ESTIMATING INVASIVE SPECIES IMPACT: INTERACTION STRENGTHS, ABUNDANCE AND THE ROLE OF PRODUCTIVITY IN A FRESHWATER INVASION

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of LESLIE ANNE RILEY find it satisfactory and recommend that it be accepted.

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ESTIMATING INVASIVE SPECIES IMPACT: INTERACTION STRENGTHS, ABUNDANCE AND THE ROLE OF PRODUCTIVITY IN A FRESHWATER INVASION

Abstract

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Abstract. Estimating the strength of interactions between species is central to diverse questions in ecology, yet the theoretical basis for interaction strengths has only been well-developed for trophic interactions in dynamic food web models. In chapter 1, we derived dynamic interaction strengths for non-trophic interactions and specifically applied this to interactions between an invasive and native species. We then demonstrate how dynamic interaction strengths can be used in current estimates of invasive impact and expand impact measures to also include reciprocal effects of resident species on the invader.

In chapter 2, we test how grazing impacts of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) varies with resource availability by measuring both *Potamopyrgus* biomass and per unit grazing effects (i.e. dynamic interaction strengths) across streams that vary in primary production. We found that *Potamopyrgus* reduced algae, regardless of resource level. We also found that grazing interaction strengths (i.e. per unit effects) were strongest in the most productive streams and snail biomass was

highest in the same streams, resulting in *Potamopyrgus* having the largest impacts on algae in the most productive streams.

In chapter 3, we tested how resource availability affects competition between the invasive *Potamopyrgus* and a native snail (*Pyrgulopsis robusta*). We measured growth rates of *Potamopyrgus* and *Pyrgulopsis* and interspecific competition between them at two experimentally-altered resource levels. We found that *Potamopyrgus* always grew faster than *Pyrgulopsis*. In the presence of interspecific competition, *Potamopyrgus* growth rates were not affected by resource levels or the biomass of *Pyrgulopsis* competitors. Alternatively, *Pyrgulopsis* grew slower at low resource levels and especially when the biomass of *Potamopyrgus* competitors was high. Competitive effects of *Potamopyrgus* on *Pyrgulopsis* were reduced at high resource levels due to faster *Pyrgulopsis* growth rates; *Pyrgulopsis*, though, does not strongly compete with *Potamopyrgus* under any resource scenario.

Overall, this study extends the use of dynamic interaction strengths to include non-trophic interactions and shows how the full range of community interactions can be included in measures of invasive species impact, facilitating comparisons of impact across species, productivity gradients and different types of community interactions.

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CHAPTER ONE

ON ESTIMATING INVASIVE SPECIES IMPACT: THE STRENGTH OF TROPHIC AND NON-TROPHIC INTERACTIONS

Abstract. Estimating the strength of interactions between species is central to diverse questions in ecology, yet the theoretical basis for interaction strengths has only been well-developed for trophic interactions in dynamic food web models. Here, we developed dynamic interaction strengths for non-trophic interactions and specifically applied this to interactions between an invasive and native species. We then demonstrate how dynamic interaction strengths can be used in estimates of invasive impact, providing an important link between potentially applied measures of impact and general ecological theory. We conclude by showing how estimates of invasive species impact can also include reciprocal effects of resident species on the invader. This study extends the use of dynamic interaction strengths to include non-trophic interactions and shows how the full range of community interactions can be included in measures of invasive species impact, facilitating comparisons of impact across species, sites and even different types of community interactions.

Introduction

Estimating the strength of interactions between species is central to diverse questions in ecology, due in part to the increased interest in trait-mediated indirect interactions (Bolnick and Preissier 2005, Werner and Peacor 2003), community interaction networks and coevolution (Novak and Wootton 2008, Bascompte and Jordano 2007), effects of invasive species in biological communities (Parker et al. 1999, Bruno et

al. 2005) and the role of weak versus strong interactions in promoting community and ecosystem stability (Sala and Graham 2002, de Ruiter et al. 1995). The idea of "interaction strength" (IS) has been used in studies of food web ecology (Hall et al. 2000, Wootton 1997) to estimate the parameters of dynamic ecological models. As a consequence, the theoretical and empirical underpinnings of estimates of the effects of consumers on resources (e.g. predator-prey, herbivore-plant) have been well developed. However, these methods are potentially widely applicable to estimating the strength of the full range of both trophic and non-trophic interactions (Wootton and Emmerson 2005).

Despite the utility of using dynamic interaction strengths to estimate a wide range of species interactions, the theoretical framework has not been developed for non-trophic interactions. Here, we review the general theoretical basis for interaction strengths and describe how to estimate consumer-resource interaction strengths. As a concrete example, we discuss the role of this theory in measuring interactions between invasive and native species in an invaded community. Next, we develop theoretical models of interaction strength for non-trophic interactions (e.g. competition and facilitation) and describe how short-term experimental studies can be used to estimate these values. We then suggest how such studies of non-trophic interactions might provide insight into long-term community dynamics. Finally, we suggest expanding on a current model (Parker et al. 1999) to include effects of not only invasive species on resident species, but also reciprocal effects of resident species on invaders.

Interaction strengths

Interaction strengths estimate the magnitude and direction of the effect of one species on another (Paine 1992, Wootton 1997, Berlow et al. 1999, Berlow et al. 2004, Wootton and Emmerson 2005). The most widely applicable interaction strengths are measured as the effect per individual or unit of biomass on another individual or another unit of biomass (Laska and Wootton 1998). Approaches to measuring per unit interaction strengths are varied and have included long-term experimental removals that examine whole-community responses (Paine's index: Paine 1966, 1992), energy flow measurements through ecosystems (Hall et al. 2000) and observational approaches based on predator and prey-specific handling times derived from dynamic food web models (Wootton 1997) or Type II functional responses (Novak and Wootton 2008).

The class of interaction strengths derived from dynamic models are considered to be most useful for addressing a range of questions in ecology for several reasons. First, dynamic interaction strengths are standardized by biomass of the species (e.g. per unit gram) or the individual (per capita) and to a unit of time (e.g. per day) so experiments can vary in densities and duration, assuming that responses are linear (but see Ruesink 1998 for non-linear responses). In addition, dynamic indices do not rely upon equilibrium assumptions; thus, these indices are more realistic because most communities are not in equilibrium (Laska and Wootton 1998), especially when invasive species are involved (Abrams 2001). Dynamic interaction strengths can also be used in theoretical community models (Laska and Wootton 1998) to predict the outcome of biotic interactions, thus uniting empirical estimates of interaction strength to model predictions (Berlow et al. 2004). Finally, dynamic models have been extensively developed for trophic interactions

in food webs, but can be expanded to also measure the strength of non-trophic interactions, which might be just as important a driver of community structure (Wootton and Emmerson 2005).

In general, dynamic interaction strengths can be calculated by changing the biomass or density of one species and measuring the resulting change in biomass or density of a second species (i.e. target species). The general equations for discrete-time versions of dynamic interactions between two species, *i* and *j,* are:

$$(1)\ M_{i,t} = M_{i,0} * \exp((r_i + \alpha_{ii} * M_{i,0} + \alpha_{ij} * M_{j,0})t)$$

$$(2)\ M_{j,t} = M_{j,0} * \exp((r_j + \alpha_{jj} * M_{j,0} + \alpha_{ji} * M_{i,0})t)$$

where $M_{i,t}$ is biomass of species *i* at time *t*, $M_{i,0}$ is biomass of species *i* at time *0*, r_i is density independent growth, α_{ii} is the interaction strength of species *i* on itself, α_{ij} is the interaction strength of species *j* on species *i*, $M_{j,0}$ is biomass of species *j* at time *0*, and *t* is time. Equation (1) represents the change in biomass of species *i* over time when interacting with both species *i* conspecifics and species *j*. The terminology in equation (2) is similar to that of equation (1), but now species *j* is the "target", representing the change in biomass of species *j* over time when interacting with both species *j* conspecifics and species *i*. These equations differ from the discrete time version of Lotka-Volterra models because here, *r* is an isolated density independent term, whereas in Lotka-Volterra equations, *r* is not an isolated term (Gotelli 1998, Hughes and Roughgarden 1998).

Interaction strengths and invasive species impact

Almost 10 years ago, Parker et al. (1999) suggested that range and abundance, or biomass, of invasive species could be combined with per unit estimates of the strength of biotic interactions between invasive and native species to quantify impact. Hence, important information about population impacts of invasive species can be obtained by measuring the strength of biotic interactions and should be included in estimates of impact. Unfortunately, the methods generally used to measure the impact of invasive species are so varied that comparing relative impacts of invaders across species, habitats and regions is difficult. Few studies have attempted to quantify interaction strength between native and invasive species.

The dynamic index of interaction strength is uniquely suited to fit into the Parker et al. impact framework because this measure provides per unit estimates standardized to biomass or the individual. This approach using a standard index facilitates comparisons of interaction strengths (1) between invasive and native species at different levels of community organization, (2) among various invasive species to determine which species have disproportionately strong effects, and (3) among different habitats to determine which communities might be most vulnerable to the effects of invasive species. This approach also unites potentially applied measures of invasive species impact to community ecology theory, thus providing insight into the role of species interactions in shaping community structure (Shea and Chesson 2002).

Experimental approaches to measuring interaction strengths

Experimental approaches to measuring interaction strengths consist of manipulating the biomass or density of one species and measuring the change in biomass or density of a target species. The general equations (1) and (2) can be rearranged to isolate interaction strengths for predation, herbivory, parasitism, competition and facilitation between any pair of species. In the following section, we first review the equations that have been derived to allow estimation of trophic interactions between consumers and their resource (e.g. predation, herbivory, parasitism) from experiments and/or observational studies. Second, we derive equations that estimate dynamic interaction strengths for non-trophic (e.g. competition, facilitation) interactions from experimental studies. For simplicity, we summarize how dynamic interaction strengths can be derived (i.e. Wootton 1997) in the context of interactions between an invasive consumer and a native prey (i.e. resource) species.

Trophic interactions.

Theoretical consumer-resource interaction strengths are well-developed and have been discussed elsewhere (Osenberg 1996, Wootton 1997, Laska and Wootton 1998, Berlow 1999, Wootton and Emmerson 2005). For predator-prey interactions with the invasive species as the predator, the native prey population can be described (Fig. 1A):

$$(3)\ M_{n,t,ti} = M_{n,0,ti} * \exp((r_n + \alpha_{ni} * M_{i,0,ti})t)$$

where $M_{n,t,ti}$ is the biomass of the native prey species at time t under the treatment biomass of the invasive predator (ti), $M_{n,0,ti}$ is the biomass of the native prey species at time 0 under the treatment biomass of the invasive predator (ti), r_n is density independent

growth of the native prey species, α_{ni} is the interaction strength of the invasive species on the native species, $M_{i,0,ti}$ is the biomass of the invasive predator at time *0,* and *t* is time. In this case, we assume that intraspecific interactions among the native prey species are negligible and thus the $\alpha_{nn} M_{n,0}$ term has dropped out of the equation. When conducting experiments, low biomass or densities of the native prey species should be used to minimize any effects of intraspecific competition.

In a simple experiment with two treatments where the invasive predator is either present ($ti > 0$) or absent ($ti = 0$) (Table 1, Fig. 1A), the native prey population can be described:

$$(4)\ M_{n,t,>0} = M_{n,0,>0} * \exp((r_n + \alpha_{ni} * M_{i,0,>0})t)$$

$$(5)\ M_{n,t,0} = M_{n,0,0} * \exp((r_n + \alpha_{ni} * M_{i,0,0})t)\ .$$

Solving equation (4) for r_n, substituting r_n into expression (5) and solving for α_{ni} results in:

$$(6)\ \alpha_{ni} = \frac{\ln(\frac{M_{n,t,>0} * M_{n,0,0}}{M_{n,0,>0} * M_{n,t,0}})}{(M_{i,0,>0} - M_{i,0,0}) * t}$$

In most predator-prey studies, the starting biomass of the native prey will be the same in treatments with and without the invasive predator. Thus the starting biomasses of the native prey will cancel out in the numerator. In addition, the biomass of the invasive predator in treatments with invasive predators absent is, by definition, zero. Thus, for the basic experiment described above, expression (6) simplifies to:

$$(7)\ \alpha_{ni} = \frac{\ln(\frac{M_{n,t,>0}}{M_{n,t,0}})}{M_{i,0,>0} * t}$$

Many variations could be added to this basic experiment. For example, a treatment with a native predator could be included to compare the strength of predation from a native species versus that of an invasive species on the same native prey.

Non-trophic interactions.

Here we will derive dynamic interaction strengths in the context of competitive/facilitative interactions between an invasive and a native species occupying the same trophic level. Even though non-trophic interactions likely also have strong effects on community structure, the connection between experiments and model estimates of per unit interaction strengths have not been developed for competition and facilitation (Berlow et al. 2004). In addition, competition between native and invasive species is quite common (reviewed in Bruno et al. 2005), but most studies do not provide a metric for the strength of competition. More recently, the importance of facilitation between native and invasive species has also been realized (Bruno et al. 2005).

For simplification, we will focus on interactions where the native is the target species. Thus, we can measure intraspecific interaction strengths (the effect of a native species on itself) as well as interspecific interaction strengths (the effect of an invasive species on the native species) (Table 2). These interaction strengths can be either positive or negative, indicating facilitation or competition, respectively. This stands in contrast to classic niche theory where positive interactions are either ignored or assumed to be constant (Bruno et al. 2003).

In general, for non-trophic interactions with the native species as the target, the native population can be described (Fig. 1B):

$$(8)\ M_{n,t,ti,tn} = M_{n,0,ti,tn} * \exp((r_n + \alpha_{nn} * M_{n,0,ti,tn} + \alpha_{ni} * M_{i,0,ti,tn})t)$$

where $M_{n,t,ti,tn}$ is the biomass of the native competitor at time *t* under the treatment biomass of the invasive competitor (*ti*) and conspecifics (*tn*), $M_{n,0,ti,tn}$ is the biomass of the native competitor at time *0* under the treatment biomass of the invasive competitor (*ti*) and conspecifics (*tn*), r_n is density independent growth of the native species, α_{nn} is the interaction strength of the native species on itself, $M_{n,0,ti,tn}$ is the biomass of the native species at time *0,* α_{ni} is the interaction strength of the invasive competitor on the native species, $M_{i,0,ti,tn}$ is the biomass of the invasive species at time *0* and *t* is time (Table 2).

For intraspecific interactions for the native species, no invasive competitors ($M_{i,0,ti,tn}$) are present. Thus, the dynamic equation simplifies to:

(9) $$M_{n,t,ti,tn} = M_{n,0,ti,tn} * \exp((r_n + \alpha_{nn} * M_{n,0,ti,tn})t)$$

For two intraspecific treatments with a high biomass of the native (*ti* = 0, *tn* = high) and a low biomass of the native (*ti* = 0, *tn* = low) (Table 3):

(10) $$M_{n,t,0,high} = M_{n,0,0,high} * \exp((r_n + \alpha_{nn} * M_{n,0,0,high})t)$$

and

(11) $$M_{n,t,0,low} = M_{n,0,0,low} * \exp((r_n + \alpha_{nn} * M_{n,0,0,low})t)$$

Solving equation (10) for r_n, substituting r_n into expression (11) and solving for α_{nn} results in:

(12) $$\alpha_{nn} = \frac{\ln(\frac{M_{n,t,0,high} * M_{n,0,0,low}}{M_{n,0,0,high} * M_{n,t,0,low}})}{(M_{n,0,0,high} - M_{n,0,0,low}) * t}$$

Under intraspecific interactions, the starting biomass of the native species differs between low (e.g. 1x) and high (e.g. 3x) treatments and thus should be included in the numerator.

(When measuring consumer-resource interaction strengths, the starting biomasses of the native prey were constant so the values canceled each other.)

For interspecific interactions between the invasive species and the native target species, we can assume that intraspecific interactions among the native species are negligible if kept at low biomass. This assumption is valid under an experimental design where the starting biomass of the native target species is much lower than their biomass under natural conditions (i.e. 0.5x). Under this assumption, $\alpha_{nn} \approx 0$ and drops out of the equation along with the second $M_{n,0,ti,tn}$. Thus, the dynamic equation simplifies to:

$$(13)\ M_{n,t,ti,tn} = M_{n,0,ti,tn} * \exp((r_n + \alpha_{ni} * M_{i,0,ti,tn})t)$$

For two interspecific treatments with a high biomass of the invasive (*ti* = high, *tn* = low) and a low biomass of the invasive (*ti* = low, *tn* = low) when the native species is the target (Table 3):

$$(14)\ M_{n,t,high,low} = M_{n,0,high,low} * \exp((r_n + \alpha_{ni} * M_{i,0,high,low})t)$$

and

$$(15)\ M_{n,t,low,low} = M_{n,0,low,low} * \exp((r_n + \alpha_{ni} * M_{i,0,low,low})t)$$

Solving expression (14) for r_n, substituting r_n into expression (15) and solving for α_{ni} results in:

$$(16)\ \alpha_{ni} = \frac{\ln(\frac{M_{n,t,high,low} * M_{n,o,low,low}}{M_{n,0,high,low} * M_{n,t,low,low}})}{(M_{i,0,high,low} - M_{i,0,low,low}) * t}$$

Under interspecific interactions, the starting biomass of the native target species does not differ between low (e.g. 0.5x) and high (e.g. 0.5x) treatments and thus could cancel out of the numerator. However, not all experiments will be designed in this way. For

consistency when comparing intra- and interspecific interactions, we have presented both interaction strengths in a similar manner.

Because the non-trophic interaction strengths presented here are equivalent to competition coefficients from the discrete time version of Lotka-Volterra equations (Laska and Wootton 1999, Berlow et al. 1999, 2004), classic Lotka-Volterra coexistence criteria could be used to predict whether a native species is likely to be displaced by an invasive species. To do so, four additional treatments with the invasive species as the target could be added to the basic experiment above. Stable coexistence should occur when intraspecific competition is stronger (more negative) than interspecific competition for both species (i.e. $\alpha_{ni} > \alpha_{nn}$ and $\alpha_{ni} > \alpha_{ii}$) (Fig. 1B).

Incorporating effects of resident species into measures of impact

Successful invasions have been attributed to characteristics of either the invader, (reviewed in Kolar and Lodge 2001), the new community (e.g., Stachowicz et al. 1999, 2002, Naeem et al. 2000), or a mismatch between the invader and residents of the new community (D'Antonio and Hobbie 2005). Impact should be highest where the mismatch is largest or where the invasive species has the largest negative effects and the resident community provides little biotic resistance or even facilitates the invader, thus highlighting the importance of including both in measures of invasive species impact. Up to this point, we have discussed impact (I) as a function of range (R), abundance or biomass (B) and per unit effect of the invasive species (E). Thus, $I \propto R \times B \times E$. However, per unit effects of the invasive species on a native species could be offset by strong intraspecific interactions among the invader. Thus, the per unit effect is a function of both interspecific and intraspecific interaction strengths. Substituting the dynamic

indices of interaction strengths:

$$I \propto R \times B \times (\alpha_{ni} - \alpha_{ii})$$

where α_{ni} is the interaction strength of the invasive species on the native species and α_{ii} is the interaction strength of the invasive species on itself.

If resident species are likely to also have some reciprocal effect on the invader these interaction strengths should also be included in estimates of impact. Any negative per unit effects a resident species has on the invasive species would lessen the overall impact of the invasive species, presuming the impact is negative. On the other hand, if the resident species has positive per unit effects on the invasive species, overall negative impacts of the invasive species might increase.

Incorporating effects of resident species into impact measures might prove most useful in critical portions of the new range where an invasive competitor is potentially displacing an already rare, threatened or locally endemic native species or where strong competitive and/or facilitative interactions are occurring between the invasive species and a resident community dominant. Thus, we could look at impact by the invasive species on a particular resident as a function of biomass and per unit effects, or $I \propto B \times E$ (same as "species impacts," Wootton 1997). By also looking at the reciprocal impacts of the resident species on the invader as a function of biomass and per unit effects, impact of the invasive species becomes:

$$I \propto (B_i \times (\alpha_{ni} - \alpha_{ii})) - (B_n \times (\alpha_{in} - \alpha_{nn}))$$

where B_i and B_n are the biomass of the invasive and native species, respectively, α_{in} is the interaction strength of the native species on the invasive species and α_{nn} is the interaction strength of the native species on itself. If the impact of the invasive species on a resident

is negative, subtracting any negative impacts from the resident (i.e. biotic resistance) will lessen overall impact. Subtracting positive impacts of the resident on the invader (i.e. facilitation) will increase overall impact of the invasive on the resident. If impacts of the resident on the invader (i.e. (B_n x ($\alpha_{in} - \alpha_{nn}$)) are equal to the impacts of the invader on the resident (B_i x ($\alpha_{ni} - \alpha_{ii}$)) then overall impact of the invader should be negligible.

Conclusions

Here, we discussed the role of dynamic modeling as it relates to measuring interactions between invasive and native species in an invaded community. We also demonstrated how interaction strengths can be measured experimentally to estimate the strength of both trophic (consumer-resource) and non-trophic (competition, facilitation) interactions. Finally, we incorporated dynamic interaction strengths into estimates of invasive species impact and illustrated how to also include reciprocal effects of resident species on invaders.

Although we have advocated the use of dynamic interaction strengths to measure the full range of species interactions, we also understand that the experimental approach presented here is not without limitations. First, experiments require sufficient replication, potentially creating logistically difficult time constraints that might not be feasible to estimate multiple interaction strength measures for an entire species-rich community (Wootton 1997). Thus, this approach works best in situations where detailed interactions among a few key species are of interest. Second, the dynamic models presented here assume that species interactions exhibit a linear functional form (Abrams 2001), which is often a valid assumption (Wootton and Emmerson 2005), but not always (Ruesink 1998, Abrams 2001). Therefore, this approach works best in situations where a system is far

from equilibrium (i.e. a dominant invader) or when the experimental duration is short enough to assume that the response is not saturated (Berlow et al. 2004).

While this discussion has emphasized the role of interaction strengths in measuring invasive species impact, it is important to note that the methods and theory developed here are relevant to a range of problems in ecology. First, understanding the context dependent nature of ecological interactions along environmental gradients has been an important question in ecology (e.g. Menge and Sutherland 1976, Huston 1976). Measuring non-trophic interaction strengths could provide an index for the importance of competition and facilitation along stress or productivity gradients. Second, non-trophic interaction strengths estimated in short-term experiments could be useful in predicting long-term population dynamics for conservation management (Strayer et al. 2006). Third, the mutually beneficial nature of plant-pollinator interactions has been responsible for a large amount of current biodiversity (Bascompte and Jordano 2007). Understanding the strength of these facilitative interactions within a community has important implications for coexistence. Dynamic non-trophic interaction strengths might be applied to complex community networks to make predictions about stability. Finally, this approach links potentially applied measures of invasive species impact to community ecology theory, thereby facilitating the use of invasive species as natural experiments to further understand the role of species interactions in shaping community structure.

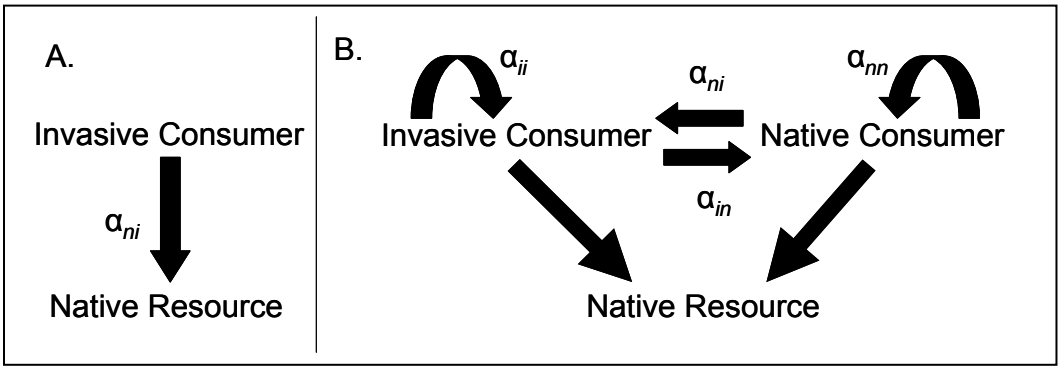

Fig. 1. Interaction networks depicting simplified experimental communities. (A) Trophic interaction strengths of invasive consumers, i.e. predators, on native resources, i.e. prey. (B) Non-trophic interaction strengths of invasive consumers and native consumers. Non-trophic interaction experiment depicts both intraspecific (α_{ii} and α_{nn}) and interspecific interaction strengths ($\alpha_{in}$and α_{ni}) for both species. The interaction strengths (α) have subscripts that match the experimental descriptions in the text.

Table 1. A simple experiment describing how to measure trophic interaction strengths.

Manipulation at time (0) $\boldsymbol{M_{i,0,ti}}$	**Response of native prey at time (t)** $\boldsymbol{M_{n,t,ti}}$
Invasive predator present $M_{i,0,>0}$	$M_{n,t,>0}$
Invasive predator absent $M_{i,0,0}$	$M_{n,t,>0}$

Table 2. Representations for mathematical terminology in the non-trophic interaction experiment when the native species is the target and the invasive species is the competitor.

Mathematical Term	Representation
$M_{n,t,ti,tn}$	biomass of the native competitor at time *t* under the treatment biomass of the invasive competitor (*ti*) and conspecifics (*tn*)
$M_{n,0,ti,tn}$	biomass of the native competitor at time *0* under the treatment biomass of the invasive competitor (*ti*) and conspecifics (*tn*)
$M_{i,0,ti,tn}$	biomass of the invasive species at time *0*
r_n	density independent growth of the native species
α_{ni}	interaction strength of the invasive competitor on the native species
α_{nn}	interaction strength of the native species on itself

Table 3. A simple experiment describing how to measure non-trophic interaction strengths.

Total biomass	Type of interaction	Manipulation at time (0) of native target species $M_{n,0,ti,tn}$	Manipulation at time (0) of invasive species $M_{i,0,ti,tn}$	Response of native target species at time (t) $M_{n,t,ti,tn}$
Low (1x*)	Intraspecific	1x $M_{n,0,0,low}$	–	$M_{n,t,0,low}$
High (3x)	Intraspecific	3x $M_{n,0,0,high}$	–	$M_{n,t,0,high}$
Low (1x)	Interspecific	0.5x $M_{n,0,low,low}$	0.5x $M_{i,0,low,low}$	$M_{n,t,low,low}$
High (3x)	Interspecific	0.5x $M_{n,0,high,low}$	2.5x $M_{i,0,high,low}$	$M_{n,t,high,low}$

* 1x = ambient biomass

CHAPTER TWO

INVASIVE SPECIES IMPACT: BIOMASS AND GRAZING EFFECTS OF THE NEW ZEALAND MUD SNAIL ACROSS A PRODUCTIVITY GRADIENT

Abstract. Traditionally, the invasiveness of species has been attributed to characteristics of either the invader or the new community. However, the emerging realization is that impacts of invasive species can depend upon changes in environmental factors. Furthermore, environmental effects on invader impact can be manifested through either their abundance or the strength of their interactions with native species. Resource availability is one factor known to promote invasiveness, but it is not yet clear whether impacts of invasive species are stronger in high resource areas and whether stronger impacts might be due to changes in biomass, the strength of species interactions or both. Here, we measured the effect of resource availability on biomass and the strength of species interactions between an invasive grazing snail (*Potamopyrgus antipodarum*) and its algal resources. We found that *Potamopyrgus* reduced periphyton abundance and productivity, regardless of resource level. However, we also found that grazing interaction strengths (i.e. per unit effects) were strongest in the most productive streams and snail biomass was highest in the same streams. Therefore, the estimated population impacts of *Potamopyrgus* on periphyton were strongest in the most productive streams and impact was influenced both by a change in grazing interaction strengths and biomass.

Introduction

Traditionally, the invasiveness of species has been attributed to characteristics of either the invader (reviewed in Kolar and Lodge 2001) or the new community (e.g., Stachowicz et al. 1999, 2002, Naeem et al. 2000). Unfortunately, there are still many unanswered questions, with the impact of successful exotic species still not well understood (Bruno et al. 2005, Strayer 1999). The emerging realization is that the impact of invasive species can depend on changes in environmental factors, such as disturbance or habitat modification (Londsdale 1999, Bando 2006, Rand and Louda 2006). Thus, impact is not independent of characteristics of the new ecosystem. Furthermore, environmental effects on invader impact can be manifested through either their abundance or the strength of their interactions with native species (per unit effects *sensu* Parker et al. 1999).

Invasive species abundance, or biomass, has often been used as the metric for impact. However, impacts of an invasive species on the native community can also be high if the strength of negative interactions of the invader on the native is high (i.e. functionally-mediated effects, Didham et al. 2007). It seems likely that the strength of these interactions might vary across the species ranges with environmental conditions. For example, the environment-dependent nature of ecological interactions along stress or productivity gradients has been realized for some time (Menge and Sutherland 1976, Huston 1976). More recently, resource availability appears to promote invasion success, whether resources are stable or fluctuating over time (Davis et al. 2000, Davis and Pelsor 2001). However, it is not clear whether increased resource availability changes the strength of interactions between invasive and native species. By measuring both biomass

and the strength of species interactions, invasive species impact along a resource gradient can be assessed.

Here, we measured the effect of resource availability on biomass and the strength of species interactions between an invasive grazing snail (*Potamopyrgus antipodarum*) and its algal resources. Previous studies show that *Potamopyrgus* biomass varies with primary production. In the native range of New Zealand, the highest densities (and presumable high biomass) of *Potamopyrgus* are found in stable, productive streams (Death 1991). Other native stream invertebrates can also reach high abundance in productive streams in both experimental (e.g Hart and Robinson 1990) and observational (e.g. Wallace and Gurtz 1986) studies. Less is known, though, about how the magnitude of grazing interactions will vary with resource availability. *Potamopyrgus* grazes on periphyton in benthic stream communities and can significantly reduce periphyton in less than one week (Riley et al. 2008). Other herbivorous grazers, including other snails, can significantly reduce periphyton (e.g. Lamberti et al.1987, Steinman 1996, reviewed in Feminella and Hawkins 1995), but the direction and magnitude of these impacts are not consistent across streams (Lamberti and Feminella 1996). In a meta-analysis, stronger grazing impacts occurred in streams with higher primary production (Feminella and Hawkins (1995). Within the Greater Yellowstone Ecosystem, *Potamopyrgus* dominates a highly productive stream (Hall et al. 2006), but we do not know how grazing per unit effects vary across a productivity gradient. Furthermore, few studies have looked at the effects of environmental variability on interaction strengths.

Our study was designed to determine whether overall grazing impacts of introduced *Potamopyrgus* will be stronger in productive streams, and whether differences

will be due to high biomass or strong grazing interaction strengths or a combination of both. We know that productivity can alter consumer biomass, but we do not know if grazing interaction strengths also change. To answer this question, we measured the effect of variation in resource availability (i.e. primary production) on 1) biomass of the invasive *Potamopyrgus* and 2) grazing interaction strengths on periphyton. By keeping the biomass of *Potamopyrgus* constant across experiments, we can determine whether changes in grazing impacts are due to biomass (i.e. numerically-mediated effects, Didham et al. 2007) or per unit effects (i.e. functionally-mediated effects, Didham et al. 2007).

Methods

Study sites and experimental design.

The invasive New Zealand mud snail (*Potamopygus antipodarum*) *Potamopyrgus* was first recorded in streams in the western U. S. in 1987 and now has a widespread, but patchy, distribution (http://www.esg.montana.edu/aim/mollusca/nzms). We measured *Potampyrgus* biomass and performed field experiments to test grazing effects of *Potamopyrgus* on periphyton in nine streams within the Greater Yellowstone Ecosystem over the course of two summers (2005 and 2007) (Table 1). Controlled field experiments are most useful for determining effects of herbivory and other factors on periphyton (Lamberti and Feminella 1996) and these streams represent the full range of primary production that *Potamopyrgus* encounters in this area (see Results). In 2005, we tested grazing effects in six streams and in 2007, added three more streams. We also repeated experiments in two highly productive streams that were used in 2005. Most streams used for the 2005 experiments fell at the low end of the range of primary production so we purposely repeated experiments in two streams that fell at the higher end of the range.

Thus, our data set included grazing effects from eleven different experiments across nine streams. For clarity, we will consider the two repeated streams as separate events, or streams, for the remainder of the methods and results.

Grazing effects.

In each stream in the summers of 2005 and 2007, we stocked 8 – 10 cage enclosures (~ 0.02 m^{-2} each) with 3 rocks from the surrounding streambed after removing other invertebrates. The periphyton was left intact. To ensure the rocks in our cages reflected ambient periphyton, we collected periphyton from 3 sets of 3 rocks that were not used in the experiment and compared chl-*a* levels on ambient rocks to those from our cages (see *Periphyton response measurements* for methods). Rocks in cages accurately reflected stream periphyton conditions. While streams differed in chl-*a* levels ($p<0.001$), ambient chl-*a* measured on rocks was not different from chl-*a* in control cages within each stream ($p=0.911$) (Fig. 1).

The cages were constructed from clear Plexiglas® tubing and openings on both ends were covered with 1-mm mesh. The cages were attached to boards of Trex® and anchored to the streambed in a manner that maximized water flow through the cages (Plate 1). Half of the cages (4-5 for each stream) served as controls and no snails were added. In the other 4-5 cages, we added 600 adult snails (3 – 5 mm). The density used in the experiments is equivalent to low to intermediate biomass levels observed in Polecat Creek and to high biomass levels observed in the Firehole River during the summer (Hall et al. 2006). We used the same biomass across all streams to avoid a further source of variation in our estimates of grazing effects.

After an average of 5.5 days post-manipulation (range: 3 – 8 days), we removed snails to measure final snail biomass and measured periphyton responses in terms of periphyton abundance (chlorophyll *a* (chl-*a*) and ash-free dry mass (AFDM)) and periphyton productivity (gross primary production (GPP)). We used short time frames for experiments to isolate direct grazing effects by reducing the possibility for any indirect effects and preventing the system from reaching equilibrium (Laska and Wootton 1998, Berlow et al. 1999, Wootton and Emmerson 2005). Dynamic interaction strengths accurately reflect theoretical interaction strengths when the system is far from equilibrium (Berlow et al. 2004). We preserved snails in 70% ethanol and measured individual snail lengths under a dissecting microscope fitted with an ocular micrometer**,** and subsequently converted to snail biomass to get final measurements of snail biomass for each experiment (Hall et al. 2006).

Periphyton response measurements. – We measured grazing effects on four periphyton response variables because the magnitude and direction of grazing effects can differ depending upon the response variable measured (Feminella and Hawkins 1995). To measure grazing effects on periphyton productivity, we placed rocks from each replicate in sealed recirculating chambers. Water was recirculated with a Watson-Marlow 323 pump (Wilmington, MA, USA) at approximately 8 mL s^{-1} to mimic stream conditions. We placed rocks in clear, 0.5 L Plexiglas® chambers for 1 h and used a dissolved oxygen meter (YSI-85; Yellow Springs, Ohio, USA) to measure oxygen generation. Net primary production (NPP) was calculated as the increase in oxygen during the chamber incubation (Bott 1996). We then incubated rocks in dark 0.5 L PVC chambers for 1 h and measured oxygen decline. Community respiration was calculated as the decrease in oxygen during

the dark chamber incubation. We calculated gross primary production (GPP) as the sum of NPP and the absolute value of community respiration and scaled these metrics by rock area (mg O_2 m^{-2} h^{-1}).

To measure grazing effects on periphyton abundance, we first removed periphyton from rocks with nylon brushes and collected two subsamples from each replicate onto pre-combusted glass fiber filters (Gelman AE; Pall Gelman Sciences, Ann Arbor, MI, USA) with 100-mL syringes. We froze the first filter for chl-*a* analysis, and then extracted chl-*a* with buffered ethanol. We measured pheophytin-corrected chl-*a* concentrations on a Turner Designs TD-700 fluorometer (Sunnyvale, CA, USA) at 436 nm excitation wavelength and 680 nm emission wavelength (Chlorophyll a: mg chl-*a* m^{-2}). We dried the second filter at 60ºC for 24 hours, recorded dry mass, and then combusted filters at 500ºC for 1 hour and recorded ash mass. We calculated ash-free dry mass as the difference between dry mass and ash mass (AFDM: mg m^{-2}). (AFDM was only measured in the 2007 experiments). Chlorophyll *a* concentrations (mg chl-*a* cm^{-2}) represent the amount of living algae present, whereas AFDM (mg AFDM m^{-2}) measures the entire organic component of the periphyton without distinguishing between algae and other organic material. Finally, we calculated chl-*a* specific production by dividing GPP by chl-*a* for each given replicate (mg O_2 mg^{-1} chl-*a*).

Statistical analysis.—Our goal was to measure grazing effects and biomass effects across streams that differed in resource availability. Thus, we first had to make sure our streams represented a gradient of productivity and periphyton abundance. We used a one-way ANOVA with stream as a fixed factor to test for variation across streams in periphyton levels with three different response variables: GPP, chl-*a* and AFDM from

control cages. The periphyton response variables were all log-transformed to meet normality assumptions for parametric analyses, but the figures present the raw data values. When a significant effect of stream was found for GPP and chl-*a*, post-hoc Bonferroni comparisons were performed. We then used a linear regression to test if chl-*a* and GPP were correlated to make sure that highly productive streams also had high periphyton abundance.

We then estimated the grazing effects that *Potamopyrgus* has on periphyton with respect to periphyton abundance and productivity. The goal was to understand the general effects that *Potamopyrgus* has on a variety of periphyton response variables. To estimate grazing effects across all streams on chl-*a* (N=97), GPP (N=96) and chl-*a* specific GPP (N=96), we used 2-way analyses of variance (ANOVAs) with stream (1-11) and treatment (control vs. snails) as fixed factors. To estimate grazing effects on AFDM (N=42), we also used a 2-way analysis of variance, but had only five levels of stream because AFDM was only measured in 2007.

Finally, we tested if grazing effects varied with productivity. We first calculated grazing interaction strengths as the difference in chl-*a* from field enclosures with snails present compared to the average chl-*a* of field enclosures with no snails present for each experiment. Thus, each experiment yielded 4 – 5 interaction strength values for a given productivity level. We used only chl-*a* to calculate interaction strengths because snails did not significantly reduce periphyton AFDM (see Results below). We calculated per biomass interaction strengths ($-c$; g^{-1} snail AFDM d^{-1}) (Wootton 1997, Riley et al. 2008) as**:**

$$-c = \frac{\ln\left(\frac{N_s}{N_0}\right)}{Mt} \qquad [1]$$

where N_s is the concentration of chlorophyll *a* with snails present, N_0 is chlorophyll *a* with no snails, M is snail biomass for N_s, and t is time (d). More-negative values indicate a greater reduction of algae/g snail biomass/d. These values are direct estimates of per biomass algal population growth and can be extrapolated to population impacts of snails when multiplied by snail population biomass. Comparisons among per biomass interaction strengths are not confounded by experimental duration or biomass of grazers, which is often the case when effect sizes are compared (i.e. ln (N_s/N_0); Feminella and Hawkins 1995). We then used a linear regression to determine the relationship between grazing interaction strengths and GPP from the control cages. Again, we log-transformed GPP to meet normality assumptions for parametric tests.

Biomass effects.

Resource availability might also affect *Potamopyrgus* biomass. To test for biomass effects across streams that varied in resource availability, we documented the relationship between primary production and *Potamopyrgus* population biomass (g AFDM m^{-2}). In each of the 9 streams, we sampled 8 benthic cobble locations with a Surber sampler (mesh size: 500 μm) during July of 2006 and preserved snails in 70% ethanol to measure biomass. We picked all snails from each of eight preserved Surber samples from each stream, and measured a random subset of ≥30 snails to estimate the length distribution and biomass for the entire sample. All snail biomass measurements were scaled to area (g snail AFDM m^{-2}). We also measured temperature because it can affect population dynamics and reproduction in *Potamopyrgus* (Winterbourn 1970, Quinn

et al. 1994, Dybdahl and Kane 2005). The average summer daytime temperature over an eight-hour day was recorded with a probe (YSI-85) during the grazing experiments in each stream.

One potential mechanism that could cause an increase in *Potamopyrgus* biomass would be an increase in birth rates. Thus, we also measured whether the number of offspring of *Potamopyrgus* was higher in productive streams after accounting for variation in snail size. Females reach their maximum size at maturity and brood their eggs and crawl-away juveniles in a brood chamber. Hence, size of first reproduction was estimated as the average size of brooding females in a sample of ≥30 snails for each of 8 replicates from the 9 streams (n >240 per stream). We then dissected the snail to check for the presence of developing offspring in the brood chamber to estimate brooding rate. For those snails that were brooding, we also measured brood number, or number of offspring present in the brood chamber at that time. Minimum sample size of brooding snails per replicate was 21, due to low snail biomass in one stream.

Statistical analyses. - To determine the relationship between *Potamopyrgus* biomass and productivity, we used a stepwise regression with GPP and average temperature as predictor variables. GPP was converted to a log scale to satisfy normality assumptions.

To examine whether snails had more offspring in more productive streams, we used a stepwise regression with snail brood number as the response variable, and snail biomass at first reproduction, average temperature and GPP as predictor variables. Fairy Creek and the Snake River were both removed from this analysis due to insufficient numbers of brooding snails. We measured 21 – 242 brooding snails in all other streams.

Population-level impacts of Potamopyrgus *on periphyton.*

We combined measures of grazing effects (as per biomass interaction strengths) on periphyton with *Potamopyrgus* population biomass in each stream to compare impacts across nine streams. Population-level impacts of *Potamopyrgus* can be estimated in all streams by multiplying population biomass by per biomass interaction strengths. Thus, impact (I) within the given range of the Greater Yellowstone Ecosystem is proportional to per biomass interaction strengths (E) multiplied by population biomass (B) (Parker et al. 1999; see also Ricciardi 2003). Grazing impacts (I) were related to GPP with a linear regression. Both variables were log-transformed.

Results

Productivity gradient.

Streams differed with respect to periphyton productivity, with GPP ranging from 70 - 950 mg O_2 $m^{-2}*h^{-1}$ ($p<0.001$, Fig. 2A). Streams also differed with respect to some measures of periphyton abundance. Chl-*a* ranged from 0.75 - 25 mg chl-*a* m^{-2} and streams on the low and high end of the range were significantly different from one another ($p<0.001$, Fig. 2B). GPP and chl-*a* across streams were highly correlated ($R^2=0.750$, $p<0.001$). AFDM ranged from 95 - 160 mg AFDM m^{-2} but there was no significant difference among streams ($p=0.135$, Fig. 2C).

Grazing effects.

We found that *Potamopyrgus* significantly reduced chl-*a* levels in streams, but not AFDM. *Potamopyrgus* reduced chl-*a* levels across all streams (treatment: $p=0.002$) and the direction of the response was the same across streams (treatment x stream interaction: $p=0.415$) (Fig. 3A). For AFDM, we found that *Potamopyrgus* grazing had no significant

effect (treatment: p=0.179) and there was no significant interaction (treatment x stream: p=0.082) (Fig. 3B).

We found that the presence of *Potamopyrgus* reduced GPP (treatment: p=0.007) (Fig. 4A) and we found a significant interaction between stream and treatment (p=0.015), but this interaction was driven by one stream (Snake River; data not shown). Interestingly, we also found that *Potamopyrgus* increased chl-*a* specific GPP when all streams were taken into account (treatment: p=0.002) (Fig. 4B), and the direction of the production response was the same across streams (treatment x stream: p=0.069). These results suggest that *Potamopyrgus* reduced chl-*a* to a greater extent than GPP, thereby increasing the amount of production that is occurring per unit of chl-*a*.

We quantified the per unit biomass effect of snail grazing on chl-*a* by calculating interaction strengths. We found that grazing interaction strengths were significantly more negative as primary production increased, although the amount of variation explained by the model was small (R^2=0.08, p=0.035) (Fig. 5).

Biomass effects.

Snail biomass ranged from 6 mg AFDM m^{-2} in the stream with the second lowest production (Snake River) to 2270 mg AFDM m^{-2} in the most productive stream (Polecat Creek). Our best model demonstrated that snail biomass was linearly related to production, with higher biomass in more productive streams. However, this model was not significant even though it explained one-third of the variation. (R^2=0.334, p= 0.063) (Fig. 6).

We examined the effect of GPP, temperature and size at maturity on brood size. The step-wise regression showed that biomass at first reproduction was a significant

predictor of brood number (R^2= 0.869, p=0.002), but that temperature and GPP did not significantly improve model fit.

Population-level impacts of Potamopyrgus *on periphyton.*

The estimated population impacts of *Potamopyrgus* on periphyton (grazing interaction strength x population biomass) were stronger as productivity increased (R^2=0.184, p=0.004) (Fig. 7). Impacts of *Potamopyrgus* on periphyton were, on average, 40 times stronger in the most productive stream, Polecat Creek, compared to many of the low production streams.

Discussion

Our study was designed to determine whether overall grazing impacts of introduced *Potamopyrgus* will be stronger in productive streams, and whether differences will be due to high biomass, strong grazing interaction strengths or a combination of both. In general, we found that *Potamopyrgus* reduced chl-*a* and GPP, but increased chl-*a* specific GPP across all streams. We also found that grazing interaction strengths were strongest in the most productive streams, even though the amount of variation explained by our model was small. Snail biomass was also highest in the most productive streams, but was not related to a change in birth rates. Thus, the estimated population impacts of *Potamopyrgus* on periphyton were strongest in the most productive streams and impact was influenced both by a change in grazing interaction strengths and biomass.

Grazers can have multiple effects on periphyton abundance and productivity (Feminella and Hawkins 1995). We expected *Potamopyrgus* to reduce periphyton abundance because snails are effective grazers in streams (e.g. Lamberti et al.1987, Steinman 1996, reviewed in Feminella and Hawkins 1995). Here, *Potamopyrgus* reduced

chl-*a*, but did not significantly reduce periphyton mass (mg AFDM m^{-2}), as has been shown in a previous study in the Greater Yellowstone Ecosystem (Riley et al. 2008). This indicates that *Potamopyrgus* consumes algal resources effectively, but might not consume the non-algal component of the periphyton as readily. *Potamopyrgus* also reduced GPP, but increased chl-a specific GPP. Grazers frequently reduce GPP (Mulholland et al. 1991, Hill et al. 1992), but can increase biomass-specific production by removing filamentous algae, which improves light and nutrient flow to periphyton (Lamberti and Resh 1983, Mulholland et al. 1991).

Potamopyrgus reduced chl-*a* and the magnitude of reduction increased in the most productive streams. Stronger grazing impacts can occur in streams with higher production and two potential mechanisms might account for this phenomenon. First, grazer densities can be higher in productive streams, resulting in stronger grazing impacts (Feminella and Hawkins 1995). However, in this study, grazer biomass was kept constant across all streams. Grazing effects were standardized to a unit of biomass, so this mechanism cannot account for the larger reduction in periphyton. Second, grazers living in more productive streams might be more efficient at harvesting the "type and amount" of periphyton present (Feminella and Hawkins 1995). While *Potamopyrgus* now occurs in all streams from this study, *Potamopyrgus* might be an effective grazer on filamentous algae occurring in productive streams, thus increasing grazing per unit effects. In less productive streams, crustose algae might be more difficult to harvest.

We expected *Potamopyrgus* biomass to be highest in the most productive streams because experimentally increasing productivity has been shown to cause an increase in grazer abundance (Rosemond 1993). Mechanisms for higher invertebrate abundance in

productive streams include faster developmental rates (Hart and Robinson 1990), higher survivorship and fecundity in caddisflies (Feminella and Resh 1990) and faster growth rates in mayflies (Hill and Knight 1987). We did not find a corresponding change in birth rates of *Potamopyrgus* that could account for changes in biomass. Thus, GPP is not driving changes in birth rates in this system, even though biomass was affected. Snails in the most productive streams reproduced earlier, but also had smaller brood sizes. After accounting for variation in snail size, birth rates were similar. If survivorship or growth of *Potamopyrgus* is higher in productive streams, reproducing earlier could cause an increase in population growth and biomass.

Stronger grazing per unit effects and high population biomass resulted in the largest impacts of *Potamopyrgus* on periphyton. However, the variation explained by the model for grazing effects was small. Thus, it appears that impacts on periphyton are driven more by changes in *Potamopyrgus* biomass than by grazing interaction strengths. In the most productive stream in this study, Polecat Creek, *Potamopyrgus* consumes >90% of total primary production (Hall et al. 2003). However, in less productive streams, *Potamopyrgus* might also consume a large percentage of available primary production. Therefore, impacts on ecosystem function could be similar, even at lower population biomass.

Productivity has the ability to alter impact of an invasive species not only through traditional metrics of impact (i.e. abundance) but also by altering the strength of species interactions. Stronger grazing impacts of *Potamopyrgus* occured in the most productive streams as a result of changes in both numerically-mediated (i.e. biomass) and functionally-mediated (i.e. per unit effects) effects (Didham et al. 2007). This study

highlights the utility of an invasive species as a natural experiment to understand the role of productivity in altering impact through changes in both biomass and the strength of species interactions.

Tables

Table 1. Stream locations and dates of experiments.

Stream	UTM coordinates*		Dates of Experiment (days)
	Easting	Northing	
Crawfish	525, 615 E	4, 888, 950 N	8 July – 15 July 2007 (7)
Fairy	512, 622 E	4, 934, 328 N	16 July – 22 or 23 July 2005 (6-7)
Iron Spring	512, 343 E	4, 922, 350 N	13 July – 19 or 21 July 2005 (6-8)
Little Firehole	510, 969 E	4, 925, 719 N	1) 8 July – 13 or 14 July 2005 (5-6) 2) 7 July – 14 July 2007 (7)
Nez Perce	513, 344 E	4, 936, 357 N	21 July- 28 July 2007 (7)
Polecat	524, 540 E	4, 884, 155 N	1) 5 July – 9 or 11 July 2005 (4- 6) 2) 11 July – 19 July 2007 (8)
Sentinel	512, 346 E	4, 934, 929 N	3 July – 6 or 7 July 2005 (3-4)
Snake	526, 260 E	4, 883, 239 N	6 July – 13 July 2007 (7)
Spirea	525, 628 E	4, 888, 964 N	26 June – 1 or 2 July 2005 (5-6)

*all UTM coordinates are from zone 12

Plates

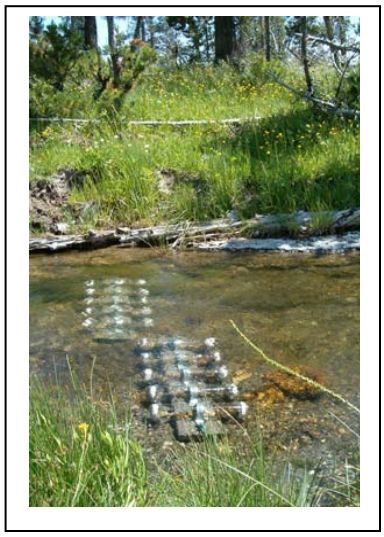

Plate 1. Cage enclosures for *Potamopyrgus* grazing experiments in one of the streams in the Greater Yellowstone Ecosystem. Photo credit: Leslie Riley.

Figures

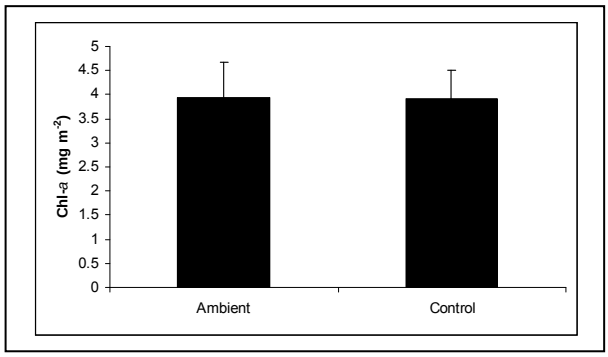

Fig. 1. Mean chl-*a* (+1 SE) standing stocks across nine streams on ambient rocks and on rocks from control cage enclosures in the absence of grazers after 1 wk.

Productivity gradient.

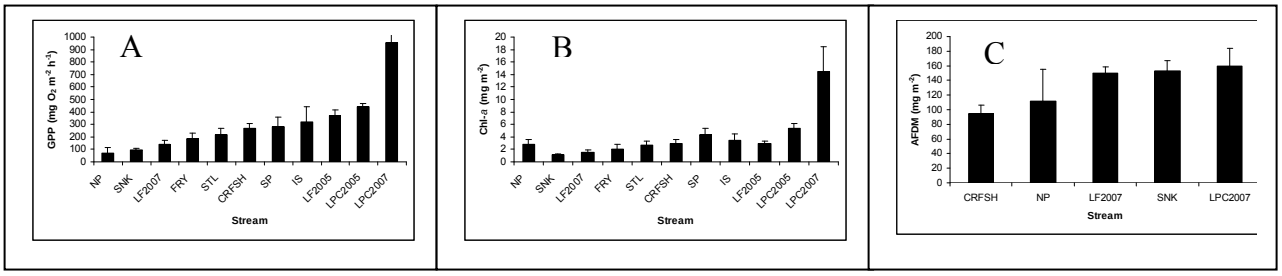

Fig. 2. Periphyton productivity and abundance in control cage enclosures across eleven experiments, measured as mean GPP (+1 SE) (A) and mean chl-*a* (+1 SE) (B). AFDM across five experiments, measured as mean periphyton AFDM (+1 SE) (C). AFDM was not measured in the first six experiments.

Grazing effects.

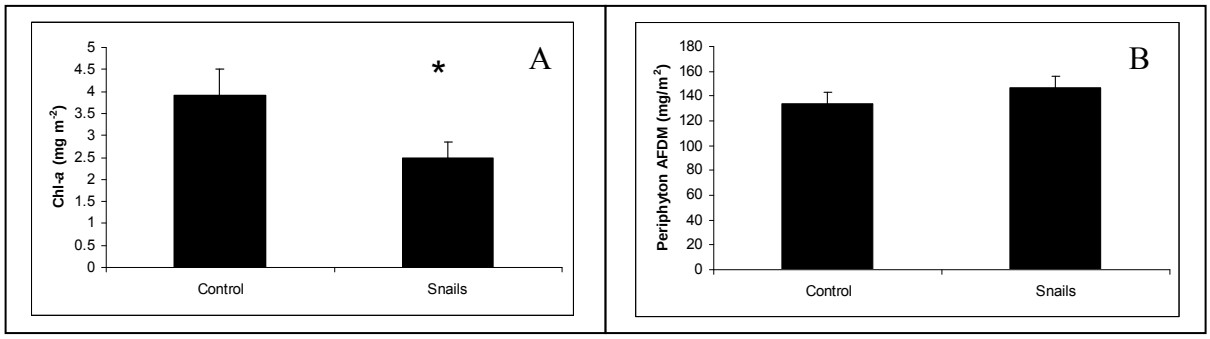

Fig. 3. Periphyton abundance after ~1 wk in cage enclosures with *Potamopyrgus* grazers (snails) and without *Potamopyrgus* grazers (control) measured as mean chl-a (+1 SE) standing stocks (A) or periphyton AFDM (+1 SE) (B).

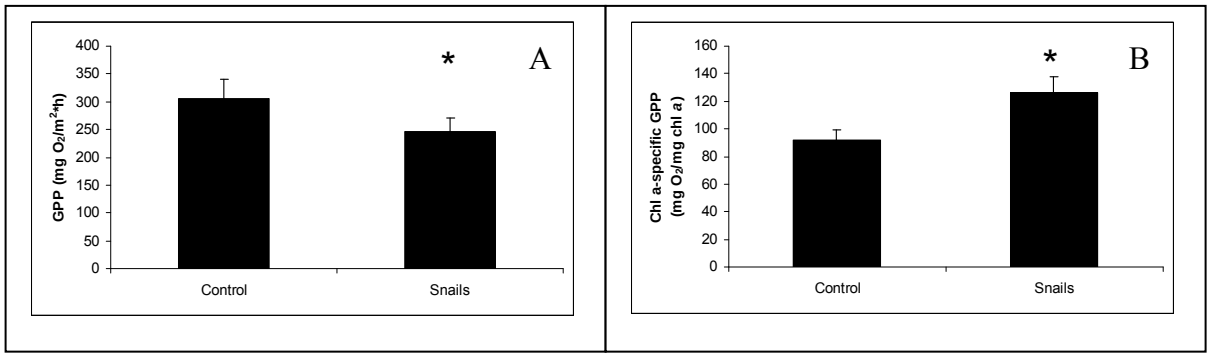

Fig. 4. Periphyton productivity after ~1 wk in cage enclosures with *Potamopyrgus* grazers (snails) and without *Potamopyrgus* grazers (control) measured as mean GPP (+1 SE) (A) or chl-a specific GPP (+1 SE) (B).

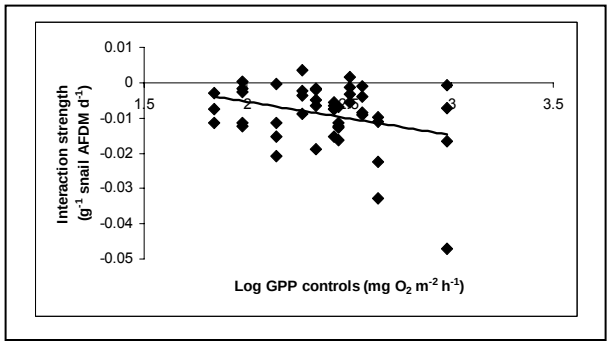

Fig. 5. Mean grazing interaction strengths on periphyton abundance, measured as chl-*a*, across eleven different experiments. The x-axis represents the log-transformed average GPP in control cage enclosures from each experiment.

Biomass effects.

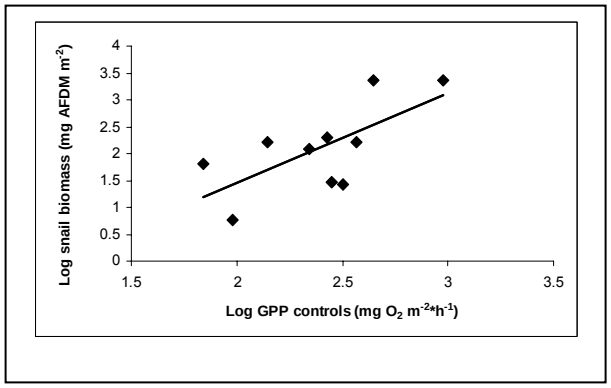

Fig. 6. Log-transformed ambient mean snail biomass across nine streams. The x-axis represents the log-transformed average GPP in control cage enclosures from each of eleven experiments.

Population-level impacts of Potamopyrgus *on periphyton.*

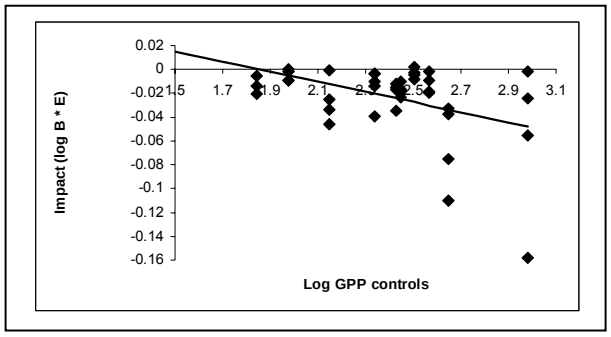

Fig. 7. Impact of *Potamopyrgus* grazers (log biomass * grazing interaction strength) on periphyton chl-*a* across eleven experiments. The x-axis represents the log-transformed average GPP in control cage enclosures from each of eleven experiments.

CHAPTER THREE

THE ROLES OF RESOURCE AVAILABILITY AND COMPETITION IN MEDIATING DOMINANCE OF AN INVASIVE FRESHWATER SNAIL

Abstract. The classic paradigm in community ecology is that competition structures communities, limiting the number of species that can coexist. Under this paradigm, highly diverse communities should be biotically resistant to invasion. However, the importance of biotic resistance in repelling invasions remains controversial and it appears that high resource availability can often neutralize competitive effects from native community members or cause an invasive species to become an even stronger competitor. Here, we experimentally test these two mechanisms in promoting dominance by measuring growth rates of invasive (*Potamopyrgus antipodarum*) and native snails (*Pyrgulopsis robusta*) and interspecific competition between them at two experimentally-altered resource levels. *Potamopyrgus* and *Pyrgulopis* are ecologically similar, compete for algal resources and are the dominant macro-invertebrates within the range of the locally endemic native *Pyrgulopsis*. We found that *Potamopyrgus* always grew faster than *Pyrgulopsis* at both high and low resource levels. In the presence of interspecific competition, *Potamopyrgus* growth rates were not affected by resource levels or the biomass of *Pyrgulopsis* competitors. On the other hand, *Pyrgulopsis* grew slower at low resource levels and especially when the biomass of *Potamopyrgus* competitors was high. These results indicate that competitive effects of *Potamopyrgus* on *Pyrgulopsis* were reduced at high resource levels due to faster *Pyrgulopsis* growth rates; *Pyrgulopsis*, though, does not strongly compete with *Potamopyrgus* under any resource scenario. In this system, the competitive dynamic between *Potamopyrgus* and *Pyrgulopsis* does not

change with increased resources. Thus, increased resource availability is not necessary for *Potamopyrgus* to dominate because competitive effects from this native community member are weak.

Introduction

The classic paradigm in community ecology is that competition structures communities, limiting the number of species that can coexist (Hardin 1960). Under this paradigm, highly diverse communities should be biotically resistant to invasion (Elton 1958), with diversity peaking when communities become saturated (Diamond 1975), and thus preventing establishment and dominance by new species. At a local scale, successful invasion can decrease with increasing species diversity in both marine and terrestrial environments (Hooper et al 2005, Tilman 1997, Stachowicz et al. 1999, 2002, Stohlgren et al. 1999, Kennedy et al. 2002, Naeem et al. 2000). Two mechanisms for repelling invaders in highly diverse systems have been proposed: niche complementarity, where a more complete use of resources limits colonizing species (Tilman 1999, Stachowicz et al. 1999, 2002), and sampling effects, where the likelihood of encountering strong resource competitors increases as species number increases (Wardle 2001).

Despite theoretical and empirical support for biotic resistance, its importance in repelling invasions remains controversial (Rejmanek 1996, Levine 2004). First, the two proposed mechanisms rely upon the notion that fewer resources (e.g. space, nutrients, light, food) are available in highly diverse environments and thus, competition is stronger. The complete use of resources, rather than diversity *per se*, is preventing invasion. In fact, many studies have demonstrated positive relationships between invasion success and native diversity at local (Sax 2002), landscape and regional scales (e.g. Stohlgren et al.

1999, 2005, Lonsdale 1999, Levine 2000), suggesting that diversity alone does not prevent invasion. In these studies, other ecological factors, such as resource availability, were more important for invasion success. Second, many studies suggest that diversity alone is unlikely to completely prevent invasions because other abiotic factors, such as disturbance (D'Antonio 2000) and fluctuating resources (Davis et al. 2000, Davis and Pelsor 2001) can allow new species to establish even in highly diverse communities. These factors increase available resources in a community and can override negative effects of a diverse array of competitors or a few strong competitors. Hence, high resource availability might offset or neutralize biotic resistance from the native community by making it unlikely that competition could completely resist invaders or prevent them from becoming dominant in a community.

As a consequence, when resource availability is high, invaders are likely to dominate, although the mechanisms are not clear. Under the Fluctuating Resource Availability hypothesis, invader dominance in high resource environments is attributed to reduced interspecific competition from native community members (Davis et al. 2000, Davis and Pelsor 2001). In contrast, under the Productivity hypothesis, invader dominance is due to stronger competitive effects on the native species, rather than reduced competition from native species, in high resource areas (Huston 2004). Both mechanisms assume that high resource availability is associated with increased growth rates by the competitively superior invasive. This assumption is likely true when successful invaders possess competitive abilities or resource requirements that are different, and potentially superior, from those already present in the established community (Tilman 2004; D'Antonio and Hobbie 2005).

Here, we experimentally test these contrasting hypotheses explaining dominance in high resources areas using the widespread invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) and a native snail from the invaded range in the western USA (*Pyrgulopsis robusta*). We measured growth rates of the two snails and interspecific competition between them at two experimentally-altered resource levels. *Potamopyrgus* and *Pyrgulopsis* are ecologically similar, compete for algal resources (Riley et al. 2008) and are the dominant macro-invertebrates within the range of the locally endemic native (Polecat Creek watershed in the Greater Yellowstone Area, USA) (Riley and Dybdahl 2005). Polecat Creek is highly productive and *Potamopyrgus* is the dominant macro-invertebrate in the main stem (Hall et al. 2006), making this study site ideal to test mechanisms of dominance.

Methods

Study site.

We performed a field experiment in Polecat Creek, a drainage of the Snake River south of Yellowstone National Parkk (UTM zone 12: 524,719 E, 4,884,045 N). We tested growth rates of *Potamopyrgus* and *Pyrgulopsis* and interspecific competition between them when subjected to two experimentally-altered resource levels (high vs. low). Under both hypotheses, we expected the invasive *Potamopyrgus* to grow faster in high resource treatments. Under the Fluctuating Resource Availability hypothesis, we expected interspecific competition between *Potamopyrgus* and *Pyrgulopsis* to be weaker in high resource treatments. However, under the Productivity hypothesis, we expected interspecific competition to be stronger in high resource treatments.

Experimentally altered resource levels.

To test for effects of resource availability on growth and competition, we first had to create two resource levels. Nutrient diffusing substrates were constructed using plastic sandwich trays (0.0169 m^2: 0.13m x 0.13m x 0.05m) filled with a 2% agar solution either with added nutrients (0.5 M NH_4Cl and 0.5 M KH_2PO_4: Nutrient treatment) or without (Control treatment) (i.e. Tank and Dodds 2003). We then placed unglazed ceramic tiles (0.00235 m^2) across the tops of the containers to serve as a substrate for periphyton colonization for 16 days (3 July 2007 – 19 July 2007) in Polecat Creek. Previous assays in this stream indicated that two weeks was sufficient time to detect significant differences in periphyton abundance between nutrient and control treatments using this method (L. A. Riley, unpublished data). A total of eighty-eight tiles were colonized (44 control and 44 nutrient tiles).

Eight replicates of each treatment were assayed for metrics of periphyton abundance and quality after the 16-day colonization period to test initial treatment differences. The remaining 72 tiles were used in the growth and competition experiment (see below). To measure periphyton abundance and quality, we removed periphyton from tiles with nylon brushes and collected four subsamples from each replicate onto four pre-combusted glass fiber filters (Gelman AE; Pall Gelman Sciences, Ann Arbor, MI, USA) with a vacuum pump. We froze the one filter for chlorophyll *a* (chl-*a*) analysis, and later extracted chl-*a* with buffered ethanol. We measured pheophytin-corrected chl-*a* concentrations on a Turner Designs TD-700 fluorometer (Sunnyvale, CA, USA) at 436 nm excitation wavelength and 680 nm emission wavelength (chl-*a*: mg m^{-2}). We dried a second filter at 60ºC for 24 hours, recorded dry mass, and then combusted filters at 500ºC

for 1 hour and recorded ash mass. We calculated periphyton ash-free dry mass (AFDM) as the difference between dry mass and ash mass (mg AFDM m^{-2}). Chl-*a* concentrations (mg chl-*a* m^{-2}) represent the amount of living algae present, whereas periphyton mass (mg AFDM m^{-2}) measures the entire organic component of the periphyton without distinguishing between algae and other material.

To measure periphyton quality, we measured C:P and C:N stoichiometric ratios on the two remaining filters from each replicate. These filters were first dried at 60ºC for 24 hours. One of the filters was analyzed for both µgC and µgN with an elemental analyzer ((ECS 4010, Costech Analytical, Valencia, CA) at the Washington State University Stable Isotope Core Laboratory. Acetanilide was used in a 1 point correction (consistent amplitude) to estimate simple C% and N%. The other remaining filter was digested in concentrated nitric acid at 115ºC for 6 hours and analyzed for µgP by inductively coupled plasma (ICP) atomic emission spectroscopy at the University of Idaho Analytical Sciences Laboratory. Laboratory quality control included reagent blanks, calibration check standards, standard reference materials and sample duplicates

Statistical analysis.- To demonstrate that the nutrient supplementation altered the quantity and quality of the resource, we used one-way ANOVAs (Systat Version 10; SPSS 2000, Chicago, Illinois, USA) to test for differences between control and nutrient tiles in the four response variables: chl-*a*, AFDM, C:N and C:P ratios.

Growth and Interspecific competition experiment.

After tile colonization, we set up experimental cages (~0.009 m^{-2} each) with high and low resource tiles for measurements of growth responses and competitive interactions. We haphazardly assigned each high resource tile to one of 36 cage

enclosures and each low resource tile to one of 36 cage enclosures. We constructed cages from clear plastic sandwich trays and placed 1-mm mesh on all sides to promote water exchange and enclose snails. We placed cages on floating rafts and anchored the rafts to a streambank (Lamberti 1987), ensuring all cages were completely submerged (Plate 1).

For our measurements of growth responses to resource levels, we set up 4 replicate cages for each species (invasive and native) and resource level treatment (high and low) (Table 1). In each replicate cage we added snails equivalent to 0.53 g snail AFDM m^{-2} (9 *Potamopyrgus* or 4 *Pyrgulopsis*/cage). We used 2.5 mm target snails of each species. We chose these sizes, which were below the asymptotic sizes of the snails (Dybdahl and Kane 2005, LAR, unpublished data), to maximize the scope for growth. We matched all treatments by biomass rather than density because *Pyrgulopsis* is wider than *Potamopyrgus*, potentially biasing any comparisons based upon abundance.

For our measurement of competitive interactions, we chose to use an additive design to test for variation in the strength of interspecific competition in response to changes in resources between a native and invasive species. In this design, the biomass of one species (the target of competition) was low, and the response of this target species was measured at different biomass levels of the competing species. In one set of treatments, the invasive was designated as target and the native as competitor, and the designation was switched in a second of treatments. For each target species, we set up 4 replicate cages for each competition treatment and resource level. Biomass levels for the target were always equal to 0.53 g snail AFDM m^{-2} and competitor biomass was either 0.53, 2.11, 4.76 or 10.04 g snail AFDM m^{-2}. Target snails and competing snails were ~2.5 mm. We chose the highest competitor biomass levels to be 2 times greater than

ambient snail conditions on stones in a place where the two species coexist in equal densities (4.47 g total snail AFDM m^{-2}). The lowest competitor biomass levels were 1/8 of total ambient snail biomass. We removed debris from cages at least once every 3 days, and only a small amount of fine sediment accumulated in the cages over the 2-wk duration of the experiment. Snail survivorship was >95% for both species and any broken cages were removed from further analyses.

For our response variables, we measured shell growth of snails over 11 days (19 July 2007 – 30 July 2007), sufficient time to measure growth in both species (Riley et al. 2008). A previous study using a response surface experiment, measured both interspecific and intraspecific competition, and showed that asymmetric competition occurred between these two species, with *Potamopyrgus* negatively affecting *Pyrgulopsis* growth and *Pyrgulopsis* facilitating the growth of *Potamopyrgus* at high biomass (Riley et al. 2008).

We measured shell growth of target snails under a dissecting microscope fitted with an ocular micrometer. We converted length measurements of *P. robusta* and *P. antipodarum* to snail biomass using length–mass regressions for each species (*P. antipodarum*: Hall et al. 2006; *P. robusta*: Riley et al. 2008). Biomass-specific growth rates g (g g^{-1} d^{-1}) (e.g., Cross and Benke 2002, Hall et al. 2006) were calculated as:

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

where M_t is total target snail biomass at the conclusion of the experiment (g AFDM), M_0 is the total initial snail biomass (g AFDM), and t is the duration of the experiment (d). Biomass-specific growth rates facilitate comparisons between organisms of different initial sizes.

Statistical analysis.— To test for differences in growth rates in response to changing resource levels, we used a two-way ANOVA with resource level (high vs. low) and species identity (*Potamopyrgus* vs. *Pyrgulopsis*) as fixed factors (Systat version 10). To isolate the effect of resources on growth rates in the absence of intraspecific or interspecific competition, we analyzed the treatments that contained each species alone at low biomass (0.53 g AFDM m^{-2}) (Table 1).

To test for the effect of resource levels on competition, we ran ANCOVAs with competitor biomass as the continuous covariate and resource level (high vs. low) as a categorical fixed factor on either *Potamopyrgus* or *Pyrgulopsis* biomass specific growth rates. A significant interaction term indicates heterogeneity of slopes, such that the strength of competition per unit of snail biomass is different across resource levels (Gotelli and Ellison 2004). A significant interaction term would also indicate that the effect of resources on competition might depend on the level of competitor biomass**.** A non-significant interaction term, on the other hand, indicates that our regression lines are parallel and the model can be reduced further (Gotelli and Ellison 2004). Biologically, this indicates that the strength of competition does not differ between resource levels. With a non-significant interaction term, one regression model can be fit to the data for both resource levels, with the slope of the line indicating the strength of competition.

Results

Experimentally altered resource levels.

Periphyton abundance differed significantly between control and nutrient tiles with respect to both periphyton mass ($p=0.02$, Fig. 1A) and chl-*a* ($p<0.001$, Fig. 1B). Chl-*a* was 12 times higher on nutrient tiles and periphyton mass was about twice as high

when compared to control tiles. Ambient chl-*a* (15.15 mg m^{-2}) in Polecat Creek during the summer of 2007 was intermediate to our control and nutrient tiles. Ambient periphyton mass (260 mg AFDM m^{-2}) was the same as our control tiles.

Periphyton quality also differed significantly between control and nutrient tiles with respect to both C:N ($p=0.01$, Fig. 2A) and C:P ($p=0.002$, Fig. 2B). C:N was 1.5 times lower on nutrient tiles and C:P was 2.5 times lower on nutrient tiles when compared to control tiles, indicating that higher quality periphyton was present on nutrient tiles. Ambient C:N and C:P of periphyton on rocks in Polecat Creek fell close to our nutrient tiles in both instances (C:N-8.77; C:P-264) and control tiles were higher.

Growth experiment.

Both *Potamopyrgus* and *Pyrgulopsis* grew during the experiment (Fig. 3). *Potamopyrgus* always grew faster than *Pyrgulopsis*, as indicated by a significant effect of species identity ($p<0.001$). However, there was no significant effect of resources on growth rates ($p=0.217$) nor was there a significant interaction between species identity and resource level ($p=0.710$). In the absence of interspecific competition, growth remained relatively constant for both species, regardless of periphyton abundance.

Competition experiment.

Potamopyrgus growth rates were not affected by resource levels ($p=0.831$) or the biomass of *Pyrgulopsis* competitors ($p=0.156$) (Fig. 4A). In addition, the interaction between periphyton abundance and snail biomass was non-significant, indicating that the slopes of the lines (i.e. the strength of competition) were not different across resource levels ($p=0.620$). *Pyrgulopsis* growth rates, on the other hand, were affected both by the level of resources ($p=0.015$) and the biomass of *Potamopyrgus* competitors ($p=0.010$).

Pyrgulopsis grew fastest with high periphyton abundance and a low biomass of *Potamopyrgus* competitors (Fig. 4B). The strength of competition per unit of *Potamopyrgus* biomass, however, did not differ across resource levels, as evidenced by a non-significant interaction term ($p=0.578$). From the reduced regression model, the slope of the line indicated the strength of competition of *Potamopyrgus* on *Pyrgulopsis* is $-0.0025\ g^{-1}$ snail AFDM d^{-1}.

Discussion

The dominance of an invader under high resource availability might be due to their increased growth rates, and either reduced competition from the native species (Davies et al. 2000, Davis and Pelsor 2001), or increased strength of competition from the invader (Huston 2004). We found that, in the absence of competition, *Potamopyrgus* always grew faster than *Pyrgulopsis* at both high and low resource levels. In the presence of interspecific competition, *Potamopyrgus* growth rates were not affected by resource levels or the biomass of *Pyrgulopsis* competitors. On the other hand, *Pyrgulopsis* grew slower at low resource levels, and the effect of resources on growth was stronger with increased biomass of *Potamopyrgus* competitors. The strength of competition of *Potamopyrgus* on *Pyrgulopsis*, though, was the same at both low and high resource levels. Slower growth rates of *Pyrgulopsis* at low resource levels and increased competitor biomass suggests *Potamopyrgus* might dominate in low resource areas even though competitive effects are constant.

In the absence of competition, it was not surprising that *Potamopyrgus* grew faster than *Pyrgulopsis*. In a previous study, *Potamopyrgus* also grew faster than *Pyrgulopsis* (Riley et al. 2008). However, the fact that growth rates of each species

remained constant across low and high resource levels was surprising. This suggests that even at low resource levels, enough periphyton was present to support maximum growth rates of each species when not competing with another species. Periphyton abundance, measured as AFDM, in the low resource treatment was the same as periphyton abundance on ambient rocks. However, periphyton abundance, measured as chl-*a*, and periphyton quality (C:P and C:N) was lower than ambient periphyton in Polecat Creek. Although *Pyrgulopsis* only occurs in this drainage, other streams where *Potamopyrgus* occurs have much lower periphyton abundance (L.A. Riley, unpublished data) and quality (Tibbetts and Krist, in prep.), suggesting that the low resource treatment in Polecat Creek might still be relatively high when compared to periphyton conditions in other streams.

In the presence of interspecific competition, *Potamopyrgus* growth was not affected by resource levels or the biomass of *Pyrgulopsis* competitors. Increasing the amount and quality of the resource did not cause *Potamopyrgus* to grow faster, suggesting that *Potamopyrgus* populations can subsist on low resource levels, even when competing with another species. Increasing the biomass of *Pyrgulopsis* competitors also did not slow *Potamopyrgus* growth. In fact, a previous study demonstrated that *Pyrgulopsis* facilitated *Potamopyrgus* growth when present at a competitor biomass of 4.65 g snail AFDM m^{-2} (Riley et al. 2008). In this study, 4.65 g snail AFDM m^{-2} was equivalent to intermediate competitor biomass levels. While this study did not demonstrate facilitative effects, together these studies indicate that *Pyrgulopsis* does not reduce *Potamopyrgus* growth, even at high biomass.

On the other hand, in the presence of interspecific competition, *Pyrgulopsis* grew slower when competing with a high biomass of *Potamopyrgus* competitors, as has been

demonstrated previously (Riley et al. 2008). *Pyrgulopsis* also grew slower under low resource conditions. While resource levels did not affect *Pyrgulopsis* growth in the absence of competition, low resources negatively affected growth when competing with *Potamopyrgus*. *Pyrgulopsis* is unable to maintain maximum growth rates in the presence of *Potamopyrgus*, especially at low resource levels. The strength of competition, though, was the same at low and high resource levels. This means that per unit of *Potamopyrgus* biomass, the rate of *Pyrgulopsis* growth was always reduced to the same extent. Thus, slower growth rates of *Pyrgulopsis* at low resource levels cannot be attributed to stronger competition from *Potamopyrgus*. These results indicate that the presence of *Potamopyrgus* exacerbates negative effects of low resources on *Pyrgulopsis* growth rates even though the strength of competition per unit of snail biomass is constant. In fact, the strength of competition measured here was similar to the strength of competition measured in a previous study in this same stream (here: -0.0025 g^{-1} snail AFDM d^{-1}; Riley et al. 2008: -0.0018 g^{-1} snail AFDM d^{-1}).

Productivity vs. Fluctuating Resource Availability Hypotheses.

Potamopyrgus is the dominant macro-invertebrate in highly productive Polecat Creek (Hall et al. 2006). Both the Fluctuating Resource Availability hypothesis and the Productivity hypothesis predict that a competitively superior invasive species will grow faster than native species in high resource areas (Davis et al. 2000, Davis and Pelsor 2001). *Potamopyrgus* does appear to be a superior competitor to *Pyrgulopsis* for two reasons: 1) the lack of negative competitive effects of *Pyrgulopsis* on *Potamopyrgus* and 2) constant growth rates of *Potamopyrgus* at both low and high resource levels, coupled with reduced growth rates of *Pyrgulopsis* at low resource levels. *Potamopyrgus*

maintains growth rates even when resources are reduced and interspecific competition is increased. Thus, high resource availability is not necessary for *Potamopyrgus* to grow fast. Successful invaders often possess competitive abilities or resource requirements that are different, and potentially superior, from those already present in the established community (Tilman 2004; D'Antonio and Hobbie 2005). *Potamopyrgus* might have lower maintenance costs or be more efficient at converting resources to growth. Under this scenario, *Potamopyrgus* could grow faster on lower resource levels than *Pyrgulopsis* (e.g. Tilman 1977), which is the case here.

Given that *Potamopyrgus* is a superior competitor, grows faster than *Pyrgulopsis* and dominates in this high resource stream, we also tested whether two alternative mechanisms might explain this dominance. Under the Fluctuating Resource Availability hypothesis, invader dominance in high resource environments is also attributed to reduced interspecific competition from native community members (Davis et al. 2000, Davis and Pelsor 2001) while the Productivity hypothesis predicts that the invasive species will have stronger competitive effects on the native species (Huston 2004). This study supports neither hypothesis. To support the Resource Availability hypothesis, competitive effects of *Pyrgulopsis* on *Potamopyrgus* should have been reduced in high resource treatments. The native community member, *Pyrgulopsis*, did not affect *Potamopyrgus* growth, even at low resource levels. To support the Productivity hypothesis, competitive effects of *Potamoyrgus* on *Pyrgulopsis* should have been stronger in high resource treatments. Instead, growth of *Pyrgulopsis* was faster at high resource levels when competing with *Potamopyrgus*. These results indicate that competition between these two species is reduced at high resource levels, although

Pyrgulopsis does not strongly compete with *Potamopyrgus* under any resource scenario. In this system, the competitive dynamic between *Potamopyrgus* and *Pyrgulopsis* does not change with increased resources. Thus, increased resource availability does not appear to be necessary for *Potamopyrgus* to dominate because competitive effects from this native community member are weak.

Plates

Plate 1. Cage enclosures for growth and interspecific competition experiment in Polecat Creek.

Tables

Table 1. Experimental design for the growth and interspecific competition experiment. Growth rates were measured on the target species (either *Potamopyrgus antipodarum* (PA) or *Pyrgulopsis robusta* (PR)). All values are g snail AFDM m^{-2}.

		Target biomass		Competitor biomass	
Experiment	Resource Level	PA	PR	PA	PR
Growth	High	0.53	-	-	-
		-	0.53	-	-
	Low	0.53	-	-	-
		-	0.53	-	-
Competition	High	0.53	0.53*	-	-
		0.53	-	-	2.11
		0.53	-	-	4.76
		0.53	-	-	10.04
	Low	0.53	0.53*	-	-
		0.53	-	-	2.11
		0.53	-	-	4.76
		0.53	-	-	10.04
	High	-	0.53	2.11	-
		-	0.53	4.76	-
		-	0.53	10.04	-
	Low	-	0.53	2.11	-
		-	0.53	4.76	-
		-	0.53	10.04	-

*Low interspecific competition treatment at low and high resource levels where growth was measured on both species.

Figures

Experimentally altered resource levels.

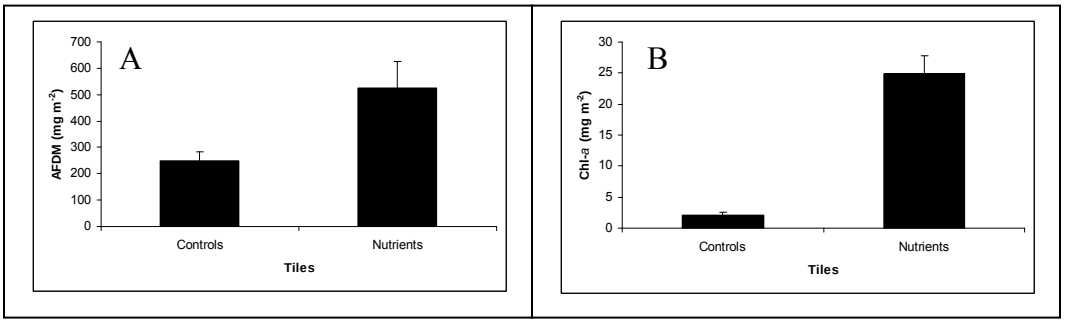

Fig. 1. Periphyton abundance on control tiles and tiles supplemented with nutrients after a 16-day colonization period in Polecat Creek. Periphyton abundance is measured as mean periphyton AFDM (+1 SE) (A) and mean chl-a (+1 SE) (B).

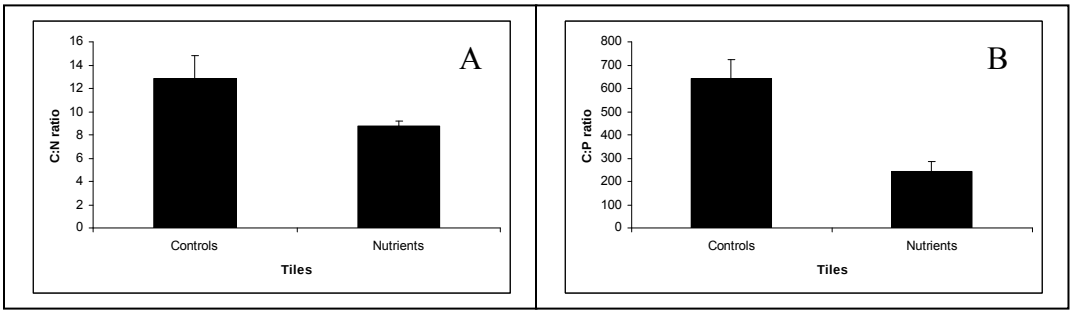

Fig. 2. Periphyton quality on control tiles and tiles supplemented with nutrients after a 16-day colonization period in Polecat Creek. Periphyton quality is measured as mean C:N ratio (+1 SE) (A) and mean C:P ratio (+1 SE) (B).

Growth experiment.

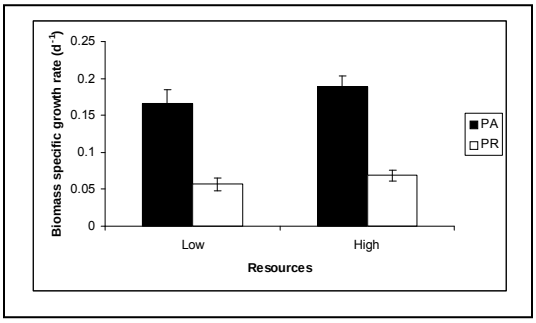

Fig. 3. Mean (+1 SE) *Potamopyrgus antipodarum* (PA) and *Pyrgulopsis robusta* (PR) biomass specific growth rates when exposed to low and high resource levels in the absence of interspecific competition. These treatments contain only the target species at low biomass (0.53 g snail AFDM m^{-2}).

Interspecific competition experiment.

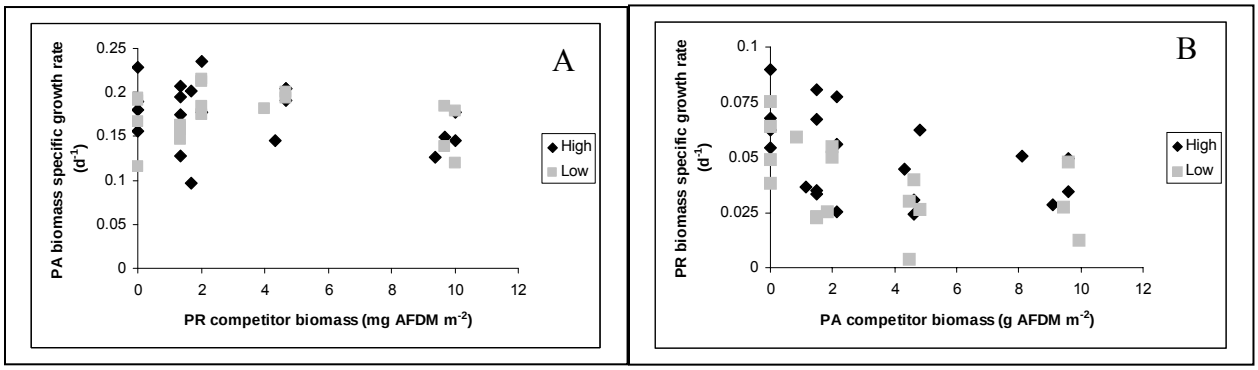

Fig. 4. *Potamopyrgus antipodarum* (A) and *Pyrgulopsis robusta* (B) biomass specific growth rates when exposed to low and high resources and various levels of interspecific competitor biomass (x-axis). Note the different scales on the y-axis.

LITERATURE CITED

Chapter One

Abrams, P. A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. Oikos 94:209–218.

Bascompte, J. and P. Jordano. 1997. Plant-animal mutualistic networks: the architecture of biodiversity. The annual review of ecology, evolution and systematics 38: 567 – 593.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224.

Berlow, E. L., A. Neutel, J. E. Cohen, P. C. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology 73:585–598.

Bolnick, D. I. and E. L. Preissier. 2005. Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. Ecology 86 (10): 2771 – 2779.

Bruno, J. F., J. J. Stachowicz and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18 (3): 119 – 125.

Bruno, J. F., J. D. Fridley, K. D. Bromberg and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13-40 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines (editors). Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Sunderland, Massachusetts.

D'Antonio, C. M. and S. E. Hobbie. 2005. Plant species effects on ecosystem processes: insights from invasive species. Pages 65 – 84 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines (editors). Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Sunderland, Massachusetts.

De Ruiter, P. C., A-M. Neutel and J.C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269: 1257 – 1260.

Gotelli, N. J. 1998. A primer of ecology. Sinauer Associates, Sunderland, Massachusetts.

Hall, R. O., J. B. Wallace and S. L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology 81: 3445 – 3463.

Hughes, J. B. and J. Roughgarden. 1998. Aggregate community properties and the strength of species' interactions. Proceedings of the National Academy of Sciences 95: 6837 – 6842.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113: 81 – 101.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199–204.

Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strengths. Ecology 79:461– 476.

Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. American Naturalist 110: 351 – 369.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying

extrinsic factors. Oikos 91: 97 – 108.

Novak, M. and J. T. Wootton. 2008. Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs. Ecology 89 (8): 2083 – 2089.

Osenberg, C. W., and G. G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pages 134–148 *in* G. A. Polis and K. O. Winemiller (editors). Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100: 65 – 75.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355: 73 – 75.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Ruesink, J. L. 1998. Variation in per capita interaction strength: Thresholds due to non-linear dynamics and non-equilibrium conditions. Proceedings of the National Academy of Sciences of the United States of America 95 (12): 6843-6847.

Sala, E. and M. H. Graham. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. Proceedings of the National Academy of Sciences 99 (6): 3678 – 3683.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for

biological invasions. Trends in Ecology and Evolution 17:171–176.

Stachowicz, J. J., R. B. Whitlach and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577 – 1579.

Strayer, D. L., V. T. Eviner, J. M. Jeschke and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology and Evolution 21 (11): 645-651.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84 (5): 1083 – 1100.

Wootton, J. T. 1997. Estimate and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Wootton, J. T., and Emmerson, M. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution and Systematics 36:419–444.

Chapter Two

APHA. 1995. Standard methods for the examination of water and wastewater. Port City Press, Baltimore, Maryland.

Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. Biological Invasions 8: 755 – 763.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224.

Berlow, E. L., A. Neutel, J. E. Cohen, P. C. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. Interaction strengths in food webs: issues and

opportunities. Journal of Animal Ecology 73:585–598.

Bott, T. L. 1996. Primary productivity and community respiration. In Hauer, F. R. and G. A. Lamberti, (eds.), Methods in stream ecology. Academic Press, pp. 533-556.

Bruno J. F., J. D. Fridley, K. D. Bromberg and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. In Sax D. F., J. J. Stachowicz and S. D. Gaines, (eds.), Species invasions: insights into ecology, evolution and biogeography, pp 13 – 40. Sinauer Associates Inc, Sunderland, Maryland.

Davis, M. A., J. P. Grime and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528 – 534.

Davis, M. A. and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4: 421 – 428.

Death, R. G. 1991. Environmental stability: its effects on stream benthic communities. PhD Dissertation, University of Canterbury, Christchurch, New Zealand.

Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology and Evolution 22 (9): 489 – 496.

Dybdahl, M. F. and S. L. Kane. 2005. Adaptation vs. phenotypic plasticity in the success of a clonal invader. Ecology 86: 1592 – 1601.

Feminella, J. W. and V. H. Resh. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology 71: 2083 – 2094.

Feminella, J. W. and C. P. Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of the North American Benthological Society 14: 465 – 509.

Hall, R. O, Jr., J. L. Tank and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1: 407-411.

Hall, R. O., Jr., M. F. Dybdahl and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. Ecological Applications 16 (3): 1121 – 1131.

Hart, D. D. 1985. Grazing insects mediate algal interactions in a stream benthic community. Oikos 44: 40-46.

Hart, D. D. and C. T. Robinson. 1990. Resource limitation in a stream community: phosphorus enrichment effects on periphyton and grazers. Ecology 71: 1494 – 1502.

Hill, W. R. and A. W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68: 1955-1965.

Hill, W. R., H. L. Boston and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Canadian Journal of Fisheries and Aquatic Sciences 49: 504 – 512.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113: 81 – 101.

Kerans, B. L., M. F. Dybdahl, M. M. Gangloff and J. E. Jannot. 2005. *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate

assemblages in the Greater Yellowstone Ecosystem. Journal of the North American Benthological Society 24:123 – 138.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199–204.

Lamberti, G. A. and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64: 1124 – 1135.

Lamberti, G. A. and J. W. Moore. 1984. Aquatic insects as primary consumers, in The Ecology of Aquatic Insects, (eds VH Resh and DM Rosenberg), Praeger Scientific, New York, pp. 164-195.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6:92 – 104.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, A. D. Steinman and C. D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70: 1840-1856.

Lamberti, G. A. and J. W. Feminella. 1996. Plant-herbivore interactions. Pages 409 – 430 *in* FR Hauer and GA Lamberti (Eds.) Methods in Stream Ecology. Academic Press: San Diego, CA.

Laska, M. S. and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strengths. Ecology 79: 461-476.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522 – 1536.

Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients: synthesis on the roles of predation, competition, and temporal heterogeneity. American Naturalist 110: 351 – 369.

Mulholland, P. J., A. D. Steinman, A. V. Palumbo, J. W. Elwood and D. B. Kirschtel. 1991. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. Ecology 72: 966 – 982.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97 - 108.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19.

Quinn, J. M., G. L. Steele, C. W. Hickey and M. L. Vickers. 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. New Zealand Journal of Marine and Freshwater Research 28: 391 – 397.

Rand, T. A. and S. A. Louda. 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. Conservation Biology 20: 1720 – 1729.

Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology 48: 972 – 981.

Riley, L. A., M. F. Dybdahl and R. O. Hall, Jr. 2008. Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. Journal of the North American Benthological Society 27 (3): 509 – 520.

Rilov, G. et al. 2004. Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. Biological Invasions 6: 47 – 364.

Rosemond, A. D. 1993. Interactions among irradiance, nutrients and herbivores constrain a stream algal community. Oecologia 94: 585 – 594.

Ruesink, J. L. 1998. Variation in per capita interaction strength: Thresholds due to nonlinear dynamics and nonequilibrium conditions. Proceedings of the National Academy of Sciences of the United States of America 95: 6843-6847.

Russell, F. L. and S. M. Louda. 2005. Indirect interaction between two native thistles mediated by an invasive exotic floral herbivore. Oecologia 146 (3): 373-384.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17 (4): 171-176.

Stachowicz, J. J., R.B. Whitlach and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286:1577 - 1579.

Stachowicz, J. J., H. Fried, R.W. Osman and R.B. Whitlach. 2002. Biodiversity, invasion resistance and marine ecosystem function: reconciling pattern and process. Ecology 83:2575 - 2590.

Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. In: Stevenson, RJ, Bothwell, ML and Lowe RL (eds) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, San Diego, California.

Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society 18: 74-98.

Sumner, W. T. and C. D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. Arch. Hydrobiol. 93:135-157.

Systat 10. 2000. SPSS, Inc. Chicago, Illinois.

Wallace, J. B. and M. E. Gurtz. 1996. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. American Midland Naturalist 115: 25 – 41.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Winterbourn, M. J. 1970. Population studies of the New Zealand freshwater Gastropod, *Potamopyrgus antipodarum* (Gray). Proceedings of the Malacological Society of London. 39: 139 – 149.

Wootton, J. T. 1997. Estimate and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67: 45-64.

Wootton, J. T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution and Systematics 36: 419 – 444.

Chapter Three

APHA 1995. Standard methods for the examination of water and wastewater. Port City Press: Baltimore, Maryland.

Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81: 1225 – 1239.

Cross, W. F. and A. C. Benke. 2002. Intra- and interspecific competition among coexisting lotic snails. Oikos 96: 251 – 264.

D'Antonio, C. M. and S. E. Hobbie. 2005. Plant species effect on ecosystem processes: insights from invasive species. Pages 65 – 84 *in* D. F. Sax, S. D. Gaines and J. J. Stachowicz (Eds.) Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Inc.: Sunderland, MA.

D'Antonio, C. M., J. T. Tunison, and R. K. Loh. 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecology 25:507-522.

Davis, M. A., J. P. Grime and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528 – 534.

Davis, M. A. and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421 - 428.

Diamond, J. M. 1975. Assembly of species communities. Pages 342 – 444 *in* M. L. Cody and J. M. Diamond (Eds.) Ecology and Evolution of Communities. Belknap: Cambridge, MA.

Dybdahl, M. F. and C. M. Lively. 1995. Host-parasite interactions: infection of common clones in natural populations of a freshwater snail (*Potamopyrgus antipodarum*). Proceedings of the Royal Society, London, B. 260: 99-103

Dybdahl, M. F. and S. L. Kane. 2005. Adaptation vs. phenotypic plasticity in the success of a clonal invader. Ecology 86: 1592 – 1601.

Elton, C. S. 1958. The ecology of invasion by animals and plants. Methuen: London.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379 – 391.

Gotelli, N. J. and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Hall, R. O., Jr., J.L. Tank and M.F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1:407 - 411.

Hall, R. O., Jr., M. F. Dybdahl and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. Ecological Applications 16 (3): 1121 – 1131.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292 – 1297.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3 - 35.

Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance and competition. Diversity and Distributions 10:167 - 178.

Kennedy, T. A. et al. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636.

Kerans, B. L., M. F. Dybdahl, M. M. Gangloff and J. E. Jannot. 2005. *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate

assemblages in the Greater Yellowstone Ecosystem. Journal of the North American Benthological Society 24:123 - 138.

Lamberti, G. A., Feminella, J. W. and Resh, V. H. 1987. Herbivory and intraspecific competition in a stream caddisfly population. - Oecologia 73: 75-81..

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852 - 854.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7:975-989.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522 - 1536.

Mittelbach, G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381 - 2396.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97 - 108.

Rejmanek, M. 1996. Species richness and resistance to invasions. Pages 153 – 172 *in* H. Orians, R. Dirzo and J. H. Cushman (Eds.) Biodiversity and ecosystem processes in tropical forests. Ecological studies Volume 122. Springer-Verlag: Berlin, Germany.

Richards, D. C. 2004. Competition between the threatened Bliss Rapids snail, *Taylorconcha serpenticola* (Hershler et al.) and the invasive, aquatic snail,

Potamopyrgus antipodarum (Gray). PhD Dissertation, Montana State University, Bozeman, Montana.

Riley, L. A. and M. F. Dybdahl. 2006. The current distribution of the Jackson Lake spring snail and interactions with the invasive New Zealand mud snail. Technical report submitted to: Grand Teton National Park, Moran, WY. Dated: 1 May 2006. 17 pp.

Riley, L. A., M. F. Dybdahl and R. O. Hall, Jr. 2006. Grazing effects of the New Zealand mud snail across a productivity gradient in the Greater Yellowstone Ecosystem. In press *in* University of Wyoming and the National Park Service Research Center Annual Report.

Riley, L. A., M. F. Dybdahl and R. O. Hall, Jr. 2008. Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. Journal of the North American Benthological Society 27 (3): 509 – 520.

Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity and Distributions 8: 193 – 210.

Stachowicz, J. J., R.B. Whitlach and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286:1577 - 1579.

Stachowicz, J. J., H. Fried, R.W. Osman and R.B. Whitlach. 2002. Biodiversity, invasion resistance and marine ecosystem function: reconciling pattern and process. Ecology 83:2575 - 2590.

Stohlgren, T. J. et al. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25 - 46.

Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. A. Villa. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. Environmental Management 29:566-577.

Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz and B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology 86:2298 - 2309.

Tank, J. L. and W. K. Dodds. 2003. Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. Freshwater Biology 48: 1031 – 1049.

Tibbetts, T. M. and A. C. Krist. Phosphorus-mediated changes in life history traits of the invasive New Zealand mud snail. Submitting to Oecoliga.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press: Princeton, N. J.

Tilman, D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. Ecology 78:81 - 92.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455 – 1474.

Tilman, D. 2004. A stochastic theory of resource competition, community assembly and invasions. Proceedings of the National Academy of Sciences USA 101: 10854 – 10861.

Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? Oikos 95:161 - 170.

Wright, D. H., D. J. Currie and B. A. Maurer. 1993. Energy supply and patterns of species richness on local and regional scales. Pages 66 – 74 *in* R. Ricklefs and D. Schulter (Eds.) Species diversity in ecological communities: historical and geographical perspectives. Chicago University Press: Chicago, IL.