



REVIEW

# The New Zealand mud snail (*Potamopyrgus antipodarum*): autecology and management of a global invader

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**Abstract** The New Zealand mud snail (*Potamopyrgus antipodarum*; NZMS) is among the most globally widespread aquatic invaders, occurring in 39 countries and 5 continents. Herein we provide a systematic review of 245 articles, focusing on the ecological impacts, spatial distribution, population dynamics, vectors of spread, and management of invasive NZMS. Most NZMS introductions originate from already-established invasive populations, which represent a small number of clonal lineages. The invasion success of NZMS stems from opportunistic traits, and while their tolerance of broad ranges of environmental conditions facilitates spread, optimal conditions for successful NZMS establishment are evident: stable hydrology, slow water velocity, high specific conductivity, and moderate salinity. NZMS can become

exceptionally abundant, driving the greatest secondary-production rates reported for any stream invertebrate. However, NZMS populations fluctuate seasonally and over longer time scales, with marked declines observed after population booms. Minimal genetic variation within and among invasive populations and minimal incidences of predation/parasitism suggest that environmental factors constrain populations. As detritivore-herbivores, NZMS impact multiple compartments of aquatic ecosystems and their functioning. NZMS alter invertebrate and algal communities and can resist digestion by many fish species, reducing fish condition. This lack of digestion combined with expanding NZMS populations suggest that snail-eating fish are unlikely to regulate NZMS populations and may aid in local range expansion.

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Management programs and technologies have recently emerged to assist resource managers, including advances in environmental DNA detection methods and effective chemical decontamination treatments. The objective of this review is to contribute to a more robust understanding of the global NZMS invasion, such that undesired impacts can be minimized or averted.

**Keywords** *Potamopyrgus antipodarum* · New Zealand mud snail · Invasive species · Impacts · Distribution · Management

## Introduction

Impacts of invasive species have emerged as a central issue for resource management and as major drivers of environmental change in ecosystems across the planet. Aquatic ecosystems are among the most heavily invaded, with freshwaters being particularly vulnerable because of inadvertent introductions through human activities, such as commerce and recreation (Mack et al. 2000; Sala et al. 2000; Ricciardi 2006). The consequences of these introductions can be economically and ecologically severe, as exemplified by zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels. Collectively known as dreissenid mussels, they have invaded freshwater and estuarine ecosystems throughout North America where they have severely impacted food web dynamics, pelagic community structure, and fundamental ecosystem attributes, such as water clarity and productivity (Higgins and Vander Zanden 2010). These species have not only caused severe ecological impacts, but also cost hundreds of millions of dollars in damage to regional infrastructure (Connelly et al. 2007). Moreover, this example illustrates how invasive species can dramatically alter freshwater ecosystems and the pressing need for early detection and research if future invasions are to be better managed.

New Zealand mud snails, *Potamopyrgus antipodarum* (Gray 1843) (hereafter NZMS), have become established in rivers, lakes, and estuaries across the globe. NZMS are caenogastropods native to the freshwater streams and lakes of New Zealand. They have invaded aquatic systems in at least 39 countries

across 5 continents, particularly in freshwaters. Their myriad effects on ecosystem processes and biological communities have placed them on the list of Europe's 100 most dangerous invasive species and spurred global concern and management initiatives (Nentwig et al. 2018).

An advantageous reproductive strategy and competitive traits enable NZMS establishment and monopolization of resources in introduced ranges (Alonso and Castro-Díez 2008). While both sexual and parthenogenic lineages of NZMS occur in New Zealand, solely clonal lineages exist in its invaded range (Zaranko et al. 1997; Dybdahl and Kane 2005). Flexible feeding abilities give NZMS access to multiple food resources, including periphyton and detritus (Dorgelo 1991; Liess and Lange 2011; Levri et al. 2017b), affording them a competitive advantage over native taxa. NZMS effectively convert these food resources into biomass, and NZMS secondary-production rates are among the greatest recorded of any stream-benthic invertebrate (Hall et al. 2006). The low prevalence of predation and infection from most natural enemies outside their native range reduces population suppression, including that by fish (e.g., Bersine et al. 2008; Rakauskas et al. 2016) and parasites (e.g., Gérard et al. 2003, 2017; Gérard and Le Lannic 2003; Morley 2008; Adema et al. 2009; Żbikowski and Żbikowska 2009; Karatayev et al. 2012; Larson and Krist 2020). In aggregate, these traits help make NZMS highly effective invaders in waters across the globe.

Although NZMS were recorded outside their native range as early as the 1850s, recent expansion of their range, particularly throughout the United States, has refocused attention on this invader. Furthermore, recent investigations have detailed NZMS impacts in new ranges (e.g., Bennett et al. 2015; Rakauskas et al. 2017); developed new technologies for early detection using environmental DNA (eDNA) (e.g., Woodell et al. 2021); and tested novel methods for management, control, and decontamination (e.g., Stockton and Moffitt 2013; De Stasio et al. 2019). Considering these recent developments, this review summarizes and synthesizes the state of the science as it relates to the global NZMS invasion. Our overarching goal is to provide researchers and resource managers with a systematic review of NZMS ecology and management, focusing on their distribution, impacts,

detection, and control. In doing so, we hope to help minimize the spread and unwanted ecological impacts of this global invader.

## Methods

We searched for published literature related to NZMS invasions, ecology, distribution, and management using the key-phrases “*Potamopyrgus antipodarum*” and its synonym “*Potamopyrgus jenkinsi*” through the ISI Web of Knowledge and Google Scholar across all available years (i.e., 1900–2021). We initially identified 563 published articles, many of which involved the use of NZMS as a model organism for ecotoxicological and evolutionary investigations; these were not included in our review. We further refined the search to 152 articles using the term “invasive”. We used the additional search terms “New Zealand Mud Snail” and “*P. antipodarum*” and targeted searches to locate additional articles using Web of Knowledge and Google Scholar. Using the World Wide Web, we also identified management and technical reports and university theses and dissertations. We deemed a total of 245 articles, reports, theses, and dissertations suitable for inclusion in our review, focusing on those that address the effects of NZMS on ecosystem structure and function, population distribution (past, present, and forecast), life-history traits, and management and control (Fig. 1).

We derived geographic information on NZMS distribution from the articles as well as online databases (USGS 2021). We extracted geographic coordinates (i.e., latitude and longitude) and date of NZMS observation and plotted them using Geographic Information Systems (GIS) (Esri® ArcMap 10.8.1) at global, North American, and North American regional scales.

## Results

### Morphology and life history

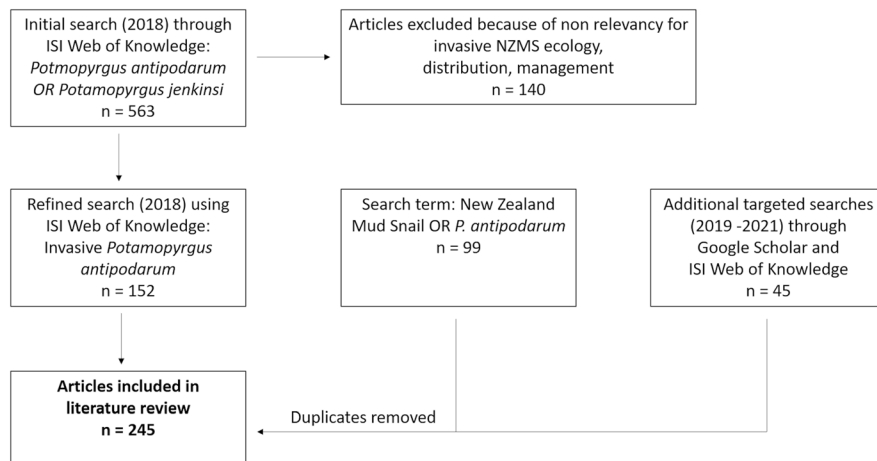
NZMS have adult shell lengths of 4–7 mm in invaded ranges and up to 12 mm in their native range (Winterbourn 1970). The cause for differences in shell lengths between invaded and native ranges is largely unknown. The shells are amber to dark brown

and narrowly conical with three to eight whorls and a mid-whorl keel in some morphotypes (Fig. 2). The invasion success of NZMS can be explained, in part, by their morphological and reproductive traits. For example, the snail has a solid operculum, allowing it to close its aperture and resist desiccation, predation, and toxic salinity levels (Oplinger et al. 2009; Alonso et al. 2016; Romero-Blanco and Alonso 2019). Much of the spatial variation in their physical characteristics (e.g., shell shape and size) and life history traits (e.g., brood size and growth rate) reflects high phenotypic plasticity (Negovetic and Jokela 2001; Kistner and Dybdahl 2013; Paolucci and Thuesen 2020; Verhaegen et al. 2021). For example, NZMS shell morphology (size, shape, and keel presence) is plastic, responding to environmental characteristics (e.g., flow rate) and predation pressure (Holomuzki and Biggs 2006; Butkus et al. 2012; Kistner and Dybdahl 2013, 2014; Verhaegen et al. 2018a, b, 2019). Their parthenogenic and ovoviviparous reproduction methods, paired with rapid growth rates, confer high fecundity. NZMS reach sexual maturity within a few months, and each individual female can produce hundreds of offspring per year (e.g., Schreiber et al. 1998; Richards 2002). Under suitable conditions, reproduction can occur year-round, resulting in the potential to produce multiple generations and tens of thousands of offspring within a population annually (Winterbourn 1970; Gangloff 1998; Schreiber et al. 1998; Richards 2002). Taken together, these traits give NZMS the ability to quickly establish populations in environments beyond their native range.

### Geographic distribution

NZMS have been found in at least 39 countries and on 5 continents (Fig. 3a) (Table 1), making them among the most widespread aquatic invasive invertebrates (Ponder 1988; Alonso and Castro-Diez 2012; Donne et al. 2020) with new detections occurring worldwide at a steady rate (e.g., Alonso et al. 2019; Butkus and Vaitonis 2019; Collado and Fuentealba 2020; Levri et al. 2020b; Woodell et al. 2021). There are three apparent global hotspots—Europe, Southeast Australia, and Western USA—with more recent records from East Asia, the Great Lakes region of North America, and South America (Fig. 3a).

The first documentation of NZMS outside of New Zealand occurred in England in 1889 (Smith 1889).



**Fig. 1** Flow diagram of search terms used to locate articles for the review



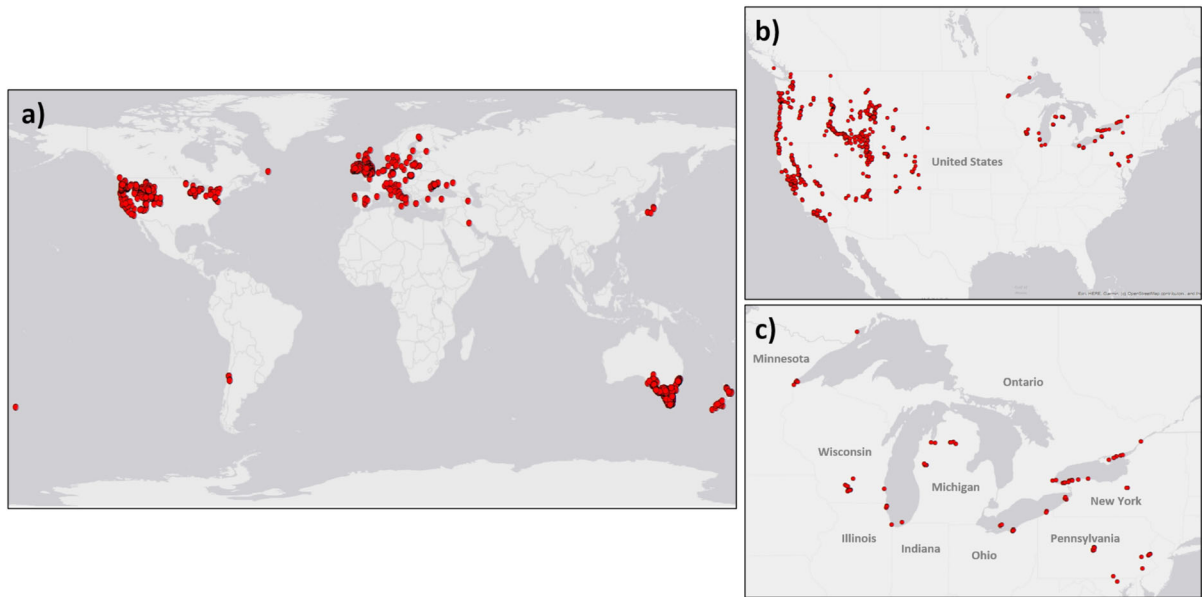
**Fig. 2** Photo of a New Zealand mud snail (*Potamopyrgus antipodarum*) with a USA one cent coin for scale. Photo credit: Gary Miller

Historic mollusk community inventories in the UK document widespread distributions of NZMS shortly after the first report and throughout the early 1900s (Boycott 1936). NZMS continued to spread broadly across Europe throughout the 1900s in Italy (Cianfanelli et al. 2007; Gaino et al. 2008), Poland (Urbański 1938), Portugal and Spain (Sousa et al. 2005; Pérez-Quintero 2009; Alonso et al. 2019), Ireland (Kerney 1999), Scotland (Boycott 1936; Ponder 1988), Greece (Radea et al. 2008), Slovakia (Čejka 2008), and Ukraine and Russia (Filippenko and Son 2008; Son 2008), among many other countries (Table 1). Several accounts of new populations occurred in the Middle East from 1990 to the early 2000s in Turkey (Kalyoncu et al. 2008) and possibly in

Iraq (Naser and Son 2009) and Lebanon (Naser and Son 2009).

In Australia, populations were discovered in Tasmania in 1872 and in Victoria in 1895 (Ponder 1988). Since their initial discovery in Australia, NZMS have expanded their range throughout south and central portions of the country with some analyses suggesting fish stocking and/or angling as a primary vector of spread within the region (Loo et al. 2007a, b). NZMS remain largely absent or undetected throughout the northern portions of the continent, which could be a result of environmental or biotic restrictions (Schreiber et al. 2003; Loo et al. 2007a, b).

In North America, NZMS are widespread throughout the United States, with established populations in 21 states (Fig. 3b). Their first discovery in North America was in 1987 (Bowler 1991) in the Snake River basin (Idaho, USA), and since then they have rapidly expanded their range across the American West (Proctor et al. 2007; Benson et al. 2015). NZMS have been established in the Laurentian Great Lakes Basin for more than three decades, being first documented in 1991 in Lake Ontario (Zaranko et al. 1997), but they have only recently been detected in streams and rivers of the region (Fig. 3c). The first record of NZMS in rivers of the Great Lakes was in an unnamed stream in New York state in 2007 (Levri and Jacoby 2008). Thereafter, NZMS were detected in Wisconsin rivers as early as 2011 (personal communication, Wisconsin Department of Natural Resources), in a Pennsylvania stream in 2013 (Levri et al. 2020b), and



**Fig. 3** **a** Global distribution of the New Zealand mud snail (NZMS); **b** North American distribution of NZMS (Canadian distribution of NZMS largely unknown); **c** distribution of NZMS in the Great Lakes region of North America

in Michigan streams as early as 2013 (personal communication, Michigan Department of Natural Resources). In many instances, NZMS introductions overlap almost exclusively with highly popular recreational fishing streams, suggesting that angling and other water-related activities are an important source of spread throughout the region. Records of NZMS in Canadian Provinces are limited, though reports have occurred in British Columbia and Ontario (Fisheries and Ocean Canada 2018; personal communication, US Fish and Wildlife Service).

More recently, NZMS have been recorded in most prefectures of Japan, with the first records in 1990 (Shimada and Urabe 2003; Urabe 2007; Hamada et al. 2013). Recent studies, some of which used molecular identification, confirm new populations of NZMS in numerous water bodies in Chile (Collado 2014; Collado and Fuentealba 2020).

#### Pathways of dispersal

NZMS are readily introduced into novel settings as a result of specific morphological and life history traits, including: a small body size, allowing easy transport and difficulty in detection; a parthenogenic reproduction strategy that allows a single individual to found a

new population; a resistant and operculate shell that allows NZMS to tolerate desiccation and passage through digestive tracts of some other organisms; and broad environmental tolerances. Because of these traits, NZMS are easily transported by numerous vectors that operate at multiple spatial scales, including vectors associated with human activity (Fig. 4) (Hosea and Finlayson 2005; Levri et al. 2007; Loo et al. 2007a; Butkus and Vaitonis 2019).

The most important contributor to long-distance transport is thought to be ballast water in transoceanic vessels (Zaranko et al. 1997; Gangloff 1998; Richards 2002; Proctor et al. 2007) (Fig. 4). Commercial trade of aquaculture products, such as fish and aquatic plants, is another common means of long- and short-distance transport (Winterbourn 1970; Richards 2002; Ponder 1988; Zaranko et al. 1997). Fish hatcheries and fisheries management involving the stocking of gamefish can contribute to interregional transport of NZMS (Haynes et al. 1985; Hosea and Finlayson 2005; Schisler et al. 2008; Stockton 2011). In the Western USA, where NZMS has invaded extensively, introduction is suspected to be due to the import of live gamefish received from invaded waters (Hosea and Finlayson 2005; Stockton and Moffitt 2013). Recreational activities, such as boating and fishing, also

**Table 1** Global records of New Zealand mud snail non-native distribution represented in the peer-reviewed literature, including continent, country, and locality with specific waterbody (when reported)

Continent/country	Locality (waterbody when provided)	Habitat type	References
<i>Asia</i>			
Japan	Hokkaido, Honshu, Ishikawa (Kanazawa), Kanagawa (Banyu Park, Tsurumaki-kita, Yagawara), Kyushu, Miyazaki (Kobayashi), Shiga (Hassaka, Kanro, Moriyama City), Tochigi (Shiobara, Nakagawa)	F/Lo	Shimada and Urabe (2003), Tatara et al. (2014), Urabe (2007)
Turkey	Aegean (Akçapınar and Akyaka Kadın Azmagi streams), Anatolia (Delice River), Çanakkale (Kocabaş Stream)	F/Lo	Kalyoncu et al. (2008), Odabaşı et al. (2019)
<i>Australia</i>			
	New South Wales, South Australia, Tasmania, Victoria (Lake Purrumbete, Tarra River),	F & B/Le & Lo	Dusting (2016), Ponder (1988), Schreiber et al. (1998, 2003)
<i>Europe</i>			
Austria	Lower Austria (Weidlingbach River, Danube), Upper Austria (Danube), Salzburg (Kaferhammer Mülbach, Natternbach, Moosebach), Tyrol	F/Lo	Patzner (1996), Zieritz and Waringer (2008)
Belarus	Pripyat River	F/Lo	Karatayev et al. (2008)
Belgium	Flanders (Willem-Leopold-Polder, Nieuve Watergang, Scheldt River)	F & B/Le	Bondesen and Kaiser (1949), Everaert et al. (2011), Städler et al. (2005), Verhaegen et al. (2018)
Bulgaria	Smolyan (Vacha River in Village of Teshel)	F/Lo	Irikov and Georgiev (2008) *empty shells only
Czech Republic	Braňany, Budyně nad Ohře (Ohře River), Central Bohemian (Slapy Reservoir, Turyňský rybník), Doksany (tributary of the Ohře River), Hradec Kolín (Elbe River), Hradec Králové, Kamenné Žehrovice, Králové (Elbe River), Libeň, Libotenice, Lysá nad Labem (Elbe River), Moravian-Silesian, Pardubice, Poodří Protected Landscape Area (Odra River), Prague (Libeňský přístav on Vltava River), South Moravian, Tovačov, Ústí nad Labem	F/Le & Lo	Beran (2002, 2007)
Denmark	Ålborg (Binderup Å), Århus (Odder Å), Bornholm, Frederiksborg (Roskilde Fjord), Grønsund Strait, København (Københavns Havn, Kongelunden Kanal), Maribo, Odense (Odense Å), Praestø (Praestø Fjord), Randers (Randers Fjord), Ringkøbing (Ringkøbing Fjord, Vilsund River, Nissum Fjord, Ferring Sø), Sortsø Gab, Western fjords	B/Le	Bondesen and Kaiser (1949), Städler et al. (2005), Thomsen et al. (2009)
Finland	Åland archipelago, Gulf of Finland, Uusimaa	F & B/Le	Bondesen and Kaiser (1949), Butkus et al. (2020), Carlsson (2000), Leppäkoski and Olenin (2000)

**Table 1** continued

Continent/country	Locality (waterbody when provided)	Habitat type	References
France	Brittany (Le Petit Hermitage, in Ille-et-Vilaine), Corsica Island, Haute-Savoie (Annecy Lake), Nord-Pas-de-Calais (Slack Estuary, Canal de Bergues), Normandy (Mont St-Michel Basin)	F & B/Lo & Le	Bondesen and Kaiser (1949), Costil et al. (2001), Gérard et al. (2003, 2018), Mouthon and Dubois (2001), Mouthon (2002), Mouthon and Magny (2004), Städler et al. (2005), Zettler and Richard (2004)
Germany	Baden-Württemberg (Lake Constance, Main River), Bavaria (Lake Mindel, Lake Constance, Main River, Krebsbach River), Hesse (Main River, Werra River), Mecklenburg-Vorpommern (Wismar Bight, Odra Estuary—Szczecin Lagoon), Rhine River, Saxony (Görlitz), Schleswig–Holstein (Kiel Canal), Thuringia (Werra River, Krebsbach River)	F & B/Le & Lo	Alonso and Castro-Díez (2012), Arle and Wagner (2012), Baur and Ringeis (2002), Baur and Schmidlin (2007), Bondesen and Kaiser (1949), Carlsson (2000), Gergs and Rothhaupt (2015), Städler et al. (2005), Verhaegen et al. (2018)
Greece	Aetolia-Acarmania (Lake Trichonis and nearby stream)	F/Le & Lo	Radea et al. (2008)
Iberian Peninsula	<i>Portugal</i> : Aveiro (Ria de Aveiro), Beja, Évora, Faro (Ribeira de Odelouca, Ribeira de Arade, Guadiana River), Galicia (River Minho Estuary), Leiria, Portulegre, Santarém, Setubal (Lago de Melides, Santo André), Viana do Castelo (Río Miño Estuary) <i>Spain</i> : Álava, Albacete (rivers in Sierra de Alcaraz), Alicante, Andalusia (Dehesas de Sierra Morena Bioreserve), Asturias (Nora River, Bay of Biscay), Badajoz (Guadiana River), Barcelona (Llobregat Delta and Vallvidrera Stream), Cáceres (Guadiana River), Cantabria, Castellón de la Plana, Ciudad Real (Guadiana River), Córdoba (Dehesas de Sierra Morena), Cuenca, Gerona, Granada, Guadalajara (Río Cañamares), Guipúzcoa, Huelva (Guadiana River), Huesca, La Coruña, Lérida, Madrid (Henares River, Perales River, Aulencia River, Guadarrama River, Lozoya River, Guadalix River, Larama River, Torote River, Tajo River), Murcia (Río Segura), Navarra, Pontevedra (Río Miño), Tarragona, Teruel, Toledo (Guadiana River), Valencia, Vizcaya, Zaragoza	F & B/Lo & Le  F & B/Lo & Le	Alonso et al. (2009, 2019), Alonso and Castro-Díez (2015), Clusa et al. (2016), Múrria et al. (2008), Pérez-Quintero (2009, 2011), Simoes (1988), Sousa et al. (2005), Soler et al. (2006), Werner et al. (1994), Zettler and Richard (2004)
Ireland	Carlow, Clare, Cork, Galway, Kerry, Kilkenny, Limerick, Louth, Mayo, Meath, Munster, Tipperary (Lough Leane), Tyrone, Waterford, Wexford (Lough Neagh)	F/Le & Lo	Bondesen and Kaiser (1949), Boycott (1936)
Italy	Aosta Valley, Abruzzo, Apulia, Basilicata, Calabria, Campania, Emilia-Romagna, Friuli-Venezia Giulia, Lazio, Liguria (Casarza Ligure), Lombardy, Marche, Molise, Piedmont, Sicily, Trentino-Alto Adige, Tuscany (Corsalone Stream and Oia Stream in National Park of the Foreste Casentinesi, Monte Falterona, and Campigna), Umbria (Upper Tiber River, Lower Mussino Stream, Upper Topino River), Veneto	F/Lo	Cianfanelli et al. (2007), Gaino et al. (2008), Gherardi (2007), Mazza et al. (2011), Städler et al. (2005)

**Table 1** continued

Continent/country	Locality (waterbody when provided)	Habitat type	References
Lithuania	Alytus (Spernia River, Lake Daugai, Lake Obelija, Lake Dusia, Lake Metelys, Lake Gilutis, Lake Serijis, Lake Lūšiai), Klaipeda (Curonian Lagoon, Nemunas Delta), Telšiai (Lake Plateliai, Babrungas River), Utena (Lake Prūtas), Vilnius (Strėva River, Lake Vilkokšnis, Verknė River, Lake Spindžiukas, Lake Spindzius, Elektrėnai reservoir, Lake Talkša)	F & B / Le & Lo	Butkus et al. (2014), Butkus and Vaitonis (2019), Rakauskas et al. (2016)
Poland	Greater Poland, Kuyavian-Pomeranian (Lake Trląg, Sosno Lake), Lesser Poland (Katowice, Czułów, Polish Jura, Oswiecín Valley), Podlaskie (Wigry Lake, Wigry National Park, Baile Wigierskie Lake, Czarne Huciańskie Lake, Koleśne Lake, Okrągłe Lake, Pierty Lake, Wigierski Pond, Kamionka River), Pomerania, Silesian (Katowice, Zebrydowice, Mleczna River, Silesian Upland, Silesian Lowland), Vistula Lagoon, Warmian-Masurian (Masurian Lakeland, Lake Inulec, Lake Głębokie), West Pomeranian (Odra Estuary-Szczecin Lagoon)	F& B/Le & Lo	Brzeziński and Kołodziejczyk (2001), Ezhova et al. (2005), Gruszka (1999), Kołodziejczyk et al. (2009), Lewin (2012), Lewin and Marszewska et al. (2018), Lewin and Smoliński (2006), Michalik-Kucharz (2008)
Romania	Dobrogea (Razim Lagoon), Oltenia (Cerna River)	F/Le & Lo	Cejka et al. (2008), Son et al. (2008)
Russia	Don River, Kaliningrad (Lake Forelevoje, Lake Golubyje, Curonian Lagoon), Krashodar Krai (Sukhoi Liman), Sea of Azov-Black Sea basin, Vistula Lagoon	F & B/Le & Lo	Ezhova et al. (2005), Filippenko and Son (2008), Son et al. (2008), Son (2008)
Slovakia	Banská Bystrica (Slatina River, Danube River), Bratislavia (Morava River, Horský Park, Danube River, Lesser Danube River), Nitra (Danube River, Váh River, Ipel' River), Trnava (Lesser Danube River, Danube River, Potok brook)	F/Le & Lo	Čejka (2008)
Sweden	Baltic Sea, Bay of Aarhus, Bothnian Bay, Gotland Island, Kattegat Sea, North Sea, Skagerrak Sea, Wadden Sea, western fjords, waters near Goteberg and Kullen	F & B/Le	Bondesen and Kaiser (1949), Leppäkoski and Olenin (2000), Thomsen et al. (2009)
Switzerland	Basel (River Rhine and tributaries—Birs and Ergolz), Neuchatel (Lake Neuchatel), Zurich (Lake Zurich)	F/Le & Lo	Baur and Ringeis (2002), Schmidlin et al. (2012), Städler (2005)
The Netherlands	Flevoland (Lake Veluwemeer, Lake Wolderwijd), Holland, Utrecht (Lake Maarsseveen I and II), Zeeland (Damse Rawart)	F/Le	Dorgelo et al. (2014), Städler et al. (2005), van den Berg et al. (1997), Verhaegen et al. (2018)
Ukraine	Black Sea (Dneiper Estuary, Dneiper-Bug Estuary, Budaki Lagoon, Berezan Estuary), Mykolaiv (tributary of Sosyk River), Odessa (Kuchurganski Liman, Lake Yalpus, Stentsovsko-Zhebriyanski Plavni wetland, Sukhoj Liman, tributaries of Dniester estuary, Dalnik River, Akkarzha Stream, Baraboj River, Fontanka River, Kuchurgan Reservoir)	F & B/Le	Son et al. (2008), Son (2008)



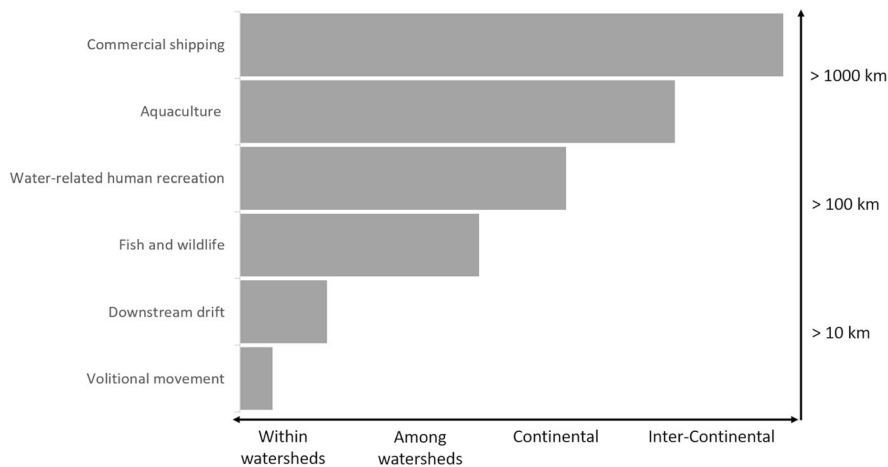
**Table 1** continued

Continent/country	Locality (waterbody when provided)	Habitat type	References
United Kingdom	<i>Northern Ireland:</i> Antrim, Armagh, Down, Londonderry	F/Le & Lo	Boycott (1936)
	<i>Wales:</i> Blaenau Gwent, Bridgend, Caerphilly, Cardiff, Carmathenshire, Ceredigion, Conwy, Denbigshire, Flintshire, Gwynedd (Portmeirion pond, Harlech), Isle of Anglesey (Llyn Maelog), Merthyr Tydfil, Monmouthshire, Neath Port Talbot, Newport, Pembrokeshire, Powys, Rhondda Cynon Taff, Swansea, Torfaen, Vale of Glamorgan, Wrexham	F/Le & Lo	Boycott (1936), Hauser et al. (1992), Städler et al. (2005)
	<i>Scotland:</i> Angus, Argyll and Bute (Tiree Island, Isle of Gigha), Caithness, Clackmannanshire, Fife, East Lothian, Midlothian, Kincardineshire, Kinrosshire, Orkney (Lock of Stenness), Perthshire, Ross and Cromarty, Shetland, Sutherland	F/Lo	Boycott (1936), Hauser et al. (1992), Ponder (1988), Städler et al. (2005)
	<i>England:</i> Bedfordshire (Ivel River), Berkshire, Buckinghamshire, Cambridgeshire, Cheshire, County Durham, Cumbria, Devon, East Riding of Yorkshire, East Sussex, Eastern portion of Norfolk, Somerset, Suffolk, Essex (Thames Estuary), Gloucestershire, Greater London (Bushy Park), Greater Manchester, Hampshire, Herefordshire, Hertfordshire, Isle of Wight, Kent (Thames Estuary), Lancashire, Leicestershire, Lincolnshire, Merseyside, North Yorkshire, Northumberland, Nottinghamshire, Norfolk, Oxfordshire, Rutland, Shropshire, South Yorkshire, Staffordshire, Surrey, Tyne and Wear, Warwickshire, West Sussex, West Yorkshire, Worcestershire	F/Lo	Bondensen and Kaiser (1949), Boycott (1936), Grant and Briggs (1998), Heywood and Edwards (1962), Ponder (1988), Städler et al. (2005)
The Americas			
Canada-USA	Great Lakes (Lake Michigan, Lake Erie, Lake Ontario, Lake Superior)	F/Le	Grigorovich et al. (2003), Levri and Jacoby (2008), Zaranko et al. (1997)
Canada	British Columbia (Vancouver Island, Port Alberni), Ontario (St. Lawrence River), Lake Ontario, Lake Superior (Thunder Bay)	F & B/Le & Lo	Davidson et al. (2008), USGS (2021)
Chile	Coquimbo (Chalinga River, Estero Consuelo, Zapallar Canal, Choapa River), Maule (Maule River), Metropolitana (O'Higgins Park, Estero La Dehesa), O'Higgins, Santiago Metropolitana (O'Higgins Park, Estero La Dehesa, El Yeso Spring), Valparaíso (Canal la Laja, Estero Romeral)	F/Lo	Collado (2014), Collado and Fuentealba (2020)

**Table 1** continued

Continent/country	Locality (waterbody when provided)	Habitat type	References
USA	Arizona (Colorado River), California (Upper Owens River, Big Springs, Hot Creek), Colorado (Boulder Creek, Platte River), Great Lakes (Lake Michigan, Lake Erie, Lake Ontario, Lake Superior), Idaho (Snake River basin), Illinois (Waukegan Harbor, Little Calumet-Galien), Maryland (Gunpowder Falls), Michigan (Au Sable River, Pere Marquette River, Boardman River, Upper Manistee River, Shanty Creek), Minnesota (Duluth Harbor, St. Louis River), Montana (Madison River), Nevada, New Jersey (Musconetcong River), New Mexico (San Juan River), New York, Ohio, Oregon (Columbia River, Tillamook Bay, Devils Lake, Yaguina Bay, Alsea Bay, Umpqua River, Coos Bay, New River, Hanson Slough, Garrison Lake, Rogue River), Pennsylvania (Presque Isle, Bald Eagle Creek), South Dakota (Beaver Creek), Utah (Bear River Basin, Colorado River, Green River, Great Salt Lake Basin, Strawberry River), Washington (Long Beach), Wisconsin (St. Louis River), Wyoming (Polecat Creek)	F & B/Le & Lo	Arango et al. (2009), Bowler (1991), Brenneis et al. (2010), Cross et al. (2010), Davidson et al. (2008), EPPO (2014), Hall et al. (2006), Herbst et al. (2008), Maret et al. (2008), McKenzie et al. (2013), Kerans et al. (2005), Levri et al. (2012), Proctor et al. (2007), Riley et al. (2008), USGS (2021), Vinson (2004), Zaranko et al. (1997)

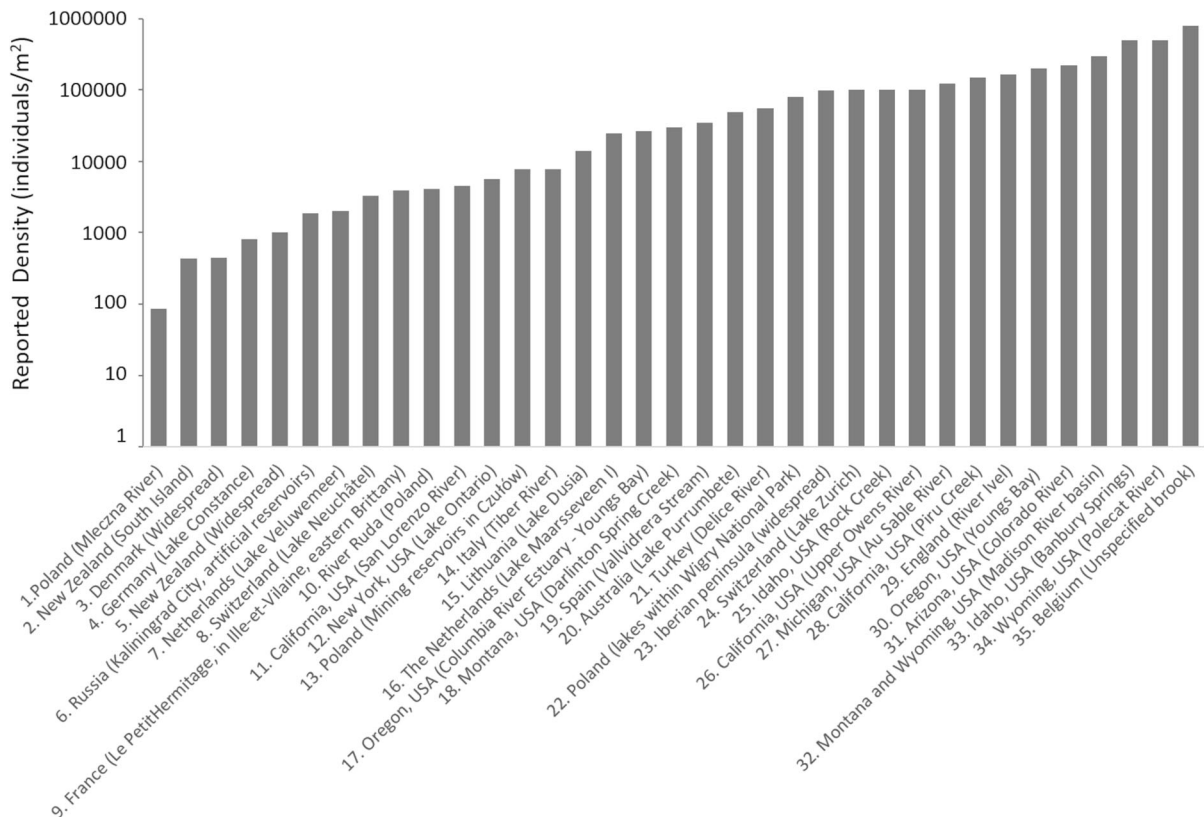
Habitat types: *F* freshwater, *B* brackish water, *Lo* lotic, *Le* lentic. Continents, countries, and localities are listed in alphabetical order



**Fig. 4** A conceptual bar chart depicting broadly estimated and relative ranges of distance associated with known (natural and anthropogenic) dispersal mechanisms of the New Zealand mud snail

transport NZMS within and among watersheds (Fig. 4). These activities often involve equipment, such as wading gear, nets, boats and other surfaces, to which NZMS can readily attach (e.g., Stockton and Moffitt 2013; Alonso et al. 2016) and, given their

small size, can easily go unnoticed. In the United States, NZMS populations are commonly found at highly popular river fishing destinations, especially cold-water trout streams, creating source populations for potential further spread.



**Fig. 5** Densities of New Zealand mud snails (NZMS) in published literature. NZMS densities represent highest reported observed means (when available) or local estimates of population densities in the respective study locations. Numbered bars and associated densities are from: 1. Lewin (2012); 2. Holomuzki and Biggs (2006); 3. Thomsen et al. (2009); 4. Gergs and Rothhaupt (2015); 5. Holomuzki and Biggs (1999); 6. Filippenko and Son (2008); 7. van den Berg et al. (1997); 8. Schmidlin et al. (2012); 9. Gérard et al. (2018); 10. Spyra et al. (2015); 11. Twardochleb et al. (2012); 12. Zaranko et al. (1997); 13. Lewin (2012); 14. Gaino et al. (2008); 15. Rakauskas et al.

(2016); 16. Dorgelo (1987); 17. Brenneis et al. (2010); 18. Cada (2004), Kerans et al. (2010); 19. Múrria et al. (2008); 20. Quinn et al. (1998) and Schreiber et al. (1998) in Alonso and Castro-Díez (2008); 21. Odabaşı (2019); 22. Brzeziński and Kolodziejczyk (2001); 23. Alonso et al. (2019); 24. Ribí and Arter (1986); 25. Maret et al. (2008); 26. Moore et al. (2012); 27. Geist et al., unpublished; 28. Bennett et al. (2015); 29. Heywood and Edwards (1962); 30. Litton (2000) in Bersine et al. (2008); 31. Cross et al. (2010); 32. Kerans et al. (2005); 33. Richards et al. (2001); 34. Hall et al. (2006); 35. Lucas (1959) in Dorgelo (1987). Note log scale of Y axis

Natural vectors also aid NZMS dispersal within and among watersheds. NZMS can attach to waterfowl and can survive through digestive tracts of fish and possibly other species, making attempted predation or incidental ingestion another potential vector of spread (Haynes et al. 1985; Vinson and Baker 2008; van Leeuwen et al. 2012). Downstream drift is probably the most important means of dispersal once populations become established in flowing waters, being orders of magnitude more rapid than volitional movement. Individuals can float freely at the water's surface using surface tension (Gangloff 1998; Levri

1998a, b; Levri and Clark 2015) and by attaching to floating vegetation mats (Dorgelo 1987; Richards et al. 2001). Volitional movement is slow at 1–3 m/hr (Richards 2002; Proctor et al. 2007; Sepulveda and Marczak 2012; Levri and Clark 2015) but allows dispersal to both upstream and downstream habitats in flowing waters. Through these and possibly other animal vectors, NZMS can have rapid and long-distance dispersal both among and within ecosystems (Fig. 4).

## Distribution of genotypes

In their native range, populations of NZMS include both sexually and asexually reproducing individuals (e.g., Jokela et al. 1997), conferring high genetic diversity (Winterbourn 1970); however, populations in invaded territories are composed solely of triploid, asexual, clonal females (Zaranko et al. 1997; Gangloff 1998; Hershler et al. 2010). The precise number of distinct genotypes in their native range is unknown, and inconsistencies in methodology and labeling make determining an exact number of invasive genotypes difficult. However, it appears that there are at least 12 parthenogenic clones that have established invasive populations in their non-native range, but it is unclear whether all known clones are differentiated genetically or if some are distinguished by geographic location alone. At any rate, there is consensus that a relatively small number of clones are responsible for the global NZMS invasion (Table 2).

Though NZMS have been present in Europe since the late 1800s, only a few lineages exist. Early assessments recognized three morphologically distinct strains in Britain, where NZMS were first documented in Europe, named A, B, and C, which were confirmed to be distinct clonal genotypes by Hauser et al. (1992) using a minisatellite core sequence. Types A and B are consistently more common than C, with type A being most common overall. Type A occurs in freshwater

habitats while type B is less common and prefers brackish waters (Hauser et al. 1992; Jacobsen and Forbes 1997; Weetman et al. 2002). However, Weetman et al. (2001) recognized four distinct clones in Britain, while Weetman et al. (2002) refined this analysis to three main clones with one additional rare clone or a potential interclonal hybridization using di- and tri-nucleotide microsatellite markers. For NZMS lineages throughout continental Europe, it appears that two clonal lineages exist; however, the use of differing methodologies and genetic markers has led to inconsistencies in labeling these clones. Donne et al. (2020) identified two groups in continental Europe, labeled EU14 and EU15, using single-nucleotide polymorphism (SNP) markers and clustering and Approximate Bayesian Computation methods. Similarly, other studies have identified two NZMS lineages in continental Europe as T and Z using mitochondrial DNA markers (Städler et al. 2005; Verhaegen et al. 2018b) and additional microsatellite markers (Butkus et al. 2020). Lineage T was widespread and found in fresh waters while lineage Z was relatively rare and found in brackish waters – a similar pattern to that in the British genotypes A and B, which have also been recorded in continental Europe (Jacobsen and Forbes 1997). Therefore, it is likely that NZMS in their invaded European range are composed primarily of two distinct clones, denoted as A and B in older literature (e.g., Jacobsen and Forbes 1997), EU14 and EU15 in

**Table 2** Global distribution of New Zealand mud snail genotypes

Location	Genetic equivalents	References
Australia	AUS2/US1/EU15/Z	Donne et al. (2020), Dusting (2016)
Britain	A/EU14/T	Hauser et al. (1992), Jacobsen and Forbes (1997), Weetman et al. (2002)
	B/EU15/Z	Hauser et al. (1992), Jacobsen and Forbes (1997), Weetman et al. (2002)
	C/EU15/Z	Hauser et al. (1992), Jacobsen and Forbes (1997), Weetman et al. (2002)
Chile	Unnamed, identical to US2/EU14/JA	Collado (2014)
Continental Europe	A/EU14/T	Städler et al. (2005), Verhaegen et al. (2018), Weetman et al. (2002)
	B/EU15/Z	Städler et al. 2005, Verhaegen et al. (2018)
Japan	JA/US2/EU14	Hamada et al. (2013)
	JB1	Hamada et al. (2013)
	JB2	Hamada et al. (2013)
United States	US1/EU15/Z/AUS2	Donne et al. (2020), Dusting (2016), Dybdahl and Drown (2011)
	US2/EU14/T	Donne et al. (2020), Dybdahl and Drown (2011)
	US1A	Dybdahl and Drown (2011)
	US3	Dybdahl and Drown (2011)

more recent (i.e., Donne et al. 2020), and T and Z in others (Städler et al. 2005; Verhaegen et al. 2018b), with the possibility of a third rare clone in Britain (C) (Table 2). Last, the two primary clones are identical to clones found in New Zealand, indicating that New Zealand is the source of the European invasion (Städler et al. 2005; Donne et al. 2020).

In the United States, there are two main clones, termed US1 and US2 (Table 2). Clone US1 is widespread in the western United States, where it was first detected in the Snake River (Idaho) in 1987 (Proctor et al. 2007; Dybdahl and Drown 2011). Clone US2 was first discovered in Lake Ontario in the 1990s and has since spread throughout the Great Lakes region (Zaranko et al. 1997; Grigorovich et al. 2003; Levri et al. 2007). Two more clones, US1A and US3, have also been discovered in the western United States but are only found in restricted geographic areas of the middle Snake River (Idaho) and are considered to be less invasive than other clones (Dybdahl and Drown 2011). Dybdahl and Drown (2011) used a three-pronged genetic approach, i.e., allozyme, mitochondrial DNA, and microsatellite DNA genetic markers, to confirm the presence of these four genotypes in the United States. Recent population genetic analyses have revealed that one of the European lineages (EU14) is responsible for the invasion in the Great Lakes region and that the other European lineage (EU15) plus two New Zealand clusters are responsible for the invasion in the western United States; this corroborates conclusions from other sources that there are probably two primary NZMS clusters in the United States and two geographically restricted clones (Donne et al. 2020).

In other parts of their invaded range (i.e., Australia, Japan, and Chile), genetic analyses have revealed low diversity, similar to findings from studies in Europe and the United States. Australia was invaded by NZMS around the same time as the European invasion, with the first reports on the island of Tasmania in 1872 and the mainland in 1895 (Ponder 1988). While there have been few genetic studies on NZMS in Australia, Dusting (2016) reported low genetic diversity among NZMS in Australian populations using mitochondrial DNA and SNP markers, similar to findings in other invaded regions. Four main clones were identified, one of which, AUS2, is identical to clone US1, indicating a close relation between their source populations (Dusting 2016) (Table 2). Using

mitochondrial DNA markers, Hamada et al. (2013) identified two clones in Japan, where NZMS were first recorded in 1990, suggesting multiple invasion events. These clones are termed JA and JB, and JB is composed of two subhaplotypes (JB-1 and JB-2). In Chile, the only location NZMS have been found in South America to date, Collado (2014) found a single haplotype in the four populations studied using mitochondrial DNA in two regions in central Chile. While the timing and origin of the invasion in Chile are unclear, this haplotype is also found in Japan (JA), the United States (US2), England (EU14), and New Zealand (Collado 2014) (Table 2). To our knowledge, no population genetic studies have been performed on NZMS populations in western Asia.

While the parthenogenic nature of the invasive clones increases their colonization success, it substantially lowers genetic diversity in their invaded range, posing a paradox regarding their high invasion success rates (Dybdahl and Drown 2011; Donne et al. 2020). Nonetheless, only a few clonal lineages of NZMS appear to be responsible for the species' global invasion (Städler et al. 2005; Proctor et al. 2007; Dybdahl and Drown 2011; Donne et al. 2020) (Table 2). Based on these data, we suggest that most NZMS introductions to previously uninvaded waterbodies within and between invaded regions are stemming from already established invasive populations rather than from native populations in New Zealand. Differences in invasion capabilities between clonal lineages may exist, perhaps owing to variation in behavior, salinity tolerance, morphology, and their ability to inhabit and adapt to new environments (Drown et al. 2011; Dybdahl and Drown 2011; Butkus et al. 2020). For example, differences in life-history traits and feeding rates between genetic lineages were observed in response to a salinity gradient (Jacobsen and Forbes 1997) and shell morphology (Verhaegen et al. 2018a), and responses to environmental contaminants can also differ between clonal lineages (e.g., Jensen et al. 2001).

## Habitat requirements

### *Habitat type*

The widespread geographic distribution of NZMS reflects their ability to invade a broad range of freshwater and brackish habitats. In their native range,

NZMS occur in freshwater streams and lakes and brackish waters, such as estuaries (Winterbourn 1970). Agriculturally dominated watersheds with low-gradient, nutrient-rich streams support particularly abundant populations of NZMS in New Zealand (Marshall and Winterbourn 1979; Quinn et al. 1998; Harding et al. 1997). Across their invaded range, they have been found in high-elevation temperate streams (e.g., Hall et al. 2006), lakes and their tributaries (e.g., Zaranko et al. 1997; Levri et al. 2007), drainage ditches (e.g., Gérard et al. 2003), reservoirs (e.g., Lewin and Smoliński 2006; Lewin 2012), and estuaries and coastal waterways (e.g., Davidson et al. 2008; Brenneis et al. 2010). The variety of aquatic environments they occupy both within and outside of their native range demonstrates their tolerance and the utility of having generalist traits for invading a broad range of habitats and environmental conditions.

### *Substrata*

NZMS are commonly referred to as ‘mud snails’ because of their association with fine substrates along mud flats and muddy banks (Winterbourn 1970), but in both native and invaded areas, they occur on substrates with a broad range of sediment sizes. In their native range, they can be most abundant on pebble and cobble (100–250 cm diameter) but with similar densities on sand (Holomuzki and Biggs 2007). NZMS often occupy subsurface space to avoid hydraulic forces and other potential threats (e.g., predation) (Holomuzki and Biggs 2007). In invaded ranges, they are abundant in vegetative and muddy substrates and on sand, leaf litter, silt, algae, gravel, boulders, wood, and artificial substrates (Richards et al. 2001; Hall et al. 2006; Proctor et al. 2007; Davidson et al. 2008). Studies characterizing physical habitat preferences and suitability in their invaded ranges are limited, though some have found relationships between NZMS occurrence and habitat characteristics. For example, in some regions of Italy, NZMS mostly occur in wide, deep streams with high densities of crevices (described by the authors as number of holes per meter) (Mazza et al. 2011). And in Piru Creek (California, USA), Bennett et al. (2015) observed higher densities of larger (> 2 mm in shell length) NZMS in macroalgae relative to substrata (i.e., mud, sand, and gravel) in riffle habitats. Similarly, Hall et al. (2006) found greater NZMS biomass and abundance in vegetated

sections of Pole Cat Creek and Firehole River (Greater Yellowstone Area, USA). Lysne and Koetsier (2006) found NZMS to prefer pebble and gravel substrates over silt and sand in experimental trials. NZMS populations appear to be habitat generalists and can persist across a broad array of aquatic systems with varying abiotic-physical characteristics but have an apparent strong association with substrata composed of larger particles (e.g., gravel, cobble) and/or areas of refuge, such as substrata subsurface, interstitial voids, and aquatic vegetation.

### *Hydrology*

The flow regime and related parameters, such as flow velocity, are key determinants of invertebrate, including NZMS, distributions in river systems (Hynes 1970; Poff et al. 1997). Within their native range, local NZMS densities are inversely related to flood frequency, with hydrologically stable streams supporting higher NZMS densities and flow velocities > 0.15 m/s being negatively associated with NZMS densities (Holomuzki and Biggs 1999, 2000, 2007). Similarly, negative relationships between densities and flow velocity occur in the Snake River (Idaho, USA) (Richards et al. 2001). Higher flow velocities can dislodge NZMS, and in an artificial stream in Australia, the minimum and mean velocities that dislodged NZMS from bricks were 0.15 and 0.68 m/s, respectively (Kefford and Lake 1999). Lysne and Koetsier (2006) observed median detachment velocities for NZMS to be 0.24 m/s while maximum detachment velocities were 0.51 m/s. In contrast to this, Spyra et al. (2015) found a positive association between the occurrence of NZMS and higher velocities (0.31–1.0 m/s) in the River Ruda (Poland). However, the study reaches where NZMS were present consisted of gravel-sand substrata and submerged macrophytes, which probably afforded NZMS refuge from the higher velocities. Furthermore, NZMS densities in their study reaches were not exceptionally high ( $\leq$  c. 4,000 ind/m<sup>2</sup>), possibly reflecting population growth constraints due to environmental conditions (e.g., high velocities). High flow velocities, therefore, probably limit NZMS populations and/or distributions.

Unstable hydrology may lead to excessive flow velocities or sediment scour and, thereby, restrict NZMS invasion success. In a California stream,

discharges between 50 and 100 m<sup>3</sup>/s dramatically lowered NZMS densities (Bennett et al. 2015), and in a Mediterranean stream, Múrria et al. (2008) observed weak effects of NZMS on benthic community structure, which they attributed to the harsh hydrologic conditions of the region (e.g., periods of drought, flashy hydrology), which minimized the ability of NZMS to establish high densities. Robinson (2019) also observed declines in NZMS abundance following periods of high flows in an unregulated Mediterranean climate stream in California (USA), whereas Hopkins et al. (2011) observed high relative abundances of NZMS in hydrologically stable streams in Idaho (USA). Hydrology, therefore, probably plays a role in determining NZMS success in invaded ranges, and, by extension, moderates their ecological impacts.

### Temperature

Water temperature affects NZMS growth, fecundity, population densities, and species interactions and imposes constraints on their distribution in time and space (e.g., Winterbourn 1970; Dybdahl and Kane 2005; Cross et al. 2010; Moffitt and James 2012a; McKenzie et al. 2013; Sardiña et al. 2015). In natural and laboratory settings, a wide temperature tolerance has been documented, ranging from 2 °C (Moffitt and James 2012b) to 34 °C (Cox and Rutherford 2000). In western USA populations, NZMS commonly occur and can reach densities of over 500,000 ind./m<sup>2</sup> in geothermally influenced streams (e.g., Hall et al. 2003; Clements et al. 2011), suggesting positive associations between population densities, relatively warm temperatures, and thermal stability.

While NZMS exhibit a wide temperature tolerance across their invaded range, the suitable range for invasion success may be narrower, with extreme lows and highs affecting reproduction. For example, Dybdahl and Kane (2005) observed that reproductive output and population growth rates were at their greatest at 18 °C (relative to 12 °C and 24 °C) using a common-garden experiment with western USA clones to test the role of trait plasticity and fitness. Furthermore, temperature had significant effects on fitness, with declines in fitness below and above 18 °C (Dybdahl and Kane 2005). Similarly, in Piru Creek (California, USA), relationships between NZMS densities and temperature occur, with densities peaking at daily temperatures of around 17 °C (Bennett et al.

2015). In invaded temperate regions, NZMS exhibit annual population cycles (see section on Population Dynamics), with abundance peaking during the summer and declining dramatically during the winter (e.g., Kerans et al. 2005; Verhaegen et al. 2021); seasonal variation in water temperatures probably directly contributes, in part, to these population dynamics, along with life cycle patterns and indirect factors, such as day length and primary productivity. Mortality is presumed to occur during winter in areas where water temperatures approach freezing (Moffitt and James 2012a, b). Consistent suitable temperatures can sustain continuous growth and reproduction of NZMS (Nebeker 1971). Thus, in systems where water temperatures are relatively stable (such as groundwater-fed systems), NZMS may be particularly likely to become established and dominate the benthic community.

### Water chemistry

NZMS invade a wide range of aquatic systems with varying levels of salinity, from fresh to mesohaline waters. NZMS have a demonstrated ability to survive in higher salinities, up to full-strength seawater (35 g/kg) for short periods (Jacobsen and Forbes 1997; Gérard et al. 2003; Drown et al. 2011; LeClair and Cheng 2011; Hoy et al. 2012; Vazquez et al. 2016). Waters with low concentrations of certain dissolved ions, however, can suppress survival, growth, and reproductive output. Herbst et al. (2008) found positive associations with NZMS growth and higher conductivities (range: 25–200 µS/cm) during experimental trials using NZMS from an invaded California (USA) river. They also documented poor NZMS survival and growth when reducing specific conductivity from 300 to 50 µS/cm and in Ca<sup>+2</sup>-free culture media relative to natural Ca<sup>+2</sup>-containing water of equal conductivity, suggesting a calcium requirement for NZMS growth. Larson et al. (2020) similarly observed lower growth rates with low conductivity (50 µS/cm), relative to higher concentrations (800 µS/cm) where NZMS grew 4.6 times faster. Low levels of conductivity can also reduce the fecundity of NZMS, as in Boulder Creek (Colorado, USA) (McKenzie et al. 2013), whereas peak fecundity (measured as brood size) correlated with peak water hardness (250–300 mg/L CaCO<sub>3</sub>). Similar effects were observed by Vazquez et al. (2016) in experimental trials that showed reduced fecundity of NZMS in

waters with low conductivity and calcium concentrations (20–200  $\mu\text{S}/\text{cm}$  and 5–17.5  $\text{mg}/\text{L}$ , respectively) using snails from Redwood National Park (California, USA). Thus, waters with low conductivity ( $< 200 \mu\text{S}/\text{cm}$ ), specifically those deficient in calcium ions, can impact NZMS growth and reproduction.

Invasive lineages appear to have a high physiological tolerance to varying salinity levels and could be opportunistically specialized to persist at higher salinities (Drown et al. 2011; Everaert et al. 2011). This is evidenced by their ability to reproduce at salinity levels between 0 and 15  $\text{g}/\text{kg}$  and survive at levels of 30–35  $\text{g}/\text{kg}$  (Jacobsen and Forbes 1997; Zaranko et al. 1997; Leppäkoski and Olenin 2000; Costil et al. 2001; Gérard et al. 2003). Despite this, higher concentrations (20–35  $\text{g}/\text{kg}$ ) of salinity can result in greater mortality and negatively affect NZMS metabolic rate, snail size, and fecundity (e.g., Paolucci and Thuesen 2020; Verhaegen et al. 2021). As such, optimal values of salinity, in terms of NZMS reproductive output, feeding, and growth rate, appear to be around 5  $\text{g}/\text{kg}$  when evaluating clonal variation in life history traits across a salinity gradient (Jacobsen and Forbes 1997). Drown et al. (2011) also evaluated differences in plasticity and performance between invasive and ancestral (i.e., New Zealand native) genotypes of NZMS across a salinity gradient of 0–15  $\text{g}/\text{kg}$  and found invasive genotype performance (as survival and reproduction) was optimal at mid-range salinities (5 and 10  $\text{g}/\text{kg}$ ). Overall, dissolved ion content is an important factor for the osmotic balance and overall physiological makeup of gastropods (McMahon 1983), and NZMS can persist across a wide range of salinities. However, differences in salinity concentrations among invaded systems can, in part, determine invasion success and influence distribution among invasive NZMS lineages (Butkus et al. 2020), and so it is likely that salinity plays a role in the invasion process and establishment of NZMS. Specifically, waters low in calcium ions (i.e.,  $< 200 \mu\text{S}/\text{cm}$ ) and those with higher salinity ( $> 15 \text{g}/\text{kg}$ ), can restrict populations and negatively affect NZMS growth and reproduction, influence distribution (e.g., Lewin 2012; Levri et al. 2014; Spyra and Strzelec 2014; Vazquez et al. 2016), and, ultimately, influence invasion success.

To our knowledge, understanding of other aspects of water chemistry (e.g., pH, nutrient status, metals, etc.) and their influence on NZMS invasions is limited.

Levri et al. (2020b) investigated range expansion of NZMS in the Great Lakes region (USA) and found positive effects of pH on the relative abundances of NZMS in invaded Pennsylvania streams. There have been studies investigating the effects on NZMS of environmental toxicants, such as ammonia, nitrite, nitrate, and copper, in which NZMS were found to be relatively intolerant compared to other invertebrates, making them a candidate biological indicator for the pollutants (Watton and Hawkes 1984; Alonso and Camargo 2003). Alonso and Camargo (2009) found NZMS to have a relatively high tolerance of long-term exposures to varying concentrations of nonionized ammonia (0.02, 0.07, 0.14  $\text{mg}/\text{L}$   $\text{N}-\text{NH}_3$ ). The effects of urban effluent on NZMS have also been evaluated by Zoukova et al. (2014), who found greater mortality and decreased embryo production of NZMS immediately downstream of a wastewater treatment plant. In all, improved understanding of additional chemical parameters of aquatic environments and their influence on NZMS is needed, as they are expected to influence NZMS populations.

## Population dynamics

### *Variation in observed population densities*

The impacts an invasive species has on ecosystems are partly determined by population density (Strayer 2020), and reported local NZMS densities range from 40 to over 800,000  $\text{ind.}/\text{m}^2$  (Fig. 4) in their invaded range (Dorgelo 1987; Thomsen et al. 2009). To a degree, variation in NZMS population densities can be explained by the time since the initial introduction, variability among clonal lineages, other biological and environmental factors, as well as differences in sampling designs. This wide range of density – spanning over four orders of magnitude – coupled with minimal genetic variation and seemingly minimal incidence of predation/parasitism, suggests that environmental factors constrain populations, and, by extension, ecological impacts. For example, quantity and quality (e.g., ratios of carbon to phosphorus in algae) of food resources over various spatial and temporal scales can limit NZMS growth and reproduction, which may contribute to variation in population abundance (e.g., Dorgelo and Leonards 2001; Richards and Shinn 2004; Tibbets et al. 2010; Neiman



et al. 2013; Dorgelo et al. 2014; Krist et al. 2014; Neiman and Krist 2016).

### *Short-term population dynamics*

NZMS population fluctuations are often pronounced in invaded systems across multiple time scales. Population density often fluctuates seasonally, with peak values occurring during the summer and declines through winter and early spring, e.g., in England (Heywood and Edwards 1962), the Netherlands (Dorgelo 1987), Australia (Schreiber et al. 1998), Germany (Verhaegen et al. 2021), and in the western United States, where densities of over 500,000 individuals/m<sup>2</sup> can occur during the late summer and fall (e.g., Vinson 2004; Kerans et al. 2005; Hall et al. 2006; Bennett et al. 2015). These changes may stem from fluctuations in food availability or type (e.g., periphyton abundance and composition), changes in hydrology (e.g., periods of high discharge), or changes in water quality characteristics (e.g., temperature) over the course of a year.

### *Long-term population dynamics*

After NZMS achieve high densities in invaded systems, marked declines in population densities have been documented at the scale of years to decades (e.g., Moore et al. 2012; Gérard et al. 2018; Greenwood et al. 2020). In a California stream, NZMS densities approached 100,000 individuals/m<sup>2</sup> after a seven-year observation period and then fell to fewer than 1,000 individuals/m<sup>2</sup> over the next three years (Moore et al. 2012). Similar declines in abundance occurred in a French stream, where during 2000–2004, NZMS made up 97% of the molluscan assemblage, while during 2009–2013, NZMS made up 44% (Gérard et al. 2018) and reduced in abundance between the two time periods by 14-fold. Greenwood et al. (2020) assessed the biomass of NZMS in Polecat Creek (Wyoming, USA) over a 16-year time frame and documented a 15-fold reduction over 10 years. The authors did observe a rebound in biomass during the next 5 years, but not to the extent of that observed prior to the decline. NZMS density often increases rapidly after introduction, but this may not necessarily predict long-term population levels or dynamics over time. Like those of other invasive species, long-term fluctuations of NZMS densities may result, in part, from density-

dependent factors that alter ecosystem characteristics, such that high populations are no longer sustained (Strayer et al. 2017). Other ecological mechanisms regulating populations, such as predation by native or non-native species (e.g., Greenwood et al. 2020), exploitation of resources (Moore et al. 2012), or abiotic environmental changes (e.g., Kołodziejczyk et al. 2009), or any combination of these, may also affect NZMS populations over time. Given that the ecological impacts of NZMS are often proportional to their population size, and their abundances exhibit short- and long-term fluctuations, ecological impacts are also likely to fluctuate.

### Ecological impacts

#### *Effects on primary producers and nutrient cycling*

NZMS impact periphyton abundance and community structure in both their native and invaded ranges (Winterbourn and Fegley 1989; Biggs and Lowe 1994). In its invaded range, NZMS significantly reduced algal standing stock and periphyton biomass relative to controls (Riley et al. 2008; Kolosovich et al. 2012; Krist and Charles 2012). Moreover, NZMS grazing can alter diatom assemblages more than that of native grazers and can reduce the abundance of medium-to-large diatoms, filamentous cyanobacteria, and green algae while increasing tough, filamentous chlorophytes (Krist and Charles 2012; Bennett et al. 2015). Grazing by the invasive snail can, therefore, affect the abundance of periphyton in addition to altering the periphyton community structure and, in some instances, altering ecosystem functioning. In invaded regions, NZMS, because of their high biomass, can consume 75% of gross primary production in streams and dominate nitrogen and carbon cycling through grazing and excretion (Hall et al. 2003; Moore et al. 2012). Arango et al. (2009) observed further effects on nitrogen cycling during an enclosure experiment in which NZMS reduced proportions of green algae relative to nitrogen-fixing diatoms. This alteration in periphyton composition and physical structure had consequences for nitrogen-fixation rates. Arango et al. (2009) observed disproportionate increases in nitrogen fixation compared with the abundance of nitrogen-fixing cells, indicating that snails indirectly increased nitrogen fixation by improving nutrient and/or light availability to

nitrogen-fixing diatoms. NZMS populations can dominate the acquisition of primary production in invaded systems, particularly at elevated densities, and greater numbers of NZMS (i.e., greater densities) increases NZMS grazing activity (e.g., Hansen et al. 2015). Therefore, their elevated densities and effective grazing can lead to record high secondary production levels (Hall et al. 2006) and altered nutrient cycling.

#### *Effects on organic-matter processing*

While NZMS are widely placed in the functional feeding group “herbivore/detritivore”, almost all studies of the impacts of invasive NZMS on basal resources have focused on periphyton, while impacts on detritus and detrital processing remain largely unknown. In their native range, NZMS consume a mixture of food sources, including epiphytic algae, bacteria, fungi, and detritus (e.g., James et al. 2000). In a mesocosm study in their invaded range (Michigan, USA), NZMS increased the rates of leaf-litter decomposition; the effects were litter-species-specific and reflected the nutritional quality of the litter (E.N. Bovee, unpublished data). In a field study in a temperate forest stream (Michigan, USA), analysis of the isotopic composition of NZMS and a 2-source mixing model, following Post (2002), using a known shredder and a known grazer revealed that 65% of NZMS body carbon originated from terrestrial litter, with the remainder originating from periphyton (K.P. Bommarito, unpublished data). Taken together, findings from diet-related studies of NZMS suggest that they have the potential to impact multiple compartments of stream food webs, including detrital pools.

#### *Effects on macroinvertebrates*

Invasive NZMS affect native macroinvertebrates at individual, population, and community levels (e.g., Richards et al. 2001; Riley et al. 2008; Rakauskus et al. 2017) through direct and indirect pathways. Native gastropods often directly compete with NZMS since they frequently use similar food resources. For example, asymmetric interactions were observed between NZMS and a native western USA snail, *Pyrgulopsis robusta*, such that NZMS negatively affected growth rates of the native snail, but *P. robusta* facilitated growth rates of NZMS (Riley et al. 2008). Riley et al. (2008) suggested three explanations for these

asymmetric interactions: 1) NZMS ate *P. robusta*; 2) *P. robusta* secreted algal-growth enhancing mucus that indirectly facilitated growth of NZMS; 3) NZMS dominated a shared and preferred algal resource, forcing *P. robusta* to consume lower-quality algae, thereby opening space for the preferred algae to grow. Riley and Dybdahl (2015) later observed that negative effects of NZMS on *P. robusta* were strongest at low resource levels at which *P. robusta* grew slower in the presence of high biomass of NZMS. Similar negative interactions have also been observed between NZMS and another native snail, *Galba* sp. (Thon 2011), as well as in *Valvata utahensis*, also native, such that increasing densities of NZMS reduced individual growth during experimental grazing trials (Lysne and Koetsier 2008).

The negative effects of NZMS on native snail growth suggest competition for shared resources and that NZMS can be a more effective grazer than native snails. In grazing trials, Larson and Black (2016) found evidence for shared resources between a native gastropod, *Fluminicola* sp., and NZMS through analysis of stable carbon isotopes. In single-species treatments evaluating fecal mass of the two competitors, NZMS consumed 4.8 times more algae than the native snail (Larson and Black 2016). Similarly, in experimental trials, Bennett et al. (2015) found that *P. antipodarum* had a much greater grazing impact per capita than a native hydrobiid snail (*Pyrgulopsis* sp.) at equal densities and altered the composition and physiognomy of algal assemblages. Bennett et al. (2015) also observed competition between NZMS and the native hydrobiid, as evidenced by greater death rates and lower birth rates of both snails when at their highest densities. These findings are consistent with strong competition between NZMS and native snails with often-significant impacts on the latter.

The competitive ability of NZMS allows them to dominate the gastropod community. During a 14-year examination of the molluscan assemblage in a French stream, NZMS were numerically dominant, making up 91% of individuals in samples (Gérard et al. 2017). In other inland waters of France and the Mont St-Michel Bay, NZMS also dominate the resident gastropod community (Gérard et al. 2003). In post-industrial ponds in Poland, NZMS comprised up to 98% of the snail community (Strzelec 2005), and in a tributary of the Snake River (Idaho, USA), NZMS densities were greater than those of native snails in all sampled

habitats (Richards et al. 2001). Using morphological and molecular analyses to determine the distribution of NZMS and native snails in central Chile, Collado et al. (2019) found NZMS in several localities from which native gastropods disappeared, suggesting a possible species replacement by NZMS. Taken together, these findings suggest that native snails are highly vulnerable to the impacts of NZMS.

NZMS can influence the foraging behavior and distribution of native aquatic invertebrates. Hansen et al. (2016) observed reduced feeding activity by the native *Galba bulimoides* in the presence of NZMS. Using experimental tiles colonized by periphyton, Kerans et al. (2010) observed that, when NZMS were present, the number of Baetidae foraging on tiles decreased, indicating competitive interference by NZMS. Kerans et al. (2005) also observed that the number of native macroinvertebrates colonizing experimentally placed tiles declined as the number of NZMS increased, suggesting a potential to displace, or at least influence, the distribution of native invertebrates. Schreiber et al. (2002) observed contrasting results from an in-situ experiment in an Australian stream where NZMS densities were positively associated with native taxa richness and densities. Coprophagy was suggested as a possible mechanism for the associations, with speculation that NZMS feeding and excretion may be improving the quality of available detritus for native detritivorous taxa. Their study, however, had temporal and spatial constraints, thereby limiting generalizations or broad scale conclusions (Schreiber et al. 2002). Competition for resources with the invasive NZMS can therefore affect the growth, development, and/or feeding behavior of functionally similar taxa and can influence distributions of native taxa.

NZMS invasions change benthic community and functional structures. During a long-term water quality assessment in Rock Creek (Idaho, USA), a reduction in Ephemeroptera-Plecoptera-Trichoptera and collector-filterer taxa, an increase in scraper abundance, and an increase in pollution-tolerant taxa occurred, which was attributed to the high densities of the invasive snail (Maret et al. 2008). Similar effects have also been reported in a temperate mesotrophic lake where Rakauskus et al. (2017) observed shifts in the benthic community, and dominant taxa transitioned from crustacean to gastropod, a result of a rapidly increasing NZMS population. Several other studies have

reported similar shifts in taxonomic and functional structure after the snail invasion and demonstrate the ability of NZMS to reorganize a native community (e.g., Richards et al. 2001; Alonso and Castro-Díez 2012; Moore et al. 2012; Spyra et al. 2015).

#### *Effects on higher consumers*

NZMS have behavioral traits that make them resistant to predation. In studies assessing their response to predator detection, NZMS displayed an array of avoidance behaviors, including surfacing, climbing, and floating in laboratory experiments exposing NZMS to fish and crayfish olfactory cues (Haddaway et al. 2014; Levri et al. 2017a); nocturnal foraging (Levri 1998a, b) and positive photokinetic and geotactic responses to novel fish predator odor (Levri et al. 2017a); burrowing into sediments in the presence of benthic fishes (Holomuzki et al. 2009); and reduced growth rates in the presence of potential fish predator odor, possibly due to reduced foraging (Levri et al. 2020a). Additionally, shell morphology may play a role in predator avoidance, with the spiny-shelled form being less palatable to small, benthivorous fishes and having a stronger ability to burrow in substrate (Holomuzki et al. 2009). The flexible nature of their response to a potential predator allows NZMS to detect and respond to threats presented by novel predators, such as those encountered in their invaded range, which may improve their invasion success (Haddaway et al. 2014; Levri et al. 2017a, 2019). Furthermore, NZMS have the ability to recognize varying degrees of danger and respond accordingly, such as differentiating predators that do and do not prey on snails (Levri et al. 2019, 2020a) and adjusting avoidance behavior based on this perception (Haddaway et al. 2014). Predator avoidance behavior differs among clonal genotypes. Invasive clones have a stronger and more plastic predatory response compared to entirely native lineages and non-native lineages with poor invasion success (e.g., US3; Levri et al. 2017a, 2019), possibly because of a feedback mechanism in which predatory avoidance behavior fosters invasion success of non-native clones and is selected for by natural processes.

Predation on NZMS has been documented in multiple invaded systems. Aquatic invertebrates, including dragonfly and damselfly naiads (Bennett et al. 2015), red swamp crayfish (*Procambarus clarkii*)

(Bennett et al. 2015; Levri et al. 2019), signal crayfish (*Pacifastacus leniusculus*), and planarians (*Dugesia* spp.) (Twardochleb et al. 2012; Greenwood et al. 2020) consume NZMS. Fish prey on NZMS, as seen in a river in Utah (USA), where brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) rapidly increased their consumption of NZMS (Vinson and Baker 2008) during the invasion period. Other accounts of NZMS consumption in the western USA by fish species include: juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin (Oregon, USA) (Bersine et al. 2008); the tidewater goby (*Eucyclogobius newberryi*) in Big Lagoon (California, USA) (Hellmair et al. 2011); and Pacific staghorn sculpin (*Leptocottus armatus*), shiner perch (*Cymatogaster aggregate*), and English sole (*Pleuronectes vetulus*) in the Columbia River estuary (Oregon, USA) (Brenneis et al. 2011). In the Great Lakes region (USA), where NZMS have recently invaded inland rivers and streams, brown trout and brook trout (*Salvelinus fontinalis*) are feeding on them at increasing rates, with gut content analysis revealing more than 50 NZMS in some individuals (J.A. Geist, unpublished). In temperate lakes of Lithuania, where NZMS dominate the benthic invertebrate community, Rakauskas et al. (2016) found NZMS in the diets of all sampled benthivorous fish species. Although consumption of NZMS in invaded regions is occurring, their abundance in gut contents varies. In some systems, the number of consumed NZMS is insignificant (e.g., Bersine et al. 2008; Hellmair et al. 2011; Rakauskas et al. 2016), whereas in other invasion locations, NZMS consumption is relatively high (e.g., Hellmair et al. 2011; Geist et al. unpublished). Therefore, the degree to which consumption of NZMS is deliberate or incidental, and if the frequency of consumption depends upon NZMS densities, time since initial invasion, and/or food preference of various fish species, is unclear.

As NZMS become incorporated into the diets of higher consumers, their hard shell and operculum make it difficult for some predators to digest and derive sufficient nutrition (Haynes et al. 1985). In both their native and invaded range, NZMS can remain viable with shell intact after consumption and egestion by some predatory fish (e.g., McCarter 1986; Holomuzki 2010). In their invaded range, Vinson and Baker (2008) found that 53% of the invasive snails consumed by rainbow trout passed through digestive

tracts alive. Similar findings have been observed elsewhere, with over 40% of NZMS surviving passage through the digestive tracts of rainbow trout (Haynes et al. 1985; Bruce 2006). In contrast, only 4.5% of NZMS survived passage through the digestive tracts of rainbow trout tested by Oplinger et al. (2009). NZMS survival through the gut tract of the common rudd (*Scardinius erythrophthalmus*) in a Lithuanian lake was more than 80% on average but 0% when consumed by tench (*Tinca tinca*) (Rakauskas et al. 2016). NZMS survival ranged from 20 to 60% in multiple central European benthivorous riverine fish species (Butkus and Rakauskas 2020).

NZMS survival rates after consumption by fish thus ranges widely across studies and fish taxa, and, therefore, digestibility of NZMS may depend on the identity of the consumer and probably on variation in feeding strategies and specialization. In their native range, the endemic and benthivorous common bully (*Gobiomorphus cotidianus*) is a widespread predator of NZMS, capable of fully digesting them and possibly regulating their population (Holomuzki and Biggs 2006). However, for many species of fish occurring in NZMS invaded ranges, such as the European perch (*Perca fluviatilis*), which passes nearly 100% of consumed NZMS undigested (Rakauskas et al. 2016), assimilation of NZMS is substantially less than that of native prey. This suggests that NZMS are a nutritionally poor food item because of the high resistance of the shell to crushing, their operculum, small size, and minimal digestible tissue (McCarter 1986; Butkus and Visinskiene 2020). An exception exists, however, in an invaded coastal waterway (Big Lagoon, California, USA), where the endangered tidewater gobies successfully prey on NZMS, as evidenced by crushed shells in the posterior gut (Hellmair et al. 2011). This may illustrate that some feeding abilities and specializations, such as presence of pharyngeal teeth, may allow certain fish species to prey on NZMS, and therefore, partially exert some degree of population regulation. As such, the physiological condition of fish that deliberately or incidentally ingest NZMS but cannot assimilate them is at risk (e.g., Vinson and Baker 2008). Moreover, the ability of NZMS to withstand the fish digestive process casts doubt on whether predation by fish can help to regulate NZMS populations in invaded ranges or rather acts as a mechanism of spread via fish movement.

The poor nutritional quality of NZMS and the inability of some fish to assimilate NZMS after consumption affect energy flow in aquatic systems. In Lake Dusia (Lithuania), where NZMS altered macroinvertebrate community structure and increased total invertebrate biomass, benthivorous fish did not consume NZMS in high quantities. This suggests that basal resources ceased to flow to higher consumers, thus remaining locked in lower trophic levels and thereby reducing fish growth and catches in the lake (Rakauskas et al. 2018). As NZMS monopolize primary production and replace preferred and higher quality native prey, energy transfer through predation may decrease in NZMS-invaded systems. As such, the fate of NZMS production in invaded systems (i.e., energy flow) remains largely unknown, with likely consequences on energy transfer throughout food webs.

#### Population detection and monitoring

Early detection of newly introduced NZMS populations can inform effective management and facilitate rapid responses (Proctor et al. 2007; Vander Zanden et al. 2010; Goldberg et al. 2013; Thomas et al. 2020; Tank et al. 2021). However, conventional benthic sampling for early detection of NZMS can be challenging and expensive (Levri et al. 2007; Trebitz et al. 2010; Goldberg et al. 2013; Woodell et al. 2021). Currently, few agencies survey broadly for aquatic invasive species in general or NZMS specifically. Most recently discovered NZMS populations have been found by accident or as part of established long-term monitoring programs conducted at designated sites. The small body and cryptic coloration of NZMS, coupled with broad similarities to some native snails, make identification and, thus, early detection of NZMS challenging (Tank et al. 2021). Reliance on professionally trained personnel is therefore needed for early detection and surveillance or, at the least, for verification, which can be expensive for agencies and other institutions. However, recent efforts have been made to develop early and effective detection methods that can be implemented broadly (e.g., Tank et al. 2021). For example, the use of environmental DNA (eDNA) can offset the costs and difficulties of sampling potentially invaded aquatic systems, detect new introductions, and identify the invasive lineages (e.g., Pilliod et al. 2012; Clusa et al. 2016; Thomas

et al. 2020; Woodell et al. 2021). Goldberg et al. (2013) developed an eDNA assay and were able to detect NZMS at densities from 11 to 144 snails/m<sup>2</sup>. Using the methods of Goldberg et al. (2013), Woodell et al. (2021) were able to detect a previously unidentified population of NZMS in a Pennsylvania stream. Easily followed protocols enable volunteer citizen scientists to collect water samples from potentially invaded streams for eDNA analysis in a laboratory that has the appropriate technology, for example, to track spread in newly invaded regions in the Midwestern United States (Bovee et al., unpublished). Both eDNA and quantitative PCR (qPCR) hold promise as a means of evaluating NZMS abundance. Additional technological advances, such as geo-spatial analysis and distribution forecast modeling, can also improve knowledge of regional spread dynamics and identify locations vulnerable to invasion (e.g., Loo et al. 2007a, b; Sanders et al. 2014; da Silva et al. 2019; Gallardo et al. 2020). Effective and standardized visual assessments and eDNA are likely to be more widely used as means of early detection for NZMS and as key steps for establishing management strategies and minimizing further spread of NZMS.

#### Spread prevention and control

Introductions of NZMS can occur through aquaculture and fish stocking (Hosea and Finlayson 2005; Proctor et al. 2007; Oplinger et al. 2009; Oplinger and Wagner 2011, 2015), prompting evaluations of the efficacy of chemical treatments for NZMS disinfection in hatcheries and other infested waters. Many of these are effective at killing NZMS and include ammonia, Bayluscide, benzalkonium chloride, Hyamine 1622, hydrogen peroxide hydrothol, Pine-Sol, Rocca-D-Plus, sodium chloride, sodium hydroxide, Steanquat 50 NF, and Virkon Aquatic. Mortality generally increases at higher concentrations (Watton and Hawkes 1984; Hosea and Finlayson 2005; McMillin and Trumbo 2009; Oplinger and Wagner 2009, 2011, 2015; Stockton-Fiti and Moffitt 2017; Barenberg and Moffitt 2018).

Concentrations of these chemicals sufficient to kill NZMS may exceed environmental regulatory levels and may be greater than what is considered safe for most fish species. Oplinger and Wagner (2009) found that commonly used chemicals for hatchery and fish-egg disinfection are lethal to rainbow trout eggs at

concentrations and/or durations necessary to kill NZMS. These chemicals included Hyamine 1622; Clorox Commercial Solutions 409 Cleaner, Degreaser and Disinfectant; formalin; and household ammonia. However, Oplinger and Wagner (2009) found that hydrogen peroxide and Pine Sol were effective at NZMS decontamination in hatcheries, but further research is needed to evaluate the effects on fish egg mortality and development. Stockton-Fiti and Moffitt (2017) evaluated the potential health impacts to steelhead trout (*Oncorhynchus mykiss*) of Virkon Aquatic, a broad-spectrum disinfectant registered by the USA Environmental Protection Agency (EPA), and found a low risk if residue of the product remained on hatchery equipment or if there were accidental spills of the solution at recommended effective concentrations (i.e., 20 g/L). As such, the controlled use of Virkon Aquatic and potentially hydrogen peroxide and Pine-Sol could adequately disinfect aquaculture facilities and prevent spread of NZMS into uninfected waterbodies through fish stocking.

Because NZMS introductions occur through transport on recreational watercraft and gear (e.g., waders and boots) (Hosea and Finlayson 2005; Schisler et al. 2008; Alonso et al. 2016), decontamination strategies that are appropriate for use by the general public need to be evaluated and implemented. Decontamination strategies using chemical treatments for recreational gear vary in effectiveness. Hosea and Finlayson (2005) tested a suite of chemicals and their efficacy in killing NZMS. Among these, 5-min exposures of copper sulfate, benzethonium chloride, or Formula 409 All Purpose Cleaner (50% dilution) were recommended for disinfecting wading gear. However, the concentration deemed effective by Hosea and Finlayson (2005) is contrary to the findings of Schisler et al. (2008) that a 5-min exposure at the same concentration was ineffective in achieving 100% NZMS mortality, although exposure to undiluted Formula 409 All Purpose Cleaner for 10 min killed 100% of NZMS. Schisler et al. (2008) found that Sparquat 256, a germicidal cleaner, was effective in achieving 100% NZMS mortality at concentrations of at least 3.1%. Both Formula 409 All Purpose Cleaner and Sparquat 256 contain quaternary ammonium compounds (QAC), which are toxic to invertebrates and a common ingredient in molluscicides (Vallejo-Freire et al. 1954). The manufacturing of Sparquat 256 has been discontinued, however, which has prompted

further investigations of effective disinfectants containing QACs as a replacement. For example, Stout et al. (2016) evaluated three products containing QACs: Quat 4, Green Solutions High Dilutions Disinfectant 256, and Super HDQ Neutral. Regardless of the brand of QAC, Stout et al. (2016) recommended a disinfection rate of 0.4% for bath (i.e., soak) and 0.8% for spray with a minimum exposure duration of 10 min for effective NZMS decontamination.

Recent studies have continued investigating the efficacy of the common household cleaning product Formula 409 All Purpose Cleaner and Virkon Aquatic for NZMS decontamination because of their wide availability. Undiluted Formula 409 All Purpose Cleaner caused 100% mortality of NZMS during 10- and 20-min laboratory exposures (J.A. Geist, unpublished). De Stasio et al. (2019) also found Formula 409 All Purpose Cleaner to be highly effective, though the presence of mud in their experimental containers, and presumably on snails, reduced effectiveness. Virkon Aquatic is specifically labeled for use in fish hatcheries and is a commonly used biocide for disinfecting hatchery and aquaculture facilities. Stockton and Moffitt (2013) found that Virkon Aquatic caused 100% mortality when NZMS on wading gear were submerged for 30 min with 20 g/L concentration. Exposure to lower concentrations and for shorter durations resulted in lower mortality. Notably, little deterioration of wading gear was observed during repeated bath disinfections. De Stasio et al. (2019) also found immersion in Virkon Aquatic to be effective at killing NZMS within 20 min at similar concentrations, while spraying was less effective. The use of QACs and other effective disinfectants can help prevent spread of NZMS into uninfected waterbodies via aquaculture and recreational means. However, practicality and attainability of an effective product are likely to be hurdles for the general public in participating in NZMS decontamination measures. Therefore, further research is needed to develop a convenient decontamination strategy and to understand the willingness of water recreationists (e.g., anglers, boaters, etc.) to adopt it.

Preventing the transport of viable individuals to uninfected systems should be a critical component of management plans. Control methods not based on chemical solutions have been evaluated to prevent NZMS introduction, eradicate NMZS, or decontaminate equipment. Hoyer and Myrick (2012) found that,

among copper-based substrates, copper sheeting or mesh were the most effective contact barriers for limiting the locomotor activity of NZMS and preventing invasion of hatcheries. Nielson et al. (2012b) found elevated partial pressures of CO<sub>2</sub> to be effective as a decontaminant and a feasible control method for disinfecting substrates and tank systems. Alonso and Castro-Díez (2012) assessed NZMS tolerance to air exposure during laboratory trials and suggested a minimum air exposure time of 53 h for effective decontamination of equipment and boats. Also evaluating the effectiveness of air-drying, Richards et al. (2004) found the highest NZMS mortality rates at higher temperatures (experimental range: 9–29 °C), with mortality increasing with exposure time. They recommended heat-drying potentially contaminated equipment at a minimum temperature of 29–30 °C at low humidity for a minimum of 24 h, or, alternatively, at 40 °C for at least 2 h. Freezing at –3 °C is also effective at killing NZMS (Richards et al. 2004), and other studies have evaluated the impacts of freezing temperatures on infested waterbodies (e.g., Cheng and LeClair 2011). Exposure to water at 54 °C for 5 min is also effective (Hosea and Finlayson 2005; Proctor et al. 2007). In all, various decontamination strategies by means other than chemical solutions can aid in preventing the spread of NZMS.

## Conclusions and future directions

The results from our systematic review reveal that the NZMS is a globally widespread aquatic invasive invertebrate, causing a wide range of impacts on native ecosystem structure and functioning. In some instances, NZMS have weak or negligible effects on native benthic fauna (e.g., Múrria et al. 2008; Brenneis et al. 2010), or, in the case of an Australian stream, positive interactions (Schreiber et al. 2002). In most instances, however, NZMS adversely impact native fauna and other aspects of the recipient system. NZMS can alter algal (e.g., Bennett et al. 2014) and native invertebrate communities (e.g., Rakauskus et al. 2017) with concomitant consequences for higher consumers (e.g., Vinson and Baker 2008) and ecosystem functioning (e.g., Moore et al. 2012). The variation in observed impacts of NZMS across spatial and temporal scales is not uncommon among invasive species (Parker et al. 1999; Strayer et al. 2006; Jokela and

Ricciardi 2008; Ricciardi and Kipp 2008; Hulme et al. 2013), and here we outline where negative impacts can be expected to be pronounced.

While NZMS occupy a broad range of aquatic ecosystems, habitat characteristics of the invaded systems can influence fundamental aspects of their ecology, including: survival; growth rates; reproductive output and population growth, and consequently, abundance; and spatial distribution (e.g., Dybdahl and Kane 2005; Mazza et al. 2010; McKenzie et al. 2013; Bennett et al. 2015; Verhaegen et al. 2021). Aquatic systems that exhibit favorable conditions may be more susceptible to not only the invasion of NZMS, but also to greater ecological impacts of their invasion by fostering rapid population growth and dominance over the resident community and resources. Based on this literature review, these favorable conditions include: systems with high primary productivity; stable temperatures of around 17–18 °C; moderate-to-high levels of water hardness; salinity levels around 5 g/kg; stable hydrology; and relatively low flow velocities and/or presence of refugia from higher velocities ( $\geq 0.15$  m/s) (Table 3). Successful invasion and large ecological impacts are expected in instances when and where these biotic and abiotic conditions overlap with high propagule pressure (e.g., sport fish hatchery operations and stocking, recreational water use). These conditions are commonly found in relatively undisturbed aquatic systems. Therefore, despite the demonstrated tolerance of NZMS to a variety of environmental conditions and pollution (e.g., Alonso and Camargo 2004, 2009; Gérard and Poullain 2005), allowing them to colonize ecologically disturbed environments (Schreiber et al. 2003), high-quality aquatic systems with minimal human impacts may be especially susceptible as well. However, human activities may increase habitat suitability for NZMS through land use alteration and associated nutrient enrichments, riparian deforestation facilitating increased primary production, and regulation of flow regimes (e.g., dam management). Nonetheless, NZMS show high levels of fitness across environmental gradients; as such, further research is needed to empirically model habitat suitability of NZMS in the various systems they invade.

NZMS exhibit dynamic population trends over short and long-term time scales, and there is little understanding of the factors that control population growth and abundance. Furthermore, while population

**Table 3** Summary of suitable and optimal physio-chemical characteristics for NZMS in invaded ranges. Information was gathered from published studies using experimental or observational investigations

Physio-Chemical Attribute	Range (experimental and/or observed)	Optimal	References
Habitats	Streams, lakes, coastal, estuaries	Various	E.g., Brenneis et al. (2010), Davidson et al. (2008), Gérard et al. (2003), Levri et al. (2007), Lewin and Smoliński (2006), Zaranko et al. (1997)
Substrata	Fine–coarse; macrophytes	Various	Bennett et al. (2015), Lysne and Koetsier (2006), Mazza et al. (2011), Spyra and Strzelec (2014), Winterbourn (1970)
Flow velocity	0–1 m/s	< 0.15 m/s	Kefford and Lake (1999), Lysne and Koetsier (2006), Richards et al. (2001), Spyra et al. (2015)
Water temperature	2–34 °C	17–18 °C	Bennett et al. (2015), Cox and Rutherford (2000), Cross et al. (2010), Dybdahl and Kane (2005), Levri et al. (2014), McKenzie et al. (2012), Moffit and James (2012), Richards et al. (2004), Sardina et al. (2015), Winterbourn (1969, 1970),
Conductivity (general)	25–10,000 µS/cm	c. 200 - 800 µS/cm	Costil et al. (2001), Drown et al. (2010), Gérard et al. (2003), Herbst et al. (2008), Hoy et al. (2012), Jacobsen and Forbes (1997), Larson et al. (2020), Leppäkoski and Olenin (2000), McKenzie et al. (2013), Paolucci and Thuesen (2020), Spyra et al. (2015), Vazquez et al. (2016), Verhaegen et al. (2020)
Salinity	0–35 g/kg	< 10 g/kg	Costil et al. (2001), Drown et al. (2010), Gérard et al. (2003), Hoy et al. (2012), Jacobsen and Forbes (1997), Larson et al. (2020), Leppäkoski and Olenin (2000), McKenzie et al. (2013), Paolucci and Thuesen (2020), Vazquez et al. (2016), Verhaegen et al. (2020)
Calcium Ca <sup>+2</sup>	< 5–314 mg/L	> 10 mg/L	Herbst et al. (2008), Spyra and Strzelec (2014), Spyra et al. (2015), Vazquez et al. (2016)

density can be a key predictor of NZMS impacts (e.g., Hall et al. 2006; Moore et al. 2012), the abundance of a population is not the only factor that predicts the magnitude of impact an invasive species will have (Strayer et al. 2019; Strayer 2020). Rather, it is a combination of the population attributes, time since initial invasion, and the characteristics of the invaded ecosystem (Lockwood et al. 2013; Strayer et al. 2017). Therefore, improved understanding is needed of the determinants of NZMS population growth (e.g., Zachar and Neiman 2013) in invaded systems and how they differ among ecosystem types and geographic regions.

Most studies involving NZMS invasions have occurred in lotic systems, with fewer conducted in lentic ecosystems (e.g., Rakauskus et al. 2016, 2018). Of the articles reviewed herein, approximately 77% either studied NZMS in or obtained snails for experimental purposes from lotic rather than lentic systems. Differences in ecosystem characteristics between lotic and lentic waters may influence NZMS invasion dynamics and impacts. NZMS invasions in brackish

waters (e.g., coastal estuaries) are similarly understudied, with only a few studies conducted throughout their invaded range (e.g., Brenneis et al. 2011; Hellmair et al. 2011). Approximately 95% of the literature reviewed studied NZMS in or obtained snails for experimental purposes from freshwater rather than brackish-saltwater systems. Additional studies in NZMS-invaded lentic systems and brackish waters may offer further insight to NZMS population and invasion dynamics and impacts.

Since NZMS can survive through the digestive tract of popular game fish (e.g., trout) (Haynes et al. 1985; Vinson and Baker 2008; Oplinger et al. 2009), their spread through commercial and private fish hatchery operations is highly probable in regions where overlap exists between NZMS invasions and fish stocking (Oplinger and Wagner 2009, 2010, 2011, 2015; Bruce and Moffitt 2010; Nielson et al. 2012a; Stockton-Fiti and Moffitt 2017). The implementation of invasive species biosecurity plans can help to minimize further introductions of NZMS within and among nearby watersheds. For example, the State of Michigan (USA)



has required preventative measures for NZMS introductions that private hatcheries must undertake when transporting and stocking fish from known infested watersheds (State of Michigan 2018; Michigan Department of Natural Resources, pers. communications 2020). Elements of the biosecurity plan include specific restrictions on water intake procedures from NZMS-invaded waters, fish purging recommendations, and directions for water disposal. The establishment and implementation of preventative measures coupled with post-invasion strategies can reduce NZMS introductions and, thereby, minimize impacts to native ecosystems.

Public participation in NZMS management can assist in early detection in waters where NZMS are suspected of occurring (Proctor et al. 2007; Tank et al. 2021) and increase public awareness of NZMS, their impacts, and best management practices. Existing community-based programs (e.g., macroinvertebrate and water quality monitoring) can integrate NZMS monitoring procedures and significantly extend the reach of agencies within a jurisdiction. Furthermore, education and outreach to the public regarding best practices when using NZMS-infested waters can reduce spread via angling and other recreational water activities. Public campaigns that emphasize techniques for spread prevention through wader and fishing-gear decontamination using extreme temperatures (e.g., Richards et al. 2004) or by chemical treatment (e.g., Stockton and Moffitt 2013; De Stasio et al. 2019) can help minimize potential NZMS transport through aquatic-related recreational activities.

The scope of our review of the worldwide NZMS invasion was limited by the available and accessible published findings, most of which are probably limited to sites of NZMS detection that are near, convenient, and important to researchers and probably, therefore, represent only a portion of the entire NZMS distribution and extent of their impacts. As NZMS continue to expand their range, resource managers, researchers, and conservationists have opportunities to improve knowledge of the determinants of their invasion success, their impacts, and methods to prevent and control their spread.

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#### Declarations

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#### References

- Adema CM, Lun C-M, Hanelt B, Seville RS (2009) Digenean trematode infections of native freshwater snails and invasive *Potamopyrgus antipodarum* in the Grand Teton National Park/John D. Rockefeller Memorial Parkway Area. *J Parasitol* 95:224–227
- Alonso Á, 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 Á, Camargo JA (2004) Sub-lethal responses of the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) to unionized ammonia: A tolerant invading species. *Fresenius Environ Bull* 13:607–615
- Alonso Á, Camargo JA (2009) Long-term effects of ammonia on the behavioral activity of the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). *Arch Environ Contam Toxicol* 56:796–802
- Alonso Á, Castro-Díez P (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? *Hydrobiologia* 614:107–116
- Alonso Á, Castro-Díez P (2012) The exotic aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca): State of the art of a worldwide invasion. *Aquat Sci* 74:375–383

- Alonso Á, Castro-Díez P (2015) El caracol acuático neozelandés del cieno (*Potamopyrgus antipodarum*): impactos ecológicos y distribución de esta especie exótica en la península ibérica. *Ecosistemas* 24:52–58
- Alonso Á, Castro-Díez P, Saldaña-López A, Gallardo B (2019) The New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1853) (Tateidae, Mollusca) in the Iberian Peninsula: temporal patterns of distribution. *Bioinvasions Rec* 8:287–300
- Alonso Á, Valle-Torres G, Castro-Díez P (2016) Survival of an invasive aquatic snail to overland translocation in non-aquatic media: Implications for spreading. *Limnologica* 57:60–65
- 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
- Arle J, Wagner F (2013) Effects of anthropogenic salinisation on the ecological status of macroinvertebrate assemblages in the Werra River (Thuringia, Germany). *Hydrobiologia* 701:129–148
- Barenberg A, Moffitt CM (2018) Toxicity of aqueous alkaline solutions to New Zealand mudsnails, Asian clams, and quagga mussels. *J Fish Wildl Manag* 9:14–24
- Baur B, Ringeis B (2002) Changes in gastropod assemblages in freshwater habitats in the vicinity of Basel (Switzerland) over 87 years. *Hydrobiologia* 479:1–10
- Baur B, Schmidlin S (2007) Effects of invasive non-native species on the native biodiversity in the river Rhine. In: Nentwig W (ed) *Biol invasions*, vol 193. Springer, Berlin, pp 257–273
- Bennett DM, Dudley TL, Cooper SD, Sweet SS (2015) Ecology of the invasive New Zealand mud snail, *Potamopyrgus antipodarum* (Hydrobiidae), in a Mediterranean-climate stream system. *Hydrobiologia* 746:375–399
- Benson AJ, Kipp RM, Larson J, Fusaro A (2015) *Potamopyrgus antipodarum* (J.E. Gray, 1853): U.S. Geological Survey, Nonindigenous Aquatic Species Database. <https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=1008>. Accessed 8 January 2021
- Beran L (2007) Vodní měkkýši přehradní nádrže Slapy (Česká republika) Aquatic molluscs of the Slapy Reservoir (Czech Republic). *Malacol Bohemoslov* 6:11–16
- Beran L (2002) Aquatic molluscs of the Czech Republic - distribution and its changes, habitats, dispersal, threat and protection, Red List. *Sborník přírodovědného klubu v Uh. Hradišti, Supplementum* 10
- 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(343):143–150
- Bersine K, Brenneis VEF, Draheim RC, Rub AMW, Zamon JE, Litton RK, Hinton SA, Sytsma MD, Cordell JR, Chapman JW (2008) Distribution of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in the Columbia River Estuary and its first recorded occurrence in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Biol Invasions* 10:1381–1388
- Biggs BJF, Lowe RL (1994) Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *N Z J Mar Freshwater Res* 28:119–134
- Bondesen P, Kaiser EW (1949) *Hydrobia (Potamopyrgus) jenkinsi* Smith in Denmark illustrated by its ecology. *Oikos* 1:252–281
- Bowler PA (1991) The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the middle Snake River, southern Idaho. *Proc Desert Fishes Council* 21:173–182
- Boycott AE (1936) The habitats of fresh-water Mollusca in Britain. *J Anim Ecol* 5:116–186
- Brenneis VEF, Sih A, de Rivera CE (2010) Coexistence in the intertidal: interactions between the nonindigenous New Zealand mud snail *Potamopyrgus antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. *Oikos* 119:1755–1764
- Brenneis VEF, Sih A, de Rivera CE (2011) Integration of an invasive consumer into an estuarine food web: Direct and indirect effects of the New Zealand mud snail. *Oecologia* 167:169–179
- Bruce RL, Moffitt CM (2010) Quantifying risks of volitional consumption of New Zealand mudsnails by steelhead and rainbow trout. *Aquac Res* 41:552–558
- Bruce RL (2006) Methods of fish depuration to control New Zealand mudsnails at fish hatcheries. Master of Science Thesis, University of Idaho
- Brzeziński T, Kołodziejczyk A (2001) Distribution of *Potamopyrgus antipodarum* (Gray, 1843) in waters of the Wigry National Park (NE Poland) and the effect of selected habitat factors on its occurrence. *Folia Malacol* 9:125–135
- Butkus R, Baltrūnaite L, Arbačiauskas K, Audzijonytė A (2020) Two lineages of the invasive New Zealand mudsnail *Potamopyrgus antipodarum* spreading in the Baltic and Black sea basins: low genetic diversity and different salinity preferences. *Biol Invasions* 22:3551–3559
- Butkus R, Rakauskas V (2020) Experimental evidence that the invasive snail *Potamopyrgus antipodarum* (Gray, 1843) survives passage through the digestive tract of common riverine fish. *Manag Biol Invasions* 11:96–104
- Butkus R, Vaitonis G (2019) New records and distribution patterns of the invasive snail *Potamopyrgus antipodarum* (Gray, 1843) in Lithuanian inland waters. *Bioinvasions Rec* 8:804–812
- Butkus R, Šidagytė E, Arbačiauskas K (2012) Two morphotypes of the New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) (Mollusca: Hydrobiidae) invade Lithuanian lakes. *Aquat Invasions* 7:211–218
- Butkus R, Šidagytė E, Rakauskas V, Arbačiauskas K (2014) Distribution and current status of non-indigenous mollusc species in Lithuanian inland waters. *Aquat Invasions* 9:95–103
- Butkus R, Višinskienė G (2020) The aquatic invader *Potamopyrgus antipodarum* (Gray, 1843) is a poorer food item for benthivorous fishes than native snails. *Aquat Invasions* 15 (in press)
- Cada CA (2004) Interactions between the invasive New Zealand Mud Snail, *Potamopyrgus antipodarum*, baetid mayflies, and fish predators. Master of Science Thesis, Montana State University
- Carlsson R (2000) The distribution of the gastropods *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) in lakes on the Åland Islands, southwestern Finland. *Boreal Env Res* 5:187–195

- Cheng YW, LeClair LL (2011) A quantitative evaluation of the effect of freezing temperatures on the survival of New Zealand mudsnails (*Potamopyrgus antipodarum* Gray, 1843), in Olympia Washington's Capitol Lake. *Aquat Invasions* 6:47–54
- 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*, vol 2. Springer, Dordrecht, pp 103–121
- Clements WH, Arnold JL, Koel TM, Daley R, Jean C (2011) Responses of benthic macroinvertebrate communities to natural geothermal discharges in Yellowstone National Park, USA. *Aquat Ecol* 45:137–149
- Clusa L, Ardura A, Gower F, Miralles L, Tsartsianidou V, Zaiko A, Garcia-Vazquez E (2016) An easy phylogenetically informative method to trace the globally invasive *Potamopyrgus* mud snail from river's eDNA. *PLoS ONE* 11:e0162899
- Collado GA (2014) Out of New Zealand: Molecular identification of the highly invasive freshwater mollusk *Potamopyrgus antipodarum* (Gray, 1843) in South America. *Zool Stud* 53:1–9
- Collado GA, Fuentealba CG (2020) Range extension of the invasive *Potamopyrgus antipodarum* (Gray, 1843) (Gastropoda, Tateiidae) in Chile, and a summary of its distribution in the country. *Check List* 16:621–626
- Collado GA, Vidal MA, Aguayo KP, Méndez MA, Valladares MA, Cabrera FJ, Pastenes L, Gutiérrez Gregoric DEG, Puillandre N (2019) Morphological and molecular analysis of cryptic native and invasive freshwater snails in Chile. *Sci Rep* 9:7846
- Connelly NA, O'Neill CR, Knuth BA, Brown TL (2007) Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities. *Environ Mgmt* 40:105–112
- Costil K, Dussart GBJ, Daguzan J (2001) Biodiversity of aquatic gastropods in the Mont St-Michel basin (France) in relation to salinity and drying of habitats. *Biodivers Conserv* 10:1–8
- Cox TJ, Rutherford JC (2000) Thermal tolerances of two stream invertebrates exposed to diurnally varying temperatures. *N Z J Mar Freshwater Res* 34:203–208
- 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
- da Silva MVA, Souza JVN, de Souza JRB, Vieira LM (2019) Modelling species distributions to predict areas at risk of invasion by the exotic aquatic New Zealand mudsnail *Potamopyrgus antipodarum* (Gray 1843). *Freshw Biol* 64:1504–1518
- De Stasio BT, Acy CN, Frankel KE, Fritz GM, Lawhun SD (2019) Tests of disinfection methods for invasive snails and zooplankton: effects of treatment methods and contaminated materials. *Lake Reserv Manag* 35:156–166
- Donne C, Neiman M, Woodell JD, Haase M, Verhaegen G (2020) A layover in Europe: Reconstructing the invasion route of asexual lineages of a New Zealand snail to North America. *Mol Ecol* 29:3446–3465
- Dorgelo J (1987) Density fluctuations in populations (1982–1986) and biological observations of *Potamopyrgus jenkinsi* in two trophically differing lakes. *Hydrobiol Bull* 21:95–110
- Dorgelo J (1991) Growth, food and respiration in the prosobranch snail *Potamopyrgus jenkinsi* (E. A. Smith) (Hydrobiidae, Mollusca). *Verh Internat Verein Limnol* 24:2947–2953
- Dorgelo J, van der Geest H, Hunting ER (2014) Dynamics of natural populations of the detritivorous mudsnail *Potamopyrgus antipodarum* (Gray) (Hydrobiidae) in two interconnected lakes differing in trophic state. *Springerplus* 3:736
- 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
- Drown DM, Levri EP, Dybdahl MF (2011) Invasive genotypes are opportunistic specialists not general purpose genotypes. *Evol Appl* 4:132–143
- Dusting A (2016) The ecology and evolution of invasive *Potamopyrgus antipodarum* in Australia. Doctor of Philosophy dissertation, University of Canberra, Australia
- Dybdahl MF, Drown DM (2011) The absence of genotypic diversity in a successful parthenogenetic invader. *Biol Invasions* 13:1663–1672
- Dybdahl MF, Kane SL (2005) Adaptation vs. phenotypic plasticity in the success of a clonal invader. *Ecology* 86:1592–1601
- Everaert G, Boets P, Lock K, Džeroski S, Goethals PLM (2011) Using classification trees to analyze the impact of exotic species on the ecological assessment of polder lakes in Flanders, Belgium. *Ecol Model* 222:2202–2212
- Ezhova E, Żmudziński L, Maciejewska K (2005) Long-term trends in the macrozoobenthos of the Vistula Lagoon, southeastern Baltic Sea. *Species composition and biomass distribution*. *Bull Sea Fisheries Inst* 1:55–73
- Filippenko DP, Son MO (2008) The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) is colonizing the artificial lakes of Kaliningrad City, Russia (Baltic Sea Coast). *Aquat Invasions* 3:345–347
- Fisheries and Oceans Canada (2018) New Zealand Mud Snail. <https://www.dfo-mpo.gc.ca/species-especes/profiles-profil/newzealandmudsnail-nassenouvellezealande-eng.html> Accessed 23 March 2021
- Gaino E, Scoccia F, Lancioni T, Ludovisi A (2008) The invader mudsnail *Potamopyrgus antipodarum* in the Tiber River basin (Central Italy). *Ital J Zool (modena)* 74:253–261
- Gallardo B, Castro-Díez P, Saldaña-López AA (2020) Integrating climate, water chemistry and propagule pressure indicators into aquatic species distribution models. *Ecol Indic* 112:106060
- Gangloff MM (1998) The New Zealand mud snail in Western North America. *Aquat Nuis Spec* 2:25–30
- Gergs R, Rothhaupt K-O (2015) Invasive species as driving factors for the structure of benthic communities in Lake Constance, Germany. *Hydrobiologia* 746:245–254

- Gherardi F (2007) Biological invaders in inland waters: Profiles, distribution, and threats. In: Drake JA (ed) *Invading nature - springer series in invasion ecology*, vol 2. Springer, Dordrecht
- Goldberg CS, Sepulveda A, Ray A, Baumgardt J, Waits LP (2013) Environmental DNA as a new method for early detection of New Zealand mudsnails (*Potamopyrgus antipodarum*). *Freshw Sci* 32:792–800
- Grant A, Briggs AD (1998) Toxicity of ivermectin to estuarine and marine invertebrates. *Mar Pollut Bull* 36:540–541
- Greenwood DJ, Hall RO Jr, Tibbets TM, Krist AC (2020) A precipitous decline in an invasive snail population cannot be explained by a native predator. *Biol Invasions* 22:363–378
- Grigorovich IA, Korniushev AV, Gray DK, Duggan IC, Colautti RI, MacIsaac HJ (2003) Lake Superior: An invasion coldspot? *Hydrobiologia* 499:191–210
- 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
- Gérard C, Hervé M, Hechinger RF (2018) Long-term population fluctuations of the exotic New Zealand mudsnail *Potamopyrgus antipodarum* and its introduced apocotylid trematode in northwestern France. *Hydrobiologia* 817:253–266
- Gérard C, Le Lannic J (2003) Establishment of a new host-parasite association between the introduced invasive species *Potamopyrgus antipodarum* (Smith) (Gastropoda) and *Sanguinicola* sp. Plehn (Trematoda) in Europe. *J Zool Lond* 261:213–216
- Gérard C, Miura O, Lorda J, Cribb TH, Nolan MJ, Hechinger RF (2017) A native-range source for a persistent trematode parasite of the exotic New Zealand mudsnail (*Potamopyrgus antipodarum*) in France. *Hydrobiologia* 785:115–126
- Gérard C, Poullain V (2005) Variation in the response of the invasive species *Potamopyrgus antipodarum* (Smith) to natural (cyanobacterial toxin) and anthropogenic (herbicide atrazine) stressors. *Environ Pollut* 138:28–33
- Haddaway NR, Vieille D, Mortimer RJG, Christmas M, Dunn AM (2014) Aquatic macroinvertebrate responses to native and non-native predators. *Knowl Manag Aquat Ecosyst*. <https://doi.org/10.1051/kmae/2014036>
- Hall RO Jr, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. *Ecol Appl* 16:1121–1131
- 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
- Hamada K, Tatara Y, Urabe M, The Biology Club of Kojo High School (2013) Survey of mitochondrial DNA haplotypes of *Potamopyrgus antipodarum* (Caenogastropoda: Hydrobiidae) introduced into Japan. *Limnology* 14:223–228
- Hansen BK (2015) A case for increased foraging success under high conspecific densities in the New Zealand mudsnail, *Potamopyrgus antipodarum*. *Natl Park Serv Res Center Ann Rep* 35:91–96
- Hansen BK, Krist AC, Tibbets TM (2016) Foraging differences between the native snail, *Fossaria* sp. and the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in response to phosphorus limitation. *Aquat Ecol* 50:297–306
- Harding JS, Winterbourn MJ, McDiffett WF (1997) Stream faunas and ecoregions in South Island, New Zealand: Do they correspond? *Arch Hydrobiol* 140:289–307
- Hauser L, Carvalho GR, Hughes RN, Carter RE (1992) Clonal structure of the introduced freshwater snail *Potamopyrgus antipodarum* (Prosobranchia: Hydrobiidae), as revealed by DNA fingerprinting. *Proc R Soc B* 249:19–25
- Haynes A, Taylor B, Varley ME (1985) The influence of the mobility of *Potamopyrgus jenkinsi* (Smith, E. A.) (Prosobranchia: Hydrobiidae) on its spread. *Arch Hydrobiol* 103:497–508
- Hellmair M, Goldsmith G, Kinziger AP (2011) Preying on invasives: The exotic New Zealand mudsnail 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 N Am Nat* 68:324–333
- Hershler R, Liu H-P, Clark WH (2010) Microsatellite evidence of invasion and rapid spread of divergent New Zealand mudsnail (*Potamopyrgus antipodarum*) clones in the Snake River basin, Idaho, USA. *Biol Invasions* 12:521–532
- Heywood J, Edwards RW (1962) Some aspects of the ecology of *Potamopyrgus jenkinsi* Smith. *J Anim Ecol* 31:239–250
- Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecol Monogr* 80:179–196
- Holomuzki JR (2010) Within-reach spatial variability of snails and molluscivory by brown trout. *N Z J Mar Fresh* 44:189–197
- Holomuzki JR, Biggs BJB (1999) Distributional responses to flow disturbance by a stream-dwelling snail. *Oikos* 87:36–47
- Holomuzki JR, Biggs BJB (2000) Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. *J N Am Benthol Soc* 19:670–679
- Holomuzki JR, Biggs BJB (2006) Habitat-specific variation and performance trade-offs in shell armature of New Zealand mudsnails. *Ecology* 87:1038–1047
- Holomuzki JR, Biggs BJB (2007) Physical microhabitat effects on 3-dimensional spatial variability of the hydrobiid snail, *Potamopyrgus antipodarum*. *N Z J Mar Fresh* 41:357–367
- Holomuzki JR, Lowe RL, Biggs BJB (2009) Spatiotemporal separation of New Zealand mudsnails from predatory fish. *J N Am Benthol Soc* 28:846–854
- Hopkins JM, Marcarelli AM, Bechtold HA (2011) Ecosystem structure and function are complementary measures of water quality in a polluted, spring-influenced river. *Water Air Soil Pollut* 214:409–421
- Hosea RC, Finlayson B (2005) Controlling the spread of New Zealand mud snails on wading gear. The State of California Department of Fish and Game
- Hoy M, Boese BL, Taylor L, Reusser D, Rodriguez R (2012) Salinity adaptation of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in the Columbia River estuary (Pacific Northwest, USA): Physiological and molecular studies. *Aquat Ecol* 46:249–260

- Hoyer SA, Myrick CA (2012) Can copper-based substrates be used to protect hatcheries from invasion by the New Zealand mudsnail? *N Am J Aquac* 74:575–583
- Hulme PE, Pyšek P, Jarošík V, Pergl J, Schaffner U, Vilá M (2013) Bias and error in understanding plant invasion impacts. *Trends Ecol Evol* 28:212–218
- Hynes HBN (1970) The ecology of running waters. University of Toronto Press, Toronto
- Irikov AA, Georgiev DG (2008) The New Zealand mud snail *Potamopyrgus antipodarum* (Gastropoda: Prosobranchia) – a new invader species in the Bulgarian fauna. *Acta Zool Bulg* 60:205–207
- Jacobsen EL, Forbes VE (1997) Clonal variation in life-history traits and feeding rates in the gastropod, *Potamopyrgus antipodarum*: Performance across a salinity gradient. *Funct Ecol* 11:260–267
- James MR, Hawes I, Weatherhead M, Stanger C, Gibbs M (2000) Carbon flow in the littoral food web of an oligotrophic lake. *Hydrobiologia* 441:93–106
- Jensen A, Forbes VE, Parker ED 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 MF, Fox JA (1997) Evidence for a cost of sex in the freshwater snail *Potamopyrgus antipodarum*. *Ecology* 78:452–460
- Jokela A, Ricciardi A (2008) Predicting zebra mussel fouling on native mussels from physicochemical variables. *Freshw Biol* 53:1845–1856
- Kalyoncu H, Barlas M, Yıldırım MZ, Yorulmaz B (2008) Gastropods of two important streams of Gökova Bay (Muğla, Turkey) and their relationships with water quality. *Int J Sci Technol* 3:27–36
- Karatayev AY, Mastitsky SE, Burlakova LE, Karatayev VA, Hajduk MM, Conn DB (2012) Exotic molluscs in the Great Lakes host epizootically important trematodes. *J Shellfish Res* 31:885–894
- Karatayev AY, Mastitsky SE, Burlakova LE, Olenin S (2008) Past, current, and future of the central European corridor for aquatic invasions in Belarus. *Biol Invasions* 10:215–232
- Kefford BJ, Lake PS (1999) Effects of spatial and temporal changes in water velocity on the density of the freshwater snail *Potamopyrgus antipodarum* (Gray). *Molluscan Res* 20:11–16
- Kerans BL, Cada CA, Zickovich J (2010) Asymmetrical behavioral interactions between the New Zealand Mud Snail, *Potamopyrgus antipodarum*, and scraping, collector-gathering and collector-filtering macroinvertebrates. *J Freshw Ecol* 25:657–666
- 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
- Kerney M (1999) Atlas of the land and freshwater molluscs of Britain and Ireland. Harley Books, United Kingdom
- Kistner EJ, Dybdahl MF (2013) Adaptive responses and invasion: the role of plasticity and evolution in snail shell morphology. *Ecol Evol* 3:424–436
- Kistner EJ, Dybdahl MF (2014) Parallel variation among populations in the shell morphology between sympatric native and invasive aquatic snails. *Biol Invasions* 16:2615–2626
- Kolosovich AS, Chandra S, Saito L, Davis CJ, Atwell L (2012) Short-term survival and potential grazing effects of the New Zealand mudsnail in an uninvaded Western Great Basin watershed. *Aquat Invasions* 7:203–209
- Kołodziejczyk A, Lewandoski 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
- Krist AC, Charles CC (2012) The invasive New Zealand mudsnail, *Potamopyrgus antipodarum*, is an effective grazer of algae and altered the assemblage of diatoms more than native grazers. *Hydrobiologia* 694:143–151
- Krist AC, Kay AD, Larkin K, Neiman M (2014) Response to phosphorus limitation varies among lake populations of the freshwater snail *Potamopyrgus antipodarum*. *PLoS ONE* 9:e85845
- Larson MD, Black AR (2016) Assessing interactions among native snails and the invasive New Zealand mud snail, *Potamopyrgus antipodarum*, using grazing experiments and stable isotope analysis. *Hydrobiologia* 763:147–159
- Larson MD, Dewey JC, Krist AC (2020) Invasive *Potamopyrgus antipodarum* (New Zealand mud snails) and native snails differ in sensitivity to specific electrical conductivity and cations. *Aquat Ecol* 54:103–117
- Larson MD, Krist AC (2020) Trematode prevalence and an invasive freshwater snail: fewer infections and parasites likely contribute to the success of an invasive snail. *Biol Invasions* 22:1279–1287
- LeClair LL, Cheng YW (2011) A review of salinity tolerances for the New Zealand mudsnail (*Potamopyrgus antipodarum*, Gray 1843) and the effect of a controlled saltwater backflush on their survival in an impounded freshwater lake. *J Shellfish Res* 30:905–914
- van Leeuwen CHA, van der Velde G, van Groenendael JM, Klaassen M (2012) Gut travelers: internal dispersal of aquatic organisms by waterfowl. *J Biogeogr* 39:2031–2040
- Leppäkoski E, Olenin S (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. *Biol Invasions* 2:151–163
- Levri EP (1998a) The influence of non-host predators on parasite-induced behavior changes in a freshwater snail. *Oikos* 81:531–537
- Levri EP (1998b) Perceived predation risk, parasitism, and the foraging behavior of a freshwater snail (*Potamopyrgus antipodarum*). *Can J Zool* 76:1878–1884
- Levri EP, Berkheimer C, Wilson K, Xu J, Woods T, Hutchinson S, Yoder K, Zhang X, Li X (2020a) The cost of predator avoidance behaviors in an invasive freshwater snail. *Freshw Sci* 39:476–484
- Levri EP, Clark TJ (2015) Behavior in invasive New Zealand mud snails (*Potamopyrgus antipodarum*) is related to source population. *Biol Invasions* 17:497–506
- Levri EP, Colledge ED, Bilka RH, Smith BJ (2012) The distribution of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in streams in the Lake Ontario and Lake Erie watersheds. *Bioinvasions Rec* 1:215–219

- Levri EP, Jacoby W (2008) The invasive New Zealand mud snail (*Potamopyrgus antipodarum*) found in streams of the Lake Ontario Watershed. *J Pa Acad Sci* 82:7–11
- Levri EP, Kelly AA, Love E (2007) The invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in Lake Erie. *J Great Lakes Res* 33:1–6
- Levri EP, Krist AC, Bilka R, Dybdahl MF (2014) Phenotypic plasticity of the introduced New Zealand mud snail, *Potamopyrgus antipodarum*, compared to sympatric native snails. *PLoS ONE* 9:e93985
- Levri EP, Landis S, Smith BJ (2017b) A periphyton-based diet results in an increased growth rate compared to a detritus-based diet in the invasive New Zealand mud snail (*Potamopyrgus antipodarum*). *Amer Malac Bull* 35:65–69
- Levri EP, Landis S, Smith B, Colledge E, Metz E, Li X (2017a) Variation in predator-induced behavioral changes in introduced and native populations of the invasive New Zealand mud snail (*Potamopyrgus antipodarum* Gray, 1843). *Aquat Invasions* 12:499–508
- Levri EP, Luft R, Li X (2019) Predator detection and a possible dispersal behavior of the invasive New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843). *Aquat Invasions* 14:417–432
- Levri EP, Macelko N, Brindle B, Levri JE, Dolney TJ, Li X (2020b) The invasive New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) in central Pennsylvania. *Bioinvasions Rec* 9:109–119
- Lewin I (2012) Occurrence of the invasive species *Potamopyrgus antipodarum* (Prosobranchia: Hydrobiidae) in mining subsidence reservoirs in Poland in relation to environmental factors. *Malacologia* 55:15–31
- Lewin I, Smoliński A (2006) Rare and vulnerable species in the mollusk communities in the mining subsidence reservoirs of an industrial area (the Katowicka Upland, Upper Silesia, Southern Poland). *Limnologia* 36:181–191
- Liess A, Lange K (2011) The snail *Potamopyrgus antipodarum* grows faster and is more active in the shade, independent of food quality. *Oecologia* 167:85–96
- Litton RK (2000) Youngs Bay benthic invertebrate study 2000. Report to Oregon Department of Environmental Quality, Permit Number 101767
- Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion ecology, 2nd edn. Wiley-Blackwell, West Sussex
- Loo SE, Keller RP, Leung B (2007a) Freshwater invasions: using historical data to analyse spread. *Diversity Distrib* 13:23–32
- Loo SE, Mac Nally R, Lake PS (2007b) Forecasting New Zealand mudsnail invasion range: Model comparisons using native and invaded ranges. *Ecol Appl* 17:181–189
- Lucas A (1959) Les Hydrobia (Bythinellidae) de l'Ouest de la France. *J Conchyliol* 99:3–14
- Lysne S, Koetsier P (2006) Experimental studies on habitat preference and tolerances of three species of snails from the Snake River of southern Idaho, U.S.A. *Amer Malac Bull* 21:77–85
- Lysne S, Koetsier P (2008) Comparison of desert valvata snail growth at three densities of the invasive New Zealand mudsnail. *West N Am Nat* 68:103–106
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Maret TR, MacCoy DE, Carlisle DM (2008) Long-term water quality and biological responses to multiple best management practices in Rock Creek, Idaho. *J Am Water Resour Assoc* 44:1248–1269
- Marshall JW, Winterbourn MJ (1979) An ecological study of a small New Zealand stream with particular reference to the Oligochaeta. *Hydrobiologia* 65:199–208
- Marszewska A, Cichy A, Bulantová J, Horák P, Žibkowska E (2018) *Potamopyrgus antipodarum* as a potential defender against swimmer's itch in European recreational water bodies—experimental study. *PeerJ*. <https://doi.org/10.7717/peerj.5045>
- Mazza G, Agostini N, Aquiloni L, Cianfanelli S, Tricarico E, Gherardi F (2011) Ecological characterisation of streams invaded by the New Zealand mud snail *Potamopyrgus antipodarum* (Gray 1843): the case study of a National Park in Italy. *Ethol Ecol Evol* 23:151–164
- McCarter NH (1986) Food and energy in the diet of brown and rainbow trout from Lake Benmore, New Zealand. *New Zeal J Mar Fresh* 20:551–559
- McKenzie VJ, Hall WE, Guralnick RP (2013) New Zealand mudsnails (*Potamopyrgus antipodarum*) in Boulder Creek, Colorado: Environmental factors associated with fecundity of a parthenogenic invader. *Can J Zool* 91:30–36
- McMahon RF (1983) Physiological ecology of freshwater pulmonates. In: Russell-Hunter WD (ed) *The Mollusca*, vol 6. Ecology. Academic Press, New York, pp 360–430
- McMillin S, Trumbo JD (2009) Field assessment of Bayluscide treatments for the control of New Zealand mudsnail *Potamopyrgus antipodarum* in a concrete-lined canal. *Calif Fish Game* 95:147–152
- Michalik-Kucharz A (2008) The occurrence and distribution of freshwater snails in a heavily industrialised region of Poland (Upper Silesia). *Limnologia* 38:43–55
- Moffitt CM, James CA (2012a) Dynamics of *Potamopyrgus antipodarum* infestations and seasonal water temperatures in a heavily used recreational watershed in intermountain North America. *Aquat Invasions* 7:193–202
- Moffitt CM, James CA (2012b) Response of New Zealand mudsnails *Potamopyrgus antipodarum* to freezing and near-freezing fluctuating water temperatures. *Freshw Sci* 31:1035–1041
- Moore JW, Herbst DB, Heady WN, Carlson SM (2012) Stream community and ecosystem responses to the boom and bust of an invading snail. *Biol Invasions* 14:2435–2446
- Morley NJ (2008) The role of the invasive snail *Potamopyrgus antipodarum* in the transmission of trematode parasites in Europe and its implications for ecotoxicological studies. *Aquat Sci* 70:107–114
- Mouthon J (2002) Changes in the composition and the structure of mollusc communities of the north part of Annecy Lake (Savoie, France) between the years 1929–1939 and the present period. *Rev Suisse Zool* 109:343–354
- Mouthon J, Dubois JP (2001) Mollusc communities of the littoral zone of Annecy Lake (Savoie, France). *Ann Limnol* 37:267–276
- Mouthon J, Magny M (2004) Malacological history of Lake Annecy (France): A comparison of Late Holocene (since 4700 BC) and present mollusc assemblages. *Arch Hydrobiol* 160:555–573

- Múrria C, Bonada N, Prat N (2008) Effects of the invasive species *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) on community structure in a small Mediterranean stream. *Fund 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
- Nebeker AV (1971) Effect of temperature at different altitudes on the emergence of aquatic insects from a single stream. *J Kans Entomol Soc* 44:26–35
- Negovetic S, Jokela J (2001) Life-history variation, phenotypic plasticity, and subpopulation structure in a freshwater snail. *Ecology* 82:2805–2815
- Neiman M, Krist AC (2016) Sensitivity to dietary phosphorus limitation in native vs. invasive lineages of a New Zealand freshwater snail. *Ecol Appl* 26:2218–2224
- Neiman M, Warren D, Rasmussen B, Zhang S (2013) Complex consequences of increased density for reproductive output in an invasive freshwater snail. *Evol Ecol* 27:1117–1127
- Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilá M (2018) More than “100 worst” alien species in Europe. *Biol Invasions* 20:1611–1621
- Nielson RJ, Moffitt CM, Watten BJ (2012a) Hydrocyclonic separation of invasive New Zealand mudsnails from an aquaculture water source. *Aquaculture* 326–329:156–162
- Nielson RJ, Moffitt CM, Watten BJ (2012b) Toxicity of elevated partial pressures of carbon dioxide to invasive New Zealand mudsnails. *Environ Toxicol Chem* 31:1838–1842
- Odabaşı S, Arslan N, Özdilek SY, Odabaşı DA (2019) An invasion report of the New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843) in Turkish freshwaters: Delice River and Kocabaş Stream. *LimnoFish* 5:213–219
- Oplinger RW, Brown P, Wagner EJ (2009) Effect of sodium chloride, tricaine methanesulfonate, and light on New Zealand mud snail behavior, survival of snails defecated from rainbow trout, and effects of Epsom salt on snail elimination rate. *N Am J Aquac* 71:157–164
- Oplinger RW, Wagner EJ (2009) Toxicity of common aquaculture disinfectants to New Zealand mud snails and mud snail toxicants to rainbow trout eggs. *N Am J Aquac* 71:229–237
- Oplinger RW, Wagner EJ (2010) Effect of potassium permanganate treatments on New Zealand mud snail behavior and survival and rainbow trout growth and condition. *N Am J Aquac* 72:207–212
- Oplinger RW, Wagner EJ (2011) Tests of the ability of five disinfectants to kill New Zealand Mud Snails. *J Appl Aquac* 23:187–197
- Oplinger RW, Wagner EJ (2015) Effects of sodium chloride and long-term, low-concentration exposures to hydrogen peroxide on New Zealand mud snails. *N Am J Aquac* 77:31–36
- Paolucci EM, Thuesen EV (2020) Effects of osmotic and thermal shock on the invasive aquatic mudsnail *Potamopyrgus antipodarum*: mortality and physiology under stressful conditions. *NeoBiota* 54:1–22
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Patzner RA (1996) Die Neuseeländische Zwergdeckelschnecke *Potamopyrgus antipodarum* (Gray 1843) im Bundesland Salzburg. *Linzer Biol Beitr* 28:1153–1159
- Pilliod DS, Goldberg CS, Laramie MB, Waits LP (2013) Application of environmental DNA for inventory and monitoring of aquatic species. U.S. Geological Survey. Accessed 8 January 2021
- Poff NL, Allan D, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. *Bioscience* 47:769–784
- Ponder WF (1988) *Potamopyrgus antipodarum* – a molluscan colonizer of Europe and Australia. *J Molluscan Stud* 54:271–285
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumption. *Ecology* 83:703–718
- Proctor T, Kerans B, Clancey P, Ryce E, Dybdahl M, Gustafson D, Hall R, Pickett F, Richards D, Draheim R, Chapman J, Wildshire RH, Becker D, Anderson M, Pitman B, Lassuy D, Heimowitz P, Dwyer P, Levri E (2007) National management and control plan for the New Zealand mudsnail (*Potamopyrgus antipodarum*). [https://anastaskforce.gov/Documents/NZMS\\_MgmtControl\\_Final.pdf](https://anastaskforce.gov/Documents/NZMS_MgmtControl_Final.pdf) Accessed 8 January 2021
- Pérez-Quintero JC (2009) Freshwater molluscs from the biosphere reserve “Dehesas de Sierra Morena”, SW Iberian Peninsula. *Iberus* 27:1–18
- Pérez-Quintero JC (2011) Distribution patterns of freshwater molluscs along environmental gradients in the southern Guadiana River basin (SW Iberian Peninsula). *Hydrobiologia* 678:65–76
- Quinn GP, Lake PS, Schreiber SG (1998) A comparative study of colonization by benthos in a lake and its outflowing stream. *Freshw Biol* 39:623–635
- 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
- Rakauskas V, Butkus R, Merkytė E (2016) Consumption of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) by benthivorous predators in temperate lakes: a case study from Lithuania. *Hydrobiologia* 775:213–230
- Rakauskas V, Šidagytė E, Butkus R, Garbaras A (2017) Effect of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) on the littoral macroinvertebrate community in a temperate mesotrophic lake. *Mar Freshw Res* 69:155
- Rakauskas V, Šidagytė E, Kesminas V, Kaminskas O (2018) Can the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) threaten fisheries of temperate lakes? A case study from Lake Dusia, Lithuania. *Acta Ichthyol Piscat* 48:37–49
- Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Drivers Distrib* 12:425–433
- Ricciardi A, Kipp R (2008) Predicting the number of ecologically harmful exotic species in an aquatic system. *Divers Distrib* 14:374–380

- Richards DC (2002) The New Zealand mudsnail invades. *Aquat Nuis Species Digest* 4:42–44
- Richards DC, Cazier LD, Lester GT (2001) Spatial distribution of three snail species, including the invader *Potamopyrgus antipodarum*, in a freshwater spring. *West N Am Nat* 61:375–380
- Richards DC, O’Connell P, Shinn DC (2004) Simple Control Method to Limit Spread of New Zealand mudsnail *Potamopyrgus antipodarum*. *N Am J Fish Manag* 24:114–117
- Richards DC, Shinn DC (2004) Intraspecific competition and development of size structure in the invasive snail *Potamopyrgus antipodarum* (Gray, 1853). *Amer Malac Bull* 19:33–37
- Riley LA, Dybdahl MF (2015) The roles of resource availability and competition in mediating growth rates of invasive and native freshwater snails. *Freshw Biol* 60:1308–1315
- 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
- Robinson C (2019) Distribution and population dynamics of the New Zealand mud snail (*Potamopyrgus antipodarum*) in the Corte Madera Creek watershed, CA. Master of Science Thesis, California State University, Stanislaus
- Romero-Blanco A, Alonso Á (2019) Tolerance assessment of the aquatic invasive snail *Potamopyrgus antipodarum* to different post-dispersive conditions: implications for its invasive success. *NeoBiota* 44:57–73
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Sanders S, Castiglione C, and Hoff M (2014) Risk assessment mapping program: RAMP. US Fish and Wildlife Service
- Sardiña P, Beringer J, Roche D, Thompson RM (2015) Temperature influences species interactions between a native and a globally invasive freshwater snail. *Freshw Sci* 34:933–941
- Schisler GJ, Vieira NKM, Walker PG (2008) Application of household disinfectants to control New Zealand mudsnails. *N Am J Fish Manag* 28:1172–1176
- 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 Freshwat Res* 49:73–78
- Schreiber ESG, Lake PS, Quinn GP (2002) Facilitation of native stream fauna by an invading species? Experimental investigations of the interactions 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
- Sepulveda AJ, Marczak LB (2012) Active dispersal of an aquatic invader determined by resource and flow conditions. *Biol Invasions* 14:1201–1209
- Shimada K, Urabe M (2003) Comparative ecology of the alien freshwater snail *Potamopyrgus antipodarum* and the indigenous snail *Semisulcospira* spp. *Venus* 62:39–53
- Simoes M (1988) Distribucion en Portugal de *Potamopyrgus jenkinsi* (Prosobranchia Hydrobiidae). *Iberus* 8:243–244
- Smith EA (1889) Notes on British Hydrobiae with a description of a supposed new species. *J Conch* 6:142–145
- 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 (2008) Rapid expansion of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the Azov-Black Sea Region. *Aquat Invasions* 3:335–340
- 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 Lim* 41:14–147
- Spyra A, Kubicka J, Strzelec M (2015) The influence of the disturbed continuity of the river and the invasive species—*Potamopyrgus antipodarum* (Gray, 1843), *Gammarus tigrinus* (Sexton, 1939) on benthos fauna: A case study on urban area in the river Ruda (Poland). *Environ Manage*. <https://doi.org/10.1007/s00267-015-0483-3>
- Spyra A, Strzelec M (2015) Identifying factors linked to the occurrence of alien gastropods in isolated woodland water bodies. *Sci Nat-Heidelberg* 101:229–239
- Städler T, Frye M, Neiman M, Lively CM (2005) Mitochondrial haplotypes and the New Zealand origin of clonal European *Potamopyrgus*, an invasive aquatic snail. *Mol Ecol* 14:2465–2473
- State of Michigan (2018) Status and strategy for New Zealand mud snail management
- Stockton KA, Moffitt CM (2013) Disinfection of three wading boot surfaces infested with New Zealand mudsnails. *N Am J Fish Manag* 33:529–538
- Stockton-Fiti KA, Moffitt CM (2017) Safety and efficacy of Virkon® aquatic as a control tool for invasive molluscs in aquaculture. *Aquaculture* 480:71–76
- Stockton KA (2011) Methods to assess, control, and manage risks for two invasive mollusks in fish hatcheries. Master of Science thesis. University of Idaho, Moscow
- Stout JB, Avila BW, Fetherman ER (2016) Efficacy of commercially available quaternary ammonium compounds for controlling New Zealand mudsnails *Potamopyrgus antipodarum*. *N Am J Fish Manag* 36:277–284
- Strayer DL (2020) Non-native species have multiple abundance-impact curves. *Ecol Evol* 10:6833–6843
- Strayer DL, D’Antonio CM, Essl F, Fowler MS, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pyšek RP, von Schmalensee M, Stefansson FA, Wright J, Jeschke JM (2017) Boom-bust dynamics in biological invasions: towards an improved application of the concept. *Ecol Lett* 20:1337–1350



- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21:645–651
- Strayer DL, Solomon CT, Findlay SEG, Rosi EJ (2019) Long-term research reveals multiple relationships between the abundance and impacts of a non-native species. *Limnol Oceanogr* 64:S105–S117
- Strzelec M (2005) Impact of the introduced *Potamopyrgus antipodarum* (Gastropoda) on the snail fauna in post-industrial ponds in Poland. *Biologia (bratisl)* 60:159–163
- Tank SN, Herbst SJ, Hayes DB (2021) Evaluation of a qualitative survey for early detection monitoring of New Zealand mudsnail. *Manag Biol Invasions* 12 (in press)
- Tatara Y, Hamada K, Urabe M, Club TB, of Kojo High School, (2014) Across-population variation in sex ratio in invasive Japanese *Potamopyrgus antipodarum* (Caenogastropoda: Rissooidea: Hydrobiidae). *Limnology* 15:185–190
- Thomas AC, Tank S, Nguyen PL, Ponce J, Sinnesael M, Goldberg CS (2020) A system for rapid eDNA detection of aquatic invasive species. *Environmental DNA* 2:261–270
- Thomsen MS, Wernberg T, Silliman BR, Josefson AB (2009) BROADSCALE PATTERNS OF ABUNDANCE OF NON-INDIGENOUS SOFT-BOTTOM INVERTEBRATES IN DENMARK. *Helgol Mar Res* 63:159–167
- Thon HN (2011) Invasive and native species interactions: Growth of a native snail is nearly halted by high levels of biomass produced by the invasive New Zealand mud snail. Master of Science Thesis, University of Wyoming
- Tibbets TM, Krist AC, Hall RO Jr, Riley LA (2010) Phosphorus-mediated changes in life history traits of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*). *Oecologia* 163:549–559
- Trebitz AS, West CW, Hoffman JC, Kelly JR, Peterson GS, Grigorovich IA (2010) Status of non-indigenous benthic invertebrates in the Duluth-Superior Harbor and the role of sampling methods in their detection. *J Great Lakes Res* 36:747–756
- Twardochleb LA, Novak M, Moore JW (2012) Using the functional response of a consumer to predict biotic resistance to invasive prey. *Ecol Appl* 22:1162–1171
- United States Geological Survey (2021) Nonindigenous Aquatic Species Database. <https://nas.er.usgs.gov/viewer/omap.aspx?speciesID=1008> Accessed 15 March 2021
- Urabe M (2007) The present distribution and issues regarding the control of the exotic snail *Potamopyrgus antipodarum* in Japan. *Jpn J Limnol* 68:491–496
- Urbański J (1938) Beiträge Zur Kenntnis der Molluskenfauna der Wojewodschaft Poznań. II. Fragm Faunist Musei Zool Polonici 3:439–467
- Vallejo-Freire A, Ribeiro OF, Ribeiro IF (1954) Quaternary ammonium compounds as molluscicides. *Science* 119:470–472
- Vander Zanden MJ, Hansen GJA, Higgins SN, Kornis MS (2010) A pound of prevention, plus a pound of cure: Early detection and eradication of invasive species in the Laurentian Great Lakes. *J Great Lakes Res* 36:199–205
- Vazquez R, Ward DM, Sepulveda A (2016) Does water chemistry limit the distribution of New Zealand mud snails in Redwood National Park? *Biol Invasions* 18:1523–1531
- Verhaegan G, Neiman M, Haase M (2018) Ecomorphology of a generalist freshwater gastropod: Complex relations of shell morphology, habitat, and fecundity. *Org Divers Evol* 18:425–441
- Verhaegan G, Herzog H, Korsch K, Kerth G, Brede M, Hasse M (2019) Testing the adaptive value of gastropod shell morphology to flow: a multidisciplinary approach based on morphometrics, computational fluid dynamics and a flow tank experiment. *Zoological Lett* 5:5
- Verhaegan G, von Jungmeister K, Haase M (2021) Life history variation in space and time: environmental and seasonal responses of a parthenogenetic invasive freshwater snail in northern Germany. *Hydrobiologia*. <https://doi.org/10.1007/s10750-020-04333-8>
- Verhaegan G, McElroy KE, Bankers L, Neiman M, Hasse M (2018) Adaptive phenotypic plasticity in a clonal invader. *Ecol Evol* 8:4465–4483
- Vinson MR, Baker MA (2008) Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodarum*. *N Am J Fish Manag* 28:701–709
- Vinson MR (2004) The occurrence and distribution of New Zealand Mud Snails (*Potamopyrgus antipodarum*) in Utah. Utah Department of Natural Resources
- Watton AJ, Hawkes HA (1984) The acute toxicity of ammonia and copper to the gastropod *Potamopyrgus jenkinsi* (Smith). *Environ Pollut Ser Ecol Biol* 36:17–29
- Weetman D, Hauser L, Carvalho GR (2001) Isolation and characterization of di- and trinucleotide microsatellites in the freshwater snail *Potamopyrgus antipodarum*. *Mol Ecol Notes* 1:185–187
- 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
- Werner H, Boeters HD, Guenther A (1994) On the freshwater mollusc fauna in the Spanish province of Cuenca. *Malakol Abh* 17:65–81
- Winterbourn MJ (1970) The New Zealand species of *Potamopyrgus* (Gastropoda: Hydrobiidae). *Malacologia* 10:283–321
- Winterbourn MJ, Fegley A (1989) Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, South Island streams. *N Z Nat Sci* 16:57–65
- Woodell JD, Neiman M, Levri EP (2021) Matching a snail's pace: successful use of environmental DNA techniques to detect early stages of invasion by the destructive New Zealand Mud Snail. *Biol Invasions* (in press)
- Zachar N, Neiman M (2013) Profound effects of population density on fitness-related traits in an invasive freshwater snail. *PLoS ONE* 8:e80067
- 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
- Zettler ML, Richard D (2004) Freshwater Molluscs from Corsica. *Malakol Abh* 22:3–16
- Zieritz A, Waringer J (2008) Distribution patterns and habitat characterization of aquatic Mollusca in the Weidlingbach near Vienna, Austria. *Large Rivers* 18:271–292

- Zoukova R, Jalova V, Janisova M, Ocelka T, Jurcikova J, Halirova J, Giesy JP, Hilscherova K (2014) *In situ* effects of urban river pollution on the mudsnail *Potamopyrgus antipodarum* as part of an integrated assessment. *Aquat Toxicol* 150:83–92
- Čejka T, Dvořák L, Košel V (2008) Present distribution of *Potamopyrgus antipodarum* (Gray, 1843) (Mollusca: Gastropoda) in the Slovak Republic. *Malacol Bohemoslov* 7:21–25

- Żbikowski J, Żbikowska E (2009) Invaders of an invader—Trematodes in *Potamopyrgus antipodarum* in Poland. *J Invertebr Pathol* 101:67–70

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