

Insights into the reproductive activity of *Omphiscola (Lymnaea) glabra* (Gastropoda: Lymnaeidae) in relation to soil geology in Central France

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Abstract – Transplantations of *Omphiscola glabra* from granite to marl, or vice versa, between farms known for cases of fasciolosis have shown differences in the maximum shell height of adult snails. To determine whether these differences were due to parasitism, soil geology, or a combination of both factors, four snail populations living on marl or granite were investigated over 12 months to specify the characteristics of egg-laying in spring, and to follow the shell growth of both snail generations. In both types of habitats, the number of egg-masses per adult snail and their size significantly decreased during the 7 weeks of snail egg-laying. During this period, each adult snail on marl laid a mean of 6.4 masses and 93.3 eggs. On granite, the mean values were 5.7 masses and 69.1 eggs, respectively. Two annual generations, the first in spring and the other in autumn, were noted in these habitats. The maximum shell height of adults was different: a mean of 19.8 and 20.5 mm on marl compared with 17.2 and 18.2 mm on granite. Soil geology thus plays a role in the egg-laying and shell growth of *O. glabra*.

Key words: Egg / fecundity / *Omphiscola glabra* / shell growth / soil geology

Introduction

On the acidic soils of Central France, *Omphiscola (Lymnaea) glabra* (O.F. Müller) is a natural snail host of the parasite *Fasciola hepatica* (Linnaeus). Three modes of snail infection were demonstrated for this lymnaeid: (i) the infection of juveniles measuring less than 2 mm in shell height at miracidial exposure (Kendall, 1950; Busson *et al.*, 1982), (ii) the co-infection of juveniles and pre-adults (3–6 mm in shell height) with *F. hepatica* and another digenean, *Calicophoron daubneyi* (Dinnik) (Abrous *et al.*, 1998) and (iii) the infection of pre-adults, coming from *F. hepatica*-infected parents, over several snail generations (Rondelaud *et al.*, 2015). Among these three modes, the co-infection of *O. glabra* with *C. daubneyi* and *F. hepatica* was the most frequent (Abrous *et al.*, 1999, 2000). The other two modes were of minor importance and were noted only in limited cases (Rondelaud, 1980; Rondelaud *et al.*, 2015).

Samples of *O. glabra* were transplanted from granite to marl by Dreyfuss *et al.* (2010) and their progeny was followed for 6 years to analyze the adaptation of these snails to these new sites and local parasites. According to these

authors, the maximum shell height of adults was different: a mean of 18.8 mm for snails transplanted on marl and 16.7 mm for controls on granite. A similar difference was also noted for snails transplanted from marl to granite: a mean of 17.5 mm for transplanted snails and 20.5 mm for controls (Dreyfuss *et al.*, 2010). In view of these findings, it is possible to ask whether the differences between these maximum shell heights were due to parasitism (the presence of the digenean can induce snail gigantism, even though the snail infection was abortive: Wilson and Denison, 1980; Chappuis, 2009), the type of soil on which snails were living, or a combination of both factors. To examine this question, we studied the reproductive activity and shell growth of snails living on marl and granite.

In Central France, *O. glabra* showed two annual generations, the first in spring and the second in autumn (Rondelaud *et al.*, 2003). Egg-masses laid by this snail were oblong, 10–15 mm long, and were composed of 15–30 eggs, each measuring 0.6–0.9 mm in diameter (Germain, 1930–1931; Macadam, 2006). According to environmental temperature, the newborns hatched 15–25 days later. The oviposition behaviour and shell growth of this lymnaeid in the field are still poorly known. Conflicting results were noted for the date of the first egg-deposits in spring because egg-laying began in

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mid-February (Macadam, 2006) or May (Welter-Schultes, 2013). The other points have not been well studied. Field studies were therefore necessary to answer the following two questions: did the characteristics of egg-masses laid by *O. glabra* show differences in relation to the location of snails on marl or granite? What was the shell growth of this lymnaeid on both types of soils? To answer the first question, weekly investigations in four *O. glabra* habitats were carried out from February to June 2015 to determine several parameters of snail reproduction during the main laying period. To respond to the second question, we sampled snails each month in these four habitats for 12 months, to monitor the shell growth of *O. glabra* in relation to each snail generation.

Materials and methods

Snail habitats

The four populations of *O. glabra* (Fig. 1) were selected in road ditches located outside cattle- or sheep-breeding farms to eliminate the risk of *F. hepatica* in these snails and analyse the sole effect of soil geology on their reproductive activity and shell growth. The first two were living in the Brenne Regional Natural Park, in the communes of Chitray (46°40'17"N, 1°18'3"E) and Thenay (46°34'47"N, 1°24'34"E), department of Indre (Central France). The areas of these habitats in January 2015 were 15.4 and 75.6 m², respectively. These sites were watered by runoff from the end of October to the next June. The bottom sediment was composed of silt and sand, and was supported by an impermeable layer of marl. Water pH varied from 6.7 to 7.8 and the dissolved calcium level from 26 to 35 mg.L⁻¹ (Dreyfuss *et al.*, 2010). Some rush clumps and a few pondweeds grew in these *O. glabra* habitats. Numerous detritus during most of the year and epiphytic filamentous algae in spring were also present. The other two populations were located on the communes of Blond (46°2'26"N, 1°1'41"E) and Le Dorat (46°11'52"N, 1°4'6"E), department of Haute Vienne. The respective areas of these habitats were 30.5 and 10.9 m² in January 2015. Water coming from a temporary spring ran to each site from the end of October to the beginning of the next July. The bottom sediment was composed of sand and gravel, supported by granite. Water pH varied from 5.6 to 7 and the dissolved calcium level was less than 20 mg.L⁻¹ (Guy *et al.*, 1996). Food available in these habitats was scarcer, with several hygrophilous grasses, a few rush clumps and epiphytic algae. The longest distance between these four habitats was 65 km.

No other lymnaeid species was living with *O. glabra* in these four habitats. These sites were subject to the same climatic conditions, with a wet temperate climate modulated by westerly oceanic winds. The mean annual rainfall noted during the 50 years preceding field investigations varied from 600 to 1000 mm, while the mean annual temperature was 10–11 °C (Dreyfuss *et al.*, 2010; Rondelaud *et al.*, 2011).

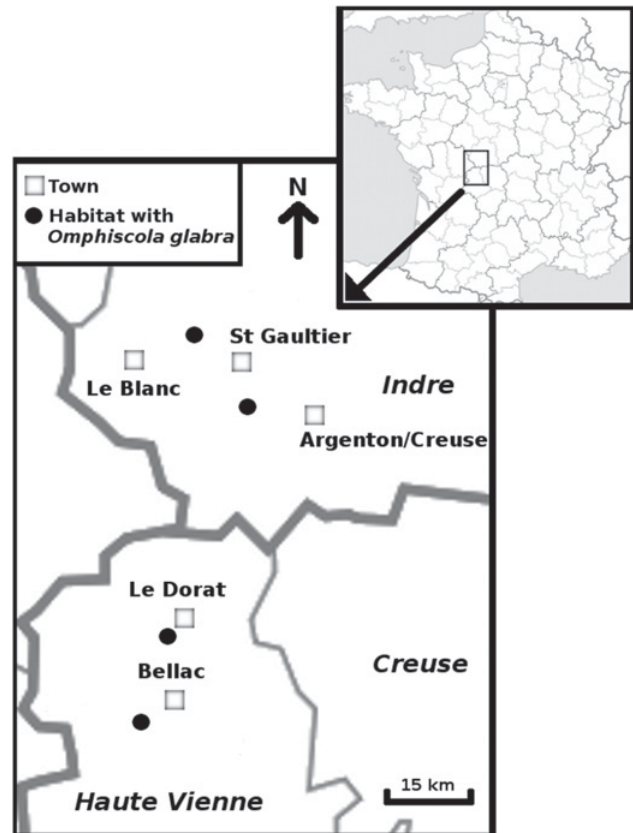


Fig. 1. Location of the four road ditches in the Brenne Regional Natural Park and northern Haute Vienne (Central France).

First series of investigations

The aim was to observe egg mass density, number of eggs per mass and viability of eggs in the four snail habitats during the main egg-laying period (spring). The protocol used for these investigations derived from that used by Vareille-Morel *et al.* (1998) to study egg-masses laid by another lymnaeid, *Galba truncatula* (O.F. Müller) on different types of French soils. Weekly observations were performed using the technique of quadrats. In each habitat, five areas of 1 m² each for Thenay and Blond, and only three for each of the other two habitats were investigated over the 7 weeks of the egg-laying period. These areas were selected in zones receiving sunlight for at least 2 h a day (egg masses were scarce in permanently-shaded places) and were covered by a low water layer (5 cm or less in depth), as the count of egg masses was difficult in deeper zones. Firstly, adult snails (12 mm and more in height) and egg masses were counted in each quadrat by two persons for 35–40 min. Secondly, 20 adult snails were collected from each habitat and their shell height was measured using electronic callipers before the replacement of these snails in their habitat. Thirdly, ten egg-masses were collected from each habitat, transported to the laboratory and placed in permanently oxygenated water coming from the habitat of origin. The other masses were removed from each quadrat to avoid recounts 7 days later. Egg-masses studied in the laboratory were subject to

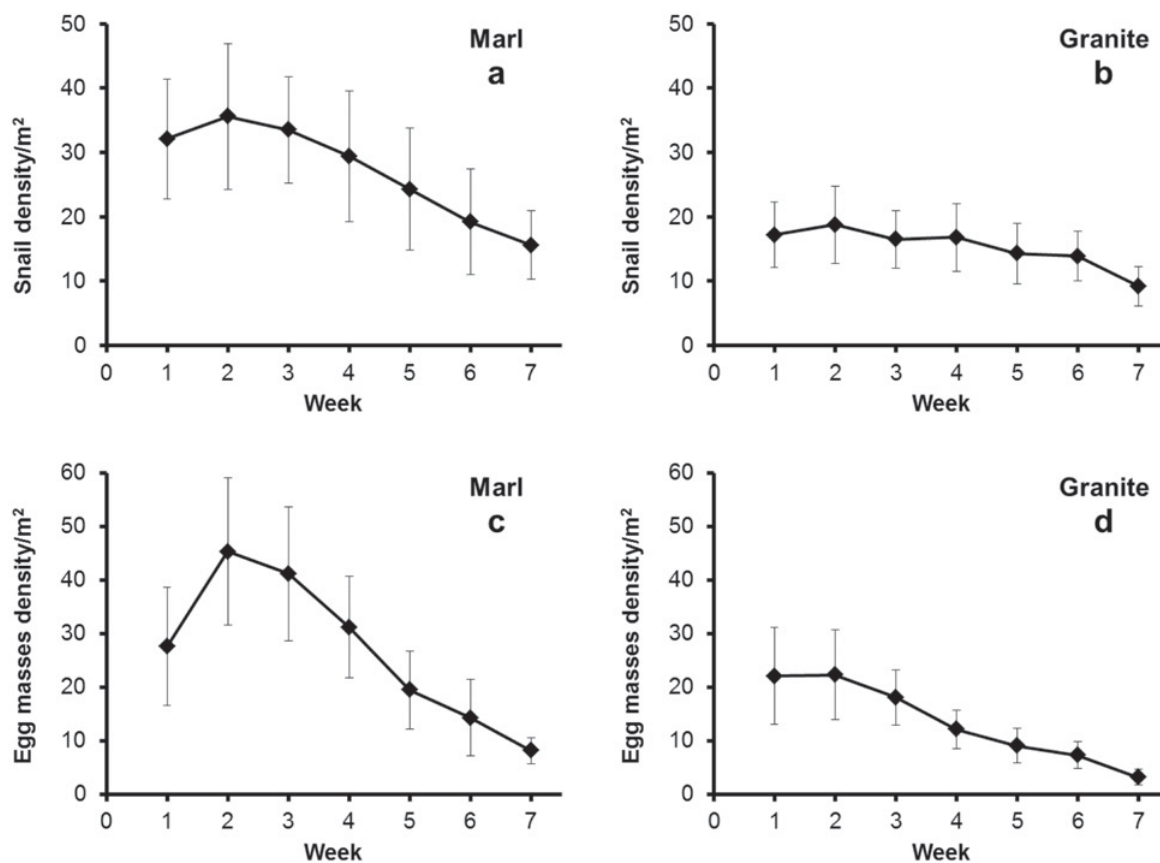


Fig. 2. Density of adult snails (a, b) and egg-masses (c, d) per m^2 of habitat in four *Omphiscola glabra* populations during the egg-laying period in relation to soil geology. Mean values are given with their standard deviation (SD).

the following conditions: temperature fluctuating each day from 8–12 °C to 22–24 °C, natural photoperiod, indirect incidence of sunlight. The number of eggs per mass and fecundity rate (number of eggs present in masses/number of newborns) were noted.

Second series of investigations

The aim was to determine any variations in shell growth of *O. glabra* according to soil geology. In each habitat, monthly samples of 100 snails each were randomly collected from January to June and from September to December 2015, whatever their shell height. No sampling was performed in July and August 2015 because of summer drying of habitats and aestivation of snails into marl (Chitray, Thenay) or among the nearest vegetation on ditch-sides in the other two habitats (Rondelaud *et al.*, 2003). The shell height of collected *O. glabra* was measured using electronic callipers. After measurement, snails were returned to their habitat.

Data analysis

Individual values noted during the first series of investigations for snail density, egg-mass density and the

number of eggs per mass were averaged and standard deviations were established taking into account soil geology (marl or granite) and the length of the egg-laying period. A similar protocol was used for shell growth during the second series of investigations taking into account soil geology, snail generation and the date of sampling. Normality of these values was analyzed using a Shapiro–Wilk normality test (Shapiro and Wilk, 1965). As their distribution was not normal, the Kruskal–Wallis test was used to establish levels of significance. All the statistical analyses were done using Statview 5.0 software (SAS Institute Inc., Cary, NC, USA).

In the first series of investigations, week 2 values noted in the habitats on marl for snail density, egg mass density, or the number of eggs per mass were compared with those found in the sites on granite, as they were the highest among values noted during the egg-laying period. In a second step, comparison of values noted from week 3 to 7 on marl and granite was also performed. In the second series of investigations, the shell heights of snails noted in June were compared, taking into account snail generation. A similar comparison was also performed for values recorded in September, October or December.

To build Figures 2–4, monthly values recorded for each type of habitat (on marl or granite) were pooled, taking into account the length of the egg-laying period (Figs. 2 and 3) or the date of snail sampling (Fig. 4).

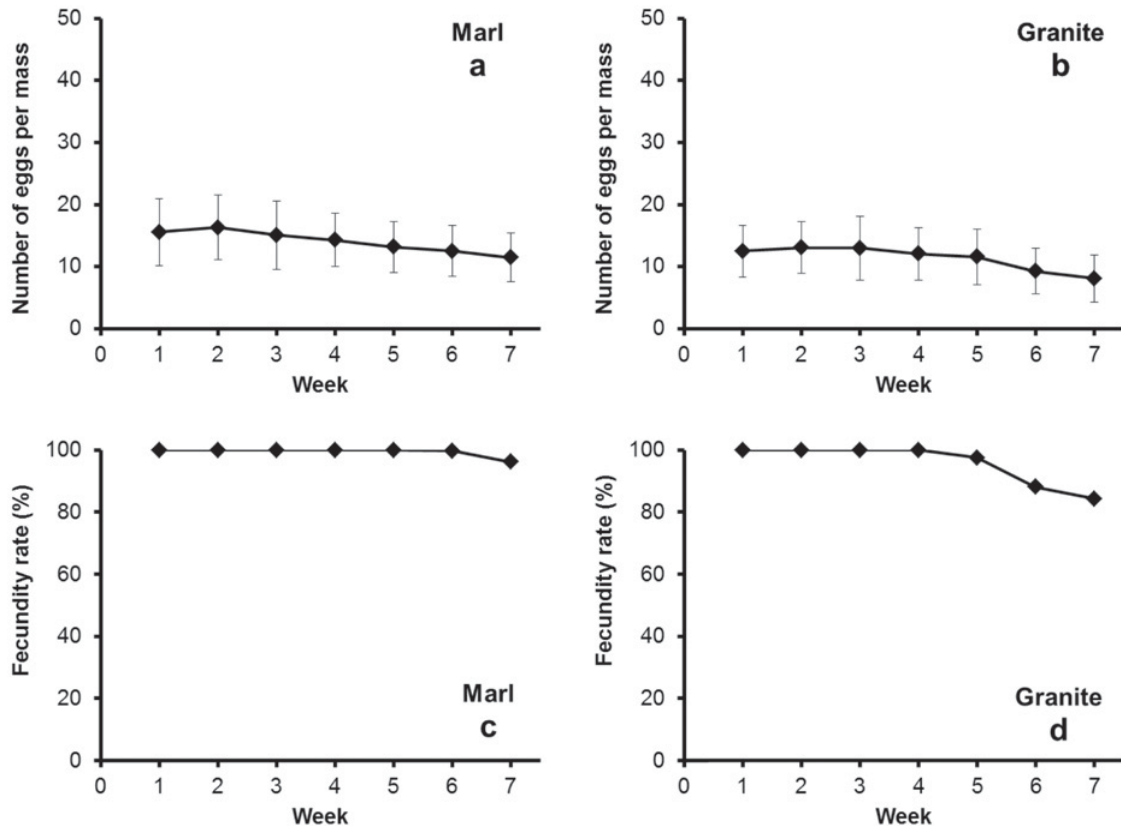


Fig. 3. Number of eggs per mass per m^2 of habitat (a, b) and fecundity rate (c, d) in four *Omphiscola glabra* populations during the egg-laying period in relation to soil geology. Mean values are given with their standard deviation (SD).

Results

Characteristics of egg-deposits

In the four snail habitats, egg-laying occurred over 7 weeks: the first egg-masses were noted at the end of April and the last at mid-June. On week 7, the shell heights of adults on marl ranged from 19.5 ± 1.7 mm to 20.6 ± 0.9 mm. The respective values on granite varied from 16.3 ± 1.4 mm to 17.2 ± 0.8 mm. A significant difference ($H = 14.67$, $P < 0.001$) between these shell heights on marl and granite was noted. In contrast, the shell heights in the two habitats on marl did not significantly differ from each other. A similar finding was also noted in the two sites on granite (data not shown).

Figure 2 shows snail density and egg-mass production in the two types of habitats (marl or granite) during the 7 weeks of the egg-laying period. The number of adult snails per m^2 of habitat peaked on week 2 and decreased thereafter until the end of egg-laying. Adult snails were significantly more numerous ($H = 7.58$, $P < 0.01$) on week 2 in the habitats on marl than in the other two sites. From week 3, the decrease in snail density was significantly greater ($H = 7.79$, $P < 0.01$) in the habitats on granite than in the two others (Fig. 2(a) and (b)). Similar findings were also noted for egg-mass density. On week 2, egg-masses were significantly more numerous ($H = 9.01$, $P < 0.01$) in the habitats on marl. In contrast, the decrease noted from

week 3 was significantly greater ($H = 10.54$, $P < 0.01$) on granite (Fig. 2(c) and (d)). This last finding is strengthened by the ratio between snail density and egg-mass density: from 1.27 to 0.52 mass throughout the 7 weeks on marl instead of 1.29–0.34 mass on granite (data not shown). If the numbers of egg-masses noted during the 7 weeks are added, each snail laid a total of 6.46 masses on marl and 5.77 masses on granite.

In both types of habitats, the number of eggs per mass (Fig. 3) peaked on week 2 and decreased thereafter until the end of the laying period. On week 2, the masses collected from marl contained more eggs than those coming from granite and the difference was significant ($H = 6.35$, $P < 0.05$). In contrast, the decrease noted from week 3 to 7 was significantly greater ($H = 8.32$, $P < 0.01$) on granite (Fig. 3(a) and (b)). If the numbers of eggs noted during the 7 weeks are added, each *O. glabra* laid a total of 93.3 eggs on marl and 69.1 eggs on granite over the 7 weeks. The fecundity rate decreased slightly from week 5 in egg-masses collected from granite (Fig. 3(d)) and from week 6 in those coming from marl (Fig. 3(c)). This last finding is due to the presence of several unfertilized eggs in these masses.

Snail growth

Figure 4 shows the shell growth of both snail generations in the two types of habitats over a year. Two growth

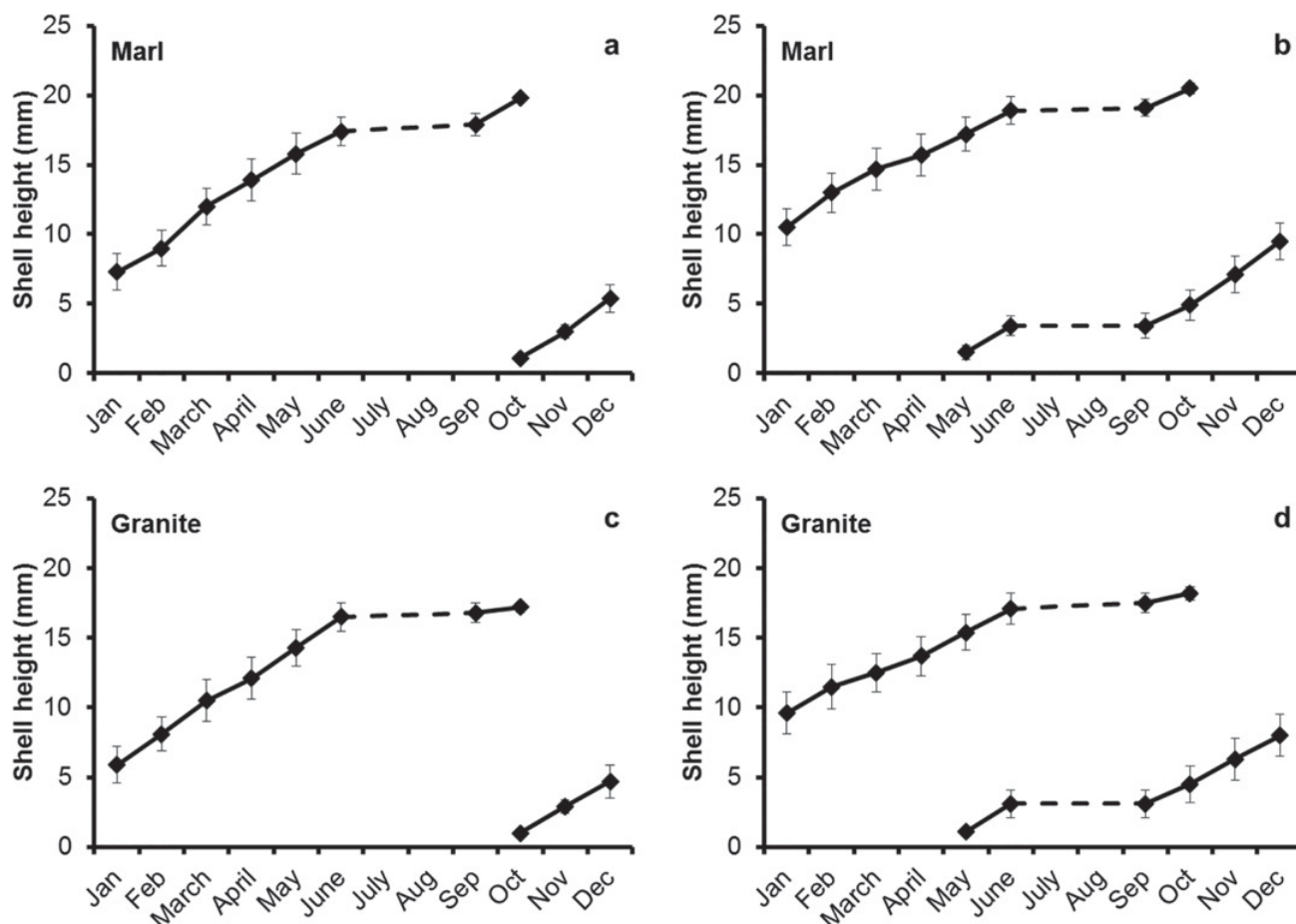


Fig. 4. Shell growth of *Omphiscola glabra* in four habitats on marl or granite: overwintering generation (a, b) and spring-born generation (c, d). Dotted lines, snail aestivation. Mean values are given with their standard deviation (SD).

periods, *i.e.*, in spring and autumn, were noted and the most important of them ranged from March to June. In contrast, the shell growth stopped during summer drought and slowed down during winter months. These two snail generations showed some differences:

- Newborns of the overwintering generation (Fig. 4(a) and (b)) appeared in October and their shell height increased up to a mean of 5.4 mm (on marl) or 4.7 mm (on granite) in December. Shell growth was slightly slowed in January (7.3 mm on marl, 5.9 mm on granite) and increased again from February up to a mean of 17.4 mm (on marl) or 16.5 mm (on granite) in June. After the first post-summer rains, several snails survived and their shell height increased again to a mean maximum height of 19.8 mm (on marl) or 17.2 mm (on granite). In December and the next June, the shell height of snails living on marl was significantly greater (December: $H = 15.23$, $P < 0.01$; June: $H = 7.99$, $P < 0.1$). In contrast, values recorded in September or in October did not significantly differ from each other.
- Egg-deposits laid in spring by the overwintering generation gave birth to another wave of newborns in May (Fig. 4(c) and (d)). The mean height of these

spring-born individuals increased up to 3.4 mm (on marl) or 3.1 mm (on granite) so that they are subject to summer drying at the juvenile state. From September, the growth of surviving snails increased up to a mean of 9.5 mm (on marl) or 8 mm (on granite) by December. After a slight slowdown in January, this growth increased again in spring to reach a mean of 18.9 mm (on marl) or 17.1 mm (on granite) in June. The few snails that survived summer drying died in September or October with a mean maximum height of 20.5 mm (on marl) or 18.2 mm (on granite). No significant difference between the shell heights of juveniles was noted in June. In contrast, significant differences were noted for adults in December ($H = 13.43$, $P < 0.01$) and June ($H = 8.54$, $P < 0.1$). Values noted in September and October in both types of habitats were close to each other and no significant difference was found.

Discussion

As little information on the dynamics of egg production for *O. glabra* is available in the literature, most of the

above results were compared with those reported by [Vareille-Morel *et al.* \(1998\)](#) for *G. truncatula*, as populations of this snail live on the same types of soils and often in the same swampy meadows ([Vareille-Morel *et al.*, 1999, 2007](#)). Firstly, there was a decrease in egg-mass production during this laying period. The number of masses per adult snail decreased from 1.27 to 0.52 mass on marl and from 1.29 to 0.34 on granite for *O. glabra* (the present study), and from 0.51 to 0.34 mass on marl and from 1.10 to 0.47 on granite for *G. truncatula* ([Vareille-Morel *et al.*, 1998](#)). This finding is mainly due to the fact that adult snails reach their maximum shell height during this period and die. However, another explanation based on greater egg production of each snail during the first weeks of the laying period, followed by its decrease during the subsequent weeks, cannot be ruled out. An argument supporting this last hypothesis is the decrease that occurs in the number of eggs per mass over time ([Fig. 3](#)). Secondly, the values recorded for egg-mass density and the number of eggs per mass was significantly higher on marl. On week 2, for example, *O. glabra* laid a mean of 45.3 masses.m⁻² on marl and 22.3 masses.m⁻² on granite, with 16.3 and 13.1 eggs per mass, respectively (the present study). In the case of *G. truncatula*, a mean of 6.31 masses.m⁻² were noted on marl and 3.92.m⁻² on granite during the same week of the laying period, while the mean numbers of eggs per mass were 12.1 and 8.75, respectively ([Vareille-Morel *et al.*, 1998](#)). These differences can partly be explained by the maximum shell height of snails, which is higher in the habitats on marl. However, other factors may also have an effect on the number and size of these egg-masses. Among these factors, the most efficient might be local microclimate, as it is known for its influence on vegetation growth and snail biology ([Smith and Wilson, 1980](#)). Thirdly, the fecundity of eggs laid by either lymnaeid slightly decreased during the last weeks of the laying period: from week 5 on granite and week 6 on marl for *O. glabra* (the present study), from week 6 in two populations of *G. truncatula* living on marl and granite ([Vareille-Morel *et al.*, 1998](#)). This fact was also observed in *Radix labiata* (Rossmässler) ([Tapie, 1996](#)). The presence of several unfertilized eggs in egg-masses laid by *O. glabra* and *G. truncatula* during the last weeks of the laying period might be due to non-viability of foreign and/or local sperm contained in the snail's carrefour ([de Jong-Brink, 1990](#)). Storage of sperm in this site over a long period would reduce its fertilizing capacity so that several spermatozoa would not be able to penetrate oocytes.

The finding of two annual generations of *O. glabra* noted in the present study was consistent with the observations of several authors. [Boycott \(1936\)](#), [Økland \(1990\)](#), [Dillon \(2010\)](#) and [Glöer and Diercking \(2010\)](#) have reported on the number of generations for several Western European freshwater pulmonate gastropods when their habitats are subject to periodic drying over the year. However, two points warrant particular comments. Firstly, the shell growth of *O. glabra* populations living on marl was significantly greater than that of snails living on granite, and this difference must be related to the type

of soil on which the snails were living. Among the factors that may explain this finding, the dissolved calcium level in running water might be the main factor responsible for this difference, as it was lower in snail habitats located on cristallophyllian soils. Calcium is already known to affect the distribution of land snails in a given country ([Boycott, 1934](#)), as well as species richness ([Horsák and Hájek, 2003](#); [Juříčková *et al.*, 2008](#)), the abundance of each snail species ([Hotopp, 2002](#); [Vadeboncoeur *et al.*, 2007](#)) and snail growth ([Beeby and Richmond, 2007](#)). Secondly, two snail categories, *i.e.*, juveniles measuring 3.1–3.4 mm in shell height and adults greater than 15 mm at the beginning of July, were subject to summer drying of their habitats. Owing to their burrowing into the soil during aestivation, the mortality of adult snails on marl was lower than that of adults on granite ([Rondelaud *et al.*, 2003](#)). In both types of habitats, the small size of juvenile snails allowed them to better resist aestivation effects, whatever the soil geology, as already reported for *G. truncatula* ([Taylor, 1965](#)).

In conclusion, the number and size of egg-masses in the field were greater on marl than on granite. Similar results were already noted for snail growth. Soil geology thus plays a role in the egg-laying and shell growth of *O. glabra*. Further studies are still necessary to analyze the impact of parasitism on the maximum shell height of this lymnaeid.

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