COEXISTENCE BETWEEN A NATIVE *(Valvata humeralis)* AND A NON-NATIVE *(Potamopyrgus antipodarum)* GASTROPOD IN THE MIDDLE SNAKE RIVER, IDAHO: IMPLICATIONS FOR INVASIVE SPECIES IMPACT

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Kiza Kristine Gates

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APPROVAL

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Kiza Kristine Gates

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Dr. Billie L. Kerans

Approved for the Department of Ecology

Dr. David W. Roberts

Approved for The Graduate School

Dr. Carl A. Fox

STATEMENT OF PERMISSION TO USE

Kiza Kristine Gates

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ABSTRACT

The dominant competitive abilities of many invasive species are frequently assumed to preclude biologically similar native species over time, but there has been little research exploring how interactions between invasive and native species may change with changes in biotic and abiotic conditions. Introduction of the invasive New Zealand mud snail *Potamopyrgus antipodarum* in the Snake River in the late 1980's raised many concerns for the native gastropods of this region; however, the native gastropod *Valvata humeralis* has maintained large populations and continued to coexist with *P. antipodarum*. I investigated the coexistence of *P. antipodarum* and *V. humeralis* in the Vista reach of the Middle Snake River. Diet, spatial, and temporal partitioning of *V. humeralis* were explored in populations that were invaded by *P. antipodarum* and uninvaded. A field growth experiment was used to measure the net intra- and interspecific effects of *V. humeralis* and *P. antipodarum* at varying densities and species proportions. Results of the field growth experiment were compared with field survey data. A laboratory growth experiment and a stoichiometric experiment were used to identify the interaction mechanisms between species. *Valvata humeralis* juveniles appeared to shift diet in the presence *P. antipodarum*. There was evidence of spatial partitioning from *P. antipodarum* by *V. humeralis* at the among population scale but not the within population or patch scales. The field growth experiment indicated that interspecific net effects of *P. antipodarum* on *V. humeralis* changed in direction with increasing *P. antipodarum* density. Field surveys showed a similar pattern. The laboratory growth experiment indicated that direct interference competition was the negative mechanism of the species interaction and confirmed field experimental results. Stoichiometric analyses suggested that *P. antipodarum* juveniles require more phosphorus than *V. humeralis* juveniles, but that stoichiometric facilitation was not likely an interaction mechanism. Facilitated growth of *V. humeralis* in the presence of *P. antipodarum* may have been caused by increased access to food and/or *P. antipodarum* digestive food conditioning. Results suggest that the impact of an invasive species on the native community may be a complex interplay between invader density, native species behavior, invader nutrient use, and environmental conditions.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Why the ecological impacts of invasive species (non-natives with a history of spread and ecological or economic impact) vary is not well understood despite the increasing prevalence of invaders (Strayer et al. 2006). As introductions of non-indigenous species have become increasingly common (Sala et al. 2000; Kolar and Lodge 2002; Leung et al. 2002; Marchetti et al. 2004) much research effort has been devoted to understanding the factors that determine the success of invasive species (Bruno et al. 2005). This research has provided valuable information concerning the mechanisms which facilitate invasions including release from predation (Adams et al. 2009; Romanuk et al. 2009), generalist feeding habits (Romanuk et al. 2009), and competitive dominance over similar native species (Byers 2000; Callaway and Aschenhoug 2000; Bando 2006). Yet, invasive species may not appreciably affect the native community in some locations creating low ecological impact (Williamson 1996) or may only exhibit invasive behavior in particular geographic locations (Kolar and Lodge 2001). A better understanding of how invasive species traits and the receiving system affect impact is needed to improve prioritization of high risk invasions (Strayer et al. 2006; Thomsen et al. 2011).

The ecological impacts of invasive species are difficult to quantify and forecast (Thomsen et al. 2011). Predictive modeling attempts have focused on identifying which species are likely to become invasive (Kolar and Lodge 2001; Kolar and Lodge 2002; Romanuk et al. 2009) and where their range is likely to expand (Loo et al. 2007).

Quantitative models that predict invader impacts have been developed for some high-profile invading species; however, these models rely on consistent and predictable impacts of the invader among different environments (Ricciardi 2003), which may not be a reasonable assumption. Predictions often rely on correlative studies that indicate invader impacts can be positively correlated with high abundance (Ricciardi 2003), rapid population growth, and high propagule pressure (Kolar and Lodge 2001), yet the presence of any of these indices may or may not ensure ecological impact. Even invasiveness, a history of high establishment success and rate of spread, is not a good indicator of the ecological impacts an invasive species will have in a new system (Ricciardi and Cohen 2007).

The coexistence of native species with similar invasive species may provide insight into mechanisms of varying invader impact on native communities. Invasive species may dominate biomass is some locations while in other locations they may coexist with native species at lower biomass levels creating variation in ecological impact (Williamson 1996; Davis 2003). The ecological impact of an invasive species may even vary among invasion sites with very similar native species assemblages. Previous research suggests that the context of an invasion in terms of the receiving community and the physical environment may provide key information for understanding varying ecological impact of invaders (Ricciardi 2003; Ricciardi and Atkinson 2004; Ricciardi and Cohen 2007; Padilla 2010; Thomsen et al. 2011). Specifically, interactions of the invader with native species of the receiving community may create variation in ecological impact among invasion sites (Crooks 2002; Lockwood et al. 2009). Understanding the coexistence mechanisms and the direct interactions between invasive species and native species may provide valuable information about how receiving native communities can mitigate the ecological impact of invaders.

The invasive aquatic gastropod *P. antipodarum* is a good model organism for investigating varying ecological impact among invasion sites. *Potamopyrgus antipodarum* has been a successful invader of lentic and lotic freshwaters of Australia (Schreiber et al. 2003), Europe (Dorgelo 1987), and more recently North America (Bowler 1991; Langenstein and Bowler 1991; Bowler and Frest 1992; Zaranko et al. 1997; Richards et al. 2001). A broad diet and physiological tolerance (Winterbourn 1970, Dorgelo et al. 1995; Collier and Winterbourn 2000) may give *P. antipodarum* a competitive advantage in many habitats (Loo et al. 2007). The ability of *P. antipodarum* to reach extremely high densities suggests it would frequently compete with native gastropods; however, prior research has demonstrated mixed responses among macroinvertebrates (Quinn et al. 1998; Kerans et al. 2005; Schreiber et al. 2002; Brenneis et al. 2010). For example, *P. antipodarum* in previously invaded habitats were found to dominate native macroinvertebrate assemblages in Australia (Quinn et al. 1998), but when *P. antipodarum* densities were manipulated over brief temporal time scales (6 days) in previously invaded Australian streams, higher invader densities were positively correlated with native macroinvertebrate diversity (Schreiber et al. 2002). Similarly, *P. antipodarum* were found to negatively affect macroinvertebrate colonization rates in the Greater Yellowstone Ecosystem (Kerans et al. 2005), but correlation analyses indicated that the community level impact was weak. These results suggest that the interactions of *P. antipodarum* with native species may change with scale, over time, or among systems.

The net interaction between *P. antipodarum* and native species could change if the components of the species interaction change individually. Species may interact in multiple ways, some positive and some negative, that sum to create a composite net interaction. *Potamopyrgus antipodarum* is frequently assumed to compete with biologically similar species for food and habitat (Richards 2004; Lysne and Koetsier 2008; Riley et al. 2008), but facilitative interactions may also occur. Potential mechanisms for facilitative effects of *P. antipodarum* on native species include stoichiometric nutrient recycling (Schreiber et al. 2002) and reproductive facilitation (Cope and Winterbourn 2004). Schreiber and colleagues (2002) hypothesized that nutrients excreted by *P. antipodarum* provided food for other macroinvertebrates thereby increasing habitat suitability. Cope and Winterbourn (2004) found that the presence of *P. antipodarum* increased the fecundity of the invading snail, *Physella acuta,* indicating a facilitative effect of *P. antipodarum* on *P. acuta* reproduction. The potential facilitative abilities of *P. antipodarum* and how they may ameliorate competitive interactions with native species is unclear and warrants further investigation.

Potamopyrgus antipodarum has rapidly invaded the Snake River drainage (Bowler 1991) and has been suggested as a probable strong competitor with native gastropods (Strayer 1999), but variation in ecological impact exists among species and locations. *Potamopyrgus antipodarum* was first documented in North America in the Snake River, Idaho in 1987 (Bowler 1991; Langenstein and Bowler 1991; Bowler and

Frest 1992). It spread rapidly throughout the Snake River drainage following its introduction; however, its distribution is patchy and its populations are highly variable in size (Bowler 1991). The native gastropod fauna of the Snake River have been adversely affected by impacts from management of scarce water resources for growing human population demands and the introduction of non-native species such as *P. antipodarum* (U. S. E. P. A. 2002; Lysne and Koetsier 2006a). Interactions between *P. antipodarum* and native gastropods have been explored with the endangered *T. serpenticola* (Richards 2004) and *V. utahensis* (Lysne and Koetsier 2008) suggesting that *P. antipodarum* negatively affects native species of conservation concern in the Snake River. Yet, little is known about more abundant native gastropod species that are able to coexist with *P. antipodarum* in some locations such as *Valvata humeralis*. *Valvata humeralis* is a colonial species that forms distinctive populations that can be found from year to year in the same location and are known to coexist with *P. antipodarum* (R. Newman, Bureau of Reclamation, personal communication). Examining *P. antipodarum* and *V. humeralis* patterns of coexistence, interaction net effects, and the mechanisms of their interaction will help further understanding of varying ecological impacts and native species persistence in the presence of invasive species.

Overview of Dissertation

In my dissertation, I examined the coexistence mechanisms of the invasive aquatic gastropod, *Potamopyrgus antipodarum*, and the native aquatic gastropod, *Valvata humeralis*, in the Vista reach of the Middle Snake River, Idaho and how they may influence the impact of *P. antipodarum* on native species. I investigated coexistence from a resource partitioning perspective (Chapter 3), a changing interaction perspective (Chapter 4), a mechanistic behavioral perspective (Chapter 5), and a nutrient recycling perspective (stoichiometric) (Chapter 5). I provide project background and a literature review in Chapter 2. In Chapter 3, I describe my exploration of diet, spatial, and temporal partitioning of *V. humeralis* in populations that were invaded by *P. antipodarum* and uninvaded. In Chapter 4, I describe a field growth experiment that measured the net intra- and interspecific effects of *V. humeralis* and *P. antipodarum* at varying densities and species proportions. I also compare the growth experiment results to field survey data. In Chapter 5, I describe a laboratory growth experiment designed to identify the competitive mechanism of the interaction between *V. humeralis* and *P. antipodarum*. I also describe a stoichiometric experiment designed to identify facilitative mechanisms between species. In Chapter 6, I summarize the results of the previous chapters and discuss the implications of my results for invasive species management and native species conservation.

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CHAPTER TWO

BACKGROUND

Understanding Varying Effects of Invasive Species

The impacts of invasive species are difficult to quantify and predict (Thomsen et al. 2011). Predictive modeling attempts have focused on identifying which species are likely to become invasive (Kolar and Lodge 2001; Kolar and Lodge 2002; Romanuk et al. 2009) and where their range is likely to expand (Loo et al. 2007). Quantitative models that predict invader impacts have been developed for some high-profile invading species; however, these models rely on consistent and predictable impacts of the invader among different environments (Ricciardi 2003). Unfortunately, the impacts of invaders often differ among environments and the mechanisms underlying this variation are unclear (Thomsen et al. 2011). Invader impacts are often positively correlated with high abundance (Ricciardi 2003), rapid population growth, and high propagule pressure (Kolar and Lodge 2001), but are not always consistent among invaded environments. Even invasiveness, a history of high establishment success and rate of spread, is not a good indicator of the impacts an invasive species will have in a system (Ricciardi and Cohen 2007). Understanding how the impacts of invasive species differ and change among systems is vital for improving predictive ability (Strayer et al. 2006).

Varying ecological impact of invaders, impact on the native community, may be caused by differences in the invaders interactions with native species. While invasive species distribution, abundance, and per capita effects on native species all contribute to the ecological impact, per capita effects are of particular interest because they reflect the direct, interspecific interactions between native and invasive species. Changes in the species composition of the native community following the establishment of an invader are commonly attributed to continued negative per capita effects on native species (Byers 1999; Wilson et al. 2004; Bruno et al. 2005; Dick 2008). Native species composition may even change over time leading to a community dominated by species that experience lower per capita effects of the invader (Vanderploeg et al. 2001; Sharp and Whittaker 2003; Cox 2004; Strayer et al. 2006). In contrast, it is also possible that invader per capita effects on native species change and thereby change the course of an invasion. For example, introduction of a nitrogen fixing tree to a nitrogen limited environment gradually increased nitrogen availability for other species (Vitousek et al. 1987). Concurrent fertilization of native trees increased native tree growth implying that the gradual addition of nitrogen to the soil by the invader could improve native plant growth. It is not known whether the positive facilitative effect of the invader ameliorated the negative competitive effect in this case, but it is likely that the facilitation changed the intensity of the interaction between species.

Per capita effects of invasive species on native species are best described quantitatively. The per capita effect of one species on another is frequently measured as the interaction strength (α) (MacArthur and Levins 1967; MacArthur 1972; Laska and Wootton 1998; Berlow et al. 1999) or as a net effect of one species on another (Gurevitch and Hedges 2001; Kawai and Tokeshi 2006; Kawai and Tokeshi 2007). With both of these metrics, positive values indicate facilitation and negative values indicate competition with changes in the metric reflecting changes in the magnitude of competitive and facilitative interactions.

The interaction between a native and an invasive may change with behavioral, physiological, or genetic changes of the invader (Strayer et al. 2006), or with changes in the physical environment caused by the invader (Vitousek et al. 1987; Crooks 2002). The latter involves physical modification, maintenance, or creation of habitat by one species that makes the habitat either more or less hospitable for other species (Jones et al. 1997; Stachowicz 2001). These habitat modifiers directly or indirectly control the availability of resources to other organisms by physically altering the environment (Jones et al. 1997) and can change their effects on other species disproportionally with abundance, creating unexpected per capita outcomes (Parker et al. 1999; Didham et al. 2007). There may be a change in the intensity of the interaction between species (increase or decrease) or a change in the direction of the interaction (negative or positive). Such changes in the positive and negative interactions that sum to create the net interaction may promote coexistence between similar native and invasive species by decreasing the intensity of negative interactions.

Positive and Negative Interactions Between Invasive and Native Species

Competition is frequently assumed to play a significant role in native species decline following invasion (Sala et al. 2000) due in part, to a historical focus on the influence of competitive interactions in ecology. The role of competition in structuring communities and determining species coexistence has been of key interest since the inception of ecology (Forbes 1887; Hairston et al. 1960; Real and Brown 1991). Early ecological publications stressed the importance of competitive mechanisms in building and maintaining community structure (Forbes 1887). The first mathematical models describing community succession and composition integrated competition in attempt to quantify the influence coexisting species could have on one another (Lotka 1932; Gause 1937; MacArthur and Levins 1967). Later competition models developed to relate similarity in resource use to competitive effects suggested that resource overlap could be used to predict the outcome of competition between two species (MacArthur and Levins 1967). An important observation following this work was that species with a greater ecological overlap had a greater tendency to compete when food or microhabitat dimensions were considered (Werner and Hall 1976; Schoener 1983). Resource overlap between an invader and a native is often cited in invasion ecology as proof of imminent native species decline because of competitive interactions. However, large ecological overlap does not always equate to competition as interspecific tolerance and exclusion may also play a role in coexistence (Colwell and Futuyma 1971; Vandermeer 1972; Abrams 1980). In addition, other factors such as environmental variability (Begon et al. 1996) may enable species with similar competitive abilities to coexist. As such, the suspected dominance of competition and competitive exclusion in structuring communities has decreased (Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003).

Recent empirical evidence implicates a greater role of facilitation in ecological communities (Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003), yet the role of positive interactions between invasive and native species is rarely considered (Bruno et al. 2005). Two potential facilitative mechanisms between native and invasive species are habitat and resource enhancement. Habitat enhancement occurs when habitat quality is increased for one species by the presence of another. This form of facilitation has been commonly identified among sessile organisms such as plants (Went 1942) and intertidal marine organisms (Bertness 1989; Bertness et al. 1999; Kawai and Tokeshi 2004). In contrast to habitat enhancement, resource enhancement typically involves species interactions with food or nutrients. For example, terrestrial herbivores may facilitate one another by creating access to better quality food through browsing or grazing (Vesey-Fitzgerald 1960; Bell 1971; McNaughton 1976). Herbivores may also enhance resources by directly increasing food quality (Hunter and Russell-Hunter 1983; Ruess and McNaughton 1984; Hillebrand et al. 2000; Liess and Hillebrand 2006; Liess and Kahlert 2007). For example, freshwater benthic grazers may function as ‘nutrient pumps’ or ‘resource engineers’ altering epilithon nutrient content via excretion of nutrient leading to higher food quality (Hillebrand and Kahlert 2001; Hillebrand et al. 2004; Evans-White and Lamberti 2005). Research with aquatic grazers has documented intraspecific stoichiometric facilitation where increased density of grazers decreased food quantity, but increased per capita food quality and thereby shifted interaction direction creating positive density dependence (Sommer 1992). Similarly, competition between aquatic grazers was reduced at increased densities when food quality increased via decreased light availability (Urabe et al. 2002). The increased evidence of positive interactions between species suggests that they are likely also common between native and invasive species.

The prevalence of facilitation driven interaction shifts between native and invasive species is not known, yet could have dramatic implications for native and invasive species coexistence. Recent research with invasive species suggests native species responses may change with invader density. Intermediate densities of some invasive species have been found to correlate with increased native species richness (Schreiber et al. 2002; Straube et al. 2009) and increased nutrient availability (Straube et al. 2009) ; however, the specific mechanisms and direct interaction have not been extensively explored. Shifting interactions between native and invasive species may contribute to variation in ecological impact of invaders among geographic locations.

Net interactions between neighboring species can change from competition to facilitation along gradients (Bronstein 1994; Bruno et al. 2003). Species often interact in multiple ways, some positive and some negative, that sum to create the net interaction. Net interactions between biologically similar species change direction along environmental stress gradients (Bertness and Callaway 1994; Callaway and Walker 1997; Brooker and Callaghan 1998; Kawai and Tokeshi 2007; Brooker et al. 2008) over different spatial scales (Bertness et al. 1999; Callaway et al. 2002) and through time (Tielborger and Kadmon 2000; Kawai and Tokeshi 2007). While much research has been devoted to exploring the effects of abiotic gradients on interactions, there is less information regarding how changes in biotic gradients (such as density) may lead to interaction changes between species. More exploration of the feedbacks that create bidirectional interactions between species is needed to understand ecological dynamics (Agrawal et al. 2007).

Interactions Between Invasive and Native Freshwater Gastropods

Introduced competitors are suggested as a driving force of extinction among native freshwater molluscs around the world (Lydeard et al. 2004). While gastropods in lentic environments have received considerable research attention (Brown 1982; Cedeño-León and Thomas 1982; Meyer-Lassen and Madsen 1989; Hershey 1990), the interactions between lotic gastropods, especially native and invasive species, remain understudied. In North America, the persistence of native molluscan fauna has been threatened by the introductions of the Zebra mussel *Dreissena polymorpha*, the Quagga mussel *Dreissena rostriformis bugensis*, the Faucet snail *Bithynia tentaculata* (Jokinen 1992; Harman 2000), the Island apple snail *Pomacea insularum*, and the New Zealand mud snail *Potamopyrgus antipodarum* (Lysne and Koetsier 2008; Riley et al. 2008). Introduced competitors may impact native molluscan fauna through habitat alteration (Tucker 1994), competition for food and space (Hadfield et al. 1993; Murray et al. 1988; Baker and Levinton 2003; Haynes et al. 2005; Kerans et al. 2005; Hall et al. 2006), or resource depletion (Holland 1993; Nichols and Hopkins 1993; Caraco et al. 1997; Hall et al. 2003). Yet, while much research has been devoted to investigating native species declines following invasive mollusc introductions, very little is known about the mechanisms of native mollusc persistence following introductions.

Previous research exploring interaction mechanisms between native and non-native gastropods has produced equivocal results. Competitive mechanisms include resource use overlap with native species leading to increased competition for food and space (Hadfield et al. 1993; Murray et al. 1988; Kerans et al. 2005; Hall et al. 2006). Competition among aquatic gastropods is commonly asymmetric (Brown 1982; Cedeño-León and Thomas 1982; Schmitt 1985; Meyer-Lassen and Madsen 1989; Baur and Baur 1990; Hershey 1990; Grudemo and Bohlin 2000; Riley et al. 2008). Other mechanisms also exist including physical interference competition (Madsen 1986; Baur and Baur 1990). Yet, research with gastropods has also provided evidence of facilitation (Brown 1982; Hershey 1990; Cope and Winterbourn 2004; Riley et al. 2008). For example, a non-native gastropod was found to increase reproduction of another non-native gastropod species (Cope and Winterbourn 2004) and in another study a native gastropod was found to facilitate growth of a non-native (Riley et al. 2008). Evidence of competition and facilitation among native and non-native gastropods suggests that interactions may vary on a species by species or system by system basis. A better understanding of the mechanisms contributing to this variation among systems would provide insight into the context specificity of invader impact on native species.

The invasive aquatic gastropod *P. antipodarum* is a good model species for investigating shifts in the strengths of net interactions. *Potamopyrgus antipodarum* has been a successful invader of lentic and lotic freshwaters of Australia (Schrieber et al. 2003), Europe (Dorgelo 1987), and more recently North America (Bowler 1991; Langenstein and Bowler 1991; Bowler and Frest 1992; Zaranko et al. 1997; Richards et al. 2001). A broad diet and physiological tolerance (Winterbourn 1970, Dorgelo et al. 1995; Collier and Winterbourn 2000) give *P. antipodarum* a potentially competitive advantage in many habitats (Loo et al. 2007). The ability of *P. antipodarum* to reach extremely high densities suggests it would frequently compete with native gastropods; however, prior research has demonstrated mixed responses among macroinvertebrates (Quinn et al. 1998; Kerans et al. 2005; Schreiber et al. 2002; Brenneis et al. 2010). In previously invaded habitats, *P. antipodarum* were found to dominate native macroinvertebrate assemblages in Australia (Quinn et al. 1998) and to negatively affect macroinvertebrate colonization rates in the Greater Yellowstone Ecosystem (Kerans et al. 2005). In contrast, when mud snail densities were manipulated over brief temporal time scales (6 days) in previously invaded Australian streams, higher densities were positively correlated with native macroinvertebrate diversity (Schreiber et al. 2002). Schreiber and colleagues (2002) hypothesized that nutrients excreted by *P. antipodarum* provided food for other macroinvertebrates thereby increasing habitat suitability, but the facilitative mechanisms involved were not explored. Cope and Winterbourn (2004) found that the presence of *P. antipodarum* increased the fecundity of the invading snail, *Physella acuta*, when both snails were kept at equal densities indicating a facilitative effect of *P. antipodarum* on *P. acuta* reproduction. The variation in responses of other gastropods to *P. antipodarum* suggests that the per capita effects of *P. antipodarum* may not be constant.

Potamopyrgus antipodarum has rapidly invaded the Snake River drainage (Bowler 1991) and has been suggested as a probable strong competitor with native gastropods (Strayer 1999), but variation in ecological impact exists among species and locations. The native gastropod fauna of the Snake River have been adversely affected by impacts from management of scarce water resources for growing human population demands and the introduction of non-native species such as *P. antipodarum* (USEPA 2002; Lysne and Koetsier 2006a). Competition between *P. antipodarum* and native gastropods has been explored in laboratory settings with the endangered *T. serpenticola* (Richards 2004) and *V. utahensis* (Lysne and Koetsier 2008) indicating negative per capita effects on biologically similar species. Little is known about other more abundant native gastropod species that are able to coexist with *P. antipodarum* in some locations such as *Valvata humeralis*. *Valvata humeralis* is a colonial species that forms distinctive populations that can be found from year to year in the same location and are known to coexist with *P. antipodarum* (R. Newman, Bureau of Reclamation, personal communication). Examining *P. antipodarum* and *V. humeralis* patterns of coexistence, interaction net effects, and the mechanisms of their interaction will help further understanding of native species persistence in the presence of invasive species.

Measuring Change in Species Interactions

Measuring species interactions in field environments has raised controversy and debate (Connell 1983; Schoener 1983; Gurevitch 1992). The rise of competition studies in ecology has been met with skepticism questioning the consistency of competition in nature (Connell 1983). This research has cascaded into a long-running debate in ecology over how influential competition is in structuring communities compared with resource availability (Wiens 1977), disturbance (Fowler 1981), environmental stochasticity (Dunham 1980; Smith 1981), and community succession (Minshall and Peterson 1985). Among the general conclusions has been the need to clearly define the mechanisms driving competition by exploring intra- and interspecific differences in an environment where other factors are controlled.

The density dependent experimental design is a clear and practical method for determining the strength and direction of interaction between species and has commonly been used to study gastropods (Schmitt 1985; Meyer-Lassen and Madsen 1989; Baur and Baur 1990; Underwood 1997; Cross and Benke 2002; Cope and Winterbourn 2004). A simple density dependent design holds the initial density of a "responding species" constant while varying the density of a potential competitor species (Morin 1999). A specific advantage to this design is that when more than two density levels are employed, one can determine whether the per capita effects of competitors increase or decrease linearly or non-linearly potentially revealing facilitative components (Morin 1999). Additionally, the density dependent design can be modified into a replacement series design to determine if frequency dependent competition occurs (i.e., intraspecific competition differs from interspecific competition) by including treatments of varying density with species alone and together (Morin 1999).

The flexibility of the density dependent design and its familiarity among ecologists make it ideal for understanding shifting interactions between native and invasive gastropods. Specifically, the net effects of *V. humeralis* and *P. antipodarum* on one another can be assessed by comparing growth and mortality among treatments of varying density and species combinations. Combined with field surveys, these results will provide insight into mechanisms of coexistence and potential influences on the varying ecological impact of *P. antipodarum.*

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CHAPTER THREE

SPATIAL, TEMPORAL, AND DIET PARTITIONING COMBINE WITH ENVIRONMENTAL STOCHASTICITY TO ENABLE COEXISTENCE BETWEEN AN INVASIVE AND A NATIVE GASTROPOD

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Kiza K. Gates

Contributions: Conceived the study, collected and analyzed output data, and wrote the Manuscript.

Co-author: Billie L. Kerans

Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Kiza K. Gates and Billie. L. Kerans
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Abstract

Understanding the mechanisms that allow similar species to coexist is a strong theme in ecological research. The coexistence of native species with similar invasive species (non-natives with a history of spread and ecological or economic impact) is of particular interest because it may provide insight into mechanisms of variable invasive impact. We investigated niche partitioning between a native, *Valvata humeralis,* and an invasive species, *Potamopyrgus antipodarum,* at an invasion site where native species have continued to coexist with the invader for over a decade. We investigated habitat use at three spatial scales over one year and diet composition of both species in the Middle Snake River. Samples were collected with a 0.25 m^2 plot, Venturi suction dredge, and SCUBA certified diver. Diet composition was determined by dissection and isolation of viscera. *Valvata humeralis* were consistently smaller in size in the presence of *P. antipodarum* suggesting competition. Juvenile *V. humeralis* appeared to shift diet to one lower in diatoms in the presence of *P. antipodarum* suggesting competition for food. There was evidence of spatial habitat partitioning between *V. humeralis* and *P. antipodarum* among populations, but not within populations or patches. Reproduction events were temporally partitioned between species and variation in flows created by upstream dams conferred an advantage to the reproductive cycle of *V. humeralis*. Niche partitioning and dam operations appeared to contribute to the coexistence of *V. humeralis* and *P. antipodarum* and to the lower impact of *P. antipodarum* on *V. humeralis* populations in our study. These results suggest that invasive species ecological impact can be mitigated by native species behavior and flow regimes that favors native species.

Introduction

Exploring the mechanisms that allow similar species to coexist remains a strong theme in ecological research (Chesson 2000). The coexistence of native species with similar invasive species (non-natives with a history of spread and ecological or economic impact) is of particular interest because it may provide insight into mechanisms of the variable impact of invaders. The impact of an invasive species on native species, ecological impact, can be highly variable among invasion sites. Invasive species may dominate biomass is some locations, whereas in other locations they may coexist with native species at lower biomass levels creating variation in ecological impact. Attempts to quantify invasive impact have highlighted the importance of understanding the context of an invasion in terms of the receiving community and the physical environment (Ricciardi 2003; Ricciardi and Atkinson 2004; Ricciardi and Cohen 2007; Padilla 2010; Thomsen et al. 2011). A better understanding coexistence mechanisms among invasive and native species is needed to improve predictions of future invader impact and identify vulnerable native species.

The cause of varying impact from one invasion site to another may be due, in part, to the interactions of the invader with native species of the receiving community (Crooks 2002; Lockwood et al. 2009). Invasive species are often managed under the assumption that all new introductions represent similar levels of threat; however, many introductions do not appreciably change the receiving community (Williamson 1996; Davis 2003) making the ecological impact low. Additionally, species often only exhibit invasive behavior in particular geographic locations (Kolar and Lodge 2001). This variation can sometimes be attributed to the invaders inability to proceed through the entire invasion process in new locations. The most commonly accepted stages of invasion include some form of transport, introduction, establishment, and spread with impact rarely occurring until the invader has proceeded through all stages (Williamson 1996; Lockwood et al. 2009). Competition with the native community is recognized as a potential influence during the invasion process that may prevent passage from one stage to the next and thus influence impact (Bertness and Callaway 1994; Stachowicz 2001; Price and Morin 2004). For example, an invasive species may fail to establish in a new location due to life history constraints, environmental stochasticity, and/or competition with native species (Petryna et al. 2002; Simberloff et al. 2002; Keeley et al. 2003).

In addition to the interactions between invasive and native species, the spatio-temporal context in which they occur may also influence the ecological impact of an invader. The effect that invasive species have on native species and vice versa is dependent on relative competitive abilities as well as spatial overlap (Shigesada and Kawasaki 1997). Native and invasive species may have the potential to compete, but habitat partitioning either within or among populations can ameliorate potential competition. For example, spatial and temporal variation in habitat use among native and invasive mosquito populations in Florida contributed to their coexistence and could possibly explain persistence of the native at larger spatial scales (Leisnham and Juliano 2009). Similarly, native whitefish spp. were found to delay negative effects of the invasive *Vendace Coregonus ablbula* by shifting microhabitat use (Gjelland et al. 2007). Such individual-level behavior may lessen invasive impact in some locations.

Furthermore, environmental variation may combine with habitat partitioning to further decrease impact at some invasion sites. For instance, researchers found that both environmental variability and community composition were important modulators of impact of marine invasive bivalves among geographic locations (Queirós et al. 2011).

We investigated native and invasive species habitat use at an invasion site where native species have continued to coexist with an invasive creating a lower perceived ecological impact. *Potamopyrgus antipodarum* is an invasive aquatic gastropod known for achieving densities in excess of 250,000 snails/m^2 (Richards et al. 2001; Kerans et al. 2005; Alonso and Castro-díez 2008). First documented in the Vista reach of the Snake River (RM 713) in 1996, *P. antipodarum* has proceeded through the invasion process, but has continued to coexist with some native gastropods and has not obtained high densities as characteristic in other invaded areas. While variation in the competitive ability of an invasive species among populations can contribute to variation in ecological impact among invasion sites (Leisnham and Juliano 2010), it is not a likely explanation for the low *P. antipodarum* abundances in the Vista reach because invasive populations are clonal with only several clones in that region (Dybdahl and Drown 2011).

The mechanisms of coexistence with native gastropods in the Vista reach are uncertain. The gastropod assemblage in this reach is diverse including *Gyraulus parvus*, *Fluminicola fuscus*, *Lymnaidae* sp., *Physella gyrina, Stagnicola* sp., *Valvata humeralis, Valvata utahensis,* and *Vorticifex effusa*. While experiments have revealed a tendency for competition with *P. antipodarum* to negatively affect growth of some native species such as *V. utahensis* (Lysne and Koetsier 2008), the native congeneric, *V. humeralis,* has maintained consistent populations in the presence of *P. antipodarum* since the invasion in the mid 1990’s. Spatio-temporal and diet partitioning between *V. humeralis* and *P. antipodarum* has not been explored and may provide insight into their coexistence.

Our goal was to explore the role of niche partitioning in enabling coexistence of a native with an invasive species. We assessed resource overlap between *V. humeralis* and *P. antipodarum* in populations of the former over one year. We investigated habitat use at three spatial scales over time and diet composition of both species. To establish whether competition with *P. antipodarum* was affecting *V. humeralis*, we compared the growth of *V. humeralis* in invaded and uninvaded populations over time. We asked, do *V. humeralis* and *P. antipodarum* spatially partition habitat among populations, within population, or within patches? We predicted that we would see evidence of competition between the two species and that *V. humeralis* would partition habitat spatially, temporally, or consumptively in order to maintain persistent populations in the presence of *P. antipodarum*.

Methods

We sampled gastropods within the Vista reach of the Middle Snake River below American Falls Dam (Latitude 42°46’03”, Longitude 112°52’46”, RM 713). The Vista reach is characterized by a narrow channel (127-165 m compared to 300+ m up and downriver) that keeps most of the riverbed watered throughout the year despite dramatic shifts in discharge from American Falls dam upriver (11-425 cubic meters/second (m^3/s)

2000-2010 mean low and high discharge). Water temperatures fluctuate from 5-22 °C throughout the year.

Annual surveys within this reach have indicated that populations of *V. humeralis* can be found in the same locations along the littoral zone from year to year (R. Newman, Bureau of Reclamation, personal communication). *Valvata humeralis* is a semelparous species that reproduces in late summer in the Middle Snake River allowing a population cohort to be followed throughout the year. We defined populations of *V. humeralis* based on previous surveys indicating that populations consist of a densely aggregated center with decreasing gastropod abundance as you move away from the center (R. Newman, personal communication). *Potamopyrgus antipodarum* was first documented in this region in the mid 1990’s and maintains a broad distribution with low-abundances (R. Newman, personal communication).

We selected four long-standing *V. humeralis* populations that were present in the reach for at least six years based on prior surveys (1998-2006). We used prior population survey data to designate the presence of *P. antipodarum* within *V. humeralis* populations a priori. Two of the four *V. humeralis* populations had a documented presence of *P. antipodarum* within them (invaded populations 1 and 2) and the other two populations did not (uninvaded populations 1 and 2). We selected populations on both sides of the river to encompass different habitat types within the reach. This design allowed us to look at *V. humeralis* behavior in the presence and absence of *P. antipodarum* at the among population scale (1-2 km), within population scale (10-20 m), and patch scale (1 m).

We sampled *V. humeralis* populations monthly from May through November of 2008. We conducted sampling during the second week of each month. Sampling months reflected the active period of the year for gastropods in the region (Cleland 1954; Hershey 1990; Lysne 2003; Lysne and Koetsier 2006b). In addition, ice build-up in the winter months prevented safe access to populations. To survey the populations each month, we placed two transects perpendicular to one-another through each population. We established a fixed transect in April which ran perpendicular to shore (perpendicular transect) through the greatest density of *V. humeralis* in each population. We marked the fixed transect on shore with rebar and revisited it each month thereafter as the reference starting point for sampling. We began sampling each month by sampling along the perpendicular transect every 2 m moving out from the rebar. Sampling along transects ceased when *V. humeralis* density decreased by 75% from the highest sample density along the transect. We placed another transect parallel to shore (parallel transect) through the greatest density of *V. humeralis* found while sampling along the perpendicular transect. We collected samples outward every 5 m along the parallel transect beginning at the intersection with the perpendicular transect and ceased sampling by the same criteria described above. We designed sampling distances along these transects to maximize area covered during sampling days.

We collected samples with a 0.25 m^2 plot, Venturi suction dredge, and SCUBA certified diver. Samples were transported to the surface in flexible piping and passed through a 1 mm sieve bucket to remove sand and silt. We separated *V. humeralis* and *P. antipodarum*, counted abundances, and measured individuals from the anterior end of the shell across to the apex with digital calipers to the nearest 0.01 mm. When samples were too large to search entirely, we thoroughly mixed contents and sub-sampled by 50%. When the number of *V. humeralis* and *P. antipodarum* individuals was too large to measure all (> 50/sample), we thoroughly mixed samples and took a sub-sample of 50 individuals of each species. We considered samples devoid of *V. humeralis* and *P. antipodarum* after 30 min. of searching. We returned all contents of the sample to the plot where they were collected after measurements were taken.

Competition Between *V. humeralis* and *P. antipodarum*

We assessed the effect of competition on the native from the invasive at the among population scale using our a priori designated invaded and univaded *V. humeralis* populations. We used *V. humeralis* size as a measure of competition with *P. antipodarum*. The semelparous life-cycle of *V. humeralis* allowed us to use mean shell length as an accurate approximation of the average size of individuals within a population each month. We assumed that if competition from *P. antipodarum* was affecting *V. humeralis* growth, average shell lengths would be smaller in invaded populations. We used a one-way ANOVA with population type (invaded or univaded) to compare monthly mean shell length of *V. humeralis*. If the effects of the ANOVA were significant, we used independent contrasts to compare *V. humeralis* shell length in invaded and uninvaded populations within month.

Valvata humeralis and *P. antipodarum* Resource Partitioning

We explored how consumptive (diet), spatial, and temporal resource partitioning by the native changed in the presence of the invasive. We assessed diet partitioning between *V. humeralis* and *P. antipodarum* by examining gut content. The food particle size consumed by gastropods varies with shell length (Fenchel 1975). To quantify potential ontogenetic differences in diet composition, we examined the gut contents of *P. antipodarum* and *V. humeralis* of varying sizes. We randomly sampled 10 adults and 10 juveniles of both species (*V. humeralis* juvenile < 2 mm and adult ≥ 2 mm, *P. antipodarum* juvenile < 3 mm and adult ≥ 3 mm) from an invaded population on August 13, 2009. To quantify any shift in diet in the presence of *P. antipodarum,* we also randomly sampled 10 adult and 10 juvenile *V. humeralis* from uninvaded populations on August 12, 2009. We sampled in August because it is the only month when both adults and juveniles are present. We immediately froze specimens to arrest digestion and returned to them to the lab for dissection (Reavell 1980). We gently crushed shells with forceps, isolated the viscera on a hemocytometer slide, flooded the gut with glycerin, and placed a cover slip over the top (Reavell 1980).

We measured gut composition as a percentage of different components from the entire flooded gut area with a hemocytometer slide grid and a 40x compound scope (Reavell 1980). We categorized contents as amorphous detritus, plant-based detritus, and diatoms. Early trials indicated that plant and amorphous detritus were difficult to distinguish and thus were combined. We square root arcsine transformed percent detritus and diatoms to meet assumptions of normality and used a one-way ANOVA to determine differences in diet composition among a combined variable that included species, age, and population (invaded or uninvaded). If the effects of the ANOVA were significant, we used independent contrasts to compare juvenile and adult gut content of *V. humeralis* in invaded and uninvaded populations as well as juvenile and adult gut content between *V. humeralis* and *P. antipodarum*.

We explored spatial partitioning between *V. humeralis* and *P. antipodarum* at three spatial scales for all sampling events combined. At the among population scale, we examined the presence of *P. antipodarum* in invaded and uninvaded *V. humeralis* populations over the course of seven months to determine if uninvaded populations remained uninvaded. We predicted that if spatial partitioning was occurring at the among population scale, uninvaded populations would remain uninvaded or with low *P. antipodarum* abundances. At the within *V. humeralis* population scale, we looked at the proportion of samples containing *P. antipodarum* in invaded populations at differing *V. humeralis* densities. We predicted that if *V. humeralis* was partitioning habitat within populations, they would be found less frequently at high densities with *P. antipodarum.* We used a chi-square analysis to compare the proportion of low, medium, and high *V. humeralis* density samples (≤ 30, $> 30 \leq 100$, and > 100 *V. humeralis*/m^2 respectively) containing *P. antipodarum*. At the patch scale, we explored the relationship between *V. humeralis* density and *P. antipodarum* density from samples taken in invaded populations. We predicted that if habitat partitioning was occurring at the smaller patch scale, we would see a negative correlation with increasing densities of both species. We used a Spearman's rank test to determine if densities of the two species were correlated over the entire sampled period.

We explored temporal habitat partitioning by comparing overlap between *V. humeralis* and *P. antipodarum* at three spatial scales monthly. At the among population scale, we qualitatively compared the percent presence of *P. antipodarum* in uninvaded populations each month from May through November. At the within population scale, we qualitatively compared the percentage of samples that contained *P. antipodarum* within invaded populations from each month. At the patch scale, we explored the relationship between *V. humeralis* density and *P. antipodarum* density in invaded populations for each sampled month with Spearman's rank tests. We predicted that if temporal habitat partitioning was occurring, we would see correlations change from month to month.

In addition to general spatial overlap, we explored overlap of reproductive events for both species. We inferred *V. humeralis* reproductive events from decreases in mean length of the population length frequency histogram from month to month. A reproductive event was considered a decrease in mean shell length and shift of the length frequency histogram to smaller shell lengths. We qualitatively compared timing of reproductive events between species to determine if the timing of reproduction differed. We predicted that if temporal partitioning was occurring, we would see peaks of juvenile *V. humeralis* abundance occurring at different times than peaks of juvenile *P. antipodarum* abundance. We performed all statistical procedures in SAS 9.3. Measures of variance listed within parenthesis are one standard error.

Habitat Assessment

We measured environmental variables concurrently with sampling to assess microhabitat associated with invaded and uninvaded *V. humeralis* populations. We took water measurements and sediment cores monthly just above the substrate at the highest *V. humeralis* density in each population. We measured water temperature, pH, dissolved oxygen, and conductivity with a Yellow Springs Instruments hand held meter. We measured water hardness with HACH Sofchek® test strips. We measured flow with a Swoffer 3000 current velocity meter. We measured depth in shallow waters (< 2.5 m) by marking the diver's wetsuit and observing standing depth. In deeper waters (> 2.5 m) we measured depth with a depth-finder attached to rear of the boat. Substrate composition was visually estimated as the predominant substrate type within the quarter meter plot by the diver because of low visibility at greater depths. To estimate benthic productivity over time, we took sediment cores to determine ash free dry mass (AFDM). We kept sediment cores on ice, returned them to the lab, and dried them in a drying oven at 21ºC until no moisture remained. We sub-sampled dried sediment, weighed it, and burned it in a muffle furnace at 550ºC for 2 hrs. We allowed samples to cool in a desiccator and we re-weighed the remaining sediment to calculate AFDM. We recorded substrate composition and macrophyte presence for every sample. We recorded sample depth for reference, but it is not presented because changing water levels from month to month made it a poor metric.

Results

Access to *V. humeralis* populations varied over the course of sampling. High and low discharge from American Falls Dam prevented safe access to some populations including uninvaded populations 1 and 2 which were not accessible in November. In addition, high flows in May and June prevented prolonged access to invaded population 1; therefore, length frequency data were available for invaded population 1 in May and June, but population density was not.

Valvata humeralis populations varied considerably in physical length parallel to the shore and width perpendicular to the shore over time (Table 3.1). Population physical size tended to decrease, whereas density increased from July to August coinciding with the semelparous reproductive period. Peak densities of *V. humeralis* occurred in different months for different populations, but were concentrated in June, July, and August.

Competition Between *V. humeralis* and *P. antipodarum*

Two-hundred and fifty samples were taken within the four populations over the course of seven months. Shell measurements were recorded from 1,542 *V. humeralis* (invaded n = 1,199, uninvaded n = 343). Uninvaded populations were both smaller in two-dimensional space and lower in *V. humeralis* density than invaded populations (Table 3.1). *Valvata humeralis* shell length was consistently smaller in invaded populations than uninvaded populations from May through October with the exception of August ($p = 0.88$) when the new cohort appeared ($F_{11,1406} = 306.88$, $p < 0.0001$) (Figure 3.1). Independent contrasts indicated that shell lengths significantly differed among invaded and uninvaded populations in May ($F_{1,1406} = 4.56$, $p = 0.03$), June ($F_{1,1406} = 8.15$, 0.004), and September ($F_{1,1406} = 3.97$, 0.05), but marginally differed in July ($F_{1,1406} = 2.97$, $p = 0.09$) and October ($F_{1,1406} = 2.55$, $p = 0.11$). Shell lengths from November were not used because only invaded populations were surveyed that month.

Valvata humeralis and *P. antipodarum* Resource Partitioning

Gut contents were primarily detritus with a small fraction of diatoms and varied significantly among species, ages, and population types ($F_{5,51} = 3.17$, $p = 0.02$). Independent contrasts revealed that juvenile *V. humeralis* in uninvaded populations had a greater percentage of diatoms than juveniles in invaded populations (juveniles invaded percent diatoms = 2.22 (0.89), juveniles uninvaded percent diatoms = 10 (3.78), $F_{1,51} = 5.50$, $p = 0.02$). Adult *V. humeralis* gut content also varied significantly between invaded and uninvaded populations with those in uninvaded populations having a smaller percentage of diatoms (adults invaded percent diatoms = 4.5 (0.5), adults uninvaded percent diatoms = 1.1 (0.66), $F_{1,51} = 6.24$, $p = 0.02$). We did not detect a difference between juvenile *P. antipodarum* and *V. humeralis* gut content in invaded populations (juvenile *P. antipodarum* percent diatoms = 3.0 (1.3) and percent detritus = 97 (1.3))($F_{1,51} = 0.02$, $p = 0.88$), but adult *P. antipodarum* and *V. humeralis* gut content did with adult *P. antipodarum* having a lower percentage of diatoms than *V. humeralis* (*P. antipodarum* 2.5 (1.12), *V. humeralis* see above, $F_{1,51} = 5.23$, $p = 0.03$).

At the among population scale, *P. antipodarum* appeared in both of the uninvaded *V. humeralis* populations. *Potamopyrgus antipodarum* densities remained low in our uninvaded populations throughout our sampling, but *P. antipodarum* were found in up to

50% of the samples during some months (Table 3.1). At the within population scale, *V. humeralis* occurred more frequently with *P. antipodarum* than by itself when *V. humeralis* densities were high, whereas when *V. humeralis* densities were low or medium, *V. humeralis* occurred in samples with and without *P. antipodarum* about equally ($\chi^2 = 25.79$, $p < 0.0001$) (Figure 3.2). At the patch scale, a positive relationship existed between *V. humeralis* density and *P. antipodarum* density in invaded populations (Spearman's Rank Correlation = 0.44, $p < 0.0001$).

Temporally, *P. antipodarum* maintained a presence in all *V. humeralis* populations throughout the sampled months. *P. antipodarum* were not found every month in the uninvaded populations, but their absence was not consistent between the two uninvaded populations. The uninvaded populations were devoid of *P. antipodarum* in April of 2008; however, *P. antipodarum* were present in uninvaded population 2 in May and uninvaded population 1 in July. The timing of highest proportion of overlap with *P. antipodarum* varied among the populations from June to October reflecting the asynchronous reproduction of *P. antipodarum* (Table 3.1). *Potamopyrgus antipodarum* densities remained low ($\leq 80/m^2$) over the year in all populations except invaded population 1 where they reached densities of $480/m^2$ in July; however, there was no pattern of overlap within the invaded populations (Figures 3.3-3.4). At the within population scale, invaded population 1 experienced the most spatial and temporal overlap with *P. antipodarum* with 100% overlap in October and 77% or greater in July, August, and September. At the patch scale, density of *V. humeralis* and *P. antipodarum* were positively correlated in June, July and October in invaded populations (Table 3.2).

Reproductive strategies of *V. humeralis* and *P. antipodarum* differed creating asynchronous reproduction between species. Population surveys confirmed that *V. humeralis* reproduced semelparously once in summer. Maximum mean shell length of *V. humeralis* occurred in July for all populations followed by the minimum mean shell length in August (Table 3.3). The largest decrease in adult *V. humeralis* (> 2 mm) in the populations occurred from July to August while the largest decrease in juveniles (< 2 mm) occurred from September to October (Table 3.3). Timing of maximum and minimum mean shell length of *P. antipodarum* varied among populations reflecting their continuous reproductive output (Table 3.3). *Potamopyrgus antipodarum* reproductive events occurred anywhere from May through October depending on the population.

Habitat Assessment

Environmental conditions associated with the highest density of *V. humeralis* were similar among populations within months (Table 3.4). Temperatures ranged from 7.84-22.68 ºC throughout the year with maximum temperatures in August and minimum temperatures in October or November. Dissolved oxygen peaked in the spring and declined into the fall both years (Table 3.4). Flow in the populations was typically very low due to their location in the littoral zone and buffering by American Falls Dam upriver (Table 3.4). Discharge from American Falls Dam ranged from 10-427 m^3/s. Discharge was above 200 m^3/s from May 1- September 23.

The organic percent of AFDM ranged from 1.1-6.4% reaching a maximum in June (Figure 3.5). Macrophytes were present only during the warmest months of June, July, and August. The most common substrate type associated with the highest densities of *V. humeralis* was small gravel followed by silt.

Discussion

Valvata humeralis size differed in the presence of *P. antipodarum* suggesting a competitive interaction. Our comparison of shell lengths between *V. humeralis* populations that were invaded and not invaded indicated that *V. humeralis* were consistently smaller and achieved a smaller adult size prior to reproduction in invaded populations. *Valvata humeralis* shell lengths were only similar among all populations during the month of September when the new cohort appeared and October when *P. antipodarum* were nearly absent. The close proximity of populations (1-2 km) and similarity of our course habitat conditions among populations suggest that patchy habitat conditions were not a major driver of the difference in *V. humeralis* growth between population types. However, the stability of our invaded/univaded population categories and decreased *V. humeralis* density in univaded populations may have also contribued to the increased shell length in univaded populations. One of the univaded populations became invaded during the spring, although *P. antipodarum* densities remained lower than in the invaded populations with the exception of during the month of May. Our uninvaded *V. humeralis* populations also had consistently less dense aggregations of *V. humeralis* than our invaded populations indicating that decreased conspecific density may have also contributed to the larger shell size of *V. humeralis* in uninvaded populations. While the differences in density and fluctations in *P. antipodarum* presence among *V.*

humeralis population types confound our shell length results to some degree, the results are still suggestive of a competitive interaction and warrant further investigation.

Our results suggest that *V. humeralis* and *P. antipodarum* may compete for food and that *V. humeralis* shifts diet and partitions food resources in the presence of *P. antipodarum*. Food resources appeared to be shared between species ontogenetically or during different ages. When *V. humeralis* and *P. antipodarum* were together, juveniles of both species had similar gut composition while adults of both species differed indicating that food resources may only be shared during the juvenile stage. Gut contents varied between *V. humeralis* juveniles and adults in invaded and uninvaded populations also suggesting that *V. humeralis* shifts diet in the presence of *P. antipodarum* regardless of age. Our results showed more diatoms in the diet of juvenile *V. humeralis* in uninvaded than invaded populations, but the opposite pattern was true for adult *V. humeralis*. Diatoms are a high nutrient food source for grazing species suggesting *V. humeralis* juveniles may select higher quality food when *P. antipodarum* is absent contributing to the larger adult size in uninvaded populations (Brendelberger 1997). The adult *V. humeralis* diet shifted to more diatoms in the presence of *P. antipodarum* suggestive of a greater competitive ability of *V. humeralis* once adult size is reached. Further study is needed to clarify food preference and competitive abilities.

Our exploration of spatial partitioning indicates the interaction between *V. humeralis* and *P. antipodarum* may vary with spatial scale and perhaps density. There was evidence of spatial habitat partitioning between *V. humeralis* and *P. antipodarum* among populations, but not within populations or patches. Although our populations started as invaded and uninvaded, *P. antipodarum* moved into all of the populations at some point during the year indicating that there was not strict population level habitat partitioning. Despite this, the larger shell lengths of *V. humeralis* in uninvaded populations suggest that there may be a benefit to some level of population scale habitat partitioning. In contrast, our measure of habitat partitioning at the within population and patch scales indicated the near opposite. Within invaded populations, *V. humeralis* were found more frequently at high densities with *P. antipodarum.* This pattern was consistent from month to month and among the two invaded populations suggesting there may be some benefit to sharing habitat with *P. antipodarum* at particular densities. This was also supported by our patch scale assessment that revealed a positive correlation between *V. humeralis* and *P. antipodarum* abundances. It is possible that heterogeneous habitat conditions could drive these patterns as well. Both of our invaded *V. humeralis* populations were larger in two-dimensions and denser than the uninvaded populations suggesting differences in habitat quality; however, the consistent pattern of high *V. humeralis* densities with *P. antipodarum* throughout the year in invaded populations and similarity of habitat conditions between population types suggests that more than habitat quality was driving the difference in population size.

Temporal partitioning of reproductive events caused by differing life history strategies may have lessened competition during critical growth periods contributing to coexistence of *V. humeralis* and *P. antipodarum.* We found that *V. humeralis* were temporally partitioning habitat with *P. antipodarum* during reproduction periods. *Valvata humeralis* populations were semelparous reproducing synchronously during

August and September which were months when *P. antipodarum* abundances were low. Even though *P. antipodarum* were found in a majority of samples from invaded populations during August and September, their abundances remained fairly low. *Potamopyrgus antipodarum* iteroparously reproduced continuously over sampled months and did not exhibit synchronized reproduction among populations. The appearance of *V. humeralis* cohorts in late summer and early fall when *P. antipodarum* were scarce may have led to higher juvenile survival due to reduced competition from *P. antipodarum* as well as optimal environmental conditions. Reproductive events for *P. antipodarum* did not coincide with the most productive season at our site and may have prevented populations from reaching high densities seen in other locations. In addition to differing life histories, *P. antipodarum* nearly disappeared from all *V. humeralis* populations in October and November. Although we did not survey during winter months, it is possible that the decline in *P. antipodarum* during winter decreases competition between species during the slowest growth period when water levels are also at their lowest.

The anthropogenically driven hydrograph below American Falls likely works in concert with life history and diet partitioning to help maintain coexistence between *V. humeralis* and *P. antipodarum* by re-setting the habitat each year. The occurrence of *P. antipodarum* reproduction throughout the year is generally considered an advantage (Dorgelo 1987; Dorgelo 1988; Alonso and Castro-diez 2008); however, in the dynamic system below American Falls Dam it may not provide the same advantage. *Potamopyrgus antipodarum* populations within this reach appeared to have 2-3 reproductive events during the year with one falling in early summer and another in early fall. The second reproductive event coincided with the dramatic decrease in discharge from American Falls dam which exposes as much as 8 m of the littoral zone for 3-5 months during the winter. The change from high to low discharge in fall, and vice versa in spring, occur over a short time period creating and then removing large areas of seasonally available habitat. The littoral zone becomes available for colonization in April and is destroyed in October essentially clearing the slate for the next year. In other words, no one species is able to maintain populations in this habitat. The re-setting of littoral habitat may keep *P. antipodarum* populations from reaching high abundances because each year they must recolonize the habitat with *V. humeralis,* but do not have enough time to dramatically increase the population size.

Although some of our results were suggestive of competition between *V. humeralis* and *P. antipodarum*, the persistence of *V. humeralis* populations and the tendency for the species to be found at higher density with *P. antipodarum* indicate that their interaction may change along a biotic or abiotic gradient. Previous work exploring community responses to *P. antipodarum* have found mixed results indicative of non-linear shifting interactions. While *P. antipodarum* has invaded many Western waters, there is considerable variability in ecological impact among sites. *Potamopyrgus antipodarum* can dominate invertebrate numbers and biomass in established areas (Kerans et al. 2005; Hall et al. 2003) facilitated by native species in some cases (Riley et al. 2008), but also experiences extreme population crashes (Dorgelo 1988) and coexists through time with native gastropod species (Siegismund and Hylleberg 1987). Schreiber et al. (2002) found that mud snails facilitated the colonization of several native taxa in an

Australian stream thereby increasing native species diversity. A similar experiment in Montana found the opposite effect that densities of *P. antipodarum* were negatively correlated with densities of several native taxa (Kerans et al. 2005). The ultimate cause of these disparities among invasion sites remains unclear, but is suggestive of a complex interplay between species interactions and environment. Further study of direct interactions between species is needed.

Our approach to exploring niche partitioning of the native species at multiple spatial scales provided varying perspectives on species coexistence and the potential mechanisms of decreased ecological impact from invaders. Niche partitioning and environmental stochasticity promoted the coexistence of *V. humeralis* and *P. antipodarum* and lower impact on *V. humeralis* populations in our study. While interactions with predators have also been shown to influence coexistence of aquatic gastropods (Covich 2010), we saw minimal evidence of heavy predation during the course of our sampling (qualitative fish gut-content analysis and crayfish abundance counts) suggesting that predation was relatively consistent among gastropod species and over time. Diet of the native species appeared to shift to one of lower nutritional quality in the presence of the invader potentially contributing to the smaller adult size of the native in the presence of the invasive. Differing reproductive strategies likely conferred an advantage to the native species because reproduction was aligned with the high flow and high productivity times of the year while potentially inhibiting the invasive. At the among populations scale, there may have been a growth advantage for the native in uninvaded populations, but at the within population and patch scales there was a tendency toward native and invasive species aggregation. These results highlight the importance of investigating native and invasive species interactions at multiple spatial scales over time and considering the environmental conditions within which they occur. In addition, these results suggest that invasive species ecological impact can be mitigated by native species behavior and flow regimes that favor native species.

Table 3.1—*Valvata humeralis* population size and density by month. Length was parallel to shore while width ran perpendicular to shore. Proportion of samples containing *P. antipodarum* is the proportion of samples containing *V. humeralis* that also contained *P. antipodarum*. A dash (-) indicates that there was no data available.

Population	Month	Population length (m)	Population width (m)	Highest *V. humeralis* density (ind./m^2)	Highest *P. antipodarum* density (ind./m^2)	Proportion of samples containing *P. antipodarum*
Uninvaded Populations						
1						
	May	40	2	32	-	0
	June	35	6	176	-	0
	July	30	6	48	32	0.11
	August	30	2	160	4	0.14
	September	15	4	80	16	0
	October	10	2	16	12	0.5
2						
	May	10	25	128	80	0.22
	June	20	10	160	24	0.33
	July	20	25	56	32	0.4
	August	0	0	4	0	0
	September	20	17	64	8	0.11
	October	5	1	8	4	0
Invaded Populations						
1						
	May	-	-	160	96	-
	June	-	-	204	20	-
	July	35	10	512	480	0.85
	August	15	8	1280	172	0.8
	September	25	12	880	48	0.77
	October	25	6	280	84	1
2						
	May	5	25	208	48	0.2
	June	15	10	256	48	0.6
	July	30	12	304	32	0.27
	August	15	2	352	32	0.5
	September	5	4	192	4	0.5
	October	10	7	28	8	0.5
	November	10	4	24	4	0

Table 3.2—Spearman's rank correlation (ρ) and associated p-values for *V. humeralis* and *P. antipodarum* density each month in invaded populations.

Month	ρ	P-value
May	-0.07	0.9
June	*0.9*	*0.02*
July	*0.55*	*0.005*
August	0.12	0.68
September	0.38	0.14
October	*0.83*	*0.0001*
November	-0.06	0.87

Table 3.3—Mean shell length of *V. humeralis* and *P. antipodarum* in each population by month. A dash (-) indicates that there were no data available.

Population	Month	*V. humeralis* mean shell length (mm)	*P. antipodarum* mean shell length (mm)
Uninvaded Populations			
1			
	May	2.71 (0.07)	-
	June	2.98 (0.07)	-
	July	3.71 (0.13)	4.27 (0.22)
	August	1.41 (0.06)	2.7 (-)
	September	1.49 (0.06)	3.69 (0.46)
	October	2.10 (0.16)	2.97 (0.36)
2			
	May	2.53 (0.08)	3.82 (0.16)
	June	2.74 (0.09)	3.61 (0.24)
	July	3.87 (0.08)	4.37 (0.18)
	August	3.63 (-)	-
	September	1.58 (0.06)	1.91 (0.09)
	October	1.67 (0.14)	2.61 (0.09)
Invaded Populations			
1			
	May	2.10 (0.07)	2.48 (0.18)
	June	2.58 (0.08)	2.87 (0.47)
	July	3.19 (0.07)	3.67 (0.09)
	August	1.47 (0.03)	2.94 (0.11)
	September	1.44 (0.02)	2.99 (0.22)
	October	1.74 (0.02)	2.19 (0.11)
	November	1.8 (0.03)	3.94 (-)
2			
	May	2.81 (0.08)	2.36 (0.14)
	June	2.90 (0.08)	4.10 (0.46)
	July	3.45 (0.06)	4.12 (0.31)
	August	1.52 (0.08)	3.66 (0.53)
	September	1.23 (0.03)	3.06 (0.53)
	October	2.29 (0.11)	3.77 (0.26)
	November	2.26 (0.11)	4.36 (0.36)

Table 3.4—Environmental parameters in *V. humeralis* populations from May through November of 2008. Measurements were taken where the highest density of *V. humeralis* were found that month.

Population	Date	Temp. (ºC)	$CaC0_3$ (ppm)	DO (mg/L)	pH	Sp. Cond. (ms/cm)	Flow (m/s)	Macro-phytes
Uninvaded Populations								
1								
	13-May	10.39	185	10.83	7.97	0.318	0.038	n
	12-Jun	13.87	120	16.4	8.44	0.37	0.06	n
	15-Jul	20.04	185	8.05	8.27	0.348	0.087	y
	11-Aug	22.61	120	7.68	8.74	0.356	0.002	y
	10-Sep	16.08	185	6.84	9.61	0.316	0.005	y
	14-Oct	8.86	120	5.05	8.4	0.303	0	n
2								
	14-May	10.4	na	11.21	8.45	0.323	0.194	n
	13-Jun	14.05	185	11.88	8.46	0.333	0.142	y
	16-Jul	20.33	185	8.48	8.38	0.351	0.292	y
	11-Aug	22.68	120	7.35	8.76	0.356	0.037	y
	10-Sep	17.03	120	7.56	9.97	0.323	0.039	y
	14-Oct	9.8	120	5.33	8.4	0.308	0	n
Invaded Populations								
1								
	14-May	9.78	185	10.57	8.22	0.319	0.053	y
	11-Jun	13.27	120	10.67	8.23	0.337	0.069	n
	14-Jul	19.27	185	7.54	8.13	0.357	0.013	y
	12-Aug	22.1	120	7.28	8.44	0.372	0.011	y
	9-Sep	17	120	8.54	9.99	0.321	0.009	y
	13-Oct	9.87	120	5.83	8.4	0.312	0	n
	13-Nov	9	120	3.08	8.4	0.354	0	n
2								
	15-May	10.37	185	10.89	8.35	0.323	0.057	n
	13-Jun	14.37	185	12.15	8.53	0.329	0.051	y
	15-Jul	20.34	185	8.45	8.29	0.354	0	y
	13-Aug	21.78	185	6.54	8.45	0.356	0	y
	11-Sep	16.04	120	7.18	9.67	0.322	0	n
	15-Oct	9.7	120	5.45	8.5	0.319	0	n

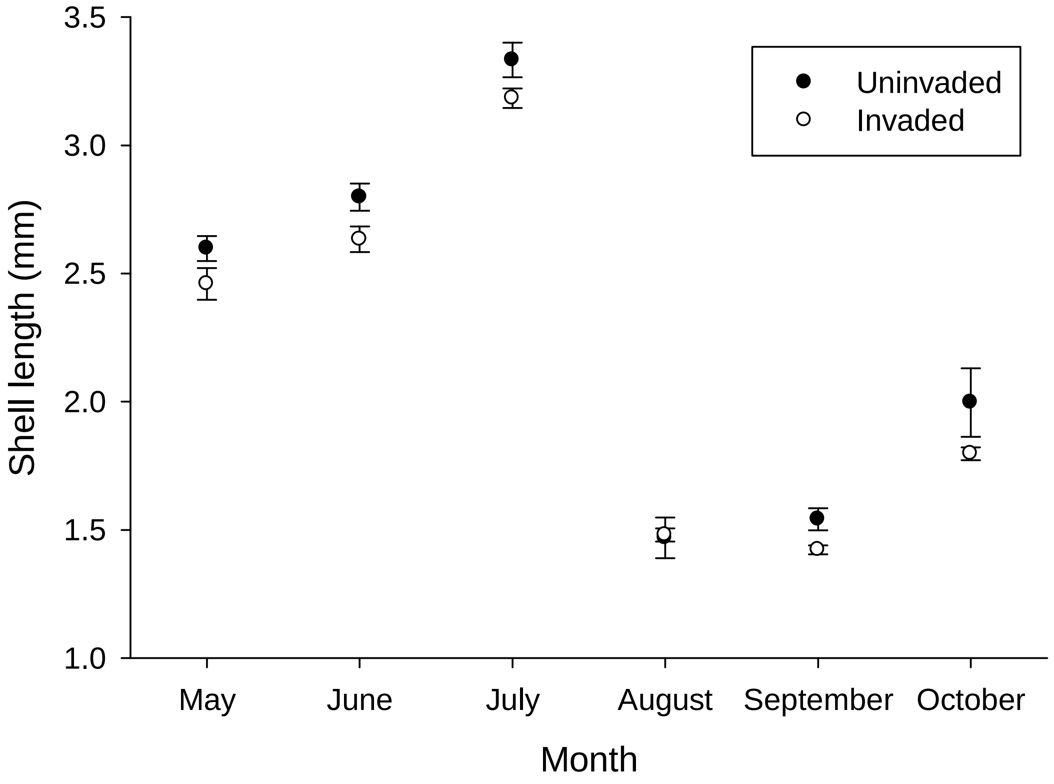


Figure 3.1.—*Valvata humeralis* mean shell length in populations invaded and uninvaded by *P. antipodarum* from May through October of 2008. Error bars indicate one standard error.

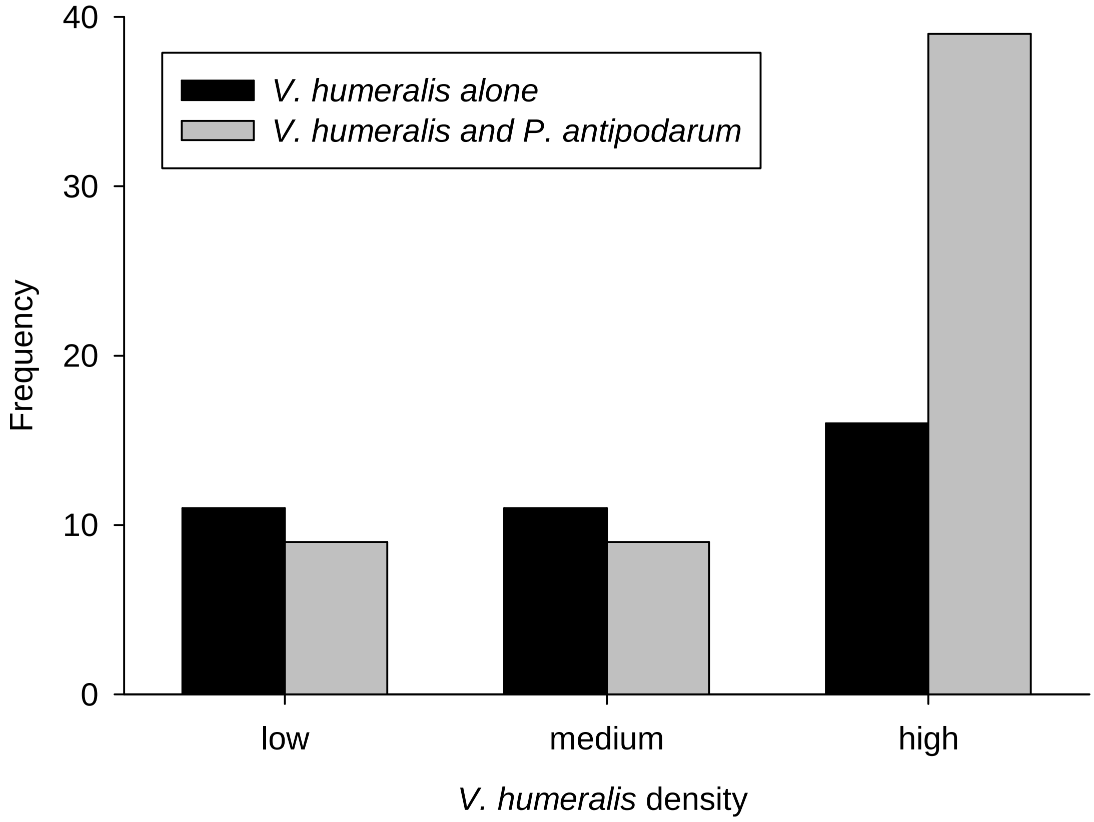


Figure 3.2.—Frequency of low (≤ 30/m^2), medium (> 30 ≤ 100 /m^2), and high (> 100/m^2) *V. humeralis* density samples containing *P. antipodarum*.

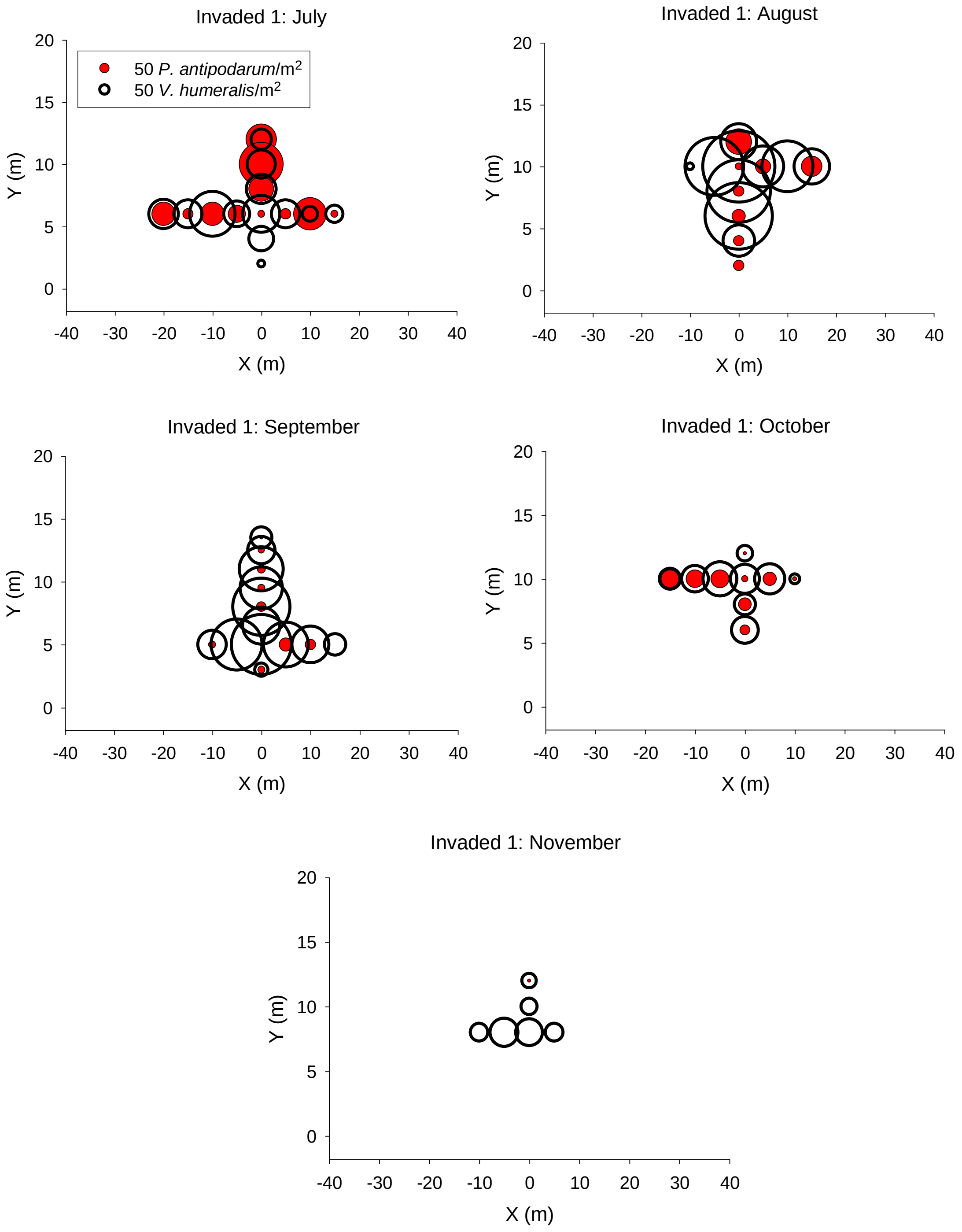
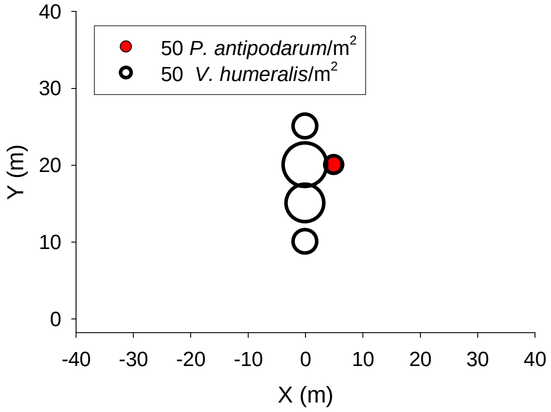
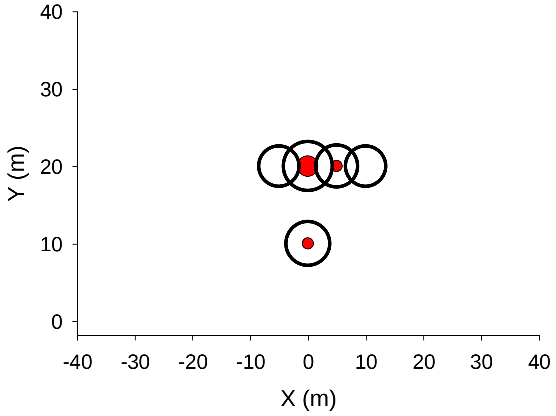


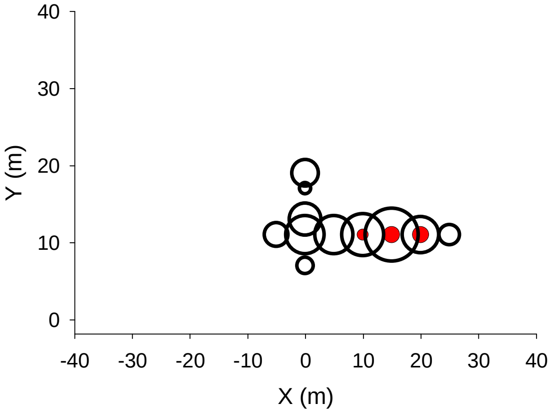
Figure 3.3—*Valvata humeralis* invaded population 1 mapped in space from July through November 2008. Each point represents a sample. Size of symbol represents density of individuals in that sample. The x-axis is parallel to the shore line and the y-axis is perpendicular to the shore line. Zero on the x-axis corresponds with the marked starting location for sampling each month.



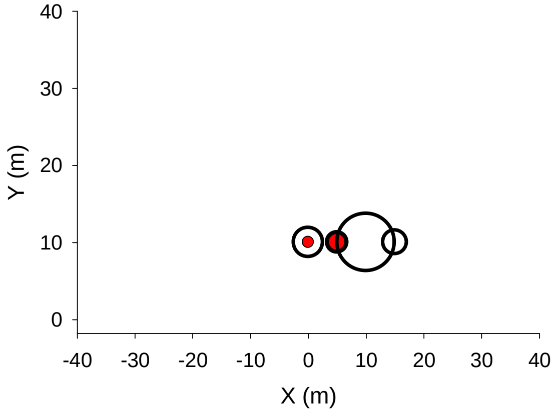
Invaded 2: May



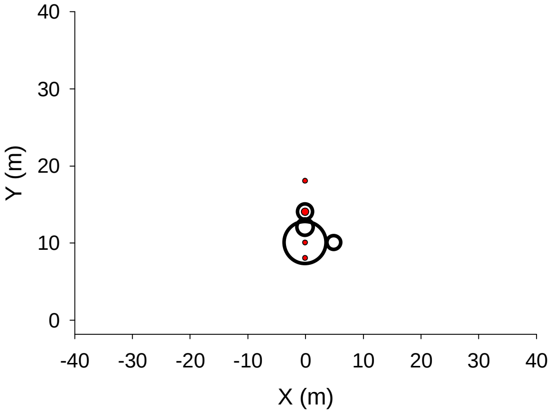
Invaded 2: June



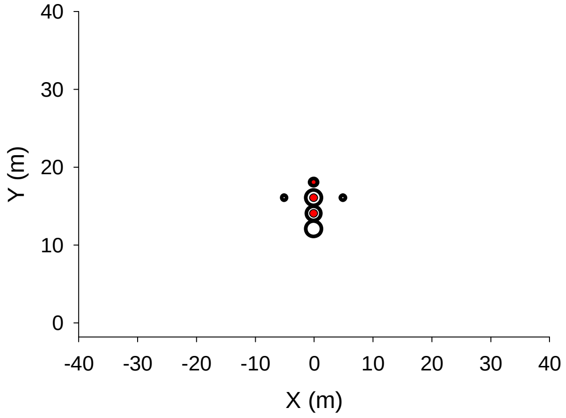
Invaded 2: July



Invaded 2: August



Invaded 2: September



Invaded 2: October

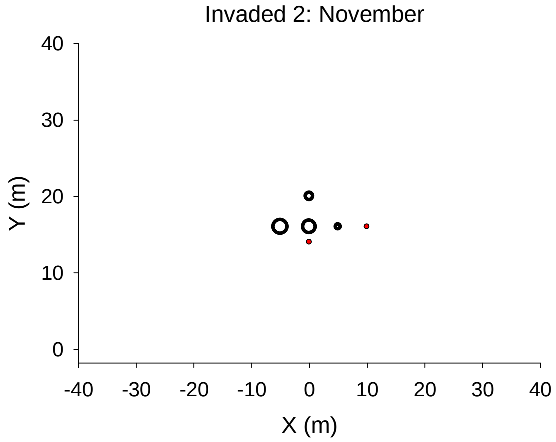


Figure 3.4—*Valvata humeralis* invaded population 2 mapped in space from May through November 2008. Each point represents a sample. Size of symbol represents density of individuals in that sample. The x-axis is parallel to the shore line and the y-axis is perpendicular to the shore line. Zero on the x-axis corresponds with the marked starting location for sampling each month.

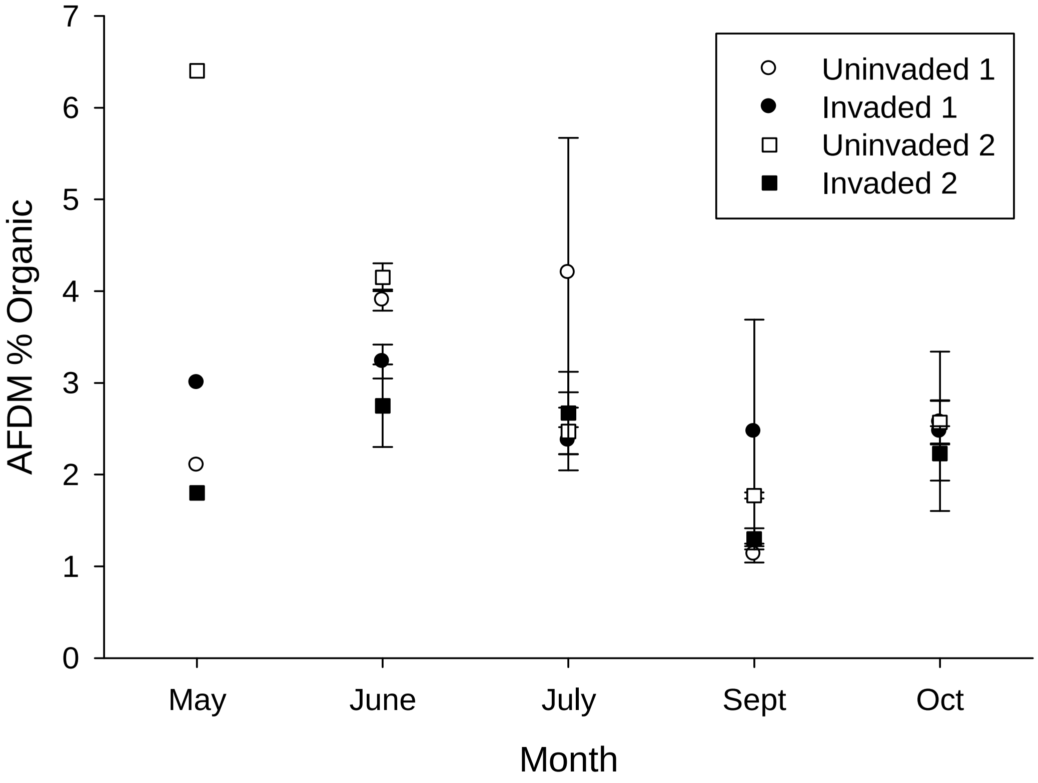


Figure 3.5—Ash free dry mass (AFDM) percent organic fraction in invaded populations and uninvaded populations. Uninvaded populations are represented with open symbols and invaded populations are represented with solid black symbols. Error bar represent one standard error.

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CHAPTER FOUR

BIOTIC INTERACTION GRADIENTS BETWEEN NATIVE AND INVASIVE SPECIES

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Kiza K. Gates

Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

Co-author: Billie L. Kerans

Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Abstract

Much research has been devoted to understanding how interactions shift along abiotic gradients of stress, but less is known about biotic gradients and how they can affect the strength and intensity of interactions between species. We explored the interaction between the native aquatic gastropod, *Valvata humeralis,* and invasive aquatic gastropod, *Potamopyrgus antipodarum,* along a biotic gradient of density in a system where we suspected that an interaction shift was occurring. We experimentally quantified the intra- and interspecific net effects of these species on each other and tested the results in a field setting by comparing them with field surveys. *Valvata humeralis* growth was significantly greater in treatments containing *V. humeralis* and *P. antipodarum* at 400/m^2 each (total gastropod density 800/m^2) when compared to growth of *V. humeralis* alone at 400/m^2. The facilitative growth effect disappeared at higher snail densities indicating it was density specific. Field surveys indicated that competition between the species at medium densities did not negatively affect *V. humeralis* growth, but did not show the same facilitation seen in the experiment. Experimental and field results combined suggest that the shifting interaction between species is intertwined with other biotic and abiotic factors in the field. Our results confirm that interactions between a native and an invasive species can shift along a biotic density gradient potentially influencing invasive species impact.

Introduction

Interactions between neighboring species are often bidirectional existing along a gradient from competition to facilitation, but are rarely studied as such (Bronstein 1994; Bruno et al. 2003). Bidirectional interactions are the result of changes in the interaction components that sum to make the net interaction. Interactions change direction along environmental stress gradients (Bertness and Callaway 1994; Callaway and Walker 1997; Brooker and Callaghan 1998; Kawai and Tokeshi 2007; Brooker et al. 2008) over different spatial scales (Bertness et al. 1999; Callaway et al. 2002) and through time (Tielborger and Kadmon 2000; Kawai and Tokeshi 2007). These bidirectional interactions create non-linear interaction coefficients which produce unexpected outcomes between species that are thought to compete (Bowden, Gates, Kerans, and Taper, in preparation). More exploration of the feedbacks that create bidirectional interactions between species is needed to understand ecological dynamics (Agrawal et al. 2007).

Much of our knowledge of changing interactions comes from research exploring the Stress-Gradient Hypothesis (SGH) with sessile organisms and abiotic stress gradients. The SGH predicts that in high stress environments, the amelioration of stress for one species, the beneficiary, by another species, the benefactor, produces a facilitation that offsets competition for resources. In other words, the occurrence of competitive and facilitative interactions varies inversely with increasing stress (Bertness and Callaway 1994; Maestre et al. 2009). Facilitation typically takes the form of habitat enhancement where habitat quality is increased (through resources or non-resources) for one species by the presence of another (Maestre et al. 2009). This form of facilitation has been commonly identified among plants (Went 1942; Callaway 1995; Callaway and Walker 1997) and intertidal marine organisms (Bertness 1989; Bertness et al. 1999; Kawai and Tokeshi 2004). Stresses that can be ameliorated by the presence of another species include exposure to heat (Kawai and Tokeshi 2006; Kawai and Tokeshi 2007), wave-action (Kawai and Tokeshi 2006; Kawai and Tokeshi 2007), or anthropogenic disturbance (Villarreal-Barajas and Martorell 2009). In all of these cases, the facilitation and shifting interaction only become apparent in high stress environments when the presence of the benefactor is facilitative for the beneficiary outweighing the competitive interactions under lower stress. In this manner, the abiotic gradient of stress determines the net species interaction.

Biotic stress gradients have not been extensively explored despite their potential to create bidirectional interactions that influence species coexistence similar to abiotic gradients. Some biotic gradient research has been conducted exploring plant interactions along a consumer stress gradient of grazing intensity (Smit et al. 2007; Smit et al. 2009; Graff et al. 2007; Graff and Aguiar 2011). This work has found evidence of interaction shifts along a consumer stress gradient, but results have been mixed with some evidence aligning with the SGH (Graff and Aguiar 2011) and some requiring modifications of the SGH (Smit et al. 2009; Soliveres et al. 2011). Another potential biotic stress gradient that has received even less attention is benefactor density (Bruno and Bertness 2001; Bulleri et al. 2011). Preliminary research with benefactor density gradients indicates that the interaction between benefactor and beneficiary can change along a benefactor density gradient, but that the outcome may also be dependent on abiotic stress levels (Irving and Bertness 2009) or individual species traits (Bulleri et al. 2011). More research is needed to better understand the influence of benefactor density gradients on species coexistence.

Inconsistent outcomes from the interactions of biologically similar species often occur in invasion ecology. Invasive species, non-native species with a history of causing ecological or economic impact, often only exhibit invasive behavior in particular geographic locations (Kolar and Lodge 2001) and many introductions do not appreciably change the receiving community (Williamson 1996; Davis 2003). Failure of an invasive species to impact native species can sometimes be attributed to their inability to proceed through the entire invasion process; yet, there can still be considerable variation in native species response among invasion sites. The mechanism of this variation is uncertain. The potential influence of positive interactions between invasive and native species is rarely considered despite the prevalence of positive interactions (Bruno et al. 2005) and existing evidence that interactions may shift along invasive density gradients promoting coexistence with native species (Straube et al. 2009).

Previous research with the invasive aquatic gastropod *Potamopyrgus antipodarum* is suggestive of shifting interactions with native invertebrates. *Potamopyrgus antipodarum* is known for achieving densities in excess of 250,000 snails/m^2 (Richards et al. 2001; Kerans et al. 2005; Alonso and Castro-díez 2008). Factors which have been suggested to contribute to the success of *P. antipodarum* in introduced systems include their parthenogenic and ovoviviparous reproduction (Dorgelo 1988), high secondary production (Hall et al. 2006), ability to reproduce throughout most of the year (Dorgelo

1987), and ability to quickly re-colonize disturbed areas (Schreiber et al. 2003). Yet while *P. antipodarum* has invaded many Western waters, there is considerable variability in invasion establishment among systems. *Potamopyrgus antipodarum* can dominate invertebrate numbers and biomass in established areas (Kerans et al. 2005; Hall et al. 2003) sometimes with the aid of native species (Riley et al. 2008), but also experiences extreme population crashes (Dorgelo 1988) and coexist through time with native gastropod species (Siegismund and Hylleberg 1987). For example, in the Vista reach of the Middle Snake River high densities of the native aquatic gastropod *Valvata humeralis* coexist with *P. antipodarum* (Gates and Kerans, Chapter 3). Despite suspected competition with *P. antipodarum* (Lysne and Koetsier 2008); the native *V. humeralis* has maintained large populations with *P. antipodarum* for over a decade in some locations. We hypothesized that coexistence of these two species was promoted by an interaction that shifts from negative to positive along a benefactor density gradient where *P. antipodarum* is the benefactor and *V. humeralis* is the beneficiary.

We explored the interaction between a native species (beneficiary) and invasive species (benefactor) along a biotic stress gradient of benefactor density in a system where we suspected that an interaction shift was occurring. We experimentally quantified the intra- and interspecific net effects of the native species *V. humeralis* and the invasive species *P. antipodarum* along a gradient of density and species proportion. We tested the hypothesis that the effect of an invasive species on a native species changes with density of the invasive species using a field experiment and tested the results in a field setting by comparing them with field surveys.

Methods

Study Species and Site

Research was conducted in the Vista reach of the Middle Snake River below American Falls Dam (Latitude 42°46’03”, Longitude 112°52’46”, RM 713). Previous surveys indicated that *V. humeralis* and *P. antipodarum* have coexisted in this reach for at least 15 years (R. Newman, Bureau of Reclamation, personal communication). The Vista reach is characterized by a narrow channel allowing most of the riverbed to remain watered throughout the year despite dramatic changes in discharge from American Falls dam upriver (11-425 m^3/s 2000-2010 mean low and high discharge). Water temperature fluctuates from 5-22 °C throughout the year.

Our target native species, *V. humeralis,* is a colonial species that forms distinctive populations that can be found from year to year in the same location and are known to coexist with *P. antipodarum* in the Middle Snake River making them a good candidate for interaction studies (R. Newman, personal communication). In addition, *V. humeralis* is semelparous reproducing in late summer in the Snake River allowing a cohort to be followed throughout the year. Our target invasive species, *P. antipodarum*, has been a successful invader of lentic and lotic freshwaters of Australia (Schrieber et al. 2003), Europe (Dorgelo 1987), and more recently North America (Bowler 1991; Langenstein and Bowler 1991; Bowler and Frest 1992; Zaranko et al. 1997; Richards et al. 2001). A broad diet and physiological tolerance (Winterbourn 1970, Dorgelo et al. 1995; Collier and Winterbourn 2000) and continuous reproduction give *P. antipodarum* a potentially competitive advantage in many habitats (Loo et al. 2007). Other gastropod species within the Vista reach include the native species *Gyraulus parvus*, *Fluminicola fuscus*, *Lymnaidae* sp., *Physella gyrina*, *Stagnicola* sp., *Valvata utahensis*, and *Vorticifex effusa*.

Field Experiment

We assessed the effects of intraspecific and interspecific density on the growth and mortality of *V. humeralis* and *P. antipodarum* with a field cage experiment modified from Underwood (1997) and Cope and Winterbourn (2004). We used growth and mortality as indicators of interaction direction and intensity. There were three densities levels; low (6 snails/cage or 400 snails snails/m^2), medium (12 snails/cage or 800 snails/m^2), and high (18 snails/cage or 1200 snails/m^2) (Table 4.1). The low density treatment corresponded with the average *V. humeralis* density found in the field during population surveys in 2008 (Chapter 3). We created seven treatments including low density *V. humeralis*, medium density *V. humeralis*, low density *P. antipodarum*, medium density *P. antipodarum*, medium density *V. humeralis* and *P. antipodarum* (1:1), high density *V. humeralis* and *P. antipodarum* (1:2), and high density *V. humeralis* and *P. antipodarum* (2:1). Within these treatments, we measured growth and mortality of *V. humeralis* in all five treatments containing *V. humeralis* and we measured growth and mortality of *P. antipodarum* in all five treatments containing *P. antipodarum* creating 10 levels of the response variable. We replicated treatments three times.

We constructed cages of clear modified plastic food storage containers (12 x 12 x 12 cm) with flow-through 0.5 mm Nitex vents on the top and two opposite sides to prevent snail movement in or out, but to allow water circulation. We covered the cage floor with local substrate (3-5 flat stones with a combined top surface area of approximately 130 cm^2) that was sifted and picked free of macroinvertebrates. We weighted cages to rest on the top surface of substrate and cage position was randomly assigned within a 5 X 5 m grid in the littoral zone at a depth of 0.5- 0.7 m. We assumed that cage effects would be minimal with this design because of the small size of gastropods used relative to the cages (1-3 mm versus 12 cm), the use of local substrate, and cage placement in local habitat.

We collected *V. humeralis* and *P. antipodarum* from the Vista reach using a Venturi suction dredge. We used juveniles of both species (*V. humeralis* < 2 mm and *P. antipodarum* < 3 mm) to capture growth potential and avoid measuring lack of growth associated with reproduction. We measured individual shell lengths to the nearest 0.01 mm with a digital micrometer on day 0 and then snails were randomly assigned to treatments. We did not mark individuals, thus a randomly selected group of six individuals of each species in each treatment were used to calculate biomass. The experiment took place over the course of 10 days from August 11- 20, 2008. August is the month that the new annual cohort of *V. humeralis* appears and between August and September they grow rapidly (R. Newman, personal communication; Chapter 3). We measured shell length as described above again on day 10 and converted shell lengths to ash free dry mass (AFDM) with an established length to mass equation for *P. antipodarum* (Hall et al. 2006). We developed our own length to mass equation for *V. humeralis* (Benke et al. 1999). The regression for *V. humeralis* was mass = $0.0868L^{3.1427}$ where mass is measured in mg (AFDM) and length (L) is measured in mm ($n = 52$, $r^2 = 0.72$) (Appendix A). Our *V. humeralis* mass includes shell mass while the *P.*

antipodarum mass does not, thus biomass was relativized with initial biomass and relative growth changes were not compared between species. We calculated biomass specific growth rates as the ratio of after biomass to before biomass in ((mg/mg)/individual)/day modified from Cross and Benke 2002 as:

$$g = \frac{((M_t - M_0)/M_0)/n}{t}$$

Where M_t is total gastropod biomass at the end of the experiment (mg AFDM), M_0 is the total initial gastropod biomass (mg AFDM), n is the number of individuals in the treatment used for the mean calculation (n = 6), and *t* is the duration of the experiment (days).

In the field experiment, we compared relative growth and mortality among treatments with a one-way multiple analysis of variance (MANOVA). If the MANOVA was significant, we used individual one-way analyses of variance (ANOVAs) for growth and mortality to explore independent effects of treatment type. If the effects in the ANOVAs were significant, we tested for significant differences among treatments with independent contrasts based on our experimental design. We compared the low density intraspecific treatment to the medium density intraspecific, medium density interspecific, and high density interspecific treatments (Underwood 1997). We arcsine square root transformed percent mortality to meet assumptions of normality. Biomass values and variance met assumptions of normality and were not transformed.

We used changes in snail tissue biomass to calculate net effect sizes. We calculated effect size as the natural log of the ratio of treatment to control biomass change (Gurevitch and Hedges 2001; Kawai and Tokeshi 2007) as:

$$\text{Net effect} = \ln(M_t/M_0)$$

Where M_t is total gastropod biomass at the end of the experiment (mg AFDM) and M_0 is the total initial gastropod biomass (mg AFDM). The control for all effect size calculations of a species was the low density intraspecific treatment. To create three replicate net effect values for each comparison, we randomly selected three control and three treatment mean ratios (M_t/M_0) from the replicates and calculated a standard error. We compared the effects of treatment type on net effect with a one-way ANOVA. If the effect in the ANOVA was significant, we tested for significant differences among treatments with individual contrasts within species. We used an alpha value of 0.05 to confer significance and did not use dead snails in any statistical analysis.

Field Surveys

We examined biomass of *V. humeralis* from a population coexisting with *P. antipodarum* in the Vista reach to determine if growth results from our experiment were concordant with those of existing populations. We divided samples taken during the field surveys into categories matching those from the density and species proportions of the field experiment when possible. The semelparous life history of *V. humeralis* allowed us to use mean individual biomass from a sampling event as the mean individual biomass of the population on that sampling date. We selected one long-standing *V. humeralis* population that had been present in the Vista reach for at least six years from prior surveys (1998-2006) and had contained *P. antipodarum* this entire time.

The *V. humeralis* population was sampled monthly during the second week of each month from May through November of 2008 and May through August of 2009.

Sampling months reflected the active period of the year for gastropods in the region when they can be found most readily (Cleland 1954; Hershey 1990; Lysne 2003; Lysne and Koetsier 2006b). We established a fixed transect in April which ran perpendicular to shore (perpendicular transect) through the greatest density of *V. humeralis* in the population. We marked the fixed transect on shore with rebar and revisited each month thereafter as the reference starting point for sampling. We began sampling each month by sampling along the perpendicular transect every 2 m moving out from the rebar and ceased when *V. humeralis* density decreased by 75% from the highest sample density. We placed another transect parallel to shore (parallel transect) through the greatest density of *V. humeralis* found while sampling along the perpendicular transect. We collected samples outward every 5 m along the parallel transect beginning at the intersection with the perpendicular transect. We ceased sampling along the parallel transect in both directions as described above.

We collected samples with a 0.25 m^2 plot, Venturi suction dredge, and SCUBA certified diver. We transported samples to the surface in flexible piping and passed through a 1 mm sieve bucket to remove sand and silt. We separated all *V. humeralis* and measured them from the anterior end of the shell across to the apex to the nearest 0.01 mm with digital calipers. We converted *V. humeralis* shell length to biomass (mg AFDM) as described previously. When samples were too large to search entirely, we thoroughly mixed contents and sub-sampled 50%. We considered samples devoid of *V. humeralis* and *P. antipodarum* after 30 min. of searching and we returned all sample contents to the plot where they were collected after measurements were taken. We counted abundance of other gastropod species present during 2009 sampling.

We compared mean individual *V. humeralis* biomass (size) from sample plots among categories matching the growth experiment with a one-way ANOVA in both years separately. If the effect in the ANOVAs was significant, we tested for significant differences among treatments with individual contrasts matching those of the field growth experiment (low density intraspecific compared to all other treatments). We used an alpha value of 0.1 to confer significance with the field survey data to balance error types and avoid being overly restrictive. We log transformed biomass to meet assumptions of normality in 2008 and 2009.

All measures of variability listed in parentheses are one standard error. We made no corrections for multiple independent contrasts following significant ANOVA effects because all contrasts were planned in the design of the experiments (Keppel and Wickens 2004). We performed all statistical procedures in SAS (9.3).

Results

Field Experiment

Mortality and relative growth varied significantly among treatments (Wilks' Lambda = 0.08, $F_{18,34} = 4.62$, $p < 0.0001$). Relative growth ($F_{9,18} = 3.14$, $p = 0.02$) and mortality ($F_{9,18} = 8.21$, $p < 0.0001$) were affected by treatment. *Valvata humeralis* growth was significantly greater in treatments containing *V. humeralis* and *P. antipodarum* at $400/m^2$ each (total gastropod density $800/m^2$) when compared to growth of *V. humeralis* alone at 400/m^2 ($F_{1,18} = 7.52$, $p = 0.01$). The increased growth of *V. humeralis* with *P. antipodarum* disappeared at higher gastropod densities (Figure 4.1). Mortality of *V. humeralis* was greatest in the low density intraspecific treatment and was marginally significantly different from mortality in the medium density intraspecific treatment ($F_{1,18} = 3.73$, $p = 0.07$) (Figure 4.1).

Although not statistically significant, *P. antipodarum* growth decreased as gastropod density increased in interspecific treatments with the exception of the high density V+2P treatment where growth matched the low density (Figure 4.2). Mortality of *P. antipodarum* was generally low and significantly higher in the medium density combined species treatment than the low density intraspecific treatment ($F_{1,18} = 6.76$, 0.02) (Figure 4.2).

Net effects varied significantly among intraspecific and interspecific treatments for both *V. humeralis* and *P. antipodarum* ($F_{5,12} = 4.98$, $p = 0.01$) (Figure 4.3). The interspecific net effect of *P. antipodarum* on *V. humeralis* was positive and significantly larger in the medium density than the high density treatment ($F_{1,12} = 5.77$, $p = 0.03$). The net effect of *V. humeralis* on itself at 800/m^2 was slightly positive and significantly smaller than the positive interspecific net effect of *P. antipodarum* on *V. humeralis* at the same density ($F_{1,12} = 4.66$, $p = 0.05$). The net effect of *P. antipodarum* on itself was negative at 800/m^2 and not significantly different from the effects of *V. humeralis* on *P. antipodarum* at 800/m^2 ($F_{1,12} = 3.74$, $p = 0.08$) or 1200/m^2 ($F_{1,12} = 0.18$, $p = 0.68$).

Field Surveys

We collected 55 samples in 2008 and 46 samples in 2009 from the *V. humeralis* population. August was the only month during both years of sampling in which the densities and proportions of *V. humeralis* and *P. antipodarum* matched those from our growth experiment. Eleven samples from 2008 and eight samples from 2009 were used in the comparisons with the field experiment.

We split samples from August 2008 into four categories and samples from August 2009 into three categories (Table 4.2). In 2008, we measured the shell lengths of 180 *V. humeralis*. Treatment category was a significant predictor of size ($F_{3,177} = 2.23$; $p = 0.09$). Matching our growth experiment, mean *V. humeralis* size in the V+P treatment was greater than those in the VV and VVV treatments although independent contrasts were not made because they were not planned. Contrary to our growth experiment, mean size in samples matching the V (n = 10) treatment was significantly greater than mean size in samples matching the VV (n = 28) ($F_{1,177} = 6.24$, $p = 0.01$), V+P (n = 87) ($F_{1,177} = 4.56$, $p = 0.03$), and VVV (n = 55) ($F_{1,177} = 5.42$, $p = 0.02$) treatments (Figure 4.4). In 2009, we measured the shell lengths of 223 *V. humeralis*. Treatment category was a significant predictor of *V. humeralis* size ($F_{2,221} = 2.31$; $p = 0.10$). Mean size in samples matching the V treatment (n = 47) were not significantly different from mean size in samples matching the V+P treatment (n = 153) ($F_{1,221} = 0.13$, $p = 0.72$), but were significantly greater than the mean size in the lower density other category (n = 23) ($F_{1,221} = 2.71$, $p = 0.10$) suggesting a benefit from the added *P. antipodarum* similar to our growth experiment (Figure 4.4).

Other species found in *V. humeralis* population samples in 2009 included *G. parvus*, *Lymnaidae* sp., *P. gyrina*, *Stagnicola* sp., *V. utahensis*, and *V. effusa.* Species other than *V. humeralis* and *P. antipodarum* were found at densities of $< 40/\text{m}^2$ in fewer than 25% of the samples with the exception of *G. parvus* which was found at densities as high as $568/\text{m}^2$.

Discussion

Our results provide evidence that interactions among native and invasive species can change in intensity and direction along invasive (benefactor) density gradients facilitating the native (beneficiary). In our growth experiment, *V. humeralis* exhibited increased growth in interspecific medium density treatments with *P. antipodarum* compared to growth in low density intraspecific treatments. The facilitative effect of *P. antipodarum* on *V. humeralis* growth was not apparent in the high density interspecific treatment suggesting that the facilitation was directly related to the medium density of *P. antipodarum*. The net effect calculations mirrored these results showing an increase in the net effect of *P. antipodarum* on *V. humeralis* size when compared with the low density intraspecific treatment and high density interspecific treatment. In contrast to *V. humeralis*, *P. antipodarum* experienced decreased growth with increasing density in the interspecific treatments but not intraspecific treatments. Intraspecific net effects of *P. antipodarum* were slightly greater than interspecific effects at the medium density suggesting that intraspecific competition may be greater than interspecific competition with *V. humeralis*.

Field surveys of *V. humeralis* size supported our experimental results on some levels but not others. Similar to our field experiment results, size in the medium interspecific treatment (hereafter referred to as facilitation treatment) in 2008 was larger than the medium density intraspecific or high density intraspecific treatment although not statistically significant. Surveys in 2009 also matched our growth experiment in that *V. humeralis* size in samples that matched the facilitation treatment was greater than size in the low density other category suggesting a benefit to the presence of added *P. antipodarum.* Yet, size in samples matching the low density intraspecific *V. humeralis* treatment were either greater (2008) or the same (2009) as size in samples matching our facilitation treatment. Sample sizes for the low density intraspecific treatment were low in 2008 and may not provide a robust estimate. Field survey results from both years indicate that the interaction between *V. humeralis* and *P. antipodarum* is influenced by other factors in a field setting such as abiotic conditions and neighboring species.

A number of factors may have contributed to the differences we saw in our field experiment and field survey data. The quantity of food was standardized in our experiment, but likely fluctuated in the field setting. Difference in the abundance and nutritional quality of food among plots could have contributed to the muted facilitative effect of *P. antipodarum* on *V. humeralis* in the field survey. In addition, other gastropod species were present in the field surveys creating more complex community interactions. Most notably, *G. parvus* densities were greater at times than our target species, *V. humeralis* and *P. antipodarum*. The influence of *G. parvus* on our target species growth is not known, but likely affected our results. Lastly, mortality in the low density intraspecific *V. humeralis* treatment was higher than in other treatments and may have contributed to the decreased growth in this treatment although no deceased gastropods were used in growth calculations.

Our research supports the hypothesis that some of the variation in the impact of *P. antipodarum* on native species among geographic locations may be explained by interaction changes along invader density gradients. The ability of *P. antipodarum* to reach extremely high densities suggests they would compete with native macroinvertebrates for habitat and food; however, prior research with *P. antipodarum* has demonstrated mixed responses. *Potamopyrgus antipodarum* have been found to dominate native macroinvertebrate assemblages in Australia (Quinn et al. 1998); however, when *P. antipodarum* densities were manipulated over brief temporal time scales (6 days) in previously invaded Australian streams, higher densities of *P. antipodarum* were positively correlated with native macroinvertebrate diversity (Schreiber et al. 2002). In a nearly opposite outcome, *P. antipodarum* densities where found to negatively affect macroinvertebrate colonization rates in the Greater Yellowstone Ecosystem (GYE) (Kerans et al. 2005); yet, later surveys revealed broad-scale reductions in density of previously high density populations (B. Kerans and R. Richards, unpublished). Mixed results from previous research exploring the impact of *P. antipodarum* on native macroinvertebrates could have resulted from shifting interactions that promote coexistence at some invader densities but not others.

Our results agree with previous experiments indicating that *P. antipodarum* can facilitate other gastropod species as well as be facilitated by them under different conditions potentially affecting invader impact. For example, *P. antipodarum* presence was found to increase the fecundity of another invading snail, *Physella acuta*, when both snails were kept at equal densities (Cope and Winterbourn 2004) suggestive of reproductive facilitation. In an opposite outcome, Riley and colleagues (2008) found that *P. antipodarum* growth was facilitated by the presence *Pyrgulopsis robusta* potentially accelerating *P. antipodarum* impact in some settings. Our experimental results showed that growth of the native *V. humeralis* was facilitated by *P. antipodarum* when densities of the invader were moderate. While our field survey results were slightly different, they still indicated that the addition of *P. antipodarum* in plots did not decrease growth of *V. humeralis* indicating a lack of or low levels of competition. Combined, our experiment and field survey results show invader impact changing non-linearly with invader density and illustrate a mechanism of varied invader impact among locations and native species.

The mechanism of *P. antipodarum*'s facilitative effect on *V. humeralis* growth and the reason why it was density specific is uncertain. Previous research with gastropods has provided evidence of facilitation among species at varying densities (Brown 1982; Hershey 1990; Cope and Winterbourn 2004; Riley et al. 2008) with coprophagy frequently proposed as a potential mechanism (Schreiber et al. 2002). There is ample evidence that invertebrate herbivores can increase the quality of food around them by grazing (Hunter and Russell-Hunter 1983; Ruess and McNaughton 1984; Hillebrand et al. 2000; Liess and Hillebrand 2006; Liess and Kahlert 2007). Freshwater benthic grazers can increase epilithon nutrient content via excretion creating higher quality in areas where they graze (Hillebrand and Kahlert 2001; Hillebrand et al. 2004;

Evans-White and Lamberti 2005). Schreiber and colleagues (2002) hypothesized that nutrients excreted by *P. antipodarum* provided food for other macroinvertebrates thereby increasing habitat suitability and increasing native species diversity. The benefit of increased food quality from *P. antipodarum* could be outweighed by increased competition as density of *P. antipodarum* increases potentially explaining why the facilitative effect of *P. antipodarum* on *V. humeralis* growth in our experiment was not apparent at higher densities. In other words, competitive interactions at higher densities may have dampened the facilitation seen at medium densities making it undetectable.

The implications of interactions shifting along biotic gradients are potentially substantial for invasive molluscan species. Introduced competitors are suggested as a driving force of extinction among global native freshwater molluscs (Lydeard et al. 2004). In North America, the persistence of native molluscan fauna has been threatened by the introductions of the Zebra mussel *Dreissena polymorpha*, the Quagga mussel *Dreissena rostriformis bugensis*, the Faucet snail *Bithynia tentaculata* (Jokinen 1992; Harman 2000), the Island apple snail *Pomacea insularum*, in addition to *P. antipodarum* (Lysne and Koetsier 2008; Riley et al. 2008). Introduced competitors may impact native Molluscan fauna through habitat alteration (Tucker 1994), competition for food and space (Murray et al. 1998; Baker and Levinton 2003; Haynes et al. 2005; Kerans et al. 2005; Hall et al. 2006), and resource depletion (Holland 1993; Nichols and Hopkins 1993; Caraco et al. 1997; Hall et al. 2003). Yet many questions remain regarding behavioral interactions that could affect the outcome of these interactions. Our results support the hypothesis that biotic and abiotic gradients may create unexpected population level impacts between native and invasive species (Dick 2008) potentially favoring native species.

Benefactor and beneficiary interactions that shift along biotic density gradients may also have widespread and potentially substantial implications for community dynamics. It has been increasingly acknowledged that shifting interactions can affect community structure and promote species coexistence (Choler et al. 2001; Peacor and Werner 2004; Gross 2008). Modeling efforts suggest that resource competitors can coexist in stable multi-species assemblages when species interactions shift from predominantly competitive to facilitative along a stress gradient even when the net interaction remains negative (Gross 2008). The facilitative species, or benefactor, may even create new interaction webs that indirectly affect other species within the community (Hacker and Gaines 1997). Indeed, recent research with freshwater bivalves suggests that species interactions may shift at higher abundances altering biodiversity affects (Allen and Vaughn 2011). If interaction shifts can occur along biotic gradients of species composition, shifting interactions may be much more common and influential in determining community structure than previously thought.

Past studies of shifting interactions between benefactor and beneficiary species have focused on abiotic drivers, but biotic gradients may be as important in structuring communities. We found the net effects between an invasive and native species shifted positively with increasing density of the invasive favoring the native's growth. Our research highlights the importance of considering biotic density gradients as drivers of species interaction shifts. Further, our research shows that non-linearity of interaction coefficients has the ability to affect invasive and native species interactions influencing the ecological impacts of invasive species. Further research is needed to explore mechanisms of biotic density gradients.

Table 4.1. Treatments for examining effects of density on growth of *V. humeralis* and *P. antipodarum* in field growth experiment. Controls are represented by ‘V’ and ‘P’ treatments alone.

	Density treatments		
	$400/m^2$	$800/m^2$	$1200/m^2$
Intraspecific effects			
Valvata humeralis	V	VV	-
Potamopyrgus antipodarum	P	PP	-
Interspecific effects			
V. humeralis + *P. antipodarum*		V+P	V+PP
P. antipodarum + *V. humeralis*		P+V	P+VV

Table 4.2.—Sample splitting from August of 2008 and 2009 field surveys. Categories were designed to match the density and proportion of species from treatments in the field growth experiment. No. indicates sample number. Target density and target proportion describe sample splitting criteria. Species densities list actual number of each species and total density of both species per m^2. Sample number (n) indicates number of shells measured in a sample and used in analysis of variance (ANOVA). Samples numbers not listed had < 20 *V. humeralis*/m^2.

No.	Category	Field exp. density	Target density	Target proportion	*V. humeralis*/m^2	*P. antipodarum*/m^2	Total/m^2	% *V. humeralis*	n
2008									
5	V	400/m^2	< 500/m^2	10:1 ± 1	276	32	308	0.90	4
9	V				438	54	492	0.89	6
7	VV	800/m^2	> 500 and < 1000/m^2	10:1 ± 1	848	0	848	1.00	16
10	VV				656	0	656	1.00	12
1	V+P			50:50 ± 10	328	172	500	0.66	82
11	V+P				320	152	472	0.68	5
2	VVV	1200/m^2	> 1000/m^2	10:1 ± 1	1280	16	1296	0.99	20
3	VVV				992	32	1024	0.97	16
4	VVV				1120	48	1168	0.96	19
2009									
3	V	400/m^2	< 500/m^2	10:1 ± 1	227	26	253	0.90	47
4	V+P	800/m^2	> 500 and < 1000/m^2	50:50 ± 10	344	216	560	0.61	84
5	V+P				126	192	318	0.40	26
7	V+P				184	216	400	0.46	33
8	V+P				88	128	216	0.41	10
2	Low other	na	> 20 and < 150/m^2	na	60	61	121	0.50	15
6	Low other				12	120	132	0.09	3
9	Low other				40	64	104	0.38	5

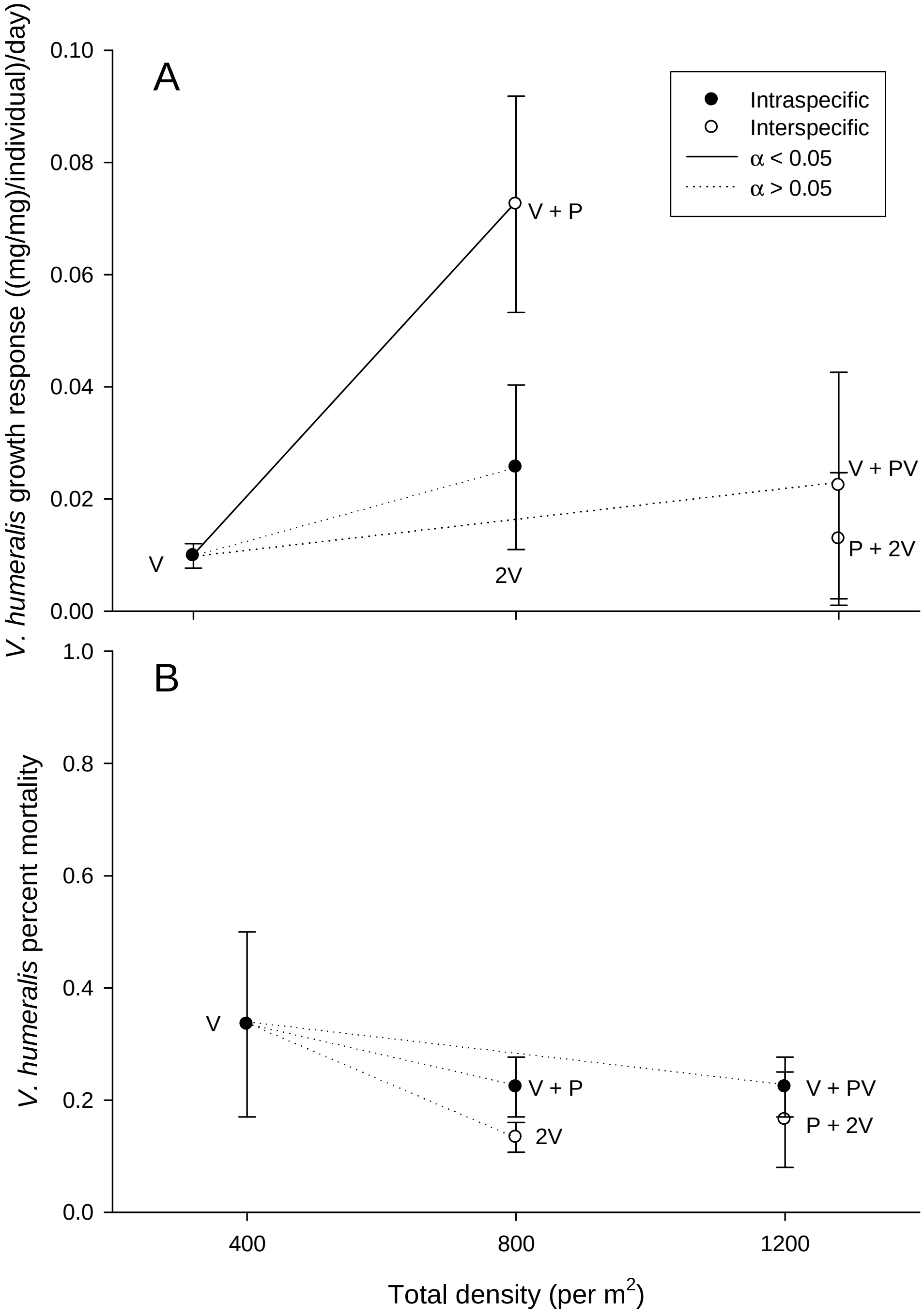

Figure 4.1.—*Valvata humeralis* individual growth response (panel A) and mortality (panel B) in the five field experiment treatments. Filled circles represent intraspecific treatments and open circles represent interspecific treatments. The x-axis indicates total gastropod densities of low (400/m^2), medium (800/m^2), and high (1200/m^2). The y-axis indicates mean growth response in ((mg/mg)/individual)/day. Lines represent independent contrasts with significance indicated in the legend. Error bars represent one stand error.

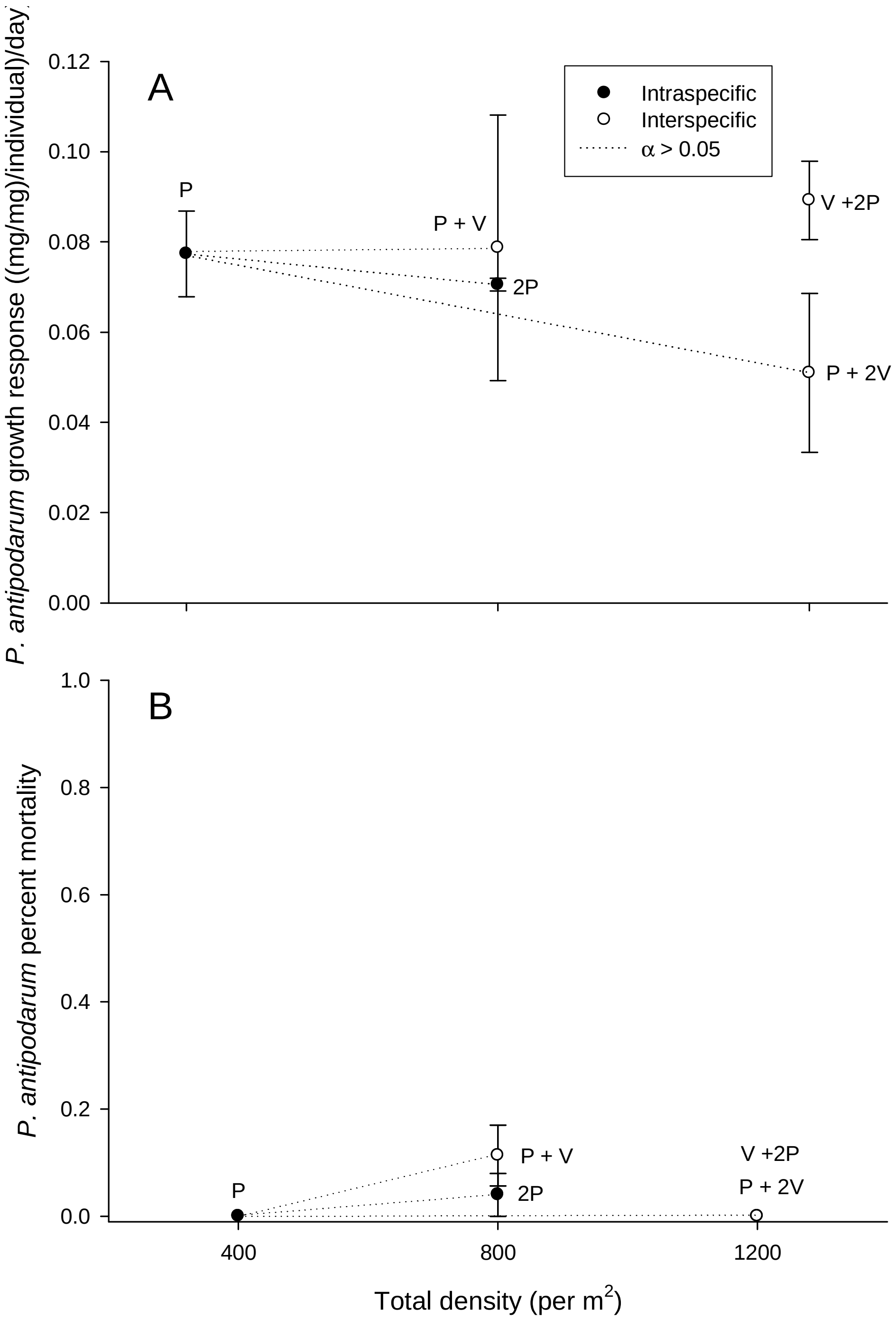

Figure 4.2.—*Potamopyrgus antipodarum* individual growth response (panel A) and mortality (panel B) in the five field experiment treatments. Filled circles represent intraspecific treatments and open circles represent interspecific treatments. The x-axis indicates total gastropod densities of low (400/m^2), medium (800/m^2), and high (1200/m^2). The y-axis indicates mean growth response in ((mg/mg)/individual)/day. Lines represent independent contrasts with significance indicated in the legend. Error bars represent one stand error.

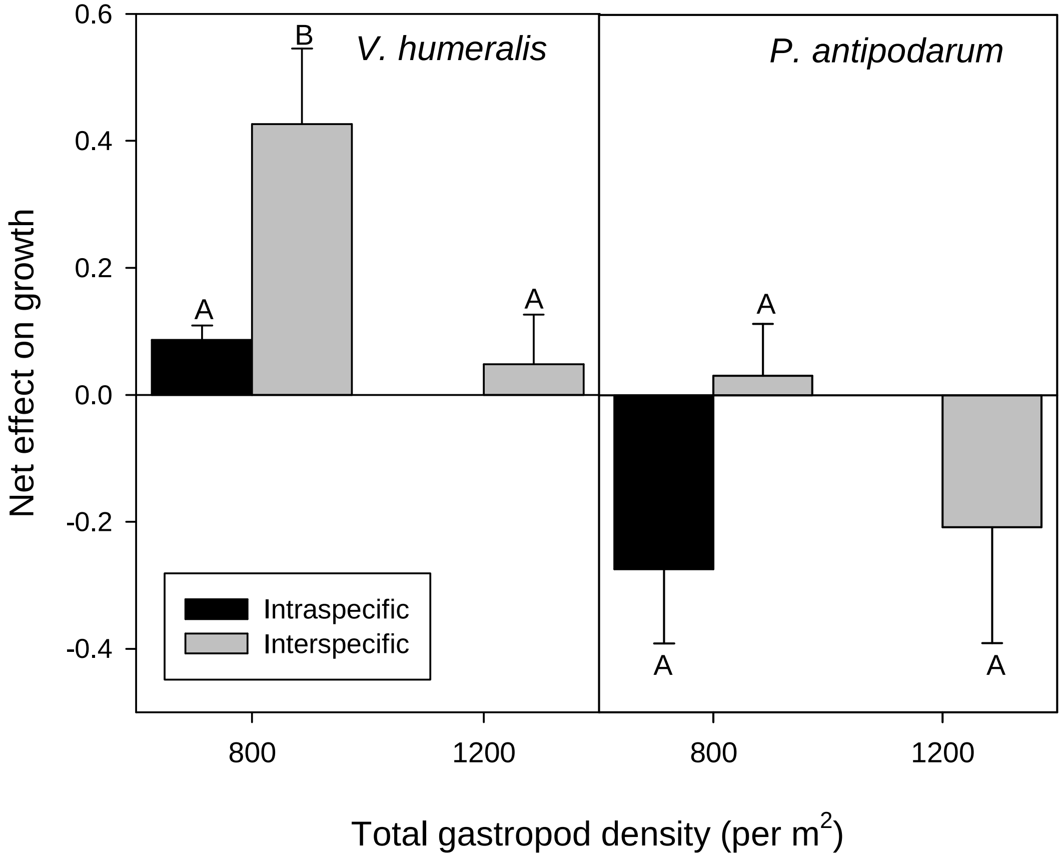

Figure 4.3.—Mean intraspecific and interspecific net effects for *V. humeralis* and *P. antipodarum* from field growth experiment. Net effects represent the magnitude and direction of the effect of the interacting species on the target species as compared to the low density (400/m^2) intraspecific treatment for the target species. Those bars within species that share the same letters do not differ significantly with significance indicated in the legend. Error bars indicate one standard error.

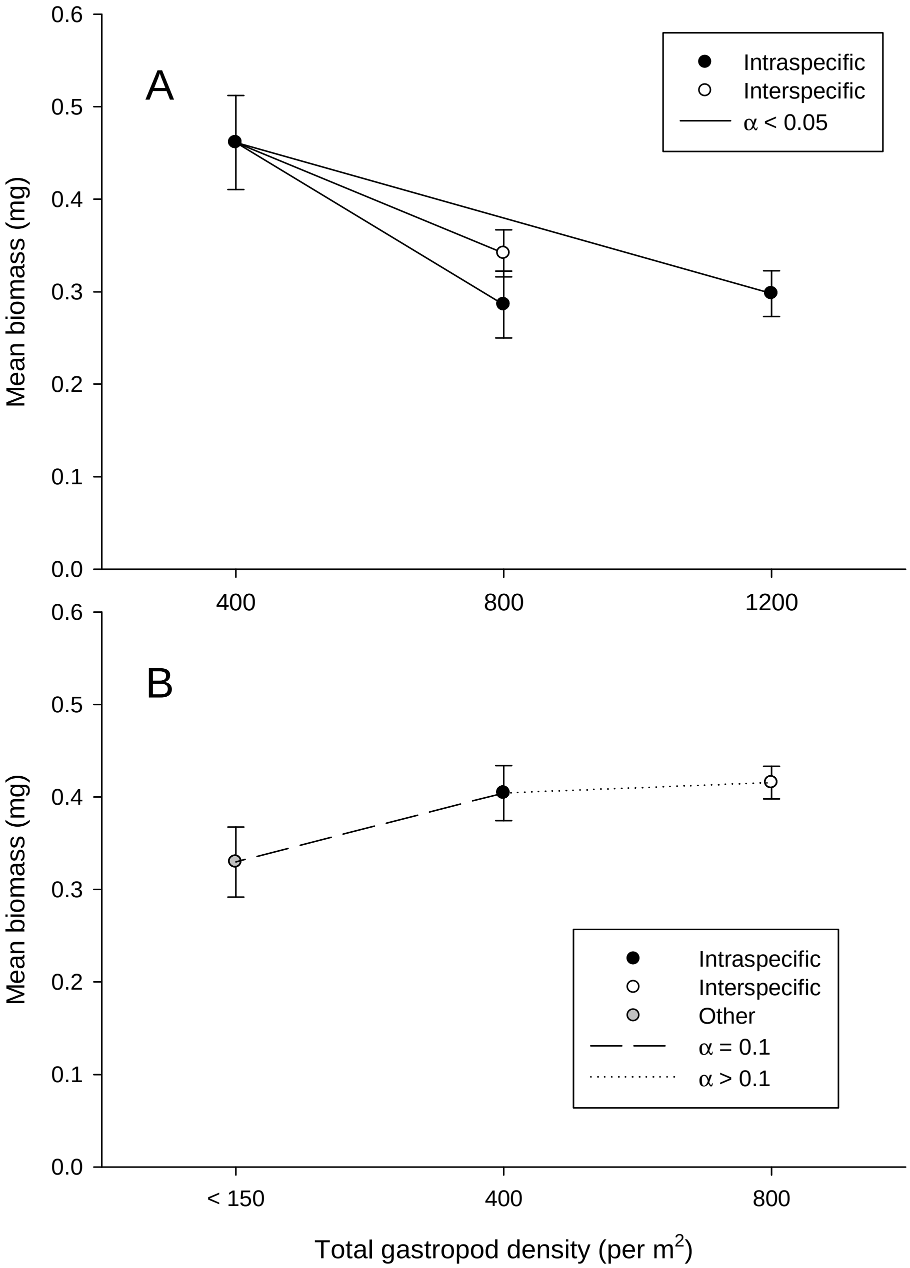

Figure 4.4.—Mean biomass of *V. humeralis* from field samples collected in August of 2008 (panel A) and 2009 (panel B) by treatment categories from the field experiment. Filled circles represent intraspecific treatments, white circles represent interspecific treatments, and grey circles represent samples that did not fit into any of our experimental categories. The x-axis indicates target gastropod densities of low (400/m^2), medium (800/m^2), and high (1200/m^2). Lines represent independent contrasts with significance indicated in the legend. Error bars indicate one standard error.

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CHAPTER FIVE

COMPETITIVE AND FACILITATIVE MECHANISMS OF A BIOTIC INTERACTION GRADIENT

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Kiza K. Gates

Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

Co-author: Billie L. Kerans

Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Abstract

In species that interact through both competition and facilitation, net interaction strength can change from negative to positive along abiotic or biotic gradients as the dominance of competition and facilitation change. We explored competition and facilitation between the aquatic gastropods *Valvata humeralis* (a native) and *Potamopyrgus antipodarum* (an invasive). To assess potential nutrient facilitation, we measured C:N and C:P ratios of *V. humeralis* and *P. antipodarum* body content, excretion, egestion, and field epilithon. To assess competition, we measured the effects of intraspecific and interspecific density and food availability on *V. humeralis* growth and mortality with a laboratory growth experiment. *Potamopyrgus antipodarum* juveniles had a lower ratio of body C:P than *P. antipodarum* adults and both ages of *V. humeralis* indicating that *P. antipodarum* juveniles have a higher phosphorus demand. We did not detect a difference between phosphorus excretion and egestion rates of *P. antipodarum* and *V. humeralis* indicating that facilitation by nutrient enhancement was unlikely. In the laboratory growth experiment, relative growth of *V. humeralis* during week one decreased with increasing density regardless of food quantity indicating that interference was the competitive mechanism. However, growth of *V. humeralis* was increased in high density interspecific treatments during the second week suggesting ontogeny influences the interaction between species. We hypothesize that the facilitative effect of *P. antipodarum* on *V. humeralis* was caused by increased access to food and potentially access to food pre-conditioning by *P. antipodarum*. Our results provide insight into how interactions between native and invasive species can change with density and ontogeny.

Introduction

Organisms may interact in multiple ways causing the effects of one species on another to vary with changing conditions (Bronstein 1994; Bruno et al. 2003). The intensity and direction of the net interaction between species may change as the strength of individual interactions change along abiotic or biotic gradients. Net interaction strength can change direction along gradients of environmental stress (Bertness and Callaway 1994; Callaway and Walker 1997; Brooker and Callaghan 1998; Kawai and Tokeshi 2007; Brooker et al. 2008), biotic stress (Smit et al. 2007; Smit et al. 2009; Graff et al. 2007; Graff and Aguiar 2011), spatial scale (Bertness et al. 1999; Callaway et al. 2002), or through time (Tielborger and Kadmon 2000; Kawai and Tokeshi 2007). The mechanisms linked to each gradient differ but are all related to a tradeoff between different simultaneous interactions. In the case of species interactions that change along biotic stress gradients related strictly to the density of one species, the mechanisms are of particular interest because they may have profound implications for species coexistence.

Competition is undoubtedly the most studied interaction between species (Connell 1983; Schoener 1983; Gurevitch 1992). In fact, biologically similar species that overlap in resource use are often assumed to compete (MacArthur and Levins 1967). Classic competition theory suggests that biological interactions between competing species take either a direct form (interference) or an indirect form (exploitation) (Elton and Miller 1954). In interference, one species directly excludes the other species from access to a common resource (Elton and Miller 1954). In exploitation, one species indirectly prevents access to a common resource by consuming it and making it unavailable to other species (Elton and Miller 1954). While not mutually exclusive, interference and exploitation competition provide a framework for understanding how net interaction strength can change with the addition of a positive interaction.

There is considerable empirical evidence suggesting that facilitation may play a greater role in structuring net interactions than previously thought (Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003). As with competition, facilitation can have direct and indirect forms, which are frequently linked to enhancement of resources by one species. For example, habitat enhancement occurs when habitat quality for one species is increased directly by the presence of another. This form of facilitation has been commonly identified among sessile organisms such as plants (Went 1942) and intertidal marine organisms (Bertness 1989; Bertness et al. 1999; Kawai and Tokeshi 2004) where the presence of an additional species directly reduces exposure of neighboring species to environmental stress. In these examples, the positive effects of stress reduction in high stress environments outweigh the negative effects of resource competition and thereby shift the net interaction from negative to positive.

Facilitative interactions may also occur indirectly through food or nutrients causing net species interactions to change. For example, terrestrial herbivores may facilitate one another by creating access to better quality food through grazing or browsing (Vesey-Fitzgerald 1960; Bell 1970; McNaughton 1976). Herbivores may also enhance resources by increasing food quality through stoichiometric facilitation (Evans-White and Lamberti 2005; Hillebrand et al. 2000; Hillebrand and Kahlert 2001; Hillebrand et al. 2004; Hunter and Russell-Hunter 1983; Liess and Hillebrand 2006;

Liess and Kahlert 2007; Ruess and McNaughton 1984). When an animal consumes a resource, it retains the nutrients needed for metabolic function and excretes or egests excess (Elser and Urabe 1999). Thus, differences in body stoichiometry (specifically carbon:nitrogen:phosphorus or C:N:P) among animals feeding on the same food source cause different rates of nutrient excretion and egestion (Elser and Urabe 1999; Evans-White and Lamberti 2005). Nutrient enrichment experiments simulating excretion and egestion indicate that the nutrient content of food resources can be increased through this process (Cross et al. 2003: Liess and Hillebrand 2006) leading to changing net interactions between organisms (Sommer 1992). Research with aquatic grazers has documented intraspecific facilitation where increased density of grazers decreased food quantity, but increased per capita food quality shifting the net interaction from negative to positive along an increasing density gradient (Sommer 1992). In this example, the indirect facilitation of increasing food quality outweighs competition for resources and thereby shifts the net interaction from negative to positive.

We explored the net interaction between the aquatic gastropods *Valvata humeralis* and *Potamopyrgus antipodarum* in a system where the former is native and the latter is invasive. The net effect of *P. antipodarum* on *V. humeralis* shifts from negative to positive to negative along a gradient of increasing *P. antipodarum* density (Chapter 4). We designed two experiments to explore the facilitative and competitive mechanisms of their net interaction.

To explore the facilitative effect of *P. antipodarum* on *V. humeralis,* we investigated the potential of indirect habitat enhancment because we assumed that direct habitat enhancement was an unlikely facilitative mechanism between mobile gastropods. We measured the potential of *P. antipodarum* to enhance food quality for *V. humeralis* through nutrient recycling and or copraphagy (consumption egestion) by exploring the body content of essential nutrients for both species as well as excretion and egestion of essential nutrients. We also measured the nutrient content of food sources in the field to assess potential nutrient limitation. We hypothesized that body nutrient content would differ between species creating different nutrient requirements and that *P. antipodarum* would excrete and or egest more nutrients that were limiting to *V. humeralis* creating the potential for stoichiometric food facilitation.

In exploring competition, we assumed that interference competition would be more important than exploitation competition because aquatic gastropods have broad diets and are known to participate in coprophagy (López-Figueroa and Niell 1987; Brendelberger 1997). In this manner, food may be changed in quality after consumption but is still available as a food source and is thus never made univalable to competitors (Lopez-Figueroa and Niell 1987; Brendelberger 1997). We therefore tested for interference competition by experimentally quantifying the net effects of *P. antipodarum* on *V. humeralis* along a gradient of gastropod density and species proportion while controlling food quantity on a per individual basis. Controlling food quantity per individual allowed us to infer a direct behavioral interaction if differences in growth occurred among treatments. We hypothesized that interference competition would cause *V. humeralis* growth to decrease linearly with increasing intraspecific density but would change non-linearly with increasing interspecific density based on previous experiments.

Methods

Stoichiometric Facilitation Experiment

We investigated stoichiometric food facilitation from the perspective of potentially limiting nutrients. We measured C:N and C:P ratios of *V. humeralis* and *P. antipodarum* body content to determine whether limiting nutrients differ between species. We determined juvenile and adult body nutrient content separately for both species, because differences in nutrient excretion and egestion among animals may be more pronounced during different life stages (Elser et al. 1996).

We sampled adult *V. humeralis* and *P. antipodarum* from the Vista reach of the Middle Snake River (Latitude 42°46’03”, Longitude 112°52’46”, RM 713) with a Venturi suction dredge and S.C.U.B.A. certified divers in July and August of 2009. The semelparous life cycle of *V. humeralis* allows a cohort to be followed through time and segregates the juvenile and adult life stages. Individuals sampled during any month are typically within 1 mm of the same size because they are from the same cohort (Gates, unpublished). Thus, we sampled adult and juvenile *V. humeralis* during the months when they were present in the population (adults in July and juveniles in August). We sampled *P. antipodarum* during July and August because they are iteroparous and both juveniles and adults were present both months. We collected fifty adult individuals of a species (*V. humeralis* > 2 mm and *P. antipodarum* > 3 mm), and fifty juveniles of a species (*V. humeralis* < 2 mm and *P. antipodarum* < 3 mm) and measured them to the nearest 0.01 mm with a digital micrometer. We stored snails on ice, returned them to the lab, wet-weighed them, de-shelled them, and froze them until further processing (Evans-White et al. 2005; Liess and Hillebrand 2005). We used pooled samples to obtain enough material for elemental analysis (seven samples per species and age group of 1.0- 1.5 mg/sample) (Evans-White et al. 2005). We freeze-dried pooled snail tissue, weighed it, and ground it to a fine powder with mortar and pestle. We analyzed subsamples for C and N in a CHN elemental analyzer and for total P (TDP) using the ascorbic acid method according to Rosemond (1993).

We measured the excretion and egestion rates of any nutrients that were significantly different between species in an additional experiment. Excretion and egestion were only measured on juveniles of both species because juveniles were used in the prior experiment. We sampled *V. humeralis* and *P. antipodarum* from the Vista reach with a Venturi suction dredge and S.C.U.B.A. certified divers in August of 2010. We collected fifty juvenile individuals of a species, measured them to the nearest 0.01 mm with a digital micrometer, and randomly pooled them into 5 replicates of 10 individuals per replicate. We placed pooled samples in 50 ml vials filled with river water filtered through glass-fiber filters to remove nutrient absorbing particles (Vanni et al. 2002). Vials contained a 1mm screen near the bottom to allow feces through and prevent coprophagy during the experiment (Whiles et al. 2009). We used five control samples to determine ambient N and P levels with filtered river water and no gastropods.

We synchronized the start of the egestion and excretion experiment among replicates. We held samples at river temperature for 2 hours in a dark cooler after which we filtered contents through pre-combusted glass-fiber filters to separate feces (egestion) and filtrate (excretion) (Vanni et al. 2002). We stored filters, containing fecal samples, and filtrate separately in vials, placed them on ice, and immediately returned them to the lab for processing (Vanni et al. 2002). We analyzed excretion samples as described above. We dried egestion samples (45 °C), weighed them, and also analyzed them as described above.

We measured C:N and C:P of epilithon samples from the field to quantify nutrient availability and the potential for resource limitation. We randomly selected five stones from the *V. humeralis* population source in the Vista reach of the Snake River for epilithon analysis during August of 2010. We rinsed stones to remove invertebrates and scrubbed them with a nylon brush in pre-filtered river water until bare. We passed dislodged material through a pre-combusted glass fiber filter. We wrapped filters in tin foil, placed them on ice, and immediately returned them to the lab for processing. We analyzed filter subsamples for C and N in a CHN elemental analyzer and for total P (TP) as described above.

Total C, N, and P of *V. humeralis* and *P. antipodarum* tissue, epilithon, and laboratory Spirulina are reported as percentages of dry masses and elemental ratios as molar ratios (C:N and C:P). We calculated mass specific excretion and egestion rates as the change in nutrient per unit time divided by the wet-mass of individuals (ug/mg wet-mass/hour) (Vanni et al. 2002). We obtained wet-mass by establishing a length to wet-mass regression for *V. humeralis* and *P. antipodarum* (Appendix B).

Interference Competition Experiment

We assessed the effects of intraspecific and interspecific density and food availability on *V. humeralis* growth and mortality with a treatment/control replacement series experiment modified from Underwood (1997) and Cope and Winterbourn (2004). Treatments consisted of different species proportions at three densities (low (3 snails/cage or 400 snails snails/m^2), medium (6 snails/cage or 800 snails/m^2), and high (12 snails/cage or 1600 snails/m^2)) (hereafter referred to as density treatments) (Table 5.1). We selected densities to match field densities from prior surveys (Chapter 3) as well as prior field experiments (Chapter 4). We conducted the experiment over 21 days from September 4-25, 2010 in the Aquatic Sciences Laboratory at Montana State University. We designed the length of the experiment to be long enough to capture growth potential, but short enough to avoid reproduction by *P. antipodarum* (Tibbets et al. 2009).

We conducted the experiment in completely enclosed food storage containers (6 X 6 X 6 cm). We aerated water within treatments with individual air stones controlled by a MEDO® LA-45B air pump. We held containers in a living stream water bath of 20° C ± 2 to maintain constant temperature among all treatments. We monitored water temperature with HOBO Pro little v2® water temperature data loggers. We replaced water within treatment containers and cleaned containers after 7 and 14 days to prevent biofilm growth. We kept light within the laboratory on a 12:12 hr light:dark regime.

We sampled *V. humeralis* two weeks prior to the start of the experiment from the Vista reach and held them in laboratory aquaria. We sampled juvenile *P. antipodarum* from a laboratory maintained Madison River, MT population because juveniles were not present in the Middle Snake River Vista reach at the time of *V. humeralis* sampling. We fed all gastropods ground *Spirulina platensis* (hereafter referred to as Spirulina) from The Vitamin Shoppe® while in holding tanks prior to the experiment (Krist and Lively 1998).

We measured individual shell lengths to the nearest 0.01 mm with a digital micrometer on day 0 and then randomly assigned individuals to treatments. We removed individuals from treatment containers on day 7, 14, and 21 to measure shell length with an ocular micrometer. We recorded any dead individuals and removed them from containers without replacement. We did not mark individuals, thus we used a randomly selected group of three individuals of each species in each treatment to calculate biomass for day 0, 7, 14, and 21. We converted shell lengths to ash free dry mass (AFDM) with an established length to mass equation for *P. antipodarum* (Hall et al. 2006). We developed our own length to mass equation for *V. humeralis* (Benke et al. 1999). The regression for *V. humeralis* was mass = $0.0868L^{3.1427}$ where mass is measured in mg (AFDM) and length (L) is measured in mm (n = 52, $r^2 = 0.72$). Our *V. humeralis* mass includes shell mass unlike the established length to mass equation for *P. antipodarum*, thus we relativized biomass measurements by initial biomass and did not make comparisons between species. We calculated growth rates for individual weeks and for the entire experiment (comparing initial biomass to final biomass) in ((mg/mg)/individual)/day as:

$$g = \frac{((M_t - M_0)/M_0)/n}{t}$$

Where M_t is total gastropod biomass at the end of the specified time period (mg AFDM), M_0 is the total initial gastropod biomass from the same specified time period (mg

AFDM), n is the number of individuals in the treatment, and *t* is the duration of the specified time period within the experiment (days).

We controlled food quantity to provide two levels: 0.23 mg of food/snail in the low food quantity treatment and 0.46 mg food/snail in the high food quantity treatment (Krist et al. 2004; Tibbets et al. 2009). These quantities of food were used to test for differences in the intra- and interspecific interactions under unlimited and limited food defined earlier work with *P. antipodarum* (Krist et al. 2004; Tibbets et al. 2009). We added food to treatment containers every other day at which time we turned off the air stone system for 4 hrs to allow the food to settle. Combining the five density treatments levels (Table 5.1) and two food treatment levels created 10 total treatments. We adjusted food level in each treatment container every seven days to reflect mortalities because food was provided on a per individual basis. We replicated treatments four times. To make comparison between food used in the laboratory experiment and field food sources, we measured C:N and C:P of the Spirulina used in experiment. Spirulina C, N, and P were quantified as described above.

Statistical Analysis

We used a two-way (species and age) ANOVA to compare the C:N and C:P body content separately of *V. humeralis* and *P. antipodarum*. If the effects in the ANOVA were significant, we made all pair-wise comparisons with a Tukey correction. If there were significant differences in body nutrient content between species, we used two-sample t-tests to compare excretion and egestion rates of the nutrients between species. All measures of variability listed in parentheses are one standard error. Unless otherwise mentioned, we made no corrections for independent contrasts following significant ANOVA effects because all contrasts were planned in the design of the experiments (Keppel and Wickens 2004).

In the laboratory growth experiment, we used a two-way (density treatment and food level) multiple analysis of variance (MANOVA) to investigate differences in final relative biomass and mortality among treatments over the entire length of the experiment (hereafter referred to as total relative biomass and mortality). If the MANOVA was significant, we used individual two-way analyses of variance (ANOVAs) for growth and mortality with density and food to explore independent effects of treatment type. If the effects in the ANOVAs were significant, we tested for significant differences among treatments with independent contrasts based on our experimental design. Within food levels, the low density intraspecific treatment was compared to the medium density intraspecific, medium density interspecific, high density intraspecific, and high density interspecific treatments. We arcsine square root transformed percent mortality to meet assumptions of normality. Biomass values and variance met assumptions of normality.

To explore the effects of density treatment and food level on *V. humeralis* growth over time, we used a two-way (density treatment and food level) repeated-measures MANOVA (profile analysis). In our MANOVA, density treatment and food level were the main between subjects factors and time was the main within subject factor (Von Ende 2001). Profile analysis analyzes the pattern of response of the within-subject factor and tests for three hypotheses of differences among treatments in parallelism (within subject interaction effects), flatness (within subject main effect), and levels (between subjects main effects) (Von Ende 2001). If the flatness and parallelism hypotheses are rejected, tests of the levels hypotheses are not reported (Von Ende 2001). The significance of the MANOVA was determined by the significance of the within subject effects of time (flatness hypothesis, indicated whether growth occurred over time), the time x density treatment interaction (parallelism hypothesis, indicated whether growth varied by density treatment over time), and the time x food level interaction (parallelism hypothesis, indicated whether growth varied by food level over time) all reported as Wilks' Lambdas (Von Ende 2001). If the MANOVA was significant, we used individual one-way ANOVAs for each seven day interval (0-7, 8-14, 15-21) to explore independent effects of the density treatment and food level on growth with a Bonferroni corrected alpha (α = 0.02) (Von Ende 2001). If the effects in the ANOVAs were significant, we tested for significant differences in growth among treatments with independent contrasts based on our experimental design. We made independent contrasts only within weeks. Biomass values and variance met assumptions of normality.

We used changes in snail tissue biomass to calculate net effect sizes. We calculated effect size as the natural log of the ratio of treatment to control biomass change (Gurevitch and Hedges 2001; Kawai and Tokeshi 2007) as:

$$\text{Net effect} = \ln(M_t/M_0)$$

Where M_t is total gastropod biomass at the end of the experiment (mg AFDM) and M_0 is the total initial gastropod biomass (mg AFDM). The control for all *V. humeralis* effect size calculations was the low density intraspecific treatment. We calculated a subset of three net effects for each treatment-control comparison by randomly selecting a control and treatment after/before biomass from the replicates and used this to calculate standard errors. We explored differences in the net effects among treatments with a one-way ANOVA. We did not use relative growth of *P. antipodarum* in any analyses but it is reported. We did not use dead snails in statistical analyses. Unless otherwise mentioned, we used an alpha value of 0.05 to confer significance and performed all statistical procedures in SAS (9.3).

Results

Stoichiometric Facilitation Experiment

Valvata humeralis and *Potamopyrgus antipodarum* P body content (C:P) varied between species and ages ($F_{3,21}$ = 5.39, p = 0.007) while N body content did not (C:N) ($F_{3,22}$ = 1.42, p = 0.26) (Figure 5.1). Species and age alone were not significant predictors of body P content (species $F_{1,21}$ = 0.55, p = 0.47, age $F_{1,21}$ = 3.24, p = 0.09), but the species by age interaction was a significant predictor of body P content ($F_{1,21}$ = 12.1, p = 0.002). *Potamopyrgus antipodarum* juveniles had a lower body C:P than *P. antipodarum* adults ($F_{1,21}$ = 14.68, p = 0.001), *V. humeralis* juveniles ($F_{1,24}$ = 7.91, p = 0.01), and marginally *V. humeralis* adults ($F_{1,24}$ = 3.4, p = 0.08) (Figure 5.4). *Valvata humeralis* adults had a lower C:P than *P. antipodarum* adults ($F_{1,24}$ = 4.28, p = 0.05) (Figure 5.1).

Phosphorus excretion and egestion rates did not differ between *P. antipodarum* and *V. humeralis* (excretion t_8 = 1.31, p = 0.23, egestion t_8 = 0.66, p = 0.52) (Figure 5.2). Epilithon samples contained 17.81% C (0.90), 1.35% N (0.08), and 0.26% P (0.02) (C:N = 15.57 (0.40), C:P = 176.77 (10.23), C and N n = 10, P n = 10).

Interference Competition Experiment

Growth and mortality differed among density treatments (Wilks' Lambda = 0.30, $F_{8,58} = 5.89$, $p < 0.0001$), but we did not detect any differences in growth and mortality between food levels (Wilks' Lambda = 0.95, $F_{2,29} = 0.81$, $p = 0.46$) or the interaction between density treatment and food level (Wilks' Lambda = 0.74, $F_{8,58} = 1.2$, $p = 0.31$). Total relative growth was affected by the density treatment decreasing with increasing density ($F_{4,30} = 15.22$, $p < 0.0001$), but not by food level ($F_{1,30} = 1.58$, $p = 0.22$), or the interaction ($F_{4,30} = 0.65$, $p = 0.63$) (Figure 5.3). Mortality was not affected by density treatment ($F_{4,30} = 0.54$, $p = 0.70$), food level ($F_{1,30} = 0.20$, $p = 0.67$), or the interaction ($F_{4,30} = 1.77$, $p = 0.16$). Total relative growth of *V. humeralis* was significantly greater in the low density intraspecific treatment than all others (Figure 5.3). Total relative growth of *P. antipodarum* was 0.29 (0.08) ((mg/mg)/individual)/day in the low food medium density interspecific treatment, 0.28 (0.05) ((mg/mg)/individual)/day in the high food medium density interspecific treatment, 0.20 (0.03) ((mg/mg)/individual)/day in the low food high density interspecific treatment, and 0.16 (0.11) ((mg/mg)/individual)/day in the high food high density interspecific treatment.

In the repeated-measures analysis, *V. humeralis* grew over time (Wilks' Lambda = 0.03, $F_{3,28} = 269.73$, $p < 0.0001$), density treatment affected growth over time (Wilks' Lambda = 0.34, $F_{12,74.37} = 3.10$, $p = 0.001$), and food level affected growth over time (Wilks' Lambda = 0.71, $F_{3,28} = 3.78$, $p = 0.02$). There was not a significant interaction of time, density treatment, and food level (Wilks' Lambda = 0.75, $F_{12,74.37} = 0.70$, $p = 0.74$). Within the three weeks of the experiment, the time effect was significant indicating that

V. humeralis grew every week (Table 5.2). The density treatment was a significant predictor of growth in the first and third week, but not the second. Food level was only significant in week three and the interaction of density treatment and food level was not significant during any week. Relative growth of *V. humeralis* from days 1-7 was significantly larger in the low density intraspecific treatment than all others, but from days 8-14 was marginally significantly larger than all others in the high density interspecific treatment (Figure 5.4). Relative growth of *V. humeralis* from days 15-21 was generally greater in high food level treatments with the highest growth occurring in the low density, high food intraspecific treatment (Figure 5.4).

Net effects varied significantly among treatments with a trend of decreasing overall effects in high density interspecific treatments ($F_{7,16} = 7.72$, $p = 0.0004$) (Figure 5.5). Intraspecific and interspecific net effects were more negative at the lower food level within treatments. The lowest net effect occurred at the medium density (800/m^2) intraspecific high food treatment and the greatest net effect occurred in the high density (1600/m^2) low food intraspecific treatment.

Spirulina used in the laboratory experiment contained 42.54% C (1.80), 8.48% N (0.38) (C:N = 5.83 (0.02) (C and N n = 5). The quantity of P within the Spirulina used in our growth experiment was too high for our laboratory calibrations and was thus obtained from the manufacturer (4.0% P and C:P = 27.31).

Discussion

Our results confirm that the intensity of a net interaction between species can change in ways not predicted by community ecology theory due to changes in the multiple interactions that make up the net. Total relative growth of *V. humeralis* decreased with increasing gastropod density regardless of the per individual food provided indicating that direct behavioral interactions were responsible for the decrease in growth rate with increasing density (interference competition). Yet, contrary to what would be predicted by theory, the intensity of competition between *V. humeralis* and *P. antipodarum* decreased with increasing *P. antipodarum* density. *Valvata humeralis* growth was increased in the high density interspecific treatments as compared to the high density intraspecific treatment. We hypothesize that *V. humeralis* competed with, but was also facilitated by *P. antipodarum* at this density changing the intensity of the net interaction.

Our results also provide insight into how net interactions between species can change with ontogeny creating non-linear interactions over time. Previous research with *V. humeralis* and *P. antipodarum* found a net interaction shift from competition, to facilitation, back to competition with increasing density of *P. antipodarum* (Chapter 4). While our current growth results do not directly match these, we saw evidence of a similar net interaction change through the course of our experiment. Growth potential was greatest from days 0-7 during which time growth rates decreased linearly with increasing total gastropod density regardless of species combinations and food levels. However, when growth potential decreased during days 8-14, there was a facilitative effect of *P. antipodarum* on *V. humeralis* growth at the highest density. By days 15-21, growth potential equalized among treatments as gastropods reached adult size and food quantity became a significant predictor of growth rate with higher growth in high food treatments. The importance of the facilitation that occurred during the second week of the experiment was confirmed in the total growth results. Growth of *V. humeralis* was greater in the high density interspecific treatment than the intraspecific treatment although an independent contrast was not made because it was not planned. The change in net effect seen through time in our experiment indicates that the facilitation of *V. humeralis* by *P. antipodarum* is related to *V. humeralis* ontogeny and may only become apparent once juveniles have begun decreasing in growth. The difference in shifting interactions seen between our laboratory experiment and previous field experiments may thus be related to the growth potential of *V. humeralis*. While juveniles were used in both experiments, it is likely that individuals varied slightly in age and growth potential among experiments.

The facilitation of *V. humeralis* growth in the presence of *P. antipodarum* may have been caused by increased access to food, increased quality of food, or a combination thereof. The high quality of Spirulina food used in the growth experiment suggests that *V. humeralis* did not experience nutrient limited growth (N or P limitation), but it is possible that the nutrients within the Spirulina were packaged in a way that decreased accessibility. The Spirulina food source used in our experiment was a filamentous cyanobacterium. While it has been commonly used as a food source for gastropods in laboratory settings (Krist and Lively 1998; Tibbets et al. 2009), the precise digestion process is unknown. If nutrient packaging within the Spirulina limited access to nutrients, digestion by *P. antipodarum* could have made the nutrients more accessible, and thus higher in quality for *V. humeralis*. Coprophagy among gastropods is a viable strategy for further acquisition of nutrients within food that is not completely or efficiently processed by one digestion (Brendelberger 1997). It is also possible that nutrient levels within the lab Spirulina were too high (Boersma and Elser 2006) and that pre-digestion by *P. antipodarum* decreased the nutrient content to a more optimum level. In addition to potential changes in food quality caused by *P. antipodarum* digestion, *V. humeralis* may have also had greater access to the Spirulina food through interference behavior. Chemical cues released by *P. antipodarum* may have also affected growth of *V. humeralis* (Dillon 2000), although water within treatment cages was replaced every seven days reducing the potentially impacts of chemical cues.

The density and species proportions at which growth of *V. humeralis* was facilitated by *P. antipodarum* differed somewhat from previous research potentially due to variation in abiotic conditions. A previous field growth experiment found the facilitation of *V. humeralis* by *P. antipodarum* occurred at 800/m^2 total gastropod density and 1:1 *V. humeralis*:*P. antipodarum* proportion while our current results found the facilitation occurred at 1600/m^2 and 1:3 proportion (Chapter 4). It is important to note that cage sizes differed between experiments and while the density per area at which the facilitation occurred differed in the lab and field, the actual number of gastropods in the treatment where the facilitation occurred were similar between experiments (previous experiment 6 *V. humeralis* individuals and 6 *P. antipodarum* individuals, current experiment 3 *V. humeralis* individuals and 9 *P. antipodarum* individuals). This suggests that the interaction may be cued more my number of individual gastropods interacting and less by small differences in the size of the area that they interact within. The differences we saw in density and proportion creating the interaction shift may also be related to other factors intertwined with the density gradient. To examine the biotic density gradient in the current growth experiment, we controlled for abiotic gradients by conducting the experiment in a low abiotic stress environment. For example, the food provided in the lab experiment was much higher in limiting nutrients than the epilithon in the field and was continuously replenished reducing the potential for nutrient or food limited growth. The conditions in the laboratory were also optimal for growth with very small temperature swings from day to night and light levels lower than that of direct sunlight. A recent study investigating growth of *P. antipodarum* found that foraging was increased in low light treatments potentially contributing to increased growth (Liess and Lange 2011) suggesting that the low light conditions in our laboratory may have increased growth rates in general. Decreasing environmental stress combined with increasing food quality and continually renewing food quantity in the current experiment could have pushed the facilitative effect to a higher density where competition was greater.

Our results are in agreement with community ecology theories of species coexistence and resource overlap. Growth patterns from our experiment indicate that *V. humeralis* may coexist with *P. antipodarum* because interspecific competition with the invader is not as strong as intraspecific competition with itself. Previous research with *P. antipodarum* and native isopods in the Columbia River similarly found that interspecific competition with *Gnorimosphaeroma insulare* was weaker than intraspecific competition between native isopods suggesting a mechanism of coexistence (Brenneis et al. 2010). Additionally, our food level treatment became significant in the last week of the study when individual size had increased. Increasing food quantity decreased the intra- and interspecific competitive effects seen in the last week of our experiment indicating that competition was for space and food.

Results from our stoichiometric experiment suggest that *P. antipodarum* may egest and excrete slightly more phosphorus than *V. humeralis*, but it is likely not enough to be the sole facilitative mechanism in this or previous experiments. The Spirulina used in our experiment contained enough phosphorus that limitation for either species was highly unlikely (Tibbets et al. 2009) although the accessibility of these nutrients within the Spirulina is uncertain as is the potential excess of nutrients (Boersma and Elser 2006). The C:P of epilithon from field samples was also greater than that thought to limit *P. antipodarum* growth and fecundity (176 compared to ~270) indicating that phosphorus limitation at our field site is not likely (Tibbets et al. 2009). It is of interest that *P. antipodarum* juveniles require more phosphorus (higher body content) than *V. humeralis* juveniles suggesting that *P. antipodarum* may become phosphorus limited as juveniles before *V. humeralis.* As adults, the pattern was switched and *V. humeralis* adults had significantly higher demand for phosphorus than *P. antipodarum* adults as may be expected for a rapidly growing invasive species with high protein synthesis rates (Elser et al. 1996). These results suggest that *P. antipodarum* growth and population expansion may be limited by juvenile growth in some locations contributing to varying impact.

These results are consistent with a previous meta-analysis suggesting that aquatic native species may out-compete invasive species under low nutrient condition where the invader’s growth is limited (González et al. 2010).

Our results confirm that the net effects of one species on another can change in intensity along biotic density gradients as a result of changes in the interactions that sum to create the net interaction. In the current study, species interacted negatively through interference competition and positively through facilitated access the higher quantity and/or quality of food. The intensity of interspecific competition in our experiment decreased as the density of the competitor increased potentially because *V. humeralis* was able to physically defend areas where food settled and benefit indirectly through acquisition of food resources. While the interaction change occurred along a density gradient, environmental conditions including food availability and temperature affected the densities at which the shift occurred as compared to previous work (Chapter 4). These results are concordant with previous biotic gradient research indicating that biotic and abiotic interaction gradients can operate concurrently (Irving and Bertness 2009; Bulleri et al. 2011).

Our results have significant implication for the management of invasive species and the role of receiving native communities in the invasion process. Competition with the native community is already recognized as a potential influence during the invasion process that may prevent progression of the invasion ultimately influencing impact (Bertness and Callaway 1994; Stachowicz 2001; Price and Morin 2004). Our results suggest further that the impact of an invader on the native community may be a complex interplay between invader density, native species behavior, and environmental conditions. The weight of each of these components likely differs among invasions sites creating context specificity.

Table 5.1. Laboratory experiment treatments for examining the effects of density, species composition, and food availability on growth and mortality of *V. humeralis*. Letters indicate treatment levels where V = 3 *V. humeralis* and P = 3 *P. antipodarum.*

	Low Food			High Food		
	Density			Density		
Intraspecific effects	400/m^2	800/m^2	1600/m^2	400/m^2	800/m^2	1600/m^2
V. humeralis	V	V + V	V + 3V	V	V + V	V + 3V
Interspecific effects						
V. humeralis + P. antipodarum		V + P	V + 3P		V + P	V + 3P

Table 5.2.—Results from repeated measures two-way analysis of variance (ANOVA) with density and food level for days 0-7, 8-14, and 15-21 of the laboratory growth experiment. Significance was assessed with a Bonferroni corrected α = 0.02 and significant p-values are italicized.

Days 0-7

Source	DF	ANOVA SS	Means Square	F	p
Time	1	4.97	4.97	293.05	< *0.0001*
Density x Time	4	0.23	0.06	3.33	*0.02*
Food x Time	1	0.02	0.02	1.06	0.31
Density*Food*Time	4	0.05	0.01	0.78	0.54
Error	30	0.51	0.02		

Days 8-14

Source	DF	ANOVA SS	Means Square	F	p
Time	1	3.14	3.14	159.76	< *0.0001*
Density x Time	4	0.18	0.04	2.27	0.09
Food x Time	1	0.02	0.02	0.79	0.38
Density*Food*Time	4	0.02	0.01	0.2	0.94
Error	30	0.59	0.02		

Days 15-21

Source	DF	ANOVA SS	Means Square	F	p
Time	1	1.08	1.08	96.73	< *0.0001*
Density x Time	4	0.15	0.04	3.31	*0.02*
Food x Time	1	0.08	0.08	6.89	*0.01*
Density*Food*Time	4	0.07	0.02	1.59	0.2
Error	30	0.34	0.01		

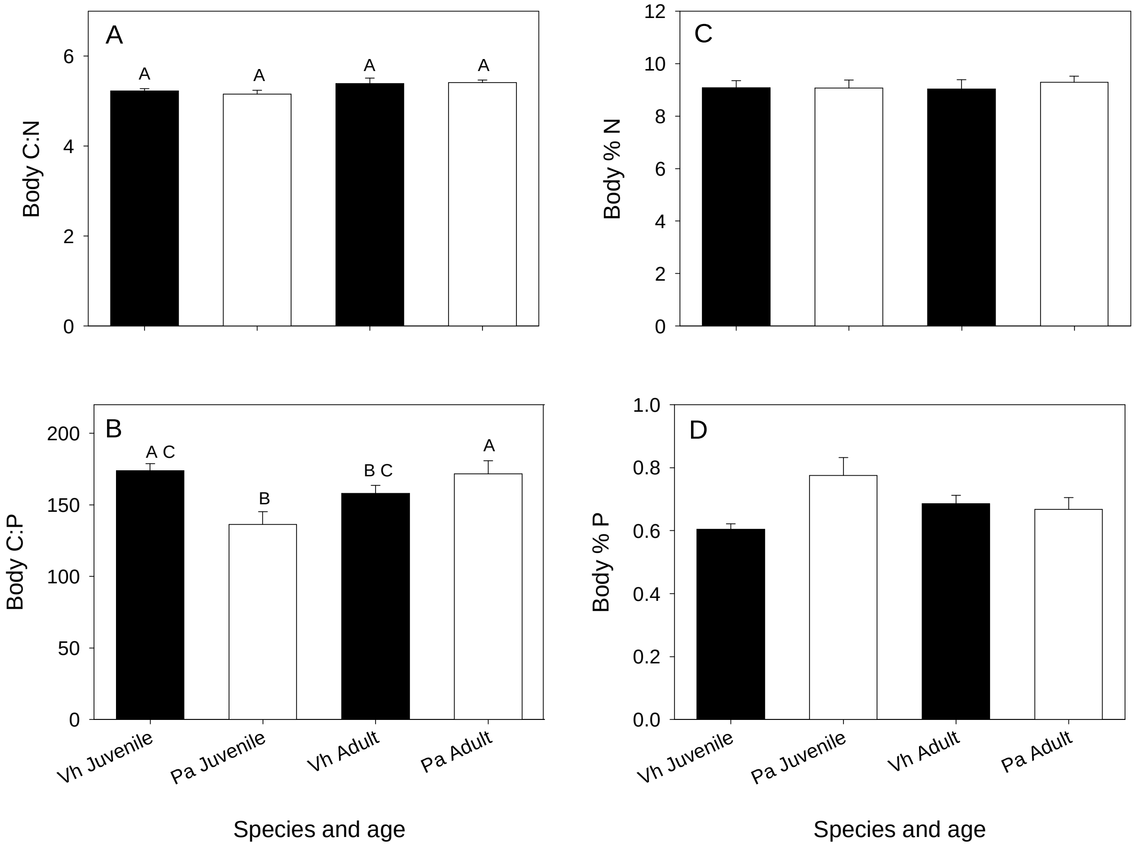

Figure 5.1.—Ratios of C:N, C:P, percent N, and percent P for *V. humeralis* (black bars) and *P. antipodarum* (open bars) body tissue. Those bars with the same letter do not differ at the $\alpha = 0.05$ significance level. Error bars indicate one standard error.

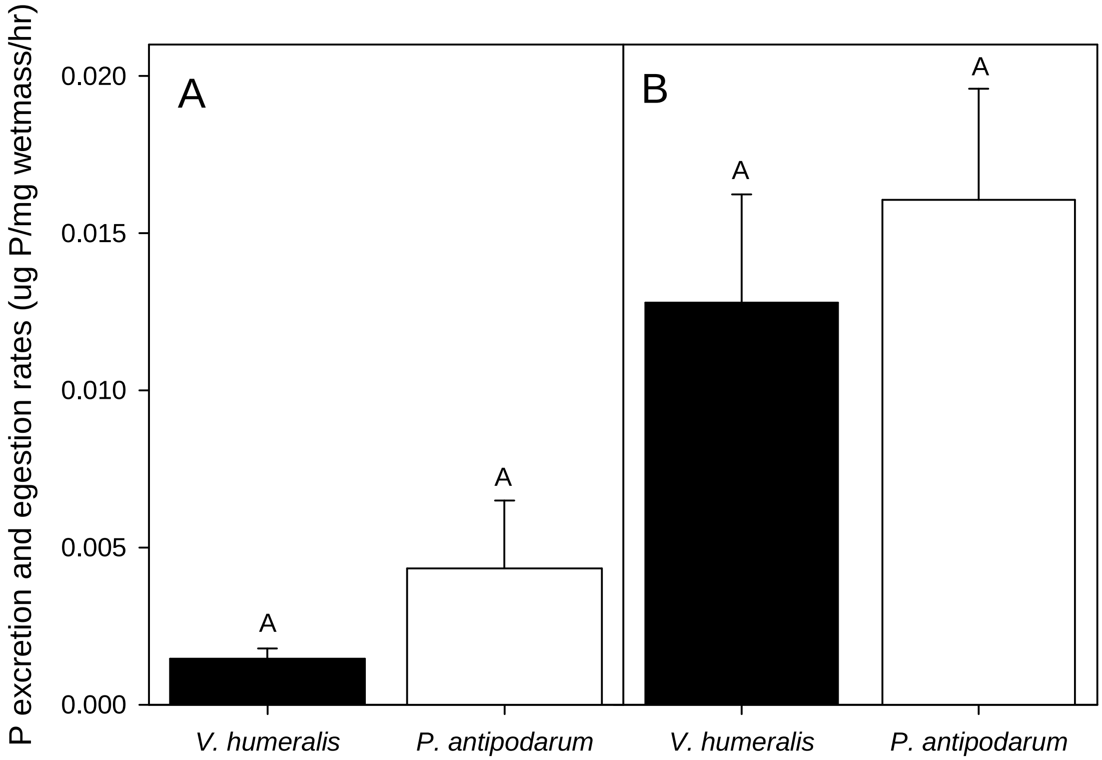

Figure 5.2.—Phosphorus excretion (panel A) and egestion (panel B) rates for *V. humeralis* (black bars) and *P. antipodarum* (open bars). Those bars with the same letter do not differ at the α = 0.05 significance level. Error bars indicate one standard error.

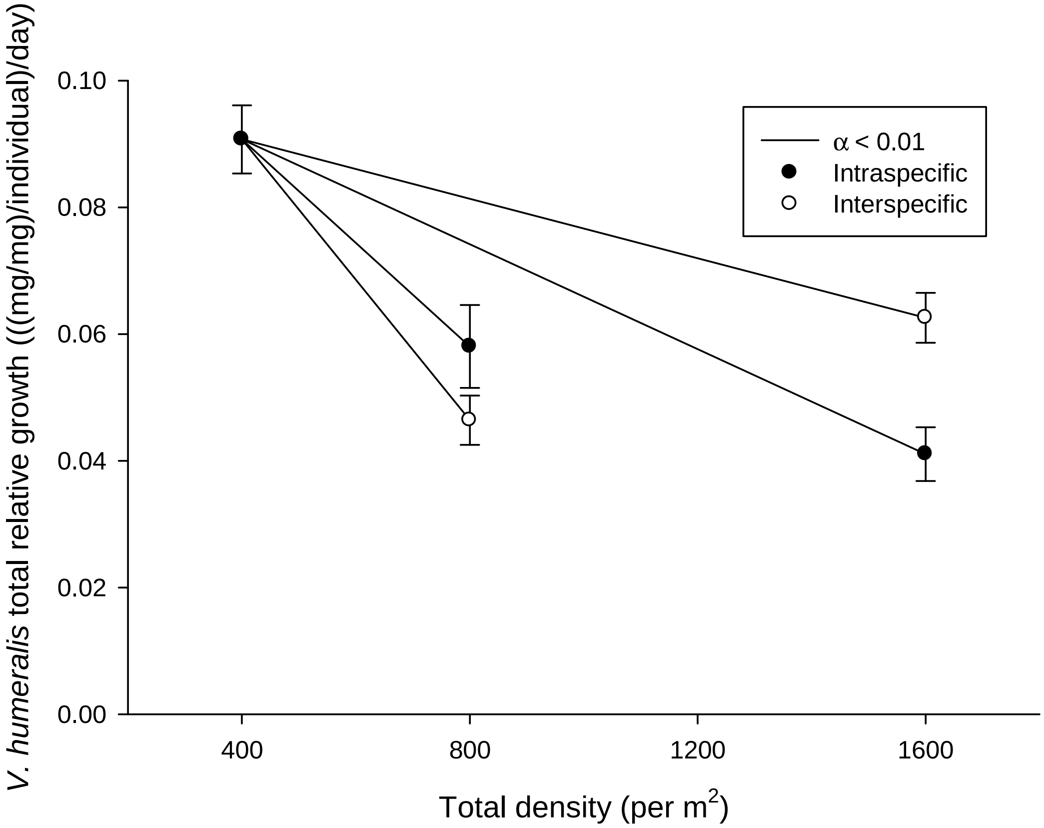

Figure 5.3.—*Valvata humeralis* total relative growth over the entire 21 day experiment in the five density treatments. Food levels were combined because of lack of significance. Filled circles represent intraspecific treatments and open circles represent interspecific treatments. The x-axis indicates gastropod densities of low (400/m^2), medium (800/m^2), and high (1600/m^2). The y-axis indicates mean growth response in ((mg/mg)/individual)/day. Lines represent independent contrasts with significance values indicated in the legend. Error bars represent one stand error.

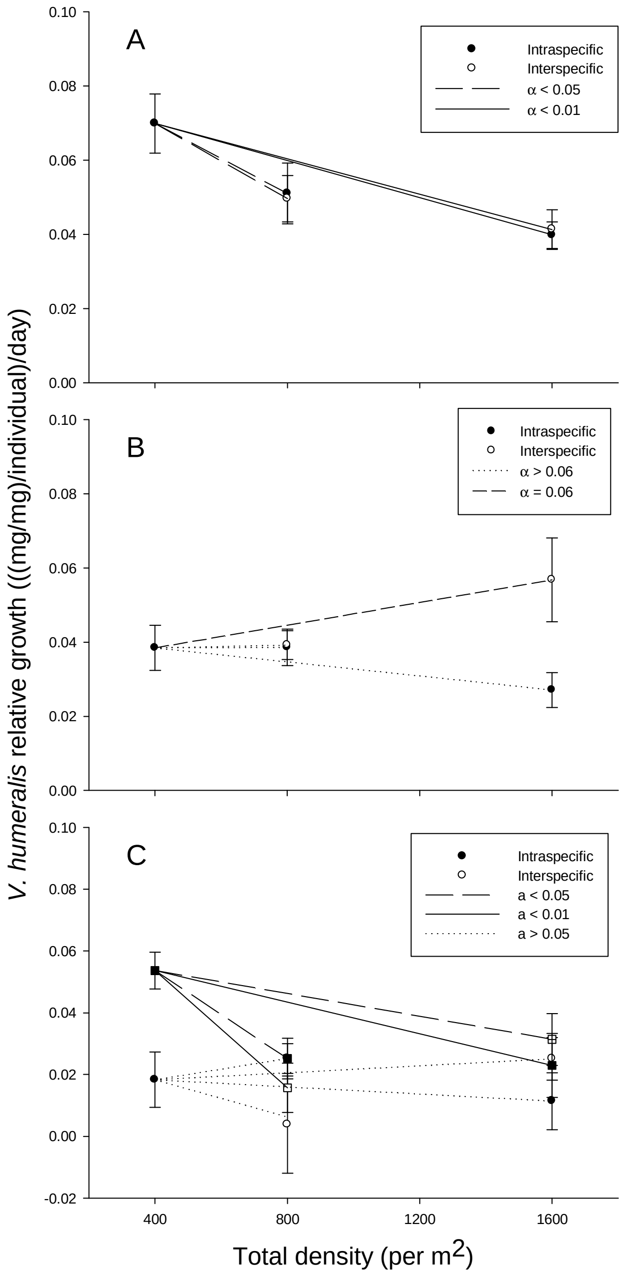

Figure 5.4.—*Valvata humeralis* individual growth response in the five treatments during day 0-7 (panel A), 8-14 (panel B), and 15-21 (panel C). Filled circles represent intraspecific treatments and open circles represent interspecific treatments. The x-axis indicates gastropod densities of low (400/m^2), medium (800/m^2), and high (1600/m^2). The y-axis indicates mean growth response in ((mg/mg)/individual)/day. Lines represent independent contrasts with significance values indicated in the legend. Independent contrasts were made within week among treatments types that were significant during that week. Error bars represent one stand error.

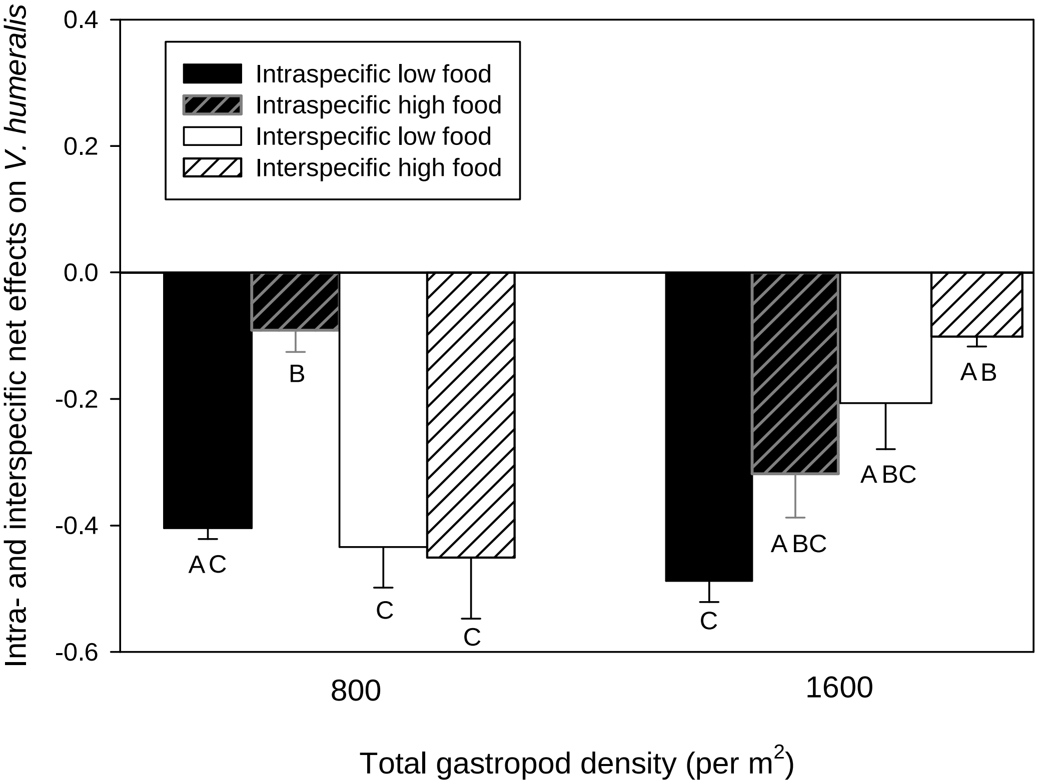

Figure 5.5.—Mean intraspecific and interspecific net effects for *V. humeralis* and *P. antipodarum* from field growth experiment. Net effects represent the magnitude and direction of the effect of the interacting species on the target species as compared to the low density (400/m^2) intraspecific treatment for the target species. Those bars with the same letter do not differ at the $\alpha = 0.05$ significance level. Error bars indicate one standard error.

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CHAPTER SIX

CONCLUSIONS

The varying impacts of invasive species are not well understood despite their increasing prevalence (Strayer et al. 2006). As non-indigenous species introductions have become increasingly common (Sala et al. 2000; Kolar and Lodge 2002; Leung et al. 2002; Marchetti et al. 2004) much research effort has been devoted to understanding the ecology of invasion fronts and the factors that determine the success of invasive species and the impact they have on native communities (Bruno et al. 2005). This research has provided valuable information concerning the mechanisms which facilitate invader impact including invader release from predation (Adams et al. 2009; Romanuk et al. 2009), generalist feeding habits of invaders (Romanuk et al. 2009), and competitive dominance of invaders over similar native species (Byers 2000; Callaway and Aschenhoug 2000; Bando 2006). However, when invasions fail to produce impact, the mechanisms are frequently unclear.

Invasive species are often managed under the assumption that all new introductions represent similar levels of threat; yet, many introductions do not appreciably change the receiving community (Williamson 1996; Davis 2003) making the ecological impact low. Additionally, species often only exhibit invasive behavior in particular geographic locations (Kolar and Lodge 2001). Attempts to quantify variation in invasive impact have highlighted the importance of understanding the context of an invasion in terms of the receiving community and the physical environment (Ricciardi

2003; Ricciardi and Atkinson 2004; Ricciardi and Cohen 2007; Padilla 2010; Thomsen et al. 2011) both of which may reduce impact allowing native species to coexist with an invader. Understanding how the physical environment and interactions with the native community interact to influence the success or failure of invasive species is vital for understanding why invader impact can vary.

The goal of this dissertation was to explore what contributed to coexistence of the invasive aquatic gastropod, *Potamopyrgus antipodarum*, and the native aquatic gastropod, *Valvata humeralis*, in the Snake River, Idaho. Previous surveys indicated that while competition was suspected (Lysne and Koetsier 2008), populations of *V. humeralis* coexisted with *P. antipodarum* throughout the year and from year to year in some locations (Ryan Newman, Bureau of Reclamation, personal communication). I investigated species coexistence mechanisms from a resource partitioning perspective (Chapter 3), a changing interaction perspective (Chapter 4), a mechanistic behavioral perspective (Chapter 5), and a nutrient recycling perspective (stoichiometric) (Chapter 5). I initially explored diet, spatial, and temporal partitioning by *V. humeralis* in populations that were invaded by *P. antipodarum* and uninvaded within the Vista reach of the Middle Snake River (Chapter 3). In the following chapter, I explored the net intra- and interspecific effects of *V. humeralis* and *P. antipodarum* at varying densities and species proportions in a field growth experiment and compared the results to field surveys matching the growth experiment treatments (Chapter 4). Lastly, I explored the positive and negative mechanisms of the intra- and interspecific interactions identified in the prior chapter with a stoichiometric experiment designed to identify facilitative mechanisms and a laboratory growth experiment designed to identify competitive mechanisms. I describe the findings of this research below and discuss the implications of my results for invasive species management and conservation of native species.

Competition between *V. humeralis* and *P. antipodarum* may negatively affect growth of *V. humeralis* in field populations. The comparison of mean individual biomass (hereafter referred to as size) between *V. humeralis* populations that were invaded and were not invaded indicated that *V. humeralis* were consistently smaller and achieved a smaller adult size prior to reproduction in invaded populations although, gastropod density and habitat heterogeneity may have also influenced this outcome. Food resources appeared to be shared between species ontogenetically or during different ages. When *V. humeralis* were in uninvaded populations, the juveniles had a higher diatom gut content than when they were found in populations invaded by *P. antipodarum* indicating potential diet partitioning. These results suggest that *V. humeralis* and *P. antipodarum* may compete for food and that *V. humeralis* may shift diets in order to partition food resources in the presence of *P. antipodarum*.

Spatial and temporal partitioning combined with habitat stability likely contributed to *V. humeralis* and *P. antipodarum* coexistence in the Vista reach. There was evidence of spatial habitat partitioning between *V. humeralis* and *P. antipodarum* at the among populations scale (1-2 km), but not within population (10-20 m) or patch (1 m) scales. The larger size of *V. humeralis* in uninvaded populations suggests that there may have been a benefit to some level of population scale habitat partitioning. In contrast, *V. humeralis* were found more frequently at high densities with *P. antipodarum* at the within population and patch scales. This pattern was consistent from month to month and among populations suggesting there may be a benefit to sharing habitat with *P. antipodarum* at particular densities. While this pattern could have also been caused by habitat heterogeneity, course habitat measurments suggested that the physical conditions among populations were similar.

Differing life history strategies created temporal partitioning of reproductive events between *V. humeralis* and *P. antipodarum* lessening competition during critical growth periods. Differing reproductive strategies conferred an advantage to the native species because reproduction was aligned with the high flow and high productivity times of the year while potentially inhibiting the invasive. By extension, the dam controlled hydrograph also likely promoted species coexistence by creating consistent high and low flow seasons that removed and replaced habitat on an annual basis. Together, these results suggest that while competition with *P. antipodarum* may negatively affect *V. humeralis* growth at the population scale, their interaction within populations is more complex.

Growth experiments indicated that the interaction between *V. humeralis* and *P. antipodarum* changed unexpectedly with increasing *P. antipodarum* density. *Valvata humeralis* exhibited increased growth in the interspecific medium density treatment with *P. antipodarum* (hereafter referred to as facilitation treatment) compared to growth in the low and high density intraspecific treatments. The change in net effect strength created a non-linear interaction between the species with increasing competitor density. The facilitative effect of *P. antipodarum* on *V. humeralis* growth was not apparent in the high density interspecific treatment suggesting that the facilitation was directly related to the medium density of *P. antipodarum*. In contrast to *V. humeralis*, *P. antipodarum* experienced decreased growth with increasing density in the interspecific treatments but not intraspecific treatments. Intraspecific net effects of *P. antipodarum* were slightly greater than interspecific effects of *V. humeralis* on *P. antipodarum* at the medium density suggesting that intraspecific competition may be greater than interspecific competition with *V. humeralis*.

Field surveys of *V. humeralis* size indicated that the non-linear interaction between *V. humeralis* and *P. antipodarum* was likely influenced by more than *P. antipodarum* density in a field setting. Similar to the field experiment, field surveys in 2008 indicated that size in the facilitation treatment was larger than other treatments although not statistically significant. Field surveys in 2009 also matched the field experiment in that *V. humeralis* size in samples matching the facilitation treatment was greater than in the lowest density treatment. Yet, size in samples matching the low density intraspecific *V. humeralis* treatment was either greater (2008) or the same (2009) as that of the facilitation treatment implying a low density growth advantage not seen in the growth experiment.

A laboratory growth experiment confirmed that the intensity of competition from *P. antipodarum* on *V. humeralis* decreased with increasing *P. antipodarum* density due to interference competition, yet the interaction also varied with ontogeny. *Valvata humeralis* size decreased with increasing gastropod density during the first portion of the experiment regardless of increasing food quantity with increasing number of individuals indicating that direct behavioral interactions were responsible for the decrease in growth rate. Over time, *V. humeralis* growth was increased in the high density interspecific treatments as compared to high density intraspecific treatments indicating that *V. humeralis* may have benefited from increased acquisition of food through interference behavior with *P. antipodarum*. Food provided in the laboratory experiment was very high in essential nutrients, nitrogen and phosphorus, suggesting that the facilitation was related solely to food quantity and not food enhancement through nutrient recycling by *P. antipodarum*. It is possible that *P. antipodarum* processed the supplied food through digestion making the nutrients more available for a second consumption. Combined, these results indicate that the interaction between *V. humeralis* and *P. antipodarum* is influenced not only by density of *P. antipodarum*, but also potentially by the behavior and age of *V. humeralis*.

Differences in the *P. antipodarum* density at which growth of *V. humeralis* was facilitated varied in the lab and field experiment potentially due to differences in abiotic conditions. In order to isolate the effects of density and species composition on growth in the lab, abiotic conditions were controlled for by conducting the experiment in a low abiotic stress environment (more consistent temperature and lower UV exposure). Decreasing abiotic stress combined with increasing food quality and continually renewing food quantity may have pushed the facilitation effect to a higher gastropod density where competition was greater.

These results together suggest that the coexistence of *P. antipodarum* and *V. humeralis* in the Vista reach of the Snake River is aided by a combination of mechanisms including a behaviorally driven interaction that changes non-linearly with density, resource partitioning, and environmental variability. The non-linear interaction between species may explain why field results were suggestive of competitive effects while laboratory experiments indicated both positive and negative effects. At large spatial scales where invader densities vary, competition from *P. antipodarum* may negatively affect *V. humeralis* growth, but diet and reproductive partitioning by *V. humeralis* could reduce competitive effects. Yet, when invader densities are held at a moderate level, behavior of *V. humeralis* may enable better access to food resources or access to food pre-digested by *P. antipodarum* increasing *V. humeralis* growth. The positive growth effects of acquiring more food in the presence of *P. antipodarum* are linked to *V. humeralis* ontogeny, *P. antipodarum* density, and potentially abiotic stress levels. Positive growth effects of *P. antipodarum* on *V. humeralis* were seen at a high density of the invader under low stress (laboratory) and a lower density of *P. antipodarum* under higher stress (field). These results suggest that variation in the impact of *P. antipodarum* on native species among geographic locations may be caused by behavioral responses of the native community.

Interaction gradients, such as that documented in this research, may create unexpected population level impacts between native and invasive species (Dick 2008). Introduced competitors are suggested as a driving force of extinction among global native freshwater molluscs (Lydeard et al. 2004), yet many questions remain regarding behavioral interactions that could affect the outcome of these interactions. In North America, the persistence of native molluscan fauna has been threatened by the introductions of the Zebra mussel *Dreissena polymorpha*, the Quagga mussel *Dreissena rostriformis bugensis*, the Faucet snail *Bithynia tentaculata* (Jokinen 1992; Harman 2000), the Island apple snail *Pomacea insularum*, in addition to *P. antipodarum* (Lysne and Koetsier 2008; Riley et al. 2008). Introduced competitors may impact native Molluscan fauna through habitat alteration (Tucker 1994), competition for food and space (Murray et al. 1998; Baker and Levinton 2003; Kerans et al. 2005; Hall et al. 2006), and resource depletion (Holland 1993; Nichols and Hopkins 1993; Caraco et al. 1997; Hall et al. 2003). The research presented in this dissertation suggests that native species may also compensate for competitive effects of invaders and persist in some circumstances aided by behavior and favorable environmental conditions. Future research efforts should focus on identifying conditions under which different assemblages of native species are able to coexist with invasive species.

These results have significant implication for the management of invasive species and the role of receiving native communities in mitigating invader impact invasion. Competition with the native community is already recognized as a potential influence during the invasion process that may prevent progression of the invasion ultimately influencing impact (Bertness and Callaway 1994; Stachowicz 2001; Price and Morin 2004). These results suggest further that the impact of an invader on the native community may be a complex interplay between invader density, native species behavior, invader nutrient use, and environmental conditions. The weight of each of these components likely differs among native species and invasion sites creating context specificity.

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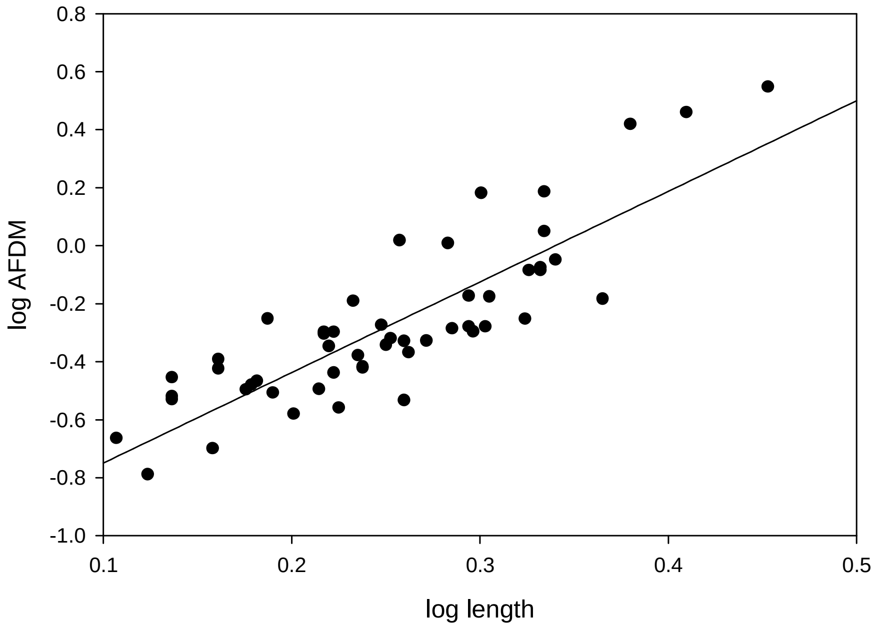
APPENDICES

APPENDIX A:

SHELL LENGTH OF VALVATA HUMERALIS TO BIOMASS

The relationship between shell length and ash free dry mass (AFDM) for *V. humeralis* was determined with individuals sampled from the Snake River Vista population. Fifty-two individuals of varying sizes were sampled in August of 2009, immediately placed on ice, and returned to the Aquatic Sciences Laboratory at Montana State University, Bozeman for processing. Shells were measured to the nearest 0.01 mm with an optical micrometer and gastropods were frozen to euthanize. Shells were not removed due to the small size of some individuals (1.2 mm) and concern over sample loss. Specimens were dried at 60°C for 24 hrs, weighed to the nearest 0.001 mg, ashed at 450°C for 2 hrs, and then placed in a glass desiccator for 2 hrs. Shell and tissue were reweighed. Ash free dry mass (AFDM) was calculated as described in Chapter 3. Length and mass values were log transformed to meet assumptions of normality. The regression for *V. humeralis* shell length to biomass was mass = $0.0868L^{3.1427}$ where mass is measured in mg (AFDM) and length (L) is measured in mm ($n = 52$, $r^2 = 0.72$).



APPENDIX B:

SHELL LENGTH OF VALVATA HUMERALIS AND POTAMOPYRGUS ANTIPODARUM TO WETMASS

The relationship between shell length and wet-mass for *V. humeralis* was determined with individuals sampled from the Snake River Vista population and *P. antipodarum* from a laboratory maintained Madison River population. Individuals of varying sizes were sampled in August of 2009 and immediately returned to the Aquatic Sciences Laboratory at Montana State University, Bozeman for holding. Shells were measured to the nearest 0.01 mm with an optical micrometer, blotted dry, and weighed to the nearest 0.001 mg with a microbalance (*V. humeralis* n = 101, *P. antipodarum* n = 51). Length and mass values were log transformed to meet assumptions of normality. The regression for *V. humeralis* shell length to wet-mass was mass = $0.9340L^{2.3626}$ where mass is measured in mg and length (L) is measured in mm (n = 101, r^2 = 0.76). The regression for *P. antipodarum* shell length to wet-mass was mass = $0.4049L^{2.2791}$ where mass is measured in mg and length (L) is measured in mm (n = 51, r^2 = 0.96).