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Aquatic Sciences

OVERVIEW

The exotic aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca): state of the art of a worldwide invasion

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Abstract Biological invasions represent a relevant ecological and economic problem of our globalized world. While a few species have been classified as invasive due to their ecological and economic impacts on the invaded ecosystems (e.g., zebra mussel), others show contrasting invasive potential, depending on the invaded ecosystem and/or the traits of the exotic species. This paper reviews the worldwide distribution, ecological impacts and the reasons that explain the invasive success of the aquatic mud snail *Potamopyrgus antipodarum* Gray (Hydrobiidae, Mollusca), which is native to New Zealand. This review shows that most studies on *P. antipodarum* distribution have been conducted in Europe, North America and Australia, and few studies in Asia. The distribution of this snail is still unknown in other parts of the world (e.g., Africa, South and Central America). The range of invaded aquatic ecosystems varies from fresh to salt water and from lentic to lotic ecosystems. The ecological impact of this species is due to the fast population growth rate and to the extremely high densities that it can reach, leading to altered C and N cycles in invaded ecosystems. However, at low densities mud snails have been shown to enhance secondary production. Additionally, *P. antipodarum* has been found to overcome the negative effects of predators and parasites (e.g., it survives the pass through the digestive tracts of fish). This review contributes to assess the magnitude and ecological risk of *P. antipodarum* invasion throughout the world.

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Introduction

Biological invasions represent a major ecological and economic problem in our globalized world. Human-mediated global change increases the chances of exotic species to successfully establish in a new region by reducing the fitness of native species within their environment (Dukes and Mooney 1999). Alien species represent one of the most important threats for the health and well-functioning of worldwide ecosystems (Gherardi 2007; Netwing 2007).

Becoming invasive in a non-native region is a complex process that includes transport, successful establishment and fast spread (Kolar and Lodge 2001; Sakai et al. 2001). The chances of an alien species to become a successful invader largely depend on the interaction between target region properties and invader traits (Kolar and Lodge 2001; Gherardi 2007; Netwing 2007). Therefore, only a few species among those arriving at a new ecosystem become invasive (Williamson and Fitter 1996; Sakai et al. 2001). These species may cause a serious impact on human and/or ecological systems (Gherardi 2007). Several species have been doubtlessly classified as invasive since they always cause obvious ecological and economic damages in the invaded ecosystems. Among them, there are several examples in aquatic ecosystems, such us the zebra mussel (*Dreissena polymorpha*), the killer shrimp (*Dikerogammarus villosus*), the golden apple snail (*Pomacea canaliculata*), caulerpa (*Caulerpa taxifolia*) and the brook trout (*Salmo trutta*) (Lowe et al. 2000; Baur and Schmidlin 2007). However, the invasion status of other exotic species

is less clear, as they show contrasting invasive behaviour and ecological impact in different regions or habitats. Sometimes these species remain at low densities for many years, but other times they quickly spread and cause a high impact in the new ecosystem (Baur and Schmidlin 2007). For instance, the clam *Corbicula fluminea*, native to South-East Asia, can impact on native benthic species or not depending on both the site properties and the structure of the host community (Left et al. 1990; Strayer 1999). This is also the case with the New Zealand aquatic mud snail (*P. antipodarum*, Hydrobiidae, Mollusca) and in some cases this species has reached a high population density, altering the structure of the native community, while in others it integrates in the host community causing no apparent negative impact (Gangloff 1998; Schreiber et al. 2002; Alonso and Castro-Díez 2008; Múrria et al. 2008). The invasion success and potential impacts from the New Zealand mud snail within aquatic ecosystems remains poorly understood.

Potamopyrgus antipodarum is a mollusc of the prosobranch family Hydrobiidae native from New Zealand. Hydrobiids constitute a cosmopolitan group of small aquatic molluscs, encompassing over 100 genera (Kabat and Hershler 1993). *Potamopyrgus antipodarum* reaches a maximum shell size of 6–7 mm in invaded ecosystems, but in its native range it can be up to 12 mm in shell length (Winterbourn 1970). This species is termed a "mud snail" since it buries itself into the sediment during dry or cold periods (Duft et al. 2003a). One peculiarity of this species is its reproductive strategy: while non-native populations are parthenogenetic, most native populations exhibit both ovoviviparous sexual and asexual reproduction (Lively 1987; Jokela et al. 1997; Gangloff 1998; Jensen et al. 2001; Duft et al. 2003a, b). Sexual maturity is reached at 3–3.5 mm of shell length (Møller et al. 1994; Richards 2002). The number of generations per year can be up to six, and the average number of offsprings per adult is 230 (Møller et al. 1994; Richards 2002). Females of this snail carry their offsprings in a brood pouch (Jokela et al. 1997). The diet of *P. antipodarum* is varied, including a wide range of living organisms (periphyton, macrophytes, etc.) and dead organic matter (Dorgelo and Leonards 2001; Jensen et al. 2001; Alonso and Camargo 2003; Duft et al. 2003a, b; Alonso 2005). In New Zealand ecosystems, mud snail occurs in fresh and brackish waters (Winterbourn 1973) and utilizes aquatic macrophytes, clay, fine sand and mud as habitats (Heywood and Edwards 1962; Marshall and Winterbourn 1979; Weatherhead and James 2001).

The aim of this study is assessing the ecological risk that this species represents for aquatic ecosystems on the basis of the published information. Specifically, we address the following questions: (1) What is the current worldwide distribution of *P. antipodarum* in aquatic ecosystems? (2) What are the effects of *P. antipodarum* in the structure and functioning of the invaded ecosystems? (3) What explains the invasion success of this species in new ecosystems? Altogether, this information will allow us to understand the global impact of this species.

Materials and methods

Scientific articles, theses and reports including the term *P. antipodarum* (or the synonymous *P. jenkinsi*) were searched for in ISI Web of Knowledge, Scirus and/or JSTOR databases (from 1900 to present day). All abstracts were read, and the articles with information on distribution, impacts and/or life-history traits of *P. antipodarum* were subsequently read. All references describing the invaded ecosystem and their location, impacts on ecosystems, and/or species or ecosystem traits explaining *P. antipodarum* success were included in our review. A total of 77 references were used in this review.

Results and discussion

Worldwide distribution

Potamopyrgus antipodarum worldwide distribution at continental, country and habitat scales is listed in Table 1. The New Zealand mud snail has been found on most continents (except Africa and Antarctica), encompassing the Palearctic, Nearctic and Australasian zoogeographical regions. The first record outside New Zealand was reported in England in 1859 (Ponder 1988), followed by a record in Tasmania in 1872, and continental Australia in 1895 (Ponder 1988). The first record in the Americas was in 1987 (Bowler 1991).

In the invaded ecosystems, *P. antipodarum* has been found in a wide range of habitats. In Europe, various types of aquatic ecosystems have been invaded, from freshwater to saltwater (estuary, polder-marsh), and from lotic (streams, rivers) to lentic ecosystems (reservoirs and lakes). In other continents, most of the reported invaded ecosystems are freshwater habitats. The older invasion history in Europe, together with the intense human activity, contributes to explain the wide range of invaded habitats and ecosystems in this continent. In general, disturbed ecosystems are more attractive to alien species than pristine ecosystems, as the latter have less available resources and less empty niches (Ross et al. 2001). In the Americas, all reported invaded ecosystems belonged to the USA and Canada. Recent studies show that this alien species is quickly spreading at continental and regional scales in North America and Australia (Loo et al. 2007a, b; Levri et al. 2008). This is the case for the Great Lakes, where this

Table 1 Worldwide distribution of *Potamopyrgus antipodarum*

Continent/country	Location	Habitat type	References
Europe			
Portugal	River Minho estuary	Freshwater tidal area	Sousa et al. (2005)
	Aveiro Ria	Saltwater	Simoes (1988)
Spain	Henares river (Guadalajara)	Stream	Alonso and Camargo (2003)
	"Dehesas de Sierra Morena" (Córdoba)	Freshwater	Pérez-Quintero (2009)
	Vallvidrera stream (Barcelona)	Stream	Múrria et al. (2008)
	Province of Madrid	Stream-rivers-channels	Soler et al. (2006)
	Province of Cuenca	Springs	Werner et al. (1994)
France	Mont St-Michel basin	Polder-marsh	Costil et al. (2001), and Gérard et al. (2003)
	Annecy lake (Savoie)	Alpine lake	Mouthon and Dubois (2001)
	Corsica island	Freshwater ecosystems	Zettler and Richard (2004)
Italy	Large distribution	Inland waters	Cianfanelli et al. (2007)
Greece	Central-Western Greece	Lakes and streams	Radea et al. (2008)
UK	Norfolk	Sea	Grant and Briggs (1998)
	Ivel river	Stream	Heywood and Edwards (1962)
	Thames estuary, several freshwater ecosystems	Estuary and freshwater ecosystems	Boycott (1936)
The Netherlands	Lake Veluwemeer	Shallow lake	Van den Berg et al. (1997)
	Lake Wolderwijd	Shallow lake	Van den Berg et al. (1997)
Poland	Upper Silesia	Ponds	Strzelec (2005)
	Upper Silesia	Reservoirs	Lewin and Smolinski (2006)
	Northern Poland	Reservoirs	Brzezinski and Kolodziejczyk (2001)
	Lakes Inulec and Głębokie	Lake	Kolodziejczyk et al. (2009)
Switzerland	Lake Zurich	Lake	Dorgelo (1987)
	Lake Neuchâtel	Lake	Schmidlin et al. (2012)
Austria	Weidlingbach river (near Vienna)	Freshwater river	Zieritz and Waringer (2008)
Germany	Main river	Freshwater	Wagner (2000)
	Lower catchment of Werra river	Salt-polluted	Huebner and Braukmann (2005)
Finland	Aland islands	Lakes	Carlsson (2000)
	Baltic sea coast	Artificial lakes	Filippenko and Son (2008)
Russia	Don river	Freshwater	Son et al. (2008)
Denmark	Open and estuarine waters	Saltwater	Thomsen et al. (2009)
Asia			
Japan	Moriyama channel	Freshwater	Shimada and Urabe (2003)
Iraq	Garmat Ali river	Freshwater	Naser and Son (2009)
The Americas			
USA	Snake river (ID)	Freshwater	Bowler (1991)
USA	Columbia river estuary (OR)	Estuary	Davidson et al. (2008)
USA	Owens river (CA)	Freshwater	Herbst et al. (2008)
USA	Colorado river (AZ)	Freshwater	Cross et al. (2010)
USA	Polecat Creek (WY)	Freshwater	Arango et al. (2009)
Canada–USA	Great Lakes	Freshwater	Zaranko et al. (1997), Grigorovich et al. (2003), and Levri et al. (2007)
Canada	Coastal aquatic systems (British Columbia)	Saltwater	Davidson et al. (2008)
Australia			
Australia	Lake Purrumbete	Freshwater	Schreiber et al. (1998)
Australia	Victorian streams	Freshwater	Schreiber et al. (2003)

Continent, country, location and habitat type are shown for each location

species is being found in new lakes every year since 1991 (Zaranko et al. 1997; Levri et al. 2008). However, at regional or local scales, *P. antipodarum* has been found to reduce its population density after a long invasion history (Levri et al. 2008).

Impacts on structure and functioning of invaded ecosystems

Table 2 summarizes the reported effects of *P. antipodarum* on the structure and functioning of several invaded aquatic ecosystems. Contrary to other alien invasive invertebrate species (such as the zebra mussel or the killer shrimp), *P. antipodarum* does not always show a clear impact on its occupied ecosystems (Table 2). Several authors have shown weak or no effects on the structure of the invaded community (Schreiber et al. 2002; Múrria et al. 2008; Brenneis et al. 2010). On the contrary, most of the revised studies show strong effects on ecosystem structure (Richards et al. 2001; Gérard et al. 2003; Kerans et al. 2005; Lewin and Smolinski 2006; Arango et al. 2009; Schmidlin et al. 2012) or on ecosystem functioning (Hall et al. 2003, 2006; Richards 2004; Arango et al. 2009). Most of these studies were conducted in freshwater ecosystems, with only two cases in estuary or saltwater ecosystems (Gérard et al. 2003; Brenneis et al. 2010). The latter studies showed contrasting results: while Gérard et al. (2003) found a high dominance of mud snail in gastropod communities in marshes; Brenneis et al. (2010) found coexistence between native estuarine invertebrates and mud snail.

Impact on nutrient cycles

The ecological impact of *P. antipodarum* can be attributed to the extremely high densities that it can reach and to the fast velocity to reach these densities (Alonso and Castro-Díez 2008). Several authors reported densities up to 500,000 individuals per square meter in invaded habitats (Richards et al. 2001; Hall et al. 2003) or even up to 800,000 (Dorgelo 1987). Such densities explain the domination of secondary productivity by *P. antipodarum*, which attains the highest value ever reported among stream invertebrates (194 g of ash free dry mass m^{-2} $year^{-1}$) (Hall et al. 2006). In a stream of Yellowstone National Park, USA, *P. antipodarum* has been found to consume up to 75% of the primary production and to excrete up to 65% of the ammonium demanded by microbes and plants of the stream (Hall et al. 2003). Therefore, in this case, *P. antipodarum* controls the C and N cycles of that stream.

In a N-limited stream in WY (USA), Arango et al. (2009) reported that *P. antipodarum* can alter the overall ecosystem nitrogen fixation rate by consuming a high proportion of green algae, which in turn increases the proportion of nitrogen-fixing diatoms (Arango et al. 2009). Besides, *P. antipodarum* was found to graze preferably on erect filamentous algae, rather than on prostate algae, such as diatoms. This increases light and nutrient availability to diatoms, causing an increase of N-fixation rates up to 50% in the periphyton community of the stream (Arango et al. 2009).

Altogether, these studies show that one of the most important impacts of *P. antipodarum* on ecosystem functioning is related to nitrogen and carbon cycles. In this way, its effect resembles those caused by other dangerous invasive alien invertebrates, such as the zebra mussel (*Dreissena polymorpha*) or apple snail (*Pomacea canaliculata*), which deeply alter nutrient cycles in aquatic ecosystems (Strayer 1999; Hall et al. 2003; Carlsson et al. 2004).

Impact on other species

Several studies have described deleterious effects of *P. antipodarum* on individual and population growth of both invertebrates and vertebrates. Riley et al. (2008) reported that this alien species significantly limits the growth of the closely related native snail *Pyrgulopsis robusta* in Polecat Creek and Marmot Spring (WY, USA) where both species feed on periphyton. Moreover, the native species seems to facilitate the growth of mud snail because native eggs constitute a food resource for mud snail and/or because native snails secrete mucus that improves the growth of algae, which are consumed by mud snail (Riley et al. 2008). Additionally, *P. antipodarum* preferentially consumes high nutrient quality algae, forcing native species to consume lower quality food (Riley et al. 2008). By contrast, Schreiber et al. (2002) showed in a field experiment that native macroinvertebrate densities were positively correlated with *P. antipodarum* densities. These authors suggested that *P. antipodarum* is capable of digesting cellulose and chitin from detritus, so that its faeces and mucus may represent a high quality food for native grazers and collectors, increasing their densities. On the contrary, Kerans et al. (2005) and Richards (2004) in field colonization experiments found low rates of native invertebrate colonization when high densities of *P. antipodarum* were present. The likely cause of these contrasting results may be the different densities of *P. antipodarum* in each experiment, which was relatively low in Schreiber et al. (2002) (approx. 3,000–4,000 individuals/m^2), while much higher in Kerans et al. (2005) and Richards (2004) (approx. 20,000–30,000 and 4,000–10,000 individuals/m^2, respectively). This fact supports the high influence of *P. antipodarum* density on the impact it causes on the invaded community, although comparison between different ecological situations is difficult. Regarding the impact on

Table 2 Reported impacts of *Potamopyrgus antipodarum* on structure and/or functioning of invaded aquatic ecosystems

Continent	Location	Ecosystem/habitat	Impact (e.g., any changes in structure and functioning)	References
Europe	Basin of the Mont St-Michel Bay (France)	Fresh- and saltwater ecosystems	Domination of gastropod communities	Gérard et al. (2003)
	The Katowicka Upland, Upper Silesia (Poland)	Reservoir	Domination of mollusc communities	Lewin and Smolinski (2006)
	Vallvidrera stream (Spain)	Stream	No effects on chlorophyll-*a* standing stocks	Múrria et al. (2008)
			No effects on taxonomical structure	
			Weak influence on macroinvertebrate distribution at microhabitat scale	
	Lake Neuchâtel (Switzerland)	Lake	Decline of invertebrates preferring hard bottom	Schmidlin et al. (2012)
			Empty shells of *P. antipodarum* enhances the number of native taxa of invertebrates preferring sandy substrate	
The Americas	Polecat Creek (WY, USA)	Stream	Domination of C and N cycles	Hall et al. (2003)
			Consumption of 75% of primary production	
			Excretion of c.a. 65% of the total ecosystem NH_4^+	
	Polecat Creek (WY, USA)	Stream	Increase of secondary productivity (7–40 times higher than that of non-invaded macroinvertebrate communities)	Hall et al. (2006)
	Polecat Creek (WY, USA)	Stream	Change of periphyton composition by reduction of green algae proportion and increasing nitrogen-fixing diatoms	Arango et al. (2009)
	Polecat Creek and Marmot Spring (WY, USA)	Streams	No effects on algal resources	Riley et al. (2008)
			Reduction of native snail growth	
	Snake river (ID, USA)	River	Higher densities than native snails in reaches of slow velocities	Richards et al. (2001)
	Banbury Springs (ID, USA)	Stream	Mud snail niche overlaps with native snail niche	Richards (2004)
			Mud snail and native snails can compete for limited food resources	
	Green river (UT, USA)	Streams and laboratory experiments	Reduction of body weight in *Oncorhynchus mykiss* (laboratory)	Vinson and Baker (2008)
			Reduction of fish health of field populations	
	Madison river basin (Montana and WY, USA)	Field experiments in streams	High densities of mud snail were associated with low colonization of slate tiles by native macroinvertebrates	Kerans et al. (2005)
	Columbia river estuary (OR, USA)	Estuary	No impact of mud snail on native amphipods	Brenneis et al. (2010)
			Positive correlations between native and exotic densities	
Australia	Tarra river (South-Eastern Australia)	Stream	Positive relationship between densities of mud snail and of native invertebrates	Schreiber et al. (2002)
			Positive relationship between density of mud snail and of a number of native taxa	

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growth of native vertebrate species, Vinson and Baker (2008) experimentally showed that *P. antipodarum* caused depletion of body weight and health condition of trouts (*Oncorhychus mykiss*) feeding mostly on *P. antipodarum*. Trout weight fell 0.14–0.48% of the initial weight per day in animals with unlimited diet of *P. antipodarum*, while the weight loss rate of starved trout was 0.52–0.54% per day (Vinson and Baker 2008).

Another factor that determines the impact of alien species on native fauna is the degree of the niche overlap with native species (Zambrano et al. 2010). In the case of *P. antipodarum*, few studies addressed this issue. Richards (2004) found niche overlap between New Zealand mud snail and a native snail *Taylorconcha serpenticola* in an Idaho stream (USA) for temperature, photophobic behaviour, habitat requirements and food resources. Consequently, both species strongly compete with each other. However, Brenneis et al. (2010) did not find competition between an estuarine isopod (*Gnorimosphaeroma insulare*) and *P. antipodarum*, in spite of their common habitat preferences. This fact can be explained by niche partitioning, either for food or for microhabitats. In this case, the intraspecific competition among isopods or among mud snails was higher than interspecific competition between both species (Brenneis et al. 2010).

What makes *P. antipodarum* a successful invader

In a previous study searching for traits that explain the invasive success of *P. antipodarum*, Alonso and Castro-Díez (2008) concluded that the wide tolerance to different physico-chemical conditions contributes to explain its successful transport and establishment. Besides, a successful establishment is possible thanks to a high capacity to overcome or avoid the biotic resistance exerted by the native community, which includes potential predators, parasites and competitors. A successful spread is explained mainly by its explosive and parthenogenetic reproduction rate and the facility to disperse by passive (birds, fish, and drift, floating macrophytes) and active (positive rheotactic) mechanisms (Alonso and Castro-Díez 2008). In the present review, we extend this knowledge by addressing the extent to which two key aspects explaining the invasive success of other species, the enemy release hypothesis and a high genotypic diversity, may also explain the invasive success of *P. antipodarum*.

The "Enemy Release" hypothesis is one of the likely causes for alien species success (Torchin et al. 2003; Gherardi 2007). This hypothesis states that exotic species flourish due to the lack of natural predators or parasites within invaded ecosystems, which provides a competitive advantage for the foreign species. Although there are some potential predators (e.g., rainbow trout) and parasites (e.g., the digenetic trematode *Microphallus* sp) (Kopp and Jokela 2007; Vinson and Baker 2008), *P. antipodarum* has been found to overcome the negative effects of these enemies with different strategies (Kopp and Jokela 2007; Vinson and Baker 2008). For instance, a high proportion of mud snails is able to survive the pass through the digestive tracts of different fish species; up to 50% in the case of rainbow trout (*Oncorhynchus mykiss*) (Vinson and Baker 2008). This ability may be attributed to its solid operculum and its strong shell (Kabat and Hershler 1993; Duft et al. 2003a, b). Moreover, this tolerance allows mud snail to use these fishes as dispersal agents. Additionally, this tolerance might increase predatory pressure on more digestible native invertebrates. On the other hand, Hellmair et al. (2011) reported that the native endangered tidewater goby (*Eucyclogobius newberryi*) may digest this hard-shelled prey, although no energetic benefit to the fish was reported. *Potamopyrgus antipodarum* has a high incidence of parasites in its native range, up to 80% of individuals being infested in some populations and up to 14 species of trematodes being found to parasite *P. antipodarum* (Winterbourn 1973). By contrast, in invaded ecosystems the number of parasite species and their incidence on *P. antipodarum* population has been reported to be very low (Zbikowski and Zbikowska 2009). Only one species of trematode uses *P. antipodarum* as intermediate host in Europe (Zbikowski and Zbikowska 2009) and its incidence is very low (3.3%). However, this can have a positive indirect effect on native fauna, as adding a new potential resistant host species can alter the native host-parasite interaction by the "zooprophylaxis" or "dilution effect" of the invasive species (Hess and Hayes 1970; Kopp and Jokela 2007).

Another key aspect of the success of an invasive species is its genotypic diversity, which helps the population to face environmental change and may increase the range of suitable niches. Given that *P. antipodarum* reproduces parthenogenetically in its invaded range, only mutation or new introductions can increase genetic diversity (Weetman et al. 2006). Mutation rate of this species has been found to be within the range of sexual-reproduction species (Weetman et al. 2006). Genetic diversity of *P. antipodarum* has been reported to be very low in North American and Australian populations where the invasion is relatively recent (Dybdahl and Drown 2011), although Hershler et al. (2010) reported 65 distinct clones in the upper Snake river basin (ID, USA), resulting from clone division in new lineages through mutations. In the case of Europe, there are several clonal lineages as a consequence of the long invasion history (Ponder 1988; Weetman et al. 2002). The lack of sexual reproduction of invasive *P. antipodarum* populations has not prevented them to rapidly spread throughout USA and Canada, although this can be a long-term handicap for the species on the face of environmental changes. However, the disadvantages of asexual reproduction may be compensated for the innate tolerance of this species to a wide range of physico-chemical and ecological properties (Alonso and Castro-Díez 2008).

Conclusions

The revised bibliography has shown that most studies on *P. antipodarum* distribution have been conducted in Europe, North America and Australia, with some punctual studies in Asia. Therefore, *P. antipodarum* distribution in other parts of the world (such as Central and South America, Africa and most of Asia) remains known poorly. A research effort on the distribution of *P. antipodarum* in these geographical areas has to be done in order to get a global view of its worldwide distribution. *Potamopyrgus antipodarum* invasion have contrasting consequences on the invaded ecosystem, from weak or even positive (e.g., increase in native populations) effects to a notable reduction of native invertebrate population, and deep changes on the nutrient cycles. These contrasting effects may be explained by differences in *P. antipodarum* population density, and by the degree of niche overlap between *P. antipodarum* and native macroinvertebrates. Several traits contribute to the successful invasion of this snail, such as its wide tolerance to different physico-chemical conditions, the low level of incidence of parasites and predators, the high reproductive rate and the high capacity to disperse by passive and active mechanisms. However, low genetic diversity shown by apomictic snails in invaded ecosystems may represent an evolutionary disadvantage as compared with native snail populations with sexual reproduction. These effects can be attenuated via mutation and immigration of new lineages. Therefore, special care should be taken to avoid new introductions in order to not increase the evolution rate of this invasive species.

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References

Alonso A (2005) Valoración de la degradación ambiental y efectos ecotoxicológicos sobre la comunidad de macroinvertebrados bentónicos en la cabecera del río Henares. Dissertation, Universiy of Alcala, Spain

Alonso A, Camargo JA (2003) Short-term toxicity of ammonia, nitrite and nitrate to the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). Bull Environ Contam Toxicol 70:1006–1012

Alonso A, Castro-Díez P (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? Hydrobiologia 614:107–116

Arango CP, Riley LA, Tank JL, Hall RO Jr (2009) Herbivory by an invasive snail increases nitrogen fixation in a nitrogen-limited stream. Can J Fish Aquat Sci 66:1309–1317

Baur B, Schmidlin S (2007) Effects of invasive non-native species on the native biodiversity in the river Rhine. In: Netwing W (ed) Biological invasions. Ecological studies, vol 193. Springer, Heidelberg, pp 257–273

Bowler PA (1991) The rapid spread of the freshwater Hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the Middle Snake River, Southern ID. Proc Desert Fishes Counc 21:173–182

Boycott AE (1936) The habitats of freshwater mollusca in Britain. J Anim Ecol 5:111–186

Brenneis VEF, Sih A, de Rivera CE (2010) Coexistence in the intertidal: interactions between the non-indigenous New Zealand mud snail *Potamopyrgus antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. Oikos 119:1755–1764

Brzeziński T, Kołodziejczyk A (2001) Distribution of *Potamopyrgus antipodarum* (Gray, 1843) in waters of the Wigry National Park (NE, Poland) and their effect of selected habitat factors on its occurrence. Folia Malacol 9:125–135

Carlsson R (2000) The distribution of the gastropods *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) in lakes on the Aland Islands, south-western Finland. Boreal Environ Res 5:187–195

Carlsson NOL, Brönmark C, Hansson L-A (2004) Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. Ecology 85:1575–1580

Cianfanelli S, Lori E, Bodon M (2007) Non-indigenous freshwater molluscs and their distribution in Italy. In: Gherardi F (ed) Biological invaders in inland waters: profiles, distribution, and threats. Springer, Dordrecht

Costil K, Dussart GBJ, Daguzan J (2001) Parameters structuring populations of aquatic gastropods in the region of Mont Saint-Michel (France). Biodivers Conserv 10:1–18

Cross WF, Rosi-Marshall EJ, Behn KE, Kennedy TA, Hall RO Jr, Fuller AE, Baxter CV (2010) Invasion and production of New Zealand mud snails in the Colorado River, Glen Canyon. Biol Invasions 12:3033–3043

Davidson TM, Brenneis VEF, de Rivera C, Draheim R, Gillespie GE (2008) Northern range expansion and coastal occurrences of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the northeast Pacific. Aquat Invasions 3:349–353

Dorgelo J (1987) Density fluctuations in populations (1982–1986) and biological observations of *Potamopyrgus jenkinsi* in two trophically differing lakes. Hydrobiol Bull (Amsterdam) 21:95–110

Dorgelo J, Leonards PEG (2001) Relationship between C/N ratio of food types and growth rate in the snail *Potamopyrgus jenkinsi* (E. A. Smith). J N Am Benthol Soc 20:60–67

Duft M, Schulte-Oehlmann U, Tillman M, Markert B, Oehlmann J (2003a) Toxicity of triphenyltin and tributyltin to the freshwater mud snail *Potamopyrgus antipodarum* in a new sediment biotest. Environ Toxicol Chem 22:145–152

Duft M, Schulte-Oehlmann U, Weltje L, Tillmann M, Oehlmann J (2003b) Stimulated embryo production as a parameter of estrogenic exposure via sediments in the freshwater mud snail *Potamopyrgus antipodarum*. Aquat Toxicol 64:437–449

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends Ecol Evol 14:135–139

Dybdahl MF, Drown DM (2011) The absence of genotypic diversity in a successful parthenogenetic invader. Biol Invasions 13:1663–1672

Filippenko DP, Son MO (2008) The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) is colonising the artificial lakes of Kaliningrad City, Russia (Baltic Sea Coast). Aquat Invasions 3:345–347

Gangloff MM (1998) The New Zealand mud snail in Western North America. Aquat Nuis Species 2:25–30

Gérard C, Blanc A, Costil K (2003) *Potamopyrgus antipodarum* (Mollusca: Hydrobiidae) in continental aquatic gastropod

communities: impact of salinity and trematode parasitism. Hydrobiologia 493:167–172

Gherardi F (2007) Biological invaders in inland waters: profiles, distribution, and threats. Springer, Dordrecht

Grant A, Briggs A (1998) Toxicity of ivermectin to estuarine and marine invertebrates. Mar Pollut Bull 36:540–541

Grigorovich IA, Korniushin AV, Gray DK, Duggan IC, Colautti RI, MacIsaac HJ (2003) Lake Superior: an invasion cold spot? Hydrobiologia 499:191–210

Hall RO Jr, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Front Ecol Environ 1:407–411

Hall RO Jr, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. Ecol Appl 16:1121–1131

Hellmair M, Goldsmith G, Kinziger AP (2011) Preying on invasives: the exotic New Zealand mud snail in the diet of the endangered tidewater goby. Biol Invasions 13:2197–2201

Herbst DB, Bogan MT, Lusardi RA (2008) Low specific conductivity limits growth and survival of the New Zealand mud snail from the upper Owens RIVER, California. West North Am Nat 68:324–333

Hershler R, Liu H-P, Clark WH (2010) Microsatellite evidence of invasion and rapid spread of divergent New Zealand mud snail (*Potamopyrgus antipodarum*) clones in the Snake River basin, ID, USA. Biol Invasions 12:1521–1532

Hess AD, Hayes RO (1970) Relative potentials of domestic animals for zooprophylaxis against mosquito vectors of encephalitis. Am J Trop Med Hyg 19:327–334

Heywood J, Edwards RW (1962) Some aspects of the ecology of *Potamopyrgus jenkinsi* Smith. J Anim Ecol 31:239–250

Huebner G, Braukmann U (2005) On the development of the sweet water molluscs (Gastropoda and Bivalvia) in the river basin of the lower Werra. Philippia 12:125–136

Jensen A, Forbes VE, Parker D Jr (2001) Variation in cadmium uptake, feeding rate, and life-history effects in the gastropod *Potamopyrgus antipodarum*: linking toxicant effects on individuals to the population level. Environ Toxicol Chem 20:2503–2513

Jokela J, Lively CM, Dybdahl ME, Fox JA (1997) Evidence for a cost of sex in the freshwater snail *Potamopyrgus antipodarum*. Ecology 78:452–460

Kabat AR, Hershler R (1993) The prosobranch snail family Hydrobiidae (Gastropoda: Rissoidae): review of classification and supraspecific taxa. Smithson Contributions Zool 547:94

Kerans BL, Dybdahl MF, Gangloff MM, Jannot JE (2005) *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone ecosystem. J N Am Benthol Soc 24:123–138

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kołodziejczyk A, Lewandowski K, Stańczykowska A (2009) Long-term changes of mollusc assemblages in bottom sediments of small semi-isolated lakes of different trophic state. Pol J Ecol 57:331–339

Kopp K, Jokela J (2007) Resistant invaders can convey benefits to native species. Oikos 116:295–301

Left LG, Burch JL, McArthur JV (1990) Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata* in a coastal plain stream. Freshw Biol 24:409–416

Levri EP, Kelly AA, Love E (2007) The invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in Lake Erie. J Gt Lakes Res 33:1–6

Levri EP, Dermott RM, Lunnen SJ, Kelly AA, Ladson T (2008) The distribution of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in Lake Ontario. Aquat Ecosyst Health Manag 11:412–421

Lewin I, Smolinski A (2006) Rare and vulnerable species in the mollusc communities in the mining subsidence reservoirs of an industrial area (The Katowicka Upland, Upper Silesia, Southern Poland). Limnologica 36:181–191

Lively CM (1987) Evidence from a New Zealand snail for the maintenance of sex by parasitism. Nature 328:519–521

Loo SE, Keller RP, Leung B (2007a) Freshwater invasions: using historical data to analyse spread. Divers Distrib 13:23–32

Loo SE, Nally RM, Lake PS (2007b) Forecasting New Zealand mud snail invasion range: model comparisons using native and invaded ranges. Ecol Appl 17:181–189

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species a selection from the global invasive species database. Published by the Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the world conservation union (IUCN), p 12. First published as special lift-out in Aliens Dec 12th 2000. (Updated and reprinted version)

Marshall JW, Winterbourn MJ (1979) An ecological study of a small New Zealand stream with particular reference to the oligochaeta. Hydrobiologia 65:199–208

Møller V, Forbes VE, Depledge MH (1994) Influence of acclimation and exposure temperature on the acute toxicity of cadmium to the freshwater snail *Potamopyrgus antipodarum* (Hydrobiidae). Environ Toxicol Chem 13:1519–1524

Mouthon J, Dubois JP (2001) Mollusc communities of the littoral zone of Annecy Lake (Savoie, France). Ann Limnol Int J Limnol 37:267–276

Múrria C, Bonada N, Prat N (2008) Effects of the invasive species *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) on community structure in a small Mediterranean stream. Fundam Appl Limnol 171:131–143

Naser MD, Son MO (2009) First record of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray 1843) from Iraq: the start of expansion to Western Asia? Aquat Invasions 4:369–372

Netwing W (2007) Biological invasions: why it matters. In: Netwing W (ed) Biological invasions. Ecological studies, vol 193. Springer, Heidelberg, pp 1–6

Pérez-Quintero JC (2009) Freshwater molluscs from the biosphere reserve "Dehesas de Sierra Morena", SW Iberian Peninsula. Iberus 27:1–18

Ponder WF (1988) *Potamopyrgus antipodarum*, a molluscan colonizer of Europe and Australia. J Molluscan Stud 54:271–286

Radea C, Louvrou I, Economou-Amilli A (2008) First record of the New Zealand mud snail *Potamopyrgus antipodarum* J.E. Gray 1843 (Mollusca: Hydrobiidae) in Greece—Notes on its population structure and associated microalgae. Aquat Invasions 3:341–344

Richards DC (2002) The New Zealand mud snail invades the Western United States. Aquat Nuis Species 4:42–44

Richards DC (2004) Competition between the threatened bliss rapids snail, *Taylorconcha serpenticola* (Hershler et al.) and the invasive, aquatic snail, *Potamopyrgus antipodarum* (Gray). Dissertation, Montana State University

Richards DC, Cazier LD, Lester GT (2001) Spatial distribution of three snail species, including the invader *Potamopyrgus antipodarum*, in a freshwater spring. Western North Am Nat 61:375–380

Riley LA, Dybdahl MF, Hall RO Jr (2008) Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. J N Am Benthol Soc 27:509–520

Ross RM, Lellis WA, Bennett RM, Johnson CS (2001) Landscape determinants of nonindigenous fish invasions. Biol Invasions 3:347–361

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Evol Syst 32:305–332

Schmidlin S, Schmera D, Baur B (2012) Alien molluscs affect the composition and diversity of native macroinvertebrates in a sandy flat of Lake Neuchâtel, Switzerland. Hydrobiologia 679:233–249

Schreiber ESG, Glaister A, Quinn GP, Lake PS (1998) Life history and population dynamics of the exotic snail *Potamopyrgus antipodarum* (Prosobranchia: Hydrobiidae) in lake Purrumbete, Victoria, Australia. Mar Freshw Res 49:73–78

Schreiber ESG, Lake PS, Quinn GP (2002) Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with native benthic fauna. Biol Invasions 4:317–325

Schreiber ESG, Quinn GP, Lake PS (2003) Distribution of an alien aquatic snail in relation to flow variability, human activities and water quality. Freshw Biol 48:951–961

Shimada K, Urabe M (2003) Comparative ecology of the alien freshwater snail *Potamopyrgus antipodarum* and the indigenous snail *Semisulcospira* spp. Venus (Tokyo) 62:39–53

Simoes M (1988) Distribución en Portugal de *Potamopyrgus jenkinsi* (Prosobranchia Hydrobiidae). Iberus 8:243–244

Soler J, Moreno D, Araujo R, Ramos MA (2006) Diversidad y distribución de los moluscos de agua dulce en la Comunidad de Madrid (España). Graellsia 62:201–252

Son MO, Nabozhenko MV, Shokhin IV (2008) The Don River basin is a new stage of expansion of *Potamopyrgus jenkinsi* (Smith, 1889) (Gastropoda, Hydrobioidea) in Europe. Dokl Biol Sci 419:129–130

Sousa R, Guilhermino L, Antunes C (2005) Molluscan fauna in the freshwater tidal area of the River Minho estuary, NW of Iberian Peninsula. Ann Limnol Int J Limnol 41:141–147

Strayer DL (1999) Effects of alien species on freshwater molluscs in North America. J N Am Benthol Soc 18:74–98

Strzelec M (2005) Impact of the introduced *Potamopyrgus antipodarum* (Gastropoda) on the snail fauna in post-industrial ponds in Poland. Biologia 60:159–163

Thomsen MS, Wernberg T, Silliman BR, Josefson AB (2009) Broad-scale patters of abundance of non-indigenous soft-bottom invertebrates in Denmark. Helgoland Mar Res 63:159–167

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Van den Berg MS, Coops H, Noordhuis R, van Schie J, Simons J (1997) Macroinvertebrate communities in relation to submerged vegetation in two Chara-dominated lakes. Hydrobiologia 342:143–150

Vinson MR, Baker MA (2008) Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodarum*. North Am J Fish Manag 28:701–709

Wagner S (2000) Mollusc population in the main river near Muehlheim/Dietesheim, Germany. Mitteilungen der Deutschen Malakozoologischen Gesellschaft 65:23–33

Weatherhead MA, James MR (2001) Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. Hydrobiologia 462:115–129

Weetman D, Hauser L, Carvalho GR (2002) Reconstruction of microsatellite mutation history reveals a strong and consistent deletion bias in invasive clonal snails, *Potamopyrgus antipodarum*. Genetics 162:813–822

Weetman D, Hauser L, Carvalho GR (2006) Heterogeneous evolution of microsatellites revealed by reconstruction of recent mutation history in an invasive apomictic snail, *Potamopyrgus antipodarum*. Genetica 127:285–293

Werner H, Boeters HD, Guenther A (1994) On the freshwater mollusc fauna in the Spanish province of Cuenca. Malakologische Abhandlungen (Dresden) 17:1–9

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666

Winterbourn MJ (1970) The New Zealand species of *Potamopyrgus* (Gastropoda: Hydrobiidae). Malacologia 10:283–321

Winterbourn MJ (1973) A guide to the freshwater mollusca of New Zealand. Tuatara 20:141–159

Zambrano L, Valiente E, Zanden MJV (2010) Food web overlap among native axolotl (*Ambystoma mexicanum*) and two exotic fishes: carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*) in Xochimilco, Mexico City. Biol Invasions 12:3061–3069

Zaranko DT, Farara DG, Thompson FG (1997) Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). Can J Fish Aquat Sci 54:809–814

Zbikowski J, Zbikowska E (2009) Invaders of an invader: trematodes in *Potamopyrgus antipodarum* in Poland. J Invertebr Pathol 101:67–70

Zettler ML, Richard D (2004) Freshwater molluscs from Corsica. Notated collections from summer 2003 with emphasis on *Theodoxus fluviatilis*. Malakologische Abhandlungen (Dresden) 22:3–16

Zieritz A, Waringer J (2008) Distribution patterns and habitat characterization of aquatic Mollusca in the Weidlingbach near Vienna, Austria. Arch fuer Hydrobiol Suppl 166:271–292