Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails

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Abstract. The strength of biotic interactions between native and invasive species is a key component of invasive species impact, but often is not quantified explicitly. We measured biotic interaction strengths between an invasive and a native endemic snail species in 2 streams in the western United States. The invasive freshwater New Zealand mudsnail, *Potamopyrgus antipodarum*, was the dominant snail in a 3rd-order stream, and a closely related endemic snail, *Pyrgulopsis robusta*, was the dominant snail in a 1st-order tributary stream. We compared consumer–resource (C–R) and consumer–consumer (C–C) per biomass interaction strengths in both streams using field enclosure experiments. Consumer effects on algal resources were strong and equivalent for both snail species in both streams. Invasion success of *P. antipodarum* could not be attributed to an unusually high rate of resource acquisition at either site because the 2 snails exerted equivalent C–R interaction strengths. However, C–C interactions were asymmetric; the invasive snail significantly limited growth of the native snail, whereas the native snail facilitated growth of the invasive snail. These effects were stronger in the stream where *P. antipodarum* was dominant. Thus, per biomass interaction strengths indicated that asymmetric interactions could be contributing to patterns of dominance by invasive and endemic stream snails.

Key words: interaction strength, per biomass effects, invasive species, competition, dominance, facilitation, grazing, *Potamopyrgus antipodarum*, *Pyrgulopsis robusta*, Polecat Creek.

Invasive species have reduced biodiversity (Wilcove et al. 1998, Mooney and Cleland 2001) and probably will influence global biodiversity in the future (Sala et al. 2000). Some of these changes arise from biotic interactions, including competition (e.g., Petren and Case 1996, Juliano 1998, Byers 2000), facilitation (Bruno and Kennedy 2000), and predation (e.g., Grosholz et al. 2000, Nystrom et al. 2001) between invasive and native species. Parker et al. (1999) proposed that the strength of biotic interactions should be a key consideration, along with range and abundance, when measuring the impact of invasive species. In this formulation, the strength of biotic interactions is measured as the effect per individual or per unit of biomass on another individual or another unit of biomass (Paine 1992, Wootton 1997, Wootton

and Emmerson 2005). Extrapolation to population impacts within a given range is accomplished by multiplying abundance or biomass by the interaction strength. Hence, important information about population impacts of invasive species can be obtained by measuring the strength of interactions. However, we know of no studies that have used this method in the context of invasive species.

We measured the strength of biotic interactions involving the invasive New Zealand mudsnail (Hydrobiidae:*Potamopyrgus antipodarum*) to estimate its effects on algal resources and an endemic snail. *Potamopyrgus antipodarum* is a worldwide invader. In North America, it was first recorded in Idaho in 1987 (Bowler 1991) and is now widespread and locally abundant across the western US (http://www.esg.montana.edu/aim/mollusca/nzms/). Invasion is occurring in many areas of conservation significance, including 4 national parks or monuments (Grand Teton, Yellowstone, Grand Canyon National Parks,

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Dinosaur National Monument). In the intermountain west, *P. antipodarum* is sympatric with many locally endemic spring snails that are threatened or endangered (US Fish and Wildlife Service 1992, Hershler 1998, Lydeard et al. 2004). However, the effect of the invasion by *P. antipodarum* on native species is not well understood.

Competitive interactions are expected to occur among aquatic gastropods (e.g., Hawkins and Furnish 1987, Schmitt 1996, Cross and Benke 2002) and can shape stream communities (Kohler and Wiley 1997). However, previous work on the competitive effect of *P. antipodarum* has produced mixed results. *Potamopyrgus antipodarum* had weak competitive effects on gastropods in its native New Zealand (Cope and Winterbourn 2004) and on stream macroinvertebrates in its invasive range of the western US (Kerans et al. 2005), but strong competitive effects on another snail in the western US (Richards 2004). On the other hand, in Australia, *P. antipodarum* facilitated colonization of other macroinvertebrates (Schreiber et al. 2002). Here, we use methods from community ecology to measure the strength of biotic interactions and the impact of *P. antipodarum* on food resources and a competitor, *Pyrgulopsis robusta*, in the western United States. These 2 species are likely to be strong interactors; they occupy similar habitats (macrophytes and stones) (Riley and Dybdahl 2006), consume algal resources (periphyton and algal detritus), and are in the same taxonomic family (Hydrobiidae) (Brown 1991, Cope and Winterbourn 2004).

Measuring interaction strength

The Parker et al. (1999) framework provides a way to quantify interactions between invasive and native species with interaction strengths from community ecology theory (Shea and Chesson 2002). Interaction strengths estimate the magnitude and direction of the effect of one species on another (Paine 1992, Wootton 1997, Laska and Wootton 1998, Berlow et al. 1999, 2004, Wootton and Emmerson 2005). Approaches to measuring interaction strengths are varied and have included examination of whole-community responses following long-term removal experiments (Paine's index: Paine 1966, 1992) and observations of predation rates between species pairs over short-term intervals (dynamic index: e.g., Wootton 1997).

We chose to use the dynamic index of interaction strength, which estimates the effect of an individual from 1 species on an individual from another species. Comparisons on the basis of abundance would be biased because the snails differ in size, whereas use of biomass alleviates this problem (Wootton and Emmer-

son 2005). Therefore, we standardized to biomass rather than abundance (i.e., the effect of 1 unit of biomass of species A on the biomass of species B or per biomass interaction strength) (see also Osenberg and Mittelbach 1996, Berlow et al. 1999 for dynamic index).

Dynamic indices have several advantages. Equilibrium assumptions are not necessary when using dynamic indices; thus, short-term experiments are useful. Dynamic indices also are realistic because most communities are not in equilibrium (Laska and Wootton 1998), especially when invasive species are involved (Abrams 2001). Last, values of dynamic indices can be used in theoretical community models (Laska and Wootton 1998) to predict the outcome of biotic interactions. For example, dynamic indices that measure competition are equivalent to competition coefficients in Lotka–Volterra equations and can be used to predict whether 2 populations might coexist. Linking experimental data regarding interactions between native and invasive species to theoretical models provides a tool for predicting displacement before it actually occurs. This approach could have important conservation implications for prioritizing efforts in areas where displacement of native species is probably caused by strong interactions with a recent invader.

Methods

Study sites

Pyrgulopsis robusta is a local endemic, currently known from 2 streams: Polecat Creek (lat 44°6′33.025″N, long 110°41′28.020″W) and Marmot Spring (lat 44°8′6.553″N, long 110°42′50.431″W) in a single drainage of the Snake River in Grand Teton and Yellowstone National Parks. Both streams are geothermally influenced and have similar water chemistry and year-round temperatures (MFD, unpublished data). Patterns of abundance in the field suggest that the invasion by *P. antipodarum* might affect the persistence of *P. robusta*. In Polecat Creek, *P. robusta* is now extremely rare, but densities of *P. antipodarum* can be >500,000 snails/m^2 (Hall et al. 2006). In Marmot Spring, *P. robusta* remains abundant along with *P. antipodarum* (Riley and Dybdahl 2006).

We investigated consumer–resource (C–R; i.e., grazing) and consumer–consumer (C–C) interactions. We measured the grazing effect of each snail on the growth of a shared resource (algal biomass and total periphyton biomass) in both streams (Wootton 1997, Laska and Wootton 1998). We also measured the shell growth of each species when subjected to intraspecific and interspecific C–C interactions in both streams and estimated the per biomass interaction strengths.

C–R interactions

First, we measured the direct interactions between consumers and resources because they can drive indirect competitive interactions between consumers. We measured grazing effects of snails on periphyton in both streams using field enclosure experiments (Marmot Spring: 5–12 July 2002; Polecat Creek: 4–11 July 2002). Before all experiments, we sampled snails on stones in Marmot Spring with a 500-µm mesh Surber sampler and converted abundance to biomass following Hall et al. (2006) to estimate ambient snail biomass levels. Average total snail biomass on stones was 4.47 ± 3.83 (SE) g/m^2 ash-free dry mass (AFDM) where the 2 species currently coexist (Marmot Spring). We then created 3 treatments (2 biomass treatments at each site to mimic ambient biomass and no-snail controls): 1) *P. antipodarum* alone at 4.98 g/m^2 AFDM (290 individuals/cage, shell length: 3–5 mm), and 2) *P. robusta* alone at 4.98 g/m^2 AFDM (170 individuals/cage, shell length: 2–4 mm). Each treatment had 6 to 8 replicates.

We conducted C–R experiments in cage enclosures within the streams. We constructed enclosures from clear plastic sandwich trays (0.0169 m^2: 0.13 × 0.13 × 0.05 m) by cutting openings on the sides and top of each tray. We covered openings with fiberglass window screening (mesh size: 1 mm), which reduced ambient light in cages by 40%. We cleaned stones of similar size, shape, and texture of benthic macroinvertebrates and haphazardly assigned stones to cover the bottom of each cage (4.7 stones/cage ± 0.1 [SE]). We then added snails to create experimental treatments and bolted the cages to bricks on the stream bed. We removed debris from the exterior of the cages at least twice during the experiments.

After 1 wk, we measured periphyton abundance on stones as chlorophyll *a* and AFDM using standard methods (APHA 1995, Steinman and Lamberti 1996). Chlorophyll *a* concentrations (µg/cm^2) represent the amount of living algae present, whereas AFDM (µg/cm^2) measures the entire organic component of the periphyton without distinguishing between algae and other material. For each cage, we scraped periphyton from all stones with toothbrushes and collected 2 subsamples of algal slurry onto precombusted glass-fiber filters (Gelman AE; Pall Gelman Sciences, Ann Arbor, Michigan) with 100-mL syringes. We traced the 2-dimensional surface of the stones onto paper to measure area. For chlorophyll *a* analysis, we extracted chlorophyll in 90% acetone and calculated pheophytin-corrected concentrations with spectrophotometric analysis (APHA 1995). For AFDM analysis, we dried filters for 24 h at 60°C, recorded dry mass, and then combusted filters at 500°C for 1 h and recorded ash mass.

Statistical analysis.—To estimate the grazing effects, we used 2-way analyses of variance (ANOVAs) with snail species and stream (Polecat vs Marmot) as factors. We used chlorophyll *a* and periphyton AFDM as response variables. We made post hoc comparisons among snail treatments with a Bonferroni test for multiple comparisons (Systat 10; SPSS Inc., Chicago, Illinois).

We estimated C–R interaction strengths as the difference in concentration of chlorophyll *a* from the field enclosures with snails present vs with no snails. We used only chlorophyll *a* to calculate interaction strengths because snails did not significantly reduce periphyton AFDM (see **Results** below). We calculated per biomass C–R interaction strengths ($-c$; g^{-1} snail AFDM d^{-1}) from the following equation, adapted from Wootton (1997):

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

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^{-1} snail biomass d^{-1}. 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.

We used a bootstrap procedure to estimate distributions of C–R interaction strengths from the replicate cages (e.g., Paine 1992). For each species, the bootstrap procedure sampled algal biomass of N_s and N_0 at random and with replacement for individual cages. C–R interaction strengths were calculated from these numbers at each site. This process was repeated 1000× and standard errors that preserved the number of replicates in the original design were generated. We determined if resampled distributions differed significantly from 0 by calculating the number of times our estimate was ≥0 for 1000 bootstrap runs (Resampling Stats 5.0.2; Resampling Stats Inc., Arlington, Virginia; Good 2001).

C–C interactions

We measured shell growth of snails subjected to intraspecific and interspecific interactions in both streams to examine interactions between *P. antipodarum* and *P. robusta* (Polecat Creek: 10–24 July 2002, Marmot Spring: 11–25 July 2002). We compared the relative importance of intraspecific and interspecific interactions for each species at each site using a

Table 1. Experimental design for the consumer–consumer interaction experiment. Growth rates were measured on target individuals of *Potamopyrgus antipodarum* (PA) or *Pyrgulopsis robusta* (PR). All biomass values are g/m^2 AFDM.

| Treatment | Interaction | Biomass of target species | | Biomass of interactor species | | Number of replicates | |
		PA	PR	PA	PR	Marmot Spring	Polecat Creek
Low	Intraspecific	0.33	–	0.33	–	2	3
High	Intraspecific	0.33	–	4.65	–	4	4
Low	Intraspecific	–	0.33	–	0.33	4	4
High	Intraspecific	–	0.33	–	4.65	4	3
Low[a]	Interspecific	0.33	0.33	–	–	5	3
High	Interspecific	0.33	–	–	4.65	4	4
High	Interspecific	–	0.33	4.65	–	4	4

[a] Low biomass interspecific treatment where growth was measured on both species

factorial response-surface design (Inouye 2001). In these experiments, biomass of a target species is held constant, and biomass levels of each competitor are varied in separate treatments (Forrester et al. 2006). The response of each species is measured as biomass of the competing species and varies independently, so that the magnitude of intraspecific and interspecific competition can be compared for both species. Response-surface designs are useful because they combine aspects of both additive designs (focus only on 1 target species) and substitution designs (vary only the relative proportions of 1 competitor species).

In our experiment, we varied 3 factors for each species: total snail biomass (high: 4.98 g/m^2 AFDM vs low: 0.66 g/m^2 AFDM), interaction type (intraspecific vs interspecific), and stream (Marmot Spring vs Polecat Creek) (Table 1). We chose the high biomass levels to mimic ambient snail conditions on stones in Marmot Spring (4.47 g/m^2 snail AFDM). Low biomass treatments were $\frac{1}{7}$ of ambient snail biomass.

For estimates of intraspecific interactions, cage enclosures contained only 1 species at high and low biomass (Table 1). For interspecific interactions, cages contained both species: the target species at low biomass (0.33 g/m^2 AFDM; equivalent to 27 *P. antipodarum* or 15 *P. robusta*/cage) and the competitor at either high or low biomass. We measured growth of the target species. Each treatment had 2 to 5 cage replicates in each stream, with an average of 3.7 replicates/treatment (Table 1). (We removed damaged cages from the experiment.) Cages housed snails and stones as described in *C–R interactions* above, except that experimental chambers were larger (0.0256 m^2: $0.16 \times 0.16 \times 0.07$ m). We removed debris from cages at least once every 3 d, 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.

The target snails were 3.04 mm ($\pm$ 0.09 SE) for *P. antipodarum* and 2.04 mm ($\pm$ 0.03 SE) for *P. robusta*. 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; in fact, both species grew during the experiment (see **Results**). In intraspecific treatments, we distinguished target snails from nontarget snails by the shorter shell lengths of target snails (Grudemo and Bohlin 2000). At the conclusion of the 2-wk experiments, we measured target snails and preserved them in 10% formalin. 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*: $M_{pr} = 0.0996\ L^{1.7158}$, where M is snail biomass [mg AFDM] and L is shell length [mm]). Biomass-specific growth rates g (g g^{-1} d^{-1}) (e.g., Cross and Benke 2002, Hall et al. 2006) were calculated as:

$$g = \frac{(\ln M_t - \ln M_0)}{t} \quad [2]$$

where M_t is snail biomass at the conclusion of the experiment (g AFDM), M_0 is the initial biomass of a snail (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.—We used 3-way ANOVAs (NCSS-PASS 2001; NCSS Statistical Software, Kaysville, Utah) to test for statistical differences in snail growth with stream, snail biomass, and interaction type (intraspecific or interspecific) as fixed factors. We analyzed each species separately. For *P. antipodarum*, we tested post hoc comparisons of snail biomass effects within each interaction type because the interaction term for biomass $\times$ interaction type term was significant (Systat 10). We used the Bonferroni method to adjust the α-level to account for extra comparisons ($\alpha = 0.025$).

We calculated C–C intraspecific interaction strengths (α_{xx} in terms of g^{-1} snail AFDM d^{-1}) as the per biomass effect of an intraspecific interactor (x) on a target individual (x), from the following equation, adapted from Wootton (1997) and Berlow et al. (1999):

$$\alpha_{xx} = \frac{\ln\left(\dfrac{M_{x,t,\text{high}} \times M_{x,0,\text{low}}}{M_{x,t,\text{high}} \times M_{x,0,\text{low}}}\right)}{(M_{x,0,\text{high}} - M_{x,0,\text{low}})t} \qquad [3]$$

where $M_{x,t,\text{high}}$ is snail biomass (g AFDM) of species x at time t from high intraspecific treatments, $M_{x,0,\text{low}}$ is snail biomass of species x at time 0 from low intraspecific treatments (0.66 g/m^2 AFDM), $M_{x,0,\text{high}}$ is snail biomass of species x at time 0 from high intraspecific treatments (4.98 g/m^2 AFDM), $M_{x,t,\text{low}}$ is snail biomass of species x at time t from low intraspecific treatments, and t is the duration of the experiment (d).

We also calculated C–C interspecific interaction strengths (α_{xy} [g^{-1} snail AFDM d^{-1}]) as the per biomass effects of the interspecific interactor (y) on the target snail (x), in a similar manner. This formulation assumes that intraspecific competition among the target species is negligible compared with interspecific competition:

$$\alpha_{xy} = \frac{\ln\left(\dfrac{M_{x,t,\text{high}} \times M_{x,0,\text{low}}}{M_{x,0,\text{high}} \times M_{x,t,\text{low}}}\right)}{(M_{y,0,\text{high}} - M_{y,0,\text{low}})t} \qquad [4]$$

where $M_{x,t,\text{high}}$ is snail biomass (g AFDM) of species x at time t from high interspecific treatments, $M_{x,0,\text{low}}$ is snail biomass of species x at time 0 from low interspecific treatments (0.33 g/m^2 AFDM), $M_{x,0,\text{high}}$ is snail biomass of species x at time 0 from high interspecific treatments (0.33 g/m^2 AFDM), $M_{x,t,\text{low}}$ is snail biomass of species x at time t from low interspecific treatments, $M_{y,0,\text{high}}$ is snail biomass of species y at time 0 from high interspecific treatments (4.65 g AFDM/m^2), $M_{y,0,\text{low}}$ is snail biomass of species y at time 0 from low interspecific treatments (0.33 g/m^2 AFDM), and t is the duration of the experiment (d).

These values indicate the degree to which competition (negative values), facilitation (positive values), or neither (0 values) is occurring and could be extrapolated to population effects for each species at each site because individual size is positively correlated with reproduction and fitness (i.e., population growth) (see Dybdahl and Kane 2005). Also, C–C interaction strengths are derived from the discrete time version of Lotka–Volterra equations, and, therefore, are equivalent to competition coefficients (Laska and Wootton 1998, Berlow et al. 1999, 2004). On the basis of classic Lotka–Volterra coexistence criteria, stable coexistence

should occur when intraspecific competition is stronger (more negative) than interspecific competition for both species (i.e., $\alpha_{xy} > \alpha_{xx}$ and $\alpha_{yx} > \alpha_{yy}$). Displacement by invasive P. antipodarum should occur when P. antipodarum exerts stronger interspecific effects on native P. robusta than P. robusta does on itself.

We used a bootstrap procedure to calculate C–C interaction strengths. The bootstrap procedure sampled final biomass of target snails in low and high treatments at random and with replacement. This process was repeated 1000×. We repeated interaction strength calculations for each species in each stream. We then tested for significant interactions by constructing 95% confidence intervals; intervals including 0 indicated that neither competition nor facilitation was occurring (Resampling Stats; Good 2001). Last, we tested pairwise comparisons of coexistence criteria using 95% confidence intervals (Resampling Stats).

Population-level impacts of P. antipodarum

Population-level impacts of the invasive P. antipodarum can be estimated in both streams by multiplying population biomass by per biomass interaction strengths. Parker et al. (1999) also proposed that range be taken into account, but P. antipodarum covers the entire range of P. robusta in Wyoming. Thus, impact (I) within this given critical range is proportional to per biomass interaction strengths (E) multiplied by population biomass (B), or $I \propto BE$ (see also Ricciardi 2003). Our measures of community interactions can be estimated on 2 levels: resources (using C–R interaction strengths) and another consumer, P. robusta (using C–C interaction strengths). Traditionally, foodweb ecologists have focused upon C–R interactions, but nontrophic interactions (i.e., competition between consumers) might be just as important for estimating effects on community structure (Berlow et al. 2004).

Results

C–R interactions

Potamopyrgus antipodarum and P. robusta reduced chlorophyll a standing stock in both streams by ~⅔ ($F = 9.96$, $p < 0.001$; Fig. 1A, B). However, neither species significantly reduced periphyton AFDM in either stream, suggesting that neither species affected detrital and nonphotosynthetic periphyton ($F = 0.75$, $p = 0.479$). Hence, we focus on effects of grazing on attached algae as estimated by chlorophyll a.

Total algal standing stock in control treatments was 2× higher in Marmot Spring than in Polecat Creek ($F = 8.63$, $p < 0.01$; Fig. 1A, B). Nevertheless, chlorophyll a was reduced by similar amounts in both streams, as
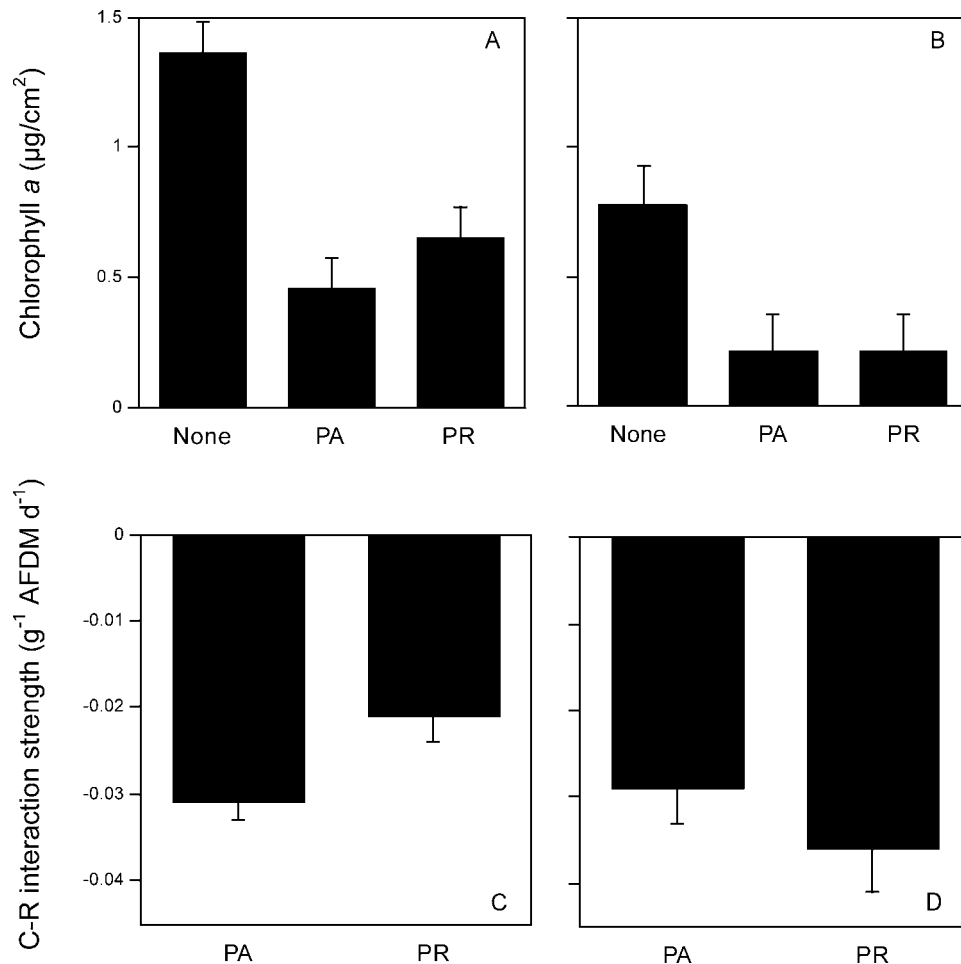
FIG. 1. Mean (+1 SE) chlorophyll *a* standing stocks after 1 wk in cage enclosures with and without grazers (*Potamopyrgus antipodarum* [PA] and *Pyrgulopsis robusta* [PR]) in Marmot Spring (A) and Polecat Creek (B) and mean (−1 SE) bootstrapped per biomass consumer–resource (C–R) interaction strengths in Marmot Spring (C) and Polecat Creek (D). AFDM = ash-free dry mass.

shown by the comparison of treatments with snails vs those without. In addition, the reduction of chlorophyll *a* did not differ significantly between species ($p > 0.05$, Bonferroni test for multiple comparisons; Fig. 1A, B).

C–R interaction strengths on chlorophyll *a* were negative and nearly identical for the 2 species in both streams (Fig. 1C, D). The stream × species interaction term was not statistically significant and indicated that the reduction in chlorophyll *a* did not depend on stream or species ($F = 0.47$, $p = 0.628$).

C–C interactions

Both *P. antipodarum* and *P. robusta* grew during the experiment in both streams (Fig. 2A–D). *Potamopyrgus antipodarum* growth rate was similar in the 2 streams (Fig. 2A, B, Table 2). On the other hand, growth rate of *P. robusta* was significantly higher in Marmot Spring than in Polecat Creek (Fig. 2C, D, Table 2).

Potamopyrgus antipodarum.—A significant snail

biomass × interaction type effect indicated that the growth response differed between intraspecific and interspecific treatments (Table 2). Growth rates of target *P. antipodarum* snails were reduced by intraspecific interactions; growth rates of *P. antipodarum* in high-biomass treatments were 67% of rates in low-biomass treatments (post hoc contrast: $F = 65.469$, $p < 0.001$; Fig. 2A, B). For interspecific treatments, growth rates of target *P. antipodarum* were 4× greater in the high than in the low *P. robusta* biomass treatments (post hoc contrast: $F = 63.553$, $p < 0.001$; Figs. 2A, B). The nonsignificant 3-way interaction term indicated that these effects did not depend on stream (Fig. 2A, B, Table 2).

Pyrgulopsis robusta.—Both intraspecific and interspecific interactions slowed growth rates. The snail biomass effect was highly significant, but the snail biomass × interaction type term was not significant (Table 2). Growth rates of *P. robusta* were reduced by
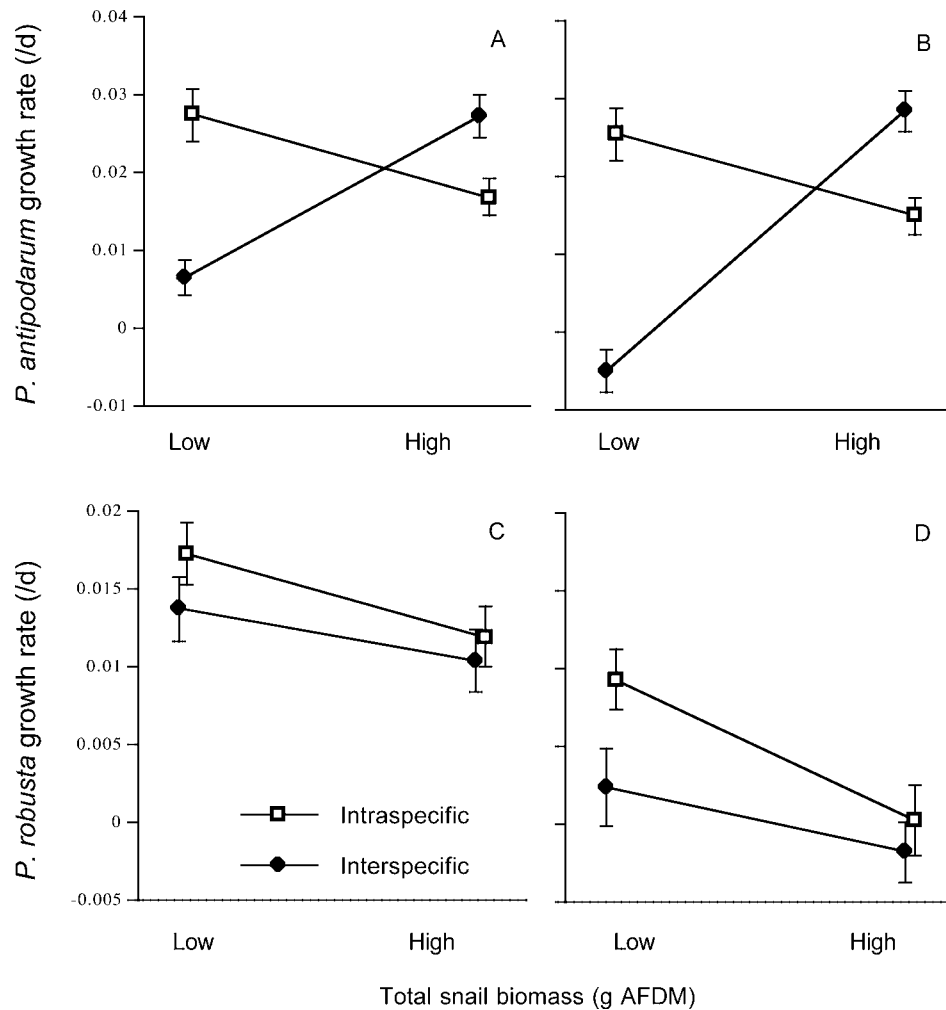
FIG. 2. Mean (±1 SE) *Potamopyrgus antipodarum* (A, B) and *Pyrgulopsis robusta* (C, D) growth rates when exposed to intraspecific and interspecific competition during consumer–consumer (C–C) interaction experiments in Marmot Spring (A, C) and Polecat Creek (B, D). Intraspecific treatments contain only the target species at a biomass of 0.66 or 4.98 g/m^2 ash-free dry mass (AFDM). Interspecific treatments have 0.33 g/m^2 AFDM of the target species and the other species at a biomass of 0.33 or 4.65 g/m^2 AFDM.

intraspecific interactions; growth rates were slower in high- than in low-biomass treatments. For interspecific treatments, growth rates of target *P. robusta* in high *P. antipodarum* biomass treatments were 50 to 80% of growth rates in the low-biomass treatments in both streams (Fig. 2C, D). Last, the nonsignificant 3-way interaction term indicated that the effects of snail biomass and interaction type did not depend on stream (Fig. 2C, D, Table 2). However, *P. robusta* grew more slowly in Polecat Creek under all treatments (Fig. 2C, D, Table 2).

We can express these effects as the magnitude and sign of the interaction strength per unit biomass. For the native snail *P. robusta*, both intraspecific and interspecific C–C interaction strengths were significantly negative in both streams (Fig. 3A, B). For *P. antipodarum*, intraspecific C–C interaction strengths

also were significantly negative in both streams, but interspecific C–C interaction strengths with *P. robusta* on *P. antipodarum* targets were significantly positive in both streams. Hence, *P. robusta* facilitated growth of *P. antipodarum* in both streams (Fig. 3A, B).

Intraspecific competition in *P. antipodarum* was stronger (more negative) than interspecific interactions with *P. robusta* in both streams (Fig. 3A, B). Intraspecific competition in *P. robusta* was stronger than interspecific interactions with *P. antipodarum* in Marmot Spring, but was equivalent to interspecific interactions with *P. antipodarum* in Polecat Creek (Fig. 3A, B). On the basis of C–C interaction strengths and coexistence criteria, *P. robusta* cannot inhibit the invasion of *P. antipodarum* through competitive interactions.

TABLE 2. Summary analysis of variance table for consumer–consumer (C–C) interaction experiment with *Potamopyrgus antipodarum* or *Pyrgulopsis robusta* growth rates as the response variables. * indicates statistically significant ($p < 0.05$).

Source	df	Mean square	F	p
P. antipodarum				
Stream	1	0.00120	3.58	0.059
Snail biomass	1	0.00617	18.33	0.000*
Interaction type	1	0.00424	12.59	0.000*
Stream × snail biomass	1	0.00094	2.79	0.096
Snail biomass × interaction type	1	0.03181	94.54	0.000*
Stream × interaction type	1	0.00023	0.69	0.407
Stream × snail biomass × interaction type	1	0.00090	2.68	0.103
P. robusta				
Stream	1	0.01252	53.65	0.000*
Snail biomass	1	0.00319	13.70	0.000*
Interaction type	1	0.00133	5.69	0.018*
Stream × snail biomass	1	0.00014	0.58	0.447
Snail biomass × interaction type	1	0.00031	1.33	0.249
Stream × interaction type	1	0.00010	0.42	0.519
Stream × snail biomass × interaction type	1	0.00005	0.24	0.628

Population-level impacts of P. antipodarum

The estimated population impacts of *P. antipodarum* on resources ($I = $ C–R interaction strengths × population biomass) and another consumer, *P. robusta* ($I = $ C–C interaction strengths × population biomass), were both much stronger in Polecat Creek than in Marmot Spring. Impacts of *P. antipodarum* on algal resources were 5 to 6× larger in Polecat Creek (-0.72 d^{-1}) than in Marmot Spring (-0.13 d^{-1}) and impacts on *P. robusta*

were 12× larger in Polecat Creek (Polecat Creek: -0.064 d^{-1} vs Marmot Spring: -0.0054 d^{-1}).

Discussion

Our goal was to measure the strength of biotic interactions involving an invasive stream snail, *P. antipodarum*, using a framework from community ecology. We showed that grazing effects of the invasive *P. antipodarum* and the endemic *P. robusta* on algal resources were similar and negative in 2 streams, as
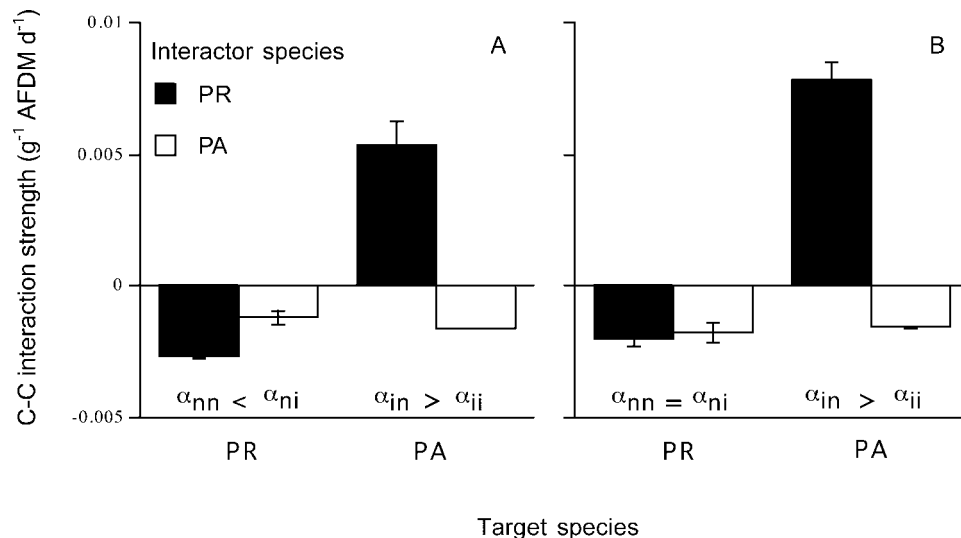

FIG. 3. Mean (±95% CI) consumer–consumer (C–C) interaction strengths in cage enclosures with *Pyrgulopsis robusta* (PR) and *Potamopyrgus antipodarum* (PA) in Marmot Spring (A) and Polecat Creek (B). Negative values indicate competition; positive values indicate facilitation. C–C interaction strengths (α) represent the magnitude and direction of the effect that 1 g of ash-free dry mass (AFDM) of the interactor species (legend) has on the biomass of the target population (*x*-axis) per day. C–C interaction strengths are equivalent to Lotka–Volterra competition coefficients for the invasive (i) and native (n) species, e.g., $\alpha_{ni} = $ per biomass effect of invasive *P. antipodarum* on native *P. robusta*.

represented by C–R interaction strengths on chloro-phyll *a*. However, C–C interactions were asymmetric. Growth rates of *P. robusta* were lowest when interacting with the invader, especially at high invader biomass. In contrast, *P. antipodarum* always grew faster than *P. robusta* and growth rates were highest when interacting with the native (endemic) species. Interactions between snails, both positive and negative, were stronger in Polecat Creek, leading to higher overall impact of the invasive snail where C–C interaction strengths were strong and biomass high.

We expected snails to reduce periphyton resources because snails are effective grazers in streams (Lamberti et al. 1987, Feminella and Hawkins 1995, Steinman 1996). We showed that, in the short term, both species reduced chlorophyll *a* by similar amounts, even though neither species significantly reduced periphyton AFDM. These results indicate that *P. antipodarum* and *P. robusta* consume algal resources and potentially compete for this portion of the periphyton. However, the similarity in algal reduction by the 2 snail species was surprising because one might expect dominance to result from: 1) a higher resource acquisition rate (e.g., Petren and Case 1996) or 2) the absence of reduction in resource levels, which should lead to resource opportunities for the dominant species (reviewed in Shea and Chesson 2002). For these mechanisms to explain the dominance of *P. antipodarum*, the grazing effect of *P. antipodarum* should have been much larger than that of the native snail. Alternatively, *P. antipodarum* could have lower maintenance costs or be more efficient at converting resources to growth, as has been suggested for *P. antipodarum* populations in Idaho (Richards 2004) and for another invasive snail in San Francisco Bay (Byers 2000). Under this scenario, *P. antipodarum* could grow faster on lower resource levels than *P. robusta* (e.g., Tilman 1977).

C–R interactions were similar between snail species, but C–C interactions were asymmetric. *Potamopyrgus antipodarum* was a superior competitor, and *P. robusta* growth rates were slower when interacting with *P. antipodarum* than with conspecifics. On the other hand, *P. antipodarum* growth rates increased in treatments with higher biomass of the native species. Hence, the native snail facilitated growth of *P. antipodarum*, and *P. antipodarum* inhibited native snail growth. Asymmetric interactions between aquatic macroinvertebrate consumers are common (Schoener 1983) and have occurred between snails and between snails and insects in freshwater habitats (Benke 1978, Brown 1982, Kohler 1992). Some interactions are so highly asymmetric that 1 species can enhance the growth (tadpoles and pulmonate snails: Brönmark et al. 1991)

or reproduction (pulmonate snails: Hershey 1990) of a 2nd species.

The mechanism by which *P. robusta* facilitates *P. antipodarum* growth is unknown, but 3 scenarios are plausible. First, *P. antipodarum* might consume *P. robusta* eggs, as has been demonstrated for both an invasive prosobranch snail in San Francisco Bay (*Ilyanassa obsoleta* on *Cerithidea californica* egg capsules; Race 1982) and a North American freshwater lymnaeid (*Stagnicola elodes* on *Physa acuta* eggs; Turner et al. 2007). Second, some snails secrete mucus that enhances algal growth (Connor and Quinn 1984). If *P. robusta* mucus has such properties, high biomass of *P. robusta* could indirectly facilitate growth of *P. antipodarum*. Third, these snails are competing for a heterogeneous resource base that consists of taxonomically and functionally diverse algae. *Potamopyrgus antipodarum* might be competitively dominant for a shared preferred algal resource, with the result that *P. robusta* could be forced to use a lower-quality resource. If *P. robusta* removed the lower-quality resource, space would be available for the preferred algae to grow, thereby indirectly facilitating the growth of *P. antipodarum*. This type of indirect commensalism has been observed between snails and tadpoles (Brönmark et al. 1991).

Interaction strengths and invasive species impact

Measuring effects of invasive species with interaction strengths has several advantages for studies of invasive species impacts. First, such studies can provide insight into whole-ecosystem responses to disturbance when before–after, control–impact experimental designs (Stewart-Oaten et al. 1986) are not possible because of the absence of long-term, before–after data (Ricciardi 2003) or suitable control sites. For example, Kohler and Wiley (1997) demonstrated that small-scale manipulations of a dominant grazer correctly predicted the direction of effects when a dominant grazer was lost at the whole-stream level, even though the magnitude was underestimated. Second, interaction strengths can be used to make comparisons across sites because values are standardized to per biomass or per capita effects, allowing for extrapolation to population impacts. Last, interaction strengths can highlight both per unit effects of the invasive species on residents and the reciprocal effects of resident species on the invader (Fig. 4). 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'An-
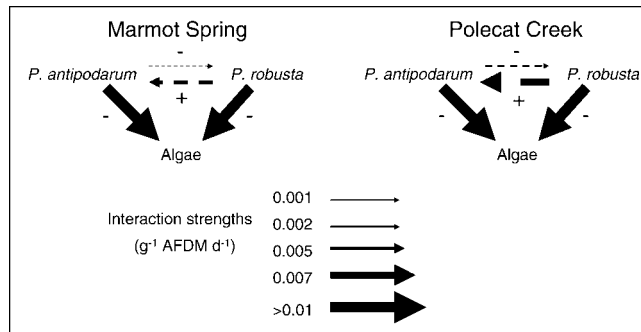
FIG. 4. Interaction networks among *Potamopyrgus antipodarum*, *Pyrgulopsis robusta*, and algae in Marmot Spring and Polecat Creek. Magnitude of interaction strength is proportional to arrow width (solid = direct effect; dashed = indirect effect). + = positive, − = negative.

tonio and Hobbie 2005). Impact should be highest where the mismatch is largest or, in this case, where the invasive species has the largest negative effects and the resident community provides little biotic resistance to the invader. Strong negative effects of *P. antipodarum* on *P. robusta* coupled with strong facilitative effects of *P. robusta* on *P. antipodarum* could lead to the largest impacts of the invasive species in Polecat Creek. Experiments conducted during other seasons could strengthen this argument, especially if competition and facilitation are important throughout the year.

Our approach using standardized measures of per biomass interaction strengths has demonstrated the potential for the invasive *P. antipodarum* to reduce resource availability and threaten an endemic snail, *P. robusta*, in a spring stream. All else equal, the overall impact of *P. antipodarum* should be magnified in Polecat Creek compared with Marmot Spring because of larger C–C interaction strengths and greater population biomass of *P. antipodarum*. Consistent with these trends, the 2 species are both abundant in the field populations of Marmot Spring, but *P. antipodarum* is dominant in Polecat Creek. Taken together, these results suggest that competition and, potentially, facilitation could contribute to *P. antipodarum* dominance in these streams. Our study highlights the potential for short-term measures of interaction strengths to estimate community-level effects, either positive or negative, at early stages of an invasion before profound changes in community structure are revealed.

Acknowledgements

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ERRATUM

On page 513 of the article by L. A. Riley et al. in the September 2008 issue (J-NABS 27:509–520), a subscript in equation 3 was reversed. The corrected equation is shown below.

$$\alpha_{xx} = \frac{\ln\left(\dfrac{M_{x,t,\text{high}} \times M_{x,0,\text{low}}}{M_{x,0,\text{high}} \times M_{x,t,\text{low}}}\right)}{(M_{x,0,\text{high}} - M_{x,0,\text{low}})t} \qquad [3]$$