

Biological invasions: the case of planorbid snails

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Abstract

A large number of planorbid snails are now commonly transported by man mainly through the aquatic plant trade. However, only a restricted number of species establish viable populations in a new habitat and a more restricted number spread. Only five planorbid species can be ranked in this last category and can be considered as pests because of their role in the transmission of parasites to humans or domestic animals: *Biomphalaria glabrata*, *B. straminea*, *B. tenagophila*, *B. pfeifferi* and *Indoplanorbis exustus*. The neotropical *B. glabrata*, *B. straminea* and *B. tenagophila* have proven their capacity to invade another continent sometimes creating new transmission foci. The African *B. pfeifferi* and the Indian *I. exustus* have also expanded their distribution area with long-distance dispersal. Other planorbid species, i.e. *Helisoma duryi*, *Amerianna carinata* and *Gyraulus* spp. have been able to establish viable populations, but not to spread, presumably because they are limited to specific habitats or/and display poor competitive abilities.

Introduction

Biological invasions linked to human activities have received special attention for many years because invasive species may become serious pests (Williamson, 1996; Pimentel, 2002). Human activities transport a fairly large number of species to areas outside their native range (Williamson, 1996). Some can then be found in the wild as feral populations, and are considered introduced. Established species refer to those species which have been able to settle a self-sustaining population, while the 'pest' status is defined based on economic impact or on impact on local biodiversity (Williamson, 1996). As a rule of thumb, Williamson (1996) suggested that out of ten species that are imported one becomes introduced (feral), then it has 10% chance to become established. Ten percent of established species become pests. In other words, most invasions fail (Hall *et al.*, 2003). A further striking aspect of invasions is the population dynamics of invasive species (see Williamson, 1996; Shigesada & Kawasaki, 1997). They typically remain cryptic for some time (very low number of

individuals and very few sites occupied), before entering a phase of rapid (e.g. exponential) growth associated with geographic spreading. At some point, all potential sites are occupied. This is sometimes associated with a collapse in the number of individuals per population (Shigesada & Kawasaki, 1997). This framework highlights the role of various evolutionary and demographic forces in biological invasions. For example, the migration regime is of prime interest when analysing the initial settlement of invasive species from their native range.

Invasive species occur in any biological group, and Mollusca is no exception. They indeed provided some famous examples of biological invasions which had a catastrophic impact on local biodiversity, leading to the extinction of local species. For example, the carnivorous land snail *Euglandina rosea* was deliberately introduced into French Polynesia in order to control the giant snail *Achatina fulica*, and this was followed by the extinction of numerous endemic land snails (Tillier & Clarke, 1983; Tillier, 1992; Civeyrel & Simberloff, 1996). Another spectacular example is the invasion of the North American lakes and rivers by the zebra mussel *Dreissena polymorpha*. Habitat degradation has presumably been the primary cause of extinction of local freshwater mussels

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during the last century but the zebra mussel invasion has accelerated regional extinction rates of local fauna by an order of magnitude (Ricciardi *et al.*, 1998). In addition *D. polymorpha* is considered as a major fouling pest obstructing flow in water conduits causing important economic damage and disturbance.

Our focus here will be on the planorbids, a group of freshwater pulmonate snails. Planorbids have been studied for many years because they are involved in the transmission of parasites, including schistosomes, to humans or domestic animals, (Malek & Cheng, 1974; Brown, 1994). Following the extension of planorbids is of prime interest, especially in the Tropics where the colonization of new sites and environments might lead to the creation of new transmission foci. As a consequence, the amount of information on the geographical – past and current – distribution of planorbids is much higher than for most other snail species. It is, for example, clear that several species have settled new populations outside their native area, and that some species have become invasive (Pointier, 2001). Given their role as intermediate hosts of parasites, some snails can be considered as pests. The present aim is to review available information on invasive planorbids.

Planorbid invasions: how many and how?

An accurate recent estimate of the number of planorbid species is not available. Baker (1945) and Hubendick (1955) considered about 350 species. However the number of valid snail species has decreased over the last decades. For example, Baker (1945) recognized 54 species in the *Biomphalaria* genus, while only 34 species are recognized today (Paraense, 1975; Brown, 1994). The number of *Bulinus* species is similar to that of *Biomphalaria* (Brown, 1994).

Species (or group of species) which have expanded their native range are reported in table 1 (see also Madsen & Frandsen, 1989; Pointier, 2001). Seven species can be considered as invasive. Several *Gyraulus* species should be added to this number, but a taxonomic identification in the reported cases of invasion is at the genus level. On the whole, about ten species can be considered as introduced, or about 0.5% of all planorbid species. This might underestimate the actual values since species from genera with limited medical interest (e.g. *Planorbis*) are less studied and taxonomic identification is not always easy. The eight species (or group of species) reported in table 1 have expanded their range both without and with long-distance dispersal. About half only can be considered as established, and half as pests. This differs from the generalizations proposed by Williamson (1996; see above).

It is noteworthy though that the most speciose genera (*Gyraulus* and *Biomphalaria*) are well-represented in the list in table 1, and it might well be that *Biomphalaria* is over-represented since this genus makes 50% of introduced species and only about 15% of planorbid species. Secondly, it should be noted that no *Bulinus* species has shown invasive capacities. As mentioned above, this genus includes about the same number of species as *Biomphalaria*, and most are involved in the transmission of

Table 1. Status of a planorbid species (or group of species) which have recently expanded their distribution area without (peripheral expansion) or with long-distance dispersal.

Species	Peripheral expansion				Long-distance dispersal			
	Area of origin	Diffusion	Pest	Invading area	Introduced	Established	Pest	Invaded area
<i>Biomphalaria glabrata</i>	Neotropics	Yes	Yes	Haiti Brazil	Yes	Yes	Yes	Egypt
<i>Biomphalaria Pfeifferi</i>	Africa	Yes	Yes	West Africa	Yes	Yes	Yes	Madagascar
<i>Biomphalaria straminea</i>	Neotropics	Yes	Yes	Lesser Antilles	Yes	Yes	Potentially	Hong-Kong, South China
<i>Biomphalaria tenagophila</i>	South America	Yes	Yes	South America	Yes	Yes?	Yes?	Congo (D.R)
<i>Indoplanorbis exustus</i>	India	Yes	Yes	South East Asia	Yes§	Yes	No	Socotra, Oman, Nigeria, Ivory Coast, Guadeloupe
<i>Helisoma duryi</i>	North America	Yes	No	South America	Yes§	Yes	No	Worldwide
<i>Amerianna carinata</i>	Australia	Yes	No	?	Yes§	Yes	No	Java, Thailand, Nigeria, Martinique
<i>Gyraulus</i> spp.	?	?	Yes	?	Yes	?	Yes	Worldwide

Introduced refers to the creation of feral populations, established to the establishment of self-sustaining population, and pest refers to parasite transmission (essentially trematodes) of medical and veterinary importance. ? refers to doubtful or unknown information. Note that details on *Gyraulus* species are vague, and taxonomic identification is at the genus level. §, in irrigation schemes and/or other artificial habitats only.

human and cattle parasites, suggesting that the two genera have been under a similar scientific focus. One can therefore safely conclude that *Biomphalaria* is much more invasive than *Bulinus*, and more generally displays good invasive capacities.

How have these species increased their range, and become invasive? In this respect, the movement of snails is essentially due to human activities. The trade of aquarium plants is probably the main vector (Madsen & Frandsen, 1989). Over the last decade or so, the demand for aquatic plants has strongly increased in order to supply private aquariums, garden tanks or botanical gardens. Breeding farms have been established, mainly in Singapore and Hong Kong, importing wild aquarium plants from other tropical areas, facilitating the introduction and dispersion of alien species (Madsen & Frandsen, 1989). The present survey suggests that this increased trade benefited only a few species, perhaps because they were located in the vicinity of places from which plants are imported. It is possible that passive transportation of snails occurs by other means and there is evidence that birds can transfer snails or snail eggs on their feet or plumage (Rees, 1965; Boag, 1986), but it is difficult to quantify such transfers.

Human activities are not only involved in the transportation of snails but can also facilitate the spread of snails via freshwater environments such as canals, hydroelectric dams and irrigation schemes. It is also likely that the creation of artificial freshwater habitats (e.g. in urban and peri-urban areas) and the degradation of water quality (e.g. eutrophication) also facilitated the expansion of some species (Southgate, 1997).

The *Biomphalaria* genus

Four species belonging to the genus *Biomphalaria* can be considered as invasive, and this is of particular importance since they are involved in the transmission of *Schistosoma mansoni*, the trematode agent of human schistosomiasis in Africa and South America (Chitsulo *et al.*, 2000). Most of the 34 recognized species are found in South America and recent phylogeographic and phylogenetic studies have established that this genus has a South American origin (Bandoni *et al.*, 1995; Woodruff & Mulvey, 1997; Campbell *et al.*, 2000; DeJong *et al.*, 2001; Morgan *et al.*, 2001). The African species (e.g. *Biomphalaria pfeifferi*) are closely related to the American *Biomphalaria glabrata*. The most parsimonious hypothesis is that the ancestor to *B. glabrata* and the African species colonized Africa about two to three million years ago (Campbell *et al.*, 2000; DeJong *et al.*, 2001).

Biomphalaria glabrata is the main snail host of *S. mansoni* in the neotropical area and, as such, the most studied *Biomphalaria* species. Its current distribution extends from the Greater Antilles to southern Brazil (Paraense, 2001). Between 1919 and 1976, a westward colonization of *B. glabrata* was observed in the state of Paraná, Brazil, followed by the expansion of schistosomiasis (Paraense, 2001). Between 1977 and 1979, Prentice (1980) carried out an extensive survey in the Lesser Antilles showing that *B. glabrata* discontinuously occurred throughout the archipelago and also

observed the introduction of the species into Dominica. In the same years, the introduction of *B. glabrata* to Haiti was also reported probably from the neighbouring country Dominican Republic (Raccurt *et al.*, 1985). Established viable populations of *B. glabrata* were subsequently observed in the northern part of the country. Although rather comprehensive phylogeographic studies, based on mitochondrial markers, have shown that this species is made of several well-differentiated clades (including one for the Greater Antilles and one for the Lesser Antilles), the South American origin of the Antillean clades remains unclear (Mavárez *et al.*, 2002; DeJong *et al.*, 2003). It seems that *B. glabrata* is presently strongly declining in several Antillean islands following the accidental or deliberate introduction of thiarid snails (Prentice, 1983; Pointier & Jourdan, 2000). The same phenomenon was also observed in some places in Venezuela (Pointier *et al.*, 1994) and Brazil (Guimarães *et al.*, 2001).

Biomphalaria glabrata was also introduced to Africa: around 1981, it was reported from several canals in Egypt (Pflüger, 1982), and from the irrigation and drainage systems in the Nile Delta area (Yousif *et al.*, 1996). More surprising was the discovery in this region of hybrids between the invader and the local *Biomphalaria alexandrina* (Kristensen *et al.*, 1999). This hybrid was also found naturally infected with *S. mansoni* suggesting that it plays a role in parasite transmission (Yousif *et al.*, 1998). More recently, in 2002–2003, an extensive survey was carried out from regions between Alexandria and Ismailia in the north of the Nile Delta, to as far south as Abu Simbel at Lake Nasser (Lofty *et al.*, 2005). According to a molecular study, surprisingly, all *Biomphalaria* collected by these authors during this survey were *B. alexandrina* and there was no evidence of the presence of *B. glabrata* or of hybridization of *B. alexandrina* with *B. glabrata* in the studied sites. If these results do not exclude the current presence of *B. glabrata* in Egypt, they suggest that *B. glabrata* is not common. The application of molluscicides in most of the putative *B. glabrata* localities by the Egyptian Snail Control Section may explain the absence of *B. glabrata* or its hybrids from the sampling carried out by Lofty *et al.* in 2002–2003. It would be of great interest to carry out subsequent extensive surveys in order to evaluate the present status of the invader and its relationships with *S. mansoni*.

Biomphalaria straminea originally has a neotropical distribution (Paraense, 2001), but has enlarged its distribution to such an extent over the last decades that it can be considered as the most invasive planorbid species. Interestingly, this species is also the one that is the most commonly found associated with aquatic plants which are transported for commercial purposes. During the last decades, *B. straminea* has invaded several Brazilian states (Barbosa, 1973; Teles *et al.*, 2003) as well as some new habitats in Paraguay, Argentina (Paraense, 1970) and Uruguay (Paraense & Corrêa, 1989). Over the same period, it has apparently displaced *B. glabrata* from several counties of the Pernambuco State (north-eastern Brazil; Barbosa *et al.*, 1981). Despite low susceptibility to *S. mansoni*, *B. straminea* is presently strongly involved in the transmission of schistosomiasis in numerous sites

from north-eastern Brazil (Carvalho, 1992; Favre *et al.*, 2002).

In the Caribbean area, its introduction was reported in Colombia in 1966 (Barbosa, 1968) and in Costa Rica in 1976 (Paraense *et al.*, 1981), as well as in several islands of the Lesser Antilles, including Martinique around 1950 (Grétilat, 1967), Grenada in 1970 (Ferguson & Buckmire, 1974), Guadeloupe in 1985 (Pointier *et al.*, 1993) and St Lucia in 1992 (Pointier, 1993). Intestinal schistosomiasis was already occurring in most of these islands with *B. glabrata* as intermediate host. Several control programmes were undertaken in the last 30 years and the parasite transmission is now interrupted or at a very low level. The role of *B. straminea* as intermediate host of *S. mansoni* has never been established on these islands.

Outside the Neotropics, *B. straminea* was introduced to Hong Kong in 1973 (Meier-Brook, 1974) and then begun to colonize the adjacent territories (Liu *et al.*, 1982; Woodruff *et al.*, 1985; Yipp, 1990). Intestinal schistosomiasis does not occur in Hong Kong and China, and the Asiatic schistosomes use local prosobranch snails as obligatory intermediate hosts; moreover, parasitological surveys carried out by Tang (1983) did not reveal the presence of trematodes infecting *B. straminea* in the invaded habitats. Consequently, this species should be considered, at least presently, only as a potential host from the viewpoint of human health.

The neotropical *Biomphalaria tenagophila* has a more restricted distribution area than the two preceding species. It was originally described from the province of Corriente, north of Argentina, by d'Orbigny (1835), and presently occurs mainly in southern Brazil throughout coastal regions from the south of Bahia to Chui (Carvalho, 1992). Up to the middle of the 20th century this species was considered as not susceptible to infection by *S. mansoni*. However, Corrêa *et al.* (1956) discovered the first transmission sites involving *B. tenagophila* as intermediate host in the Paraíba valley, state of São Paulo. In the following years schistosomiasis spread throughout the valley showing that schistosomes have adapted to this new host (Paraense, 2001). *Biomphalaria tenagophila* has also been recorded sporadically in other South American countries such as Peru, Bolivia and Uruguay but it is difficult to consider these records as colonization events because of the lack of historical malacological data (Paraense, 2001).

There is strong evidence that *B. tenagophila* colonized Africa very recently (Pointier *et al.*, 2005). Several malacological surveys carried out in the early 1970s and in the following years in the Kinshasa area, Democratic Republic of Congo, detected a species first identified as *B. camerunensis* (this species occupied the western part of central Africa). Concomitant parasitological studies also showed the presence of numerous snails infected by *S. mansoni*, demonstrating for the first time an active transmission in this area (Colaert *et al.*, 1977). However, conchological, anatomical and molecular studies clearly showed that this snail is in fact the introduced neotropical *B. tenagophila* (Pointier *et al.*, 2005).

The last species in the *Biomphalaria* genus is the African *B. pfeifferi*, the main snail host of *S. mansoni* in Africa. This species probably has the largest distribution among *Biomphalaria* species (and perhaps of all planorbids),

covering most of tropical Africa, part of the Arabic peninsula and Madagascar (see fig. 122 in Brown, 1994). This species has enlarged its distribution in several directions, especially northwards in western Africa partly due to human activities. For example, the building of a large dam on the Senegal River for irrigation purposes induced the creation of artificial habitats such as irrigation canals, and the subsequent extremely fast colonization and spread of *B. pfeifferi* (Southgate, 1997). A consequence of *B. pfeifferi* invasion was the appearance and rise of intestinal schistosomiasis (Picquet *et al.*, 1996).

The occurrence of *Biomphalaria pfeifferi* in Madagascar has been recorded for about a century. However this is probably the result of a recent introduction by humans, and genetic data suggest that at least five genetically differentiated African populations served as the source of colonizers (Charbonnel *et al.*, 2002; N. Charbonnel & P. Jarne, unpublished data). The Malagasy high plateaux (e.g. near Antananarivo) are currently being colonized by *B. pfeifferi*, with a rise in intestinal schistosomiasis (P. Brémond, personal communication).

Other invasive planorbids

Four other species of planorbids can be considered as invasive to various degrees. The first one is the North American *Helisoma duryi*. This species has become a very popular aquarium snail which might explain why numerous introductions have been reported all over the world (see reviews in Frandsen & Madsen, 1979; World Health Organization, 1984; Brown, 1994). However, despite numerous and repeated introductions, this snail has almost never shown important abilities to spread, remaining restricted to a limited number of sites. For example, its arrival in Guadeloupe was reported in the 1960s (Courmes *et al.*, 1964) but it has not since then been detected at more than a few sites, despite the occurrence of numerous apparently favourable habitats. However, *H. duryi* has been more successful in the Nile Delta in Egypt where it occurs in all categories of canals and drains, co-existing to various degrees with other snail species (Yousif *et al.*, 1993). The recent survey carried out by Lofty *et al.* (2005) also showed that the distribution of *H. duryi* extended to north-central Delta, Ismailia and Aswan City. The reason why *H. duryi* has generally not been able to spread might be related to poor competitive capacities against other planorbid snails. They have been investigated in a series of experiments involving interactions with various species of *Biomphalaria* or *Bulinus* (see the review in World Health Organization, 1984). In spite of promising results, all field experiments carried out in various types of habitats such as in Tanzania or Saudi Arabia were not conclusive (Madsen, 1990).

Indoplanorbis exustus was described in 1838 from the south-western coast of Malabar, India but is widely distributed in this country where it serves as intermediate host for several cattle schistosomes (Mishra & Agrawal, 1998). It is also widespread in south-east Asia, following several introductions by man (Brandt, 1974). *Indoplanorbis exustus* was also introduced to the Socotra Island (Wright, 1971) and the Arabian Peninsula (Wright & Brown, 1980).

It has also been discovered in Nigeria (Kristensen & Ogunnowo, 1987) and Ivory Coast (Mouchet *et al.*, 1987). Its first record from the neotropical area dates from 2002 when a few adult specimens were discovered in the Mare à Boire pond from the Grande-Terre of Guadeloupe, Lesser Antilles. Most of the pond was colonized by the next year in spite of the presence of two other alien species, *B. straminea* and *Melanoides tuberculata*, suggesting that *I. exustus* has strong competitive abilities in this type of habitat. It should be noted that the shell of *I. exustus* might easily be confused with that of *H. duryi* (though the two species differ strongly in anatomy), suggesting that invasion of some sites by *I. exustus* might have been overlooked.

The Australian *Amerianna carinata* also proved to have invasive capabilities. It was reported for the first time out of its area of origin in Java in 1951 by Butot (1954) in aquariums and ponds of the Bogor Botanic Gardens. Its spread in Java was confirmed in the following years by Benthem-Jutting (1956). *Amerianna carinata* was then reported from Thailand (Brandt, 1974), Nigeria (Brown, 1983) and the Lesser Antilles (Pointier, 1996). Little is known about its ecology and invasive capabilities. However this snail seems to limit its invasion to particular habitats such as artificial ponds, botanical gardens or small ditches along river banks.

The genus *Gyraulus* includes species of wide distribution in Europe, Asia or Africa and also endemic taxa in ancient Palaeartic lakes (Meier-Brook, 1983; Brown, 1994). Several species which are often difficult to identify are commonly found on aquarium plants and consequently have been transported all around the world. The presence of the North American species *Gyraulus parvus* in Cuba is most probably the result of this type of transportation (Aguayo & Jaume, 1954). Another unidentified species has also been recorded in a watercress bed in Martinique in 1987 (Pointier, 2001). In South America the occurrence of *Gyraulus* spp. in nature is not clear. More information should be gained about invasions of *Gyraulus* species, since in Asia some of them serve as first intermediate hosts of intestinal flukes of cattle such as echinostomes or paramphistomes (Rolfe *et al.*, 1991; Lo, 1995).

Conclusions

Several species of planorbid snails have spread to new areas, possibly as a result of human activities. However, few species establish viable populations in a new habitat and a more restricted number become invasive (see table 1). Only five species (four *Biomphalaria* and *I. exustus*) can be ranked in this last category which generally have medical and veterinary implications. Other species have been able to establish viable populations, but not to spread, presumably because they are limited to specific habitats.

The present survey of invasive planorbid species essentially reports the current extension of some species. Only a few studies have been undertaken for further understanding the invasion of planorbid species. For example, genetic markers can be used to analyse the origin of invaders (see e.g. Charbonnel *et al.*, 2002; Facon

et al., 2003; Genner *et al.*, 2004). Their subsequent spread can also be analysed using genetic markers (Charbonnel *et al.*, 2002), but population dynamics offers the possibility of a refined approach, in order to estimate the rate of spread. This is of particular interest since planorbids, and freshwater organisms in general, occupy patchy environments in which the classical framework, based on the analysis of wave spread (see Williamson 1996; Shigesada & Kawazaki, 1997) is not always appropriate (Facon, 2003). A further research path is the influence of invaders on local biodiversity or health. With reference to health, little is known other than the fact that invasive species have opened up new foci for parasite transmission.

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