the percentage of juveniles decreased to 36.5% (of these 7.9% subadult) and, besides hibernating snails, few hatchlings appeared. Usually at the beginning of August the proportion of juveniles was the smallest (12–16%), and then increased rapidly. At half of September the juveniles (hatchling to subadult) constituted on average 32.6% of the population, and at the beginning of October – 43.5% (wide variation from 23.6 to 72.4%, depending on the year). At the end of October mainly adults were found among the grasses (few), with apertures sealed with mucous epiphragms. In the studied population the active period (growth, reproduction) was distinctly shorter, compared to Sharland's data from Wales (CAMERON 2003).

In the sample taken on 16.09.2007 on the lakeshore the age structure was the following (n=60): 53.3% individuals hatched in 2007 (33.3% juvenile + 20.0% adult), 28.3% hatched in the previous year, 11.7% hatched two years earlier and 6.7% hatched three years earlier. In the sample of 2.10.2007 from the meadow the age structure was similar (n=72): 65.3% hatched in 2007 (23.6% juvenile + 41.7% adult), 25.0% hatched in the previous year, 8.3% hatched two years earlier and 1.4% hatched three years earlier. In the lakeshore sample of 1.10.2008 the age structure was somewhat different (n=87): 34.5% hatched in 2008 (26.4% juvenile + 8.1% adult), 55.2% hatched in the previous year, 9.2% hatched two years previously and 1.1% hatched three years before. The age of the oldest snails (bleached shells with a distinct stria) found in October was 36–38 months.

Most of the empty adult shells found in the autumn showed a distinct stria and periostracal lesions only on the apex (life span of about one year), fewer had a stria and small periostracal lesions on the whole surface (two years). Shells with no stria and no periostracal lesions (life span 1.5–2.5 months) and bleached shells with a distinct stria (life span of about three years) were foud rather rarely.

In the literature (CAMERON 2003, CAMERON et al. 2003) the species is generally regarded as annual, with a variable proportion of snails surviving till the second year.

Shell variation. The sinistral, spindle-shaped shells were usually brown, less often yellow-brown or horny-brown. The surface of middle whorls, except the embryonic shell and body whorl, was covered by

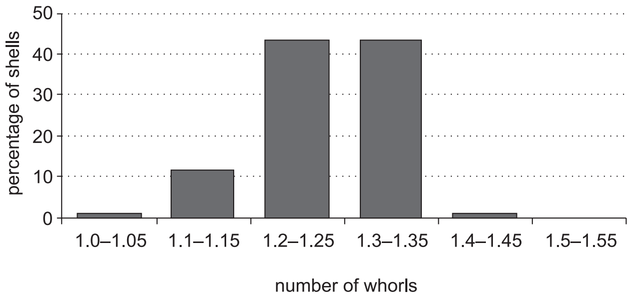


Fig. 10. *Vertigo angustior*: variation in the number of whorls of embryonic shells (n=97)

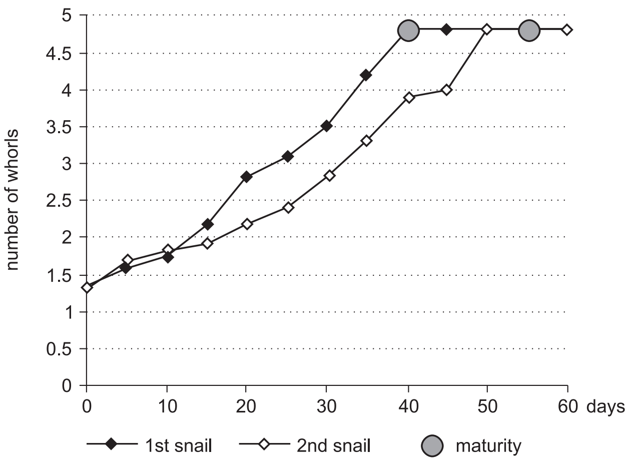


Fig. 11. *Vertigo angustior*: growth curves in the laboratory

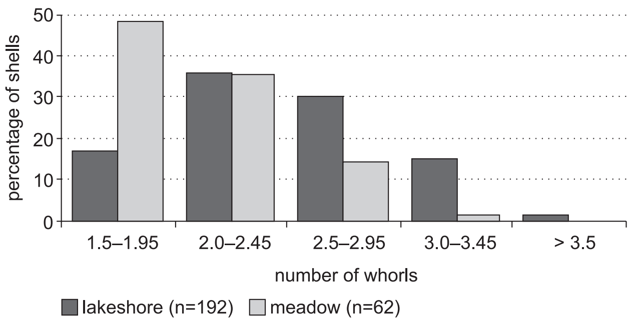
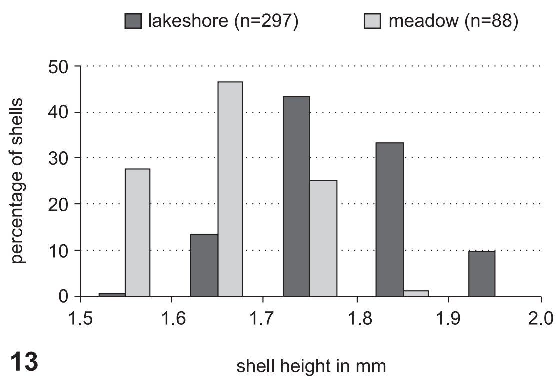


Fig. 12. *Vertigo angustior*: variation in the position of single light stria on the shell

distinct striae or riblets. Adult shells had four lamellate teeth in the aperture (parietal, angular, columellar and upper palatal) and fairly often one tuberculate tooth (lower palatal); a tuberculate basal tooth was rarely present, and sporadically strongly marked.

The measurements of adult shells from the lakeshore site were (n=295): height 1.59–1.98 mm (mean 1.78 mm, SD=0.08), width 0.92–1.06 mm (mean 0.99 mm, SD=0.03), number of whorls 4.5–5.35 (mean 4.90, SD=0.16), height/width ratio 1.59–2.05 (mean 1.81, SD=0.08). The largest shells found in that site were: I – height 2.02 mm, width 1.01 mm, 5.35 whorls; II – height 2.00 mm, width 0.99 mm,



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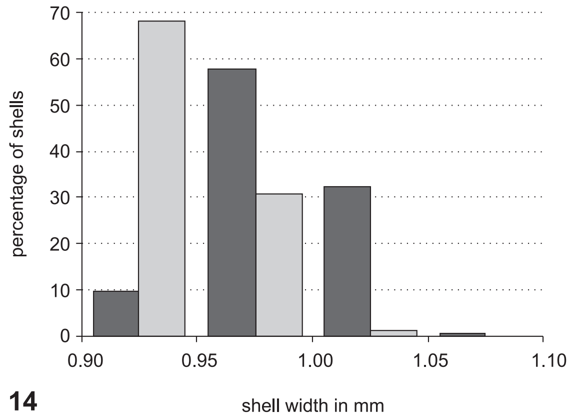

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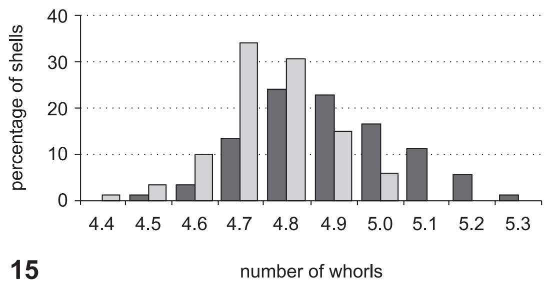

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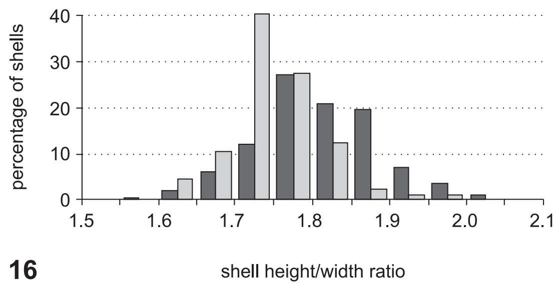

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Figs 13–16. *Vertigo angustior*: shell size variation

5.35 whorl (both subadult – no crest, only columellar and parietal teeth developed). Shells from the meadow site were slightly smaller (n=88): height 1.50–1.84 mm (mean 1.64 mm, SD=0.07), width 0.90–1.01 mm (mean 0.94 mm, SD=0.02), number of whorls 4.4–5.0 (mean 4.76, SD=0.12), height/width ratio 1.60–1.97 (mean 1.74, SD=0.06). Shell variation in the two populations is presented in Figs 13–16. Pearson's correlation coefficients between pairs of shell parameters were: for the lakeshore population (n=295): height/width r=0.40, height/number of whorls r=0.84, width/number of whorls r=0.25; for the meadow population (n=88): height/width r=0.57, height/number of whorls r=0.72, width/number of whorls r=0.28.

Accompanying species. The species composition of the malacocoenoses of which *V. angustior* was a component was rather varied. Examples of malacocoenoses:

– northern end of Lake Sosnowe – sample of 15.08.2004 (n=47): *Vertigo angustior* (33), *Vertigo pusilla* (5), *Punctum pygmaeum* (3), *Euconulus fulvus* (2), *Carychium tridentatum* (1), *Columella aspera* (1), *Vertigo substriata* (1), *Nesovitrea hammonis* (1). Sample of 2.10.2005 (n=28): *Punctum pygmaeum* (10), *Vertigo angustior* (6), *Arianta arbustorum* (5), *Vertigo pusilla* (2), *Vertigo pygmaea* (1), *Truncatellina cylindrica* (1), *Euconulus fulvus* (1), *Vallonia excentrica* (1), *Cepaea hortensis* (1). Besides, other samples from the site taken in various years and seasons contained *Vertigo ronnebyensis*, *Vitrina pellucida*, *Arion circumscriptus*, *Arion subfuscus*, *Arion rufus* and *Deroceras laeve*, and at high water level in the lake also *Euconulus alderi* and *Vallonia pulchella*,

– southern end of Lake Sosnowe – sample of 12.10.2008 (n=24): *Vertigo angustior* (8), *Vertigo pygmaea* (4), *Punctum pygmaeum* (3), *Carychium tridentatum* (1), *Pupilla muscorum* (1), *Euconulus fulvus* (1), *Vallonia costata* (1), *Vallonia excentrica* (1), *Nesovitrea hammonis* (1), *Vitrina pellucida* (1), *Euomphalia strigella* (1), *Arion circumscriptus* (1),

– meadow on the Brda – sample of 26.02.1992 (n=39): *Vertigo angustior* (19), *Carychium tridentatum* (4), *Succinea oblonga* (4), *Cochlicopa lubrica* (3), *Pupilla muscorum* (2), *Vallonia pulchella* (2), *Deroceras laeve* (2), *Vertigo pygmaea* (1), *Euconulus alderi* (1), *Nesovitrea hammonis* (1).

Other information. On the shore of Lake Sosnowe the snail density varied very much between the years and sampling plots (from about a dozen to 500–600 individuals per square metre). The greatest density was observed on the meadow on the Brda, where a moss tuft detached from the substratum, 0.10 × 0.20 m in size, contained 19 *V. angustior* (950 when converted to 1 square metre).

Vertigo moulinsiana (Dupuy, 1849)

Habitat. In the studied area the snail occurred in a narrow rush and reed belt around a small lake near the village of Korne. The lake was surrounded by cultivated fields (for details see MYZYK 2004). Since the spring of 2005 the snails were found also along the ditch draining the lake, but in 2008 the vegetation next to the ditch was partly damaged as a result of herbicide use, and then by the beaver dam-building.

Reproduction. Of the six snails hatched and grown in the laboratory (each kept separately), five started to lay eggs in the year of hatching, 1–15 days after shell growth completion, and one – next year, 142 days after shell growth completion. In the year of hatching the reproduction started between July 28 and September 12, and ceased between September 3 and 16 (duration of breeding period 5–50 days). After hibernation the reproduction started on 13–29 April and ceased between June 28th and August 27th (breeding period of 64–137 days). Usually, one egg was laid every 2–3 days (rarely daily), but sometimes irregular intervals between consecutive egg-layings could last even 42 days.

Adults collected in the field in early spring (end of March – beginning of April) started reproducing after 8–20 days, those collected later (half of May – end of July) often laid eggs after a few hours. Those hibernating in the laboratory laid their first eggs at about half of April. Most snails produced eggs with equal intensity at the beginning (April-beginning of May) and end of the breeding period (June-August, depending on the snail). During the breeding period usually one egg was produced every 2–3 days (less often daily, or even two eggs during 24 hours); the maximum number of eggs produced during one month was 26. Outside that main breeding period irregular long intervals between consecutive eggs occurred, and on the spring/summer boundary the reproduction sometimes stopped for 1–3 months. The breeding period usually ended in July-August, and only one snail continued laying eggs till October (Table 1). The time between the first and the last egg during the season was usually 63–132 days (maximum 189 days).

The number of eggs produced per season was 2–36 (mean 19, SD=9, n=22). Adults collected in the field on April 10th 2004 and reproducing only during one season produced 14–36 eggs (mean 27, SD=6, n=8), but other individuals, collected on March 26th 2005, laid only 7–14 eggs (mean 11, SD=2, n=6). Another example of varied reproduction: a snail collected on 27.07.2004 (newly adult, hatched in the previous year), laid 26 eggs from 27.07 to 25.08.2004, and only two eggs after hibernation: on 17.05 and 27.07.2005. The maximum number of eggs produced during life time (three seasons) was 60 (34+11+15) (Table 1). Snails hatched in the laboratory produced 18–34 eggs per lifetime (mean 25, SD=5, n=6), of these 2–13 in the year of hatching and 11–32 next year.

In the wild, eggs were found mainly in thick tussocks of grass growing along the water edge and in the moss layer. During the breeding period some adults were hidden under objects laying on the ground (stones, pieces of bark, thick branches) and may have been laying eggs there. The earliest-laid eggs were found in the sample of May 20th 2007 (oval immobile embryos), and in the sample of 11.06.2006 the advancement of embryonic development varied widely (from a few blastomeres to hatching). Intensive reproduction continued till as late as the end of July (e.g. 10 snails collected on July 27th 2005 produced 17 eggs within about a dozen hours after placing them in the laboratory). Only single eggs with much advanced embryos were found (shells of 1.3–1.4 whorl) at the end of August and beginning of September.

Egg. Eggs of *V. moulinsiana* were covered by three envelopes, like those of *V. angustior*, but the surface of external envelope was always smooth. The gelatinous envelope was relatively thick and usually composed of 10–15 layers. The average total thickness of the envelopes constituted 15.5% of egg diameter. The egg measurements (n=507) were: diameter 0.55–0.87 mm (mean 0.737 mm, SD=0.041), egg chamber diameter 0.43–0.73 mm (mean 0.623 mm, SD=0.042) (for details see MYZYK 2005b).

Embryonic development. Most eggs were laid at the stage of one cell (some at the stage of oocyte II), but in some the advancement of embryonic development indicated a few days of retention (embryo usually prior to shell formation, and only in one egg it had a broken shell of ca. 0.3 whorl). The course of development showed no significant differences compared to *V. angustior*. At the temperature of 24°C hatching took place after 10–11 days, at 20°C usually after 15–16 days, at 17°C after 21 days (Fig. 17), and at ca. 13°C after 67 days (not shown in the figure). In some eggs the duration of embryonic development was distinctly longer compared to most eggs incubated at the same temperature. Pearson's correlation coefficient between the temperature and the duration of development was r=–0.77, n=67. In eggs submerged in water the development progressed like in those kept on damp leaves, and the hatchlings emerged above the water crawling on the container walls. According to the literature (CAMERON et al. 2003) the duration of embryonic development is

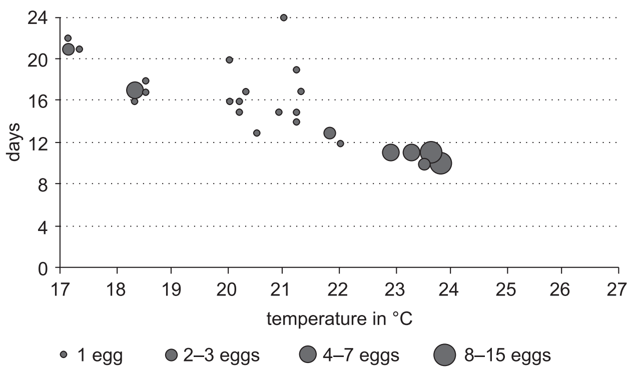


Fig. 17. *Vertigo moulinsiana*: duration of embryonic development dependent on the mean temperature (n=66)

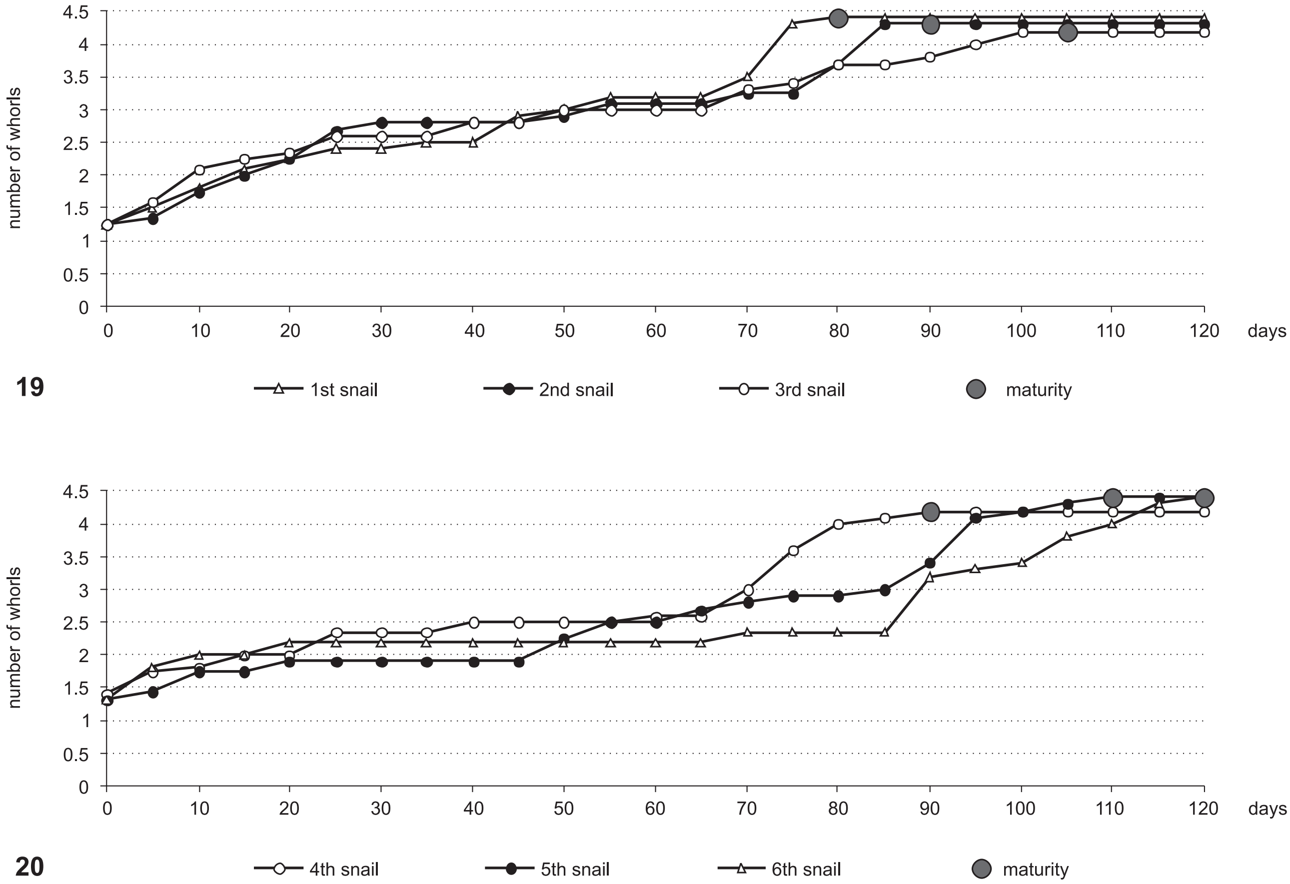
shorter than two weeks, but there is no information on the incubation temperature.

Growth. Embryonic shells were usually composed of 1.25–1.3 whorl (mean 1.28, SD=0.08, n=152, range 1.1–1.5) (Fig. 18). The shell width was 0.55–0.69 mm (mean 0.630 mm, SD=0.028, n=92). The surface of embryonic shells was covered by fine irregular tubercles, and postembryonic increments were often separated by a narrow stria of growth disturbance.

Among 22 juvenile snails hatched/placed in the laboratory only six became mature (27.3%). The remaining ones died 4–90 days from hatching, with shells of 1.2–3.7 whorls. The whole shell growth period for the six snails could be divided in three stages (Figs 19–20). Just after hatching the growth was relatively fast; they reached two whorls within 9–15 days (rarely longer). Twenty-thirty days after hatching (mean 24), at shell size of 1.9–2.8 whorls (mean 2.4), the growth was distinctly inhibited. The duration of slow growth period ranged from 40 to 65 days (mean 49) and at the end of it the shells reached 2.35–3.25 whorls (mean 2.9). It was followed by another period of fast growth (15–40 days, mean 26), and the shells reached their ultimate size of 4.15–4.4 whorls (mean 4.3), while the lip became reflexed. The time from hatching till maturity was 79–119 days (mean 99 days, SD=14, n=6). The time elapsing from the appearance of the first teeth to formation of reflexed lip (subadult stage) was 4–10 days. During adult life the reflexed lip showed some increment (in specimens collected in the field up to ca. 0.20 mm) and its damage was regenerated. Besides, callus and additional tuberculate teeth were formed on the basal and platal wall.

Fig. 18. *Vertigo moulinsiana*: variation in the number of whorls of embryonic shells (n=152)

Hatching in the wild started at about half of June (e.g. on 11.06.2006 some embryos had already broken the internal egg envelopes), and ended in September. When conditions were favourable (plus temperatures in day and night) some snails were still feeding at the end of November. The growth rate of juveniles was rather varied. From 10 to 15% of juveniles became mature in the year of hatching (usually after the



Figs 19–20. *Vertigo moulinsiana*: growth curves of two groups snails kept in the laboratory; 19 – snails hatched in May 2004; 20 – snails hatched in May 2005

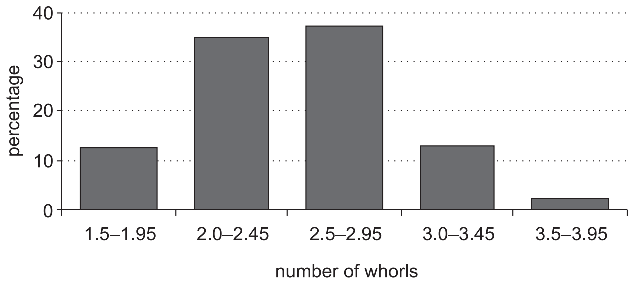


Fig. 21. *Vertigo moulinsiana*: variation in the position of single light stria on the shell (n=419)

reproductive period ended). Hibernating snails, both juvenile and adult, were usually found in wisps of dried sedge and grass blades hanging 20–50 cm above the ground or water table, and inside thick tussocks of sedges and grasses (rarely in the litter and moss on the ground). After hibernation a distinct light stria was marked on ca. 60% of shells; only slight traces of growth disturbance were visible on the remaining shells (resembling summer growth disturbances). The mean shell size of hibernating juveniles, based on the position of the light stria, was 2.50 whorls (SD=0.45, n=419, range 1.5–3.9) (Fig. 21). Some juveniles resumed growth at about half of April, others as late as at the beginning of May (samples from the end of April contained both shells with fresh increments of up to ca. 0.5 whorl, and shells with no such increments). Maturation of hibernating snails usually took place in June or at the beginning of July, but in some years juveniles with a stria on their shells were sporadically found even at the beginning of November.

Longevity. The life span of snails hatched and grown in the laboratory was 422–508 days (mean 456, SD=27, n=6). All of them died one year after hatching, between July and September, 5–29 days (mean 17) after laying the last egg.

Most of the snails collected as adults and placed in the laboratory died after 3–5 months, three survived much longer. One, collected on 16.05.2004 (shell with no stria and no periostracal lesions – hatched and adult in 2003), survived till 25.09.2006 (life span ca. 39 months). The second, collected on 26.03.2005 (shell with a stria and periostracal lesions on all surface – hatched in 2003 and adult in 2004), survived till 25.09.2006 (life span 37–38 months). The third, collected on 27.07.2004 (shell with a stria and small peirostracal lesions on apex – hatched in 2003 and adult in 2004), survived till 15.09.2005 (life span ca. 24 months). In the laboratory dying out usually took place in the period end of June – end of September, 2–71 days (mean 31) after the last egg laying.

In the wild most adults died in the second year of life, but some lived longer and hibernated for the second time. A small proportion (3–5%) hibernated for the third time and some reached the age of 38–39 months (bleached shells with a distinct stria). The age structure in the sample of 13.04.2008 (n=131) was the following: 82.4% snails hatched in the previous year (74.0% juvenile + 8.4% adult) and 17.6% hatched two years before. The sample of 9.11.2008 (n=145) contained 72.4% snails hatched in 2008 (66.9% juvenile + 5.5% adult), 24.1% snails hatched in the previous year, 2.8% hatched two years before and 0.7% hatched three years before (bleached shell with a distinct stria). During almost the whole year the samples contained, besides live snails, juvenile and adult shells which constituted 5–10% of the sample size. Among the empty shells, the juvenile:adult ratio was similar to that among the live part of the same sample.

Population structure. Except winter months, samples for the analysis of age structure were taken from September 2003 till September 2005 (Fig. 22). In the summer and autumn the number of live snails in the samples ranged from 134 to 293, and in the spring – from 71 to 97. Each sample contained snails collected in a few places and at different heights above the ground.

Both juveniles and adults were present in the studied population during the whole year (Fig. 22). In order to visualise the changes in the age structure, juveniles were divided into three groups: small, up to

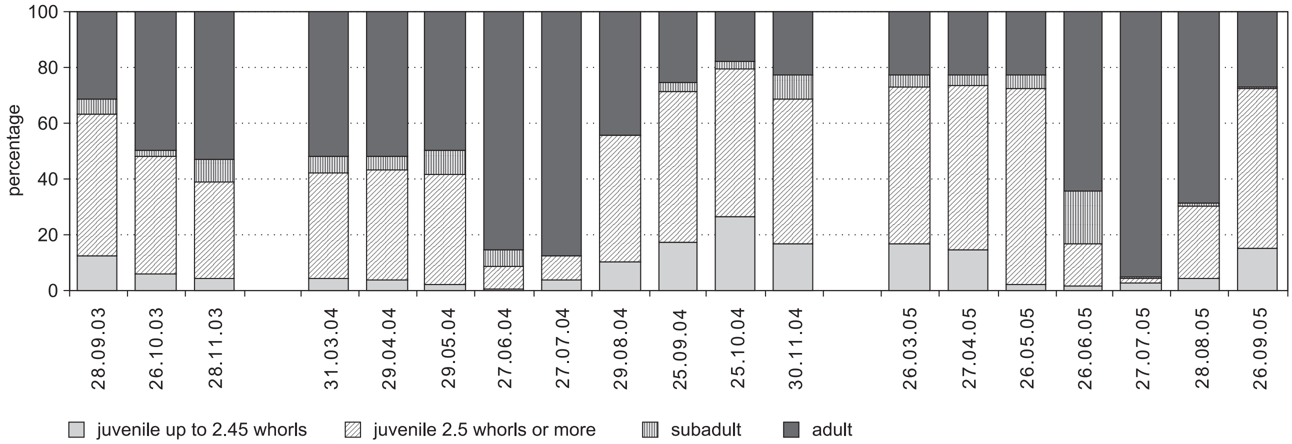
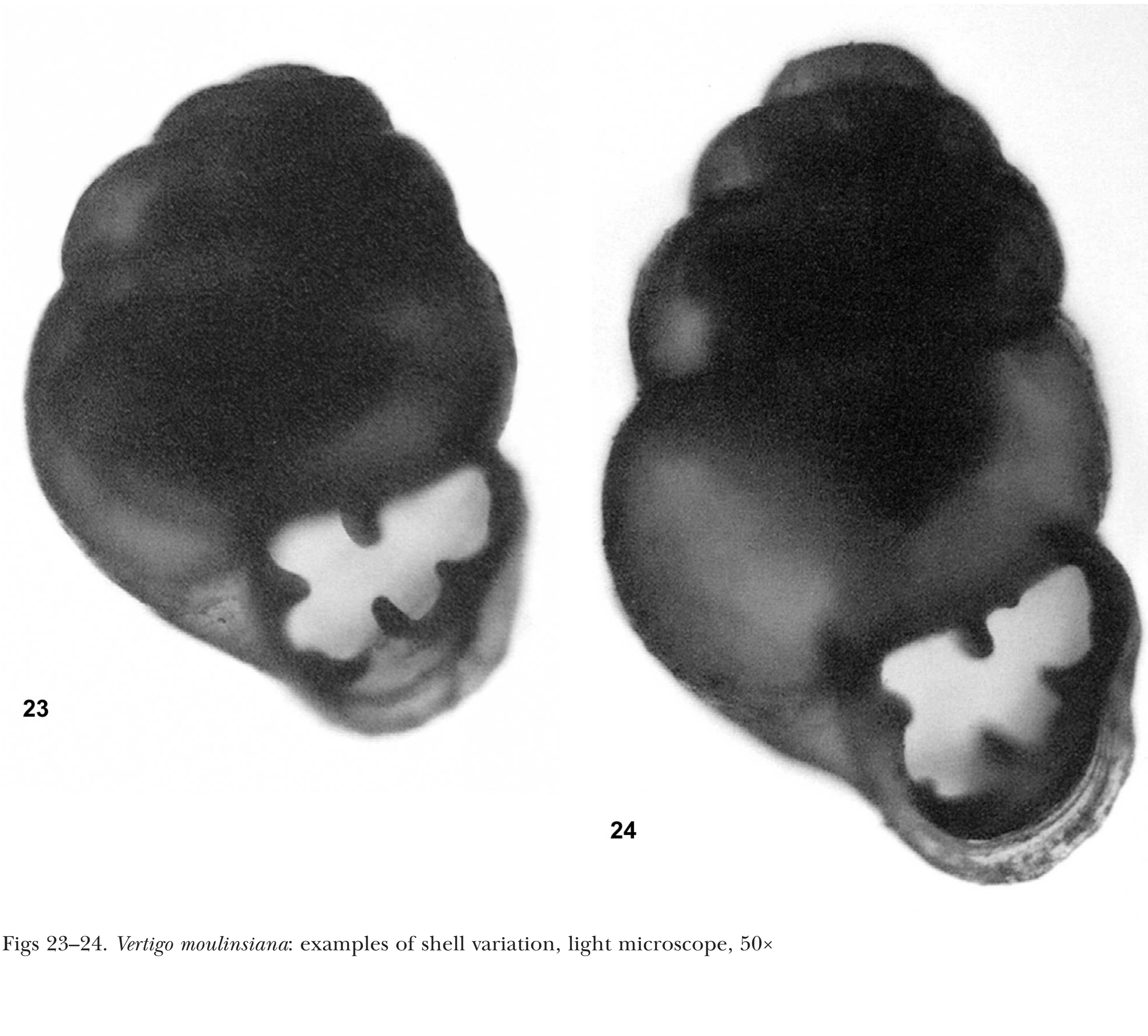


Fig. 22. *Vertigo moulinsiana*: variation in the population structure from September 2003 to September 2005

2.45 whorls (their percentage in the samples was clearly underestimated), large, above 2.5 whorls, and subadult, with teeth visible in the aperture. From March till May the total proportion of juveniles in the samples remained roughly constant (47–77%, depending on the year), but their mean shell size gradually increased. At the end of May and in June the proportion of subadults (small teeth in the aperture) ranged from 5.1 to 19.4% of all sampled snails and soon they reached maturity. Samples taken at the end of June contained 14–36% juveniles, and few hatchlings appeared. The proportion of juveniles was the smallest at the end of July (4.9–12.4%), and from August their percentage increased very fast (mass hatching); the abundance of juveniles reached its peak (69–82%) in September or October. Since massive hatching in October was unlikely, it can be supposed that this was the effect of dying out of numerous adults (a change in the distribution of shell appearance was also observed), or of the appearance of juveniles hatched in September on the plants (higher air humidity). Later, the total proportion of juveniles was close to their percentage found at the beginning of the season, but at the end of November the proportion of subadult snails was rather high (maturation of the present year's hatchlings). Similar seasonal changes in the population structure in a locality in England were observed by KILLEEN (2003).

Shell variation. The dextral, ovate or ovate-conical shells (Figs 23–24) were almost smooth, with weak irregular striation, and brown or horn-brown in colour. The apertural barriers in the studied populations consisted of 4–5 distinct teeth and a varied number of fine tuberculate teeth. The frequency of occurrence of angular tooth was correlated with the shell height. In small shells below 2.1 mm it was very rarely present (mean 12.5 %), in shells exceeding 2.4 mm it occurred very frequently (mean 87.5%) (Fig. 25).

The adult shell measurements were (samples of 2002/2003, n=275): height 2.05–2.58 mm (mean 2.29 mm, SD=0.09 mm), width 1.40–1.63 (mean 1.51 mm, SD=0.04 mm), number of whorls 4.1–4.8 (mean 4.39, SD=0.14), height/width ratio 1.40–1.70 (mean 1.52, SD=0.05) (for details see MYZYK 2004). The smallest shells were found in March 2005: I – height 2.02 mm,



Figs 23–24. *Vertigo moulinsiana*: examples of shell variation, light microscope, 50×

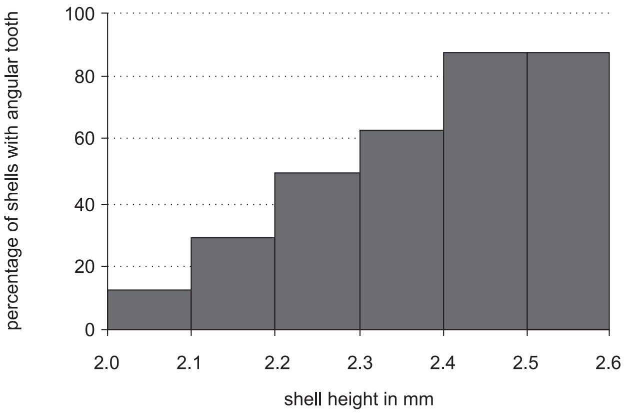


Fig. 25. *Vertigo moulinsiana*: relation between shell height and frequency of shells with angular tooth

width 1.54 mm, 4.0 whorls; II – height 2.02 mm, width 1.38 mm, 4.1 whorls.

Shells of snails hatched and grown in the laboratory were somewhat smaller than those from the natural population (n=6): height 1.98–2.25 mm (mean 2.14 mm), width 1.40–1.47 mm (mean 1.43 mm), number of whorls 4.15–4.4 (mean 4.3), height/width ratio 1.41–1.55 (mean 1.49).

Other information. In the laboratory adult snails often stayed in the upper part of the container, though they fed and laid eggs on the leaves on the bottom. On dry substratum they crawled at ca. 0.5 mm/s (=3 cm/min). The mantle cavity of adults was rather large and the air accumulated in it enabled them to float when dropped in the water (*V. antivertigo*, living in similar habitats, sinks).

In the wild the population structure varied with the place of sampling (vegetation) and height above the ground (water). Both the youngest juveniles and adults were found next to the ground surface, while only larger juveniles and adults climbed higher, and almost exclusively adults climbed to the height of about 1 m. Besides, the proportion of juveniles was somewhat higher in samples taken after a rain or during fog. Shaking snails out of the vegetation gave satisfactory results only in the spring. In the summer and autumn it was not very effective because of the sticky mucus which glued the snails to the substratum (most snails remained on the vegetation, and fresh increments of juveniles often became damaged).

The substratum in places of occurrence of the snails usually had an acid pH: mean soil pH 6.5 (range 6.3–6.7, only in one place, on dumped rubble, it was 7.0–7.5), mean water pH 6.3 (range 5.8–6.8, n=15). Despite the abundant occurrence of live snails on the vegetation, empty shells in the litter were very few.

Vertigo pygmaea (Draparnaud, 1801)

Habitats. In the environs of Sąpolno the snail was fairly common in open habitats (meadows, balks, wasteland), but usually did not reach high densities. Besides, it was found in small, sparse forests, in grassy places where its densities were somewhat higher than in the open (dampness persisting for a longer time favoured reproduction).

Reproduction. Adults collected in the spring (March–May) started egg-laying after 2–4 weeks of feeding, those collected in July and August usually laid eggs on the next day after placing them in the laboratory. A snail collected on 15.08.2005 as a juvenile (shell with a stria) became mature on August 21th and laid its first egg after four days. Snails hibernating in the laboratory started reproducing between April 17 and June 5. Some snails produced series of eggs, others laid one egg every 2–3 days (rarely daily). During the period of the most intensive reproduction a maximum of 26 eggs was produced during one month. At the end of the breeding period most snails showed irregular, long intervals between consecutive eggs (even up to three weeks). Some snails showed similarly long intervals also in the middle of the season (e.g. June or July). The reproduction in the laboratory usually lasted 32–140 days and it was shorter only in the case of snails collected in the summer. The last egg of the season was usually laid between July and beginning of September (sometimes earlier). In most containers eggs were laid on the leaf fragment which was the last to dry during dry periods, usually along the main nerves of the leaf. Very often the eggs were embedded in a layer of detritus.

Among the 20 snails placed in the laboratory only 10 laid eggs. Most of them produced eggs only during one season. The number of eggs per season ranged from 6 to 70 (mean 22, SD=18, n=13). Snails reproducing during two seasons showed a higher fecundity: one, collected on 29.03.2005, laid 79 eggs (70+9), the second, collected on 23.07.2005, produced 52 eggs (25+27) (Table 1). Another, collected on 25.08.2005 as juvenile, during its lifetime produced 32 eggs (15+17).

In the wild, reproduction started in June, but initially it was not very intensive. The latest-laid eggs were found on 10.09.2006 (embryos with shells of 0.3 and 0.9 whorls).

Egg. Eggs of *V. pygmaea* were covered by three envelopes, like in *V. angustior*, but the surface of the external envelope was always smooth. Compared to the eggs of *V. moulinsiana*, they were usually distinctly smaller, their gelatinous envelope was relatively thin and composed of only a few layers with distinct borders. The internal envelope was usually fairly thick (up to ca. 0.005 mm). The mean total thickness of envelopes was 9.1% of egg diameter. The egg measurements (n=211) were: diameter 0.42–0.60 mm (mean 0.540 mm, SD=0.025), egg chamber diameter 0.38–0.55 mm (mean 0.491 mm, SD=0.025) (for details see MYZYK 2005b).

Embryonic development. Most eggs were laid at one-cell stage, but in some eggs (especially those laid

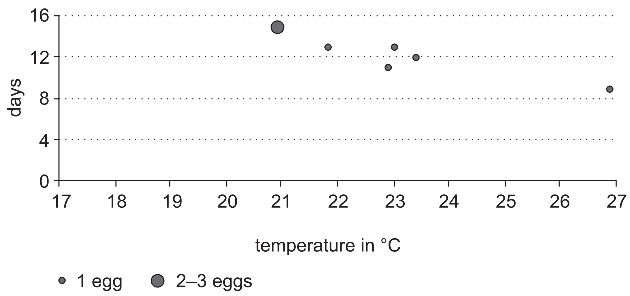


Fig. 26. *Vertigo pygmaea*: duration of embryonic development dependent on the mean temperature (n=7)

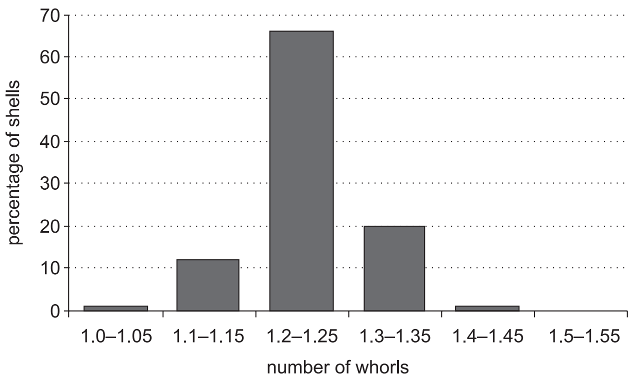


Fig. 27. *Vertigo pygmaea*: variation in the number of whorls of embryonic shells (n=100)

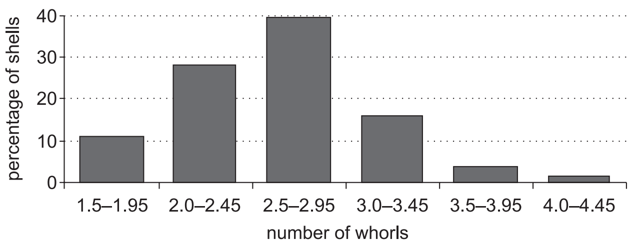


Fig. 28. *Vertigo pygmaea*: variation in the position of single light stria on the shell (n=237)

in series) the advancement of development indicated 1–3 days of retention. The rate of embryonic development was slightly smaller than in *V. angustior* at the same temperature (Fig. 26). Pearson's correlation coefficient between the temperature and the duration of development was: r=–0.93, n=7.

Growth. Most embryonic shells had 1.2–1.25 whorl (mean 1.23, SD=0.06, n=100, range 1.05–1.4) (Fig. 27). The width of the 14 measured shells was 0.42–0.53 mm (mean 0.499 mm, SD=0.026). The embryonic shell surface was covered by fine irregular tubercles. Embryonic shells of some snails collected in the field bore striae marking a growth disturbance (probably desiccation).

Hatching in the wild started in July (in some years slightly earlier), and ended in the second half of September. On average 18% juveniles reached maturity in the year of hatching. Shells of hibernating juveniles nearly always bore a light stria. The mean shell size of hibernating juveniles, based on the position of the single light stria, was 2.59 whorls (SD=0.49, n=237, range 1.6–4.45) (Fig. 28). Adult shells with two light striae were found rarely (ca. 6%), and the distance between the striae was usually 0.2–1.0 whorl (sporadically up to 1.7). The time of activity resumption by hibernating juveniles varied. Some juveniles resumed growth in the second half of May, and at the beginning of June fresh increments of up to ca. 0.6 whorl were visible on their shells. Maturation usually took place in July and August, but in some years juveniles with a light stria on their shells were found as late as the beginnng of October.

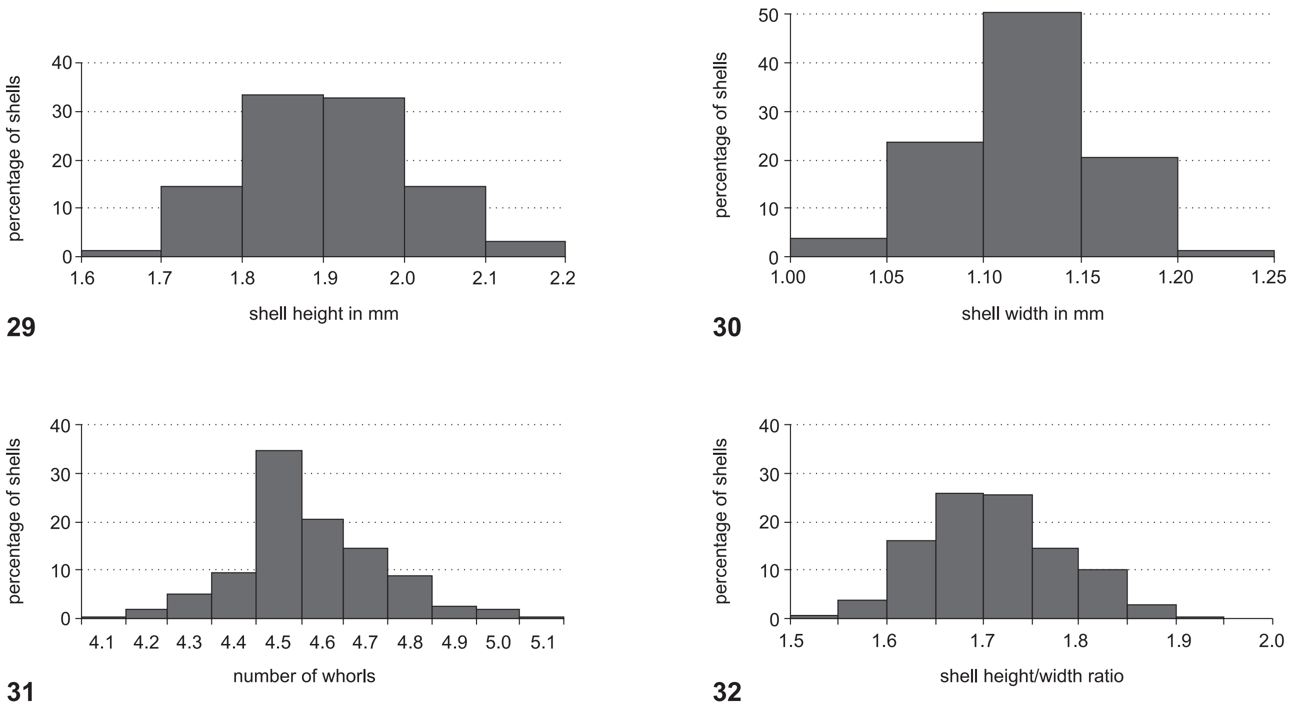
Longevity. Adults collected in the field mostly died after 2–3 months, and only three survived much longer. One, collected on 29.03.2005 (shell with a stria and fine periostracal lesions on the whole surface – hatched in 2003 and adult in 2004), survived till 18.06.2006 (life span ca. 34 months). Another, collected on 23.07.2005 (shell with a stria, with no periostracal lesions – hatched in 2004 and adult in 2005), survived till 25.09.2006 (life span ca. 25 month). The third, collected as juvenile on 15.08.2005 (shell with a stria – hatched in 2004), lived till 30.07.2006 (life span ca. 23 months). In the laboratory dying out of adults usually occurred between the end of July and end of September (rarely earlier), 3–22 days after the last egg-laying.

The age structure of several samples taken in October 2008 was the following (total n=33): 39.4% hatched in 2008 (33.3% juvenile + 6.1% adult), 48.5% hatched in the previous year and 12.1% hatched two years before. The oldest snails found in the summer (July–August) had shells with much damaged periostracum (bleached) and a distinct stria (age ca. 3 years).

Shell variation. The dextral shells of *V. pygmaea*, ovate and elongated to various degree, were brown or yellow-brown. The surface of some of them was smooth, in other shells it was covered by a dense network of fine wrinkles. The apertural barriers usually consisted of five distinct teeth: columellar, parietal, two palatals and one basal. Some shells lacked the basal, and sporadically the basal was bifid. Only one shell had a very small tuberculate angular. The adult shell measurements (n=314) were: height 1.61–2.18 mm (mean 1.90 mm, SD=0.10), width 1.01–1.20 mm (mean 1.11 mm, SD=0.04), number of whorls 4.1–5.1 (mean 4.57, SD=0.16), height/width ratio 1.52–1.94 (mean 1.71, SD=0.07) (Figs 29–32). Pearson's correlation coeffcients between the shell parameters were (n=314): height/width r=0.58, height/number of whorls r=0.84, width/number of whorls r=0.32.

Vertigo antivertigo (Draparnaud, 1801)

Habitats. The snail was found only in places with high constant humidity, for example river banks, lake shores, near field ponds and on marshy meadows. In



Figs 29–32. *Vertigo pygmaea*: shell size variation (n=314)

the studied area it was rather common but usually did not reach high densities.

Reproduction. Snails hatched in the laboratory started laying eggs 32–50 days from hatching (5–6 days after reaching maturity). The breeding period was very short (15–19 days), and produced few eggs (6–17).

Adults collected in the field in May-June started reproducing 6–25 days after placing them in the laboratory. Hibernating adults (or those collected in winter) laid their first eggs between April 8th and 22nd. The intensity of reproduction from May to August was usually rather high (one or two eggs laid nearly every day), and some snails produced up to 46 eggs during one month. The breeding period usually lasted 50–88 days and only in the case of snails hibernating in the laboratory it was much longer – up to 172 days (e.g. from April 20th till October 8th). The last egg of the season was laid by some snails in May, by others in November.

The number of eggs produced in one season varied widely and ranged from 6 to 184 (mean 55, SD=49, n=14). Most snails laid eggs only during one season (maximum 56) and died. The most fecund snails were those reproducing during two seasons: one, collected on 6.02.2005, produced 218 eggs (184+34), another, collected on 6.02.2005, laid 192 eggs (135+57) (Table 1), the third, collected on 16.05.2004, laid 138 eggs (96+42).

In the wild, egg-laying started at half of May, and the earliest-laid eggs were found on 20.05.2007 (oval, immobile embryos). The end of the reproductive season could not be ascertained.

Egg. Eggs of *V. antivertigo* differed from the eggs of the preceding species in the presence of an additional mucous envelope of variable density and thickness (usually 0.03–0.06 mm, sometimes up to 0.10 mm). The egg size, disregarding the mucous layer, was (n=674): egg diameter 0.55–0.78 mm (mean 0.648 mm, SD=0.034), egg chamber diameter 0.47–0.64 mm (mean 0.559 mm, SD=0.029) (for details see MYZYK 2005b). The mean total thickness of the envelopes (without mucous layer) was 13.7% of egg diameter.

Embryonic development. Most eggs were laid at one-cell stage (some at the stage of oocyte II). Very rarely the development in newly laid eggs was distinctly advanced (1–3 days of retention). The rate of development at corresponding temperature did not differ from that of *V. angustior*. At the temperature of 27°C hatching took place after 8 days, at 23°C usually after 11 days, at 19°C after 16 days (Fig. 33), but at ca. 14°C only after 68 days (omitted in the figure). Pearson's correlation coefficient between the temperature and the duration of embryonic development was: r=–0.78, n=22. Eggs submerged in water developed like those resting on damp leaves; the hatch-

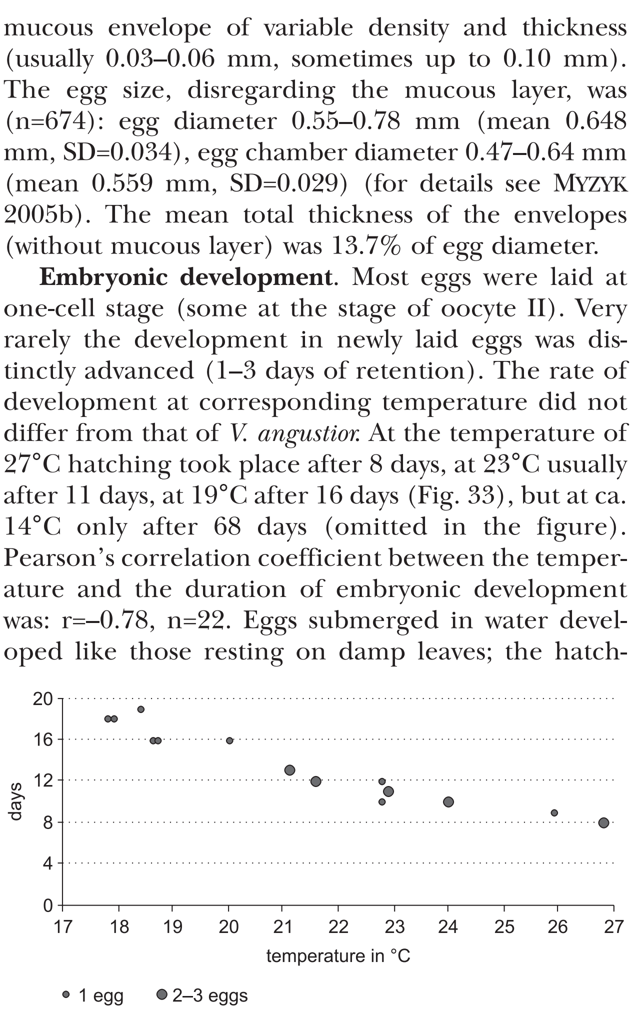


Fig. 33. *Vertigo antivertigo*: duration of embryonic development dependent on the mean temperature (n=20)

lings soon emerged from the water crawling up the container walls.

Growth. Embryonic shells were mostly composed of 1.2–1.3 whorl (mean 1.25, SD=0.06, n=114, range 1.05–1.4) (Fig. 34). The width of the 29 measured shells was 0.48–0.60 mm (mean 0.533 mm, SD=0.027). The surface of embryonic shell was covered by fine, irregular tubercles.

The growth of snails hatched in the laboratory was fairly fast (Fig. 35). The shells reached their ultimate size and the lip became reflexed 26–45 days from hatching.

Hatching in the wild started at about half of June, and at half of August some of the individuals hatched in the same year became adult. In all, on average 71% of the snails reached maturity in the year of hatching. The mean size of shells of hibernating juveniles, based on the position of the single light stria, was 2.38 whorls (SD=0.51, n=61, range 1.5–3.4) (Fig. 36). Hibernating adults were mainly found in the litter and moss near water bodies, but sometimes also among dry grass blades hanging over the frozen water surface (even a few metres from the shore). Since in the spring juveniles were found very rarely, it was impossible to ascertain the dates of growth resumption and maturation of the previous year's hatchlings.

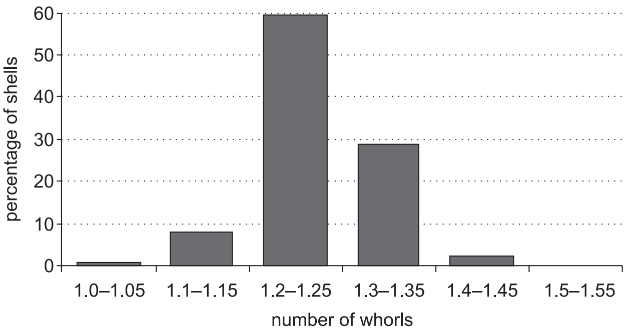


Fig. 34. *Vertigo antivertigo*: variation in the number of whorls of embryonic shells (n=114)

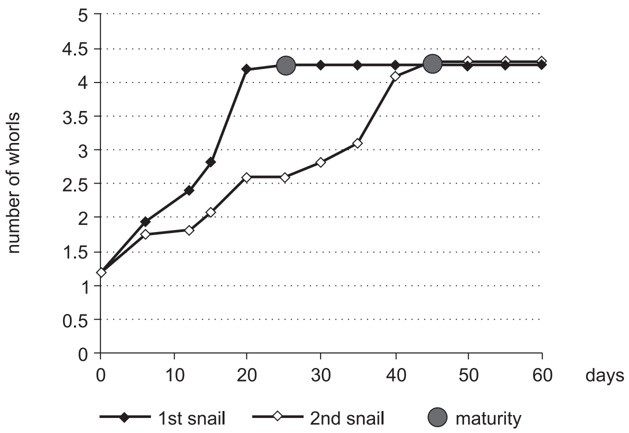


Fig. 35. *Vertigo antivertigo*: growth curves in the laboratory

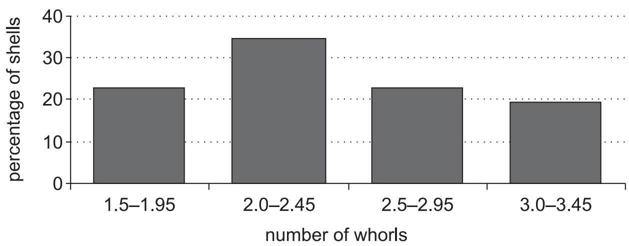


Fig. 36. *Vertigo antivertigo*: variation in the position of single light stria on the shell (n=61)

Longevity. The life span in the laboratory was 63–68 days and the adults died out at half of August.

Among adults collected in the wild some died after 2–3 months in the laboratory, others after 14–18 months. The longest-lived snails were: one, collected on 16.05.2004 (shell with a stria, of 2.5 whorl and small periostracal lesions – hatched in 2002 and adult in 2003), which survived till 29.06.2005 (life span ca. 34 months); and another two, collected on 6.02.2005 (shells without striae, or periostracal lesions – hatched and adult in 2004), which survived till 18.06 and 24.07.2006 (life span 23 and 24 months, respectively). In the laboratory dying out of adults usually occurred in the period June-August, 4–20 days after the last egg-laying.

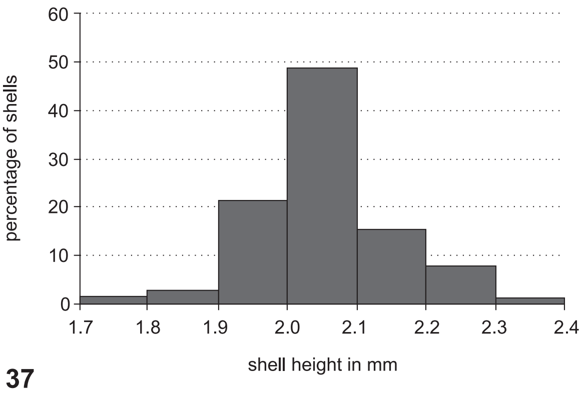
Among adults collected in the field in October (juveniles were found very rarely) ca. 65% were snails hatched in the same year, ca. 23% – hatched in the previous year, and ca. 12% – hatched two years before (mean values of 2004–2008). The oldest snails found in the spring (April-June) had much damaged periostracum (bleached) and a distinct stria (life span ca. 3 years).

Shell variation. The dextral ovate shells of *V. antivertigo* were brown or dark brown. Their surface was nearly smooth or with delicate irregular striae. The apertural barriers in most shells consisted of nine teeth (rarely more or less). The adult shell size (n=225) was: height 1.72–2.35 mm (mean 2.05 mm, SD=0.10), width 1.17–1.43 mm (mean 1.29 mm, SD=0.04), number of whorls 4.0–5.1 (mean 4.52, SD=0.17), height/width ratio 1.43–1.76 (mean 1.59, SD=0.06) (Figs 37–40). Pearson's correlation coefficient for pairs of shell parameters was (n=225): height/width r=0.72, height/number of whorls r=0.84, width/number of whorls r=0.50. Snails wintering as juveniles usually had larger shells that those that became adult in the year of hatching (among the shells exceeding the height of 2.20 mm ca. 71% had a marked light stria).

Vertigo pusilla O. F. Müller, 1774

Habitats. The species was fairly common in deciduous and mixed forests, and rarely found in open habitats (e.g. meadows, balks).

Reproduction. Adults collected in the field in the spring (April–May) started egg-laying after 5–15 days, those collected later usually started reproducing already after 1–2 days (like those which reached matur-



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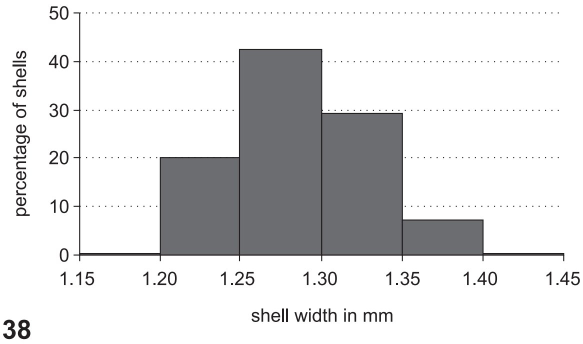

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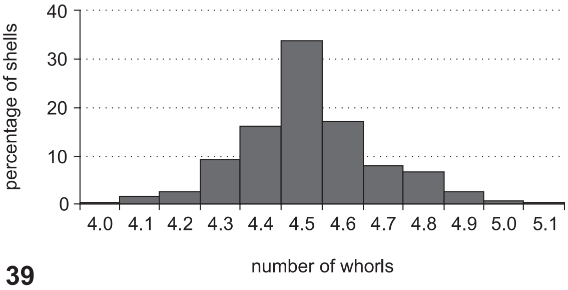

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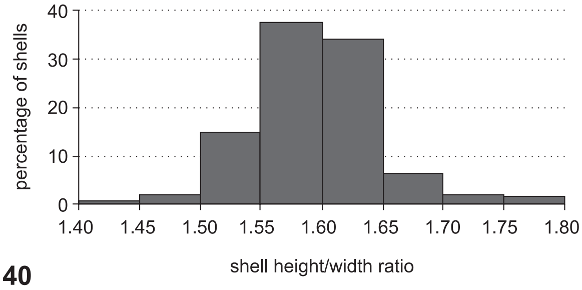

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Figs 37–40. *Vertigo antivertigo*: shell size variation (n=225)

ity in June–July). Snails hibernating in the laboratory started laying eggs between April 20th and May 18th. During the season the eggs were laid with varied intensity: in the beginning usually daily (up to 30 eggs per month), then at irregular intervals of a few days. The breeding period usually lasted 13–52 days (rarely longer, up to 134 days). Some snails laid their last egg of the season at the end of May, others at the beginning of September (only one egg was laid at half of November – Table 1).

The number of eggs produced during one season was 4–74 (mean 29, SD=18, n=12). Most snails laid eggs during one season (maximum 29) and died. Two snails which matured in the laboratory died, having produced 17 and 20 eggs (one season). Snails reproducing during two seasons were more fecund: one, collected on 15.08.2004, produced 102 eggs (28+74), another, collected on 3.05.2004, laid 89 eggs (52+37) (Table 1), the third, collected on 11.07.2004, laid 39 eggs (35+4).

In the wild, egg laying started in the second half of May (when there was rain). The earliest-laid egg was found on 27.05.2007 (spherical, immobile embryo). Most eggs were laid at the end of June and in July, in August the reproduction gradually ceased.

Egg. Eggs of *V. pusilla* were very similar to those of *V. antivertigo*. The egg size, without the mucous layer (n=337) was: egg diameter 0.52–0.70 mm (mean 0.629 mm, SD=0.027), egg chamber diameter 0.44–0.62 (mean 0.559 mm, SD=0.027) (for details see MYZYK 2005b). The mean total thickness of envelopes (without mucous layer) was 11.1% of egg diameter.

Embryonic development. Most eggs were laid at one cell stage (some at the stage of oocyte II), but in some the advancement of development indicated a few days of retention. The rate of embryonic development was somewhat smaller than in *V. angustior* at the same temperature. At the temperature of 27°C hatching took place after 11 days, at 24°C usually after 12 days, at 19°C after 18–19 days (Fig. 41). Compared to the data of POKRYSZKO (1990a) the duration of development was distinctly longer. Correlation coefficients between the temperature and the duration of embryonic development was: r=–0.88, n=28.

Growth. Embryonic shells were usually composed of 1.25–1.3 whorl (mean 1.30, SD=0.08, n=106, range 1.1–1.5 whorl) (Fig. 42). The shell width was 0.52–0.60 mm (mean 0.561 mm, SD=0.022, n=28). The embryonic shell surface was covered by small irregular tubercles.

Hatching in the wild started at about half of June (the earliest hatchling was found on 26.06.2007) and continued till September. Juveniles mostly stayed in the litter just next to the soil surface. Their growth rate was fairly varied. On average 16% of the snails reached maturity in the year of hatching, usually at the end of reproductive season or after it ended (second half of August – beginning of October). Almost all hibernating juveniles had a distinct light stria on their shells, followed by a constriction of the whorl. The mean shell size of most hibernating juveniles, based on the position of the single light stria, was 2.63 whorls (SD=0.53, n=241, range 1.5–4.5) (Fig. 43). The time of activity resumption by hibernating juveniles

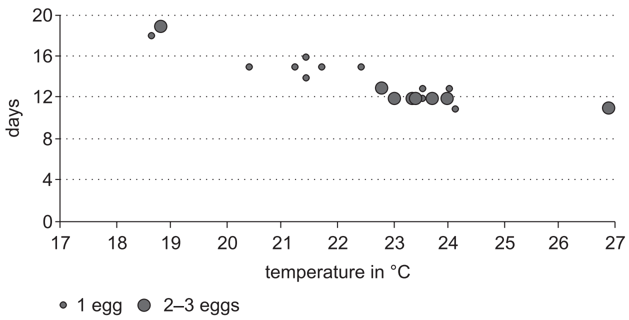


Fig. 41. *Vertigo pusilla*: duration of embryonic development dependent on the mean temperature (n=28)

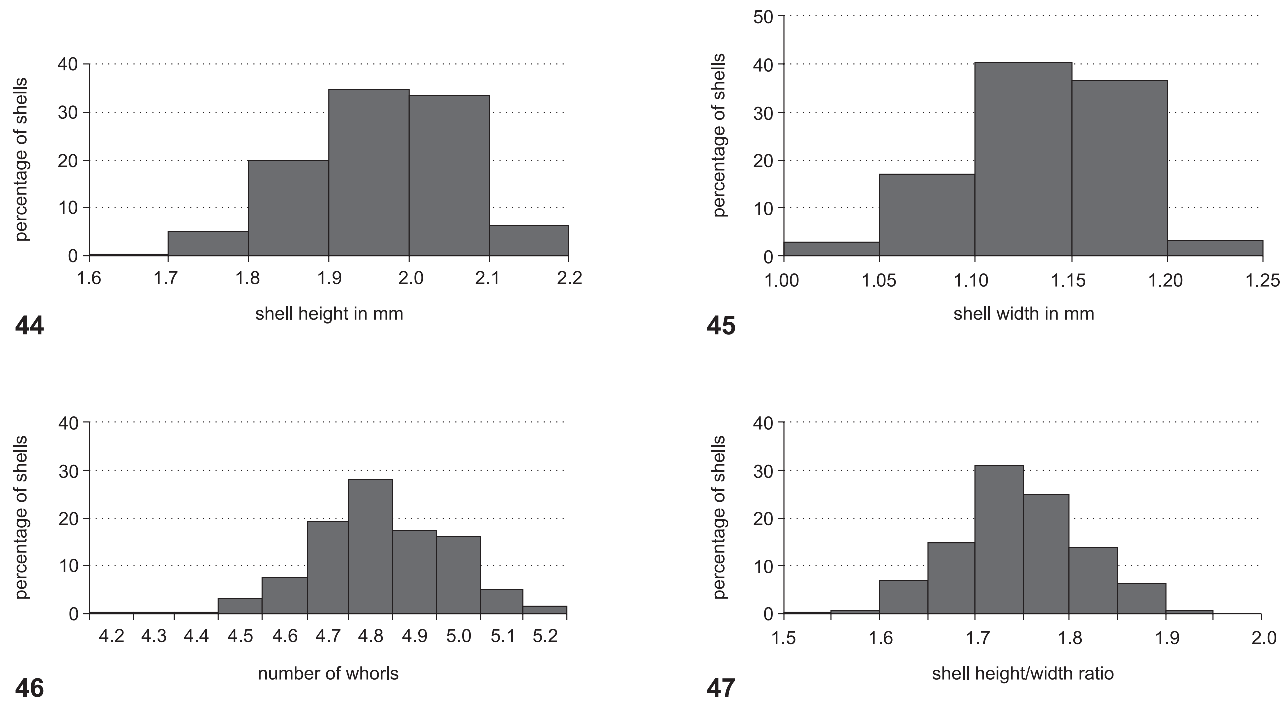
Fig. 42. *Vertigo pusilla*: variation in the number of whorls of embryonic shells (n=106)

Fig. 43. *Vertigo pusilla*: variation in the position of single light stria on the shell (n=241)

was varied. Some resumed growth already in the first half of April, others at the end of May. Mostly, they became mature in the period June-August, but juveniles with a distinct stria were sometimes found even at half of September. Shells of *V. pusilla* showed two (or more) light striae with a subsequent whorl constriction much more often (ca. 14%) than those of other species, and the distance between the striae was sometimes up to 2.5 whorls. It could not be ascertained if some of the striae arose during longer dry periods in the summer, or if some snails hibernated as juveniles twice. For example, on 3.05.2008 a juvenile was found with a shell of 3.8 whorls, with two striae at 1.9 and 3.7 whorl, and till the stria at 3.7 whorls the periostracum was slightly damaged (fine spots), while below the stria the shell wall was very thin (new increment).

These observations differ from the data of Pokryszko (1990a) with respect to both time of hatching and the growth rate (possible reproduction in the year of hatching).

Longevity. The life span of two snails collected on 19.06.2005 as subadult (both shells with a stria – hatched in 2004) which became adult in the laboratory was 11–12 months (both dead on 23.07.2005). Most adults collected in the field died after 1–2 months and only three survived much longer. One, collected on 11.07.2004 (shell with stria and fine periostracal lesions on the whole surface – hatched in 2002 and adult in 2003), survived till 25.06.2005 (life span 34 months), another, collected on 15.08.2004 (shell with a stria and periostracal lesions on the apex – hatched in 2003 and adult in 2004), survived till 12.09.2005 (life span 24–25 months), the third, collected on 3.05.2004 (shell without stria or periostracal



Figs 44–47. *Vertigo pusilla*: shell size variation (n=343)

lesions – hatched and adult in 2003), lived till 25.06.2005 (life span 24 months). Dying out of adults in the laboratory usually took place in June and July, 3–15 days after the last egg laying.

At half of September 2007 (a few samples) the age structure was the following (total n=153): 15.0% individuals hatched in 2007 (11.1% juvenile + 3.9% adult), 71.2% hatched in the previous year, 11.8% hatched two years before, 2.0% hatched three years before.

Shell variation. The sinistral, ovate shells, elongated to various degree, were yellowish or yellow-brown. The shell surface was nearly smooth or with weak irregular striae. The apertural barriers were composed of six main teeth and a variable number of fine tuberculate teeth: on parietal wall usually two lamellate teeth: parietal and angular), and sporadically (1.2% of shells) a tuberculate infraparietal. The number and shape of teeth of the basal wall varied much (e.g. some bifid teeth). The adult shell measurements were (n=343): height 1.66–2.18 mm (mean 1.96 mm, SD=0.09), width 1.01–1.20 mm (mean 1.12 mm, SD=0.04), number of whorls 4.2–5.25 (mean 4.82, SD=0.16), height/width ratio 1.52–1.94 (mean 1.74, SD=0.07) (Figs 44–47). Pearson's corelation between pairs of shell parameters (n=343) was: height/width r=0.61, height/number of whorls r=0.88, width/number of whorls r=0.41.

Vertigo ronnebyensis (Westerlund, 1871)

Habitats. In the environs of Sąpolno the species occurred in forest interiors in damp places (lake shores, forest valleys, young dense forests etc.) (for details see MYZYK 2004).

Reproduction. Some of the adults collected in the field started laying eggs just after placing them in the laboratory, others only after 3–5 weeks. Snails hibernating in the field laid their first eggs between April 8th and 13th. In the period of intensive reproduction (May–July) most snails laid one egg every other day (less often daily, up to 25 eggs in a month). In the remaining period there were irregular long intervals between consecutive egg-layings; they sometimes lasted even 1–2 months. The duration of the breeding period was usually 40–85 days (rarely longer, up to 132 days). Some snails laid their last egg of the season in May, others only in October.

The number of eggs laid during the season ranged from 1 to 55 (mean 23, SD=15, n=12). Snails reproducing during two seasons laid a total not exceeding 52 eggs (Table 1).

In the wild, egg-laying started at the beginning of June (in some years maybe even earlier), and ended at the beginning of September. The latest laid egg was found on 5.09.2006 (embryo with shell of 0.3 whorl).

Egg. Eggs of *V. ronnebyensis* were similar to those of *V. antivertigo*, but the number of layers of the gelatinous envelope was smaller (3–6). The egg size, disregarding the mucous layer (n=237), was: egg diameter 0.58–0.78 mm (mean 0.699 mm, SD=0.024), egg chamber diameter 0.49–0.70 mm (mean 0.622 mm, SD=0.025) (for details see MYZYK 2005b). The mean total thickness of the envelopes (without the mucous layer) was 11.0% of egg diameter.

Embryonic development. Most eggs were laid at one cell stage but in some the advancement of development indicated a few days of retention. The duration of embryonic development was somewhat longer than in *V. angustior* at the same temperature (Fig. 48). Pearson's correlation between the temperature and the duration of development was r=–0.92, n=8.

Growth. Embryonic shells were mostly composed of 1.2–1.3 whorl (mean 1.24, SD=0.08, n=120, range 1.0–1.45 whorl) (Fig. 49). The width of the 11 measured shells was 0.51–0.63 mm (mean 0.599 mm, SD=0.032). The embryonic shell surface was covered by fine irregular tubercles.

Hatching in the wild started in the second half of June (the earliest date of finding a new hatchling was 29.06.2007) and continued till September. Ca. 30% of the snails reached maturity in the year of hatching. Nearly all hibernating juveniles had a light stria on their shells. Two (or more) such striae were visible on 5.5% of adult shells, and the distance between them varied widely (usually 0.1–0.5 whorl, sometimes even up to 2.5 whorls). The mean shell size of hibernating juveniles, based on the position of the single light stria, was 2.33 whorls (SD=0.57, n=170, range 1.5–4.5) (Fig. 50). Further growth started in May, and at the

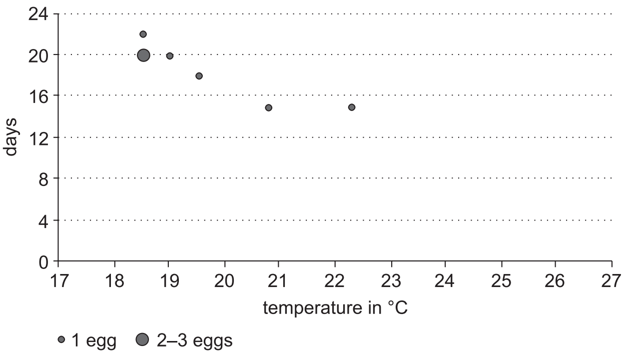


Fig. 48. *Vertigo ronnebyensis*: duration of embryonic development dependent on the mean temperature (n=8)

Fig. 49. *Vertigo ronnebyensis*: variation in the number of whorls of embryonic shells (n=120)

Fig. 50. *Vertigo ronnebyensis*: variation in the position of single light stria on the shell (n=170)

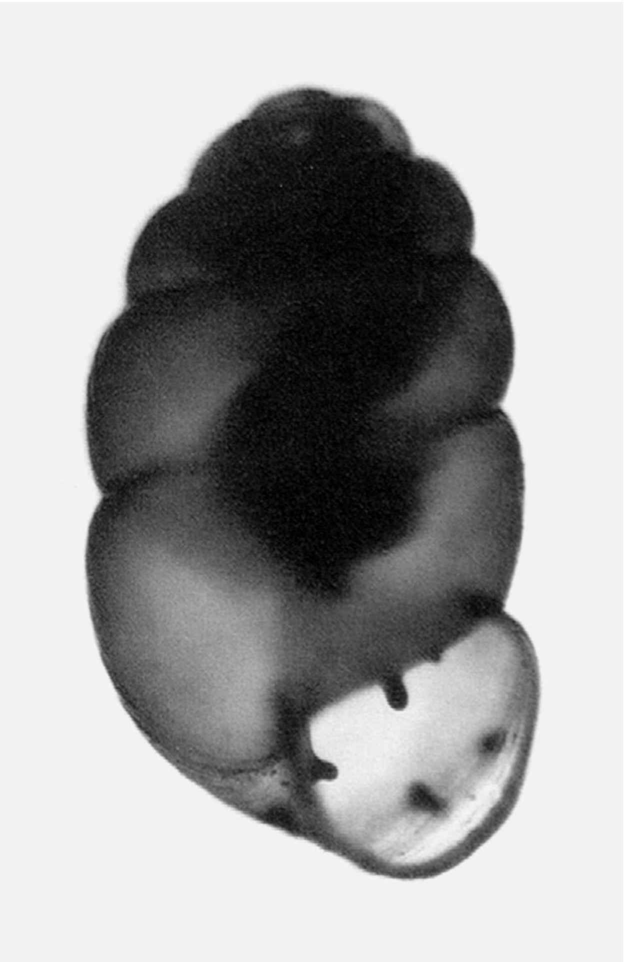


Fig. 51. *Vertigo ronnebyensis*: shell with angular tooth, light microscope, 50×

end of this month most shells showed fresh increments. The time of maturation varied and dependend on the shell size during hibernation. Juveniles with a light stria on their shells were rather often found at half of September, and in some years even at the beginning of October (some perhaps hibernated twice as juveniles).

Longevity. Some adults collected in the field died after 1–3 months in the laboratory, others only after 10–13 months. The longest-lived snails: one, collected on 3.05.2004 (shell with a stria and fine periostracal lesions – hatched in 2002 and adult in 2003), survived till 24.05.2005 (life span ca. 33 months). Another two, collected on 15.08.2004 (both shells with a stria and fine periostracal lesions on the apex – hatched in 2003 and adult in 2004), survived till the beginning of June 2005 (died on 5.06 and 12.06), their life span was 22–23 months. In the laboratory adults died almost during the whole year (April–October).

The age structure in the sample of 30.09.2007 was the following (n=35): 14.3% individuals hatched in 2007 (11.4% juvenile + 2.9% adult), 68.6% hatched in the previous year and 17.1% hatched two years before. After one year (autumn 2008) the density of the population decreased rapidly.

Shell variation. The dextral, ovate-cylindrical shells (often nearly cylindrical) were light brown or yellow-brown. The surface of the mid whorls was covered by fine, regular striae. The apertural barriers were composed of 2–5 teeth (usually poorly developed) (Fig. 51). The shell measurements (n=250) were: height 1.91–2.28 mm (mean 2.09 mm, SD=0.07), width 1.13–1.33 mm (mean 1.21 mm, SD=0.03), number of whorls 4.3–5.0 (mean 4.64, SD=0.14), height/width ratio 1.57–1.88 (mean 1.73, SD=0.06) (for details see MYZYK 2004).

Other information. Most populations were very unstable in terms of the occupied area. In favourable conditions (frequent rains in the summer) they occupied almost all the forest floor, in dry years they were found only in damper places (e.g. lake shores, depressions). Also vegetational changes (e.g. clearfelling, growth of young trees) had a strong effect on the occurrence and abundance of the species.

Vertigo substriata (Jeffreys, 1833)

Habitats. The species was rather common in deciduous and mixed forests, but only locally reached higher densities. In small numbers it also occurred on marshy unmeliorated meadows with tall grasses.

Reproduction. Adults collected in the field in the spring started egg-laying after 1–17 days in the laboratory (second half of April – beginning of June). Those hibernating in the laboratory laid their first eggs at about half of April. Most snails reproduced intensively from May till August (less often already in April or as late as September). In that period one egg was laid every other day (less often daily, maximum 32 eggs in a month). The intensity of egg laying distinctly increased when algae- and lichen-covered twigs were placed in the containers. In the remaining periods eggs were laid irregularly, and intervals between consecutive egg-laying episodes ranged from a few days to a few weeks. The last egg of the season was usually laid in June-July, but at room temperature some snails laid eggs till the beginning of January.

The number of eggs produced during the season ranged from 7 to 82 (mean 38, SD=23, n=11). Most snails laid eggs in one season (maximum 34) and died. Snails reproducing during two seasons were more fecund: one, collected on 15.08.2004, laid 120 eggs (38+82), another, collected on 3.06.2004, produced 110 eggs (75+35) (Table 1).

In the wild, reproduction usually started in June (in some years perhaps already in May) and continued till the beginning of September. The latest-laid egg was found on 5.09.2006 (embryo with a shell of 0.8 whorl).

Egg. Eggs of *V. substriata* were very similar to those of *V. antivertigo*. The egg measurements, disregarding the mucous layer (n=394) were: egg diameter 0.56–0.72 mm (mean 0.637 mm, SD=0.027), egg chamber diameter 0.50–0.64 mm (mean 0.564 mm, SD=0.026) (for details see MYZYK 2005b). The average total thickness of envelopes (without mucous layer) was 11.5% of egg diameter.

Embryonic development. Most eggs were laid at one cell stage (some at the stage of oocyte II), but in some the advancement of development indicated a few days of retention. The rate of embryonic development was somewhat smaller than in *V. angustior* at the same temperature (e.g. at 23°C hatching took place after 12–13 days). Besides, the duration of development varied widely among the eggs, irrespective of the temperature (Fig. 52). Pearson's correlation between the temperature and the duration of embryonic development was: r=–0.59, n=32. At the temperature of 24°C the duration of one cell division (between the first and second divisions) was ca. 2 hours.

Growth. Embryonic shells were usually composed of 1.2–1.25 whorl (mean 1.21, SD=0.07, n=141, range 1.0–1.35) (Fig. 53). The shell width was 0.39–0.56 mm (mean 0.519 mm, SD=0.028, n=45). The embryonic shell surface was covered by fine irregular tubercles.

Hatching in the wild usually started in July and ended in September. From 15 to 20% of the snails reached maturity in the year of hatching. Only some shells (50–60%) of hibernating juveniles bore a light stria. The mean shell size of hibernating juveniles, based on the position of the single light stria, was 2.45 whorls (SD=0.50, n=118, range 1.5–3.5) (Fig. 54). Some juveniles resumed growth already in the first half of May, others only in June. Maturation mostly took place in July or August (rarely somewhat later).

Longevity. Some adults collected in the field died after 1–2 months in the laboratory, others after 11–13 months. The longest-lived snail, collected on 3.06.2004 (shell with a stria, 1.7 whorl and fine periostracal lesions on the whole surface – hatched in 2002 and adult in 2003), survived till 10.07.2005 (life span 34–35 months). Another, collected on 15.08.2004 (shell with no stria but periostractum much damaged on the apex – hatched on 2003 and adult in 2004), survived till 2.08.2005 (life span ca. 24 months). Dying out of adults in the laboratory usually took place between the end of May and the beginning of August, 4–22 days after the last egg-laying (only in one case soon after hibernation).

In the wild, snails hatched in the same year, in the previous year and two years before (shells with a stria and periostracal lesions on whole surface) were present at the beginning of October. In the spring and early summer also snails with bleached shells (devoid of periostracum) and a distinct stria were present (age ca. 3 years).

Shell variation. The dextral, ovate or ovate-cylindrical shells were mostly yellowish, rarely yellow-brown. The surface of middle whorls was covered by regular, delicate riblets or distinct striae, and the body whorl surface was covered by a network of fine wrinkles. The apertural barriers usually included six teeth (columellar, parietal, angular, two palatals and basal). The adult shell measurements (n=301) were: height 1.50–2.00 mm (mean 1.74 mm, SD=0.10), width 0.99–1.17 mm (mean 1.08 mm, SD=0.04), number of whorls 3.9–4.8 (mean 4.38, SD=0.16), height/width ratio 1.37–1.80 (mean 1.62, SD=0.08) (Figs 55–58). Pearson's correlation between pairs of shell parameters was (n=301): height/width r=0.53, height/number of whorls r=0.88, width/number of whorls r=0.40.

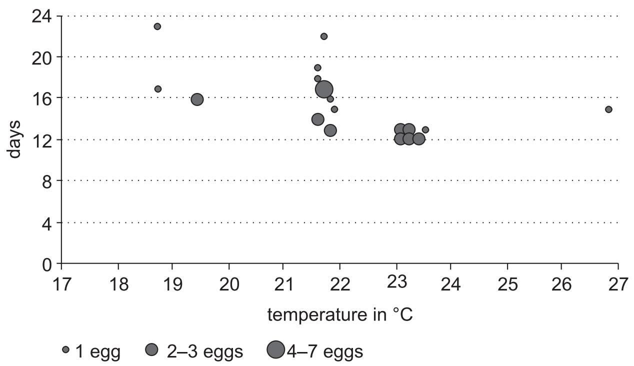


Fig. 52. *Vertigo substriata*: duration of embryonic development dependent on the mean temperature (n=32)

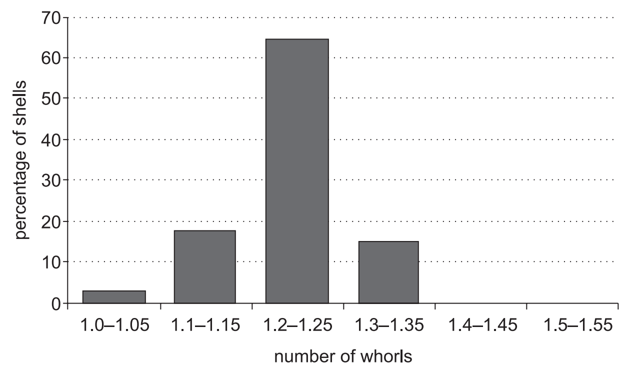


Fig. 53. *Vertigo substriata*: variation in the number of whorls of embryonic shells (n=141)

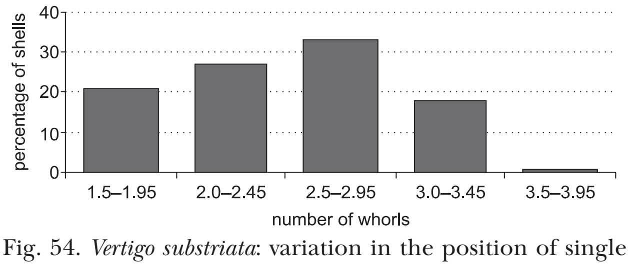
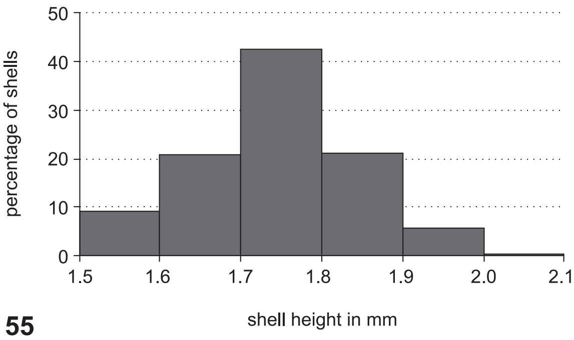


Fig. 54. *Vertigo substriata*: variation in the position of single light stria on the shell (n=118)



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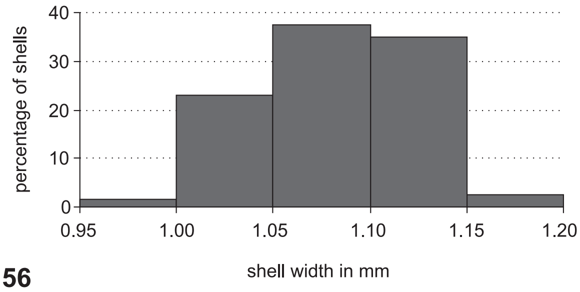

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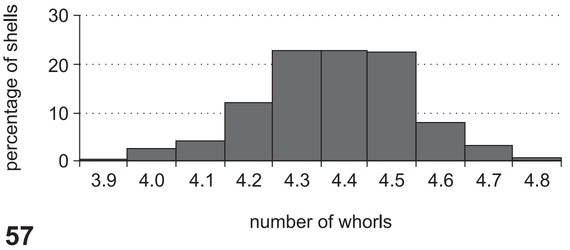

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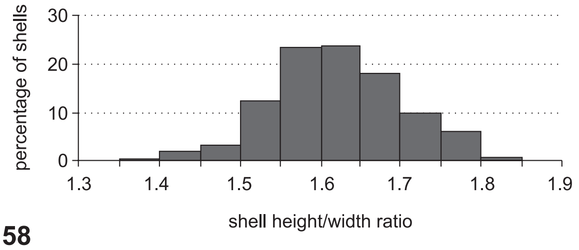

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Figs 55–58. *Vertigo substriata*: shell size variation (n=301)

Truncatellina cylindrica (Férussac, 1807)

Habitats. In the environs of Sąpolno the species was rather common in open and relatively dry habitats (railway embankment, balks, wasteland, house gardens etc.). Besides, it occurred in a small sparse deciduous forest in grassy places.

Reproduction. Adults placed in the laboratory laid eggs from half of June till the end of August. The number of eggs was small (4–11 per snail). No eggs could be found in the field, but the time of appearance of hatchlings indicated a similar reproductive season.

Egg. Eggs of *T. cylindrica* differed distinctly from those produced by members of the genus *Vertigo*. The were opaque, milky white and, depending on the parent, were spherical, lenticular (flattened sphere) or flattened ovate. The egg was covered by three envelopes: internal (thin, parchment-like), gelatinous 0.015–0.030 mm thick (layered, with borders between layers usually poorly visible) and external, 0.006–0.011 mm thick. The surface of the external envelope bore numerous calcium carbonate crystals of varied shape and size of 0.004–0.006 mm. The crystals partly protruded to the outside and, when dissolved, left irregular pits in the envelope.

Embryonic development. Observation of early development stages was rendered difficult by the calcified egg envelope. At the temperature of 21–23°C the development usually lasted 16–17 days (rarely longer, even up to 24 days), but in eggs devoid of external envelope hatching sometimes occurred on day 12 or 13.

During drying out the shrinking egg envelopes caused the calcium crystals to adjoin each other closely and inhibited further water loss (the embryos remained alive even on completely dried leaves). During incubation the crystals usually dissolved. However, with consecutive incubations on the same piece of leaf, an increasingly smaller number of crystals dissolved or even all of them remained in the egg envelopes after hatching. During incubation on a very damp substratum the external envelope usually broke and ceased to play its drought-protecting role. In eggs devoid of the external envelope (when they were not exposed to dessication) embryonic development and shell formation were similar to those in intact eggs. The observations suggest that the calcium carbonate crystals played mainly a protective and buffering role, and were not used to build the embryonic shell.

Growth. Embryonic shells were usually composed of 1.2–1.3 whorl (mean 1.26, SD=0.06, n=173, range 1.0–1.45) (Fig. 59). Their width was 0.45–0.53 mm (mean 0.496 mm, SD=0.018, n=37). The embryonic shell surface was covered by fine, partly fused tubercles. Near the aperture the tubercles were arranged in rows parallel to the aperture edge.

Hatching in the wild usually started in the first half of July, and ended at half of September. The sample of 25.08.2006 (n=44) contained 88.6% juveniles (54.5% with shells 3.0–3.95 whorls, and 4.5% of more than 5.0 whorls). In the samples collected later (11.09 and 3.10.2006) the proportion of juveniles with shells exceeding 5.0 whorls increased (17.6% and 21.3%, respectively). In a sample from another site, of 2.10.2004 (n=26), 84.6% of the individuals were juvenile (46.2% with shells of 2.0–2.95 whorls, 26.9% exceeding 5.0 whorls). The mean percentage of snails reaching maturity in the year of hatching was ca. 32%. Most of hibernating juveniles had a light stria and a

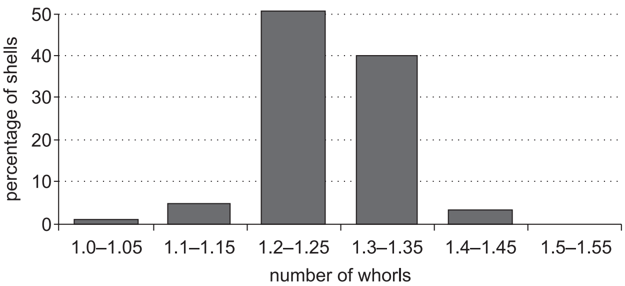


Fig. 59. *Truncatellina cylindrica*: variation in the number of whorls of embryonic shells (n=173)

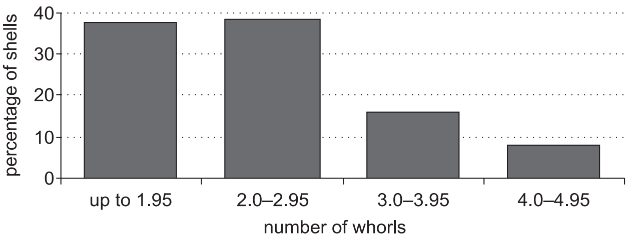


Fig. 60. *Truncatellina cylindrica*: variation in the position of single light stria on the shell (n=99)

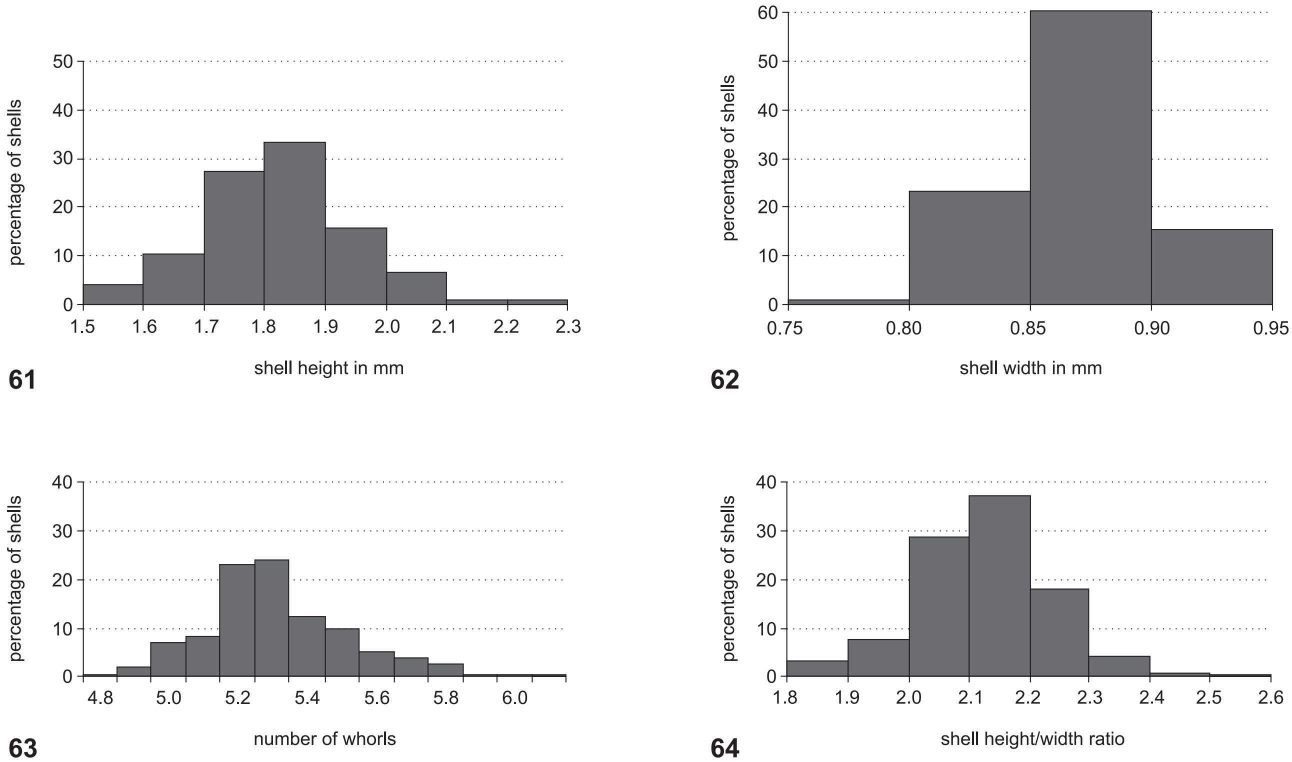
growth disturbance marked on their shells. The mean shell size of hibernating juveniles, based on the position of the stria, was 2.43 whorls (SD=0.77, n=99, range 1.5–4.7) (Fig. 60). In the spring the proportion of juveniles in the samples varied (38–75%, depending on the year). In favourable conditions some snails resumed growth in the first half of May (high temperature and humidity of the substratum, e.g. in regularly watered gardens). Usually, however, fresh increments were visible in June. The time of maturation varied according to the shell size prior to hibernation: some of the snails completed growth at the end of May, others in September, and in some years juveniles with a light stria on their shell were still found at the beginning of October.

Longevity. Adult snails collected in the spring and placed in the laboratory died after 1–3 months. Also field observations showed that most (70–85%) of the snails died after reproduction at the age of about one year. The remaining ones hibernated and lived till the age of about two years.

Shell variation. The dextral cylindrical shells were horny-brown or yellow-brown in colour. The shell surface till the aperture was covered by delicate regular ribs. In mature snails the aperture edge became reflexed or, less often, only thickened. The shell measurements (n=307) were: height 1.52–2.25 mm (mean 1.82 mm, SD=0.13), width 0.78–0.94 mm (mean 0.86 mm, SD=0.03), number of whorls 4.8–6.1 (mean 5.32, SD=0.22), height/width ratio 1.82–2.53 (mean 2.12, SD=0.12) (Figs 61–64). Pearson's correlation between pairs of shell parameters was (n=307): height/width r=0.64, height/number of whorls r=0.87, width/number of whorls r=0.45.

Columella aspera Waldén, 1966

Habitats. In the environs of Sąpolno the species was common and occurred in nearly all mixed and some deciduous forests; outside the compact forest areas it was very rare and found only on forest edges (among grasses in very shaded places).



Figs 61–64. *Truncatellina cylindrica*: shell size variation (n=307)

Reproduction. In the laboratory reproduction took place only in the containers which, besides tree leaves (mainly birch), contained the moss *Hylocomium splendens* (often occurring in places inhabited by the snail). Some eggs were laid on the upper (concave) side of the moss leaves which, with decreasing humidity, tightly adhered to the stem, providing additional protection. The eggs were laid during periods of intense rains and temperatures of 17–20°C (rarely somewhat higher). Snails collected at the beginning of May started egg-laying after about two weeks, those collected later – often after two days. In the laboratory the reproductive season ended at the beginning of September (the latest-laid egg 4.09.2006). The smallest snail which produced an egg had a shell 1.9 mm high, composed of 4.8 whorls. The number of eggs produced in the laboratory was small (maximum 5 eggs per snail).

In the wild eggs were laid from June (in some years perhaps even at the end of May). In an egg found on 29.06.2007 the embryo had a shell of ca. 1.0 whorl. Latest-laid eggs were found on 10.09.2006 (embryos at various development stages, from an irregular, rotating lump to embryos with shells of 1.35 whorl).

Egg. Eggs of *C. aspera* were uncalcified and nearly colourless. They were oval and distinctly flattened. The egg chamber was covered by three envelopes: internal (very thin, parchment-like), gelatinous (the thickest, of 3–4 layers) and external (relatively thin with numerous small folds). The folds of the external envelope were arranged spirally on one flattened side of the egg, and irregularly on the other side. The external measurements of the eggs (n=48) were: length 0.69–0.86 mm (mean 0.780 mm, SD=0.036), width 0.68–0.82 mm (mean 0.741 mm, SD=0.030). The egg chamber measurements were: length 0.59–0.76 mm (mean 0.683 mm, SD=0.036), width 0.58–0.72 mm (mean 0.641 mm, SD=0.030). The length/width ratio of the egg was 1.013–1.099 (mean 1.052, SD=0.019, n=48). The egg envelope thickness was 0.031–0.062 mm (mean 0.049 mm, SD=0.006, n=96) and fairly often varied along the perimeter. The mean total thickness of the envelopes was 12.4% of egg length.

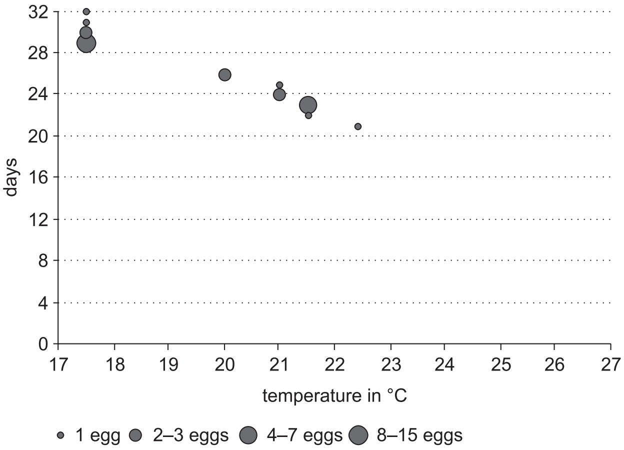


Fig. 65. *Columella aspera*: duration of embryonic development dependent on the mean temperature (n=35)

Fig. 66. *Columella aspera*: variation in the number of whorls of embryonic shells (n=144)

Embryonic development. On finding the eggs most embryos were at early development stages (from two divisions to gastrula). Like in *Vertigo*, polocytes I and II were rather often visible in the egg chamber, indicating fertilisation inside the formed egg. The duration of embryonic development was much longer than in *Vertigo* at the same temperature. At the temperature of 21.5°C hatching took place after 23 days, and at 17.5°C usually after 29–30 days (Fig. 65). Pearson's correlation between the temperature and the duration of development was: r =–0.97, n=35.

Growth. Embryonic shells were usually composed of 1.35–1.4 whorl (mean 1.36, SD=0.09, n=144, range 1.1–1.55) (Fig. 66). The width of the 38 measured embryonic shells was 0.58–0.69 mm (mean 0.643 mm, SD=0.024). The embryonic shell surface was covered by relatively large regular tubercles. Embryonic shells of some snails hatched in the wild bore radial striae indicating arrested development (probably dessication).

Hatching in the laboratory started at about half of June and continued till the end of September. Growth of juveniles was rather slow and usually soon ceased (lack of adequate food?).

In the wild the timing of hatching was similar as in the laboratory (beginning of July – end of September). The growth was probably also rather slow and most snails hibernated for the first time as juveniles. In the samples taken in March-April the shell size of hibernating juveniles varied from 2.6 to 5.3 whorls (some shells with a light stria even at 1.6 whorl). When conditions were favourable, already at the beginning of March some snails had food in their intestines, but fresh shell increments were visible only in May. Most hibernating snails became mature in the summer, but some could hibernate for the second time as juveniles (e.g. sample of 30.09.2007 contained a snail with a shell of 3.9 whorls, stria at 1.9 whorl and periostracal lesions on the apex). During the whole year, snails with 4.0–4.95 whorls dominated in the samples (mean 59.2%), while those with larger shells exceeding 5.0 whorls were much less frequent (mean 22.0%, n=191). The shell growth usually continued till the end of life, but in mature snails it was much slower.

Shell variation. The generally conical-cylindrical shells were yellow-brown or horny-brown. The shell surface was matt, densely covered by regular striae (in some populations the striae were visible only on some whorls). The largest shells collected near Sąpolno were: I – height 2.41 mm, width 1.40 mm, 5.7 whorls; II – height 2.41 mm, width 1.33 mm, 5.7 whorls; III – height 2.32 mm, width 1.45 mm, 5.5 whorls. Pearson's correlation between pairs of shell parameters (n=60) were: height/width r=0.45, height/number of whorls r=0.96, width/number of whorls r=0.33. The height/width ratio increased with the number of whorls and for shells of 5.0 whorls was on average 1.53, and for those of 5.5 whorls – 1.69.

Other information. The velocity of crawling on dry substratum was ca. 0.5 mm/s (=3 cm/min).

Columella edentula (Draparnaud, 1805)

Habitats. In the environs of Sąpolno the species occurred patchily in the valley of the Brda River and on the northern side of the railway embankment. In the last ten years it was also found in two sites on the shore of Lake Sosnowe. Where populations of *C. edentula* and *C. aspera* adjoined, the two species co-occurred along a narrow belt, with *C. edentula* always occupying the lower situated area (closer to the river or lake). Very rarely it was found in rather dry forests but did not form permanent populations there.

Reproduction. Adults collected in the field in early spring (end of March – beginning of April) in the laboratory laid eggs at about half of April (e.g. snails of April 10th laid eggs on April 23–25). During field work I could not find eggs, only hatchlings.

Egg. Eggs of *C. edentula* were very similar to those of *C. aspera*, and their probable calcification mentioned in my earlier paper (MYZYK 2005b) is erroneous. The external egg measurements (n=8) were: length 0.69–0.76 mm (mean 0.729 mm, SD=0.024), width 0.64–0.72 mm (mean 0.696 mm, SD=0.027). The egg chamber measurements were: length 0.61–0.64 mm (mean 0.627 mm, SD=0.009), width 0.57–0.61 mm (mean 0.597 mm, SD=0.016). The length/width ratio was 1.015–1.079 (mean 1.049, SD=0.22, n=8). The egg envelopes were 0.036–0.062 mm thick (mean 0.050 mm, SD=0.008, n=16) and rather often their thickness varied along the perimeter. The mean total thickness of egg envelopes was 13.8% of egg length.

Fig. 67. *Columella edentula*: variation in the number of whorls of embryonic shells (n=159)

Embryonic development. In six eggs, on finding, the embryos were at early development stages (from a few divisions to gastrula). After transferring them to another piece of leaf they developed for a few days and then died. Only two eggs, found at a more advanced stage (embryos with shells of 1.2 and 1.25 whorl), developed till hatching (21–22.05). In two egg chambers polocytes I and II were visible, indicating fertilisation inside the formed egg.

Growth. Embryonic shells were usually composed of 1.4–1.45 whorl (mean 1.40, SD=0.08, n=159, range 1.15–1.55) (Fig. 67). The width of the nine measured embryonic shells (from the laboratory and collected in the field) was 0.56–0.63 mm (mean 0.607 mm, SD=0.021). The shell surface was covered by relatively large regular tubercles, and postembryonic increments were usually separated by a narrow stria.

Hatching in the wild occurred at the end of May and beginning of June (e.g. litter sample of 3.06.2007 contained both hatchlings with no increment and juveniles with a small increment of ca. 0.15 whorl). The growth was probably rather slow and most snails hibernated for the first time as juveniles. The shell size of hibernating snails varied very widely (1.7–5.8 whorls), and nearly half of them (42–49%) had more than 5.0 whorls (adults). When weather permitted the snails fed even in the winter (e.g. January 29th 2008 at a daytime temperature of ca. 10°C), but new shell increments were usually visible only in May. Still at the beggining of June the smallest hibernating snails had shells of ca. 2.2 whorls. The shell growth usually continued till the death of the snail.

Shell variation. Juvenile shells were conical, those of older snails cylindrical with a conical apex. Some big shells (6 or more whorls) had the penultimate whorl narrowed and a slightly wider body whorl. The shell was usually lighter than in *C. aspera*, light horny or yellowish. The shell surface was covered by sparse irregular striae. The largest shells collected in the environs of Sąpolno had the following mesurements: I – height 2.87 mm, width 1.33 mm, 6.5 whorls; II – height 2.85 mm, width 1.43 mm, 6.5 whorls; III – height 2.81 mm, width 1.33 mm, 6.6 whorls. Pearson's correlation between pairs of shell prameters (n=35) was: height/width r = 0.65, height/number of whorls r=0.96, width/number of whorls r=0.63. The height/width ratio increased with the number of whorls and for shells of 6.0 whorls it was on average 1.94, for those of 6.5 whorl – 2.06.

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