# Introduction and spread of *Thiara granifera* (Lamarck, 1822) in Martinique, French West Indies

# J. P. POINTIER

Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne, Laboratoire de Biologie Marine et Malacologie, EPHE, UMR 5555 du CNRS, Université de Perpignan, 52 avenue de Villeneuve, 66860, Perpignan, France

# S. SAMADI and P. JARNE

Génétique et Environnement, CC065, Institut des Sciences de l'Evolution, UMR 5554 du CNRS, Université Montpellier II, Place Bataillon, 34095 Montpellier cedex 5, France

# B. DELAY

CEFE-CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

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We followed the invasion dynamics of the Oriental thiarid snail *Thiara granifera* on the Martinique island, French Antilles. This freshwater species was first discovered in 1991 in the Charpentier River, and its spread has since been analysed based on a yearly survey of the malacological fauna at more than 100 sites covering the whole island and representing 50 river systems and three pools. Four river systems were sampled at many sites. Thirteen river systems were colonized by 1997. Colonization within river systems occurred at a speed greater than 1 km per year, probably resulting from both active and passive dispersal. Our results can, on the whole, be explained by a simple diffusion process. However, stratified diffusion has to be invoked in at least one river. Moreover, colonization was faster downstream than upstream, suggesting that current velocity plays a significant role in dispersal. Dispersal also occurred between river systems at a mean distance of almost 10 km, though with a large variance, in accordance with the scattered colony model of stratified diffusion. The relative frequencies of T. granifera and Melanoides tuberculata, another recent invader of Martinique, were followed at three sites on the Lézarde River. The first species quickly outnumbered the second, though never wiped it out. The data therefore do not support any exclusion phenomena between these two parthenogenetic invaders. Our analysis does not indicate any obvious influence of the rise of T. granifera on the local freshwater fauna.

Keywords: invasion; stratified diffusion; Martinique; freshwater snails; biological control; Thiaridae; Thiara granifera; Melanoides tuberculata.

## Introduction

Biological invasions have been on of the serious biological consequences of human activities. Their influence on local biodiversity is sometimes catastrophic, leading to extinction of local species. For example, the introduction of the land snail *Euglandina rosea* in French Polynesia was followed by the extinction of several *Partula* species (Tillier and Clarke, 1983; Tillier, 1992; Civeyrel and Simberloff, 1996). The dynamics of invasions have been detailed through a series of examples (review in Drake *et al.*, 1989; Shigesada and Kawasaki, 1997). Two broad models have been proposed and detailed analytically. The first one assumes that invasion occurs at a single site, and then diffuses through space at a rate depending on the local intrinsic rate of increase of populations and the diffusion coefficient (measuring the rate of dispersal). The second assumes in addition long-distance dispersal, and diffusion is then termed stratified (Shigesada and Kawasaki, 1997, Chapter 3). The basic model assumes a homogeneous and infinite environment. However, heter-ogeneous or finite environments are mathematically tractable in some cases, even if few such empirical examples have been studied in detail.

Along this line, we consider here the example of the invasion of a freshwater environment (typically heterogeneous) within a tropical island (finite) by a snail species. Drought and floods, which are prominent factors shaping freshwater environments in the tropics, have been viewed as important factors in snail migration (Jarne and Städler, 1995); the study of the invasion process may then help to clarify the role of these factors, as well as those due to human activities (passive dispersal) and active dispersal, after the initial introduction events, provided that the invasion process is thoroughly followed in time and space. If examples of invasions can be found among freshwater species, such as Potamopyrgus jenkensi (Doby et al., 1969) and Lymnaea truncatula (Jabbour-Zahab et al., 1997), such a thorough analysis has been conducted in very few instances, the best example being the thiarid Melanoides tuberculata (Pointier et al., 1993). This study focuses on the tropical freshwater prosobranch Thiara granifera (Lamarck, 1822), a native to Southeast Asia and now with a world-wide distribution. It was introduced into the New World in Lithia Spring, Florida, USA, around 1940 by an aquatic-plant and fish dealer (Abbott, 1952). At the same time, established populations of this species were recorded at several sites in Texas and Florida (Murray, 1964; Murray and Wopschall, 1965). In the following years, Harry and Aldrich (1958) reported its introduction to Puerto-Rico and Vieques. It then spread quickly throughout the whole Caribbean area: the Dominican Republic was reached in 1967, and Grenada, Cuba and Venezuela in 1970 (Jaume, 1972; Chrosciechowski, 1973; Ferguson, 1977).

Regular sampling of the freshwater snail fauna has been carried out in Martinique for more than 25 years (Guyard and Pointier, 1979; Guyard *et al.*, 1983; Pointier *et al.*, 1989, 1993). As a consequence, a significant set of data has been gathered on the introduction, spread and distribution of several foreign freshwater snails. For instance, three distinct morphs of the Oriental thiarid *Melanoides tuberculata* as well as the Australian planorbid *Amerianna carinata* were introduced over the last two decades (Starmühlner, 1984; Pointier, 1989, 1996; Pointier *et al.*, 1992). In 1991, *T. granifera* was discovered for the first time in Martinique in the Charpentier River. The origin of this introduction is unknown but probably linked, as in the United States, to the aquatic-plant and fish trade. Sampling has since been conducted in 50 river systems, covering the whole hydrographic system of the island. Some rivers were sampled at several sites. Our objectives were: (i) to follow the colonization of *T. granifera*, both within and between rivers, and relate it to current models of invasion; and (ii) to evaluate the consequences of this invasion on the local freshwater molluscs, including the previous invader *M. tuberculata*.

#### Methods

Martinique is a small volcanic island of the Lesser Antilles with numerous streams and rivers, most of which are permanent, and characterized by short and rocky watercourses

descending rapidly from the mountains. The upper stretches located in the rain forest constitute very poor habitats and harbour very few freshwater snails. On the other hand, several species can be found in the lower course of rivers. Several malacological surveys have been conducted in Martinique between 1972 and 1986 in the lower course of all rivers as well as in other aquatic habitats such as ditches, springs or ponds (Guyard and Pointier, 1979; Guyard *et al.*, 1983). More regular surveys have been conducted since 1986, with about 60 sites sampled per year at the end of the dry season in March or April. Numerous sites located along the same watercourses have been added to the annual surveys since 1994, increasing the total number of sampling sites to 109. In four river systems (Lézarde, Galion, Pilote and Simon), several sites have been sampled along the main river and its tributaries.

At each site, snails (T. granifera, as well as M. tuberculata; see below) were handcollected by one or two persons over a period of 10–20 minutes. The taxonomic status was ascertained visually (see Pointier, 1989), and all snails were then preserved in 70% ethanol. Thiara granifera was recorded for the first time in 1991. Extensive surveys, especially in the four river systems cited above, allowed its subsequent spread to be followed. The speed of spread within a river system was estimated as the distance separating newly invaded sites from one year to the next. This distance was measured on a map (1:25 000, IGN map). In the Lézarde River, T. granifera was introduced (at least) twice (in 1992 and in 1996). The second introduction was not considered when estimating the speed of spread, because it may have resulted from passive transport from the lower parts of the same river, or from another site. Two distances were estimated to analyse dispersal between river systems. We first calculated the minimum dispersal distance for each newly colonized river system (d) as the smallest distance between this river at year i and all sites colonized at year i - 1. This obviously underestimated the actual dispersal distance. Secondly, we calculated the maximum possible dispersal distance for each year  $(d_{max})$  and the whole island as follows: using the distribution of the minimum distance between all colonized rivers and a free river,  $d_{\text{max}}$  is the largest of these distances each year.  $d_{\text{max}}$  decreases with time as increasing areas are colonized. It should be noted that  $d_{\text{max}}$  is estimated prior to sampling, while d is estimated after sampling on a given year.

We have already pointed out that the rivers on Martinique have also been invaded by another thiarid snail, M. tuberculata, over the last two decades. This species has often been confused with T. granifera (see Ferguson, 1977; Prentice, 1983; Gomez et al., 1986). Typically, the shells of T. granifera have axial and spiral sculptures which give rise to tubercles (Fig. 1A). The body whorls are flat and the height of the aperture is more than half that of the total height of the shell. Shells of *M. tuberculata* are more elongated and the height of the aperture is always less than half of the total shell height. In addition, the body whorls are more or less rounded with spiral grooves and more or less marked axial ribs. This species also exhibits a substantial shell polymorphism. For example, several morphs have been distinguished in the French West Indies, based on the type of ornamentation and sculptures (Fig. 1B, C, D; Pointier, 1989). Some of these morphs, especially those with well marked axial and spiral sculptures, may be confused with T. granifera (Prentice, 1983; Gomez et al., 1986). On the other hand, little conchological variation has been observed in this latter species. The consequences of T. granifera invasion has been observed in this latter species. The consequences of T. granifera invasion upon the recently established populations of M. tuberculata have been estimated by following the frequency distributions of the two species, every year



Figure 1. Shells of *Thiara granifera* (A) and *Melanoides tuberculata* (B) MAD morph; (C) PAP morph; (D) FAL morph, from Martinique.

since 1991, at three sites located along the Lézarde River (Glotin, Désirade and Soudon, see Fig. 2).

#### Results

Thiara granifera was first observed in the Charpentier River on the northeastern coast of Martinique in 1991 (Fig. 3). It was recorded in 1992 at two sites along the Lézarde River. The number of river systems colonized from 1991 to 1997 were then 1, 2, 2, 8, 10, 12 and 13 (out of 50). Colonization was fast within each river system, as illustrated by the distribution of snails in the Lézarde River (Fig. 4): two sites were occupied in 1992, and upstream migration was observed during the following years. The whole river system was still not colonized by 1997. As mentioned above, a second introduction of *T. granifera* occurred in the upper part of this river in 1996 and was not considered in our estimate of spread speed. In the Lézarde, Galion, Pilote and Simon river systems, the average speed of spread was 1277 m year<sup>-1</sup> (range = 0-5175 m; sD = 1501; n = 26). However the upstream speed of spread (mean = 753 m year<sup>-1</sup>; range = 0-3725 m; sD = 1151; n = 17) significantly differed from the downstream one (mean = 2267 m year<sup>-1</sup>; range = 0-5175 m; sD = 1646; n = 9) as assessed by a Mann-Whitney test (U = 34, p = 0.022). Of these four rivers, only the Simon river was fully occupied by 1997.

The average minimum dispersal distance for newly colonized river systems (d) was equal to 8.6 km (range = 1.7-18.7 km; sD = 6.6; n = 12). The average d value per year is given in Table 1, together with the maximum possible dispersal distance per year ( $d_{max}$ ). Both values decreased with time, though more markedly for the latter.

Mixed populations of *M. tuberculata*, comprising both the morphs MAD and PAP (see Fig. 1B and C), were detected at the three sites studied in the Lézarde River. *Thiara* 



**Figure 2.** Frequency distributions of *Thiara granifera* (black) and *Melanoides tuberculata* (three morphs taken together, white) at three sites sampled along the Lézarde River.

granifera was the most abundant species from 1993 to 1995. However, its frequency decreased in 1996 and 1997 (Fig. 2).

#### Discussion

1991 may reasonably be considered as the year of introduction of *T. granifera* in Martinique based on regular sampling of snails over the whole island from 1986 onwards (Pointier *et al.*, 1993). As observed in Florida (USA) by Abbott (1952), this introduction is probably the consequence of the trade in aquatic plants used in aquariophily. This activity has indeed significantly increased over the past decades in the French West Indies. The



**Figure 3.** Introduction and colonization of the hydrographic system of Martinique by *Thiara* granifera. White circles: sampled water bodies; black circles: water bodies colonized by *T. granifera*. 1, Charpentier River; 2, Marigot River; 3, Sainte-Marie River; 4, Epinette River; 5, Galion River; 6, Blanche River; 7, Lézarde River; 8, Perriolat River; 9, Pilote Little River; 10, Pilote River; 11, Moulin l'Etang Pond; 12, Lorrain River; 13, Saint-Jacques River; 14, Pont de la Digue River; 15, Latouche River; 16, Simon River.

spread of *T. granifera* in Martinique was very fast. This is in line with field observations made in Puerto Rico between 1964 and 1969 demonstrating the capacity of this species to colonize rapidly many types of habitats and thereafter form dense populations (Chaniotis *et al.*, 1980).

With respect to within-river colonization, rivers are continuous one-dimensional environments and therefore are well suited for analysing colonization as a diffusion process. In the basic diffusion model, under which colonization occurs at a single site and is followed by a diffusion of the invaders, the speed of spread is determined by both the local intrinsic rate of population increase and the diffusion coefficient (assuming no interspecific competition; Shigesada and Kawasaki, 1997, Chapter 2). We have no estimate of these two values. However, one at least should be very high in order to explain the extremely fast spread of T. granifera. Both the parthenogenetic reproduction of T. granifera and the extremely high densities of individuals observed during one regular surveys (peaking at hundreds of individuals per m<sup>2</sup>) are certainly compatible with a high rate of increase. The space available to T. granifera within the four rivers studied has been occupied extremely quickly, and is already saturated in the Simon River. As already mentioned, the upper parts of rivers in Martinique constitute a hostile environment for most snails, being too poor in nutrients, especially calcium and periphyton. Our data also indicate that colonization proceeds downstream much faster than upstream. This suggests that the natural river flow is a favouring factor in the colonization process. However, upstream colonization, probably through active crawling, is not prevented at all by downstream currents,

**Figure 4.** Occurrence of *Thiara granifera* along the Lézarde River system from 1992 to 1997. White circles: sampled sites along the river and its tributary; black circles: sites colonized by *Thiara granifera*. 1, Sainte Céline; 2, Rivière Lézarde; 3, Morne Vaudin; 4, Saint-Etienne; 5, Glotin; 6, Grande Trace; 7, Saint-Maurice; 8, Désirade; 9, Soudon; 10, Presqu'île; 11, La Charmille; 12, Choco; 13, Goureau; 14, Bouliki.



Year	1992	1993	1994	1995	1996	1997
d	16	0	9.6	10.4	8.6	1.7
	(1)	(0)	(6)	(2)	(2)	(1)
$d_{\rm max}$	42	26.5	26.5	18.5	16	13

**Table 1.** Minimum dispersal distance for newly colonized river systems (d) and maximum possible dispersal distance per year ( $d_{max}$ ) are given in km for each year of sampling. d is given together with the number of colonization events (in parenthesis) upon which it was estimated

as long as the upper parts of the rivers are not reached. Our results directly prove that migration may be an active process in freshwater snails, and is correctly considered in models of population biology, especially population genetics (Jarne and Städler, 1995). However it should be modelled as an asymmetric process.

It should be mentioned that our analysis is too crude in both space and time (or the spread was too fast) to follow the details of the spread. For example, invasions often begin with a phase during which the invasive species remains at a very low density (see Shigesada and Kawasaki, 1997, Chapter 2). Whether such an establishment phase occurred during the *T. granifera* invasion is hard to tell from our data. However, the analysis is precise enough to show that the basic diffusion model may not always be appropriate.

Long-range dispersal indeed occurred in the Lézarde river, suggesting that within-river colonization may follow a stratified model (see Shigesada and Kawasaki, 1997, Chapter 5). It is, however, not clear whether long-range dispersal involved individuals from the Lézarde river only.

Colonization also involved dispersal between rivers (we assume a single, or a few, introductions in Martinique). Our results indicate that, on average, more than two river systems have been colonized per year since the introduction of *T. granifera*. The variance is, however, quite large, with no river colonized in 1993 and six the following year. Only a quarter of the rivers were colonized by 1997, and the western part of Martinique remains poorly occupied (Fig. 3), suggesting that space is saturated unevenly. The average minimum dispersal distance for newly colonized river systems (*d*) was quite large (almost 10 km), given that sites in our study are not separated by more than 60 km. Of course, *d* decreases with time, as a consequence of spatial saturation. In a finite environment such as an island, the decrease of *d* with time is larger when its initial value is high. Similarly, the maximum possible dispersal distance per year ( $d_{max}$ ) decreases with time, as the environment is saturated.

These results clearly indicate that the colonization of Martinique by *T. granifera* follows a model of stratified diffusion, including long-range dispersal and therefore fits the scattered colony model (see Shigesada and Kawasaki, 1997, pp. 80–85). Long-range dispersal of snails requires agents of dispersion. It may result from the movements of birds (Boag, 1986) or mammals (Madsen and Frandsen, 1989), or may be mediated through human activities. The very high density of human populations and the heavy traffic through a well-developed road network may constitute preponderant factors. We finally note that models of colonization have been developed to cope with heterogeneous environments, that is environments in which the intrinsic rate of increase of the invader varies. Freshwater species represent an extreme case, with environments in which life is possible (rivers, ponds, etc.) and all others in which it is impossible. Including such environments and a

finite space in a single model of colonization with stratified diffusion needs to be undertaken, if we want to understand more clearly the dynamics of *T. granifera* in Martinique.

Up to now, we have assumed that T. granifera invaded Martinique without any competitive interactions with other species. However, our surveys have also provided data on the consequences of the introduction and spread of T. granifera on other components of the freshwater fauna. First, there is clear influence on the distribution of another recent colonizer of Martinique, M. tuberculata. At the three sites that were specifically followed to analyse the distribution of both species. T. granifera became quickly dominant in number. We note however that its frequency decreased in 1996 and 1997. Our long-term studies will indicate whether there is a tendency towards a quasi-stationary distribution of the two species. The situation in Martinique is similar to that observed in the rivers of the littoral central region of Venezuela where M. tuberculata appeared in 1972, together with T. granifera (Chrosciechowski, 1973). A malacological survey conducted 20 years later showed that the density of T. granifera was much higher than that of M. tuberculata. Why should T. granifera outnumber M. tuberculata? The simple models of colonization show that the frequencies of two interacting species depend on their intrinsic rate of increase and the coefficient of diffusion (Shigesada and Kawasaki, 1997, Chapter 6). As mentioned above, we have little idea of the values of these parameters. However they might be lower for *M. tuberculata* than for *T. granifera*, because the latter is better able to resist currents. Indeed, M. tuberculata occurs along the banks in rapidly flowing rivers, whereas T. granifera is distributed over the whole river bed, suggesting that this latter species can support faster currents. Tropical rivers are often submitted to flooding, in which case T. granifera may be more able to resist dislodgement. In quieter rivers, a more contrasted distribution is observed, suggesting that interspecific competition occurs between species (Pointier et al., 1994). A similar distribution was observed when studying two morphs of *M. tuberculata* in the Lézarde River in Martinique. Competition seems here to occur at the infraspecific level (Samadi et al., 1997).

Secondly, we mentioned above that T. granifera quickly invaded Puerto Rico in the 1960s. As a consequence, populations of *Biomphalaria glabrata*, one of the intermediate snail hosts of schistosomes, were strongly limited, or even excluded (Butlers et al., 1980). In Martinique, the malacological situation when T. granifera arrived in 1991 was quite different from that of Puerto Rico. Several morphs of *M. tuberculata* had already colonized the whole hydrographic system for more than ten years and already strongly limited the local populations of B. glabrata and B. straminea, both of which are involved in schistosomiasis transmission (Pointier et al., 1989; Pointier and Guyard, 1992). It is difficult to evaluate the influence of the introduction of T. granifera on these two species, and therefore as a possible agent in the biological control of schistosomiasis. T. granifera, as well as other thiarid species (e.g. M. tuberculata), may influence other components of the malacological fauna. However, few studies have been conducted on their impact on local species other than *Biomphalaria* spp. and especially on other prosobranch snails. Murray (1971) indicated that Goniobasis comalensis, an endemic mollusc of Texas, became extremely rare in New Braunsfels, following the spread of thiarids. In Florida, Roessler et al. (1977) found *M. tuberculata* together with *Neritina virginea* in a mangrove swamp of Florida and noted possible competition between the two species. M. tuberculata was found in Lake Yojoa (Honduras) in 1980 together with dense populations of *Biomphalaria ha*vanensis and Pachychilus largillierti. Five years later, M. tuberculata became dominant throughout the lake and both local species became very rare (Clarke, 1987). In Martinique, five other prosobranch species are present in the rivers: *Pomacea glauca* (Ampullariidae), *Nerililia succinea, Neritina virginea, N. punctulata* (Neritidae) and *Potamopyrgus parvulus* (Hydrobiidae). No apparent exclusion can be noted 18 years after the first records of thiarids, and populations of ampullarid and neritid snails are commonly encountered together with thiarid snails. With respect to *P. parvulus* the situtation is more difficult to evaluate because this species was not very common in Martinique before the introduction of thiarids (Guyard and Pointier, 1979) and a specific survey would be necessary in order to ascertain the present situation.

The introduction of a species also opens the possibility of introducing new diseases or parasites (see Drake *et al.*, 1989; Shigesada and Kawasaki, 1997). Freshwater snails are intermediate hosts for a series of human-infecting parasites, including numerous trematodes of large economic impact (see Brown, 1994). It has been asserted that *T. granifera* may act as intermediate host of *Paragonimus westermanii* (Abbott 1952; McMullen, 1973), casting some doubts on the use of this species to control schistosome vectors. However, Michelson (1992) argued that these assertions are based on scanty empirical evidence. It is therefore unlikely that the spread of *T. granifera* leads to paragonomiasis transmission. Moreover, we have not been able to detect trematodes in *M. tuberculata* individuals from Martinique (Pointier and Delay, unpublished data), showing that parasites are not systematically introduced with their hosts. In addition a size-specific predation by the prawn *Macrobrachium lar* upon *T. granifera* has been recorded in some streams from Guam island, South Pacific (Camacho and Nelson, 1997). However, in Martinique, predation seems limited to birds and rats and no malacophagous fishes or crustaceans have been encountered in the rivers. These aspects deserve further empirical evaluation for *T. granifera*.

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## References

- Abbott, T.T. (1952) A study of an intermediate snail host (*Thiara granifera*) of the oriental lung fluke (*Paragonimus*). *Proceedings of the United States National Museum*, **102**(3292), 71–116.
- Boag, D.A. (1986) Dispersal in pond snails: potential role of waterfowl. Can. J. Zool. 64, 904-9.
- Brown, D.S. (1994) Freshwater snails of Africa and their medical importance, 2nd edn. London: Taylor & Francis, 608 pp.
- Butlers, J.M., Ferguson, F.F., Palmer, J.R. and Jobin, W.R. (1980) Displacement of a colony of *Biomphalaria glabrata* by an invading population of *Tarebia granifera* in a small stream in Puerto Rico. *Carib. J. Sci.* 16, 73–9.
- Camacho, F and Nelson, S. (1997) Size-specific predation by the Tahitian prawn *Macrobrachium lar* on the freshwater snail *Thiara granifera*. *Pacific Science Inter-Congress*, Suva, 11.
- Chaniotis, B.N., Butlers, J.M., Ferguson, F.F. and Jobins, W.R. (1980) Bionomics of *Tarebia granifera* (Gastropoda: Thiaridae) in Puerto Rico, an asiatic vector of *Paragonimus westermani*. *Carib. J. Sci.* **1R6**, 81–90.
- Chrosciechowski, P. (1973) Un caracol en busca de nueva residencia. El Lago 39, 813-14.

- Civeyrel, L. and Simberloff, D. (1996) A tale of two snails: is the cure worse than the disease? *Biodivers. Conserv.* 5, 1231–52.
- Clarke, A.H. (1987) Apparent competitive exclusion of *Biomphalaria havanensis* and *Pachychilus largillierti* by *Melanoides tuberculata* in a large Honduran lake. *First International Congress on Medical and Applied Malacology, Monterrey*, International Society for Medical and Applied Radiology Publishers, p. 24.
- Doby, J.M., Chabaud, A., Mandahl-Barth, G., Rault, B. and Chevallier, H. (1969) Extension en Corse du mollusque gastropode *Potamopyrgus jenkinsi* (Smith, 1889) (Hydrobiidae). *Bulletin du Museum National d'Histoire Naturelle* 37, 833–43.
- Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. and Williamson, M. (1989) *Biological Invasions. A global perspective.* SCOPE 37. New York: J. Wiley & Sons, 525 pp.
- Ferguson, F.F. (1977) *The role of biological agents in the control of schistosome-bearing snails*. US Department of Health Education and Welfare, Public Health Service, Centre for Disease Control, Bureau of Laboratories, Atlanta, Georgia 30333, 107 pp.
- Gomez, J.D., Vargas, M. and Malek, E.A. (1986) Freshwater mollusks of the Dominican Republic. *Nautilus* 100(4), 130–4.
- Guyard, A. and Pointier, J.P. (1979) Faune malacologique dulçaquicole et vecteurs de la schistosomose intestinale en Martinique (Antilles françaises). *Annales de Parasitologie* **54**(2), 193–205.
- Guyard, A., Pointier, J.P., Theron, A. and Dumoutier-Gilles, A. (1983) La bilharziose intestinale en Martinique en 1983. CRDP des Antilles et de la Guyane, 28 pp.
- Harry, H.W. and Aldrich, D.V. (1958) The ecology of *Australorbis glabratus* in puerto Rico. *Bull. World Health Organization* 18, 829–32.
- Jabbour-Zahab, R., Pointier, J.P., Jourdane, J., Jarne, P., Oviedo, J.A., Bargues, M.D., Mas-Coma, S., Angles, R., Perera, G., Balzan, C., Khallayoune, K. and Renaud, F. (1997) Phylogeography and genetic divergence of some lymnaeid snails, intermediate hosts of human and animal fasioliasis with special reference to lymnaeids from the Bolivian Altiplano. *Acta Tropica* 64, 191–203.
- Jarne, P. and Städler, T. (1995) Population genetic structure and mating system evolution in freshwater pulmonates. *Experientia* **51**, 482–97.
- Jaume, M.L. (1972) Nuevo género y especie de molusco fluvial para la fauna malacológica cubana (Gastropoda: Prosobranchia: Thiaridae). Circulares del Museo y Bibliotheca de Zoología de la Habana 1523–5.
- Madsen, H. and Frandsen, F. (1989) The spread of freshwater snails including those of medical and veterinary importance. *Acta Tropica* **46**, 139–46.
- McMullen, D.B. (1973) Biological and environmental control of snails. In *Epidemiology and control* of schistosomiasis, pp 533–91. Basel: Karger and Baltimore: University Park Press.
- Michelson, E.H. (1992) Thiara granifera: a victim of authoritarianism. Malacol. Rev. 25, 67-71.
- Murray, H.D. (1964) Tarebia granifera and Melanoides tuberculata in Texas. American Malacological Union, Incompany, 15–16.
- Murray, H.D. (1971) The introduction and spread of thiarids in the United States. *The Biologist* 53, 133–5.
- Murray, H.D. and Wopschall, L.J. (1965) Ecology of *Melanoides tuberculata* (Müller) and *Tarebia granifera* (Lamarck) in South Texas. *American Malacological Union, Incompany*, 25–6.
- Pointier, J.P. (1989) Conchological studies of *Thiara (Melanoides) tuberculata* (Mollusca: Gastropoda: Thiaridae) in the French West Indies. *Walkerana* **3**(10), 203–9.
- Pointier, J.P. (1996) An Australian planorbid freshwater snail recently introduced to the island of Martinique: Amerianna carinata (H. Adams, 1861). Haliotis 25, 25–31.
- Pointier, J.P. and Guyard, A. (1992) Biological control of the snail intermediate hosts of *Schistosoma mansoni* in Martinique, French West Indies. *Trop. Med. Parasitol.* **43**, 98–101.

- Pointier, J.P., Guyard A. and Mosser, A. (1989) Biological control of *Biomphalaria glabrata* and *B. straminea* by the competitor snail *Thiara tuberculata* in a transmission site of schistosomias in Martinique, French West Indies. *Ann. Trop. Med. Parasitol.* 83(3), 263–9.
- Pointier, J.P., Delay, B., Toffart, J.L., Lefevre, M. and Romero-Alvarez, R. (1992) Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. J. Mollusc. Stud. 58, 415–23.
- Pointier, J.P., Thaler, L., Pernot, A.F. and Delay, B. (1993) Invasion of the Martinique island by the parthenogenetic snail *Melanoides tuberculata* and the succession of morphs. *Acta Oecologica* 14(1), 33–42.
- Pointier, J.P., Incani, R.N., Balzan, C., Chrosciechowski, P. and Prypchan, S. (1994) Invasion of the rivers of the littoral central region of Venezuela by *Thiara granifera* and *Melanoides tuberculata* (Mollusca: Prosobranchia: Thiaridae) and the absence of *Biomphalaria glabrata*, snail host of *Schistosoma mansoni*. Nautilus 107(4), 124–8.
- Prentice, M.A., (1983) Displacement of *Biomphalaria glabrata* by the snail *Thiara granifera* in field habitats in St Lucia, West Indies. *Ann. Trop. Med. Parasitol.* **77**, 51–9.
- Roessler, M.A. Beardsley, G.L. and Tabb, D.C. (1977) New records of the introduced snail, *Melanoides tuberculata* (Mollusca: Thiaridae) in South Florida. *Florida Sci.* **40**(1), 87–94.
- Samadi, S., Balzan, C., Delay, B. and Pointier, J.P. (1997) Local distribution and abundance of thiarid snails in recently colonized rivers from the Caribbean area. *Malacol. Rev.* 30 (45–52).
- Shigesada, N. and Kawasaki, K. (1997) *Biological invasions: theory and practice*. Oxford: Oxford University press, 205 pp.
- Starmühlner, F. (1984) Occurrence, longitudinal distribution and geographical range of the fresh and brackish water molluscs of the Lesser Antillean islands (Guadeloupe, Dominica and Martinica). Soosiana 12, 83–102.
- Tillier, S. (1992) Introduced land snails in New Caledonia: A limited impact in the past, a potential disaster for the future. *Pac. Sci.* **46**, 396–7.
- Tillier, S. and Clarke, B.C. (1983) Lutte Biologique et destruction du patrimoine génétique: le cas des mollusques gastéropodes pulmonés dans les territoires français du Pacifique. *Génétique Sélection et Evolution* **15**, 559–66.

### Appendix

Sampling sites in Martinique

- 1 Briquetterie Pond
- 2 Vatable River
- 3 Pagerie River
- 4 Morne Blanc Pond
- 5 Fond Placide River
- 6 Pilote Little River at Baudelle
- 7 Pilote Little River at Mauny
- 8 Pilote Little River at Pont Madeleine
- 9 Pilote Little River at Rivière Pilote (no. 9 Fig. 2)
- 10 Pilote River at Rivière Pilote (no. 10 Fig. 2)
- 11 Pilote River at Lescouét
- 12 Pilote River at Cassis Germont
- 13 Canari Cassé River at Josseaud
- 14 Canari Cassé River at Canari Cassé
- 15 Massel River
- 16 Fond Repos River
- 17 Crève Coeur River
- 18 Vauclin River at Vauclin
- 19 Vauclin River at la Broue
- 20 Coulée d'Or River at la Baume
- 21 Coulée d'Or River at la Neveu
- 22 Simon River (no. 16 Fig. 2)
- 23 La Digue River
- 24 Perriolat River (no. 8 Fig. 2)
- 25 Saint-Pierre River at Usine
- 26 Saint-Pierre River at Rouchy
- 27 Saint-Pierre River at Baringhton
- 28 Saint-Pierre River at Lourdes
- 29 Saint-Pierre River at Sainte-Rose
- 30 Saint-Pierre River at la Roman
- 31 Saint-Pierre River at Morne Cabrits
- 32 Saint-Pierre River at La Beauville
- 33 Saint-Pierre River at Morne Caret
- 34 Saint-Pierre River at Bois Neuf
- 35 Saint-Pierre River at Fond Savanne
- 36 Manzo Lake at the outlet
- 37 Manzo Lake at the dam
- 38 Coulisses River at Petit Bourg
- 39 Coulisses River at Petit Fond
- 40 Grande Case River
- 41 Beauséjour River
- 42 Roussane River
- 43 Fond Coulisse River
- 44 Bonny River
- 45 Fond Nicolas River

- 46 Cacao River
- 47 Petite Rivière River
- 48 Galion River at Brevette
- 49 Galion River at Bassignac (no. 5 Fig. 2)
- 50 Galion River at Fond Moulin
- 51 Galion River at Sainte Luce
- 52 Galion River at Tamarin
- 53 La Tracée River at Desforts
- 54 La Tracée River at Birot
- 55 La Tracée River at Petite Tracée
- 56 La Tracée River at Dumaine
- 57 Lézarde River at Soudon (no. 7 Fig. 2)
- 58 Lézarde River at Désirade
- 59 Lézarde River at Saint Maurice
- 60 Lézarde River at Grande Trace
- 61 Lézarde River at Glotin
- 62 Lézarde River at Saint Etienne
- 63 Lézarde River at Morne Vaudin
- 64 Lézarde River at Rivière Lézarde
- 65 Lézarde River at Sainte Céline
- 66 Blanche River at Presqu'île (no. 6 Fig. 2)
- 67 Blanche River at la Charmille
- 68 Blanche River at Choco
- 69 Blanche River at Goureau
- 70 Blanche River at Bouliki
- 71 Gondeau River
- 72 Monsieur River
- 73 Madame River at Pont de Chaînes
- 74 Madame River at Desbrosses
- 75 Case Navire River
- 76 Fond Lahaye River at Fond Lahaye
- 77 Fond Lahaye River downstream of the dam
- 78 Fond Lahaye River upstream of the dam
- 79 Fond Lahaye River at Fond Duclos
- 80 Fond Bourlet River
- 81 Case Pilote River
- 82 Fond Capot River
- 83 Carbet River
- 84 Anse Latouche River (no. 15 Fig. 2)
- 85 Pointe la Mare River
- 86 Céron River
- 87 Lagarde River
- 88 Petel Canal
- 89 Basse Pointe River
- 90 Moulin l'Etang Pond (no. 11 Fig. 2)
- 91 Capot River at le Poteau

- 92 Capot River at Mackintosh
- 93 Capot River at Conserverie
- 94 Carrière Falaise Spring
- 95 Claire River at Rivière Claire
- 96 Claire River at Maxime
- 97 Grande Anse River at Fond Brûlé
- 98 Grande Anse River at Fond Grande Anse
- 99 Crochemort River
- 100 Fond Massacre River

- 101 Lorrain River (no. 12 Fig. 2)
- 102 Marigot River (no. 2 Fig. 2)
- 103 Charpentier River (no. 1 Fig. 2)
- 104 Saint-Jacques River (no. 13 Fig. 2)
- 105 Sainte-Marie River (no. 3 Fig. 2)
- 106 Numa River
- 107 Pont de la Digue River (no. 14 Fig. 2)
- 108 Baie de la Crique River
- 109 Epinette River (no. 4 Fig. 2)