Int. J. Lim. 2022, 58, 11
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https://doi.org/10.1051/limn/2022011

Available online at:
www.limnology-journal.org

Research Article Open Access

Decline in the number and size of populations of two Lymnaeidae living in central France over the last decade

Philippe Vignoles, Gilles Dreyfuss* and Daniel Rondelaud

Laboratory of Parasitology, Faculty of Pharmacy, 2, rue du Docteur Raymond Marcland, 87025 Limoges Cedex, France

Received: 15 February 2022; Accepted: 25 July 2022

Abstract – Field investigations in 2013–2014 on acid soils and in 2016–2017 on sedimentary soils showed that populations of two lymnaeids had decreased in number in central France since 1998. As several heat waves occurred in this region in 2018, 2019 and 2020, it was useful to check whether this decline had further increased in recent years. Surveys in 56 farms in the north-west and west of the Haute Vienne department (acid soils) and 37 farms in the south of Indre (sedimentary soils) were therefore carried out in 2020 and 2021 and the results obtained were compared with those recorded by our team in the same farms in 2013–2014 and 2016–2017. On acid soils, the overall number of populations decreased by 34.7% for *Galba truncatula* (out of 813 populations in 2013–2014) and 22% for *Omphiscola glabra* (out of 550), while it decreased by 25% for *G. truncatula* (out of 361 in 2016–2017) and 15.2% for *O. glabra* (out of 205) on sedimentary soils. Similarly, the overall density of overwintering snails significantly decreased by 80.7% for *G. truncatula* and 70.2% for *O. glabra* on acid soils, while it significantly decreased by 64.1% and 38.3%, respectively, on sedimentarym soils. In both cases, these decreases were more marked on acid soils than on sedimentary soils. In contrast, the habitats of *G. truncatula* and most of those colonized by *O. glabra* showed no significant variation in their area between the two periods of study. The decline in the number of these lymnaeid populations, observed since 1998, is still continuing today in central France and may be due in part to heatwave episodes s that occurred in 2018, 2019 and 2020 in this region.

Keywords: *Galba truncatula* / habitat / Lymnaeidae / *Omphiscola glabra* / population / population dynamics

1 Introduction

One of the major effects of humans on nature has been to increase the rate of extinction of animal and plant species well above natural levels. Currently, the rate of extinction is accelerating so much that biodiversity is declining rapidly and many ecosystem processes are degraded or lost (see review by Johnson, 2020). The main direct causes of extinction are (a) loss and degradation of habitats due to human use of land and sea, (b) overexploitation of wild populations and (c) impact of pollution and/or climate change on populations and ecological communities of invasive alien species (Maxwell *et al.*, 2016; Díaz *et al.*, 2019; Leclère *et al.*, 2020). Among these causes, climate change appears to be the most worrying current process due to the continued increase of greenhouse gases in the atmosphere (IPPC, 2020) and its most important effect may well be to increase the frequency or magnitude of extreme events. These include many elements that recent experience shows have great potential to damage biodiversity, such as intense tropical cyclones, marine heat waves, and El Niño and La Niña events (Collins *et al.*, 2019; Johnson, 2020). Extreme events that affect large areas can result in large, abrupt, and unexpected declines of many species at the same time (Johnson, 2020).

Changes in climatic parameters have a direct impact on the structure and dynamics of helminth populations which cause parasitic diseases in humans and animals (Mas-Coma *et al.*, 2009). Among these parasitoses, the fasciolosis caused by *Fasciola hepatica* Linnaeus, 1758 has been the subject of several reports on its development in the years to come (Poulin, 2006; Mas-Coma *et al.*, 2009; Van Dijk *et al.*, 2010; Fox *et al.*, 2011; Lofty, 2014; Short *et al.*, 2017) because this disease is highly dependent on temperature and rainfall (Ollerenshaw and Smith, 1969). The increase in temperature can directly affect the prevalence of this parasitosis in a given area (Short *et al.*, 2017). The onset of milder, wetter winters allows more metacercariae to overwinter in pastures (Taylor, 2009). The same is true for freshwater snails which ensure the development of *F. hepatica* larval forms (Van Dijk *et al.*, 2010).

*Corresponding author: gilles.dreyfuss@unilim.fr

In its life cycle, the parasite needs a definitive host (generally a mammal) which harbours the adult form of this digenean and an intermediate host (generally a lymnaeid) which ensures the development of its larval forms (Andrews *et al.*, 2022). At least 20–22 species of Lymnaeidae have been recorded worldwide as natural or experimental intermediate hosts of *F. hepatica* (Correa *et al.*, 2010, 2011; Vázquez *et al.*, 2019). *Galba truncatula* (O.F. Müller, 1774) is considered the main snail host of *F. hepatica* in Western Europe (Dreyfuss *et al.*, 2015; Knubben-Schweizer *et al.*, 2022). In central France, *Omphiscola glabra* (O.F. Müller, 1774), also known under the name of *Lymnaea glabra*, is also a potential intermediate host but its role is limited because most of naturally infected individuals come from co-infections with the miracidia of *F. hepatica* and those of another parasite, *Calicophoron daubneyi* Dinnik, 1962 (Vignoles *et al.*, 2018). On acid soils, both Lymnaeidae can live on the same surface drainage networks or the same road ditches, but their habitats are generally separated by 15–30 m from each other (Vareille-Morel *et al.*, 1999, 2007). The same fact was also observed on sedimentary soils, but the distance between the populations of the two species was then reduced: from 3 to 10 m (Vignoles *et al.*, 2018).

In central France, a decline in the number of populations and their size has already been reported in both species when they live on the acid soils of Limousin (Dreyfuss *et al.*, 2016a, b) and on sedimentary lands surrounding this region (Dreyfuss *et al.*, 2018a). Field investigations were first carried out in 2013 and 2014 on the lymnaeid habitats in 162 farms on acid soils and the results were compared with those that our team noted in these same farms from 1976 to 1992 (*G. truncatula*) and from 1986 to 1997 (*O. glabra*). The overall number of populations decreased by 34% (out of 3015 populations) for *G. truncatula* and by 23.4% (out of 1131) for *O. glabra*. The overwintering snails were also less numerous in 2013–2014 in five types of habitats for *G. truncatula* and in three types only for *O. glabra* (Dreyfuss *et al.*, 2016a, b). Similar results were then observed in 2016–2017 in 57 farms on sedimentary soils, with an overall decline rate of 30.8% (out of 483 populations) for *G. truncatula* and 38.6% (out of 269) for *O. glabra*. Significantly lower densities of overwintering snails were noted for *G. truncatula* in two habitat types, while no significant difference was noted for *O. glabra* (Dreyfuss *et al.*, 2018a). Among the causes identified to explain this decline, human activity on permanent meadows and road ditches (mechanical cleaning, *etc.*) as well as climate change have been incriminated (Dreyfuss *et al.*, 2016a, b). Few studies have still been carried out on the effects of this climate change on the populations of freshwater snails living in western Europe (Cordellier and Pfenninger, 2009; Salo *et al.*, 2017; Leicht and Seppälä, 2019). According to Cordellier *et al.* (2012), global warming will lead to changes in the distribution of native freshwater species: some ones will migrate to colder places, while others might have a limited distribution. Non-native species should take over and expand their distribution areas. In view of these data, it seemed useful to verify whether this observed decline in the number and size of populations has further increased in central France following several heatwave episodes that occurred in 2018, 2019 and 2020 (Météo France, 2018, 2019, 2020).

In order to verify this possibility, investigations were carried out in 56 farms located in the Haute Vienne department on acid soils and in 37 farms in the department of Indre on sedimentary soils. The permanent meadows located in the perimeter of each farm and the road ditches around them were investigated and the results were compared with those provided by surveys carried out by our team in the same farms in 2013–2014 (acid soils) and 2016–2017 (sedimentary soils). Several results noted in 2020 in the grasslands of 38 farms on acid soils have already been published (Rondelaud *et al.*, 2021). These first results were verified and supplemented in 2021 by addressing a higher number of farms on acid and sedimentary soils to determine whether this observed decline was a general process affecting all lowland populations of *G. truncatula* and *O. glabra* living in central France.

2 Materials and methods

2.1 Farms studied

Two groups of farms were selected according to their following characteristics: (a) these farms are located in two neighbouring French departments (Haute Vienne, Indre) so that the maximum distance between the most distant farm on acid soils and the most distant farm on sedimentary soils does not exceed 120 km (Fig. 1); (b) they are in the same altitude range: between 80 and 250 m, as the number of lymnaeid populations on acid soils decreases significantly when the altitude of municipalities increases (Dreyfuss *et al.*, 2018b, c) (c) these farms raise cattle or sheep on permanent grasslands not treated with lime and the farming technique used has not changed over the past 30 years; (d) the permanent meadows within the perimeter of these farms are hygro-mesophilous with a mesophilous zone dominant in area on the other zone; (e) these grasslands are subject to alternating grazing by ruminants and mowing during the summer (usually late July to September depending on the intensity of summer drying); (f) the habitats of *G. truncatula* and those of *O. glabra* present in these grasslands and the roads, that surround them, are quite numerous during surveys carried out by our team from 2013 to 2017 in these stations (Dreyfuss *et al.*, 2016a, b, 2018b, c).

The 56 farms on acid soils are located in the north-west or west of the Haute Vienne department (Fig. 1). Their altitude ranges from 155 to 241 m. Thirty-nine farms raised cattle and the other 27 raised sheep. The subsoil of these farms is granitic (37 cases) or gneissic (19) (Chèvremont, 2008). A surface drainage network, whether or not supplied by one or more temporary sources, is present in each of the 257 permanent pastures. This network is only cleaned up every three, four or five years depending on its state of degradation. In road ditches around these farms, vegetation was only gyro-crushed two or three times a year. Water, which flows through drainage systems or road ditches, is generally present from early October to late June or early July with a maximum from January to late April. The pH of this water varies from 5.8 to 7, while the concentration of dissolved calcium ions is less than 20 mg/L (Guy *et al.*, 1996).

The 37 farms on sedimentary soils are located in the south and south-east of the Brenne Regional Natural Park, department of Indre (Fig. 1). The altitude of these stations ranges from 87 to 103 m. Twenty farms raised cattle, while the other 17 raised sheep. In 35 cases, grasslands and road ditches are located on an impermeable sandstone or clay subsoil at shallow

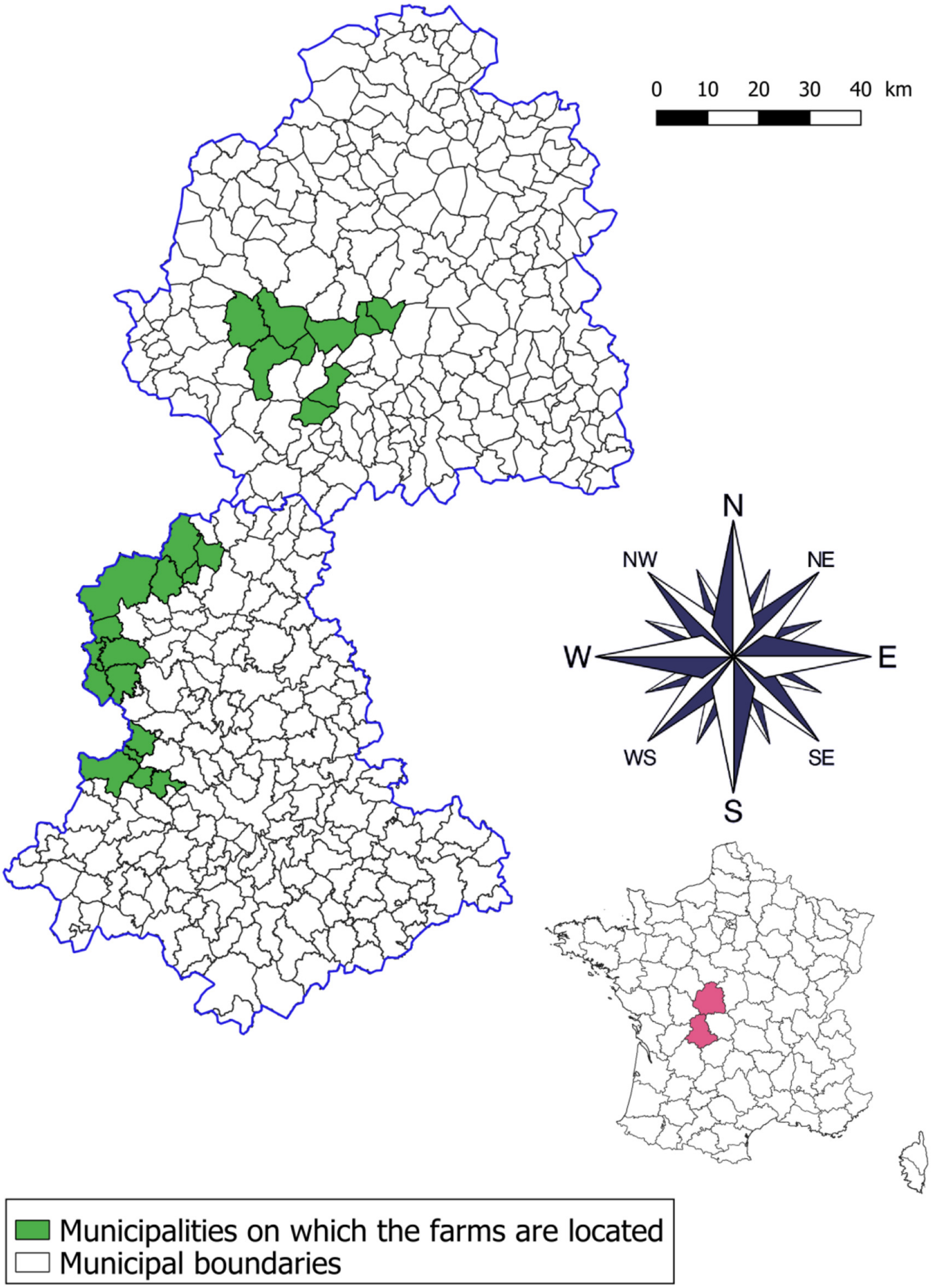

Fig. 1. Geographical location of Indre and Haute Vienne departments in central France (lower right map) and the municipalities of both departments (the other map) where the farms are located: Indre (upper position) and Haute Vienne (lower position).

depth (from 40 to 80 cm). In the north of the municipality of Migné, two farms are located on a limestone subsoil. The 184 meadows studied are hygro-mesophilous, generally with a small hygrophilous zone. Rainwater drainage is usually provided by a surface drainage system and sometimes by one or two swales only. The conditions for maintaining grasslands and road ditches are identical to those described above for farms on acid soils. Due to the heterogeneity of soils, the pH of running water in snail habitats ranges from 6.8 to 8.1 and the level of dissolved calcium ions is between 28 and 41 mg/L (Dreyfuss *et al.*, 2018a).

All these farms are subjected to a continental climate strongly attenuated by the wet winds coming from the Atlantic Ocean. In the farms on acid soils, the mean annual precipitation ranged from 850 to 1100 mm per year, while mean annual temperature ranged from 10.5 to 11.5 °C for most farms (Rondelaud *et al.*, 2011). In those of sedimentary soils, the mean annual precipitation ranged from 750 to 850 mm depending of the year, while the mean annual temperature fluctuated from 11.5 to 12 °C at most stations (Dreyfuss *et al.*, 2018a).

2.2 Types of snail habitats

In the grasslands on acid soils, several habitat types have been defined by Vareille-Morel *et al.* (1999, 2007) for *G. truncatula*: (a) the peripheral end of a surface drainage swale with or without a temporary source flowing into it, (b) a hillside source, surrounded by rushes, (c) the main drainage ditch, (d) an area trampled by cattle or sheep when the walls of the adjacent drainage swale or main ditch are levelled, (e) the edges of a pond, usually at the inlet of the water body, and (f) the banks of a stream or river. In the case of *O. glabra*, Rondelaud *et al.* (2017) found the same habitat types, with the exception of type (a) because the lymnaeid usually colonizes the course of the drainage swale (Fig. 2). Both lymnaeids also colonize the road ditches located around these farms. In grasslands, there were generally no macrophytes on the course of drainage swales and ditches. In contrast, riparian vegetation was often well developed with numerous rushes and sedges. Around hillside sources, the vegetation was often sparse with clumps of rushes interspersed with rare plants of the Poaceae family. In trampled areas, the vegetation was denser with a clear predominance of Poaceae over rushes and sedges. Snail habitats on the banks of ponds and streams were generally bare with sparse macrophytes belonging to various taxa (Rondelaud *et al.*, 2011; Vignoles *et al.*, 2017, 2018).

On the sedimentary soils of Indre, five types of snail habitats were considered for either lymnaeid: (a) surface drainage swales, (b) spring pools (<20 m^2 in area) supplied or not by a temporary source, (c) road ditches when waterlogged during winter and spring, (d) small streams, and (e) the banks of large ponds near their inlet. In the swales and pools as well as on their periphery, the vegetation was fairly dense and consists primarily of many plants in the Poaceae family, with rare clumps of rushes and sedges. In contrast, rushes and sedges were more abundant in road ditches and along the banks of streams and ponds (Dreyfuss *et al.*, 2018a; Vignoles *et al.*, 2018).

2.3 Protocol for field investigations

Investigations on permanent meadows and the ditches that border them were carried out in 2013–2014 in farms on acid soils and in 2016–2017 in those on sedimentary soils in order to identify the populations of the two lymnaeid species and determine the characteristics of their habitats. Pastures and ditches were then re-examined in 2020 and 2021 to count the populations present, measure the area of their habitats and count the overwintering individuals in each population.

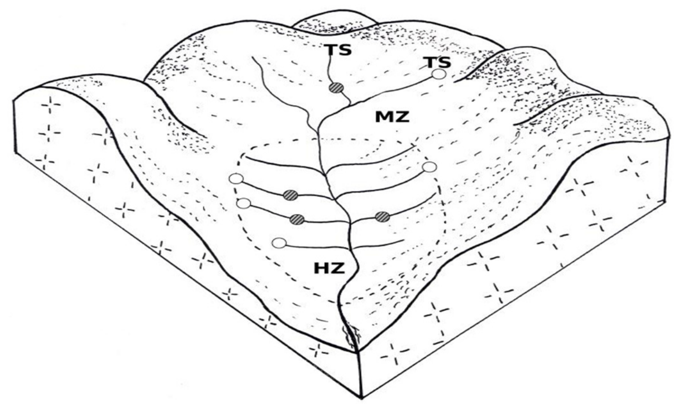

Fig. 2. Block diagram showing the location of the most frequent habitats colonized by *Galba truncatula* (○) and *Omphiscola glabra* (●) in a central French grassland on acid soil. Most of these meadows have a surface drainage system to evacuate runoff. In the example shown in this figure, four swales on each side open into the main ditch. Two temporary sources (TS), located on the hillsides, discharge their water at the upstream end of the drainage ditch. HZ, hygrophilous zone; MZ, mesophilous zone.

Depending on the year, these investigations were carried out in March-April and sometimes in February when the clemency of the temperature allows it. This period was selected for the following two reasons: (a) the habitats were then waterlogged and (b) they are populated only by adults belonging to the generation born during the previous autumn (overwintering snails). When a population of lymnaeids was not found in 2020 and 2021 in a meadow, the breeder was questioned to find out the possible cause behind this disappearance.

Adults higher than 4 mm for *G. truncatula* and 12 mm for *O. glabra* were counted by sight or using a colander (mesh size, 3 mm) depending on the height of the water layer. In 2013, 2014, 2016 and 2017, each count in habitats located along a drainage network or in a road ditch was performed by two people for 30–40 min, while on pond edges and stream banks each count was performed by one person for 15–20 min. In 2020 and 2021, each count was performed by one person for 15–20 min per habitat (when there is a population). The area of each habitat was then determined. Measuring areas occupied by *G. truncatula* or *O. glabra* is easy in the case of drainage swales due to their constant width and sometimes in the main ditches. The same is true for habitats located on the banks of ponds and streams because the lymnaeids are generally close to the edges. When the shape of the habitat was irregular (those located at the upstream end of a swale, around a source, or on a trampled area), the only solution was to draw a map and determine the area of this habitat according to its shape and dimensions.

When a habitat identified in 2013, 2014, 2016 or 2017 in a drainage network or road ditch was observed in 2020 or 2021 on a section located further downstream, the distance between the initial site and that observed in 2020 or 2021 has been measured. If the two species of lymnaeids formed a mixed community (Dreyfuss *et al.*, 2014), the area occupied by each species in the common habitat as well as the corresponding individuals were considered separately.

Two types of controls were carried out to confirm or not the disappearance of a snail population from its initial habitat. In 2020

Table 1. Number of populations for *Galba truncatula* and *Omphiscola glabra* in 2013–2014 and 2020–2021 in the farms investigated in the department of Haute Vienne on acid soils.

Habitat type	Number of populations and decline rate (%) between the two periods					
	Galba truncatula			*Omphiscola glabra*		
	2013–14	2020–21	Decline	2013–14	2020–21	Decline
Drainage swales	413	256	38.1	233	177	24.1
Hillside sources	178	133	25.3	142	121	14.8
Drainage ditches	47	26	44.7	32	23	28.2
Trampled areas	11	4	63.7	3	0	100
Road ditches	152	110	27.7	114	98	14.1
Pond banks	5	0	100	9	4	55.6
Stream banks	7	2	71.5	17	6	64.8
All types	813	531	34.7	550	429	22.0

or 2021, the sections of the drainage network or road ditch located downstream of the initial site were first examined for 30–45 min on the same day of the survey to see whether the population had not moved downstream under the effect of the current or another factor. When this research was negative, a second check was carried out at the end of July 2021 during a period of excess rain (Météo France, 2021) in order to verify the absence of offspring from this population and thus confirm its complete disappearance.

2.4 Parameters studied

The first was the number of populations our team found for each lymnaeid species, each habitat type and each period of investigation. These values were compared using Fisher's exact test. In addition, the Fisher.multcomp function from the RVAideMemoire package (R Core Team, 2016) was used as a post-hoc test to perform pairwise comparisons.

The other three parameters were the overall surface area of habitats, the density of overwintering snails per m^2 of habitat, and the distance between the initial habitat of a population in 2013–2014 (or 2016–2017) and that observed in 2020–2021 when this population has moved downstream. Individual values obtained for the areas were reduced to an average, framed by a standard deviation, taking into account the species of lymnaeids and the type of habitat. A similar protocol was used for snail densities. The three types of data were first analysed using the Shapiro-Wilk test of normality (Shapiro and Wilk, 1965). As the distribution of these values was not normal in the three cases, the Kruskal-Wallis test was used to establish the levels of statistical significance. These analyses were performed using R 3.3.0 software (R Core Team, 2016).

The rate of decline between the 2013–2014 (or 2016–2017) values and those noted in 2020-2021 was calculated only for the number of populations and the density of overwintering individuals.

3 Results

3.1 Number of populations

Compared to surveys carried out in 2013 and 2014 in farms on acid soils, the overall number of populations in 2020 and 2021 fell by 34.7% for *G. truncatula* and 22% for *O. glabra* (Tab. 1) and this difference between the two species was significant ($p < 0.001$). When each habitat type is considered separately, the decrease in three habitat types (swales, hillside sources, road ditches) was significantly higher ($p < 0.05$ in each case) in *G. truncatula* than in *O. glabra*. In contrast, no clear difference between the values recorded for the two species was noted in the case of drainage ditches (Tab. 1). In the other three habitat types, the low number of values did not statistically show a clear trend. On the other hand, eighteen populations of *G. truncatula* were observed in 2020 or 2021 on the course of the swales themselves or on the main ditch, whereas they occupied the peripheral end of these swales in 2013 and 2014. Similarly, eight populations of *O. glabra* were observed in 2020 or 2021 at the downstream end of these swales or on the main ditch. The distance recorded between the habitats of 2013–2014 and those of 2020–2021 ranged from 5 to 32 m for *G. truncatula* and from 4 to 18 m for *O. glabra* (data not shown). In addition, eight mixed communities living in swales and three in road ditches were observed in 2020–2021.

Table 2 lists the number of populations for each snail species and each period of investigation in farms on sedimentary soils. Compared to values recorded in 2016 and 2017, the overall number of populations in 2020–2021 decreased by 25.0% for *G. truncatula* and 15.2% for *O. glabra*. The percentage noted for *G. truncatula* between the two study periods was significantly higher ($p < 0.001$) than that for *O. glabra*. When each type of habitat is considered for *G. truncatula*, significant differences between the two study periods were noted for swales ($p < 0.01$) and road ditches ($p < 0.05$) while there was no significant difference for the other habitat types. In the case of *O. glabra*, no significant difference was noted, whatever the type of habitat considered. In grasslands and road ditches, 37 and 19 populations of *G. truncatula*, respectively, moved downstream a few meters. As the distance between the population of *G. truncatula* and that of *O. glabra* is limited (from 3 to 10 m) when the two species lived in the same type of habitat, mixed communities, where the two lymnaeids share the same area, were noted: 17 in drainage swales and 13 in road ditches (data not shown).

The decrease in the number of *G. truncatula* populations was significantly higher ($p < 0.001$) on acid soils than on sedimentary soils. A similar finding was also noted for *O. glabra* with a significantly higher numerical decrease ($p < 0.05$) on acid soils.

Table 2. Number of populations for *Galba truncatula* and *Omphiscola glabra* in 2016–2017 and 2020–2021 in the farms investigated in the department of Indre on sedimentary soils.

Habitat type	Number of populations and decline rate between the two periods					
	Galba truncatula			*Omphiscola glabra*		
	2016–17	2020–21	Decline	2016–17	2020–21	Decline
Drainage swales	162	110	32.1	71	57	19.8
Spring pools	46	36	21.8	22	18	18.2
Road ditches	136	117	13.9	110	98	11.9
Pond banks	11	4	63.7	1	1	0
Stream banks	6	4	33.3	1	0	100.0
All types	361	271	25.0	205	174	15.2

3.2 Area of snail habitats

The values recorded on acid soils during the two investigation periods are presented in Figure 3. In 2013–2014, the mean area of sites colonized by *G. truncatula* ranged from 1.6 to 6.5 m^2 per habitat type, resulting in an overall mean value of 2.9 m^2. In 2020–2021, the mean values ranged from 1 to 4 m^2 per habitat type and the overall mean value was 1.8 m^2. No significant difference between the mean values recorded in 2013–2014 and 2020–2021 was noted for any habitat type. Compared to values found for *G. truncatula*, the area of habitats colonized by *O. glabra* in 2013–2014 showed mean values ranging from 2.7 to 13.5 m^2 per habitat type and an overall mean value of 9.1 m^2. In 2020–2021, mean areas per habitat type ranged from 2.2 to 12.5 m^2 with an overall mean value of 5.4 m^2. The area of habitats located in swales was significantly lower ($H = 21.12$; $p < 0.001$) in 2020–2021 than in 2013–2014, while there was no clear difference between means of other habitat types. This affects the overall means for all habitats, with a significantly lower value ($H = 11.02$; $p < 0.01$) in 2020–2021.

Figure 4 shows the areas found in habitats on sedimentary soils. In 2016–2017, mean values ranging from 1.6 to 3.2 m^2 were found in the five habitat types colonized by *G. truncatula*, while they fluctuated from 1.1 to 2.5 m^2 in 2020–2021. The overall means recorded during these two periods were therefore 2.3 and 1.7 m^2, respectively, so that no significant difference was noted between these mean values. In the case of *O. glabra*, the mean values observed in 2016–2017 ranged from 4.1 to 17.8 m^2 in the habitat types taken separately with an overall mean value of 13.3 m^2. In 2020–2021, mean values per habitat type ranged from 3.9 to 15.2 m^2, resulting in an overall mean value of 11.6 m^2. No significant difference was found between these averages, whatever the method of comparison.

No significant difference between the overall means recorded in the two studied regions was noted for *G. truncatula* as for *O. glabra*.

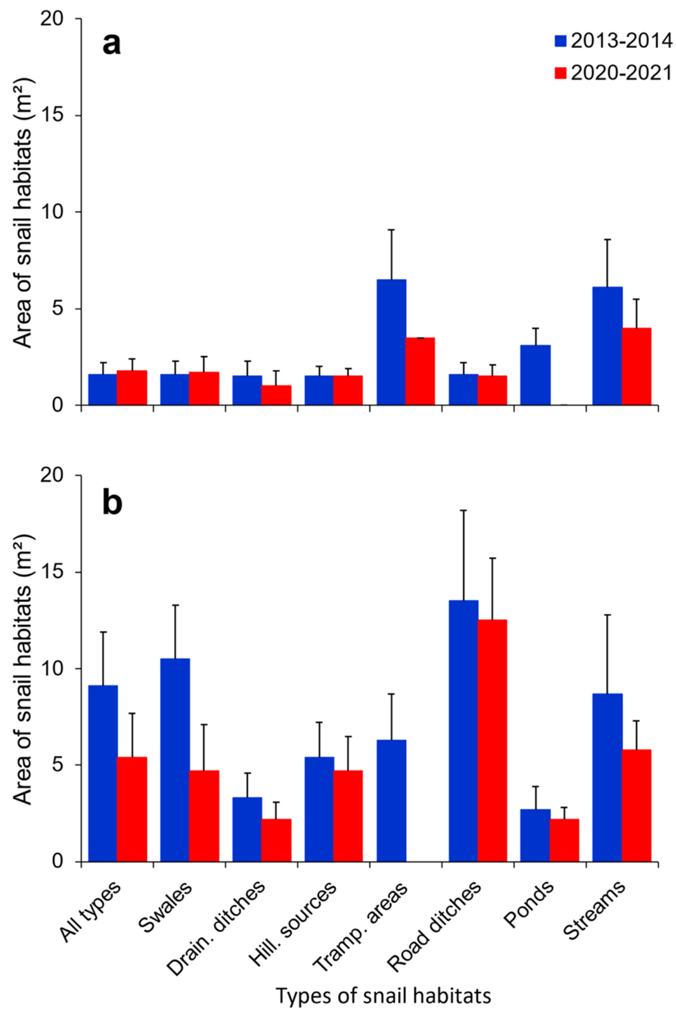

Fig. 3. Area of habitats colonized by the two Lymnaeidae in 2013–2014 and 2020–2021 in 56 farms investigated on acid soils: *Galba truncatula* (3a) and *Omphiscola glabra* (3b). Hill., hillside; tramp., trampled.

3.3 Density of overwintering snails per m^2 of habitat

Values recorded in the populations of both lymnaeids on acid soils are presented in Figure 5. Compared to 2013–2014 surveys, the overall number of overwintering *G. truncatula* counted in 2020–2021 decreased by 80.7% (a total of 14,797 snails in 2013–2014 and 2871 in 2020–2021). Similarly, the overall number of *O. glabra* in 2020–2021 also showed a decrease by 70.2% (3025 snails in 2013–2014 and 901 in 2020–2021). However, this decline rate varied depending on

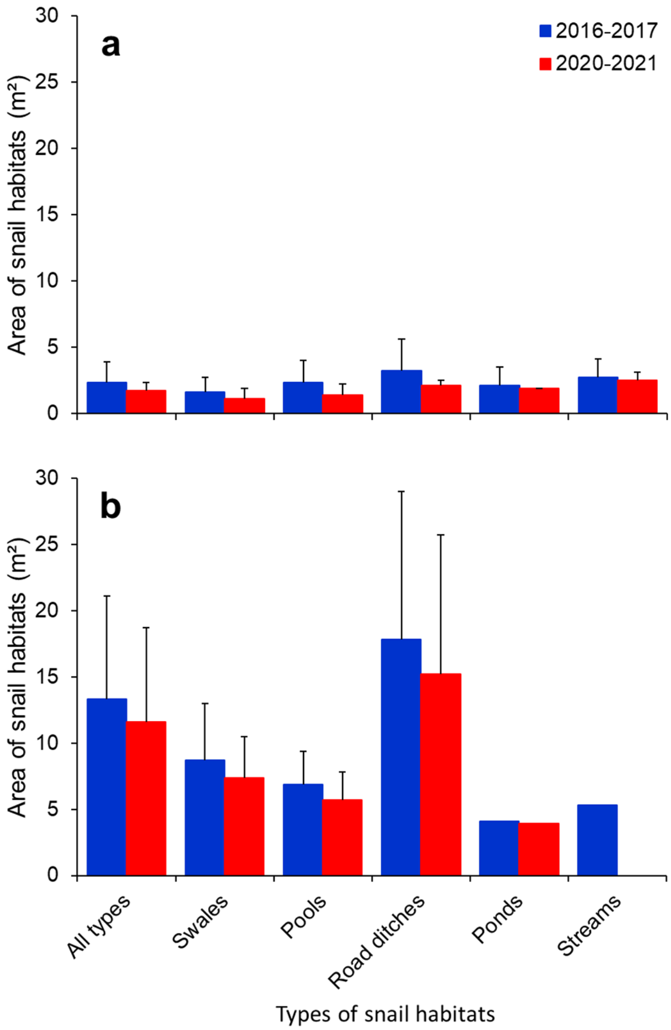

Fig. 4. Area of habitats colonized by the two Lymnaeidae in 2016–2017 and 2020–2021 in 37 farms investigated on sedimentary soils: *Galba truncatula* (4a) and *Omphiscola glabra* (4b).

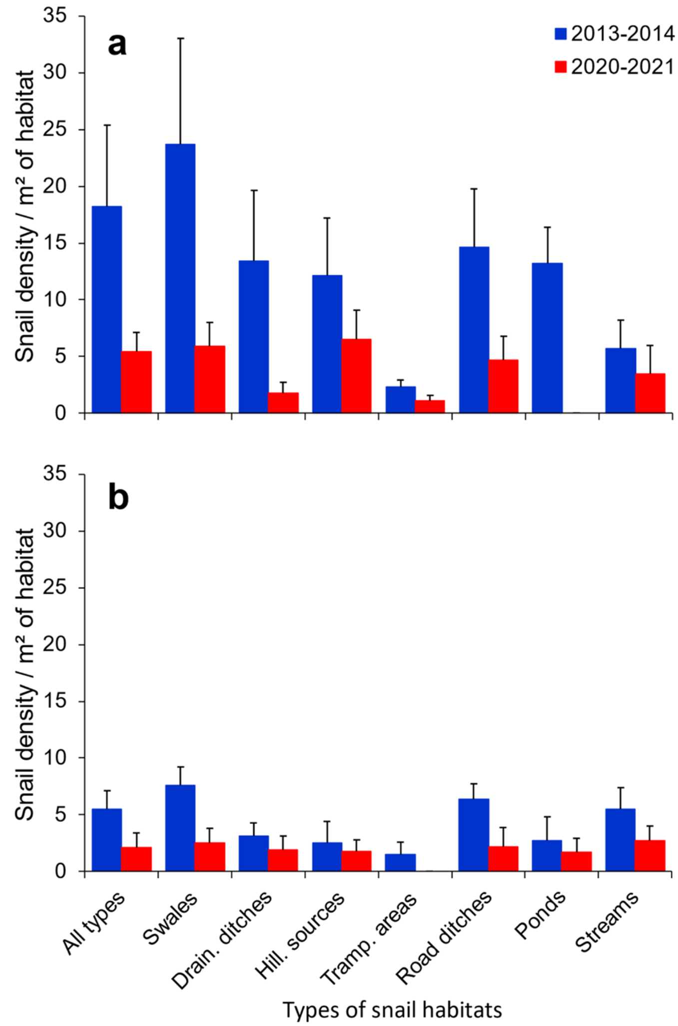

Fig. 5. Density of overwintering snails for two Lymnaeidae in 2013–2014 and 2020–2021 in 56 farms investigated on acid soils: *Galba truncatula* (5a) and *Omphiscola glabra* (5b). Hill., hillside; tramp., trampled.

the type of habitat. For *G. truncatula*, the numerical decrease was greater for drainage ditches (87%) and swales (75.2%) than in road ditches (67.9%) and hillside sources (46.3%). The percentages are much lower for *O. glabra*: 67.2% in swales, 65.7% in road ditches, 38.8% in drainage ditches and only 28% in hillside sources. In both species, the low number of populations in the other three habitat types did not allow us to identify a clear trend for this decline. Decreases in *G. truncatula* densities between the two study periods were significant for all habitat types ($H = 27.71$; $p < 0.001$) as well as for four habitat types considered separately: swales ($H = 31.78$; $p < 0.01$), drainage ditches ($H = 16.34$; $p < 0.001$), hillside sources ($H = 7.43$; $p < 0.01$) and road ditches ($H = 4.98$; $p < 0.05$). In contrast, there was no significant difference for the other three habitat types. For *O. glabra*, decreases in the values were significant for all habitat types ($H = 13.32$; $p < 0.001$) as well as for swales ($H = 16.51$; $p < 0.001$), road ditches ($H = 11.78$; $p < 0.001$) and stream banks ($H = 7.46$; $p < 0.01$). In contrast, no clear difference was noted for main drainage ditches and hillside sources.

Compared to values recorded in 2016–2017 for all habitat types on sedimentary soils (Fig. 6), the overall density of overwintering snails in 2020–2021 decreased by 64.1% for *G. truncatula* (a total of 5271 snails in 2016–2017 and 1897 in 2020–2921) and 38.3% for *O. glabra* (1353 snails in 2016–2017 and 836 in 2020–2021). However, variations in these percentages can be noted for each type of habitat. For *G. truncatula*, the decrease in snail numbers ranged from 63.1% to 74.2% in swales, ponds and stream banks, while it was close to 40% in pools and road ditches. In *O. glabra* populations, the decrease in overwintering snails was much lower in 2020–2021: 37.9% in swales and less than 24% in pools and road ditches. Decreases in the densities of *G. truncatula* between the two study periods were significant in all habitat types ($H = 16.87$; $p < 0.001$) as well as for swales ($H = 25.56$; $p < 0.001$), pools ($H = 7.89$; $p < 0.01$), road ditches ($H = 7.57$; $p < 0.01$) and pond banks ($H = 8.54$; $p < 0.01$). For *O. glabra*, decreases in the values were significant for all

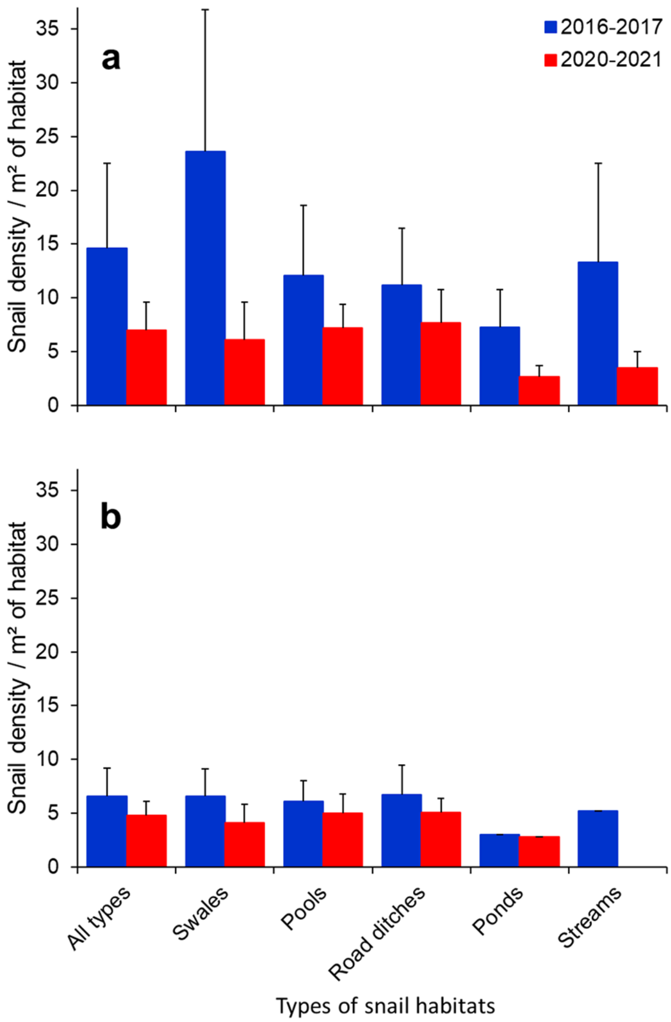

Fig. 6. Density of overwintering snails for two Lymnaeidae in 2016–2017 and 2020–2021 in 37 farms investigated on sedimentary soils: *Galba truncatula* (6a) and *Omphiscola glabra* (6b).

habitat types ($H = 5.12$; $p < 0.05$) and swales ($H = 5.26$; $p < 0.05$), whereas no clear differences were noted for spring pools and road ditches was noted.

The decrease in *G. truncatula* densities was significantly greater ($H = 21.34$; $p < 0.001$) on acid soils than on sedimentary soils. The same observation was noted for *O. glabra* with a significantly higher numerical decrease ($H = 7.48$; $p < 0.01$) on acid soils.

4 Discussion

Despite projections by Cordellier and Pfenninger (2009) and Cordellier *et al.* (2012) on the fate of freshwater snail populations in the face of global warming in north-western Europe, it is still difficult, currently, to predict future changes in habitat characteristics and population dynamics in the two species of lymnaeids which intervene as intermediate hosts in the life cycle of *F. hepatica* in central France. The results of studies that our team has carried out on *G. truncatula* populations living in semi-arid or arid climate regions such as Algeria (Mekroud *et al.*, 2002, 2004), Morocco (Goumghar *et al.*, 2001a, b; Belfaiza *et al.*, 2008, 2009) or Tunisia (Ayadi *et al.*, 1993), cannot be fully transposed to central France because of the remarks that Woodward *et al.* (2010) formulated for water collections in the face of climate change: (a) many species such as snails in these fragmented habitats have limited abilities to disperse as the environment changes, (b) temperature and water availability are dependent on local climate, and (c) many anthropogenic stressors are already affecting these water collections. As a result, future changes in the dynamics of precipitation, evaporation, and flooding will lead to changes in water levels, the structure of snail habitats, and the time they live in wetlands (Heino *et al.*, 2009; Domisch *et al.*, 2011; Hershkovitz *et al.*, 2013). Under these conditions, the data from this study constitute only a first approach to the problem and need to be completed by further research on the same meadows and ditches in order to generalize the impact of climate change on areas subject to a temperate climate.

Compared to surveys carried out in 2013–2014 on acid soils and 2016–2017 on sedimentary soils, the decrease in population numbers noted in 2020–2021 was more marked for *G. truncatula* than for *O. glabra*. It was also more marked on acid soils than on sedimentary soils, whatever lymnaeid species. The decline observed in recent years in the number of these lymnaeid populations is consistent with the observations that many authors have reported for other communities of terrestrial or aquatic snails (Lydeard *et al.*, 2004; Burgmer *et al.*, 2007; Cordellier *et al.*, 2012; Pearce and Paustian, 2013; Caminade *et al.*, 2019) as well as for other biological taxa such as invertebrates (Ponder and Lunney, 1999), birds and mammals (Spooner *et al.*, 2018). This decline can also be considered as one of the direct consequences that climate change can cause over time in the temperate countries of Western Europe (Cordellier *et al.*, 2012). Three arguments explain the differences between the results of *G. truncatula* and those of *O. glabra* in the two regions studied. The first is the behaviour of each lymnaeid during the aestivation of its habitats because the two species do not have the same capacities to bury themselves in the drying sediment. In the lowlands of central France, only juveniles of *G. truncatula*, measuring less than 2 mm in height, could burrow into the sediment during habitat aestivation, while *O. glabra* could burrow, whatever its size, during the same period, provided that there is a fairly thick sandy-muddy sediment, mixed or not with organic debris, on the bottom of its habitat (Dreyfuss *et al.*, 2015; Vignoles *et al.*, 2018). The second argument concerns the physical characteristics of the habitats which differ according to the region studied. On acid soils in the Haute Vienne, the sediment is usually made up of sand and gravel in the surface drainage networks and hillside sources while it includes a mixture of mud, sand and rare silt in road ditches (Dreyfuss *et al.*, 2021). It is therefore not very suitable for burying molluscs. In contrast, conditions are more favourable on the sedimentary soils of Brenne because the sediments are usually made of mud and clay, mixed with variable amounts of organic debris (Dreyfuss *et al.*, 2018a). The last argument concerns the development of macrophytes in the habitats of each species during the summer months. Vegetation was then quite high and dense around and/or in the habitats of *O. glabra*, while development was more limited and macrophyte density was much lower around sites colonized by

G. truncatula (Rondelaud *et al.*, 2011; Vignoles *et al.*, 2017). Despite the habitat characteristics related to the geology of each region and the behaviour of each lymnaeid species, one cannot be excluded that the decline in populations, which is much more marked on acid soils, would not be due to the time interval between the two series of investigations (at least 6–7 years on acid soils instead of 3–4 years on sedimentary soils).

In addition to this decrease in the number of populations, two other consequences also emerge from this study. The first is the displacement of 55 populations of *G. truncatula* and 27 of *O. glabra* downstream of a drainage network or road ditch between the two survey periods. This finding is much more difficult to comment on because the literature does not provide data on the reasons for such a transfer. One explanation would be to invoke a forced displacement of each population downstream under the effect of a flood caused by an excess of runoff. However, this hypothesis does not fit well with the ecological needs of each species because both *G. truncatula* and *O. glabra* are capable in winter and spring of moving upstream into a drainage swale or a road ditch at its peripheral end, whether or not there is a source at its end (Rondelaud *et al.*, 2005, 2006). As no snails were observed migrating along the drainage swale or road ditch located between their initial habitat and that observed during our 2020–2021 investigations, it can be assumed that each population would have voluntarily moved downstream to escape a habitat that had become unfavourable due to climatic conditions in order to colonize a new site more compatible with the life of the species. The second consequence is the formation of mixed communities with both species of lymnaeids occupying the same habitat, whereas these communities were rare in the two regions studied, whatever the soil type (Vignoles *et al.*, 2018). Human activity cannot be proposed to explain the formation of these mixed communities, at least in the case of permanent grasslands, because the maintenance of the drainage network is identical to that applied in the other farms studied. In our opinion, the formation of these habitats with a mixed community could be an indirect consequence of global warming because there was, in each case, a displacement of *G. truncatula* from its initial habitat (the upstream end of the swale) to the area where *O. glabra* lived. The distribution of individuals of each species in this common habitat was consistent with observations that several authors have reported on other freshwater gastropod communities living in south-eastern or north-western USA (Osenberg, 1989; Cross and Benke, 2002; Hoverman *et al.*, 2017) According to these authors, competition for food generally occurred at sites colonized by two or more gastropod species, limiting the range and size of each population.

As for the number of populations, the overwintering snails showed a significant decrease in their densities between the two survey periods, with varying percentages depending on the lymnaeid species and the region studied. The three arguments, which we proposed above to comment on the decline in population numbers, can also be used here to explain the decrease in abundance of each population. However, these findings do not fit well with what is known about the population dynamics of each lymnaeid species. The introduction of low numbers of snails of either species into new habitats on acid soils most often resulted in the development of new populations whose numbers peaked in the second or third year after introduction, with a gradual return to lower values close to each other in subsequent years (Rondelaud *et al.*, 2019; Dreyfuss *et al.*, 2021). In contrast, in the meadows of the 38 farms investigated by Rondelaud *et al.* (2021) and our team in 2020–2021, the number of overwintering snails remained low over the three years of the study, whatever snail species. To explain this difference between the results of Rondelaud *et al.* in 2019 (or Dreyfuss *et al.* in 2020) and the low number of snails recorded in the 38 farms mentioned above, it can be assumed that the occurrence of heat waves for several successive years such as those which occurred in central France (Météo France, 2018, 2019, 2020) would probably affect the dynamics of either lymnaeid species by limiting the reproductive activity of the snails that survived each aestivation, which would not allow the development of populations during the following winter and spring. Populations affected by this numerical decrease will certainly be able to recover if climatic conditions become favourable again, but several years will be necessary for each population to regain its initial size (Sabourin, 2018). The development of these populations over time will therefore depend on the intensity of the ongoing climate change and its length.

In this study, the habitats of *G. truncatula* and most sites colonized by *O. glabra* showed no significant variation in their area between the two study periods. This finding is surprising, as many environmental and biotic factors are known to influence the area of habitats that freshwater gastropod snails colonize in the field (Hubendick, 1958; Brönmark, 1985; Olkeba *et al.*, 2020). The lack of significant variation for *G. truncatula* in any study area must be related to the location of most of these habitats on the drainage network or road ditch (generally at the upstream end according to Moens, 1991). In the case of *O. glabra*, the variation was only significant for the drainage swales on acid soils and several hypotheses were proposed to explain this result. On the acid soils of Haute Vienne, Rondelaud *et al.* (2021) explained their data by the presence or absence of a temporary spring in the drainage swales, which would maintain some moisture in the soil during aestivation (if this spring exists) and promote burial of *O. glabra* over the entire area of the habitat when burial is possible. Another explanation provided by these authors concerns the quality and abundance of vegetation around or in the habitats of *O. glabra*. As this variation was not found in habitats on sedimentary soils, another hypothesis must be proposed. In our opinion, the ability of *O. glabra* to disperse in its habitat (it is common to observe adult individuals swimming on the surface of the water in April–May according to Vignoles *et al.*, 2018) could explain the lack of variation in the area of most habitat types for this species.

Given the numerical decrease in snail populations in the two regions studied, one may wonder what will be the consequences of this process on the transmission of local fasciolosis. The disappearance of these host snails may be due to snail infection with the parasite. Indeed, infections of snails with a digenean may increase their mortality and, in the same time, reduce their fecundity, which reduce their number and that of the subsequent generations (Dreyfuss *et al.*, 2015). However, it is possible that the parasite adapts quickly to this situation by using aquatic or terrestrial mollusc species which are not potential intermediate hosts under usual conditions. Other lymnaeid species such as *Radix balthica*

(Linnaeus, 1758), *Stagnicola fuscus* (C. Pfeiffer, 1821) or *S. palustris* (O.F. Müller, 1774) can ensure the larval development of *F. hepatica* provided they are infected in their first days of life (Boray, 1978; Caron *et al.*, 2007, 2014; Novobilský *et al.*, 2013) or that miracidial infection occurs in juveniles and pre-adults from previously infected parents over several successive generations (Rondelaud *et al.*, 2014; Vignoles *et al.*, 2016). DNA from *F. hepatica* has also been detected by molecular biology in the body of *Omalonyx matheroni* (Potiez and Michaud, 1838) and in that of *Succinea putris* (Linnaeus, 1758) (Relf *et al.*, 2009; Novobilský *et al.*, 2014). However, it is not yet known whether these two succineids are potential intermediate hosts of *F. hepatica* capable of ensuring the complete larval development of the parasite or non-target molluscs that attract miracidia by a decoy effect.

In conclusion, the decline observed in the number and size of *G. truncatula* and *O. glabra* populations since 1998 is still continuing today in central France. In view of this decline, the future of these lymnaeid species must be questioned because *O. glabra* is currently seriously threatened in Western Europe while *G. truncatula* is not a major problem (Welter-Schultes, 2012). Research at the same stations should be carried out at regular intervals in order to determine the extent of this decline over time in central France and to take appropriate measures to ensure the conservation of these two species in the future.

Acknowledgements. The authors are grateful to the 93 breeders who accepted that snail investigations be carried out on their grasslands in 2013–2014 (or 2016–2017) and in 2020 and/or 2021. They also thank A. Thomas for his assistance in computerizing the data collected in 2020 and 2021 and several anonymous reviewers for their helpful comments.

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Cite this article as: Vignoles P, Dreyfuss G, Rondelaud D. 2022. Decline in the number and size of populations of two Lymnaeidae living in central France over the last decade. *Int. J. Lim.* 58: 11: