INTERACTIONS BETWEEN THE INVASIVE NEW ZEALAND MUD SNAIL, *POTAMOPYRGUS ANTIPODARUM,* BAETID MAYFLIES, AND FISH PREDATORS

by

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Chelsea Ann Cada
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ABSTRACT

The nonindigenous gastropod *Potamopyrgus antipodarum* is quickly spreading through aquatic environments in the western United States, and populations often occur at very high densities. In previous studies, densities of baetid mayflies were lower in reaches with high densities of *Potamopyrgus* than in reaches with low densities of *Potamopyrgus* in Darlinton Spring Creek (Madison River drainage, Montana, USA), suggesting exploitation or interference competition. To determine when *Potamopyrgus* had the greatest effect on baetids, I quantified densities and biomasses of *Potamopyrgus* and baetids in low-snail and high-snail reaches over 18 months in Darlinton Spring Creek. *Potamopyrgus* had little effect on the densities or biomasses of baetids. Measurement of periphyton biomass at the same times as macroinvertebrate densities indicated that *Potamopyrgus* depressed periphyton biomass.

Using an *in situ* experiment, I quantified intra- and interspecific competition between baetids and *Potamopyrgus* by measuring survivorship and body growth. *Baetis* and *Diphetor* survivorship decreased when combined with *Potamopyrgus*, but there was no effect of interspecific competition on body growth. *Potamopyrgus* survivorship decreased when combined with *Diphetor* or *Baetis,* and *Potamopyrgus* growth was negatively affected by intraspecific competition.

To explore the effects of *Potamopyrgus* on secondary consumers, I compared the diets and growth of *Salmo trutta* and *Cottus bairdi* in an enclosure experiment in reaches with high and low-densities of *Potamopyrgus*. Only one *Potamopyrgus* was found in the stomachs of the fishes, indicating that *Potamopyrgus* was not an important food source. There were no differences in growth for either fish species between high-snail and low-snail reaches. Additionally, there was little evidence suggesting that these fishes shifted their diets to compensate for changes in food availability associated with high densities of *Potamopyrgus*.

My results indicated that *Potamopyrgus* and baetids competed in the experiments; however, the effects of competition were not evident in the field surveys even though *Potamopyrgus* depressed periphyton biomass. Additionally, fishes were not negatively affected by *Potamopyrgus*. During my studies, *Potamopyrgus* densities were moderate. Thus, moderate densities of this invader may not have a large effect on communities. I caution against interpreting these results to mean that *Potamopyrgus* will not have effects in other aquatic systems.

CHAPTER 1

INTRODUCTION

Invasive species pose one of the largest threats to biodiversity, second only to habitat destruction (Baskin 1998) by causing endangerment or extinction of native species (Coblentz 1990, Jenkins 1996). Invasive species threaten the integrity of ecosystems by altering interactions at various levels of biological scale from species interactions and population dynamics to community dynamics (e.g., competition, shifts in taxa richness or functional dominance), to ecosystem dynamics (e.g., nutrient cycles, primary and secondary production, and trophic interactions) (Vander Zanden et al. 1999, Crooks 2002).

Not only do biological invasions threaten the quality and biodiversity of terrestrial and aquatic ecosystems, but they can also negatively affect industries such as agriculture, tourism and outdoor recreation (e.g., fly-fishing in Montana) and result in serious economic loss. Fly-fishing retail (not including additional inputs from tourism such as hotel, food, etc) in the Bozeman area generates approximately $3.5 million annually (The River's Edge, Bozeman, MT), and may be adversely affected by the changes in lotic systems caused by invasive species such as *Myxobolus cerebralis* (the "whirling disease" parasite) and *Potamopyrgus antipodarum*, the New Zealand Mud Snail. Furthermore, local agencies, recreational groups, and the general public express concern about the potential effects of invasive species on aquatic ecosystems.

Interactions between an invasive species and the invaded ecosystem merit scientific attention for several reasons. Understanding these interactions increases knowledge that is useful for controlling, managing, preventing and even predicting invasions (Kolar and Lodge 2001). For example, invasion success of a competitor may depend upon its relative abilities to convert resources to growth (Byers 2000) or to compete in human-disturbed environments (Petren and Case 1996). Furthermore, an invasive species may have characteristics that suggest it will have a strong effect in an invaded ecosystem (e.g., occupying a niche previously unoccupied in the environment, Simon and Townsend 2003). Therefore, information regarding invasive species' interactions, effects, and success in an invaded system can suggest which species or communities are more vulnerable to species invasions. Finally, species invasions provide an opportunity to examine and better understand important ecological interactions such as competition (Coblentz 1990).

Because invasive species are known to compete with and change population distribution and abundance of native or resident organisms (Shigesada and Kawasaki 1997, Mooney and Cleland 2001), it is reasonable to hypothesize that an invasive gastropod such as *Potamopyrgus antipodarum* will compete with native herbivores. Additionally, gastropods can exert strong influences on benthic communities through grazing of periphyton assemblages. Gastropod grazers often strongly compete with other snail species (Fenchel 1976, Underwood 1978, 1984, Schmitt 1996) as well as with other herbivorous macroinvertebrates (Hill 1992). Furthermore, biological attributes of *Potamopyrgus* suggest it could exert a strong competitive effect upon macroinvertebrate populations. Thus, exploration of competitive interactions between *Potamopyrgus* and macroinvertebrates and the consequences for trophic dynamics will provide necessary information to understand the effects of *Potamopyrgus* on species interactions, trophic dynamics and ultimately, ecosystem function.

In this master's thesis, I determined how an invasive species, *Potamopyrgus antipodarum*, affected mayflies (Baetidae) and how these effects changed temporally using field surveys and experimental manipulations. Additionally, I explored the potential effects of *Potamopyrgus* establishment on the diet and growth of the introduced brown trout (*Salmo trutta*) and the native mottled sculpin (*Cottus bairdi*).

CHAPTER 2

BACKGROUND

Competition between invasive and native species

Concern about competitive interactions between invasive and resident species arises from the possibility that invasive species are superior competitors (Byers 2000), causing population reduction or displacement of resident species. For example, an introduced gastropod reduced the abundance and changed the distribution of a native mud snail through exploitation competition (Byers 2000). Exploitative competition with an introduced gecko caused displacement of a native gecko through decreased fecundity and survivorship (Petren and Case 1996). Competitive interactions with invaders are also suggested to be the mechanism of decreased abundances of native ants (Holway 1999), native sunfish (*Lepomis gibbosus*, Huckins et al. 2000), native crayfish (Hill and Lodge 1999), and native galaxiid fishes (Flecker and Townsend 1994). Consequently, *Potamopyrgus antipodarum* has the potential to cause profound effects on biota in aquatic systems through competitive interactions.

The outcome of competitive interactions in lotic systems may not be straightforward because the levels of patchiness and variability characteristic of streams may promote coexistence of invasive and resident competitors rather than allow competitive exclusion of an entire population or species. Competition theory suggests that environmental variation (e.g., temporal or spatial) often allows the coexistence of competitors (Chesson 1985). According to Lehman and Tilman (1997), coexistence in a patchy environment occurs because no competitor can occupy all sites at any one time.

Thus, two species might experience local exclusion with regional coexistence in a spatially dynamic environment. Conversely, temporal variability in competitive interactions may cause “ecological crunches” during certain times that have a strong influence on populations even after competitive interactions decrease or cease (Wiens 1977).

Relatively few studies have examined the variability in competitive interactions (Cedeno-Leon and Thomas 1982) and the combination of current theory with real-world dynamics remains in its “infancy” (Roos and Sabelis 1995). Even so, examining competition among various habitats or time periods provides ecologists with much more insight than studies examining one particular time or place (Fletcher and Underwood 1987). Indeed, studies focusing on a particular time or place can lead to conclusions and applications of information beyond the scope in which the hypotheses were tested. For example, intensity of competitive interactions between grazing mayflies and *Glossosoma* caddisflies may change as a function of stream flow due to changing grazing efficiency of *Glossosoma* (Kuhara et al. 2000). If competitive interactions for these species were examined at only flow level, the authors would have made an incomplete or even incorrect conclusion about the dynamics of these species interactions.

Temporal variation in competitive interactions among aquatic biota could occur within an organism’s life cycle, among seasons, or among years. For example, when intraspecific competition between larval stoneflies occurred during early-instar stages, per capita growth was negatively affected, but competition between last-instar individuals did not affect body size because stonefly feeding decreased as they approached emergence (Peckarsky and Cowan 1991). Additionally, larval body-size in stoneflies directly correlates with female fecundity: small larvae may have low fecundity as adults (Peckarsky and Cowan 1991). Thus, the consequences of competitive interactions for stonefly populations might depend upon the timing of interactions within the life cycle. In another example, Wissinger (1989) showed that intraspecific competition among larval odonates decreased growth during spring months but not during autumn months, which was probably due to seasonal variation in resource abundance. However, it was not clear how the seasonal variation in competitive interactions among larvae affected odonate reproductive capability and population dynamics. Environmental variation among longer time periods (e.g., annual) can also influence the strength and occurrence of competitive interactions, which has implications for how community structure changes over time (e.g., for sessile invertebrates like barnacles and mussels) (Lively et al. 1993).

Designing competition studies

Competition is often suggested as the causal mechanism behind abundance and distributional patterns that scientists observe in nature (Leff et al. 1990, Ricklefs and Miller 2000). However, these conclusions are often reached by inference based on correlative data from which causation cannot be determined (e.g., Cedeno-Leon and Thomas 1982, Feminella and Resh 1991, Huckins et al. 2000), Reynoldson and Bellamy (1971) developed five criteria that should be met to confirm that interspecific exploitation competition occurs in a particular circumstance: 1) indirect evidence of resource limitation; 2) indirect evidence for intraspecific competition; 3) patterns of potentially competing species that suggest interspecific competition; 4) direct evidence from controlled experiments of resource limitation and intraspecific competition; 5) direct evidence of interspecific competition from controlled experiments.

Common patterns that suggest competition include non-overlapping distributions of ecologically similar species and lower abundance of competitors where they exist together compared to where they exist separately (Connell 1961, McAuliffe 1984, Byers 2000). Field studies are important component of investigations on competition because they indicate whether competitive interactions influence distribution and abundance of natural populations. However, field studies only satisfy the first three of Reynoldson and Bellamy's (1971) criteria and are limited in their ability to support hypotheses of competitive interactions. For example, predator-prey interactions can result in patterns consistent with competition called "apparent competition" (Holt 1977, Schmitt 1987). This indicates that alternate hypotheses also need exploration when studying competition through field studies and that field studies do not determine the causal mechanisms behind patterns (Miller 1986).

The two additional methods for studying competition, field and laboratory experiments, involve manipulations of one or more variable(s) while others are held constant. These methods provide direct evidence for competition and consequently satisfy the last two criteria recommended by Reynoldson and Bellamy (1971). Experiments can provide the strongest evidence that competition occurs because they have the ability to limit confounding variables and manipulate target variables. Consequently, they allow the exclusion of alternate explanations for results and observed patterns. Additionally, experiments allow the testing of specific hypotheses about the nature of the competitive interactions. For example, the manipulation of multiple density combinations between competitors makes it possible to compare the strengths of intraspecific and interspecific competition (Kohler 1992). Experiments also allow comparisons of competitive ability between taxa or of variation in competition intensity over time or space (Goldberg and Scheiner 2001).

Laboratory experiments conducted in micro- or mesocosms are typically criticized for their lack of applicability to the natural environment. For example, laboratory experiments often hold temperature constant, which does not reflect the diel changes in water temperatures of streams. Field experiments do not necessarily provide better information than laboratory experiments because they do not always achieve isolation of confounding variables (Miller 1986). Experiments are also limited in application for the same reasons that they are so insightful: the simplified environment that eliminates confounding variables does not reflect the characteristics of a natural community. So, when seeking evidence of competitive interactions, a combination of experimental and observational approaches offers the best of both worlds (Miller 1986) by providing evidence that competition occurs in the natural environment and more rigorously testing hypotheses about the nature of the competitive interactions.

Design of competition experiments often falls under one of three basic treatment arrays: substitutive, additive or response-surface (Goldberg and Scheiner 2001, Inouye 2001). *Substitutive designs* maintain the same total density while replacing individuals of species A with those of species B. Substitutive experiments are limited in the scope of hypotheses that can be tested. Specifically, this design can only test the relative intensities of inter- and intraspecific competition (Goldberg and Scheiner 2001, Inouye 2001). *Additive designs* manipulate only the density of the associate species to determine its effect on the target species. Consequently, additive designs do not allow determination of the effects of competition on both species nor do they allow separation of intra- and interspecific competition. Even so, additive designs are often used in studies of competition (Inouye 2001). *Response-surface* designs manipulate densities of both the target and associate species for several different densities and are thus the ideal design for two-species interactions (Inouye 2001). They allow distinction between intra- and interspecific competition and make it possible to examine the effects on both species. Furthermore, response-surface arrays can provide the data needed for parameter estimation and population modeling (Inouye 2001). When one desires to estimate model parameters, Inouye (2001) suggests using a wide range of density treatments including those above carrying capacity and those at very low densities because a wider range provides more accurate estimation of population parameters. Unfortunately, response-surface arrays require a larger number of density treatments than additive or substitutive designs, which makes them more difficult to execute (Inouye 2001).

Extrapolating experiments to the environment

Experimental and observational results do not always agree. One problem with extrapolating results from an experiment to the natural environment is the confounding influence of scale, both spatial and temporal (Wiens 1989). In streams, factors operating at a large spatial scale (e.g., geology) may overwhelm the importance of small-scale factors (e.g., individual behavior) for population or community dynamics (Peckarsky et al. 1997). Similarly, effects of interactions observed in experiments on a relatively small spatial scale do not always “scale-up” in the direction or the magnitude of the interaction to a larger spatial scale (i.e., stream or drainage) (Thrush et al. 1997), again suggesting that large-scale processes can overwhelm the importance of small-scale interactions. Even in the case of strong competitive interactions among individuals, the effects at the community level can be weak (Pacala and Levin 1997), but “weak interactors” (sensu Berlow 1999) may play an important role in community structure by increasing variation among patches in time and space and promoting coexistence of species (Berlow 1999). Consequently, strong competitive effects observed locally in a field study or experiment might have little influence on the overall abundance or distribution of the populations. For example, I might observe strong competitive effects on the response variables in my experiments, but I might not observe any effect, or the same magnitude or direction of an effect in my field study.

Extrapolation of results from an experiment to the population or community level may also be affected by species interactions (Billick and Case 1994). Competition between two species in an enclosure experiment eliminates the interactions of other species in that community (“higher-order interactions,” Neill 1974, Case and Bender 1981) or can prevent density-dependent dispersal of competitors. For example, the extrapolation of predator-prey interactions from microcosm experiments to population distribution and abundance often did not predict observed patterns in nature (McIntosh et al. 2002). Furthermore, life history attributes may confound extrapolation from small-scale experiments because they can influence the effects of competitive interactions for stream insects. More specifically, species with short adult stages experience greater population-level consequences of larval interactions than species with longer adult stages (McPeek and Peckarsky 1998). Species with longer adult stages that typically feed as an adult (e.g., Trichoptera, Plectoptera) may be able to compensate as adults for competitive effects that occurred during the larval stage (e.g., size at emergence, biomass, fat content). Furthermore, resource allocation to reproduction may not occur until the adult stage (Thorp and Covich 1991) with the potential result that competitive interactions as larvae would not affect adult fecundity. Conversely, species with short adult stages (e.g., Ephemeroptera) and with adults that do not feed cannot compensate for competitive effects that occurred during larval stages when an adult. Furthermore, mayflies primarily develop ova as larvae (Needham et al. 1935), so that competitive interactions as a larvae may decrease fecundity. Since baetid mayflies have short adult stages lasting only days to a few weeks (Merritt and Cummins 1996) and do not feed as adults, competitive interactions with *P. antipodarum* as a larvae are more likely to influence mayfly population dynamics than taxa with longer-lived adult stages.

Invasive and competitive characters of *Potamopyrgus antipodarum*

The New Zealand Mud Snail, *Potamopyrgus antipodarum* (Gray, 1843), synonymous with *Potamopyrgus jenkinsi* (Winterbourn 1970a), has invaded many freshwater and brackish ecosystems in Europe (Bondesen and Kaiser 1949, Ribi and Arter 1986, Strzelec and Krodkeiwska 1994, Cunha and Moreira 1995), Australia (Schreiber et al. 1998) and the United States (Bowler 1991, Zaranko et al. 1997) including the Madison River drainage in southwestern Montana (Kerans et al. in press)

(Fig. 2.1). *Potamopyrgus antipodarum* inhabits a wide range of habitat types including fresh and brackish waters (Winterbourn 1970a) in lotic and lentic habitats (Dorgelo 1987, Talbot and Ward 1987, Bowler 1991) and is thus likely to invade a wide range of aquatic systems in the United States. However, systems with extreme environmental stability may not allow coexistence or high densities of *Potamopyrgus* (Death 1991) because it may be a poor competitor in comparison with other New Zealand macroinvertebrates, leading to competitive exclusion in a stable environment. Similarly, severely instable environments may preclude successful populations of *Potamopyrgus* because frequent flood events in an unstable environment cause high mortality (80%) of *Potamopyrgus* (Holomuzki and Biggs 2000), which may prevent populations from reaching high densities.

Figure 2.1. The known distribution of *Potamopyrgus antipodarum* (a) (indicated by grey dots) in the western United States as of July 1, 2004 courtesy of D. L. Gustafson, Montana State University, from http://www.esg.montana.edu/cgi-bin/aimmap. The dotted oval indicates the location of the Madison River drainage (b). The arrow indicates the location of the study site, Darlinton Spring Creek, which is shown in (c). The plus signs in (c) indicate reaches with high densities of *Potamopyrgus* (also numbered 1 and 2) and reaches with low densities of *Potamopyrgus* (numbered 4 and 5); the diagonal arrows in (c) indicate the direction of water flow.

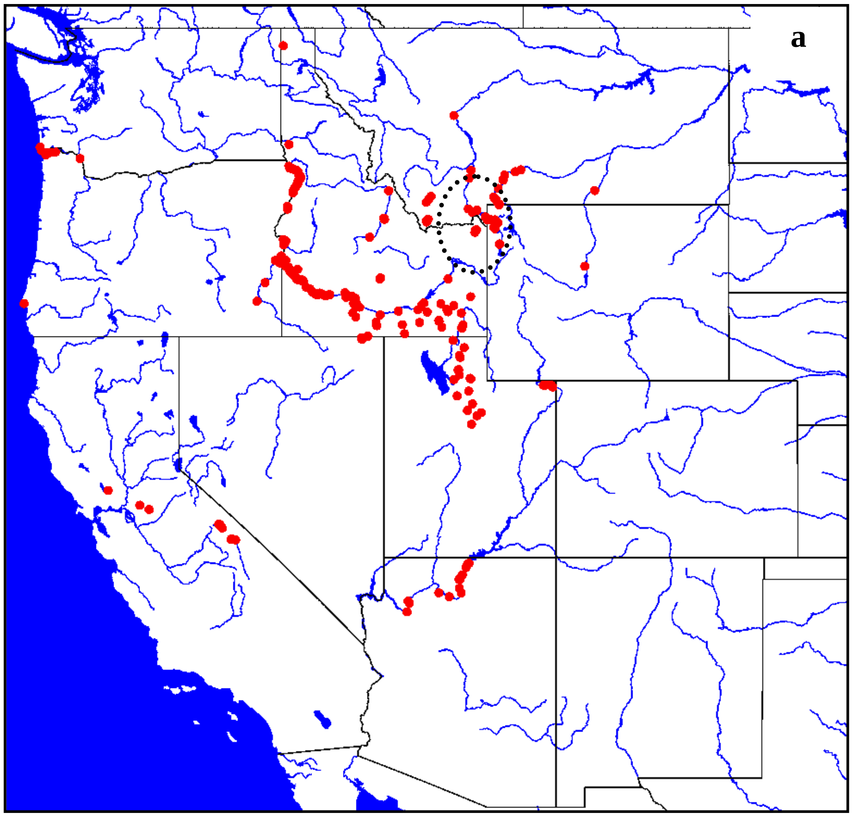
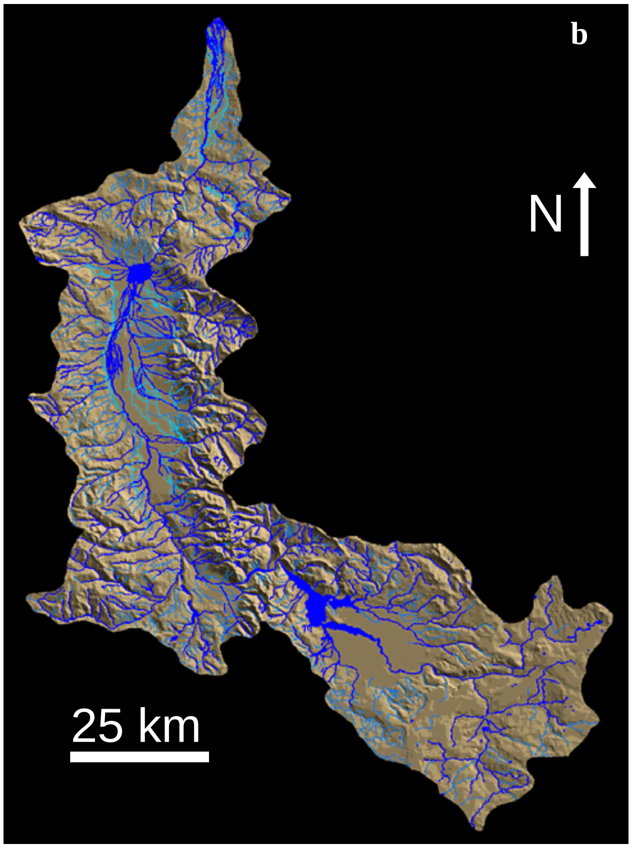
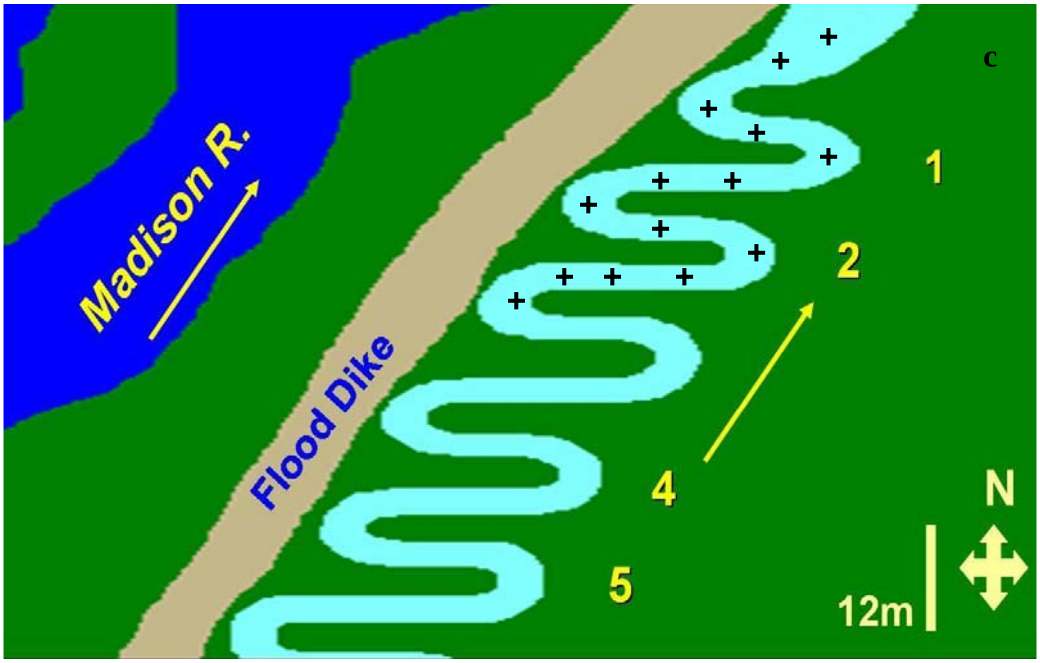


Figure 2.1 continued





Several biological attributes of *P. antipodarum* suggest the nature and magnitude of its potential effects on invaded systems. First, invasive populations of *P. antipodarum* often exist at very high densities: 43,000 to 800,000 individuals m^{-2} (Heywood and Edwards 1962, Dorgelo 1987, Hall et al. 2003). In the Madison River drainage within Yellowstone National Park, Kerans et al. (in press) found mean densities greater than 200,000 m^{-2}. Mean densities in invaded reaches of the study site examined in this thesis, Darlinton Spring Creek (Fig 2.1), range from 8,864 m^{-2} to 27,996 m^{-2} in spring 2001 and autumn 2000, respectively (Cada and Kerans, in preparation). In comparison, *P. antipodarum* densities ranged from eight to twenty-nine times greater than densities of baetid mayflies in the same location (Cada and Kerans, in preparation). Thus, dense populations will occupy a large area of habitat, reducing the area that could be occupied by other taxa and increasing the probability of agonistic encounters.

Second, gastropods eat periphyton and detritus, and thus their diet overlaps with the diets of many common macroinvertebrate taxa (Cummins and Klug 1979, Thorp and Covich 1991). According to Haynes and Taylor (1984), *P. antipodarum* prefers plant and animal detritus but often grazes green algae and diatoms. Additionally, Dorgelo et al. (1995) reported highest growth rates of *P. antipodarum* when its diet included plant and animal material. In general, gastropods are known to interact strongly with periphyton, often controlling biomass in aquatic systems or altering physiognomic characteristics of the algal community (Lamberti et al. 1989).

Third, like other invasive species (Mack et al. 2000, Grewal et al. 2002), *P. antipodarum* may be released from predation and parasitism when nonindigenous.

Several species of trematode larvae commonly parasitize P. *antipodarum* in New Zealand, which results in sterilization and “genetic death” (Jokela and Lively 1995, Fox et al. 1996). It is unknown whether any of these parasites invaded with *P. antipodarum* or whether any North American parasite fauna cause similar effects. Known natural predators of *P. antipodarum* include dabbling ducks (Krist et al. 2000, Jokela et al. 1999) and bullies, (fishes of the genus *Gobiomorphus*) (Levri 1998, Winterbourn 1970b). However, the extent to which *P. antipodarum* provides a useable and important food source for these various predators and the degree to which *P. antipodarum* populations are controlled by predators has not been studied. Natural predators that coevolved with *P. antipodarum* are not present in Montana and consequently cannot exert control over *P. antipodarum* populations.

Finally, the reproductive biology of *P. antipodarum* makes it easy for this invasive species to invade and establish new populations. Invasive populations are almost entirely clonal females (<1% are male) (D. Gustafson, Montana State University, unpublished data) and reproduction occurs via parthenogenesis (Fox et al. 1996). Consequently, a new population can easily become established. Additionally, reproduction occurs quickly and females produce large broods of offspring. Under laboratory conditions, reproductive capability is reached in about six months (2.5 to 3.5mm in length), and juveniles are subsequently born at three-month intervals (Winterbourn 1970b, Richards and Lester 2000). Unlike most gastropods, *P. antipodarum* is ovoviviparous, embryos develop in an internal brood pouch, and females bear live young (Winterbourn 1970a). The number of embryos per female varies seasonally, typically peaking in spring months (Schreiber et al. 1998), and depends upon female size but can range from 60-120 (Winterbourn 1970b, Strzelec and Serafinski 1996, Richards and Lester 2000).

Preliminary field studies on *P. antipodarum* and macroinvertebrates

A study of the macroinvertebrate assemblages in Darlinton Spring Creek (Fig. 2.1) suggested that *P. antipodarum* negatively affected the densities of resident macroinvertebrates in autumn but not in spring (Cada and Kerans, in preparation). Baetid mayflies were among the taxa exhibiting the largest decrease in density between reaches with low and high densities of *Potamopyrgus* in November 2000. Cada and Kerans hypothesized that this was due to competitive interactions between *Potamopyrgus* and baetids. Additionally, periphyton biomass was lower in reaches with high densities of *Potamopyrgus* compared with reaches containing low densities of *Potamopyrgus*, indicating an effect of *Potamopyrgus* on periphyton resources and the possibility of resource limitation. However, the negative association between baetids and *Potamopyrgus* was observed in only one of two time periods, suggesting that competitive interactions varied on a temporal basis.

Biology and ecology of baetid mayflies

Five species of Baetidae are known to inhabit Darlinton Ditch: *Baetis tricaudatis*, *Acerpenna pygmaeus*, *Diphetor hageni*, *Plauditus punctiventris,* and *Callibaetis* sp. (D.L. Gustafson, pers. comm.). The genus *Baetis* is well studied in comparison with other genera (Merritt and Cummins 1996) and is abundant in Darlinton Spring Creek (Cada and Kerans, in preparation). Because of its feeding ecology and decreased abundance when sympatric with *P. antipodarum*, *Baetis* has a high potential for competitive interactions with *P. antipodarum*. Additionally, the wealth of published knowledge and the widespread distribution of *Baetis* spp. within North America indicated that the results of my study could be applicable in many geographical locations.

Baetis spp. (Insecta: Ephemeroptera: Baetidae) are ubiquitous and abundant in many North American stream ecosystems (Merritt and Cummins 1996). As grazers, they can strongly depress periphyton biomass and alter periphyton physiognomy (Hill and Knight 1987). Baetid mayflies provide food for stream predators such as stoneflies (Perlodidae) (Peckarsky and Cowan 1991, Kerans et al. 1995), benthic-feeding sculpins and drift-feeding trout (Allan 1978, Forrester 1994, Miyasaka and Nakano 2001).

Baetis spp. feed on epilithic periphyton, especially those diatoms tightly adhered to the substrate's surface (Mullholland et al. 2000). However, they tend to act as generalist herbivores, in that they collect periphyton by both scraping and gathering methods (Merrit and Cummins 1996). *Baetis* spp. can graze periphyton to very low levels, and other species in the same family can decrease periphyton biomass by five times its original biomass and change the physiognomy of periphyton forms (Hill and Knight 1987). However, *Baetis* typically leave the substrate and enter the drift when food availability becomes "low" (Kohler 1985), which is often before other species (e.g., *Glossosoma*) leave in search of food (Kohler 1992).

During long summers, *Baetis* spp. can complete two life cycles within a year (bivoltine): a quick-growing summer generation with emergence in August or September and a slow-growing over-wintering generation (possibly diapausing as eggs; Thorp and

Covich 1991) with spring emergence. Mayflies are hemimetabolous (egg-larvae-adult) insects with an indeterminate number of larval instars (Thorp and Covich 1991). Larvae emerge as subimagos before molting into the adult imago stage and live only a few days to a few weeks (Thorp and Covich 1991). Adults do not feed (Thorp and Covich 1991), and consequently, size at emergence directly correlates to fecundity of females (Hinterleitner-Anderson et al. 1992, McPeek and Peckarsky 1998). Mating occurs in swarms (Thorp and Covich 1991). Oviposition by *Baetis* occurs by crawling from the emergent surface of a rock to its submerged surface where it lays fan-shaped masses of eggs (Encalada and Peckarsky 2002).

Many Ephemeroptera species compete intra- and interspecifically (Hill and Knight 1987, Kohler 1992, Kuhara et al. 2000), indicating that competition between *P. antipodarum* and baetids is likely to occur. For example, growth of *Ameletus validus* decreases by one-third to one-half due to intraspecific competition (Hill and Knight 1987). Intraspecific competition of *Baetis* spp. resulted in low survivorship and decreased growth (34.7% less than expected), and interspecific interactions with a grazing caddisfly, *Glossosoma*, affected growth (25% decrease) but not survivorship (Kohler 1992). *Baetis* was also subject to interference competition with a sessile, territorial caddisfly, *Leucotrichia*, and responded to agonistic encounters by quickly leaving the substrate (McAuliffe 1984).

Trophic interactions

In addition to interacting competitively with taxa in the same trophic level, *P. antipodarum,* like many invasive species, is likely to cause changes in other trophic levels (Strayer et al. 1999, Vander Zanden et al. 1999). One possible change in the food web may occur through interactions with primary producers, especially periphyton. Stream grazers, especially gastropods, can be powerful controllers of periphyton biomass and can alter algae physiognomy (Feminella and Resh 1991, Lamberti 1996). For example, snail grazing reduced the relative abundance of erect and loosely-attached algae but increased that of adnate diatoms (Lamberti et al. 1989). Similarly, snail grazing slowed the accumulation of algal biomass (Lamberti et al. 1989) and caddisfly grazers maintained algal biomass at low levels even in early autumn (Feminella and Resh 1991). Indeed, periphyton biomass was 32% lower even at relatively low densities of *Potamopyrgus* (i.e., >50,000m^{-2}) (Cada and Kerans, in preparation). However, grazing in streams can also stimulate primary production by removing senescent layers and increasing photo-exposure of the underlying algae (Lamberti and Feminella 1996, Allan 1995). Furthermore, competitive interactions between two grazers alter their effects on the algal assemblage: exploitative competition results in further depression of periphyton biomass (Schmitt 1996, Byers 2000), whereas interference competition decreases depression of periphyton biomass (Kerans et al. 2002).

Potamopyrgus may also interact with the secondary-consumer trophic level, especially with benthic and drift feeding fishes such as sculpin and trout. Although *Potamopyrgus* almost certainly provides a food resource for native fishes such as *Gobiomorphys* spp. (Levri 1998), as well as nonnative species such as *Anguilla* spp. (Ryan 1982) in New Zealand, the role of *Potamopyrgus* as a prey item in western U.S. streams is unclear. *Potamopyrgus* may be a poor quality food resource for many fishes because the operculum seals the shell aperture (Winterbourn 1970a, 1970b), which prevents digestive fluids from acting on tissue. For example, *Potamopyrgus* survived six hours in the digestive system of rainbow trout, *Oncorhynchus mykiss,* and subsequently birthed live young (Haynes et al. 1985). However, trout with extended gut-retention time may be able to digest through the shell and assimilate nutrition and energy from *Potamopyrgus.* Furthermore, it is unclear whether salmonids consistently feed on *Potamopyrgus* (Winterbourn 1970b, Sagar and Glova 1995, Levri 1998, Wells and Clayton 2001, W.P. Dwyer, USFWS, personal communication). Feeding on *Potamopyrgus* could reduce energy assimilation in an individual's diet, negatively affecting body growth and allocation of resources to reproduction. Despite predator avoidance tactics (e.g. behavioral modification of foraging in presence of fish chemicals; Levri 1998), *Potamopyrgus* is available as a food resource for trout in lotic systems because of its propensity to drift when disturbed (personal observation).

Indirectly, *Potamopyrgus* may interact with secondary consumers that rely on macroinvertebrates as a food source. That is, interference and exploitative competition between *Potamopyrgus* and other macroinvertebrates can reduce the density of macroinvertebrates during certain times of the year (Cada and Kerans, in preparation), which may limit food availability for secondary consumers. Consequently, secondary consumers may experience reduced growth and fecundity when *Potamopyrgus* does not function as a quality food resource.

Clearly, *Potamopyrgus* has the potential to interact with several trophic levels. Moreover, effects at one trophic level can propagate both directly and indirectly through a food-web. Trophic cascades (Paine 1980) or tri-trophic interactions (Price et al. 1980) as a result of species invasions are well documented (Mooney and Cleland 2001). For instance, the establishment of the zebra mussel, *Dreissena polymorpha,* caused decreased abundance of planktivorous filtering communities, increased abundance of detritivorous collecting communities, and even affected fish population sizes in the Hudson Bay ecosystem (Strayer et al. 1999, Strayer 1998). Flecker and Townsend (1994) reported that the displacement of the native galaxiids by brown trout (*Salmo trutta*) in New Zealand caused top-down trophic effects including decreased insect density and increased algal biomass. Consequently, the effects of *Potamopyrgus* on primary producers or primary and secondary consumers may propagate through the food-web.

Thesis goals

To further explore the hypothesis that interactions between *Potamopyrgus* and baetids varied temporally, I quantified macroinvertebrate abundance in reaches with high and low densities of *Potamopyrgus* on a monthly basis for one year. Additionally, to provide stronger evidence for competition and to determine the effects of competition upon fitness-related response variables, I performed controlled experimental manipulations of baetids and *Potamopyrgus*. The results of the field survey and competition experiments are in Chapter 3. To explore the potential effects of *Potamopyrgus* on secondary consumers, I compared the diets and growth of two fish species: *Salmo trutta* and *Cottus bairdi,* in an enclosure experiment in reaches with high-densities and low-densities of *Potamopyrgus*. These results are presented in Chapter 4.

CHAPTER 3

COMPETITIVE INTERACTIONS BETWEEN *POTAMOPYRGUS ANTIPODARUM* AND BAETID MAYFLIES

Introduction

Invasive species[1] often strongly affect resident species[2] and may cause extensive ecological changes through a wide array of species interactions. For example, competition between invaders and residents often limits the distribution and reduces the abundance of the resident species (Petren and Case 1996, Byers 2000, Huckins et al. 2000). In addition, invasive predators, through the threat of predation, may alter habitat use and suppress individual growth and reproduction of a resident species (Fraser and Gilliam 1992). Both of these types of species interactions can lead to extirpation or extinction of a resident species. While much attention focuses on the deleterious effects of invasive species, some may actually facilitate resident species, often through indirect species interactions. Indeed, invasions have even resulted in increased species richness (Hutchison 1989, Strayer et al. 1999). Finally, combined interactions from a set of invasive species may be multiplicative, not additive, which can lead to an "invasional meltdown" of an ecological system (Simberloff and Von Holle 1999). Because of the myriad of potential interactions between resident and invasive species or among several

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[1] Using the definition of Kolar and Lodge (2001), an invasive species is a nonindigenous species that spreads from the point of introduction and becomes abundant.
[3] A resident species is one that lives in its natural or historical range and zone of dispersal.

invasive species, understanding the effects of invasive species on aquatic ecosystems is complex.

Ideally, scientists and resource managers need to predict the effects of a particular invasive species in their systems. However, an accepted framework to predict the outcome and consequences of particular invasions has not yet emerged (Heger and Trepl 2003, Peterson and Fausch 2003). In part, this is due to gaps in knowledge about species interactions in population and community dynamics. Focusing on understanding the mechanisms by which a particular invasive species has an effect, especially across multiple habitat types and ecosystems, should increase our ability to predict the success of a species introduction in a new location (Peterson and Fausch 2003, Ricciardi 2003). Additionally, by quantifying the strength of interactions between an invasive and resident species (i.e., the per capita effect of the invasive species on the survival, growth or fecundity of a resident species), knowledge is gained about the magnitude of effect caused by that species, which should also increase our ability to predict the success of an introduction into a new location.

An additional challenge to synthesizing a predictive framework for the effects of invasive species originates with the lack of sufficient knowledge about the ecology of invasive species in many taxonomic groups (e.g., gastropods, insects, mammals; Kolar and Lodge 2001). In the case of the invasive species that is the focus of this study, *Potamopyrgus antipodarum* (the New Zealand Mud Snail), little research on its invasion ecology exists (Richards et al. 2001, Schreiber et al. 2002, Schreiber et al. 2003, Kerans et al. in press). Furthermore, only a few invasive species studied are gastropods and little knowledge on the effects of invasive gastropods in freshwater is available.

Despite the lack of research on *P. antipodarum* as an invasive species, predictions about its potential effects can be made based on its biological attributes and knowledge from other species invasions. First, *P. antipodarum* can occupy a wide range of aquatic habitats and tolerates brief removal from water, which suggests it could be easily transported and become broadly distributed throughout the United States (Bondesen and Kaiser 1949, Winterbourn 1970a, Talbot and Ward 1987, Cunha and Moreira 1995, Schreiber et al. 1998). Second, parthenogenetic reproduction (Fox et al. 1996) and high recruitment allows populations to quickly reach high densities. Additionally, invasive species are often abundant due to release from predation and parasitism (Mack et al. 2000, Grewal et al. 2002) and this may indeed be the case for *P. antipodarum*. Trematode parasites (Lively 1992) and native fish or waterfowl predation (Winterbourn 1970b, Sagar and Glova 1995) may control densities of *P. antipodarum* populations in New Zealand, but few fishes may feed on *P. antipodarum* in the intermountain west and few parasitized *P. antipodarum* have been found (Beck et al. 2004), suggesting that non-native populations are not controlled by these mechanisms (but see Gerard et al. 2003). Indeed, *P. antipodarum* reaches very high densities in the western United States. For example, densities exceeded 200,000 m^{-2} in the upper Madison River (Kerans et al. in press) and 800,000 m^{-2} in Polecat Creek, Yellowstone National Park (Hall et al. 2003). Thus, high-density populations, through the occupation of habitat and antagonistic encounters, may cause competition for space with other macroinvertebrates. Third, *P.*

antipodarum shares food resources with many aquatic macroinvertebrates, particularly invertebrate grazers (Cummins and Klug 1979, Haynes and Taylor 1984, Thorp and Covich 1991, Dorgelo et al. 1995), and it seems reasonable to expect it to limit primary food resources when at high densities, which could result in competition for food. Finally, effects of invasive species can propagate through trophic levels (Vander Zanden et al. 1999, Mooney and Cleland 2001), which suggests it may affect predatory invertebrates and fishes.

One aquatic system that may experience strong effects of invasion by *P. antipodarum* is the Madison River drainage in southwestern Montana (Richards et al. 2001). Based upon presence and absence in 8-km units, 46.7% of the Madison River supports populations of *P. antipodarum*, but most of these occur upstream of Hebgen Reservoir (D. Gustafson, Montana State University, unpublished data). Additionally, Kerans et al. (in press) documented a negative correlation between the colonization of macroinvertebrates and the abundance of *P. antipodarum* in field experiments in the Madison River. Furthermore, I documented a general depression of macroinvertebrate densities and periphyton biomass in stream reaches containing high densities of *P. antipodarum* in comparison with reaches containing low densities (Cada and Kerans, in preparation). Mayfly larvae from the family Baetidae, a common taxon that shares food resources with *P. antipodarum*, were among those exhibiting the largest decreases in densities. These patterns of abundance suggest competition between baetids and *P. antipodarum*, possibly by exploitation.

To better understand the observed patterns and the effects this invasive species can have, I investigated the nature and magnitude of interactions between *P. antipodarum,* periphyton, and baetid mayflies. The specific objectives were to: (1) identify times of potential competition between *P. antipodarum* and baetid mayflies by comparing density and biomass of baetids in reaches with high and low densities of *P. antipodarum*, (2) determine whether the life history of baetid mayflies differed between reaches with low and high densities of *P. antipodarum,* (3) determine how grazing by *P. antipodarum* influenced periphyton biomass, (4) determine the relative strength of inter- and intra-specific competition between *P. antipodarum* and baetid mayflies using survivorship and per capita growth rates as measurements of fitness in a response-surface field experiment.

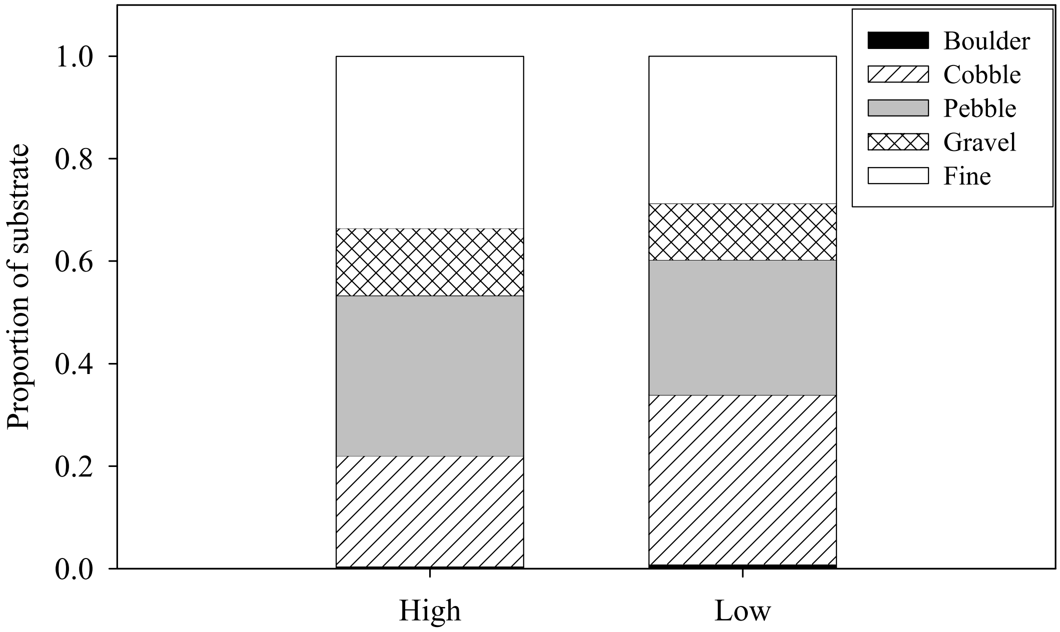
Study Site

I conducted this study in Darlinton Spring Creek at the Montana Fish, Wildlife and Parks Cobblestone fishing access site in south-central Montana, USA (45.8638°N, 111.4947°W) (see Fig. 2.1). Darlinton Spring Creek is an artificial side channel (~18 km length) of the upper Madison River that was created in the form of a borrow-pit in 1948 by the Army Corp of Engineers (Decker-Hess 1989). It carries primarily surfacing groundwater, but base flow is supplemented in the summer months by irrigation water diverted from the Madison River. Darlinton Spring Creek supports typical “spring” creek fauna such as Amphipoda, Decopoda, Diptera, and Ephemeroptera. Mayfly species in the family Baetidae that occur in Darlinton Spring Creek include *Baetis tricaudatis, Diphetor hageni*, *Acerpenna pygmaea, Plauditus punctiventris,* and *Callibaetis* sp (D. L.

Gustafson, Montana State University, personal communication). Resident fishes include *Catostomus commersoni* (white sucker), *Salmo trutta* (brown trout), *Cottus bairdi* (mottled sculpin), *Phoxinus eos* (northern redbelly dace), *Rhinichthys cataractae* (longnose dace), *Pimephales promelas* (fathead minnow), and *Gila atraria* (Utah chub) (Cope et al. 1991). It is bordered on the west by cattle-grazed farmland and the riparian vegetation consists primarily of grasses. Consequently, water can reach high temperatures (20 ºC) in the summer and can change 10 ºC within 24 hrs. In 1982, 0.8 km of the channel was engineered to improve habitat for brown trout, *Salmo trutta,* including construction of meandering reaches of pools and riffles (Decker-Hess 1989). Within these reaches, substrate is primarily cobbles, pebbles and sand (Fig 3.1).

After invasion into Darlinton Spring Creek in the 1990's, *P. antipodarum* spread both downstream and upstream into the engineered reaches (see Fig. 2.1). However, density decreases dramatically as distance from the point of introduction increases. It was therefore possible to sample upstream in "low-density-*Potamopyrgus*" reaches and downstream in "high-density-*Potamopyrgus*" reaches (hereafter referred to as "low-snail" and "high-snail"). The reaches in Darlinton were an ideal location to make comparisons between communities because of the relative homogeneity of habitat and the relatively simple community structure. Indeed, comparison of physicochemical conditions within low-snail and high-snail reaches indicates little difference (Tables 3.1 and 3.2, Fig 3.1).

Figure 3.1 - Comparison of substrate composition between high and low-snail reaches of Darlinton Spring Creek. At each time period, we sampled substrate composition in each reach using a modified (n=50) Wolman pebble count (Wolman 1954). Size classes were boulder (>256 mm), cobble (64-256 mm), pebble (16-64 mm), gravel (2-16 mm), and fine (<2 mm). The data were pooled within snail-treatment and across time.



Methods

Field surveys

I examined the densities and biomasses of *P. antipodarum* and baetids, and periphyton biomass, in low-snail and high-snail reaches to identify time periods when competition potentially occurred. I expected baetid density and biomass and periphyton biomass to be greater in low-snail than in high-snail reaches. Both macroinvertebrate and periphyton samples were collected roughly monthly (April 2002 to May 2003, plus July, August and October 2003) from two downstream high-snail reaches and two upstream low-snail reaches, each reach about 30 m in length.

Table 3.1. Temporal trends in the mean physicochemical conditions in Darlinton Spring Creek indicate little difference between high- (H) and low-snail (L) reaches in 2002 and 2003. I recorded temperature, conductivity, percent dissolved oxygen (%DO), and pH from each reach at each sampling date using a Yellow Springs Instrument (YSI) model 6000X. Missing values are indicated by "---", which resulted primarily from malfunctioning of the YSI.

Sampling date	Temperature (ºC)		Conductivity (mS)		%DO		pH	
	H	L	H	L	H	L	H	L
Apr-02	11	11	0.307	0.306	107.5	118.6	7.7	7.5
Aug-02	21	21	0.271	0.267	126.6	127.5	8.8	8.7
Sep-02	18	18	0.256	0.256	103.5	103.7	8.7	8.8
Oct-02	8	8	0.283	0.282	92.2	91.8	8.2	8.3
Nov-02	9	7	0.281	0.276	98.4	89.9	8.4	8.2
Jan-03	6	5	0.264	0.260	66.1	64.9	8.2	8.4
Feb-03	5	4	0.287	0.253	50.5	48.5	8.2	8.2
Mar-03	8	11	0.282	0.299	41.7	43.6	8.3	8.3
May-03	11	12	0.306	0.343	30.0	68.8	8.4	8.1
Jul-03	21	20	0.249	0.247	132.6	130.8	---	---
Aug-03	22	23	0.275	0.277	139.1	136.7	---	---

Macroinvertebrates.—I sampled *Potamopyrgus* and baetids using cobble samples, which target the grazing community (Kerans et al. 1995). Thirty-two cobbles, 8 per reach with 2 reaches per snail density, were haphazardly taken each sampling date. To reduce loss of organisms due to drift when disturbed, I placed a Surber sampler (132-µm-mesh) downstream of the rock and then gently lifted both in unison from the water (Kerans et al. 1995). Invertebrates were removed from cobbles and the Surber sampler as in Kerans et al. (1995) and then preserved in Kahle's solution (Pennak 1978). Dimensions of cobbles were measured according to Graham et al. (1988) for subsequent calculation of surface area and macroinvertebrate density.

Table 3.2. Temporal trends in the mean physical conditions in Darlinton Spring Creek, which indicate little difference between high- (H) and low-snail (L) reaches in 2002 and 2003. I collected water velocity, channel depth, and channel width along a permanent transect in a riffle of each reach. Ten velocity and depth measurement were collected along the transect using a Swoffer 3000 flow meter. Wetted-channel width was measured perpendicular to the direction of stream flow. Missing values are indicated by "---".

Sampling date	Water velocity (m/s)		Depth (cm)		Width (m)	
	H	L	H	L	H	L
Apr-02	0.147	0.165	25	27	4.09	3.74
Aug-02	0.570	0.850	53	38	---	---
Sep-02	0.568	0.570	43	53	---	---
Oct-02	0.165	0.291	27	23	---	---
Nov-02	0.223	0.175	33	41	4.40	4.30
Jan-03	0.063	0.218	33	23	4.60	4.63
Fb-03	0.166	0.172	21	21	4.39	3.80
Mar-03	0.228	0.170	18	22	4.33	3.69
May-03	0.048	0.105	31	22	4.23	4.05
Jul-03	0.467	0.467	47	47	4.40	4.90
Aug-03	0.538	0.547	40	39	4.80	4.50
Oct-03	0.149	0.183	21	0	4.45	4.30

I identified and enumerated *Potamopyrgus* and baetids to species using a dissecting microscope at 6.3X to 40X magnifications. I calculated densities for each sample by dividing the taxa abundance by surface area of the corresponding cobble. For baetids, I measured head capsule width (largest transect between lateral edges of head) of

~20 randomly chosen individuals per species per reach per sampling date to 0.01mm using an ocular micrometer at 40X magnification, categorized individuals into developmental stages based on wing-pad size (I, II, III, or IV) as defined by Deluchi and Peckarsky (1989), and recorded sex of stage III-IV individuals based on the presence of the enlarged second pair of compound eyes of males (Peckarsky et al. 1993). For *P. antipodarum*, I measured shell length (as defined by Winterbourn 1970a) and determined both reproductive status and fecundity by dissecting randomly chosen *P. antipodarum* (n ~ 40 per reach and sampling date). Reproductive status was defined as the presence or absence of embryos in a brood pouch, whereas fecundity was defined as the number of embryos present in the brood pouch.

<u>Periphyton.—</u> I compared periphyton biomass between high- and low-snail reaches using chlorophyll *a* and pheophytin *a*. Chlorophyll *a* estimates biomass of living periphyton, whereas pheophytin *a*, a degradation product of chlorophyll *a*, estimates biomass of senescent periphyton (Iguchi and Abe 2002). I collected 8 cobbles per reach per sampling date, which were frozen and stored in the dark until chlorophyll extraction (< 30 d). I extracted photosynthetic pigments in 90% ethanol by submerging each cobble, and I used spectrophotometry to measure pigment concentrations in a subsample of each extract (Cada and Kerans in preparation). Direct extraction of photosynthetic pigments was chosen over other periphyton sampling methods such as scraping or brushing of the cobbles primarily because these methods can underestimate biomass through loss of tightly adhered diatoms (Aloi 1990, Cattaneo and Roberge 1991). Biomass was calculated as the product of the extract's concentration and volume divided

by the estimated surface area of the rock. I estimated surface area of the cobbles as noted for macroinvertebrates.

To evaluate densities and biomasses of *P. antipodarum* and baetid species and the biomass of periphyton, I used repeated measures, nested 2-way MANOVA (Von Ende 2001) with the response variable repeated over time. The 2 main factors (levels listed in parentheses) included snail-density (low or high) and reach (A or B) nested within snail-density. I was particularly interested in the time*snail-density interaction to determine whether the snail-density effect differed across time for any of the response variables (e.g., was mean density of a baetid species the same in low and high snail reaches in June 2002 but different between low and high snail reaches in November 2002?). The test statistic I used for MANOVA was Wilk's Lambda (λ), from which an F statistic is approximated (Gotelli and Ellison 2004). In the case of the repeated measures MANOVA, λ cannot be calculated for the snail factor because complete sums of squares and cross-products matrices cannot be generated. Consequently, an exact F statistic was calculated (without approximation from λ, as was done for the other factors) and reported for the snail factor. Baetids were evaluated both as a family (data pooled across species) and as individual species. To satisfy assumptions of normality and equality of variance, density data for all species were ln+1 transformed. Biomass data of *P. antipodarum* were quarter-root transformed, whereas *Diphetor* and *Acerpenna* biomass data were ln+1 transformed.

To analyze life history attributes of *Potamopyrgus* , I used 1-way ANOVA with the factor time (each sampling date as a level) for three response variables—mean length, proportion of the population brooding, and mean number of embryos per reproductive individual. Proportion of the population brooding was calculated as the number of individuals with embryos present divided by the total number of individuals. The mean number of embryos per reproductive individual was calculated from only the individuals subsampled for embryo counts. Additionally, I used linear regression to evaluate the relationship between the number of embryos per reproductive individual and shell length. Only data from high-snail reaches was used in these analyses. *Potamopyrgus* length data were ln transformed.

To analyze life history attributes of Baetidae mayflies, I compared mean head width for stages III and IV of each mayfly species using a 1-way ANOVA across all time periods with the factor snail (high and low density). I used only stages III and IV in this comparison because I expected older larvae to potentially exhibit greater differences between high- and low-snail reaches than younger larvae. For each species, I tested males and females separately as mayflies exhibit some sexual dimorphism, but where non-significant, I report values for males and females analyzed together. Because of the synchronous life-cycles of *Diphetor* and *Acerpenna*, pooling head size across time should not influence the results. However, pooling head size across time may be less realistic for *Baetis* because emergence occurred over many months (see Results) and size at emergence increases later in the season (Block and Stoks 2004). Head width data for *Diphetor* were square-root transformed.

In addition to comparing mean head width between high- and low-snail reaches, I compared the percentage of females for *Baetis*, *Diphetor* and *Acerpenna* using 1-way

ANOVA with the factor snail (low or high). I also used the presence of emerging larvae to compare the timing of emergence between high- and low-snail reaches. I looked for seasonal patterns in head width and the occurrence of emerging larvae to broadly describe the life cycle of *Baetis*, *Diphetor* and *Acerpenna*.

All statistical analyses were performed using SAS 9.0 for Windows (SAS Institute Inc., Cary, North Carolina, USA). All ANOVA, MANOVA, and regression analyses were completed with PROC GLM.

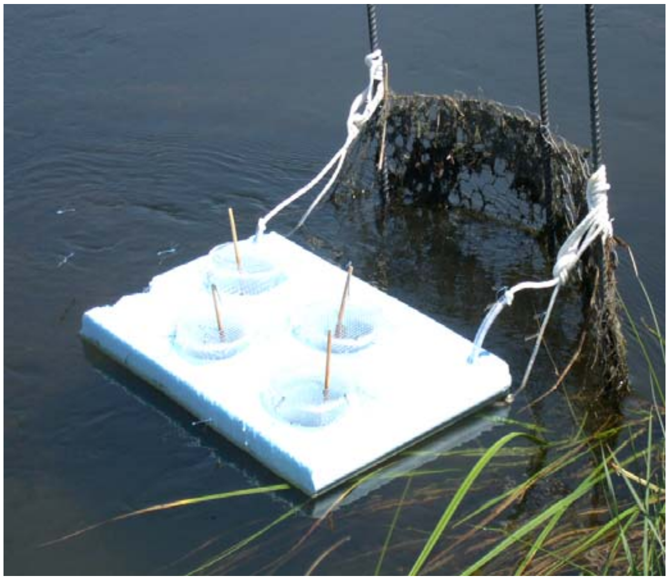
Competition experiments

To determine the strength of competitive interactions between *P. antipodarum* and baetid mayflies, I conducted two *in situ* experiments in artificial chambers stocked with various density combinations of baetid mayflies and *P. antipodarum* in late summer (28 July – 13 August 2003, Experiment 1) and early winter (23 October – 11 November 2003, Experiment 2) to compare the magnitude of competition between seasons. Experiments occurred in different seasons (summer and winter) to compare the magnitude of competition between seasons. Experiment 1 was 4 days shorter than Experiment 2 because invertebrate growth is temperature dependent and body growth of individuals should have accumulated more quickly in Experiment 1. Additionally, because emergence increased over time in Experiment 1, I wanted to limit the loss of mayflies before sample size became too small.

The circular chambers were 11 cm diameter x 14 cm depth with two 4 x 7 cm holes covered by 500-μm nytex mesh on opposing sides of the chamber to allow water exchange. Chambers were mounted in polystyrene floats (1.2 m x 0.6 m x 0.05 m, 4 chambers per float) that were secured in the stream channel with rebar and protected from debris by 0.64 cm wire-mesh attached to the rebar upstream of the floats (Fig. 3.2). Each chamber received 3 similarly sized pebbles (total surface area of about 125 cm^2) prior to invertebrate stocking. I collected the pebbles from the stream channel and carefully removed visible invertebrates to minimize disturbance of periphyton. Extra pebbles were collected and frozen for analysis to determine periphyton biomass at the beginning of the experiment (n=4 for Experiment 1 and n=18 for Experiment 2). I measured water velocity at the upstream and downstream edges of each float and at two depths (0.6X channel depth and 5 cm below the water's surface, which corresponded with the depth of the water-exchange holes) with a Swoffer 3000 flow meter (Appendix D). Onset® temperature probes, secured at the upstream-most and downstream-most floats, recorded water temperature at 1-hr intervals throughout the experiments (Appendix D).

Stocking abundances reflected the range of densities observed at Darlinton Spring Creek (10,000-20,000 m^{-2}). In Experiment 1, I compared *Diphetor* and *Potamopyrgus*, whereas in Experiment 2, I compared *Baetis* and *Potamopyrgus*. I used *Diphetor* rather than *Baetis* in Experiment 1 because most *Baetis* I collected were too small and might have escaped the chambers, but *Diphetor* was within the appropriate size range. Experiment 1 examined competitive interactions where intra- and interspecific competition cannot be separated (Goldberg and Scheiner 2001) and consisted of 3 treatments in an substitutive design where the total number of individuals in a replicate was constant at 250: *Diphetor* alone (D), *Potamopyrgus* alone (P), and *Diphetor* plus *Potamopyrgus* together (D+P). In contrast, Experiment 2 estimated both intraspecific and interspecific interactions and was comprised of 7 treatments in a response-surface design (Table 3.3). Assignment of treatments to chambers was completely randomized across floats.

Figure 3.2. This photograph shows chambers used in the competition experiments in Chapter 3. There were 10 floats, each of which supported 4 chambers into which *Potamopyrgus* and baetids were stocked at various density combinations. The wire mesh reduced debris clogging the nytex mesh on the chambers.



Invertebrate stocking of the experimental chambers occurred over 2 d. I collected invertebrates using kick nets and pipetted a known number of individuals into temporary containers. I chose *P. antipodarum* ~2 mm length and young baetid nymphs (wing-pads present but not darkened or thickened) for stocking. These sizes precluded prior embryo development by *P. antipodarum* (Richards et al. 2001) in addition to allowing growth by both species and field identification.

Table 3.3. Experimental design of field competition Experiment 2 indicating the species and density combinations for each treatment, the number of individuals stocked per chamber, and the number of replication for each treatment. B=*Baetis tricaudatis*. P=*Potamopyrgus antipodarum*.

Species	Density	# Individuals	n
Baetis	low	120B	6
Potamopyrgus	low	120P	5
Baetis + *Potamopyrgus*	low	60B + 60P	6
Baetis	high	240B	6
Potamopyrgus	high	240P	5
Baetis + *Potamopyrgus*	high	120B + 120P	6
Control	na	0	5

Maintenance of chambers and floats occurred every ~3 days. I cleaned the nytex and wire meshes of debris to aid water exchange and removed dead invertebrates by pipetting to prevent deterioration of water quality. For Experiment 2, maintenance included removal of snow and ice from the surfaces of chambers and floats. At the end of each experiment, I enumerated and preserved live individuals in Kahle’s solution. Additionally, pebbles from the experimental chambers (n=3 per chamber) were frozen for chlorophyll and pheophytin analysis and calculation of periphyton biomass (see methods in field surveys).

I quantified the effect of competition using two characters related to fitness—daily survivorship and daily per capita body growth. Because *Potamopyrgus* reproduced in some replicates in Experiment 1, the response variable in that case is per capita population growth rather than survivorship. I calculated survivorship or per capita population growth according to equation 3.1.

Daily survivorship or per capita population growth = Eq. 3.1

ln[(final number of species y alive at experiment end)/(initial number of species y added at the beginning of the experiment)] / (number of days in experiment)

In Experiment 1, survivorship of *Diphetor* was corrected for loss of individuals due to emergence (i.e., mean daily emergence was added to each final abundance).

I calculated the second fitness characteristic, daily per capita growth, for both species according to equation 3.2.

Daily per capita body growth = Eq. 3.2

Eq. 3.2

ln[(biomass of species y alive at experiment end)/(biomass of species y added at the beginning of the experiment)] / (number of days in experiment)

To estimate initial and final biomasses, I measured shell length or head-capsule width and converted these measurements to dry-mass according to equations 3.3 from Cada and Kerans (in preparation) and 3.4. from Benke et. al (1999).

Potamopyrgus dry weight [mg] = length [mm]$^{2.3697}$ * 0.117 Eq. 3.3

Diphetor or *Baetis* dry weight [mg] = width [mm]$^{3.326}$ * 1.2688 Eq. 3.4

For initial biomass, I measured 40 individuals per species, which I subsampled from the individuals available for stocking. For final biomass, I measured up to 40 individuals per species per replicate, depending on survivorship of the invertebrates.

In Experiment 1, I used 1-way ANOVA to test for a treatment effect for each response variable (survivorship and growth) for each competitor. Factor levels were

Diphetor alone (D) or *Potamopyrgus* alone (P) and *Diphetor* plus *Potamopyrgus* (D+P). Because the response variables were not independent of each other, I used Bonferroni corrections. Additionally, I compared overall survivorship and growth between competitors using two-sample t-tests. To determine whether treatment-levels affected chlorophyll *a* or pheophytin biomass through differential grazing pressure, I used 1-way ANOVA with 5 factor levels. This analysis included an "initial" factor level that represented periphyton from the stream channel at the start of the experiment and a "control" factor level that represented periphyton biomass from experimental chambers with no invertebrates, in addition to the invertebrate treatments D, P or D+P. Chlorophyll *a* and pheophytin data were ln transformed

In Experiment 2, I used 2-way ANOVA for each competitor for each response variable with treatment ("solitary" or "B+P") and density ("low" or "high") as the factors. Because the response variables were not independent of each other, I used Bonferroni corrections. I compared overall survivorship and growth between competitors using two-sample t-tests.

I estimated competition coefficients (α) based on survivorship. I did not estimate coefficients based on per capita growth because of insignificant results for this response variable (with the exception of *Potamopyrgus* intraspecific competition) (see Results). Intraspecific competition is indicated as α_{BB} for *Baetis* and α_{PP} for *Potamopyrgus*. Interspecific competition is represented as α_{BP} for the effect of *Potamopyrgus* on *Baetis* or α_{PB} for the effect of *Baetis* on *Potamopyrgus*. Values of $\alpha < 1$ indicate a negative effect of competition; $\alpha = 1$ indicates no effect; and $\alpha > 1$ indicates a positive effect and is not considered competition. Intraspecific coefficients were calculated from the transformed means of each treatment level as in equation 3.5.

$$\alpha_{BB} \text{ or } \alpha_{PP} = \text{solitary}_{high} - \text{solitary}_{low} \qquad \text{Eq. 3.5}$$

Interspecific coefficients were also calculated from the transformed means for each treatment level as in equations 3.6 and 3.7.

$$\alpha_{BP} = B{+}P_{high} - \text{solitary}_{\mathit{Baetis}\text{—low}} \qquad \text{Eq. 3.6}$$

$$\alpha_{PB} = B{+}P_{high} - \text{solitary}_{\mathit{Potamopyrgus}\text{—low}} \qquad \text{Eq. 3.7}$$

I calculated 95% confidence intervals around the mean competition coefficients using the standard error corrected for comparisons of 2 or more means (Elliot 1971).

To determine whether the treatment (solitary and B+P) and density (low and high) factors affected food resources, I used 2-way ANOVA for the response variables, chlorophyll *a* and pheophytin. This analysis included additional levels in the density factor: ‘initial’, that represented periphyton biomass from the stream channel at the start of the experiment as well as a “control” level that represented periphyton biomass from experimental chambers with no invertebrates. Neither chlorophyll *a* or pheophytin data required transformation.

Results

Objective 1: Densities and biomass

Potamopyrgus .— As expected, densities and biomasses of *P. antipodarum* in high-snail reaches were greater than densities and biomasses in low-snail reaches (snail effect, Table 3.4a, Fig. 3.3a), with considerable temporal variation (time effect, Table 3.4a). Mean densities of *P. antipodarum* in high-snail reaches ranged from 868 m^{-2} in

May 2003 to 24,750 m^{-2} in July 2002, whereas mean densities in low-snail reaches ranged from 0 m^{-2} in November 2002 to 424 m^{-2} in September 2002 (Fig. 3.3a). In general, densities after May 2003 were lower than densities in the same months in 2002. Mean *Potamopyrgus* biomass followed a similar pattern over time as that observed for mean densities (Fig. 3.3b). Mean *Potamopyrgus* biomass peaked at 26 g m^{-2} in July 2002 in high-snail reaches and did not exceed 0.54 g m^{-2} in low snail reaches (Fig. 3.3b). Unexpectedly, between October 2002 and January 2003, densities and biomasses of *P. antipodarum* in the high-snail reaches decreased dramatically and then returned to levels previously observed, which probably contributed to the significant time*snail interaction (Table 3.4a). In addition, there was a significant reach(snail)*time interaction for biomass (Table 3.4a), indicating that within the high-snail reaches, one reach did not consistently have greater biomasses than the other (see Appendix B).

Mayflies.—I encountered 5 species of baetid mayflies in the study area: *Baetis tricaudatis, Diphetor hageni, Acerpenna pygmaea, Plauditus punctiventris,* and *Callibaetis* sp. Both *P. punctiventris* and *Callibaetis* sp. occurred in less than 1% of samples at very low densities (< 20 m^{-2}) and were excluded from further analyses. Mean densities of Baetidae (*Baetis*, *Diphetor* and *Acerpenna* pooled) peaked in late fall and winter months (October and November 2002, January 2003) (17,848 m^{-2} in low-snail reaches of November 2002) and were lowest in summer months (June to September 2002, July and August 2003) (741 m^{-2} in low-snail reaches of June 2002) (Fig 3.3 c). The mean biomass of Baetidae followed a temporal pattern similar to that of Baetidae density, peaking slightly later in winter in January 2003 at 4951 mg m^{-2} in low-snail reaches; the lowest mean biomass was observed in June 2002 at 299 mg m^{-2} (Fig. 3.3d). Mean Baetidae density and biomass changed significantly across time periods (Table 3.4b) but did not differ significantly between high- or low-snail reaches or with the interaction between time and snail-density (Table 3.4b). There was a significant reach(snail-density)*time interaction for both baetid density and biomass (Table 3.4b), indicating that within the high-snail reaches and within the low-snail reaches, one reach did not consistently have greater densities or biomasses than the other.

Figure 3.3 - Temporal trends in the densities and biomasses (mean ± 1 SE) of *Potamopyrgus antipodarum* and Baetidae mayflies in high-snail (filled circle) and low-snail reaches (open circle). For each snail type and each time period, 16 cobble samples were taken for a total of n = 384 invertebrate samples.

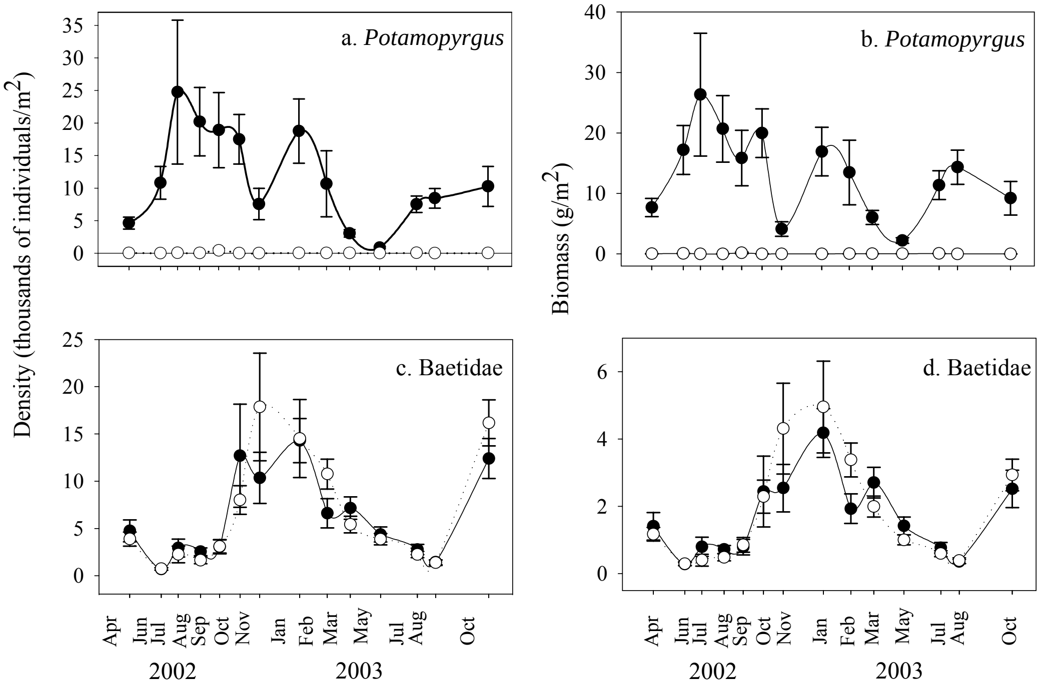


Table 3.4. Results of repeated measures 2-way MANOVA for *P. antipodarum* (a) and Baetidae mayflies (pooled by family) (b) where density and biomass were repeatedly measured over time. Note that "$^{+}$" indicates that instead of λ, the value reported is the F-statistic from the between-subjects effect repeated measures analysis.

a. *Potamopyrgus antipodarum*

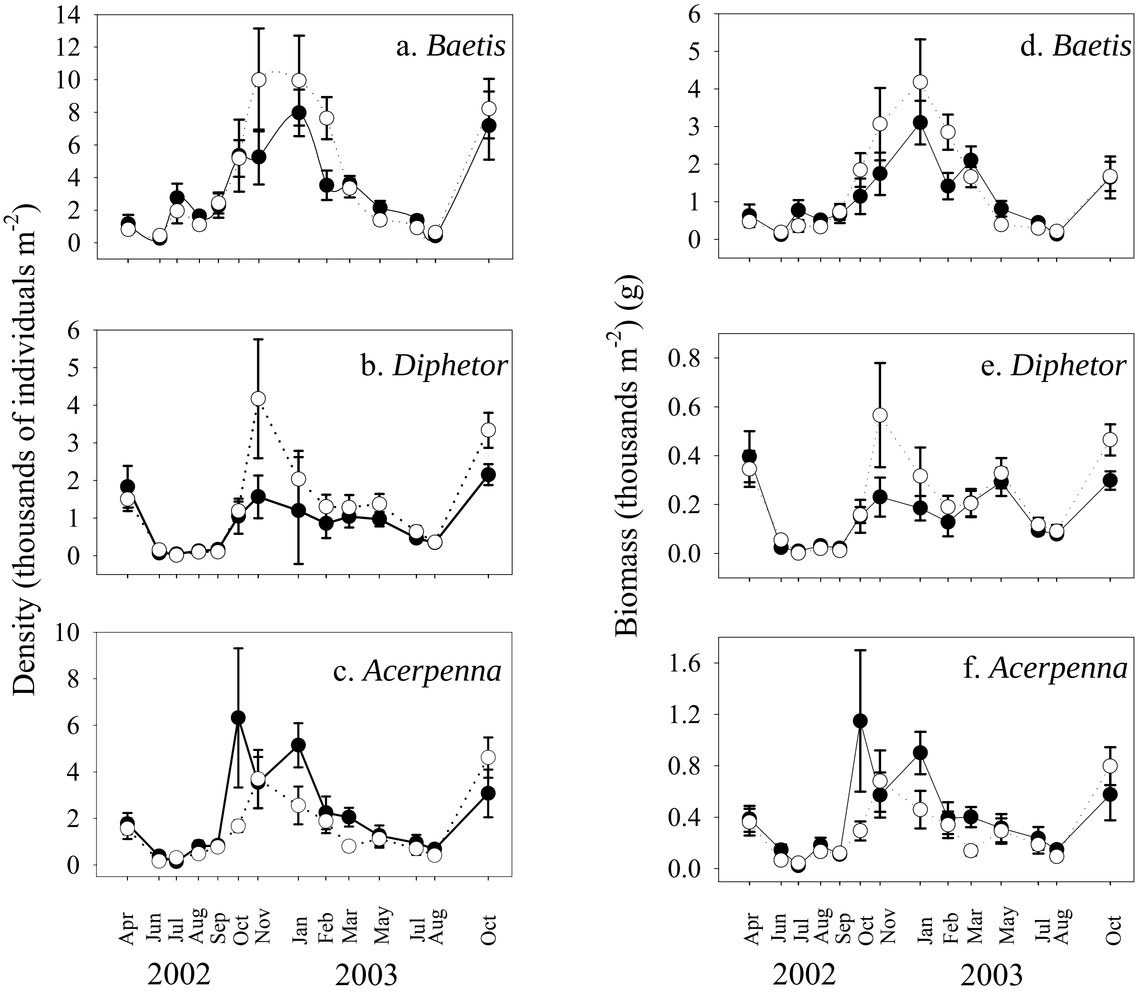
Source of variation	df	Wilk's lambda	*P*
		Density	
Time	13, 16	0.106	**<0.0001**
Snail	1, 28	1926.7^{+}	**<0.0001**
Time*Snail	13, 16	0.141	**0.0001**
Time*Reach(Snail)	26, 32	0.208	0.1511
		Biomass	
Time	13,16	0.203	**0.0019**
Snail	1, 28	3346.6^{+}	**<0.0001**
Time*Snail	13,16	0.198	**0.0016**
Time*Reach(Snail)	26, 32	0.091	**0.0027**

b. Baetidae

Source of variation	df	Wilk's lambda	*P*
		Density	
Time	13, 16	0.0354	**<0.0001**
Snail	1, 28	0.24^{+}	0.6248
Time*Snail	13, 16	0.542	0.4624
Time*Reach(Snail)	26, 32	0.0621	**0.0003**
		Biomass	
Time	13, 16	0.0357	**<0.0001**
Snail	1, 28	0.18^{+}	0.675
Time*Snail	13, 16	0.55	0.488
Time*Reach(Snail)	26, 32	0.0524	**<0.0001**

Densities and biomasses of all three mayfly species varied over time (Table 3.5, Fig. 3.4). Even though I did not observe a statistically significant snail-density or time*snail-density effect for Baetidae, it is possible that the species differed in their response to *Potamopyrgus*.

Figure 3.4 - Temporal trends in the densities (mean ± 1 SE) of *Baetis tricaudatis*, *Diphetor hageni*, and *Acerpenna pygmaeus* in high-snail (filled circle) and low-snail reaches (open circle). For each snail type and each time period, 16 cobble samples were taken for a total of n = 384 invertebrate samples.



For *B. tricaudatis,* mean density and biomass tended to be greater in low- than in high-snail reaches in fall and winter (February 2003, November 2002, and January 2003) (Table 3.5, Fig. 3.4a and d). Mean density and biomass of *D. hageni* tended to be greater in low- than in high-snail reaches in fall and winter (November 2002, Jan 2003 and October 2003) (Table 3.5, Fig. 3.4b and e).

Table 3.5. Results of repeated measures 2-way MANOVA for *Baetis tricaudatis, Diphetor hageni* and *Acerpenna pygmaea,* where density and biomass were repeatedly measured over time. Note that “$^{+}$” indicates that instead of λ, the value reported is the F-statistic from the between-subjects effect repeated measures analysis.

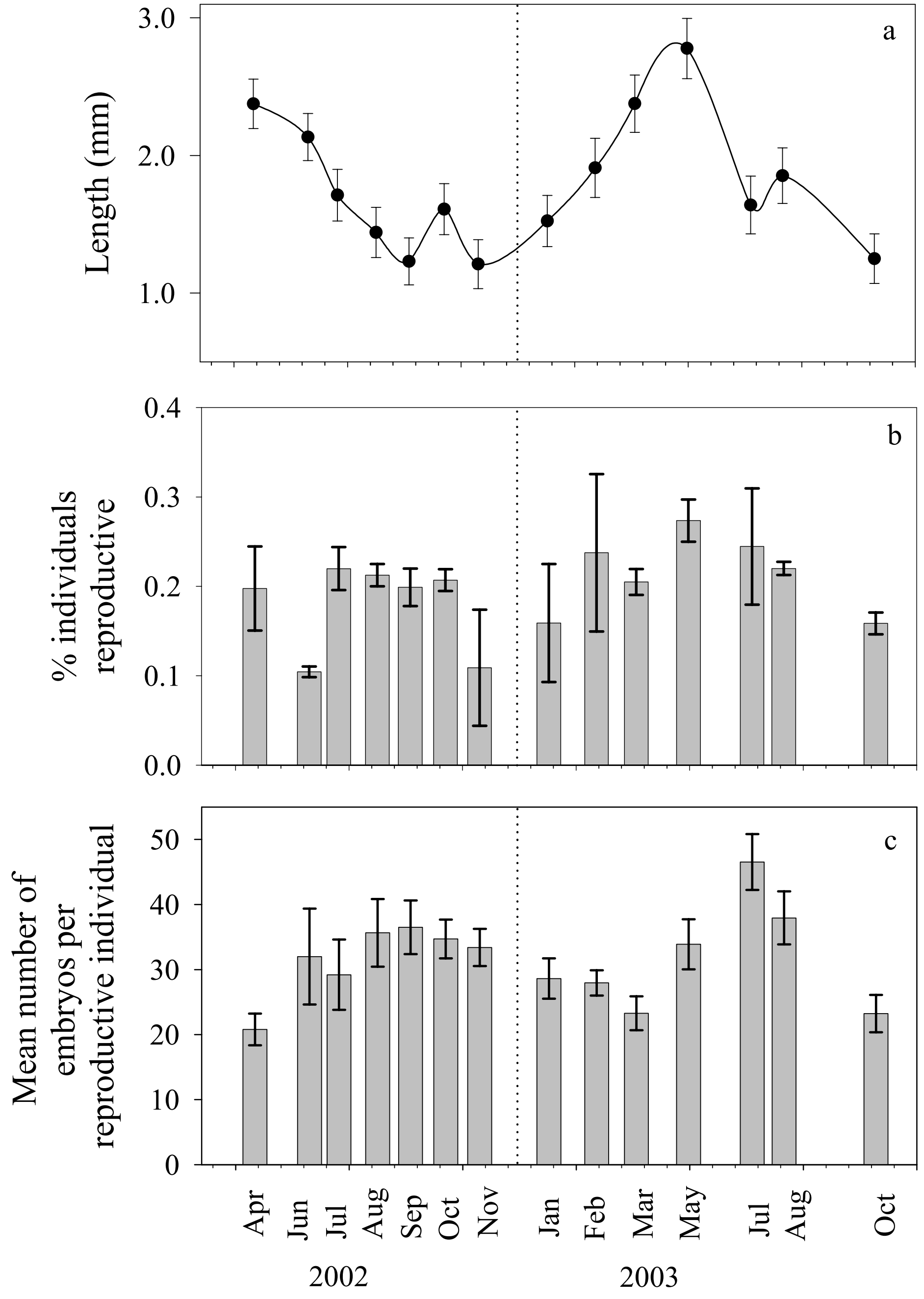
Density				Biomass			
Source of variation	df	Wilk's lambda	*P*	Source of variation	df	Wilk's lambda	P
Baetis							
Time	13, 16	0.059	<**0.0001**	Time	13,16	0.044	< **0.0001**
Snail	1, 28	0.1+	0.7545	Snail	1, 28	0.09+	0.763
Time*Snail	13, 16	0.485	0.3023	Time*Snail	13,16	0.444	0.2043
Time*Reach (Snail)	26, 32	0.065	**0.0004**	Time*Reach (Snail)	26, 32	0.057	0.0002
Diphetor							
Time	13, 16	0.066	<**0.0001**	Time	13, 16	0.054	< **0.0001**
Snail	1, 28	0.51+	0.4790	Snail	1, 28	0.66 +	0.4218
Time*Snail	13, 16	0.409	0.1368	Time*Snail	13, 16	0.408	0.1358
Time*Reach (Snail)	26, 32	0.137	**0.0239**	Time*Reach (Snail)	26, 32	0.129	**0.0181**
Acerpenna							
Time	13, 16	0.055	<**0.0001**	Time	13, 16	0.059	< **0.0001**
Snail	1, 28	1.72+	0.1998	Snail	1, 28	1.74 +	0.1979
Time*Snail	13, 16	0.453	0.2239	Time*Snail	13, 16	0.482	0.2932
Time*Reach (Snail)	26, 32	0.059	**0.0002**	Time*Reach (Snail)	26, 32	0.06	**0.0002**

In contrast to *Baetis* and *Diphetor*, mean densities of *A. pygmaea* tended to be greater in high- than in low-snail reaches in fall and winter (October 2002, January and March 2003) (Table 3.5, Fig. 3.4c and f). However, none of the differences in densities or biomasses between low-snail and high-snail reaches were statistically significant (Table 3.5, Fig. 3.4), although the P-value for the *Diphetor* time*snail-density interaction was low ($P < 0.14$).

Objective 2: Life histories

Potamopyrgus .—Mean length of *Potamopyrgus* varied through time ($F_{13,1157} = 11.11$, $P < 0.0001$). Specifically, mean length decreased from spring through summer months and remained small (1.3 – 1.6 mm) through mid-winter (e.g., January 2003) (Fig. 3.5a), indicating reproduction throughout this time period. Mean lengths increased through winter and spring of 2003, suggesting a possible cohort of individuals resulting from late summer and early autumn reproduction. However, both large adults (≥ 4.8 mm) and newly birthed individuals (< 0.5 mm) occurred year-round, suggesting that reproduction occurred throughout the year. Similarly, individuals containing developing embryos were present year-round (Fig. 3.5b), but the proportion of the population brooding (overall mean proportion= 0.18, n = 1,249) did not differ significantly over time ($F_{13,14} = 1.31$, $P = 0.31$). The mean proportion of the population brooding did not exceed 0.30 at any time. Individuals above the observed threshold for reproduction (see below) composed the greatest proportion of the population in April and June 2002, as well as March and May 2003, whereas newly birthed individuals composed the greatest proportion of the population in September and November 2002 (Appendix A).

Figure 3.5 - Temporal trends in the life history characteristics of *P. antipodarum* including shell length (mean ± 1 SE) (a), the percentage of individuals carrying embryos (mean ± 1 SE) (b) (n=80 snails per time), and the number of embryos per gravid individual (mean ± 1 SE) (c).



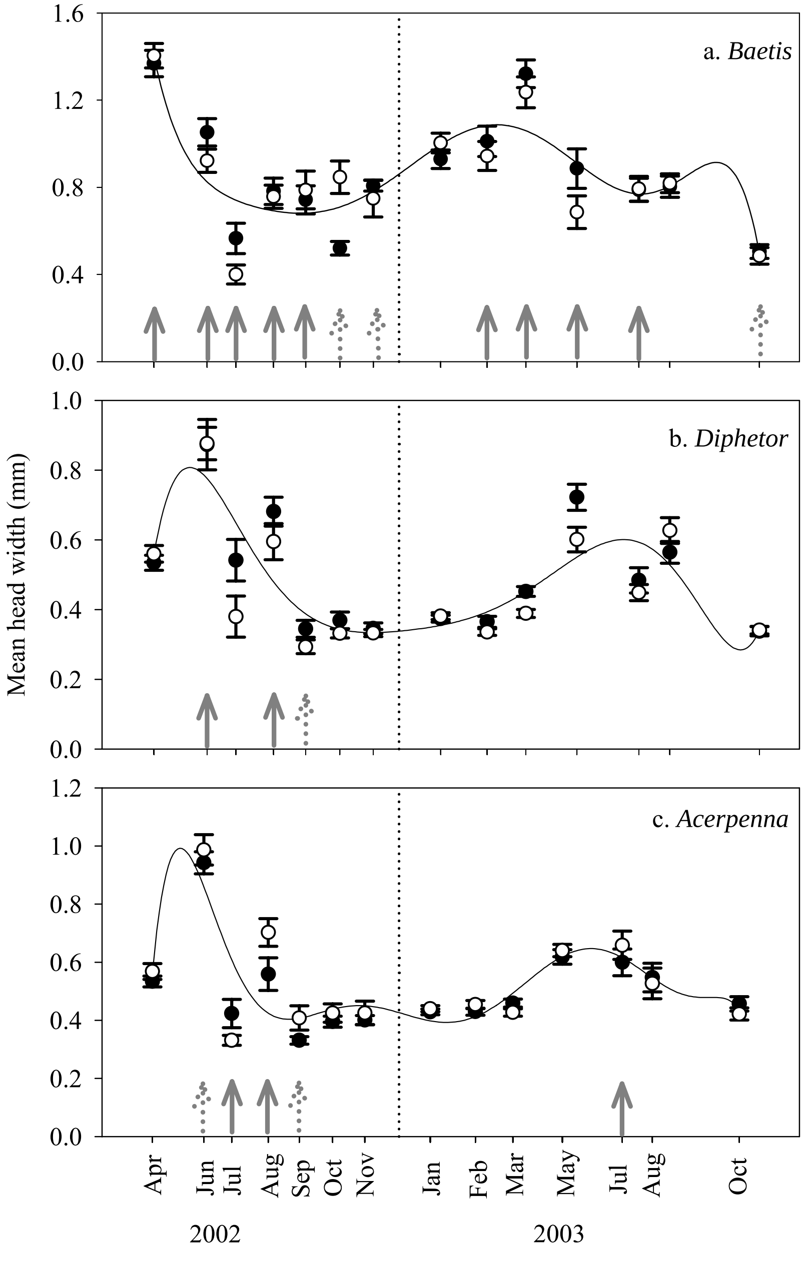
Of the *P. antipodarum* individuals reproducing (n = 228), the number of embryos present in the brood pouch ranged between 1 and 83 and averaged 32.1 (± 1.13) embryos. The mean number of embryos per reproductive individual varied over time ($F_{13,214}$ = 3.13, P = 0.0003) and was greatest in mid-summer of 2003 (Fig. 3.4c). The minimum length at which embryos were present was 2.2 mm. There was a positive correlation between the number of embryos per brood pouch and shell length (t_{231} = 6.80, P < 0.001), but the regression explained only a small amount of the variation (r^2 = 0.167).

Interestingly, I encountered a small proportion of male *P. antipodarum* (0.94 % of 1171 snails), which had a mean shell length of 3.4 ± 0.07 (SE) mm. Of the males encountered, 54.5% (6/11) occurred in March 2003.

Mayflies.— I did not detect a snail effect on the mean head widths of stage III and IV *Baetis* ($F_{1,247}$ = 0.50, P = 0.4795) (Fig. 3.6a) and III and IV *Acerpenna (*$F_{1,102}$ = 0.16, P = 0.6940) (Fig. 3.6c); however, *Diphetor* males of stages III and IV were larger in low-snail reaches (1.3 ± 0.039 mm) than in high-snail reaches (1.2 ± 0.027 mm) ($F_{1,23}$ = 4.34, P = 0.0484). Female *Diphetor* in stages III and IV occurred only in high-snail reaches, suggesting that development from stage III to emergence in low-snail reaches occurred between sampling periods.

The overall percentages of females were 61% for *Baetis*, 73% for *Diphetor,* and 63% for *Acerpenna* (all sexed mayflies, n=810; females, n=449). However, the percentage of *Acerpenna* females was greater in high-snail reaches (64.4%) than low-snail reaches (61.5%) ($F_{1,9}$ = 7.87, P = 0.0206), but I was unable to detect a snail effect for *Baetis* ($F_{1,23}$ = 0.05, P = 0.8180) or *Diphetor* ($F_{1,8}$ = 0.06, P = 0.8071).

Figure 3.6 - Temporal trends in the head width (mean ± 1 SE) of *Baetis*, *Diphetor*, and *Acerpenna*. Filled circles represent high-snail reaches whereas open circles represent low-snail reaches. Arrows indicate the presence of emerging nymphs: solid (both high and low snail reaches), dotted (either high or low snail reaches). Vertical dotted lines separate 2002 from 2003.



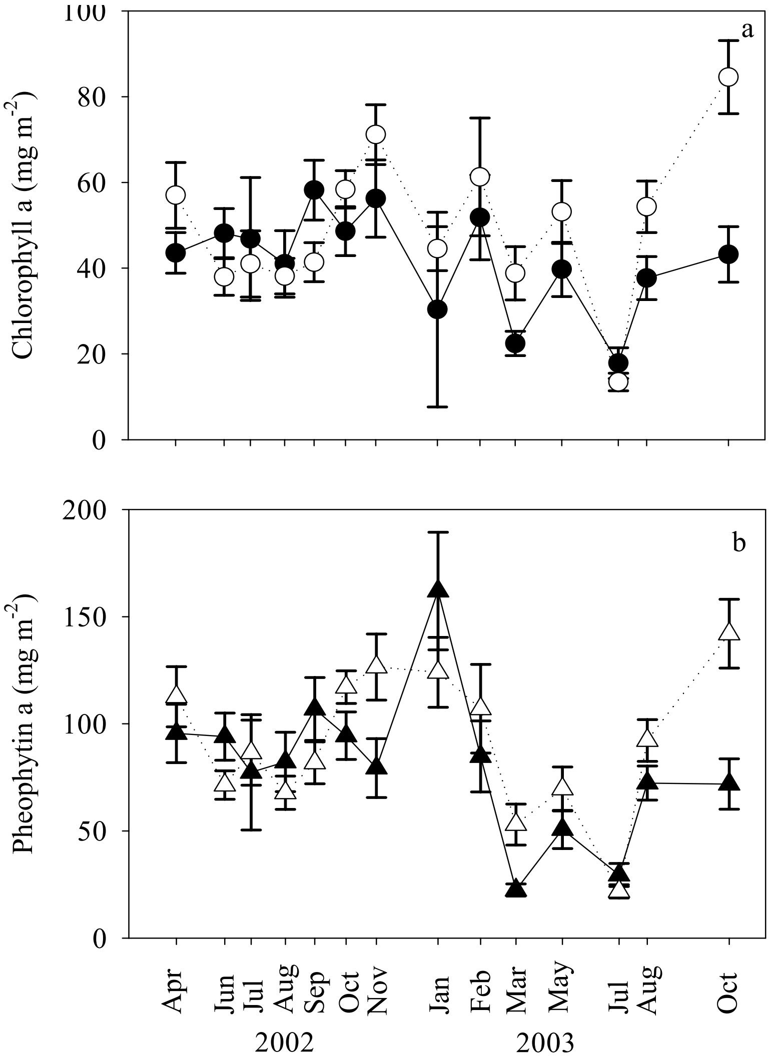
Mean head width for all baetid species showed strong seasonal patterns (Fig. 3.6). *Baetis* mean head width was greatest in spring (April 2002 and March 2003) and remained small to intermediate sized throughout summer and fall 2002 (Fig. 3.6a). Mean head width of *Diphetor* peaked in June 2002 and May 2003 (Fig. 3.6b), slightly later in the year than *Baetis*. Similar to *Diphetor*, mean head width of *Acerpenna* peaked in June 2002 and late spring-early summer 2003 (May and July) (Fig. 3.6c). *Diphetor* and *Acerpenna* head widths remained constant from September 2002 through February 2003, indicating a lack of winter nymph growth, whereas *Baetis* head width increased over fall and winter months.

Emerging *Baetis* were present in samples from winter (February 2003) through summer and even early fall (Fig. 3.6). In contrast, emerging *Diphetor* and *Acerpenna* nymphs were present for shorter time periods (~3 months), from June to September.

Objective 3: Food resources in the field

Chlorophyll *a* biomass increased in fall and early winter 2002 and reached similar levels in October 2003 as October 2002 (Fig 3.7a, Table 3.6). Chlorophyll *a* biomass exhibited no clear trend over time during winter of 2003 and reached the lowest levels in July 2003. Chlorophyll *a* tended to be greater ($P < 0.06$, Table 3.6) in low-snail reaches than in high-snail reaches (Fig. 3.7b), suggesting that food resources for *Potamopyrgus* and baetids were depressed by *Potamopyrgus* in high-snail reaches. This difference between low-snail and high-snail reaches tended to vary over time (time*snail effect, $P<0.09$, Table 3.6), the greatest difference occurring in winter months.

Figure 3.7 - Chlorophyll *a* biomass (mean ± 1 SE) (a) and pheophytin *a* biomass (b) compared between high-snail and low-snail reaches over time from the field surveys. The filled symbols represent high-snail reaches and open symbols represent low-snail reaches.



Similar to chlorophyll *a*, pheophytin tended to decrease over summer and then increase in fall and winter 2002 (Fig 3.7a, Table 3.6). I observed a significant reach(snail)*time interaction, which indicates that within high-snail and within low-snail reaches, pheophytin trends over time did not follow the same pattern. Pheophytin biomass did not differ between high-snail and low-snail reaches (Fig. 3.7b, Table 3.6). Large differences between reaches, which act as replicates for the snail-density treatments, may have contributed to our inability to statistically detect a snail or time*snail effect for pheophytin.

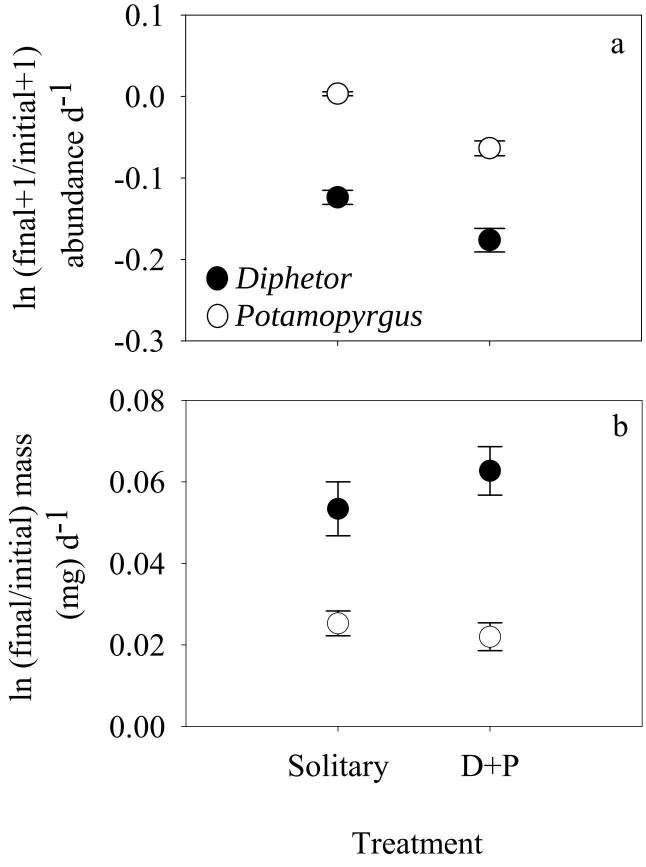
Table 3.6. Results of repeated measures 2-way MANOVA for chlorophyll *a* and pheophytin *a* biomass where periphyton biomass was repeatedly measured over time. Note that "$^+$" indicates that instead of λ, the value reported is the F-statistic from the between-subjects effect repeated measures analysis.

Source of variation	df	Wilk's lambda	*P*
		Chlorophyll *a*	
Time	13, 11	0.1049	**0.0012**
Snail	1, 23	3.9600 $^+$	0.0587
Time*snail	13, 11	0.2671	0.0850
Time*reach(snail)	26, 22	0.1164	0.1230
		Pheophytin *a*	
Time	13, 11	0.0491	< **0.0001**
Snail	1, 23	1.0600 $^+$	0.3136
Time*snail	13, 11	0.2740	0.0939
Time*reach(snail)	26, 22	0.0541	**0.0085**

Objective 4: Competition Experiments

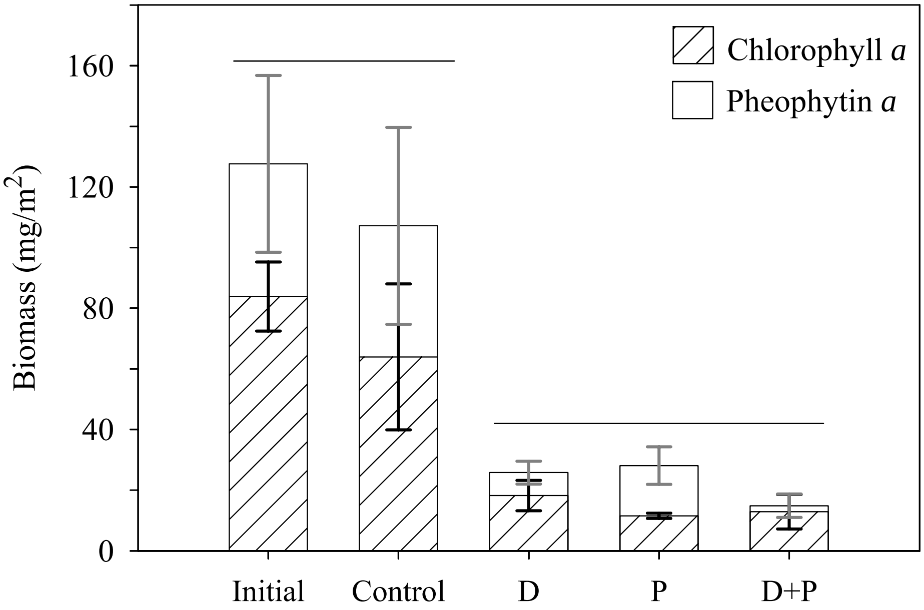
Experiment 1.—In tests of competition between *Potamopyrgus antipodarum* and *Diphetor*, *Potamopyrgus* survivorship was greater than survivorship of *Diphetor* (t_{14}=6.51, P<0.0001; Fig. 3.8a). Survivorship was greater for both species in the intraspecific treatment than in the interspecific treatment (*Potamopyrgus*: $F_{1,6}$ =50.14, P = 0.0004; *Diphetor:* $F_{1,6}$ = 9.61, P = 0.0211). Mean individual growth per day (Fig 3.8b) did not differ between treatments for either species (*Potamopyrgus*: $F_{1,316} = 0.51$, $P = 0.4757$; *Diphetor:* $F_{1,132} = 1.26$, $P = 0.2640$), but *Diphetor* growth was greater than that of *Potamopyrgus* ($t_{199} = 5.78$, $P < 0.0001$).

Figure 3.8 - Survivorship or per capita population growth (a) and body growth (b) for *Potamopyrgus* and *Diphetor* from competition Experiment 1. Treatments were either *Potamopyrgus* or *Diphetor* alone ("solitary") or both species together ("D+P"). *Potamopyrgus* reproduced in solitary treatments resulting in positive per capita population growth.



Grazing pressure in the chambers decreased periphyton biomass. Chlorophyll *a* and pheophytin biomasses in Experiment 1 were greater in the initial and control treatments than in D, P or D+P treatments (chlorophyll *a*: $F_{5,19} = 8.58$, $P = 0.0004$; pheophytin: $F_{4,19} = 11.58$, $P < 0.0001$; Tukey's HSD $P < 0.05$) (Fig 3.9). *Potamopyrgus* and *Diphetor* did not differ in their effect on periphyton biomass (Fig 3.9).

Figure 3.9 - Chlorophyll *a* and pheophytin *a* biomass (mean ± 1 SE) from competition Experiment 1. Treatments included biomass from the stream channel at the start of the experiment (Initial), a control with no invertebrates added (Control), *Diphetor* only (D), *Potamopyrgus* only (P), or both species (D+P). Horizontal lines indicate those treatment means that are statistically similar to each other from Tukey's HSD multiple comparisons ($p < 0.05$).



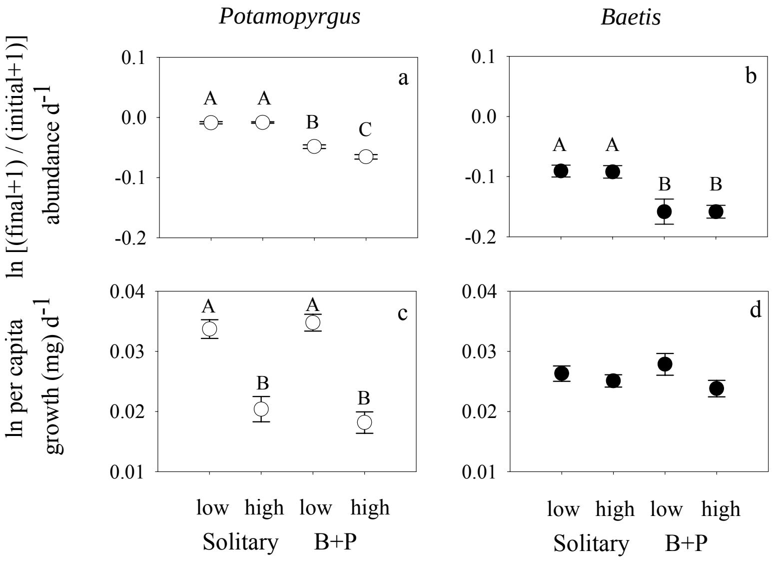
<u>Experiment 2.—</u>Overall, *Potamopyrgus* survivorship was greater than that of *Baetis* (t_{37}=8.2, P<0.0001). The mean survivorship for *Potamopyrgus* was greater when

maintained only with conspecifics than when combined with *Baetis* (i.e., B+P; Fig. 3.10a) (treatment: $F_{1,18} = 287.31$, $P < 0.0001$). Density negatively affected survivorship only when *Potamopyrgus* was combined with *Baetis* (B+P) (density: $F_{1,18} = 8.44$, $P = 0.0095$; treatment*density: $F_{1,18} = 6.30$, $P = 0.007$). Similarly, the mean survivorship of *Baetis* was greater when with conspecifics than in combined treatments with *Potamopyrgus* (Fig. 3.10b) (treatment: $F_{1,20} = 24.01$, $P < 0.0001$). However, *Baetis* survivorship did not differ between low and high densities (density: $F_{1,20} = 0.0$, $P = 0.9520$; treatment*density: $F_{1,20} = 0.0$, $P = 0.9609$).

The overall mean daily growth of *Potamopyrgus* did not differ from that of *Baetis* (t_{1341}=1.14, P=0.2533). *Potamopyrgus* growth did not differ between solitary and mixed treatments (Fig. 3.10c) ($F_{1,873} = 0.36$, $P = 0.5487$). However, increased density negatively affected *P. antipodarum* growth (density: $F_{1,873} = 91.55$, $P < 0.0001$; treatment*density: $F_{1,873} =0.79$, $P = 0.376$). In contrast, *Baetis* growth did not differ between solitary and mixed treatments nor between low and high densities (Fig. 3.10d) (treatment: $F_{1,430} = 0.15$, $P = 0.7019$; density: $F_{1,430} = 1.68$, $P = 0.1961$; treatment*density: $F_{1,430} = 0.40$, $P = 0.5260$).

The estimated strength of the intraspecific competition coefficients (mean and 95% confidence intervals) were α_{PP}=1.0004 (0.9972 – 1.004) and α_{BB}=0.9985 (0.9786 – 1.018). Both values are equivalent to no intraspecific competition. The interspecific competition coefficient for the effect of *Potamopyrgus* on *Baetis* was α_{BP}=0.9345

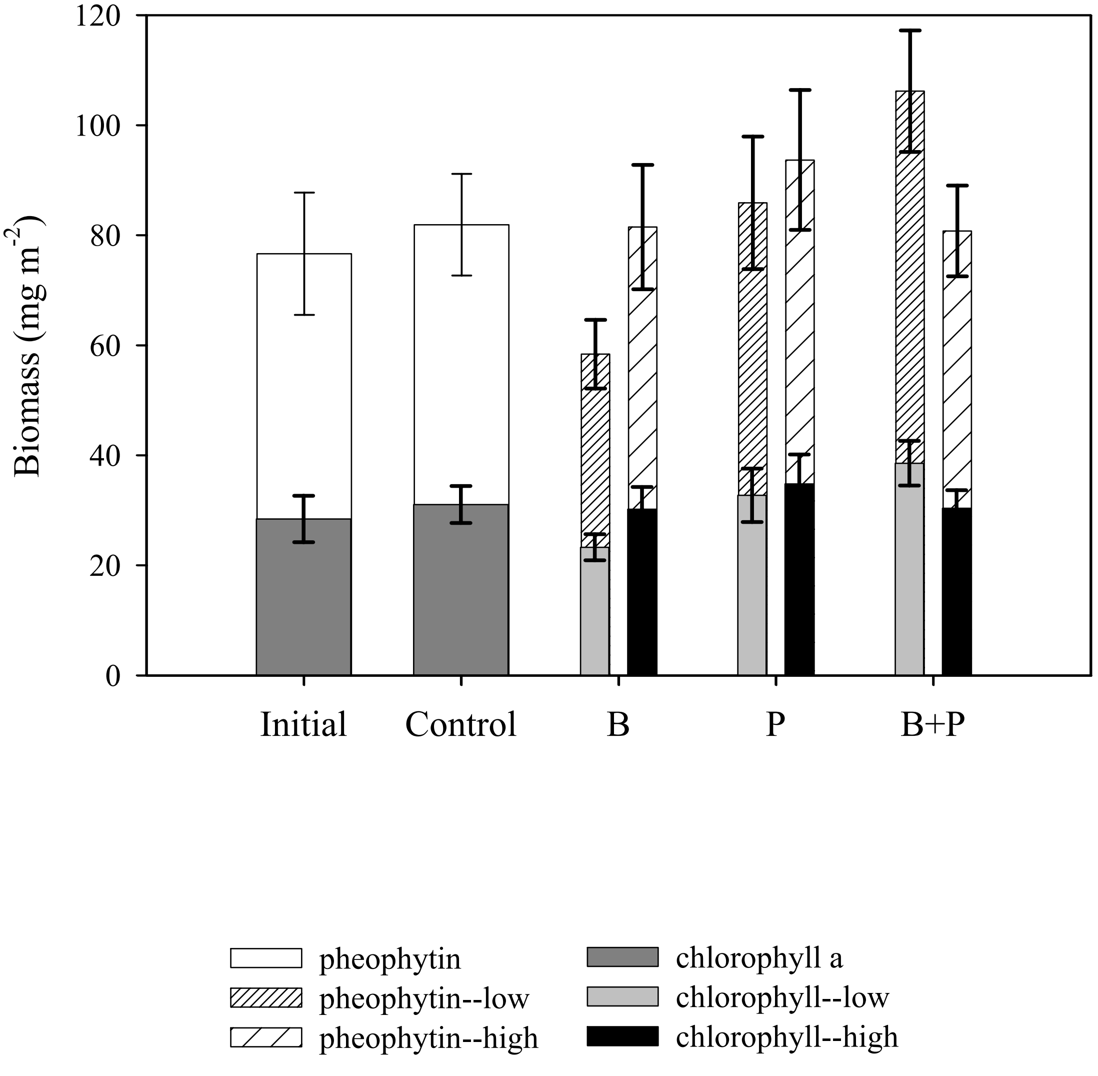
Figure 3.10 - Survivorship (a & b) or growth (c & d) (mean ± 1 SE) for *Potamopyrgus* and *Baetis* from competition Experiment 2. Filled circles represent *Baetis* whereas open circles represent *Potamopyrgus*. Treatments included *Baetis* only at low and high densities and *Potamopyrgus* only at low and high densities ("solitary"), or both species at low and high densities (B+P). Different upper-case letters above data points indicate differences among means using Tukey's HSD multiple comparisons ($p < 0.05$).



(0.9138 – 0.9553), and the coefficient for the effect of *Baetis* on *Potamopyrgus* was α_{PB}=0.9450 (0.9390 – 0.9404) indicating that competition between *Baetis* and *Potamopyrgus* was symmetrical.

Mean chlorophyll *a* biomass was somewhat lower in *Baetis*-only treatments (Fig. 3.11) (species: $F_{2,92}$ = 2.73, P = 0.0703) in comparison to the initial and control levels as well as to *Potamopyrgus*-only and B+P treatments, indicating that chlorophyll *a* biomass was depressed in the experiment only when *Baetis* grazed by itself. Density did not affect chlorophyll *a* biomass (density: $F_{1,92}$ = 0.01, P = 0.9396; species*density: F = 1.98,

Figure 3.11 - Chlorophyll *a* (shaded) and pheophytin *a* (open) biomasses (mean ± 1 SE) from competition Experiment 2. Treatments included biomass from the stream channel at the start of the experiment (Initial), a control with no invertebrates added (Control), *Baetis* only at both densities (B), *Potamopyrgus* only at both densities (P), or both species at both densities (B+P).



P = 0.1432). Similarly, mean pheophytin *a* biomass was lower in *Baetis*-only treatments (species: $F_{2,92} = 4.25$, P = 0.0172) in comparison to all other treatment levels, indicating that only grazing by *Baetis* was able to depress pheophytin biomass lower than the initial and control levels of biomass. An interaction effect indicates that pheophytin *a* biomass was lower in the high B+P treatment in comparison with the low B+P treatment (density: $F_{1,92} = 0.10$, $P = 0.752$; treatment*density: $F_{2,92} = 4.43$, $P = 0.0145$). Additionally, both chlorophyll a and pheophytin a biomass results suggest that *Baetis* may be able to graze algae to lower levels than *Potamopyrgus.*

Discussion

Competition in the field

Densities of baetid mayflies (see Fig. 3.3 and 3.4) did not respond as strongly to high-densities of *Potamopyrgus* as I expected; i.e., I expected mayfly densities to be higher in low-snail reaches than in high-snail reaches at least during fall months as I observed in November 2000 (Cada and Kerans, in preparation). High variability among samples and between reaches undoubtedly decreased my ability to detect statistical differences between mean mayfly densities in high-snail and low-snail reaches.

It is important to note that “high” *Potamopyrgus* densities within our field study do not represent the range of densities that *Potamopyrgus* can attain in other locations (Kerans et al. in press, Hall et al. 2003). In a broader perspective, the densities observed in Darlinton Spring Creek would more correctly be considered “moderate”. As a result, the effect of *Potamopyrgus* on baetid mayflies in locations of “high” (i.e., > 50,000 m^{-2}) and extremely high (i.e., > 150,000 m^{-2}) densities could be much stronger and more apparent than observed in this study. Moreover, consequences of *Potamopyrgus* invasion at low (i.e., >10,000 m^{-2}) and very low densities (i.e., 1000-2000 m^{-2}) are largely unknown, although some evidence suggests that *Potamopyrgus* may positively affect macroinvertebrate colonization at very low densities (Schreiber et al. 2002). Consequently, to understand the circumstances under which *Potamopyrgus* has or does not have an effect, it will be valuable to ask similar questions as pursued in this study in locations where *Potamopyrgus* populations reach lower or higher densities.

I observed an unexpected decline in *Potamopyrgus* density in November 2002 followed immediately by a return to previously observed densities. Interestingly, *Acerpenna* densities follow this same trend in high-snail density reaches, which suggests a positive relationship between *Acerpenna* and *Potamopyrgus*. Concurrent with *Acerpenna* and *Potamopyrgus* declines, both *Diphetor* and *Baetis* densities reach high levels (see Fig. 3.4), which suggests a negative relationship between *Acerpenna-Potamopyrgus* and *Diphetor-Baetis*. However, these relationships are relatively weak and lack further support. Additionally, for *Potamopyrgus*, one plausible explanation for the drop in density may be burrowing behavior. Snails within the same family, Hydrobiidae, burrow in intertidal habitats to reduce physiological stresses (Race 1982), and Holomuzki and Biggs (2004) found some evidence that *Potamopyrgus* burrows in soft sediments to escape flooding disturbance. One reason *Potamopyrgus* might have chosen to burrow was the incidence of colder temperatures in October 2002 (compared with October 2003) (see Appendix C).

Life histories

Potamopyrgus densities and biomasses peaked during summer months of 2002 but reached their lowest levels in spring 2002 and 2003 (see Fig 3.3). *Potamopyrgus* reproduced year-round and did not exhibit clear cohorts (see Fig. 3.5a and b), which is consistent with other findings on *P. antipodarum* reproduction (Winterbourn 1970b). However, a pulse of reproduction may have occurred in the fall, with individuals growing throughout the winter, because the largest proportion of recently birthed individuals occurred from September to November 2002 (see Appendix A). This fall pulse of reproduction contradicts other observed peaks in reproduction, which were observed in spring or summer months (Winterbourn 1970b, Talbot and Ward 1987, Schreiber et al. 1998). By spring, this pulse of individuals reached reproductive size and dominated the population. Because *Potamopyrgus* can produce a new brood, at the most, every three months after reaching maturity (about 9 months age) (Winterbourn 1970b), several generations per year occurred in Darlinton Spring Creek. The number of embryos per reproductive individual (see Fig. 3.5c) were similar to the range reported in New Zealand (Winterbourn 1970b), Australia (Schreiber et al. 1998), and Europe (Strzelec 1999) indicating that *Potamopyrgus* fecundity in Darlinton Spring Creek was similar to its native and non-native habitats. In contrast to Darlinton Spring Creek, other locations in the United States may have greater fecundities because densities reach much higher levels. Thus, a comparison of *Potamopyrgus'* fecundity among non-native populations of varying densities may provide important insight on the limiting factors of *Potamopyrgus* as an invasive species in the western United States.

Potamopyrgus densities may have been lower in 2003 than 2002 because of biology and life history attributes or as a consequence of invasion dynamics. *Potamopyrgus* may be sensitive to cold temperatures (Hylleberg and Siegismund 1987), and an early, particularly low-temperature event may have decreased survival of individuals in late winter and early spring 2003 (see Appendix C). In support of this hypothesis, minimum and maximum temperatures in October were nearly three degrees cooler in 2002 than in 2003 (2.76-14.11 ºC and 5.42-17.59 ºC, respectively). However, Kerans et al. (in press) suggest that low temperatures are not the primary factor controlling *Potamopyrgus* densities in the upper Madison River because they observed winter declines in density in the Firehole River near thermal inputs; they propose that limited food availability may be the cause. Additionally, many invasive species exhibit dynamic population behavior with large cycles or experience a "boom and bust" where populations decline markedly after initial high abundances (Williamson and Fitter 1996). Furthermore, large intra-annual changes in *Potamopyrgus* densities have been observed (Dorgelo 1987, Schreiber et al. 1998). For example, densities in the River Ivel dropped from 65,900 m^{-2} in August to 5000 m^{-2} the following April (Heywood and Edwards 1962). Thus, it seems likely that variation in population density commonly occurs for *Potamopyrgus* and that the Darlinton population fluctuates temporally as some function of the winter environment (e.g., low primary productivity).

All three mayfly species exhibited patterns of abundance (see Fig. 3.4) and size-class distributions (see Appendix A) consistent with univoltine life history strategies. Young *Baetis* individuals (stage I) formed a large proportion of the population as early as

July and were the dominant life stage in fall and early winter (see Appendix A). *Baetis* individuals close to emergence and maturity (stage IV) were present over a wide range of months from late-winter through mid-summer suggesting that emergence occurred throughout these months and was not tightly synchronized. In contrast with *Baetis*, young *Diphetor* and *Acerpenna* individuals did not comprise a large proportion of the population until September and consisted of more than 90% of the population through February (see Appendix A). This indicates eggs began hatching in late summer and may have continued throughout winter. In addition, little if any individual growth occurred during winter months as mean head width did not change during that time period. Stage IV individuals of *Diphetor* and *Acerpenna* occurred from late spring throughout the summer, indicating emergence occurred primarily in summer months. *Diphetor* emergence may have begun slightly before *Acerpenna* (see Fig 3.6 and Appendix A). Differential timing of emergence between *Diphetor* and *Acerpenna* may be caused by different temperature requirements for developmental (Jackson and Sweeny 1995, Kosnicki and Burian 2003,) or could be a result of past competitive interactions (Connell 1980) and temporal habitat partitioning (Sweeny and Vannote 1981).

I observed little evidence that interactions between *Potamopyrgus* and baetids affect the size of mayflies when nearing emergence (see Fig 3.6), with the exception that stages III and IV *Diphetor* males were slightly larger in low-snail reaches than in high-snail reaches and that *Diphetor* females may have emerged earlier in low-snail reaches compared to high-snail reaches. A lack of effect is not surprising as I was unable to detect any effects of *Potamopyrgus* on density or biomass of baetids. However, the size of male baetids at emergence may be important to an individual's fitness, as size can be an important characteristic for mating success among some aquatic insects (*Baetis bicaudatis*: Peckarsky et al. 2002, caddisflies: Gullefors and Petersson 1993, stoneflies: Taylor et al. 1998, waterstriders: Ferguson and Fairbairn 2000). Furthermore, the size of female baetids at emergence is important to population dynamics as fecundity is closely related to size at emergence (Peckarsky et al. 1993). Thus, if interactions with *Potamopyrgus* affect size at emergence, population demographics and dynamics could be affected. Consequently, I think that exploration of the effects of competitive interactions between *Potamopyrgus* and baetids on mayfly size at emergence merits further research attention.

Effects on periphyton

In the field survey, both chlorophyll *a* and pheophytin *a* biomass were lower in high-snail reaches compared with low-snail reaches (see Fig 3.7), suggesting that *Potamopyrgus* exerted a negative effect on periphyton biomass, the hypothesized resource for which competition between *Potamopyrgus* and baetids occurs. Chlorophyll *a* and pheophytin biomass tended to track *Potamopyrgus* density from April 2002 through February 2003. However, periphyton biomass did not increase when *Potamopyrgus* density and biomass decreased markedly after February 2003, as one would expect when algae is released from heavy grazing pressure. The presence of other grazers may partially explain this inconsistency. Additionally, dramatic daily changes in water flow in Darlinton Spring Creek during summer months of 2003 (personal observation) could explain the especially low biomass of periphyton in July 2003. Water flow may have decreased periphyton biomass because the sloughing of algal cells from the substrata, especially senescent algae, increases with increasing flow (Peterson 1996). Because I did not observe a clear effect of *Potamopyrgus* on baetid mayflies in the field study, it seems likely that *Potamopyrgus* did not depress resources sufficiently to limit resources and strongly influence baetid densities.

There was not a clear difference between *Potamopyrgus* and *Diphetor* (see Fig. 3.9) or *Potamopyrgus* and *Baetis* (see Fig. 3.11) in the depression of periphyton biomass. In Experiment 1, *Potamopyrgus* tended to graze chlorophyll *a* biomass to lower levels than *Diphetor* whereas *Diphetor* tended to graze pheophytin biomass to lower levels than *Potamopyrgus*, but these trends were not statistically significant. When both species were combined, both chlorophyll *a* and pheophytin biomass were depressed to low levels. This suggests that *Diphetor* and *Potamopyrgus* may have differences in their food preference (i.e., *Diphetor* may prefer senescent cells over live ones and vice versa for *Potamopyrgus*) so that their niches only partially overlap. In contrast to *Diphetor*, *Baetis* depressed periphyton biomass to lower levels than *Potamopyrgus* in Experiment 2 (see Fig. 3.11). A better ability by *Baetis* in consuming periphyton at low levels of biomass agrees with data from a previous behavioral experiment where *Baetis* decreased the ability of *Potamopyrgus* to depress periphyton biomass (Cada and Kerans, unpublished data). A similar relationship between competing cogeneric snails, where one species employed “area intensive grazing” and the other employed “area extensive grazing,” was implicated as the mechanism for coexistence between these two competitors (Schmitt 1996).

Although there may be differences in foraging ability between baetids and *Potamopyrgus*, as suggested by these experiments, there may also be differences in assimilation ability. For example, some snails are more efficient at converting food resources to body tissues than other snails (Byers 2000). Furthermore, there is often a trade-off between ingestion and assimilation ability for grazers (Thorp and Covich 1991). Whether assimilation or ingestion abilities actually differ between *Baetis* and *Potamopyrgus* may influence or even mediate the interactions between these species in the natural environment.

Even though *Baetis* may be better able to graze periphyton at low levels of biomass relative to *Potamopyrgus*, *Baetis'* behavioral decisions may change the interaction between these species in the natural environment. *Baetis* is thought to actively enter the drift when food levels reach a certain threshold (Kohler 1985), and rather than remaining in an area of decreased periphyton biomass that results from the presence of *Potamopyrgus*, *Baetis* may choose to drift and seek areas of higher food availability. However, by choosing to drift *Baetis* increases its probability of death by predation, decreases the relative amount of time spent foraging, and risks drifting to an unsuitable habitat, all of which may ultimately decrease fitness.

Competition experiments

For *Potamopyrgus*, I generally observed negative effects of baetid mayflies on survivorship but not on growth (see Fig. 3.8 and 3.10). For survivorship, I did not observe differences between low and high densities when *Potamopyrgus* was alone, indicating a lack of intraspecific competition at the densities investigated in this study. In contrast, *Potamopyrgus* survivorship was greater in treatments without *Baetis* or *Diphetor* than treatments with the competitors, which indicates interspecific competition. In the first experiment, *Potamopyrgus* growth tended to be greater in the presence of *Diphetor* than when alone, which may indicate either a release from intraspecific competition or facilitation. In contrast to the first experiment, *Potamopyrgus* growth decreased from low to high density treatments, indicating intraspecific competition. Additionally, I did not observe an effect of *Baetis* on *Potamopyrgus* growth.

Potamopyrgus negatively affected the survivorship but not the growth of *Diphetor* (see Fig. 3.8). For *Baetis*, I did not observe an effect of conspecific density on survivorship, which indicates a lack of intraspecific competition (see Fig. 3.10). However, *Baetis* survivorship was lower in combination treatments with *Potamopyrgus* , indicating the presence of interspecific competition (see Fig. 3.10). Additionally, high and low densities with *Potamopyrgus* did not differentially affect *Baetis* survivorship, indicating that the intensity of competition did not increase as density increased. In contrast to survivorship, I did not detect any effects of *Potamopyrgus* on *Baetis* growth, either intra- or interspecific.

One reason I did not detect any effects of *Potamopyrgus* on the growth of *Diphetor* or *Baetis* was the low survivorship of mayflies in the experiments. Low survivorship resulted in fewer individuals from which to estimate growth in each replicate; i.e., a small sample size. Additionally, if I assume that only the most healthy individuals survived, these may be less affected by competition than by unhealthy individuals and result in a biased sample. Furthermore, baetid mortalities may have decreased densities sufficiently to reduce density-dependent effects upon growth.

Conclusions

Contrary to previous research (Cada and Kerans, in preparation), this study does not demonstrate a strong effect of *Potamopyrgus* on the density or biomass of baetid mayflies in the field. Factors such as high levels of patchiness (Simon and Townsend 2003) and environmental variation, in combination with the invasion process, may decrease the ability to detect the effects of species interactions at a larger spatial scale (Kerans et al. in press). In addition, my field observations did not separate different types of interactions between *Potamopyrgus* and baetid larvae, which could be a combination of both negative and positive interactions of differing magnitudes that sum to a smaller net negative interaction (Berlow 1999). Similarly, competitive interactions between closely related species, such as between baetid species, may obscure the responses of baetids to *P. antipodarum.* Furthermore, periphyton is not the only resource for which *Potamopyrgus* may compete with baetid mayflies. Space is likely to be an important factor because high densities of *Potamopyrgus* will limit habitat availability (Zaranko et al. 1997, Kerans et al. in press).

In contrast to the field observations, the competition experiments demonstrated a negative effect of *Potamopyrgus* on baetid mayfly survivorship. Decreased survivorship may affect population dynamics of baetid species and may ultimately have negative implications for the persistence of some mayfly populations in the presence of *Potamopyrgus*. However, these experimental results do not agree with my field observations, which indicated no effect of *Potamopyrgus* on baetids. Experimental results do not always agree with observational studies because factors operating at a large spatial scale may overwhelm the importance of small-scale factors (Peckarsky et al. 1997, Thrush et al. 1997). Additionally, extrapolation of results from an experiment to the population or community level may also be affected by species interactions (Billick and Case 1994) that aren't included within the experiment.

My competition experiments also demonstrated a negative effect of baetid mayflies on *Potamopyrgus* survivorship, which may adversely affect the degree of success of *Potamopyrgus* populations. That is, *Potamopyrgus* densities in Darlinton Spring Creek may be limited, at least in part, by competition with baetids. This relationship is known as the "biotic resistance hypothesis" and has been proposed as one way to understand why invasion success varies (Baltz 1993).

Experiments and observations in this thesis also showed that *Potamopyrgus* can depress periphyton food resources, but whether to a level that limits other species will depend upon biological attributes and competitive abilities of each species.

Because this study does not demonstrate an effect of *Potamopyrgus* on baetid mayflies in the field but does indicate that *Potamopyrgus* can negatively affect baetid survivorship, it forces the question—"under what circumstances might *Potamopyrgus* affect baetids, as well as other macroinvertebrates?" One working hypothesis is that *Potamopyrgus* does not negatively affect baetids until densities reach a certain level—perhaps >50,000 or >100,000 m^{-2}. An additional hypothesis may be that the effect of *Potamopyrgus* on baetids may change over time, having a greater effect during times of lower productivity (winter) or during different developmental ages of baetid larvae. For *Potamopyrgus*, as well as other invasive species, this question is important to ask and answer so that accurate predictions about the consequences of the invasive species can be made. Furthermore, I want to caution against interpreting the results of this study to mean that *Potamopyrgus* will not have an effect in other invaded locations.

CHAPTER 4

TROPHIC EFFECTS OF THE NEW ZEALAND MUD SNAIL, *POTAMOPYRGUS ANTIPODARUM,* ON A TROUT AND A SCULPIN SPECIES

Introduction

Trophic cascades (Hairston et al. 1960, Paine 1980) and tri-trophic interactions (Price et al. 1980), the propagation of effects by a species to other species via an intermediate species, are important structuring mechanisms in aquatic communities (Bronmark et al. 1997). With the arrival of invasive species, trophic cascades have caused dramatic changes in ecosystems because invasive species interact with organisms in many trophic levels, radiating throughout the community (Strayer et al. 1999, Vander Zanden et al. 1999, Mooney and Cleland 2001). For example, the establishment of the zebra mussel, *Dreissena polymorpha,* caused decreased abundance of planktivorous filtering organisms, increased abundance of detritivorous collecting organisms, and even affected fish population sizes in the Hudson Bay ecosystem (Strayer et al. 1999, Strayer 1998). Flecker and Townsend (1994) reported that non-native brown trout (*Salmo trutta*) in New Zealand not only displaced native galaxiids (Galaxiidae) but caused a top-down trophic cascade where insect density decreased and algal biomass increased. Thus, understanding how invasive species interact with organisms in multiple trophic levels increases our ability to predict the effects an invasive species will have in an ecosystem.

Potamopyrgus antipodarum is an invasive gastropod that may interact with species in multiple trophic levels, possibly causing changes that radiate through a community. In the western United States, *Potamopyrgus* populations commonly reach high densities (e.g. 200,000m^{-2} to 800,000 m^{-2} Kerans et al. in press, Hall et al. 2003), and through the occupation of habitat and antagonistic encounters, may exclude other macroinvertebrates. In addition, *Potamopyrgus* shares food resources with many aquatic macroinvertebrates, particularly grazers (Cummins and Klug 1979, Haynes and Taylor 1984, Thorp and Covich 1991, Dorgelo et al. 1995), and it may limit primary food resources when densities are high, resulting in competition for food. Consequently, the effects *Potamopyrgus* exerts either directly or indirectly on primary producers as well on primary and secondary consumers may propagate through the food-web. Directly, the edibility and food quality of *Potamopyrgus* may be poor (Haynes et al. 1985) for benthic and drift feeding fishes (e.g., sculpin and trout) in western U.S. streams and rivers. Indirectly, competitive interactions between *Potamopyrgus* and macroinvertebrates may reduce food availability for consumers of those macroinvertebrates, which is problematic for fishes if *Potamopyrgus* does not replace those macroinvertebrates as a quality food resource.

Although *Potamopyrgus* almost certainly provides a food resource for native fishes such as *Gobiomorphys* spp. (Levri 1998) in New Zealand, as well as nonnative species such as *Anguilla* spp. (Ryan 1982), the role of *Potamopyrgus* as a prey item in western U.S. streams is unclear. *Potamopyrgus* potentially represents a poor quality food resource for many fishes primarily because the operculum closes the shell aperture and creates a tight seal (Winterbourn 1970a, 1970b), which prevents digestive fluids from acting on tissue. For example, *Potamopyrgus* survived six hours in the digestive system of rainbow trout, *Oncorhynchus mykiss,* and subsequently birthed live young (Haynes et al. 1985). On the other hand, trout with extended gut-retention time may be able to digest through the shell and assimilate nutrition and energy from *Potamopyrgus.* Because *Potamopyrgus*' operculum acts as a predator defense mechanism, feeding on *Potamopyrgus* could reduce the nutritive value and energy assimilation in an individual fish's diet, negatively affecting body growth and allocation of resources to reproduction. Furthermore, it is unclear whether salmonids consistently feed on *Potamopyrgus* (Winterbourn 1970b, Death 1991, Sagar and Glova 1995, Levri 1998, Wells and Clayton 2001, W.P. Dwyer, USFWS, personal communication).

Potamopyrgus may indirectly affect secondary consumers that rely on macroinvertebrates as a food source (e.g., predatory stoneflies and beetles, benthic and drift feeding fishes). That is, interference and exploitative competition between *Potamopyrgus* and other macroinvertebrates can reduce the density of macroinvertebrates during certain times of the year (Cada and Kerans, in preparation), which may limit food availability for secondary consumers. Consequently, secondary consumers may experience reduced growth and fecundity when *Potamopyrgus* does not function as a quality food resource.

To explore the potential effects of *P. antipodarum* on secondary consumers, I estimated growth of two fish species, *Salmo trutta* (brown trout) and *Cottus bairdi* (mottled sculpin), in areas with high and low densities of *Potamopyrgus*. I chose these species because they feed on macroinvertebrates, are abundant in southwestern Montana, and are important as game or prey fishes. *Salmo trutta* has been widely introduced in the

United States because of its popularity as a game fish and has been in the Madison River since 1889 (Brown 1971). *Cottus bairdi*, the only native sculpin in southwestern Montana, is also abundant and widely distributed east of the continental divide (Brown 1971). Both species rely on aquatic invertebrates as a food source but feed using different methods: *S. trutta* mostly pick from the drift (Elliot 1973) whereas *C. bairdi* remove invertebrates from the benthos (Dineen 1951). Additionally, trout lack pharyngeal teeth (Brown 1971) which molluscivorous fishes use to crush shells (Bond 1996), but sculpin have palatine teeth (Bond 1996, Brown 1971), which may confer the ability to crush shells and thus use *P. antipodarum* as a food source. As a result of these differences between *S. trutta* and *C. bairdi*, decreased macroinvertebrate densities and biomasses might translate differently to each species. Furthermore, both species are also prey for many different organisms including larger fish, aquatic mammals, many species of birds, and even snakes (Wilzbach et al. 1986) and thus form an important component of Rocky Mountain ecosystems.

My objectives were to 1) estimate the difference in growth for both species of fish, in areas with high and low densities of *Potamopyrgus*, 2) determine whether *S. trutta* or *C. bairdi* fed upon *P. antipodarum,* and 3) compare the diet for both species of fish between areas with high and low densities of *Potamopyrgus*.

Methods

I compared fish growth and diet in Darlinton Spring Creek, Montana (see Chapter 2 for study site description, Fig. 2.1) between reaches with low and high densities of *Potamopyrgus antipodarum* (hereafter referred to as high-snail or low-snail). To estimate the effects of *P. antipodarum* density on the growth rates of *Salmo trutta* and *Cottus bairdi,* I used an *in situ* enclosure experiment in high-snail (n=3 enclosures per fish species) and low-snail reaches (n=3 enclosures per fish species). Enclosures were constructed from 2.5 x 3.8 cm wooden frames to dimensions of 61 x 61 x 30.5 cm for *C. bairdi* and 61 x 91.5 x 91.5 cm for *S. trutta* and were wrapped with 0.85 cm nylon-netting or 0.64 cm hard-wire cloth, respectively. Bottoms and tops of enclosures were covered with nylon window-screening rather than netting or hard-wire cloth. I placed trout enclosures near the thalweg and added several large cobbles and a willow-bunch (*Salix* spp.) to provide a flow-refuge (Wilzbach et al. 1986). I placed sculpin enclosures in riffles and covered the bottom with pebbles to provide suitable habitat (Hendricks 1997). Both enclosure types were secured to rebar posts driven into the stream bed. The rebar posts, about 30 cm upstream of each enclosure, also supported chicken-wire that served to reduce clogging of the enclosures' mesh and improve water flow within enclosures. All mesh was cleaned of debris every 2-3 days throughout the duration of the experiment. I measured water flow at the front and rear of each enclosure using a Swoffer 3000 flow meter and measured physicochemical water conditions at each enclosure using a Yellow Springs Instrument (physicochemical data are presented in Appendix E).

I collected age-0 brown trout (*Salmo trutta*, 7 cm length) and sculpin (*Cottus bairdi*, 7-12 cm length) for the enclosures by electrofishing 1 July 2003. Fishes were anesthetized using MS-222 for handling. For each individual, I measured fork length (nearest mm) and wet mass (nearest 0.1 g) at the beginning and the end of the experiment (Wilzbach et al. 1986). Three sculpin per enclosure were stocked 1 July 2003, and 5 *S.*

trutta per enclosure were stocked on 2 July 2003, after being held overnight within Darlinton Spring Creek. Abrupt changes in water level between 9 July and 14 July disrupted two enclosures containing *S. trutta* (one high-snail and one low-snail), and individuals were redistributed within high-snail or low-snail enclosures so that enclosures thereafter contained only 3 *S. trutta*. I terminated the sculpin experiment 31 July 2003 and the trout experiment 6 August 2003.

I estimated daily growth of *S. trutta and C. bairdi* according to Equation 4.1 (Busacker et al. 1990). I used 2-way ANOVA to compare growth between species (trout and sculpin) and between snail treatments (low and high density).

$$\text{Growth (g)} = \ln(\text{weight final} - \text{weight initial})/\text{days in experiment} \qquad \text{Eq. 4.1}$$

To determine whether *C. bairdi* and *S. trutta* in Darlinton Spring Creek feed on *P. antipodarum*, I used gastric lavage (Bowen 1983) to examine the stomach contents of 29 *S. trutta* and 18 *C. bairdi*, which were caught by electrofishing on 1 July 2003 (these stomach samples hereafter referred to as from the stream “channel”). These stomach contents were used as a reference-diet that I compared to the diets of fish held in the enclosures. To assess differences in fish diet between reaches with high and low densities of *Potamopyrgus*, I used gastric lavage to obtain stomach contents of *S. trutta* and *C. bairdi* at the end of the enclosure experiment (these stomach samples hereafter referred to as from the “experiment”). All stomach contents samples were preserved in Kahle’s solution (Pennak 1978) and then stored in 70% ethanol. I identified and enumerated invertebrates to family for insects and to order for non-insect taxa, except *Potamopyrgus antipodarum*, according to Merritt and Cummins (1996).

To assess changes in the fishes' diets associated with the presence of *Potamopyrgus*, I compared three metrics among high- and low-snail enclosures and the fish collected from the stream channel. From the stomach contents data of both fish species, I calculated the mean number of prey individuals per fish, the mean number of taxa per fish, and the relative abundance of taxa in stomach samples from both the stream channel and the experiment. I used 2-way ANOVA with the factors species (trout or sculpin) and snail (low-snail enclosures, high-snail enclosures, and high-snail from the stream channel) to compare the mean number of prey and the mean number of taxa. The additional level for the snail factor, designated as high-snail from the stream channel, tested for an enclosure effect. For the third metric, I contrasted the relative abundance of taxa in stomach samples from high- and low-snail enclosures and from the stream channel.

To compare *Potamopyrgus* and other macroinvertebrate densities between high- and low-snail enclosures, I sampled macroinvertebrates from the sculpin enclosures using cobble samples (n=3 per enclosure) according to the same procedures in Chapter 3. Because I assumed that food availability of macroinvertebrates in trout enclosures was directly dependent on the composition of the drift, benthic macroinvertebrate densities within trout enclosures were not sampled. I compared the mean density of *Potamopyrgus* and of macroinvertebrates (all taxa excluding *Potamopyrgus*) in sculpin enclosures using 2-way ANOVA with a factor named snail (high or low density of *Potamopyrgus*) and a factor to include a nested enclosure effect. I was able to assess the effects of the enclosures on the density of macroinvertebrates by comparing the mean density of

Potamopyrgus and Baetidae between high-snail sculpin enclosures the stream channel (high-snail reaches only) using two-sample t-tests. For stream channel macroinvertebrate densities, I used samples from August 2003 that were obtained as a component of Chapter 3. Baetidae was used as a response variable, rather than total macroinvertebrate density, because macroinvertebrate samples in Chapter 3 were analyzed for the taxon Baetidae.

Results

Fish Growth

In the growth experiment, *S. trutta* gained weight whereas *C. bairdi* lost weight (Fig. 4.1; species effect $F_{1,6} = 14.16$, $P = 0.0094$). Although growth for both species appeared higher in the low-snail reaches, there was no difference in between snail reaches for either species (snail effect $F_{1,6} = 1.58$, $P = 0.2553$; species*snail interaction $F_{1,6} = 0.0$, $P = 0.9646$).

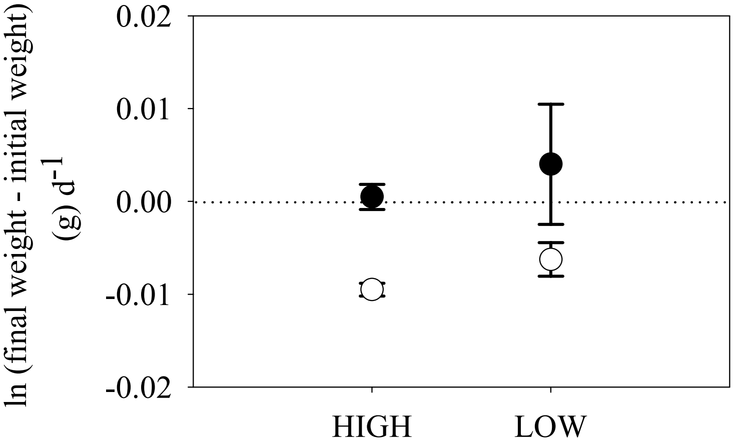
Potamopyrgus as a food source

Potamopyrgus was found in one stomach out of all stomach samples (from the channel and from the experiment) for both *C. bairdi* and *S. trutta* (n=27 and n=42, respectively). The *Potamopyrgus* individual, less than 0.5 mm shell-length, was in the stomach of a 23 cm (fork-length) *S. trutta* captured from the stream channel that was not used in the enclosure experiment; all other *S. trutta* were small (6.0 – 9.4 cm fork length).

Fish diets

For stomach samples obtained from fishes in the stream channel, only 1 of 29 *S. trutta* had an empty stomach, and all *C. bairdi* (n=17) contained at least 1 prey item. In the enclosures, there were 4 out of 13 *S. trutta* with 0 prey in their stomachs (evenly distributed between high- and low-snail enclosures), and there were 2 out of 10 *C. bairdi* with 0 prey in their stomach samples, both from the high-snail enclosures.

Figure 4.1. Comparison of fish growth in high-snail and low-snail density reaches from the enclosure experiment for *Salmo trutta* (filled circles) and *Cottus bairdi* (open circles). The dotted line represents no growth; above it is weight gain and below it is weight loss.



The number of prey per fish (mean ± 1 SE) did not differ between *S. trutta* (8.1 ± 1.5) and *C. bairdi* (5.9 ± 1.8) ($F_{1,63}$=0.73, P=0.3951) and there was not a species*snail interaction ($F_{2,63}$=0.12, P=0.8849). However, there were fewer prey items per fish in the high-snail (2.1 ± 0.58) and low-snail enclosures (2.3 ± 1.0) than in the stream channel (9.8 ± 1.6) ($F_{2,63}$ = 12.73, P < 0.0001), but the high-snail and low-snail enclosures did not differ.

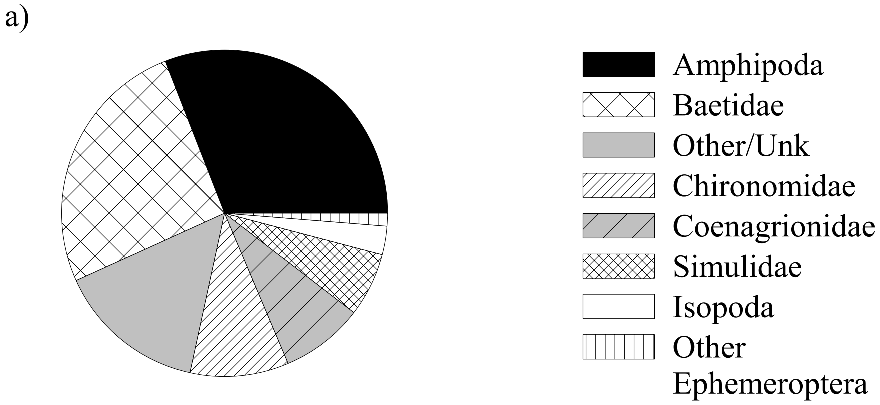
Similarly, the number of taxa per fish (mean ± 1 SE) was not different between *S.*

trutta (2.8 ± 0.32) and *C. bairdi* (2.3 ± 0.32) ($F_{1,63}$=0.14, P=0.7092), and there was not a species*snail interaction ($F_{2,63}$=0.2, P=0.8220). The mean number of taxa per fish was greatest in the stream channel (3.3 ± 0.28) than in the high-snail (1.4 ± 0.38) or low-snail enclosures (1.0 ± 0.19) ($F_{2,63}$=14.45, P<0.0001), but the enclosures did not differ.

For *S. trutta* from the stream channel, Amphipoda and Baetidae composed more than 50% of the macroinvertebrates in the stomachs. (Fig 4.2 a). *Salmo trutta* stomachs also contained a diverse assemblage of macroinvertebrates, as indicated by the relatively large percentage in the Other/Unk category. Similar to *S. trutta*, Amphipoda (38%) were the most abundant prey item of *Cottus bairdi* (Fig. 4.2 b) from the stream channel. In contrast to *S. trutta*, Isopoda instead of Baetidae, composed a large percentage of macroinvertebrates (32% and 13 % respectively) in the stomach samples of *C. bairdi*.

Similar to *S. trutta* samples from the stream channel, Baetidae was a large component of the *S. trutta* diet in both high- and low-snail enclosures (Fig. 4.3). *Salmo trutta* stomachs in high-snail enclosures contained few Amphipoda in comparison with stomachs in low-snail enclosures and with samples from the channel (Fig 4.3 a & b). In contrast to the stomach contents of *C. bairdi* from the stream channel, Amphipoda were not present in sculpin stomachs at the end of the experiment, and Isopoda did not comprise a large percentage of the stomach contents for samples from the high-snail enclosures (Fig. 4.3 c & d). Baetidae and Chironomidae composed the largest proportion of *C. bairdi* diet in high-snail reaches, but Baetidae did not occur in stomach samples in low-snail reaches. The stomach contents from the low-snail enclosures were different from those in the high-snail enclosures; they contained only two taxa, Isopoda and Chironomidae.

Figure 4.2. The relative abundance of macroinvertebrates in stomach samples of *Salmo trutta* (a) and *Cottus bairdi* (b) taken from the stream channel.



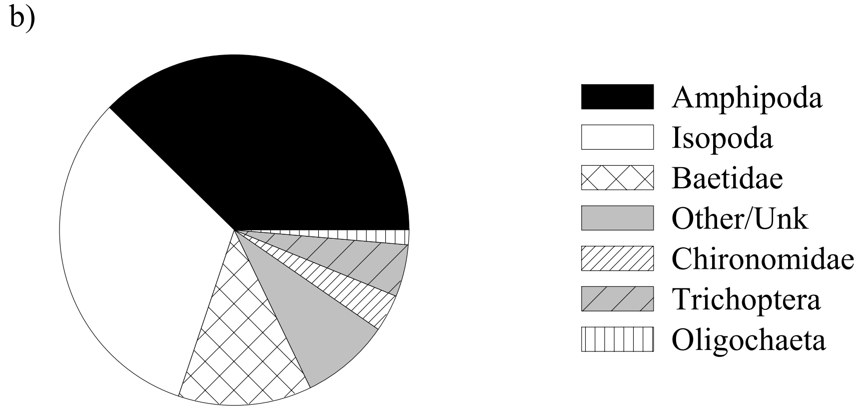
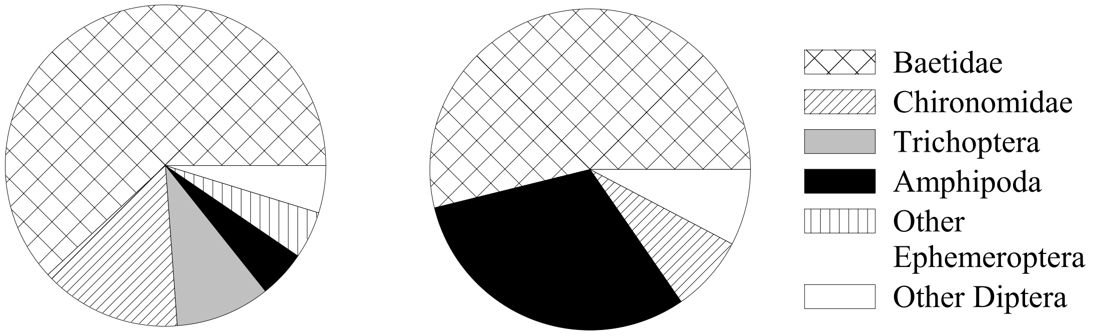


Figure 4.3. The relative abundance of macroinvertebrates in stomach samples from the end of the enclosure experiment for *Salmo trutta* in high- (a) and low-snail (b) reaches and for *Cottus bairdi* in high- (c) and low-snail (d) reaches.

Salmo trutta

a) high-snail

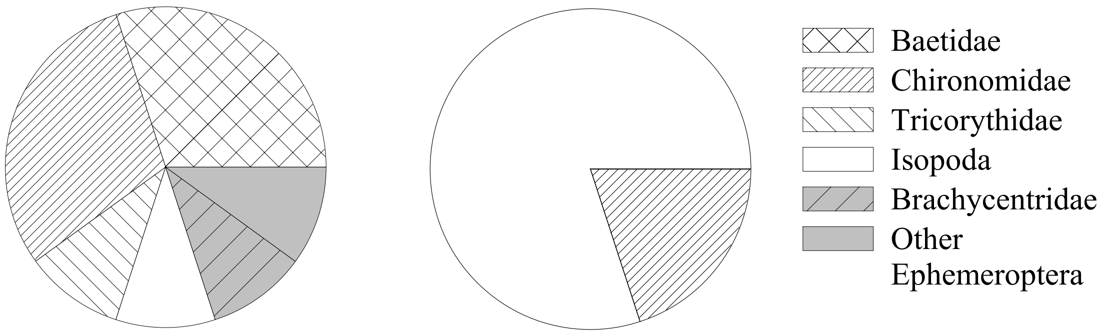
b) low-snail



Cottus bairdi

c) high snail

d) low snail



Macroinvertebrates

In the sculpin enclosures, the density of *Potamopyrgus antipodarum* was greater in the high-snail enclosures than in the low-snail enclosures (Table 4.1) ($F_{1,12} = 59.54$, $P < 0.0001$).

Table 4.1. Comparison of benthic macroinvertebrate density between sculpin enclosures in high-snail (n=9) and low-snail (n=9) reaches in Darlinton Spring Creek, July, 2003. Data are presented as the number per m^2 (mean ± 1SE) and relative abundance (%). Values marked with * indicate the percentage of the community represented by *Potamopyrgus* when *Potamopyrgus* is included in the calculations, whereas all other relative abundance values represent the percentage of the community when *Potamopyrgus* density is excluded.

	High snail				Low snail			
Taxa	Number			%	Number			%
Potamopyrgus antipodarum	8174	±	1745	60*	381	±	292	7*
Lymnaedae	248	±	66	5	137	±	93	5
Baetidae	387	±	86	7	339	±	109	7
Other Ephemeroptera	367	±	181	7	326	±	90	7
Chironomidae	1536	±	329	28	1976	±	274	41
Other Diptera	85	±	38	2	337	±	157	7
Trichoptera	1571	±	731	29	858	±	218	18
Elmidae	126	±	40	2	12	±	12	<1
Amphipoda	59	±	43	1	41	±	30	<1
Oligochaeta	9	±	9	<1	0	±	0	<1
Isopoda	27	±	27	<1	19	±	19	<1
Copepoda	356	±	120	7	520	±	139	11
Acari	273	±	207	5	19	±	19	<1
Turbelleria	336	±	247	6	47	±	24	<1
Terrestrial	68	±	39	1	117	±	35	2
Unknown	0	±	0	0	68	±	45	1
Total excluding *Potamopyrgus*	5448	±	1401		4816	±	630	

However, I did not detect a difference in the mean density of macroinvertebrates (excluding *Potamopyrgus*) between high-snail and low-snail enclosures (Table 4.1) ($F_{1,12} = 0.02$, $P = 0.8923$). The mean density of *Potamopyrgus* in the high-snail enclosures (Table 4.1) was similar to the mean density of *Potamopyrgus* in the stream channel (8443 ± 1506), but the mean density of Baetidae in the enclosures (Table 4.1) was lower than their density in the stream channel (1418 ± 194.6) ($t_{48} = 2.94$, $P = 0.005$).

Trichoptera and Chironomidae dominated the macroinvertebrate assemblage in both high-snail and low-snail enclosures (Table 4.1). Both Amphipoda and Isopoda, which were an abundant component in sculpin stomach samples prior to the experiment (Fig 4.2), were at low densities in the enclosures and were less than 1% of the invertebrate assemblage (Table 4.1).

Discussion

In the enclosure experiment, the growth of *S. trutta* and *C. bairdi* was not influenced by the density of *P. antipodarum*, and the fish did not eat more prey or more taxa in high-snail enclosures compared to low-snail enclosures. In addition, enclosure effects reduced the number of prey eaten per fish and the number of taxa eaten per fish. Contrary to the responses of fish growth, diet quantity and diet diversity, the diet composition of both *S. trutta* and *C. bairdi* differed between high- and low-snail enclosures. Furthermore, I found little evidence that *S. trutta* or *C. bairdi* consistently fed on *Potamopyrgus*.

The inability to detect a snail-effect on the growth of *S. trutta* or *C. bairdi* can be attributed to several factors. The variability due to the snail-effect was small relative to the variability due to other effects. Additionally, the small sample size for *C. bairdi*, which was caused by mortality in some replicates, probably contributed as well. Because densities of *Potamopyrgus* were relatively low prior to and during the enclosure experiment (see Fig 3.3), there were no differences in baetid density in high- and low-snail reaches (see Table 3.4) nor were there differences between Baetidae density or total invertebrate density between high-snail and low-snail enclosures (see Table 4.1). Under these circumstances, food availability should be equally abundant in high- and low-snail reaches and there would not be a snail-effect to detect. This experiment clearly needs replication in order to increase sample size and reduce variability, as well as to occur when *Potamopyrgus* densities are relatively high.

I did not detect differences between the mean number of prey (quantity) or the mean number of taxa (diversity) between high- and low-snail enclosures, which may be due to a lack of difference in macroinvertebrate density between the enclosure types. Although I lack data on the benthic macroinvertebrate density in trout enclosures and on the quantity of macroinvertebrate drift, densities in the sculpin enclosures indicate there was not a difference between high- and low-snail enclosures. This indicates that macroinvertebrate densities were not negatively associated with high-densities of *Potamopyrgus* during this experiment. In further support of this hypothesis, densities of Baetidae were not lower in high-snail than in low-snail reaches (see Chapter 3). On the other hand, densities of *Potamopyrgus* during the experiment were relatively low in comparison with previous observations in Darlinton Spring Creek and in the Madison

River, and as a consequence, any effect on macroinvertebrate abundance would be negligible.

Despite a lack of difference in the growth, prey quantity, and prey diversity, I observed differences in diet composition between high- and low-snail enclosures for both *S. trutta* and *C. bairdi* (see Fig 4.3). This might indicate that individuals are adjusting their diet to the relative abundance of macroinvertebrates to compensate for decreases in food type and availability associated with *Potamopyrgu.s* A shift in diet between high-snail and low-snail areas would not necessarily translate to a change in growth for fishes in high-snail reaches if macroinvertebrates are similar in food quality. However, the similarity of macroinvertebrate density in high-snail and low-snail enclosures does not support the hypothesis that fishes are adjust their diet due to changes associated with *Potamopyrgus*. It may simply be that diet variation within and among individuals accounts for the observed differences in diet composition between high- and low-snail reaches.

Based on the macroinvertebrate composition eaten by the fish, it appears that *S. trutta* and *C. bairdi* showed strong selection for Amphipoda and Isopoda, respectively (see Fig. 4.3). That is, densities of Amphipoda and Isopoda comprised only a small percentage (<1%) of the macroinvertebrates in the enclosures, but they composed a relatively large component of the fishes' stomach contents, which suggests that *S. trutta* and *C. bairdi* selectively fed upon these taxa. This is not surprising as both crustacean taxa are a common component of salmonid (Ware 1972) and sculpin diets (Dahl 1998). However, what appears as strong selection for Amphipoda and Isopoda as prey may be misleading because they could be more abundant in the environment than indicated by our data. The method of macroinvertebrate sampling may not be adequate for collection of these highly mobile taxa, and I could have underestimated the densities of these taxa. Thus, the fishes might not have preferentially selected Amphipoda and Isopoda but fed in proportion to the prey's abundance in the environment.

The diets of *S. trutta* and *C. bairdi* suggest that the enclosures negatively affected prey quantity and diversity. The abundance of potential prey within the enclosures may have decreased due to predatory mortality (Flecker 1984, Englund and Olsson 1996) or antipredator behavior (Peckarsky 1980, Huhta et al. 2000). For example, mayflies actively drift as a result of contact with predators (Peckarsky 1980). In addition, the cage structure may have strongly affected food availability because the mesh of the enclosures quickly clogs with organic debris, resulting in decreased macroinvertebrate drift within the enclosures. This would decrease food availability for *S. trutta* as well as negatively affect colonization of macroinvertebrates into the enclosures.

Limited food availability within the enclosures may have had negative consequences for *C. bairdi* because individuals lost body mass over the course of the experiment. Food limitation may also have starved several *C. bairdi* in the enclosure experiment, resulting in their death. Because several *C. bairdi* were held in each enclosure, intraspecific competitive interactions (Resetarits 1995) likely exasperated any food limitation caused by the enclosures. Repetition of this experiment with lower stocking abundance per enclosure (e.g., 1 individual per enclosure) should reduce food limitation and intraspecific competition and consequently increase the success of this experiment. In contrast to *C. bairdi, Salmo trutta* seemed to be less affected by food limitation in the experiment because they tended to gain weight. Trout are generalist feeders and can adjust to what is available (Giroux et al. 2000). By shifting or expanding their diet composition, they may be able to fulfill energy requirements. Consequently, trout may be able to compensate for reductions in macroinvertebrate density that is correlated with *Potamopyrgus* density.

In addition to fewer prey per fish, I observed a diet shift between stomach samples collected in the stream channel (see Fig 4.2) and in the enclosures for both *S. trutta* and *C. bairdi* (see Fig 4.3). This diet shift could be an artifact of reduced densities and community composition differences in the enclosures compared to the channel. However, the time difference between the diet samples from the channel and from the enclosures was approximately 1 summer month. Because warm temperatures speeding up insect development (Wallace and Anderson 1996), macroinvertebrate communities change rapidly during summer months. Thus, the macroinvertebrate community in Darlinton could have changed dramatically between the two diet samplings, causing the differences in diet composition between the channel and the enclosures.

This study suggests that some fishes in Montana do not utilize *Potamopyrgus* as a food resource. Both *C. bairdi* and *S. trutta* were initially collected from a stream reach abundant with *Potamopyrgus* (>50,000 m^{-2}, personal observation), yet only one fish (23 cm *S. trutta*) contained *Potamopyrgus.* Moreover, *C. bairdi* did not contain *Potamopyrgus* in their stomach contents from the enclosure experiment even though they were losing weight and *Potamopyrgus* was abundant in the enclosures.

Potamopyrgus might not be expected as a prey item of *S. trutta* and other salmonids because salmonids feed primarily from the drift. However, *Potamopyrgus* can be present in the drift (Sagar and Glova 1995) and exhibits active drift behavior in experimental situations (personal observation). Moreover, salmonids tend to be generalist and opportunistic feeders and often feed upon those prey that are abundant (Giroux et al. 2000).

Salmo trutta in this study may have been biased against *Potamopyrgus* because we used age-0 individuals, which might not be able to consume *Potamopyrgus* due to of the size of *Potamopyrgus* relative to mouth size. However, juvenile *S. trutta* may only be gape-limited for medium to full-sized *Potamopyrgus,* with age-0 *S. trutta* being capable of feeding on small *Potamopyrgus.* For example, juvenile *S. trutta* (≥10 cm) fed on small individuals (2 mm length) of the gastropod *Lymnaea peregra,* and as trout length increased, the size of *L. peregra* eaten increased multiplicatively (Steingrimsson and Gislason 2002). Thus, larger juveniles (20-30 cm) and adult *S. trutta* should not find the size of *Potamopyrgus* a limiting factor as a potential prey item. Furthermore, because fishes commonly exhibit ontogenetic diet shifts caused by factors other than mouth size (e.g., improvement of coordination, changes in habitat-use) (Wootton 1990), a lack of feeding on *Potamopyrgus* by age-0 *S. trutta* does not necessarily indicate that older individuals will continue to ignore *Potamopyrgus* as a food source.

In conclusion, I did not find evidence supporting the hypothesis that decreased fish growth is associated with high densities of *Potamopyrgus*. Because of the relatively small sample sizes used in the growth experiment, I am currently repeating this experiment to increase statistical power and to clarify these results. Furthermore, this study does not support the hypothesis that *S. trutta* or *C. bairdi* feed on *Potamopyrgus*. However, in areas with extremely high densities of *Potamopyrgus* (e.g., 100,000 m^{-2}), *Potamopyrgus* may have a dramatic effect on the abundance of other macroinvertebrates and consequently negatively affect fish growth.

CHAPTER 5

CONCLUSIONS

The field survey results from Darlinton Spring Creek in Chapter 3 demonstrated that *Potamopyrgus* did not have an effect on the density or biomass of mayflies in the family Baetidae. Densities of baetids were not greater in high-snail reaches compared to with low-snail reaches. However, closer post-hoc examination of individual time periods where there appeared to be a difference in baetid density and biomass between low- and high-snail reaches showed that *Baetis* was negatively associated with *Potamopyrgus* whereas *Acerpenna* was positively associated with *Potamopyrgus* during some time periods. *Diphetor* was not significantly associated with *Potamopyrgus*. Thus, related species such as *Baetis* and *Acerpenna* may exhibit completely different responses to an invading species. Furthermore, two-species interactions can be changed by other species within the community. For example, competitive interactions between *Baetis* and *Potamopyrgus* that negatively influence the abundance of *Baetis* may reduce competitive interactions between *Baetis* and *Acerpenna*. Therefore, a species in a multi-species competitive assemblage may exhibit a different response to competition with *Potamopyrgus* than the same species would exhibit when isolated in an environment with *Potamopyrgus*.

From the field survey in Darlinton Spring Creek, I also showed that *Potamopyrgus* did not have an effect on the size (head-capsule) of baetids in Darlinton Spring Creek. However, *Diphetor* males were one exception because their size was greater in low-snail reaches than in high-snail reaches. Small male body size can decrease mating success (Peckarsky et al. 2002), although whether the difference in size was biologically significant is unknown. Thus, these results suggest that *Potamopyrgus* had little influence on size-at-emergence. Because female size-at-emergence is positively correlated with fecundity (Peckarsky et al. 1993), my results do not indicate that interactions with *Potamopyrgus* decreased baetid fitness in the natural environment. However, my examination of the potential effects that *Potamopyrgus* may have on baetid size-at-emergence was not thorough, and I think that this warrants further attention because size-at-emergence is an important variable to baetid population dynamics.

In contrast to the field survey, the experimental manipulations of *Potamopyrgus* and *Baetis* or *Potamopyrgus* and *Diphetor* in Chapter 3 suggest that competitive interactions can negatively affect both baetids and *Potamopyrgus*. *Baetis* survivorship was greater in high density treatments that contained only conspecifics in comparison with high-density treatments that contained equal numbers of conspecifics and *Potamopyrgus*. *Baetis* growth was not affected by conspecifics or by *Potamopyrgus*. These results indicate that interspecific competition negatively affected the survivorship of *Baetis*. Intraspecific competition of *Baetis* was not readily apparent, probably because the densities used in the experiment may have been too high, and the intraspecific effects of competition were so large in both low and high treatments that I was unable to distinguish any differences between those treatments. Consequently, it seems likely that intraspecific competition was present, but I was unable to measure it due to experimental design. Similar to *Baetis*, *Potamopyrgus* survivorship was greater in high density treatments that contained only conspecifics in comparison with high-density treatments that contained equal numbers of conspecifics and *Baetis*. *Potamopyrgus* body growth was lower in high-density treatments than low-density treatments but was not negatively affected by *Baetis*, signifying that interspecific competition with *Baetis* negatively affected *Potamopyrgus* survivorship, whereas intraspecific competition negatively affected *Potamopyrgus* growth. In sum, the results of this experiment demonstrate that both species were subject to density-dependence.

Also from the *Baetis-Potamopyrgus* competition experiment, I estimated the strength of the competitive interaction, alpha (α). The effect of *Potamopyrgus* on *Baetis*, α_{BP}, was similar in magnitude to the effect of *Baetis* on *Potamopyrgus* α_{PB}. This indicates that the strength of competitive interactions in these experiments was symmetrical so that neither species was a dominant competitor. Because α_{BP} and α_{PB} were relatively close to 1, the strengths of interspecific interactions were relatively weak. Furthermore, predictions of coexistence between competitors can be made by comparing intra- and interspecific competition coefficients. Because interspecific competition was greater than intraspecific competition for both species, populations should tend to diverge from a stable equilibrium state, and the outcome of the competitive interactions will depend upon the initial densities of the species (Ricklefs and Miller 2000). So, if *Baetis* initially had a numerical advantage over *Potamopyrgus*, discrete-time Lotka-Volterra models for two competing species would predict that *Baetis* would win over *Potamopyrgus*. In this case, I might expect *Potamopyrgus* abundance to decline in Darlinton Spring Creek. However, predictions on the outcome of competitive interactions between *Baetis* and *Potamopyrgus* based on the results of the experiment in Chapter 3 may not be correct because, as discussed above, I was not able to estimate intraspecific competition for *Baetis*, and α_{BB} and α_{PP} are critical for making predictions on the outcome of interspecific interactions. Additionally, these predictions are based upon interactions between two species and do not account for multi-species interactions, which may affect the nature of interactions between *Potamopyrgus* and *Baetis*. Furthermore, models of competition that include a spatially structured environment predict the coexistence of competitors (Tilman 1994), suggesting that competitive exclusion between *Potamopyrgus* and *Baetis* may not occur.

In Chapter 3, I also demonstrated that low-snail reaches often had greater periphyton biomass than high-snail reaches, which indicates that *Potamopyrgus* can cause resource depression. But because I did not observe a strong, negative association between *Potamopyrgus* and baetids, the overall grazing pressure exerted by *Potamopyrgus* was not strong enough to limit food availability to the point that baetid mortality, growth or emigration occurred. Furthermore, although periphyton biomass can be a good indicator of food availability, it does not always accurately reflect primary production. A more informative way of quantifying food availability may be to measure primary productivity rather than periphyton biomass.

Despite the ability of *Potamopyrgus* to cause resource depression, *Baetis* seems able to graze periphyton biomass to lower levels than *Potamopyrgus* in experimental situations (Cada and Kerans, in preparation, see Fig. 3.11). In addition to the weak interaction strength of *Potamopyrgus* on *Baetis*, differential grazing ability may allow

Baetis to be a slightly better competitor than *Potamopyrgus*. However, this hypothesis may not hold true in the natural environment because the experiments restricted movement and dispersal of *Potamopyrgus* and *Baetis*. *Baetis* may leave a rock at low levels of periphyton biomass in search of more abundant resources rather than remain to graze more intensively. Because this behavioral decision reduces foraging time, *Baetis* may lose any competitive advantage over *Potamopyrgus*. Furthermore, by increasing its time spent drifting, *Baetis* faces an increased risk of predation and of immigration to a poor quality or unsuitable habitat. As invasion of *Potamopyrgus* within Darlinton and the Madison River becomes less patchy and more extensive, a choice by *Baetis* to drift rather than remain may become more risky and cause decreased body growth or greater rates of mortality.

The experimental results in Chapter 4 did not support the hypothesis that fish growth was lower in high-snail reaches than low-snail reaches although stomach contents analyses indicated there might have been differences in diet composition between high and low-snail reaches. Furthermore, I found little evidence that *Potamopyrgus* was consumed by *Salmo trutta* or *Cottus bairdi*.

In this thesis, I focused on negative effects and tended to ignore the possibility of positive effects of *Potamopyrgus* on baetids, periphyton and fishes. That is, all examinations of interactions between baetids and *Potamopyrgus* focused on competition, or net negative interactions between species. Any two-species interaction is likely to be composed of both positive, negative, and neutral effects that, when summed, result in a net effect that is positive, neutral or negative (Berlow 1999). Thus, any two-species or multi-species interactions may include both facilitation and competition.

Because species interactions can be a net result of several separate interactions, I would like to present the following hypothesis: I suggest that the densities that *Potamopyrgus* achieves will dictate the outcome (+, 0, -) of its interactions with other species in an environment. That is, at low densities, *Potamopyrgus* may interact with producers and other grazers so that the net effect is positive rather than negative, as demonstrated by Schreiber et al. (2002). A positive effect of *Potamopyrgus* at low densities may occur because intermediate levels of grazing can stimulate primary productivity by reducing the proportion of senescent periphyton that shades live cells (Lamberti et al. 1989), increasing food availability and decreasing food limitation. In addition, fecal material from *Potamopyrgus* may provide a substrate for bacteria, increasing food resources for detritivores. In contrast, at moderate densities of *Potamopyrgus* (i.e., 25,000 m^{-2}), grazing pressure may exceed primary productivity so that any positive effects are canceled by negative effects related to *Potamopyrgus*, such as food limitation. In this situation, the net effect of *Potamopyrgus* would be negligible. The field survey in Chapter 3, where the effect of *Potamopyrgus* on baetids was negligible, provides some evidence in support of this idea that moderate densities result in a neutral effect. Furthermore, when *Potamopyrgus* reaches high (i.e., > 50,000 m^{-2}) or very high densities (i.e., >100,000 m^{-2}), the grazing pressure may cause severe food limitation for herbivorous macroinvertebrates, and the net effect of *Potamopyrgus* on macroinvertebrates would be negative. Thus, the effects of *Potamopyrgus* establishment in a system may result in facilitation at low densities and switch to competition at high densities.

This study did not demonstrate a negative effect of *Potamopyrgus* on baetid mayflies or fish growth in the field but did indicate that *Potamopyrgus* can depress periphyton biomass in the field and negatively affect baetid survivorship in experiments. Thus, the question becomes—"under what circumstances might *Potamopyrgus* affect macroinvertebrates and fishes in the natural environment?" My results suggest that *Potamopyrgus* will not have a large effect when at relatively moderate densities (e.g., 10,000-15,000 m^{-2}). However, a previous study (Cada and Kerans, in preparation) suggests that *Potamopyrgus* will have a negative effect on macroinvertebrates at densities of *Potamopyrgus* as low as 25,000 m^{-2}. Because *Potamopyrgus* densities in other invaded systems are usually much higher than 15,000 m^{-2} or 25,000 m^{-2}, it is likely it will negatively affect other macroinvertebrates in these locations. That is, when densities of *Potamopyrgus* become high (e.g., >100,000 m^{-2}), I expect there will be a strong negative effect on periphyton biomass and macroinvertebrate density. For *Potamopyrgus*, as well as other invasive species, it is important to define the conditions that will and will not result in large effects so that accurate predictions about the consequences of the invader can be made. Furthermore, I want to caution against interpreting the results of this study to mean that *Potamopyrgus* will not have an effect in other invaded systems, especially where *Potamopyrgus* densities are very high.

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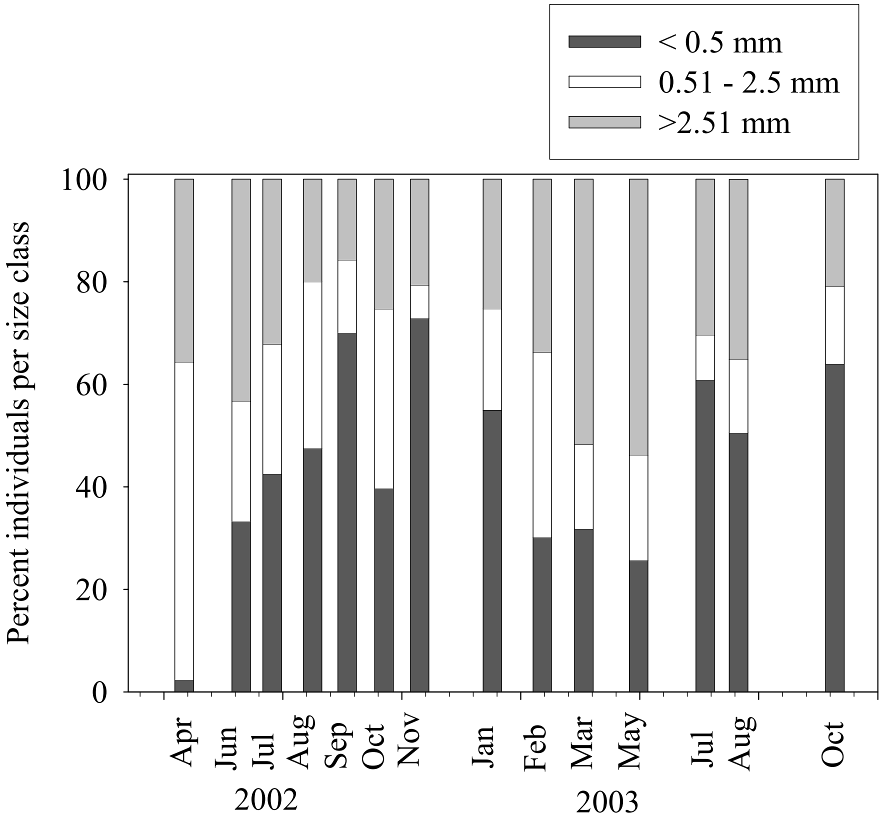
APPENDICES

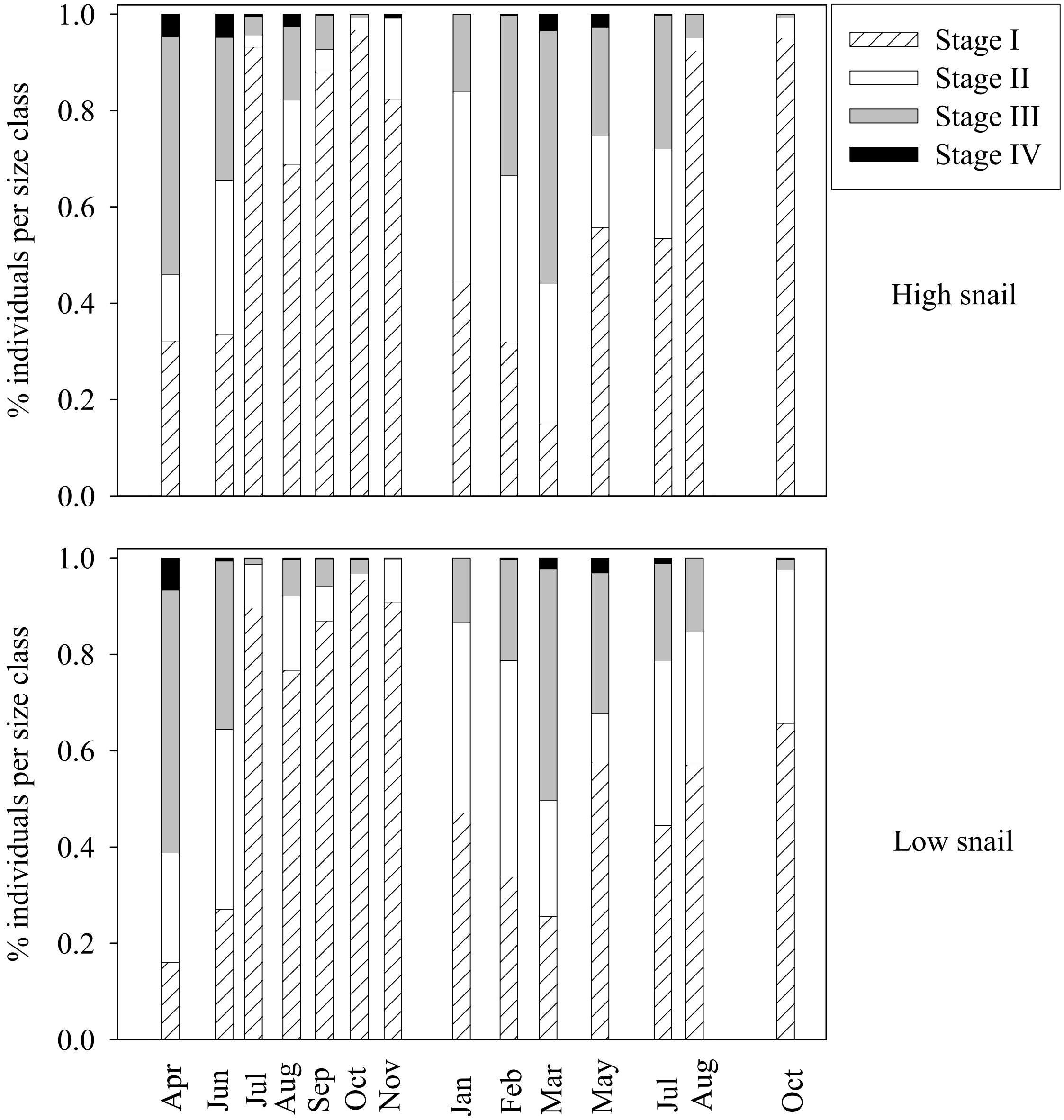
APPENDIX A

Size class distributions for *Potamopyrgus* and baetid mayflies

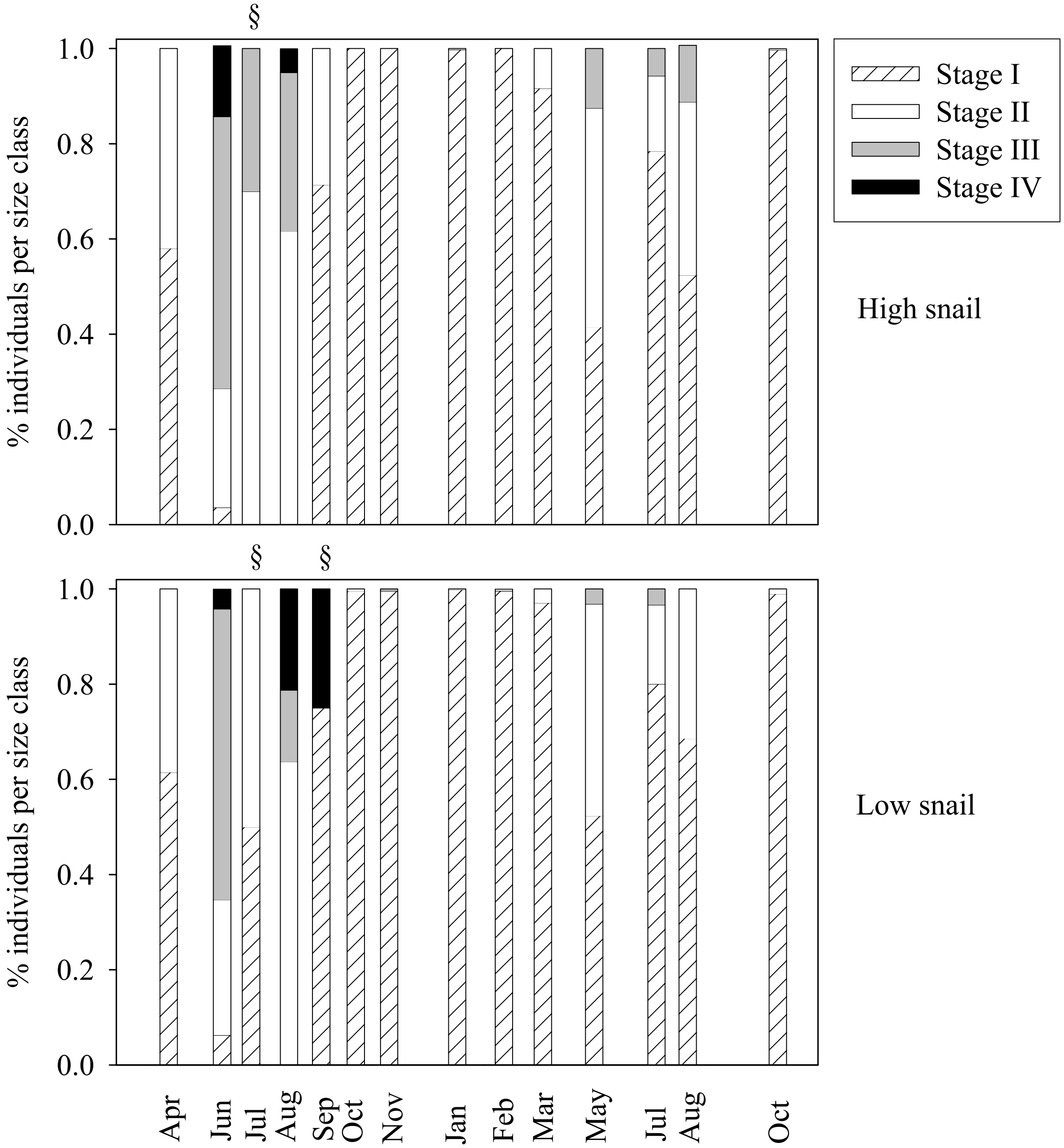
Temporal trends in the size class distribution of *Potamopyrgus antipodarum* from high-snail reaches only (n=880 individuals). Size classes were chosen based on reproductive age determined within this study: individuals < 0.5 mm were recently birthed; individuals between 0.51 and 2.5 mm were pre-reproductive; and individuals > 2.51 mm were capable of reproducing.



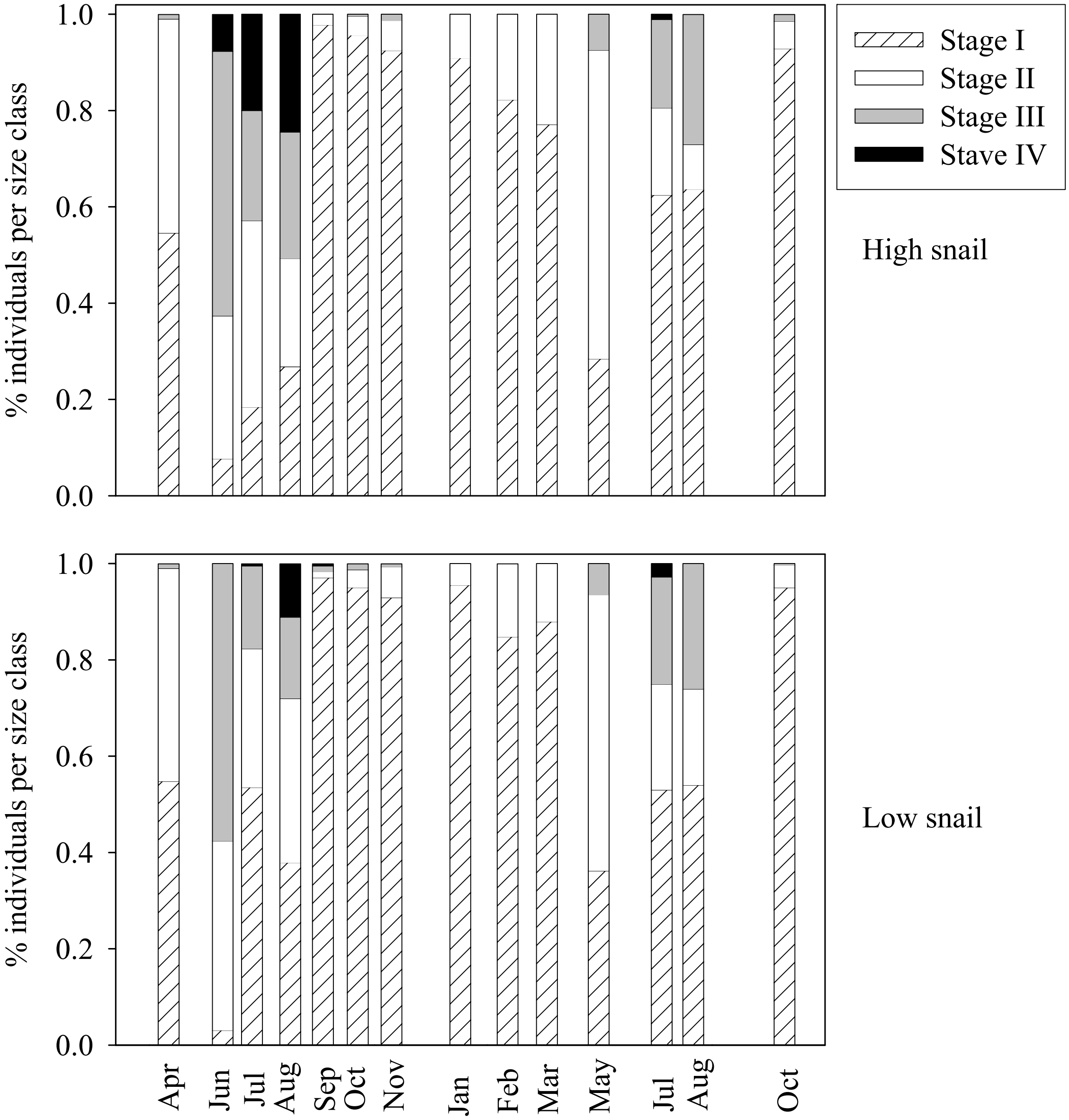
Temporal trends in the size-class distributions of *Baetis tricaudatis* based on developmental stage for high-snail and low-snail reaches (n=406 individuals). Developmental stage, based on Deluchi and Peckarsky (1989), divided mayflies into 4 categories based on maturity of wing-pads where Stage I, the youngest category, represents individuals without wing pads, Stage II represents individuals with wing pads wider than long, Stage III represents individuals with wing pads longer than wide, and Stage IV, the stage just prior to emergence, represents individuals with thickened and blackened wing pads.



Temporal trends in the size-class distributions of *Diphetor hageni* based on developmental stage for high-snail and low-snail reaches (n=326 individuals). See the figure for Baetis (p) for details on the developmental stages. § indicates n < 5 individuals for that time-period and snail-treatment.



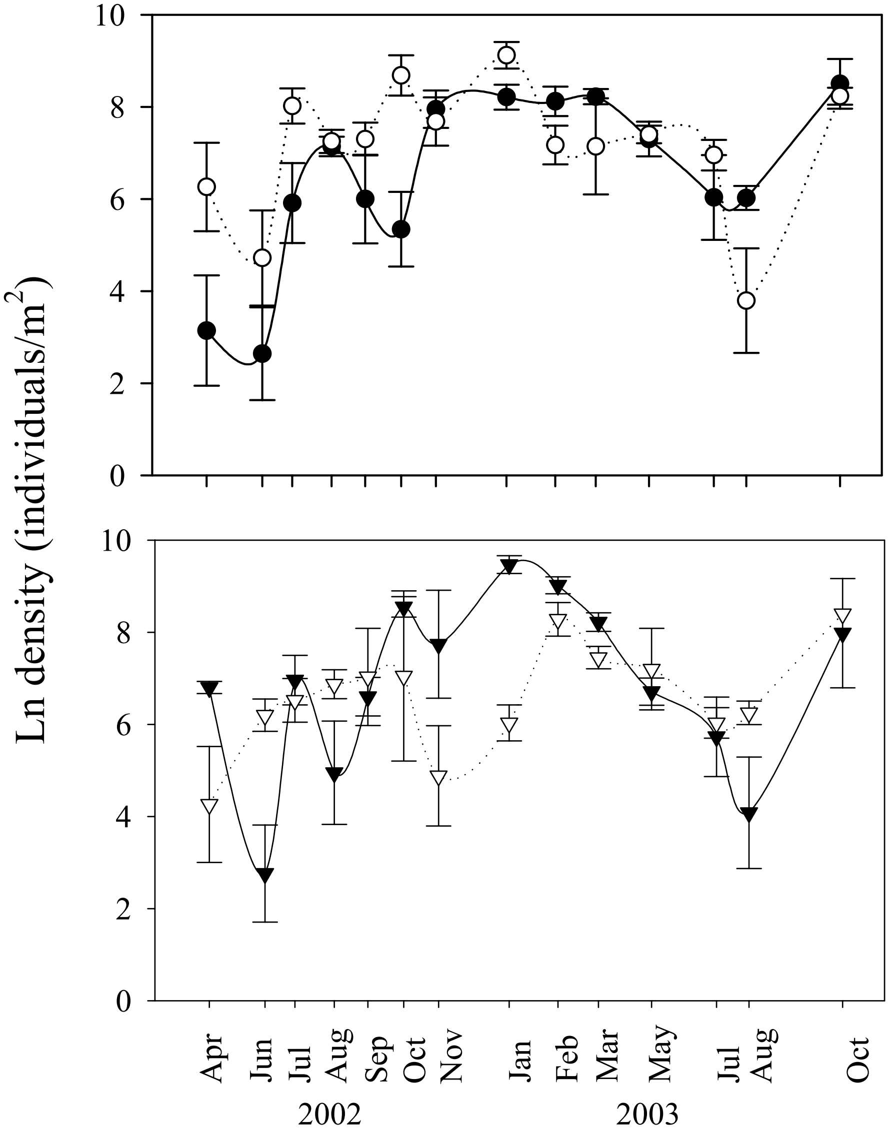
Temporal trends in the size-class distributions of *Acerpenna pygmaeus* based on developmental stage for high-snail and low-snail reaches (n=385 individuals). See the figure for Baetis (p) for details on the developmental stages.



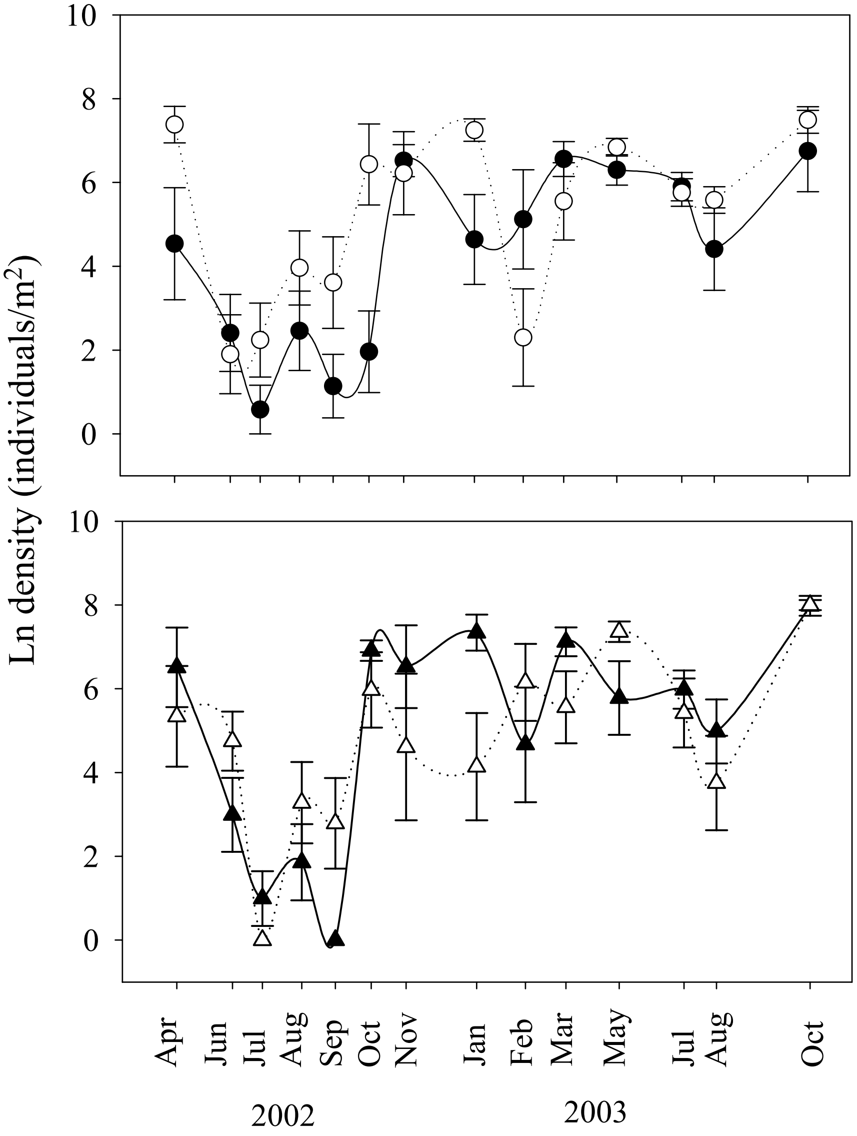
APPENDIX B

Baetid densities by reach

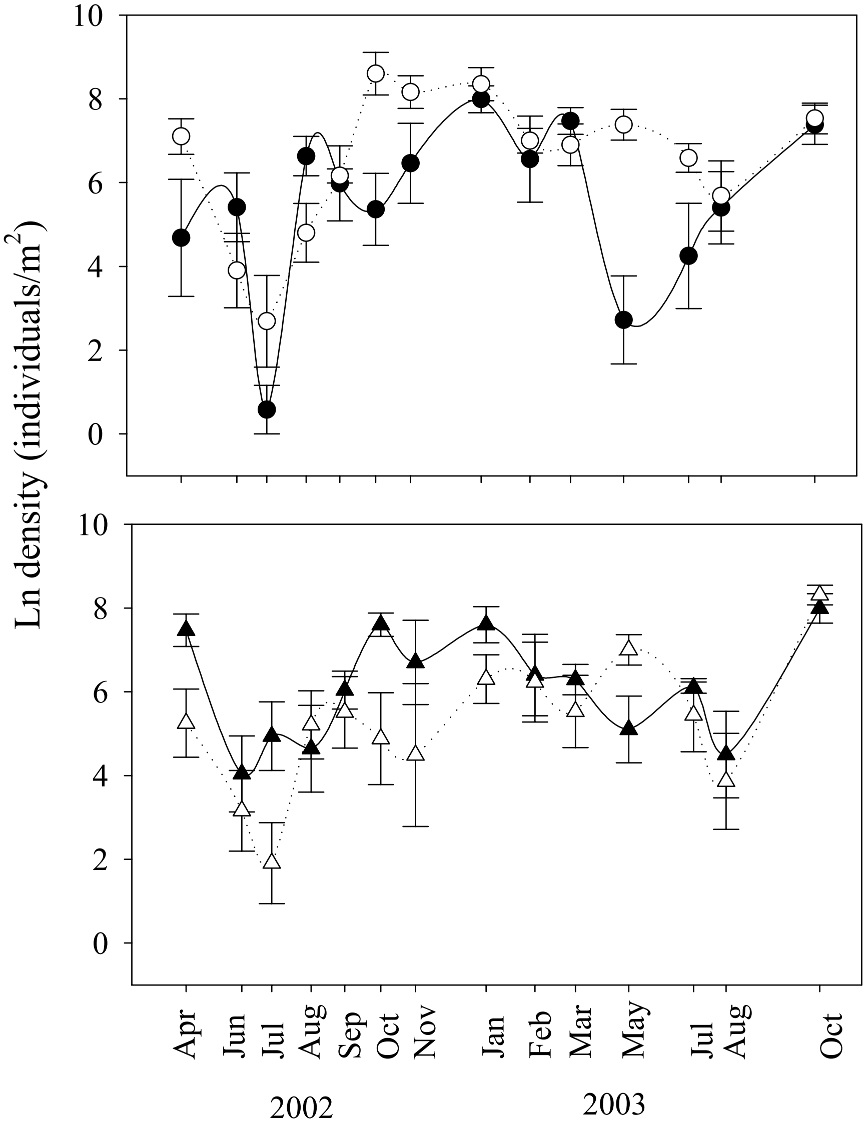
Repeated measures MANOVA results indicated a significant time*reach(snail) interaction for *Baetis tricaudatis* densities (see Table 3.5). Thus, these graphs show mean ln densities (± 1 SE) by reach, nested within snail, across times for interpretation of the interaction. High snail reaches are represented by circles, whereas low-snail reaches are represented by triangles.



Repeated measures MANOVA results indicated a significant time*reach(snail) interaction for *Diphetor hageni* densities (see Table 3.5). Thus, these graphs show mean ln densities (± 1 SE) by reach, nested within snail, across times for interpretation of the interaction. High snail reaches are represented by circles, whereas low-snail reaches are represented by triangles.



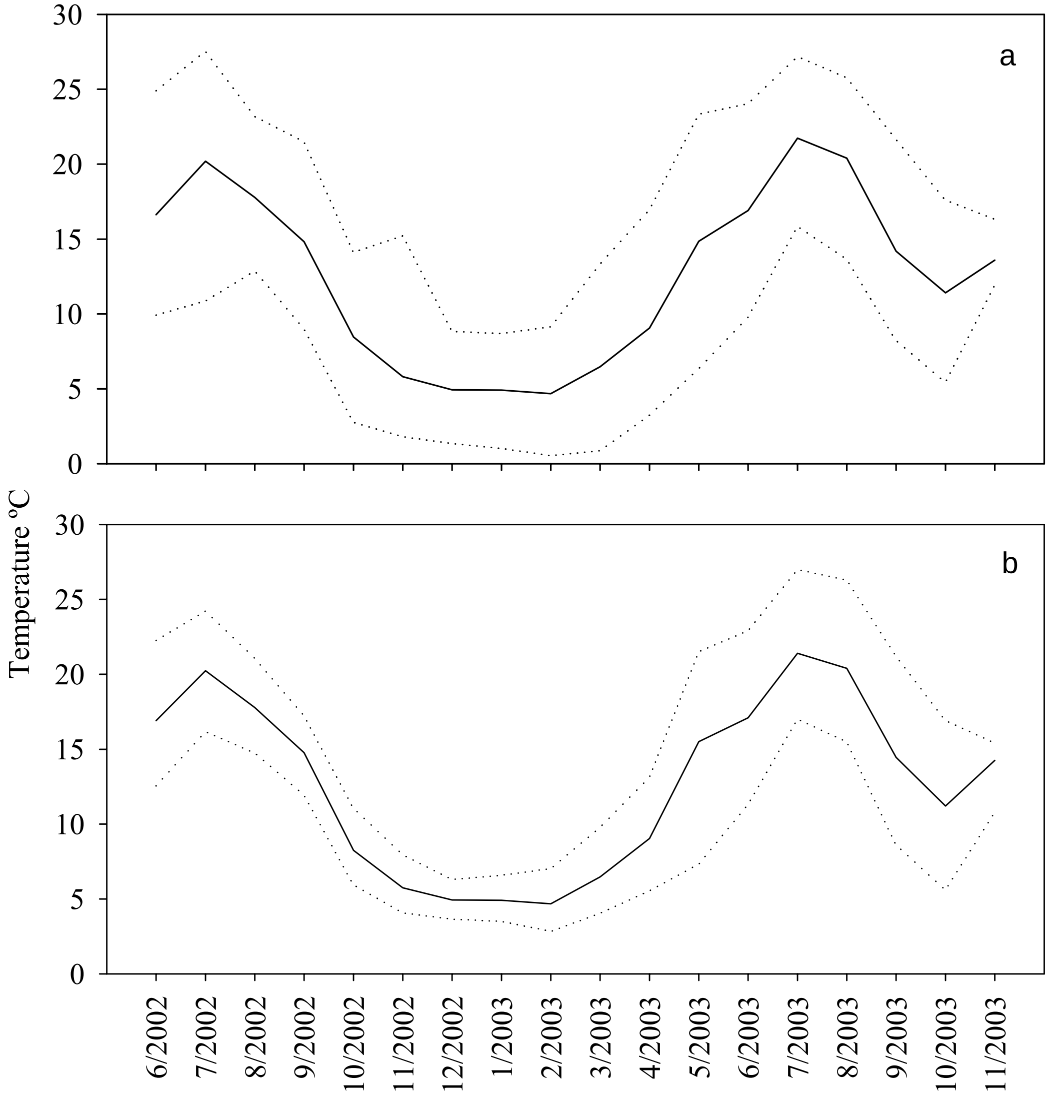
Repeated measures MANOVA results indicated a significant time*reach(snail) interaction for *Acerpenna pygmaeus* densities (Table 3.5). Thus, these graphs show mean ln densities (± 1 SE) by reach, nested within snail, across times for interpretation of the interaction. High snail reaches are represented by circles, whereas low-snail reaches are represented by triangles.



APPENDIX C

Mean monthly temperature in Darlinton Spring Creek

Temporal trends in the monthly water temperature (ºC) with mean (solid line), minimum (dotted line), and maximum (dotted line) values from Meander 1 (a) and Meander 5 (b) of Darlinton Spring Creek. Water temperature was measured using Onset® temperature probes that recorded temperature on an hourly basis.



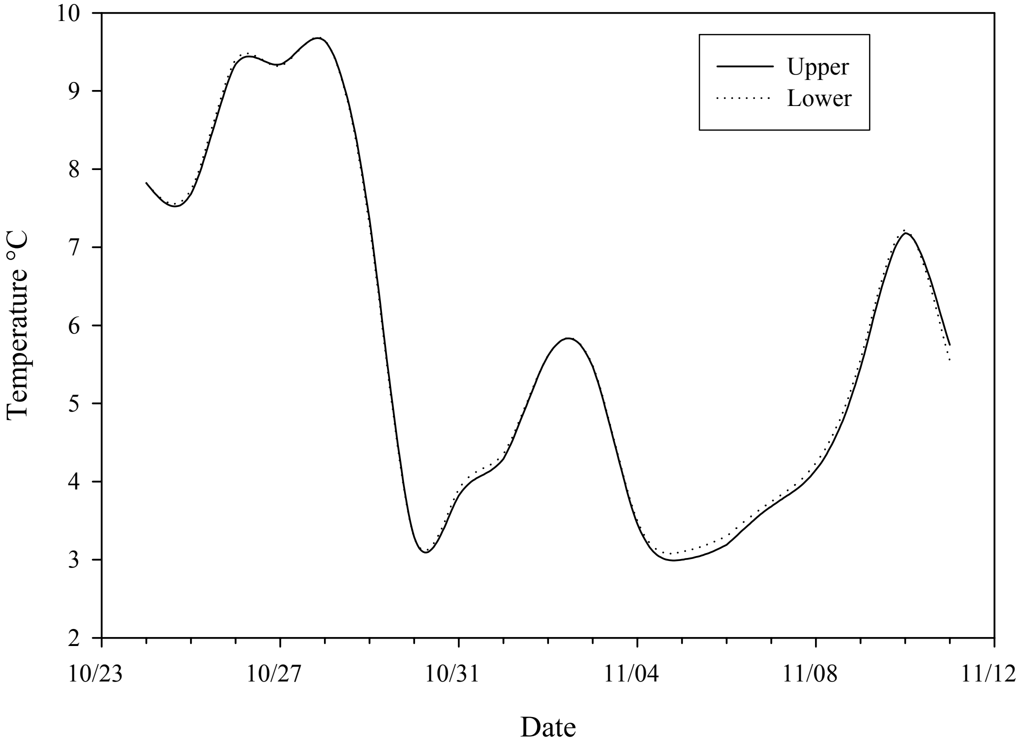
APPENDIX D

Physiochemical conditions for competition experiments in Chapter 3

Physicochemical conditions at the end of Experiment 2 at each experimental float. I collected depth and flow using a Swoffer 3000 flow meter; flow was measured at 0.6 of the water depth (0.6X) and at 5cm below the water's surface (5 cm). This second flow measurement targeted flow at the same depth as the experimental chambers. I collected conductivity, % dissolved oxygen and pH using a Yellow Springs Instrument 6000X.

Float	Depth (m)	Flow (m/s) 0.6X	Flow (m/s) 5 cm	Conductivity (mS)	%DO	pH
1	0.35	0.121	0.124	0.261	44.6	8.38
2	0.39	0.034	0.060	---	---	---
3	0.37	0.046	0.232	---	---	---
4	0.4	0.039	0.105	---	---	---
5	0.41	0.049	0.230	0.257	36.2	8.28
6	0.37	0.067	0.220	---	---	---
7	0.39	0.041	0.146	---	---	---
8	0.56	0.020	0.007	---	---	---
9	0.42	0.177	0.260	---	---	---
10	0.56	0.118	0.071	0.258	37.3	8.14
Mean	0.42	0.07	0.15	0.259	39.4	8.27
StdErr	0.02	0.02	0.03	0.001	2.6	0.07

Mean daily temperature during Experiment 2 at the upper-most (float 10) and downstream-most (float 1) boundaries of the section of stream where Experiment 2 occurred. Temperature was measured using 2 Onset® temperature probes set to record at 1 hr intervals.



APPENDIX E

Physicochemical conditions from Chapter 4

The mean physicochemical conditions (± 1 SE) for the fish growth experiment at the front and at the rear of the enclosures. Table "a" presents the data for *Salmo trutta* enclosures whereas table "b" provides the data for *Cottus bairdi* (n = 6 except for flow and depth in "a" where n = 12).

a) *Salmo trutta*

Variable	Front			Back		
Temperature (°C)	21.70	±	0.128	NA		
Conductivity (mS)	0.24	±	0.001	NA		
Dissolved oxygen (%)	129.90	±	1.171	NA		
Flow (m/s)	0.34	±	0.054	0.112	±	0.031
Depth (m)	0.45	±	0.010	0.43	±	0.014

b) *Cottus bairdi*

Variable	Front			Back		
Temperature (°C)	21.70	±	0.131	NA		
Conductivity (mS)	0.24	±	0.001	NA		
Dissolved oxygen (%)	129.10	±	0.900	NA		
Flow (m/s)	0.35	±	0.045	0.18	±	0.029
Depth (m)	0.37	±	0.010	0.36	±	0.017