

THE INVASIVE NEW ZEALAND MUDSNAIL, *POTAMOPYRGUS ANTIPODARUM*, REDUCES GROWTH OF THE NATIVE SNAIL, *FOSSARIA SP.*

AMY C. KRIST ♦ DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY
UNIVERSITY OF WYOMING ♦ LARAMIE

MARK F. DYBDAHL ♦ SCHOOL OF BIOLOGICAL STUDIES
WASHINGTON STATE UNIVERSITY ♦ PULLMAN

♦ INTRODUCTION

Invasive species are one of the greatest threats to global biodiversity. Hence, understanding the role of invasive species is of grave importance to managing and minimizing the impact of biological invasions. To date, the ecological impacts of biological invasions have received significant attention, but little effort has been made to address the evolutionary impact (Sakai *et al.* 2001, Cox 2004). This is despite the fact that evolutionary impacts are likely to be widespread; invasive species have been shown to alter patterns of natural selection or gene flow within native populations (Parker *et al.* 1999), and many of the best examples of rapid evolution involve invasive species interacting with native species (Reznick and Ghalambor 2001, Strauss *et al.* 2006). We have begun to address some of the evolutionary consequences of the invasion of the New Zealand mud snail, (*Potamopyrgus antipodarum*) on a species of native snail in the Greater Yellowstone Area (GYA).

Potamopyrgus antipodarum are a likely selective agent on native snails because they have achieved very high densities in the invasive range (500,000/m² in some areas of the Greater Yellowstone Ecosystem; Hall *et al.* 2003) and dominate these communities (Kerans *et al.* 2005, Hall *et al.* 2006). These densities translate into a strong

impact on the biotic and abiotic environment. For example, Hall and colleagues (2003) showed that *P. antipodarum* consumed 75% of gross primary productivity, and Riley and colleagues (*in review*) showed that they reduce periphyton biomass (the microscopic algae, fungi, and bacteria on substrata). Because the growth of individuals and populations of algivores can be limited by the abundance of algae (reviewed in Lamberti 1996), this consumption of the majority of resources by *P. antipodarum* is likely to have a negative effect on other benthic herbivores. Hence, one way *P. antipodarum* may be impacting native snails and other benthic herbivores is by reducing their evolutionary fitness through consumption of resources. These detrimental consequences to the fitness of native invertebrates may either reduce their population sizes or, with sufficient time and genetic variation, lead to evolutionary change in populations of natives.

Indeed, consumption of resources by *P. antipodarum* has been shown to cause exploitative competition with a native snail. In experimental chambers, *P. antipodarum* reduced the growth rate of the native hydrobid *Pyrgulopsis robusta* in two streams in the GYA (Riley *et al.* *in review*). We used two methods to determine whether *P. antipodarum* are competing with another native snail (*Fossaria* sp.). First, we sampled every 150 m along a 900 m stretch of Polecat Creek to determine whether the

densities of the two species are correlated. If competition is occurring and reducing their population sizes, the densities of the invasive snail should be negatively correlated with densities of the native snail. Second, we conducted an experiment to determine whether interspecific or intraspecific competition reduces growth and reproduction of the native *Fossaria* and the non-native *P. antipodarum*. Although *P. antipodarum* may be competing with native invertebrates for either food or space (Kerans *et al.* 2005), our experiment only addressed competition for food. We only report on the results of the competition experiment because the data on the relationship between densities of the invasive and the native snail in Polecat Creek are still being collected.

We conducted an experiment to examine growth and reproductive output in interspecific and intraspecific competition treatments at two different densities. To address intraspecific competition, we used experimental chambers with high or low densities of one species. To address interspecific competition, we mixed both species at high or low densities. For each species, we asked whether interactions with conspecifics or the other species had a greater effect on growth and reproduction.

◆ METHODS

Experimental design

We performed a field experiment in the summer of 2005 in Polecat Creek (Roosevelt National Parkway) to assess the competitive interactions between the invasive *P. antipodarum* and the native snail *Fossaria* sp., in terms of on growth and reproduction. For each species, there were two levels of density (low and high) and two types of competition (intraspecific and interspecific). We determined the biomass for the density treatments by measuring the densities of both species in four random samples from the site of the experiment. Low density (1x, 550 mg AFDM/m²) was within the range of ambient density for both species. High density was eight times the ambient density (8x, 4400 mg AFDM/m²). We varied densities to determine whether competition occurred under current conditions (low density) or only when resources are very limited (high densities). Intraspecific competition was addressed in half of the experimental chambers containing only one species (all *Fossaria* or all *Potamopyrgus*). Interspecific competition was addressed in the rest of the chambers containing a mixture of both species.

To examine the impact of competition on the growth of each species, we designated 15 target snails in each experimental chamber. These animals were marked by placing a dab of water-proof paint on their shell. We measured the length of the shell of each target snail at the beginning of the experiment and at the end of the experiment (two weeks later). Since the growth of *P. antipodarum* decreases markedly after sexual maturity (Jokela and Lively 1995), we selected small snails that were likely to be immature for the target snails of this species. For *P. antipodarum*, the mean size of the target snails was 2.17 mm (min. = 1.61 mm, max. = 3.02 mm). Likewise, small *Fossaria* were marked as target snails. These snails were sorted by hand from the random samples that we collected. The mean size of the target *Fossaria* was 6.54 mm (min. = 2.59 mm, max. = 7.97 mm). Although little is known about the life history of this species, in the congener *Fossaria cubensis*, size at maturity is between 10 and 12 mm (Gutierrez *et al.* 2000).

We controlled for biomass in each experimental chamber by converting the length of the snails to ash free dry mass (AFDM) using length-mass regressions for *Fossaria* (Riley, unpublished) and *P. antipodarum* (Hall, unpublished). Then, we placed equal amounts of AFDM for each density (550 mg AFDM/m² for low density and 4400 mg AFDM/m² for high density) into the experimental chambers. This also serves to control for differences in body size since adult *Fossaria* are much larger than *P. antipodarum*. For the interspecific competition treatment, the differences in density were achieved by altering the non-target (other) species; the numbers (AFDM) of the target species (target and reproductive snails) were the same for both densities (Table 1).

To examine the impact of competition on the reproduction of each species, we included reproductive snails in addition to the target snails. To match the biomass across experimental chambers of the same density treatment, the AFDM of the target snails was subtracted from the total biomass needed and we then added the appropriate number of reproductive snails to yield the treatment biomass for that species. Hence for the experimental chambers with interspecific competition, there were 15 target individuals of species A, reproductive adults of species A (number varies by density treatment, Table 1), and a variable number of snails of species B to equal the total biomass of that density treatment (mg of AFDM for each density given above). Overall, there were 8 treatments, low and high density for intraspecific and interspecific competition for both

species (2 density x 2 competition x 2 species = 8), with three replicates per treatment.

| Competition Treatment | Density | Target species | N target | N reproductives | N (other species) |
|-----------------------|---------|----------------|----------|-----------------|-------------------|
| Intraspecific | Lo | Fossaria | 15 | 18 | 0 |
| Intraspecific | Hi | Fossaria | 15 | 80 | 0 |
| Interspecific | Lo | Fossaria | 15 | 9 | 86 |
| Interspecific | Hi | Fossaria | 15 | 9 | 692 |
| Intraspecific | Lo | Potamopyrgus | 15 | 172 | 0 |
| Intraspecific | Hi | Potamopyrgus | 15 | 778 | 0 |
| Interspecific | Lo | Potamopyrgus | 15 | 86 | 16 |
| Interspecific | Hi | Potamopyrgus | 15 | 86 | 127 |

Table 1. Number of snails placed in each experimental chamber by treatment. Because we controlled for biomass across treatments, the total biomass in each experimental chamber for a given density are equivalent, whether the biomass is composed of a single species (intraspecific competition) or mixed species (interspecific competition). Since the two species of snails differ in size, the numbers of each species vary. N refers to the sample size of the target snails, the reproductive snails (same species as target snails), and number of snails of the other species.

Experimental cages were constructed from 0.0182 m² plastic storage containers. We cut out the plastic from each side and from the top and replaced it with 122 μ m mesh Nytex screen. The screen allowed water to flow through the chambers but kept the egg masses of *Fossaria* and the newly hatched juveniles of *P. antipodarum* inside.

To assemble the experimental chambers, we attached each plastic chamber to a brick by threading a 14 cm long bolt through a hole in the bottom of the chamber and attaching nuts and washers to the bottom of the brick to secure the two together. Next, we placed between five and six rocks from the surrounding stream in each experimental chamber. These rocks, which had been cleaned of benthic invertebrates, possess periphyton and provide nutrients for the snails. Snails were added to each chamber according to the appropriate biomass and species combination. Then, we placed the chambers in the stream to a depth that covered the rocks in the chamber but also allowed some air at the top of the cage. The air pocket was required because *Fossaria* possess lungs and breathe air.

The experiment was set-up on July 1 and 2, 2005. Every two days during the duration of the experiment, we visited the site of the experiment to check the depth of the experimental chambers and to remove detached algae from the mesh. The experimental chambers were removed from the creek on 15 and 16 July; each experimental chamber remained in the creek for 14 days. At the end of the experiment all of the contents of the chambers

(snails, egg masses, algae), except the rocks, were rinsed through a 250 μ m metal sieve and preserved in 70% ethanol. Each of the rocks were scrubbed for analysis of chlorophyll *a*.

Measurements of resource use

We also measured use of algal resources by measuring the concentration of chlorophyll *a* for each rock. In addition to the experimental chambers containing snails, we also had three experimental chambers that had no snails in them. These chambers served as controls to compare the grazing effect among the treatments. The controls also allow us to determine whether one species utilizes the resource more completely and whether resource use was the cause of competition.

We scraped the periphyton off of each rock with toothbrushes and then collected a volume of the slurry on a glass fiber filter (Gelman AE) using vacuum filtration. We calculated chlorophyll *a* concentrations with a 90% acetone extraction and spectrophotometric analysis of the extract (APHA 1998). We estimated the exposed surface area of each of the rocks using paper tracing. Hence, we will be able to calculate the concentration of chlorophyll *a* per unit area. These results are not reported here because they are not yet complete.

Statistical analyses

We omitted one replicate from each treatment because some of the experimental chambers failed (the Nytex mesh did not remain attached on one or more of the "windows"). In these replicates, the number of snails in the chamber was either higher or lower than the starting number (escapes and émigrés). Therefore, we analyzed the remaining two replicates per treatment.

To determine the effect of the experimental conditions on growth, we converted the length measurements to biomass (AFDM) and compared the biomass measurements at the beginning and end of the experiment among groups. We used a two-way ANOVA with biomass (mg of AFDM) as the dependent variable and with the categorical independent variables, density (low or high) and type of competition (intraspecific and interspecific). We did not use repeated measures ANOVA because snails were marked so that they could be distinguished from the reproductive adults, but not marked individually. Therefore, we have biomass measurements for the group at the beginning and at the end of the experiment.

The rate of reproduction in each chamber was calculated as rate of reproduction = $o / (r - m)$ where o is the total number of offspring (juvenile *P. antipodarum*, and juvenile and egg masses of *Fossaria*) in each container, r is the total number of reproductive adults, and m is the total number of snails of the target species that died in each container. Since the timing of mortality is unknown, excluding the dead animals may underestimate the number of animals contributing to reproduction. Despite this potential risk, we excluded the dead animals because of high mortality of *Fossaria* in the high density treatments. Reproductive rates were also analyzed with a two-way ANOVA. Again the categorical, independent variables were density and type of interaction. All statistics were conducted using the R statistical package (R Development Core Team, 2005).

◆ RESULTS AND DISCUSSION

Growth

Both density and type of competition had significant effects on biomass in the native *Fossaria* sp. (Table 2A). Not surprisingly, *Fossaria* showed a significantly higher increase in biomass in the low density treatment than in high density (Table 2A, Fig. 1). This result indicates that a high density of individuals lead to decreased growth, probably because of reduced resources. Importantly, *Fossaria* also gained significantly less biomass in the interspecific competition treatment than in the intraspecific treatment (Table 2, Fig.1). This result indicates that the invasive snail, *P. antipodarum* had a more detrimental effect on *Fossaria*'s growth than conspecifics. A significant interaction term between density and type of competition was caused by a larger gain in biomass in the intraspecific treatments at low density that at high density (Fig. 1).

In contrast to the native *Fossaria*, only density had a significant effect on biomass in the invasive *P. antipodarum* (Table 2B); there was no effect of type of competition and no significant interaction term. Similar to *Fossaria*, the gain in biomass was significantly higher in the low density treatment (Table 2B, Fig. 2). Again, this result suggests that in the high density treatment, the presence of many individuals decreased resources which led to decreased growth. Although an accumulation of nitrogenous wastes may also stunt growth, this explanation is unlikely in this experiment because fresh water flowed constantly through the experimental chambers.

| A. <i>Fossaria</i> | | | | |
|------------------------|------|--------|---------|---------------|
| Source | d.f. | M.S. | F value | P |
| Density | 1 | 30.30 | 14.66 | 0.0002 |
| Competition | 1 | 17.80 | 8.61 | 0.0038 |
| Density * | 1 | 10.99 | 5.32 | 0.0222 |
| Competition error | 187 | 2.07 | | |
| B. <i>Potamopyrgus</i> | | | | |
| Source | d.f. | M.S. | F value | P |
| Density | 1 | 0.0576 | 4.53 | 0.0347 |
| Competition | 1 | 0.0003 | 0.02 | 0.8886 |
| Density * | 1 | 0.0058 | 0.45 | 0.5011 |
| Competition error | 189 | 0.0127 | | |

Table 2. The results of a two-way ANOVA of the effects of density (low and high) and type of competition (intraspecific and interspecific) on the AFDM (mg) of the target snails before and after the experiment. Separate analyses were conducted for *Fossaria* (A.) and *Potamopyrgus* (B.) Statistically significant effects are bolded.

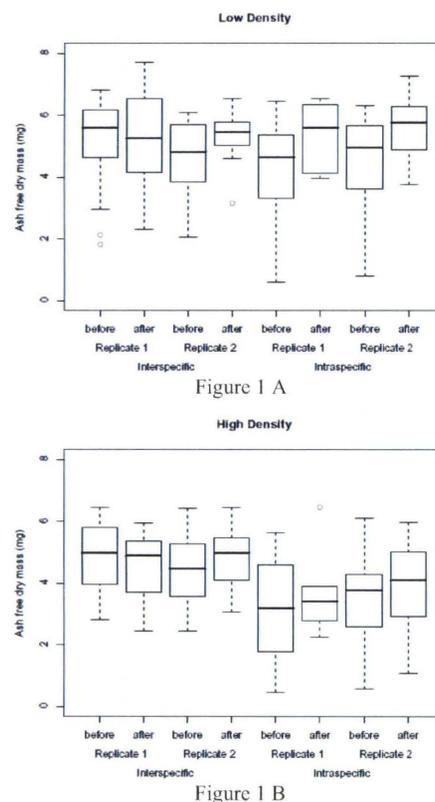


Figure 1. The change in biomass (AFDM in mg) of *Fossaria* between the beginning of the experiment (before) and two weeks later at the end of the experiment (after), for each replicate for interspecific and intraspecific competition treatments. In these boxplots, the dark, horizontal line is the median, the box bounds the 75th and 25th percentiles, and the whiskers bound the 90th and 10th percentiles. Any outliers are plotted as open circles. The low density treatments are shown in A) and the high density in B).

Despite the fact that conspecifics can have identical resource needs, interspecific interactions had a greater impact on the growth rate of *Fossaria* than did intraspecific interactions. This result is

surprising and suggests that *P. antipodarum* may be depressing the periphyton resource to a greater extent than *Fossaria*. This explanation would also explain why there was no effect of competition type in *P. antipodarum* (intraspecific and interspecific competition treatments had an equivalent effect on growth). We will be able to address this hypothesis with the data on concentrations of chlorophyll *a*.

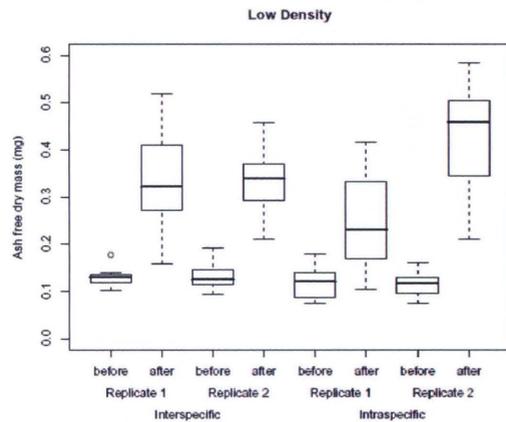


Figure 2A

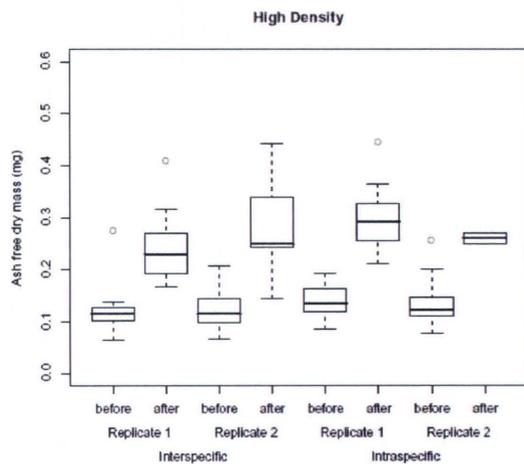


Figure 2 B

Figure 2. The change in biomass (AFDM in mg) of *Potamopyrgus antipodarum* between the beginning of the experiment (before) and two weeks later at the end of the experiment (after), for each replicate for interspecific and intraspecific competition treatments. In these boxplots, the dark, horizontal line is the median, the box bounds the 75th and 25th percentiles, and the whiskers bound the 90th and 10th percentiles. Any outliers are plotted as open circles. The low density treatments are shown in A) and the high density in B).

Reproduction

Overall, reproductive rate was less affected than growth. In the native *Fossaria*, there were no significant effects on reproductive rate by either density or type of competition (Table 3A, Table 4A). These results suggest that allocation to reproduction is prioritized over growth; when environmental

conditions were poor (e.g. under competition in high density) growth was compromised but not reproductive rate. Another possible explanation is that fourteen days is not long enough to detect a response in reproduction.

| A. <i>Fossaria</i> | | | | |
|------------------------|------|-------|---------|---------------|
| Source | d.f. | M.S. | F value | P |
| Density | 1 | 6.42 | 0.92 | 0.3907 |
| Competition | 1 | 24.09 | 3.47 | 0.1361 |
| Density * Competition | 1 | 4.83 | 0.69 | 0.4514 |
| error | 4 | 6.95 | | |
| B. <i>Potamopyrgus</i> | | | | |
| Source | d.f. | M.S. | F value | P |
| Density | 1 | 0.765 | 2.41 | 0.1954 |
| Competition | 1 | 0.004 | 0.01 | 0.9180 |
| Density * Competition | 1 | 2.556 | 8.07 | 0.0469 |
| error | 4 | 0.317 | | |

Table 3. The results of a two-way ANOVA of the effects of density (low and high) and type of competition (intraspecific and interspecific) on the reproductive rate of the target snails. Separate analyses were conducted for *Fossaria* (A.) and *Potamopyrgus* (B.) Statistically significant effects are bolded.

Results for the invasive *P. antipodarum* were similar. Reproductive rate of *P. antipodarum* was not affected by either density or type of competition (Table 3B, Table 4B). However, there was a significant interaction between density and competition; in the interspecific competition treatment, reproduction was highest in the high density treatments. In contrast, in the intraspecific competition treatment, reproductive rate was highest in the low density treatments (Table 4B).

◆ CONCLUSIONS

The two species differed in their responses to the experimental conditions. In *Fossaria*, growth was negatively affected by density and by *P. antipodarum* but not by conspecifics. Reproduction in this species was not affected at all. In contrast, growth of *P. antipodarum* was only affected by density and there was no difference in growth between the intraspecific and interspecific competition treatments. Similar to *Fossaria*, reproduction in *P. antipodarum* was not significantly affected by the experimental conditions. These results suggest that *P. antipodarum* is the stronger competitor. This asymmetrical relationship actually suggests that the interaction between the two species might best be described as amensal (Begon *et al.* 1990). Competition involves two species that have negative effects on each other. Inconsistent with this definition, *P. antipodarum* has a negative effect on *Fossaria*, but *Fossaria* does not have a significantly negative effect on *P. antipodarum*. An asymmetrical

relationship was also found between *P. antipodarum* and *P. robusta* (Riley *et al.* in review).

Regardless of whether the interspecific interaction is best termed competition or amensalism, in an experimental setting, *P. antipodarum* had a negative effect on the growth of the native snail, *Fossaria*. The reduction in growth of the native *Fossaria* can lead to reduced population sizes, eventual population declines and possibly local extirpation. If these demographic consequences are not severe, the decrease in fitness of the native caused by reduced growth might lead to selection. For example, selection might favor traits in *Fossaria* that reduce the overlap in resource use. With sufficient genetic variation and time, this selection can result in evolutionary change in heritable traits. Alternatively, if competition causes age-specific mortality, it might lead to evolution in life-history traits. The possibility that invasive species can have an evolutionary impact within native communities has often been neglected (Sakai *et al.* 2001).

| A. <i>Fossaria</i> | | | |
|------------------------|---------|-----------|-------------------|
| Competition treatment | Density | replicate | Reproductive rate |
| Intraspecific | Low | 1 | 4.57 |
| Intraspecific | Low | 2 | 3.07 |
| Intraspecific | High | 1 | 0.48 |
| Intraspecific | High | 2 | 0.48 |
| Interspecific | Low | 1 | 3.08 |
| Interspecific | Low | 2 | 8.40 |
| Interspecific | High | 1 | 3.00 |
| Interspecific | High | 2 | 8.00 |
| B. <i>Potamopyrgus</i> | | | |
| Competition treatment | Density | replicate | Reproductive rate |
| Intraspecific | Low | 1 | 1.63 |
| Intraspecific | Low | 2 | 1.26 |
| Intraspecific | High | 1 | 1.26 |
| Intraspecific | High | 2 | 2.66 |
| Interspecific | Low | 1 | 2.47 |
| Interspecific | Low | 2 | 2.76 |
| Interspecific | High | 1 | 0.57 |
| Interspecific | High | 2 | 1.67 |

Table 4. Reproductive rate for each replicate in each treatment. The rate of reproduction in each chamber was calculated as $o / (r - m)$, where o is the total number of offspring (juvenile *P. antipodarum*, and juvenile and egg masses of *Fossaria*) in each replicate, r is the total number of reproductive adults, and m is the total mortality of the target species in each container.

The reduction in growth in the native species most likely resulted from exploitative competition for algal resources. Both of these species consume periphyton and periphyton-covered rocks were the only resource available to the snails in the experimental chambers. The data on chlorophyll *a* will indicate whether competition occurred over resources.

Whether or not exploitative competition is also occurring in the natural environment depends on whether aquatic algivores are typically limited by the abundance of periphyton. Although we do not have these data, several pieces of evidence suggest that algivores probably are limited by the abundance of periphyton. First, several studies have shown that *P. antipodarum* significantly reduce the biomass of periphyton in experimental conditions (Riley *et al.* in review, Winterbourn and Fegley, 1989). Second, Kolher and Wiley (1997) showed that population sizes of many aquatic insect taxa were maintained at low levels because of limited periphyton. Third, several studies have suggested that growth of benthic algivores is limited by algal abundance (reviewed by Lamberti 1996). Therefore, while individual streams may vary, it is likely that periphyton is a limiting resource and hence competition over periphyton limits growth and population size of aquatic grazing species.

These results verify that the mud snail invasion should be a concern to biologists and managers. This and other studies (Riley *et al.* in review) suggest that the mudsnail is having a negative effect on native species. These negative impacts could lead to population declines of natives, local extirpation, or an evolutionary response in the natives. Our results also suggest that density dependent effects on growth and reproduction of *P. antipodarum* are much smaller than those of the natives (Tables 2 and 3). These results suggest that *P. antipodarum* is a superior competitor and further spread of this species is unlikely to be halted by competitive interactions with native organisms.

Studies of severe population declines of a strong grazing competitor in streams, showed the importance of competition in both the composition of aquatic benthic communities and the population dynamics of individual species in the communities (Kohler and Wiley 1997). Hence, the strong competitive interactions by *P. antipodarum* in this study, suggest that they too could change the composition of stream communities and population sizes of species in the communities. In addition, reduced fitness in the native snail in the presence of mudsnails also makes evolutionary change in the native species possible. Hence, the impact of the mudsnail on native communities and species is likely to be widespread and detrimental.



LITERATURE CITED

- APHA (American Public Health Association). 1998. Standard methods for the examination of water and wastewater. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, D.C., USA.
- Begon, M., J.L. Harper, and C.R. Townsend, 1990. Ecology: Individuals, Populations, Communities, 2nd edition. Blackwell Scientific Publications, Cambridge, U.S.A.
- Cox, G.W. 2004. Alien Species and Evolution: The evolutionary ecology of exotic plants, animals, microbes, and interacting native species. Island Press, Washington, D.C., USA.
- Gutierrez, A.G. Perera, M. Yong, J. Sanchez, L. Wong. 2000. Life-history traits of *Fossaria cubensis* (Gastropoda: Lymnaeidae) under experimental exposure to *Fasciola hepatica* (Trematoda: Digenea). Mem Inst Oswaldo Cruz, Rio de Janeiro 95: 747-752.
- Hall, R.O. Jr., J.L. Tank, 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., M.F. Dybdahl, and M.C. VanderLoop. 2006. Invasive species and energy flow: Extremely high secondary production of introduced snails in rivers. *Ecological Applications*. In Press
- Jokela, J. and C.M. Lively. 1995. Parasites, sex, and early reproduction in a mixed population of freshwater snails. *Evolution* 49: 1268-1271.
- 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. *J.N. Am. Benthol. Soc.* 24:123-138.
- Kohler, S.L. and M.J. Wiley. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78:2164-2176.
- Lamberti, G.A. 1996. The role of periphyton in benthic food webs. In *Algal Ecology: Freshwater Benthic Ecosystems* (Stevenson, R.J., Bothwell, M.L. and Lowe, R.L. eds). Academic Press, San Diego, USA.
- 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.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Reznick, D.N. and C.K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112-113:183-198.
- Riley, L.A., M.F. Dybdahl, R.O. Hall, Jr. *in review*. Grazing and competition interaction strengths match patterns of introduced species dominance. *Biological Invasions*.
- Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, S.G. Weller. 2001. The Population Biology of Invasive Species. *Annu. Rev. Ecol. Syst.* 32:305-32.
- Strauss, S.Y., J.A. Lau, and S.P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 9:357-374.
- Winterbourn, M.J. and A. Fegley. 1989. Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, south island streams. *New Zealand Natural Sciences* 16:57-65