COMPETITION BETWEEN THE THREATENED BLISS RAPIDS SNAIL, *TAYLORCONCHA SERPENTICOLA* (HERSHLER ET AL.) AND THE INVASIVE, AQUATIC SNAIL, *POTAMOPYRGUS ANTIPODARUM* (GRAY)

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David Charles Richards

I dedicate this dissertation to all those that helped me make it through the tough times: *Ursus arctos* for showing me humility, all of the members of the Corvid family, particularly the ravens and magpies, for showing me that most intellectual pursuits aren't all that serious and the giant Ponderosa pines and Doug firs for giving me perseverance. I also dedicate this dissertation to the north rim of the Grand Canyon, the backcountry of the Bob and the A-B and the GYE, as yet, unexplored coral reefs and all the other relatively empty places on the map, for giving me hope. To the rivers that inspire me: the Belly, the S.F. of the Flathead, the Colorado and all the tribs too numerous to mention, thank you. And last but not least, to the little things, like snails, that remind me that everything has its place and time on this wonderful, ephemeral planet.

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ABSTRACT

Due primarily to habitat loss and invasive species, extinction rates for North American mollusk taxa are among the highest for any taxonomic group in the world. Competition between invasive and native species often leads to decreases in native populations. For example, a primary reason for listing the Bliss Rapids snail, *Taylorconcha serpenticola* as threatened in the Snake River drainage was the perceived impacts of the highly invasive New Zealand mudsnail, *Potamopyrgus antipodarum*. Despite federal protection of *T. serpenticola* and the known presence of *P. antipodarum* in the Snake River drainage for almost 20 years, almost nothing is known about their ecology and competitive interactions. For this dissertation I conducted both field and laboratory studies to determine niche overlaps, spatial patterns, and some life history characteristics of both species. I compared optimal growth temperatures and estimated temperature tolerances for each species, under laboratory conditions; 2) examined stage (size) class fecundity rates and growth rates; and 3) examined photophobic tendencies of both species. I then explored environmental conditions and spatial patterns of both species in Banbury Springs, a tributary of the Snake River, near Hagerman, Idaho, that may have affected their distribution and abundance using regression tree analysis and geostatistical methods. I then conducted several competition experiments between both species under controlled conditions at Banbury Springs, developed competition coefficients, and related their growth rates and competitive outcomes to periphyton abundance and diversity. Finally, I monitored and then modeled seasonal and yearly population density trends of both species in a section of Banbury Springs, where both coexist, using time series analysis. Results of this study show that that both species have niche overlaps (i.e. temperature overlaps, photophobic tendencies, and somewhat similar habitat requirements) and can compete for limited food resources, but may have just enough niche separation or their occupied habitat is heterogeneous enough for them to coexist, at present. It is possible however that not enough time has elapsed for the effects of competition with *P. antipodarum* to push *T. serpenticola* to extinction.

INTRODUCTION

Invasion of exotic species is rapidly approaching habitat destruction as the number one cause of biodiversity loss worldwide, and is responsible for 20 to 40 percent of extinctions of vertebrate taxa (Reid and Miller 1989, Cox 1999, Enserink 1999). This loss is particularly pronounced in aquatic environments (Cohen and Carlton 1998, Byers 2000) where extinction rates of North American freshwater mollusks are among the highest for any taxonomic group in the world (Ricciardi and Rasmussen 1999). Despite this unprecedented loss of biodiversity in modern times (Pimm et al. 1995), predicting where invasive species will become established and their impact on native species and ecosystems has been difficult, at best (Boraas et al. 1990, Coblenz 1990, Reichard and Hamilton 1997, Shigesada and Kawasaki 1997, Simon and Townsend 2003). Many studies (e.g. Huffaker 1971, Lawton and Brown 1986) have emphasized the absence of natural predators as a primary reason for the establishment and rapid spread of invasive species, but competitive abilities may also be a crucial but underestimated characteristic (Herbold and Moyle 1986, Byers 2000, Amarasekare 2003, Levine et al. 2003). Recent research has shown that competition between invasive and native species often leads to decreases in native populations (U.S. Congress 1993, Cox 1999, Byers 2000). There is also growing evidence that degraded or disturbed habitats are more susceptible to invasion than intact systems (Drake et al. 1989, Burke and Grime 1996, Mack et al. 2000) and that it is often a combination of competitive abilities and disturbance that allows for species invasions (Corbin and D'Antonio 2004).

In the mid-Snake River drainage in south central Idaho, six species of aquatic snails have been listed as federally Threatened and Endangered. One of which, the

Threatened Bliss Rapids Snail, *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler, and Thompson, a small (< 3.0 mm) hydrobiid, is the subject of this investigation. Perceived loss of habitat, primarily from hydroelectric generating facilities on the main stem of the Snake River and degraded water quality resulting from aquaculture and non-point agriculture sources were two of the reasons for these listings (Desert Fishes Council 1992, U.S. Fish and Wildlife Service, 1995). The third potential threat influential in the listing of these native snail species was competition with the recently established, (circa.1985-87), highly, invasive, New Zealand mudsnail, *Potamopyrgus antipodarum* (Gray)(Hydrobiidae)(Desert Fishes Council 1992, U.S. Fish and Wildlife Service 1995).

Potamopyrgus antipodarum has become widely established throughout the Snake River drainage, including sections of the river and adjacent springs where extant *T. serpenticola* colonies persist. This highly invasive snail often reaches densities > 100,000/m^2 within remaining occupied *T. serpenticola* habitat in the mid-Snake River drainage (Richards et al. 2000, Cazier 1997) and > 500,000/m^2 in a headwater tributary of the Snake River near Yellowstone National Park (Hall et al. 2003).

Little is known about the life histories and ecologies of *T. serpenticola* and *P. antipodarum* in the Snake River. Less is known about competitive impacts of *P. antipodarum* on surviving colonies of *T. serpenticola.* In this dissertation, I will investigate basic life history characteristics and competitive interactions between *P. antipodarum* and *T. serpenticola*, which occur sympatrically in a freshwater spring, Banbury Springs, mid-Snake River drainage near Hagerman, Idaho. These two species, along with the common Pebble snail, *Fluminicola* sp. dominate the macroinvertebrate assemblage and account for over 95% of faunal biomass at the study site at Banbury

Springs (Richards et al. 2000). Because laboratory and controlled field experiments offer unique advantages in assessing species life histories and competitive interactions (Miller 1986), I will use both arenas in this investigation.

Literature Review

Competition

There are many working definitions of competition (Pianka 1999, Begon et al. 1996, Tillman and Kareiva 1997, Gotelli 1998). Generally, competition occurs when one organism consumes or precludes the use of a resource that could have been available to another organism (Begon et al. 1996). Competitive displacement can occur when a species reduces the limiting resource below the level required for sustained growth by the competing species (Fredrickson and Stephanopoulus 1981, Boraas et al. 1990). In 1978, Hutchinson proposed the now well- known 'competitive exclusion principal', which basically states, "complete competitors can not coexist." By analyzing Lotka-Volterra two-species competition models, Gotelli (1998) further refined the competitive exclusion principal, to state that, " the more similar species are in shared resources, the more precarious their coexistence."

Despite our knowledge of competition, its importance in structuring natural communities continues to be debated (Wiens 1977, Connell 1980, Roughgarden 1983, Fletcher and Underwood 1987). The debate occurs, in part, because many of the patterns found in species distributions, which researchers attributed to competitive effects, could also have been caused by other processes (Connell 1980, Fletcher and Creese 1985, Underwood 1986) or could have been generated randomly (Strong 1980, Connor and

Simberloff 1983, Fletcher and Underwood 1987). In addition, competition may be difficult to observe in natural environments because native species in an ecosystem have evolved together over millennia and therefore 'have worked out their competitive differences' and now their fundamental niches have diverged sufficiently to limit competition (Connell 1980, Begon et al. 1996). Invasive species, by default, did not evolve with native species, therefore, it should follow that affects of interspecific competition between invasive and native species would be more easily observed than between two native species. Even though interspecific competition between invasive species and native species allows us a better opportunity to understand the effects of competition, competitive exclusion theory has not been incorporated into empirical studies of species invasion (Byers 2000, Shea and Chesson 2002). Although the debate over the effects and the nature of competition still continues, there is accumulating evidence that interspecific competition can often have profound effects on the structuring of aquatic communities (Morin 1999, Simon and Townsend 2003).

Competitive Dominance

Competition between invasive and native species can occur in a number of ways including, but not limited to, exploitative (Byers 2000, Begon et al. 1998) and interference competition (Gotelli 1998, Morin 1999), and several hypotheses have been proposed for species traits that lead to competitive dominance. The competitive dominant may have; 1) higher reproductive success [the R-max hypothesis (Goulden et al. 1978, Amarasekare 2003)], 2) more efficient food assimilation [(the low food efficiency (R*) hypothesis (e.g. Lampert and Schober 1980, Romanosky 1984, Byers 2000)], or 3) better dispersal abilities into unoccupied habitats (Amarasekare 2003).

Bengtsson (1987) outlined several additional hypotheses, some apparently conflicting, that lead to competitive dominance including; 1) the size-efficiency hypothesis (Brooks and Dodson 1965, Gerritsen 1984) where large species are better competitors than small ones, 2) the small body size hypothesis (Hanski and Ranta 1983) where small species are better competitors, and 3) that susceptibility to predation and competitive ability are positively related. Shigesada and Kawaski (1999) proposed that competition between a biological invader and a native species could lead to three possible population outcomes; 1) the native species becomes extinct in some or all patches, 2) co-existence occurs in patches, or 3) the invader species fails to become established in some patches.

Competition is common among aquatic snails, including competition between invasives and natives (Fenchel and Kofoed 1976, Schmitt 1985, 1996, Osenberg 1989, Skilleter and Underwood 1993, Byers 2000). For example, in field experiments designed to study competition between an expanding population of an invasive mudsnail and a declining population of a native mudsnail in a northern California estuary, Byers (2000) concluded that exploitative competition occurred and that the invader was more efficient at converting limited food resources to tissue growth. Byers (2000) also suggested that the higher food resource conversion efficiency of the invasive mudsnail could explain its success and be responsible for the exclusion of the native mudsnail from its former habitat.

Density-dependent, intraspecific competition can also: affect population dynamics (Cappuccino and Price 1995), the stability of populations (Forrester and Steele 2004), and in turn influence interspecific competition (Begon et al. 1996, 1998, Gotelli 1998). For example, in species that reproduce sexually (i.e., *T. serpenticola*),

intraspecific competition often leads to size hierarchies (stage classes) within a population (Weiner and Solbrig 1984, Uchmanski 1985, Gribbin and Thompson 1990, Adams and Tschinkel 1995, and Geffen 1996). Size often influences the outcome of intraspecific and interspecific competition. Because *P. antipodarum* is apparently a clonal species in the western USA, all individuals in a population should be genetically similar (M. Dybdahl, Washington State University, personal communication) and therefore, it is unknown if intraspecific competition in *P. antipodarum* populations could partially be responsible for size hierarchies observed in rivers in the western USA and what effect size hierarchies might have on interspecific competition with native species.

Spatial Ecology and Competition

The intensity of the effects of density dependence on population dynamics may also vary spatially (Forrester and Steele 2004). Spatial ecology (Tilman 1994) and metapopulation ecology (Hanski and Gilpin 1997, Hanski 1999) are relatively new advances in population ecology of small, isolated populations and have their foundations in island biogeography (MacArthur and Wilson, 1963, 1967, Simberloff 1974, 1996, Simberloff and Abele 1976). Basically, metapopulations are a network of fragmented populations that have low migration rates and extinction rates of individual populations are stochastically uncorrelated (Hanski and Gilpin 1997, Hanski 1999). If migration between populations is unrestricted then it is basically one continuous population. Fragmented populations with no immigration would be considered isolated. Often the causes of fragmentation are the result of human activity (Hanski and Gilpin 1997, Hanski 1999) and not all fragmented populations should be considered metapopulations if there is no immigration.

According to Hanski (1999), "an important recurring theme in the dynamics of two or more interacting populations is the creation and maintenance of aggregated spatial distributions of species in the absence of any environmental heterogeneity." In a heterogenous environment, the competitive dominant does not always have to exclude other competitors (Lehman and Tilman 1997). Therefore, native species populations may become more fragmented due to competitive effects of the invasive species. This may be occurring between the already fragmented populations of *T. serpenticola* and *P. antipodarum* in the Snake River drainage (Richards et al. 2000).

Habitat heterogeneity may allow for the coexistence of competing species and thus should be considered when assessing interspecific competition (Wissinger 1992, Lehman and Tilman 1997). Specifically, habitat edges, ("the edge effect") have been shown to reduce species diversity (Leopold 1933, Yahner 1988, and Paton 1994) or alternatively, may allow for the coexistence of competitive species (Tilman and Kariveva 1997). Although very limited data suggest that *T. serpenticola* only occurs on cobble habitats (Bowler 1990, Frest and Johannes 1992), it is unknown if it occurs in other habitats (e.g., vegetation) at other locations or how edge effects between habitats influences its abundance or interspecific competition.

Bliss Rapids snail, *Taylorconcha serpenticola*

The Bliss Rapids snail, *Taylorconcha serpenticola*, was first recognized as a new taxon in 1959 (Taylor 1982) and formally described by Hershler et al. (1994). Adults are usually 2.0 to 2.5 mm in shell length, have three whorls, are roughly ovoid in shape, and reproduce sexually (Figure 1).

Figure 1.♂ *Taylorconcha serpenticola* (Family Hydrobiidae)(Photo courtesy of Dr. Dan Gustafson, Montana State University, Bozeman, MT)

Taylorconcha serpenticola survives in fragmented habitat patches in the mainstem of the mid-Snake River, near Hagerman, Idaho, and is found in Banbury Springs, Box Canyon, The Nature Conservancy's Thousand Springs, Niagara Springs and several other springs in the area (Figure 2). It is also found in some of the free-flowing sections of the main-stem of the mid-Snake River downstream of Lower Salmon Dam. In this area, it is assumed to be associated with spring influences or rapids-edge environments and tends to flank shorelines, but has not been recorded in impounded sections of the mid-Snake River (Frest and Johannes 1992, U.S. Fish and Wildlife Service 1995, Cazier 1997, Richards et al. 1999). *Taylorconcha serpenticola* is considered moderately photophobic and resides on the lateral sides and undersides of

rocks during daylight (Bowler 1990). It can be locally quite abundant, especially on smooth rock surfaces with common encrusting red algae (Frest and Johannes 1992).

The Bliss Rapids snail, a relict of Pliocene Lake Idaho, was known historically from the mainstem middle Snake River and associated springs between Indian Cove Bridge (rkm 945.9) and Twin Falls (rkm 982.9) (Hershler et al. 1994). Taylor (1982) believed that "...prior to dam construction there was probably a single population throughout this range, and plausibly upstream as well… Based on live collections, the species currently exists as discontinuous populations within its historic range (Figure 2)." Cazier (2000) has also found a possible disjunct population of *T. serpenticola* near River KM 367 in Hells Canyon of the Snake River. Based on the somewhat outdated report of the U. S. Fish and Wildlife Service (1995), Cazier (2000), and results from this investigation, I suggest that populations of *T. serpenticola* may now be fragmented in such a way as to be considered a mixture of isolated populations and metapopulations.

New Zealand Mudsnail, *Potamopyrgus antipodarum*

The invasive New Zealand mudsnail, *Potamopyrgus antipodarum* (Gray)(Hydrobiidae)(Figure 3) is rapidly spreading throughout river systems in the western USA. It first became established in the mid-Snake River, Idaho in the mid-1980's (Bowler 1991) and has since spread to most major western river systems (for the most recent maps of *P. antipodarum* distribution in the western USA visit the New Zealand mudsnail web site; http://www.esg.montana.edu/aim/mollusca/nzms). *Potamopyrgus antipodarum* is native to New Zealand and is well established throughout many rivers and estuaries in Australia, Europe, and Asia (Bondesen and Kaiser 1949, Michaut 1968, Lassen 1978, Ribi 1986, Ponder 1988).

Figure 2. Current distribution of *Taylorconcha serpenticola* populations in Snake River drainage, Idaho, USA.

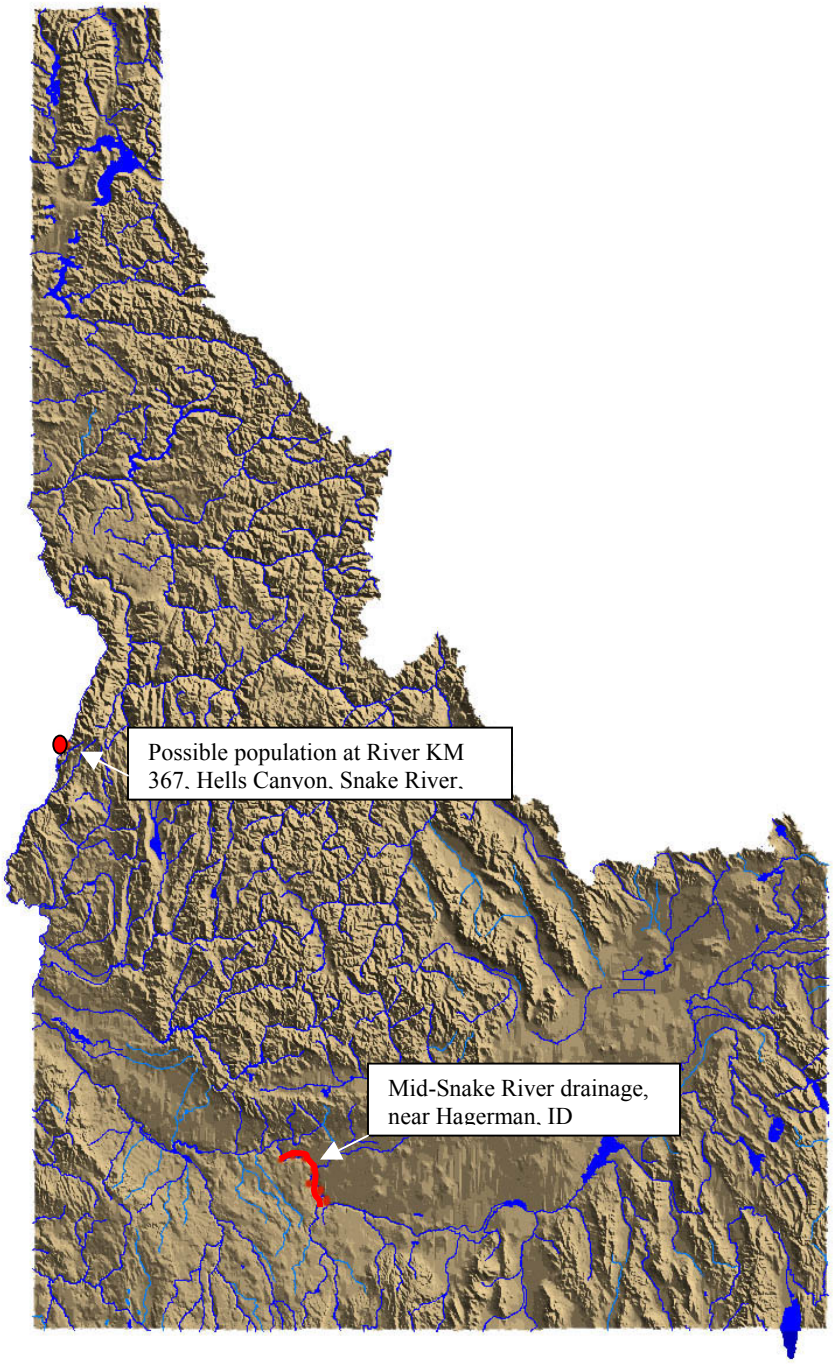
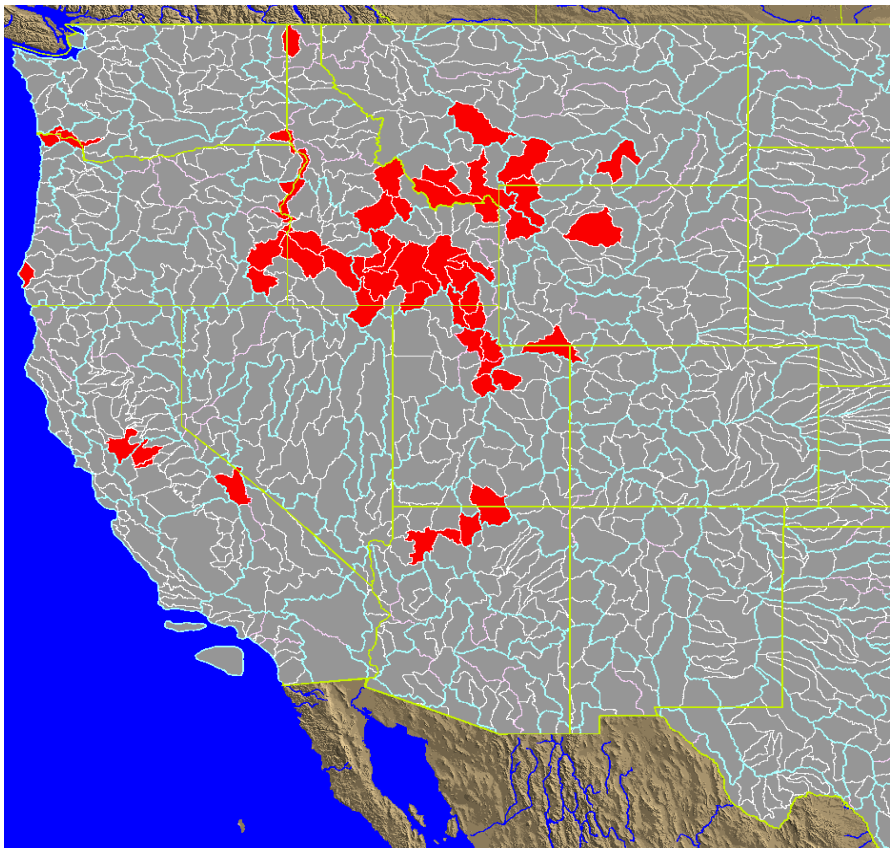


Figure 3. *Potamopyrgus antipodarum* (Family Hydrobiidae)(Photo courtesy of Dr. Dan Gustafson, Montana State University, Bozeman, MT)

Figure 4. Reported distribution of *P. antipodarum* west of 100º West longitude, USA, as of 2004 (from www.esg.montana.edu/aim/mollusca/nzms) (map cells represent USGS HUC cataloging units)



In the western USA, densities can often exceed 300,000/m^2 (Richards et al. 2001, Kerans et al. in press) and have been reported as high as 500,000/m^2 in a tributary of the Snake River in Yellowstone National Park (Hall et al. 2003). *Potamopyrgus antipodarum* is now often the most abundant macroinvertebrate species in known habitats occupied by *T. serpenticola* (W. Clark, Idaho Power Company, personal communication; D. Richards unpublished data).

Although it is thought to be primarily a parthenogenic livebearer in the western USA (M. Dybdahl, Washington State University, personal communication), males have recently been found to comprise from 1- 3% of a population in SW Montana (C. Cada, Montana State University, personal communication). In the western USA, adult *P. antipodarum* are typically 4 to 5 mm shell length and, like *T. serpenticola,* have been reported to be somewhat photophobic (Levri 1998). *Potamopyrgus antipodarum* now often comprises 85% to 95% of the invertebrate assemblages both in biomass and abundance in many rivers in the western USA (Bowler 1991, Richards et al. 2001, Kerans et al. in press, Shannon et al. 2003).

To date, limited research on the ecological impacts of *P. antipodarum* on western USA aquatic ecosystems has been published. C. Cada and B. L. Kerans (Montana State University, unpublished manuscript) documented lower periphyton biomass and fewer individuals of some invertebrate taxa in sections of their study site in a tributary of the Madison River, MT containing many *P. antipodarum* versus sections with few *P. antipodarum*. In addition, Kerans et al. (in press) showed that the numbers of other invertebrates colonizing slate tiles in the Madison River were negatively correlated to the abundance of *P. antipodarum*. Moreover, preliminary evidence suggested growth rates

of mottled sculpins in sections of a stream where *P. antipodarum* was abundant were lower than in sections where it was absent. Hall et al. (2003) documented > 75% of gross primary production in a river in Yellowstone National Park having been diverted through *P. antipodarum*. Their data showed that *P. antipodarum* consumed nearly 100% of the algal primary production and that algal growth rates were slower with increased *P. antipodarum* biomass, which suggested that *P. antipodarum* was consuming high-turnover algal taxa and that its impacts on the aquatic environment were comparable to that of the zebra mussel (*Dreissenia polymorpha*) in the eastern USA (Hall et al. 2003).

It appears that not only is *P. antipodarum* a highly invasive species, but that it has the potential to affect populations of native species and alter ecosystem function. Because *P. antipodarum* can often reach extremely high densities and, under certain conditions, appears to be capable of affecting whole ecosystem processes, understanding its population dynamics becomes critical if we are to control its spread and limit its impact.

Goals

Even though little was known about the life history and ecology of *T. serpenticola,* it was federally listed as Threatened, in part because of potential competitive interactions with *P. antipodarum* (USFWS 1995). Therefore, before I addressed competition between the two species, I needed more information on basic life history traits, environmental niche overlaps and population dynamics, of both species than was available in the literature.

In Chapter 2, I; 1) compared optimal growth temperatures and estimated temperature tolerances for each species, under laboratory conditions; 2) examined stage (size) class fecundity rates and growth rates; and 3) examined photophobic tendencies of both species,

In Chapter 3, I explored environmental conditions in Banbury Springs that may have affected *T. serpenticola* and *P. antipodarum* distribution and abundance, particularly differences in edge effects between vegetation and run habitats. In this chapter, I also explored the spatial distributions of *T. serpenticola*, *P. antipodarum*, and *Fluminicola* sp. in the same section of Banbury Springs. I focused on possible spatial autocorrelation patterns of the three species using geostatistical methods and then formally test whether each species is distributed randomly, uniformly, or clumped and if each species was statistically associated or disassociated with one another using the statistical program, Spatial Analysis by Distance Indices (Perry 1999). Based on the results of the spatial analyses, I estimated abundances of each species in the study area, results of which can be directly useful to managers, particularly for management of the threatened Bliss Rapids snail, *T. serpenticola*.

In Chapter 4, I conducted a laboratory experiment to determine if size hierarchies could arise in *P. antipodarum* populations due only to intraspecific competition for limited food resources. Density dependent size hierarchies in either species could affect interspecific competition outcomes.

In Chapter 5, I conducted several competition experiments with *P. antipodarum* and *T. serpenticola* under controlled conditions at Banbury Springs. I also developed competition coefficients for the two species and related their growth rates and

competitive outcomes to periphyton abundance and diversity. Results from these competition experiments showed that competition could occur between *T. serpenticola* and *P. antipodarum* under controlled conditions, but these experiments did not address the potential importance of spatial habitat heterogeneity and real world conditions. I therefore, monitored and then modeled seasonal and yearly population density trends of both species in a section of Banbury Springs, where both coexist, using time series analysis in Chapter 6.

SOME LIFE HISTORY STUDIES OF *TAYLORCONCHA SERPENTICOLA* AND *POTAMOPYRGUS ANTIPODARUM*

Introduction

The idea of 'niche' originated at least since Darwin (1859) and is a general concept meant to summarize many aspects of an organism's biology and ecology (Leibold 1995). Modern niche theory proposes a "total" niche, which is comprised of an organism's "requirement" niche and "impact" niche (Leibold 1995). The "requirement niche" or "fundamental, N-dimensional hypervolume niche" contains all the environmental conditions or limiting factors that control the organisms fitness and can include; abiotic factors (such as temperature, dissolved oxygen), habitat requirements, predators, and resources (Hutchinson 1957, 1978, Leibold 1995). Limiting factors in the "requirement" niche, such as food resources, can also alter population dynamics (Begon et al. 1996). The "impact" niche is what the species role is or what it is doing and its subsequent impact on the environment (Elton 1927, Leibold 1995). For example, most freshwater aquatic snails, including *T. serpenticola* and *P. antipodarum*, are considered herbivore-grazers. Understanding both the "requirement" and "impact" niches can help answer the questions, "Under what conditions can *T. serpenticola* and *P. antipodarum* co-occur " and " is continued coexistence of these two species possible?"

Although *T. serpenticola* was petitioned for listing as a threatened species more than 20 years ago (U.S. Fish and Wildlife Service 1992) and *P. antipodarum* has been established in the Snake River for almost the same amount of time (Bowler 1991), almost nothing was known about their basic biology or ecology (niches) in this system. For

example, no data are available on important life history traits ("requirement" niches) that may influence interspecific competition and coexistence, such as; 1) temperatures for optimal growth or the range of temperature tolerances for either species; 2) stage or size class fecundity and growth rates of *P. antipodarum*; or 3) photophobic tendencies of either species.

Water temperature is one of the most important regulators of distributions of freshwater organisms (Giller and Malmqvist 1999, Allan 2001). Reports of temperature tolerances of *P. antipodarum* vary from < 0˚ C in slightly saline waters (Hylleberg and Siegismund 1987) up to 32˚ C in experimental tests (Quinn et al. 1994). Temperature tolerances of *T. serpenticola* have not been reported, but extant populations are usually found in cold-water springs or river habitats influenced by cold-water springs from the Snake River aquifer (Frest and Johannes 1992). Therefore, its upper temperature tolerance may be lower than *P. antipodarum*. Water temperatures of several of the cold - water springs where populations of *T. serpenticola* persist are uniformly constant throughout the year and range between 13 and 16˚ C (Richards et al 2001, Shinn 1999). In the flowing sections of the mid-Snake River where populations of *T. serpenticola* persist, river water temperatures fluctuate daily and seasonally and range from a high of $\geq$ 22˚ C in summer to a low of 0˚ C in winter (Shinn 1999). However, it is unknown if these temperature measurements were recorded near sections of the river influenced by upwelling from the Snake River aquifer (Shinn 1999). There is no evidence that either these cold-water springs or river temperature regimes allow for optimal growth of *T. serpenticola* or *P. antipodarum*. Therefore, I conducted laboratory experiments on growth rates of both species at several temperatures.

There are also no data available on growth rates of *P. antipodarum* in relation to stage or size classes in the western USA. Sizes of *P. antipodarum* populations vary in the western USA; individuals present at any one time may range from ≅ 0.75 mm newborns, to 4.0- 5.0 mm adults or larger, of unknown ages. This size-at-birth is in the range reported in European, clonal *P. antipodarum,* which can range from 0.5 - 1.0 mm (Dahl and Winther 1993) or from ≅ 0.9 - 1.7 mm (Jacobsen and Forbes 1997). In the western USA, it is unknown if smaller snails grow at a faster rate than larger snails, given ample food resources. It is also unknown if stage classes observed in the field could be a result of differential growth rates. To address this problem, I estimated growth rates, measured as shell length and biomass, of *P. antipodarum* over several months under laboratory conditions.

Both species have been reported to be photophobic (Bowler 2001, Levri 1998a), possibly as an avoidance response to visual predators (Levri 1998b), but photophobic tendencies of either species in the Snake River drainage have not been experimentally tested. If both species are photophobic than they could compete, via interference, for habitat, diurnally and/or for food resources, nocturnally. Therefore, I sampled cobble habitat and conducted an *in situ* experiment to establish the photic tendencies of both species.

Materials and Methods

Growth Rates of *T. serpenticola* and *P. antipodarum* at Six Temperatures

I measured shell growth of ten *T. serpenticola* and ten *P. antipodarum* at six temperatures, 6, 15, 17, 20, 22, and 26˚ C (42.8, 59, 62.6, 68, 71.6, and 78.8˚ F

respectively)(N = 120) in EcoAnalysts Inc. Research Laboratory, Bozeman, Montana. Snails were reared in the laboratory from stock from Banbury Springs, near Hagerman, Idaho. Snails were individually placed in 21 mm (inner diameter); double open-ended glass tubes that were 7 cm in length. Tubes were covered on each end with 1mm nylon mesh secured with rubber bands. I used 1 mm nylon mesh instead of smaller diameter because it was the largest size that would contain snails and allow for sufficient gas exchange between the tube and surrounding water and a mesh size larger than 1 mm would have allowed snails to escape.

Approximately 200 glass tubes were conditioned with periphyton from a 160-gallon aquarium containing a wide variety of periphyton taxa (> 12 identified taxa), for two weeks before stocking. Tubes were then visually examined and those (N = 120) that appeared to have approximately equal amounts of periphyton growing inside were selected for the experiment. Because there was ample periphyton growing in the tubes at the end of the experiment, it is highly unlikely that snails were food limited. Tubes with snails were then placed into 10-gallon aquaria. Two replicate aquaria were maintained at each of the six temperatures (12 total aquaria) to address the effects of individual aquaria on growth. Five tubes with individual snails were placed in one of each aquarium. Tubes were placed near aeration sources in an effort to maximize the oxygen available to the snails and to facilitate gas exchange from the water within the tube into the surrounding water. Dissolved oxygen was measured from within one of the five tubes in each of the 12 aquaria weekly, using a Technika® dissolved oxygen meter. Dissolved oxygen ranged from 6.4 to 7.5 ppm for all temperatures.

Sixty active *T. serpenticola* between 1.4 mm and 1.9 mm shell length (mean = 1.67, s.d. = 0.126) and sixty active *P. antipodarum* between 1.6 mm and 2.3 mm (mean = 2.01, s.d. = 0.148) were selected. I chose these shell lengths because *T. serpenticola* smaller than 1.4 mm could escape through the mesh and because it reaches a maximum of about 3.0 mm shell length. I had to choose slightly larger *P. antipodarum* than *T. serpenticola* because *P. antipodarum* shells are more elongate- conical than the globose *T. serpenticola* shells and < 1.6 mm *P. antipodarum* could pass through the 1 mm diameter nylon mesh. I also avoided using *P. antipodarum* larger than 3.0 mm, because at that size they start producing embryos (Richards et al. 2000) and may have diverted their energy from shell growth to embryo production. Even though I only measured temperature effects on these size groups, growth rates are often directly related to fecundity (citation) and none of their reported or observed life history characteristics suggest that temperature affects snail growth at different size classes. I therefore assume that these results will be similar for other size classes of both species.

At 30 days snails were removed from the tubes and measured to the nearest 0.05 mm. They were then replaced into the same tubes for an additional 15 days to determine if they laid eggs and were allocating some energy to reproduction, rather than solely to growth during the experiment. I did not determine the sex of *T. serpenticola* used in this experiment because that would entail dissection. It is also unknown at what size *T. serpenticola* begins to reproduce. I did not observe any *T. serpenticola* eggs during 15 days after termination of the experiment.

Average growth rate per day was determined for each of the 120 snails. Because growth rates were non-normally distributed, I used nonparametric Kruskal-Wallis test of

ranks to determine if growth rates of each species varied between temperatures. In addition, I used two-sample Wilcoxon test for comparing several findings. I also report the percent mortality for both species at each temperature.

Stage Structured *P. antipodarum* Population Growth Rates and Fecundity

I observed adult *P. antipodarum* in laboratory aquaria on a daily basis until young were observed. Under laboratory conditions, pulses of newborns occur from many similar sized adults releasing young within several days of each other. Fifty young *P. antipodarum* with a mean 1.48 (± 0.01 se) mm shell length were collected within ≅ 7-10 days after birth and placed in individual 21 mm (inner diameter), double open-ended glass tubes that were 7 cm in length in a ten-gallon aquarium in the laboratory. Water temperature was maintained at 17° C under a 14:10 light: dark regime. Snails were fed ¼ Wardley™ brand algal disks once every week and remaining wafers were removed to prevent fungal growth and provide equal amounts of food availability. Shell length was measured every 7 days for 98 days (N = 14). Mortality was recorded at each measurement period. Shell lengths were transformed to biomass using a previously calculated regression formula: biomass (mg) = 1.91 –2.29*shell length + 0.88* shell length^2. Mean, standard error (s.e.) and coefficient of variation (CV) were calculated for biomass, increase in biomass per week, shell length, and increase in shell length per week for each of the 15 time periods (including time 0).

In addition, I examined a total of 902 *P. antipodarum* that were collected in 1999 and 2000 from various habitats in the Banbury Springs Complex, mid-Snake River drainage, southern Idaho (N = 481) and Darlinton Spring Creek, Madison River drainage, SW Montana (N = 421) for embryo production. Shell length for each snail was measured

to the nearest 0.01 mm. Each snail was gently rolled between a finger and glass dish with increasing pressure until the shell cracked. Neonates ($\geq$ 0.05 mm) were then dissected away from the brood pouch and counted. I then compared the relationship between the number of neonates produced and shell length using regression analysis. For a more detailed analysis of number of neonates in relation to shell length at various seasons and locations see Richards et al. (2000).

Photic Tendencies of *T. serpenticola* and *P. antipodarum*

Artificial Substrate Experiment. Twelve artificial substrates were placed in a northern section of Morgan Lake at Banbury Springs, Idaho, during April 2000 (Figures 5 and 6). Substrates were made of untreated 1.27 cm diameter plywood, 30.48 cm x 30.48 cm square and were conditioned in the lake for 2 weeks prior to start of experiment. Top and bottom of substrates were randomly chosen by coin toss to determine which side was placed up. This was done to reduce any bias resulting from differences in periphyton abundance and composition between tops and bottoms. Substrates were placed 20-30 cm below the water surface and were buoyed in place by attached 9.07 kg test monofilament line anchored to the bottom of Morgan Lake and by a 1.27 cm nylon rope strung between 1.91 cm diameter rebar above the surface (Figure 6). Substrates were contained within a 6.10 m x 3.05 m exclosure made of 1 mm mesh nylon attached to the rebar, which spanned from the bottom of the lake to 20 cm above the water line. This enclosure was erected to prevent *P. antipodarum* and floating mats of green algae from entering the study site and to allow for regulation and manipulation of *P. antipodarum* abundances on substrates. Even though the 1 mm mesh enclosure was designed and intended to limit colonization by *P. antipodarum*, large numbers of them

found their way on to the substrates. These were counted, and became an important component of this study. All algal mats were cleared from within the enclosure on a daily basis. Each of the twelve substrates was stocked with 50 *T. serpenticola* on the topside (day 0). No (0) *P. antipodarum* were stocked on any of the substrates. Snails were counted at 10 AM on day 1, 3, 6, 9, 12, and 14 and counted on days 12 and 14 at 12 AM (midnight). Snails that were on the sides of substrates were equally assigned to tops or bottoms. During counts, a 1 mm mesh net was held below substrate and any snails that fell off were replaced on the topside. In addition, five standard Surber samples (1 mm mesh) were collected in Morgan Lake adjacent to the enclosure on day 0, to estimate background densities of *T. serpenticola* and *P. antipodarum* in the area at that time.

Figure 5. Exclosure site at Morgan Lake, Banbury Springs, near Hagerman, Idaho. Exclosure was 6.10 m x 3.05 m using 1 mm mesh nylon.

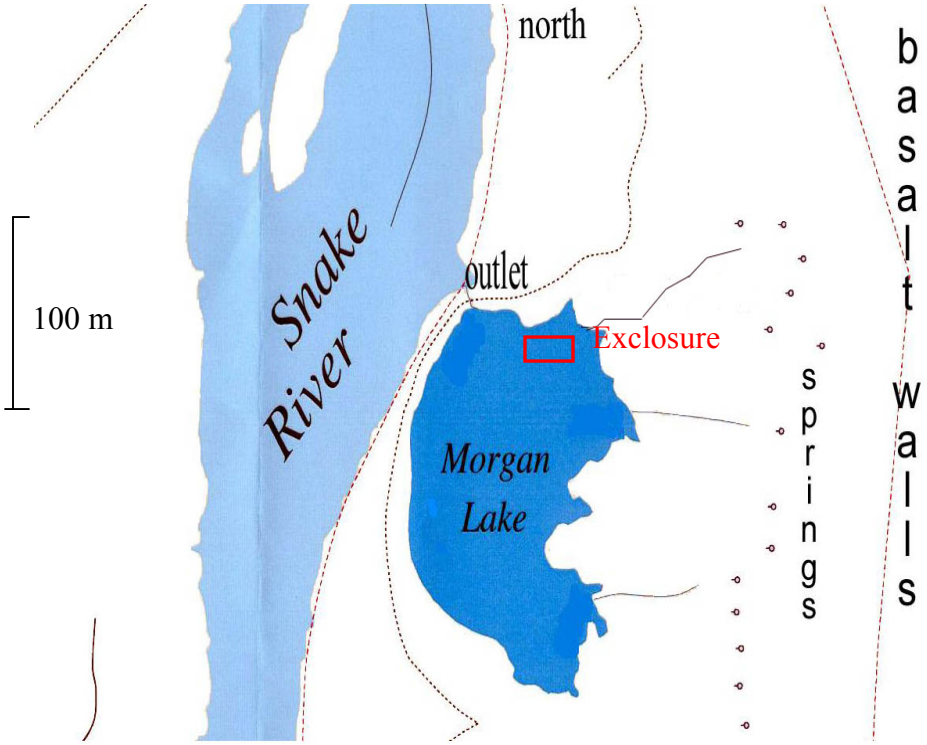
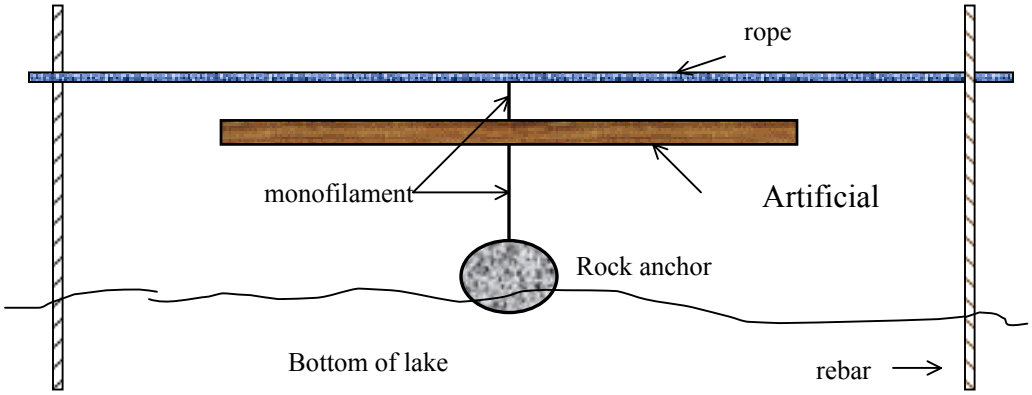


Figure 6. Artificial substrate (N = 12) within exclosure at Morgan Lake, Banbury Springs, Idaho. Substrate was 30.48 cm x 30.48 cm, 1.27 cm diameter, untreated plywood, conditioned for 2 weeks in Morgan Lake.



Descriptive statistics of mean (95% CI's) and percent number of *T. serpenticola* and *P. antipodarum* on top and bottom of artificial substrates were made for the seven daylight observations (day 0 = control with 50 *T. serpenticola* per substrate and 0 *P. antipodarum* per substrate) and 2 night observations on days 12 and 14. Mean frequencies of *P. antipodarum* on the tops of substrates were compared for night observations (N = 2) and day observations (N = 7) using two-sample t-test. There were no *T. serpenticola* found during night observations (day 12 and 14), so no comparisons were made. For all analyses in this study I used S-PLUS 6.1 for Windows (Insightful 2000).

Spatial Distribution of Snails on Undisturbed Cobbles. Between 12:00 and 4 PM, April 21, 2000, twenty rectangular shaped cobbles were examined at the outlet of Morgan Lake where it enters the Snake River (Figure 5). Counts were made of *T. serpenticola*

and *P. antipodarum* on tops, sides, and bottoms of cobbles. The length, width, and height of the cobbles were also measured

Snail counts on cobbles were transformed into densities (snails/m2) on top, sides, and bottoms. I conducted a non-parametric Moods median test on the snail densities because transformations did not normalize their distribution and because there were many outliers in the data. Moods median test is less sensitive to outliers than the non-parametric Kruskal-Wallis test (Conover 1999). I also compared 95% CI's of densities between top, sides, and bottom of cobbles for both species. If their 95% CI's did not overlap, I considered them significantly different.

Results

Growth Rates of *T. serpenticola* and *P. antipodarum* at Six Temperatures

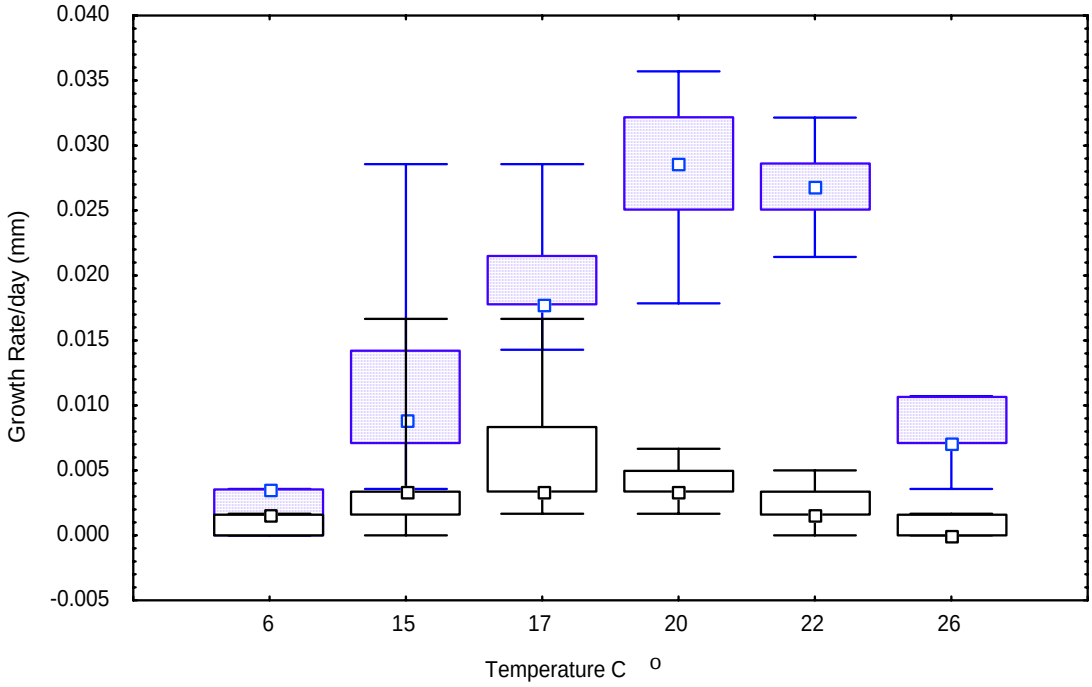
Taylorconcha serpenticola Growth Rates. There were significant differences in growth rates between the 6 temperatures ($H = 25.15$, $df = 5$, $N = 55$, $p < 0.01$). Post hoc power analysis using the mean of the variances = 0.0027 for all six temperatures and a detectable difference of 0.005 gave a power value of 0.88, which indicated good replication. Median growth rates of *T. serpenticola* were 0.003 mm/day for 15, 17 and 20˚ C. The highest mean growth rate was 0.006 mm/day at 17˚ C. Maximum growth rates were 0.017 mm/day at 15 and 17˚ C and minimum growth rates for *T. serpenticola* were at 6 and 26˚ C (Figure 7). By examining descriptive statistics and box and whisker plots of the growth data, I determined that the significant differences in growth rates occurred between either the lowest temperature of 6˚ C or the highest temperatures of 26˚ C and the two middle temperatures of 17 and 20˚ C (Figure 7). The two-sample

Wilcoxon test comparing 15 and 22˚ C resulted in a p- value of 0.07, which suggested growth rates at these two temperatures were marginally statistically different. No mortality occurred at 15, 17, and 20˚ C, however, mortality was 10% at 22˚ C and 20% at 6 and 26˚ C.

Potamopyrgus antipodarum Growth Rates. There were statistically significant differences in growth rates between the 6 temperatures ($H = 48.51$, $df = 5$, $N = 60$, $p < 0.01$). Post hoc power analysis using the mean of the variances = 0.0043 for all six temperatures and a detectable difference of 0.007 gave a power of 1.00 and therefore, excellent replication. Median growth rates for *P. antipodarum* were highest at 20 and 22˚ C at 0.0285 mm/day and 0.0267 mm/day, respectively (Figure 7). Growth rates were lowest at 6 ˚C (median = 0.0035mm/day) and at 26˚ C (median = 0.0071mm/day)(Figure 7). No mortality occurred for *P. antipodarum* at any temperature.

Comparison of *T. serpenticola* and *P. antipodarum* Growth Rates. At all temperatures, *P. antipodarum* growth rates were significantly higher than for *T. serpenticola* except at 15˚ C (Figure 7). At 15˚ C, the fastest growing *T. serpenticola* individual (0.017mm/day) grew at rates higher than the upper quartile of *P. antipodarum* and the slowest growing *P. antipodarum* individual (0.0035mm/day) grew at a rate about equal to the upper quartile of *T. serpenticola*, which was probably why there was no significant difference in growth rates at this temperature (two-sample Wilcoxon test; $p = 0.515$) (Figure 7). At 20 and 22˚ C, *P. antipodarum* grew 9.5 X and 13.35 X faster than *T. serpenticola* (Figure 7). Even though there was a slight overlap in growth rates of the two species at 17˚ C, they were statistically significantly different (two-sample Wilcoxon test; $df = 9$, $t = 0.000$, $z = 2.665$, $p < 0.01$).

Figure 7. *T. serpenticola* vs. *P. antipodarum* growth rates (mm/day) at 6 temperatures (min, max, 25% to 75%, and median values)(*T. serpenticola* growth is in black; *P. antipodarum* growth is in blue)(N = 10 snails/temperature treatment)



Stage-structured *P. antipodarum* Population Growth Rates and Fecundity

Most mortality in the laboratory occurred at the smallest sizes and followed a Type III survival curve (Figure 8). None of the 902 *P. antipodarum* with a ≤ 2.99 mm shell length collected in the field had embryos. At 3.00 mm, field collected *P. antipodarum* were producing embryos, and there was a significant linear relationship (R^2 = 0.44, P = 0.00) between shell length and number of embryos in brood pouches for snails that contained embryos (Figure 9).

In the laboratory study, shell length and biomass increased more quickly at the intermediate age classes than at the early and late age classes (Figure 10 and Appendix 1). Most biomass increase occurred between shell lengths of 2.75 and 4.30 mm (days 42-

70). There was a large amount of variability (coefficient of variation, CV) in individual biomass increase in snails measured on day 14 (≃ 1.75 mm shell length)(CV = 2.69), day 35 (≃ 2.20 mm shell length)(CV = 2.39), and days 91 and 99 (> 4.44 mm shell length)(CV = 1.83, 1.46, respectively).

Figure 8. Type III survivorship curve for *P. antipodarum* under laboratory conditions.

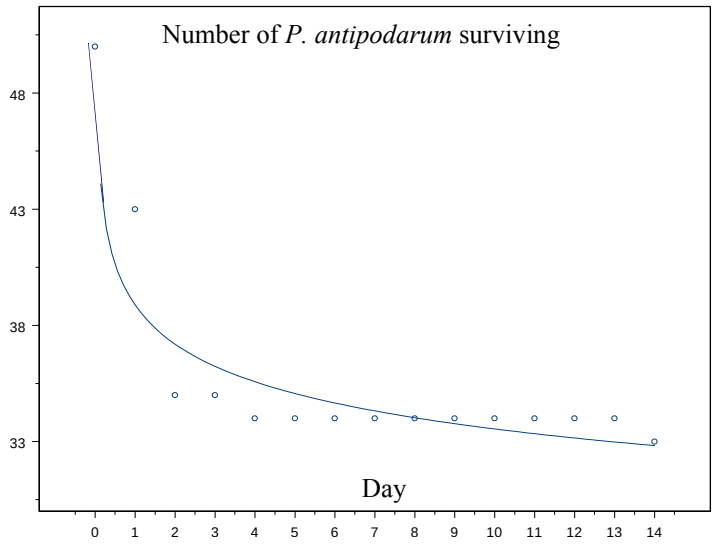


Figure 9. Relationship between *P. antipodarum* shell length and number of embryos in brood pouches from snails with embryos. Best- fit regression model (lowest AIC): number of embryos = -81.71 + 25.73*shell length (N = 257, P-value = 0.00, R^2 = 0.44).

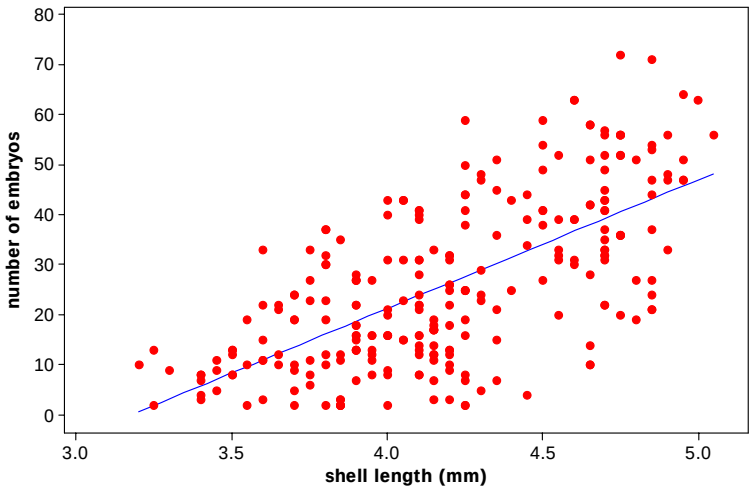
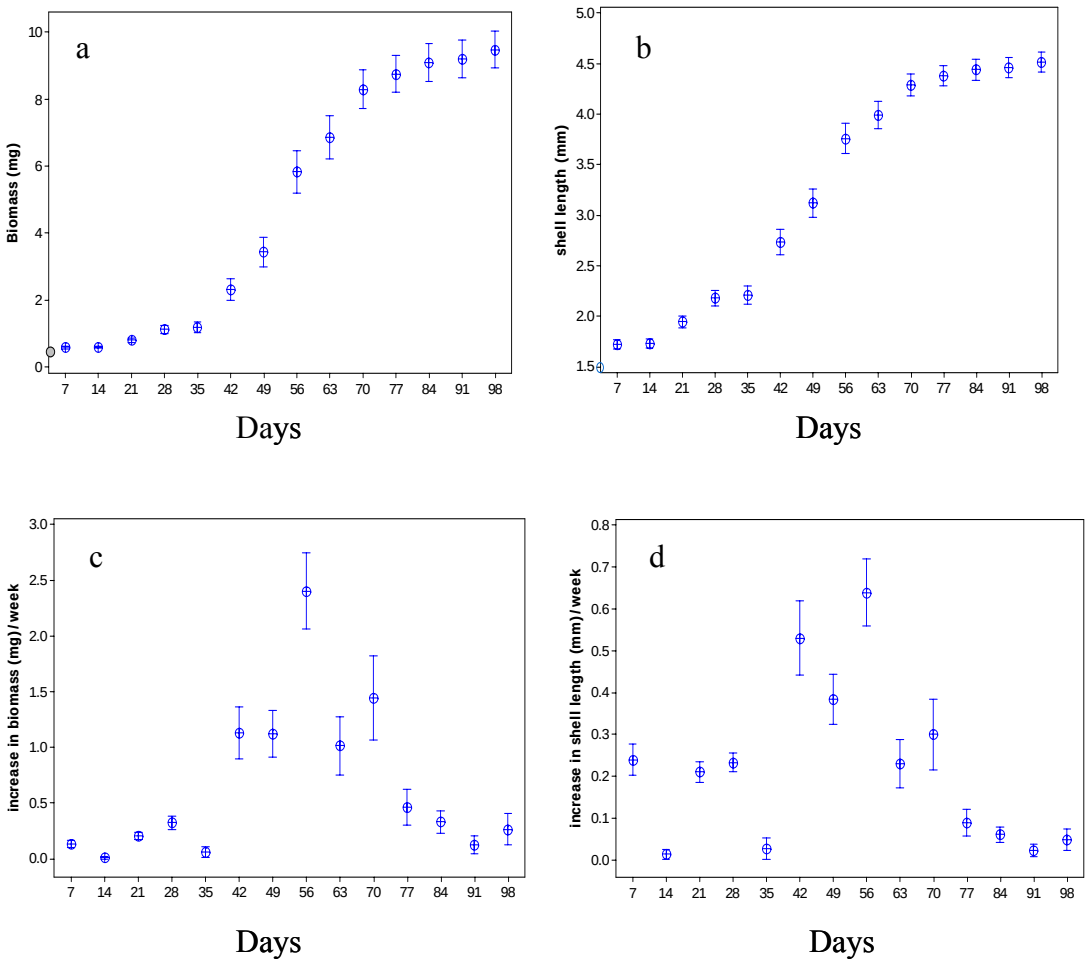


Figure 10. Changes in biomass and shell length of *P. antipodarum* (N = 50, 1.5 mm individuals at start). Snails were measured at seven-day intervals. a) biomass (mg), b) shell length (mm), c) increase in biomass (mg/week), d) increase in shell length (mm/week)



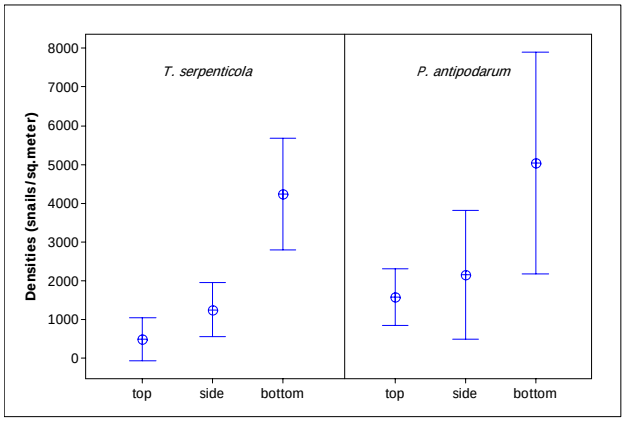
Photic Tendencies of Both Species

Artificial Substrate Experiment. After day 1, all remaining *T. serpenticola* were found on the bottoms of the substrates during the 10 AM counts and by day 12, all *T. serpenticola* had abandoned the substrates entirely. The mean frequency (%) of *P. antipodarum* on the tops of substrates during daylight observations (N = 7) was 0.04 (95% CI; 0.03, 06) and was significantly lower than for night observations (N = 2) with a

mean frequency of 0.73 (95% CI: 0.68, 0.78; p-value = 0.01). Daylight visual inspections of the top of the substrates revealed that there were many more *P. antipodarum* on the tops of the substrates at 7 am (prior to direct sunlight) than at 10 am ($\simeq$ 1 hour after direct sunlight) when snails were counted, suggesting that *P. antipodarum* was moving to the bottom of the substrates, as the day progressed and light intensity increased.

Distribution of Snails on Undisturbed Cobbles. Abundances of *T. serpenticola* and *P. antipodarum* were significantly different on tops, sides, and bottoms of the cobbles (Moods median; $\chi^2 = 17.20$, df = 2, $P < 0.01$ and $\chi^2 = 8.40$, df = 2, $P < 0.02$, respectively). Abundance of *T. serpenticola* was significantly greater on the sides and bottoms of cobbles than on tops, but not significantly different between sides and bottom (overlap in 95% CI's)(Figure 11). Abundance of *P. antipodarum* was significantly greater on the bottoms than tops of cobbles (no overlap in 95% CI's) but not significantly different between tops and sides or sides and bottom (overlap in 95% CI's).

Figure 11. Densities of *T. serpenticola*/m^2 and *P. antipodarum*/m^2 on tops, sides, and bottom of cobbles (N = 20) at the outlet of Morgan Lake into the Snake River, 12pm, April 21, 2000 (mean and 95% CI's)



Discussion

Based on the temperature experiment, it appears that *T. serpenticola* grows best between 15 and 20˚ C and probably does a little better at 15 to 17˚ C. These are slightly higher temperatures than at Banbury Springs, where the test snails were originally collected and suggest that individuals of *T. serpenticola* in Banbury Springs and surrounding springs may not be growing at their maximum potential. *Potamopyrgus antipodarum* appears to grow better at warmer temperatures than does *T. serpenticola*, which may partially explain why *P. antipodarum* is not found in abundance in the upper, colder reaches of Banbury Springs. Results of this experiment are also consistent with a previous temperature-growth experiment, where out of five temperatures studied, *P. antipodarum* growth rates were highest at 21˚ C (Richards et al 2000).

Based on the variability in growth rates, I suggest that observed size structures of *P. antipodarum* found in aquatic habitats in the western USA may not reflect age or timing of release of embryos. For example, high abundance of small (< 2.20 mm) and large (> 4.30 mm) snails with an absence or low abundance of snails between 2.20 – 4.30 mm may not indicate a break in birth sequences. This observed size class structure could be a result of the timing of sampling events greater than the length of time ($\approx$ 40 days) that snails were in this size class. Rapid growth rates of snails in these size classes could be attributed to higher feeding rates (Levri 1996).

The large amount of variability (CV = 2.69) in increase in biomass of individuals at the 1.75 mm size class could be due to smaller newborn snails not finding food (by chance) or because they were less fit and therefore, grew less. Others at this age may have grown quicker because, by chance, they were able to find the food resource or had

greater fitness. Most mortality occurred for the smallest sizes; again this could have been due either not finding food or lower fitness. Although *P. antipodarum* has been shown to locate food resources using chemoreception (Haynes and Taylor 1984), it is unknown to what extent this is learning experience. Also, at the smallest sizes, stored energy reserves from hatching only allow for a limited amount of time and effort for finding food resources. Travel time to food resources may be positively related to body size. Small (0.5 mm) newborn *P. antipodarum* in New Zealand and Europe can take up to two months to reach 1.0 mm (Winterbourne 1970, Dorgelo 1991), longer than was found in this experiment, but consistent with the idea that it is more difficult for smaller newborns to locate food resources.

The large amount of variability (CV = 1.83 and 1.46) for the increase in biomass of individuals at the largest two sizes (> 4.44 mm) could be attributed to those snails that already had reached the larger size classes having slower growth rates, while those that lagged behind were able to catch up. Larger snails may also have stopped growing because they were preparing to release embryos (Jokela and Winterbourn 1970, Lively 1995). There was also a large amount of variability (CV = 2.39) in the increase in biomass of individuals around the 2.20 mm sizes. This may have been due to an allometric relationship between shell length and biomass, where increases in shell length occurred more rapidly than for biomass.

In the photophobic study, both *T. serpenticola* and *P. antipodarum* preferred the bottom of the substrates during daylight hours and *P. antipodarum* preferred the tops at night. Both species were also more abundant on sides or bottoms of undisturbed cobbles. I also observed substrates irregularly throughout the day on days when snails were not

counted and there appeared to be a decrease in numbers of snails on the tops of substrates as the day progressed. Under experimental conditions, Bowler (2001) concluded that *P. antipodarum* was not photophobic, although in his study, snails were only subjected to light for 10- minute intervals under artificial conditions and no delineation of size class differences was reported. Levri (1998b) however, reported that in general, larger *P. antipodarum* and in particular, larger brooding snails spend less time on the tops of substrates diurnally than do smaller snails under natural conditions. This was presumably to avoid visual predators, primarily waterfowl and fish. I did not measure *P. antipodarum* shell lengths on the artificial substrates, but typically in April in Banbury Springs and Morgan Lake adults are fully reproductive (unpublished data) and many of these snails could have been brooding. Also at this time, waterfowl are abundant at Morgan Lake, as are several species of potential fish predators (personal observation).

Bowler (2001) also reported that *T. serpenticola* was photophobic, hiding beneath rocks in daylight and grazing in the open, nocturnally. I did not measure periphyton on the cobbles or other environmental variables, therefore, I do not know if *T. serpenticola* and *P. antipodarum* avoided the tops of cobbles in response to light, food resource availability, or a combination of these. Routine observations of *T. serpenticola* in my laboratory also suggest that individuals are much more abundant on the sides and undersides of cobbles than on tops of cobbles during lighted conditions, although the periphyton density is visually greater and probably different in composition on the tops as compared to the bottoms of cobbles. Further research is required to determine if there is a relationship between periphyton abundance/composition and *T. serpenticola* photophobic behavior. Although I did not formally test if *T. serpenticola* was more

abundant on tops of substrate or natural cobbles at night, this study, in general, supports the idea that both *T. serpenticola* and *P. antipodarum* are photophobic. Because both species apparently migrate daily in response to light, they are likely to compete for habitat, wherever their ranges overlap.

It is interesting that the combination of an exclosure area and the suspension of the artificial substrates off the bottom of the lake did not prevent *P. antipodarum* migration and colonization. *Potamopyrgus antipodarum* individuals either: floated in on algal mats, drifted in the water column, or were able to climb a single strand of monofilament to reach the suspended substrates. The ability of this highly mobile snail to locally invade unoccupied habitats should be considered in future ecological studies and management activities.

Conclusion

Although more life history studies of *T. serpenticola* and *P. antipodarum* are needed for us to fully understand their ecology, these studies provide some insight. From these and from previous studies, it appears that; 1) temperature niches of *T. serpenticola* and *P. antipodarum* overlap, 2) observed stage structure may not reflect age class for *P. antipodarum*, and 3) both species are photophobic. In locations where *T. serpenticola* populations persist and water temperature requirements are met for both species, interspecific competition for space may increase, particularly in shaded habitats during daylight hours.

SPATIAL AND ENVIRONMENTAL RELATIONSHIPS OF *T. SERPENTICOLA*, *FLUMINICOLA* SP., AND *P. ANTIPODARUM* IN A FRESHWATER SPRING: WITH ESTIMATES OF THEIR ABUNDANCE

Introduction

Homogenous habitats rarely exist in nature (Tilman and Kareiva 1997, Dale 1999). Even monocultural agriculture lands and the open oceans are heterogenous, if examined on an appropriate spatial scale [(i.e. grain, extent (Cox et al. 1997, Dungan et al. 2002)]. Studying spatial patterns of organisms can often lead to an understanding of underlying processes, such as interactions between a species and its environment or interspecific competition, which can then allow us to better manage ecosystems and threatened and endangered species (Perry et al. 2002). Because habitats are patchy and dispersal of organisms tends to decrease with increasing distance, the distribution of organisms is often spatially autocorrelated.

Spatial autocorrelation is the lack of independence between pairs of observations at given distances (Bailey and Gatrell 1995, Diniz-Filho et al. 2003). Because of the lack of independence in spatially correlated data, Type I errors can be inflated, therefore, understanding spatial patterns allows for refinement of statistical tests and improvement of sampling design (Perry et al. 2002, Legendre 1993, Legendre et al. 2002). It has also been suggested that spatial autocorrelation generates “red herrings” (diversions that keep us from detecting meaningful relationships of variables) and that all past statistical analyses that did not account for spatial autocorrelation were flawed (Lennon 2000), although this suggestion seems to be overstated (Diniz-Filho et al. 2003)

Numerous methods are available (from a variety of disciplines) for analyzing spatial patterns; thus it is often difficult to choose the most appropriate method (Perry et al. 2002). Point-referenced data with attributes (*x, y, z*) are commonly used for analysis of plant and animal spatial patterns (autocorrelation)(Rossi et al. 1992, Perry et al. 2002), where 'x' and 'y' are location variables and 'z' is the variable of interest. Two methods that use point-referenced data are geostatistical kriging, which is based on variogram models, and **S**patial **A**nalysis by **D**istance **I**ndic**e**s (SADIE).

Variograms are based on the idea that spatial autocorrelation declines and variance increases with increased distance between sample points, until some maximum variance is reached and the *z* data are no longer correlated with each other (Rossi et al. 1992, Perry et al. 2002). This distance, known as the 'range', can be interpreted as an estimate of patch and gap size (Perry et al. 2002). Variograms can then be used for spatial interpolation, modeling, and simulation (Isaaks and Srivastava 1989, Rossi et al. 1992).

SADIE was designed to detect spatial patterns of individual populations in the form of clusters, either as patches or gaps (Perry et al. 1999) and can also measure and test for spatial association between two species (Perry and Dixon 2002). If more than one *z* value (e.g. additional snail species abundance) is measured for each *x* and *y* value, then it is possible to explore and test whether the *z* values are positively associated or 'dissociated' after any similarity or dissimilarity due to individual *z* spatial structure is accounted for (Clifford et al. 1989, Bocard et al. 1992, Dutilleul 1993, Perry et al. 2002, Liebhold and Sharov 1998).

Interspecific competition may cause two species to be spatially dissociated or they may be randomly distributed with respect to one another. Spatial interactions between two species are dynamic and can be influenced by other species or environmental conditions (Perry and Dixon 2002). The null hypothesis in SADIE is that any association between the two species does not exist, although both may still show individual spatial patterns. Therefore, SADIE; 1) describes spatial patterns of individual species and then tests these spatial patterns separately, 2) removes the effects of their individual spatial patterns, and 3) tests the spatial association/disassociation between the species of interest (Perry and Dixon 2002).

In addition to methods specifically developed for spatial analysis, many multivariate and regression statistical methods allow for exploration and modeling species-environmental relationships (Digby and Kempton 1994, Jongman et al. 1995, McCune and Grace 2002). Of these methods, regression tree analysis (RTA) offers advantages over other better-known methods when applied to species abundance data (Urban 2002). RTA analyzes all explanatory variables and determines which binary division of a single explanatory variable best reduces deviance (defined as squared residuals) in the response variable (Breiman et al. 1984, Efron and Tibshirani 1991). The process is repeated for each resulting group of data and continues splitting the data until homogenous end points (terminal nodes or "leaves") are reached in a hierarchical tree (Lawrence and Ripple 2000). As a nonparametric method, RTA is robust to many of the problems that can affect parametric models and is often able to reveal relationships that are understandable ecologically, but are difficult to interpret using conventional linear models (Urban 2002). Both multiple linear regression and RTA are based on minimizing

squared residual deviance; therefore, the amount of variation explained by these two models can be directly compared (Lawrence and Ripple 2000). RTA usually statistically over fits the model (Venables and Ripley 2002), which can lead to spurious conclusions and/or limit its usefulness as a predictive model for other data sets; therefore, regression trees often are simplified or "pruned". Pruning provides for a balance of accuracy and robustness (Urban 2002).

Very few data are available on the spatial distributions of three snail species, *T. serpenticola*, *P. antipodarum* or *Fluminicola* sp. in the middle Snake River drainage. These three species comprise > 95% of the invertebrate biomass in Banbury Springs, Idaho (Richards et al. 2001). Almost nothing is known about how environmental or interspecific interactions affect their spatial distribution and abundance, and no estimates of their abundances in unsampled areas incorporating spatial autocorrelation have been attempted.

I tested the following hypotheses: within the study site at Banbury Springs abundances of the three species were; 1) related to environmental and spatial variables and to each other's abundance, 2) spatially autocorrelated, 3) spatially associated with the other species, and 4) different in three delineated habitat types; run, edge, and vegetation.

In the first portion of this study, I explored environmental and spatial relationships of *P. antipodarum, T. serpenticola,* and *Fluminicola* sp., in Banbury Springs using regression tree analysis (RTA) and Spatial Analysis by Distance Indices (SADIE). I also estimated the total abundance of each of the three species in the study site explicitly incorporating spatial autocorrelation patterns.

In the second portion of this study, I analyzed densities and spatial distribution data of the three snail species as related to three assumed habitat types: run, edge, and vegetation. I also related shell lengths of *P. antipodarum* with water velocity and habitat type in Banbury Springs.

Methods

Spatial and environmental relationships and abundances

Sample collection. I measured densities of *T. serpenticola*, Fluminicola sp., and *P. antipodarum* at 57 randomly chosen sample locations in a 25 m x 25 m plot in the northern most spring of Banbury Springs near its confluence with Morgan Lake (Figures 12, 13, and 14), in May 1999. Samples were collected using a 1.0 mm diameter mesh Surber sampler with collection area of 15cm by 15cm. Sample locations were randomly chosen in the 25 m x 25m plot at 0.10 m increments. The sampler collection area was then centered in the chosen location. If a sample location occurred outside of a wetted area (e.g. an island), another set of random numbers was chosen and a new sample location selected. Contents of each sample were placed in a shoebox-sized, clear, plastic tub, filled with spring water and the snails were counted. All *T. serpenticola* and Fluminicola sp. were released downstream of the study site and all *P. antipodarum* were preserved in 95% ethanol.

Figure 12. Study area at Banbury Springs, near Hagerman, Idaho, USA. Study plot was 25m x 25m of heterogenous habitat several meters upstream of Morgan Lake.

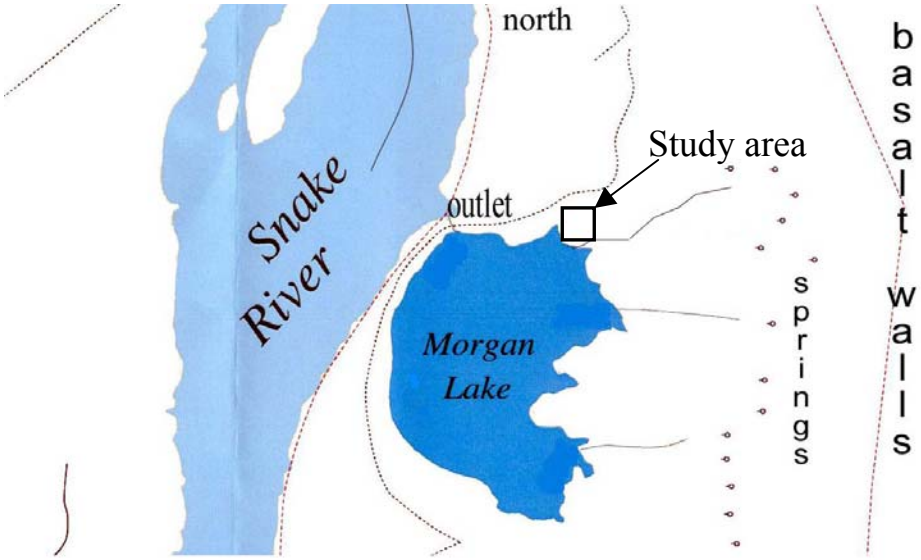
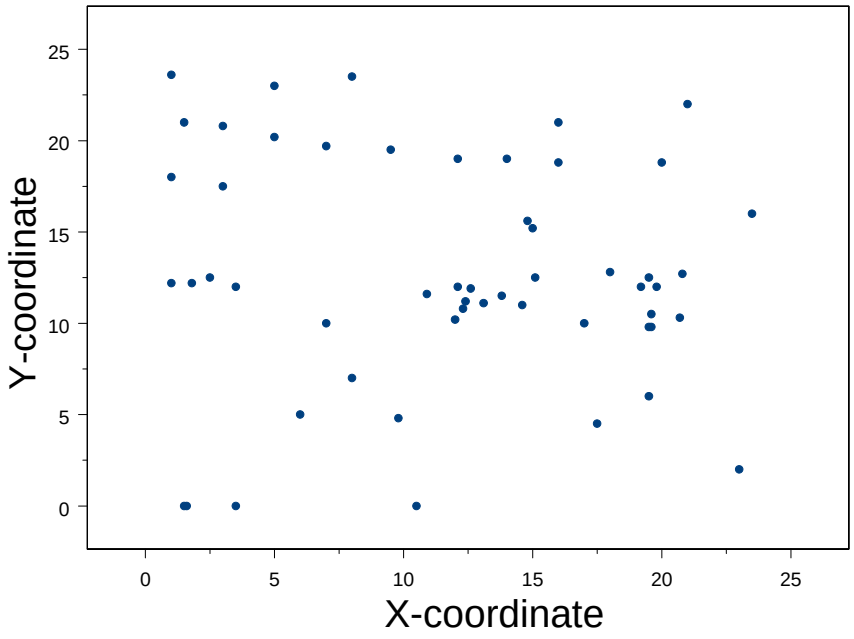


Figure 13. Southeast portion of study plot showing vegetation and run habitats and start of canopy cover. Morgan Lake is downstream.

Figure 14. Random sample locations (N = 57) in 25 by 25 m plot at Banbury Springs, Idaho



In addition, I recorded eight environmental and spatial variables: x-coordinate, y-coordinate, water temperature, velocity, aquatic vegetation density, canopy cover, water depth, and substrate size. Hourly water temperatures (N = 4919) were recorded at the upper and lower portions of the study plot between 13 April and 5 November 1999 using HOBO temperature data loggers (Onset Computer Corp. 1998). The x-coordinates and y-coordinates were measured in 0.1 m increments beginning at 0,0 at the NW corner. The y-coordinate equated to distances upstream of Morgan Lake. Vegetation density and canopy cover were recorded on an ordinal (categorical) scale from 1 – 5; with 1 = no vegetation or canopy cover up to 5 = very dense vegetation or canopy cover. Mean substrate size (mm) was estimated at each sample location by randomly selecting and measuring 10 particles enclosed by the sampler. Average depth (mm) was estimated

from 5 measurements taken within the area encompassed by each Surber sample at each location and average velocity was estimated from 5 velocity recordings (m/s) in each sampling area using a Marsh-McBirney pygmy current meter.

Descriptive statistics, histograms, and several bivariate plots were generated to explore distribution of the three snail species in relation to x and y coordinates and to each other. For these analyses, I used S-PLUS 6.1 for Windows (Insightful 2002).

I used regression tree analysis (RTA in S-PLUS) to model each snail species' abundance (response variable) using the eight explanatory variables and the other two species' abundances. Because data for *T. serpenticola* were not normally distributed, I based its regression tree on a log +1 transformation. There was one outlier in the *T. serpenticola* data, which I removed from the analysis. The outlier had a high residual and leverage value and much larger Cooks distance D value than the other values. For *P. antipodarum*, I used a log + 1 transformation and for *Fluminicola* sp. I used raw abundance data. I "pruned" the regression trees using cost-complexity pruning methods in S-PLUS.

To validate the models, I withheld 10 random samples from the original data set and conducted a validation regression tree model for each species on the 47 remaining original data (N = 46 for *T. serpenticola*). I decided to only withhold 10 samples because I wanted to have enough samples to create the validation regression tree models. Each of the species' regression tree models was used to predict abundance values for the 10 samples withheld. Predicted abundance values were then compared with actual values using linear regression. Validation models for all three species predicted the withheld sample abundance values fairly well (r^2 = 0.32, 0.54, and 0.49; p-values = 0.09, 0.03, and

0.02) considering that I only withheld a samples size of N = 10 to validate. Validation models generated the same subsets of predictor variables, as did the final models based on the entire data set. To further evaluate these models, I developed best multiple linear regression models for each species and compared these with the final RTA models. For all three species, final RTA models explained more variability in snail abundance than did multiple linear regression models.

To formally quantify spatial patterns and associations between the three snail species, I used a non-parametric version of the computer program **S**patial **A**nalysis by **D**istance **I**ndic**E**s (SADIE) developed by Perry and Hewitt (1991) on the raw density data. For each of the three snail species, SADIE equated the degree of spatial pattern in the observed arrangement of snail counts to the minimum distance that the individual snails in the study site needed to move to achieve a completely regular pattern in which counts in each sample were equal. This minimum distance, referred to as distance to regularity, *D*, was derived by a transportation algorithm (Kennington & Helgason 1980, Perry and Hewitt 1991) which rearranges the data to determine the minimum distance. The observed value of *D* divided by the mean value from 5967 randomizations gave an index of aggregation, I_a, where values of $I_a = 1$ would have indicated randomly arranged counts and $I_a > 1$ would have indicated aggregation. I tested the null hypothesis that counts were randomly arranged by comparing the observed value of *D* with the tails of the distribution of values from 5967 permutations. I also used SADIE to compute a distance to crowding, C, and associated index of clustering J_a. The index, J_a is not viable when there is more than one cluster (Perry and Dixon, 2002) also, I_a and J_a may be less

reliable when clusters are mostly located near the edges of a study site (Xu and Madden 2003).

Because any spatial disassociation between pairs of the three species might have suggested interspecific competition, I also tested the null hypothesis of lack of any association between each pair of snail species using the SADIE spatial association software and its associated index of association, X_a (Perry and Dixon 2002).

I performed separate, all subsets, ordinary least squares regression with *T. serpenticola*, Fluminicola sp., and *P. antipodarum* densities as the dependent variables versus the independent location variables x, y, x*y, x^2, and y^2 to determine suitable trend surface models. For *T. serpenticola*, the best trend surface model (lowest AIC, Cp) was [density = 8.56 + (-0.85*x) + (-0.39*y) + (0.09*x*y)]($r^2 = 0.30$, p-value < 0.01) for raw counts, minus the outlier. I then created a variogram model based on the trend surface model residuals for *T. serpenticola*, which continued to show spatial autocorrelation (2^{nd} order effects). I validated this model by randomly withholding 10 sample residuals from the trend surface model. From the remaining 46 sample residuals, I developed a variogram model and block kriged estimates for unsampled sites. I then compared the withheld residual values with the kriged prediction values at those sites using linear regression. For variogram and kriging predictions, I used the computer program GS+ (Gamma Design Software 1998). To estimate total abundance ($\hat{\tau} \pm$ s. e.) of *T. serpenticola* using kriging prediction, I added back the trend surface residuals and summed predicted values for the study area (N = 27,777, 0.15 m x 0.15 m intervals).

Because *P. antipodarum* was spatially distributed into two very distinct sections in the y-coordinate direction (Figure 21) I also analyzed these areas separately. No

suitable trend surface model was found for either of these sections. No suitable trend surface model was found for *Fluminicola* sp., either. Because there was no apparent spatial autocorrelation for *P. antipodarum* in both sections of the site and for *Fluminicola* sp. in the entire site (Figure 35), I could not use predictive kriging to estimate total abundances for either species. I therefore estimated the total abundance of *P. antipodarum* in the study site by estimating its abundance in each section separately and combining the two estimates. Total abundance ($\hat{\tau} \pm$ s.e.) in each section was estimated by bootstrapping (B = 10,000) the sample abundances in each section and then multiplying the bootstrapped mean ($\bar{y}$) by the number of quadrats (N) of size 0.0225 m^2.

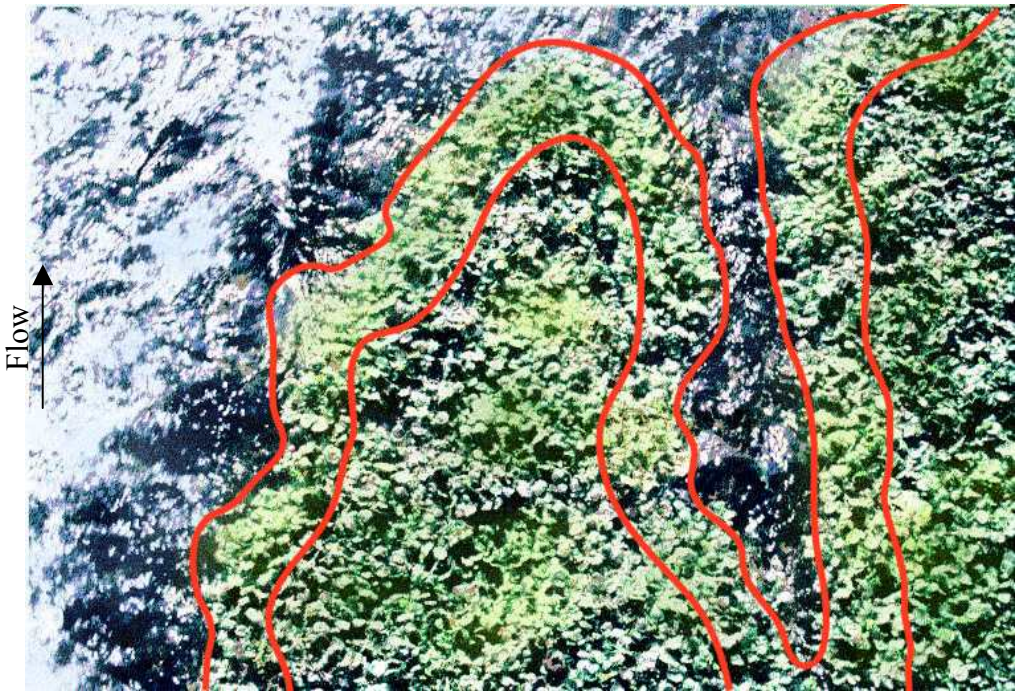
For comparison of estimation methods, I also estimated total abundance ($\hat{\tau} \pm$ s.e.) for each species by bootstrapping (B = 10,000) their raw means and multiplying the bootstrapped mean ($\bar{y}$) by the number of quadrats (N = 27,777.88) of size 0.0225 m^2. There was approximately 35 m^2 surface area of unsuitable island habitat in the study site. I therefore, estimated the total number of each species predicted in these unsuitable habitats and subtracted this amount from the total snails estimated in the models and bootstrapped estimates. I created distribution and abundance maps of *P. antipodarum* and *Fluminicola* sp. using default extrapolation methods in S-PLUS (Insightful 2002).

Habitat Preferences

I selected 54 of the 57 random samples based on three delineated habitat types: run, edge, and vegetation. The three samples that were excluded were in silt substrate, without vegetation, had low water velocity and did not fit into any of the three delineated habitat categories. Also, because there were only three samples, I felt they didn't warrant their own separate category. Of the 54 samples, 17 were in run habitats, 14 in edge

habitats, and 23 in vegetation habitats. I delineated a run habitat as any riffle or flowing section that did not have emergent, aquatic vegetation growing and that was dominated by gravel or larger sized substrates. An edge habitat was that portion of the emergent aquatic vegetation habitat that was within 15 cm of a run. I chose a 15 cm distance for edge habitat because that was the length of the sampler. Vegetation habitat was defined as being more than 15 cm from a run habitat and composed of emergent, aquatic vegetation (Figure 15). Samples collected in the vegetation and edge habitats included both macrophytes and substrate.

Figure 15. Run, edge, and vegetation habitats. Edge was 15 cm from run into vegetation.



To determine whether there was a relationship between size of *P. antipodarum* and habitat type, I measured 760 *P. antipodarum* shell lengths to nearest 0.05 mm: 235

from edge, 250 from vegetation, and 275 from run habitats. I also measured 889 *P. antipodarum* from an additional 12 samples in the study site from habitats with varying water velocities to determine whether there was a relationship between shell length and water velocity.

Descriptive statistics (including skewness and kurtosis), histograms, normal expected frequencies, Shapiro-Wilk *W*-tests, and normal probability plots of the 3 snail species densities were generated and analyzed for comparison of habitat densites. Densities that did not follow a normal distribution were log-transformed and reexamined. All log-transformed densities subsequently appeared to follow a normal distribution. A one-way ANOVA and Tukey HSD post hoc comparison were conducted on log-transformed densities of the 3 snail species for each species to determine if there were any differences in snail densities in the 3 habitats. *Potamopyrgus antipodarum* mean shell lengths were compared among the 3 habitats using one-way ANOVA and Tukey post hoc comparison. I also used Pearson product-moment correlation for examining the relationship between *P. antipodarum* shell lengths and water velocity. I used STATISTICA for Windows (Statsoft, Inc. 1995) for all statistical analyses in this portion of the study.

Results

Spatial and Environmental Relationships and Abundance

Sample counts for all three species were right skewed indicating non-normal distributions (Figures 16, 17, and 18), and many of the samples for *T. serpenticola* (N = 11) and *P. antipodarum* (N = 7) had zero counts (Figures 16 and 17). Spearman rank

order correlations suggested that *T. serpenticola* was negatively associated with *P. antipodarum* (Figure 19) and positively associated with *Fluminicola* sp. (Figure 20) but not significantly associated or disassociated with other variables (Table 1).

Potamopyrgus antipodarum was negatively associated with *T. serpenticola* (Figure 19), y-coordinate (Figure 21), depth, substrate size, velocity, and canopy cover (Table 1). This translated to an open-canopied, shallower, slower water velocity, sand/silt, habitat closer to Morgan Lake. As was anticipated, velocity, depth, and substrate size were significantly lower in the vegetation habitat (Table 1). *Potamopyrgus antipodarum* was also weakly associated ($p = 0.10$) with vegetation density (Table 1). As mentioned in the methods section, there was an abrupt decline in *P. antipodarum* density at about 13.4 meters upstream (Figure 21), where canopy cover began.

Fluminicola sp. was positively associated with *T. serpenticola* (Figure 20), vegetation density, canopy cover and lower water velocities (Table 1). This translated to more closed-canopy, vegetated habitats.

Table 1. Spearman rank order correlations for *T. serpenticola* (*Tse*), *P. antipodarum (Pan), Flumincola* sp (*Fl*.sp.) and seven environmental variables at Banbury Springs study site (N = 57 samples)(* = P-value $\leq$ 0.05, ** = P-value $\leq$ 0.01)

	Tse	Xcoord	Ycoord	Veg	Depth	Subsize	Veloc	Canopy
X-coord	0.10							
Y-coord	0.18	-0.18*						
Vegetation	-0.03	-0.24	0.16					
Depth	0.06	-0.24	0.39**	-0.45**				
Subsize	0.11	-0.04	0.39**	-0.43**	0.47**			
Velocity	0.10	-0.00	0.35*	-0.60**	0.64**	0.59**		
Canopy	0.18	-0.21	0.63**	0.10	0.20	0.27*	0.28*	
Pan	-0.30*	0.04	-0.57**	0.22	-0.45**	-0.53**	-0.53**	-0.58**
Fl.sp.	0.53**	-0.05	0.20	0.41	-0.21	-0.10	-0.33*	0.29*

Figure 16. Frequency histogram and some summary statistics for *T. serpenticola* at Banbury Springs study site. (CV = s / $\bar{x}$)

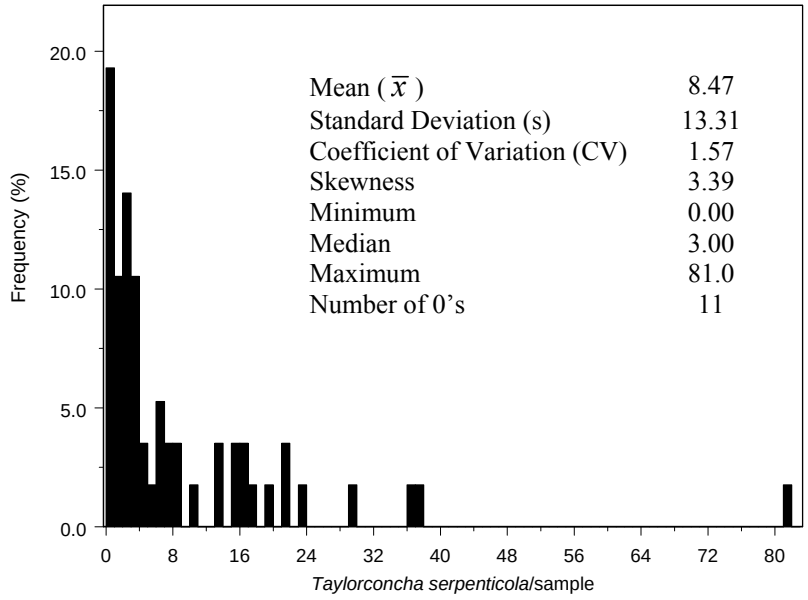


Figure 17. Frequency histogram and some summary statistics for *P. antipodarum* at Banbury Springs study site. (CV = s / $\bar{x}$)

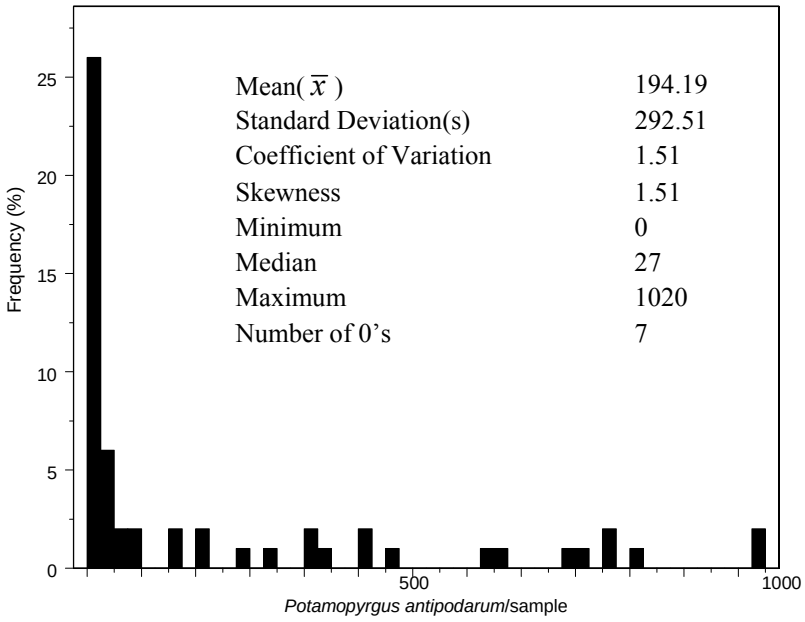


Figure 18. Frequency histogram and some summary statistics for *Fluminicola* sp. at Banbury Springs study site. (CV = s / $\bar{x}$)

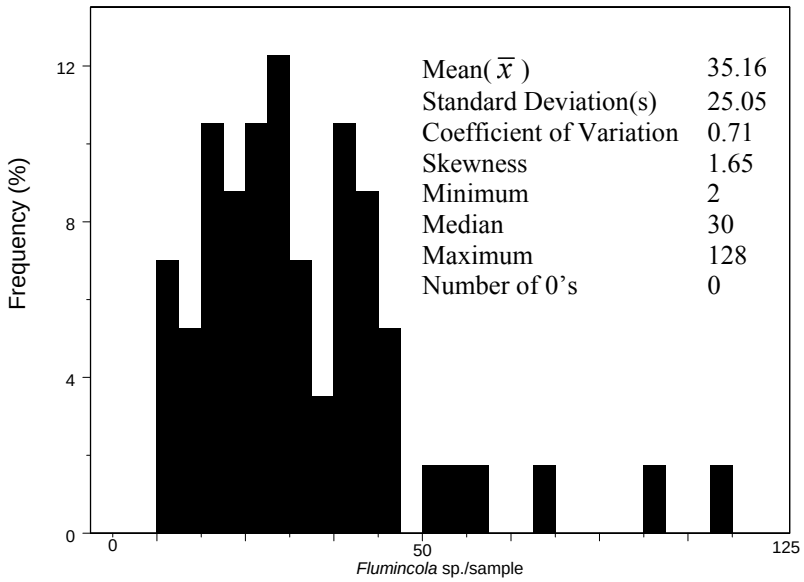


Figure 19. Number of *T. serpenticola*/sample vs. number of *P. antipodarum*/sample at Banbury Springs study site. (*r* is Pearson product-moment correlation, ρ is Spearman rank correlation)

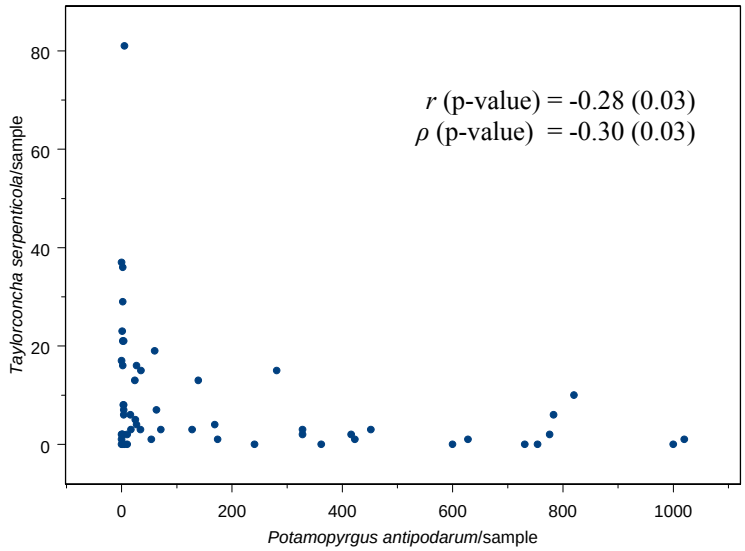


Figure 20. Number of *T. serpenticola*/sample vs. *Fluminicola* sp. at Banbury Springs study site. (*r* is Pearson product-moment correlation, ρ is Spearman rank correlation)

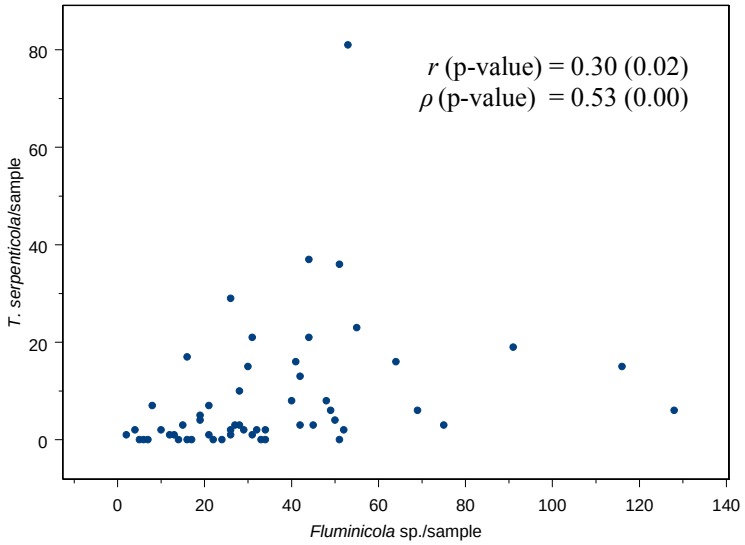
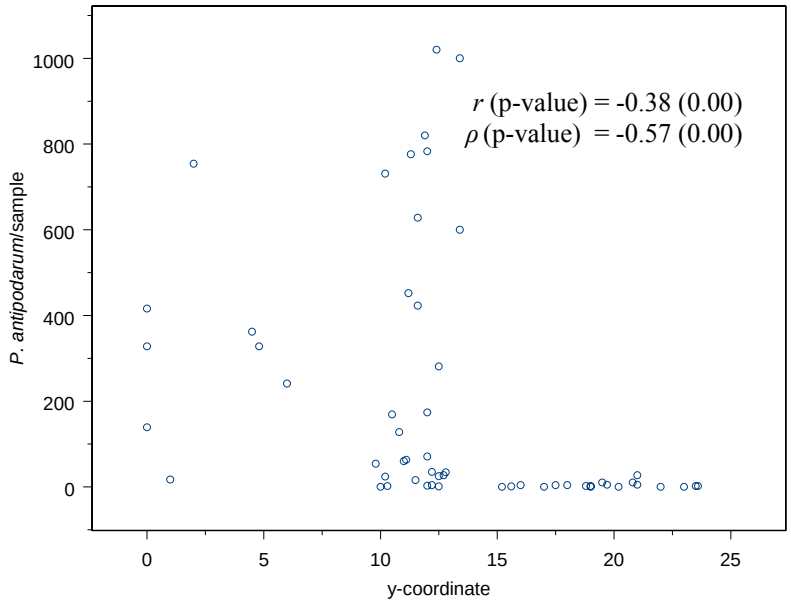


Figure 21. Number *P. antipodarum*/sample vs. y-coordinate at Banbury Springs study site. (*r* is Pearson product-moment correlation, ρ is Spearman rank correlation)



Pruned regression trees explained 59.50, 79.80, and 39.50 % of the variability of *T. serpenticola*, *P. antipodarum*, and *Flumincola* sp. abundance, respectively (Figures 22, 23, and 24). The most important RTA model explanatory variable for *T. serpenticola* was *Fluminicola* sp., followed by water velocity and then substrate size at velocities < 0.18 m/s and *Fluminicola* sp. abundance < 37 (Figure 22). Its predicted highest abundance (≅ 18) was in areas of the study site with more than 37 *Fluminicola* sp. and velocities > 0.08 m/s. The most important RTA model explanatory variables for *P. antipodarum* were y-coordinate, substrate size, and then *T. serpenticola* (Figure 23). *Potamopyrgus antipodarum* highest predicted abundance (≅ 555) was in areas downstream of y-coordinate 14.30 with *T. serpenticola* abundance < 2.50. Its predicted lowest abundance (≅ 4) was in areas upstream of y-coordinate 14.30. Predicted abundance of *Fluminicola* sp. was dependent on *T. serpenticola* abundance and depths (Figure 24).

The final spherical variogram model of *T. serpenticola* distribution gave an estimated patch size of 3.12 m (Figure 25). *Taylorconcha serpenticola* was significantly aggregated into several patches and gaps (Table 2), mostly in the upstream portion of the study site (Figure 26). There were however, two small patches in the downstream corners of the site (Figure 26). Because *T. serpenticola* was distributed into several distinct patches, the index of clustering, J_a, was invalid (Perry and Dixon 2002).

Figure 22. Final regression tree for *T. serpenticola* abundance. Tree pruned to 5 terminal nodes, tree model: *T. serpenticola* abundance (log +1) = *Fluminicola* sp. + velocity + substrate size, $R^2 = 0.60$. Values at terminal nodes are abundances (per 15 cm x 15 cm sample) of *T. serpenticola*.

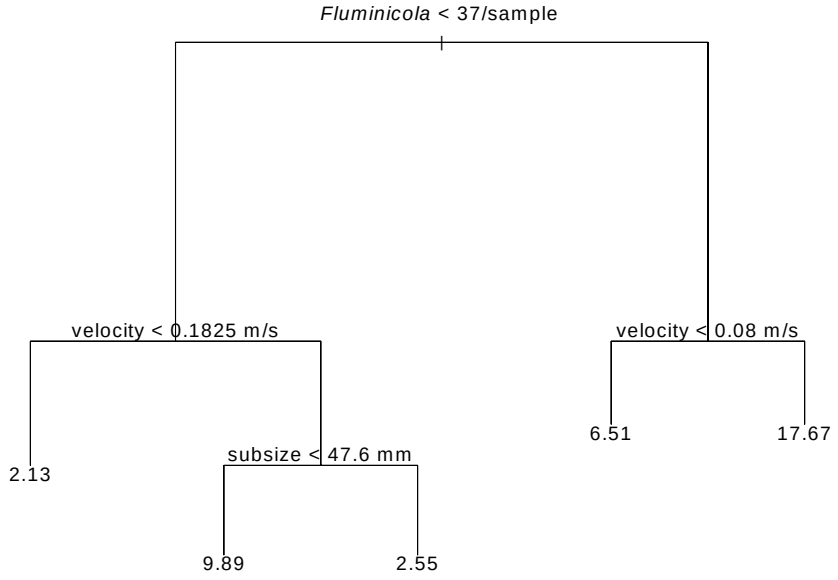


Figure 23. Final regression tree for *P. antipodarum* abundance. (tree pruned to 5 terminal nodes, tree model; *P. antipodarum* abundance(log +1) = y-coordinate + substrate size + *T. serpenticola* ($R^2 = 0.80$). Values at terminal nodes are abundances (per 15 cm x 15 cm sample)of *P. antipodarum*.

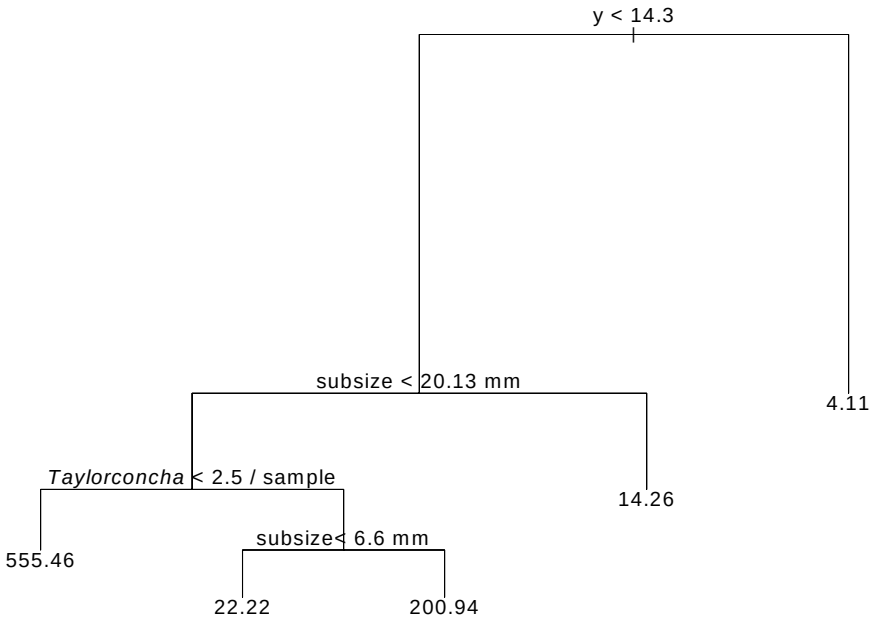


Figure 24. Final regression tree for *Fluminicola* sp. abundance. (tree pruned to 3 terminal nodes, tree model: *Fluminicola sp.* abundance = *T. serpenticola* + depth, $R^2 = 0.40$). Values at terminal nodes are abundances (per 15 cm x 15 cm sample) of *Fluminicola* sp.

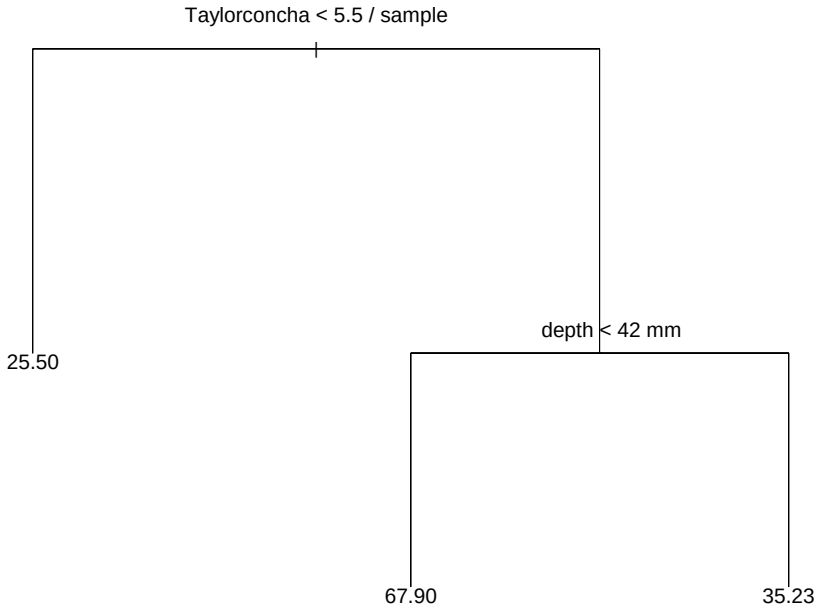
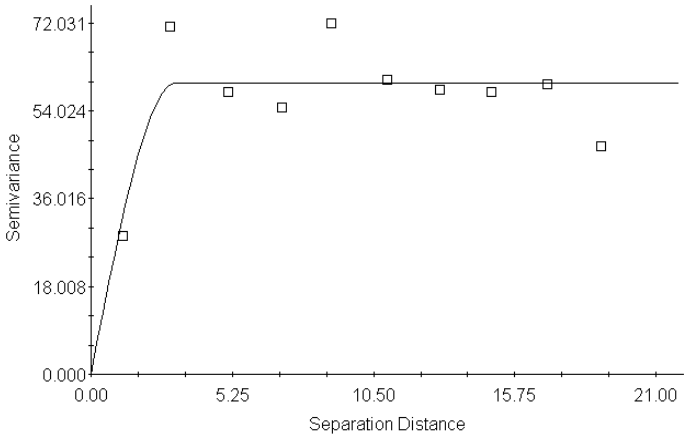


Figure 25. Final spherical variogram model for *T. serpenticola* abundances based on residuals from best trend surface model [abundance =
8.56 + (-0.85*x) + (-0.39*y) + (0.09*x*y)] (Nugget = 0.10, sill = 59.65, range = 3.12, R^2 = 0.64).



Using data for the entire study area, *P. antipodarum* was significantly aggregated (Table 2) into one large almost continuous patch in the downstream section (<13.40 m y-coordinate) nearest Morgan Lake and away from the canopy and one large gap upstream of 13.40 m y-coordinate (Figure 27). The large downstream patch was in the shallower, smaller substrate (i.e. silt/sand) section with lower water velocities. Analyzed separately, *P. antipodarum* was not significantly different from a random distribution in either the downstream, high-abundance patch or the upstream low-abundance gap (Table 2).

Fluminicola sp. did not occur in any significant patches or gaps and was more randomly distributed within the site (Table 2 and Figure 28). Both *T. serpenticola* and *Fluminicola* sp. were significantly spatially disassociated with *P. antipodarum* and were significantly associated with each other (Table 2).

Table 2. **S**patial **A**nalysis by **D**istance **I**ndic**E**s (SADIE); index of aggregation, I_a, index of clustering, J_a, and index of association X_a for the three snail species.

	T. serpenticola[2]	*P. antipodarum*			*Fluminicola* sp.
		Entire site	Downstream	Upstream	
I_a	1.31	1.94	1.06	1.27	1.04
(p-value[1])	(0.06)	(< 0.00)	(0.35)	(0.16)	(0.37)
J_a	0.95	1.13	1.16	1.12	0.99
(p-value[1])	(0.86)	(0.00)	(0.15)	(0.32)	(0.84)

Species associations	*T. serpenticola* vs. *P. antipodarum*	*P. antipodarum* vs. *Fluminicola* sp.	*Fluminicola sp.* vs. *T. serpenticola*
X_a	-0.39	-0.36	0.33
(p-value)	(0.02)	(0.01)	(0.02)

[1]Adjusted Dutilleul p-value for spatial autocorrelation effects (Perry and Dixon 2002)
[2]Cluster index J_a was invalid for *T. serpenticola* because of more than one distinct cluster (Perry and Dixon 2002). See krig map (Figure 26)

Figure 26. Predictive ordinary block kriging map of *T. serpenticola* based on residuals from best trend surface model. (N = 27,778 estimated kriged values at 0.15 m intervals) (Values are abundances in 15 cm x 15 cm samples)

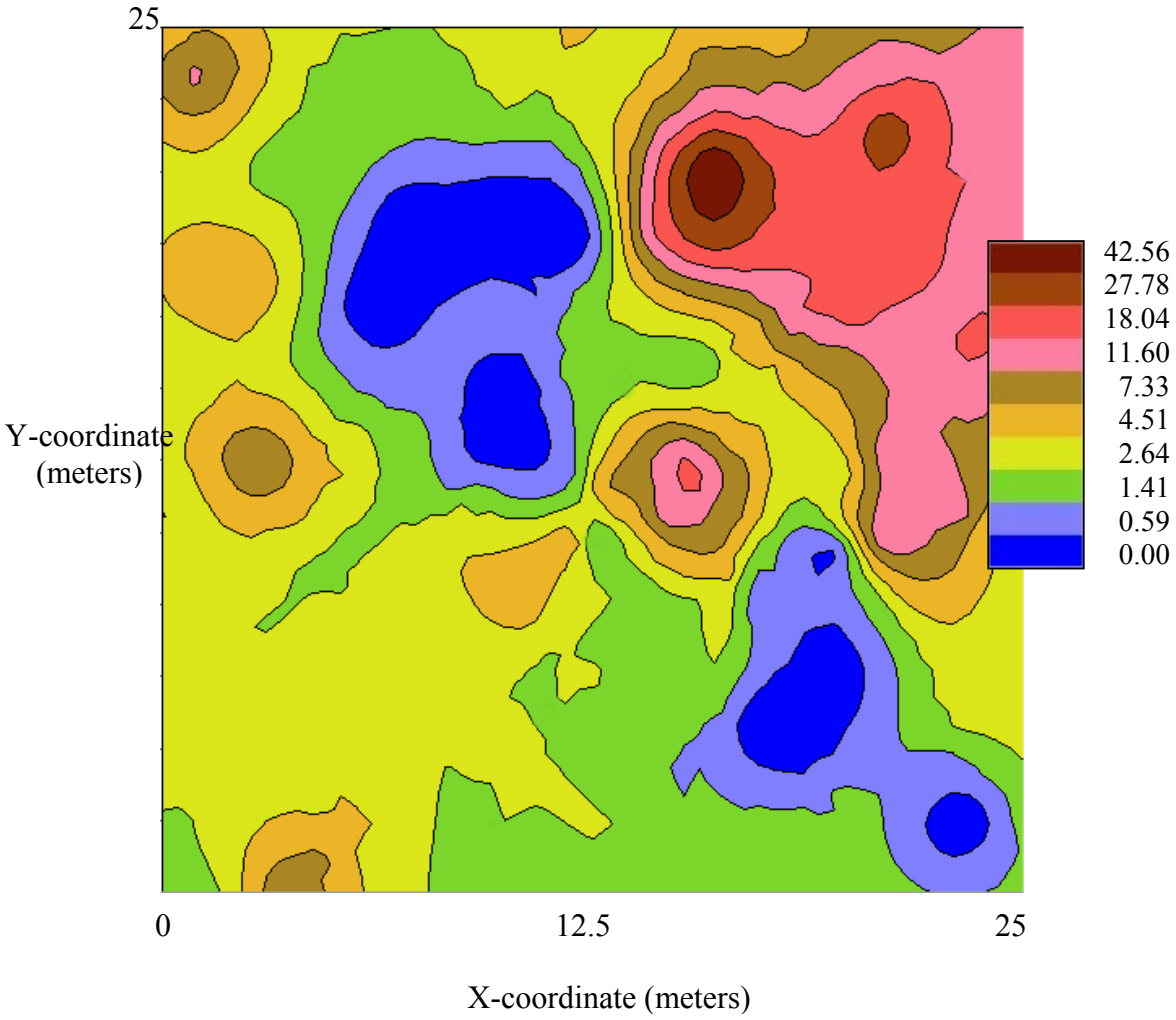


Figure 27. Prediction map of *P. antipodarum* extrapolated using bivariate algorithm (outside convex hull)(Values are abundances in 15 cm x 15 cm samples)

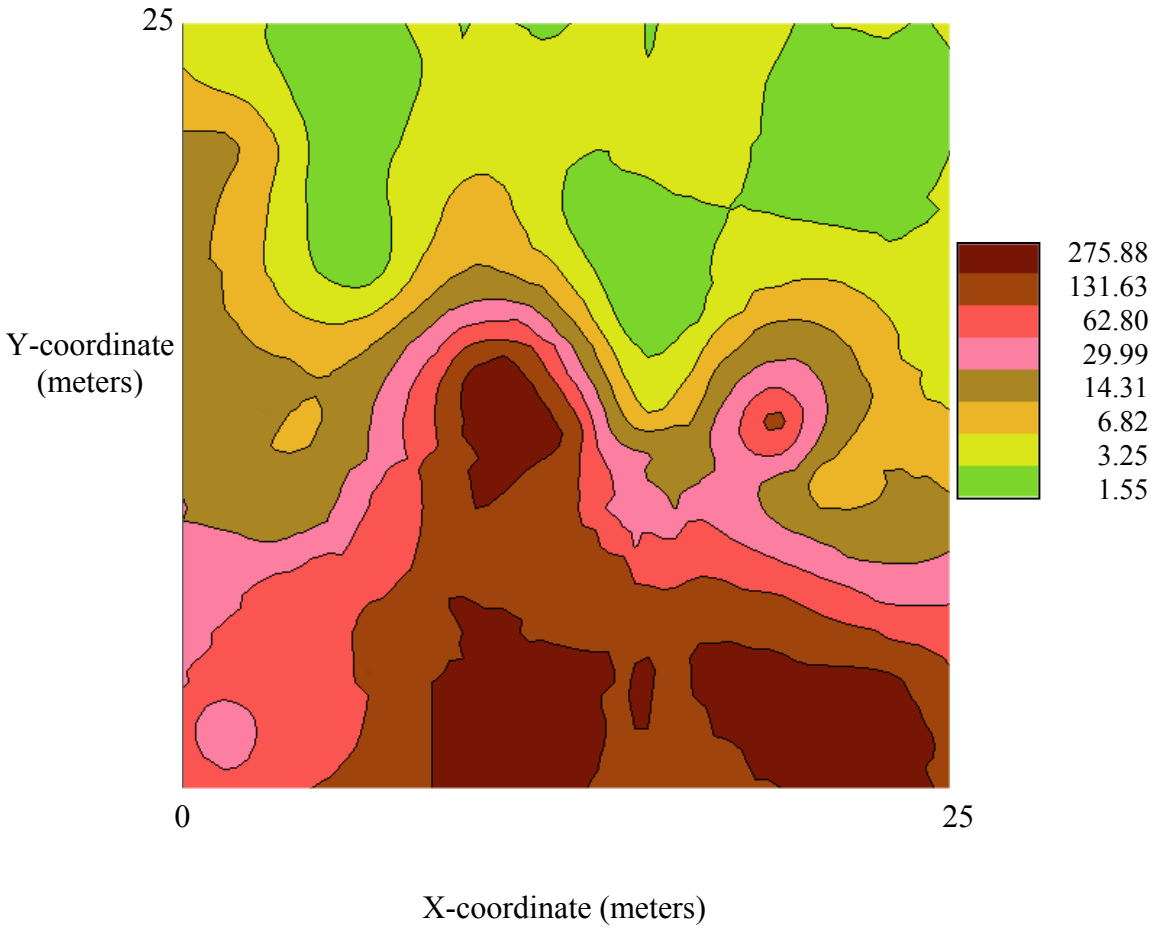
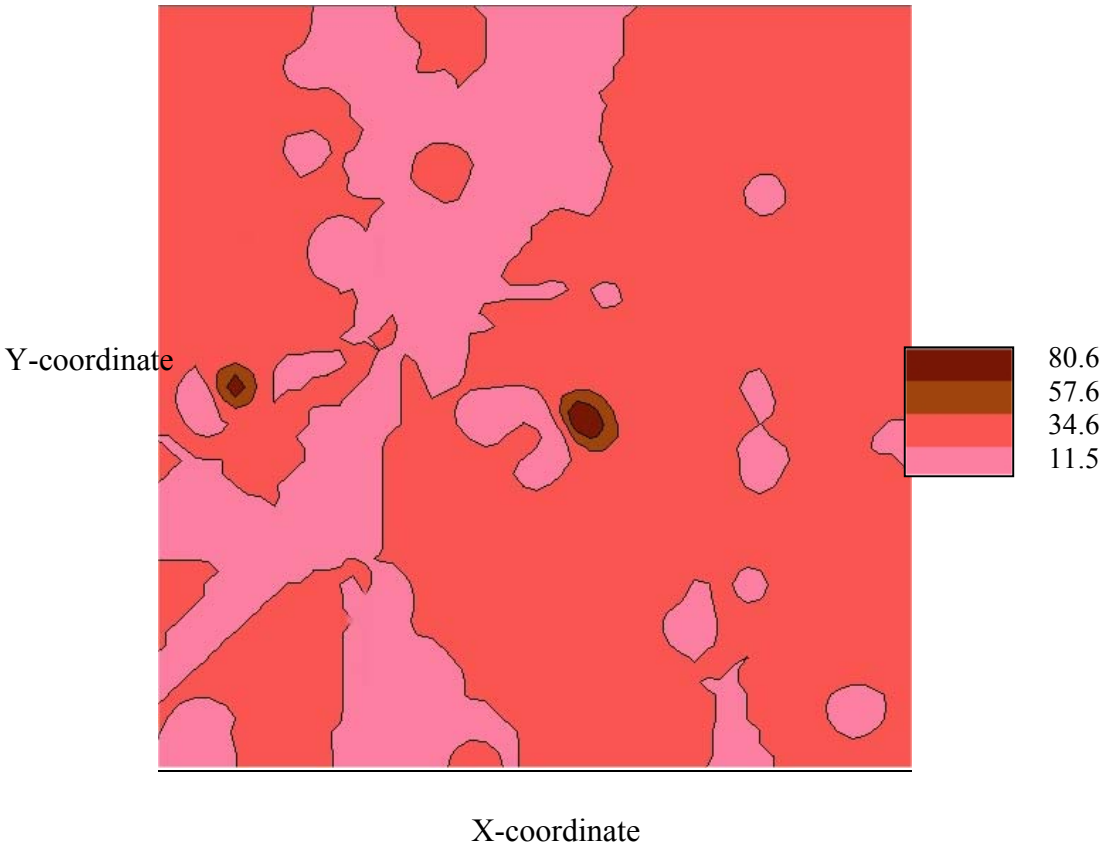


Figure 28. Prediction map of *Fluminicola* sp. extrapolated using bivariate algorithm (outside convex hull)(Values are abundances in 15 cm x 15 cm sample)



Abundance estimates of *T. serpenticola* using the kriged prediction model (outlier removed) were greater than the bootstrapped estimates of the raw values with the outlier removed. Because the *T. serpenticola* predictive model was able to predict high abundance locations and adjust for the effects of removing the outlier, its estimate was similar to the bootstrap estimate of raw values containing the outlier (Table 3) but its 95% confidence intervals were wider. The total estimate ($\hat{\tau}$) for *P. antipodarum*, using the predictive model was approximately 1.0 x 10^6 less than that of the bootstrapped raw values (Table 3). Because they were based on spatial patterns, the predictive models probably gave more realistic estimates.

Table 3. Estimated total abundance ($\hat{\tau} \pm 95\%$ CI) of the three snail species in the study area comparing predictive ordinary block kriging, raw mean, median, and bootstrapped mean values. Abundance values for all values were adjusted for 35 m^2 of unsuitable island habitat.

	T. serpenticola	*P. antipodarum*[2]	*Fluminicola* sp.[3]
Predictive model (95% CI)	239,761[1] (49,790; 429,506)	4,308,075 (3,536,411; 5,063,791)	NA
Bootstrap raw mean[4] (95% CI)	235,083 (162,767; 370,228)	5,391,667 (3,514,319; 7,682,411)	975,556 (817,739; 1,183,188)
Bootstrap (-outlier) (95% CI)	199,583 (142,861; 274,306)	NA	NA

[1]based on kriged estimates of residuals from best trend surface model
[2]Combined bootstrapped estimates of *P. antipodarum* in lower and upper sections
[3]No predictive model available for *Fluminicola sp.*
[4]number of bootstrap samples B = 10,000; 95% CI's based on percentiles

Edge effects

There did not appear to be a sharp edge effect for *T. serpenticola* between run habitat and vegetation habitat (Figure 29). Edge habitat was transitional in density between the high densities of *P. antipodarum* in the vegetation habitat and the lower densities in the run habitat (Figure 30). There was a sharp edge effect on *Fluminicola* sp. densities (Figure 31).

Fig. 29. Comparison of *T. serpenticola* m^{-2} in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999(mean, std. error, and std. deviation)

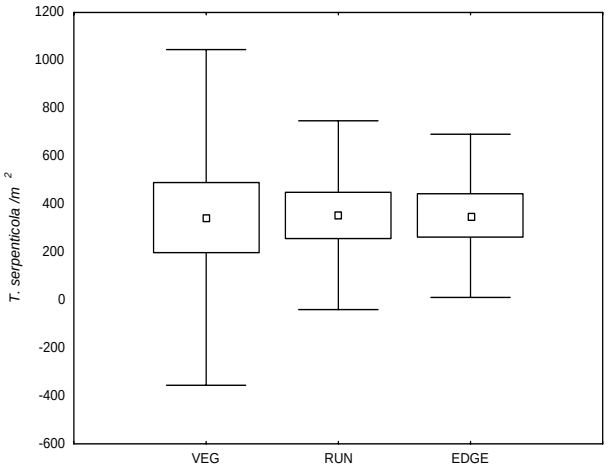


Figure 30. Comparison of *P. antipodarum* densities m^{-2} in 3 habitat types (vegetation, run, and edge) in the Banbury Springs study site, 1999(mean, std. error, and std. deviation)

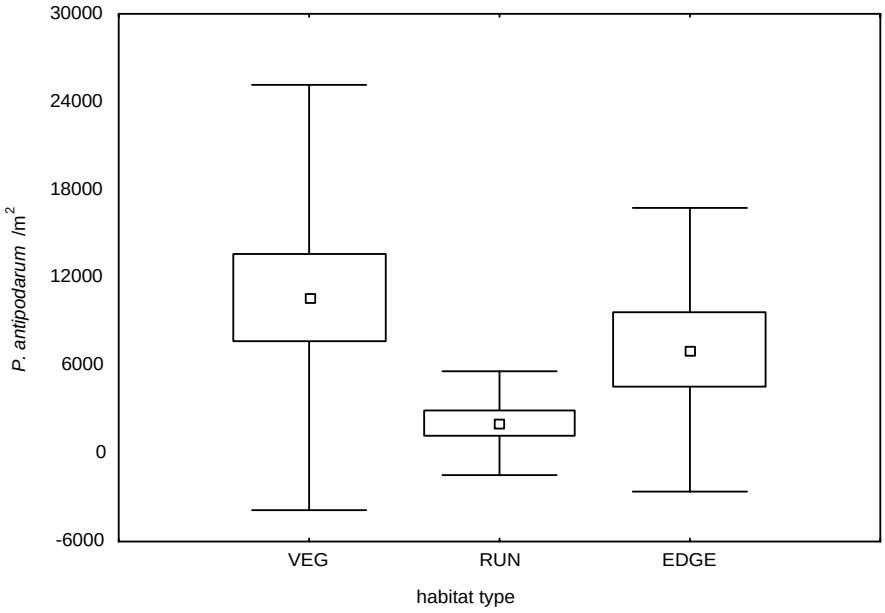
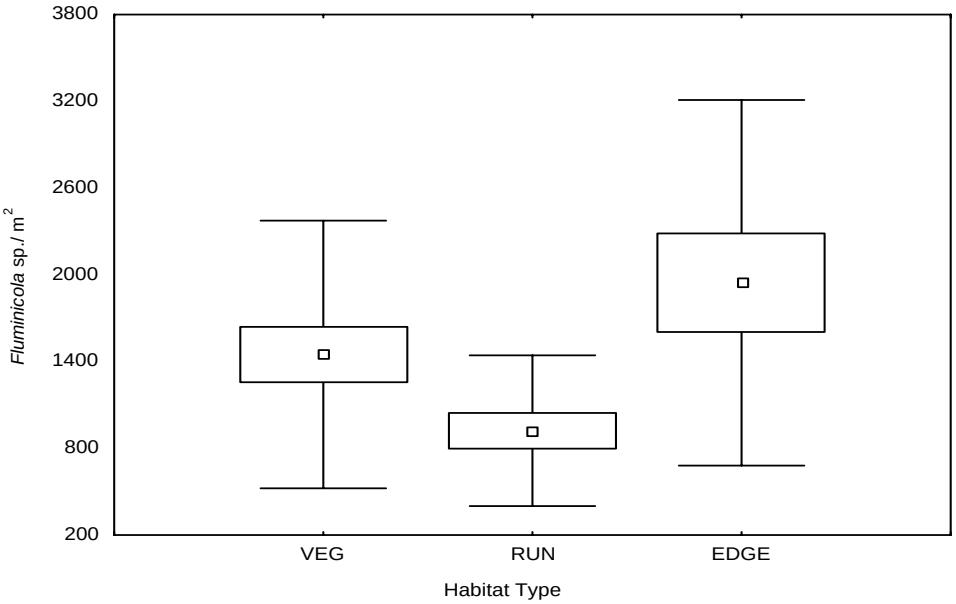


Figure 31. Comparison of *Fluminicola* sp. densities m^{-2} in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999(mean, std. error, and std. deviation)



P. antipodarum had the highest densities of the 3 snail species in all 3 habitats, but was more similar to *T. serpenticola* and *Fluminicola* sp. densities in the run habitat. Log-transformed mean densities of *P. antipodarum* were marginally different among habitats (one-way ANOVA, $F = 3.02$, df 2,26, p-value = 0.07). Mean densities (log-transformed) of *P. antipodarum* were significantly higher in the vegetation than the run habitat (Tukey HSD post hoc comparison, p-value = 0.05) but were not significantly greater in the edge than the run habitat (p-value = 0.36) or between the vegetation and edge habitats (p-value = 0.53). *Fluminicola* sp. mean densities (log transformed) were significantly different among the 3 habitats (one-way ANOVA, $F = 6.21$, df = 2,26, and p-value = 0.00). *Fluminicola* sp. mean densities were significantly greater in the vegetation and edge habitats than in the run habitat (Tukey HSD post hoc comparison, p-value = 0.07 and 0.01, respectively) but were not significantly different between the edge and vegetation habitats (p-value = 0.48). Mean densities (log-transformed) of *T. serpenticola,* were not significantly different among any of the 3 habitats (one-way ANOVA, $F = 0.63$, df = 2,26, p-value = 0.53), but were most variable and had the lowest median density in the vegetation habitat (Fig 31).

Water temperature was constant throughout the study site and season. Mean hourly temperatures recorded between 13 April and 5 November 1999 were 14.19°C (±0.38°C *s*; min = 12.93°C; max = 14.85°C; $N = 4919$) at the upstream portion of the study site and 14.29°C (± 0.57°C *s.d.*; min = 12.93°C; max = 16.38°C; $N = 4919$) at the downstream portion. Water velocities ranged from 0 m s^{-1} in thicker vegetation habitats to 0.52 m s^{-1} in runs. Mean water velocity was 0.04 m s^{-1} (± 0.03 s.e.) for vegetation, 0.08 m s^{-1} (± 0.12 s.e.) for edge, and 0.34 m s^{-1} (± 0.15 s.e.) for run habitat. Velocities

were significantly different (p-value < 0.05) between run and vegetation, and run and edge habitats, but not between vegetation and edge habitats.

Mean shell lengths of *P. antipodarum* were significantly correlated with water velocity using Pearson correlation ($N = 12$, $r = 0.68$, p-value = 0.02). Mean shell lengths of *P. antipodarum* were also significantly greater in the run habitat than in edge or vegetation habitats (p-value < 0.00 for both), but not significantly different between edge and vegetation habitats (p-value = 0.87). I did not measure surface areas of macrophytes collected in the vegetation and edge samples. Therefore, results show only densities of snails in a 2-dimensional plane within the 3 habitats.

Discussion

The three primary statistical methods used in this analysis, regression tree, geostatistics, and SADIE provided varying types of analysis and answered different spatial questions. Regression tree analysis determined which environmental factors, including other snail species, were the best predictor of species abundance. These factors varied with each species. Geostatistics provided several answers that the other two methods could not, particularly for *T. serpenticola*. Because *T. serpenticola* was spatially autocorrelated, a variogram provided an approximation of its patch size and allowed me to more realistically estimate, via kriging, its total abundance in the study site. SADIE supported the geostatistical results of presence or absence of spatial autocorrelation for all three species but did this by formally testing the null hypothesis of lack of spatial autocorrelation. SADIE also allowed me to formally test whether the species were associated or disassociated with one other. For example, SADIE showed that *T.*

serpenticola and *Fluminicola* sp. were significantly spatially disassociated with *P. antipodarum*, whereas this (dis)association was not included in the regression tree analysis and it was difficult to discern in the geostatistical analysis.

Non-random spatial patterns are usually the rule, not the exception (Perry et al. 2002) although, spatial patterns are obviously scale dependent (Keitt et al. 2002). Within this small 25-m x 25-m area, *T. serpenticola* and *P. antipodarum* were spatially autocorrelated and distributed into patchy aggregations but *P. antipodarum* distribution in the upstream and downstream sections analyzed separately (and *Fluminicola* sp. distribution in the entire site) were not significantly different than random. This apparently random distribution could be a result of the scale at which the snails were measured.

Potamopyrgus antipodarum abundance and distribution in the study area was primarily due to first order effects, with an obvious sharp decrease in abundance upstream of Morgan Lake near where canopy cover started. First order effects here refer to environmental gradients such as x and y coordinates and elevation, whereas, second order effects refer to the spatial autocorrelation structure. I have found extremely high densities of *P. antipodarum* in Morgan Lake and this appears to be the focus of its distribution and spread throughout Banbury Springs into the headwaters sections (Richards et al. 2001). Conditions further upstream from Morgan Lake appear to limit its abundance. Because water temperatures were constant within the study site and did not appear to be a factor, a likely explanation for the sharp decline in upstream abundance of *P. antipodarum* was that there may have been large differences in either primary production, food resources, or both between the shaded, canopy-covered, upstream

portion of the site and the open, sunlit, downstream section. Further investigation is required. The apparent random pattern of *P. antipodarum* distribution in the lower portion of the study area and the absence of second order spatial pattern in the entire study area was probably because it is a highly mobile snail species and easily disperses (Ribi 1986). I have observed all three species in the field and in the laboratory for several years and *P. antipodarum* is by far the most mobile. I have estimated that it can disperse ≅ 1 m/hr and could have easily occupied the entire study site since it first became established, at least ten years prior to this study. *Potamopyrgus antipodarum* is highly fecund with a potential for rapid population growth (Bowler 1991) and its dispersal abilities may allow it to avoid crowding from intraspecific competition.

The spatial pattern observed for *T. serpenticola* was likely due to both first order and second order effects. *Taylorconcha serpenticola* occurred mostly upstream from Morgan Lake (1^{st} order effect), but because *T. serpenticola* does not readily detach from the substrate and moves very slowly, it has limited dispersal capability and therefore, occurred in patches (2^{nd} order effects).

For the predictive krig mapping and total abundance estimation of *T. serpenticola*, one outlier and high leverage point was identified and removed. This sample had over twice as many *T. serpenticola* as did the next largest value and was in a cluster of other samples with large values. Because *T. serpenticola* is listed as threatened species and it is unlawful to intentionally harm them, I wanted to have as little impact on individuals as possible while conducting the study and did not measure or record shell sizes. Therefore, this outlier may have been a sample that contained many smaller, younger, *T. serpenticola* that had not dispersed. Determining the reason for this high-density sample,

however, could be important toward understanding the ecology of *T. serpenticola* (Rossi et al. 1992).

Both *T. serpenticola* and *Fluminicola* sp. were spatially disassociated with *P. antipodarum* and positively associated with each other. This positive association between *T. serpenticola* and *Fluminicola* sp. may be the result of coevolution in similar habitats in the Snake River drainage. The disassociation between both *T. serpenticola* and *Fluminicola* sp. with *P. antipodarum* may have been primarily due to environmental constraints, although both SADIE and RTA results suggested that interspecific competition may also have been involved (Perry and Dixon 2002, Keitt 2002, Tilman and Kareiva 1997). It is unknown if *T. serpenticola* or *Fluminicola* sp. would have been more abundant downstream in the study area occupied by *P. antipodarum* or if *P. antipodarum* would have been more abundant in upstream areas if *T. serpenticola* was less abundant. *Potamopyrgus antipodarum* may actually be an inferior competitor to *T. serpenticola* but its high fecundity, recruitment ability, and long-dispersal range may allow it to exploit resource rich disturbed habitats and allow it to coexist with *T. serpenticola* (Amarasekare 2003). *Taylorconcha serpenticola* appears to be more fecundity- recruitment- and dispersal-limited than *P. antipodarum* (Taylor 1987, Frest and Johannes 1992, U. S. Fish and Wildlife Service 1992 and 1995) and thus not able to exploit resource rich conditions, such as recently disturbed (early successional) habitats but may be able to out-compete *P. antipodarum* in stable, resource limited habitats (Amarasekare 2003), such as the upper sections of Banbury Springs. In Chapter 5, I discuss results from competition experiments between *P. antipodarum* and *T. serpenticola* that further support this idea.

Spatially predicted estimates of total abundances of *T. serpenticola* and *P. antipodarum* were somewhat different than the often-used bootstrap method of estimation. These differences could become more pronounced if used on a larger scale or in different habitats and therefore, bootstrap estimation may become less reliable. Models that ignore spatial autocorrelation may not reflect true abundance, species interactions, or environmental relationships (Lennon 2000, Keitt 2002, Diniz-Filho 2003) and may not give best estimates of abundance.

Estimating total abundance is important for understanding and evaluating anthropomorphic effects on a species, particularly threatened or endangered species. Threatened species risk assessments, sensitivity analyses, population viability analyses, and management options often require an estimate of total abundance. By examining spatial patterns, a better understanding of species interactions (i.e. competition), species-environmental relationships, abundance and distribution, and anthropomorphic effects is possible.

In Banbury Springs, it appears that *P. antipodarum* may be establishing itself into the upper portion of the springs, mostly by spreading through vegetation and edges of the faster-flowing waters and then moving into new habitats, particularly unoccupied vegetation habitat. Faster water velocity possibly limits colonization of *P. antipodarum* into run habitats. The vegetation habitat with its associated slower water velocity seems to provide refuge for small-sized *P. antipodarum* and might also act as a nursery. Velocity could also affect smaller *P. antipodarum* more than larger ones due to a combination of physical, behavioral, physiological, or morphological factors. Water velocity more easily dislodges *P. antipodarum* than *T. serpenticola* individuals. During this study, *T.*

serpenticola remained attached to rock substrates when disturbed, whereas *P. antipodarum* immediately detached themselves from any substrate and often entered the drift after disturbance. Interestingly, I found *P. antipodarum* to be the 2nd most abundant macroinvertebrate collected in 24-hour drift net samples at Banbury Springs, and have often found them in floating vegetation mats in Morgan Lake. Continued invasions of *P. antipodarum* are likely, particularly in habitats with low water velocity and large amounts of vegetation (e.g., ponds, lakes, reservoirs, slower rivers, and backwaters), but may be limited in habitats with higher water velocities. Although, there was little water temperature gradient in the study area, temperature may be important for snail distribution and abundance in this and other aquatic environments (see Chapter 2). In the temperature-growth rate experiment in Chapter 2, *P. antipodarum* growth rates were much lower at 15˚ C than at their maximum growth rate of 21˚ C and were similar to *T. serpenticola* growth rates at 15˚ C. It is possible that the combination of high water velocities and cold-water temperatures limit the upstream distribution and densities of *P. antipodarum* in Banbury Springs.

Conclusion

Interspecific competition between *T. serpenticola* and *P. antipodarum* may occur in areas where their distributions overlap. Historically (Taylor 1987, U. S. Fish and Wildlife Service 1995), *T. serpenticola* was found only on large cobble substrates. In this study, *T. serpenticola* was equally abundant in vegetation habitat as it was in run habitat with larger substrates. Future surveys of *T. serpenticola* should include vegetation habitat.

Although edge habitat between run and vegetation habitat did not affect *T.*

serpenticola densities, it did have a transitional affect on *P. antipodarum* densities and a sharp affect on *Fluminicola* sp. densities. These boundaries may therefore, influence abundance and distribution of these three species and may affect interspecific competition. Because *T. serpenticola* appears to be dispersal limited and its abundance is spatially autocorrelated at a small scale, appropriate analyses incorporating its spatial dynamics are required to further understand its ecology and to better manage its populations and habitats. Appropriate scale dependent spatial analyses should also be used for *P. antipodarum*, as well.

INTRASPECIFIC COMPETITION AND DEVELOPMENT OF SIZE STRUCTURE IN THE INVASIVE SNAIL *POTAMOPYRGUS ANTIPODARUM*

Introduction

Intraspecific competition (density-dependence) is an important regulator of populations (Gotelli 1998) and could influence *P. antipodarum* population dynamics, including individual growth rates. Size structures of *P. antipodarum* populations vary in the western USA; sizes of individuals present at any one time may range from 0.5 -1 mm newborns, to 4 - 5 + mm adults of unknown ages. Because *P. antipodarum* is a clonal species, some researchers have attempted to use size classes to infer age structure; based on the assumption that genetically identical *P. antipodarum* within a population should grow at approximately the same rate as compared with sexual snails with more genetic variability. This assumption may be inappropriate because "asymmetric" or "one-sided" intraspecific competition could influence the size hierarchy of a population (Begon 1984, Weiner 1990, Begon et al. 1996), possibly even in a clonal species. Asymmetric competition occurs when larger individuals are able to obtain more resources than smaller individuals and thus suppress the growth of the smaller individuals (Weiner 1986, Begon et al. 1996). Size hierarchies induced by asymmetric competition have been reported for many organisms (Obeid et al. 1967, Ross and Harper 1972; Branch 1975, Uchmanski 1985, Gribbin and Thompson 1990, Adams and Tschinkel 1995, Geffen 1996).

The ecological and evolutionary significance of competition induced size hierarchies are numerous (Begon et al. 1996). For example, because asymmetric competition suppresses growth in smaller individuals it could cause density-dependent

mortality or decreased fitness in smaller individuals (Rubenstein 1981, Weiner 1985, Begon et al. 1996). Correlations between fitness (fecundity) and size have been well studied (Begon et al. 1996, McPeek and Peckarsky 1998, Taylor et al. 1998). I have demonstrated that larger *P. antipodarum* produce more offspring (Richards et al. 2000) and survive desiccation longer than do smaller *P. antipodarum* (Richards et al. 2004), both of which may have ecological consequences. Thus, understanding the cause of size hierarchies in *P. antipodarum* populations becomes important.

For this study, I conducted growth experiments on *P. antipodarum* in the laboratory to determine if intraspecific competition for limited food resources would cause shifts in the size hierarchy of *P. antipodarum* populations. Because results from laboratory experiments are usually less variable and, therefore, more precise than are field experiments (Miller 1986), I chose to conduct laboratory experiments. This allowed me to control other variables that could have contributed to differences in growth. Also, it is extremely difficult and costly to conduct exclosure experiments with *P. antipodarum* at field sites in the Snake River because of the sheer numbers of less than 1.5 mm newborn snails usually present, which can pass through any mesh large enough (1mm) to allow for flows that provide gas exchange and metabolic waste removal.

Materials and methods

I stocked individually measured *P. antipodarum* with shell lengths between 2.00 to 2.10 mm in double open-ended glass tubes (inner surface area 22.0 cm^2) at 1-snail/tube (20 replications) and 10-snails/tube (20 replications). I covered both tube ends with 1mm nylon mesh to allow passage of dissolved gases, including metabolic wastes. I have used

this experimental design in numerous growth and competition studies and have found them to provide ample flow and gas exchange, even using snail species such as the oxygen demanding Bliss Rapids snail, *T. serpenticola* (Richards et al. unpublished data).

All snails were individually color-coded by application of a small drop of various colors of acrylic fingernail paint to their apex. Stocked tubes were randomly placed in plastic test tube racks and submerged into a 160- gallon freshwater aquarium (water temperature 20^0 C). I placed snails into clean tubes with new mesh weekly, to prevent establishment of periphyton in the tubes. One milligram of commercial *Spirulina* sp. dissolved in 5 ml of water was injected into each tube through the nylon mesh using a hypodermic syringe, once per week. Because *Spirulina* sp. is a poor food resource for most snails, I was assured that all snails were food resource limited. After one month, I measured growth of individuals to the nearest 0.05 mm.

I compared growth rates (mm/month) of individuals from 1-snail/tube and 10-snails/tube. Various indices (metrics) for measuring and comparing variability, evenness, and size hierarchies are often used in ecological studies (Knox et al. 1989, Damgaard and Weiner 2000) for example; skewness, coefficient of variation, the Shannon-Weiner index (Zar 1999), and the Gini coefficient '*G*' (Dixon 2001). According to Weiner and Thomas (1986), size variability is best measured in terms of inequality (hierarchy) and of these metrics; the Gini coefficient is considered to be the most relevant (Weiner and Solbrig 1984, Dixon et al. 1987, Knox et al. 1989). For this study, I focused the analysis on the Gini coefficient, *G*.

Because I used all twenty of the individual growth rates of snails at 1-snail/tube in the calculation of the no competition *G* (N = 20 data points), it would have been less

accurate to compare the with-competition *G* derived from 10- snails/tube (N = 10 data points). Therefore, to create with-competition *G*'s derived from 20 data points, I randomly sampled an individual snail from each of the twenty 10-snails/ tube 1000 times using a random sampling algorithm and then calculated 1000 with-competition *G*'s. I then compared 95% confidence intervals for the 1000 with-competition *G*'s with the single no-competition *G*. I also conducted a one-tailed t-test comparing differences in means between the no-competition *G* and the 1000 with-competition *G*'s. I used SAS for Windows (SAS Institute 2001) for the t-test and the program 'Gini' developed by Dr. John Borkowski, Montana State University (2002) in SAS for Windows (SAS Institute 2001) for generation of *G*.

G is a summary statistic that measures size hierarchy (inequality) in a population. It ranges from 0 for populations with all individuals of equal size, to 1 where every individual except one has a size of zero. I used the *G* formula presented by Dixon (2001):

$$G = \frac{\sum_{i=1}^{n} (2i - n - 1) X_i}{(n-1) \sum_{i=1}^{n} X_i}$$

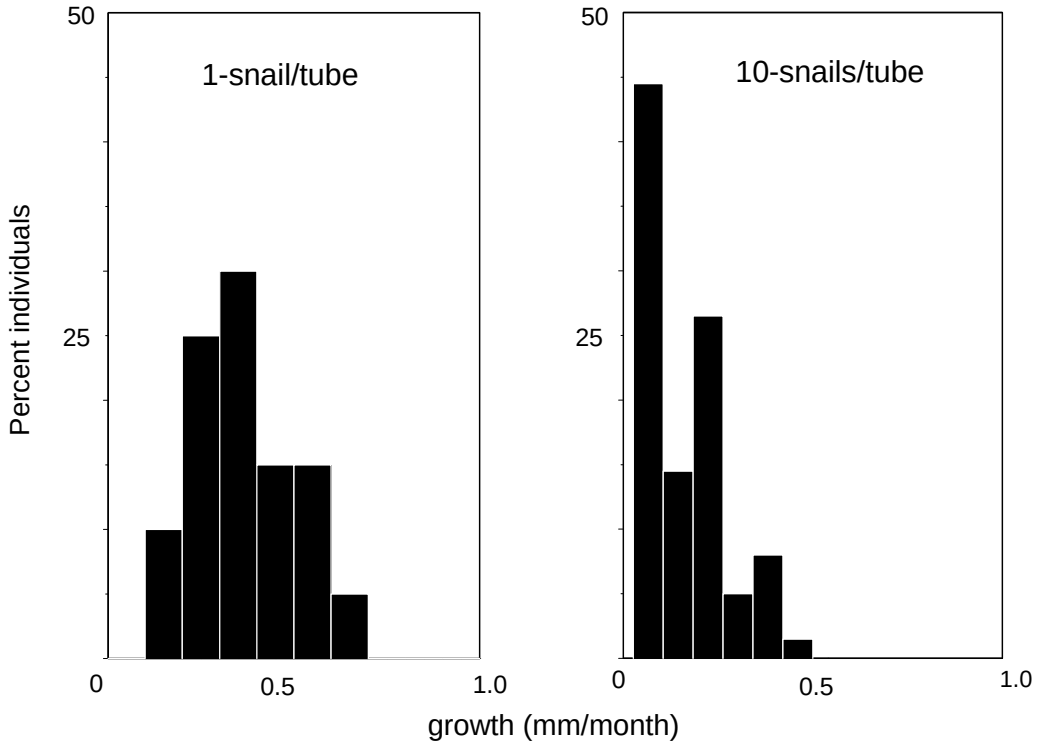
Here *n* equals the number of individual snails and X_i is the size of the i^{th} snail when they are sorted from smallest to largest.

Results

There was a shift from no size hierarchy for *P. antipodarum* grown at no-competition to a strong size hierarchy for *P. antipodarum* grown with-competition (Figure 32). The no-competition *G* was 0.251 and the mean with-competition *G* was

0.461 (95% upper and lower CI = 0.458, 0.465; min. = 0.286; max. = 0.650), which was significantly greater than the no-competition *G* (one-tailed t test for differences in means; N = 1000; t = 135.36; p < 0.000). The distribution of growth rates of *P. antipodarum* at no-competition was normally distributed (N = 20; Shapiro-Wilk W = 0.967; p = 0.696) while those grown with-competition were right-skewed and non-normally distributed (N = 200; Shapiro-Wilk W = 0.852; p < 0.000) (Figure 32). *Potamopyrgus antipodarum* grown at no-competition (mean growth = 0.338 mm/month, std. dev. = 0.146) grew significantly more (non parametric Kolmogorov-Smirnov t-test, p < 0.005) than those grown with-competition (median growth = 0.100 mm/month, 25% quartile = 0.050, 75% quartile = 0.200).

Figure 32. *Potamopyrgus antipodarum* growth (mm/month) with no competition (1 snail/tube; N = 20) and with intraspecific competition (10 snails/tube; N = 200).



Discussion

Intraspecific competition for limited food resources caused decreased growth of *P. antipodarum* reared in the laboratory. One snail in a 22 cm^2 tube translates to roughly 455 snails/ m^2 and 10-snails/tube translates to roughly 4555 snails/m^2, fairly low compared to naturally-occurring densities of *P. antipodarum*, which are often between 20,000 and 40,000/m^2 and occasionally exceed 500,000/m^2 in rivers in the western USA. Obviously, other environmental and ecological factors affect *P. antipodarum* populations in waters in the western USA. It is likely however, that intraspecific competition occurs in waters infested with *P. antipodarum*, particularly in late autumn and early winter when primary production is reduced and *P. antipodarum* populations are high. Intraspecific competition may partially explain why many researchers report marked decreases in *P. antipodarum* densities and a scarcity of smaller individuals in winter (D. Shinn unpublished data, D. Richards unpublished data, B. Kerans and C. Cada unpublished data; and D. Gustafson, personal communication). I have shown that in a freshwater spring with fairly constant year round temperatures (approx. 14° C) and flows that *P. antipodarum* densities also decrease in autumn and winter, which indicates that temperature and flow are not entirely responsible (Richards et al. 2001).

In this experiment, asymmetric competition resulted in a well-defined size hierarchy. These results suggest that size hierarchies in *P. antipodarum* populations in the western USA may not be entirely based on age class. Because asymmetric competition affects smaller individuals more than larger individuals, it might also result in reproductive hierarchies. Previously I found that in several rivers in the western USA, larger *P. antipodarum* produce more embryos; snails < 3.00 mm did not reproduce at all

(Richards et al. 2000). Reproductive hierarchies could result in self- thinning populations and/or dominant and suppressed size classes (Ford 1975, Ford and Diggle 1981). I do not know if the effects of inequality in individual reproductive output are greater than the effects of their inequality in size. Even though *P. antipodarum* in the western USA is a clonal species, reproductive hierarchies could increase the proportion of genes represented by the larger, more fecund individuals in future generations (Heywood 1986, Damgaard and Weiner 2000).

COMPETITION BETWEEN *T. SERPENTICOLA* AND *P. ANTIPODARUM*

Introduction

Because of the enormous impacts of humans on the world's biodiversity, primarily only 'weed' species, 'relict' species, or 'ghost' species remain (Meyer 2004, Vitousek et al. 1997). Weed species are those that can survive and flourish under human disturbed conditions and include most invasive species. Relict species are those that remain in heavily managed ecosystems, reserves, or zoos and/or are afforded legal protection (i.e. Endangered Species Act), without which, they would soon disappear. Ghost species are those that only persist due to extreme management effort, but do not have viable populations (Meyer 2004). Ghost species are considered part of the extinction 'debt' (Meyer 2004, Tilman et al. 1994) and relict species can quickly become ghost species (Meyer 2004). *Potamopyrgus antipodarum* is widespread throughout the world and can be considered an invasive 'weed' species. *Taylorconcha serpenticola*, due to its Threatened status and limited distribution can be considered a 'relict' species. Competition between weed species and relict species is inevitable (Meyer 2004) and in previous chapters, I have shown that competition between *P. antipodarum* and *T. serpenticola* was likely. In this chapter, I directly examined competition between the two species using controlled field experiments.

I conducted exclosure/enclosure competition experiments between *P. antipodarum* and *T. serpenticola* at the confluence of Banbury Springs and Snake River (Figure 33), in the summers of 1999 and 2000. For this study I tested the hypothesis that

increased densities of *P. antipodarum* in cobble habitats negatively affected *T. serpenticola* densities.

I then conducted controlled experiments at two locations in Banbury Springs, Idaho during four seasons, spring (March/April), summer (June/July), autumn (September/October) and winter (December/January) 2002. This set of experiments was designed to examine intra and interspecific competition effects on growth rates of *T. serpenticola* and *P. antipodarum*. From this set of experiments, I developed competition coefficients for both species and measured amounts of periphyton (food resource) needed for each species' growth (biomass) as well as explored and compared periphyton community structure in experimental chambers and under natural conditions. For this set of experiments I tested the following hypotheses; 1) intraspecific competition results in decreased growth in *T. serpenticola* and *P. antipodarum, 2)* interspecific competition results in decreased growth in *T. serpenticola* and *P. antipodarum*, 3) growth rates of *T. serpenticola* and *P. antipodarum* were affected by competition, season, and habitat, 4) periphyton biomass and diversity was different between experimental chambers (treatments) and natural conditions, seasons, and locations.

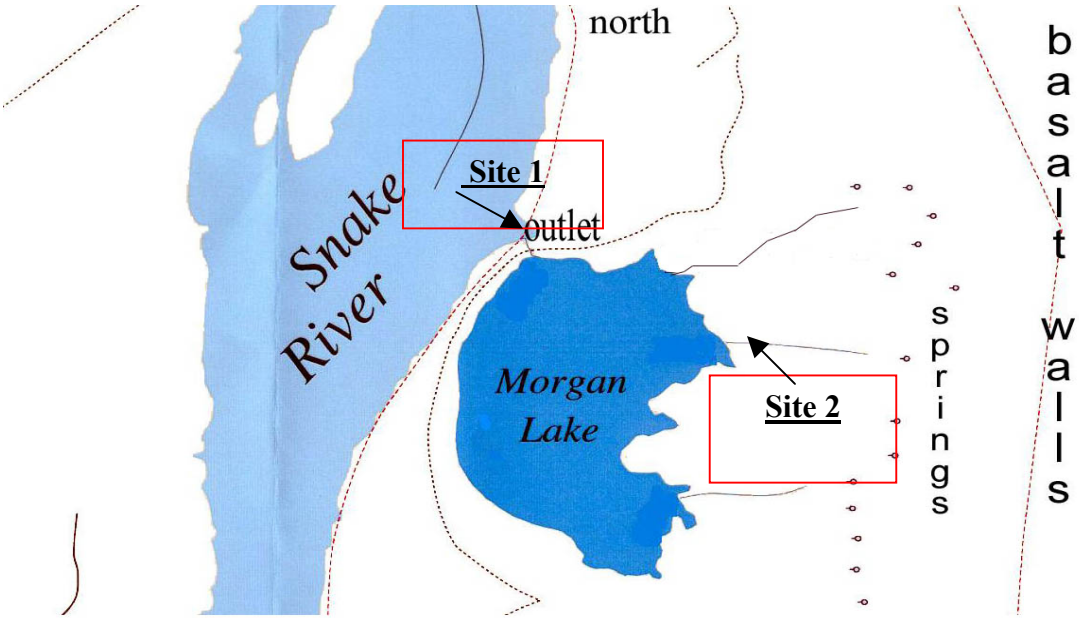
Materials and Methods

Exclosure/enclosure experiments

I surveyed *T. serpenticola* and *P. antipodarum*, in August 1999, to determine natural snail densities on cobble habitat in the study site at the outlet of Banbury Springs (Figure 33). *Taylorconcha serpenticola* mean density on cobble habitat was estimated at 1721.07/m^2 (std. dev. = 1277.28) and *P. antipodarum* mean density was 4919.62/m^2 (std.

dev. = 3325.64). Based on these natural densities, I stocked *T. serpenticola* at densities of approximately 1500/m^2 on 40 measured cobbles in specially designed enclosure/exclosure cages (Figures 34 and 35). For the repeat of the experiment in 2000, I reduced the number of replicates to 20 cobbles based on a power analysis of results from 1999. I then stocked *P. antipodarum* on these same cobbles at five different densities: 0/m^2 (control), 1000/m^2, 2000/m^2, 4000/m^2, and 10,000 /m^2 at 8 replications/treatment in 1999 and 4 replications/treatment in 2000.

Figure 33. Banbury Springs study site near Hagerman, in south central Idaho. Site 1 is at the outlet of Morgan Lake and Banbury Springs. Site 2 is the second spring from the north entering into Morgan Lake.

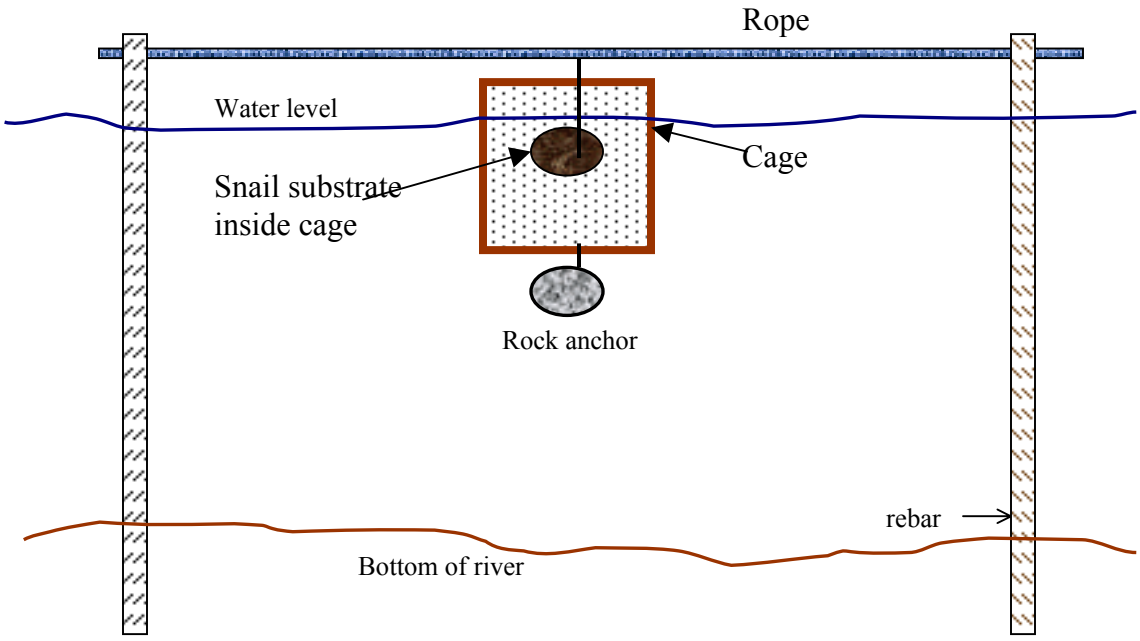


Enclosure/exclosure cages were made with ¼- inch plywood and 0.5 mm diameter nylon mesh to form a box (Figures 34 and 35). To counter act the buoyancy of the plywood and to submerge the cage to the desired level, a single cobble was attached

to the outside bottom of the plywood by 20 lb. test monofilament and snap swivel. All of the cages were hung in a random series in the water from a 1/2-inch nylon rope strung between ½- inch embedded rebar. Cobbles were all of volcanic origin and were measured for total surface area and then pre-conditioned for 3-weeks in the cages prior to the experiment. After conditioning, cobbles were suspended from the rope, via fine gauge, picture wire, and submerged under water inside each cage. They were then stocked with *T. serpenticola* and *P. antipodarum*. Suspending the cobbles in the cages prevented any snails from leaving the cages and reduced the number of *P. antipodarum* entering the cages.

Figure 34. Exclosure/enclosure cages used in experiment using 0.5 mm mesh. Cages were half submersed in water to prevent snails from escaping or entering.

Figure 35. Exclosure/enclosure cages used in competition experiments.



I used only *T. serpenticol*a and *P. antipodarum* whose shell lengths were between 2.0 mm and 2.5 mm, for several reasons. First, I wanted to preclude any potential inter or intra-specific competitive affects resulting from different size classes. Second, I had recently conducted an analysis of number of neonates (embryos) produced in relation to shell lengths of *P. antipodarum* from Banbury Springs and found that *P. antipodarum* did not produce neonates at shell lengths < 3.0 mm (Chapter 2). *Potamopyrgus antipodarum* with shell length $\geq$ 3 mm can release young throughout the spring, summer, and autumn at Banbury Springs and any such newly born *P. antipodarum* released in the cages during the experiments could have affected results. Also, *T. serpenticola* does not often exceed 2.5 mm as adults.

Cobbles in the enclosure cages were examined 3 days after deployment and any snails that had fallen off into the cage were placed back on to the cobbles. Weekly visual examinations were conducted and any *P. antipodarum* that abandoned the cobbles were returned to the cobbles, whereas any *T. serpenticola* that migrated off of the cobbles were removed from the cage and released unharmed into the study site. I repeated the counts at 1, 2, and 3 months in 1999. During counts, I held a 1 mm diameter- mesh aquarium net below the cobble to catch any snails that fell off while counting or while I was replacing the cobbles back into the water. Any snails that fell off while counting were placed back onto the cobbles. After 1 month (August, 1999), abandonment from the cobbles was great enough by both species that any competition effects were not detectable (Richards and Lester 1999); therefore, I conducted the experiment for only 1 month in August 2000.

Statistical Analysis

A single factor, fixed- effects model analysis of variance (ANOVA) was conducted on 1999 and 2000 data separately and for 1999 and 2000 data combined to determine if *P. antipodarum* densities affected *T. serpenticola* densities. Simple linear regression was conducted using densities of *P. antipodarum* as the predictor variable and densities of *T. serpenticola* as the response variable for 1999 and 2000 data combined. I also created a linear regression model and projected an estimate of *P. antipodarum* density that would result in *T. serpenticola* densities of $0/m^2$. All statistical analyses were conducted using the statistical packages MINITAB (2000) and STATISTICA (Statsoft Inc. 1995).

Competition and Growth Rates

Study Sites. In 2002 and 2003, I chose two sites at Banbury Springs (Figure 33) that represented different habitats. The first site was at the outlet of Banbury Springs into the Snake River below Morgan Lake (Figure 36). This site appeared to be much more productive than the second site due to the influence of the nutrient rich Snake River and it contained sizable populations of both species. I estimated that *P. antipodarum* ranged from 3000/m^2 to > 300,000/m^2 in this area and *T. serpenticola* in summer, often reached > 3000/m^2. The second location was the second inflowing spring from the northern end of Banbury Springs just upstream of Morgan Lake (Figure 37). This site was entirely spring influenced, had constant year round cool temperatures, and had very few or no *P. antipodarum.* Densities of *T. serpenticola* at the second site were about 300/m^2 (Richards et al. 2001).

Procedures and Methods

I compared mean growth rates of *T. serpenticola* and *P. antipodarum* in double open-ended enclosure tubes at eight levels of snail densities (treatments) at each location and season. Each of the eight treatments had 5 replicates. Treatment densities are shown in Table 4, with a description of comparisons needed to determine intra and interspecific competition. Snail densities in tubes were representative of densities found in Banbury Springs. Tubes were placed in the sites and preconditioned with periphyton for 3 weeks prior to the experiment. Pre-measured snails (2-3 mm) were randomly placed in tubes, which were then randomly placed in four different tube racks at 10 tubes/rack at each site. I used multiple tube racks instead of one rack to reduce any potential crowding

effects on tubes. Snails were allowed to grow for 1 month, then were removed, re-measured and either released (*T. serpenticola*) or preserved (*P. antipodarum*).

Figure 36. Site 1. Snake River alcove at outlet of Banbury Springs, Idaho (top photo). The whitewater in photo is main outlet of Banbury Springs. Seep area (bottom photo) is to the left of top photo.

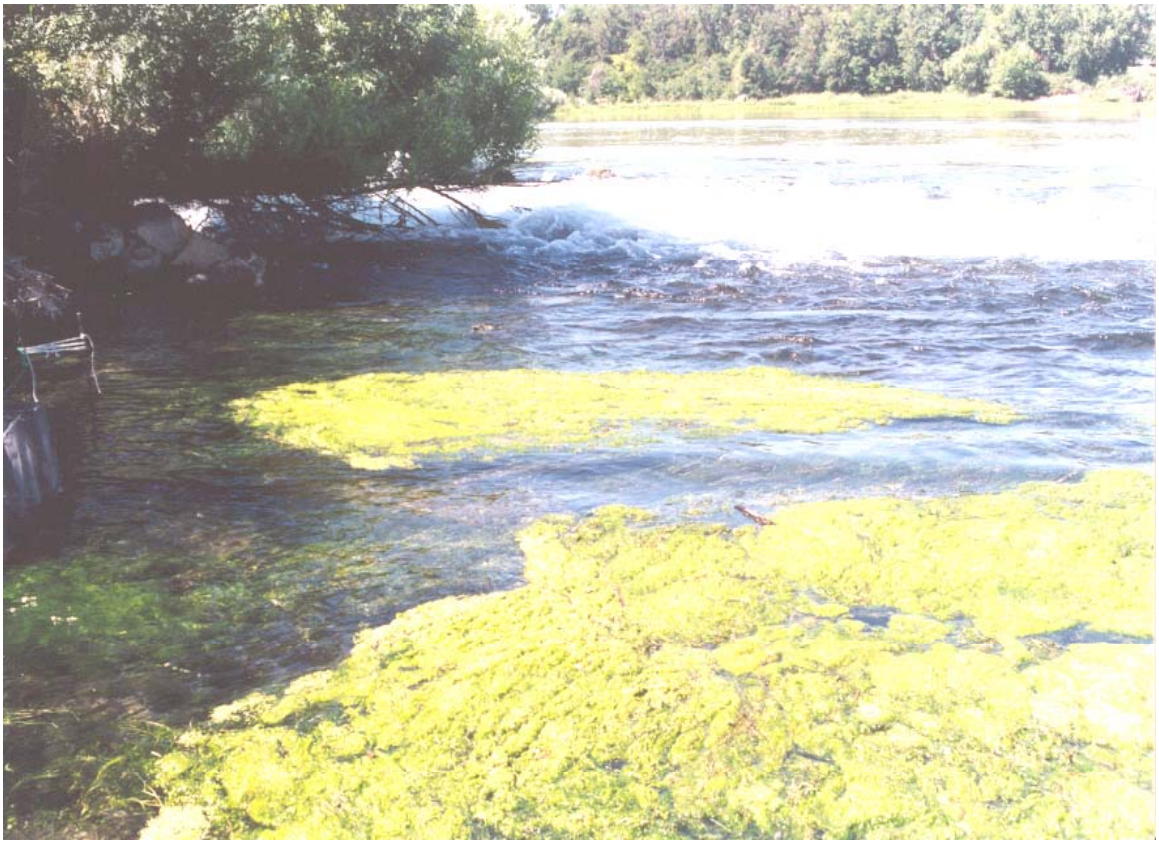


Figure 37. Site 2. Springs site looking downstream into Morgan Lake, Banbury Springs, Idaho.

Table 4. Stocking densities (snails/tube) and outcomes of competition experiment (area of vials = 22 cm^2)

	treatment							
	1	2	3	4	5	6	7	8
T. serpenticola/tube	1	4	12	0	0	0	2	6
P. antipodarum/tube	0	0	0	1	4	12	2	6

Intraspecific competition

1) *T. serpenticola*: Treatment 1 vs. 2 vs. 3
2) *P. antipodarum*: Treatment 4 vs. 5 vs. 6

Interspecific competition

1) Effects of *P. antipodarum* on *T. serpenticola*
    a. Treatment 2 vs. 7 (low densities) and treatment 3 vs. 8 (high density)
2) Effects of *T. serpenticola* on *P. antipodarum*
    a. Treatment 5 vs. 7 (low densities) and treatment 6 vs. 8 (high density)

Figure 38. Periphyton conditioned tubes in tube racks stocked with snails at Site 2, Banbury Springs, Idaho, 2002 (top photo). Close-up of similar tube racks in laboratory (lower photo)

Statistical Analysis

I conducted two-factor, fixed effect ANOVA's for each species at each season. The two factors were densities (treatments) and location plus the interaction term.

Homogeneity of variance tests and plots of residuals and normal probability plots were used to determine if the raw data was appropriate for ANOVA. I used raw data for all ANOVA's, except for *P. antipodarum* winter data, which I log transformed and for *T. serpenticola* autumn data which I used the best fit Box Cox transformation of $\lambda = 0.3$. Statistical significance in this experiment will be at p-value < 0.05, unless otherwise stated. I created interaction plots if there were significant interactions between treatment and location in ANOVA results. I also conducted preplanned comparisons to test if mean growth rates at low interspecific competition (treatments 2 vs. 7 and 5 vs. 7)(Table 4) were significantly different and if mean growth rates at high interspecific competition (treatments 3 vs. 8 and 6 vs. 8)(Table 4) were significantly different, for both locations. For these comparisons, I used 95% confidence intervals (CI) values. If CI's included 0, then I considered means not to be significantly different.

I also used preplanned orthogonal contrasts to determine if there was a linear trend in mean growth rate from no intraspecific competition (treatments 1 and 4)(Table 1) to low intraspecific competition (treatments 2 and 5)(Table 1) to high intraspecific competition (treatments 3 and 6)(Table 1) at both locations. I also created interval plots for each of the above three comparisons and contrasts using mean, and 95% CI's.

Competition Coefficients and Snail Growth Efficiencies

I estimated mean (95% CI's) competition coefficient values for both species at the low (4 snails/tube) and high (12 snails/tube) treatments for both locations and all four seasons and then calculated an overall mean (95% CI's) competition coefficient value where; α_{ij} is effect of one *P. antipodarum* on x-number of *T. serpenticola* and α_{ji} is effect of one *T. serpenticola* on x-number *P. antipodarum*. Mean and 95% CI competition

coefficients were calculated by bootstrapping (N = 10,000) the formula; mean growth rates for intraspecific competition (N = 5) divided by mean growth rate values for interspecific competition (N = 5), at the various treatment levels using S-PLUS 6.1 (Insightful Corp. 2002). The overall mean (95% CI's) competition coefficient value was calculated by bootstrapping (N =10,000) mean competition coefficients (N =4) for four seasons. 95% CI's were selected from 2.5 % and 97.5% BCa percentiles (Bias Corrected and accelerated Method).

Snail growth efficiencies were calculated by estimating the amount of ash free dry mass (AFDM) of periphyton consumed by snails in the high-density intraspecific competition treatments (3 and 6) needed to grow 1 mg of snail biomass (wet weight) in one month. This was done by bootstrapping (N = 10,000) the following formula: [mean AFDM periphyton in tubes saved at the start of the experiment (N = 5) - mean AFDM values of treatments 3 or 6 (N = 5)]/[mean biomass of snails at end of experiment (N = 5) - mean biomass of snails at beginning of experiment for treatments 3 or 6 (N = 5)]. Biomass of snails was estimated from shell lengths using previously developed shell length/biomass regression formulas: *T. serpenticola* wet weight (mg) = -5.00 + 3.69*shell length (mm) and *P. antipodarum* wet weight (mg)= 1.91 – 2.29*shell length (mm) + 0.88*length (mm)(Richards unpublished data). Two assumptions were made in estimating amounts of periphyton consumed: 1) that there was little or no periphyton growth in the high-density intraspecific treatments during the experiment and 2) snail grazing did not cause periphyton to be dislodged and therefore, unavailable for consumption. Most likely, neither of these assumptions was valid; therefore, the final growth efficiency values were probably biased and not exact estimates, although

comparisons between growth rate efficiencies of *T. serpenticola* and *P. antipodarum* would have been less affected.

Periphyton Biomass and Diversity

At the start of experiments, five conditioned tubes at each location for each season were immediately frozen and stored under dark conditions. Five randomly chosen cobbles from each location during spring and autumn were thoroughly scrubbed and contents combined and stored in Lugol's solution. Tube contents (N = 5) were combined as were cobble samples (N = 5) and were subsampled and analyzed for ash free dry mass (mg/cm^2)(APHA 1995) and chlorophyll a (mg/cm^2, pheophyton corrected)(USEPA 1997). In addition, samples from spring and autumn were analyzed for taxon specific biovolume. Samples were analyzed by EcoAnalysts Inc., Portland, Oregon. For a detailed description of methods see Appendix 1.

I calculated and compared several richness and evenness indices on taxa biovolume for tube samples and cobble samples between sites and seasons. These indices included:

1) taxa richness, S (total number of taxa),

2) Pielou's evenness index, J = H/ln(S),

3) Shannon-Wiener index, $H = 1 - \sum_{i}^{s} p_i^2 - \sum_{i}^{s} p_i \ln (p_i)$, and

3) Simpson's diversity index, $D = 1 - \sum_{i}^{s} p_i^2$

where p = percent individuals of each taxa. All indices were calculated using PC-ORD for Windows (McCune and Mefford 1999).

Results

Exclosure/enclosure Experiments

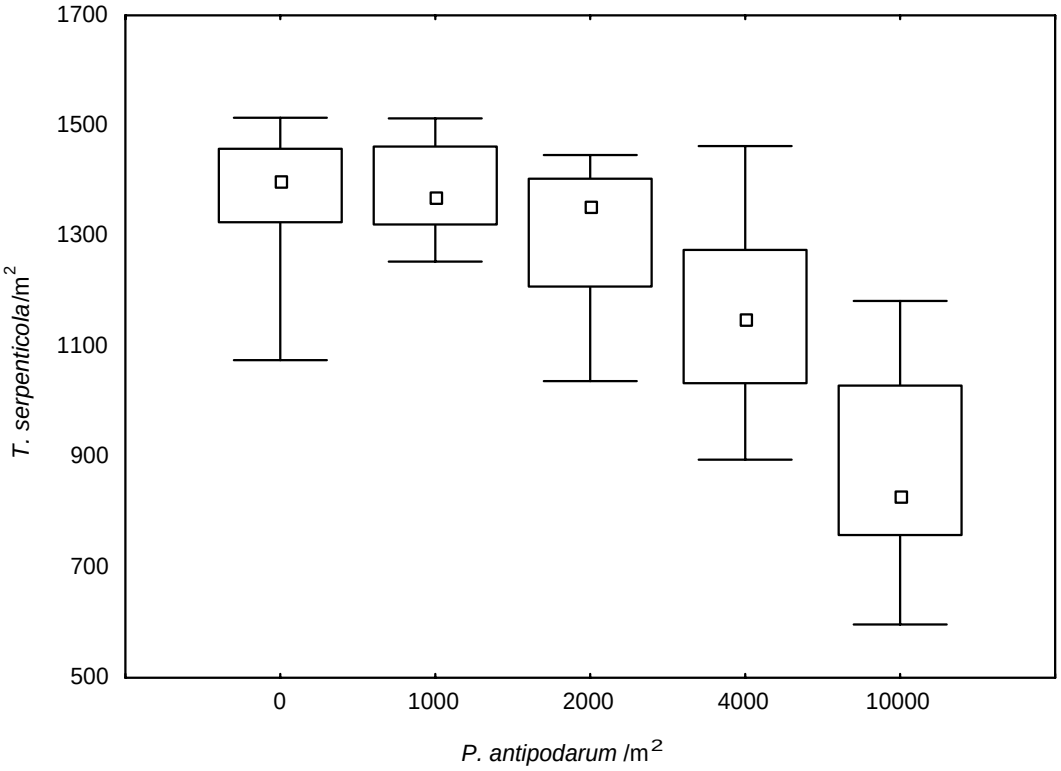
Natural densities of both *T. serpenticola* and *P. antipodarum* on cobble habitat at the outlet of Banbury Springs were higher in 2000 than in 1999 (Table 5). Densities of *P. antipodarum* were significantly greater than densities of *T. serpenticola* in 1999 (t-test, p-value < 0.01) but were not significantly different than those of *T. serpenticola* in 2000 (p-value = 0.21).

Table 5. Natural densities of *T. serpenticola* and *P. antipodarum* at the confluence of Banbury Springs and the Snake River (N = 20 cobbles). Collected on 5 August 1999 and 2 September 2000.

	Mean	Median	Minimum	Maximum	Std. Dev.
1999					
T. serpenticola	1721.07	1396.50	72.08	4789.51	1277.27
P. antipodarum	4919.62	4177.04	1361.27	12,831.01	3325.64
2000					
T. serpenticola	5558.39	3338.69	606.06	14,350.00	4751.74
P. antipodarum	4774.92	2325.94	458.43	15,625.00	4949.45

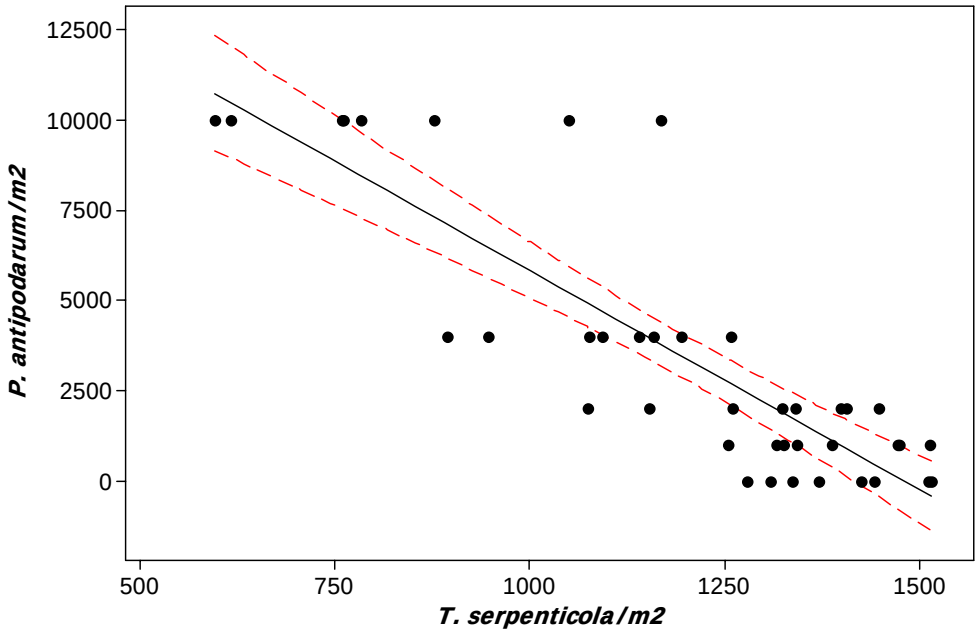
Results for 1999 and 2000 experiments were similar; therefore I will only further discuss combined data. Densities of *T. serpenticola* differed significantly between treatments (densities of *P. antipodarum*)($P < 0.01$) and a plot of the median, minimum, maximum, and quartiles for each treatment at 1 month showed a decrease in *T. serpenticola* densities with increased *P. antipodarum* densities (Figure 39).

Figure 39. *Taylorconcha serpenticola* densities at five densities of *P. antipodarum* after 1 month in enclosure cages at Banbury Springs, 1999 and 2000 data combined (median, 25-75 quartiles, minimum and maximum values)



Densities of *T. serpenticola* for 1999 and 2000 data combined declined significantly with increasing *P. antipodarum* densities (Figure 40). Predicted *P. antipodarum* density at *T. serpenticola* density of 0/m^2 was 18,018/ m^2 (95% CI = 15,033/ m^2, 21,002/m^2) based on a best-fit regression model. This prediction obviously violated rules of regression analysis by estimating values outside of the range of data based, predictor values.

Figure 40. Relationship between densities of *T. serpenticola* and *P. antipodarum* for 1999 and 2000 data combined. The regression formula was: *P. antipodarum*/m^2 = 18018 – 12.17 *T. serpenticola*/m^2 (N = 60, R^2 = 0.73, p-value < 0.01)(± 95% CI's)



Competition and Growth Rates

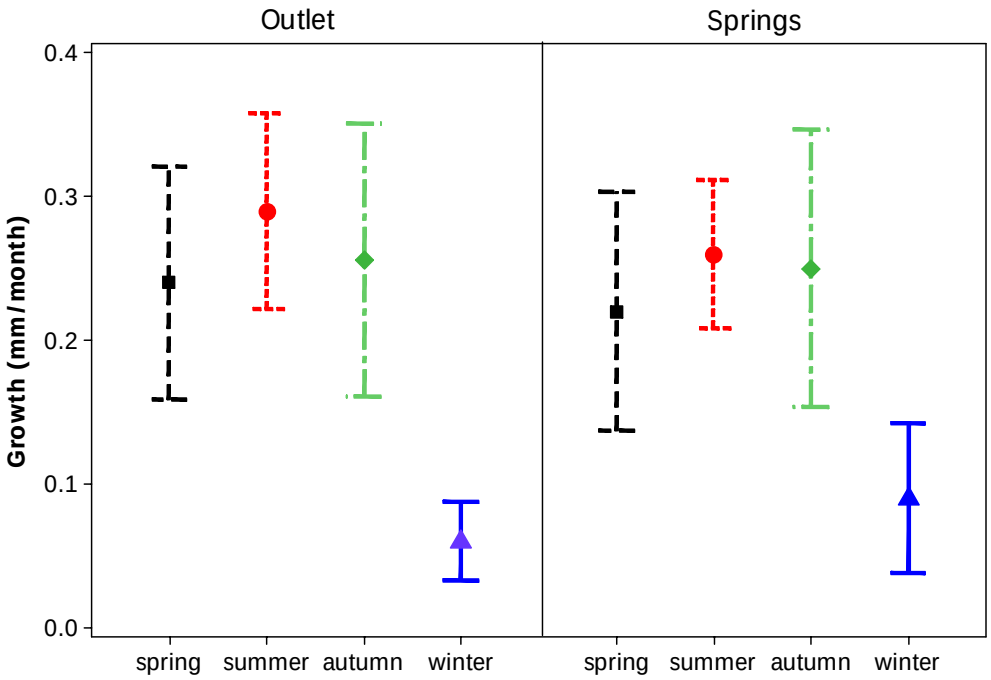
Taylorconcha serpenticola Growth with No Inter or Intraspecific Competition.

There was a significant seasonal effect but no location or interaction effects on *T. serpenticola* growth rates without competition (Treatment 1)(Table 6) with growth rates significantly lower during winter at both locations (Figure 41). The ANOVA model explained 69.51% of the variability in growth rates of *T. serpenticola*.

Table 6. ANOVA for *T. serpenticola* growth rates (mm/month) with no intra or inter specific competition at four seasons and two locations (R^2 = 0.70)

Source	df	SS	MS	F statistic	P-value
Season	3	0.25	0.08	23.78	< 0.01
Location	1	< 0.01	< 0.01	0.12	0.73
Season*location	3	0.01	< 0.00	0.50	0.69
Error	32	0.11	< 0.01		
Total	39	0.36			

Figure 41. Mean (± 95% CI) growth rates of *T. serpenticola* at four seasons and two locations.



Taylorconcha serpenticola: Spring (March/April) 2002. There was a significant treatment effect, but no significant location or interaction effect and the ANOVA model explained 62.51% of the variability in growth rates of *T. serpenticola* (Table 7). There was a significant negative linear trend ($t > t^*$) in growth rates under intraspecific competition at both locations (Figure 42), but there were no significant differences in growth at low interspecific competition (Figure 43) or high interspecific competition (Figure 44).

Table 7. Analysis of Variance for *T. serpenticola* growth (mm/month) at 6 densities (treatments) and 2 locations ($R^2 = 0.63$)

Source	df	SS	MS	F statistic	p-value
Treatment	5	0.24	0.05	15.56	< 0.01
Location	1	< 0.00	< 0.00	1.17	0.29
Treatment*location	5	< 0.00	< 0.00	0.21	0.96
Error	48	0.15	< 0.01		
Total	59	0.39			

Figure 42. Mean (± 95% CI) *Taylorconcha serpenticola* growth rates (mm/month) at three intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) and at two locations; outlet and springs, during spring (March/April) 2002 at Banbury Springs, Idaho. There was a significant negative linear trend ($t > t^*$) for both locations ($df = 2$, $t = 2.89$ for outlet, $t = 2.71$ for springs, $t^* = 2.01$)

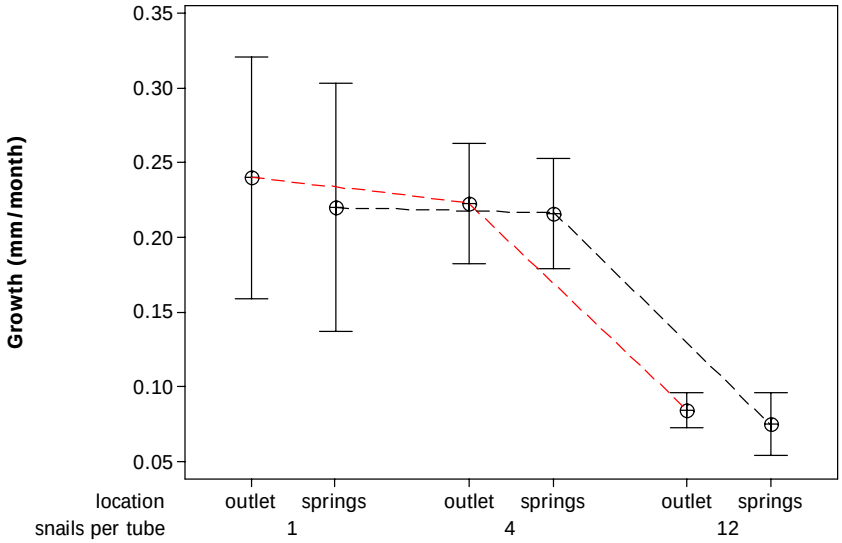


Figure 43. Mean (± 95% CI) *Taylorconcha serpenticola* growth rates (mm/month) at low intraspecific competition (4 *T. serpenticola*/tube) vs. low interspecific competition (2 *T. serpenticola*/tube and 2 *P. antipodarum*/tube) at two locations, outlet and springs at Banbury Springs, Idaho during spring (March/April) 2002. No significant differences in growth [95% CI for $\hat{D}$ = (–0.04, 0.10) and (-0.07, 0.07) for springs and outlet, respectively]

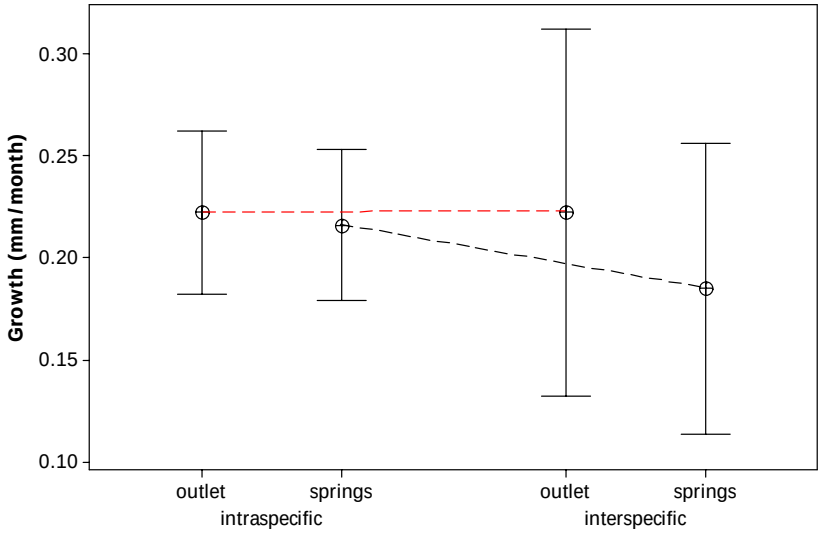
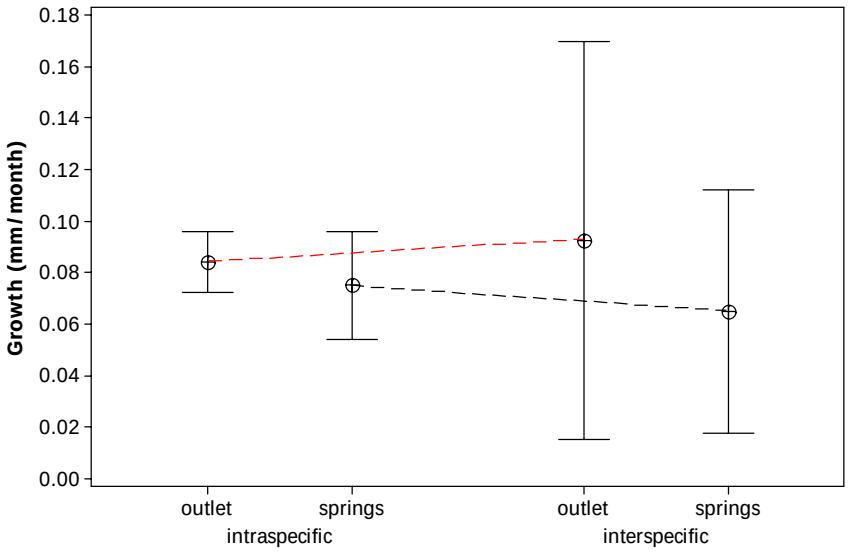


Figure 44. Mean (± 95% CI) *Taylorconcha serpenticola* growth rates (mm/month) at high intraspecific competition (12 *T. serpenticola*/tube) vs. high interspecific competition (6 *T. serpenticola*/tube and 6 *P. antipodarum*/tube) at two locations, outlet and springs at Banbury Springs, Idaho during spring (March/April) 2002. No significant differences in growth [95% CI for $\hat{D}$ = (–0.07, 0.07) and (-0.06, 0.08) for springs and outlet, respectively]



Taylorconcha serpenticola: Summer (June/July) 2002. There were significant treatment and location effects but no interaction effect, and the ANOVA model explained 91.00 % of the variability in growth rates of *T. serpenticola* (Table 8). There was also a significant negative linear trend (t > t*) in growth rates of *T. serpenticola* under intraspecific competition locations (Figure 45). Overall, *T. serpenticola* grew significantly more in the outlet than in the springs. *Taylorconcha serpenticola* grew significantly less under both low and high interspecific competition with *P. antipodarum* at both locations (Figures 46 and 47).

Table 8. Analysis of Variance for *T. serpenticola* growth (mm/month) at 6 densities (treatments) and 2 locations at Banbury Springs, Idaho, Summer (June/July) 2002. (R^2 = 0.91)

	df	SS	MS	F statistic	P-value
Treatment	5	0.37	0.07	90.65	< 0.01
Location	1	0.01	0.01	7.19	0.01
Treatment*location	5	< 0.01	< 0.01	0.74	0.60
Error	48	0.04	< 0.01		
Total	59	0.42			

Figure 45. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at three intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) and at two locations; outlet and springs, during summer (June/July) 2002 at Banbury Springs, Idaho. There was a significant negative linear trend (t > t*) for both locations (df = 2, t =13.97 for outlet, t = 11.17 for springs, t* = 2.01)

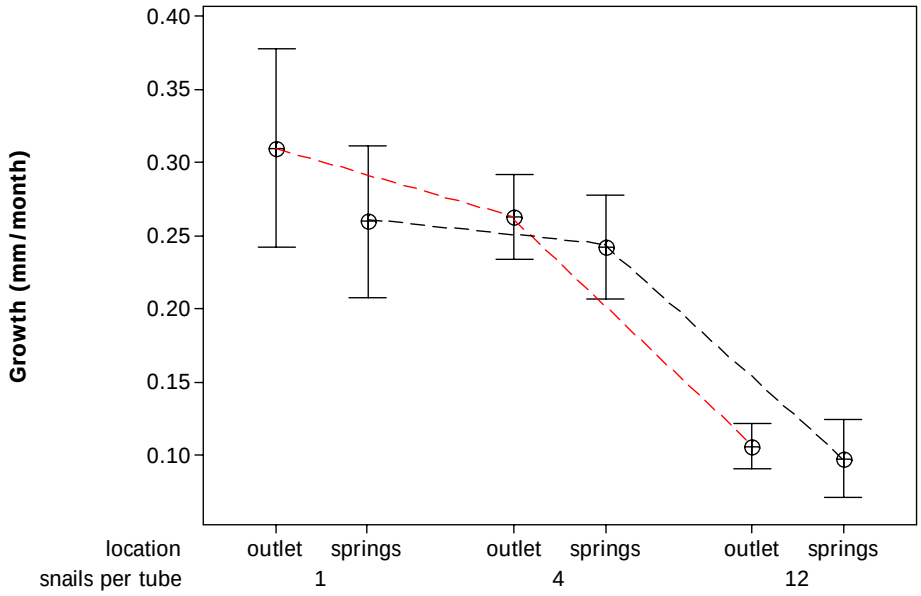


Figure 46. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at low intraspecific competition (4 *T. serpenticola*/tube) vs. low interspecific competition (2 *T. serpenticola*/tube and 2 *P. antipodarum*/tube) at two locations, outlet and springs at Banbury Springs, Idaho during summer (June/July) 2002. Significant differences in growth at both locations [95% CI for $\hat{D}$ = (0.06, 0.10) and (0.07, 0.11) for springs and outlet, respectively]

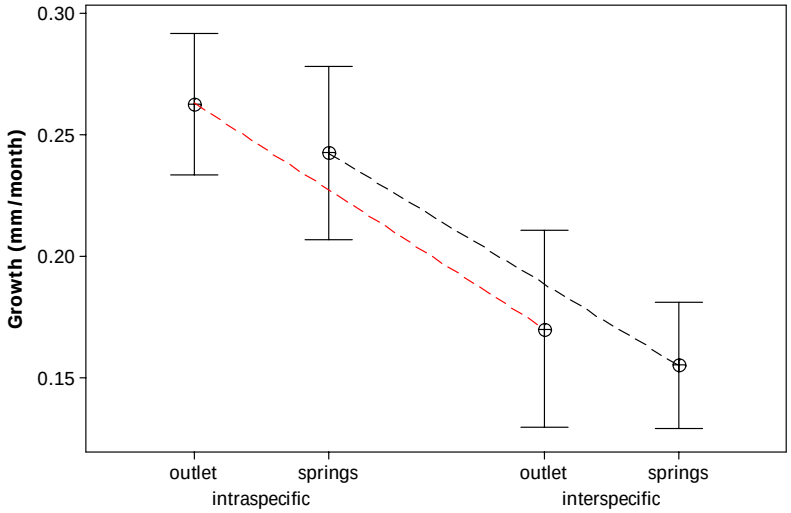
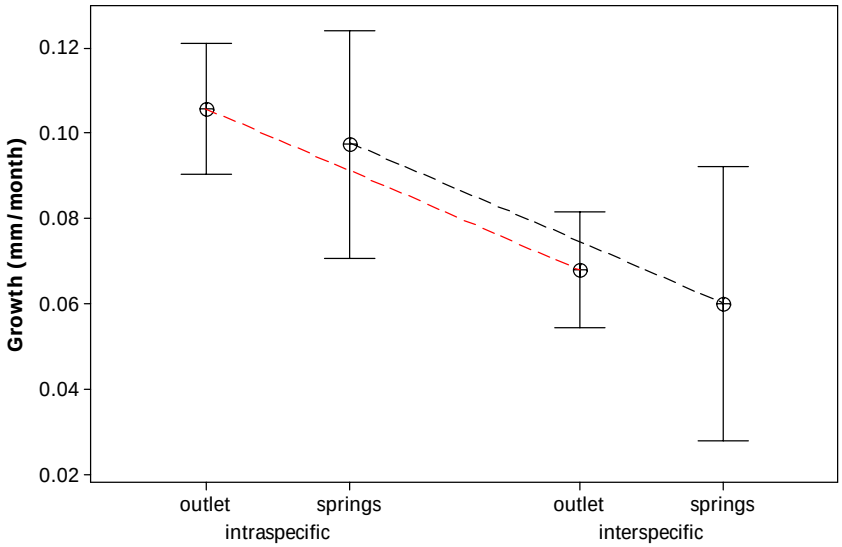


Figure 47. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at high intraspecific competition (12 *T. serpenticola*/tube) vs. high interspecific competition (6 *T. serpenticola*/tube and 6 *P. antipodarum*/tube) at two locations, outlet and springs at Banbury Springs, Idaho during summer (June/July) 2002. Significant differences in growth at both locations [95% CI for $\hat{D}$ = (0.02, 0.06) and (0.02, 0.06) for springs and outlet, respectively]



Taylorconcha serpenticola: Autumn (September/October) 2002. There was a significant treatment effect but no location or interaction effect and the ANOVA model explained 62.24% of the variability in *T. serpenticola* growth (Table 9). There was also a significant negative linear trend ($t > t^*$) at both locations. *Taylorconcha serpenticola* grew less under both low and high interspecific competition with *P. antipodarum* at both locations, although at high densities this difference was not significant (Figures 48, 49, and 50).

Table 9. Analysis of Variance for *T. serpenticola* growth (mm/month) at 6 densities (treatments) and 2 locations ($R^2 = 0.62$) during autumn (September/October) 2002

	DF	SS	MS	F statistic	P-value
Treatment	5	0.41	0.08	15.66	< 0.01
Location	1	< 0.01	< 0.01	0.08	0.77
Interaction	5	< 0.01	< 0.01	0.14	0.98
Error	48	0.25	0.01		
Total	59	0.66			

Figure 48. Mean (95% CI) *T. serpenticola* growth rates ($\lambda = 0.3$ transformed; mm/month) at three intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) and at two locations; outlet and springs, during autumn (September/October) 2002-2003 at Banbury Springs, Idaho. There was a significant negative linear trend ($t > t^*$) at both locations ($df = 2$, $t = 2.25$ for outlet, $t = 2.21$ for springs, $t^* = 2.01$)

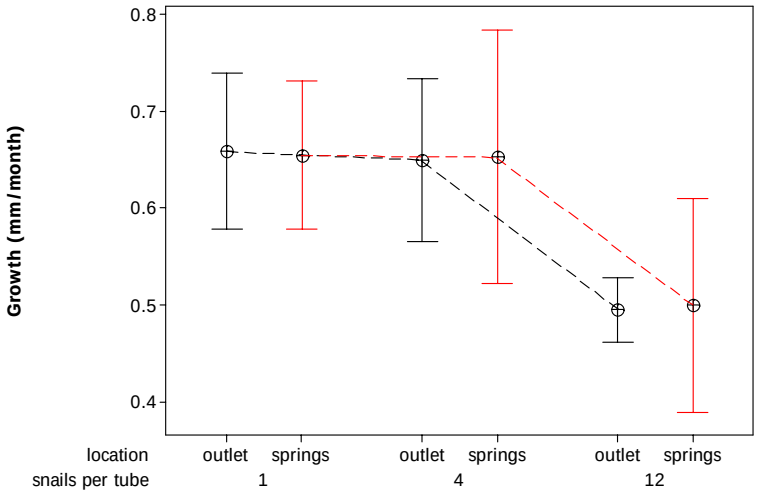


Figure 49. Mean (95% CI) *T. serpenticola* growth rates (λ = 0.3 transformed; mm/month) at low intraspecific competition (4 *T. serpenticola*/tube: 0 *P. antipodarum*/tube) vs. low interspecific competition (2 *T. serpenticola*/tube and 2 *P. antipodarum*/tube) at two locations at Banbury Springs, Idaho, during autumn (September/October) 2002. No significant differences in growth at either location

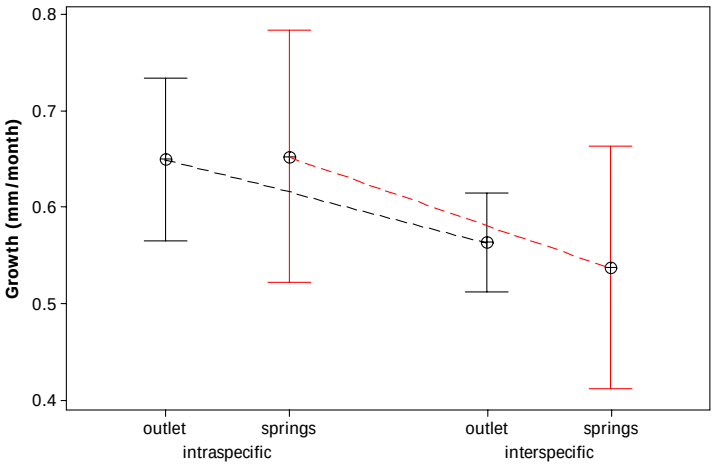
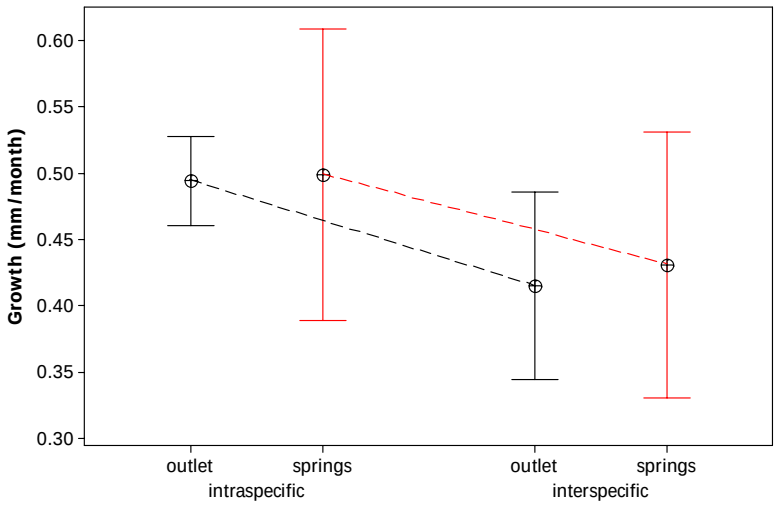


Figure 50. Mean (95% CI) *T. serpenticola* growth rates (λ = 0.3 transformed; mm/month) at high intraspecific competition (12 *T. serpenticola* / 0 *P. antipodarum* per tube) vs. high interspecific competition (6 *T. serpenticola* / 6 *P. antipodarum* per tube) at two locations, outlet and springs at Banbury Springs, Idaho, autumn (September/October) 2002. No significant differences in growth at either location (95% CI for $\hat{D}$ not applicable for springs and outlet, respectively)



Taylorconcha serpenticola: Winter (December/January) 2002-2003. There were significant treatment and interaction effects, a marginal location effect and the ANOVA model explained 69.76% of the variability in growth rates of *T. serpenticola* (Table 10). There was also a significant negative linear trend ($t > t^*$) in growth rates under intraspecific competition at both locations (Figure 51). There were no significant differences in growth at low interspecific competition (Figure 52) or high interspecific competition (Figure 53).

Table 10. Analysis of Variance for *T. serpenticola* growth (mm/month) at 6 densities (treatments) and 2 locations ($R^2 = 0.70$) during winter (December/January) 2002-2003

	df	SS	MS	F statistic	p-value
Treatment	4	0.03	0.01	19.37	< 0.00
Location	1	< 0.00	< 0.00	2.84	0.10
Treatment*location	4	< 0.00	< 0.00	2.99	0.03
Error	40	0.02	< 0.00		
Total	49	0.05			

Figure 51. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at three intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) and at two locations; outlet and springs, during winter (December/January) 2002-2003 at Banbury Springs, Idaho. There was a significant negative linear trend ($t > t^*$) for both locations ($df = 2$, $t = 2.25$ for outlet, $t = 3.01$ for springs, $t^* = 2.02$)

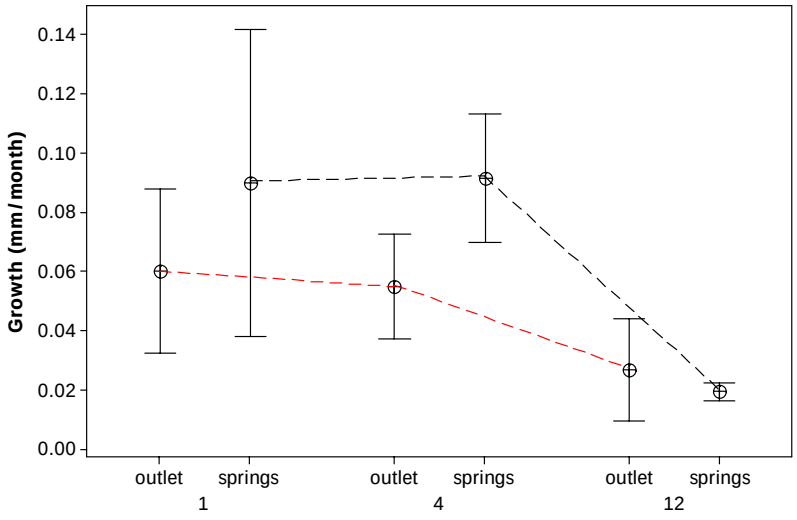


Figure 52. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at low intraspecific competition (4 *T. serpenticola*/tube) vs. low interspecific competition (2 *T. serpenticola*/tube and 2 *P. antipodarum*/tube) at two locations at Banbury Springs, Idaho during winter (December/January) 2002-2003. No significant differences in growth at either location (95% CI for $\hat{D}$ = –0.01, 0.04 and -0.02, 0.04, for springs and outlet, respectively)

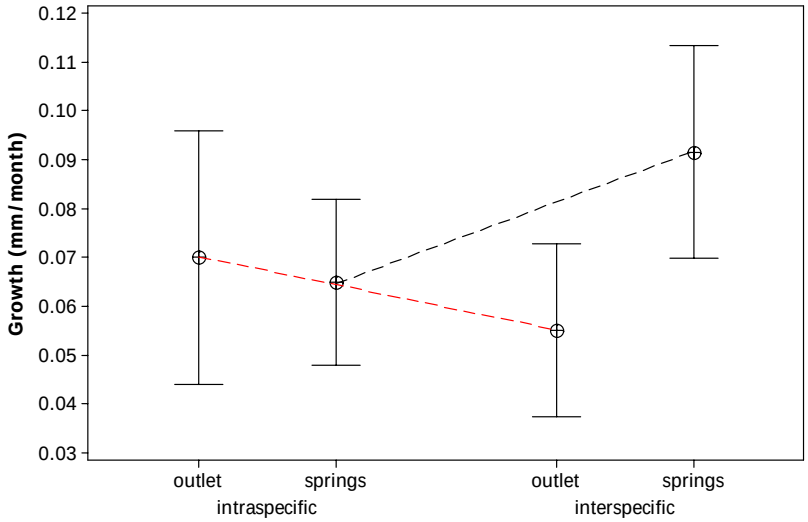
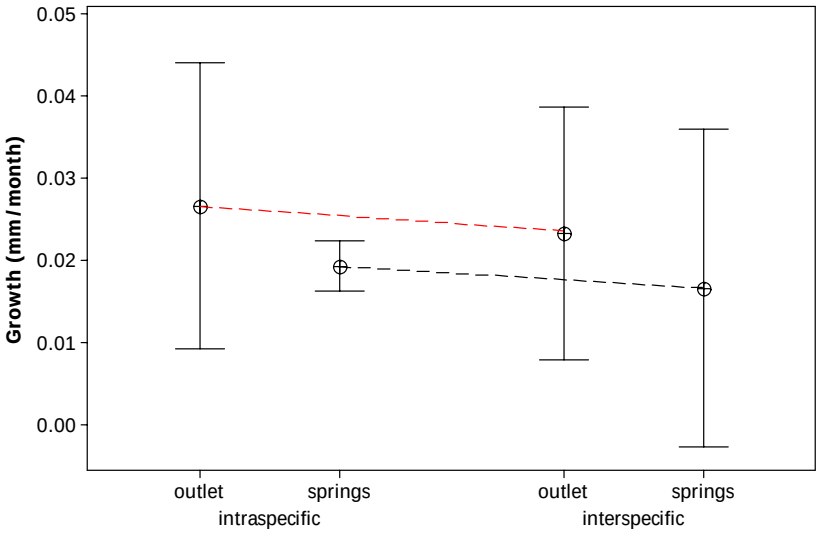


Figure 53. Mean (95% CI) *T. serpenticola* growth rates (mm/month) at high intraspecific competition (12 *T. serpenticola* / 0 *P. antipodarum* per tube) vs. high interspecific competition (6 *T. serpenticola* / 6 *P. antipodarum* per tube) at two locations, outlet and springs at Banbury Springs, Idaho during winter (December/January) 2002-2003. No significant differences in growth at either location (95% CI for $\hat{D}$ = -0.02, 0.04 and -0.02, 0.04, for springs and outlet, respectively)



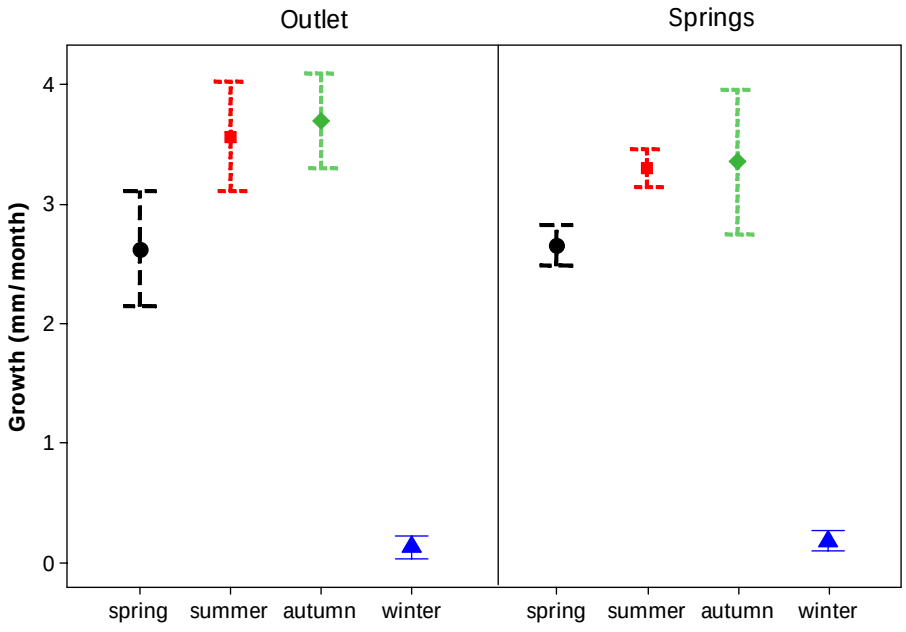
Potamopyrgus antipodarum growth with no inter or intraspecific competition.

There was a significant seasonal effect but no location or interaction affects on *P. antipodarum* growth rates without competition (Treatment 4)(Table 3) with growth rates significantly lowest during winter and highest in summer and autumn, at both locations (Figure 54). The ANOVA model explained 96.53% of the variability in growth rates of *P. antipodarum* (Table 11).

Table 11. ANOVA for *P. antipodarum* growth (mm/month) with no intra or interspecific competition at four seasons and two locations

Source	df	SS	MS	F statistic	p-value
Location	1	0.18	0.18	2.09	0.16
Season	3	74.41	24.80	294.96	< 0.01
Location*season	3	0.30	0.10	1.21	0.32
Error	32	2.69	0.08		
Total	39	77.58			

Figure 54. Mean (± 95% CI) growth rates of *P. antipodarum* at four seasons and two locations.



Potamopyrgus antipodarum: Spring (March/April) 2002. There was a significant treatment effect, but no location or interaction effect. The ANOVA model explained 84.45 % of the variability in growth rates of *P. antipodarum* (Table 12). There was a significant negative linear trend (t > t*) in growth rates of *T. serpenticola* under intraspecific competition locations (Figure 55). There was no significant difference in mean growth rate of *P. antipodarum* at low interspecific competition at either location (Fig. 56) but *P. antipodarum* growth rates were significantly greater at high interspecific competition than high intraspecific competition in both locations (Fig. 57).

Table 12. Analysis of Variance for growth ($R^2 = 0.84$)

	df	SS	MS	F statistic	p-value
Treatment	5	13.59	2.72	49.74	0.00
Location	1	0.02	0.02	0.39	0.54
Treatment*location	5	0.34	0.07	1.23	0.31
Error	43	2.35	0.05		
Total					

Figure 55. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at three intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) and at two locations during Spring (March/April) 2002 at Banbury Springs, Idaho. There was a significant negative linear trend (t > t*) for both locations (df = 2, t =6.58 for outlet, t = 7.35 for springs, t* = 2.01)

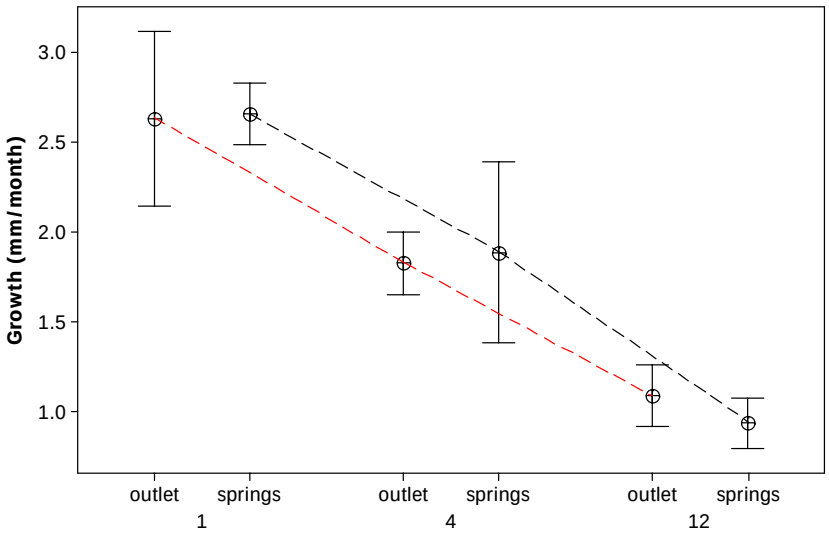


Figure 56. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at low intraspecific competition (4 *P. antipodarum*/tube and 0 T. *serpenticola*) vs. low interspecific competition (2 *T. serpenticola*/tube and 2 *P. antipodarum*/tube) at two locations at Banbury Springs, Idaho. No significant differences in growth at either location (95% CI for $\hat{D}$ = -0.31, 0.35 and –0.25, 0.41 for springs and outlet, respectively)

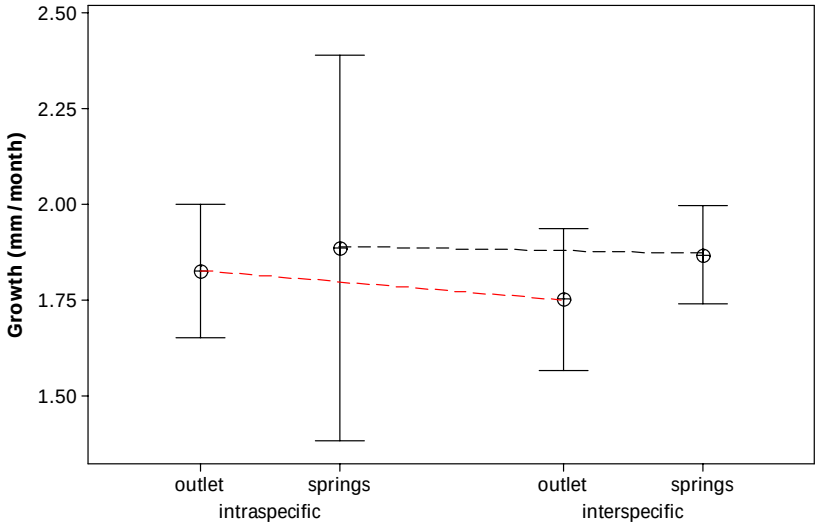
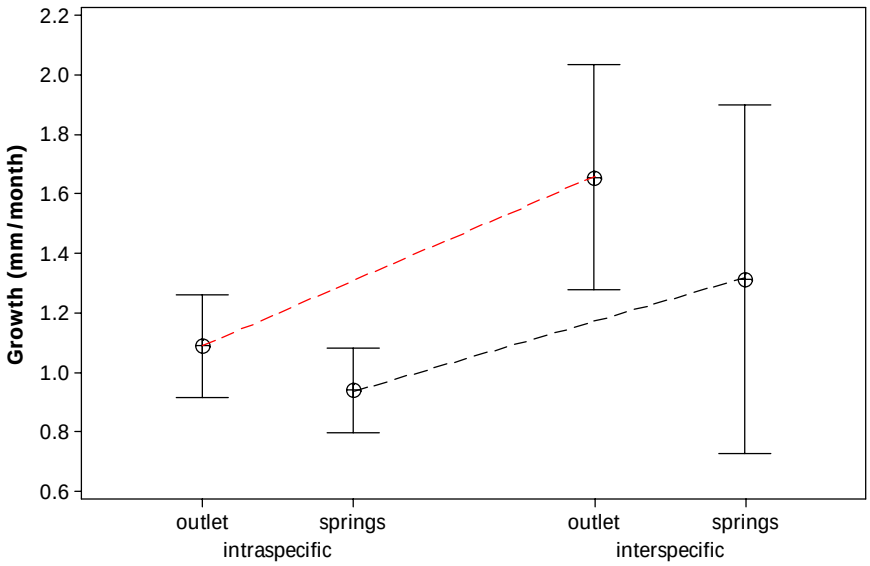


Figure 57. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at high intraspecific competition (12 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. high interspecific competition (6 *P. antipodarum* and 6 *T. serpenticola* per tube) at two locations, outlet and springs at Banbury Springs, Idaho, during summer (June/July) 2002. Significant differences in growth at both locations (95% CI for $\hat{D}$ = 0.40, 0.71 and 0.24, 0.90 for springs and outlet, respectively)



Potamopyrgus antipodarum: Summer 2002. There was a significant treatment and location effect, no interaction effect. The ANOVA model explained 91.16 % of the variability in growth rates of *P. antipodarum* (Table 13). There was a significant negative linear trend ($t > t^*$) in growth rates under intraspecific competition in both locations (Fig. 58). Overall, *P. antipodarum* grew significantly more in the outlet than in the springs. There was no significant difference in mean growth rates for *P. antipodarum* at low interspecific competition at either location (Fig. 59) or at high interspecific competition in the outlet but mean growth rates were significantly less at high intraspecific densities compared with high interspecific densities in the springs (Fig. 60).

Table 13. ANOVA for *P. antipodarum* growth (mm/month) at 6 densities (treatments) and 2 locations at Banbury Springs, Idaho, Summer 2002. ($R^2 = 0.91$)

	df	SS	MS	F statistic	p-value
Treatment	5	27.30	5.46	92.06	< 0.00
Location	1	1.84	1.84	31.01	< 0.00
Treatment*location	5	0.20	0.04	0.69	0.64
Error	48	2.85	0.06		
Total	59	32.19			

Figure 58. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at three intraspecific densities; no (1 snail/tube), low (4 snails/tube) and high competition (12 snails/tube) and at outlet and springs. Summer 2002 at Banbury Springs, Idaho. (Linear contrast: df = 2, t = 15.60 for outlet, t = 8.99 for springs, t* = 2.01)

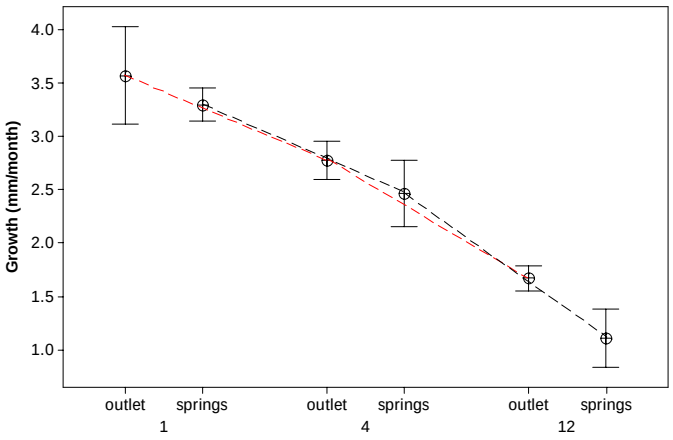


Figure 59. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at low intraspecific competition (4 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. low interspecific competition (2 *T. serpenticola* and 2 *P. antipodarum* per tube) at two locations at Banbury Springs, Idaho, during summer (June/July) 2002. No significant differences in growth at either location (95% CI for $\hat{D}$ = -0.25, 0.37 and -0.03, 0.07 for springs and outlet, respectively)

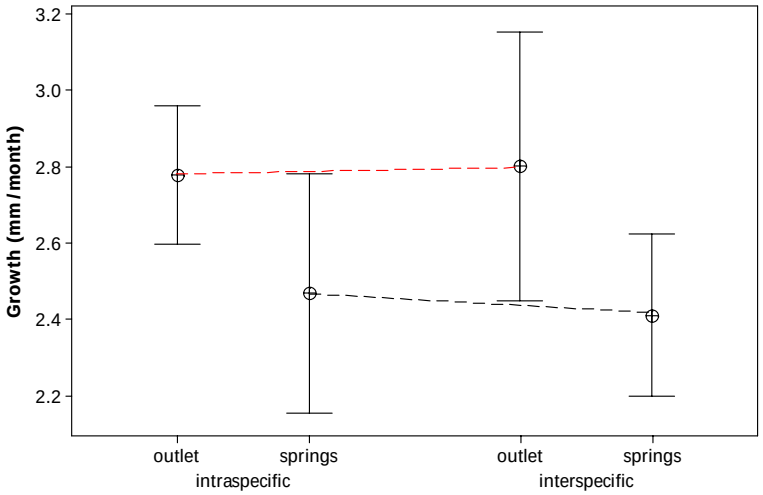
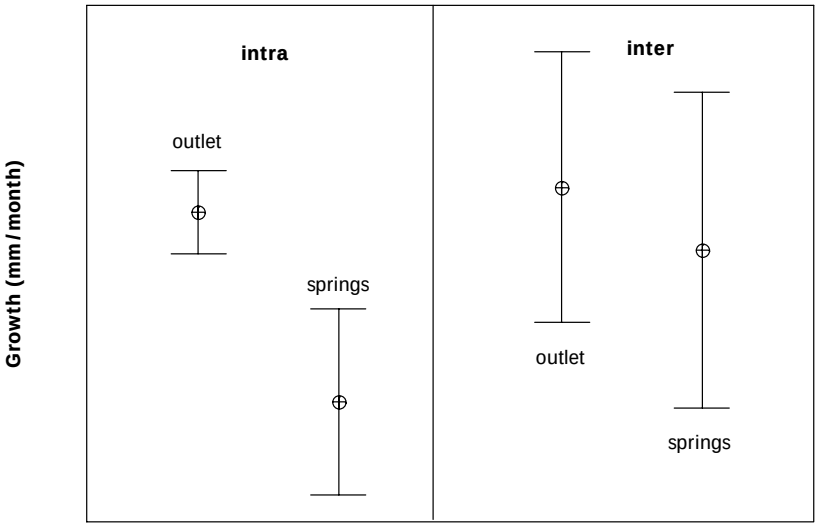


Figure 60. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at high intraspecific competition (12 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. high interspecific competition (6 *T. serpenticola* and 6 *P. antipodarum* per tube) at two locations at Banbury Springs, Idaho, during summer (June/July) 2002. *P. antipodarum* growth rates were significantly less at high intraspecific densities compared with high interspecific densities (95% CI for $\hat{D}$ = 0.14, 0.76) in the springs but not in the outlet (95% CI for $\hat{D}$ = -0.26, 0.36)



Potamopyrgus antipodarum: Autumn (September/October) 2002. There were significant treatment and location effects but no interaction effect and the ANOVA model explained 83.34% of the variability in growth rates of *P. antipodarum* (Table 14). There was also a significant negative linear trend ($t > t^*$) in growth rates of *P. antipodarum* under intraspecific competition at both locations (Figure 61) and it grew significantly more at high interspecific competition than at high intraspecific competition (Figure 63).

Table 14. Analysis of Variance for *P. antipodarum* growth (mm/month) at 6 densities (treatments) and 2 locations at Banbury Springs, Idaho, Summer (June/July) 2002. (R^2 = 0.83)

Source	df	SS	MS	F statistic	p-value
Location	5	35.37	7.07	56.40	< 0.01
Season	1	2.75	2.75	21.94	< 0.01
Location*season	5	0.61	0.12	0.97	0.45
Error	48	6.02	0.13		
Total	59	44.75			

Figure 61. Mean (95% CI) intraspecific *P. antipodarum* growth rates (mm/month); no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube) at two locations; outlet and springs, during autumn (September/October) 2002 at Banbury Springs, Idaho. There was a significant negative linear trend ($t > t^*$) for both locations (df = 2, t = 5.11 for outlet, t = 6.24 for springs, t^* = 2.01)

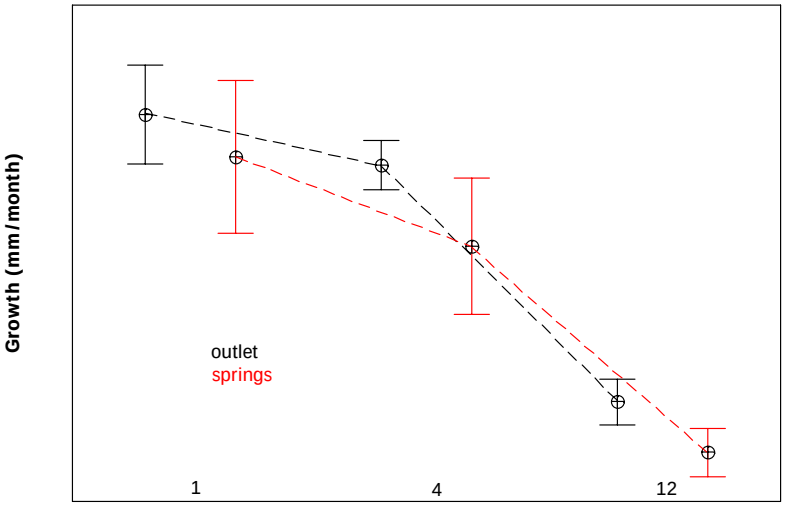


Figure 62. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at low intraspecific competition (4 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. low interspecific competition (2 *T. serpenticola* and 2 *P. antipodarum* per tube) at two locations at Banbury Springs, Idaho during autumn (September/October) 2002. No significant differences in growth at either location (95% CI for $\hat{D}$ = -0.11, 1.05 and 0.01, 0.75 for springs and outlet, respectively)

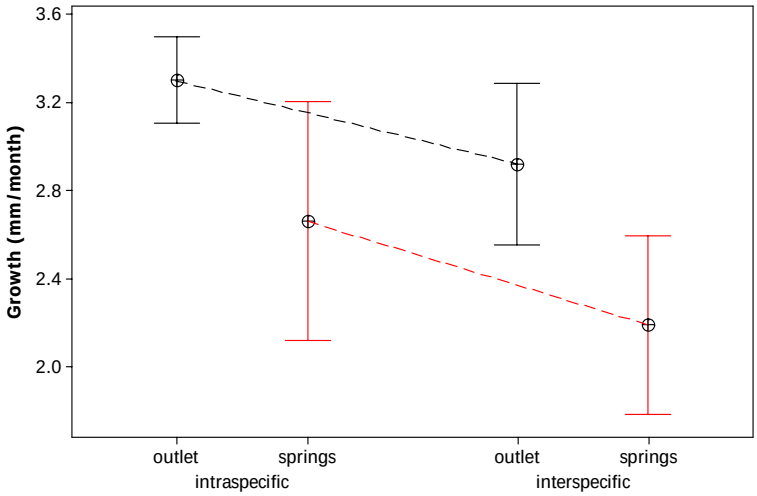
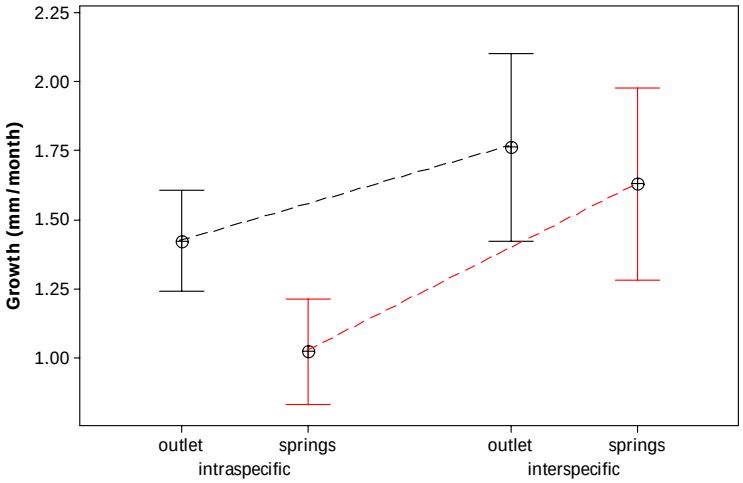


Figure 63. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at high intraspecific competition (12 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. high interspecific competition (6 *T. serpenticola* and 6 *P. antipodarum* per tube) at two locations at Banbury Springs, Idaho, during autumn (September/October) 2002. *Potamopyrgus antipodarum* growth rates were significantly less at high intraspecific densities compared with high interspecific densities (95% CI for $\hat{D}$ = na) in the springs but not in the outlet (95% CI for $\hat{D}$ = na)



Potamopyrgus antipodarum: Winter (December/January) 2002-2003. There was a significant treatment but no location or interaction effect, and the ANOVA model explained 73.19 % of the variability in growth rates of *P. antipodarum* (Table 15). There was also a significant negative linear trend ($t > t^*$) in growth rates of *P. antipodarum* under intraspecific competition in both locations (Figure 64). There was no significant difference in mean growth rates for *P. antipodarum* at low interspecific competition at either location (Figure 65) or at high interspecific competition at either location (Figure 66).

Table 15. Analysis of Variance for *P. antipodarum* growth (mm/month) at 6 densities (treatments) and 2 locations at Banbury Springs, Idaho, winter (December/January) 2002-2003. ($R^2 = 0.73$)

	df	SS	MS	F statistic	p-value
Treatment	4	17.91	4.48	25.44	0.00
Location	1	0.06	0.06	0.33	0.57
Treatment*location	4	1.25	0.31	1.78	0.15
Error	40	7.04	0.18		
Total	49	26.26			

Figure 64. Mean (95% CI) *P. antipodarum* growth rates (mm/month), intraspecific densities; no competition (1 snail/tube), low competition (4 snails/tube) and high competition (12 snails/tube), two locations; outlet and springs, winter 2002-2003, Banbury Springs, Idaho. There was a significant negative linear trend ($t > t^*$) for both locations ($df = 2$, $t = 2.87$ for outlet, $t = 3.85$ for springs, $t^* = 2.01$)

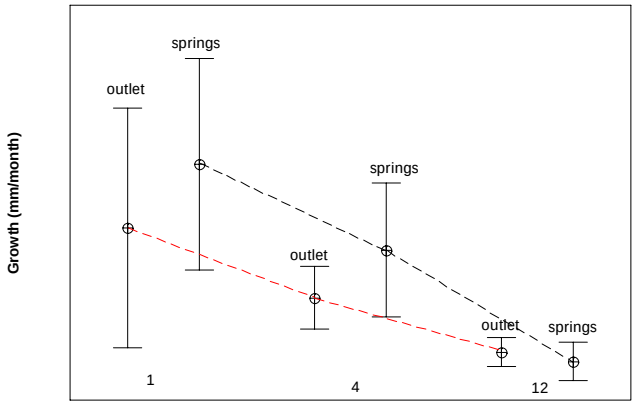


Figure 65. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at low intraspecific competition (4 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. low interspecific competition (2 *T. serpenticola* and 2 *P. antipodarum* per tube) at two locations at Banbury Springs, Idaho, during winter (December/January) 2002-2003. No significant differences in growth at either location (95% CI for $\hat{D}$ = -0.03, 0.07 and -0.03, 0.07 for springs and outlet, respectively)

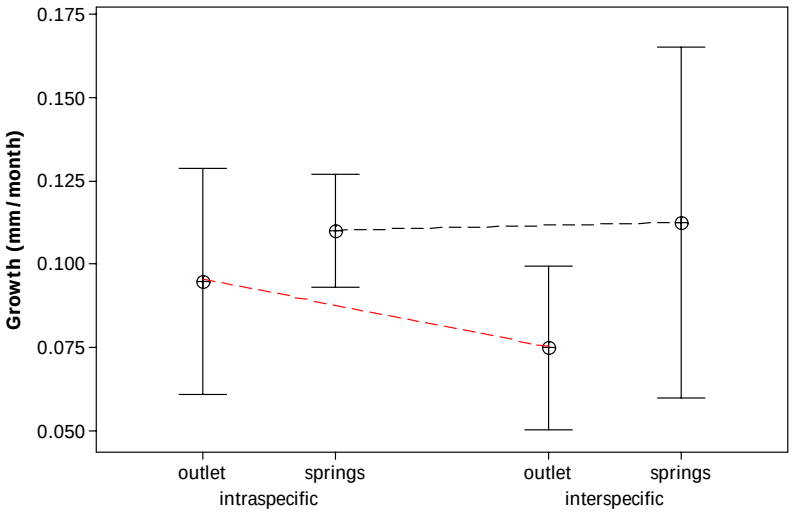
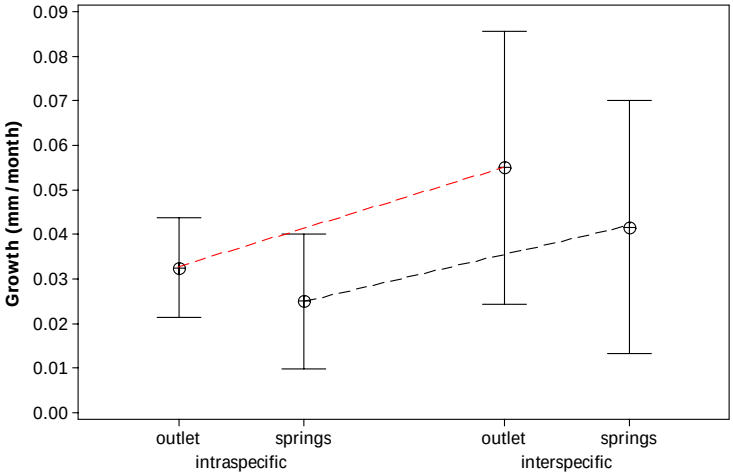


Figure 66. Mean (95% CI) *P. antipodarum* growth rates (mm/month) at high intraspecific competition (12 *P. antipodarum* and 0 *T. serpenticola* per tube) vs. high interspecific competition (6 *T. serpenticola* and 6 *P. antipodarum* per tube) at two locations, outlet and springs at Banbury Springs, Idaho, during winter (December/January) 2002-2003. Significant differences in growth at both locations (95% CI for $\hat{D}$ = -0.04, 0.06 and -0.02, 0.04 for springs and outlet, respectively)



Competition Coefficients and Growth Efficiencies

Although competition coefficient results were highly variable, *P. antipodarum* had about the same effect on the growth rate of one *T. serpenticola,* as did ≈1.50 *T. serpenticola* (Table 16). Conversely, *T. serpenticola* had about the same effect on the growth rate of one *P. antipodarum*, as did about 0.86 *P. antipodarum* (Table 17). Thus, under the experimental conditions, interspecific competition was asymmetrical and almost always favored *P. antipodarum*. In autumn, *P. antipodarum* had the largest mean effect (mean α_{ij} = 1.98) on *T. serpenticola* and in winter it had the lowest mean effect (mean α_{ij} = 1.12) on *T. serpenticola* (Table 16).

Figure 67 is a simple Lotka-Volterra competition model based on grand mean competition coefficient values in Tables 16 and 17. If competition for limited food resources is the only limiting factor and mechanism regulating both snails' populations, then this model suggests that *P. antipodarum* will exclude *T. serpenticola*. There is only one equilibrium point at which *P. antipodarum* will reach K_1, its carrying capacity and *T. serpenticola* declines to extinction.

Table 16. Means (95% CI's) of competition coefficient $\boldsymbol{\alpha_{ij}}$ (effect of *P. antipodarum* on *T. serpenticola*) at two density treatments low (4 snails/tube) and high (12 snails/tube); two locations, springs and outlet; and four seasons at Banbury Springs

	Springs		Outlet		
	Low	High	Low	High	Overall
Spring	1.27	1.38	1.12	1.46	1.31
	(0.96, 1.64)	(0.97, 1.81)	(0.78, 1.47)	(0.67, 2.50)	(1.19, 1.44)
Summer	1.59	1.64	1.84	1.60	1.67
	(1.39, 1.85)	(0.98, 2.83)	(1.62, 2.06)	(1.33, 1.91)	(1.60, 1.78)
Autumn	2.11	2.00	1.76	2.06	1.98
	(1.37, 1.85)	(1.07, 3.13)	(1.13, 2.38)	(1.28, 2.90)	(1.84, 2.09)
Winter	1.40	1.16	0.79	1.15	1.12
	(1.04, 1.90)	(0.62, 4.23)	(0.53, 1.23)	(0.53, 2.95)	(0.88, 1.34)

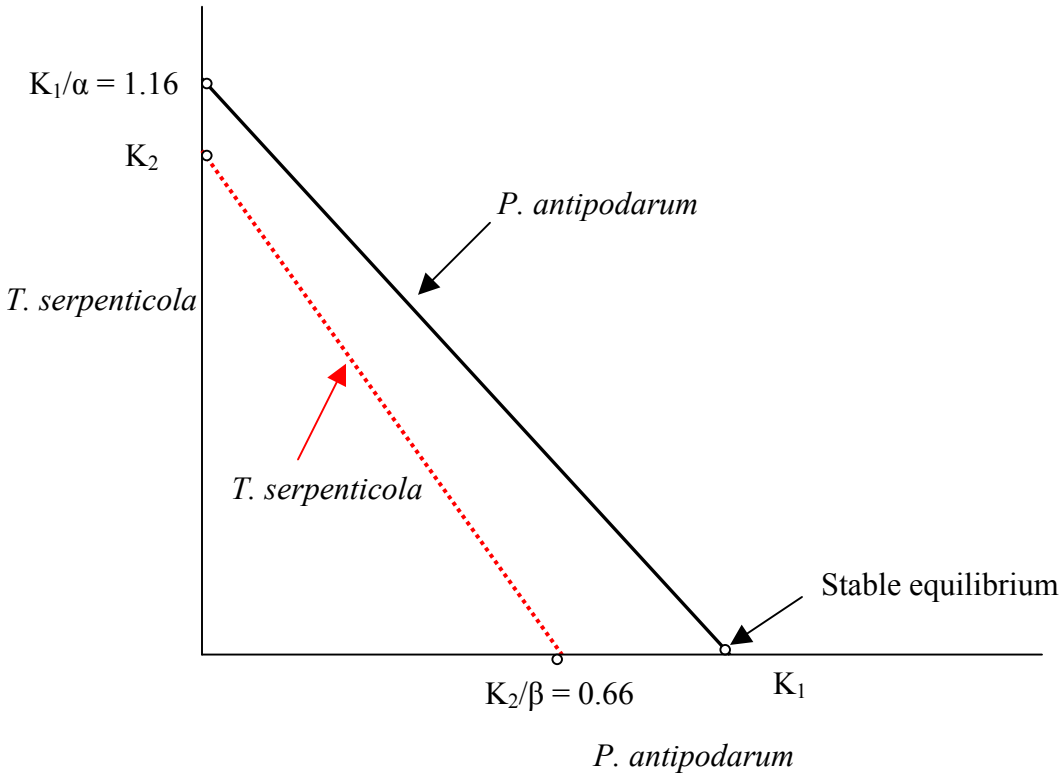
Grand mean (95% CI's) = 1.52 (1.22, 1.83)

Table 17. Means (95% CI's) of competition coefficient α_{ji} (effect of *T. serpenticola* on *P. antipodarum*) at two density treatments low (4 snails/tube) and high (12 snails/tube); two locations, springs and outlet; and four seasons at Banbury Springs

	Springs		Outlet		
	low	high	low	high	overall
Spring	1.01	0.72	1.05	0.66	0.86
	(0.91, 1.12)	(0.60, 0.87)	(0.97, 1.13)	(0.57, 0.75)	(0.76, 0.96)
Summer	1.03	0.71	0.99	0.97	0.93
	(0.95, 1.17)	(0.58, 0.87)	(0.93, 1.07)	(0.77, 1.08)	(0.85, 0.99)
Autumn	1.21	0.63	1.13	0.81	0.94
	(1.06, 1.39)	(0.55, 0.72)	(1.06, 1.21)	(0.72, 0.90)	(0.68, 1.15)
Winter	0.82	0.75	0.80	0.50	0.72
	(0.58, 1.10)	(0.40, 1.33)	(0.64, 1.00)	(0.28, 0.80)	(0.64, 0.79)

Grand mean = 0.86 (0.76, 0.93)

Figure 67. Competitive exclusion of *T. serpenticola* by *P. antipodarum* based on competition coefficients developed in this experiment. K_1 and K_2 are standardized carrying capacities of *P. antipodarum* and *T. serpenticola*, respectively. $K_1/\alpha = 1.00/0.86$ (mean α_{ji} from Table 20) = 1.16; $K_2/\beta = 1.00/ 1.52$ (mean α_{ij} from Table 19) = 0.66



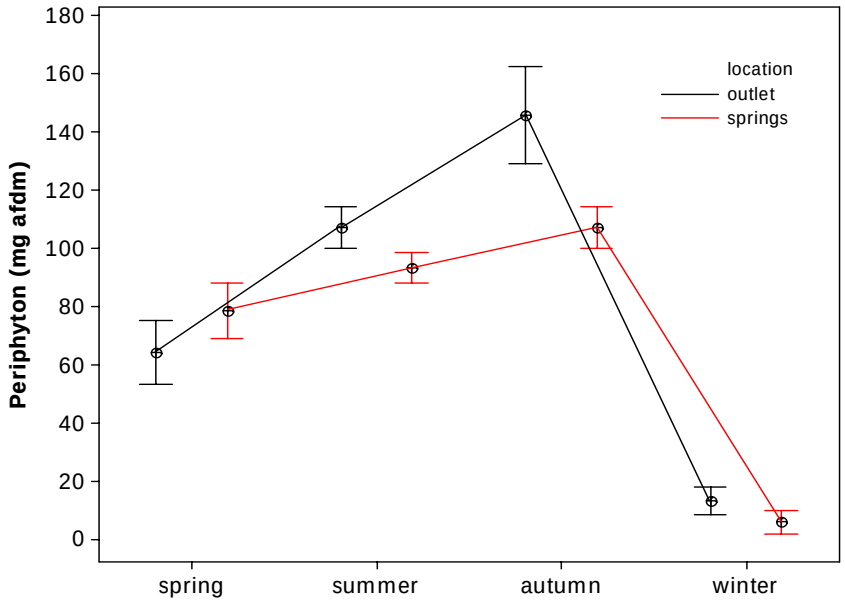
Periphyton Biomass, Diversity, and Richness

There were significant differences in periphyton biomass (AFDM) between locations (outlet vs springs), seasons, and their interaction in ungrazed tubes at the start of the experiments (Table 18). Periphyton biomass increased significantly from spring to autumn and decreased significantly in winter. Periphyton biomass was also significantly greater in the outlet than in the springs during summer and autumn (Figure 68).

Table 18. Two-way ANOVA: AFDM versus location, season ($R^2 = 0.98$)

	DF	SS	MS	F	P
Location	1	1311.1	1311.1	24.57	< 0.00
Season	3	75891.2	25297.1	474.1	< 0.00
Interaction	3	3582.2	1194.1	22.38	< 0.00
Error	32	1707.5	53.4		
Total	39	82492.0			

Figure 68. Mean (± 95% CI) periphyton ash free dry mass (AFDM)(mg) at start of experiments at four seasons and two locations (N = 5 for each season and location)(If 95% CI's overlaped then they weren't considered significantly different)



Periphyton taxa richness and frequency in tubes at the start of experiments in spring (N = 5 combined) and autumn (N = 5 combined) were somewhat similar, both in the springs and outlet (Table 19 and Figure 69). Tubes were mostly dominated by early successional diatoms *Achnanthes* sp. and *Cocconeis* sp., as well as *Navicula* sp. (Figure 69). There was no moss (Bryophyta) in the tubes at either season or location.

Periphyton taxa richness and frequency on the cobbles at the start of experiments in spring (N = 5 combined) and autumn (N = 5 combined) also were dominated by *Achnanthes* sp. and *Cocconeis* sp. but also had high frequencies of late successional diatom species *Gomphonema* sp. and *Rhoicosphenia* sp. (Figure 69). Cobbles in spring had high frequencies of the diatom *Tabellaria* sp. in the outlet but not in springs, where as cobbles in autumn had high frequencies of the green alga, *Oocystis* sp. particularly in the outlet (Figure 69). The mosses *Fontinalis* sp. and *Leptodictyum* sp. comprised ≈90-95% of the plant biovolume on cobbles in spring and autumn in the springs and ≈ 5 – 15% plant biovolume on cobbles in spring and autumn at the outlet.

Three of the four periphyton diversity and evenness indices comparing both tubes and cobble values between spring and autumn values were significantly different (Table 19), indicating that there were more species but less evenness in autumn than in spring. Noticeable differences in the periphyton communities included: dominance of *Cocconeis* sp. in tubes in the springs during autumn, dominance of *Tabellaria* sp. (diatom) on cobbles at the outlet in spring, and the appearance of the blue-green alga *Oocystis* sp. on cobbles in autumn, particularly at the outlet (Figure 69).

Table 19. Diversity and evenness indices of periphyton taxa in tubes and cobbles.

	Spring[1]				Autumn[1]			
	Springs		Outlet		Springs		Outlet	
	Tubes	Cobbles	Tubes	Cobbles	Tubes	Cobbles	Tubes	Cobbles
S[2]	9	7	8	8	9	12	11	13
E[3]	0.77	0.86	0.79	0.73	0.50	0.66	0.55	0.64
H[4]	1.68	1.67	1.65	1.52	1.10	1.63	1.31	1.65
D[5]	0.76	0.78	0.77	0.71	0.49	0.64	0.55	0.70

[1]Spring sample (tubes and cobbles) diversity indices were significantly different from autumn sample diversity indices using Wilcoxon rank-sum test for S (N = 4, p = 0.04), E (N = 4, p = 0.03) and D (N = 4, p = 0.03), but not H (N = 4, p = 0.15)

[2]Richness: S = number of taxa

[3]Pielou's evenness index: J = H/ln(S)

[4]Shannon-Wiener index: $H = 1 - \sum_{i}^{s} p_i^2 - \sum_{i}^{s} p_i \ln (p_i)$

[5]Simpson's diversity index: $D = 1 - \sum_{i}^{s} p_i^2$,

where p = percent individuals of each taxa

Relative Growth Efficiencies of *Taylorconcha* and *Potamopyrgus*

Potamopyrgus antipodarum was from 3-6 times more efficient at converting periphyton into biomass than was *T. serpenticola* in spring, summer, and autumn in both habitats, but was less efficient than *T. serpenticola* in winter. *Taylorconcha serpenticola*'s growth efficiency did not vary much between seasons or locations (Figures 70 and 71). Both species grew significantly less in winter than in the other season.

At the outlet, in spring, summer, and autumn, *P. antipodarum* required significantly less periphyton for growth than did *T. serpenticola* but in winter there was no significant difference. *Potamopyrgus antipodarum* also required significantly more periphyton for growth in winter than at the other 3 seasons and significantly more periphyton in autumn than in spring, at the outlet.

Figure 69. Five dominant and 'other' periphyton genera in tubes (N = 5 combined) and on cobbles (N = 5 combined) for spring and autumn at the springs and outlet sites. *Values in 'other' category are the number of remaining genera, including dead Bacillariophyta cells that weren't the five most dominant. All dominant genera were Bacillarioiphyta (diatoms) except for *Oocystis* sp., which is a Chlorophyta (green algae)

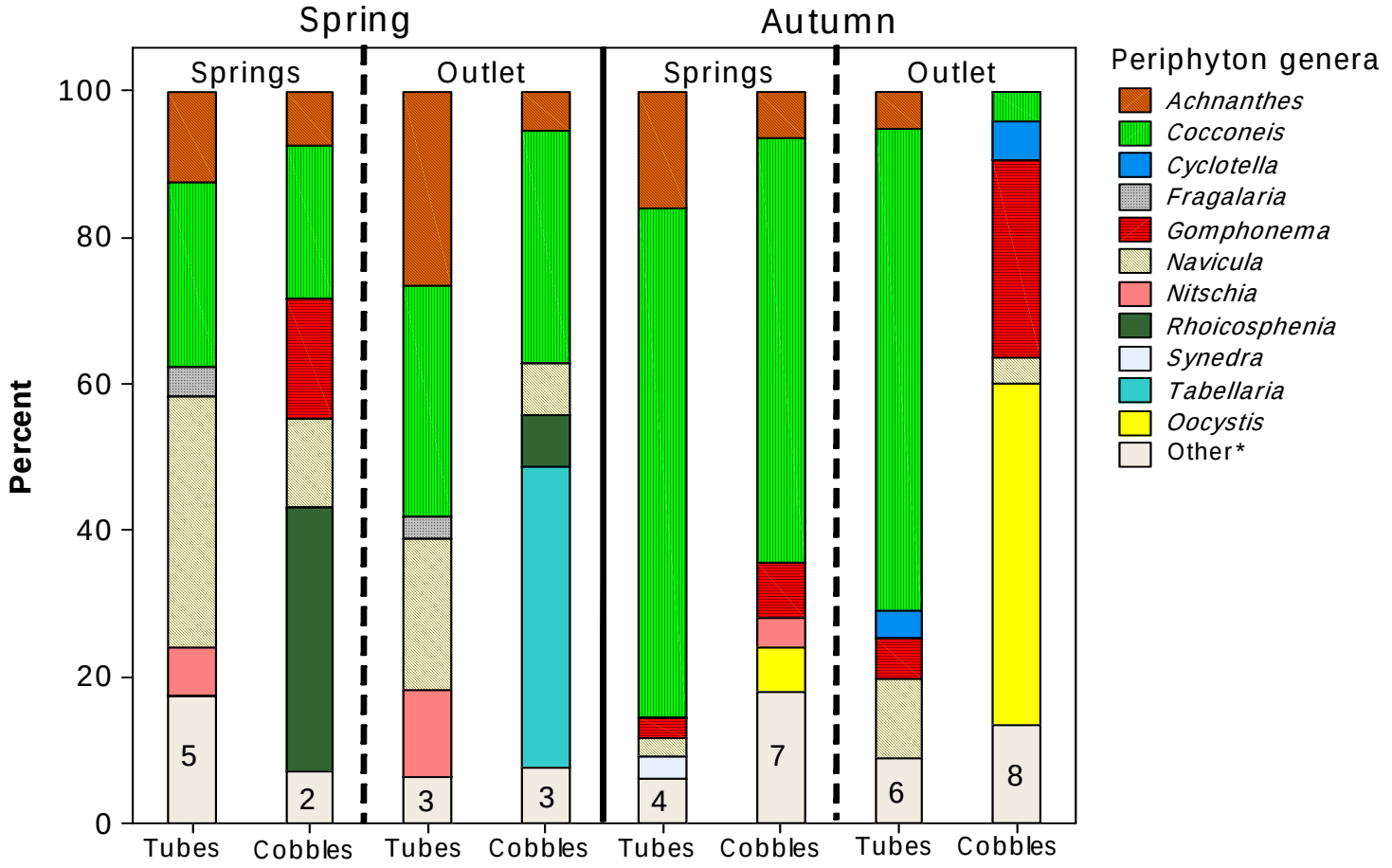


Figure 70. Mean (95% CI) growth efficiency [mg periphyton (AFDM)/ 1 mg increase in biomass (wet weight)/month] of *T. serpenticola* and *P. antipodarum* at four seasons, 2002 in the springs

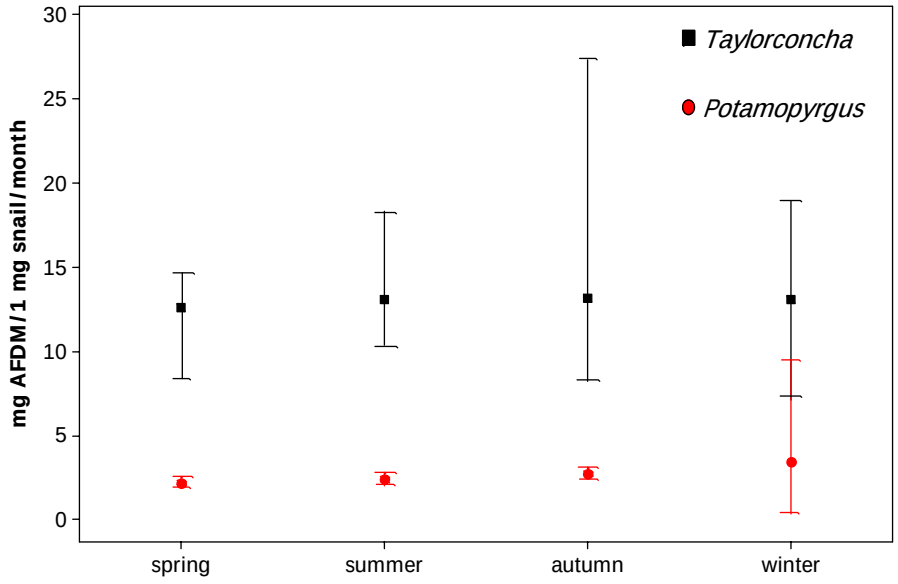
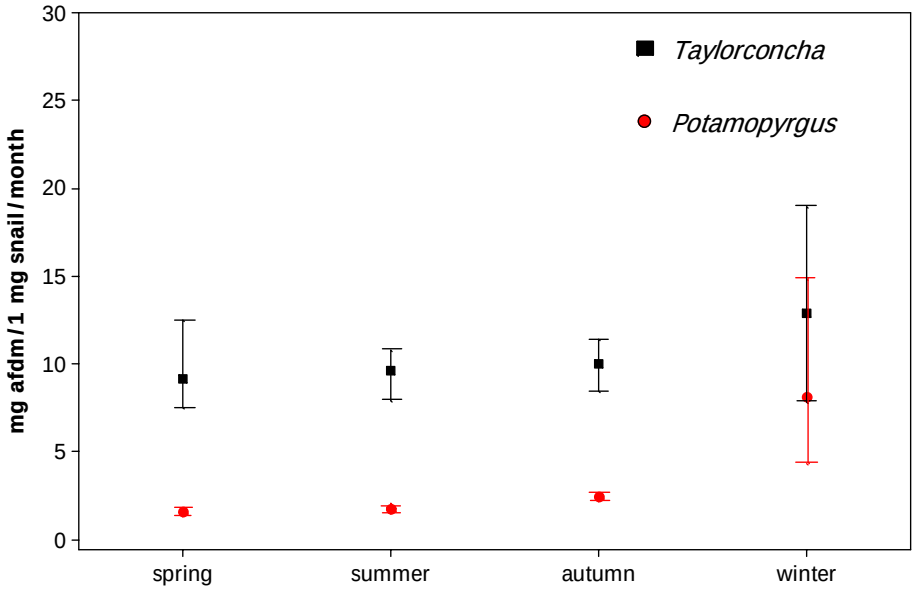


Figure 71. Mean (95% CI) relative growth efficiency [mg periphyton (AFDM)/ 1 mg increase in biomass/month] of *T. serpenticola* and *P. antipodarum* at four seasons, 2002 at the outlet



Discussion

Although, it is difficult to project what effects *P. antipodarum* had on *T. serpenticola* outside of the exclosure/enclosure competition experiments, the data suggests that *P. antipodarum* may cause *T. serpenticola* to abandon cobble habitats when *P. antipodarum* densities are between 4000/ m^2 to 10,000/m^2. These densities are similar to densities of *P. antipodarum* found throughout the year on the undisturbed cobbles at Banbury Springs (Chapter 6); therefore, *T. serpenticola* densities in these cobble habitats could have been greater in the absence of *P. antipodarum*.

The exclosure/enclosure competition experiment did not address effects of increased intraspecific competition on *T. serpenticola.* I could have measured this by increasing the densities of *T. serpenticola* to the five density levels of *P. antipodarum* on the cobbles in the absence of *P. antipodarum*. The reason I did not conduct these additional trials was because I was primarily concerned with competitive impacts of *P. antipodarum* on *T. serpenticola* and not of *T. serpenticola* on *P. antipodarum.* I also assumed that the competitive effect of *P. antipodarum* was greater on *T. serpenticola* than was that of *T. serpenticola* on itself. Any interspecific competition effects observed in this experiment would have indicated that *T. serpenticola* was negatively affected by *P. antipodarum* and that *T. serpenticol*a's densities would have been greater in its absence.

The exclosure/enclosure experiment also did not examine possible competitive mechanisms (i.e., interference or exploitative competition). In addition, results of these experiments cannot be expected to closely reflect real conditions, although, on occasion, small -scale competition experiments, such as this, can sometimes predict larger spatial

scale changes (Kohler and Wiley, 1997, Giller and Malmqvist 1999). Under natural stochastic conditions with a full community of organisms interacting in a heterogenous environment, competitive interactions between *T. serpenticola* and *P. antipodarum* may be exacerbated or inhibited (i.e. indirect effects) (Lehman and Tilman 1997, Tilman 1997). Spatial patterns in the landscape may allow *T. serpenticola* populations to coexist with *P. antipodarum* for many generations at the local or regional scale (Vanderlaan and Hogeweg 1995), even in habitats where *P. antipodarum* populations appear to completely dominate the macroinvertebrate community.

In the growth rate experiment, in all instances, increased intraspecific competition (density-dependence) caused decrease growth. This suggests that whenever food resources become limited, density-dependent effects could regulate populations of both species. During this experiment, food resources decreased through time due to grazing and by the end of the experiment competition should have been the most intense. Due to the set-up of the experiment, I did not measure snail growth until the termination of the experiment and had no data on daily growth rates. I was therefore, unable to determine which species had the lowest R* (species that can maintain a positive growth rate at lowest resource level)(Tilman 1982). Tilman's R* rule predicts that the invader would out compete the resident if its R* was less than the resident, either because it had a higher resource acquisition rate or lower maintenance requirement, or both (Tilman 1982, Shea and Chesson 2002).

I only used snails between 2.0 – 2.5 mm shell length for both species in this experiment. *Taylorconcha serpenticola* rarely exceeds 2.50 mm and *P. antipodarum* often reaches $\geq$ 5.00 mm shell length in the study area. At about 3.00 mm, visible

neonates begin to develop in *P. antipodarum* brood pouches (Chapter 2), and *P. antipodarum* food assimilation, in addition to adult growth is also directed into neonate growth. I previously reported that in the study area *P. antipodarum* reproduce throughout the year, while *T. serpenticola* may only reproduce once or twice seasonally (Richards et al. 2000) and have shown that *P. antipodarum* growth rates are highest between 2.25 - 3.50 mm (Chapter 2). It is therefore, likely that the interspecific competition effects of *P. antipodarum* on *T. serpenticola* reported in these experiments do not represent the full range of competition effects resulting from differences in resource demands of *P. antipodarum* at different sizes or reproductive stage.

Potamopyrgus antipodarum is not a typical grazer found in rivers and streams in the western USA. Compared with many native snails, particularly the slow-moving *T. serpenticola, P. antipodarum* is highly mobile (Haynes et al 1985), but unlike other mobile non-snail grazers, such as Baetidae mayflies, *P. antipodarum* possesses a radula for efficient scraping and grazing. Both *P. antipodarum* and *T. serpenticola* are apparently photophobic and avoid feeding on exposed surfaces (Chapter 2), thus they may share and compete for the same habitat resource were both species co-occur. *Potamopyrgus antipodarum* spatial grazing pattern is also different than many of the native hydrobiid snails. Because *P. antipodarum* is highly mobile and constantly on the move during feeding (personal observations), I would consider it to be a 'lawnmower' type grazer (spatially homogenous grazing)(Sommer 1999, Chase et al. 2001) whereas, many other native snail species, including *T. serpenticola* are slower- moving 'bulldozer' type or 'digger' type grazers (all-or-nothing homogeneous grazing)(Sommer 1999, Chase et al. 2001). *Potamopyrgus antipodarum* and *T. serpenticola* therefore, may avoid

competition with each other by feeding on different types of periphyton or microhabitats, particularly in heterogenous landscapes. This is supported by my spatial distribution analysis of *P. antipodarum* and *T. serpenticola* in Banbury Springs (Chapter 3).

Alternatively, *P. antipodarum* may have allowed for higher densities of *T. serpenticola* at the outlet of Banbury Springs, through facilitation. Although, the importance of facilitation in structuring communities continues to be overlooked by most ecologists (Bruno et al. 2003), *P. antipodarum* has been show to facilitate native benthic fauna in Australia (Schreiber et al. 2002). It is therefore, possible that under certain conditions (e.g. low to medium densities), *P. antipodarum* may facilitate *T. serpenticola* by altering the periphyton community via grazing or through changes in nutrient availability and primary production (Bronmark et al. 1991, Hall et. al. 2003). More research is needed to address the role if any, of facilitation between these two species.

Tubes used in the growth rate experiment were empty of any periphyton at the start of conditioning and only the rapidly colonizing periphyton species became established during the experiment. These periphyton taxa could be considered early successional species under early successional conditions. The ability of *P. antipodarum* to utilize this early successional, albeit, artificial periphyton community more efficiently than *T. serpenticola* and consequently have higher growth rates in this experiment is consistent with present competition theory, where 'inferior competitors have greater resource-exploitation ability by virtue of higher fecundity and faster growth' (Amarasekare 2003). Current ecological theory suggests that species require life history trade-offs in order to coexist with competitors in a community (Shea and Chesson 2002, Kneitel and Chase 2004) and it may be that *T. serpenticola* is a superior competitor to *P.*

antipodarum in undisturbed, late- successional, stable, habitats where it is often found. *Potamopyrgus antipodarum*, on the other hand, has higher fecundity, higher dispersal and recruitment ability and appears to be able to exploit resource–rich or early successional habitats better than *T. serpenticola*: all traits that are characteristic of inferior competitors (Amarasekare 2003). In past studies (Frest and Johannes 1992, U. S. Fish and Wildlife Service 1992), *T. serpenticola* was observed to be more abundant on red algal encrusted cobbles and from my past research (Richards et al. 2001), *T. serpenticola* was more abundant than *P. antipodarum* in areas and substrates that appeared to be more stable (i.e. spring influenced). It is likely that *T. serpenticola* is more specialized for feeding on the types of periphyton found in these areas than those offered in the experiment. This could partially explain why *T. serpenticola* was less efficient at converting periphyton in the experimental tubes into growth than was *P. antipodarum*. Also, in all treatments without competition, growth rates of *T. serpenticola* were significantly greater in the outlet during summer than in the headwater springs. This may reflect why densities of *T. serpenticola* are consistently greater in the outlet than in the springs.

The simple Lotka-Volterra competition model derived from competition coefficients generated in the growth rate experiment showed that *P. antipodarum* should exclude *T. serpenticola* and drive it to extinction. This basic model does not include any spatial or temporal dynamics or other factors that could allow for coexistence of the two species and is very limited in its utility. Because both species currently coexist in the Snake River drainage, this model does however suggest two possible competitive outcomes; 1) both species will coexist because their populations are not regulated by interspecific competition for limited food resources, or 2) *P. antipodarum* will eventually

out compete *T. serpenticola* but not enough time has elapsed for this to occur. Often the effects of an invasive species are not fully known until 50 to 100 years after it becomes established (Elton 1958 and Cox 1999). Because almost no research has been conducted on the ecology of *P. antipodarum* or on any of the threatened and endangered gastropods in the Snake River system, it is difficult to predict the fate of any of these species, due to competition with *P. antipodarum*, at this time.

Conclusion

From these experiments, it appears that interspecific competition favors *P. antipodarum,* possibly to the exclusion of *T. serpenticola*. Although other factors including habitat heterogeneity, environmental stochasticity, niche partitioning, migration and dispersal, and life histories can affect the outcomes of interspecific competition and allow for their coexistence, *T. serpenticola* populations are probably negatively affected by *P. antipodarum*. Any management strategies and actions designed to protect and enhance remaining threatened *T. serpenticola* populations should incorporate the likely impacts of the highly, invasive New Zealand mudsnail, *P. antipodarum*.

POPULATION DYNAMICS OF *T. SERPENTICOLA* AND *P. ANTIPODARUM* AT BANBURY SPRINGS OUTLET, 1999-2004, USING TIME SERIES ANALYSIS

Introduction

In Chapter 3, I showed that both *T. serpenticola* and *P. antipodarum* densities and distributions in Banbury Springs were influenced by spatial habitat heterogeneity and were spatially disassociated with each other, potentially from interspecific competition. In Chapter 4, I showed that intraspecific competition for limited food resources could create size hierarchies in *P. antipodarum* populations, which in turn could affect population dynamics, including interspecific competition. In Chapter 5, I demonstrated that both intra and interspecific competition could affect growth rates of both *T. serpenticola* and *P. antipodarum*, although competition was primarily asymmetrical in favor of *P. antipodarum*. All of these results, including some of the life history studies reported in Chapter 2 (i.e. overlapping temperature tolerances and photophobic tendencies), suggested that *P. antipodarum* populations could negatively affect *T. serpenticola* populations. However, none of these studies examined how *T. serpenticola* population densities were related to *P. antipodarum* population densities over time in habitats where both species occur, which is the ultimate measure of the effects of interspecific competition. In this chapter, I measured and modeled *T. serpenticola* and *P. antipodarum* densities over a 5 year time period in a section of Banbury Springs where both species co-exist.

Materials and Methods

Study Site

The study site was an ≅ 3 x 3 m section of the northern-most seep within an alcove that was formed by the junction of the Snake River and the outlet of Banbury Springs (Figures 33, 36, and 72). This site had a dense canopy cover of alder, willow, and exotic Russian olive. The snail habitat was primarily basalt cobble substrate covered with periphyton and moss (see Figure 69 and pages 121-124, Chapter 5 for description of periphyton and moss composition on cobbles). The alcove proper was a heterogenous mixture of primarily sand and silt with some cobble substrate. During most of the year, except winter, algal mats and macrophyte vegetation were abundant and there were extremely high densities of *P. antipodarum*. Water levels of the Snake River at this site fluctuated irregularly, both daily and seasonally, due to power generation activities from the Bell Rapids Dam several miles downstream. At high river levels, the study site seep was completely covered with river water, while at low river water levels, the seep extended several meters out to the Snake River alcove. I chose this location because it had very high densities of *T. serpenticola* relative to any other known colonies in the Snake River drainage (D. Shinn, Idaho Power Company, personal communication) and also high densities of *P. antipodarum*, therefore; interspecific competitive effects on population densities and growth rates could be monitored and modeled.

Figure 72. Study site spring seep at outlet of Banbury Springs. The seep was caused by water from Morgan Lake eroding a portion of a man-made dike impoundment that created Morgan Lake

I estimated densities of *T. serpenticola* and *P. antipodarum* at the study site by counting snails of both species on individual, randomly selected cobbles (N = 20) at two-month time intervals (January, March, May, July, September, and November), between March 1999 and September 2001 (N = 16). Cobbles were randomly selected by using the standard stream pebble count method of standing in the center of the plot, closing eyes and picking up the first cobble that is touched by an extended finger tip. Due to time and budget constraints, from November 2001 to May 2004, I did not count snails or estimate snail densities on individual cobbles, but estimated total densities by combining snails

from randomly selected cobbles (N = 20) into a water-filled, shoe-box sized, plastic container and counting the total number of each species. This was done during the same two-month time intervals (N = 16). Snails were counted live and released.

To determine densities of snails/m^2, I measured the three main axes of the cobbles (mm)(N = 20 cobbles/sampling period) and calculated surface area (m^2) available to snails by subtracting the surface area of the cobble that was embedded in the substrate and then divided the number of snails by available cobble surface area. Cobbles were almost always quadrate in shape and typically were uniformly covered with pits and indentations; therefore, surface area of each cobble was probably, slightly underestimated.

I used S-PLUS 6.1 for Windows (Insightful 2002) and MINITAB 14.0 (Minitab Inc. 2003) for statistical and time series analysis. I estimated variability of snail densities on individual cobbles for the March 1999 through September 2001 samples. For time series analysis, I used total number of each species counted at each time period divided by total available surface area of cobbles for each time period, from 1999-2004 (N = 32). Time series analysis methods were preferred over standard regression methods because they incorporated and adjusted for autocorrelation between time steps. Population dynamics of all organisms are autocorrelated, that is, the number of individuals observed at any time step, N is dependent on time step $N-1$ (Venables and Ripley 2002). Alternatively, regression analyses assume independence in data values. I used multiplicative decomposition analysis to generate time series models for each species. This method separated the times series into linear trend, seasonal components, and error (Minitab Inc. 2003). I used a seasonal component length of one year, grouped by the 2-

month intervals (N =6). I used multiplicative instead of additive decomposition because multiplicative decomposition assumed that as the data values increased, so did the variability in the seasonal pattern. Most time series plots exhibit such a pattern (Minitab Inc. 2003). In the multiplicative model, the trend and seasonal components were multiplied and then added to the error component (Minitab Inc. 2003). I compared the multiplicative decomposition time series models with linear, quadratic, exponential, and S-curve (Pearl-logistic) trend analysis models, which did not incorporate seasonal components. For comparison of models, I used two measures of accuracy: MAPE and MAD. For both, the smaller the value, the better the fit of the model. I also computed autocorrelation functions (correlograms) and 5% significance limits for both species to determine if there was any significant autocorrelation for lags from 2 – 48 months, at two-month intervals. If autocorrelation values for a lag was outside the 5% significance limit, I considered them significant. I conducted time series model seasonal analysis using four methods; 1) a seasonal index that standardizes densities such that values below 1.0 are < the average density value and values above 1.0 are > than the average density value, 2) the percent variation at each seasonal period, 3) the median, 25^{th} and 75^{th} percentiles, and range of the detrended (removal of increasing trend) data by seasonal period, and 4) the median, 25^{th} and 75^{th} percentiles, and range of the residuals by seasonal period. I also estimated the finite rate of increase, $\lambda = 1 + r$, where r is the discrete growth factor, for both species from the best -fit trend line.

Results

From March 1999 to September 2001, densities of both species varied on individual cobbles and *P. antipodarum* densities were almost always greater than *T. serpenticola* at each time period, except September 2000 (Table 20). Cobble samples contained primarily *T. serpenticola* and *P. antipodarum*, which I estimated to be > 90% of the total number of individual organisms in the samples at all sampling periods. For example, the cobble sample in July 2001 contained 7631 individual macroinvertebrate organisms, of which 59.34% were *P. antipodarum*, 33.05% were *T. serpenticola*, and 6.68% were Turbellaria. The remaining 0.93% individuals were from 11 different taxa.

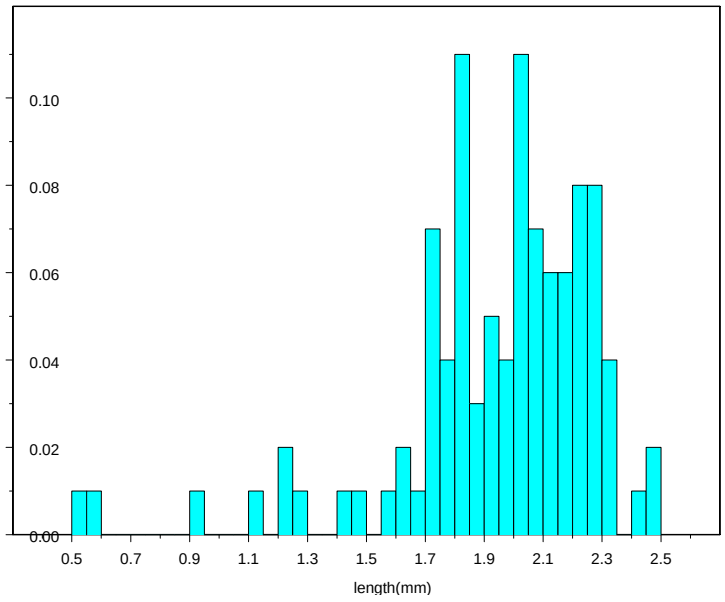
Taylorconcha serpenticola Time Series Model

For *T. serpenticola*, the multiplicative decomposition model was more accurate than the time series models that did not incorporate seasonality. The May 2003 density value was determined to be an outlier because it was well outside the 95% CI values of the mean of the densities. The reason its value was so large was because there was an abundance of very young, small snails < 1.5 mm, which comprised about 10% of the abundance and represented a recent birthing event (Figure 73). This was atypical of most *T. serpenticola* samples examined. Most samples examined had < 1- 2% young snails; therefore, I reduced the abundance value of the May 2003 sample by 8% after which, it was no longer an outlier.

Table 20. Mean and std.dev. of *T. serpenticola* /m^2 and *P. antipodarum*/m^2 at the outlet of Banbury Springs from 1999-2001.

	T. serpenticola		*P. antipodarum*	
	Mean	Std.Dev.	Mean	Std.Dev.
1999				
March	973.31	567.13	2112.90	1970.65
May	2142.45	826.71	5797.79	2748.77
July	2286.46	1263.19	6832.04	4893.12
September	3511.24	1421.65	7845.25	3105.06
November	4794.26	2291.47	8547.39	5482.33
2000				
January	864.43	644.06	3265.87	1853.03
March	1573.82	932.94	2114.45	1564.67
May	3422.61	2007.00	6589.31	4910.59
July	2656.76	2019.52	3857.60	2699.57
September	5592.52	3976.49	4633.87	4355.28
November	5627.74	4674.23	5711.42	3809.15
2001				
January	536.97	619.82	2149.92	1185.69
March	1579.84	1708.08	2115.78	1956.66
May	2453.22	1890.48	7516.63	5185.18
July	1385.00	865.35	9554.00	4758.95
September	2860.04	1678.77	10636.01	6955.79

Figure 73. Length frequency of *T. serpenticola* collected May 2003 at outlet of Banbury Springs (N = 100 snails measured to nearest 0.05 mm), ≈ 10% were ≤ 1.5 mm.



There was an obvious seasonal trend and a slight, increasing, linear trend in *T. serpenticola* densities (Figure 74). The seasonal trend was confirmed by the autocorrelation function (correlogram) cycling period of about 12 months (Figure 75) and a significant correlation at lag of 12 months. The model predicted an increase in density of 141.26 snails/m^2/year and a model based finite rate of increase, λ of 1.06 (Figure 74). The model tended to underestimate the high abundance years and overestimate the low abundance years (Figure 74). Densities were highest in September and lowest in January (Figure 76a) and were most variable in November and least variable in January (Figure 76b).

Figure 74. *Taylorconcha serpenticola* time series decomposition multiplicative model (measured at 2-month intervals; January, March, May, July, September, and November). The fitted linear trend equation with the May 2003 outlier reduced by 8% was: Y_t = 2223.42 + 23.5426*t. Accuracy measures: MAPE = 30, MAD = 811

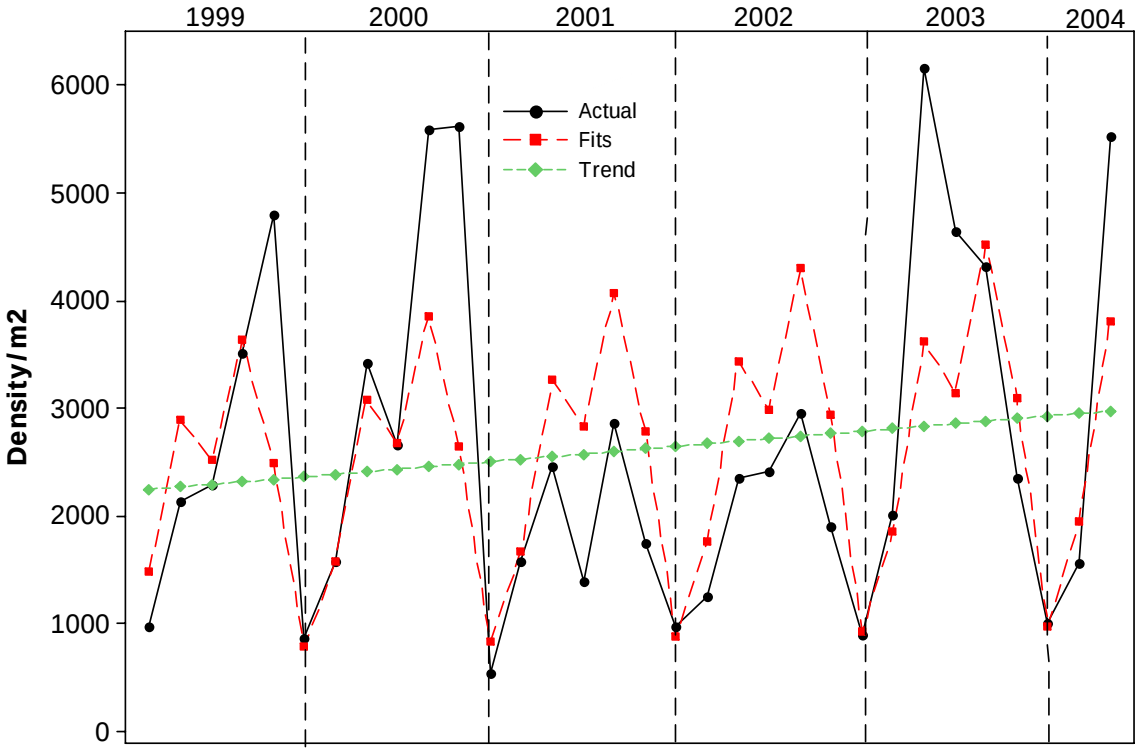


Figure 75. *Taylorconcha serpenticola* autocorrelation function (correlogram) and 5% significance limits. There was a cycle of about 12 months and a significant lag at 12 months. Lag of 1 is not included because it is assumed to = 1.0 and each time step is correlated to the previous or subsequent time step (Venables and Ripley 2002)

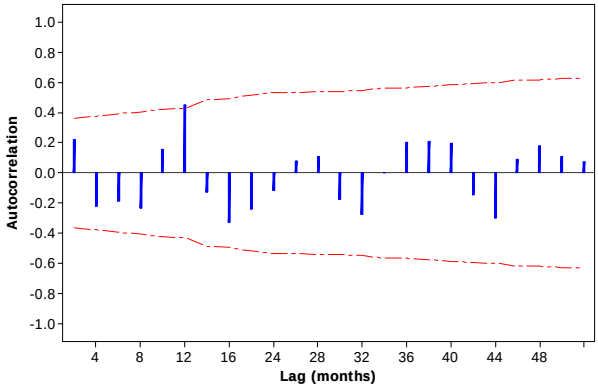
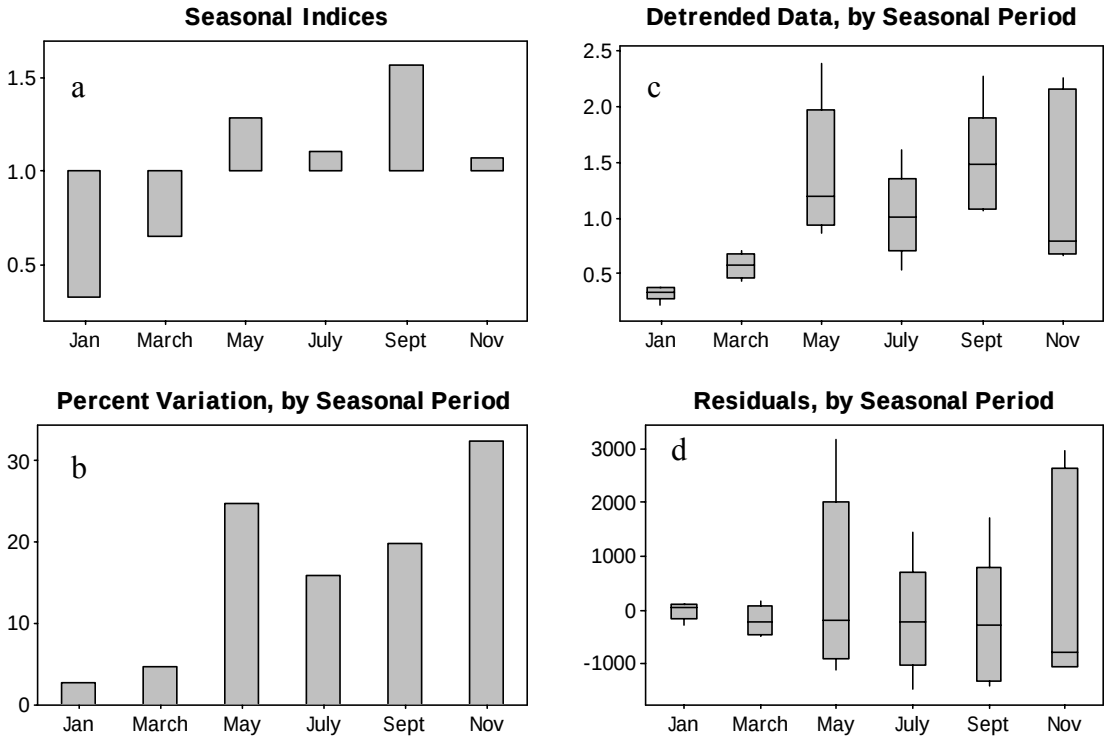


Figure 76. *Taylorconcha serpenticola* multiplicative time series model seasonal analysis; a) seasonal index that standardizes densities such that values below 1.0 are < the average density value and values above 1.0 are > than the average density value, b) percent variation at each seasonal period, c) median, 25th and 75th percentiles, and range of the detrended (removal of increasing trend) data by seasonal period, and d) median, 25th and 75th percentiles, and range of the residuals by seasonal period



Potamopyrgus antipodarum Time Series Model

For *P. antipodarum*, the multiplicative decomposition model was also more accurate than the models that did not incorporate seasonality. There was an obvious seasonal and increasing, linear trend in densities (Figure 77). The seasonal trend was confirmed by the non-decaying, autocorrelation function (correlogram) cycling period of 12 months (Figure 78). There was also a significant negative correlation between densities at a lag of 6 months (Figure 78). The model predicted an increase in density of 544.31 snails/m^2/year and a model based finite rate of increase, λ of 1.12 (Figure 77). The model tended to slightly underestimate the high abundance years and slightly overestimate the low abundance years (Figure 77). There was a marginally significant autocorrelation at a lag of 2-months, which suggested that *P. antipodarum* densities at each seasonal sample period were dependent on the previous seasonal time period densities (Figure 78). Densities were highest in July and September and lowest in January and March (Figure 79) and were most variable in September and least variable in January (Figure 79).

Comparison of *T. serpenticola* and *P. antipodarum* Time Series

From March 1999 until May 2004, *P. antipodarum* densities were almost always greater than *T. serpenticola*, except in 2000 when their densities were similar and in May 2003 when *T. serpenticola* densities were higher than *P. antipodarum* (Figure 80). In 2001, when *P. antipodarum* densities were high, *T. serpenticola* densities were low. In general, *P. antipodarum* densities peaked (July) before *T. serpenticola* (September/November)(Figure 80).

Figure 77. *Potamopyrgus antipodarum* time series decomposition multiplicative model from March 1999 to May 2004 (measured at 2-month intervals; January, March, May, July, September, and November). The fitted linear trend equation was: $Y_t = 4413.46 + 90.72*t$. Accuracy measures: MAPE = 23, MAD = 1207

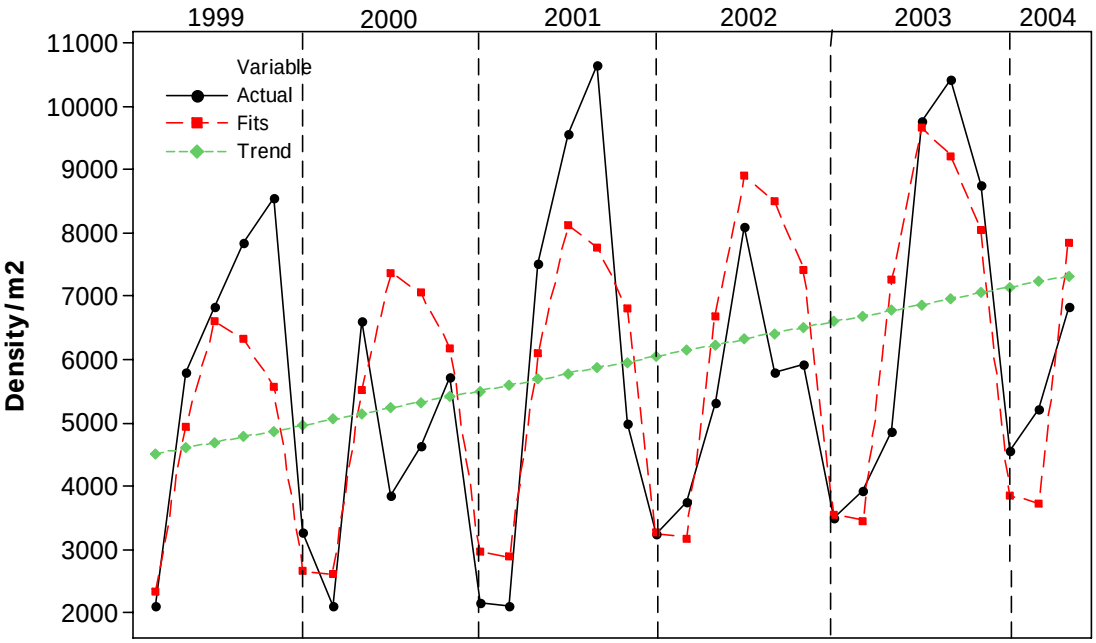


Figure 78. *Potamopyrgus antipodarum* autocorrelation function and 5% significance limits. There was a cycle of 12 months and a significant lag at 2 and 6 months. Lag of 1 is not included because it is assumed to = 1.0 and each time step is correlated to the previous or subsequent time step (Venables and Ripley 2002)

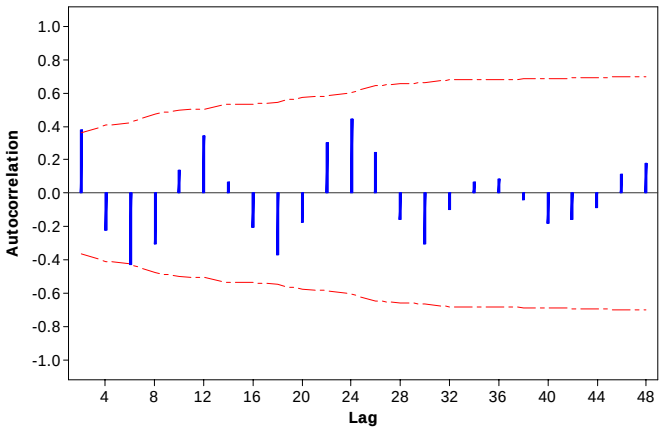


Figure 79. *Potamopyrgus antipodarum* multiplicative time series model seasonal analysis. a) seasonal index that standardizes densities such that values below 1.0 are < the average density value and values above 1.0 are > than the average density value, b) percent variation at each seasonal period, c) median, 25th and 75th percentiles, and range of the detrended (increasing trend removed) data by seasonal period, and d) median, 25th and 75th percentiles, and range of the residuals by seasonal period

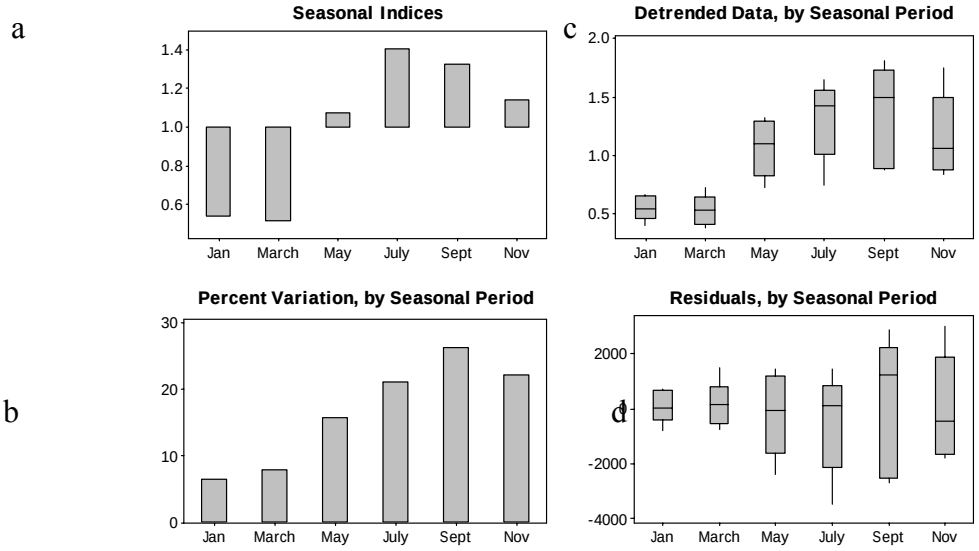
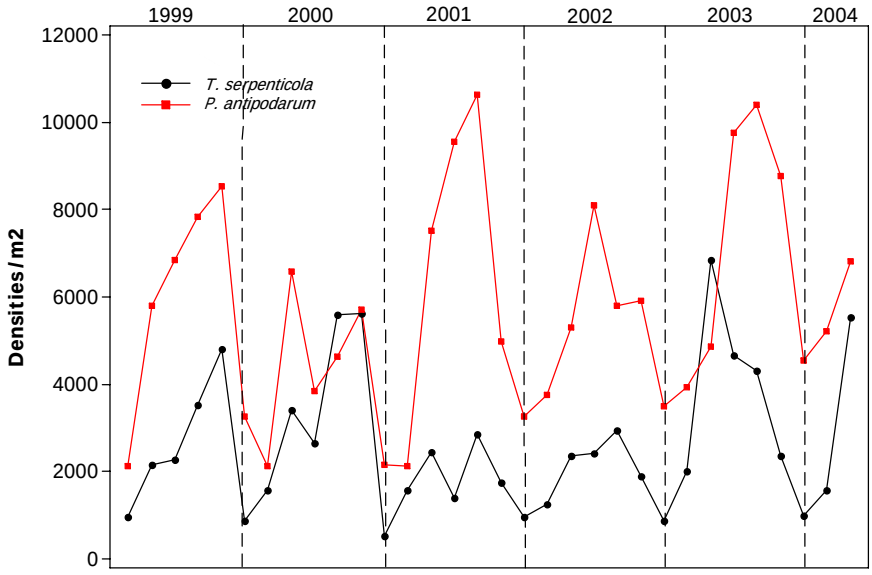


Figure 80. Time series of *T. serpenticola* and *P. antipodarum* densities/m^2 on cobble habitat at outlet of Banbury Springs, Idaho, March 1999 to May 2004 (measured at 2-month intervals; January, March, May, July, September, and November)



Discussion

Densities of *P. antipodarum* in the study site were within the range of densities that, as reported in Chapter 5, caused *T. serpenticola* to abandon cobbles. Therefore, densities of *T. serpenticola* may have been higher or its population dynamics may have been different in the absence of *P. antipodarum*.

Taylorconcha serpenticola appears to reproduce primarily at two time periods, late spring and early autumn (also reported by Frest and Johannes 1992) but I have found low numbers of very small < 1.5 mm individuals throughout the year. *Potamopyrgus antipodarum* reproduces throughout the year, but large numbers of newborn individuals < 1.5 mm typically appear between spring and autumn. Although *T. serpenticola* density estimates and time series model were probably not heavily influenced by newborns, except in May 2003, density estimates and the time series model of *P. antipodarum* could have been, particularly from spring to autumn.

The finite rate of increase λ values were based on single point estimates of density in the time series models and did not incorporate any variability associated with sampling error. Therefore estimated λ values are only mean values and could have been somewhat lower or higher. A reasonable conclusion would be that both populations were not decreasing from 1999-2004.

Because this time series was conducted for < 6 years, no valid trends were detected for cycles or oscillations in densities for either species, other than the seasonal cycle. Environmental factors, resource abundance or quality, or predation and parasite interactions could lead to 2-year, 4-year, or even longer cycles (Begon et al. 1996). Even small changes in intra and interspecific competition can lead to random or chaotic

fluctuations in densities (Akcakaya et al. 1999, Morin 1999). Continued monitoring of these populations is required to detect any long-term oscillations.

Potamopyrgus antipodarum densities were extremely high (> 500,000/m^2 during summer and autumn) in the alcove ≈ 2 meters downstream of the study site, whereas their densities never exceeded 11,000/m^2 on cobbles within the study site. This could be because the alcove was better habitat (i.e. warmer temps, less velocity, more food resources, different substrate, etc.) for *P. antipodarum* than the spring influenced cobble habitat in the study site and it only moved into the cobble habitat as a result of intraspecific competition in the alcove or because of its natural tendency to disperse. I did not find any *T. serpenticola* in the alcove away from the cobble habitat in the study site where densities of *P. antipodarum* were high. Conditions presumably rapidly deteriorated for *T. serpenticola* away from the study site. Because the *T. serpenticola* population at the study site is isolated from other populations, random or chaotic fluctuations in densities could increase its extinction risk (Morin 1999). Whereas constant immigration of *P. antipodarum* from the alcove decreases its risk of extinction in the study site to almost zero.

In the previous chapter, I showed that *P. antipodarum* could compete with *T. serpenticola* for limited food resources and habitat under controlled conditions. The length of this study was not sufficient to detect any possible long-term trends, increased fluctuation in population variability, or chaotic patterns in the *T. serpenticola* population; therefore, continued monitoring of this population is required. At this time, however it appears that *T. serpenticola* can co-exist with *P. antipodarum* at this site.

DISCUSSION AND CONCLUSION

Invasive species are causing large losses in biodiversity and ecological changes worldwide (Sala et al. 2000, Lodge 2001). In the western USA, the "weedy" invasive *P. antipodarum* is here to stay and its impacts will be either direct or indirect on the aquatic ecosystems it invades. The "relict" threatened *T. serpenticola* on the other hand, has lost most of its historic habitat and now occupies limited and highly fragmented sections in the mid-Snake River.

I have shown that both species can compete for limited food resources, have niche overlaps (i.e. temperature overlaps, photophobic tendencies, and somewhat similar habitat requirements) but may have just enough niche separation or their occupied habitat is heterogeneous enough for them to coexist, at present. It is possible however that not enough time has elapsed for *T. serpenticola* abundance to decline due to competition with *P. antipodarum*. For example, it has been hypothesized that time to competitive exclusion could be inversely related to body size, temperature, and metabolism [(e.g. metabolic theory of ecology) (Brown et al. 2004)], all of which are small for both *P. antipodarum* and *T. serpenticola* compared to larger organisms. It has also been suggested that for most invasions, their ecological impacts are not fully realized for 50 to 100 years (Elton 1958).

Because *P. antipodarum* is; 1) highly mobile, 2) easily disperses, 3) reaches extreme high densities, and 4) shows strong interspecific interactions, its effects on the benthic communities and ecosystem processes in the Snake River drainage should be substantial (Dangles and Malmqvist 2004). *Potamopyrgus antipodarum* is now the most dominant macroinvertebrate species in the Snake River (Bowler 1991, Cazier 1997) and I

have observed it to be > 90% of the total number of invertebrates in many Snake River locations. Limited research suggests that *P. antipodarum*'s effects on stream ecosystems is more a result of its high abundance and not its per capita feeding efficiency (Hall et al. 2003), although in Chapter 5, I found it to be more efficient than *T. serpenticola* in converting periphyton to biomass, at least from periphyton taxa that colonized experimental tubes. Because *P. antipodarum* has a broad ecological niche and often reaches high densities (the niche hierarchy model; Sugihara et al 2003), its effects on aquatic ecosystems will probably be through direct, via high abundances, or indirect competitive interactions (Dangles and Malmqvist 2004). Although not documented for *P. antipodarum* in the western USA, it recently has been demonstrated that the invasive golden apple snail (*Pomacea canaliculatea*) has altered ecosystem functioning by causing a complete collapse of an aquatic plant community, thus inducing a shift to an alternative stable state (Carlsson et al. 2004, Scheffer et al. 2001).

I have also shown that intraspecific competition for limited food resources can cause size hierarchies in *P. antipodarum* populations. Although many population dynamics models are based on the assumption that variability of individual growths does not occur (Metz and de Roos 1992), sized based interactions can shape population and community dynamics (de Roos et al. 1992, 2002, Kooten et al. 2004). Therefore, future ecological modeling of *P. antipodarum* should include size-structure (Kooten et al. 2004).

Taylorconcha serpenticola, unlike *P. antipodarum* appears to be more restricted in its habitat requirements. This is most likely due to its evolutionary history. *Taylorconcha serpenticola* is a relict of Pliocene Lake Idaho and presumably evolved on

wave swept, well-oxygenated shorelines (Frest and Johannes 1992). It is also assumed that until recently (the last 100 years), *T. serpenticola* populations were more or less continuously distributed in the mid Snake River and associated springs (Frest and Johannes 1992). Over the last 100 years, the Snake River has been substantially degraded due to; agricultural activities, confined-animal feeding operations, rangeland grazing, recreational activities, logging, and atmospheric deposition, industrial discharges, municipal wastewater-treatment facilities, fish farms, non-point agriculture sources, dewatering, numerous hydroelectric facilities, and the invasive *P. antipodarum* (Clark 1998, Bowler 1991). A 'sea' of *P. antipodarum* and poor water quality now surrounds remaining *T. serpenticola* populations. Connectivity of *T. serpenticola* populations has most certainly been severed or reduced, further increasing its extinction probability (Hanski 2002). Fragmented habitats are also highly susceptible to invasions (Bierregaard et al. 2002).

Water temperatures have increased and flows have been altered in the Snake River due to human impacts and droughts over the last decade and will probably continue, due to effects of global climate change. These conditions will most likely result in increased *P. antipodarum* abundance and decreased *T. serpenticola* abundance. Changes in water temperatures have been linked with changes in species abundance. For example, paleoclimatic records have shown shifts in distributions or abundance of species with change in temperature (Kennett and Stott 1991, Schiel et a. 2004). It has been shown that aquatic benthic communities changed in structure and the majority of species abundances changed as a result of increased water temperatures of only 3.5º C over 18 years, on a coastline in California (Schiel et al. 2004). Ecological shifts can involve

many factors and result in modified food webs and species interactions (Wootton 1993), depending on the strength of the interactions (Menge 2000). In the Schiel et al. 2004 study, increases in grazers were preceded by simplification of the algal community. Once changes occurred in the dominant algae, grazers increased in abundance, which was not unexpected. They did however; observe large and unforeseen changes in the community that was atypical of the surrounding area. Ecological shifts can also be exacerbated by exotic species invasions (Groshotz 2002) and may be occurring where *P. antipodarum* densities become exceedingly large (Hall et al. 2002).

The combination of degraded habitats and species invasions can result in biotic (taxonomic) homogenization (i.e. increase in species similarity)(Vitousek et al. 1997, McKinney and Lockwood 1999, Olden and Poff 2004), including reduction in snail species diversity (Cowie 2001). We now live in what has been called the 'Great Homogocene' (Rosenzweig 2001) or the 'New Pangea' (Mooney and Cleland, in press), where "weedy" species dominate and "relict" species survive under intensive management effort and substantial economic investment (Meyer 2004). Two of these competing species are the "weedy" *P. antipodarum* and "relict" *T. serpenticola*.

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