SHELL MORPHOLOGY, GROWTH PATTERN AND POPULATION DYNAMICS OF THE LAND SNAIL *XEROLENTA OBVIA* (MENKE, 1828) IN TWO AREAS OF DIFFERENT CLIMATIC CONDITIONS WITHIN A TEMPERATE CLIMATE REGION

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To determine the relative role of climatic variables (temperature and precipitation) on land snail *Xerolenta obvia* populations, field surveys were conducted in Poland at two sites (SW and NE) with striking differences in climatic regime during two growing seasons. In a temperate climate of Central Europe *X. obvia* is an annual species with the majority of snails hatching in autumn. They overwinter as juveniles, continue their growth in spring and summer, and reproduce in the following autumn. Due to the comparatively milder climate, the SW population is more plastic, some individuals can live and reproduce longer. The two variants of the growth model are presented. We found that the length of growing season and temperature were additional factors determining differences in snails' growth and population dynamics between the sites. The growth rate of *X. obvia* is negatively correlated with the initial size of their shells and varies among sites. These two geographically distant populations differ in terms of their shell size and morphology. The SW population is characterised by larger, dark banded shells compared to the NE one, which is dominated by snails with smaller, white shells. A pattern of decreasing body size in areas with shorter growing season may explain differences in the shell size of *X. obvia*. Larger shells in regions with warmer and drier environment perhaps constitute responses to selection by environmental factors.

Key words: growth rate, size structure of population, life cycle, terrestrial molluscs, Geomitridae, land snail, shell morphology.

INTRODUCTION

Variation in life history strategy in response to climate is an important factor in determining the distribution of many animal species, but until recently such variation has received little attention in land snails (Peake 1978). Such intraspecific variation in life history in relation to climate is known for just a few species of terrestrial pulmonates, for example *Oreohelix cooperi*

(Anderson *et al.* 2007), *Vestia gulo* (Sulikowska-Drozd 2011), *Bradybaena fruticum* (Proćków *et al.* 2012), *Alinda biplicata* (Sulikowska-Drozd *et al.* 2013). In Greece, where the climate varies from Mediterranean to temperate or continental, a variety of life history patterns have been found within the Geomitridae (Lazaridou-Dimitriadou 1981, Staikou & Lazaridou-Dimitriadou 1991), and Lazaridou and Chatziioannou (2005) demonstrated such variation with climate in two populations of *Xerolenta obvia*, now classified as a geomitrid (Razkin *et al.* 2015). In Central Europe there are field studies of life histories of the xerophilic geomitrids *Candidula unifasciata* and *Helicella itala* (Hänsel *et al.* 1999). Further east, there is also a study of *Xerolenta obvia* in Belarus (Zemoglyadczuk 2019), where the species is not native.

Xerolenta obvia thus exhibits wide ecological amplitude in terms of macroclimate. Its distribution ranges from Asia Minor to the Balkans, the Carpathians, along the Baltic coast, and in the Mediterranean region to the south-east of France (Falkner 1990). The studies in two areas in northern Greece (Lazaridou & Chatziioannou 2005) and in one site in Belarus (Zemoglyadchuk 2019) showed substantial differences in life-cycle strategies between populations. While the breeding season was in the autumn in all populations, an annual life cycle was recorded both in the Belarusian population (Zemoglyadchuk 2019) and in the population from a temperate montane site in Greece, where there was a short but very favourable season for growth. Adult size was modest, and eggs and hatchlings were large. By contrast, in the coastal Greek population the life cycle spanned two years, the adults were larger and laid large clutches of smaller eggs. Growth and activity do not occur during the adverse periods of winter and of summer drought in lowland Greece (Lazaridou & Chatziioannou 2005).

In Poland *X. obvia* lives in sunny open habitats, dry grassy slopes, also fallows, gravel pits, railway embankments and road margins, often estivating in large numbers in the low vegetation (Wiktor 2004). This Pontic species is not native in Poland but is now widely distributed in lowlands (Wiktor 2004). The moderate and highly variable climate in Poland is influenced by both maritime (western part) and continental elements (eastern part).

The aim of this study was to examine whether there were differences in (1) growth pattern, (2) population dynamics and (3) shell morphology of *X. obvia* inhabiting two sites with striking differences in the climatic regime, i.e. an oceanic-influenced area in SW Poland and a cold polar area in NE Poland.

MATERIAL AND METHODS

Study areas

The south-western site lies in Piotrkowiczki village ca. 20 km north of Wrocław in the Silesian Lowland, and the north-eastern site is near Żytkiejmy village about 40 km

north-west of Suwałki in the Lithuanian Lakeland. They are separated by *ca.* 650 km. The localities belong to regions with contrasting climatic conditions; that of the SW region is maritime-influenced and is one of the warmest in Poland, whereas that of the NE region is continental and the coldest in Polish lowlands (Matuszkiewicz 2008). The detailed habitat characteristics of these two sampling sites are given in Table 1.

Sampling and analyses

The study was carried out during two growing seasons in 2015 (May–November) and 2016 (April–November). The last sample was taken after winter in April (May) 2017. Seasonal changes in the size structure of *X. obvia* populations were traced based on regular monthly samples made by visual search. On each occasion, snails were collected for 1 hour, from an area of 25 m². Growth rates and longevity estimates were based on monthly marking with nail varnish (each month a different colour). Marking was done by painting a narrow stripe on the shell, just next to the aperture margin, so that the shell increment could be read on recapture. For each recaptured individual the whorl increment since the last marking and the date of the last marking were noted, then the individual was marked again and released. The average growth rate was estimated for all marked-recaptured snails in both populations. The growth rate was expressed by whorl increment (whorls counted according to Ehrmann's (1933) method) and six size classes were distinguished (Table 2). Additionally, the shell width and shell height of all collected snails were measured with Vernier callipers to 0.01 mm.

Climatic data were obtained from meteorological stations (IMGW-PIB data) in Wrocław (28 km from SW site) and Suwałki (40 km from NE site), which were the ones

Table 1. Habitat characteristics of sampling sites.

Locality	Piotrkowiczki	Żytkiejmy
Location name	SW - southwestern site	NE - northeastern site
Coordinates	51°16′07.5″N, 17°02′07.5″E	54°20′36.8″N, 22°40′52.7″E
Altitude a.s.l.	183 m	168 m
Vegetation	*Artemisia campestris, Papaver rhoeas, Euphorbia cyparissias, Vicia angustifolia, Taraxacum officinale, Trifolium arvense, Achillea millefolium, Anchusa officinalis, Atriplex* sp.	*Lotus corniculatus, Artemisia campestris, Hieracium pilosella, Solidago virgaurea, Rumex* sp.
Growing season[a]	224 days	194 days
Mean annual temperature[a]	8°C	6.2°C
No. of days with $t_{max} < 0°C$[a]	33	66
No. of days with $t_{max} > 25°C$[a]	36.9	25
No. of days with snow-cover[a]	54	100

[a]Data from Matuszkiewicz (2008); growing season, i.e. number of days in a year with a mean temperature over 5°C

Table 2. Size classes of *X. obvia.*

Size class	Number of whorls
I	2.5–3.0
II	3.1–3.5
III	3.6–4.0
IV	4.1–4.5
V	4.6–5.0
VI	5.1–5.4

closest to the sampling localities. These were used to extract temperature and precipitation regimes at each site during the study period, referring exactly to the periods when the snails' growth was recorded, i.e. the days between subsequent recaptures.

Differences in mean shell size between the populations were tested using t-tests since the data followed a normal distribution. The Mann-Whitney *U* test, which evaluates differences in medians, was used to test the differences in shell growth. Statistica PL 12.5, Microsoft Excel 2016 and PAST were used for statistical analyses of the data.

Analysed material

The total number of individuals collected on each occasion in the SW site ranged from 55 to 252. The total number of marked snails was 1079 and 510 of them (47%) were recaptured: once, 196 individuals (38%), twice 152 individuals (30%), three times 73 individuals (14%), four times 60 individuals (12%), five times 18 individuals (4%), six times 10 individuals (2%) and seven times one individual (< 1%). In the NE population, the number of individuals collected on each occasion ranged from 24 to 229. The total number of marked snails was 1703 and 413 of them (24%) were recaptured: once 308 individuals (75%), twice 77 individuals (19%), three times 19 individuals (4%), four times 8 individuals (2%), and five times one individual (<1%).
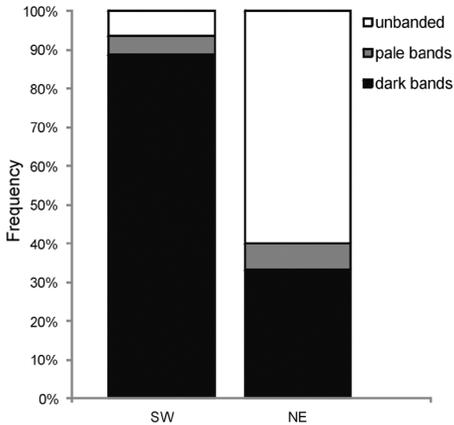
RESULTS

Morphological differences

The two populations of *X. obvia* differed in terms of shell morphology. The SW population was characterised by larger shells. With the same number of whorls, these shells were wider by 1–2 mm than the shells of the NE population (t = 9.5, $p < 0.0001$, $n = 28$). The differences increased with increasing number of whorls and reached its maximum in snails with 5.0–5.2 whorls (Fig. 1). Shell height in both populations was similar and the difference between the two populations was statistically insignificant (t = –1.5, $p = 0.15$, $n = 28$). The maximum shell width recorded was 16.12 mm in the SW population and 14.08 mm in the NE population, while the maximum height was 7.85 mm and 7.91 mm, respectively. *Xerolenta obvia* shells are white with three types of pattern: unbanded, with distinct dark bands and with light and weakly visible bands. In both populations all three types of shell-colouration were present. In the SW population, distinctly banded shells dominated (89%), while white shells were the most frequent in the NE population (60%) (Fig. 2). The proportion of pale banded shells was marginal, i.e. 4.1% and 6.7% in SW and NE populations, respectively.
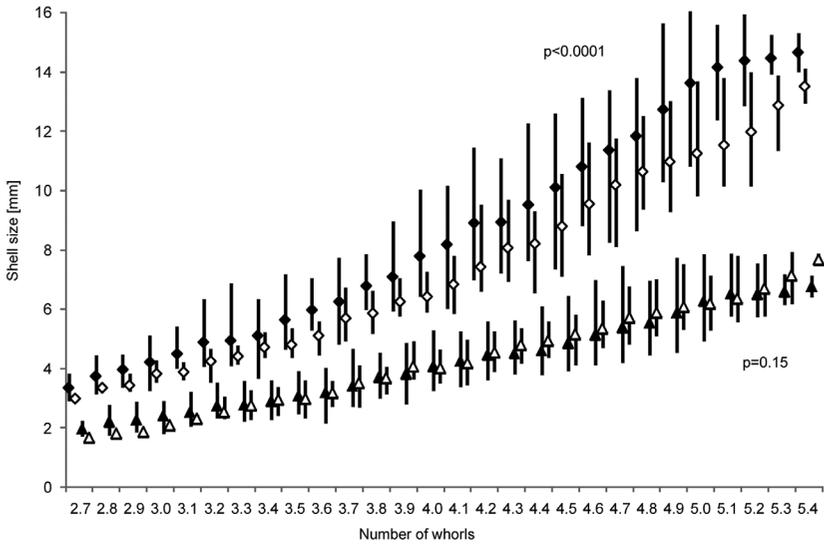
Fig. 1. Shell size differences of *Xerolenta obvia* at different stage of growth in SW (filled symbols) and NE (empty symbols) populations; diamonds = mean shell width, triangles = mean shell height, lines = range of size

Population structure

The changes in size distribution over the study period in both sites (Fig. 3) demonstrate that the youngest snails (2.5–3.0 whorls) appeared first in April and were present to June (August) in the SW site and to May (June) in the NE site depending on the growing season. In the SW population, they were most

Fig. 2. Distribution of shell pattern types of *Xerolenta obvia* snails in the two populations studied, SW (*n* = 781) and NE (*n* = 1387)

abundant in May and June 2015 as well as in May 2017 constituting more than 20% of all snails recorded. In later months, they appeared much less frequently. The number of individuals from the second size class (3.1–3.5 whorls) increased in abundance between April and June (July) in both sites, but only in the SW site they were also present in the subsequent months, i.e. August to November, represented only by a small number of individuals. Similarly, snails of size class III (3.6–4.0 whorls)

appeared in almost all months (April–October) in the SW site, but only from April till July in the NE site, having the peak abundance in May (SW) and in June (July) (NE). Size class IV (4.1–4.5 whorls) was present in almost all months in both sites, being most abundant from August to November (SW), and in June and July (NE). The abundance of snails from size class V (4.6–5.0 whorls) fluctuated during periods of the growing seasons and started to increase from July in both sites. The number of snails from size class VI was more or less constant from July to November in the SW site in each season, but increased slightly over the same period in the NE site.
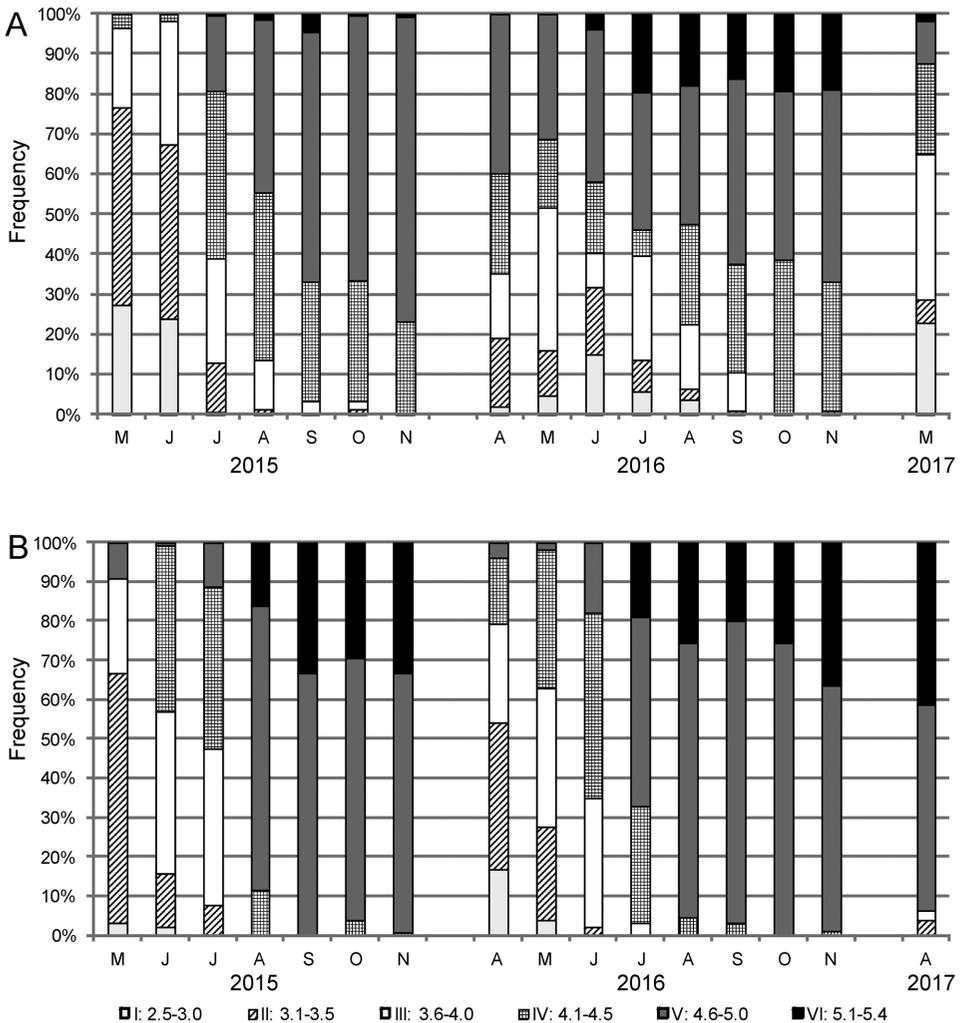

Fig. 3. Relative distribution of size classes (I–VI) over the whole activity period studied in SW (A) and NE (B) populations of *Xerolenta obvia*

Table 3. Average growth rate [no. of whorls/month] in different size classes of *Xerolenta obvia* in SW and NE populations. Significant differences are marked in bold.

No. of whorls	SW				NE				Mann-Whitney U test
	mean	min.-max.	*SD*	*n*	mean	min.-max.	*SD*	*n*	
2.5–3.0	0.87	0.30–1.20	0.49	3	0.63	0.50–0.80	0.24	2	$p > 0.05$
3.1–3.5	0.51	0.10–1.20	0.31	15	0.36	0.20–0.60	0.11	17	$p > 0.05$
3.6–4.0	0.40	0.10–1.50	0.30	66	0.40	0.10–0.80	0.15	53	$p > 0.05$
4.1–4.5	0.30	0.05–0.90	0.21	149	0.23	0.05–0.60	0.14	90	**$p < 0.05$**
4.6–5.0	0.18	0.05–0.70	0.13	143	0.10	0.05–0.30	0.07	49	**$p < 0.05$**
5.1–5.4	0.12	0.05–0.20	0.07	9	–	–	–	–	–

Growth

The growth rate (expressed as the increase in the number of whorls) depended on the initial size of the individual snail; the smaller the individual the greater its monthly whorl increment (Table 3, Fig. 4). This trend is stronger in the NE population ($r = –0.6$, $p < 0.0001$) than in the SW population ($r = –0.3$, $p < 0.0001$). Mean monthly whorl increment during all growing periods was 0.5 and 0.4 whorls per month in the SW and NE populations, respectively.
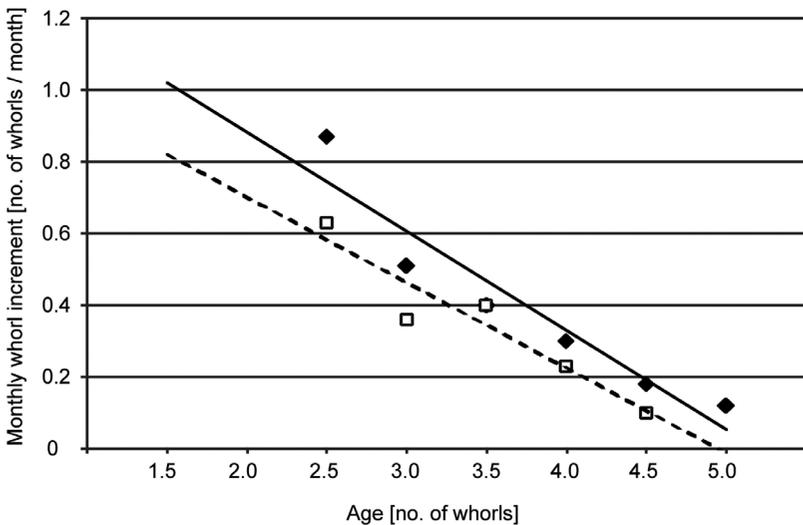
Fig. 4. Average monthly whorl increment of *Xerolenta obvia* at different stages of growth in SW (diamonds with the solid trend line) and NE (squares with the dashed trend line) populations

The influence of climatic conditions on the growth of X. obvia

Correlations of the average growth with climatic variables, such as temperature, precipitation and percentage of rainy days, revealed that the mean monthly whorl increment in the SW population does not directly depend on any of the variables considered (*p* > 0.05). In the NE population, the mean monthly growth significantly increased with increasing mean temperature (correlation coefficient r = 0.7, *p* < 0.01).

Analysing the two seasons separately, the whorl increment in 2015 was larger in the SW population than in the NE one, with a temporary reversal in July (Fig. 5A). This appears to relate to heat and drought in this month (Figs 5B, 5C). In 2016, snails in the NE population started growing a month later and ended growth a month earlier than those in the SW; growth in the SW was stronger until June, and lasted longer (Fig. 5A).

Lifespan

Among all the marked-recaptured snails, only three individuals (0.3%) survived two winters: two from the SW population (first observed at the stage of 4.0 and 4.1 whorls) and one from
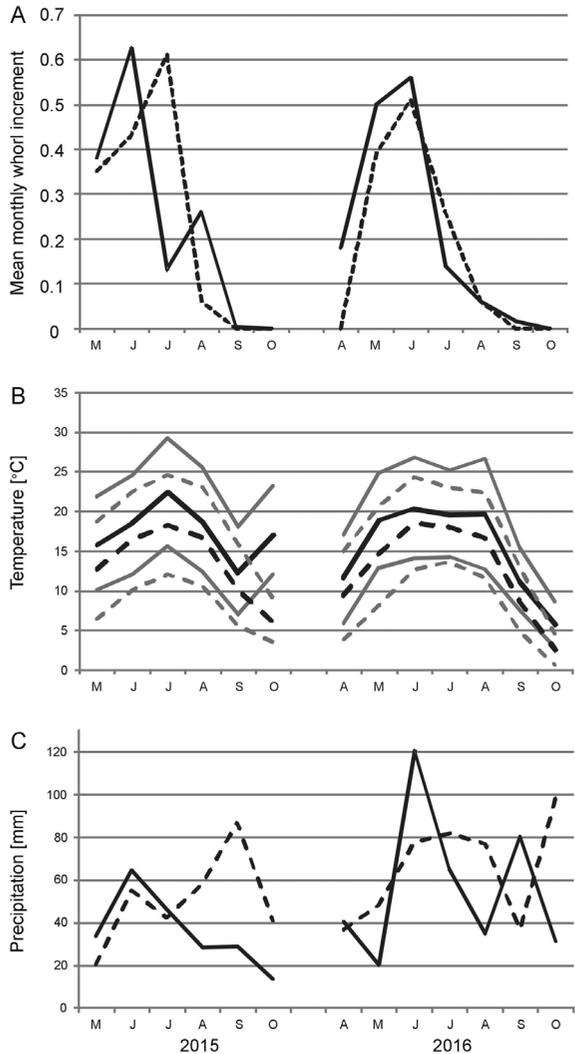
**Fig. 5.** A) Mean monthly whorl increment of *Xerolenta obvia* in two growth seasons in SW (solid line) and NE (dashed line) populations; B) mean (black lines), maximum and minimum (grey lines) monthly temperature, and C) total monthly precipitation during the study period in SW (solid lines) and NE (dashed lines) sites. Data from nearest meteorological stations in Wrocław and Suwałki (IMGW-PIB data)

the NE population (3.7 whorls). These animals were last observed in April or May 2017 (the final sample), each with 5.0 whorls. The actual time of observation of these individuals is 21–22 months and the estimated life expectancy is minimum of two years (24–25 months).

DISCUSSION

The data on seasonal changes in size structure combined with those for growth rate enable us to reconstruct the life cycle of *X. obvia*. The growth model under natural conditions (Fig. 6) was based on the different growth rates in the SW and NE populations. The lack of growth in April in the NE population was also taken into account (Fig. 5A). Additionally, our laboratory data show that hatchlings have shells of ca. 1.5–2.0 whorls (Kuźnik-Kowalska *et al.* 2019). In the field we did not observe any individuals smaller than 2.5 whorls (probably overlooked due to their very small dimensions, hiding in vegetation or litter). Our model therefore considers two variants of hatching time. In the first model variant (Fig. 6), the juveniles hatch in autumn, they grow for a short period, then overwinter. In spring they continue their growth. At the end of summer and in early autumn most individuals from both populations are able to reach maturity and start to reproduce. In the second model variant (Fig. 6), at least some snails hatch in spring, which means that some overwinter in the form of eggs. Our direct field observations show that *X. obvia* lays eggs in mid-October, and in the laboratory conditions juveniles hatch within ca. 18 days (range 11–28 days, Kuźnik-Kowalska *et al.* 2019). Given that in lower temperatures the time to hatch may take as long as 28 days, it seems likely that hatching at the end of November would be harmful. While
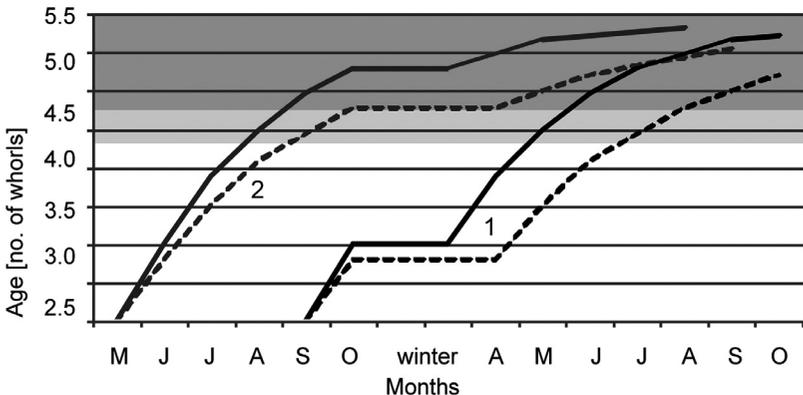
Fig. 6. *Xerolenta obvia* growth model under natural conditions. Size ranges of sexually mature snails are shown in dark grey (4.5–5.4 whorls) and light grey (4.25–4.4 whorls); solid lines = SW population, dashed lines = NE population; 1 = first model variant, 2 = second model variant (details in text)

in the second model snails from the SW population could reach maturity in the same year and lay eggs in September/October, the snails from the NE population would reach at most only the minimum size at which they can start to reproduce (the smallest individual that reproduced in the laboratory had 4.25 whorls, the remaining ones had more than 4.5 whorls), but most individuals would do it after winter.

Recorded changes in the percentages of size classes over the activity seasons (Fig. 3) indicate that all snails from the NE population and most from the SW population correspond to the first growth model. The smallest recorded snails (with 2.5-3.0 whorls) were present in April and May, which means they had hatched earlier. Our findings and those of ZEMOGLYADCHUK (2019) show that in a temperate climate of Central Europe *X. obvia* is mainly an annual species. Most snails hatch in autumn, they overwinter as juveniles, continue growth in spring and summer and finally they reproduce in autumn.

The pattern of growth and reproduction in the SW population is more plastic than in that of the NE; growth and reproduction are not so tightly synchronised. Reproduction is not confined to autumn, and juveniles of the smallest recorded age class were found in all months from April to August. Some adults may survive for more than one season. The milder climate of the SW seems likely to account for these differences. The timing and length of the reproductive season of *X. obvia* are not rigid and variations occur from one year to the next and differ between localities. Similar plasticity was observed in *X. obvia* inhabiting Mediterranean areas where growth rates and length of life cycle varied in response to climatic conditions (LAZARIDOU & CHATZIIOANNOU 2005).

The fastest proportional growth occurred in the youngest snails, and decreased later over time (Fig. 4). Snails from the SW population grew faster than those from the NE. Since SW snails are larger than those from the NE for any given number of whorls, the same whorl increment indicates a greater increase in biomass, increasing the difference between the populations. While this difference might be attributed in part to the climatic difference between the sites, any direct dependence of growth rate on temperature was found only in the NE site, where generally lower temperatures and higher precipitation prevail. Exceptionally high temperatures may have inhibited growth in the SW site (especially in summer 2015, Fig. 5A), as it was associated with, significantly lower rainfall than normal in spring and summer 2015 (Fig. 5C). This confounding of temperature and rainfall effects may have obscured any direct effects of temperature in the SW site. Hence in August 2015 captured snails were aestivating, and no growth had occurred. More generally, growth in *X. obvia* may be constrained by either temperature or humidity. In the NE population, the former is dominant; both play a part in the SW population,

while in Greece humidity is the main determining factor for both growth rate and life history variation (Staikou *et al.* 1990, Lazaridou & Chatziioannou 2005). In that type of climate aestivation restricts activity and winter temperatures are not limiting.

The difference in climate between the two sites also affects the length of time in which growth and activity are possible. The growing season at the SW site is 30 days longer than that of the NE site (Matuszkiewicz 2008 and Table 1). It has half as many days with snow cover and days in which the maximum temperature remains below 0°C. As a consequence, snails from the SW population continued to grow for two more months than those in the NE (cf. April-October 2016, Fig. 5A). This temperature constraint has been found in other snails from temperate regions, where more time is required to reach maturity/final size in areas with a shorter growing season (Umiński 1975, Terhivuo 1978, Baur & Raboud 1988, Sulikowska-Drozd 2010, 2011). In the Mediterranean region, an analogous slowdown in growth rate is caused by heat and drought (Kiss *et al.* 2005, Lazaridou & Chatziioannou 2005).

The variation in these aspects of growth between years in the SW site suggest that snails are capable of an immediate response to climatic variations, rather than having fixed properties determined by selection over the long term. It would be of interest to obtain longer time series from particular populations and to study many over a range of climatic regimes. Variation in weather certainly influences growth and longevity in other snail species (Sulikowska-Drozd 2011, Prόćków *et al.* 2012, 2013).

A pattern of decreasing body size with shorter growing seasons and harsh climates more generally has been regularly reported among arthropods (e.g. Blanckenhorn 1997, Fischer & Fiedler 2002, Chown & Klok 2003, Blanckenhorn & Demont 2004, Puzin *et al.* 2014, Horne *et al.* 2015, Ramírez-Delgado *et al.* 2016). While this pattern is also present when comparing the SW and NE populations of *X. obvia* in this study and might reflect the same constraints, this is not reflected so consistently among snails (Baur & Raboud 1988, Gittenberger 1991, Kotsakiozi *et al.* 2013, Giokas *et al.* 2014, Prόćków *et al.* 2017). An extensive literature review (Goodfriend 1986) noted some individualistic responses in body size of land snails along altitudinal, moisture, temperature/insolation and calcium availability gradients. In four of five taxa, he documented negative correlations between shell size and elevation, which is undoubtedly influenced by the change in climatic conditions with altitude. Smaller shells were also reported in *Faustina faustina* from higher latitudes of Poland (Marzec 2013). Observations of land snails across larger scale (northwestern Europe, eastern North America and New Zealand), however, showed only weak altitudinal variation in community body sizes which is probably obscured by other strong local environmental gradients such as precipita-

tion (Nekola et al. 2013). Additionally, larger shells of *X. obvia*, recorded in warmer and drier habitat, may constitute responses to selection by environmental factors. According to the Desiccation Resistance hypothesis (Remmert 1981), larger invertebrates should be more resistant to desiccation because of their lower ratio of surface area to volume. Nevo et al. (1983) found a positive relationship between shell size and aridity in four snail species in Israel and hypothesized that large shells are superior in dry habitats since they lose relatively less water due to their lower surface to volume ratio. Desiccation is a major constraint for snails in arid environments (Giokas et al. 2005, Entling et al. 2010).

Shell colouration in land snails, and most particularly in those that are polymorphic in this respect, affects their thermal properties. These may affect fitness under different climatic conditions as pale shells reflect more solar radiation (Jones et al. 1977, Lazaridou & Chatziioannou 2005, Ożgo 2005). Differences in thermal balance influence many behavioural and life cycle traits (Abdel-Rehim 1983, 1986, 1988, Cowie & Jones 1985, Burla & Costelli 1993, Staikou 1999, Pruitt et al. 2011, Goulet et al. 2017). In many species, including *X. obvia* from the Mediterranean region, pale or unbanded snails are more frequent in hotter and more exposed sites (Lazaridou & Chatziioannou 2005, Johnson 2011). Our results were opposite, as unbanded snails were most common in the region with a colder climate (Table 1). While the relationship of thermal balance in relation to shell colour has recently been criticised (Scheil et al. 2012), we note that there are more hours of sunshine during the active season in the NE site, a consequence of latitude. Shell polymorphisms in snails are known to be affected by factors other than climate. Selection for crypsis and the tendency for different morphs to select appropriate microhabitats may all have effects (Jones et al. 1974, Allen & Weale 2005, Holmes et al. 2017, Rosin et al. 2018). With only two populations available, we cannot comment further other than to note that *X. obvia* and other species of open, lime-rich sites such as *Granaria frumentum* may be subject to heavy predation (Němec & Horsák 2019), and that genetic drift and founder effects may be significant in small, isolated populations (Jones et al. 1977, Cook 1998, Ożgo 2008). Such isolation is typical for *X. obvia* populations in Poland (Wiktor 2004).

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