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Aplexa hypnorum (Gastropoda: Physidae) exerts competition on two lymnaeid species in periodically dried ditches

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Abstract – Samples of adult *Aplexa hypnorum* were experimentally introduced into periodically dried ditches colonized by *Galba truncatula* or *Omphiscola glabra* to monitor the distribution and density of these snail species from 2002 to 2008, and to compare these values with those noted in control sites only frequented by either lymnaeid. The introduction of *A. hypnorum* into each ditch was followed by the progressive colonization of the entire habitat by the physid and progressive reduction of the portion occupied by the lymnaeid towards the upstream extremity of the ditch. Moreover, the size of the lymnaeid population decreased significantly over the 7-year period, with values noted in 2008 that were significantly lower than those recorded in 2002. In contrast, the mean densities were relatively stable in the sites only occupied by *G. truncatula* or *O. glabra*. Laboratory investigations were also carried out by placing juvenile, intermediate or adult physids in aquaria in the presence of juvenile, intermediate or adult *G. truncatula* (or *O. glabra*) for 30 days. The life stage of *A. hypnorum* had a significant influence on the survival of each lymnaeid. In snail combinations, this survival was significantly lower for adult *G. truncatula* (or *O. glabra*) than for intermediate snails. In contrast, the survival of juveniles was similar to that noted in the corresponding controls. This interspecific competition between the physid and either lymnaeid may not be due to food present in their habitat, but might be due to the toxicity of mucus secreted by intermediate and adult *A. hypnorum*.

Key words: *Aplexa hypnorum* / colonization / density / ditch / *Galba truncatula* / Gastropoda / Lymnaeidae / *Omphiscola glabra* / Physidae

Introduction

Fasciolosis due to *Fasciola hepatica* (Linnaeus) has a worldwide distribution, with human and animal cases being reported on the five continents. To accomplish its life-cycle, this fluke needs a definitive host (generally a mammal) that harbours the adult parasite and an intermediate host (a freshwater pulmonate gastropod) that ensures the development of larvae. In Western Europe, the most common host snail is *Galba truncatula* (O.F. Müller) (Taylor, 1965; Torgerson and Claxton, 1999). Another lymnaeid, *Omphiscola glabra* (O.F. Müller) also can sustain larval development of *F. hepatica* (Abrous *et al*., 1999, 2000; Rondelaud *et al*., 2015). The control of these invertebrate populations has been proposed by numerous authors as one of the means to eliminate the fluke from farms (Taylor, 1965). On the acidic soils of central France, the use of open drainage only limited the size of snail populations because of the summer drought which was too short: 5–6 weeks (Rondelaud *et al*., 2006). A terrestrial snail, *Zonitoides nitidus* (O.F. Müller), able to actively prey on these lymnaeids, was also applied in several cattle-breeding farms. However, this method has not become generalized because of the complexity of applying this control in the field by non-specialists (Rondelaud *et al*., 2006).

Another method of control is to use a freshwater snail, which is not a compatible host for *F. hepatica*, as a competitor of these lymnaeid populations. Several gastropods have already been used as competitors in the past to control intermediate hosts for schistosomes, but the success of these biological agents varied according to the snail species and the country in which they were introduced (Brown, 1994). As no freshwater pulmonate gastropod was reported as a competitor of *G. truncatula* and *O. glabra* in the literature, it was reasonable to search for a candidate among species belonging to the same snail community. In Western Europe, these lymnaeids are

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known to live in periodically dried habitats with the physid *Aplexa hypnorum* (Linnaeus) and planorbids such as *Anisus leucostoma* (Miller) or *A. spirorbis* (Linnaeus) (Costil *et al.*, 2001; Vignoles *et al.*, 2015). As another physid, *Physella acuta* (Draparnaud) was already reported as a competitor against *Bulinus truncatus* (Audouin) in Egypt (El-Hassan, 1974), the competition of *A. hypnorum* against *G. truncatula* and *O. glabra* was investigated.

A. hypnorum is known for its distribution in most European countries (Welter-Schultes, 2012, 2013) and North America (Dillon *et al.*, 2006). But in some countries, the numbers of these snails were small such as in woodland ponds from Southern Poland (Spyra, 2010) and a few ponds of the upper Rhine valley (Mosimann, 2000; Bauer and Ringeis, 2002). This physid colonizes small and temporary waterbodies rich in vegetation, located in lowlands. It is also found on swampy and forested margins of lakes, in swampy deciduous forests, and very moist meadows (Welter-Schultes, 2013). However, the species prefers ditches, temporary ponds and pools, which it shares with other gastropod species adapted to seasonal habitats (Kerney, 1999; Anderson, 2006). The bottom of these habitats often consisted of mud (Glöer and Diercking, 2010). In addition, a positive relationship was noted in Germany between the abundance of snails and sand and/or clay soil types (Den Hartog, 1963; Glöer and Diercking, 2010). The future of *A. hypnorum* is particularly worrying in Western European countries due to destruction of its moist habitats owing to land drainage and the general intensification of agriculture (Kerney, 1999).

In these periodically dried habitats, community dynamics depend on species-specific abilities to withstand drought periods (Dillon, 2004). However, periodic drought is not the sole factor that acts on the dynamics of these populations, as the composition of this freshwater pulmonate community also has also an effect on variations in snail numbers. In the Brenne Regional Natural Park (Central France), the densities of adult *O. glabra* were similar when this lymnaeid was living alone or with *A. spirorbis* in its habitat. In contrast, the size of each *O. glabra* population fell strongly when *A. hypnorum* or *P. acuta* occupied the same habitats (Vignoles *et al.*, 2015). In view of these results, the two following questions arose: was competition for trophic resources between *A. hypnorum* and *O. glabra* the reason for the observed population dynamics in coexistence? Might the numerical decrease of *O. glabra* result from a lethal action of *A. hypnorum* on eggs and juveniles of the lymnaeid? To answer the first question, field investigations were carried out during seven successive years to monitor the dynamics of *G. truncatula* and *O. glabra* populations living in ditches where *A. hypnorum* was experimentally introduced. The answer to the second question was provided by monitoring population dynamics in laboratory aquaria with *A. hypnorum* and *G. truncatula* or *O. glabra*. In both cases, controls were road ditches colonized by *G. truncatula* or *O. glabra* (but without *A. hypnorum*), or aquaria containing *G. truncatula* or *O. glabra* only.

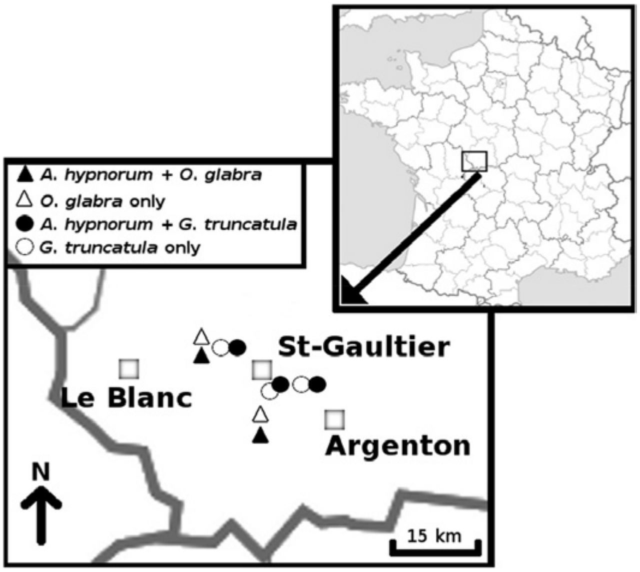

Fig. 1. Location of the ten road ditches in the Brenne Regional Natural Park, department of Indre (Central France).

Materials and methods

Snail identification was done on the basis of shell shape and size, and also length of reproductive organs according to the keys by Glöer and Meier-Brook (2003).

Field investigations

Snail habitats

The field part of the investigation included a total of ten ditches inhabited by either *G. truncatula* or *O. glabra*. These ditches were located within the municipalities of Chitray, Luzeret, Migné and Thenay, department of Indre, Central France (Fig. 1). The first six ditches were only inhabited by *G. truncatula* in March 2002. At this date, 50 adults (shell height > 12 mm) of *A. hypnorum* from a nearby upstream pond (46°45′14″N, 1°11′7″E) were introduced in the deepest zone of each of three *G. truncatula* ditches (46°35′53″N, 1°27′27″E; 46°36′38″N, 1°27′10″E; 46°40′33″N, 1°22′44″E). The remaining three *G. truncatula*-only ditches (46°35′2″N, 1°27′18″E; 46°36′40″N, 1°27′8″E; 46°40′27″N, 1°21′23″E) served as controls. The length and area of these first six habitats ranged from 42 to 87 m and from 18.9 to 39.1 m^2, respectively, in March 2002. Following the same methods as above, 50 adult *A. hypnorum* were introduced to the deepest zone of each of two *O. glabra*-only ditches (46°33′37″N, 1°24′18″E; 46°40′17″N, 1°18°3″E), while the other two *O. glabra* ditches (46°34′47″N, 1°24′34″E; 46°42′47″N, 1°19′69″E) served as controls. The length of these last four habitats ranged from 81 to 146 m in March 2002 and their area from 36.4 to 65.7 m^2. The longest distance between these ten snail habitats was 18 km. All these ditches contained rain water during most of the year (from the end of October to mid-June).

The bottom sediment was composed of silt and sand, and was supported by impermeable subsoil generally formed by sandstone and/or clay. Water pH varied from 6.7 to 7.8 and the dissolved calcium level ranged from 26 to 35 mg.L^{-1} (Dreyfuss *et al.*, 2010). In the *G. truncatula* habitats, vegetation was mainly composed of scattered clumps of rushes. Numerous rush clumps and a few pondweeds grew in the *O. glabra* habitats. In all these ditches, there were detritus during most of the year and epiphytic filamentous algae in spring. These habitats were subjected to the same climatic conditions, with a wet temperate climate modulated by westerly oceanic winds. The mean annual precipitation noted during the 50 years preceding field investigations is 800 mm, while the mean annual temperature is 10.5–11 °C (Dreyfuss *et al.*, 2010; Rondelaud *et al.*, 2011). Mean annual values recorded for each parameter during the years of investigation were similar to those reported above.

Protocol of investigations

During seven successive years (2002–2008), snails were counted in mid-May in the ten ditches during the warmest hours of the day (1–4 p.m.) because they were present at that time in the upper layer of water. This period was chosen because all snails belonging to the spring and/or overwintering generations were at the adult stage. First, the length of the ditch colonized by each species was determined by noting the presence or absence of the snail from the downstream to the upstream parts of each habitat. Secondly, eight quadrants of 1 m^2 each (A–H), located from the downstream to the upstream parts of each habitat and separated from each other by a 3–6 m interval (habitats with *G. truncatula*) or 6–12 m interval (those with *O. glabra*), were selected in each ditch to count snails. In each quadrant, snails were collected using a 20-cm diameter sieve (mesh size, 3 mm) if the depth of the water layer was more than 10 cm or by sight in the other cases (water depth less than 10 cm, or reduced to a film). This area was controlled 15 min later to collect snails that could have escaped during the first count. Snails were then classified according to their species before being replaced in each area.

Parameters studied

The first parameter considered was the length of the ditch colonized by each snail species over the 7-year period. Values recorded at the sites occupied by *A. hypnorum* and *G. truncatula* or by *G. truncatula* only were pooled and expressed as percentages in relation to the total length of each habitat (Fig. 1(A) and (B)). A similar protocol was also used for values noted in habitats colonized by *A. hypnorum* and *O. glabra* or by *O. glabra* only (Fig. 1(C) and (D)). The second variable was the density of each snail species in the eight 1-m^2 quadrants of each habitat. Normality of snail densities was analysed using the Shapiro–Wilk test (Shapiro and Wilk, 1965). As the distribution of these values was not normal, the Kruskal–Wallis test was used to compare snail densities noted in each quadrant in 2002 and 2008. All the statistical analyses were performed using Statview 5.0 software (SAS Institute Inc., Cary, NC, USA).

Laboratory investigations

The behaviour of *G. truncatula* or *O. glabra* in the presence or the absence of *A. hypnorum* was studied during three successive years between 2010 and 2013. Three life stages were considered for *A. hypnorum* and *O. glabra*: juveniles (2–3 mm), intermediates (4–5 mm) and adults (12–13 mm). In the case of *G. truncatula*, shell heights of the three life stages were 1.5–2, 3–4 and 6–7 mm, respectively. The *A. hypnorum* were collected in March from a small pond (46°45′14″N, 1°11′7″E), while the *G. truncatula* originated from a road ditch (46°40′24″N, 1°20′45″E) and the *O. glabra* from another road ditch (46°41′0″N, 1°25′33″E) located in the municipalities of Nuret-le-Ferron and Chitray, respectively. All snails collected from the field were subjected to a 48-h period of acclimatization to laboratory conditions (see below) before being used for experiments. As parasitism may have an effect on snail ecophysiology, reproduction output and behaviour (Zbikowska, 2011), 50 snails for each species and each life stage were collected each year from their natural habitat in March and were dissected in the laboratory under a stereomicroscope to detect the presence of monogenean or digenean larval forms.

Each life stage of *A. hypnorum* was introduced into a covered 5-L aquarium containing lymnaeids (*G. truncatula* or *O. glabra*) which had the same or a different life stage. The number of snails per recipient was five physids and ten lymnaeids. These snail numbers were selected on the basis of snail densities noted in May 2008 in ditches colonized by *A. hypnorum* (see above). Tables 1 and 2 indicate the different types of pairwise combinations formed with the physid and either lymnaeid (nine types of combinations in each case). Five aquaria were used each year for each snail combination (a total of 25 individuals for *A. hypnorum* and 50 for either lymnaeid). Following the same method, control groups were constituted for each snail species and each life stage. Three replicates for each snail combination or each control group were performed in March between 2010 and 2013. All aquaria were placed at a constant temperature of 20° ± 1 °C and a natural photoperiod of 12 h light. The dissolved calcium content in spring water was 35 mg.L^{-1}. Pesticide-free, dried lettuce leaves and dead *Molinia caerulea* leaves were given *ad libitum* as food for snails. Each week, spring water and food were changed. After 1 month, physids and/or lymnaeids surviving in each aquarium were counted.

The parameter for the three snail species was the number of live individuals on day 30 of the experiment. Normality of snail numbers was analysed using the Shapiro–Wilk test (Shapiro and Wilk, 1965). As the distribution of these values for *G. truncatula* was not normal, the Scheirer–Ray–Hare test coupled with the Steel-Dwass

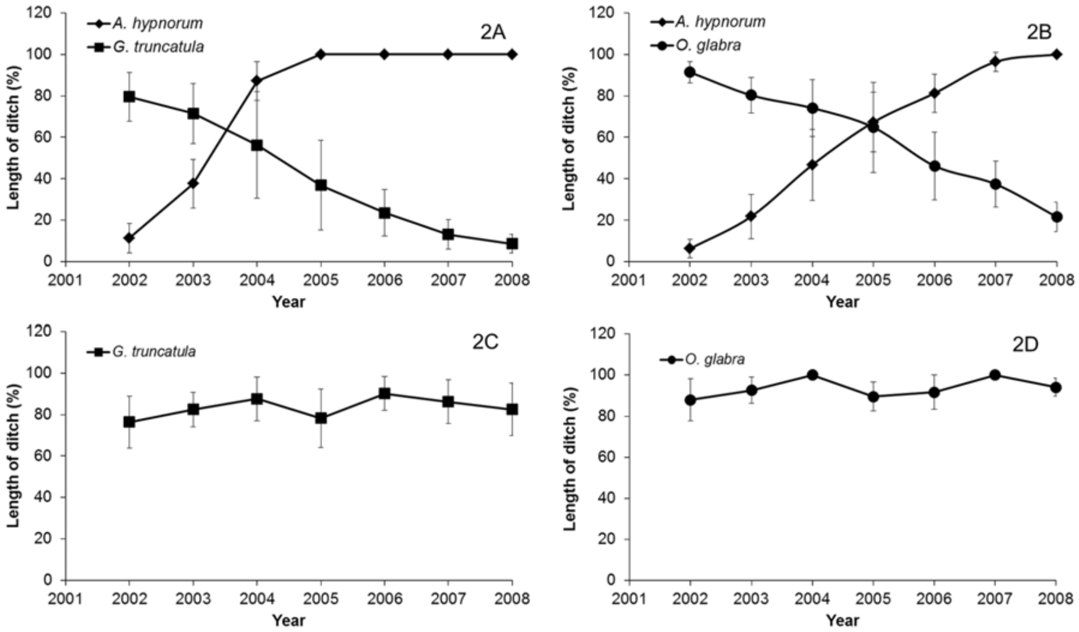

Fig. 2. Length (%) of habitat colonized by each snail species over a 7-year period: *A. hypnorum* and *Galba truncatula* (2A), *A. hypnorum* and *Omphiscola glabra* (2B), *G. truncatula* only (2C) and *O. glabra* only (2D).

post-hoc test (Siegel and Castellan, 1988) was used to compare the differences between the snail combinations and control groups. A similar method was also used for results noted with *A. hypnorum* and *O. glabra*. All the analyses were performed using Statview 5.0 software (SAS Institute Inc., Cary, NC, USA).

Results

Field investigations

A. hypnorum completely colonized road ditches inhabited by *G. truncatula* in 4 years (2002–2005) (Fig. 2(A)). In the case of *G. truncatula*, there was a progressive reduction of ditch lengths from 2002 to 2008 so that the lymnaeid in 2008 only occupied 8.7% of its habitat at the upstream extremity. Like for *G. truncatula* habitats in which the physid was introduced, complete colonization of ditches by *A. hypnorum* and the progressive limitation of lengths occupied by the lymnaeid were also noted in habitats occupied by *O. glabra* (Fig. 2(B)). In 2008, the *O. glabra* populations only inhabited 21.6% of their original sites and were found at the upstream extremity of their habitats (Fig. 2(B)). In the control groups, *G. truncatula* (Fig. 2(C)) and *O. glabra* (Fig. 2(D)) occupied the major or total length of their habitats throughout the entire study.

In ditches inhabited by *A. hypnorum* and *G. truncatula*, the density of the physid remained somewhat stable at 14.9–30.6 snails.m^{-2} in the final year, with statistically similar densities among quadrants (Fig. 3(A)). *G. truncatula* was found in 2008 only in two quadrants at the upstream end of its habitat with densities that were significantly lower than in 2002 (Fig. 3(B)). In control ditches, the densities of *G. truncatula* in 2002 and 2006 were close to each other, whatever the quadrant considered and no significant difference between the 2 years was noted (Fig. 3(C)).

In the other experimental ditches, the density of *A. hypnorum* in 2008 did not show significant variations among quadrants (Fig. 4(A)). The three quadrants located at the upstream extremity of these sites showed only the presence of *O. glabra* in 2008, with snail densities significantly lower than in 2002 (Fig. 4(B)). The control popuations of *O. glabra* occupied the greater part of their habitat in 2002 and 2008, and all the differences between snail densities recorded during these 2 years were not significant (Fig. 4(C)).

Laboratory investigations

Tables 1 and 2 give the numbers of surviving lymnaeids in snail combinations (*A. hypnorum* + *G. truncatula* or *O. glabra*) and control groups at the end of the 1-month period. In both species of lymnaeids, similar results were noted. The life stage of *A. hypnorum* had a significant influence (*G. truncatula*: $H = 30.48$, $P < 0.001$; *O. glabra*: $H = 28.96$, $P < 0.001$) on survival of each lymnaeid. The life stage of each lymnaeid and the interaction between the life stages of the physid and the lymnaeid had no clear effect on these results. In snail combinations, the survival of lymnaeids was significantly lower for adult *G. truncatula* ($P < 0.001$) and *O. glabra* ($P < 0.001$) than for intermediates (*G. truncatula*: $P < 0.01$; *O. glabra*: $P < 0.01$). In contrast, the survival of juvenile

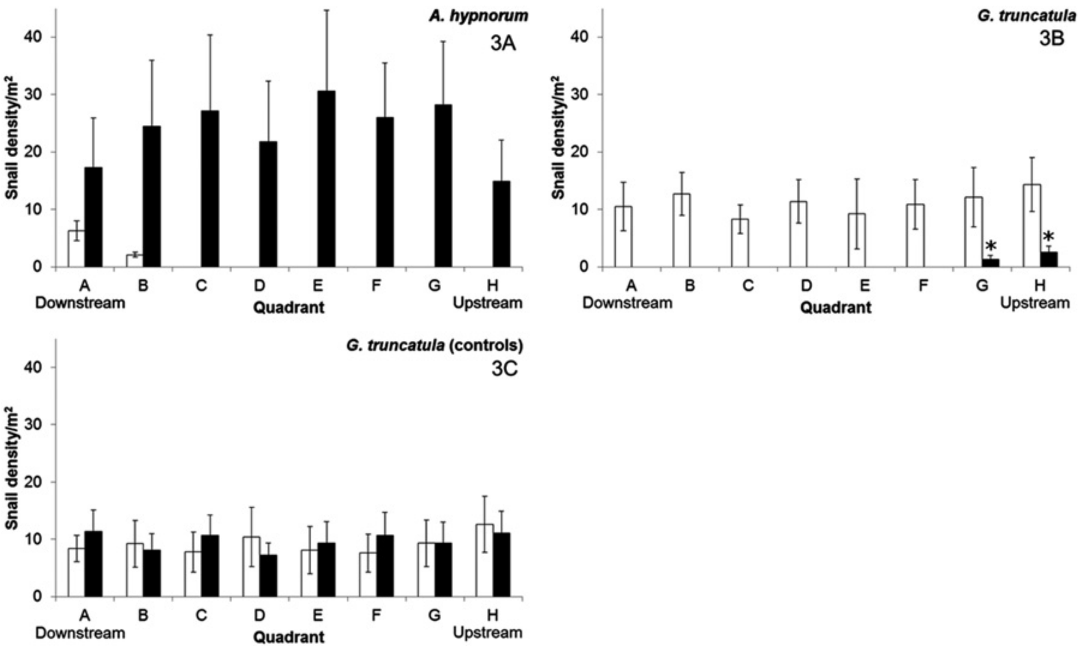

Fig. 3. Distribution of *Aplexa hypnorum* and *Galba truncatula* in eight 1-m^2 quadrants, located from downstream to upstream, in 2002 and 2008: habitats colonized by *A. hypnorum* (3A) and *G. truncatula* (3B), or by *G. truncatula* only (3C). Graph 3B: significant differences ($P < 0.01$) between 2002 and 2008 (*).

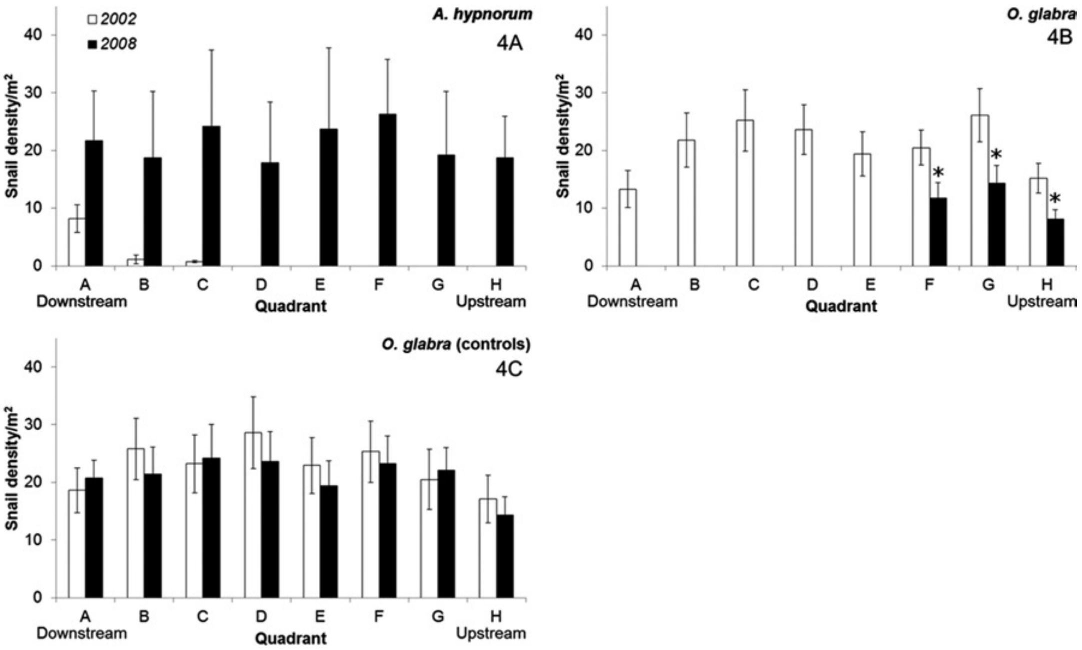

Fig. 4. Distribution of *A. hypnorum* and *Omphiscola glabra* in eight 1-m^2 quadrants, located from downstream to upstream, in 2002 and 2008: habitats colonized by *A. hypnorum* (4A) and *O. glabra* (4B), or by *O. glabra* only (4C). Graph 4B: significant differences ($P < 0.01$) between 2002 and 2008 (*).

lymnaeids was similar to that noted in the corresponding controls.

On day 30 of the experiment, the survival rates of *A. hypnorum* in snail combinations were 92.0% for juveniles, 97.4% for intermediates, and 100% for adults (out of a total of 75 individuals in each group at the beginning of the experiment). In the control groups, the percentages were 93.4, 97.4 and 98.7%, respectively (data not shown).

No sign of lymnaeid predation by *A. hypnorum* was noted in the different snail combinations formed with *G. truncatula* or *O. glabra*. In contrast, several cadavers

Table 1. Mean numbers (SD) of *Galba truncatula* surviving at the end of a 1-month period in pairwise combinations formed by *Aplexa hypnorum* + *G. truncatula* (25 + 50 snails per combination, respectively) and control groups (50 *G. truncatula* per group).

		Number (SD) of live *G. truncatula*		
Snail group	Life stage of *A. hypnorum*	Juveniles	Intermediates	Adults
Snail couples	Juveniles	38.3 (7.9)	41.6 (8.3)	45.2 (6.4)
	Intermediates	24.0 (2.7)	18.7 (5.2)	11.2 (5.2)
	Adults	5.1 (1.6)	3.0 (0.9)	1.5 (1.4)
Controls	No physids	45.3 (3.7)	47.9 (2.1)	49.6 (0.5)

Table 2. Mean numbers (SD) of *Omphiscola glabra* surviving at the end of a 1-month period in pairwise combinations formed by *Aplexa hypnorum* + *O. glabra* (25 + 50 snails per combination, respectively) and control groups (50 *O. glabra* per group).

		Number (SD) of live *O. glabra*		
Snail group	Life stage of *A. hypnorum*	Juveniles	Intermediates	Adults
Snail couples	Juveniles	43.2 (7.1)	46.1 (3.9)	47.4 (2.1)
	Intermediates	37.0 (5.2)	31.8 (7.2)	24.8 (5.4)
	Adults	9.6 (3.7)	7.5 (2.9)	3.7 (1.5)
Controls	No physids	45.7 (4.2)	48.2 (1.1)	49.8 (0.3)

of juvenile and intermediate lymnaeids after exit from their shells were partly eaten by pre-adult and adult *A. hypnorum*.

Discussion

Among the freshwater gastropods that live in periodically dried habitats present in Western Europe, *A. hypnorum*, *G. truncatula* and *O. glabra* were considered to be the most able to withstand drying of their habitats (Kerney, 1999; Anderson, 2006; Glöer and Diercking, 2010). Their ability to resist this process is thought to be species specific. *A. hypnorum* was able to resist drought at the egg stage (Den Hartog and De Wolf, 1962). In contrast, the eggs of both lymnaeids did not withstand summer drying. Juvenile and pre-adult *O. glabra* burrowed into the soft mud at the beginning of summer drying and aestivated at a depth of 1–6 cm when the bottom sediment was marl (Rondelaud *et al.*, 2003). In the same way, the juvenile and pre-adult *G. truncatula* could also burrow into the upper layers of the soil, mainly at altitude (Goumghar *et al.*, 2001) or settle on a support structure that varies in nature depending on the type of habitat (Rondelaud *et al.*, 2009).

In road ditches occupied by *G. truncatula* or *O. glabra*, the introduction of *A. hypnorum* was followed by progressive colonization of the entire area by the physid and gradual reduction of areas occupied by the lymnaeid towards the upstream extremity of the habitats. The strong resistance of *A. hypnorum* eggs to desiccation (Den Hartog and De Wolf, 1962) and its high mobility (the physid moves more quickly than lymnaeids) may partly explain colonization of experimental ditches by this species. In addition, the size of the lymnaeid population significantly decreased over 7 years of the study, so that values noted in 2008 were significantly lower than those recorded in 2002. In contrast, mean densities were relatively stable at sites only occupied by *G. truncatula* or *O. glabra*. Several authors (Økland, 1990; Moens, 1991; Vareille-Morel *et al.*, 1999) have already reported the marginalization of most *G. truncatula* habitats at the peripheral extremity of open drainage and rainwater-draining furrows. According to these authors, *G. truncatula* was outcompeted by other lymnaeids, including *O. glabra* which may even drive *G. truncatula* to local extinction (Rondelaud *et al.*, 2005). Our results demonstrate that *A. hypnorum* also exerted an evident negative effect on *O. glabra*, though to a lesser extent than on *G. truncatula* because of the two following reasons: (i) the complete colonization of *O. glabra* habitats by the physid took longer than that of the other lymnaeid (7 years instead of 4 years, respectively: Figs. 2(A) and (B)); and (ii) the populations of *O. glabra* in their habitats invaded by *A. hypnorum* occupied greater areas in 2008 and their sizes were larger than those noted for *G. truncatula*.

On day 30 of the experiment, the survival of each lymnaeid in snail combinations significantly decreased when the shell height of *A. hypnorum* increased (Tables 1 and 2), suggesting that the inhibitory action of *A. hypnorum* over the lymnaeids seems to be higher when the physid actively grows in size. This inhibition essentially affected adult lymnaeids and, to a lesser extent, intermediates, whereas the juveniles did not seem to suffer from the presence of the physid. As competition of one species over another had an effect on survivorship, growth or reproduction of the individuals concerned (Begon *et al.*, 1996), the low values noted in the intermediate and adult lymnaeids are more difficult to comment, as only snail survival was considered in the present study. Because *A. hypnorum* was never observed to prey on live lymnaeids and the three species fed on lettuce and grass leaves that were given *ad libitum*, the most reliable hypothesis is to incriminate the mucus of intermediate and adult physids that may be toxic for the other freshwater gastropods. Several arguments support this last hypothesis. When *G. truncatula* and *O. glabra* were raised together in the same breeding Petri dishes, the former species quickly died when its shell height reached 6 mm, while the latter survived longer up to the maximum height limit of the adult stage. According to Dreyfuss *et al.* (2006), this rapid death of *G. truncatula* at the adult stage may be due to the toxicity of the mucus secreted by adult *O. glabra*. Another argument comes from the planarian predation experiment described by Lombardo *et al.* (2012): planarians, whose body size was roughly the same as most temperate-climate freshwater snails (~ 10–15 mm in body length), often hunted by roaming and leaving a mucus trail in which small prey such as juvenile *P. acuta* may become entangled. The planarians then revisited the mucus trail and obtained an "easy meal". In contrast, larger snails such as adults were too large to become entangled in the planarian mucus. However, one could question whether the mucus hypothesis is applicable in the field, like it is based on laboratory data. The mucus of *A. hypnorum* may be physically and/or chemically unstable *in situ*, with soft sediment and water flow that could bury it in sediment and/or reduce its toxicity.

Owing to food that was given *ad libitum* to snails in their aquaria, the results noted in the laboratory experiment excluded the occurrence of exploitation competition and suggested evidence of strong interference competition between the physid and either lymnaeid. Several previous authors had already reported cases of interference competition. Gresens (1995) found that snails (*Physa gyrina*) had a strong effect on reproductive output and, consequently, on densities of coexisting chironomid and chydorid crustaceans, even if trophic resources (periphyton) were not depleted. According to this author, chironomids and chydorids were less active in the snail's presence, showing an interference effect on behaviour. The reciprocal effect of chironomids and chydorids on snails was much lower so that the snails were declared as the "winners". Other cases of interference competition for freshwater gastropods were also reported, for example, by Brown (1982) and Lombardo and Cooke (2004).

This interspecific competition between *A. hypnorum* and either lymnaeid requires 7 years in the field to reach complete colonization of the lymnaeid habitat by the physid, a reduction of areas occupied by the lymnaeid, and a limitation of its population size. These results suggest that *A. hypnorum* was a poor competitor. It is possible to question whether these effects in periodically dried ditches persist over time. Indeed, even though *P. acuta* was considered a competitor in Egypt (El-Hassan, 1974), populations of this species often co-existed with planorbids in other countries in Africa (Brown, 1994).

In conclusion, the presence of *A. hypnorum* in habitats colonized by *G. truncatula* or *O. glabra* resulted in a progressive decrease in areas occupied by lymnaeids and their population size. This interspecific competition between the physid and either lymnaeid may not be due to food present in their habitat, but might be due to the toxicity of mucus secreted by intermediate and adult *A. hypnorum*.

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