THE NEW ZEALAND MUD SNAIL (*POTAMOPYRGUS ANTIPODARUM*) ECOLOGY AND MANAGEMENT OF A GLOBAL INVADER

by

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To my family

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ABSTRACT

THE NEW ZEALAND MUD SNAIL
(*POTAMOPYRGUS ANTIPODARUM*)
ECOLOGY AND MANAGEMENT OF A GLOBAL INVADER

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The New Zealand mud snail (*Potamopyrgus antipodarum*; NZMS) is among the most globally widespread aquatic invaders, colonizing at least 40 countries across 6 continents. NZMS have recently colonized rivers of the Laurentian Great Lakes region. where little is known about their impacts on the native communities of the ecosystems they invade. In chapter one, I present the results of a systematic review of 245 articles, and outline NZMS impacts, distribution, population dynamics, vectors of spread, and management. The invasion success of NZMS stems from their opportunistic traits allowing them to tolerate broad ranges of environmental conditions. However, optimal conditions for successful establishment are evident. NZMS can become exceptionally abundant and impact multiple facets of aquatic ecosystems, though populations can fluctuate seasonally and over longer time scales, likely due to environmental constraints. In chapter two, I tested the efficacy of three different chemical reagents for NZMS decontamination on recreational fishing gear and combined these results with results of a self-administered public survey gauging the level of willingness individuals have to

participate in a given NZMS decontamination technique. The greatest mortality of NZMS was caused by Formula 409, and participants of the survey revealed Formula 409 to be the chemical they'd be most willing to use. Chapter three outlines an investigation of the effects of NZMS on the diets and condition of fish in a recently invaded stream, the Au Sable River (Michigan, USA). Trout consumed NZMS throughout the duration of the study, while sculpin minimally consumed NZMS. Of the 83 trout collected, 60% contained NZMS in their stomachs. Age 2 trout that consumed NZMS exhibited reduced condition relative to those that contained fewer NZMS. Lastly, chapter four consists of a study to characterize NZMS population dynamics and their effects on native benthic invertebrates in the Au Sable River. NZMS populations exhibited pronounced seasonality with peak densities typically occurring during the Summer and Autumn of each year. NZMS numerically dominated the benthic community and were associated with differences in the overall benthic community composition. The results of these studies highlight how NZMS can affect native communities and higher consumers in rivers of the Great Lakes region and contribute to a more robust understanding of the global NZMS invasion, such that undesired impacts can be minimized or averted.

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CHAPTER ONE

THE NEW ZEALAND MUD SNAIL (*POTAMOPYRGUS ANTIPODARUM*): AUTECOLOGY AND MANAGEMENT OF A GLOBAL INVADER

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; Rakauskus 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 to 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. 1.1).

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 scale.

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. 1.2). 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 40 countries and on 6 continents (Fig. 1.3a) (Table 1.1), 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. 1.3a).

The first documentation of NZMS outside of New Zealand occurred in England in 1889 (Smith 1889). 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 1.1). 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 is widespread throughout the United States, with established populations in 19 states (Fig. 1.3b). 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. 1.3c). 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 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. 1.4) (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; Proctor et al. 2007; Richards 2002) (Fig. 1.4). Commercial trade of aquaculture products, such as fish and aquatic plants, is another common means of long- and short-distance transport (Winterbourn 1970; Ponder 1988; Zaranko et al. 1997; Richards 2002). 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 transport NZMS within and among watersheds (Fig. 1.4). 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.

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 1998; 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. 1.4).

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 1.2).

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 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 1.2). 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 1.2). 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 1.2). 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 1.2). 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 1.2). 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 and Hickey 1990; 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 2013). 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 (≤ c. 4,000 ind/m^2), 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 50–100 m^3/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; McKenzie et al. 2013; Moffitt and James 2012a; 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^2 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^{+2}-free culture media relative to natural Ca^{+2}-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 $CaCO_3$). 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 µS/cm and 5–17.5 mg/L, respectively) using snails from Redwood National Park (California, USA). Thus, waters with low conductivity (< 200 µS/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 g/kg and survive at levels of 30–35 g/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 g/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 g/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 g/kg and found invasive genotype performance (as survival and reproduction) was optimal at mid-range salinities (5 and 10 g/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 µS/cm), and those with higher salinity (> 15 g/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 mg/L N-NH_3). The effects of urban effluent on NZMS have also been evaluated by Zounkova 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 ind./m^2 (Fig. 1.5) 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^2 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^2 after a seven-year observation period and then fell to fewer than 1,000 individuals/m^2 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 suggests 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 1998) 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 (Oregan, 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 dominates 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, its 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^2. 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-minute 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-minute exposure at the same concentration was ineffective in achieving 100% NZMS mortality, although exposure to undiluted Formula 409 All Purpose Cleaner for 10 minutes 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 minutes for effective NZMS decontamination.

Recent studies have continued investigating the efficacy of the common household cleaning products 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-minute laboratory exposures (Geist et al., unpublished data). 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 minutes 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_2 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 hours 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 minutes 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 up to 5 g/kg; stable hydrology; and relatively low flow velocities and/or presence of refugia from higher velocities (≥ 0.15 m/s) (Table 1.3). 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 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.

Table 1.1. Global records of NZMS non-native distribution represented in the peer-reviewed literature, including continent, country, and locality with specific waterbody (when reported). Habitat types: F = freshwater, B = brackish water, Lo = lotic, Le = lentic. Continents, countries, and localities are listed in alphabetical order.

CONTINENT/COUNTRY	LOCALITY (WATERBODY WHEN PROVIDED)	HABITAT TYPE	REFERENCES
ASIA			
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** (Akçapinar and Akyaka Kadin Azmagi streams), **Anatolia** (Delice River), **Çanakkale** (Kocabaş Stream)	F/Lo	Kalyoncu et al. (2008), Odabaşi et al. (2019)
AUSTRALIA			
	New South Wales, **South Australia**, **Tasmania**, **Victoria** (Lake Purrumbete, Tarra River),	F & B/Le & Lo	Dusting (2016), Ponder (1988), Schreiber et al. (1998, 2003)
EUROPE			
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 Kolin** (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), **Arhus** (Odder Å), **Bornholm**, **Frederiksborg** (Roskilde Fjord), Grønsund Strait, **København** (Københavns Havn, Kongelunden Kanal), **Maribo**, **Odense** (Odense Å), **Præstø** (Præstø 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)
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), **Thüringia** (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-Acarnania** (Lake Trichonis and nearby stream)	F/Le & Lo	Radea et al. (2008)
Iberian Peninsula	*Portugal:* **Aveiro** (Ria de Averio), **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)	F & B/Lo & Le	Alonso et al. (2006, 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)
	Spain: **Álava**, **Albacete** (rivers in Sierra de Alcaraz), **Alicante**, **Andalusia** (Dehesas de Sierra Morena Bioreserve), **Asturias** (Nora River, Bay of Biscay), **Badajos** (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),	F & B/Lo & Le	

	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**		
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)
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 Spindžius, Elektrénai 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, Oswiecin Valley), **Podlaskie** (Wigry Lake, Wigry	F& B/Le & Lo	Brzeziński and Kołodziejczyk (2001), Ezhova et al. (2005),

	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)		Gruszka (1999), Kołodziejczyk et al. (2009), Lewin (2012), Lewin and Marszewska et al. (2018), Michalik-Kucharz (2008), Smoliński (2006)
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 Yalpug, 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)
United Kingdom	*Northern Ireland:* **Antrim**, **Armagh**, **Down**, **Londonderry**	F/Le & Lo	Boycott (1936)
	Wales: **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)
	Scotland: **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)
	England: **Bedfordshire** (Ivel River), **Berkshire**, **Buckinghamshire**, **Cambridgeshire**, **Cheshire**, **County**	F/Lo	Bondensen and Kaiser (1949), Boycott (1936),

	Durham, **Cumbria**, **Devon**, **East Riding of Yorkshire**, **East Sussex**, **Eastern portion of Norfolk**, **Somerset**, **Surfolk**, **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**, **Northumerland**, **Nottinghamshire**, **Norfolk**, **Oxfordshire**, **Rutland**, **Shropshire**, **South Yorkshire**, **Staffordshire**, **Surrey**, **Tyne and Wear**, **Warwickshire**, **West Sussex**, **West Yorkshire**, **Worcestershire**		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)
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	F & B/Le & Lo	Arango et al. (2009), Bowler (1991), Brenneis et al. (2010), Cross et al. (2010), Davidson et al.

	basin), **Illinois** (Waukegan Harbor, Little Calumet-Galien), **Maryland** (Gunpowder Falls), **Michigan** (Au Sable River, Pere Marquette River, Boardman River, Upper Manistee River), **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)	(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)

Table 1.2. Global distribution of NZMS genotypes

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

Table 1.3. 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., Zaranko et al. (1997), Levri et al. (2007), Davidson et al. (2008), Gérard et al. (2003), Lewin and Smoliński (2006), Brenneis et al. (2010)
Substrata	Fine–coarse; macrophytes	Various	Winterbourn (1970), Mazza et al. (2010), Bennett et al. (2015), Lysne and Koetsier (2006), Spyra and Strzelec (2014)
Flow velocity	0–1 m/s	< 0.15 m/s	Richards et al. (2001), Lysne and Koetsier (2006), Kefford and Lake (2013), Spyra et al. (2015)
Water temperature	2 °C–34 °C	17–18 °C	Winterbourn (1969, 1970), Cox and Rutherford (2000), Richards et al. (2004), Dybdahl and Kane (2005), Cross et al. (2010), McKenzie et al. (2012), Moffit and James (2012), Levri et al. (2014), Bennett et al. (2015), Sardina et al. (2015)
Conductivity (general)	25–10,000 µS/cm	> 200 µS/cm	Jacobsen and Forbes (1997), Leppäkoski and Olenin (2000), Costil et al. (2001), Gérard et al. (2003), Herbst et al. (2008), Drown et al. (2010), Hoy et al (2012), McKenzie et al. (2013), Spyra et al. (2015), Vazquez et al. (2016), Larson et al. (2020), Paolucci and Thuesen (2020), Verhaegen et al. (2020)
Salinity	0–35 g/kg	< 10 g/kg	Jacobsen and Forbes (1997), Leppäkoski and Olenin (2000), Costil et al. (2001), Gérard et al. (2003), Drown et al. (2010), Hoy et al (2012), McKenzie et al. (2013), Vazquez et al. (2016), Larson et al. (2020), Paolucci and Thuesen (2020) Verhaegen et al. (2020)
Calcium Ca^{+2}	< 5–314 mg/L	> 10 mg/L	Herbst et al. (2008), Spyra and Strzelec (2014), Spyra et al. (2015), Vazquez et al. (2016)

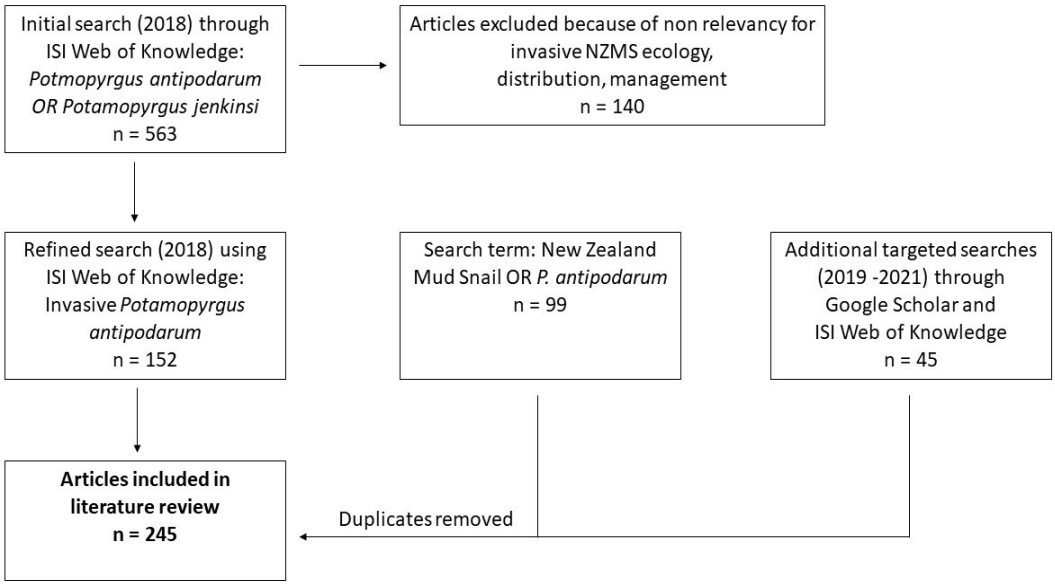

Figure 1.1. Flow diagram of search terms used to locate articles for the review

Figure 1.2. Photo of a New Zealand mud snail with a USA one cent coin for scale. Photo credit: Gary Miller

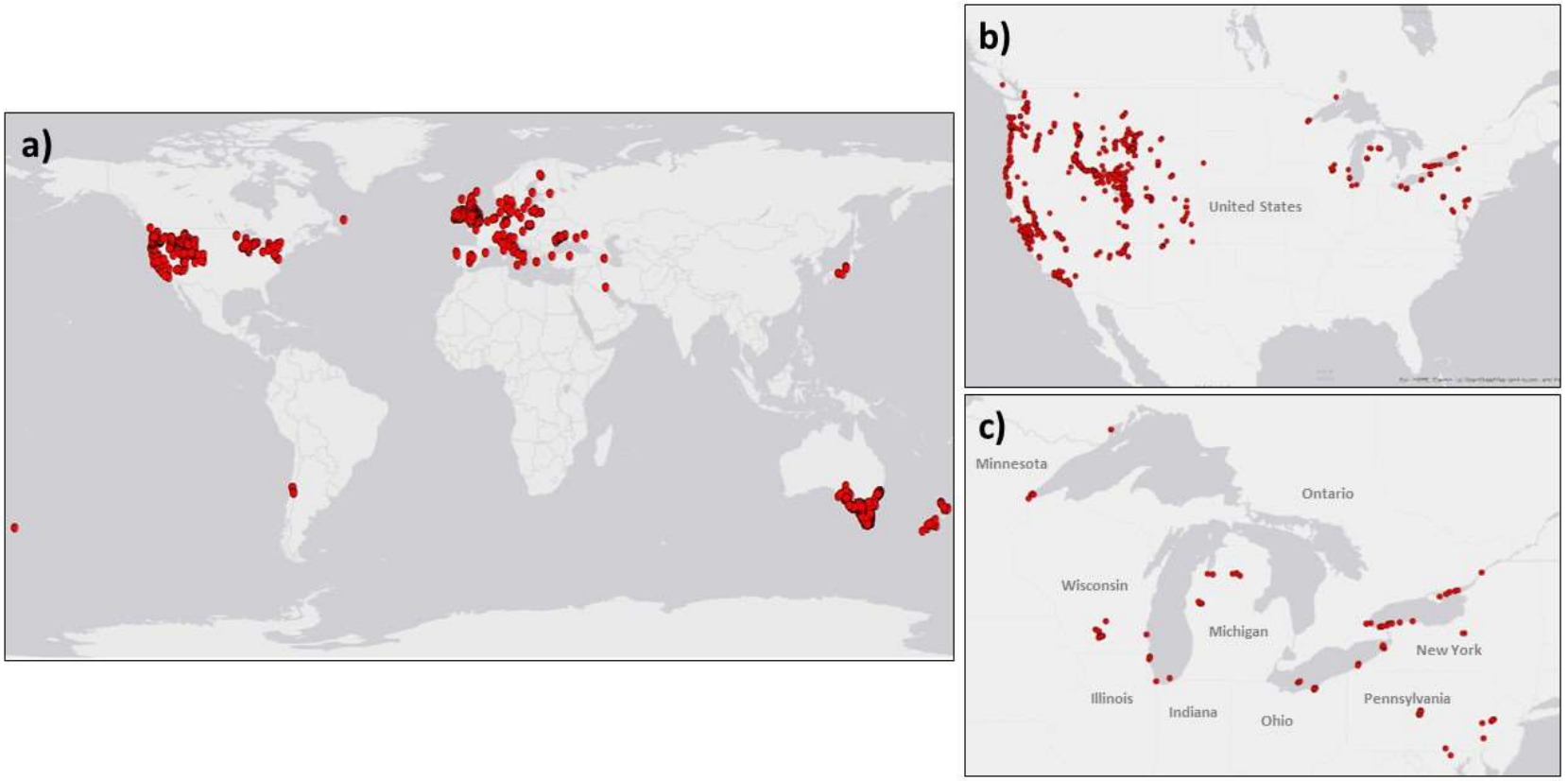

Figure 1.3. a) Global distribution of NZMS; b) North American distribution of NZMS (Canadian distribution of NZMS largely unknown); c) distribution of NZMS in the Great Lakes region of North America.

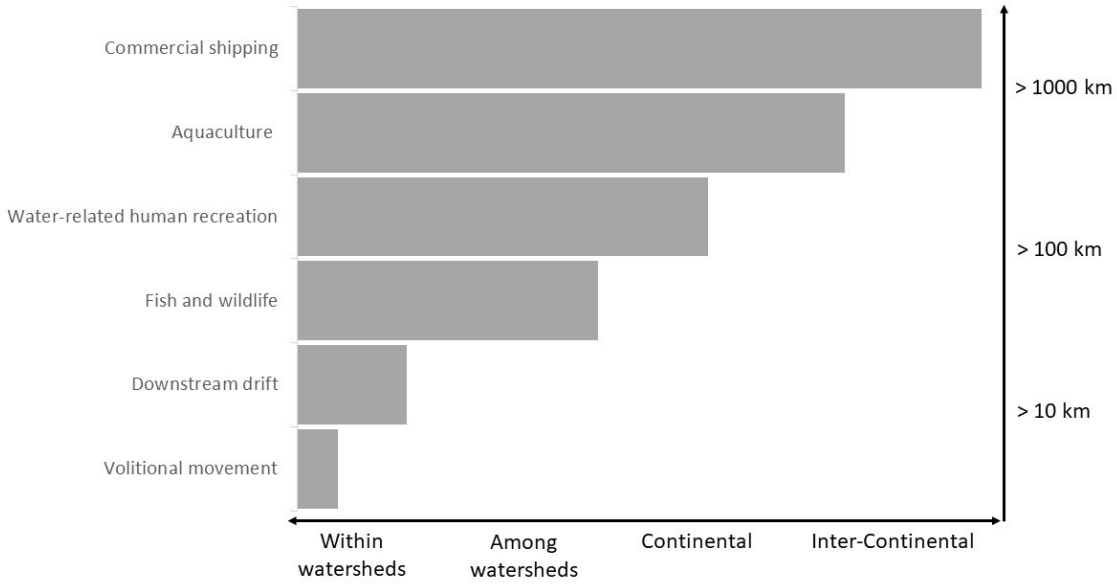

Figure 1.4. A conceptual bar chart depicting broadly estimated and relative ranges of distance associated with known (natural and anthropogenic) dispersal mechanisms of the New Zealand mud snail

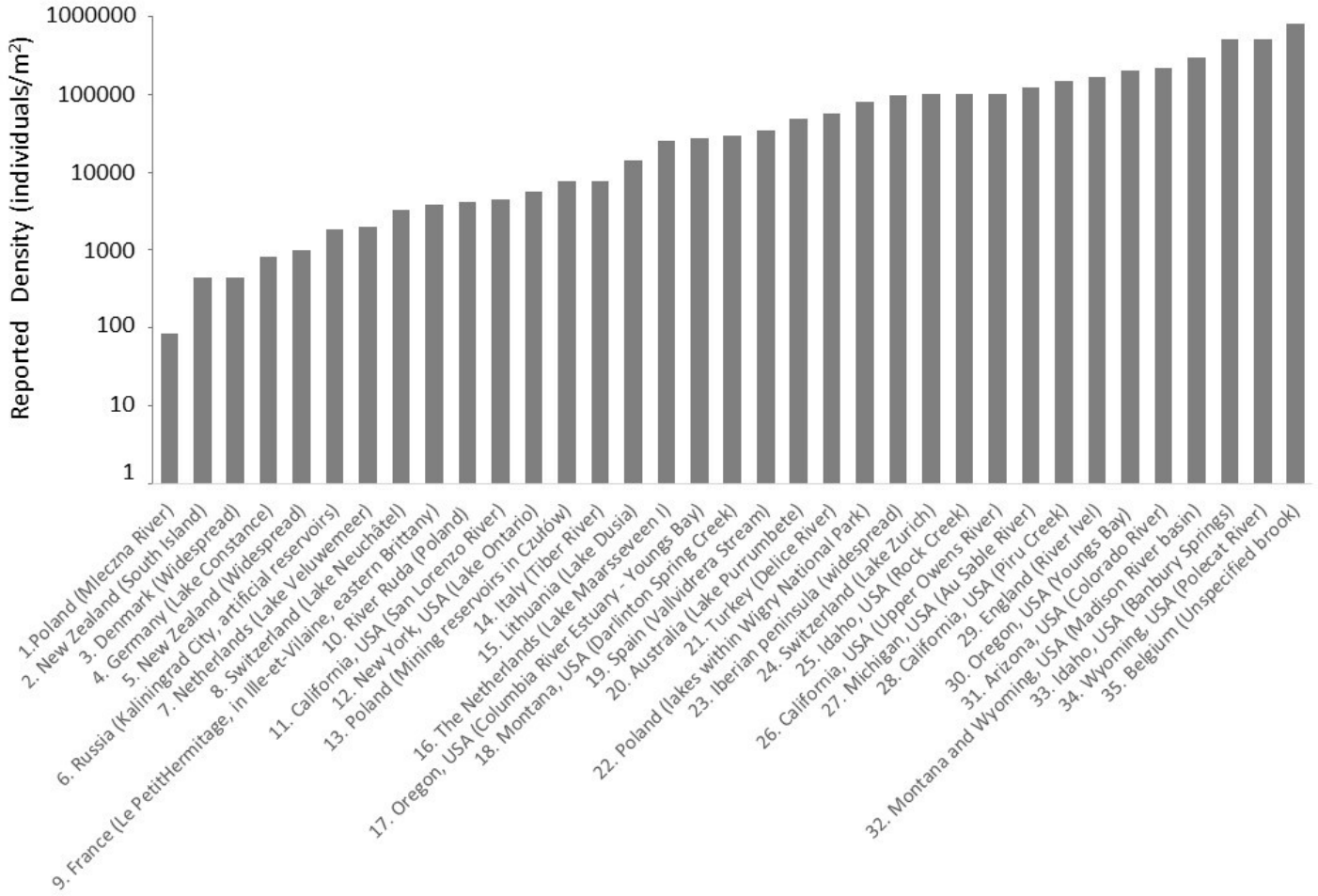

Figure 1.5. Densities of NZMS in published literature. NZMS densities represent highest reported observed means (when available) or local estimates of population densities in the respective study locations.

CHAPTER TWO

COUPLING GEAR-DECONTAMINATION TRIALS AND ANGLER SURVEYS TO MINIMIZE SPREAD OF INVASIVE NEW ZEALAND MUD SNAILS

Introduction

Introductions of invasive species into new habitats, particularly freshwaters, have accelerated during the past century due to human activities such as commerce, transport, and recreation (Mack et al. 2000; Sala et al. 2000; Kolar and Lodge 2001; Ricciardi 2006). In turn, research has documented widespread impacts on the biodiversity, ecosystem processes, and ecosystem goods and services of invaded ecosystems (Wilcove et al. 1998; Cox and Rutherford 2000; Kolar and Lodge 2001; Lodge and Shrader-Frechette 2003). Once established, invasive species can be extremely difficult to remove from an area, and resource managers are now increasingly emphasizing the prevention of new introductions as a key facet of effective management (Leung et al. 2002).

New Zealand mud snails (NZMS), *Potamopyrgus antipodarum* (Gray 1843), are prolific invaders and have become established across the globe. NZMS are native to the streams and lakes of New Zealand but are now found in 40 countries across 6 continents (Geist et al. 2022; Taybi et al. 2021). NZMS are successful invaders due, in part, to their high reproductive capacity and competitive aptitude, while largely being released from predation in their non-native range. The reproductive strategy of invasive NZMS populations is solely parthenogenic, and invasive populations are predominantly made up of females, a trait that enables a single individual to establish a new population (Zaranko et al. 1997; Dybdahl and Kane 2005). In addition, NZMS have a solid operculum, giving

the snail the ability to enclose itself within its elongated shell to resist environmental stressors (e.g., desiccation) and persist across a broad range of conditions (Geist et al. 2022). The advantageous life-history traits of NZMS, coupled with increasing globalization, facilitate further spread, posing threats to aquatic systems worldwide.

Impacts of invasive NZMS on resident communities and ecosystem function are complex and vary widely. NZMS can cause major shifts in algal assemblages (e.g., Krist and Charles 2012; Bennett et al. 2015), and native invertebrate communities (e.g., Kerans et al. 2005; Rakauskus et al. 2017), and impact fish diets and physiological condition (Vinson and Baker 2008; Geist et al. in prep). In other instances, NZMS have weak or negligible effects on invaded systems (e.g., Múrria et al. 2008; Brenneis et al. 2010), and in the case of an Australian stream, positive effects on native invertebrate densities (Schreiber et al. 2002). The negative effects of NZMS on invaded systems, in part, stems from their extremely high densities, in some instances over 500,000 individuals/m^2 (e.g., Dorgelo 1987; Hall et al. 2006). When elevated densities are achieved, NZMS can consume as much as 75% of gross primary production and alter nitrogen and carbon cycling (Hall et al. 2003; Moore et al. 2012). Overall, the impacts associated with NZMS can be severe, and their ongoing spread poses threats to the structure and functioning of aquatic systems.

As NZMS continue to expand their range, identifying pathways of spread and minimizing their effectiveness are key steps towards preventing further invasion into uninfected water bodies (U.S. Fish and Wildlife Service/Fish and Aquatic Conservation 2015). In the United States, NZMS populations usually occur in popular angling destinations, suggesting a relationship between recreational fishing and NZMS spread

(Geist et al. 2022). Recreational angling often involves gear such as waders, wading boots, and other equipment to which NZMS can attach and be spread within and among watersheds (Hosea and Finlayson 2005; Stockton 2013; State of Michigan 2018).

Preventing NZMS spread through individual efforts (e.g., gear decontamination by recreationists) can be effective at reducing introductions into uninvaded waterbodies at local and regional scales (Proctor et al. 2007; State of Michigan 2018). Several chemical reagents have been found to be effective at decontaminating equipment (e.g., boats, fishing equipment) and infrastructure (e.g., fish hatcheries). These include copper sulfate, benzethonium chloride, Pine-Sol, Formula 409, Virkon Aquatic, Sparquat 256, Quat 4, Green Solutions High Dilutions Disinfectant 256, and Super HDQ (Hosea and Finlayson 2005; Schisler et al. 2008; Stockton and Moffitt 2013; Stout et al. 2016; De Stasio et al. 2019). These reagents vary in their effectiveness, availability, and ease of use. Given this variation, it is important to understand the willingness of anglers to use a particular decontamination strategy. Additionally, various strategies for NZMS decontamination are currently recommended by different state and federal agencies, organizations, and recreational user groups, resulting in lack of clarity and consistency about best practices.

Coupling data on the effectiveness of different chemical reagents with data on anglers' willingness to use a treatment should lead to optimized decontamination and reduced NZMS spread into new areas. However, combining data on the willingness to implement a particular protocol with its effectiveness has only rarely been implemented. Angler willingness, and more broadly the likelihood of the public to adopt a spread prevention strategy, is often an undervalued component to the overall effort to reduce

invasive species spread and minimize new introductions. Here, we evaluate the efficacy of different chemical reagents on NZMS mortality along with the willingness of anglers to implement specific decontamination strategies. We experimentally tested 3 different chemical reagents for their ability to kill NZMS: Virkon Aquatic, Formula 409 Multi-Purpose Cleaner (hereafter, Formula 409), and bleach. The selected chemicals are currently being advocated by various state and federal agencies as effective NZMS decontaminants for recreational fishing gear. We also developed and distributed an online survey that was completed by 339 members of the regional angling community to gauge their general understanding of the NZMS invasion and their willingness to use specific recommended decontamination strategies. By coupling the results from the experimental trials and the survey, we provide a recommendation to resource managers and the public for a practical and optimized strategy for decontaminating recreational angling gear to minimize new introductions of NZMS.

Methods

Test Organisms

We collected approximately 500 live NZMS by handpicking sediments from the East Branch Au Sable River (Michigan, USA). We placed NZMS into a 23-L container filled with stream water and transported them to the laboratory where we transferred them to a 38-L holding tank filled with ~20°C dechlorinated tap water. We also collected rocks, algae, and organic matter (e.g., leaves) from the Au Sable River and placed them in the holding tank to provide food and habitat. We selected 64 adult snails (mean length=4.59 mm, SD=0.05) from the holding tank for experimental trials. Prior to

experimental trials, we assessed snails for viability (via volitional movement) and determined shell length to the nearest millimeter.

Evaluation of 3 Disinfectants for New Zealand Mud Snail Decontamination on Waders

We used a fully crossed 4 x 2 x 2 factorial design (3 chemical treatments and 1 control × 2 exposure durations × 2 application types) to test the effectiveness of chemical disinfectants at killing NZMS and different means of applying them. The 3 chemical reagents were: Virkon Aquatic, Formula 409 All Purpose Cleaner (hereafter, Formula 409), a bleach solution, and deionized water as a control (Fig. 2.1). Chemical disinfectants were prepared according to manufacturer recommendations. We diluted 21 mL of Virkon Aquatic concentrate in 30 liters of deionized water to reach a 2% concentration (equivalent to label recommendation). We then used Virkon dilution test strips (Snydel Company) to validate the pre-measured and diluted solution to ensure the appropriate concentration. To obtain a 10% household bleach solution, we diluted 5.25% sodium hypochlorite (Clorox Bleach) in 30 L of deionized water (equivalent to the recommended concentration for household bleach [OSHA and Center for Disease Control and Prevention 2016]). Formula 409 was not altered from its manufactured concentration.

To evaluate the effectiveness of NZMS decontaminants on the surfaces of angling equipment believed to be important for transporting NZMS, we applied chemical treatments to snails attached to fabric that is commonly used in waders. Nylon/polyester wader fabric was cut from Cabela's Breathable Waders to the size of the experimental chambers (60 x 15 mm polystyrene Petri dishes). We sprayed cut wader material with

deionized water immediately before the start of the experiment to simulate the wet conditions NZMS experience when exiting a waterbody while attached to angling gear.

We tested 2 exposure durations: 10 and 20 minutes, and 2 application types: spraying the chemical onto NZMS and fully submerging NZMS in the chemical (hereafter, soaking). We designated 16 individual NZMS for each chemical treatment with 4 individual NZMS for each experimental treatment combination (1 of the 3 chemicals with either spray or soak application for either the 10- or 20-minute exposure duration). We assigned NZMS to a designated treatment then placed NZMS directly onto the wader material in each experimental chamber for treatment exposure.

For the spray application, we transferred each chemical solution and water as a control to identical spray bottles of the same manufacturer (Lowe's 32 oz. All Purpose Sprayer) to standardize spray volume and velocity when applying chemicals to NZMS on wader surfaces. We primed each standardized spray bottle by discharging 2 test sprays away from NZMS to ensure a full spray (approximately 1 mL) at the time of exposure. With the spray bottle head positioned approximately 10 cm away, we sprayed NZMS with the chemical and control to ensure full coverage and exposure. For the soak application, we poured enough chemical solution into the experimental chamber, with the wader material, to fully submerge NZMS (approximately 5 mL), and then placed NZMS into the chamber. We interspersed and randomly arranged the experimental chambers and treatment combinations in the testing area. After the designated duration of the chemical exposure (and control) ended, snails were removed from the experimental chambers, rinsed with clean tap water for 5 seconds, and placed into a recovery chamber (100 x 15 mm polystyrene petri dish) with tap water (approximately 5 mL). To assess mortality, we

marked NMZS initial placement in the recovery chambers and observed snail movement immediately and at 1, 6, 24-, 48-, 72-, and 96-hours post-treatment.

Angler Survey

We developed and distributed an online survey to anglers consisting of 36 questions regarding angler behaviors, invasive species, and NZMS decontamination strategies. We solicited participation in the survey through email to a targeted sample demographic consisting of members of the non-governmental freshwater conservation and recreational fishing organizations Trout Unlimited and Fly Fishers International. This sample population is a likely transport vector for NZMS since NZMS spread is speculated to be associated with recreational angling (Bruce and Moffitt 2010; Alonso and Castro-Díez 2012; Stockton and Moffitt 2013). We administered the survey via Google Forms and collected survey data from November 2018 through March 2019.

The survey consisted of 3 discrete sections (Appendix B) and included questions about 1.) the respondent's angling behaviors, 2.) their general awareness of regional invasive species - specifically, NZMS, and 3.) willingness to implement a specific NZMS decontamination strategy after fishing. Decontamination strategies (i.e., chemical, application technique, duration) presented in the survey were the same as those used in the experimental trials of this study and previously published studies and available state and federal management documents (Hosea and Finlayson 2005; Proctor et al. 2007; Stockton and Moffitt 2013; De Stasio et al. 2019). In brief, we asked participants how willing they would be to apply a specific chemical decontaminant (i.e., Virkon Aquatic, Bleach or Formula 409) to their wading gear to help prevent the spread of NZMS. Each question included a decontamination strategy with a combination of 1 of the 3 chemicals,

1 of 2 types of application methods (i.e., spraying the chemical on wading gear or soaking wading gear in the chemical), and 1 of 2 exposure durations (10 min or 20 min).

Statistical analysis

Statistical analyses were conducted using R (version 4.0.3; The R Foundation for Statistical Computing Platform 2020). For the decontamination experiment, we compared mean percent mortality using a 3-way analysis of variance (ANOVA) to test for differences in chemical treatment (4 levels), application technique (spray or soak), and exposure duration (10 or 20 minutes) on NZMS mortality. Post-hoc Tukey HSD (Honestly Significant Difference) tests were used to determine significant differences between groups. We conducted a survival analysis of NZMS for each decontamination treatment using Kaplan-Meier estimates (R package: Survival Analysis; Therneau et al. 2020), a computation of successive survival probabilities over time to estimate survival function. Survival probabilities are computed using the following equation:

$$S_{t+1} = S_t * ((N_{t+1} - D_{t+1})/N_{t+1})$$

Where S_t = probability of an individual surviving at a given time; N = number of individuals alive at the given time; D = number of individuals dead. We tested for significant differences among survival function curves using a pairwise log-rank test, and adjusted p-values using a Bonferroni correction.

For the online survey, questions regarding a respondent's willingness to implement various decontamination strategies were developed using a 7-point Likert-type scale (1 = not likely, 7 = very likely) to provide categorical ordinal data. Measures of central tendency (i.e., mean, median and mode) were calculated for each question. We used the median answer to characterize the sample population's degree of willingness in

using a particular decontamination strategy. Additional questions regarding angler behaviors, and invasive species and NZMS awareness included various response options specific to the question – we summarized these answers by calculating the percentage of each response option selected.

Angler Decontamination Metric

By coupling the results of the experimental evaluation of 3 disinfectants for NZMS decontamination on wader surfaces with the angler survey, we developed an NZMS Angler Decontamination Metric (ADM) that helps determine the decontamination strategy that will maximize NZMS mortality. This metric was calculated using the following equation:

$$ADM = SMR * \%M$$

Where SMR = survey median response of an angler's willingness to implement each treatment combination/decontamination strategy and %M = mean percentage of NZMS killed with each experimental treatment combination. Higher scores indicate a decontamination strategy that yields greater NZMS mortality and greater willingness of an angler to implement the strategy.

Results

Evaluation of 3 Disinfectants for New Zealand Mud Snail Decontamination on Waders NZMS mortality differed widely among decontaminants (ANOVA, $P < 0.001$) (Fig. 2.2, Table 2.1). The greatest mean NZMS mortality (± SE) at 1 hour after exposure to the decontaminants across all applications and durations was caused by Formula 409, with lower mortality from bleach and even lower mortality from Virkon. Neither exposure duration (10-minute vs. 20-minute) ($P = 0.48$) nor application method

(spraying vs. soaking) ($P = 0.16$) affected NZMS mortality (Fig. C.1 and C.2), nor were there any significant interactions in the fully crossed ANOVA model (Table 2.2).

Kaplan-Meier analysis showed a 6.3% survival probability after 1 hour for NZMS treated with Formula 409 across all applications and exposure durations (Fig. 2.3). After 24 hours, survival probability was 0% (Fig. 2.3). NZMS treated with bleach had an 81.2% probability of survival after 1 hour and 62.5% after the final 96-hour viability assessment (Fig. 2.3). NZMS treated with Virkon Aquatic had a 37.5% survival probability after 1 hour and 18.8% after 96 hours (Fig. 2.3). NZMS in the control treatment (i.e., water) had a 100% survival probability throughout the entire 96-hour duration (Fig. 2.3). Significant differences in survivorship curves were observed between Bleach and Formula 409 ($P < 0.001$), Bleach and Virkon Aquatic ($P = 0.034$), Bleach and water ($P = 0.044$), Virkon and Water ($P < 0.001$), and Formula 409 and water ($P < 0.001$) (Table 2.3).

Angler Survey

In total, 339 individuals responded to the online questionnaire, with most respondents answering most questions (Table D.1). Most of the sample population prefers to fish in rivers vs. lakes (91% and 9%, respectively), fish multiple rivers in a year (median = 4.5 rivers), fish mostly during summer months, June – August (58%), and prefers wading vs. accessing rivers in a boat (81% and 19%, respectively) (Table D.1). Wading gear and material preferences of the sample population were for rubber-soled wading boots vs. felt (67% and 29%, respectively) and Gore-Tex or other breathable vs. neoprene/nylon/rubber (82% and 18%, respectively) (Table D.1). Awareness and knowledge of invasive species, specifically NZMS, varied, with 62% of the respondent's

claiming knowledge of NZMS invaded rivers in the Great Lakes region and 43% able to identify NZMS (Table D.1). When asked to gage their own knowledge of NZMS in the Great Lakes region on a scale of 1-7 (1 = no knowledge, 7 = very knowledgeable), the responses fell in the intermediate range (median = 4) (Table D.1).

The decontamination strategy that anglers are most likely to use (based on a 7-point Likert-type scale [1 = not likely, 7 = very likely]) is Formula 409 by spray, regardless of the exposure duration (median = 5, mode = 7) (Table D.2; Fig. 2.4). Participants were less likely to use Virkon Aquatic by spray application with either exposure duration (median = 4, mode = 1), and even less likely to use Bleach as a decontaminant by spray application with either exposure duration (10-minute: median = 3, mode = 1; 20-minute: median = 2, mode = 1) (Table D.2; Fig. 2.4). The willingness of the sample population to use any of the chemicals in a soak application, regardless of exposure duration, was low (all combinations: median = 1, mode = 1) (Table D.2; Fig. 2.4). When asked if the survey participants knew where to purchase the chemicals, 99% responded yes to Bleach, 88% responded yes to Formula 409, and 12% responded yes to Virkon Aquatic.

Angler Decontamination Metric

Angler decontamination metric values (higher values indicate greater angler willingness and greater chemical effectiveness) for specific treatment combinations/decontamination strategies ranged from 0.5–5 (Bleach: Soak: 20 minute - Formula 409: Spray: 20 minute, respectively) (Table 2.4). The mean (± SD) ADM value per chemical reagent was 3 (± 2.31) for Formula 409; 1.13 (± 0.60) for Virkon Aquatic; and 1.13 (± 0.49) for Bleach across all applications types and exposure durations. The

mean value (± SD) for spray application was 2.80 (± 1.85) and soak application was 0.83 (± 0.20) across all chemical reagents and exposure durations. The mean value (± SD) for a 10-minute chemical exposure duration was 1.85 (±1.59) and for a 20-minute chemical exposure duration was 1.63 (± 1.69) across all chemical reagents and application types (Table 2.4).

Discussion

Preventing the spread of NZMS through fishing gear decontamination is a key step to help limit the range of NZMS and their ecological impacts. However, there remains confusion within the angling community about which decontaminant is most effective and uncertainty regarding which decontamination strategies anglers are willing to adopt. Here we present a decontamination protocol for fishing gear that maximizes NZMS mortality and is most likely to be used by an angler. Based on this determination, we recommend the following for decontaminating gear that was exposed to a known or suspected NZMS-invaded river:

1. Visually inspect wading and fishing gear and remove NZMS.
2. Brush (using a stiff-bristled brush) and/or wipe off organisms, debris, and organic material from wading and fishing gear.
3. With the angler positioned out of and away from surface waters, spray wading and fishing gear liberally with Formula 409 (as prepared by the manufacturer), completely covering all material that was in contact with the waterbody.
4. Let Formula 409 remain on fishing and wading gear for at least 10 minutes.
5. With the angler positioned out of and away from surface waters, rinse fishing and wading gear with clean water to remove residual Formula 409.

Our results indicate that Formula 409 is the most effective chemical reagent for killing NZMS using either spray or soak application, with either a 10- or 20-minute exposure duration. Formula 409 contains quaternary ammonium compounds (QAC), which are toxic to many invertebrates and are commonly found in molluscicides (Vallejo-Freire et al. 1954). Regardless of whether Formula 409 was sprayed or applied via soaking or left on angling gear for 10 or 20 minutes, it killed 100% of NZMS.

Our findings on the efficacy of Formula 409 and NZMS mortality are consistent with Schisler et al. (2008) who also observed 100% mortality of NZMS when exposed to undiluted Formula 409 for 10 minutes. De Stasio et al. (2019) also found Formula 409 to be highly effective, although less so when mud was present. This suggests that NZMS need to be in direct contact with the chemical reagent for it to have maximum effectiveness. Furthermore, NZMS can become attached to gear in crevices, under fabric flaps, and-or stuck in Velcro which may provide conditions that may prohibit full exposure to Formula 409. As such, care should be taken to remove mud and organic material, fully examine wading gear for the presence of NZMS, and treat all suspected areas with the chemical decontaminant. The conditions of waders and boots directly after exiting an infested waterbody are also likely still damp and exhibit moist conditions, which may dilute Formula 409 and reduce efficacy. While we did not test a diluted solution of Formula 409 nor an exposure duration of Formula 409 for less than 10 minutes, Hosea and Finlayson (2005) found Formula 409 at full strength and 50% dilution to be effective at killing most or all NZMS with a 5-minute exposure duration. This contradicts Schisler et al. (2008), who observed 50% survival of NZMS when exposed to 50% diluted Formula 409 for 5 minutes. As such, we recommend using full

strength Formula 409 for an exposure duration of no less than 10 minutes to achieve maximum NZMS mortality.

Virkon Aquatic is commonly used in fish hatcheries and other aquaculture facilities and is currently recommended for NZMS by many agencies (Hosea and Finlayson 2005; Stockton and Moffitt 2013). We found that Virkon Aquatic killed fewer NZMS in all applications and durations than Formula 409 and usually underperformed bleach (Fig. 2.2, Table 2.1) in 1-hour trials. However, survival analysis indicates Virkon Aquatic to have the second lowest survival probability (Formula 409 being the lowest) after the full 96-hour assessment duration (Figure 2.3). Furthermore, other studies have shown Virkon Aquatic to be effective at killing NZMS. Stockton and Moffitt (2013) found fully submerging wading gear in Virkon Aquatic for 30 minutes to be 100% effective at killing NZMS at the same concentration as our treatments (i.e., 20g/L) and 99% effective when sprayed and left on wading gear for 30 minutes. If used for NZMS decontamination, concentrations of Virkon Aquatic should be at least 20 g/L and should be applied via soaking (i.e., full submersion) for at least 30 minutes.

Bleach is commonly used for microbial decontamination and has also become an option for anglers as a decontaminant of NZMS (Michigan Department of Natural Resources, personal communication). However, there have been limited studies evaluating the efficacy of bleach on NZMS mortality. Our study indicates that bleach can be effective if NZMS are soaked in a 10% concentration solution, but a spray application of bleach did not result in 100% NZMS mortality (Table 2.1). Some studies have found that soaking gear in a 5% bleach solution was effective at killing NZMS (Medhurst and Herbst 2003 [via Hosea and Finlayson 2005]), but another study reported that this

procedure was ineffective (Hosea and Finlayson 2005). Though NZMS exposed to higher concentrations of bleach (17% and undiluted) was more effective (Hosea and Finlayson 2005). Overall, the concentrations of bleach that are effective at achieving high levels of NZMS mortality on fishing gear remains unclear.

Responses from the survey of angler behavior and NZMS awareness support the speculation that recreational anglers like those in our survey are probably unintentional vectors of NZMS spread (Table D.1). Ninety-one percent of the respondents indicated that they fish mostly in rivers rather than lakes, aquatic systems where NZMS have been prominently documented throughout their invasive range (Geist et al. 2022). Further, 99% of the respondents indicated that they fish more than 1 river in a typical year, suggesting the potential for NZMS spread among watersheds via attachment and transport on fishing gear. Most survey respondents (81%) fish while wading, which entails direct contact with benthic habitats, including NZMS in invaded systems. Additionally, most respondents prefer to fish during summer (i.e., June–August), during which NZMS densities are typically greatest (e.g., Vinson 2004; Kerans et al. 2005; Hall et al. 2006; Bennett et al. 2015), increasing the likelihood of anglers contacting NZMS. While anglers like those in our sample population have the potential to spread NZMS, they also have some level of awareness of the invasive NZMS issue (Table D.1). Widespread use of an effective and convenient decontamination strategy will help to limit the spread of NZMS through this vector.

Responses from survey questions regarding willingness to implement various decontamination strategies strongly indicates that Formula 409 is the preferred chemical, with a spray application preferred over soaking (Table D.2, Fig. 2.4). The preference for

Formula 409 may be a result of familiarity and accessibility of the product (i.e., it is available at most convenience stores and markets and requires no preparation prior to use), whereas Virkon Aquatic requires purchase from an online manufacturer and a multi-step process for effective use (i.e., mixing a specific amount of powder with water to achieve the desired concentration). Bleach, while widely available, was not a preferred chemical reagent to use by the sample population, perhaps because of its widespread reputation for damaging fabrics, perhaps including waders.

A small number of studies show that chemical decontaminants can damage waders. Bleach can affect wader fabric and boots resulting in leaks, cracking and tears (Hosea and Finlayson 2005). Repeated use of Virkon Aquatic can cause leaking along seams, legs, crotch, and knees (Stockton and Moffitt 2013), and soaking wading gear in 50% diluted Formula 409 can cause surficial cracking of rubber toes of wading boots (Hosea and Finlayson 2005). Damage probably increases with continuing use but rinsing gear with clean water after the required exposure duration can reduce potential damage (e.g., Stockton and Moffit 2013). Further studies evaluating the long-term effects of chemical reagents used for decontamination of fishing gear are needed.

Preventing the spread of NZMS and other aquatic invasive species through attachment and transport on water-related recreational gear will help limit new introductions into uninvaded aquatic systems. While the goal of our study was specific to the invasive NZMS, this approach (i.e., coupling experimental findings with gaged public willingness) could be used to develop spread prevention techniques for other invasive species, and other decontamination protocols. As such, further research is needed to

investigate the efficacy of Formula 409 as a decontaminant for other aquatic invasive species.

We recognize the limitations and drawbacks from our approach combining the experimental results with the results of our angler survey data (i.e., Angler Decontamination Metric). Because we used ordinal data as a multiplier for the index, the magnitude of differences among ADM values cannot be assessed. We believe that this technique – combing survey data on the willingness to use a particular decontamination protocol with data on the effectiveness of that protocol at causing mortality to an invasive – can be built upon and improved in future research to maximize invasive-species mortality. Furthermore, as a companion to our ADM, we graphically displayed the coupling of our experimental results with our survey (Fig. 2.5) and hope that together these can provide insight for researchers, resource managers and the public on the most effective NZMS decontamination strategy that anglers are most willing to use. In all, future research should be directed towards the development of robust and wide-ranging spread prevention strategies that consider public willingness and that adapt to a broad range of recreational styles (fly fishing, spin fishing, boating, etc.) and invasive species, and here we present a general approach to quantify these very different types of data. Our survey was limited to participants that were willing to respond, and as such, may be more likely to implement a decontamination strategy relative to those who did not respond. The inherent bias associated with the targeted sample population should be considered when interpreting our results. Nevertheless, recommendations of an effective and convenient decontamination strategy for anglers and other water-related recreationists should increase adoption of the strategy.

As invasive species continue to spread and impact aquatic ecosystems, effective tools are needed that are not only effective preventing spread, but are also readily adopted and implemented by groups that are responsible for the transport of the invader. Here we combine these very different types of data and approaches to develop a protocol that optimizes mortality to a global invader that is continuing to expand its range – the New Zealand mud snail. Through this effort we hope to assist in more effective management and conservation of freshwaters where these invaders are increasingly found.

Table 2.1. Summary of NZMS decontamination trials. Values shown are mean percent mortality 1 hour after treatment exposure for each chemical treatment, application type, and exposure duration; and the mean (± SD) time of apparent mortality throughout the viability assessment duration (96 hours). Values in parentheses are SDs.

Chemical	Application	Exposure Duration (min)	Percent Mortality (± SD) (after 1 hour)	Mean (± SD) Time in Hours to Mortality
Water	Spray	10	0 (0)	>96 (0)
	Soak	10	0 (0)	>96 (0)
	Spray	20	0 (0)	>96 (0)
	Soak	20	0 (0)	>96 (0)
Bleach	Spray	10	50 (57)	>96 (0)
	Soak	10	100 (0)	60 (45.96)
	Spray	20	75 (50)	66 (45.43)
	Soak	20	50 (57)	60 (45.96)
Virkon Aquatic	Spray	10	50 (57)	25.5 (47.09)
	Soak	10	25 (50)	48 (43.82)
	Spray	20	75 (50)	2 (2.71)
	Soak	20	75 (50)	0.25 (0.5)
Formula 409	Spray	10	100 (0)	0 (0)
	Soak	10	100 (0)	6 (12)
	Spray	20	100 (0)	0 (0)
	Soak	20	100 (0)	0 (0)

Table 2.2 Results of a three-way ANOVA testing for differences in New Zealand mud snail mortality based on chemical treatment, application technique (spray versus soak), and exposure duration (10 versus 20 min).

	Degrees of freedom	F-value	P-value
Chemical	3	22.333	<0.001
Duration	1	0.500	0.483
Application	1	2.000	0.164
Chemical: Duration	3	0.167	0.918
Chemical: Application	3	1.000	0.401
Duration: Application	1	0.500	0.483
Chemical: Duration: Application	3	1.500	0.226

Table 2.3**.** Differences in New Zealand mud snail survivorship functions after 96-h viability assessments. All chemical treatments differed except for Formula 409 and Virkon aquatic (significance accepted at ≤ 0.05). The adjusted P – values (after Bonferroni correction) from pairwise log-rank tests are shown.

	Formula 409	Bleach	Virkon Aquatic
Bleach	<0.001	-	-
Virkon Aquatic	0.142	0.034	-
Water	<0.001	0.044	<0.001

Table 2.4. Results from the angler decontamination metric (ADM) equation. Higher scores indicate a decontamination strategy that yields greater New Zealand mud snail (NZMS) mortality and/or greater willingness of an angler to implement the strategy. Strategies are ordered based on the highest to lowest ADM values. Mean ADMs (with SD in parentheses) for each chemical, application technique, and exposure duration are also provided.

Decontamination Strategy	Mean NZMS Mortality (%M [Decimal])	Survey Median Response (SMR)	Angler Decontamination Metric (ADM = %M*SMR)
409:Spray:10-min	1	5	5
409:Spray:20-min	1	5	5
Virkon:Spray:10-min	0.5	4	2
Bleach:Spray:10-min	0.5	3	1.5
Bleach:Spray:20-min	0.75	2	1.5
409:Soak:10-min	1	1	1
409:Soak:20-min	1	1	1
Bleach:Soak:10-min	1	1	1
Virkon:Spray:20-min	0.25	4	1
Virkon:Soak:10-min	0.75	1	0.75
Virkon:Soak:20-min	0.75	1	0.75
Bleach:Soak:20-min	0.5	1	0.5
Mean (+/- SD) ADM: Formula 409			3 (+/- 2.31)
Mean (+/- SD) ADM: Bleach			1.125 (+/-0.49)
Mean (+/- SD) ADM: Virkon			1.125 (+/- 0.60)
Mean (+/-SD) ADM: Spray application			2.80 (+/-1.85)
Mean (+/-SD) ADM: Soak application			0.83 (+/-0.20)
Mean (+/-SD) ADM: 10-min duration			1.85 (+/-1.59)
Mean (+/-SD) ADM: 20-min duration			1.625 (+/-1.69)

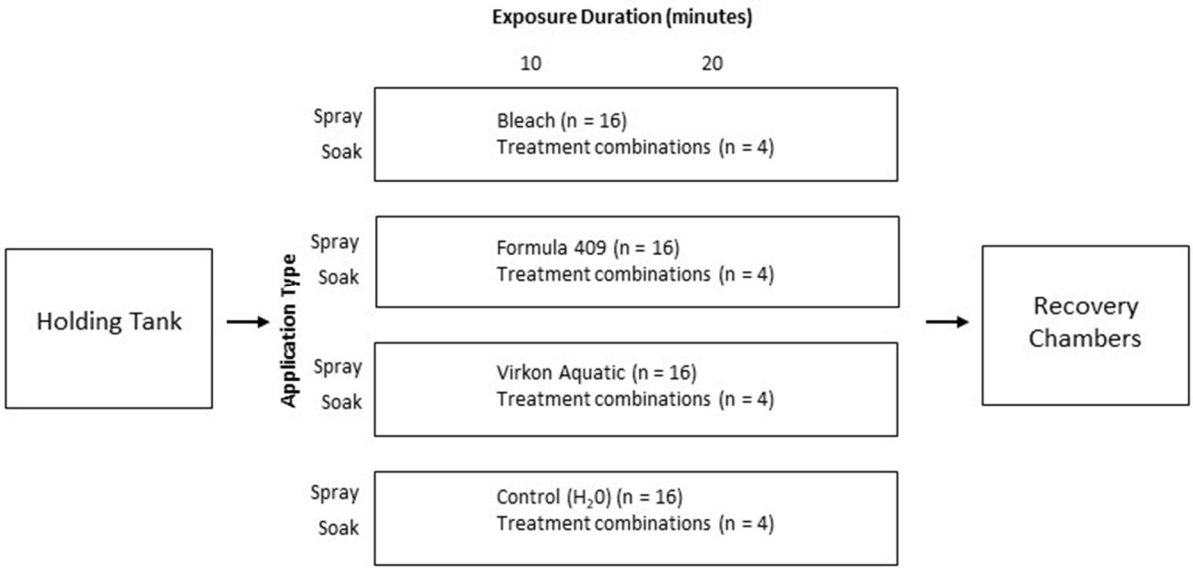

Figure 2.1. Conceptual schematic of experimental design used to assess the effects of 3 different chemicals on NZMS mortality with 2 application types (spray or soak) and 2 exposure durations (10 or 20 minutes). Experimental treatments/chambers were interspersed and randomly assigned. Viability assessments occurred at 1, 6, 24-, 48-, 72-, and 96-hours post-treatment.

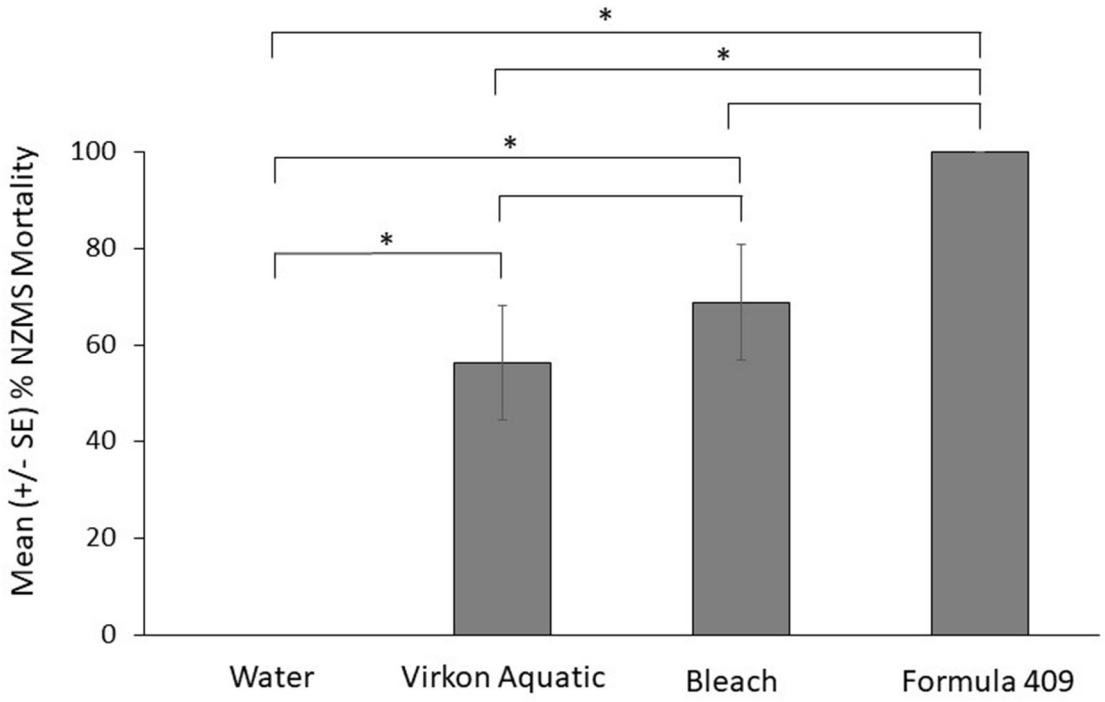

Figure 2.2. Percent NZMS mortality (± SE) across all treatment combinations one hour after applying reagents. Differences were observed across all chemical reagents (* indicates significant difference between chemicals). Post-hoc analysis indicates a significant difference on NZMS mortality between Formula 409 and Virkon Aquatic ($P = 0.005$). No significant differences were found between Formula 409 and Bleach ($P = 0.07$) and Virkon Aquatic and Bleach ($P = 0.75$). All 3 disinfectants were significantly different from water ($P < 0.001$). Significance accepted at ≤ 0.05.

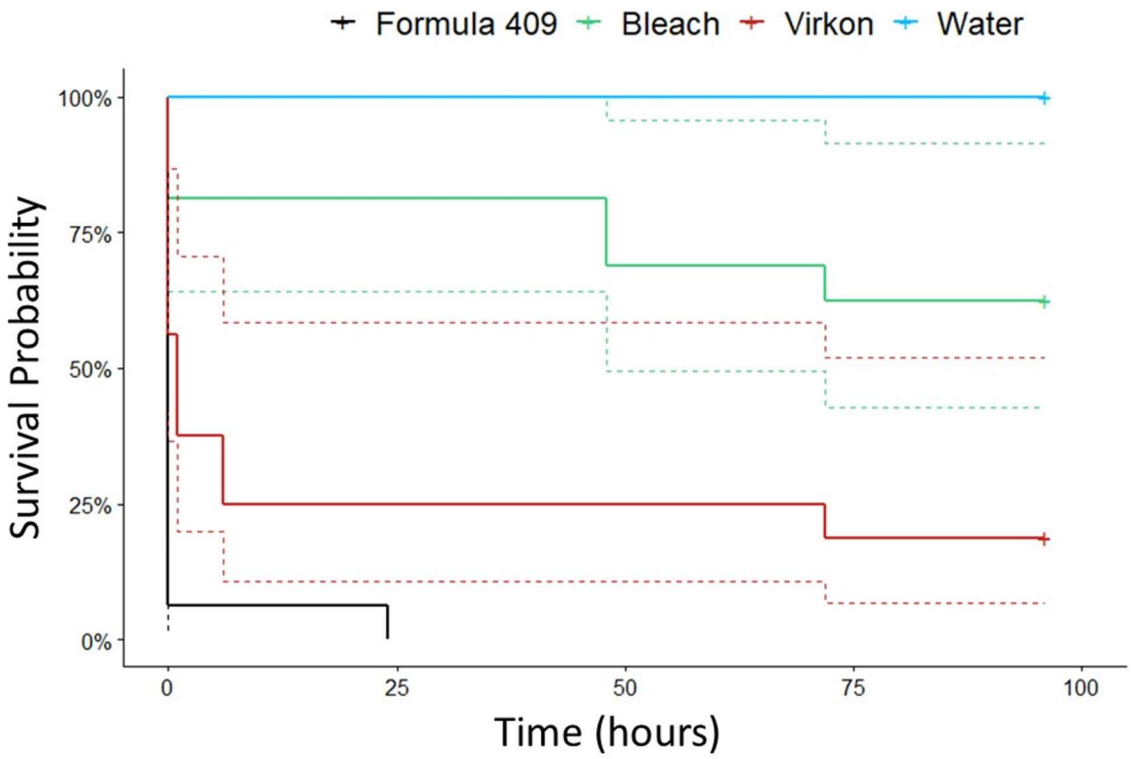

Figure 2.3. Results of the Kaplan-Meier survivorship analysis. There were significant differences among survival function curves ($P < 0.001$). Probabilities of NZMS survival 96hrs after exposure are: Water - 100%; Bleach - 62%; Virkon Aquatic - 18%; Formula 409 - 0%. Dashed lines represent upper and lower boundaries of the 95% confidence intervals and are color associated with the respective chemical treatment.

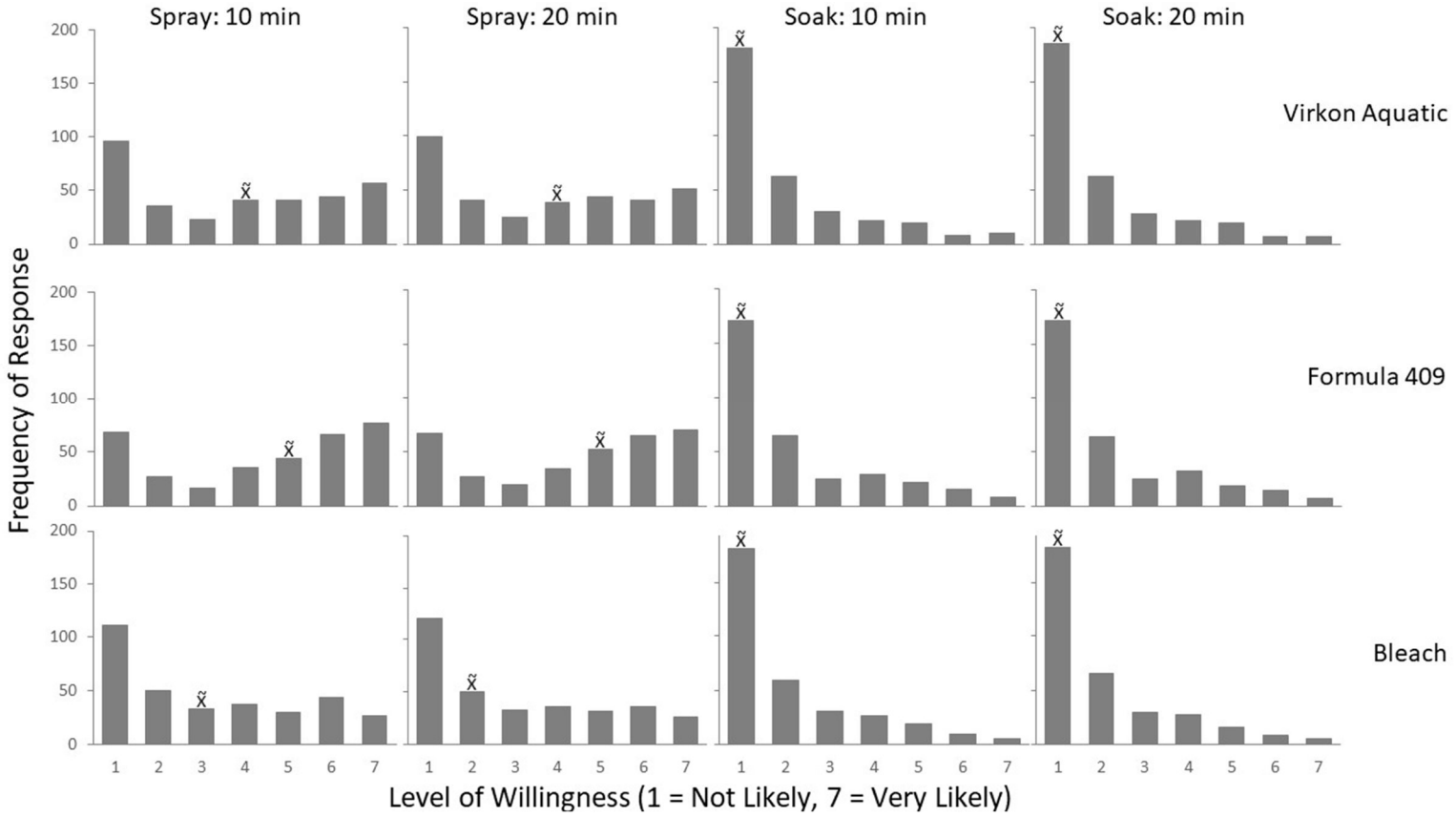

Figure 2.4. Responses of survey participants (n = 339) to questions relating to willingness to implement different NZMS decontamination strategies. Decontamination strategies include 1 of 3 chemicals (Virkon aquatic, Formula 409, Bleach); 1 of 2 application methods (spray, soak); and 1 of 2 exposure durations (10-min, 20-min). x̃ indicates median response for each treatment combination.

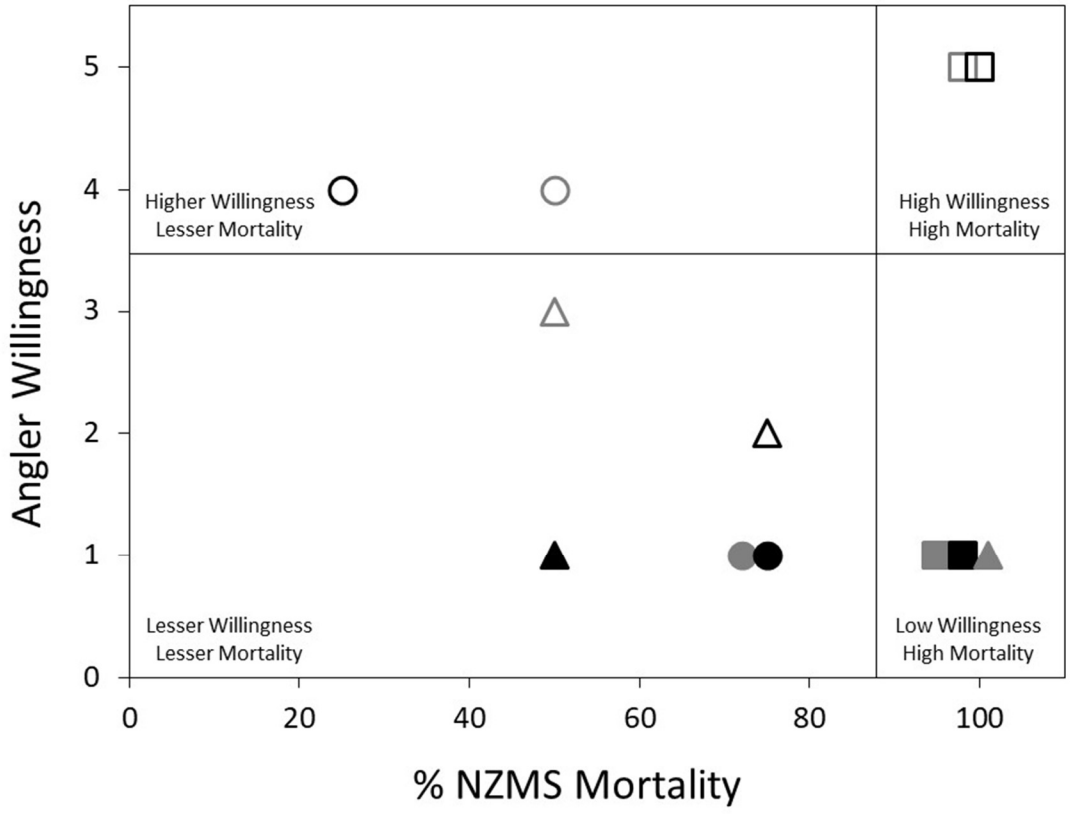

Figure 2.5. Summary plot of the Angler Decontamination Metric, depicting responses of the angler survey plotted against the results of the chemical efficacy trials for NZMS. Squares represent Formula 409; circles represent Virkon Aquatic; triangles represent bleach. Filled shapes represent soaking application and open shapes represent spray application of each chemical. Grey shapes represent 10-minute exposure durations and black shapes represent 20-minute durations for each chemical. Some data points have been jittered to avoid overlap. Spray application of Formula 409 is the decontamination strategy that yields the highest NZMS mortality and is the most willing to be used by the survey participants.

CHAPTER THREE

NEW ZEALAND MUD SNAIL INVASION IMPACTS THE DIETS AND CONDITION OF RESIDENT TROUT

Introduction

Invasive species impart negative ecological impacts in their invaded range through multiple pathways; they physically alter habitats, disrupt food webs, reorganize community structure, compete with native species, and alter ecosystem processes (Sala et al. 2000; Lodge and Shrader-Frechette 2003; Pimentel et al. 2001; Strayer 2010, Lockwood et al. 2013; Ricciardi et al. 2013). They can also influence communities by providing a novel food resource to resident predators. Predator-prey interactions involving invasive species have implications not only for consumers of invasive species, but also for the invasive populations if consumers can exert control over their population growth (Carlsson et al. 2009). However, invasive species that can evade top-down controls in their invasive range are more likely to become established and spread (Lockwood et al. 2013).

New Zealand mud snails (NZMS), *Potamopyrgus antipodarum* (Gray, 1843), are global invaders that have become established in at least 40 countries across 6 continents (Geist et al. 2022). NZMS are caenogastropods, with adult shell lengths of 4–7 mm in invaded ranges and up to 12 mm in their native range (Winterbourn 1970). The shells are amber to dark brown and narrowly conical with three to eight whorls and a mid-whorl keel in some morphotypes. Flexible in its feeding strategy, NZMS feed upon algae and organic detritus (Winterbourn 1970). Their success as an invasive species is due, in part,

to their parthenogenic reproductive strategy, high reproductive capacity, and competitive aptitude. Further, NZMS have a solid operculum and can enclose themselves within their elongated shell, conferring survival across a broad range of environmental conditions, and resistance to predation (Alonso and Castro-Díez 2008) and environmental stressors (e.g., desiccation).

In their invaded range, NZMS impact multiple levels of biological organization, from individual species to community-level dynamics to ecosystem processes (e.g., Riley et al. 2008; Arango et al. 2009; Krist and Charles 2012). Most ecological impacts stem from the ability of NZMS to achieve extremely high densities (> 500,000 individuals/m^2 [e.g., Hall et al. 2006; Dorgelo 1987]) and the fact that NZMS can consume up to 75% of gross primary production (Hall et al. 2003; Moore et al. 2012). NZMS also alter algal and macroinvertebrate communities (e.g., Kerans et al. 2005; Krist and Charles 2012; Bennett et al. 2015; Rakauskas et al. 2017) and impact fish health and food-web dynamics (e.g., Vinson and Baker 2008; Rakauskas et al. 2016).

As NZMS invade aquatic systems, they can displace native benthic invertebrates (e.g., Kerans et al. 2005; Rakauskus et al. 2017), reducing native prey availability for predators. Higher consumers may then incorporate NZMS into their diet as they become an abundant prey item. For example, consumption of NZMS has been documented in the western United States by freshwater, brackish water, and marine species: brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) (Vinson and Baker 2008), juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (Bersine et al. 2008), the tidewater goby (*Eucyclogobius newberryi*) (Hellmair et al. 2011), Pacific staghorn

sculpin (*Leptocottus armatus*), shiner perch (*Cymatogaster aggregate*), and English sole (*Pleuronectes vetulus*) (Bersine et al. 2008). In lakes of Lithuania, NZMS dominate benthic invertebrate communities and are incorporated in the diets of many benthivorous fish species (Rakauskas et al. 2016).

The hard shell and operculum of NZMS provides protection against digestion by predatory fishes, limiting the amount of nutrition that can be obtained (Haynes et al. 1985; Butkus and Visinskiene 2020). Remarkably, NZMS are frequently found alive while in the gut contents of fish and can survive passage through entire gastrointestinal tracts (e.g., McCarter 1986; Vinson and Baker 2008; Holomuzki 2010). Therefore, in instances when native consumers are able to feed on NZMS, the snails may represent a potential 'trophic dead end', with carbon flow to higher consumers being interrupted.

Herein, we report the first documentation of fish, specifically brown trout, brook trout (*Salvelinus fontinalis*), and mottled sculpin (*Cottus bairdii*), feeding on NZMS in the Great Lakes region. Our objectives were to evaluate the frequency and magnitude of NZMS consumption by fish over a 5-year study period in an economically important cold-water stream where NZMS were recently introduced – the Au Sable River (Michigan, USA). We also evaluated the trends of benthic NZMS densities and NZMS consumption by trout, and whether consumption of NZMS affects trout physiological condition.

Methods

Study Area

Our study area was the Au Sable River (Michigan, USA). The Au Sable, in the northeastern region of Michigan's Lower Peninsula, has a watershed area of 5,004 km^2 and drains into Lake Huron. The main stem of the Au Sable is approximately 208 km long, with an additional 558 km of tributaries (Michigan Department of Natural Resources, 1987). The Au Sable is classified as a cold-water system and is a designated trout stream (Michigan Department of Natural Resources, 1987). It is managed as a "blue-ribbon" trout stream with introduced and stocked game species, such as brown trout, rainbow trout and brook trout. The river is a highly popular destination for angling and boating for visitors from across North America and other continents. The East Branch of the Au Sable River, located within the city limits of Grayling, Michigan is approximately 27 km long and flows north to south. NZMS were first detected in the East Branch in 2015 (M.R. Luttenton, unpublished; Michigan Department of Environmental Quality, pers. communications 2016). Since then, NZMS have spread throughout the watershed, and the Au Sable is a potential source population for further NZMS spread given the popularity of the river for recreation.

Field Sampling and Diet Analysis

We collected brown trout, brook trout, and mottled sculpin throughout 5 stream reaches, each approximately 100 m long and 100 m apart, in the lower and most heavily NZMS-invaded portion of the East Branch Au Sable for 5 years during the late summer/early autumn from 2016–2020. We collected fish through a single-pass sampling

effort using a pulsed DC backpack electro-fishing unit (Smith-Root LR-24 backpack electro-fisher) with a circular anode and rattail cathode. Electrofishing was conducted with one person operating the electro-fisher and two netters.

After measuring total lengths and weights of individual trout to the nearest millimeter and gram, respectively, we performed pulsed gastric lavage on trout following the methods of Foster (1977). We used a 50-ml syringe attached to a ~ 50-mm-long catheter-like tube. We filled the syringe with stream water and gently inserted the attached tube down the esophagus of the fish into the stomach cavity. We then pulsed water from the syringe into the fish while massaging the abdomen to flush gut contents, which we then placed into a polypropylene storage container. We stored the containers on ice during transport back to the laboratory where we kept them at -18 °C in ethanol until sample processing. To ensure the complete removal of all gut contents, we euthanized trout and transported them to the Aquatic Ecology Laboratory at Oakland University for complete gut content removal via dissection. We did not conduct gastric lavage on collected sculpin; we euthanized sculpin and transported them back to the laboratory for dissection. In the laboratory, we extracted NZMS, and other prey items retrieved from the gut contents via gastric lavage and full dissection, which we sorted, identified, and enumerated.

In the field we conducted standardized quantitative benthic sampling to obtain NMZS population estimates to evaluate the relationship between benthic densities of NZMS and trout diets. After we sampled fish, we collected three replicate benthic-invertebrate samples from haphazardly chosen riffle- and pool-type habitats, throughout

the same sampling reaches from which we collected fish, using a Wildco 0.086 m^2 Hess-Sampler (Wildlife Supply Co., mesh size 500 μm). For each replicate sample, we drove the Hess sampler into the stream bed, scrubbed large rocks clean of all invertebrates by hand, and agitated the remaining substrate for approximately 60–90 seconds to dislodge invertebrates into the collection chamber. We preserved benthic samples in 90% ethanol for transport to the laboratory until processing. In the laboratory we enumerated NZMS in the benthic samples.

Evaluation of NZMS Consumption and Statistical Analysis

We quantified the absolute abundance of NZMS in trout guts and the proportional abundance of NZMS relative to the number of other diet items across all sampling sites and years. We estimated NZMS benthic densities for each year across all sites and evaluated annual differences using a repeated measures ANOVA with year as a within-subject factor and sampling site as a between-subject factor. Similarly, we conducted a repeated measures ANOVA using year as a within-subject factor and sampling site as a between-subject factor to determine differences in the absolute and proportional abundance of NZMS in trout gut contents across years, (R package: lme4, version 3.1-3 [Kuznetsova et al. 2020]). Post-hoc pairwise comparisons were conducted to identify differences in absolute abundances of NZMS in trout gut contents among sampling years, and proportional abundance of NZMS in trout gut contents among sampling years. P-values were adjusted using the Tukey method (R package: emmeans, version 1.7.3 [Lenth et al. 2022]). We used a negative binomial regression model to evaluate the relationship between the absolute abundance of NZMS (i.e., counts) in trout gut contents and trout

length, and a logistic regression model fit to evaluate the proportional abundance of NZMS in trout gut contents and trout length.

We calculated Fulton's Condition Factor (K) (Ricker 1975) for each trout as a generally accepted metric of trout health, with higher values indicating better overall trout condition. Condition factor enables the quantitative comparison of individuals within a fish population to determine if NZMS negatively affected trout health. We calculated Fulton's Condition Factor for each individual trout using the equation:

$$K = (100{,}000*W)/L^3$$

Where K = fish condition; W = the weight of the fish in grams; L = the total length of the fish in millimeters.

We evaluated the effects of NZMS consumption on the condition of trout with mixed-effect models (R package: lme4; lmerTest, version 3.1-3 [Kuznetsova et al. 2020]). For the models, we used the degree of NZMS consumption by trout and trout age class (0, 1, 2, and 3-yr), as determined by total length (mm), as fixed effects. We defined the degree of NZMS consumption by trout with two categories – high and low – where "high" levels of NZMS consumption were represented by trout that contained ≥ 5 NZMS in their gut contents or had NZMS constituting ≥ 1/3 of their total gut contents, and "low" being anything less. We used age class as a fixed effect to determine if condition factor values differed among trout age. Sampling year was used as a random factor to best account for any interannual variation. We assessed normality of the residuals of the models visually using quantile-quantile plots. We then conducted post-hoc pairwise comparisons to evaluate differences between high and low levels of NZMS consumption

on trout condition within age classes. P-values were adjusted using the Tukey method (R package: emmeans, version 1.7.3 [Lenth et al. 2022]). Additionally, we conducted linear regressions to evaluate the relationship between the absolute abundances of NZMS in trout gut contents, proportional abundances of NZMS in trout gut contents, and condition factor values for age class specific trout.

Lastly, to evaluate differences between consumption by trout and sculpin we used a Student's t-test. All statistical analyses were conducted using R (version 4.0.3; The R Foundation for Statistical Computing Platform, 2020).

Results

We collected 83 trout and 75 sculpin during the 5-year study period. Brown trout was the numerically dominant species caught (n=77) over brook trout (n=6). Mean (± SD) brown trout length and weight across all years were 182 mm (± 65) and 76 g (± 75), respectively (Fig. 3.1a). Mean (± SD) brook trout length and weight across all years were 170 mm (± 50) and 48 g (± 34), respectively (Fig. 3.1b). Mean (± SD) sculpin length and weight across all years were 76 mm (± 11) and 5 g (± 2), respectively.

Across all sampling years and all trout, 60% ± 14% (mean ± SD) had one or more NZMS in their gut contents (Table 3.1). Of the trout that contained NZMS, 75% had 5 or fewer NZMS in their gut contents (Fig. 3.2). NZMS abundances in gut contents ranged from 0–52 snails, with a mean (± SD) of 7.32 (± 10.2) snails (Table 3.1). The proportion of NZMS in gut contents for individual trout ranged from 0–1 with a mean (± SD) of 0.19 (± 0.24) across all sampling years (Table 3.1).

Densities of NZMS in the benthos varied widely among Hess samples and sampling years. Mean (± SD) NZMS density across all years and sites was 9,628 ind./m^2 (± 18,960) and localized densities ranged from 0–122,867 individuals/m^2, with 2018 having the highest observed mean density relative to other sampling years (Table 3.1, Fig. 3.3). Despite the observed increased densities during 2018, we found only marginally significant differences of NZMS densities among years throughout our study period (Repeated Measures: $F = 2.21$, $P = 0.07$).

We found significant differences in the absolute abundance of NZMS in trout gut contents across sampling years (Repeated Measures: $F = 3.22$, $P = 0.04$). Post-hoc pairwise comparisons revealed absolute abundances of NZMS in trout guts increased from a mean (±SD) of 1.2 (± 0.47) to 9.2 (± 7.9) between 2016 and 2018 ($P = 0.03$) (Fig. 3.4a). We also found significant differences in the proportional abundances of NZMS in trout gut contents across sampling years (Repeated Measures: $F = 4.14$, $P = 0.017$). Post-hoc pairwise comparisons revealed proportional abundances of NZMS in trout guts increased from a mean (±SD) of 0.07 (± 0.04) to 0.267 (± 0.11) between years 2016 and 2017 ($P = 0.03$), and to 0.275 (± 0.14) from 2016 to 2018 ($P = 0.02$) (Fig. 3.4b).

The prevalence of NZMS in trout guts depended on trout size. Larger trout contained more NZMS than smaller trout, evidenced by significant positive relationships between trout length and the abundance of NZMS in trout gut contents ($P < 0.001$) (Fig. 3.5a), and the proportion of NZMS relative to total gut contents ($P < 0.017$) (Fig. 3.5b).

Our mixed-effects models indicated significantly lower condition of trout that contained greater abundances of NZMS. Condition factor (K) of all trout ranged from

0.54–2.39 with a mean (± SD) of 0.96 (± 0.25). Trout that had greater numbers of NZMS (>5) in their gut contents had significantly lower condition relative to trout that contained fewer NZMS ($F = 5.49$, $P = 0.02$). Age class did not influence condition factor values of trout ($F = 0.90$, $P = 0.45$) in the model, nor was there an interaction between age class and the degree of NZMS consumption on condition ($F = 0.71$, $P = 0.49$). Trout that had higher proportional abundances of NZMS in their gut contents (> 1/3) also had significantly lower condition relative to trout that had lower proportional abundances ($F = 5.02$, $P = 0.03$). Age class also did not influence condition factor values of trout ($F = 0.85$, $P = 0.47$) in the model, nor was there an interaction between age class and the degree of NZMS consumption ($F = 1.13$, $P = 0.33$).

Post-hoc pairwise comparison within each age class revealed that trout condition significantly differed within age 2 trout and was influenced by the degree of NZMS consumption. Age 2 trout that had > 5 NZMS in their gut contents had significantly lower condition relative to those that had fewer ($P = 0.02$) (Fig. 3.6a). Additionally, age 2 trout that had NZMS constituting > 1/3 of the proportional abundance of their gut content had significantly lower condition relative to age 2 trout that had less ($P = 0.01$) (Fig. 3.6b). Furthermore, when evaluating the relationship of NZMS consumption and trout condition of age 2 trout, we found a negative relationship between condition factor and abundance of NZMS in gut contents ($P < 0.015$, $R^2 = 0.24$) (Fig. 3.7a). Condition factor for age 2 trout also significantly declined with increasing proportions of NZMS relative to total gut contents ($P < 0.053$, $R^2 = 0.16$) (Fig. 3.7b).

The frequency of NZMS consumption was less in mottled sculpin than trout. Of the mottled sculpin we sampled in the field, we randomly subsampled 38 individuals (approximately 50%) for dissection to determine the occurrence and magnitude of NZMS consumption. We found only 1 sculpin with 1 NZMS within its gut contents, a frequency of occurrence of 2.6%. Trout contained significantly greater numbers of NZMS than mottled sculpin ($P < 0.001$).

Discussion

As invasive species expand their ranges, they create novel predator-prey interactions, the outcomes of which are uncertain and wide-ranging. Here we present the first report of consumption of NZMS by trout in the Great Lakes region and relate NZMS consumption to considerable reductions in trout condition factor. Trout consumed NZMS during each year of our 5-year-long study. While most of the collected fish contained 10 or fewer of the invasive snail, NZMS did make up a substantial proportion of prey of some individual trout. Among our sample population, trout contained up to 52 NZMS, and NZMS contributed up to 100% of the total gut contents. These results add to the growing documentation of resident fish preying on NZMS in invaded ranges (e.g., Bersine et al. 2008; Brenneis et al. 2011; Hellmair et al. 2011), and point to the need for effective management of NZMS populations.

NZMS usually constitute a negligible part of fish diets in invaded regions. For example, the frequency of NZMS consumption by juvenile Chinook salmon in the Columbia River Estuary was only 0.03%, with gut contents containing a total of ≤ 6 NZMS (Bersine et al. 2008). Other fish including the Pacific staghorn sculpin

(*Leptocottus armatus*), Shiner perch (*Cymatogaster aggregata*), and English sole (*Pleuronectes vetulus*) (also collected from the Columbia River Estuary [Oregon-Washington, USA]) had similarly low frequencies of NZMS feeding occurrence (≤ 10%) and NZMS abundances in gut contents (total of ≤ 2 for most species and 20 NZMS in one species) (Brenneis et al. 2011). In NZMS-invaded lakes of Lithuania, multiple fish species consume NZMS, but NZMS tend to be low in abundance (≤ 10 NZMS individuals) (Rakauskas et al. 2016). In contrast, NZMS was preyed upon by the tidewater goby in Big Lagoon (California, USA) where 80% of sampled gobies ate NZMS with as many as 27 NZMS/gut (Hellmair et al. 2011). Overall, the degree of NZMS consumption likely depends on interacting factors including NZMS densities, the feeding guild to which fish belong, and the character of the overall native invertebrate community. NZMS densities were high relative to other native macroinvertebrate prey at our study sites (see Chapter 4).

The absolute and proportional abundances of NZMS in trout guts significantly increased during the first 3 years of our study period. We documented a marginally significant change in annual benthic NZMS densities throughout our study period ($P = 0.07$), and spatial and temporal variability of NZMS densities were apparent, and therefore, probably influences the degree of NZMS consumption by trout. Furthermore, changes in NZMS abundances in trout diets could reflect increased predation on NZMS as NZMS become more established in the system over time. This pattern parallels the known feeding habits of trout – the consumption of a particular prey item/type is proportional to the prey abundance and availability (e.g., Hubert and Rhodes 1989;

Hilderbrand and Kershner 2004). In contrast to trout, NZMS consumption by mottled sculpin was very low and did not vary with NZMS densities. This may be a result of different feeding strategies between trout and sculpin. Sculpin are exclusively benthivores during all life stages and may have greater selectivity when foraging, and as such, may be more effective at differentiating among prey types during this stage of the NZMS invasion. In all, the degree to which the consumption of NZMS by trout or sculpin in the East Branch Au Sable River is incidental or deliberate remains largely unclear at this stage of the NZMS invasion.

The nutritional gain to trout when consuming NZMS, relative to native prey, and the physiological consequences for trout consuming NZMS, is uncertain, but our results relate NZMS presence in trout guts with lower trout condition. These findings are consistent with those of Vinson and Baker (2008) who also observed significantly lower condition in rainbow trout and brown trout that were experimentally fed NZMS relative to those that were fed native crustaceans. Our results specifically indicated that adult trout of age 2+ that contained greater abundances of NZMS in their gut contents (> 5 individual NZMS, and > 1/3 proportional abundance) exhibited significantly lower condition relative to age 2+ trout that did not. The mechanism of the adverse effect on age 2 trout is unknown, though it may be related certain ontogenetic changes during this life-stage related to feeding behaviors and-or habitat preference that may coincide with NZMS presence, which may then increase the likelihood of NZMS consumption. As such, the presence of numerous NZMS in trout guts may give trout the sensation of being fed, limiting feeding on native and presumably more-nutritious prey.

The reduced condition among trout that consume NZMS may be, in part, because of the morphological traits of the invasive snail. NZMS possess a hard shell, are small, and are able to close their aperture, providing considerable protection from digestion (McCarter 1986; Butkus and Visinskiene 2020). NZMS can remain intact after being consumed by fish (e.g., McCarter 1986; Holomuzki 2010) and can pass the gastrointestinal tract of fish alive. While we did not experimentally evaluate the survival of NZMS through trout digestive tracts, we observed the survival of NZMS after egestion by a brook trout. Among studies that have experimentally evaluated NZMS survival after consumption, Vinson and Baker (2008) found 53% of NZMS survived after being consumed and egested by rainbow trout, and other studies have observed similar findings (e.g., Haynes et al. 1985, Bruce 2010). In addition to the consequences for fish condition factor, their ability to survive passage through trout guts makes trout an potentially important source of upstream NZMS dispersal given that upstream volitional migration rates are very low.

Invasive NZMS can impact ecosystems through multiple pathways (Geist et al. 2022), and in the case of higher consumers, NZMS can directly and/or indirectly affect fish condition. Our study is one of few that has evaluated predator-prey interactions among native/resident fish and NZMS, and the first to document trout feeding on NZMS in the flowing-water ecosystems of the Great Lakes region. Our study spanned a 5-year period, with fish sampling occurring once annually and early in the NZMS invasion process. However, more research is needed to evaluate the seasonal and long-term dynamics and effects of NZMS on higher consumers, since NZMS populations are

dynamic over the short and long term (e.g., Vinson 2004; Hall et al. 2006; Moore et al. 2012; Bennett et al. 2015; Greenwood et al. 2020; Geist et al. 2022). Improved understanding of the relationship between native consumers and invasive NZMS populations, and by extension, food web dynamics, will help direct research and management efforts for this increasingly relevant aquatic invader.

Table 3.1. NZMS densities and NZMS consumption by Brook trout and brown trout in the East Branch Au Sable River (Michigan, USA).

				No. of NZMS Consumed			Proportion of Diet		
Year	Mean NZMS Density (ind. per m^2) (± SD)	No. Trout Collected (n)	Proportion of Trout that Consumed NZMS	Min	Mean (± SD)	Max	Min	Mean (± SD)	Max
2016	5639 (3209)	26	0.44	0	1.2 (0.2)	7	0	0.072 (± 0.04)	0.33
2017	6340 (5627)	16	0.60	0	4.7 (4.8)	41	0	0.267 (± 0.1)	1
2018	19479 (20779)	15	0.80	0	9.2 (7.9)	52	0	0.27 (± 0.14)	0.81
2019	4470 (2750)	16	0.57	0	3 (3.7)	25	0	0.174 (± 0.12	0.66
2020	8223 (7196)	10	0.55	0	2.6 (1.5)	13	0	0.149 (± 0.08)	0.59

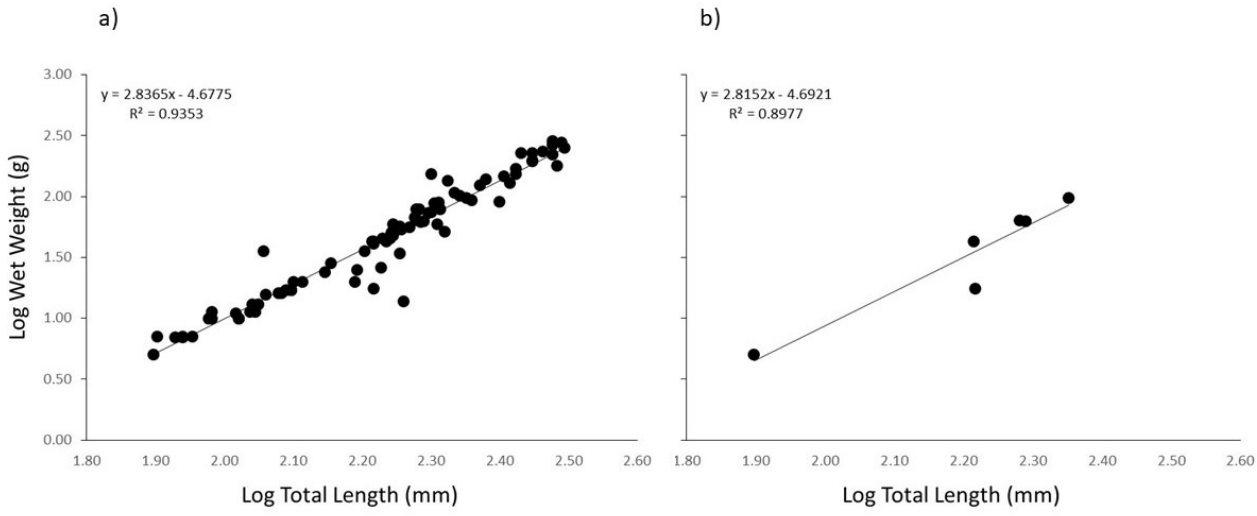

Figure 3.1. Length-weight regression of a) brown trout (n = 77) and b) brook trout (n = 6), across all years (2016-2020) and sites.

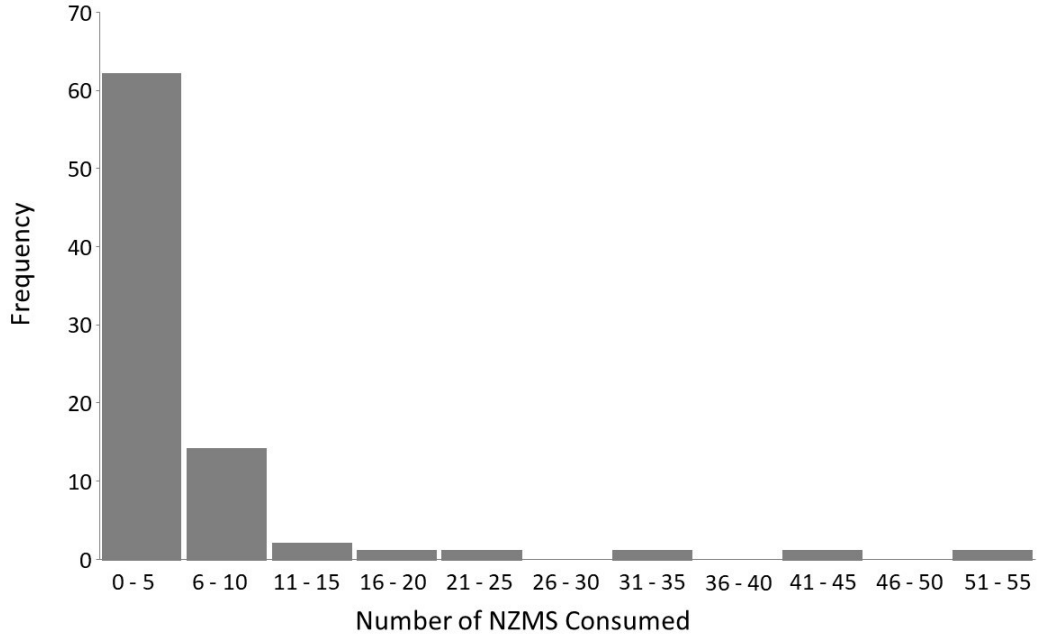

Figure 3.2. Number of NZMS contained in the gut contents of all sampled trout (n = 83) across all years.

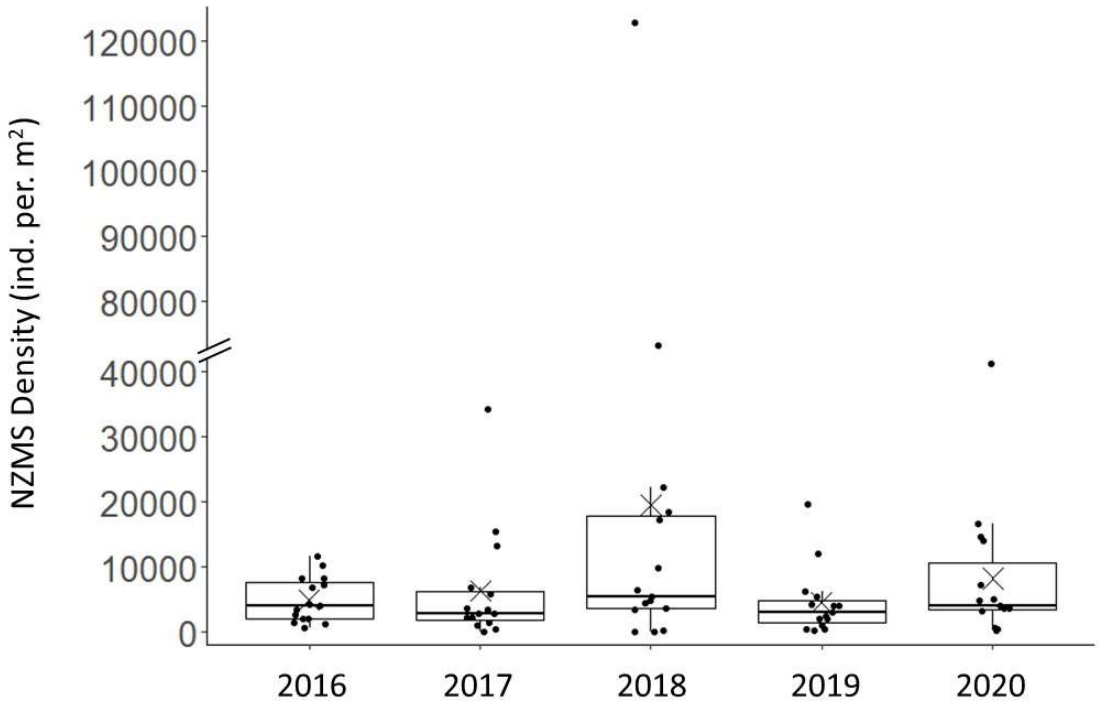

Figure 3.3. Box plot of NZMS density estimates across all sampling sites during each sampling year. Boxes represent the interquartile range (IQR). Closed circles are individual data points, with minimum and maximum values represented by the whiskers (outliers indicated by data points beyond whiskers). X marks the mean value, and line within the box marks the median value. Mean (± SD) NZMS density across all years and sites was 9,628 ind. per m^2 (± 18,960) and localized densities ranged from 0–122,867 individuals/m^2. Marginally significant differences of NZMS densities were observed among years throughout our study period (Repeated Measures: $F = 2.21$, $P = 0.07$), with 2018 having the highest observed mean density relative to other sampling years.

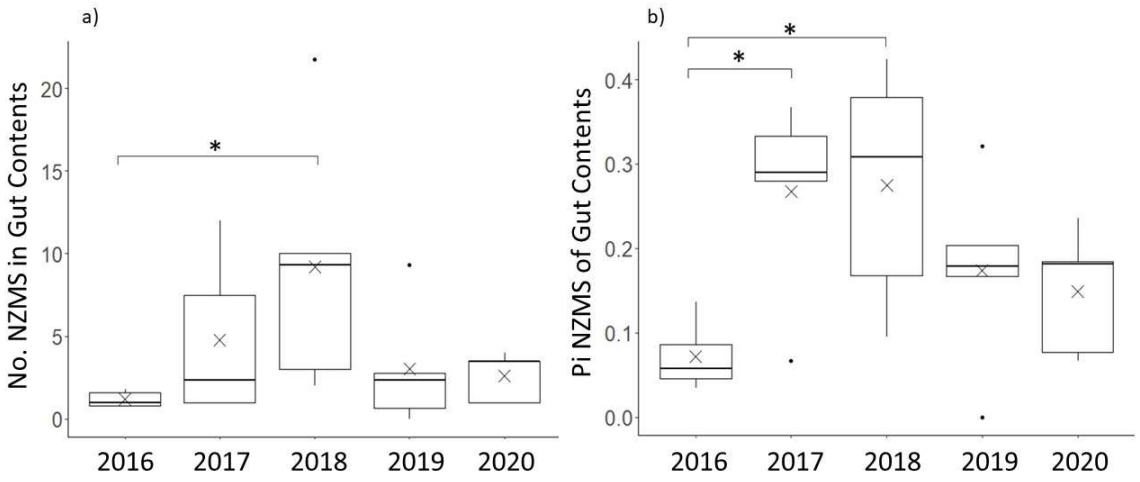

Figure 3.4. Box plots of absolute and proportional abundances of NZMS in trout gut contents during each sampling year across all sites. Boxes represent the interquartile range (IQR) with minimum and maximum values represented by the whiskers (outliers indicated by dots beyond whiskers). X marks the mean value, and line within the box marks the median value. Significant differences were found in a) the absolute abundances of NZMS in trout gut contents between sampling years 2016 and 2018, and b) the proportional abundances of NZMS found in trout gut contents between sampling years 2016 and 2017, and 2016 and 2018.

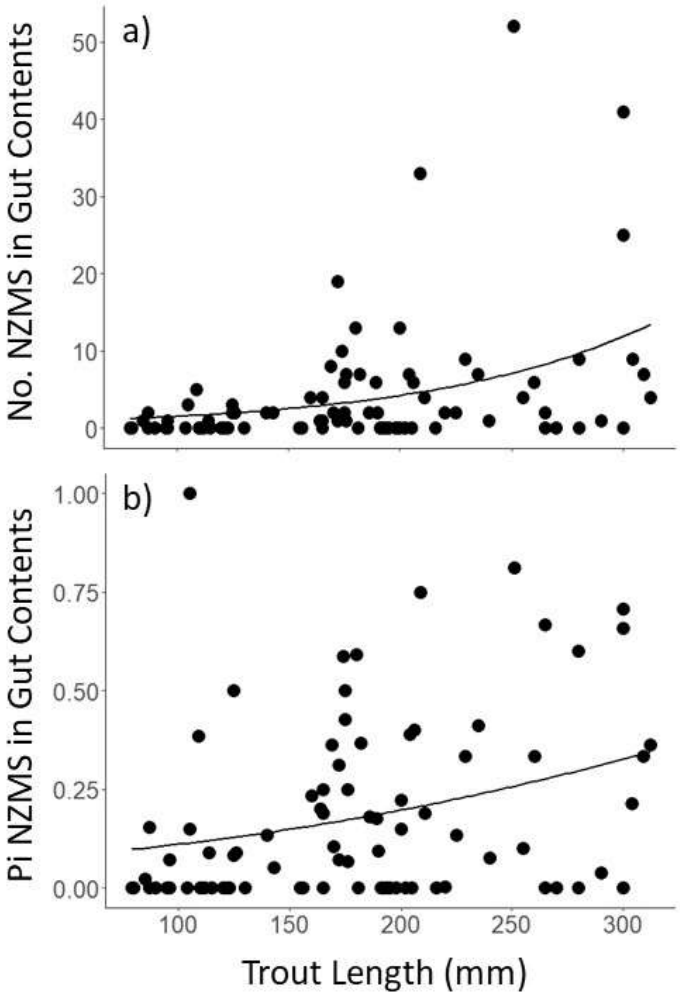

Figure 3.5. a) Negative binomial regression model fit for trout length and the number of NZMS in trout gut contents across all years and sites (n = 83) ($P < 0.01$); b) Logistic regression model fit for trout length and the proportional abundance of NZMS in trout gut contents across all years and sites (n = 83) ($P = 0.017$).

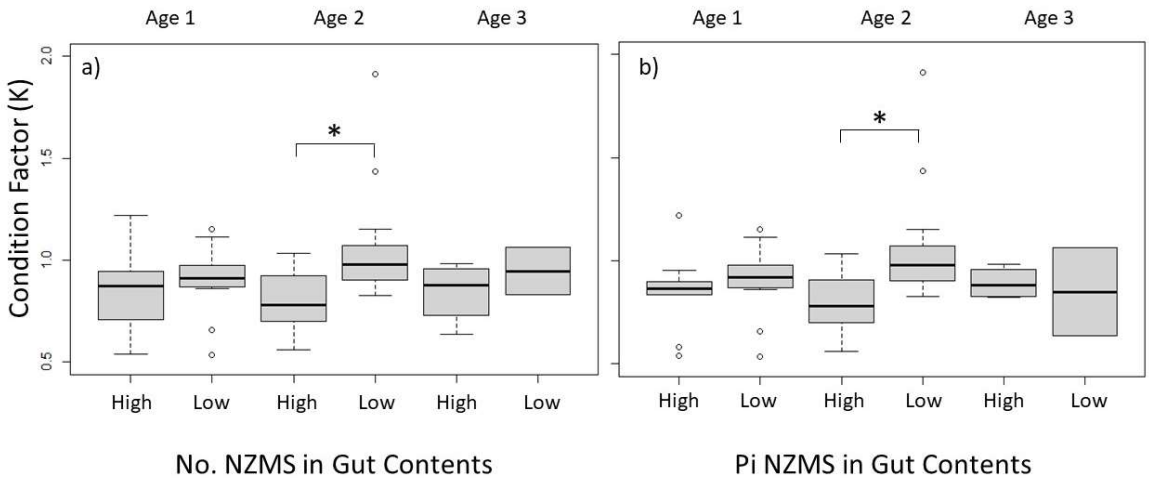

Figure 3.6. Comparison of trout condition, within each age class, between high and low levels of NZMS consumption. Significantly lower condition was found between a) age 2 trout that contained greater numbers of NZMS (> 5) relative to trout that had fewer (P = 0.02) and b) age 2 trout that contained greater proportions of NZMS (> 1/3) in their gut contents relative to trout that contained less (P = 0.01). Note: age zero trout were omitted from the figure due to a lack of comparability between high and low levels of NZMS consumption (i.e., no age 0 trout contained "high" levels of NZMS).

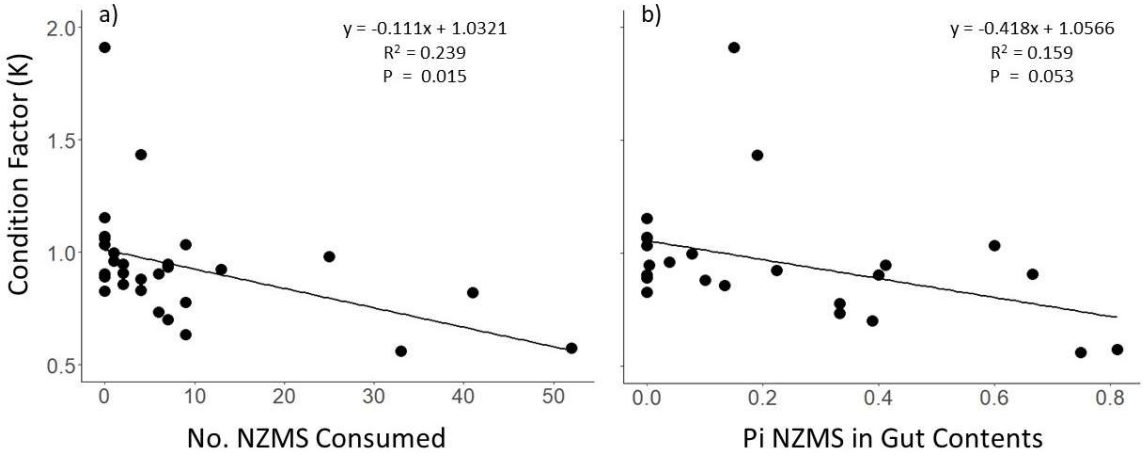

Figure 3.7. Negative relationships between trout condition (Fulton's condition factor, K), and a) the number of NZMS in age 2 trout gut contents across all years and sites, and b) proportion of NZMS in age 2 trout gut contents across all years and sites.

CHAPTER FOUR

POPULATION DYNAMICS OF THE INVASIVE NEW ZEALAND MUD SNAIL AND EFFECTS ON NATIVE MACROINVERTEBRATE COMMUNITIES

Introduction

Biological invasions are a leading threat to the structure and functioning of ecosystems worldwide (Vitousek et al. 1996; Sala et al. 2000; Lodge and Shrader-Frechette 2003; Strayer 2010). Few habitats on earth remain free of invasions, with aquatic systems being among the most heavily invaded, particularly freshwaters (Sala et al. 2000). The Laurentian Great Lakes are a hot spot for exotic species introductions. To date, over 180 non-native aquatic species have been documented (National Oceanic and Atmospheric Administration 2020), making the Great Lakes one of the most invaded ecosystems throughout the world (Riccardi and MacIsaac 2000; Holeck et al. 2004).

New Zealand mud snails (NZMS), *Potamopyrgus antipodarum* (Gray, 1843) have colonized at least 40 countries across 6 continents (Geist et al. 2022) and have recently been detected in rivers and streams of the Great Lakes. NZMS are caenogastropods that opportunistically feed upon algae and organic detritus (Winterbourn 1970; E.N. Bovee unpublished data). They possess several life-history traits, such as high fecundity and asexual reproduction, that enable them to reach high population densities quickly after colonizing new habitats (Alonso and Castro-Diez 2008). NZMS can persist across a broad range of environmental conditions and are mostly released from predation in their invaded ranges (but see Geist et al. In prep).

NZMS populations exhibit a wide range of densities across their invaded range. Maximum reported densities of NZMS across studies range from 40 to over 800,000 ind./m^2 (Dorgelo 1987; Thomsen et al. 2009). The mechanisms behind such variation in NZMS population densities are largely unknown, though may in part be explained by the time since initial introduction, differences in invasion capabilities among clonal populations, and/or ecological factors such as the productivity or condition of the invaded system (Geist et al. 2022). Further research is needed to better understand NZMS population dynamics, and its drivers.

Cyclical boom-and-bust patterns of NZMS population abundance are frequently documented in invaded systems across multiple time scales. For example, seasonal variations in population abundance – where densities peak during summer and decrease during winter – are commonly observed (e.g., Heywood and Edwards 1962; Dorgelo 1987; Vinson 2004; Kerans 2005). Similarly, dynamic NZMS populations have also been observed over longer timescales, wherein abundances increased over several years, following invasions, before decreasing rapidly (Moore et al. 2012; Gerard et al. 2018). The driving factors behind intra-annual fluctuation of population densities are not well understood but may include variation in resource availability (e.g., algal abundance) and/or seasonal changes in hydrology or water quality characteristics. Longer-term patterns may be the result of NZMS altering ecosystem characteristics such that they limit population densities. Given that the ecological impacts may be proportional to their population size and NZMS abundances can exhibit short- and long-term fluctuations,

variation in the level of ecological impacts is likely to occur within an invaded system over time.

Dense NZMS populations can impact multiple levels of biological organization and ecosystem processes. NZMS alter periphyton assemblages (Arango et al. 2009; Bennett 2014) and adversely impact (e.g., homogenize) macroinvertebrate communities (e.g., Richards et al. 2001; Richards 2004; Kerans et al. 2005; Rakauskas et al. 2017). For example, in the Greater Yellowstone Area, NZMS densities exceed 500,000 ind./m^2 (Hall et al. 2006) (Fig. 4a). These extremely high densities coupled with rapid per-capita growth translated to levels of secondary production that exceed those of all native invertebrate taxa in that community combined (Hall et al. 2006). NZMS can also affect higher consumers, such as fish, by altering their diets and reducing their physiological condition (Vinson and Baker 2008; Geist and Tiegs In prep). These results suggest that NZMS monopolize resources that otherwise would be available to native invertebrates and can cause subsequent impacts to the structure and functioning of the invaded ecosystem.

The effects NZMS have on native communities are likely to be context dependent. Thus, improved understanding is needed on how population dynamics and effects depend on the ecological setting to better direct management and research. Furthermore, investigations on the effects of NZMS on native invertebrate communities in the Great Lakes region are lacking, making it difficult to predict their population dynamics and ecological impacts in this recently invaded range. Here, we determine NZMS presence and the extent of their distribution in a recently invaded system, the Au

Sable River Watershed (MI, USA). Moreover, we characterize NZMS population dynamics and document the effects of NZMS on resident stream-invertebrate communities through seasonal sampling of the benthic community over a 5-year study period. We hypothesized that NZMS populations would increase annually over the study period, with fluctuations occurring on a seasonal basis, as seen elsewhere in NZMS invaded ranges (e.g., Kerans et al. 2005; Hall et al. 2006). Furthermore, we hypothesized that increasing densities of NZMS would have adverse impacts on the native invertebrate community composition, particularly that of native taxa that share similar feeding strategies.

Methods

Study Area

Our study area was in the Au Sable River watershed (Michigan, USA). The Au Sable River, located in the northeast of Michigan's Lower Peninsula, has a watershed area of 5,004 km^2 and drains into Lake Huron. The main stem of the Au Sable River is approximately 208 km long, with an additional 558 km of tributaries (Michigan Department of Natural Resources, 1987). The Au Sable River is classified as a cold-water system and is a designated trout stream (Michigan Department of Natural Resources, 1987). It is managed as a "blue-ribbon" trout stream, with introduced and stocked game species, such as brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), and brook trout (*Salvelinus fontinalis*). As such, the river is a highly popular destination for tourism, especially river-oriented recreation, such as angling and boating, attracting visitors from across North America and other continents. The East Branch of the Au

Sable River, near the town of Grayling, is approximately 27 km long and flows north to south and is where NZMS were first detected in the watershed in 2016 (Michigan Department of Environmental Quality, pers. communications 2016). Since then, NZMS have spread throughout the watershed, making the Au Sable River a potential source population for further NZMS spread.

Macroinvertebrate Sampling and Habitat Variables

We conducted quantitative benthic sampling seasonally during a 5-year study period in 6 stream reaches in the lower, most-heavily NZMS-invaded portion of the East Branch Au Sable River. Additionally, we sampled selected tributaries and the Main Branch of the Au Sable. Benthic sampling occurred seasonally (i.e., 4 times/year) from late summer/early autumn 2016 to summer 2020 (Fig. 4.1).

To obtain NZMS and native invertebrate population estimates, we collected three replicate benthic-invertebrate samples from haphazardly chosen riffle and pool habitats throughout each sampling reach using a Wildco 0.086 m^2 Hess-Sampler (Wildlife Supply Co., mesh size 500 μm). For each replicate sample, we drove the Hess sampler into the stream bed, scrubbed large rocks clean of all invertebrates by hand, and agitated the remaining substrate for approximately 60–90 seconds to dislodge invertebrates into the collection chamber. We preserved benthic samples in 90% ethanol for transport to the laboratory until processing.

In the laboratory, we sieved benthic samples using 63-, 2,000- and 4,000-micron mesh sizes to separate organic and inorganic materials from the macroinvertebrates. We used fixed-fraction subsampling methods (Hilsenhoff, 1987) to select a proportion of the

whole sample for identification and enumeration. In brief, the contents of the sieved sample were emptied into a gridded enamel panel, which was divided into 6 equal compartments. We then randomly selected 2 of the compartments for subsampling. All organisms within the selected compartments were picked and sorted. NZMS were identified, separated from other organisms, and enumerated. Native macroinvertebrates were sorted, identified to the family taxonomic level (Bouchard 2004; Merritt et al. 2009), and enumerated.

We collected stream habitat measurements on 27 July 2018 that included canopy cover, water velocity, water depth, and substrate composition to evaluate associations with NZMS, native invertebrates, and stream habitat characteristics. We collected habitat measurements during base/low discharge using standardized methods and protocols.

Statistical Analysis

Statistical analyses were conducted using R (version 4.0.3; The R Foundation for Statistical Computing Platform, 2020). We calculated NZMS population densities based on the samples from all sites and plotted densities across all sampling seasons and years. We tested for differences between seasons and years using a Repeated Measures Analysis of Variance (RMANOVA) (R package: lme4; lmerTest, version 3.1-3; Kuznetsova et al. 2020), where Site was a random factor, and Year and Season were fixed factors. We assessed normality of the residuals of the models visually using histograms and quantile-quantile plots. If the RMANOVA detected differences among treatments, we used a pairwise post-hoc analysis using the estimated marginal means (R package: emmeans,

version 1.7.2; Russell et al. 2022) to locate differences. We adjusted P-values after post-hoc tests using the Tukey method.

To evaluate differences in benthic macroinvertebrate community composition among years, we conducted multivariate analysis using non-metric multidimensional scaling (NMDS) (package: vegan; version 2.5-7; Oksanen et al. 2020) with a Bray-Curtis dissimilarity matrix to visualize differences in community composition over the study period. We performed a post-hoc Adonis test to identify differences in community structure among years and used a pairwise permutation multivariate analysis of variance (PERMANOVA) to locate differences. Additionally, we organized data into three classes based on NZMS densities: low (0-1,000 NZMS individuals/m^2), medium (1,000 – 7,275 NZMS individuals/m^2) and high (> 7,275 NZMS individuals/m^2) and used NMDS ordinations to evaluate the effects of NZMS density on the native invertebrate community composition for each sampling year. NZMS density levels were semi-arbitrarily determined and based on data centrality and quartile ranges.

We performed a Canonical Correspondence Analysis (CCA) (package: vegan; version 2.5-7; Oksanen et al. 2020) to separate variation in our data from statistical noise to evaluate associations between native macroinvertebrate communities, NZMS, and stream habitat characteristics. We used proportional abundances of individual invertebrate taxa for each site across all sampling years and seasons (excluding NZMS) as the response variables in the analysis and stream habitat measurements, as well as proportional abundances of NZMS, as predictor terms. We used a permutation analysis

of variance to assess the significance of the CCA model and to assess the significance of each predictor term used in the analysis.

We used bivariate regression analysis to determine relationships between NZMS abundances, functional feeding guilds of native invertebrate taxa, and other various metrics of the native macroinvertebrate community. Specifically, we used logistic regression models to evaluate relationships between NZMS proportional abundances and proportional abundances of native taxa belonging to each functional feeding guild (scraper, shredder, collector-gatherer, collector-filterer, and predator), as well as individual taxa that were most common in our benthic samples that belonged to the scraper functional feeding guild (those deemed most likely to be impacted by NZMS given overlap in feeding strategy). We log (+1) transformed absolute abundance data for NZMS and native taxa and used linear regression analysis to evaluate relationships between NZMS and taxa belonging to the scraper, shredder, and collector-gatherer functional feeding guilds. Additionally, we evaluated relationships between NZMS proportional abundance and native invertebrate taxonomic family richness, native invertebrate community species evenness (Pielou's J), and diversity (Shannon-Weiner Diversity H'). We assessed the normality of the residuals of all models visually using histograms and quantile-quantile plots and compared these to alternative models (e.g., Poisson) to select those that provided the best fit.

Results

NZMS distribution expanded during the study period, with new populations detected in tributaries and other locations throughout the Au Sable watershed (Fig. 4.1,

Table E.1.). Specifically, since 2016 (the first sampling year), NZMS were detected at 5 additional sampling locations located in the main stem of the Au Sable (2), the South Branch Au Sable (1), and North Branch Au Sable (2). Densities of NZMS within the East Branch Au Sable (believed to be the site of initial NZMS introduction in the Au Sable watershed) varied widely. Mean (± SD) NZMS density in the East Branch Au Sable across all years and sites was 7,275 ind./m^2 (± 15,197) (Fig. 4.2); local densities ranged from 0–122,860 ind./m^2 (Fig. 4.3). The sampling sites with the greatest mean NZMS densities were EB01 (mean ± SD = 7,205 ± 4,038, max density = 118,500 ind./m^2) and EB04 (mean ± SD = 11,312 ± 5,346, max density = 122,860 ind./m^2) (Fig. 3). NZMS densities in other tributaries of the Au Sable were less than the East Branch (Fig. E.1).

We observed pronounced seasonality among NZMS populations during the 5-year duration of our study, with peak densities typically occurring during summer and autumn. We detected significant differences in mean (± SD) NZMS densities among seasons (RMANOVA: $F = 4.21$, $P = 0.006$), and post-hoc pairwise comparisons revealed differences of NZMS densities between autumn and spring ($P = 0.03$), autumn and winter ($P < 0.001$), and summer and winter ($P < 0.01$) (Fig. 4.4). We did not detect significant differences in NZMS densities among years (RMANOVA: $F = 1.59$, $P = 0.17$) (Fig. E.2).

NZMS numerically dominated the benthic community across all sites during most years (Fig. E.3), and NZMS proportional abundances in benthic samples ranged widely from 0–0.99. Contrary to our hypothesis, we did not observe any relationships between the proportional abundances of NZMS and taxa belonging to functional feeding guilds of

scrapers (P = 0.15), shredders (P = 0.79) and collector-gatherers (P = 0.14) (Fig. 4.5a–4.5c). However, we observed positive relationships between the absolute abundances of NZMS and taxa belonging to functional feeding guilds of scrapers ($P < 0.01$, $R^2 = 0.24$), shredders ($P < 0.001$, $R^2 = 0.08$), and collector-gatherers ($P = 0.03$, $R^2 = 0.029$) (Fig. 4.6a – 4.6c). We did not observe any relationship between the proportional abundances of NZMS and the 4 most abundant scraper taxa: native snails (collectively), Baetidae, Elmidae and Helicopsychidae (Fig 4.7a–4.7d). Further, there was no relationship between NZMS proportional abundance and native invertebrate family richness ($P = 0.32$, $R^2 = 0.003$) (Fig. 4.8a), species evenness (J) ($P = 0.91$, $R^2 = -0.006$) (Fig. 4.8b), and diversity (H') ($P = 0.59$, $R^2 = 0.001$) (Fig. 4.8c).

We observed differences in the overall benthic community composition among years, evidenced by NMDS ordination (Fig. 4.9) (Post-hoc Adonis: P = 0.04). Pairwise PERMANOVA indicated differences in benthic community composition between years 2017 and 2019 (P = 0.012), 2018 and 2019 (P = 0.03), 2018 and 2020 (P = 0.018), 2019 and 2020 (P = 0.012) (Fig. 4.9). We also observed differences in the native benthic community composition across NZMS density categories (low, medium, and high), in years 2018 (Post-hoc Adonis: P = 0.002) and 2019 (Post-hoc Adonis: P = 0.001) (Fig. 4.10). In 2018, native invertebrate community composition differed between low and medium NZMS densities (PERMANOVA: P = 0.01) and low and high NZMS densities (PERMANOVA: P = 0.003) (Fig. 4.10). In 2019, native invertebrate community composition differed between low and medium NZMS densities (PERMANOVA: P = 0.004) and low and high NZMS densities (PERMANOVA: P = 0.003) (Fig. 4.10).

Our CCA model was marginally significant (P = 0.055) and indicated fewer native taxa being associated with NZMS (Fig. E.4). Sites EB01 and EB04, the sampling sites with the greatest NZMS densities during the study period, were located in the quadrat that NZMS were associated with (Fig. E.4). Of the environmental predictors, velocity was the only significant term influencing invertebrate community composition (P = 0.006).

Discussion

The impacts an invasive species has on its ecosystem are often proportional to its population size (Bradley et al. 2019), and NZMS can reach population densities up to 800,000 ind./m^2 (e.g., Dorgelo 1987). Here, we present NZMS population dynamics and their relationships with native invertebrate communities early in the invasion process in Michigan streams. In our study area, NZMS densities were highly dynamic, and in some instances, local densities reached over 100,000 ind./m^2.

NZMS densities were highly variable among seasons, with the greatest densities typically occurring during summer and autumn, often followed by precipitous declines during winter and spring. These seasonal changes in NZMS population densities are consistent with observations seen elsewhere in their invaded range. For example, in the Western U.S., NZMS can achieve densities of over 500,000 ind./m^2 during the late summer and autumn, which then fall considerably during the late winter (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. Furthermore, invasive NZMS populations are seemingly restricted to temperate latitudes (see Geist et al. 2022), and as such, seasonal changes in NZMS populations may be an inherent facet of their ecology in invaded ranges.

We did not observe any significantly longer-term population fluctuations (e.g., at the scale of years), although such fluctuations occur elsewhere in NZMS invaded ranges. For example, in a California stream, NZMS densities reached nearly 100,000 ind./m^2 after a seven-year observation period and then fell to fewer than 1,000 ind./m^2 over the next three years (Moore et al. 2012). Similar declines in abundance occurred in a French stream, where during years 2000–2004, NZMS made up 97% of the molluscan assemblage, while during 2009–2013, the relative abundance of NZMS decreased to 44% (Gérard et al. 2018). These fluctuations may, in part, be a result of density-dependent factors altering ecosystem characteristics, such that large populations can no longer be sustained. Alternatively, other ecological population-regulation mechanisms may be important, such as predation, the exploitation of resources, or abiotic environmental changes. In all, long-term data, spanning multiple years to decades, is needed to better characterize patterns of NZMS population dynamics in the Au Sable watershed and help predict their potential impacts.

NZMS densities were related to differences in community composition of native macroinvertebrates, as evidenced by our NMDS. However, contrary to our hypothesis, we did not detect any relationships between NZMS proportional abundances and those of scrapers, shredders, and collector-gatherers. Furthermore, we did not observe any

associations between NZMS and native invertebrate community species evenness (J) and diversity (H') of the native invertebrate community. We did, however, observe positive relationships between absolute densities of NZMS and taxa of similar feeding strategies (i.e., scraper, shredder, collector-gatherer), to which we attribute to environmental conditions suitable for supporting NZMS and native taxa of those feeding guilds. Adverse impacts of NZMS on native invertebrate community structure has been seen elsewhere in their invaded range. For example, in Rock Creek (Wyoming, USA), the alteration of macroinvertebrate community structure and shifts in functional assemblage occurred, with reductions in EPT taxa, an increase in scraper abundance, and an increase in pollution-tolerant taxa, which was attributed to high densities of the invasive snail (Maret et al. 2008). Similarly, Rakauskus et al. (2017) observed shifts in the lentic benthic community, where dominant taxa changed from crustacean to gastropod, a result of a rapidly increasing NZMS population. Several other studies have reported similar shifts in the taxonomic and functional structure after NZMS invasion and demonstrate the ability of NZMS to reorganize a native community (e.g., Richards et al. 2001; Moore et al. 2012; see Alonso and Castro Diez 2012; Spyra et al. 2014).

Native gastropods and other taxa with similar feeding strategies, in particular, can be in direct competition with NZMS because they use similar resources (Kerans et al. 2010; Geist et al. 2022). Surprisingly, we did not observe any relationship between taxa that share similar feeding strategies (i.e., scrapers, shredders, and collector-gatherers) and NZMS proportional abundance. Furthermore, we did not observe any association between proportional abundances of NZMS and the most common scraper taxa (native

snails, Helicopsychidae, Baetidae and Elmidae) of our samples. However, the impacts of NZMS on native invertebrate community composition are commonly observed in other NZMS-invaded ranges. For example, Kerans et al. (2005) observed negative associations between native invertebrate colonization and NZMS in the Western USA. The number of native macroinvertebrates colonizing experimentally placed tiles declined as the number of NZMS increased, suggesting a potential to influence the distribution of native invertebrates.

Our study is the first to document and characterize seasonal and annual NZMS population dynamics in the Midwest United States. Additionally, we address associations between NZMS and native invertebrates in the East Branch Au Sable River (the site of initial introduction of NZMS in the Au Sable watershed). Like that of other invasive populations in the Western United States, NZMS densities in the East Branch Au Sable can reach elevated levels, exceeding 100,000 ind./m^2. Furthermore, NZMS often numerically dominated the benthic community and comprised up to 99% of our benthic samples. However, we only observed moderate effects of NZMS on native invertebrate community composition and no apparent impacts to taxa of similar feeding strategies (e.g., scrapers). We recognize that our study occurred over a relatively short time frame in the overall invasion process, and as such, more research is needed to document longer-term trends in invasive NZMS population dynamics and effects on native invertebrates to improve our understanding of this widespread invasive species and to better aid management efforts.

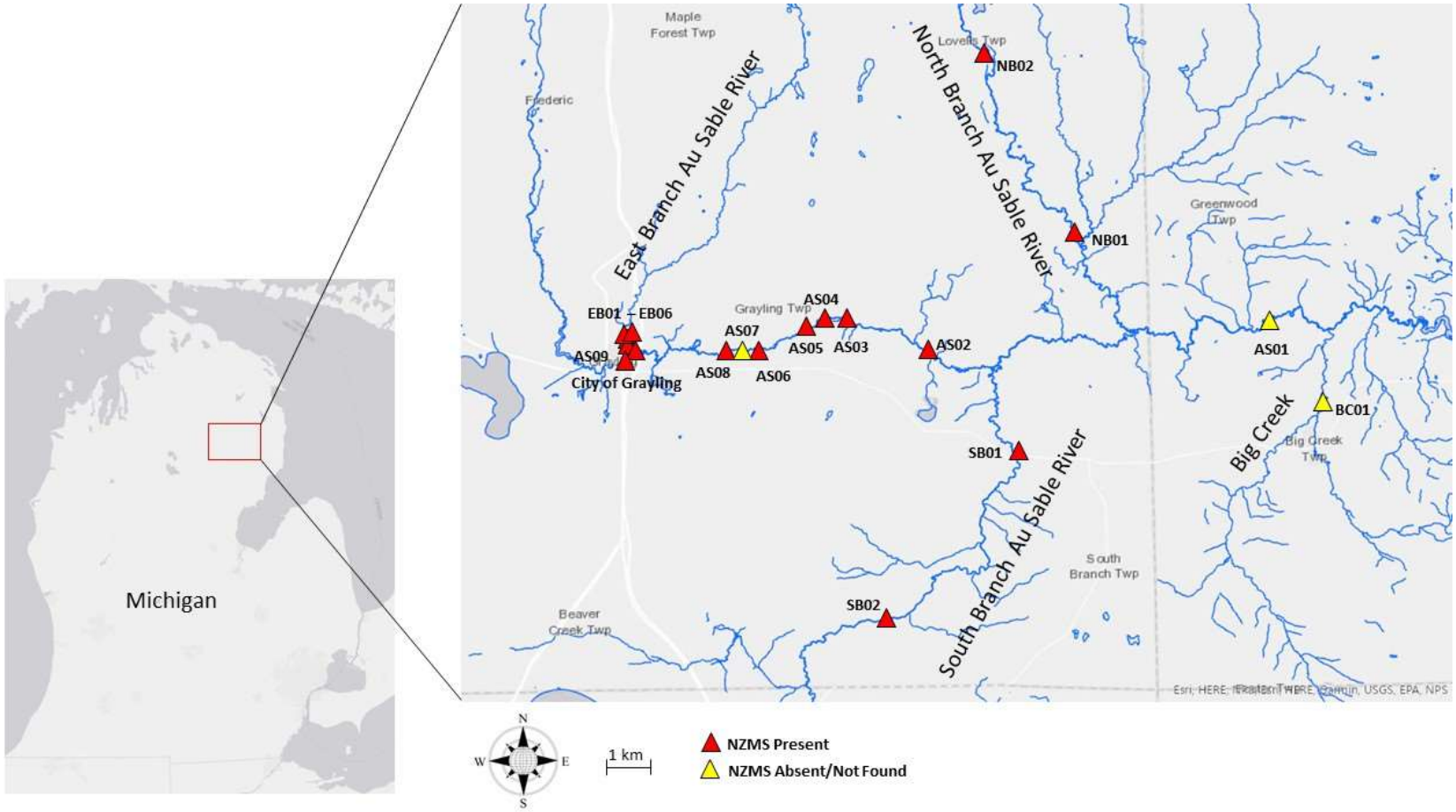

Figure 4.1. Presence/absence of NZMS in the Au Sable watershed (Michigan, USA) across all years, seasons and sites.

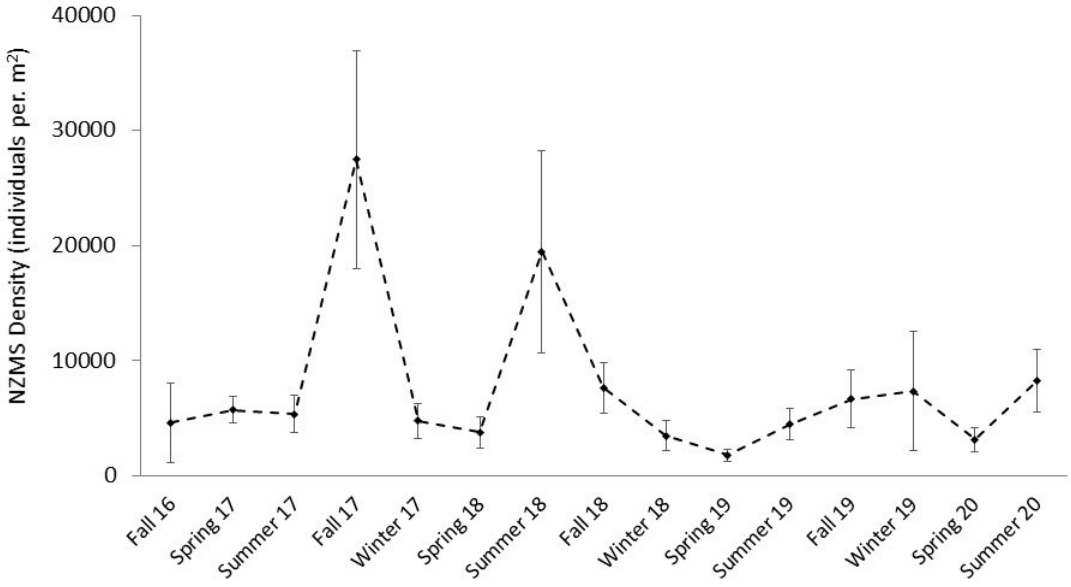

Figure 4.2. Mean (± SE) NZMS densities in the East Branch Au Sable River (Michigan, USA) across all sampling sites (n = 6) and seasons/years

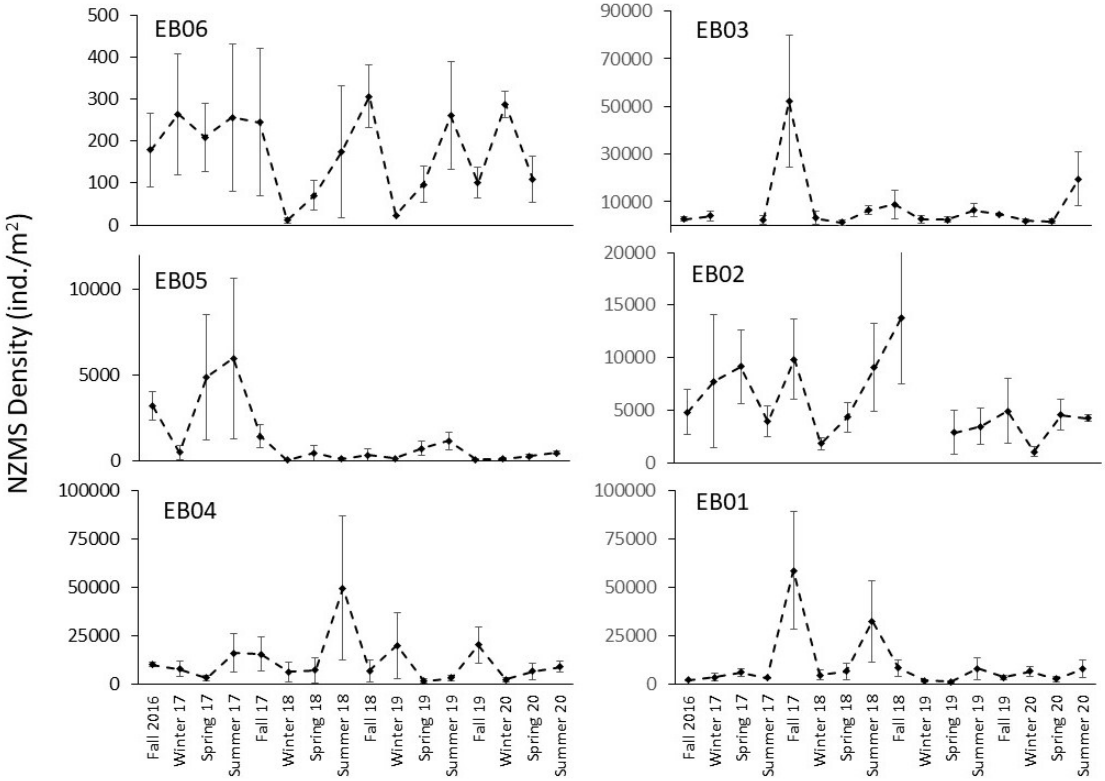

Figure 4.3. Mean (± SE) NZMS densities at each sampling site (6) in the East Branch Au Sable River across all sampling seasons and years. Data gaps represent season/year where data was not collected at the site.

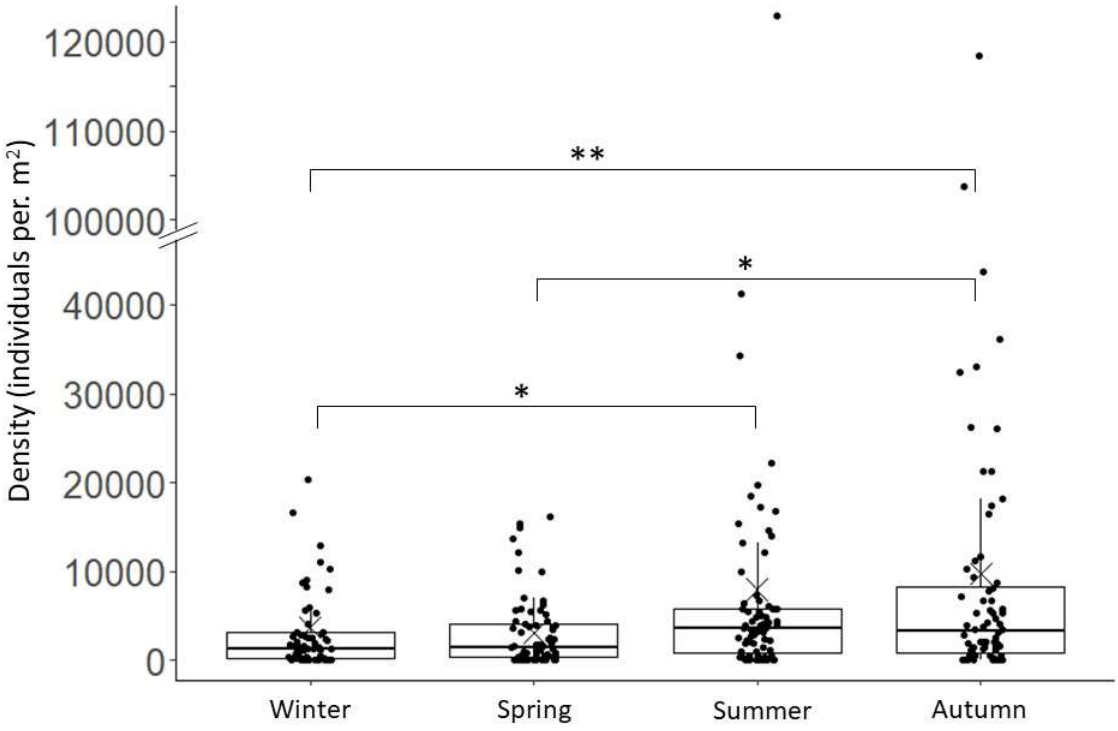

Figure 4.4. Differences between NZMS densities among seasons in the East Branch Au Sable River across all years and sites. Boxes represent the interquartile range (IQR). Circles are individual data points, with minimum and maximum values represented by the whiskers (outliers indicated by data points beyond whiskers). X marks the mean value, and the line within the box marks the median value. Horizontal brackets indicate significant differences between seasons. * indicates $P \leq 0.05$, ** indiacates $P \leq 0.01$.

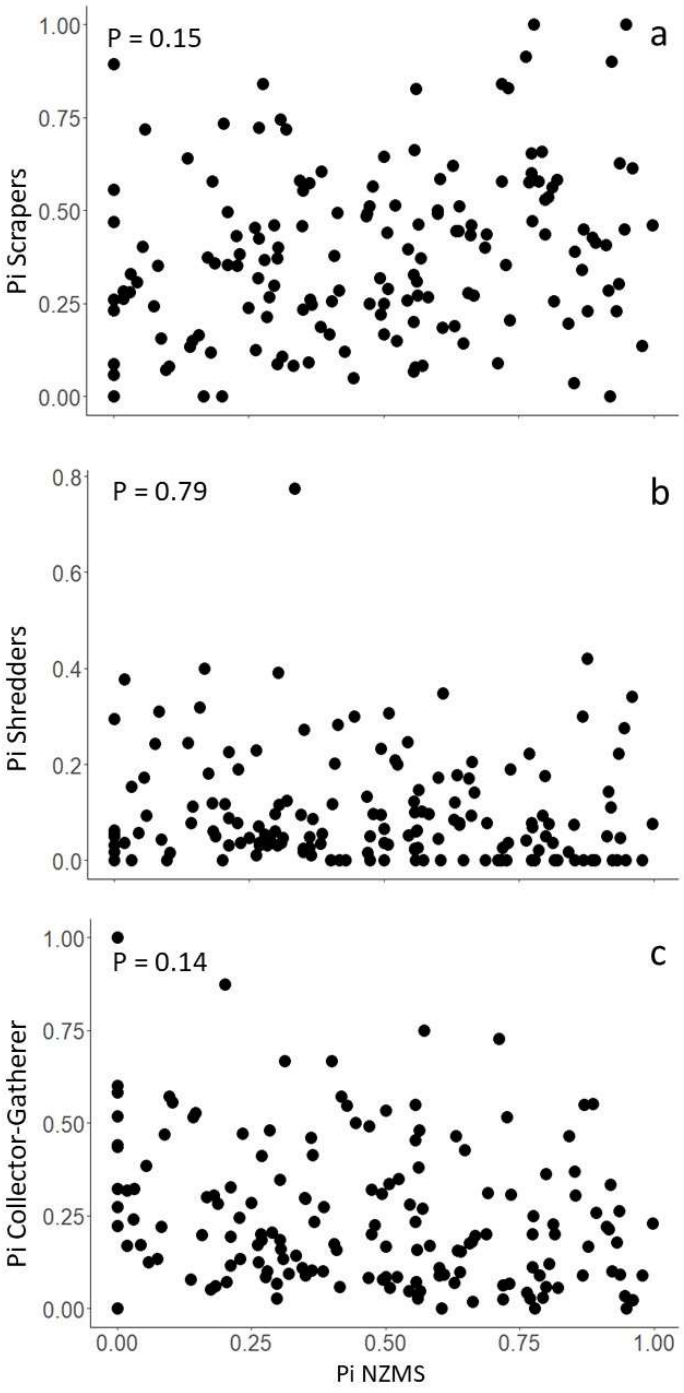

Figure 4.5. Logistic regressions showing no relationship between NZMS proportional abundances and native taxa of the functional feeding guilds a) scraper b) shredder and c) collector-gatherer.

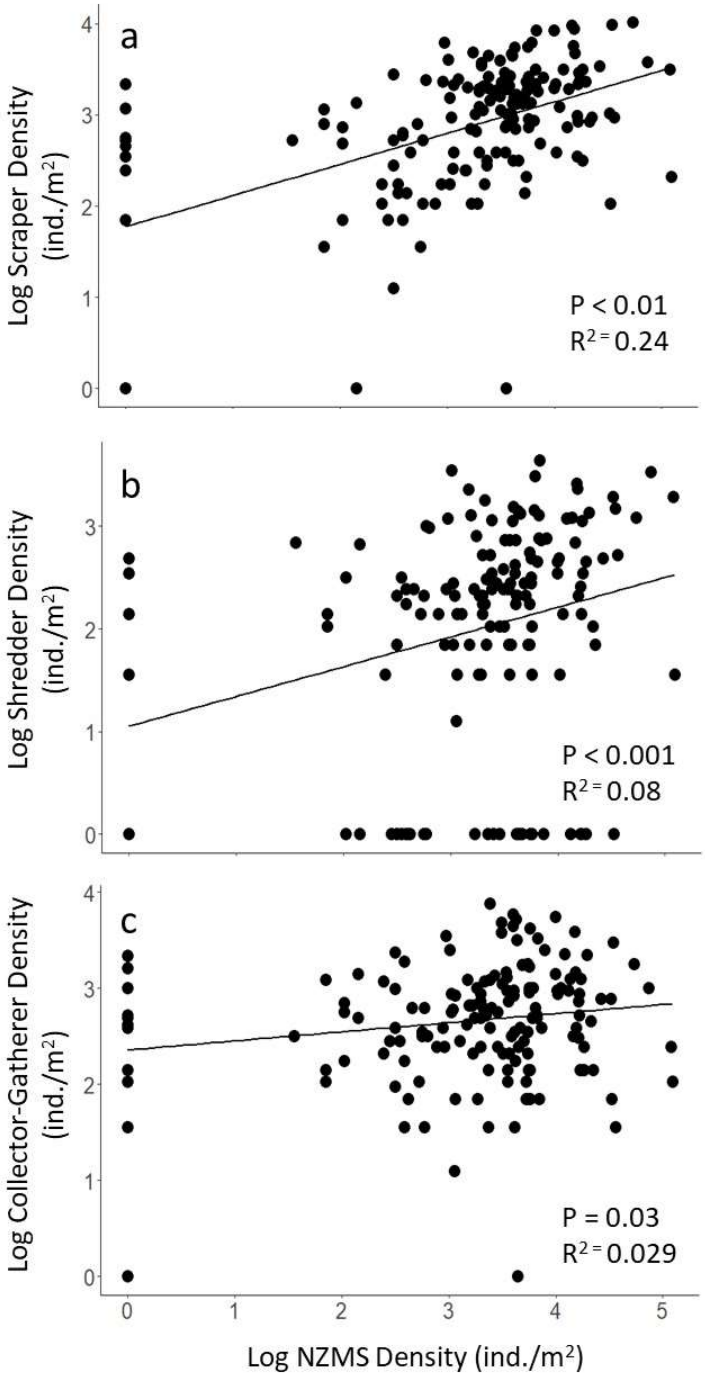

Figure 4.6. Linear regressions showing positive relationships between (Log transformed) NZMS absolute abundances and native taxa of the functional feeding guilds a) scraper b) shredder, and c) collector-gatherer.

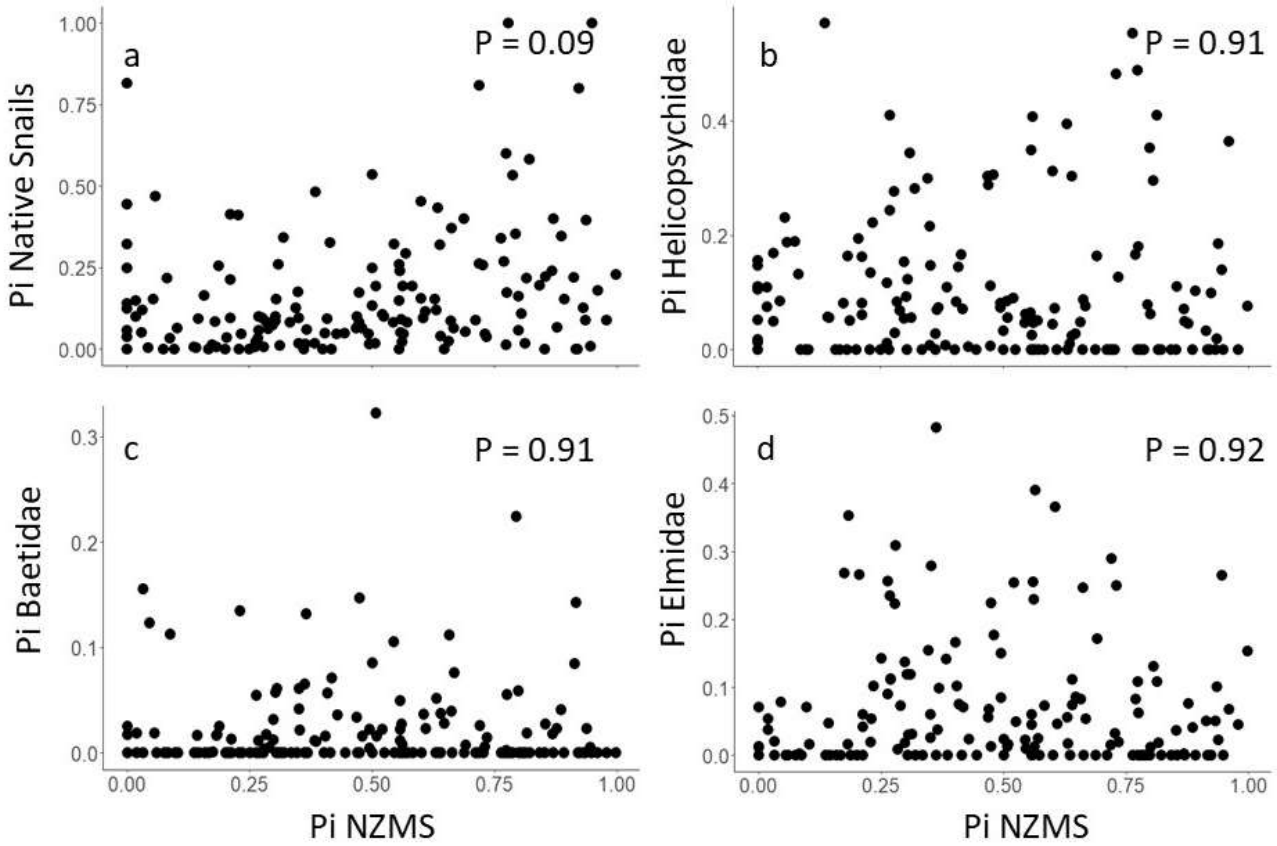

Figure 4.7. Logistic regressions showing no relationships between NZMS proportional abundance and the proportional abundances of the 4 most abundant native scraper taxa a) native snails (collectively) b) Helicosychidae c) Baetidae and d) Elmidae, found in the East Branch Au Sable River.

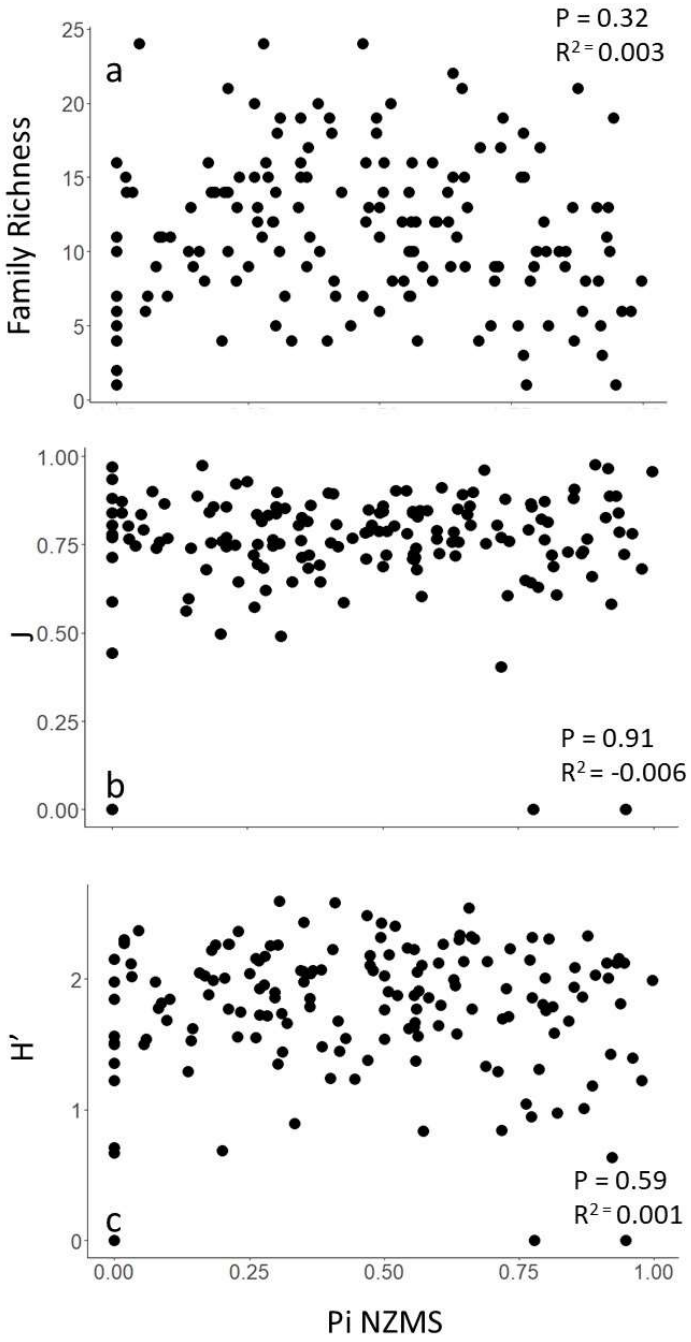

Figure 4.8. Evaluation of NZMS density on macroinvertebrate community parameters: a) no relationship observed between family richness of the native macroinvertebrate community and proportional abundance of NZMS; b) no relationship between native macroinvertebrate community evenness (J) and proportional abundance of NZMS; c) no relationship between native macroinvertebrate community diversity (H') and proportional abundance of NZMS.

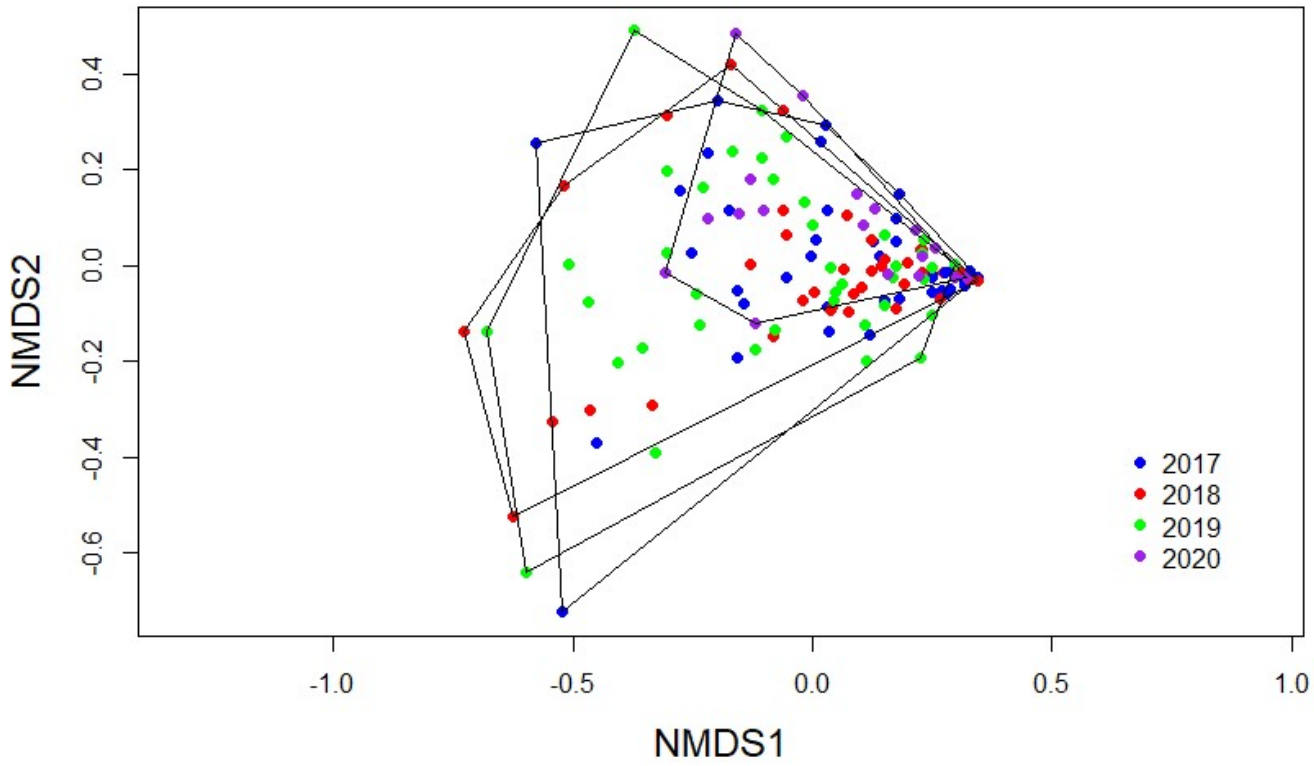

Figure 4.9. Ordination plot (nonmetric multidimensional scaling) of the benthic community in the East Branch Au Sable River among years, across all sampling sites and seasons. Pairwise PERMANOVA indicated differences in benthic community composition between years 2017 and 2019 (P = 0.012), 2018 and 2019 (P = 0.03), 2018 and 2020 (P = 0.018), 2019 and 2020 (P = 0.012)

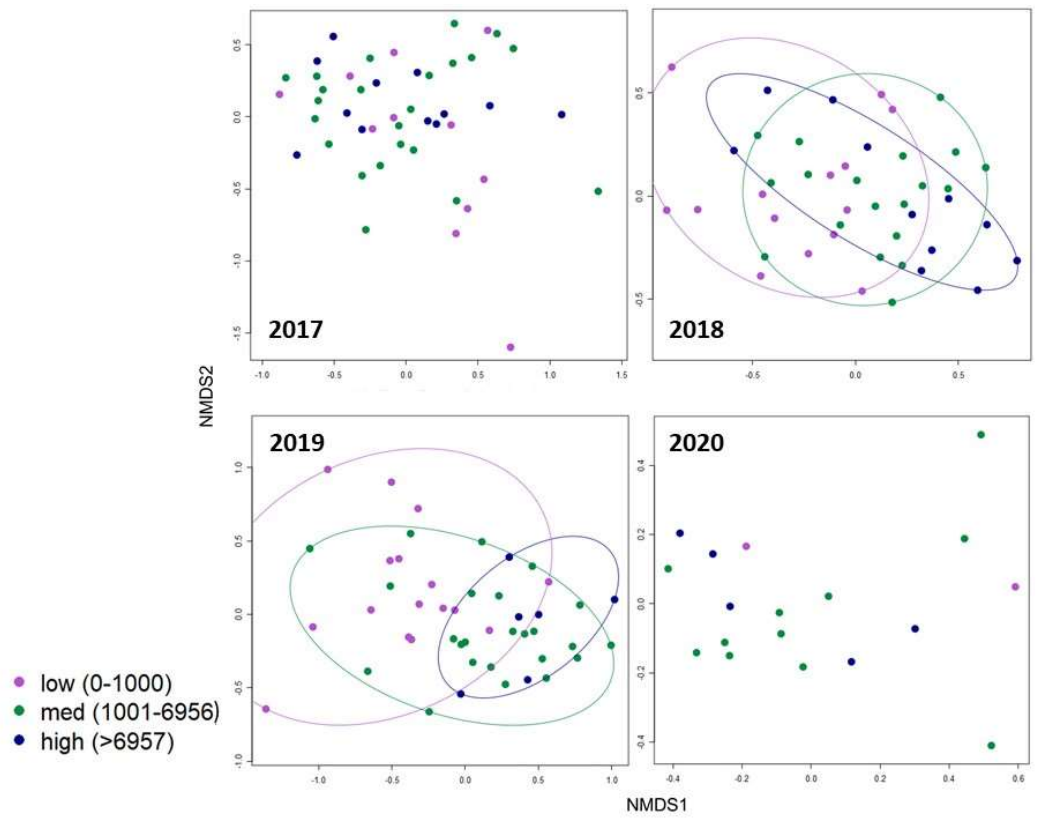

Figure 4.10. Ordination plots (nonmetric multidimensional scaling) of native macroinvertebrate communities in the East Branch Au Sable River for each year of the study period, 2017 - 2020. In 2018, native invertebrate community composition differed between low and medium NZMS densities (PERMANOVA: P = 0.01) and low and high NZMS densities (PERMANOVA: P = 0.003). In 2019, native invertebrate community composition differed between low and medium NZMS densities (PERMANOVA: P = 0.004) and low and high NZMS densities (PERMANOVA: P = 0.003).

APPENDIX A

INSTITUTIONAL REVIEW BOARD (IRB) APPROVAL LETTER

FOR THE ANGLER SURVEY

OAKLAND UNIVERSITY

Institutional Review Board for the Protection of Human Subjects

DATE:	March 29, 2018
TO:	Scott Tiegs, PhD
FROM:	Oakland University IRB
PROJECT TITLE:	Citizen Science and New Zealand Mud Snails: Fly Fishers as Sentinels and Deterrents of Range Expansion
REFERENCE #:	1213995-1
SUBMISSION TYPE:	New Project
ACTION:	DETERMINATION OF EXEMPT STATUS
DECISION DATE:	March 29, 2018
REVIEW CATEGORY:	Exemption category # 2

Thank you for your submission of New Project materials for this project. The Oakland University IRB has determined this project is EXEMPT FROM IRB REVIEW according to federal regulations. The following documents were reviewed:

- IRB Application
- Solicitation Email
- Survey
- Consent Form (**Please note that the Consent Form has been date-stamped and published under Board Documents. You must use the published Consent Form, version 3/29/2018, in the recruitment and consent of all research participants**.)

The exemption is made with the understanding that NO CHANGES may be made to the project until such changes have been reviewed by the IRB. Please contact me to determine appropriate revision form(s) that may be needed. Do not collect data while the revisions are being reviewed. Data collected during this time cannot be used.

Please retain a copy of this correspondence for your records.

If you have any questions, please contact Stephanie Edwards at (248) 370-4329 or sedwards@oakland.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Oakland University IRB's records.

APPENDIX B

ANGLER SURVEY FOR NZMS DECONTAMINATION

Angler Survey for NZMS Decontamination

Background Questions:

1. What TU Chapter are you affiliated with?
2. What river/stream do you consider 'home waters?
3. What river/stream do you fish the most?
4. When do you fish most?
    a. Spring (March – May)
    b. Summer (June – August)
    c. Fall (September – November)
    d. Winter (December – February)
5. What type of freshwater body do you fish in most?
    a. Rivers
    b. Lakes
6. Please give your best estimate of the number of times you fish during the spring season (March – May)?
    a. 0-5 times
    b. 6-10 times
    c. 11-15 times
    d. 16-20 times
    e. Over 21 times
7. Please give your best estimate of the number of times you fish during the summer season (June – August)?
    a. 0-5 times
    b. 6-10 times
    c. 11-15 times
    d. 16-20 times
    e. Over 21 times
8. Please give your best estimate of the number of times you fish during the fall season (September – November)?
    a. 0-5 times
    b. 6-10 times
    c. 11-15 times
    d. 16-20 times
    e. Over 21 times
9. Please give your best estimate of the number of times you fish during the winter season (December – February)?
    a. 0-5 times

b. 6-10 times
c. 11-15 times
d. 16-20 times
e. Over 21 times

10. Do you travel to other states/countries to fish?
    a. Yes
    b. No
11. If answered yes to the previous question, where do you commonly travel to fish? (check all that apply).
    a. Western United States
    b. Around the Great Lakes region
    c. Eastern United States
    d. Southern United States
    e. Other countries
12. Which type of wader boot surface do you primarily use?
    a. Felt
    b. Rubber
13. What type of material are your primary waders made from?
    a. Breathable nylon
    b. Neoprene
    c. PVC/Rubber
14. Do you practice any type of wader/gear decontamination after a fishing trip?
    a. Yes
    b. No
15. If so, describe.

Invasive Species (New Zealand mud snail) Questions:

16. On a scale of 0-7 (0 = no knowledge, 7 = very knowledgeable), how well would you rate your knowledge on invasive species issues in the Great Lakes Region?
17. How familiar are you on the topic of the New Zealand mud snail?
    a. Not familiar
    b. Somewhat familiar
    c. Very familiar
18. Do you know which rivers currently have existing populations of New Zealand mud snail in Michigan?
    a. Yes
    b. No
19. Do you know how to identify a New Zealand mud snail?

a. Yes
b. No

20. Do you know who to contact if you find a New Zealand mud snail?
    a. Yes
    b. No

Wader decontamination questions:

21. To help prevent spread of NZMS, how likely are you to spray your wading gear with Virkon Aquatic decontamination solution (concentrated disinfectant powder available via online purchase) and let sit for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

22. To help prevent spread of NZMS, how likely are you to spray your wading gear with Virkon Aquatic decontamination solution and let sit for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

23. To help prevent spread of NZMS, how likely are you to spray your wading gear with Formula 409 (home and industrial cleaning product available at most convenience stores) and let sit for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

24. To help prevent spread of NZMS, how likely are you to spray your wading gear with Formula 409 and let sit for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

25. To help prevent spread of NZMS, how likely are you to spray your wading gear with a bleach solution and let sit for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

26. To help prevent spread of NZMS, how likely are you to spray your wading gear with a bleach solution and let sit for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

27. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub of Virkon Aquatic decontamination solution for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

28. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub of Virkon Aquatic decontamination solution for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

29. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub with Formula 409 for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

30. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub with Formula 409 for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

31. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub with a bleach solution for **10 minutes** between water bodies?

    Not likely 0 – 7 Very likely

32. To help prevent spread of NZMS, how likely are you to soak your wading gear in a tub with a bleach solution for **20 minutes** between water bodies?

    Not likely 0 – 7 Very likely

33. Do you know where to purchase Bleach?
    a. Yes
    b. No
34. Do you know where to purchase Formula 409?
    a. Yes
    b. No
35. Do you know where to purchase Virkon Aquatic?

a. Yes
b. No

36. Would you like to become more involved in a current NZMS project?
    a. Yes
    b. No

APPENDIX C

SUPPLEMENTAL RESULTS OF THE CHEMICAL EFFICACY TRIALS FOR CHAPTER TWO

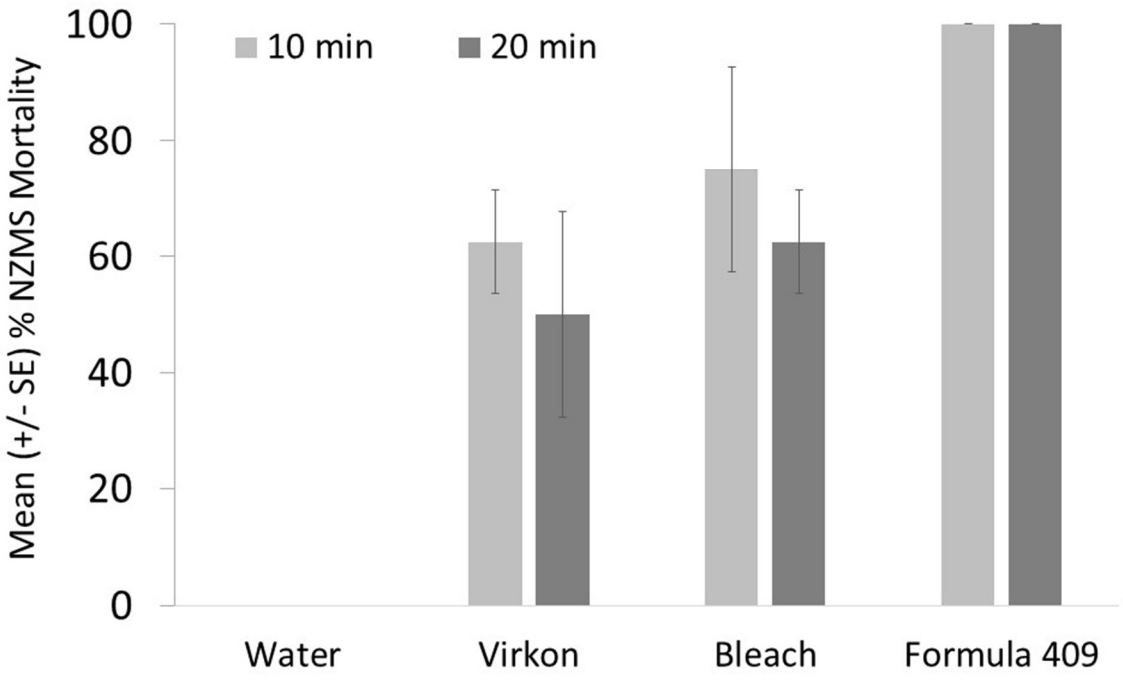

Figure C.1. Effects of chemical treatment and exposure time on NZMS mortality. No significant differences were found between 10- and 20-minute exposure durations.

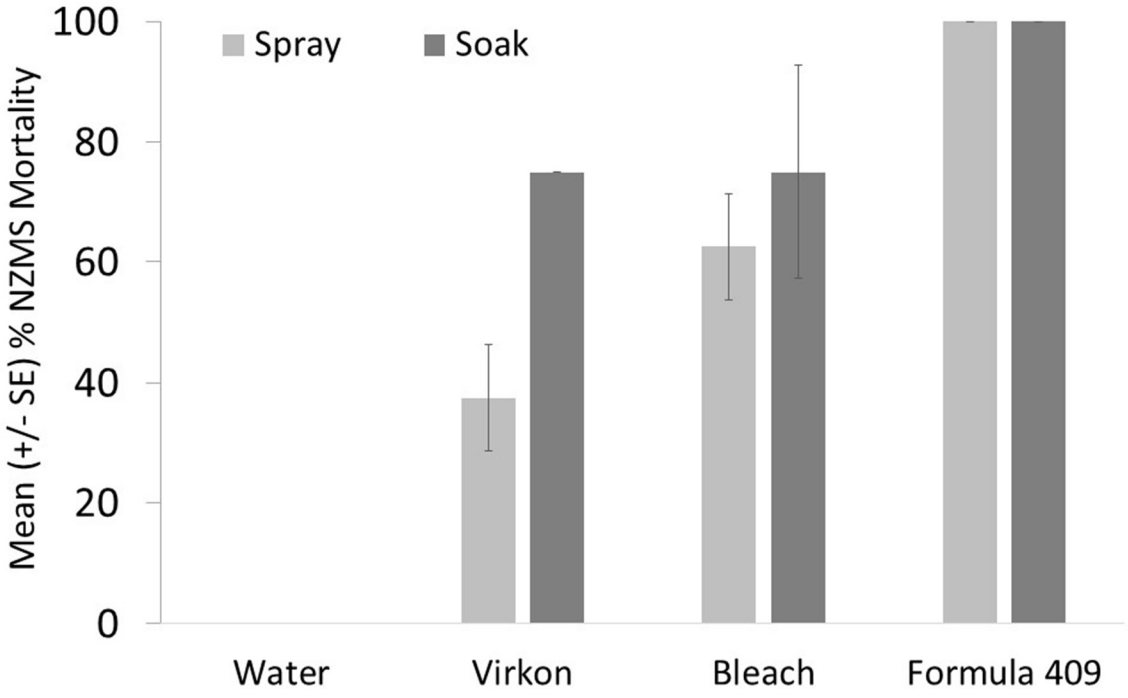

Figure C.2. Effects of chemical treatment and application technique on NZMS mortality. No significant differences were found between spraying and soaking.

APPENDIX D

PARTICIPANT RESPONSES TO THE ANGLER SURVEY FOR CHAPTER TWO

Table D.1. Responses from 339 respondents to angling behavior and preference.

Angling Behavior and Preference	*n*	%
Type of freshwater body fished the most		
Lake	30	9
River	307	91
Travel to other states/countries to fish		
Do not	97	29
Do	241	71
No. of different rivers typically fish in a year		
0	2	1
1-3	108	32
4-5	126	37
6-7	49	14
Over 7	53	16
Mostly fish by		
Boat	63	19
Wading	270	81
Preferred season to fish		
Spring (March-May)	88	26
Summer (June – August)	197	58
Fall (September – November)	50	15
Winter (December – February)	3	1
Wader boot sole type		
Rubber/synthetic	225	67
Felt	98	29
Both	7	2
Other	5	1
Wader material type		
Gore-tex or other breathable	273	82
Neoprene	24	7
Nylon	28	8
PVC/Rubber	9	3
Current decontamination practice after fishing		
Brush and remove debris	203	42
Spray or soak with a decontamination chemical	18	4
Let dry for a minimum of 48hrs	226	47
Freeze for a minimum of 6hrs	13	3
Soak in 120 degrees or hotter water for a minimum of 5 min	4	1
Other	15	3
Nothing	3	1

	n	%
Awareness of rivers in the Great Lakes Region that have populations of New Zealand mud snail		
No	130	38
Yes	208	62
Know how to identify New Zealand mud snail		
No	191	57
Yes	145	43
Know who to contact if New Zealand mud snail is found		
No	216	64
Yes	121	36
Knowledge of invasive species in the Great Lakes Region (1 = no knowledge, 7 = very knowledgeable)		
1	1	0
2	19	6
3	41	12
4	74	22
5	89	26
6	75	22
7	39	12
Knowledge of invasive NZMS in the Great Lakes Region (1 = no knowledge, 7 = very knowledgeable)		
1	28	8
2	62	18
3	50	15
4	68	20
5	57	17
6	51	15

7	23	7
Know where to purchase Bleach		
No	5	1
Yes	329	99
Know where to purchase Formula 409		
No	40	12
Yes	297	88
Know where to purchase Virkon Aquatic		
No	297	88
Yes	40	12

Table D.2. Responses from 339 respondents to questions regarding their willingness to implement a specific decontamination strategy (i.e., treatment combination). Responses were collected using a Likert-type scale of 1-7 (1 = not likely, 7 = very likely).

Treatment Combination	Mean Response	Median Response	Mode	n
Virkon Aquatic:Spray:10-min	3.75	4	1	338
Virkon Aquatic:Spray:20-min	3.64	4	1	338
Formula 409:Spray:10-min	4.39	5	7	335
Formula 409:Spray:20-min	4.35	5	7	334
Bleach:Spray:10-min	3.18	3	1	331
Bleach:Spray:20-min	3.06	2	1	332
Virkon Aquatic:Soak:10-min	2.10	1	1	334
Virkon Aquatic:Soak:20-min	2.03	1	1	332
Formula 409:Soak:10-min	2.23	1	1	332
Formula 409:Soak:20-min	2.19	1	1	332
Bleach:Soak:10-min	2.05	1	1	330
Bleach:Soak:20-min	2.02	1	1	333

APPENDIX E

SUPPLEMENTAL RESULTS FOR CHAPTER FOUR

Table E.1. Presence/absence records of NZMS in the Au Sable watershed (Michigan, USA) across sampling years.

					NZMS Presence				
No.	Waterbody	Site ID	Lat	Long	2016	2017	2018	2019	2020
1	Au Sable R.	-	44.6599	-84.1266	No	-	-	-	-
2	Au Sable R.	AS01	44.6766	-84.2925	No	No	No	No	-
3	Au Sable R.	AS02	44.6586	-84.505	No	No	No	No	-
4	Au Sable R.	AS04	44.6791	-84.5733	Yes	Yes	Yes	Yes	Yes
5	Au Sable R.	AS03	44.6764	-84.5621	-	Yes	Yes	Yes	-
6	Au Sable R.	AS05	44.6747	-84.5895	-	Yes	Yes	Yes	-
7	Au Sable R.	AS06	44.6651	-84.6275	-	Yes	Yes	Yes	Yes
8	Au Sable R.	AS07	44.6657	-84.6375	-	-	Yes	Yes	Yes
9	Au Sable R.	AS08	44.6629	-84.6466	No	Yes	Yes	Yes	Yes
10	Au Sable R.	AS09	44.6618	-84.7072	No	Yes	No	No	-
11	Au Sable R.	-	44.6598	-84.7131	No	-	-	-	-
12	South Branch	SB02	44.5406	-84.5503	No	No	No	No	Yes
13	South Branch	SB01	44.6147	-84.4556	Yes	Yes	Yes	Yes	-
14	Big Creek	BC01	44.6376	-84.2612	-	No	No	No	No
15	North Branch	NB02	44.8036	-84.4813	No	No	No	No	-
16	North Branch	NB01	44.7164	-84.42	-	No	Yes	Yes	No
17	East Branch	EB01	44.6654	-84.7036	Yes	Yes	Yes	Yes	Yes
18	East Branch	EB02	44.6661	-84.7047	-	Yes	Yes	Yes	Yes
19	East Branch	EB03	44.6672	-84.7045	-	Yes	Yes	Yes	Yes
20	East Branch	EB04	44.6683	-84.7054	Yes	Yes	Yes	Yes	Yes
21	East Branch	EB05	44.6699	-84.7044	-	Yes	Yes	Yes	Yes
22	East Branch	EB06	44.6712	-84.7054	Yes	Yes	Yes	Yes	Yes

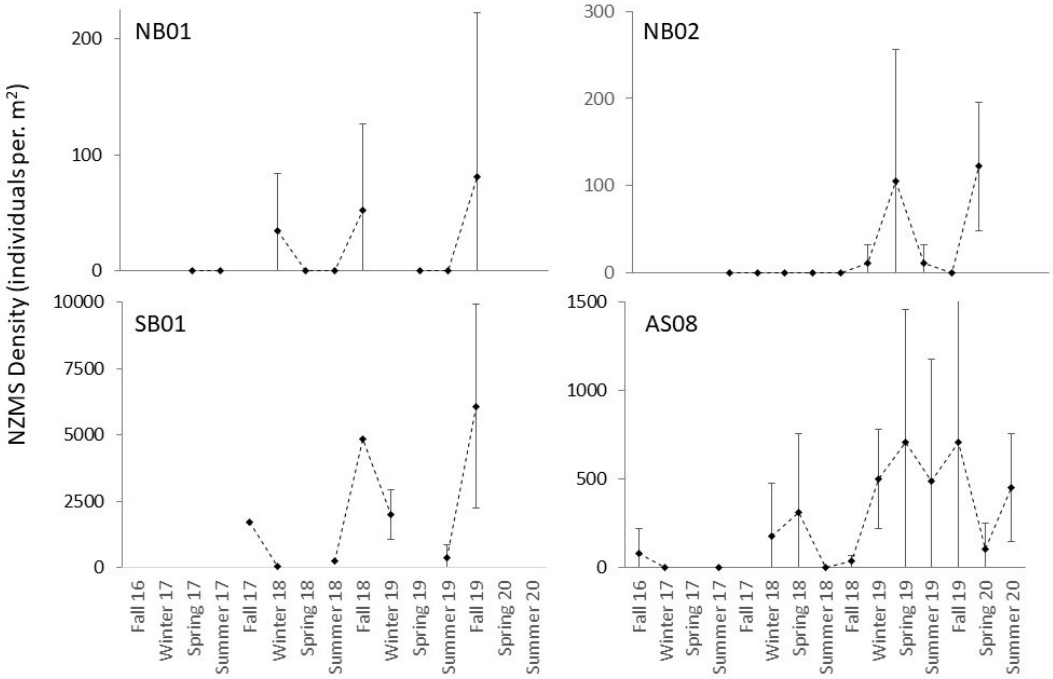

Figure E.1. Mean (± SE) NZMS densities of select tributaries and the main branch of the Au Sable River across all sampling seasons and years. NB = North Branch Au Sable River; SB – South Branch Au Sable River; AS = Main Branch Au Sable River. Data gaps represent season/year where data was not collected at the site.

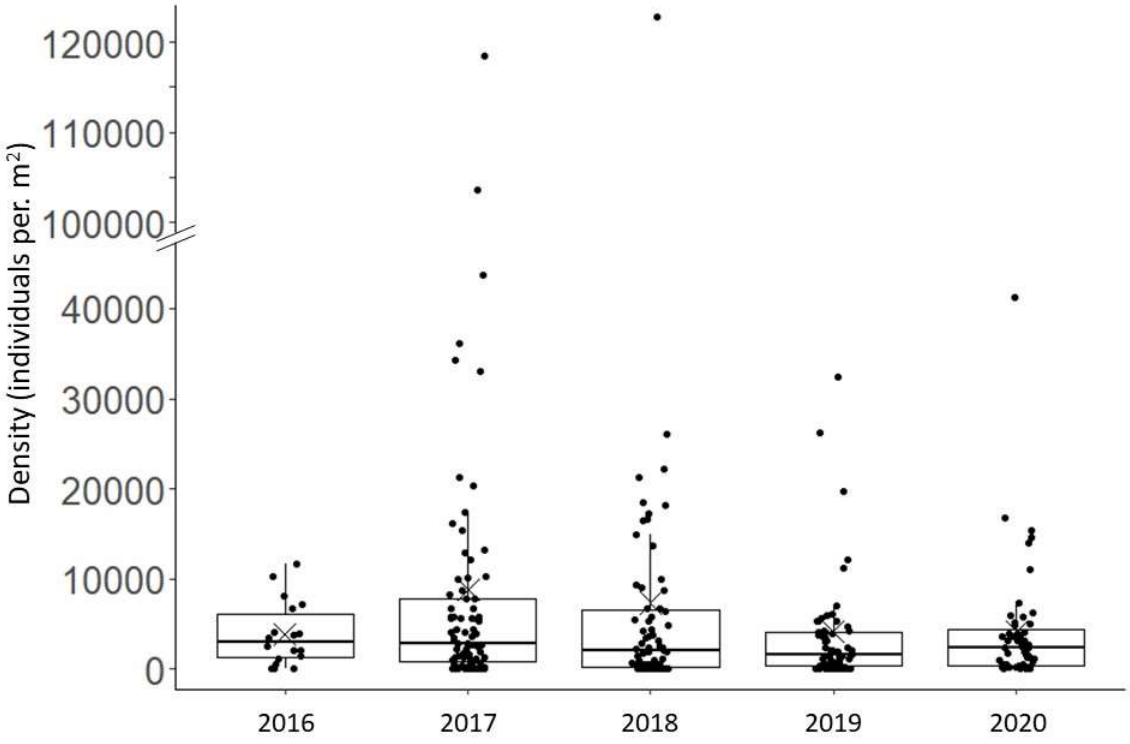

Figure E.2. Annual NZMS densities in the East Branch Au Sable River across all years and sites. Boxes represent the interquartile range (IQR). Closed circles are individual data points, with minimum and maximum values represented by the whiskers (outliers indicated by data points beyond whiskers). X marks the mean value, and line within the box marks the median value.

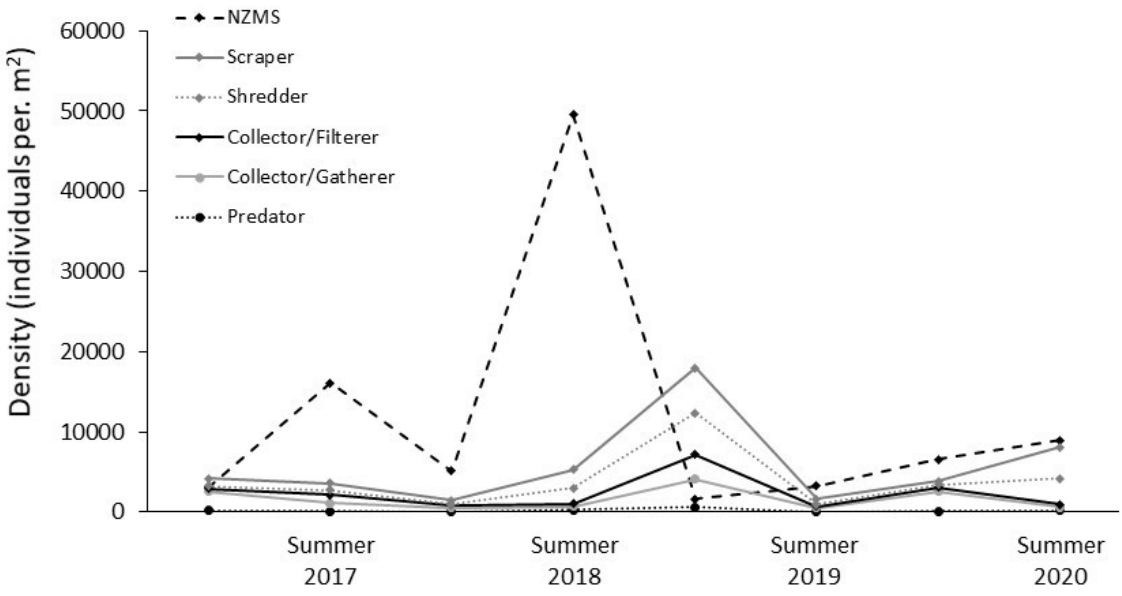

Figure E.3. Mean densities of NZMS and native invertebrates, organized into functional feeding groups, in the East Branch Au Sable River across all sampling seasons and years.

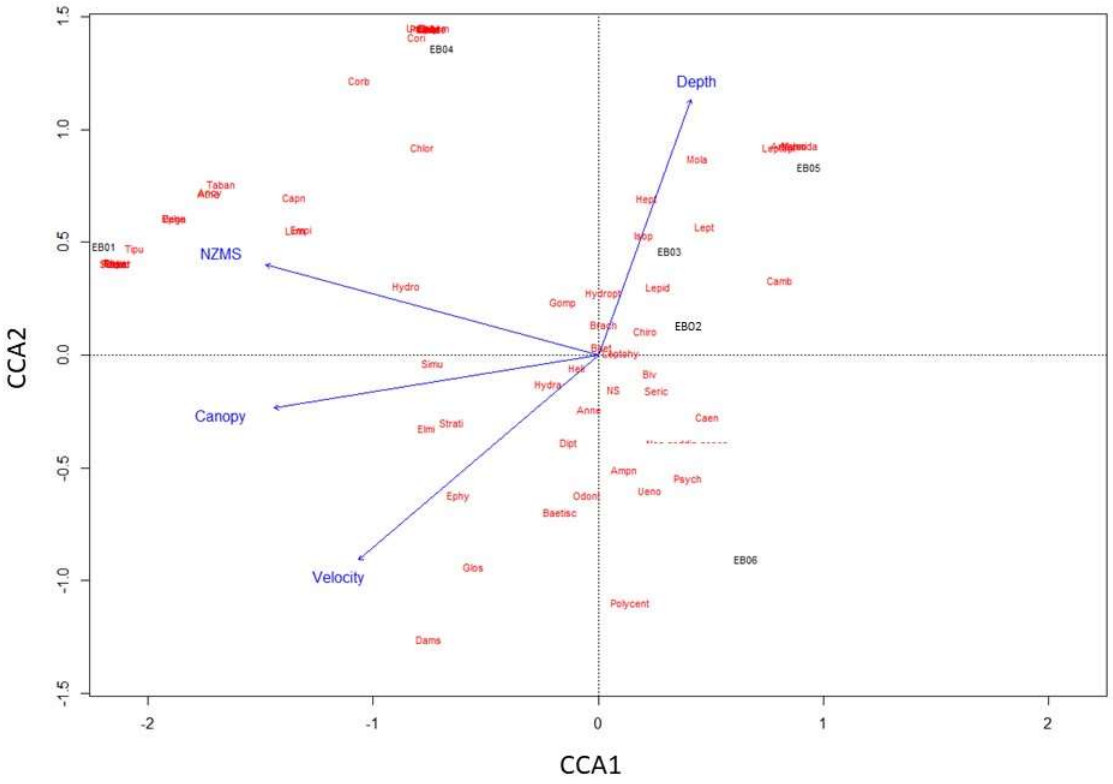

Figure E.4. Canonical correspondence analysis was marginally significant (P = 0.055) and indicated relatively fewer native taxa being associated with NZMS as a predictor term. Sites EB01 and EB04 are driven by NZMS and are the sampling sites with the greatest NZMS densities across the study period.

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