# Chapter 9
# The Biological Control of the Snail Hosts of Schistosomes: The Role of Competitor Snails and Biological Invasions

**Jean-Pierre Pointier, Patrice David, and Philippe Jarne**

**Abstract** Biological control of the snail hosts of schistosomes has been considered in the last few decades as an alternative to molluscicides. Several groups of organisms have been proposed to control snail hosts, but very few have proven their efficacy in the field. Competitor snails can be considered as the most efficient biological control agents and numerous promising laboratory studies and field experiments have been carried out, mainly in the Caribbean. Two species of competitor caenogastropod snails belonging to the Ampullariidae (*Marisa cornuarietis*) and Thiaridae (*Melanoides tuberculata*) families have succeeded in eliminating or reducing populations of schistosome-transmitting snails, especially *Biomphalaria glabrata* in several different habitats in St Lucia, Martinique, and Guadeloupe. However, their efficiency is context-dependent. Caenogastropods are good competitors in relatively stable habitats only when long-term resource exploitation rather than colonization is the limiting factor. At the same time, unassisted invasions by these species and by other freshwater snails, including numerous pulmonates, were detected in the 1950s, followed by rapid spread in the following decades to most Neotropical areas. These invasions were largely responsible for the general decline of *B. glabrata* in islands, such as Martinique and Guadeloupe, replicating at a larger scale the results of biological control programs. No extinction of local snail species occurred following the invasion by exotic snails, except for *B. glabrata* in Martinique. Thus, biological invasions could qualify as efficient "unintentional biological control" agents. However, the downside of biological invasions is that snail hosts can be invasive and establish new sites of parasite transmission in formerly parasite-free areas. Moreover, the apparent lack of extinctions may mask the ongoing declines of local species leading to future extinctions, especially if new invaders continue to appear on a yearly basis.

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## 9.1 Introduction

Schistosomiasis control has a long history, and our understanding of both local parasite transmission and the array of control techniques has gradually improved. The first control programs mainly focused on populations of snail vectors but the discovery of new diagnostic methods, new effective drugs, and powerful molluscicides led to the development of more integrated approaches implementing several types of interventions simultaneously (Bruun and Aagaard-Hansen 2008). Snail control has remained an essential component of these integrated control programs, but chemical molluscicides are expensive; the organization needed to spray them is complex, and they may negatively impact local faunas (McCullough 1992). Over the last several decades, biological control has been considered as an alternative approach to molluscicides. The logic underpinning biological control is to introduce a new species ("natural enemy") that has the ability to establish self-sustained populations and to eliminate – or to limit the density of – populations of the target species. A scheme for screening and evaluating the cost-efficiency and environmental impact of biological control agents has been proposed by the World Health Organization (1982). This protocol includes five stages of laboratory and field studies before using any biological agent at large scale in integrated disease control operations. However, few biological agents have proven their efficiency against vector snails in the field despite several decades of work. On the other hand, many unassisted biological invasions took place in the whole tropical areas during the same period inducing long-term changes in snail communities.

Four main groups of organisms have been proposed for controlling snail hosts of schistosomes: pathogens, predators, parasites, and competitors. Several micropathogens, mainly bacteria and fungi, and protozoans have been studied, but research remained at the laboratory stage. A long list of micropathogens of freshwater snails is available in the literature (see the review by Madsen 1995). However, very little work has been done for systematically screening snails for micropathogens and more thorough studies on the fitness impact of pathogens on snails are required.

Predators of freshwater snails have been studied more extensively. They include almost all groups of the animal kingdom, including planarians, leeches, insects, and their larvae, crustaceans, fishes, birds and mammals. A lot of empirical observations and laboratory studies are available in the literature on these predators, particularly the sciomyzid flies and cichlid malacolophagous fishes (see the review by Madsen 1995); field experiments remain scarce. An exception is the investigation on the crayfish *Procambarus clarkii* in Kenya (Hofkins et al. 1991; Loker et al. 1993; Mkoji et al. 1995). Moreover, introducing predators is notoriously dangerous, as the lack of specificity of predators may lead to ecological disasters. For example, the introduction of the land snail *Euglandina rosea* into the Society Archipelago, French Polynesia, is responsible for the extinction of a remarkable endemic land snail fauna (Tiller and Clarke 1983).

Parasites, especially larval trematodes, have been also considered as control agents, and three main characteristics of the snail–parasite interactions have attracted the attention of researchers: (1) the antagonism between larvae of different trematode species within the snail host (Lie et al. 1965; Lie 1967; Lie and Heynemann 1972), (2) the parasitic castration of the snail host (Jourdane and Kulo 1981), and (3) the pathogenic or lethal action of larval trematodes on snails (Jourdane and Kulo 1982). Here , field experiments are also scarce and they either failed (Lie et al 1974) or had only ephemeral success (Nassi et al. 1979).

Competitor snails have been considered as the most promising biological control agents; many encouraging laboratory studies have been conducted using several competitor species (Madsen 1995), and trials have proven their efficacy in the field (Pointier and Jourdane 2000). These field experiments were mainly conducted in the Caribbean over the last half-century using ampullariids and thiarid snails. However, several species of the same group accidentally invaded numerous Caribbean islands and countries during the same period, and the number of newcomer freshwater snails steadily increased. These newcomers had substantial influence on those snail species acting as intermediate hosts for schistosomes. Our aim here is to illustrate key aspects of the impact of competitor snails on the snail hosts of schistosomes and on native ecosystems. We consider both intentional introductions of a snail competitor and bioinvasions, drawing heavily from the few situations that have been studied thoroughly, to allow some inferences on biological control and species interactions. These studies were mainly conducted in the Lesser Antilles (Jobin et al. 1977; Prentice 1983; Pointier et al. 1989; Pointier and Guyard 1992; Facon et al. 2005, 2008; Facon and David 2006).

## 9.2 Field Experiments Using the Ampullariid Snail *Marisa cornuarietis*

One of the classical examples of biological control of schistosome transmitting snails is that of *Biomphalaria glabrata* by the ampullarid snail *Marisa cornuarietis.* This species is native to Venezuela and has been introduced to Florida and several Caribbean islands as an ornamental snail by aquarists (Madsen and Frandsen 1989). Its ability to eliminate *B. glabrata* was reported for the first time in 1952 in natural water bodies on the island of Puerto Rico (Oliver-González et al. 1956). In 1956, a first field trial using *M. cornuarietis* was carried out in 111 irrigation ponds located on the south coast of Puerto Rico. By 1965, *B. glabrata* had been displaced in 89 out of 97 ponds (92%) still in operation (Ruiz-Tibén et al. 1969). Other field experiments confirmed the efficiency of *M. cornuarietis* against *B. glabrata* in other types of Puerto Rican habitats, such as artificial lakes (Jobin et al. 1977) or flowing waters (Jobin and Laracuente 1979). In Tanzania, *M. cornuarietis* was successfully introduced to a dam harboring large populations of *Biomphalaria pfeifferi, Bulinus tropicus* and *Lymnaea natalensis*. Two years after the introduction of the ampullariid snails, all three pulmonate species had been eliminated (Nguma et al. 1981).

A similar field experiment was initiated in 1987 in Grande-Terre of Guadeloupe using *M. cornuarietis* against *B. glabrata* (Pointier and David 2004). Grande-Terre harbors about 2,000 ponds over an area of about 700 km$^2$ and a few small rivers. The competitor snail was introduced to 15 experimental ponds, while 15 control ponds were left unchanged. Populations of all species of freshwater molluscs as well as representative plant species were surveyed twice a year for the 13 subsequent years. *B. glabrata*, which was initially seen frequently in the studied ponds (and over the entire island), rapidly disappeared from the experimental sites. Concomitantly, a slow and continuous decrease in the number of control ponds harboring *B. glabrata* was observed from 1994 to 2000 (Fig. 9.1). This trend was not restricted to the study sites but rather represented a progressive, general decline in the occurrence of *B. glabrata* over the whole island. In fact, *B. glabrata* occurred in 26.6% of 188 ponds surveyed in 1980–1981 (Pointier et al. 1985), whereas this proportion had decreased to 2% by 2000 (authors' unpublished data; 150 ponds). This decline probably results from both an increase in the rate of local extinction and a decrease in recolonization rates. Although periodic drying of the ponds normally results in a regime of local extinctions during each dry season, additional extinctions have taken place because of competitive interactions with introduced species. The latter include *M. cornuarietis* (in the experimental ponds, see above) and also, in many other ponds, two exotic species, *Biomphalaria kuhniana* (a member of the *Biomphalaria straminea* species complex, formerly identified as *B. straminea* in Pointier et al. 1993a) and *Melanoides tuberculata*. These two species invaded many sites without assistance between 1980 and 2000 (Pointier et al. 1993a; Pointier and Delay 1995; authors' unpublished data). The entire system of ponds can be considered as a single metapopulation of *B. glabrata* and is subject to recurrent extinction–colonization dynamics. The metapopulation structure amplifies

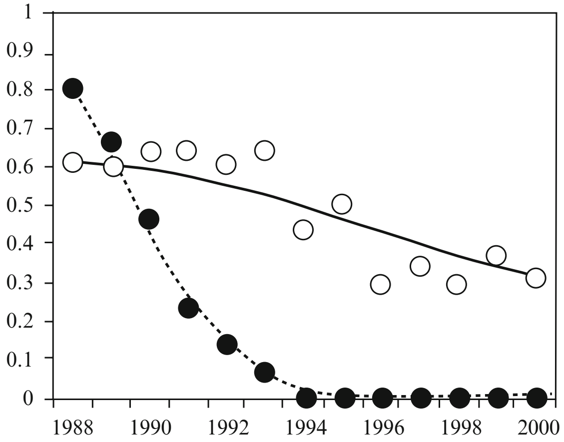

**Fig. 9.1** Temporal variation in the frequency of ponds occupied by *Biomphalaria glabrata* in a biological control trial implemented in Grande-Terre (Guadeloupe) using the competitor snail *Marisa cornuarietis*. *Black circles*: experimental ponds ($N=15$) where *M. cornuarietis* was introduced at the end of 1987; *white circles*: control ponds ($N=15$). Note a slow, delayed decline of *B. glabrata* in the control ponds from 1994 on

the effects of removing favorable sites through the action of biological control agents. Because sites are sources of colonizers to each other, such a removal can disproportionately decrease the equilibrium occurrence of a species on a metapopulation scale (Pointier and David 2004). According to the hypothesis of metapopulation collapse, and assuming that the presence of *M. cornuarietis* makes a pond unavailable for the establishment of *B. glabrata*, the frequency of the latter should decrease even in sites where *M. cornuarietis* is absent, which is exactly what was observed. Of course, the 15 experimental ponds represent a small fraction of the suitable sites for *B. glabrata*. However, the introduction of *M. cornuarietis* to other ponds (not part of the experiment), as well as the spread of two other alien species may have affected a sufficient number of sites to seriously lower the colonization rate, even in sites devoid of exotic species. This interactive effect is probably the key to the slow decline of *B. glabrata* in Grande-Terre of Guadeloupe in the last few decades.

Importantly, other pulmonate species, such as *Biomphalaria schrammi, Drepanotrema surinamense* or *Drepanotrema depressissimum* were apparently not affected by the presence of *M. cornuarietis*. This observation was interpreted as the consequence of strong differences in life-history traits between these species and *B. glabrata*. More rapid growth and a much shorter life span provide a strong advantage to these species at the beginning of the rainy season (Lévèque and Pointier 1976). They are able to colonize some refuges much more rapidly than *B. glabrata* after the dry season and can resist more effectively competitor introduction. It also appears clearly from this report that biological control might be less straightforward than initially imagined, and may have consequences at scales larger than that at which the control experiment was conducted (Pointier and David 2004).

The efficiency of *M. cornuarietis* against vector snails is probably linked to its feeding habits. It is indeed a voracious snail consuming many types of submerged or floating aquatic plants. Another typical example of biological control mediated through plant destruction can be drawn from Guadeloupe. In the Grand Etang Lake (Basse-Terre) the exclusive habitat of *B. glabrata* was constituted by a belt of the floating plant *Pistia stratiotes*. The introduction of *M. cornuarietis* in 1987 resulted in its complete destruction in the course of 3 years and consequently in the elimination of the only snail host from that lake. This was followed by the eradication of *Schistosoma mansoni* in the animal reservoir *Rattus rattus* (Pointier et al. 1991; Fig. 9.2).

Regarding the 15 experimental ponds of Grande-Terre, the main visible consequence of the introduction of *M. cornuarietis* on the aquatic vegetation was a significant decline of the water lily *Nymphaea ampla* (Pointier and David 2004). Fortunately, this plant is very common in the Caribbean islands and in South America, and its extinction seems very unlikely due to the large number of ponds still free of *M. cornuarietis* and the poor dispersal capacities of this snail (Pointier and David 2004). Caution remains necessary, however, in using it in biological control programs as it can become a pest for cultivated rice, water-cress (*Nasturtium officinale*) or dasheen (*Colocasia esculenta*). The invasion of several South-Eastern Asian countries by ampullariid species from South America, and their impact on agriculture is quite illustrative of this problem (Cowie 2002).

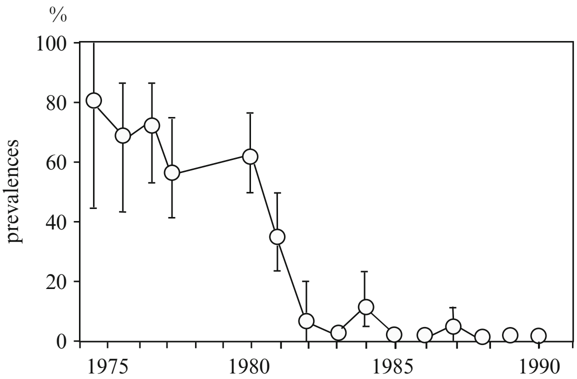

**Fig. 9.2** Infection rate of rats, *Rattus rattus*, by *Schistosoma mansoni* at Grand Etang Lake, Basse-Terre of Guadeloupe between 1974 and 1990. The parasite has been eradicated by 1990 following the elimination of the snail host *Biomphalaria glabrata* through biological control

## 9.3 Field Experiments Using Thiarid Snails

Thiarid snails, native to the Paleotropics, have invaded the Neotropics since the 1930s. They soon attracted the attention of researchers who assessed their efficiency as biological control agents in controlled trials. The history of thiarid introductions to Caribbean countries is well documented (Fig. 9.3). All are unintentional except in the island of St Lucia (see Prentice 1983). Water birds and passive transport by cars or cattle are probably involved in the local spread of invasive species from one watershed to the other, or to nearby islands, yet aquarist trade is probably more efficient as a means of long-distance (transcontinental) introductions, as these species are often associated with aquarium plants (Abbott 1952; Madsen and Frandsen 1989). Two species are mainly concerned, *Tarebia granifera* and *M. tuberculata* (Fig. 9.3).

A first field experiment of biological control using thiarid snails against the snail hosts of schistosomes was conducted in St Lucia in 1978 (Prentice 1983). *M. tuberculata* (erroneously identified as *T. granifera* by Prentice) was introduced to seven sites, including dasheen (*C. esculenta*) and water-cress (*N. officinale*) marshes drained by small streams or springs. Other similar sites, left unchanged, were used as controls. These habitats were very common in St Lucia and highly favorable to *B. glabrata* and to schistosomiasis transmission. Two years later, the competitor snail was widespread in these sites and had eliminated *B. glabrata* (Fig. 9.4). Following this success, *M. tuberculata* was introduced to other sites on the island (A. Calender, pers com). A malacological survey of the whole hydrographic system in 1992 revealed that *M. tuberculata* had become the most common freshwater snail in St Lucia. This survey was undertaken in sites where large populations of *B. glabrata* had been found in the past, and showed (1) the absence of the planorbid snail from seven sites extensively colonized by *M. tuberculata*, (2) the presence of *B. glabrata* at low to very low densities in 17 sites together with *M. tuberculata*, and (3) the presence of *B. glabrata* in large populations in the only two sites where

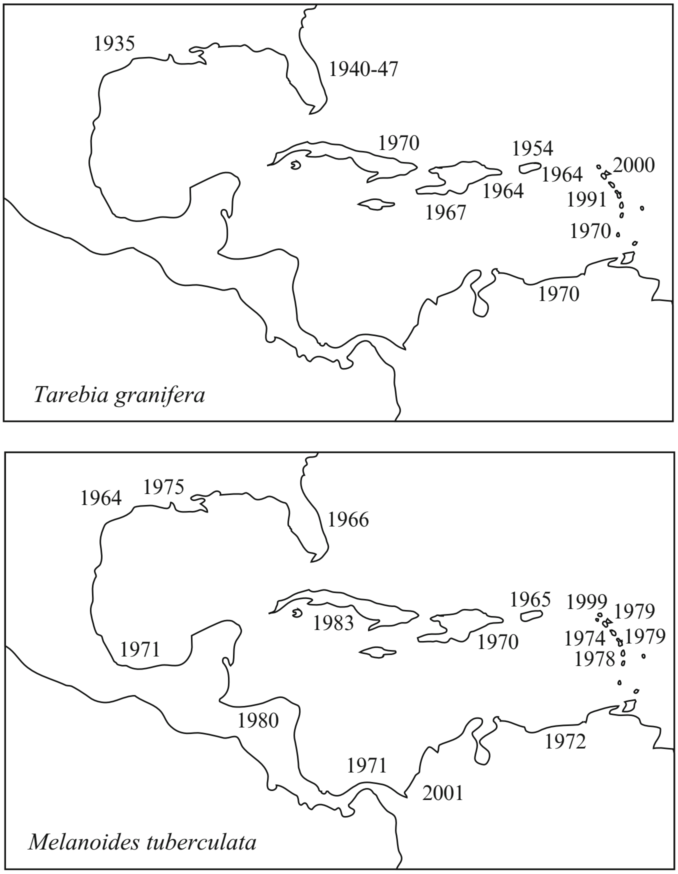

**Fig. 9.3** Introduction of thiarid snails to the Caribbean area. *Top map*: *Tarebia granifera*. Sources are Murray and Woopschall (1965) for San Antonio, Texas, USA, Abbott (1952) for Lihia Springs, Florida, USA, Harry and Aldrich (1958) for Puerto Rico, Ferguson (1977) for Vieques and the Dominican Republic, Robart et al. (1979) for Haiti, Ferguson (1977) for Grenada, Chrosciechowski (1973) for Venezuela, Jaume (1972) for Cuba, Pointier et al. (1998) for Martinique and Pointier (2008) for Guadeloupe. *Bottom map*: *Melanoides tuberculata*. Sources are Murray (1964) for Texas, Abbott (1973) for Puerto Rico, Clench (1969) for Florida, Gomez et al. (1986) for Dominican Republic, Abbott (1973) for Mexico and Panama, Chrosciechowski (1973) for Venezuela, Pointier unpublished data and Starmühlner (1984) for Dominica, Dundee and Paine (1977) for Louisiana, Prentice (1983) for St Lucia, Pointier and McCullough (1989); Pointier and Delay (1995) for Martinique and Guadeloupe, Clarke (1987) for Honduras, Perera et al. (1987) for Cuba, Stevens and Waldmann (2001) for Montserrat. Note that the invasion sequence is very difficult to interpret because *M. tuberculata* is in fact a single name for independent strains which were introduced and are still being introduced at different places at different times

*M. tuberculata* was absent (Pointier 1993). Its scarcity in habitats which were formerly important transmission sites in St Lucia probably means that transmission is presently low or very low if it indeed still occurs. Although other ecological or anthropogenic factors may be involved, there is no doubt that the thiarid snail

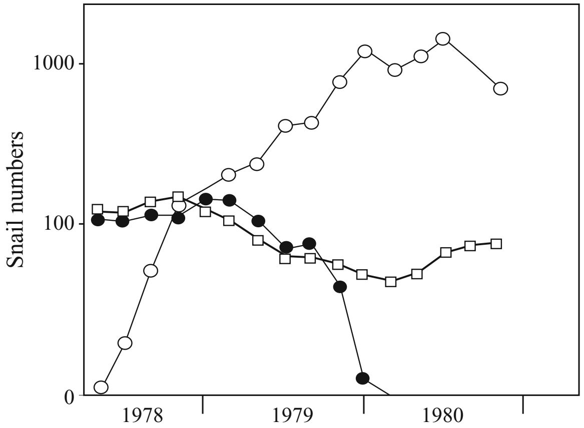

**Fig. 9.4** Temporal variation of snail number (log scale) in a dasheen marsh in St Lucia during a biological control trial of *Biomphalaria glabrata* (*black circles*) by *Melanoides tuberculata* (*white circles*). *White squares*: *B. glabrata* in the control site without *M. tuberculata*

*M. tuberculata* played a major role in the decline of *B. glabrata* populations. Also of importance is the long-term permanence of dense populations of the thiarid snail, maintaining *B. glabrata* at a very low level and preventing the recolonization of sites where the planorbid snail has been eliminated.

Biological control using *M. tuberculata* has also been conducted in Martinique. This species was discovered there for the first time in 1979, and then spread rapidly. In 1982, *B. glabrata* and schistosome transmission were still occurring in several water-cress cultures (Pointier et al. 1984). The biological control program took advantage of previous studies of snail population dynamics conducted in 1982. *M. tuberculata* was introduced in 1983 to a group of water-cress cultures and eliminated the snail hosts *B. glabrata* and *B. kuhniana* (formerly identified as *B. straminea*) in less than 2 years (Pointier et al. 1989; see Fig. 9.5). Following this success, *M. tuberculata* was introduced to other groups of water-cress beds. In 1990, *B. glabrata* and *B. kuhniana* had totally disappeared from eight sites and a few individuals only were recorded from the remaining sites (Pointier and Guyard 1992).

The last example we present is that of Guadeloupe where the marshy forest of *Pterocarpus officinalis* located behind the mangrove swamp is a schistosomiasis focus. The reservoir of adult schistosomes is the black rat *R. rattus* (Théron and Pointier 1995). This focus includes the marshy forest and a wet meadow zone. The area extending from the marshy forest to the herbaceous zone irregularly experiences periods of flooding and drying following the rainfall regime. It is mainly devoted to dasheen culture and harbors large populations of *B. glabrata*. The herbaceous zone used for cattle grazing is also suitable for this snail. Additionally, permanent ponds fed by groundwater can be found in both the marshy forest and herbaceous zones. They are used for watering cattle or for growing water-cress and providing favorable habitats for *B. glabrata*. A biological control trial was initiated in 1984. *M. tuberculata* was introduced to the three main types of habitats of this area,

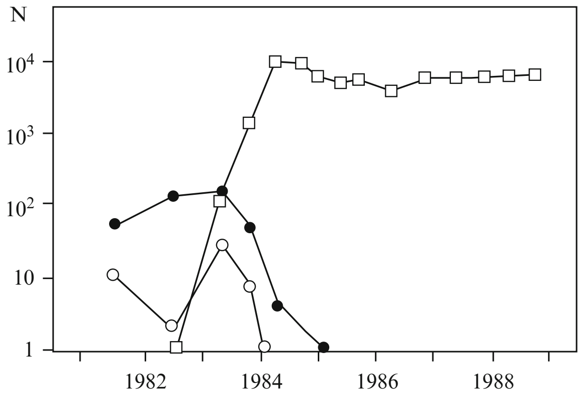

**Fig. 9.5** Temporal variation of snail number (log scale) in a water-cress bed of Martinique during a 7-years trial of biological control of *Biomphalaria glabrata* (*black circles*) and *B. kuhniana* (*white circles*) by *Melanoides tuberculata* (*white squares*)

and snail dynamics was followed over the next 6 years (Pointier et al. 1993b). Colonization by *M. tuberculata* was successful in all habitats, but the impact on the snail host differed with habitats. In permanent ponds, *M. tuberculata* rapidly reached high densities 6–10 months after its introduction (see the example in Fig. 9.6, top). Initially low, the densities of *B. glabrata* declined and the snail population disappeared almost completely. In contrast, colonization of the dasheen cultures was more difficult presumably because of irregular periods of desiccation during the dry season. *M. tuberculata* densities remained low and *B. glabrata* densities fluctuated markedly, but there was no apparent correlation between the two species (Fig. 9.6, bottom). These contrasted results can be explained by the quite opposite demographic strategies exhibited by the two snail species. *M. tuberculata* has slow growth, low reproductive rate, and a long life span, whereas *B. glabrata* exhibits rapid growth, high reproductive rates, and a very short life span. Thus, *B. glabrata* has a strong advantage on *M. tuberculata* in unstable and temporary habitats such as dasheen cultures. On the contrary, *M. tuberculata* has enough time to reach and maintain high densities in permanent and stable habitats, such as water-cress cultures, and thus is able to become a serious competitor for food and space (Pointier et al. 1993b).

To summarize, the competitor species *M. cornuarietis* and *M. tuberculata* have been quite successful in eliminating or reducing populations of schistosome-transmitting snails, especially *B. glabrata*. However, their efficiency is context-dependent; these caenogastropods are efficient competitors in sufficiently stable habitats only where long-term resource exploitation rather than colonization ability is the limiting factor. Species with more colonization-oriented life histories, especially other pulmonates, may be more efficient than caenogastropods to limit *B. glabrata* in isolated and unstable habitats, such as small ponds. The combined presence of introduced caenogastropods and introduced pulmonates (the latter being nonassisted invasions) can dramatically limit, if not eliminate, *B. glabrata* populations at the regional scale.

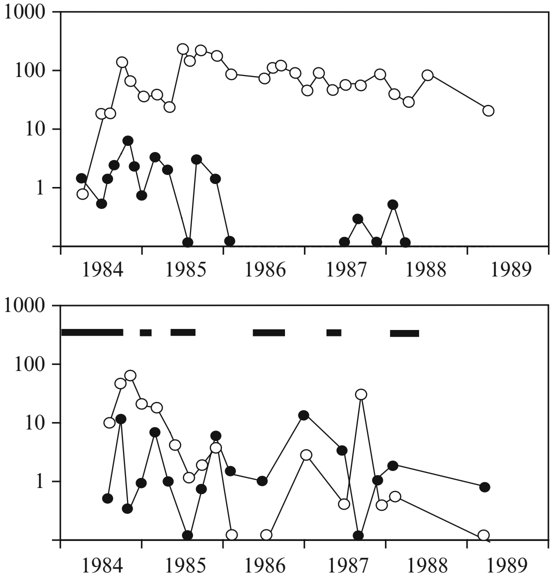

**Fig. 9.6** Temporal variation of snail number (log scale) in the marshy forest of Guadeloupe during a 6-years trial of biological control of *Biomphalaria glabrata* (*black circles*) by *Melanoides tuberculata* (*white circles*). Snail dynamics in a permanent pond (*top*) and in a dasheen culture (*bottom*). *Horizontal black bars* indicate periods of site drying

## 9.4 Snail Invaders and French Antillean Islands: The Decline of *Biomphalaria glabrata*

Unassisted invasions of exotic snails have considerably modified most tropical freshwater faunas in recent decades. Invasive species have often ended up behaving as efficient, if involuntary, control agents against schistosome-transmitting snails, especially *B. glabrata*. In Guadeloupe and Martinique, the initiation of field trials in biological control programs (see above) was paralleled by rapid and unassisted invasions of entire hydrographic systems. They have been well documented by long-term malacological studies initiated in the beginning of the 1970s (Golvan et al. 1981; Pointier and David 2004; Facon and David 2006).

In Martinique (Fig. 9.7), this fauna was first investigated at the end of the nineteenth century by Mazé (1874) and Bordaz (1899) who reported ten species, including *B. glabrata*. Dreyfuss (1953) confirmed the presence of four planorbid species. At that time, *B. glabrata* was apparently widely distributed throughout the island. Starting with the discovery of *B. kuhniana* in 1967 (*Biomphalaria havanensis* in Grétillat (1967)), a continuous influx of exotic species has been detected (Guyard and Pointier 1979; Pointier 2008) so that the number of introduced species now

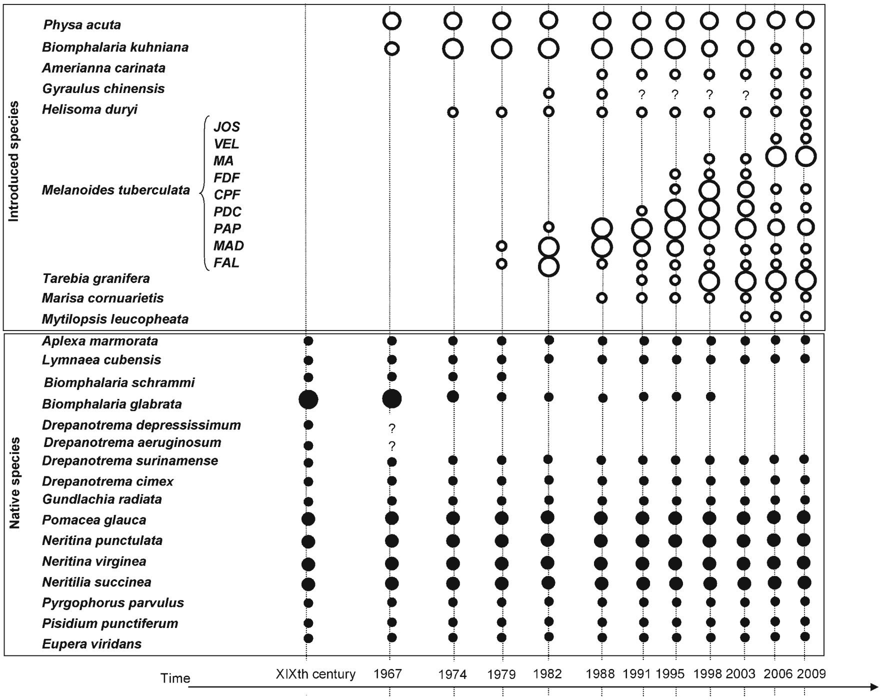

**Fig. 9.7** Changes in the freshwater malacofauna of Martinique during the twentieth century distinguishing introduced (*white*) and native (*black*) species. *Circle size* corresponds to taxa abundance; *small circles*: taxon very localized and/or rare; *medium circle*: taxon either found at many sites and low densities, or localized and abundant; *large circle*: dominant taxon, very common and widespread. From Mazé (1874), Bordaz (1899), Dreyfuss (1953), Grétillat (1967), Guyard and Pointier (1979), Pointier et al. (1993c), Pointier (1996, 2008), Facon et al. (2003), Facon and David (2006), and authors (unpublished data)

approximately matches that of native species (Fig. 9.7). The most spectacular invasions are those by members of the Thiaridae family, *M. tuberculata* and *T. granifera*. The former is characterized by a high morphological and genetical diversity; it consists of several well-individualized strains (see Fig. 9.7) perpetuating through clonal reproduction that can ecologically be considered as a different species. These strains can be recognized in the field based on shell sculpture and colors (Fig. 9.8). Those occurring in Martinique, depicted in Fig. 9.7, have been independently introduced from outside, with the exception of two (named CPF and FDF) which are local hybrids produced by rare sexual reproduction events among previously established strains (Facon et al. 2003, 2008).

The freshwater malacological fauna of Guadeloupe includes a larger number of native species than Martinique because of the diversity of habitats offered by the contrasted geomorphological characteristics of the two main islands of the

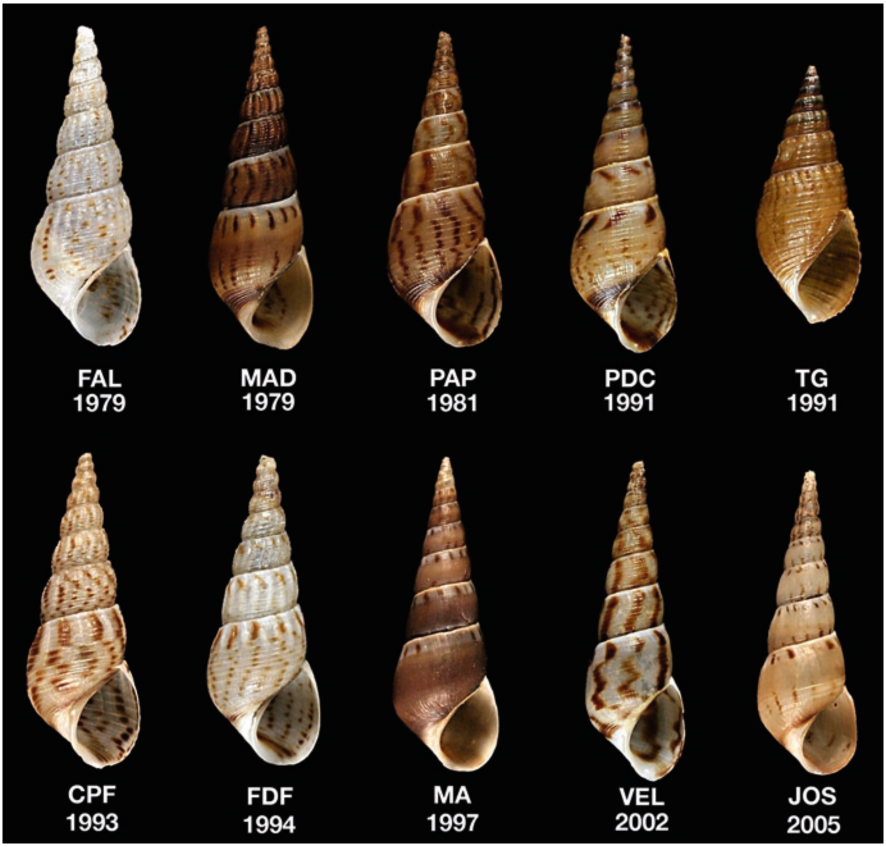

**Fig. 9.8** Thiarid snails that have invaded Martinique over the last 30 years with introduction year. FAL, MAD, PAP, PDC, CPF, FDF, MA, VEL, and JOS are morphs of *Melanoides tuberculata* which have been recognized based on shell and genetical characteristics. TG = *Tarebia granifera*

Guadeloupean archipelago (Fig. 9.9). Basse-Terre is a volcanic mountainous island with numerous rivers, streams, and canals, whereas Grande-Terre is flat, calcareous, offering numerous lentic habitats, such as natural or artificial ponds and marshes. The introduction history is summarized in Fig. 9.9 and shows marked similarities with that of Martinique. Many species have invaded the two islands at approximately the same time (*T. granifera* and *M. tuberculata*) or at different times (*B. kuhniana*). However, other invasions have reached a single island, some of which concern taxa that are now both abundant and widespread (e.g., the PDC and MA strains of *M. tuberculata* in Martinique, the GOS strain of *M. tuberculata* and the lymnaeid *Pseudosuccinea columella* in Guadeloupe). To some extent, the two islands can, therefore, be considered as independent natural experiments. The current status of introduced species is very diverse and

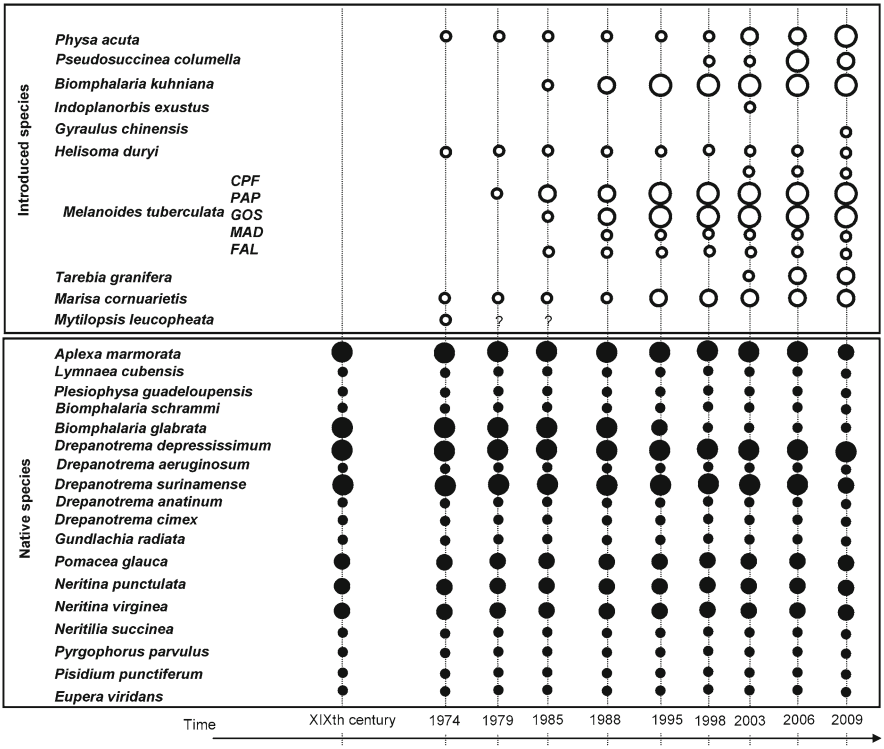

**Fig. 9.9** Changes in the freshwater malacofauna of Guadeloupe during the twentieth century. *Circle size* corresponds to taxa abundance, as in Fig. 9.7. From Schramm (1869), Mazé (1890), Floch (1969), Pointier (1974), Pointier et al. (1993a), Pointier and Delay (1995), Pointier (2008), and authors (unpublished data)

a large range of situations may be encountered (see Table 9.1). Some taxa are now widely distributed throughout the islands and may even occur in huge populations (e.g., the PAP and MA strains of *M. tuberculata* and *T. granifera* in Martinique) while others are declining (the FAL morph of *M. tuberculata* and *B. kuhniana* in Martinique) or are restricted to a particular type of aquatic environment (e.g., *Amerianna carinata* and *Gyraulus chinensis* to oxbow lakes, *Helisoma duryi* to artificial habitats). Others even failed to persist for more than 2 or 3 years after their introduction (e.g., *Indoplanorbis exustus* in Guadeloupe).

As already pointed out, although ecological and anthropogenic factors may also be involved, a clear correlation has been observed in the Caribbean area in the last 30 years between the invasion by exotic snails and the decline of *Biomphalaria* species. In Martinique, for example, *B. kuhniana* (which was itself a previously established invader) has strongly regressed in the last decades, while thiarid snails were on the rise, and *B. glabrata* can be considered as eradicated since 2005

**Table 9.1** Introduced species of freshwater snails in Martinique and Guadeloupe (in chronological order), and current status

| Introduction year | Alien species | Present status |
|---|---|---|
| Martinique | | |
| ? | *Physa acuta* | Widely distributed mainly in anthropized sites |
| 1953–1967 | *Biomphalaria kuhniana* | Strongly regressed between 1979 and 2009 |
| 1972–1978 | *Helisoma duryi* | Restricted to a very few sites (artificial tanks and ponds) |
| 1979 | *Melanoides tuberculata* FAL and MAD | FAL morph widely distributed in 1986, now strongly regressed. MAD now widely distributed |
| 1981 | *Melanoides tuberculata* PAP | Widely distributed |
| 1982 | *Gyraulus chinensis* | Restricted to some oxbow lakes |
| 1987 | *Marisa cornuarietis* | Restricted to two marshes |
| 1987 | *Amerianna carinata* | Restricted to some oxbow lakes |
| 1990 | *Melanoides tuberculata* PDC | Widely distributed |
| 1991 | *Tarebia granifera* | Widely distributed |
| 1993 | *Melanoides tuberculata* CPF | Uncommon |
| 1994 | *Melanoides tuberculata* FDF | Appeared at a single site in 1994. Now disappeared |
| 1997 | *Melanoides tuberculata* MA | Widely distributed. Probably the most competitive taxon |
| 2002 | *Melanoides tuberculata* VEL | Restricted to a few sites |
| 2005 | *Melanoides tuberculata* JOS | Restricted to a very few sites |
| Guadeloupe | | |
| 1969 | *Helisoma duryi* | Restricted to a very few sites (artificial tanks and Grand Etang Lake) |
| Around 1970 | *Physa acuta* | Widely distributed (invasion in progress?) |
| 1973 | *Marisa cornuarietis* | Widely distributed in ponds of Grande-Terre. Invasion in progress in marshes |
| 1979 | *Melanoides tuberculata* PAP | Widely distributed |
| 1984 | *Melanoides tuberculata* GOS | Widely distributed |
| 1984 | *Melanoides tuberculata* FAL | Restricted to a few sites |
| 1985 | *Biomphalaria kuhniana* | Widely distributed in Grande-Terre. Restricted to a few rivers in Basse-Terre |
| 1986 | *Melanoides tuberculata* MAD | Restricted to a few sites |
| 1997 | *Pseudosuccinea columella* | Widely distributed in Grande-Terre. Invasion in progress in Basse-Terre |
| 2000 | *Tarebia granifera* | Restricted to few ponds of Grande-Terre. Invasion in progress in Basse-Terre since 2007 |

(continued)

**Table 9.1** (continued)

| Introduction year | Alien species | Present status |
|---|---|---|
| 2002 | *Indoplanorbis exustus* | Introduced to a single pond. Species not collected after 2004. Example of an invasion failure |
| 2008 | *Gyraulus chinensis* | Restricted to some oxbow lakes in Basse-Terre |

Morphs of *Melanoides tuberculata* have names based on a three-letter code. CPF is an hybrid between FAL and PAP, and FDF between FAL and PDC (see Samadi et al. 1999)

(Pointier and Théron 2006; see Fig. 9.10). In Guadeloupe, the situation is quite different. *B. kuhniana* has invaded numerous ponds of Grande-Terre from 1985 on and is now a major component of malacological communities in this area. Thiarids reach insufficient abundance in most temporary ponds to eliminate *B. kuhniana*. In contrast, *B. kuhniana* seems to have much more difficulty in invading streams and rivers of the Basse-Terre Island, probably because these habitats were already widely occupied by thiarids. In the 1970s, this island harbored the largest foci of intestinal schistosomiasis and huge populations of the snail host *B. glabrata* (Théron and Pointier 1995). In the last several decades, *B. glabrata* has strongly regressed from Basse-Terre following the invasion by thiarids and the elimination of numerous canals that had become useless. It is currently restricted to a few sites such as Vieux Fort pool in the Northern part of the island (authors' unpublished data). In Grande-Terre, the situation depends on the type of aquatic environment. As already pointed out, a phenomenon of metapopulation collapse was observed for *B. glabrata* in ponds (see the first paragraph on field experiments using *M. cornuarietis*). The situation is quite different in the marshy forest zone located behind mangrove swamps (see above). The impact of the introduction of alien species, such as *M. tuberculata* or *P. columella* upon *B. glabrata* populations, was apparently limited and this aquatic environment may be considered as a refuge for the planorbid snail. A consequence is the persistence in this area of an active focus of schistosomiasis transmission. This situation might change with the recent arrival of *M. cornuarietis* in some of these sites (authors' unpublished data). To summarize, unassisted snail species introductions in Martinique and Guadeloupe have reproduced at a larger scale the results of field experiments: introduced species have been instrumental in reducing populations of schistosome-transmitting snails (*Biomphalaria spp.*) in the habitats that were massively invaded, such as streams and rivers in which thiarids snails literally thrive. This resulted in the regional collapse of *Biomphalaria spp*. populations in Martinique and Basse-Terre where these habitats are dominant. However, the impact of alien species has been more limited in some specific habitats (marshy forest in Guadeloupe) where invasive snails did not outcompete local ones, and where they now coexist with *B. glabrata*.

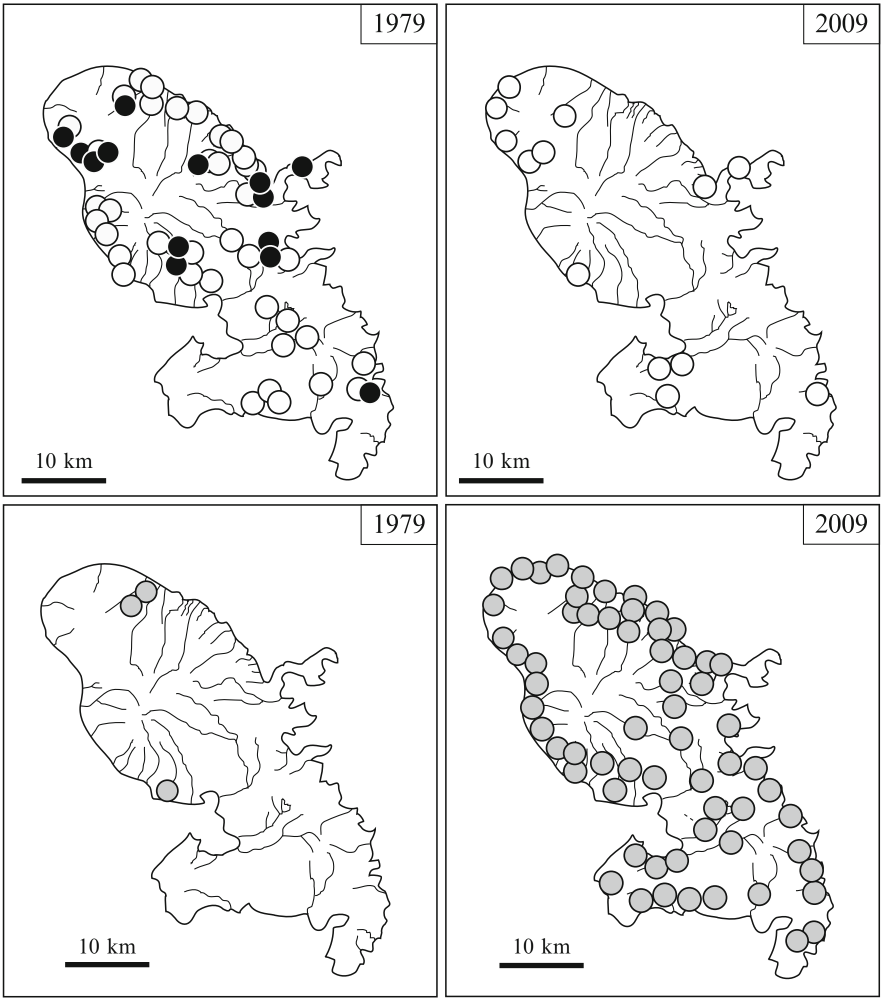

**Fig. 9.10** *Top*: distribution of *Biomphalaria glabrata* (*black circles*) and *Biomphalaria kuhniana* (*white circles*) in 1979 and 2009 in Martinique. *Bottom*: distribution of thiarid snails (*gray circles*) in 1979 (introduction time) and 2009

## 9.5 Freshwater Snail Invasions: Threats for Environment and Biodiversity?

We have so far described the effects of exotic snail introductions (whether unassisted or done on purpose) on schistosome-transmitting snails, and found that introduced competitors have been the most powerful cause of decline of the latter, especially *B. glabrata*. However, assessing the overall cost-benefit balance of snail introductions requires considering the threats that introduced snails pose to biodiversity and environment. Two types of threats can be considered (we do not consider herein the economic costs entailed by the introduction of apple snails, especially in Asia, since they are unrelated to *Biomphalaria* species; see Cowie 2002 for a review): the first is that introduced species may carry new parasites, especially trematodes parasitizing humans or domestic animals; the second is that they may alter competitive or predator–prey equilibria in such a way that extinctions of local species occur, and species diversity or genetic diversity decrease in native communities and taxa.

On the first aspect, several species belonging to the genus *Biomphalaria* can be considered as invasive in different parts of the world, and this is of particular importance since they are involved in the transmission of *S. mansoni*. An example is the accidental introduction to Egypt of *B. glabrata*, the best snail host for this parasite, originally restricted to the Neotropical area (around 1981; Pflüger 1982). During the following years, *B. glabrata* invaded the irrigation and drainage systems of the Nile Delta area (Yousif et al. 1996) and hybridized with the local *B. alexandrina* (Kristensen et al. 1999). This hybrid was also found naturally infected with *S. mansoni* suggesting that it played a role in the parasite transmission (Yousif et al. 1998). A recent extensive survey failed to detect any *B. glabrata* or hybrids (Lofty et al. 2005). The application of molluscicides in most of the putative *B. glabrata* localities by the Egyptian Snail Control Section may explain this absence.

*B. straminea* is also of Neotropical origin, but it has increased its distribution to such an extent over the last few decades that it can be considered, together with *Physa acuta*, as the most invasive mollusc species. It has invaded several Brazilian States as well as new habitats in Paraguay, Argentina and Uruguay (Paraense and Corrêa 1989; Paraense 2001; Teles et al. 2003). Despite its low susceptibility to *S. mansoni, B. straminea* is presently heavily involved in the transmission of schistosomiasis in numerous sites from North-Eastern Brazil (Carvalho 1992). In the Caribbean area, the introduction of *B. kuhniana* (a member of the *B. straminea* complex) was reported in Colombia in 1966 (Barbosa 1968), in Costa Rica in 1976 (Paraense et al. 1981), as well as in several islands of the Lesser Antilles, including Martinique around 1950 (Grétillat 1967), Grenada in 1970 (Ferguson and Buckmire 1974), Guadeloupe in 1985 (Pointier et al. 1993a) and St Lucia in 1992 (Pointier 1993). Intestinal schistosomiasis was already occurring in most of these islands with *B. glabrata* as intermediate host, and the role of *B. kuhniana* in parasite transmission has never been clearly established except in Martinique (WL Paraense, pers. comm.). Outside the Neotropics, *B. straminea* was introduced to Hong Kong in 1973 (Meier-Brook 1974) and then began to colonize the adjacent territories (Yipp 1990). The study of Tang (1983) did not reveal the presence of trematodes infecting *B. straminea* in the invaded habitats. The Neotropical *Biomphalaria tenagophila* has a more restricted distribution area than *B. glabrata* and *B. straminea*. However, this snail was recently introduced to Africa where it colonized the Kinshasa area, Democratic Republic of Congo and was responsible for the creation of a new focus of intestinal schistosomiasis (Pointier et al. 2005a).

Another trematode parasite, the liver fluke *Fasciola hepatica*, was introduced to the New World over the last 400 years through cattle importation. Recent studies have demonstrated that the snail host *Lymnaea truncatula* was also introduced to several South American countries and was responsible for parasite transmission to humans (Jabbour-Zahab et al. 1997; Pointier et al. 2009). Another lymnaeid species, *P. columella* also has a successful history of introductions and is now one of the most widespread freshwater snails worldwide (in tropical as well as in temperate countries). It occurs in a large fraction of ponds in Guadeloupe (Pointier 2008). This species can also serve as intermediate host for the liver fluke. Fascioliasis has never been reported in Guadeloupe, but the current presence of *P. columella* must be considered as a serious threat.

*M. tuberculata* may also serve as intermediate host for numerous trematodes infecting wild animals. It is also the snail host of *Centrocestus formosanus*, the parasite responsible for a food-borne intestinal infection in Asia. The source of infection for humans is freshwater fish (when eaten raw or improperly cooked). This parasite was introduced to Oaxaca State, Mexico (Amaya-Huerta and Almeyda-Artigas 1994). More recently, *C. formosanus* was discovered in Medellín, Colombia with a prevalence of 73% in the snail host *M. tuberculata* (Velásquez et al. 2006).

From these examples, we see that the increased rate of biological invasion over the last few decades has both positive and negative effects on parasite transmission to humans: while host snails have been outcompeted by invasive species in some regions (such as Guadeloupe and Martinique), other regions have been invaded by susceptible snails. This resulted in new foci of parasitic transmission, sometimes with dramatic sanitary consequences (e.g., liver fluke transmission in the Altiplano region).

The second threat deriving from the introduction of exotic snails is their potential impact on native biodiversity. Generally, this impact appears to have been very modest. Strikingly, we are aware of no example of local snail species that became extinct at a regional scale following invasions by exotic freshwater snails, to the exception of *B. glabrata* in Martinique and probably in St Lucia ("welcome" extinctions, considering that the relictual populations of *B. glabrata* were associated with the last foci of schistosome transmission). Because of the absence of extinctions, the two aquatic snail communities that have been followed in most detail (Guadeloupe and Martinique) experienced a steady increase in snail biodiversity with the accumulation of exotic species (see Figs. 9.7 and 9.9). This is because of the diversity of habitats that offer gradients from temporary to permanent, from lotic to lentic, and from easily accessible to completely isolated habitats. As already mentioned, local pulmonate species are adapted to more or less rapidly colonize the habitats created by occasional changes in water level. Different species will occupy different positions in this spatial and temporal mosaic, and it appears that these habitats are not collectively saturated in terms of pulmonate diversity, at least in islands such as Guadeloupe and Martinique. Moreover, these islands were initially mainly devoid of benthic caenogastropods (the only important species were the ampullariid *P. glauca* and the neritids *Neritina punctulata* and *Neritina virginea*). This group had no obvious effect on either *P. glauca,* or *Neritina* spp. Thiarids can occur in both rivers and permanent ponds where they might potentially compete with virtually all resident species. Several pulmonate species (including *B. glabrata* and *B. kuhniana*) have decreased following the invasion of thiarids, but have been able to escape extinction whenever they were able to occupy unstable habitats unfavorable to thiarids. The rarity of such habitats in Martinique may explain why *B. glabrata* did go extinct there. In fact, the most intense competitive interactions occur among introduced species (or strains of *M. tuberculata*) with similar ecologies. For example, the invasion of *T. granifera* in Martinican rivers, and later that of the MA strain of *M. tuberculata*, drastically impacted the other strains of *M. tuberculata*, leading one of them (FDF) to extinction, and several others (FAL and CPF) became rare. It is possible that species diversity might be adversely affected in countries where the diversity of indigenous thiarids and other benthic caenogastropods would not be as low as in Guadeloupe or Martinique. For example, Genner et al. (2004) showed that the diversity of endemic thiarids in the Great African Lakes could be threatened by the invasion of Asian strains of *M. tuberculata*. Similar threats are expected wherever thiarid diversity exists, such as in the Greater Antilles or continental South America where numerous endemic *Hemisinus, Aylacostoma* and *Pachychilus* occur (Pointier et al. 2005b; Simone 2006). Studying such situations in details through temporal surveys would certainly bring clearer answers.

Another lesson from the history of aquatic snail invasions in the Lesser Antilles is that invasive populations should not be regarded as genetically depauperate. Owing to many successive introductions, the *M. tuberculata* populations in Martinique and Guadeloupe have indeed accumulated high levels of genetic diversity, in terms of both genetic variation and ecologically important traits (Facon et al. 2008). Remarkably, rare sexual events between introduced lines give rise to natural hybrids (FDF and CPF) which to our knowledge do not occur anywhere else in the world. These hybrids strikingly differ from their parents in both morphology and life history, and have locally outperformed them (Facon et al. 2005). This story illustrates that invasions can sometimes be evolutionarily creative. Yet the long-term balance of invasions is difficult to establish, especially in the Lesser Antilles. The apparent absence of extinctions may mask ongoing declines of local species leading to future extinctions, especially if new invaders continue to appear year after year.

## 9.6 Concluding Remarks

There is little doubt that both voluntary introductions within biological control programs and unassisted invasions are strongly associated with the general decline of populations of schistosome-transmitting snails (*B. glabrata*) in several places, especially the Caribbean area, over the last several decades. However, very different results have been reported at the local level depending on the species involved, certainly resulting from a wide diversity of ecological situations. In this respect, the *B. glabrata* model in the Caribbean area seems to be exemplary, as it encompasses a variety of freshwater habitats and eco-epidemiological situations from small-scale insular systems (Lesser Antilles) to large-scale continental systems (Venezuela, Brazil). In general, the impact of exotic snail introductions on freshwater biodiversity has been moderate until now, although this does not mean that it will remain so in the decades to come.

Species introductions, whether voluntary or unassisted, come with another potential risk, namely, the establishment of new transmission foci, for example, schistosomiasis and fasciolosis. Several examples have been provided above calling for scrutiny whenever a new potential host is detected somewhere.

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