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INVASIVE FRESHWATER MOLLUSCS

Effects of the invasive aquatic snail *Potamopyrgus antipodarum* (Gray, 1853) on ecosystem properties and services

Álvaro Alonso · Gonzalo A. Collado · Claudia Gérard · Edward P. Levri · Rodrigo B. Salvador · Pilar Castro-Díez

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Abstract Ecosystems provide benefits to humans, including provisioning, regulating, and cultural services. However, invasive species can threaten ecosystem well-functioning and services provided. One invasive species with such potential is the New Zealand mud snail (NZMS) *Potamopyrgus antipodarum*. The aims of this study are focused on the quantitative review of (1) the NZMS impacts on ecosystem properties and their direct links with ecosystem services, and (2) the ecosystem services that can be affected by the NZMS. The high density reached by this species in most of the invaded ecosystems and its highly competitive ability affect ecosystem structure and functioning. However, some facilitation processes on native species may result in an improvement of some services. The NZMS tends to positively affect cultural services (88% positive cases) but negatively to provisioning services (77% of cases). Regarding, regulating and maintenance services, the proportions of positive and negative effects were similar (45% vs 36%, respectively). Therefore, the NZMS is a species with numerous negative impacts on ecosystem services. However, ecosystem services related to health (e.g., dilution effect against parasites) and research (e.g., biomonitoring) are cultural services that the NZMS can improve. No economic assessment of the impacts of the NZMS is available in the literature.

Keywords Invasive species · Ecosystem functioning · Cultural services · Provisioning services · Regulating and maintenance services · Ecological impacts

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Introduction

Ecosystem services are the benefits that ecosystems directly provide to human welfare through markets or other non-market values (Hooper et al., 2005; Millennium Ecosystem Assessment, 2005; Vilà & Hulme, 2017; Haines-Young & Potschin, 2018). These include provisioning services, i.e., goods obtained from ecosystems (e.g. food, water, fibers, or medicines), regulating services, i.e., the capacity of ecosystems to maintain their "homeostasis" and prevent catastrophic events (e.g. climate regulation, prevention of floods or pests, water purification), and cultural services, i.e., spiritual values that also contribute to human welfare (e.g. recreation, esthetic assets, and spiritual fulfillment) (Millennium Ecosystem Assessment, 2005; Haines-Young & Potschin, 2018). In recent decades, the growing demand of resources by humans is endangering ecosystem integrity, and thus, the capacity of ecosystems to provide services in a sustainable way (Millennium Ecosystem Assessment, 2005; Nishijima & Belgrano, 2020; O'Brien et al., 2021; Ashrafi et al., 2022). In fact, pollution, overexploitation of resources, and the introduction of exotic species are major threats to many ecosystem services (Millennium Ecosystem Assessment, 2005; Shin-ichiro et al., 2009; Lodge et al., 2012; Vilà & Hulme 2017; Cañedo-Argüelles, 2020).

Biological invasions represent one of the greatest threats to ecosystems and biodiversity (Gherardi, 2007; Shin-ichiro et al., 2009; Havel et al., 2015; Corrales et al., 2020). Specifically, aquatic ecosystems are exposed to a continuous increase in introductions of exotic species worldwide (Gherardi, 2007; Strayer, 2010; Lodge et al., 2012; Katsanevakis et al., 2014; Nunes et al., 2015; Corrales et al., 2020). Some introductions have been intentional, such as those fish, molluscs, and crayfish that have been intentionally introduced as food resources or to control disease vectors (Gofas & Zenetos, 2003; Gherardi, 2011; Deines et al., 2016; Heikal et al., 2018). Others have been accidental, such as those aquatic invertebrates introduced through ballast waters, attached to ships, or by inland canals (Gofas & Zenetos, 2003; Alonso & Castro-Díez, 2008; Nunes et al., 2015; Gilioli et al., 2017; Gallardo et al., 2019). In fact, invasive alien species are an important component of the global change that threatens the well-functioning of ecosystems and many of the services they provide (Gherardi, 2007; Strayer, 2010; Lodge et al., 2012; Katsanevakis et al., 2014; Corrales et al., 2020).

Aquatic ecosystems are particularly vulnerable to invasive species (Gherardi, 2007; Strayer, 2010; Nunes et al., 2015; Moorhouse & Macdonald, 2015; Corrales et al., 2020). That vulnerability is likely caused by (1) the higher dispersal ability of freshwater species as compared with terrestrial organisms, (2) the high rates of endemism (and often low biodiversity) of inland waters, and (3) the intense use of aquatic ecosystems by humans for recreational, commercial, and food resources (Gherardi, 2007). Invasive aquatic species may modify the structure and functioning of aquatic ecosystems (Shin-ichiro et al., 2009; Havel et al., 2015; Petsch, 2016; Corrales et al., 2020), which in turn may cause direct or indirect harmful impacts on human societies and economies (Shin-ichiro et al., 2009; Lodge et al., 2012; Laverty et al., 2015; Deines et al., 2016). However, biotic changes in aquatic ecosystem, including changes caused by exotic species, may increase some ecosystem services while simultaneously decreasing others (Hooper et al., 2005; Shin-ichiro et al., 2009; Limburg et al., 2010; Lodge et al., 2012; Katsanevakis et al., 2014; Laverty et al., 2015; Deines et al., 2016). For instance, some dreissenid mussels (*Dreissena polymorpha* (Pallas, 1771) and *Dreissena burgensis* (Andrusov, 1897)) can increase water clarity through filtration, but also increase nuisance algae (Limburg et al., 2010). Most introduced crayfish are a food supply for people, thus increasing a provisioning service; yet they are also important vectors of parasites and pathogens (Lodge et al., 2012). Thus, there is growing recognition that exotic species may either increase or decrease ecosystem services (Limburg et al., 2010; Lodge et al., 2012; Deines et al., 2016; Vilà & Hulme, 2017; Kourantidou et al., 2022). Many changes in ecosystem services are caused by the profound impacts of these species on the properties of aquatic ecosystems, mostly when they become invasive (Shin-ichiro et al., 2009; Limburg et al., 2010; Lodge et al., 2012; McLaughlan et al., 2014; Walsh et al., 2016). Therefore, the development of studies on the effects of exotic species on ecosystem services is important to aid and inform decision making by aquatic ecosystem managers and policymakers.

Ecosystem properties include both ecological compartments (e.g., pools of organic matter) and rates of processes (e.g., fluxes of energy among

compartments), they are different across ecosystems, but not inherently "good" or "bad" (Hooper et al., 2005). By contrast, ecosystem services contribute to human welfare, so they are considered as "good" for human well-being (Hooper et al., 2005; Millennium Ecosystem Assessment, 2005). Some changes in ecosystem properties are directly related to certain ecosystem services. For example, the shells of dreissenid mussels on submerged surfaces can cause an increase in biofouling with a direct cost for the maintenance of infrastructure (Nakano & Strayer, 2014). However, other changes in ecosystem properties caused by invasive species are not so clearly related to ecosystem services, and their impact on services is difficult to discern (Charles & Dukes, 2007). Therefore, there is a need of knowledge on the links between changes of ecosystem properties by invasive species and their impact on ecosystem services (Walsh et al., 2016).

The impacts of various invasive alien species of crayfish (*Procambarus clarkii* (Girard, 1852), *Pacifastacus leniusculus* (Dana, 1852), *Orconectes* spp., *Cherax* spp.), bivalves (*Dreissena polymorpha* and *D. burgensis*), and gastropods (*Pomacea* spp.) on ecosystem services have been extensively studied (Limburg et al., 2010; Lodge et al., 2012; McLaughlan et al., 2014; Gilioli et al., 2017). However, alterations caused by other aquatic invertebrate species have been more studied from the perspective of their immediate ecological impacts than from the perspective of ecosystem services and "disservices." This is the case of the New Zealand mudsnail (NZMS) *Potamopyrgus antipodarum* (Gray, 1853). The impacts of this successful invader on aquatic ecosystems, along with the causes of its ecological success, have been previously reviewed (Alonso & Castro-Díez, 2008, 2012) and recently updated (Geist et al., 2022). Even though this species is highly invasive, the benefits and harms of the NZMS on ecosystems services have received much less attention compared to other invasive invertebrates.

The NZMS is an aquatic gastropod of the family Tateidae; it is native to New Zealand but reported on most continents (except Antarctica) (Alonso & Castro-Díez, 2012; Taybi et al., 2021; Geist et al., 2022). This species presents a high reproductive rate and the ability to quickly monopolize invertebrate secondary production, helping to explain its high impact in most of the invaded ecosystems (Alonso & Castro-Díez, 2008). Previous studies showed that the NZMS highly affects both the structure and functioning of aquatic ecosystems (for more details, see reviews by Alonso & Castro-Díez, 2008, 2012; Geist et al., 2022). The secondary production reported for this species is one of the highest for a stream invertebrate (Hall et al., 2006). This finding is in accordance with the high densities found in some invaded ecosystems, reaching up to 800,000 individuals per square meter (Dorgelo, 1987). This species can consume up to 75% of the primary production of streams (Hall et al., 2003), successfully competing against native species while also benefiting a few other native fauna (Schreiber et al., 2002; Alonso & Castro-Díez, 2008; Riley et al., 2008; Rakauskas et al., 2016, 2018). Despite the severe impacts reported in the scientific literature for the NZMS, there is scarce information on how it increases or decreases specific ecosystem services.

The aim of this study is to review the scientific literature to identify both positive and negative effects of the NZMS on a wide range of ecosystem services throughout the introduced range. We also aim to identify how this species alters ecosystem properties and the direct effects of these changes on ecosystem services. This review provides (1) impacts of the NZMS on ecosystem properties and how these effects may be directly linked with improvements or impairments on the ecosystem services, and (2) information on the ecosystem services that can be potentially (directly or indirectly) affected by this invasive species.

Materials and methods

We focus on the effects of the NZMS on ecosystem properties and services in its non-native range. We used the term "effects" to document changes produced by the NZMS on aquatic ecosystem properties. Additionally, we attempt to estimate the type of the change caused by the NZMS on each ecosystem service (increase or decrease or non-change in the services).

Autoecology of the NZMS

Most of the non-native populations of the NZMS are composed of parthenogenetic females and no evidence of sexual reproduction has been reported outside of its native range (Alonso & Castro-Díez, 2008; Butkus et al., 2020). This species is ovoviviparous,

and its sexual maturity is reached at shell length ranging from 2.0 to 3.5 mm (Lassen, 1979; Richards, 2002; Alonso & Castro-Díez, 2008; Gaino et al., 2008; McKenzie et al., 2013). In the brood pouch, which is formed by an elongated oviduct, adult females carry about 60 eggs and up to 147 embryos at different stages of development (Lassen, 1979; Gaino et al., 2008; Verhaegen et al., 2018, 2021). Up to six generations per year have been reported and the NZMS is a prolific reproducer that can produce a mean number of 230 offspring per adult female per year (Lassen, 1979; Richards, 2002). Field studies show the existence of drastic differences in space and time for fecundity of this species (Verhaegen et al., 2021). In any case, the NZMS is reported as a gastropod with a high reproductive effort, with a clear r-selected strategy (Lassen, 1979).

In its native New Zealand range, the NZMS not only is abundant in freshwater ecosystems (lakes, ponds, rivers, and streams) (Winterbourn, 1969, 1970; Alonso & Castro-Díez, 2008), but it also lives in water with up to 26‰ of salinity (Winterbourn, 1969, 1970; Alonso & Castro-Díez, 2008). The species can tolerate a wide range of environmental conditions in both native and invaded areas (Winterbourn, 1969; Alonso & Castro-Díez, 2008, 2012), but relative high temperature of water (> 30 °C) appears to restrict its distribution in New Zealand (Winterbourn, 1969). Clements et al. (2011) found populations of the NZMS in geothermal streams (Yellowstone National Park, USA) at water temperatures up to 35.3 °C. Low temperatures can also limit the species as Moffitt and James (2012) showed that the size of the NZMS populations is controlled by near-to-below freezing winter, with very low densities or lack of detection in field populations at freezing areas (Idaho, USA). Additionally, low water conductivity, low calcium ion concentration, and a high velocity of water have likewise been reported as limiting factors for the distribution of this snail (Vazquez et al., 2016, Verhaegen et al., 2019; Larson et al., 2020a). Acidic waters would also appear to limit species as low pH is a common limiting factor to molluscs (Okland, 1992; Levri et al., 2020).

Literature search

We performed a literature search of scientific publications on the NZMS using the *Web of Science* (https://www.webofscience.com/) in February 2022. The search covered the years from 1904 to 2022 and used different keywords and search strings (Table S1). With these combinations, scientific publications on ecosystem services and impacts on ecosystem properties were gathered. Additionally, technical reports and gray literature were also included. For this, Google Scholar search, and the Google search using the custom IGO (intergovernmental organizations), and NGO (non-governmental organizations) search tools were used in conjunction with expert knowledge by the authors regarding publications that cannot be found online.

Data compilation

The documents retrieved from the literature search were filtered according to the following procedure. (1) We checked whether the title was related with any target ecosystem properties/services (see below). (2) We read the abstract and, if the publication was clearly related with ecosystem properties and/or services, it was selected. (3) All selected publications were thoroughly checked to summarize all information on the potential effects of the NZMS on ecosystem properties and/or services in its non-native range. Ecosystem properties include both ecological compartments (e.g., pools of organic matter) and rates of processes (e.g., fluxes of energy among compartments) (Hooper et al., 2005). Changes on ecosystem properties were considered when authors of publications assessed any change caused by the NZMS in its non-native range (e.g., changes in secondary production). For each selected publication, the likely direct changes on ecosystem services (Provisioning, Regulation and Maintenance, and Cultural services) were also identified (Haines-Young & Potschin, 2018). The expert opinion of the authors was used to determine which ecosystem services would be directly affected by the changes in ecosystem properties. Since most of the available information does not allow a quantification of the ecosystem service, the collected data are largely qualitative.

For linking the variables reported by documents to ecosystem services, we used the Common International Classification of Ecosystem Services (CICES) (Haines-Young & Potschin, 2018). Three main groups of ecosystem services were analyzed: provisioning, regulation and maintenance, and cultural services.

Each service is subsequently classified into several final sub-categories that are the ultimate benefits for people (e.g., food provisioning). Some of the outputs from ecosystems can be less tangible, such as the cultural services (e.g., recreational services or scientific value). In the compiled publications on ecosystem services, any aspect that can link with changes caused by the NZMS on ecosystem services, directly or indirectly, was selected. For that, the expert opinion of authors was followed (Drescher et al., 2013). The background ecological knowledge of the authors (e.g., parasitology, ecosystem function, autoecology, ecotoxicology, biomonitoring, behavior, community ecology, etc.) allowed an effective and rigorous classification of the possible impacts of the species on contrasting ecosystem services. Each effect on ecosystem services was classified in the most appropriate category (or categories) according to CICES (Haines-Young & Potschin, 2018). For each publication and service, the direction of the change was established ("+" the service increases, "−" the service decreases, and "0" the service is unchanged). The description of the change was established in a qualitative way.

Statistical analysis

The frequency of positive, neutral, and negative effects of the NZMS on the three main groups of ecosystem services (provisioning, regulation and maintenance, and cultural services) was compared by means of Fisher's exact test (Field et al., 2012). When the frequency of positive, neutral, or negative cases is higher than expected by chance, the Fisher's exact test reports a p value less than 0.05 (Field et al., 2012). Additionally, pairwise comparisons using Fisher's exact test for count data were used to compare the sign of cases among ecosystem services. Statistical analysis was conducted by means of the *fisher.test* and *fisher.multcomp* functions in R 4.0.5. Software (R Core Team, 2021).

Results

A total of 805 scientific publications were retrieved from the search in *Web of Science*. Among them, a total of 88 publications and documents, containing information of the effects of the NZMS on ecosystem properties and services, were finally selected. 37 out of them provided information on ecosystem properties (Supplementary S1) and 67 on ecosystem services (Supplementary S2). Table 1 summarizes the effects of the NZMS in its non-native area on ecosystem properties related to ecological compartments and rates of processes, and how these changes can cause direct effects on the main ecosystem services (provisioning, regulating and maintenance, and cultural services). In general, the NZMS affects the ecosystem properties in several ways, which can alter ecosystem services, mostly provisioning and cultural ones (Table 1). However, the revised literature shows that the three main ecosystem services could be directly affected by this species. Eight direct impacts of the NZMS on provisioning services, four in regulating and maintenance services, and eight in cultural services were identified (Table 1). Table 2 summarizes the effects of the NZMS for likely direct and indirect modifications on ecosystem services considering the CICES (Haines-Young & Potschin, 2018).

Across all publications and documents selected, a total of 90 case studies on the effects (positive, neutral, and negative) of the NZMS on the ecosystem services were collected (Fig. 1). For cultural services, most of the cases were positive (88%) (Fig. 1). On the contrary, for provisioning services, most of the cases were negative (77%). The regulating and maintenance services showed a relatively similar number of positive and negative effects (45% and 36%, respectively). Only provisioning, and regulating and maintenance services showed neutral cases, with 11 and 18% of cases, respectively (Fig. 1). The frequency of cases was different than expected by chance (Fisher's exact test $P < 0.001$) (Fig. 1). The frequency of positive and negative cases was the main cause of the differences between services ($P < 0.001$; pairwise Fisher's exact test).

Discussion

Effects of the NZMS on ecosystem properties

Effects on native fauna

The NZMS reaches a high density in most of the invaded ecosystems with up to 800,000 individuals per square meter (Dorgelo, 1987; Alonso & Castro-Díez, 2012; Geist et al., 2022). These characteristics,

Table 1 Effects of *Potamopyrgus antipodarum* on ecosystem properties (related to ecological compartments and rates of process) and its likely direct effects on ecosystem services (provisioning, regulating & maintenance, and cultural services)

Ecosystem properties related to	Change	Probable direct effect on			References
		Provisioning services	Regulating and maintenance services	Cultural services	
Ecological compartments	Extremely high density and biomass (up to 800,000 individuals per square meter). Dominance of macroinvertebrate community Competition with native invertebrates	Reduction of wild invertebrate populations	Changes in water properties by shell accumulation (i.e., less availability of calcium)	Reduction of invertebrate stocks supporting angling activities	Dorgelo (1987), Richards et al. (2001), Gérard et al. (2003, 2017), Hall et al. (2003, 2006), Cada (2004), Richards (2004), Kerans et al. (2005, 2010), Strzelec (2005), Lewin & Smolinski (2006), Vinson et al. (2007), Lysne & Koetsier (2008), Riley et al. (2008), Moore et al. (2012), Bennett et al. (2015) and Riley & Dybdahl (2015)
Ecological compartments	Facilitation of native invertebrates	Increase of wild invertebrate populations	–	Increase of invertebrate stocks supporting angling activities	Schreiber et al. (2002) and Brenneis et al. (2010, 2011)
Ecological compartments	Reduction of body weight and health of fish Low assimilation by fish	Reduction of wild fish populations	–	Reduction of fish stocks for angling activities	Cada (2004), Vinson & Baker (2008), Rakauskas et al. (2016), Butkus & Rakauskas (2020) and Butkus & Visinskiene (2020)
Ecological compartments	Carries parasites to fish and waterfowl	Reduction of wild fish-farmed fish and waterfowl populations	–	Reduction of fish and waterfowl stocks for angling or hunting activities Losses for ornamental waterfowl trade	Beverley-Burton (1972), Hine (1978), Morley (2008) and Gérard et al. (2017)
Rates of processes	Extremely high secondary production	Reduction of wild invertebrate populations Displacement or extinction of native snails	Changes in water properties by shell accumulation (i.e., less availability of calcium)	Reduction of invertebrate stocks supporting angling activities. Water fouling by blockage of pipes	Ponder (1988), Kerans et al. (2005), Hall et al. (2006), Collado et al. (2019a, b) and Collado & Fuentealba (2020)

Table 1 (continued)

Ecosystem properties related to	Change	Probable direct effect on			References
		Provisioning services	Regulating and maintenance services	Cultural services	
Rates of processes	High consumption of primary production	Reduction of wild and cultivated aquatic plants	–	–	Hall et al. (2003), Riley et al. (2008), Krist & Charles (2012), Bennett et al. (2015) and Larson & Black (2016)
Rates of processes	Excretion up to 65% of the ammonium demanded by plants and microbes Increase of N fixation by consuming green algae and facilitate nitrogen-fixing diatoms Changes in nitrogen cycle by systematic depletion of δ15N signatures	Increase of wild and cultivated aquatic plants Reduction of water quality for human consumption	Alteration of water properties	Reduction of the recreational usefulness of water bodies (i.e., eutrophication)	Hall et al. (2003), Arango et al. (2009) and Moore et al. (2012)
Rates of processes	Increase of leaf litter processing	–	Alteration of water properties	Reduction of the recreational usefulness of water bodies (i.e., eutrophication)	Geist et al. (2022)
Rates of processes	Reduction of energy flow from basal resource to fish predators	Reduction of wild fish populations	–	Reduction of fish stocks for angling activities	Vinson & Baker (2008) and Rakauskas et al. (2018)

References are in Supplementary S1

Table 2 Effects of *Potamopyrgus antipodarum* on ecosystem services (provisioning, regulating and maintenance, and cultural services). For each service, the sign of change is shown ('+' increase the service, '−' reduce the service, or '0' no effect on service)

Ecosystem services	Division	Group	Sign of change	Effect description	References
Provisioning	Biomass	Cultivated aquatic plants for nutrition, materials, or energy	−	Impact on plant production. NZMS consumes a high amount of primary production	Holomuzki et al. (2006), Krist & Charles (2012) and Laverty et al. (2015)
Provisioning	Biomass	Reared animals for nutrition, materials, or energy	−	*Potamopyrgus antipodarum* as a host of parasites	Adema et al. (2009), Jones et al. (2015) and Laverty et al. (2015)
Provisioning	Biomass	Reared animals for nutrition, materials, or energy	− 0+	*Potamopyrgus antipodarum* as a likely host of parasites. *Fasciola hepatica* DNA has been detected in *P. antipodarum* tissues without confirmation by means of dissection. It could be a positive (dilution effect), neutral or negative (new host) effect	Jones et al. (2015)
Provisioning	Biomass	Reared aquatic animals for nutrition, materials, or energy	−	*Potamopyrgus antipodarum* as a host of parasites Cost of disinfection procedures in hatchery environment	Gérard & Le Lannic (2003), Hoyer & Myrick (2012), Laverty et al. (2015), Gérard et al. (2017) and Oliver et al. (2021)
Provisioning	Biomass	Wild animals (terrestrial and aquatic) for nutrition, materials, or energy	−	*Potamopyrgus antipodarum* as a host of parasites Poor diet for native fish Poor diet for rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) *Potamopyrgus antipodarum* has the potential to severely impact freshwater fisheries Negative impact on native invertebrates The presence of *Potamopyrgus antipodarum* led to short term, asymmetric, apparent competition between native crayfish	Evans et al. (1981), Richards (2002), Gérard & Le Lannic (2003), Gérard et al. (2003), Cada (2004), Kopp & Jokela (2007), Proctor et al. (2007), Morley (2008), Vinson & Baker (2008), Adema et al. (2009), Bruce et al. (2009), Zbikowski & Zbikowska (2009), Davies & Moeltner (2010), Brenneis et al. (2011), Rakauskas et al. (2016), Cichy et al. (2017), Gérard et al. (2017, 2018), Rakauskas et al. (2018) and Butkus & Visinskine (2020)

Table 2 (continued)

Ecosystem services	Division	Group	Sign of change	Effect description	References
Provisioning	Biomass	Wild animals (terrestrial and aquatic) for nutrition, materials, or energy	+	*Potamopyrgus antipodarum* is found in the diet of native fish For crustaceans, the energy provided by ingestion of *Potamopyrgus antipodarum* and native prey was higher than that of native prey alone	Brenneis et al. (2011) and Hellmair et al. (2011)
Provisioning	Biomass	Wild animals (terrestrial and aquatic) for nutrition, materials, or energy	0	For fish, the energy provided by ingestion of *Potamopyrgus antipodarum* did not differ from that of native preys Fish were not negatively affected by different *Potamopyrgus* densities	Cada (2004) and Brenneis et al. (2011)
Provisioning	Biomass	Wild animals (terrestrial and aquatic) for nutrition, materials, or energy	− 0+	*Potamopyrgus antipodarum* as a diet for Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)) shows positive, neutral, or negative effects	Bersine et al. (2008)
Provisioning	Water	Surface water used for nutrition, materials, or energy	−	*Potamopyrgus antipodarum* is a biofouler for pipes and filters	Moseley (2003) and Nakano & Strayer (2014)
Regulation and maintenance	Transformation of biochemical or physical inputs to ecosystems	Mediation of wastes or toxic substances of anthropogenic origin by living processes	+	Accumulation of Cu from water in the tissues of *Potamopyrgus antipodarum*	Ramskov et al. (2015)
Regulation and maintenance	Regulation of physical, chemical, biological conditions	Pest and disease control	+	Dilution effect of *Potamopyrgus antipodarum* against pathogens *Potamopyrgus antipodarum* may limit or decrease abundance of snail hosts of pathogens of medical and veterinary importance (*Bulinus truncatus*/*Schistosoma* spp.) by means of competition	Marszewska et al. (2018), Mulero et al. (2021) and Zbikowska et al. (2021)

Table 2 (continued)

Ecosystem services	Division	Group	Sign of change	Effect description	References
Regulation and maintenance	Regulation of physical, chemical, biological conditions	Pest and disease control	0	No dilution effect of *Potamopyrgus antipodarum* against pathogens	Larson et al. (2020b)
Regulation and maintenance	Regulation of physical, chemical, biological conditions	Water conditions	−	Hoard of carbon from terrestrial leaf litter by *Potamopyrgus antipodarum* Hoard of secondary production by *Potamopyrgus antipodarum*	Hall et al. (2003), Arango et al. (2009), Moore et al. (2012) and Geist et al. (2022)
Regulation and maintenance	Regulation of physical, chemical, biological conditions	Water conditions	− 0+	Herbivory by *Potamopyrgus antipodarum* increases nitrogen fixation	Arango et al. (2009)
Cultural	Direct, in situ, and outdoor interactions with living systems that depend on presence in the environmental setting	Physical and experiential interactions with natural environment	−	Recreational access restrictions in waters invaded by *Potamopyrgus antipodarum*	Proctor et al. (2007) and Hoyer & Myrick (2012)
Cultural	Direct, in situ, and outdoor interactions with living systems that depend on presence in the environmental setting	Intellectual and representative interactions with natural environment	+	Development of new ecotoxicological bioassays with *Potamopyrgus antipodarum* *Potamopyrgus antipodarum* is a sensitive species for ecotoxicological bioassays and the monitoring of aquatic ecosystems *Potamopyrgus antipodarum* as a model species for genetic studies	Duft et al. (2002), 2003, 2007), Gagnaire et al. (2008), Gust et al. (2010, 2011, 2014), Schmitt et al. (2010a, b, 2011), Vincent-Hubert et al. (2012), Orlova & Komendantou (2013), Wilton et al. (2013), Zounkova et al. (2014), Tallarico (2015), Alonso et al. (2016), Ruppert et al. (2016), Cresswell et al. (2017), Geiss et al. (2017), Ruppert et al. (2017), Alonso & Valle-Torres (2018), Capela et al. (2020) and Subba et al. (2021)

The 'Division' and 'Group' of the Common International Classification of Ecosystem Services (CICES) have been also included for each ecosystem service (Haines-Young & Potschin, 2018). Description of the effects of *P. antipodarum* on each ecosystem service is also included. References are in Supplementary S2

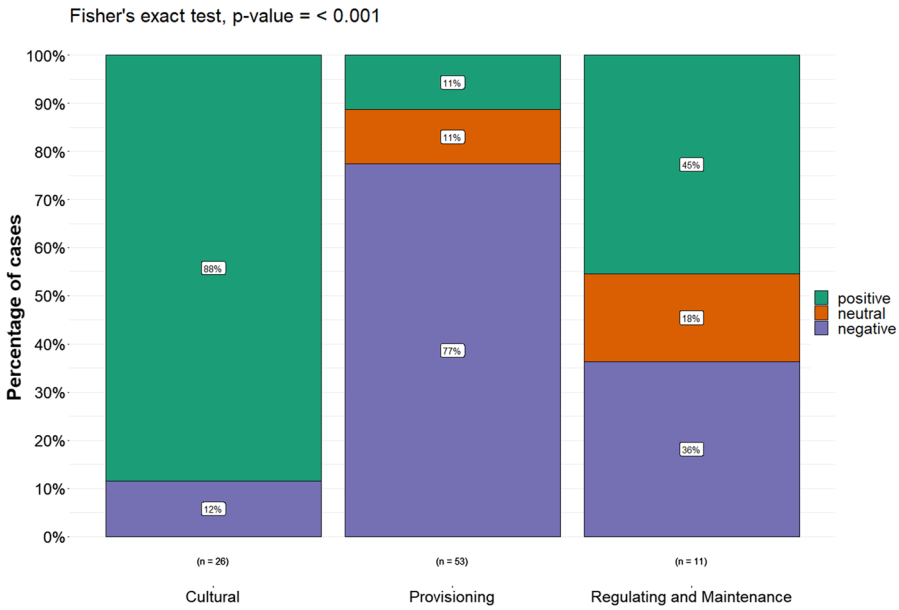

Fig. 1 The percentage of positive, neutral, and negative impacts of the NZMS on each ecosystem services (cultural, provisioning, and regulating and maintenance) are presented. The number of total cases and the percentage of cases for each service is showed in each column. Fisher's exact test result is presented at the top of the graph, showing that the frequency of positive, neutral, or negative cases are higher than expected by chance. The frequencies of positive and negative cases were significantly difference of chance for each pair of ecosystem services ($P < 0.001$; pairwise Fisher's exact test)

along with its competitive ability, allow the NZMS to greatly affect both ecosystem structure and functioning (Dorgelo, 1987; Richards et al., 2001; Hall et al., 2003; Alonso & Castro-Díez, 2012; Geist et al., 2022). Both high reproductive potential and competitive superiority of the NZMS over native invertebrate species result in its dominance of invertebrate communities (Alonso & Castro-Díez, 2008, 2012; Geist et al., 2022 for reviews). The reduction in wild invertebrate populations of the native fauna supposes a direct deterioration in the provisioning services (e.g., reduction in invertebrate animals for food supply or/and as supporting vertebrate fauna), which can also cause a reduction in cultural services (i.e., reduction of bait for angling activities). However, the extreme density reached by the NZMS may have an indirect positive effect on regulating ecosystem services when the affected native species are vectors of diseases such as *Bulinus truncatus* (Audouin, 1827) and lymnaeids, gastropods which transmit liver flukes among them schistosomes (Jones et al., 2015; Mulero et al., 2021).

Several studies show that the NZMS may facilitate some native invertebrates (Schreiber et al., 2002; Brenneis et al., 2010). When these invertebrates have culinary interest or are used as bait for angling activities, the NZMS may be improving provisioning and cultural services. A field experiment conducted in an Australian stream shows that NZMS density correlates positively with some common aquatic invertebrates and with richness of native taxa (Schreiber et al., 2002; Rakauskas et al., 2018). In a North American estuarine system, no negative competitive impact of the NZMS on native benthic invertebrates is found, but a positive correlation is demonstrated between the NZMS and common native epibenthic invertebrates (Brenneis et al., 2010). Additionally, Brenneis et al. (2011) show, by means of an experimental approach that the native crayfish *Pacifastacus leniusculus* consumes and digests the NZMS, which could be an important food source for this species in areas invaded by the NZMS. Crayfish species are used as a source of food and disease control in many parts of the world (Gherardi, 2011; Nonaka, 2012; Heikal et al., 2018; Smietana et al., 2021). Thus, the NZMS may potentially increase the many ecosystem services reported for crayfish species (Gherardi, 2011), which can be important in aquatic ecosystems

where the NZMS is an abundant prey. However, it is also possible that the benefit to crayfish may result in negative ecosystem effects as several species of crayfish are highly invasive (Gherardi et al. 2011), and NZMS facilitation of them may magnify their invasion capacity.

Even though the NZMS appears to be a good food source for crayfish, several studies demonstrate that the NZMS is likely to be a poor source of food for several species of fish. A low rate of assimilation and weight loss are associated with the consumption of the NZMS by fish (Cada, 2004; Vinson & Baker, 2008; Rakauskas et al., 2016). This may entail a direct reduction in provisioning services and in cultural services, since wild fish populations used for food provisioning or sport fishing could be affected (Vinson & Baker, 2008; Davis & Moeltner, 2010). The main reason for the low nutritional value of the NZMS for fish is the great resistance of the shell and the operculum that allows a large percentage of eaten individuals that to pass through the digestive tract of fish undigested, and even alive (Alonso & Castro-Díez, 2008; Vinson & Baker, 2008; Geist et al., 2022). However, there are also exceptions of fish species that can digest the NZMS (Hellmair et al., 2011; Rakauskas et al., 2016).

Effects on food webs, nutrient cycling, and water quality

The NZMS is well known for monopolizing the secondary production of the benthic macroinvertebrate community and for a high consumption of the primary production of the invaded ecosystems (Hall et al., 2003, 2006; Alonso & Castro-Díez, 2008, 2012; Riley et al., 2008; Geist et al., 2022). Consequently, the NZMS almost monopolizes the nitrogen cycle in some ecosystems since it excretes up to 65% of the ammonium demanded by primary producers and microbes (Hall et al., 2003). The NZMS consumes high amounts of green algae, which in turn may favor diatoms (Arango et al., 2009). As the latter can fix atmospheric nitrogen, the NZMS indirectly promotes this ecosystem function up to 50% in the periphyton of some streams (Arango et al., 2009). Additionally, the NZMS is reported to increase the rates of leaf litter decomposition (Geist et al., 2022). This can result in an increase of inorganic nutrient availability, especially if the organic matter comes from the terrestrial ecosystem. All this may cause various impacts on ecosystem services, related to possible effects of eutrophication and alteration of the physico-chemical properties of water, which can be detrimental to the use of water bodies for recreational uses (i.e., impact on cultural services) or for human consumption (i.e., impact on provisioning services). Previous studies highlight the impact that molluscs have on nutrient cycling, in many cases due to changes in the dominance of the different primary producers (McLaughlan et al., 2014; Gilioli et al., 2017). These changes caused by exotic species in the nutrient cycling can impact the freshwater quality by means of algal blooms (e.g., *Dreissena polymorpha*) or increase the phosphorous in the water column (e.g., *Pomacea maculata* (Perry, 1810)) (McLaughlan et al., 2014; Gilioli et al., 2017).

The high densities reached by the NZMS result in a considerable increase of shells on the substratum. As these shells accumulate calcium from the water in calcium carbonate (Medakovic et al., 2003; White et al., 2007), this may also result in a direct change in the chemical composition of water, which could be significant in extremely invaded ecosystems. However, this effect has not been well studied associated with mollusc invasions, so there is a high degree of uncertainty about its actual effects.

Effects of the NZMS on ecosystem services

Effects on provisioning services

In general, most of the revised studies show impacts of the NZMS on provisioning services. In fact, biomass, including that of primary producers, invertebrates, and fish is the division of provisioning services with the largest number of cases. The high rates of consumption of primary producers by the NZMS may lead to a drastic decrease in the biomass of some of those producers (Holomuzki et al., 2006; Krist & Charles, 2012; Laverty et al., 2015). Additionally, the NZMS provides a poor diet for many fish species, which can cause a decline in fish stocks (Cada, 2004; Vinson & Baker, 2008; Rakauskas et al., 2016). Moreover, the NZMS can host some parasites, posing another threat to the fish stock (Evans et al., 1981; Cichy et al., 2017; Gérard et al., 2017).

A “disservice” related to the high NZMS density is the high risk of biofouling for pipes and filters,

causing a negative impact on provisioning services (Nakano & Strayer, 2014). This is a common effect caused by invasive species of molluscs, such as *Dreissena* spp., *Corbicula* spp., or *Limnoperna fortunei* (Dunker, 1857) (Nakano & Strayer, 2014). The damage to pipes and filters caused by the NZMS corresponds to an intermediate impact in comparison with other invasive invertebrates with less than ten cases reported in a literature review (Nakano & Strayer, 2014). Even so, the NZMS can cause an accumulation of living and non-living materials (e.g., shells) on and around water distribution pipes and filters, which may result in a relatively high economic cost (Nakano & Strayer, 2014). However, this issue needs further research for the NZMS, as most studies have focused on the biofouling effects of other species of molluscs.

Changes caused by other exotic molluscs on the trophic webs have been previously reported (Locke et al., 2014; Cattau et al., 2016; Zhang et al., 2019), including positive effects for terrestrial birds (Cattau et al., 2016). In fact, the facilitation of native species by trophic interactions with invasive species is not an unusual occurrence in the ecology of invasions (Rodriguez, 2006; Cattau et al., 2016). However, although the NZMS can be consumed by some species of fish and invertebrates, little is known of its nutritional value, so the effects on the improvement of the provisioning services of other components of the food webs (e.g., predators of fish or water birds) are largely unknown. However, the high density of the NZMS in some cases can produce a positive effect for several species of fish and crustaceans when successfully consumed (Brenneis et al., 2011; Hellmair et al., 2011).

Effects on regulation and maintenance services

The NZMS causes several changes in regulation and maintenance services related to water quality and pest/disease control. For instance, the NZMS may improve the water quality by reducing the presence of copper in water through bioaccumulation (Ramskov et al., 2015). As it can reach high densities, its bioaccumulation capacity may be a mechanism of metal removal from the water column and sediment. In any case, the NZMS shows bioaccumulation capacity of metals, as other invasive molluscs, which is useful in biomonitoring and water quality programs (Johns, 2012; Benito et al., 2017; Spyra et al., 2019). However, this direct improvement of water quality could become a problem as it may produce the biomobilization of metals through the food web, which could impact the provisioning services (Bray et al., 2015; Benito et al., 2017).

Pest and disease control can be improved by the NZMS by means of competition with native snail hosts of pathogens or as an unsuitable intermediate host for native pathogens (Jones et al., 2015; Marszewska et al., 2018; Mulero et al., 2021). The NZMS presents a potential dilution effect against native trematode parasites, consequently reducing infection level (both prevalence and abundance) of native intermediate and definitive host species, such as gastropods and vertebrates. Such a dilution effect has been demonstrated in Europe against the bird schistosome *Trichobilharzia regenti* (Horák, Kolářová & Dvořák, 1998) infecting lymnaeids and responsible for swimmer's itch (Marszweska et al., 2018), but not against native trematodes of *Physa* spp., *Galba* spp., and *Pyrgulopsis* spp. in North America (Larson et al., 2020b). The dilution effect implies that native parasite species cannot develop in the NZMS, which, thus, constitutes a dead end with benefits for native host species. However, on evolutionary terms, the NZMS may become a new intermediate host allowing development of native parasite species, and thus, becoming a vector of disease (negative effect). Native parasite species are rarely recorded in the NZMS in its non-native areas [e.g., *Fasciola hepatica* (Linnaeus, 1758) infecting livestock (Jones et al., 2015), three echinostomes at metacercarial stage (*Echinostoma revolutum* (Fröhlich, 1802), *Echinoparyphium aconiatum* (Dietz, 1909), and *Hypoderaeum conoideum* (Block, 1872)) (Zbikowski and Zbikowska, 2009)], and up to now, it is unknown whether the NZMS is a dead end or a new intermediate host for these parasites (Marszewska et al., 2018; Larson et al., 2020b; Mulero et al., 2021). Therefore, the influence of the NZMS on ecosystem services associated with health presents a high degree of uncertainty. Even though they may currently be positive (e.g., dilution effect for native parasites), evolutionary processes may change towards disservices (e.g., transmission of native parasites). The risk for native species to become infected by exotic parasites introduced with the NZMS (i.e., new diseases) is limited, as the NZMS rarely harbors parasites native to New Zealand in its introduction

areas. In fact, only two New Zealand parasite species have been reported so far, both in Europe: *Notocotylus gippyensis* (Beverley-Burton, 1958) infecting ducks as definitive hosts (Morley, 2008) and Aporocotylid I infecting fish as definitive hosts (Gérard et al., 2017). Only the Aporocotylid species has been proved to be persistent over time in Europe, but with very low prevalence (<<1%) (Gérard et al., 2018).

Effects on cultural services

The cultural services provided by the NZMS are summarized in two groups. One "disservice" is related to the access restrictions that the authorities impose in NZMS-infested ecosystems (Proctor et al., 2007). Another disservice is the loss of recreational opportunities when stocking of fish from NZMS-positive facilities is limited to infested ecosystems (Hoyer & Myrick, 2012). Both facts prevent the recreational use of certain areas (bathing, fishing, boating, etc.), reducing the cultural services provided by aquatic ecosystems. Access restrictions to areas invaded by exotic species are proposed as a measure to avoid their dispersal to new ecosystems (Proctor et al., 2007; Pejchar & Mooney, 2009; Otero et al., 2013; USDI, 2016). However, natural vectors, such as water birds, terrestrial animals, fish, etc., can successfully contribute to the dispersion of the NZMS (Alonso & Castro-Díez, 2008; van Leeuwen & van der Velde, 2012). Therefore, access restriction measures may make sense at very early stages of invasion, but not when the species is widely distributed in the affected area.

Finally, a common cultural service provided by the NZMS is its use as a model organism for ecotoxicological and genetic studies, and as a biomonitoring species to assess the water quality of ecosystems. Several studies show the usefulness of the NZMS to assess the adverse effects of pollutants, including the development of a standardized OECD reproduction test (Geiss et al., 2017). Tests reveal that this species is a suitable organism for reproduction, growth, and behavioral bioassays in ecotoxicology (Pedersen et al., 2009; Geiss et al., 2017; Alonso & Valle-Torres, 2018). The maintenance of stable populations in laboratory is relatively feasible with several exotic species, which present a high reproductive capacity. Thanks to this, toxicological and genetic bioassays can be carried out under laboratory conditions (controlled temperature and water physico-chemical parameters, health conditions of the organisms, known age, etc.), which are not possible with wild populations (Orlova & Komendantov, 2013). Other invasive species of molluscs, such as *Dreissena* spp. or *Corbicula fluminea* (Müller, 1774), are amply used in ecotoxicology and biomonitoring studies (Binelli et al., 2008; Barenberg & Moffitt, 2018; Miserazzi et al., 2020). However, the NZMS is not always a sensitive species for all toxicants and environmental conditions (Jacobsen & Forbes, 1997; Alonso & Camargo, 2004), which must be considered when this species is used for biomonitoring.

Conclusions

Our review highlights that the NZMS, *Potamopyrgus antipodarum*, causes important impacts on several ecosystem properties. Most of them can be related to direct impacts on ecosystem services, mainly due to the high density and secondary production that this species can reach in invaded ecosystems. However, facilitation processes of the NZMS on native species may result in a direct improvement of some services. In general, there are few studies quantifying the relationships between the impacts of the NZMS on ecosystem properties and ecosystem services. Therefore, further studies linking ecosystem functions and services are necessary, in such a way that an impact assessment of exotic species on the ecosystem functioning is a good basis for the evaluation of the likely changes on ecosystem services. Most analyzed ecosystem services were negatively affected by the NZMS, which makes this invasive species a threat to the quality of ecosystem services provided by aquatic ecosystems. On the contrary, ecosystem services related to health (e.g., dilution effect) and research (e.g., biomonitoring, model species for ecotoxicological and genetic bioassays) are two groups of cultural services that the NZMS improves. However, health services present a high degree of uncertainty regarding their potential benefit. In general, the bibliography provides scarce quantification of the ecosystem services that the NZMS may provide/affect in the invaded ecosystems, with most studies showing qualitative results. Finally, we could not find economic assessment on the impact of the NZMS on ecosystem

services (e.g., cost of biofouling), which would be highly relevant for managers and policymakers.

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Data availability Not applicable.

Declarations

Conflict of interest Authors declare no conflict of interest.

Ethical approval Not applicable.

Consent for publication Authors provide consent for publication.

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