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REVIEW ARTICLE

What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)?

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Abstract The spread of non-native species is one of the most harmful and least reversible disturbances in ecosystems. Species have to overcome several filters to become a pest (transport, establishment, spread and impact). Few studies have checked the traits that confer ability to overcome these steps in the same species. The aim of the present study is to review the available information on the life-history and ecological traits of the mud snail, *Potamopyrgus antipodarum* Gray (Hydrobiidae, Mollusca), native from New Zealand, in order to explain its invasive success at different aquatic ecosystems around the world. A wide tolerance range to physico-chemical factors has been found to be a key trait for successful transport. A high competitive ability at early stages of succession can explains its establishment success in human-altered ecosystems. A high reproduction rate, high capacity for active and passive dispersal, and the escape from native predators and parasites explains its spread success. The high reproduction and the ability to monopolize invertebrate secondary production explain its high impact in the invaded ecosystems. However, further research is needed to understand how other factors, such as population density or the degree of human perturbation can modify the invasive success of this aquatic snail.

Keywords *Potamopyrgus antipodarum* · Snail · Tolerance · Life-history traits · Colonization · Spread

Introduction

The spread of non-native species can be one of the most harmful and least reversible disturbances in ecosystems (Strayer, 1999; Ricciardi & MacIsaac, 2000; Rahel, 2002). Biological invasions may alter the properties of the invaded habitat, decline biodiversity and induce biotic homogenization (Enserink, 1999; Kolar & Lodge, 2001; Cambray, 2003; Mills et al., 2003). Nowadays, human activities, such us agriculture, aquaculture, recreation and international trade are increasing the range of some species (Leppäkoski & Olenin, 2000; Ricciardi & MacIsaac, 2000; Kolar & Lodge, 2001; Darrigran, 2002; Grigorovich et al., 2003). Moreover, global change may increase the chance of success of exotic species by declining the fitness of local species to the new environment (Dukes & Mooney, 1999).

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Before a species becomes a pest in an ecosystem, it must successfully overcome several filters (Kolar & Lodge, 2001; Sakai et al., 2001). First, the species must travel from its native range to a new ecosystem (*transport*). Second, it must survive, grow and reproduce under the new environmental conditions (*establishment*). Third, it must acquire a high rate of population growth, invading new regions (*spread*). Finally, the alien species must alter the structure and functioning of the invaded ecosystem (*impact*) (Parker et al., 1999). Different traits may confer success to overcome each step, so all of them must coincide in the same species to assure its invasive success (Williamson & Fitter, 1996; Sakai et al., 2001). Most studies on invasion processes have searched for functional traits explaining the spreading success (Table 1). However, fewer studies have searched for traits explaining success in the previous invasive phases (Kolar & Lodge, 2001), partly because exotic species do not catch the attention of researches before being widely spread. Therefore, it remains unknown whether the traits explaining spread success of a given species also contribute to explain its success in transport, establishment and impact, or different sets of traits are required to pass each filter. In order to answer this question, detailed information of the whole invasive process of a species is needed.

The New Zealand mud snail, *Potamopyrgus antipodarum* Gray (=*P. jenkinsi* Smith) (Hydrobiidae, Mollusca), meets the above condition. This invertebrate, native from New Zealand and adjacent islands (Gangloff, 1998; Ponder, 1988), has successfully spread through fast rivers, slow-flowing and brackish water ecosystems of four continents (Heywood & Edwards, 1962; Quinn et al., 1998; Leppäkoski & Olenin, 2000; Shimada & Urabe, 2003; Cada, 2004; Kerans et al., 2005; Strzelec, 2005; ANS, 2007). Its first occurrence in Europe was dated in England in 1859 (Ponder, 1988). In Australia, the species was first reported in Tasmania in 1892, and then in Victoria in 1895 (Ponder, 1988). In North America, this species was first cited in the Middle Snake River (Idaho, north-west of USA) in 1987, probably escaped from a fish farm (Bowler, 1991). In 1991, mud snails were found in Lake Ontario (North-East USA) and in 1997 in Columbia River (Oregon, north-west of USA), where they probably arrived via ballast water from commercial ships (Zaranko et al., 1997; Gangloff, 1998). Recently, this species has been cited in Japan (Shimada & Urabe, 2003). In spite of this rapid and well-documented spread, little is known about the potential effect of mud snail on the native communities. Moreover, most of the available information has been gathered at a local scale, and no attempt has been done to put these pieces together to gain insight on the whole process of invasion.

The aim of this work was to investigate whether the attributes which confer mud snail success in transport, spread, establishment and impact are the same or not by reviewing all published information on this mollusc.

Table 1 Functional traits reported in bibliography to explain the spreading success of alien species

Trait	References
Rapid growth rate	Baruch & Bilbao (1999), Pattison et al. (1998)
Early sexual maturity	Richardson et al. (1990)
High fecundity	Richardson et al. (1990), **Møller et al. (1994), Zaranko et al. (1997), Richards (2002)**
Low size of propagules	Rejmánek & Richardson (1996)
Vegetative and **parthenogenetic reproduction**	Huenneke & Vitousek (1990), **Lively (1992)**, Lake & Leishman (2004), Reichard & Hamilton (1997)
Low susceptibility to natural enemies	**Gérard et al. (2003)**, Maron et al. (2004), Vilà et al. (2005), **Vinson & Baker (2008)**
Ability to tolerate wide range of abiotic conditions	**Alonso & Camargo (2003, 2004)**, Baruch & Bilbao (1999), **Morton (1996), Gérard et al. (2003), Strayer (1999)**
High evolutionary potential to adapt to new environments	Hänfling & Kollmann (2002), Lee (2002)

Bold letters highlight those functional traits present in *P. antipodarum* and the studies reporting them

Life-history traits and colonized habitats

P. antipodarum is a prosobranch snail (Hydrobiidae, Mollusca), which reaches a maximum size of 6–7 mm in invaded regions, but can be up to 12 mm in New Zealand (Winterbourn, 1970). This snail has a solid operculum and its shell is long (Duft et al., 2003a, b). Although, in its natural range, both sexual and asexual reproduction coexists, non-native populations are parthenogenetic, consisting almost exclusively of females (Lively, 1987; Jokela et al., 1997; Gangloff, 1998; Jensen et al., 2001; Duft et al., 2003a, b). This invertebrate is ovoviviparous, and females brood their offsprings to the "crawl-away" developmental stage in a brood pouch (Jokela et al., 1997). It reaches sexual maturity at 3–3.5 mm of shell length (Møller et al., 1994; Richards, 2002). The number of generations per year ranges from 1 to 6, and one adult individual can produce an average of 230 juveniles per year (Møller et al., 1994; Richards, 2002). Its diet includes periphyton, macrophytes and detritus (Dorgelo & Leonards, 2001; Jensen et al., 2001; Alonso & Camargo, 2003; Duft et al., 2003a, b; Alonso, 2005). This snail can dwell on different substrata, such as aquatic macrophytes, clay, fine sand and mud (Heywood & Edwards, 1962; Marshall & Winterbourn, 1979; Weatherhead & James, 2001). In addition, it buries itself in the sediment to stand dry or cold periods (Duft et al., 2003a).

Within its native range mud snail lives in freshwater ecosystems, except temporary ponds, and also inhabits brackish waters (Winterbourn, 1973). However, in the invaded regions, it can be found in a higher variety of habitats (Table 2). Although in most cases *P. antipodarum* lives in freshwater habitats, it has also been found in brackish and even salty water. Regarding water speed, mud snail has colonized streams, lakes, reservoirs, estuaries and even open seas (Table 2).

Transport

There are several transport mechanisms that have been reported in literature for *P. antipodarum* (Table 3). The most frequently cited long-distance transport is through ballast water of commercial ships (Zaranko et al., 1997; Gangloff, 1998; Leppäkoski & Olenin, 2000; Leppäkoski et al., 2002; Richards, 2002), which may explain transoceanic transport (e.g. from Australia to Europe). Other reported long- or short-distance transport means relate with commercial movements of aquaculture products, or aquatic ornamental plants; mud snails may also travel within freshwater tanks and water pipes, or within the mud attached to bills or legs of birds, or even inside the gut of birds or fishes (Haynes et al., 1985; Ponder, 1988; Aarnio & Bonsdorff, 1997; Zaranko et al., 1997; Gangloff, 1998; Leppäkoski & Olenin, 2000; Richards, 2002). Finally, other transport mechanisms are recreational vessels (e.g. kayaks and rafts) and sport fishing tools (e.g. waders and boots), where mud snails may adhere (Hosea & Finlayson, 2005; ANS, 2007).

Although the arrival to any of these transport means may be a matter of chance, the survival during the journey requires wide tolerance to physicochemical conditions. For example, a successful transport via ballast water requires high tolerance to salinity (Leppäkoski & Olenin, 2000; Richards, 2002; Gérard et al., 2003). In fact, this snail has been reported to survive after short-term exposures to salinities as high as 32‰, and it can feed, grow and reproduce at 15‰ salinity (Jacobsen & Forbes, 1997; Costil et al., 2001; Gérard et al., 2003).

Long distance travels also require wide tolerance to temperature change. Some authors have found that this species tolerates temperature from 0 to 28°C (Winterbourn, 1969; Hylleberg & Siegismund, 1987). In an experimental study, Vareille-Morel (1985a, b) found a range of temperature tolerance between 9 and 27°C among individuals of different populations. In other experimental study, Dybdahl & Kane (2005) tested the growth of *P. antipodarum* to a range of temperatures from 12 to 24°C, finding the highest growth rate at 18°C. But to our knowledge, no study has assessed the reproductive success after exposure to extreme temperatures.

Successful transport on mud, fishing tools or recreational vessels requires a high tolerance to desiccation. Several authors have reported that this snail can survive after short desiccation periods (Bowler, 1991; Zaranko et al., 1997; Cada, 2004; Lysne & Koetsier, 2006), although desiccation tolerance declines at increasing temperature, and with decreasing snail size (Richards et al., 2004). Fewer studies have tested the reproductive success of *P. antipodarum* after desiccation and for different environmental conditions (Vareille-Morel, 1985a, b; Bowler, 1991; Quinn et al., 1994; Zaranko

Table 2 Habitats colonized by the mud snail *Potamopyrgus antipodarum*. Habitat type, water salinity and population densities are shown for each site whenever available

Continent/Country	Habitat	Salinity (‰)	Densities (snails/m^2)	Reference
Europe				
Mont St-Michel Basin (France)	Polder-marsh	0–28	–	Costil et al. (2001), Gérard et al. (2003)
Baltic Sea (North Europe)	Sea	Brackishwater	–	Leppäkoski & Olenin (2000)
Norfolk (UK)	Sea	3.5	–	Grant & Briggs (1998)
Ivel river (UK)	Stream	Freshwater	2,750–164,000	Heywood & Edwards (1962)
Henares river (central Spain)	Stream	Freshwater	–	Alonso & Camargo (2003), Alonso (2005)
Lake Veluwemeer, Lake Wolderwijd (The Netherlands)	Shallow lakes	Freshwater	2,000	Van den Berg et al. (1997)
Upper Silesia (southern Poland)	Post-industrial ponds	Freshwater	100	Strzelec (2005)
Upper Silesia (southern Poland)	Reservoirs	Freshwater	2–2,422	Lewin & Smolinski (2006)
Northern Poland	Reservoirs	Freshwater	220–25,500	Brzezinski & Kolodziejczyk (2001)
Lake Zurich (Switzerland)	Lake	Freshwater	800,000	Dorgelo (1987)
Finland	Isolated coastal lakes	Freshwater	–	Leppäkoski (1984), Leppäkoski & Olenin (2000)
North America				
Yellowstone National Park (USA)	Geothermal stream	Freshwater	20,000–500,000	Hall et al. (2003)
Greater Yellowstone (USA)	Stream and Creek	Freshwater	22–299,000	Kerans et al. (2005)
Idaho (USA)	Stream	Freshwater	17,550–500,000	Richards et al. (2001)
Great Lakes Basin (Canada–USA)	Lake	Freshwater	–	Mills et al. (2003), Grigorovich et al. (2003)
Columbia River (USA)	Estuary	Saltwater	–	Zaranko et al. (1997)
Australia				
Lake Purrumbete (Victoria)	Lake	Freshwater	1,770–49,260	Quinn et al. (1998), Schreiber et al (1998)
Curdies river (Victoria)	Stream	Freshwater	–	Quinn et al. (1998)
Southern Victoria	Stream	Freshwater	–	Schreiber et al. (2003)
Asia				
Tone River (Japan)	River	Freshwater	–	Katayama & Ryoji (2004)
Moriyama (Japan)	Channel	Freshwater	–	Shimada & Urabe (2003)

et al., 1997). These studies suggest that transport means implying desiccation are only effective for short distance movements, therefore contributing to snail spread once the species has reached a new area. The same can be argued for travels in other animal's gut, as mud snail can only stand such conditions for a few hours (Haynes et al., 1985; Bowler, 1991; Aarnio & Bonsdorff, 1997; Zaranko et al., 1997; Cada, 2004; Lysne & Koetsier, 2006). In summary, wide tolerance range to physico-chemical variables is a key trait assuring travel success of mud snail, both at long and short distances.

Establishment

A wide tolerance range to multiple environmental factors also increases the chances of an exotic species survival once it has arrived in a new environment.

Table 3 Summary of transport, establishment, spread and impact mechanisms reported in scientific bibliography for *Potamopyrgus antipodarum*

Invasion step	Mechanism	Reference
Transport	Ship ballast water	Zaranko et al. (1997), Gangloff (1998), Leppäkoski & Olenin, (2000), Richards (2002), Leppäkoski et al. (2002)
	Holding on aquatic ornamental plants	Ribi (1986)
	Movements of aquaculture products	Bowler (1991)
	Freshwater tanks	Ponder (1988)
	Water pipes	Ponder (1988)
	Bird and fish guts; Bills or legs of birds	Haynes et al. (1985), Aarnio & Bonsdorff (1997), Zaranko et al. (1997)
	Others: holding on recreational vessels, sport fishing tools, etc.	Hosea & Finlayson (2005); ANS (2007)
Establishment	Tolerance to wide range of environmental conditions	
	High tolerance to salinity	Leppäkoski & Olenin (2000), Richards (2002), Gérard et al. (2003)
	High tolerance to extreme temperatures	Winterbourn (1969), Hylleberg & Siegismund (1987)
	High tolerance to human perturbations	Alonso & Camargo (2003), Alonso (2005)
	High competition ability as compared with invertebrate native fauna (dependent on snail density)	Gangloff (1998), Schreiber et al. (2002, 2003), Hall et al. (2006)
Spread	Passive methods	
	Dispersal by birds and fish	Lassen (1975), Haynes et al. (1985)
	Drift	Richards et al. (2001)
	Holding in floating aquatic macrophytes	Ribi (1986)
	Active methods	
	Positive rheotactic	Haynes et al. (1985)
Impact	High consumption rate of primary production	Hall et al. (2003)
	High secondary production	Hall et al. (2006)
	Reduction in the colonization ability of other invertebrates	Ponder (1988), Kerans et al. (2005)
	Asymmetrical competition with native snail	Riley et al. (2008)

However, the species still have to overcome the biological resistance opposed by the local community (competition, predation, diseases, etc.) to assure a long-term successful establishment. Theoretically, the exotic species can take advantage of two different, but not exclusive, strategies to do so: to possess a high potential to overcome biological resistance (by means of high competitive potential, escape from natural enemies, etc.), and/or to be a successful colonizer of empty spaces, where disturbances have reduced or eliminated local populations.

In non-native regions, mud snail has been mainly found in human-disturbed environments (Zaranko et al., 1997; Mouthon & Charvet, 1999; Gérard et al., 2003; Schreiber et al., 2003; Cada, 2004; Richards et al., 2004; Alonso, 2005), as occurs with other exotic species (Rejmánek & Richardson, 1996; Almasi, 2000; Lake & Leishman, 2004). Human-induced disturbances increases the chance of success for recently arrived species, either by increasing resource availability (i.e. eutrophication), or by releasing resources capitalized by local populations (Thompson et al., 2001; Schreiber et al., 2003). In habitats altered by human activities, *P. antipodarum* performs as a successful early colonizer (Quinn et al., 1998) dominating the incipient community (Schreiber et al., 2003; Strzelec, 2005; Strzelec et al., 2005; Lewin & Smolinski, 2006), probably due to the low biotic resistance exerted by the remaining simplified native communities. The escape from parasites can additionally contribute to explain mud snail successful establishment, as it seems to leave their trematode parasites behind when invading new regions (Gérard et al., 2003). Experimental studies have shown that *P. antipodarum* growth was reduced by the presence of trematodes (Krist & Lively, 1998). Finally, mud snails are also resistant to many native predators, because of its hard shell and solid operculum (Zaranko et al., 1997; Vinson & Baker, 2008). All these traits can help mud snail for a successful establishment in a new area.

Spread

Mud snail may disperse both by passive and active methods (Table 3). Passive methods have been described as the principal way of spread in European waters for *P. antipodarum* (Hubendick, 1950; Lassen, 1975). Among them, several authors reported birds and fish as dispersal agents (Haynes et al., 1985; Ribi, 1986; Aarnio & Bonsdorff, 1997; Zaranko et al., 1997), while others reported passive drift or dispersal by holding in floating aquatic macrophytes (Ribi, 1986; Richards et al., 2001). Mud snail was found to be one of the most abundant macroinvertebrate in drift net samples in Banbury Springs (Idaho, USA) (Richards et al., 2001). These authors also showed that *P. antipodarum* used floating vegetation mats to colonize a lake. However, these mechanisms are only effective to colonize lakes or currents downstream from the initial population. In Australia, Loo et al. (2007a) found that fish stocking and anglers were two passive spread mechanisms to *P. antipodarum*.

Regarding active dispersal mechanisms, some authors have found that positive rheotactic response can facilitate spread in invaded streams and rivers (Adam, 1942; Haynes et al., 1985), and that high water speed produces a more consistent upstream movement (Haynes et al., 1985). Adam (1942) found in Belgium that mud snails can spread 60 m in three months by active upstream movements. At this spread rate a single mud snail might can move upstream up to 240 m in just one year. Furthermore, as each snail can produce more than 230 juveniles per year, the number of snails in the reach can dramatically increase, as it moves upstream in a reach (Møller et al., 1994; Richards, 2002). By contrast, Richards et al. (2001) reported that *P. antipodarum* is prone to detach from substrate in high-speed waters, suggesting that fast waters can limit colonization. They also found that aquatic macrophytes are a good refuge for juveniles of *P. antipodarum*, which are more sensitive to velocity than adults. According to these authors, low-speed waters with high densities of macrophytes are more susceptible to mud snail spread than high-speed waters. These contradictory results indicate the necessity of further research on the active dispersal method of mud snail.

All these ecological traits help mud snail to a rapid spread around different aquatic ecosystems. Recent predictive models developed for *P. antipodarum* have shown that the future spread of mud snail through Australia and North America could be very fast unless prevention measures are rapidly implemented (Loo et al., 2007b).

Impact

The principal impact of mud snail in invaded ecosystem can be attributed to its high reproductive capacity, which leads to an explosive population growth, a fast spread and a high consumption rate of the available primary production of the ecosystem. *P. antipodarum* is a successful early colonizer (Quinn et al., 1998) dominating the incipient community (Schreiber et al., 2003; Strzelec, 2005; Strzelec et al., 2005; Lewin & Smolinski, 2006). In a highly productive stream of Wyoming (USA), Hall et al. (2003) found that mud snail consumed 75% of the primary production and excreted about 65% of the total NH_4^+ demanded by microbes and plants, therefore dominating both C and N cycles. These authors compared the effects of mud snail to those of zebra mussel (*Dreissena polymorpha*), an invasive bivalve which can consume nearly all the primary production of the community (Strayer, 1999; Hall et al., 2003). The same authors found in another study that the secondary productivity of *P. antipodarum* was one of the highest ever reported for a stream invertebrate (194 g AFDM m^{-2} yr^{-1}), being 7–40 times higher than that of any macroinvertebrate in Greater Yellowstone area (Wyoming, USA) (Hall et al., 2006). In a tributary of Snake River (Idaho, USA), mud snail densities were reported to be higher than those of native snails in three different habitats (run, edge and vegetation) (Richards et al., 2001). In ditches and canals of the Basin of the Mont St-Michel Bay

(France), mud snail dominates the gastropod communities in fresh- and salt-water ecosystems (Gérard et al., 2003). Lewin & Smolinski (2006) reported that mud snail made up 83% of the mollusc community in a reservoir near an industrial area in Poland. Experimental studies also showed that mud snail reduced colonization by other invertebrates in the early stages of succession (Kerans et al., 2005; Ponder, 1988).

Several authors have compared the densities of mud snail between degraded and intact stream. Alonso (2005) found high densities of *P. antipodarum* in human-polluted reaches of the Henares River, whereas no snails were found in well-preserved areas. Similarly, Schreiber et al. (2003) found higher density of *P. antipodarum* in areas with multiple human land uses than in low-impact sites of Victoria streams (Australia). Moreover, at low population density, *P. antipodarum* has been even found to facilitate some native invertebrates, as its faeces, which contain processed cellulases and chitinases plus mucoproteins and mucopolysaccharides, constitute a suitable food for native grazers and deposit-feeders (Gangloff, 1998; Schreiber et al., 2002).

According to the five-level framework put forward by Parker et al. (1999) to assess the impact of an invader, mud snail impacts on the invaded ecosystems are related mainly with two levels: (1) the population effects, given that *P. antipodarum* possess a population density in the invaded ecosystem higher than most native invertebrates and (2) effects on ecosystem processes, as the mud snail can consume most of the primary production of the stream, and therefore it can dominate the secondary production of the invertebrate community.

This revision shows that the invasion success of mud snail can be largely dependent on the conservation state of the invaded habitat, and that *P. antipodarum* is a very successful colonizer of empty spaces, typically occurring at early stages of succession, but less successful at overcoming the biological resistance of an intact native community.

Concluding remarks

The revised bibliography has shown that a wide tolerance to physico-chemical conditions contributes to explain the success of mud snail in the two former steps to become an invasive species (transport and establishment). However, a successful establishment also relies on a high capacity to overcome biotic resistance, either by successfully colonizing early stages of succession in human-altered habitats, or by leaving behind parasite and predator control. Its high reproductive rate, together with its ability to disperse by active and passive mechanisms, explains mud snail potential for an efficient spread. Finally, mud snail ability to alter the structure and function of invaded ecosystems (impact) is again due to the high reproductive rate, which leads to extremely high population density and to the consumption of most of the primary productivity of the ecosystem. Therefore, the coincidence of wide tolerance to abiotic factors and high reproductive capacity on the same species may have allowed it overcome most of the filters to become a pest. Human-disturbed ecosystems are more susceptible to mud snail invasion than intact ones, although the latter may be also affected by mud snail.

Future research on mud snail invasion should address several open questions: (1) To assess the reproductive viability of mud snail after exposure to gradients of different conditions (humidity, temperature, etc.) to understand its transport-spread potential, (2) to study the potential impacts of mud snail on native faunas at different densities, especially in perturbed ecosystems, where it apparently shows higher success and (3) to identify the ecosystems that are susceptible to invasion in order to prevent spread of *P. antipodarum* into these regions.

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