Competition and coexistence between the federally-threatened Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) and a non-native snail (*Succinea sp*. B)

Final Progress Report to the U.S. Fish and Wildlife Service – July 2010

Steven P. Campbell, Jacqueline L. Frair, and James P. Gibbs

Department of Environmental and Forest Biology
246 Illick Hall, 1 Forestry Drive
SUNY College of Environmental Science and Forestry
Syracuse, New York 13210

Executive Summary

Background

The Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) (COAS) is a terrestrial succineid snail that is endemic to the spray zone of Chittenango Falls within Chittenango Falls State Park in Madison County, New York. COAS is designated as an endangered species by the New York State Department of Environmental Conservation and as a threatened species by the United States Fish and Wildlife Service (USFWS). The USFWS recovery plan for COAS has identified its small population size, limited distribution, and negative interactions with an introduced snail, *Succinea* sp. B (Sp. B), as the primary threats to the snail's existence. Nevertheless, the nature and severity of these threats remain poorly understood, which has hampered the development and implementation of recovery efforts. To better understand these threats, USFWS enlisted researchers at SUNY College of Environmental Science and Forestry in 2005 to conduct a study titled "Field investigation of the interactions between Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) (COAS) and invasive snails". The main objectives of the study were to:

1. analyze a COAS monitoring database to produce population estimates and extract natural history information,
2. study the interactions between COAS and invasive Sp. B, and
3. evaluate the intensity of Sp. B removal needed to control their numbers.

We approached this study with the overall goal of determining if the native COAS and the non-native Sp. B are capable of coexisting without management intervention. As such, our focus was on understanding the competitive interactions between the two species to determine potential mechanisms for coexistence and avenues for population management. This approach encompassed all of the objectives and leads to recommendations that are directly relevant to the management of COAS.

Methods

To examine the potential for coexistence of COAS and Sp. B, we combined quantitative field data on the competitive interactions, habitat use, and population ecology of the two snail species. Specifically, we 1) performed *ex situ* competition experiments in 2008 and 2009 to establish the nature and strength of the competition between the species, 2) quantified habitat use of each species in 2008 to examine their potential for resource use overlap (a necessary condition for *in situ* competition), and 3) conducted mark-recapture surveys in 2008 and 2009 to examine the population-level effects of the invasive snail on the native snail as well as elucidate factors that may mediate the interactions between the species such as within year changes in abundance and size distribution. We also reanalyzed the data from mark-recapture surveys in 2002-2005 and 2007 using more rigorous methods of population estimation and combined it with the estimates from 2008 and 2009 to examine population trends.

Results and Discussion

Our work on the competitive interactions between COAS and Sp. B, their habitat use, and population ecology provides evidence for both competition and coexistence. In our experiments, COAS growth rates slowed by as much as 80% and mortality rates increased with increasing density, and larger body sizes, of Sp. B, indicating the potential for long-term competitive exclusion of COAS. However, our examination of habitat use and density *in situ* suggests that there may be enough mitigating factors to favor coexistence at the falls. First, spatial partitioning at very local scales through differential use of living and dead plant material (i.e., COAS preferring wood, detritus, and decaying plant matter, Sp. B. preferring living plant material), and differential selection of plant species (e.g., COAS selecting *Eupatorium purpureum* while avoiding *Nasturtium officinale*, Sp. B. selecting *Impatiens* spp. and *Pilea pumila*), is likely to favor coexistence – increasing intraspecific competition relative to interspecific competition. Second, rigorous population estimates indicate that the natural population densities of COAS and Sp. B have remained well below the densities at which we observed negative competitive effects in our experiments (roughly 8:1 at the falls versus 25-50:1 in our experiments), suggesting that these two species are not strongly competing *in situ*. It is likely that environmental fluctuations of limiting abiotic factors (e.g., temperature and moisture) maintain populations of each species at sufficiently low densities such that resources are abundant, encounters among individuals are rare, and competition remains relatively unimportant. Population trends since 2002 corroborate this conclusion given a high correlation between raw COAS and Sp. B counts among years, and concurrent periods of increase and decline. Moreover, intra-annual patterns from the mark-recapture surveys suggest that there may be a temporal partitioning of resources as a result of a trade-off between growth and longevity of COAS and Sp. B (i.e., COAS is a slower growing, and smaller biennial species and Sp. B is a faster growing and larger annual species). The annual die-off of adult Sp. B late in the summer and their replacement by a new cohort of newly hatched individuals may lead to a less competitive environment for COAS during this time.

Management Recommendations

Despite the potential for competition to occur should the ratio of Sp. B to COAS increase roughly 3-6 times over current levels, our data indicate that these species are capable of coexisting at the falls. Since 2002 (with the exception of 2006), Sp. B has been manually removed from the shelf every two weeks as part of the annual COAS population survey. Anecdotal observations of high Sp. B abundance as soon as 1 day following removals, combined with data showing increased numbers of Sp. B throughout early- to mid-summer despite removals, indicates that the removals have not been an effective means of controlling Sp. B numbers. Further, our experiments indicate that the observed densities of COAS and Sp. B at the falls are not likely to drive COAS to local extinction. Therefore, more intensive management to control Sp. B seems unwarranted at this time, and reduced control efforts seem unlikely to cause any detriment to COAS persistence.

Although COAS population estimates have reached as high as 784 ± 38 snails since 2002, and the animals appear robust to catastrophic events (the 2006 landslide) and competition by Sp. B, in the majority of years of our study population estimates fell below 339 ± 53 snails. Thus, existing at low densities in a single, concentrated population continues to put COAS at risk of extinction. For this reason continued monitoring of COAS at the site, with or without habitat management or Sp. B control measures, remains warranted as is establishment of captive populations that could be used as sources for translocations to establish new populations elsewhere (or back to the falls should COAS become locally extinct). *In situ* monitoring of COAS may well be accomplished with surveys of less intensity than previously conducted (e.g., monthly rather than bi-monthly surveys, or every other year rather than annual surveys), or with any number of indices based on raw COAS counts (e.g., any single survey in July or August, or surveys of only sections 7-10) that correlate well to robust estimates of population size. Reduced intensity monitoring is likely to benefit COAS due to reductions in trampling damage at the site. Given the potential for a catastrophic event to cause serious harm to the population, we do recommend at least some level of monitoring on an annual basis. However, should an index to population size be employed we further recommend conducting a formal population estimate at least every 2-3 years to ensure that the relationship between the index and true population abundance remains valid.

Additional experiments are also recommended to clarify COAS habitat requirements so as to effectively manage habitat at the falls and identify potential areas for establishing additional COAS populations. A captive population could be used to test plant species preferences, as well as determine whether live versus decaying material is truly preferred by COAS or used only as a means of niche differentiation when competing with Sp. B. Further, experimental releases of captive COAS in other suitable locations in the state could help clarify the factors truly limiting population distribution and abundance.

Introduction

The invasion of ecosystems by non-indigenous species is one of the most serious threats to global biodiversity (e.g., Williamson 1996, Walker and Steffen 1997, Cohen and Carlton 1998, Wilcove et al. 1998, Sala et al. 2000). Invading species can have strong ecological effects at different organization levels, ranging from changes in behaviors of individuals and decline or extinction of vulnerable endemic species to changes in community structure and composition, habitat degradation, declines in ecosystem services (e.g., water quality), and alterations of ecosystem processes (e.g., increase in fire frequency) (e.g., Parker et al. 1999, Simon and Townsend 2003, Clout and Williams 2009). For example, nearly 80% of endangered species worldwide are adversely affected by competition or predation by invasive species (Pimentel et al. 2005). The effects are not just ecological. In the Unites States alone, the economic costs associated with invasive organisms exceed $120 billion/year in lost production, maintenance, eradication efforts, and health costs (Pimentel et al. 2005).

The complexity of invaded systems and the idiosyncrasies of each invader and of the species each invader affects makes it difficult to address the threat of invasive species in a comprehensive way. This problem is further exacerbated by the paucity of detailed, mechanistic information about the interactions between non-native and native species (Byers and Goldwasser 2001). A better understanding of these interactions and their outcomes is necessary if we hope to identify the factors that facilitate the establishment and spread of invaders, predict the effects that a given invasion will have on native species and their ecosystems, and effectively manage ecological systems where invasive species have become established (Parker et al. 1999).

Ecological theory indicates that native species and non-native invaders that are closely related or ecological analogues are more likely to utilize similar resources and thus compete. Based on the principle of competitive exclusion (Hardin 1960), competitively superior invasive species are predicted to drive native competitors to extinction. Nevertheless, competition rarely leads to the exclusion of "inferior" species (see reviews by Branch 1984, Underwood 1992) and much recent ecological theory has sought to explain how species coexist when they compete for one or a small number of shared limiting resources. (Tilman 1994, Chesson 1991, Loreau and Mouquet 1999, Chesson 2000a, Hastings and Botsford 2006, Volkov et al. 2007). Niche differentiation is often proposed as the primary mechanism for coexistence. Its general premise is that important ecological differences between the competing species distinguish their niche and lead to a reduction in interspecific competition relative to intraspecific competition which in turn leads to their stable coexistence (Chesson 1991, 2000a, Wright 2002, Kneitel and Chase 2004).

Niche differentiation is usually represented as trade-offs among species (Kneitel and Chase 2004). Trade-offs are exhibited as a negative functional interaction between traits: performing one ecological function well comes at the cost of performing another function (e.g., growth and reproduction) (Stearns 1989, Zera and Harshman 2001). Some of the most common and important tradeoffs among species include differences in spatiotemporal partitioning of habitats and resources (Hairston 1951, Whittaker 1967, Pianka 1969, Diamond 1973, MacArthur 1972, Tilman 1982, Leisnham and Juliano 2009, Veen et al. 2010), susceptibility to predators (Holt et al. 1994, Leibold 1996), tolerance to abiotic environmental conditions, exploitation of patchy environments (Chase et al. 2001), response to disturbance or stress, and fitness in a temporally variable environment (Chesson and Huntly 1997).

Interspecific trade-offs are typically purported to be a prerequisite for species coexistence at small spatial scales (MacArthur 1972, Tilman 1982, 2000, Petraitis et al. 1989, Tilman and Pacala 1993, Chesson and Huntly 1997, Grover 1997), but it is not always necessary to invoke trade-offs to explain coexistence. For example, environmental variability *per se* can maintain populations of potential competitors at low enough densities so that resources are sufficiently abundant and competition is insignificant (e.g., Connell 1978, Sousa 1984). Neutral models (Hubbell and Foster 1986, Hubbell 2001, 2005) have also been proposed to explain coexistence. Under neutral theory, competitors are assumed to have equal fitness under all conditions and coexistence is long-term but not indefinite because extinctions can still occur via random walks. As such, this type of coexistence is different than the long-term stability marked by the tendency of a species to recover after falling to a low density (Chesson 2000a).

Elucidating the presence and mechanisms of coexistence can have important practical consequences for invasive species management because the ability to distinguish nonnative species with negligible effects (e.g., those that can stably coexist with native species) from those causing significant damage (e.g., those competitively excluding native species) would allow managers with limited money, time, and personnel resources to prioritize their efforts (Hiebert 1997). Assessing coexistence requires knowledge of the species' life cycle, basic habitat requirements, means of dispersal, reproductive capacity, and function in its invaded range (Grice 2009). Unfortunately there is little published quantitative information on the effects of most nonnative species, so management actions often are based on anecdotal information or subjective assessments (Parker et al. 1999). Further, the invasion literature may be biased toward studies finding large ecological impacts because positive results are more likely to be published (Simberloff 1981, 1986), leading to the conclusion that most invasive species will be destructive and will need to be aggressively controlled. Better information on low-impact species will help to distinguish these from high-impact species and lead to a better understanding of the relative harm a species may cause (Byers et al. 2002).

In this paper we examine the interactions between the native Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) (COAS) and the closely-related nonnative *Succinea* sp. B (Sp. B) with the goal of determining if these species are capable of coexisting. To this end, we combined quantitative field data on the competitive interactions, habitat use, and population ecology of the two snail species to examine their potential for coexistence. Specifically, we performed *ex situ* competition experiments to establish the nature and strength of the competition between the species, we quantified habitat use to examine their potential for resource use overlap (a necessary condition for *in situ* competition), and we conducted mark-recapture surveys to examine the population level effects of the invasive snail on the native snail (e.g., population trends) as well as factors that may mediate the interactions between the species such as within year changes in abundance and size distribution. Using the results of this work, we examine the roles of competitive exclusion and coexistence in the long-term persistence of this species and propose a novel mechanism that may be promoting their coexistence. We conclude by discussing the implications of this research for the management of these two species and of invasive species in general.

Methods

Study system

The Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) (COAS) is a federally-threatened and state-endangered species of terrestrial succineid snail that is endemic to the spray zone of a single waterfall in central New York (Plate 1A). Specifically, it occurs at the base of the 51-m (167-foot) tall Chittenango Falls (N 42.97869 / W 75.84161) that are formed by Chittenango Creek as it flows northward out of Cazenovia Lake to its outlet in Oneida Lake (Plate 2). The falls and gorge are entirely within Chittenango Falls State Park in Madison County, New York.

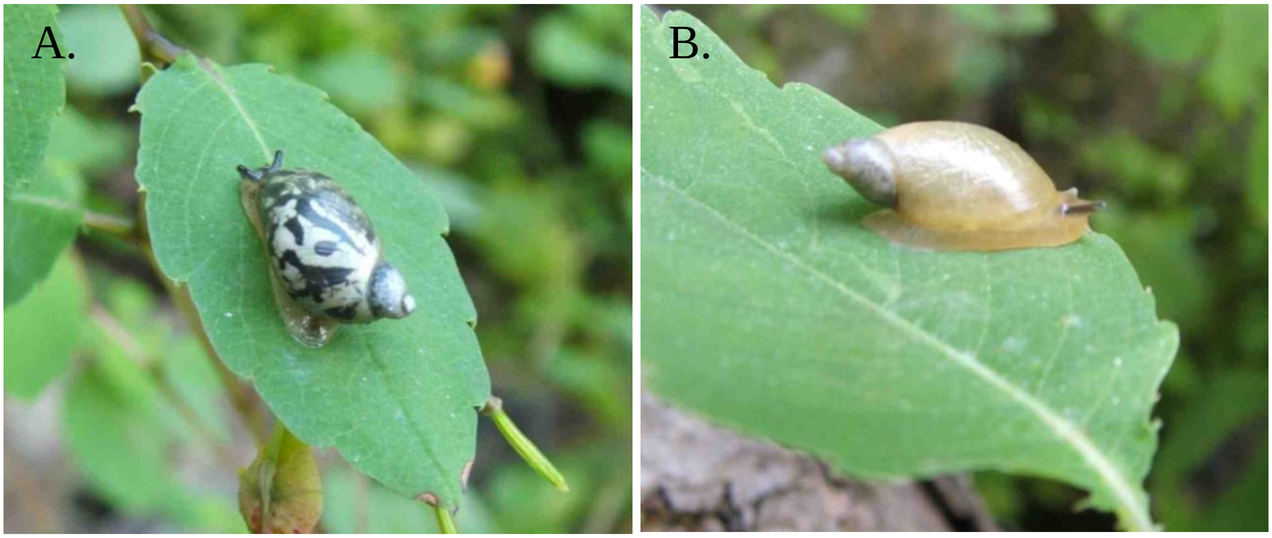

Plate 1. Comparison of the Chittenango Ovate Amber Snail (*Novisuccinea chittenangoensis*) (A) and *Succinea* Sp. B (B).

The invasive snail *Succinea* sp. B (Sp. B) is a related species from the *S. putris* species complex that may (Hubricht 1985) or may not have been introduced from Europe (Hoagland and Davis 1987) (Plate 1B). Regardless of its origin, it is thought to have arrived at the falls at least by 1981, after which its population increased rapidly from 200-300 adults in 1982 to over 3000 adults in 1984 (pers. comm., A. Breisch to J. Deisler, 1986). Sp. B occurs throughout the Chittenango Creek watershed, the neighboring watersheds of the Chenango River and Oneida Creek (Molloy 1995), and is likely widespread outside of these watersheds. It is currently the most abundant snail at the falls.

Little is known about COAS biology and ecology, in part because early efforts to study COAS were complicated by identification problems. Because of its similarity to COAS, the arrival of Sp. B went unnoticed for several years and studies during that time mistakenly grouped these two species together (Aloi and Ringler 1982, Aloi 1985, Thomee 1986). However, Hoagland and Davis (1987) resolved the identification problems of the succineid snails at Chittenango Falls using electrophoresis, shell morphology, and internal anatomy. Subsequent work on COAS has reliably distinguished between these two species. In 2003, King (unpublished data) further investigated the relationship between COAS and Sp. B by amplifying and sequencing regions of mitochondrial and nuclear DNA in COAS and Sp. B. He found a sequence divergence of 10-15 percent, which suggests large differences between the two species, and no evidence of hybridization.

The reliable information that exists on COAS biology and ecology is largely from anecdotal observations, efforts to establish a captive population (Molloy 1995), and informal population surveys (USFWS 2006). From these sources of information, we know that COAS is restricted to a vegetated limestone rock ledge immediately east of the base the falls (Plate 3). This location provides a relatively cool, partially sunlit area of lush herbaceous growth within the spray zone of the falls. COAS mates from May through July and oviposits clusters of 8-14 eggs (Molloy and Norton 1993) from June through July at the base of plants, under matted vegetation, or in loose, wet soil. The young snails hatch in 2 to 3 weeks, measuring 2 mm in length. Although it remains unclear when the snails mature, they probably reach maturity in five to eight months (i.e., the spring following hatching) when they measure around 10 mm (Grimm 1981, Aloi and Ringler 1982). By the end of the following year, the adult snails reach a length of approximately 21 mm; they then die, completing a life span of about 2.5 years (USFWS 2006). COAS is thought to feed on microflora and be preyed upon by beetles and sciomyzid fly larvae, salamanders, small mammals, and birds but neither of these aspects of its biology have been thoroughly studied. Until this study, rigorous and reliable population estimates have been made for COAS.

Plate 2. The Chittenango Ovate Amber Snail is endemic to the spray zone of Chittenango Falls within Chittenango Falls State Park in Madison County, New York.

Even less is known about Sp. B at the falls. Prior to this study, Molloy (1995) examined substrate preference of Sp. B along the stream banks of Chittenango Creek upstream from the falls and its dispersal ability through the water. Due to its numerical dominance and co-occurrence with COAS, Sp. B is presumed to be competing with COAS, but there is no empirical evidence to support or refute this claim.

We examined the interactions of these two snails within a 15 m × 3m transect that extends eastward along the rock ledge away from the falls (Plate 3). While some snails occur in the largely inaccessible area directly above the transect, the transect encompasses nearly the entire range of COAS. The rock ledge is covered by scree to the east (farthest from the falls) and lush vegetation to the west (closest to the falls). The vegetation is dominated by *Nasturtium officinale* closest to the falls, and *Impatiens* spp. and *Eupatorium purpureum* farther away from the falls.

Plate 3. Section of vegetated limestone rock ledge to which COAS is restricted. Orange flags mark the baseline of the transect used in the mark-recapture and habitat surveys.

Field methods

Competition experiments

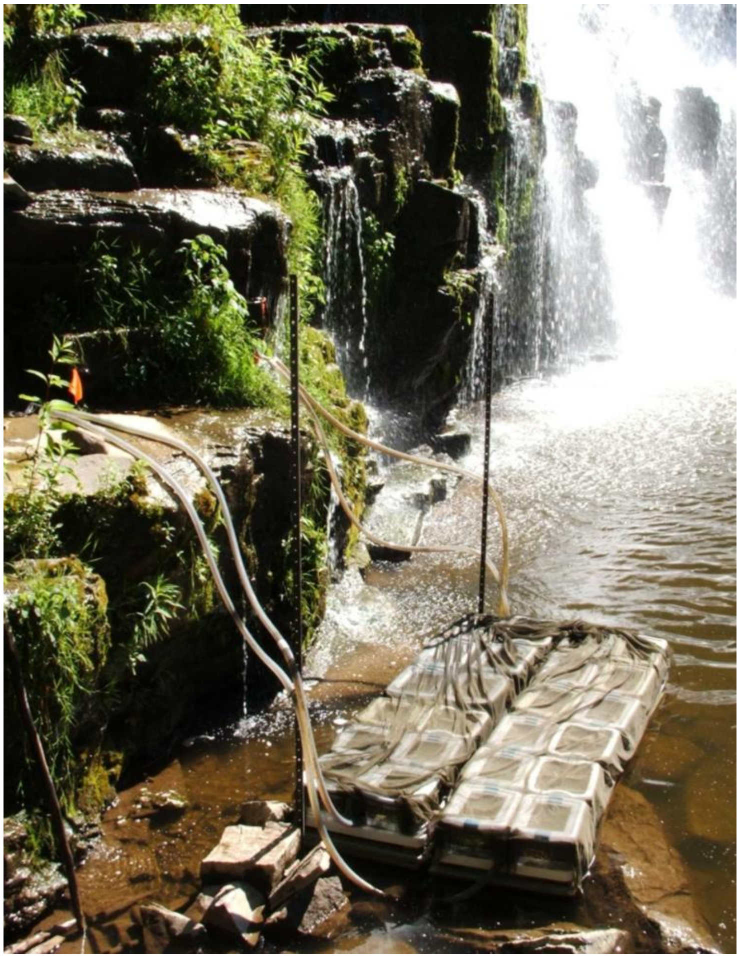

Plate 4. Experimental setup to assess competition between COAS and Sp. B.

We assessed the competitive effects of Sp. B on COAS by evaluating growth rates of COAS and Sp. B under increasing densities of Sp. B within experimental enclosures constructed from 24 13.2-L (12-quart) rectangular plastic containers with locking tops. The sides, top, and bottom of each container were removed such that only the frame remained. Each container was divided in half (17L×25W×15D cm = 6375 cm^3), yielding a total of 48 experimental enclosures, and lined with mosquito netting to allow contact with ambient air. We placed 12 enclosures (6 containers) each on four floating platforms near the base of falls and irrigated the enclosures with water from the falls (Plate 4).

We performed two competition experiments using this experimental setup. In the first experiment (i.e., density competition) we examined the effects of Sp. B density on the growth and mortality of COAS and itself using a randomized block design in which 3 replicates of 4 density treatments were randomly distributed on each of the four floating platforms. Treatments consisted of 1 COAS with 0, 10, 25, or 50 individuals of Sp. B. These ratios spanned the range of natural densities of Sp. B and COAS. We haphazardly selected snails for inclusion in the experiment (i.e., we made no effort to control the size of the snails). Nevertheless, there were no differences in the average size of snails among the treatments (COAS: ANOVA, $F_{3,34} = 0.30$, $p = 0.8265$; Sp. B: Nested ANOVA, $F_{2,30} = 0.56$, $p = 0.5757$). Concerns for the small population size of COAS prevented experiments with reciprocal treatments (i.e., 1 Sp. B with 0, 10, 25, or 50 COAS).

A total of 1068 snails (48 COAS and 1020 Sp. B) were required to populate the experiment. To reduce the handling time for snails, we initiated the experiment over a two-day period (9 and 10 July 2008). Most snails were gathered on 9 July during a mark-recapture survey and additional individuals of Sp. B were gathered from vegetation below the base of the falls. One COAS and 10 Sp. B were marked in each treatment, with the exception of the treatment with no Sp. B (where only the single COAS was marked). We measured the shell length of marked snails and placed them in enclosures with the appropriate number of unmarked snails, approximately 125 g (wet mass) of *Nasturtium officinale*, and a roughly fist-sized rock.

Nasturtium officinale was used as a standardized food source because it was widely available outside the study area and was known to be used by both COAS and Sp. B.

Each enclosure remained in the experiment for 15 days, at which point we measured the surviving marked snails and counted the number of dead snails in each enclosure to quantify mortality for each treatment. We did not measure snails that were dead because they were unable to grow for the full time period and because shells may decrease in size after the death of the snail. Upon completion of the experiment COAS were released back into their range whereas Sp. B were released downstream of the falls.

Based on our initial observations, we designed a second experiment in 2009. This experiment investigated the interaction between the size and density of Sp. B. on the growth and mortality of both COAS and Sp. B (i.e., size × density competition). The setup for this competition experiment was the same as that of the density competition experiment except for the treatments and timing of the experiment. There were five treatments allocated among the 48 enclosures: 8 enclosures with 1 COAS and 0 Sp. B that acted as controls and 10 enclosures each containing 1 COAS with 10 small (6-10 mm) Sp. B, 50 small Sp. B, 10 large (> 13 mm) Sp. B, or 50 large Sp. B. The average size of "small" ($\bar{x}$ = 8.5 mm, sd = 1.1 mm) and "large" ($\bar{x}$ = 14.5 mm, sd = 1.7 mm) snails used in the treatments were significantly different and showed little overlap in their distributions. We randomized the locations of the treatments among all the enclosures and populated the enclosures with 1248 snails (48 COAS, 600 small Sp. B and 600 large Sp. B) on 16 and 17 July. Each enclosure remained in the experiment for 14 days at which time snails were measured and released.

Habitat use surveys

To assess habitat segregation via differential resource use, we examined *in situ* habitat use of COAS and Sp. B at two levels: the specific plant species and substrate on which snails occurred as well as the "patch" type within which snails were found. To determine on which plant species and substrate types each snail species was occurring we searched for snails along a 12-m transect running east from the falls into the talus slope. We divided the transect into 1-m intervals and searched for snails within 1 m on either side of the transect (i.e., 2-m^2 blocks). Each block was searched 5 times from 21 July and 21 September 2008 between 10:00 and 14:00 and under wet and dry conditions. We searched each block exhaustively for COAS and stopped searching for Sp. B after 3 individuals were encountered. Upon encountering a snail we recorded its coordinates from the 1-m node of the transect (x = parallel to transect, y = perpendicular to transect), species, shell length, and tag (if marked). We also recorded the plant species or substrate type (detritus, wood, soil, rock) on which the snail occurred (Table 1). If the snail was on a plant we recorded the decay class (living, intermediate, dead) of the part of the plant on which the snail was found.

For patch-level habitat use we determined the availability of vegetation and substrate types in the study area by mapping the vegetation within the 2 m × 12 m transect from 19-27 August 2008. This area covered the entire area of the habitat use surveys and overlapped a significant portion of the area in which most of the snails were collected during the mark-recapture surveys. Within this area we delineated vegetation and substrate patch type based on the dominant plant species or substrates of each patch and plotted the locations of snails on the resulting vegetation map to assess how snails were distributed among the patch types.

Table 1. Plant species and substrate types on which at least three snails were found during habitat use surveys between 21 July and 21 September.

Plant Species		
Common Name	Scientific Name	Species Code
Clearweed	*Pilea pumila*	Pipu
Graminoid		Gram
Low Herbaceous		Lohe
Moss		Moss
Northern White Cedar	*Thuja occidentalis*	Thoc
Peppermint	*Mentha piperita*	Mepi
Purple Loosestrife	*Lythrum salicaria*	Lysa
Purple-stemmed Aster	*Aster puniceus*	Aspu
Sweet-scented Joe-Pye Weed	*Eupatorium purpureum*	Eupu
Touch-me-not or Jewelweed	*Impatiens sp.*	Imsp
True Forget-me-not	*Myosotis scorpioides*	Mysc
Turtlehead	*Chelone glabra*	Chgl
Unknown 2[a]		Unk2
Watercress	*Nasturtium officinale*	Naof
White Snakeroot	*Eupatorium rugosum*	Euru
Wild Mint	*Mentha arvensis*	Mear
Willow	*Salix sp.*	Salix
Substrate Type		
Detritus		Det
Soil		Soil
Rock		Rock
Wood		Wood

[a] Plant species still needs to be identified.

Mark-recapture surveys

We conducted mark-recapture surveys to estimate the population size of COAS between 2002-2005 and 2007-2009. In 2006, surveys were not conducted due to safety concerns following a rockslide. These surveys also yielded data on the abundance and spatial distributions of COAS and Sp. B. and the size structure of COAS populations. The size structure for Sp. B populations was only collected in 2008 and 2009.

Surveys were conducted weekly for 16 weeks during 2002 and for 10 weeks during 2007 but in the remaining years 10-12 surveys were conducted every two weeks. Surveys occurred between 4 May and 15 October of each year (Table 2). We conducted mark-recapture surveys along a 15-m transect that overlapped the habitat use transect and extended three more meters into the talus slope (Plate 5). The transect was divided into 1-m block intervals, with each block arbitrarily divided into lower, middle, and upper zones (based on terrain). Each zone was searched for 5 minutes. We placed all snails encountered in containers labeled with the respective block and zone. Surveys were generally started between 9:30 and 10:00 in the morning and continued until all blocks were sampled.

Plate 5. Volunteers helping in a mark-recapture survey in 2008.

We separated and counted snails by species. Snails that we could not reliably identify, typically because they were too small (< 5 mm), were measured and counted as unknown. For all COAS, we measured the shell length (apex of the spire to the anterior-most part of the shell), and for those > 8.5 mm we marked them by affixing bee tags (www.beeworks.com) to the ventral surface of the shell's spire with a drop of cyanoacrylate gel adhesive (Plate 6). All COAS and unknown snails were returned to the zones from which they were removed. We also recorded shell lengths of Sp. B and the zones in which they were found before disposing of them by freezing.

Table 2. Basic information for mark-recapture surveys of the Chittenango Ovate Amber Snail from 2002-2009.

Year	Start Date	End Date	No. of Surveys	Days Between Surveys
2002	1 July	16 October	16	7
2003	4 June	8 October	10	14
2004	5 May	6 October	12	14
2005	4 May	21 September	11	14
2006	1 June	---[a]	1[a]	---[a]
2007	28 June	30 August	10	7
2008	12 June	15 October	10	14
2009	18 June	22 October	10	14

[a] Due to a rockslide, surveys were curtailed for safety reasons in 2006.

Plate 6. Tags used for marking snails. Tags, which are the same as those used for marking queen bees (www.beeworks.com), come in five colors (white, blue, neon green, orange, and neon yellow) and are numbered from 1 to 99.

Data analysis

Competition experiments

We examined the nature and strength of competition between COAS and Sp. B using the growth rate of snails. Up to 10 marked Sp. B and one COAS survived in each enclosure, so we used average growth rate of Sp. B and growth rate of COAS in each enclosure as our dependent variables in the ANOVAs. For the density competition experiments, we examined the differences in average growth rates among the four density treatments (1 COAS and 0, 10, 25, or 50 Sp. B). For the size × density competition experiments, we were interested in the tradeoff between density and size in combination (e.g., is the competition intensity between 10 large Sp. B equal to 50 small Sp. B), so we examined the five size and density combinations as main effects rather than as interactions between size and density. To test for differences in all pair-wise comparisons, we used the post hoc Fisher's least significant difference test. Where necessary we log transformed growth rates to meet the assumptions of normality and equality of variance, however the test results were qualitatively the same as the untransformed data so we present the results of the untransformed data.

Because some snails died during the experiment we also compared percent mortality among the treatments of each experiment. There was only one COAS per enclosure, so percent mortality for a treatment was calculated as the percentage of enclosures in a given treatment in which a snail died (i.e., there was only one measure per treatment). However there were 10 Sp. B in each enclosure, so percent mortality was calculated for each enclosure before comparing among treatments. To compare mortality among treatments for Sp. B, we used ANOVAs followed by Fisher's least significant difference tests where the ANOVA indicated a significant difference among the means.

Habitat use surveys

We tested for differences between COAS and Sp. B in their use of plant species and substrate types and decay classes of plants with χ^2 tests of independence. If there was a lack of fit, we examined the adjusted residuals of each cell of the contingency table to see where the lack of fit occurred. Cells with adjusted residuals that exceeded two in absolute value were considered to have contributed significantly to the overall lack of fit (Agresti 1996). To meet the assumptions of the χ^2 test, we combined 13 plant species and substrate types that were rarely used into an "other" category.

Because we encountered a different number of COAS and Sp. B, species' use is presented as a percentage of the total number of conspecifics in the sample. We also note that comparisons should be limited to within a given plant species or substrate types and decay class because differences in our search effort and snail detectability on different plants and substrates bias the comparisons among plant and substrates. For example, both species appeared to use *Eupatorium purpureum* and *Impatiens sp.*, more than other plant species. However, we spent more time searching the leaves of *Eupatorium purpureum* late in the season because COAS tended to occur there. Therefore we were more likely to find more snails of both species using this plant relative to other plants. Likewise, the more open architecture of *Impatiens sp.* probably made it easier to detect snails on those plants than on plants in which many of the leaves and stems were obscured from view.

For patch level habitat associations, we did not collect enough data for individual snails to estimate individual use and some individual animals were not identified, so our study design was based on collective use vs. collective availability (Design I *sensu* Thomas and Taylor 1990, 2006). Specifically, we used a χ^2 goodness-of-fit test to examine if there was an overall difference in use and availability followed by an examination of confidence intervals on the proportional use to see if proportional use was greater or less than the proportion expected based on availability (Neu et al. 1974, Alldredge and Griswold 2006). For this analysis, we combined 10 patch types into an "other" category because their areas were so small that their expected counts led to the violation of assumption of a chi-square analysis. Together these habitat types represented only 16% of the total area.

During data collection, some marked COAS were observed more than once, so for the χ^2 tests we only used one randomly selected incident of each marked snail to avoid pseudoreplication (i.e., an artificial increase in sample size due to the disproportionate representation of some individuals). In contrast, many of the snails we observed were unmarked, leading to an unknown degree of pseudoreplication. However, given that few marked snails (19%) were observed more than once, despite the greater detectability caused by the tags, we believe that unmarked snails were even less likely to be re-sampled, making the issue of pseudoreplication nominal among this portion of the sample.

Mark-recapture surveys

To estimate population size, we assumed that the population was open, because individuals most likely moved between the part of the ledge we could sample and a higher part of the ledge, which we could not readily sample. We also limited our data to snails that were living at the time they were found. Marked snails that were dead when recovered were removed from consideration following the recovery occasion. Thus, we used Jolly-Seber models, which allow for open populations.

We used the POPAN formulation of the Jolly–Seber model in Program MARK (White and Burnham 1999) to estimate abundance. Under this formulation, model parameters include probability of capture at sampling occasion i (p_i), apparent survival between occasions i and $i + 1$ (φ_i), and the probability of an animal entering the population (b_i) between occasions i and $i + 1$ and surviving to occasion $i + 1$ (Schwarz and Arnason 2008). Abundance (N) is derived from these parameters. For each year we built four *a priori* candidate models based on the combinations of p and φ being variable with time or constant and b being variable with time (i.e., [$p(t)$, $\varphi(t)$, $b(t)$], [$p(.)$, $\varphi(t)$, $b(t)$], [$p(t)$, $\varphi(.)$, $b(t)$], [$p(.)$, $\varphi(.)$, $b(t)$]). Parameters were estimated via numerical likelihood and the best models were selected using the sample-size corrected AIC ($\mathrm{AIC_c}$) or the quasi-likelihood adjusted AIC ($\mathrm{QAIC_c}$), when data were overdispersed. The models with the lowest $\mathrm{AIC_c}$ or $\mathrm{QAIC_c}$ were ranked the best. Before models were compared we conducted goodness-of-fit tests on the most parameterized (i.e., saturated) models using the sub-module Release and adjusted the likelihood of the models if the data were overdispersed (i.e., if the variance inflation factor exceeded unity) (Cooch and White 2008).

Although we recorded the number of Sp. B we collected, we did not mark Sp. B so we were unable to directly estimate its population size in the sampling area. Instead, we obtained estimates of population size for Sp. B by regressing the MARK population estimates of COAS on the total number of COAS captures for the year and used this fitted regression line to estimate the population size of Sp. B in each year based on its total number of captures in that year.

We calculated growth rates of each marked COAS in a year using the difference in lengths measured at the earliest and latest dates of recapture divided by the number of days comprising that period. Growth rates were then scaled to a two-week interval for comparison with the growth rates from the competition data. We also calculated growth rates of COAS during early (before 8 August) and late (after 8 August) periods of each year. These periods corresponded to the times of the year when the size distribution Sp. B was dominated by large and small individuals, respectively (see *Results: Mark-recapture surveys*). Most of the length data for these analyses came from mark-recapture surveys, but we also measured lengths of marked snail during habitat use surveys, before they were used in the competition experiment, and during chance recaptures. Observations of snails after they were used in the competition experiments were not used in the calculation of growth rates. To minimize the influence of measurement errors over short time intervals, we excluded snails with length measurements that were made less than two weeks apart. Growth rates were not normal, so we tested for differences among years and between early and late periods using Kruskal-Wallis tests.

Results

Competition experiments

In the density competition experiment, the magnitude and trends of COAS and Sp. B growth rates were similar. Over the two-week period growth rates for both species declined at increasing densities of Sp. B (Fig 1). COAS growth rates were not affected by the presence of 10 Sp. B, but were 73 and 83% lower at densities of 25 and 50 Sp. B, respectively (Fig. 1A; $F_{3, 34} = 10.45$, $p < 0.0001$). Growth rates of Sp. B showed no difference between treatments containing 10 and 25 snails, but there was a 62% reduction in growth rate in the presence of 50 conspecifics (Fig. 1B; $F_{2, 30} = 10.71$, $p = 0.0003$). A total of 7 COAS (14%) died during the experiment with a tendency for higher mortality at higher densities of Sp. B (Fig. 2A). Sp. B mortalities did not differ with densities of conspecifics (ANOVA: $F_{2,32} = 0.85$, $p = 0.4365$); however, mortality rates at a given density were greater for Sp. B than COAS (Fig. 2A).

In the size × density competition experiment, Sp. B growth rates were 2.6-6.3 times greater on average than were COAS growth rates (Fig. 3). Similar to the previous experiment, COAS growth rates did not decline in the presence of 10 small Sp. B, but they did decline in the presence of greater numbers and larger sizes of Sp. B ($F_{4, 38} = 10.34$, $p < 0.0001$). On average, COAS growth rates were depressed by 40 and 50% in the presence of large versus small snails present at low and high densities, respectively (Fig. 3A). Interestingly, 50 small Sp. B had an equivalent competitive effect on COAS growth rates as 10 large snails. The average growth rates of Sp. B were 56 and 75% lower on average in the presence of large versus small snails at low and high densities, respectively ($F_{3, 36} = 53.53$, $p < 0.0001$). The intraspecific competitive effect was greater for large conspecifics, with the presence of 10 large snails reducing Sp. B growth rates more than 50 small snails.

Differences in mortality rates in the size × density competition experiment were consistent with the expectations of intraspecific competition ($F_{3,35} = 6.85$, $p = 0.0009$). In general morality rates were higher for Sp. B than COAS and mortality rates were highest in the treatment with 50 large Sp. B (Fig 2B). Only 4 COAS died in the size × density competition experiment and there was no discernable pattern to their mortality.

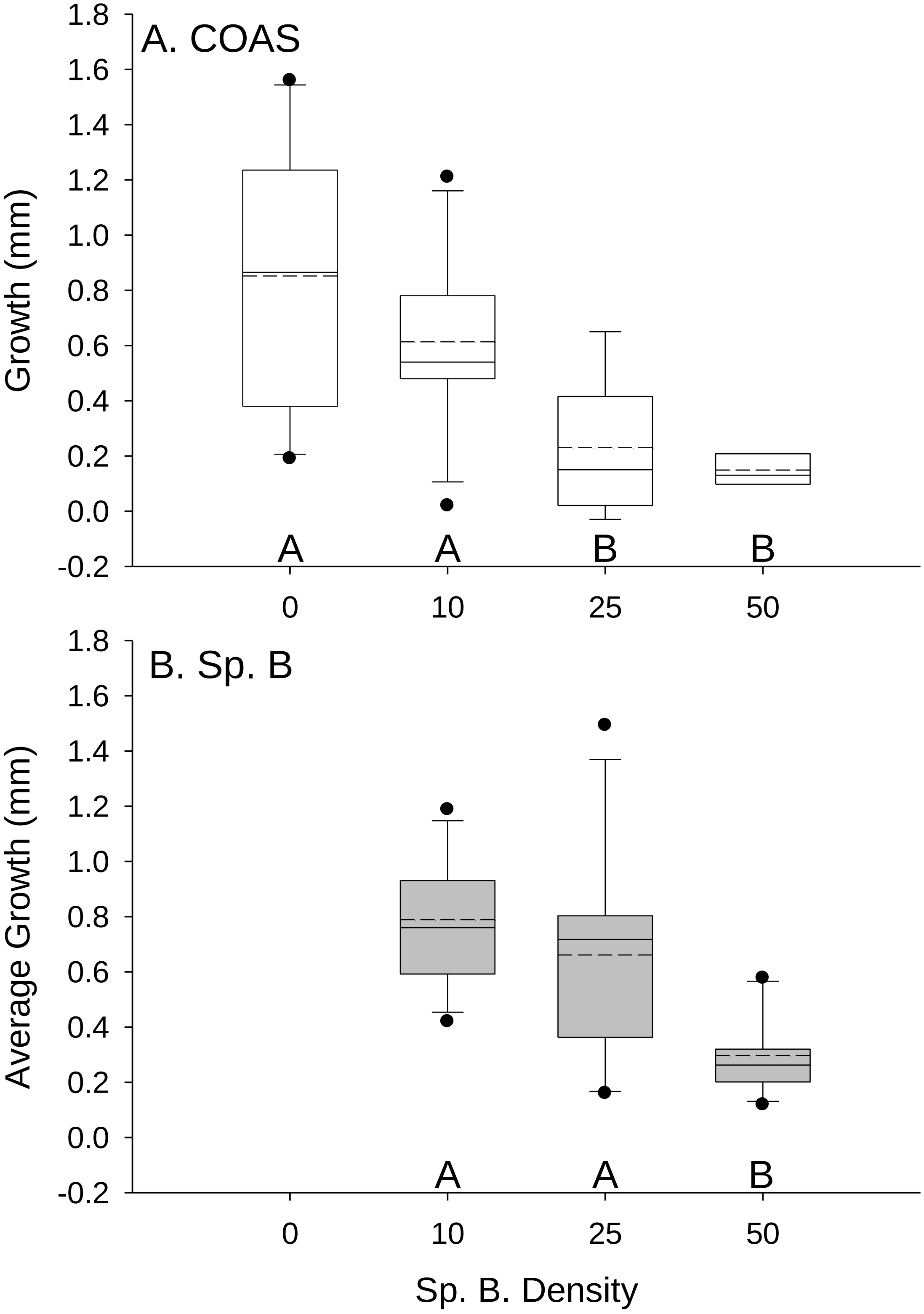

Figure 1. Growth of COAS and average growth per experimental enclosure of Sp. B at different densities of Sp. B. Average growths per enclosure of Sp. B are based on a maximum of 10 individuals. Different letters indicate groups are significantly different. Dashed horizontal lines represent average growth and whiskers represent the 10th and 90th percentile.

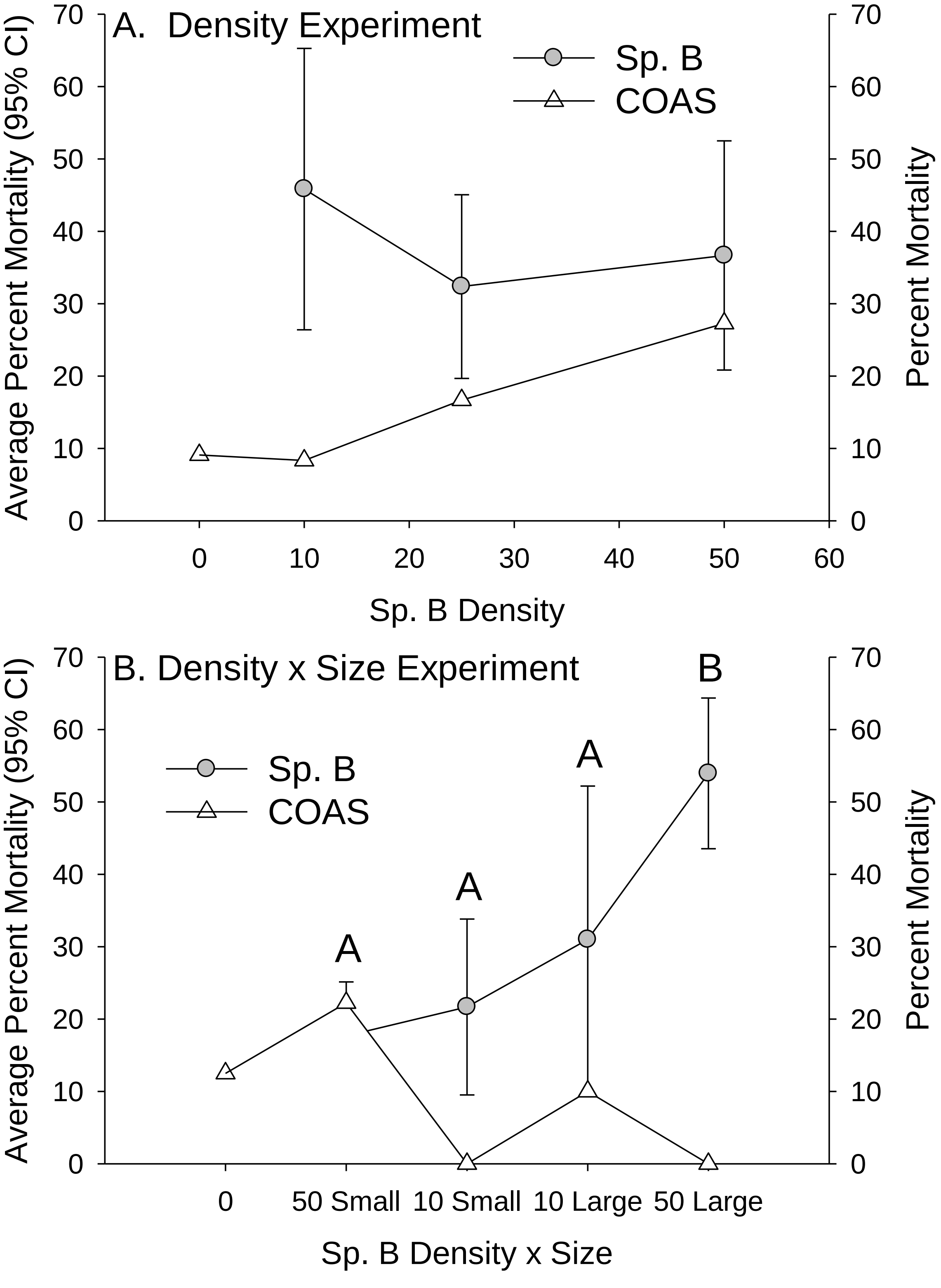

Figure 2. Percent mortality of COAS in each treatment and average percent mortality of Sp. B in each enclosure over a two week period when subjected to different densities of Sp. B (A) and different combinations of densities and sizes of Sp. B (B).

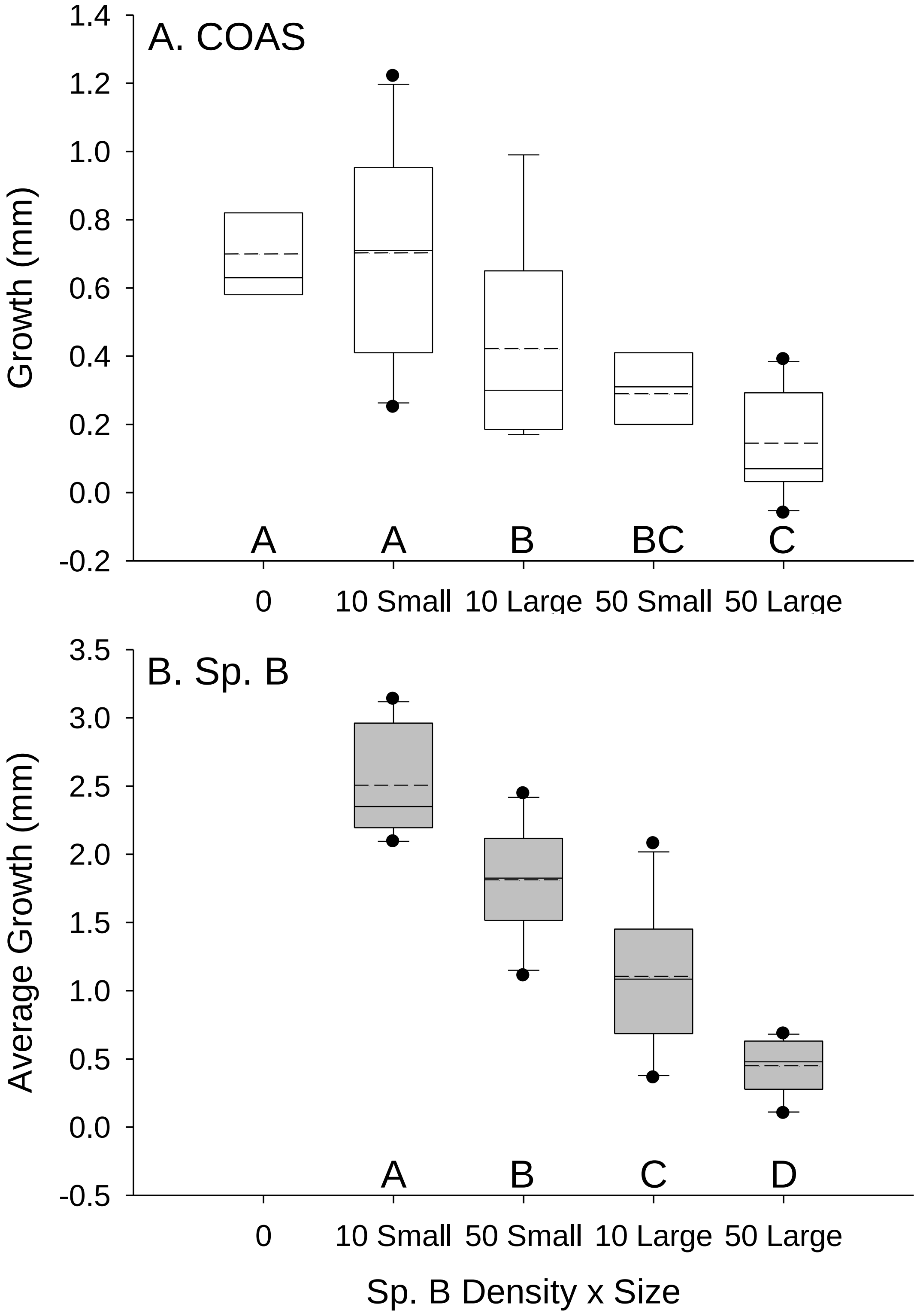

Figure 3. Growth of COAS and average growth per experimental enclosure of Sp. B at different combinations of size and density of Sp. B. Average growths per enclosure of Sp. B are based on a maximum of 10 individuals. Different letters indicate groups are significantly different. Note the different order of the treatment combinations on the x-axis. Dashed horizontal lines represent average growth and whiskers represent the 10th and 90th percentile.

Habitat use surveys

We obtained 285 observations of habitat use: 151 Sp. B, 130 COAS, and 4 snails that were too small to be accurately identified to species. Fifty-three observations of COAS were from 42 marked individuals (3 snails appeared 3 times, 5 snails appeared twice, and 34 snails appeared once). After randomly removing repeat occurrence of these individuals, 119 observations of COAS remained.

COAS and Sp. B exhibited a high degree of overlap in the plant species and substrate types on which they were found (Fig. 4). Nevertheless, some differences existed (χ^2_{10} = 27.86, p = 0.0019). Most notably, Sp. B was more prevalent on *Nasturtium officinale* than was COAS (adjusted residual = 4.03). In contrast, COAS used dead wood, detritus, and *Eupatorium purpureum* more than Sp. B, but only the use of wood was significantly different (adjusted residual = 2.28). COAS also occurred more often on parts of plants that were dead (adjusted residual = 4.62) whereas Sp. B occurred more often on parts that were living (adjusted residual = 4.23) (χ^2_2 = 22.97, p < 0.0001) (Fig. 5). Each species used the intermediate decay class equally.

The map of the dominant vegetation and substrate types across the study area showed that *Nasturtium officinale* dominated the end closest to the falls and rocks from the rockslide in 2006 dominated the end farthest from the falls (Fig. 6). The central part of the transect was composed primarily of patches of *Impatiens* sp. and *Eupatorium purpureum*. Neither snail species was distributed randomly with respect to these different patch types (COAS: χ^2_5 = 32.92, p < 0.0001; Sp. B: χ^2_5 = 103.23, p < 0.0001). COAS selected patches of *Eupatorium purpureum* and avoided areas dominated by rocks and *Nasturtium officinale* (Table 3). COAS also selected the aggregate “other” category, but its mixture of patch types make its interpretation difficult. Sp. B selected patches of *Impatiens sp*. and *Pilea pumila* and avoided rocky areas (Table 3). The other areas were used in proportion to their availability.

Mark-recapture surveys

The best models for estimating COAS survival rates and population size (i.e., models with lowest AIC_c and $QAIC_c$ scores) varied among years, but in general models in which survival was constant were selected as the best (Table 4). The population estimates from these models indicate that the population size was lowest in 2003 and that over the next two years there was a large increase in the population size (Fig. 7). It peaked in 2005, the year before the rockslide, at 784 snails and declined in the two years after the rock slide before stabilizing in 2008 at 323 individuals and increasing slightly in 2009 to 339 individuals (Table 4). Survival and recapture probabilities and population estimates for each sampling occasion are listed in Appendix A.

The temporal patterns in the number of observations of each species of snails were relatively consistent among years (Fig. 8). Numbers of Sp. B in a survey peaked around mid-June and were lowest in mid-August before showing a secondary peak in numbers in mid-September (Fig. 8B). This pattern corresponds with shifts in the size distribution of the population (Figs. 9B and 10B), such that early in the season the majority of the population is large (> 10 mm) and total counts are high and late in the season most of the population is composed of small snails (< 10 mm) and the total counts are low. Thus, the bimodal distribution of counts is likely a result of a size-dependent detection bias combined with a shifting size distribution of the population. Early in the season, the total counts are high because the majority of the population is large and easier to detect. Late in the season the large snails are replaced with small individuals that are difficult to detect. As these snails grow, their detectability increases, as does their occurrence in the sample. The same patterns of abundance and size distribution did not exist for COAS. The size distribution and number of snails collected fluctuated but remained more uniform over the course of a year (Figs. 8A, 9A and 10A).

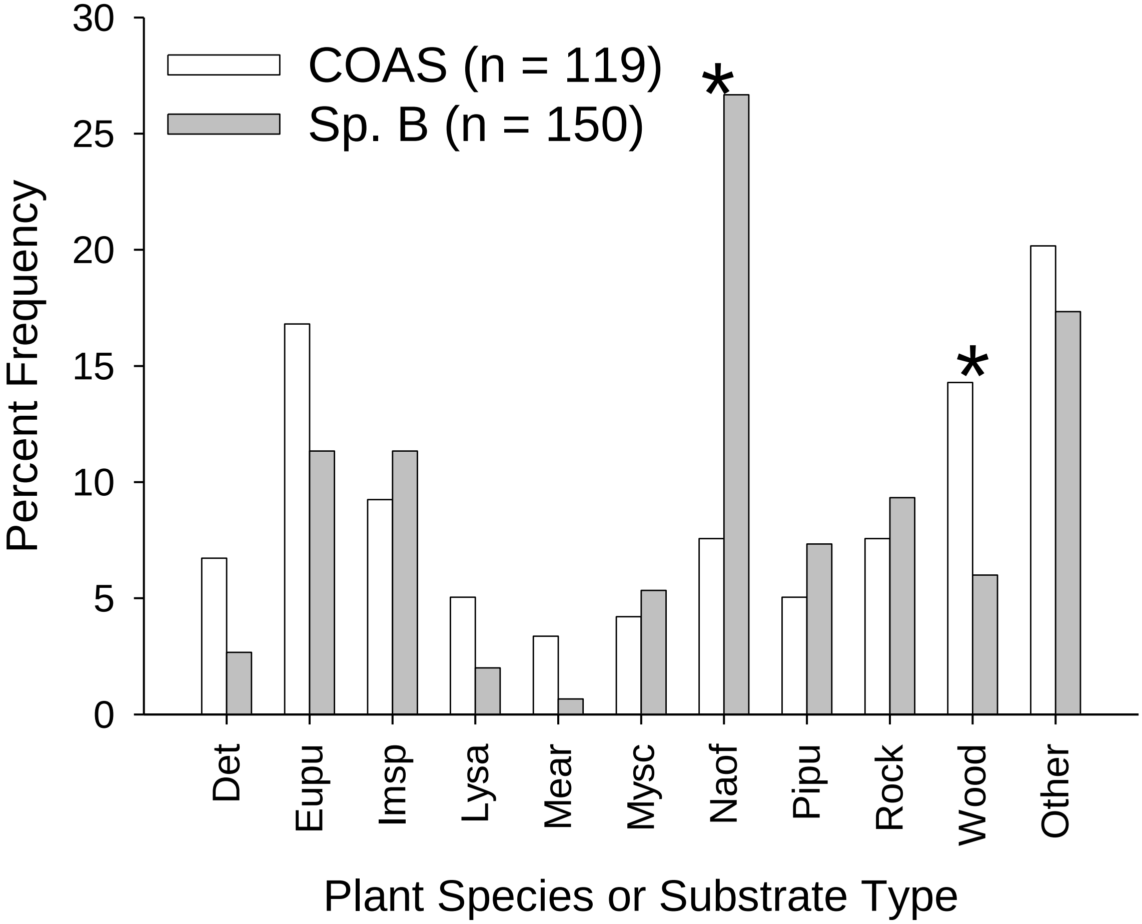

Figure 4. Comparison of relative use of plant species and substrate types use by COAS and Sp. B. Asterisks indicate which plant species and substrate types contributed to the overall difference between species (i.e., had adjusted residuals greater than 2 in absolute value). Codes for plant species and substrate types are in Table 1.

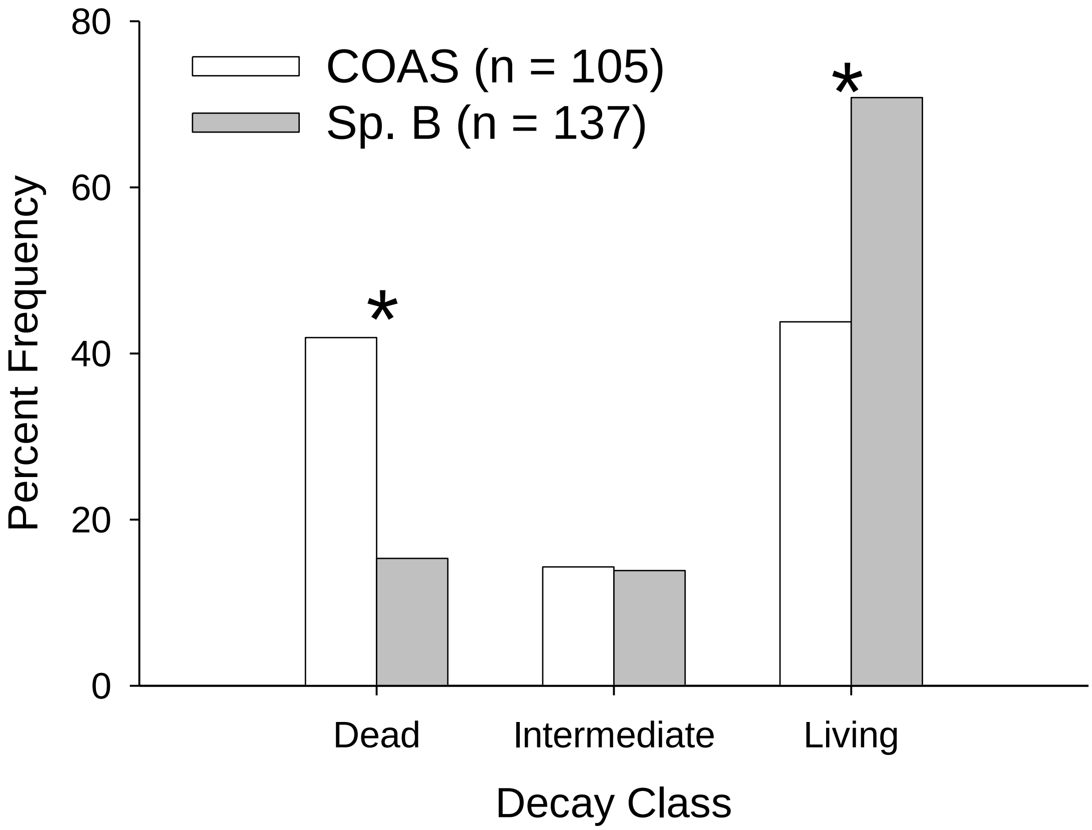

Figure 5. Comparison of relative use of decay classes of plants used by COAS and Sp. B. Asterisks indicate which plant species and substrate types contributed to the overall difference between species (i.e., had adjusted residuals greater than 2 in absolute value).

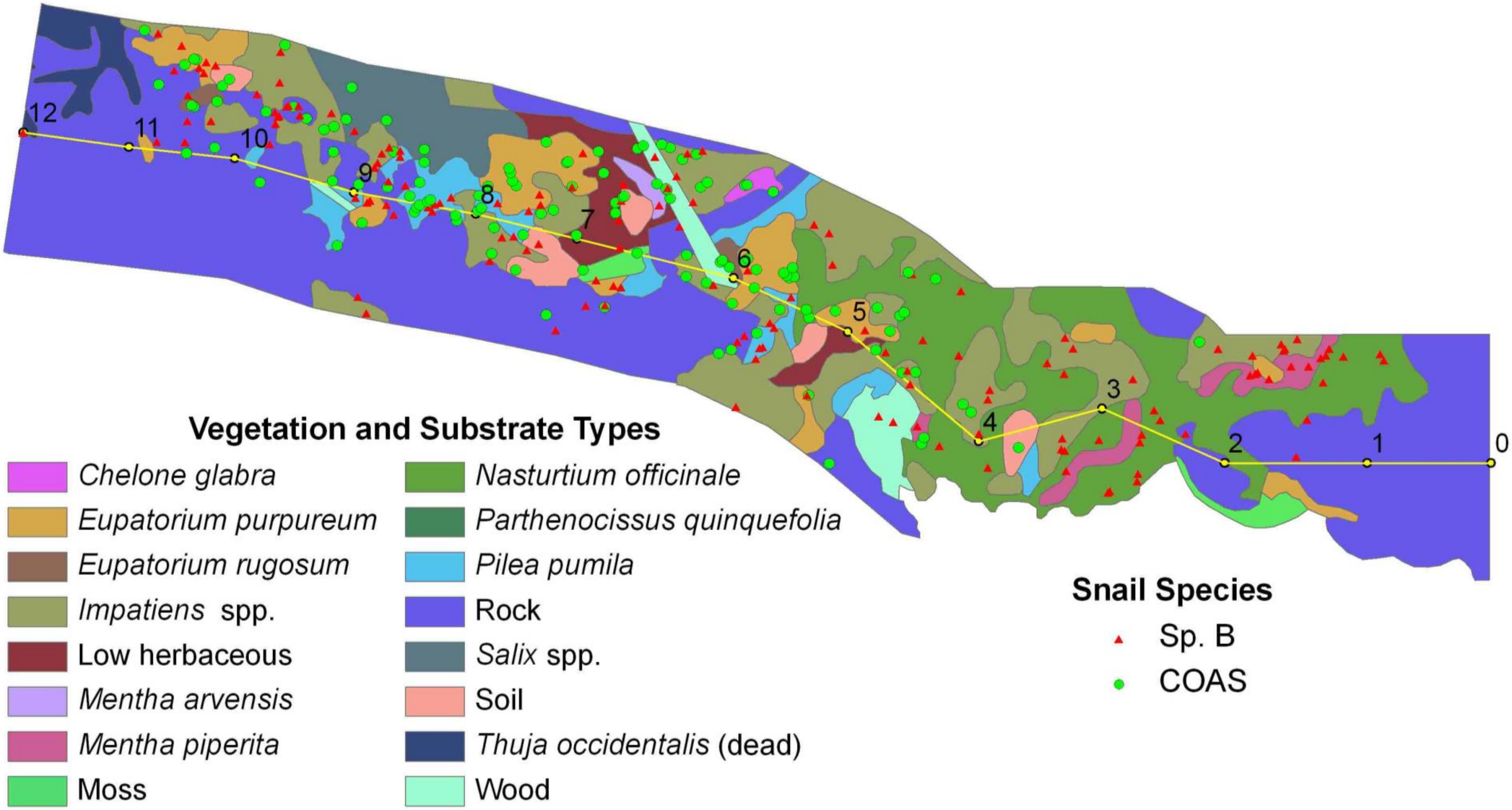

Figure 6. Map of vegetation and substrate types and locations of snails observed during habitat use surveys. Vegetation and substrate types are categorized by dominant plant species and substrates. Transect is approximately 2 m × 12 m.

Table 3. Observed and expected occurrence of COAS and Sp. B on different vegetation and substrate types near the base of Chittenango Falls in 2008 and the selection of each vegetation and substrate type based on the comparison of proportional use and availability.

Species	Vegetation or Substrate	Code	Area (m^2)	Prop. of Total Area	No. of Snails Observed	Expected No. of Snails[a]	Prop. Observed in each Type	90% CI on Prop. Observed[b]	Selection
Sp. B	*Eupatorium purpureum*	Eupu	1.419	0.06	17	9	0.11	0.05-0.17	None
	Impatiens sp.	Imsp	4.139	0.18	44	28	0.29	0.20-0.38	Selected
	Rock	Rock	9.401	0.41	30	63	0.20	0.12-0.27	Avoided
	Nasturtium officinale	Naof	3.543	0.15	24	23	0.16	0.09-0.23	None
	Pilea pumila	Pipu	0.881	0.04	18	6	0.12	0.06-0.18	Selected
	Other	Other[c]	3.701	0.16	20	24	0.13	0.07-0.20	None
Total			23.085		153				
COAS	*Eupatorium purpureum*	Eupu	1.419	0.06	19	7	0.16	0.08-0.25	Selected
	Impatiens sp.	Imsp	4.139	0.18	27	21	0.23	0.14-0.33	None
	Rock	Rock	9.401	0.41	19	48	0.16	0.08-0.25	Avoided
	Nasturtium officinale	Naof	3.543	0.15	8	17	0.07	0.01-0.13	Avoided
	Pilea pumila	Pipu	0.881	0.04	12	5	0.10	0.04-0.17	None
	Other	Other[c]	3.701	0.16	31	19	0.27	0.17-0.37	Selected
Total			23.085		116				

[a] Expected number of snails in a vegetation or substrate type is based on the number that would be occurring in that type if it were being used in exact proportion to its availability. (e.g., $153 \times 0.06 \approx 9$)

[b] Confidence intervals are adjusted so that the 90% confidence level applies to all intervals of a species simultaneously.

[c] Other category includes *Salix* sp. (Salix), low herbaceous (Lohe), Wood, Soil, *Thuja occidentalis* (Thoc), *Mentha piperita* (Mepi), Moss, *Eupatorium rugosum* (Euru), *Mentha arvensis* (Mear), and *Chelone glabra* (Chgl).

Table 4. AIC$_c$- and QAIC$_c$-selected best models used to estimate of population size of COAS populations from 2002-2009.

Year[a]	Best Model[b]	Population Estimate	SE
2002	*p*(.), φ(.), *b*(*t*)	262.4	35.68
2003	*p*(.), φ(.), *b*(*t*)	225.1	31.76
2004	*p*(*t*), φ(.), *b*(*t*)	716.5	68.97
2005	*p*(.), φ(*t*), *b*(*t*)	784.2	38.10
2007	*p*(*t*), φ(.), *b*(*t*)	551.1	50.01
2008	*p*(*t*), φ(.), *b*(*t*)	322.6	27.59
2009	*p*(*t*), φ(.), *b*(*t*)	339.2	52.85

[a] In 2006, surveys were curtailed following a rock slide for safety reasons.

[b] Model parameters include probability of capture (*p*), survival (φ), and probability of entering the population (*b*) that vary over sampling occasions within a year (*t*) or are constant (.).

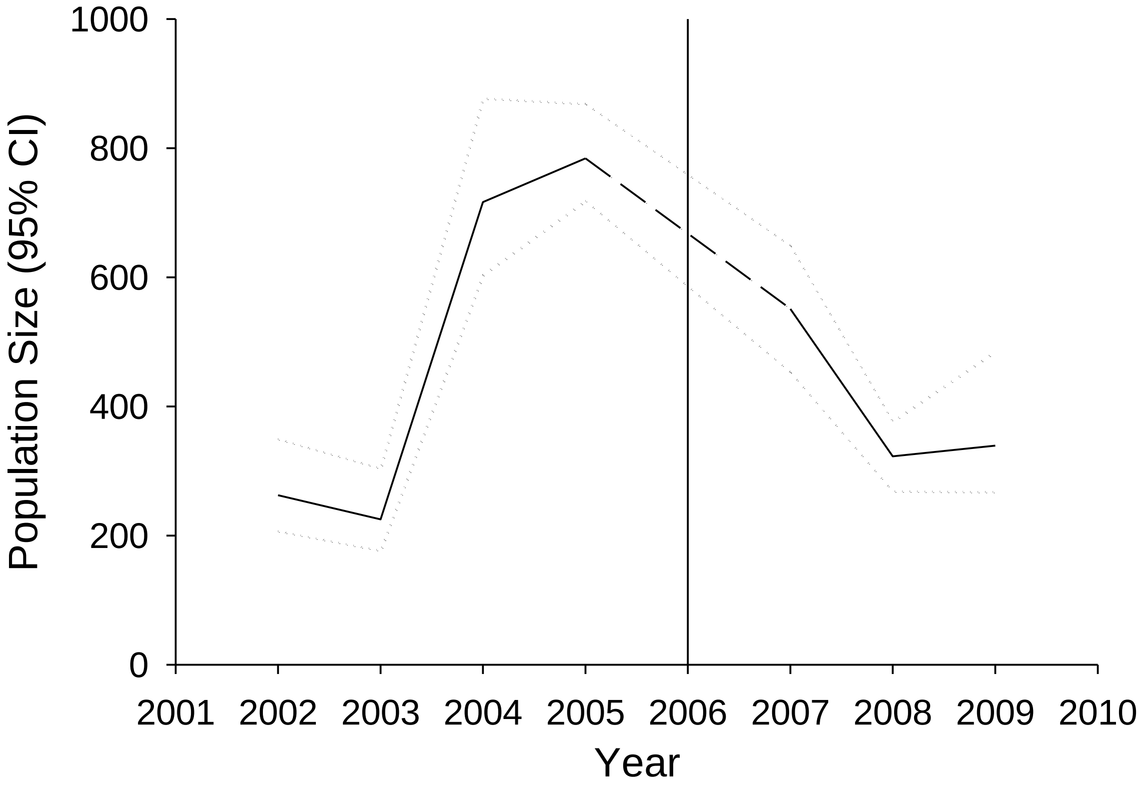

Figure 7. Trend in population size of COAS from 2002 to 2009 based on mark-recapture surveys. Vertical line denotes the year rockslide in which part of the species range was buried; surveys were not conducted in this year because of safety concerns.

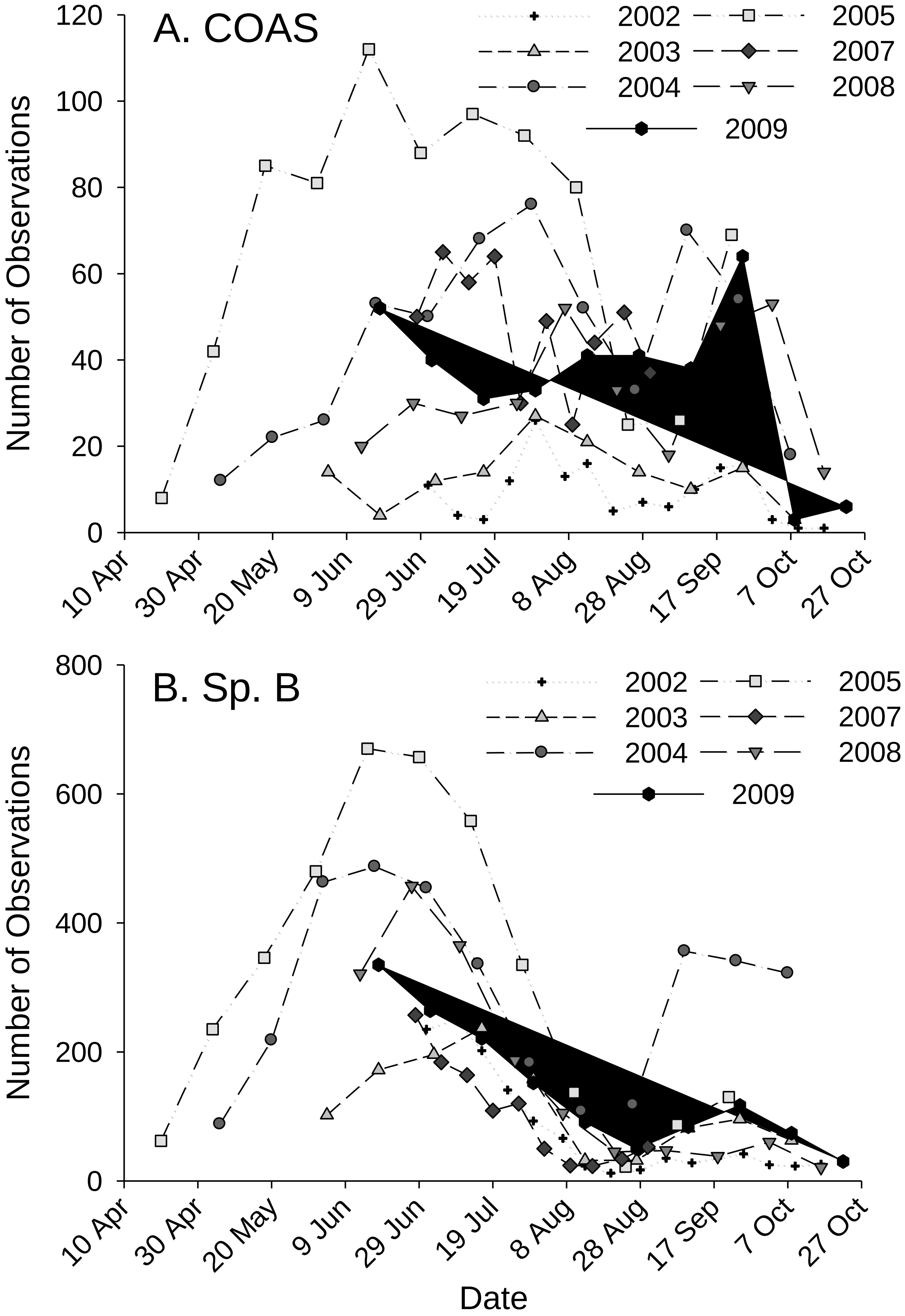

Figure 8. Number of COAS and Sp. B collected in each mark-recapture survey in 2002-2005, 2007-2009.

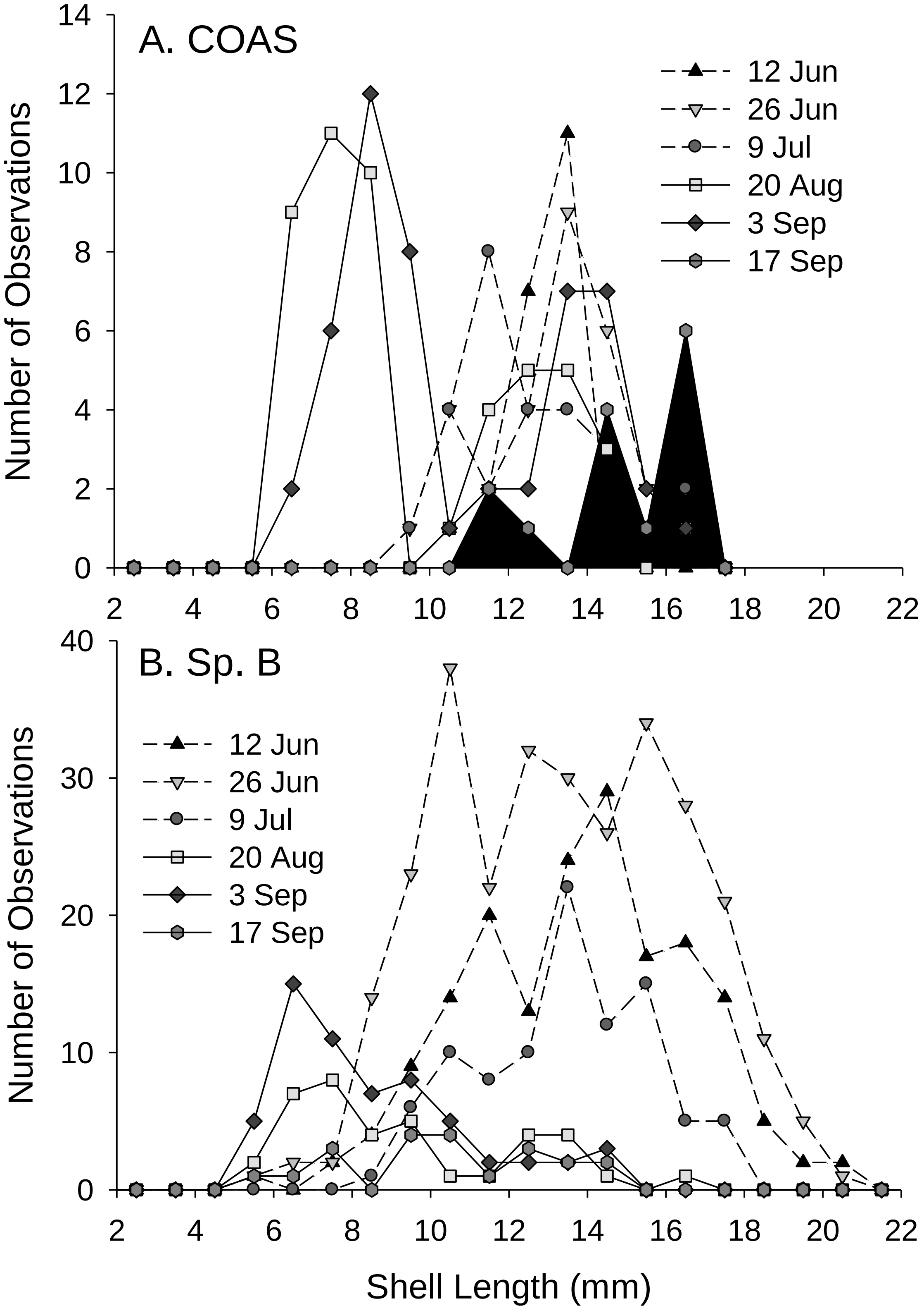

Figure 9. Frequency polygons of the shell lengths of COAS and Sp. B from Surveys 1-3 (dashed lines) and Surveys 8-10 (solid lines) in 2008.

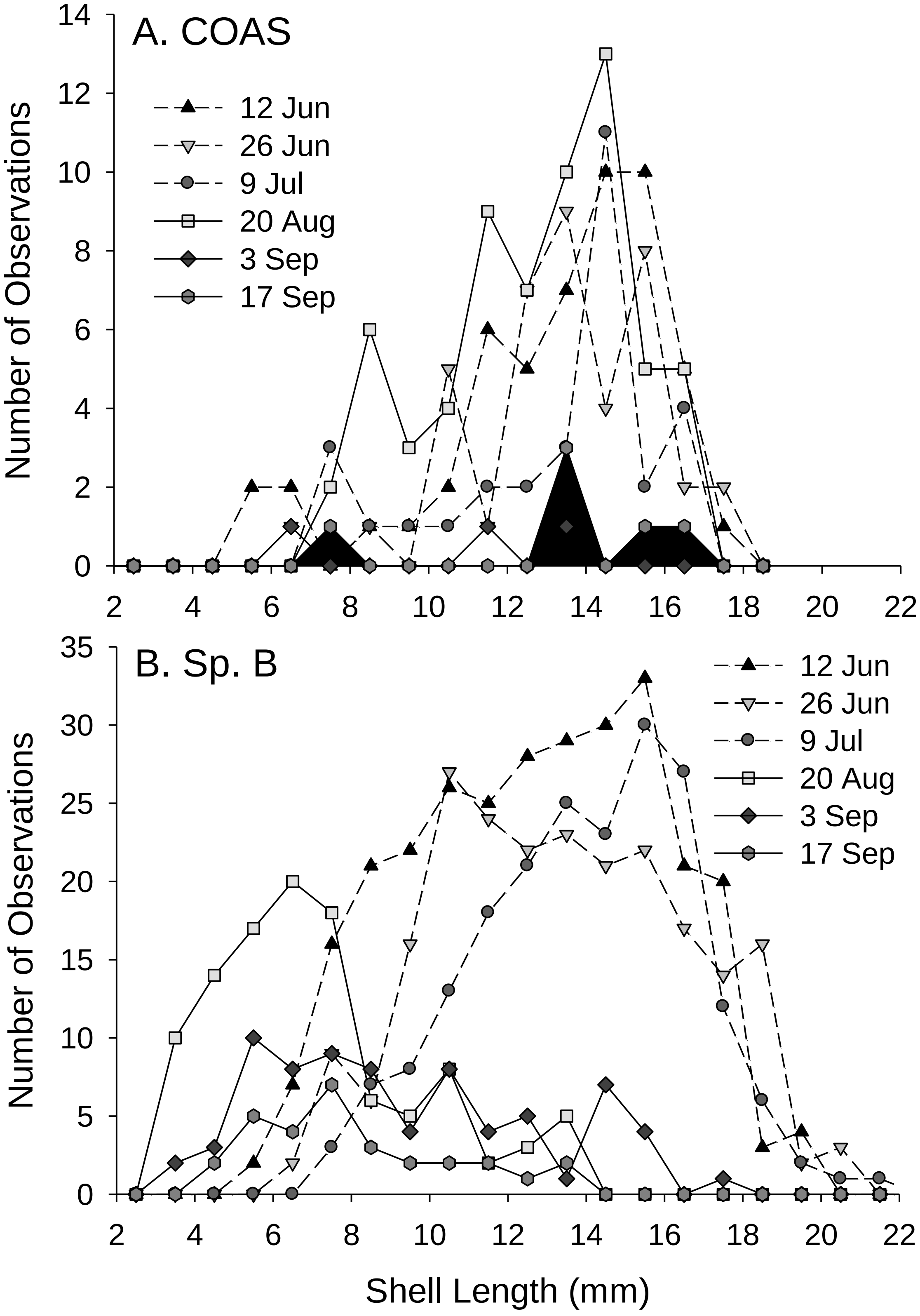

Figure 10. Frequency polygons of the shell lengths of COAS and Sp. B from Surveys 1-3 (dashed lines) and Surveys 8-10 (solid lines) in 2009.

The ratio of the number of Sp. B to COAS that were encountered during individual surveys from 2002-2009 ranged from 0.5 to 67. The distribution of ratios was highly right skewed, so that 75% of the ratios were less than 8 (Fig. 11). Despite the variation in captures within a survey, the numbers of COAS and Sp. B captured at each occasion were correlated ($r = 0.58$, $p < 0.0001$, $n = 80$). When counts were summed over the year, the total numbers of COAS and Sp. B captured were more highly correlated ($r = 0.80$, $p = 0.0298$, $n = 7$). At this temporal scale, the ratio of total numbers of Sp. B to COAS ranged from 2 to 9.

The population estimates of COAS for each sampling occasion (Appendix A) were highly correlated with the number of COAS captured at that occasion ($r = 0.71$, $p < 0.0001$, $n = 64$). Population estimates of COAS for each year were even more highly correlated with the total number of COAS captured each year ($r = 0.95$, $p = 0.0012$, $n = 7$,). We used the relationship between the population estimate and total counts of COAS (*estimate* = 95.83 + 0.914[*total count*]) to estimate the number of Sp. B in the study area in each year (Table 5). Using the estimates from Program Mark for COAS and the regression estimates for Sp. B, the ratio of Sp. B to COAS only ranged from 2 to 5. However, the estimates for Sp. B determined by this relationship are likely to be conservative because the small size of Sp. B late in the season caused low contributions to the total counts.

There were clear and consistent differences in the spatial distributions of COAS and Sp. B along the transect. Sp. B was more evenly spread across the survey area, with a tendency in most years to occur closer to the falls than COAS (Fig. 12B). In contrast, COAS showed a more symmetric distribution centered around Block 8, with few snails occurring outside blocks 3 and 13 (Fig. 12A). These distributions largely corresponded with those we observed in our habitat use surveys (Fig. 6). Namely, Sp. B was widespread over the entire area that was sampled, whereas COAS was largely restricted to Blocks 4-11.

Growth rates of recaptured marked COAS varied over years (Kruskal Wallis: $p = 0.0407$), but did not exhibit a consistent trend (Fig. 13). When growth rates were calculated for early and late summer periods of each year (i.e., times of the year when the population of Sp. B was composed of primarily of large and small individuals, respectively), the growth rates were significantly lower later in the summer (Kruskal-Wallis, $p < 0.0001$) (Fig. 14).

Discussion

Our work on the competitive interactions between the native COAS and non-native Sp. B, their habitat use, and population ecology provides evidence for both competition and coexistence. The competition experiment clearly demonstrated that COAS grew more slowly and generally suffered higher mortality at higher densities and larger body sizes of Sp. B, indicating that these two snail species compete. Nevertheless, our examination of habitat use and population ecology suggests that there may be enough mitigating factors to favor coexistence. The relative influence of mechanisms of competition and coexistence have direct and important ramifications for how COAS is managed (e.g., control of Sp. B or do nothing).

Evidence for competition

The differential changes in growth and mortality rates over different densities and sizes of snail supported the contention that COAS and Sp. B compete (USFWS 2006). At higher densities and larger sizes of Sp. B, growth rates of both species were reduced and mortality rates generally increased, indicating interspecific competition for COAS and intraspecific competition for Sp. B (Figs. 1-3).

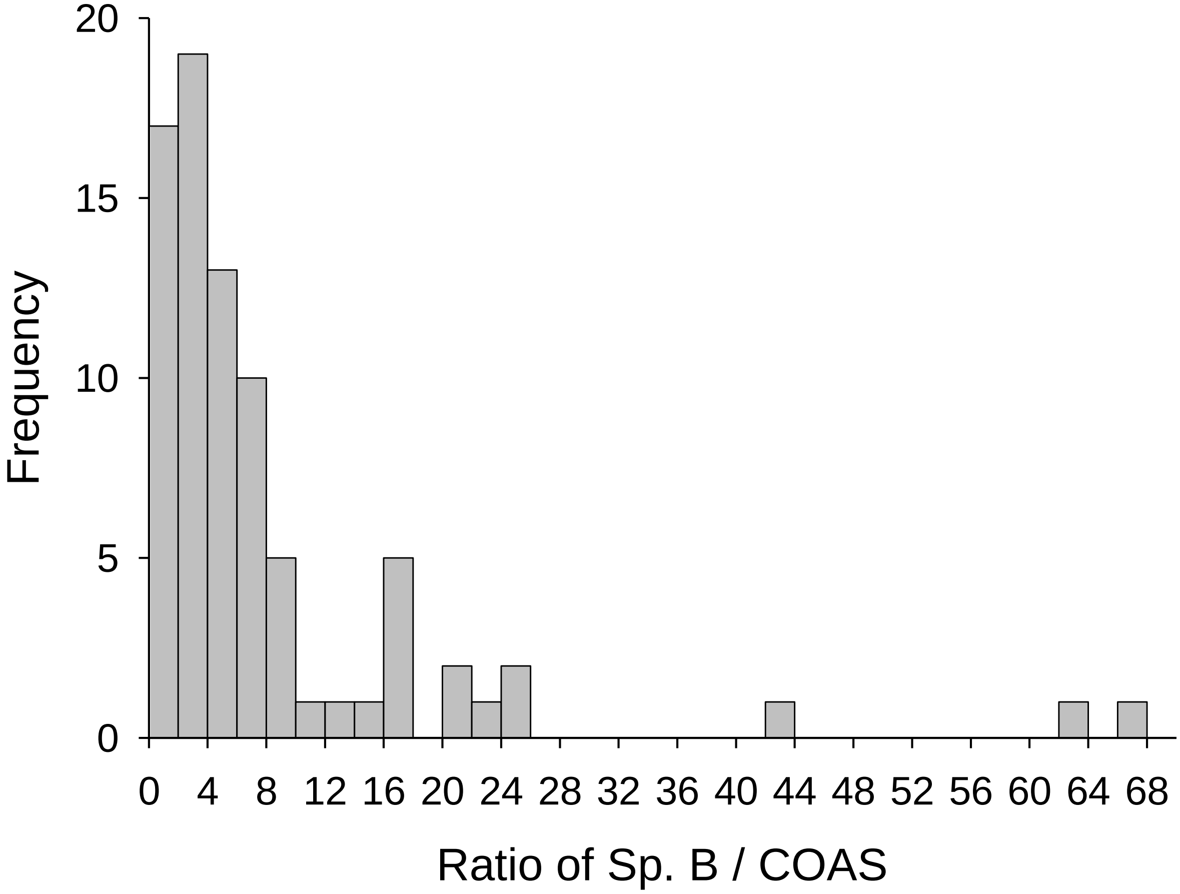

Figure 11. Distribution of the ratio of the number of Sp. B to the number of COAS collected during each mark-recapture survey from 2002-2009.

Table 5. Regression estimates of population sizes of COAS and Sp. B derived from the relationship between each year's Program MARK population estimate for COAS and the total number of COAS captured in a year (*estimate* = 95.83 + 0.914[*total count*]). Total estimate of both species combined is the sum of the Program Mark Estimate for COAS and the regression estimate for Sp. B.

	COAS			Sp. B		Both
Year[a]	Total Count	Program MARK Estimate	Regression Estimate	Total Count	Regression Estimate	Total Estimate
2002	149	262.4	232.0	1253	1240.8	1503.2
2003	134	225.1	218.3	1170	1165.0	1390.1
2004	534	716.5	583.8	3474	3270.4	3986.9
2005	805	784.2	831.4	3719	3494.3	4278.5
2007	473	551.1	528.1	1018	1026.1	1577.2
2008	325	322.6	392.8	1646	1599.9	1922.5
2009	349	339.2	414.7	1418	1391.6	1730.8

[a] In 2006, surveys were curtailed following a rock slide for safety reasons.

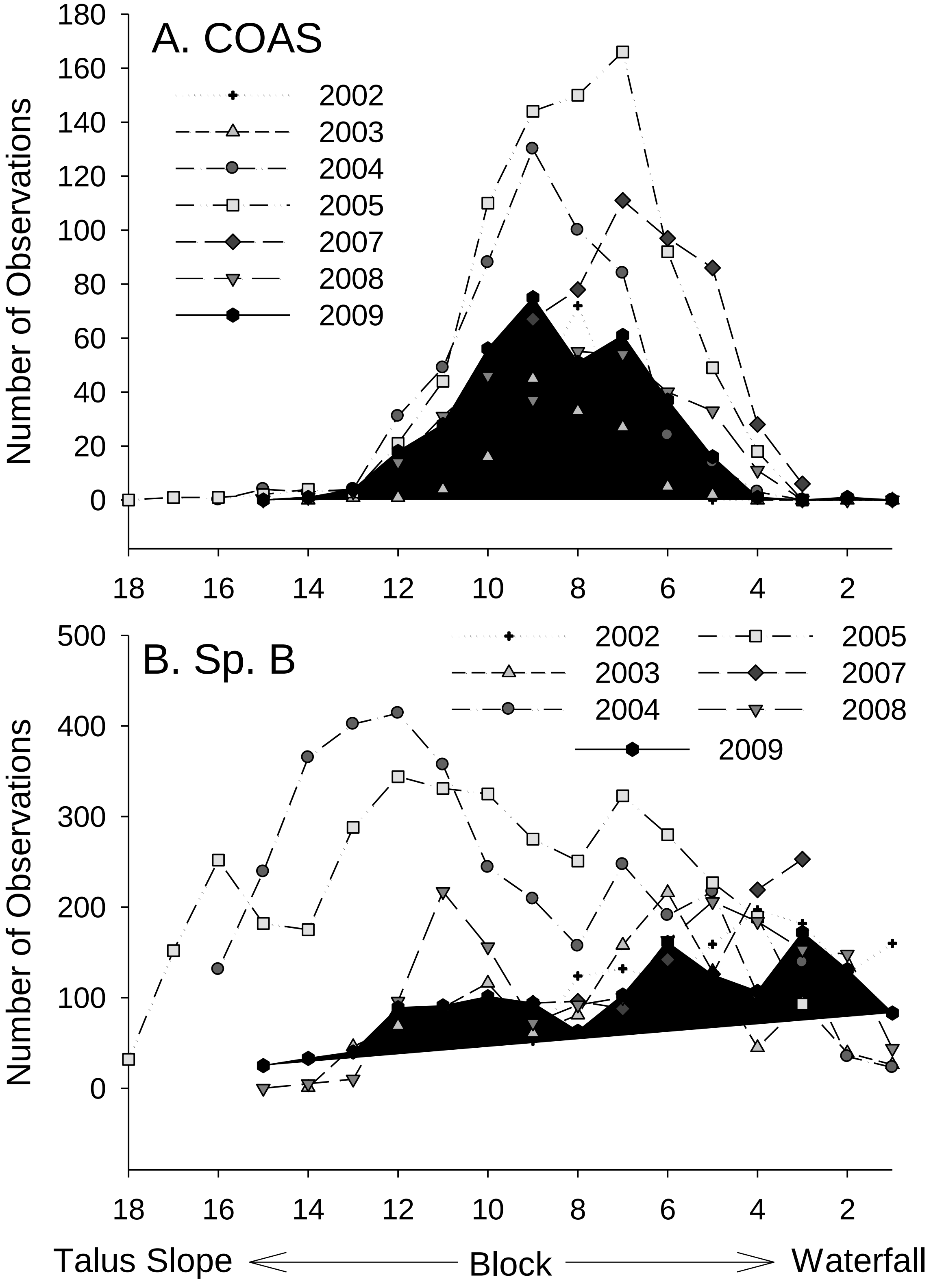

Figure 12. Total captures per year of COAS and Sp. B in each block along the mark-recapture survey transect.

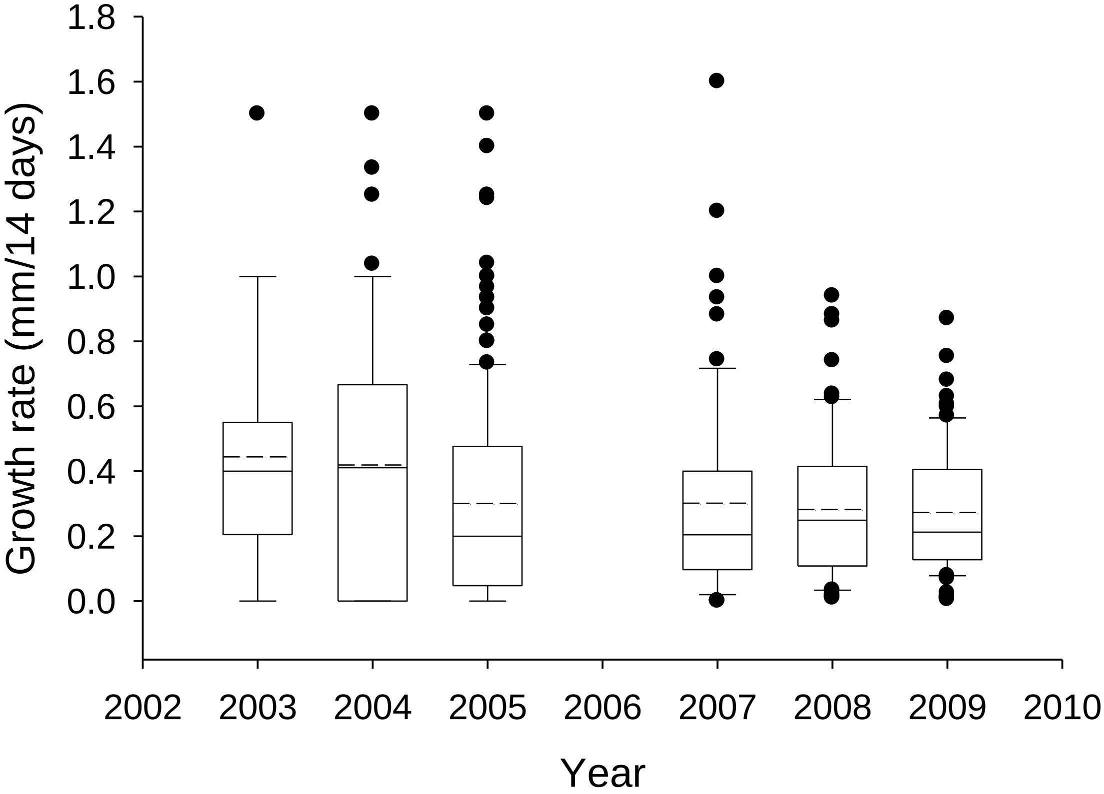

Figure 13. Growth rates of COAS based on recaptured marked individuals from 2002 to 2009. Growth rates are adjusted to 14 days for comparison with Figures 1 and 3. Dashed horizontal lines represent average growth rate and whiskers represent the 10th and 90th percentile.

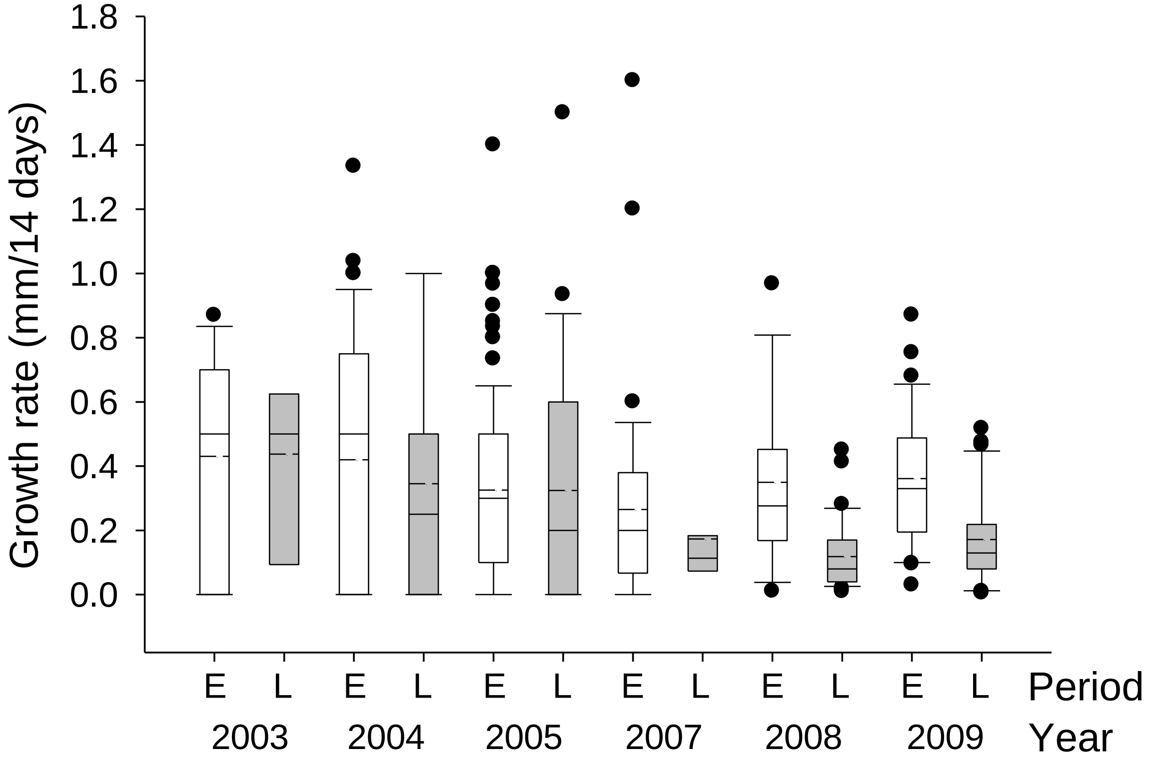

Figure 14. Growth rates of COAS based on marked individuals recaptured during the early periods of the year (E = before 8 August) when the population of Sp. B is composed of large individuals and during the late periods (L = after 8 August) when the population of Sp. B is composed of small individuals (See Fig. 8). Growth rates are adjusted to 14 days for comparison with Figures 1 and 3. Dashed horizontal lines represent average growth rate and whiskers represent the 10th and 90th percentile.

Because both species feed on similar plants, we assumed that decline in growth rates was a result of exploitation competition for limited food resources, but our experiments do not allow us to definitively elucidate the mechanism of competition. For example, competition for space could elicit a similar pattern in growth rates, or competition could have resulted from interference competition resulting from the presence of mucus trails (Cain 1983, Goodfriend 1986, Baur and Baur 1990). Likewise, we only tested for competition on one species of plant present at the falls, so we do not know if the intensity of the inter- and intraspecific competitive interactions vary based on the plant species on which they cooccur. Additional experiments should be conducted to investigate the interactions on different plant species, specifically focusing on *Eupatorium purpureum* (selected by COAS, used proportionate to its occurrence by Sp. B), and both *Impatiens* spp. and *Pilea pumila* (selected by Sp. B, used proportionate to its occurrence by COAS). Such experiments, potentially conducted with captive COAS, may help direct management to increase habitat quality for COAS at the falls.

While our findings on growth and mortality show strong evidence for competition under the conditions within the experimental enclosures (e.g., only a single plant species was available and the snails were confined to a relatively small volume), the question remains if they compete *in situ* (i.e., in their natural habitat). Previous research has shown that competing species can coexist because of spatial separation due to attraction of competitors to different environmental conditions. In other words, if spatial aggregation is greater between species than within species, differences in habitat use will decrease the frequency of interaction between species and thus reduce the intensity of interspecific competition relative to intraspecific competition (Ives 1988, Chesson 2000b, Hartley and Shorrocks 2002, Leisnham and Juliano 2009). This was not the case for COAS and Sp. B, as their spatial distributions were coincident at multiple scales. Sp. B was widespread across the study area and entirely encompassed the limited range of COAS. Snails of both species showed a high degree of overlap in the use of patches of dominant vegetation and substrate types (Fig. 6). While both species avoided rocky area, neither species selected another vegetation type that the other avoided. Within these patches, both species used many of the same plant species and substrates (Fig. 4). Spatial overlap at all these scales suggests the potential for a high level of interaction between these two species. Therefore, some level of competition is likely to exist under natural conditions.

Further evidence for *in situ* competition is provided by the higher average growth rates of individual COAS in the experiment (Figs. 1 and 3) compared to the average growth rates of naturally occurring COAS (Fig. 13). Although the relative contribution of intraspecific competition and interspecific competition to these differences is unknown, the considerably lower growth rates under natural conditions suggests that one or both types of competition are depressing the *in situ* growth rates of COAS.

Evidence for coexistence

Ecological theory indicates that coexistence is possible when intraspecific competition is stronger than interspecific competition (Chesson 1991, 2000a, Wright 2002, Kneitel and Chase 2004). Unfortunately, we were not able to assess these quantities directly. Because Sp. B and COAS grow at different rates, quantifying the relative strengths of intra- and interspecific competition for Sp. B and COAS would require examining the growth rates of snails in the different treatments as a proportion of each species maximum growth (Cross and Benke 2002). While our experiments allowed us to examine the interspecific effects of Sp. B on COAS growth rate and to a lesser extent the intraspecific effects of Sp. B on its own grown rate, the endangered status of COAS prevented us from performing experiments with reciprocal treatment densities. Thus, we were unable to obtain data on the maximum growth rate of Sp. B and the effects of varying density of COAS on Sp. B. Nevertheless, there are several lines of indirect evidence from our work on each species' population ecology and habitat use that collectively suggest that the two species are coexisting.

First, the persistence of COAS for over 30 years in the presence of Sp. B is itself strong evidence for stable coexistence. However, we lack pre-invasion population estimates for COAS, so we do not know if COAS was more abundant and widespread before the arrival of Sp. B. Even so, after this much time, it is likely that the population of Sp. B has reached the limits of its population size and range at the falls. Unless conditions change, it has probably reached its maximum level of impact.

Second, the recent trend in COAS population sizes suggests that Sp. B is not causing an attenuated extinction of COAS (Fig. 7). The population size has declined in recent years, which may have been a result of the loss of habitat from the rock slide in 2006. However, the low population size prior to the rock slide suggests that the population is more likely to be fluctuating. Further, the over 3-fold increase from 2003 to 2004 shows that the population of COAS retains a high capacity for growth when conditions are suitable. Additionally, there was a high positive correlation between the total numbers of snails of each species captured each year (Table 5). The coincident population trends suggest that these species are responding similarly to environmental conditions (i.e. a good year for one species is good year for the other) and that COAS can increase even as the population of Sp. B grows.

Third, our estimates of the ratios of Sp. B to COAS captured during each of the surveys (Fig. 11) indicate that Sp. B rarely outnumbers COAS to the degree that caused significant reductions in the growth of COAS in our experiments. In only 3 of the 80 surveys did the ratio of Sp. B to COAS exceed 30. Moreover, the natural densities are considerably lower than those in the competition experiment. We estimated the total density of snails in the study area using the Program MARK population estimates for COAS and the regression estimates for Sp. B (Table 5). Based on the 45 m^2 area that we sampled, total density of snails ranged from $31/m^2$ to $95/m^2$. By comparison, the density of snails in the competition experiment ranged from $235/m^2$ to $1176/m^2$. Although both sets of densities are clearly rough estimates, they illustrate the disparity between the densities in the experiments that were necessary to elicit a negative response and the natural densities of snails.

Finally, although there was a large degree of overlap in the use of different plant and substrate use, some differences did exist in plant species and substrate types used by each species, which suggests differential resource use. Most notably, COAS tended to be found more often on decaying plant matter (e.g., detritus, dead leaves, wood) than Sp. B and Sp. B was more often found on living plant matter (Fig. 5). Although these differences in resource use may be minor, they can still contribute to the coexistence of competing species. For example, Veen et al. (2010) found that minor habitat differences between the closely related Collared (*Ficedula albicollis*) and Pied (*Ficedula hypoleuca*) Flycatchers lead to temporal differences in availability of similar food resources and differential effects on reproductive success, which in turn favored coexistence.

Mechanism for coexistence

Although the evidence suggests that coexistence is more likely than competitive exclusion over short temporal scales further study is needed to ensure that this is the case for longer time scales. Even slight reductions in growth due to competition could have long-term fitness consequences. In terrestrial gastropods fecundity and age at first reproduction are often directly related to shell size (Wolda 1963, Oosterhoff 1977, Carter and Ashdown 1984, Baur 1988, Baur and Raboud 1988). Size and age at first reproduction are critical life-history traits that can influence the rate of increase in a population by affecting the amount and timing of reproduction (Cole 1954, Lewontin 1965, Murphy 1968). Thus, snails with reduced growth rates could lead to long-term declines in population size.

Given the potential for long-term decline it is important to have a mechanistic understanding of the interactions between the snails and between the snails and their environment. We propose at least three non-mutually exclusive mechanisms facilitating the coexistence of COAS and Sp. B where their ranges overlap: two familiar (environmental fluctuations and spatial partitioning) and one novel (temporal partitioning based on differences in life history strategies). Although further study is necessary to determine the importance of each of these mechanisms, the combination of our results on the competition experiments, habitat use, and population ecology suggests that these mechanisms may be important in this system.

Compared to the densities in the competition experiment, the natural population densities of COAS and Sp. B may be low enough that they are not strongly competing. It is possible that environmental fluctuations of limiting abiotic factors (e.g., temperature and moisture) are maintaining populations of each species at low enough densities, such that resources are abundant, encounters among individuals are rare, and competition is unimportant (e.g., Connell 1978, Sousa 1984). Similarly, predators can reduce numbers of prey below the threshold of competition (e.g., Paine 1966), thereby allowing species with varying competitive abilities and a high degree of niche overlap to coexist (e.g., Dayton 1971, Huston 1979, Sousa 1979, Dudley et al. 1990, Hemphill 1991). Although we did not attempt to ascertain the factors that influence the population size of COAS and Sp. B in this study, a comprehensive understanding of competition and coexistence would require that the effects of these factors on population growth be quantified. Experimental translocations to areas where conditions are more constant or where there are less potential predators could help elucidate important limiting factors. Based on our study, the presence of Sp. B at a potential release site should not preclude COAS translocation.

As previously mentioned, spatial partitioning appears to be occurring at very small spatial scales through trade-offs in the use of living and dead plant material (Fig. 5). Differential resource use can lead to coexistence when each species has density-dependent feedback loops with its resources that limits itself intraspecifically and other species interspecifically. Limited resource overlap and trade-offs in resource use can concentrate intraspecific competition relative to interspecific competition, which is the basis of coexistence (Chesson 2000a). Whether or not these small-scale differences in plant use are enough to promote coexistence depends on the quality of these different habitats for each species. It is possible that these differences in use do not reflect preference or the quality of these resources. The “selection” of dead wood, detritus and decaying plant matter by COAS may result from the displacement from its more preferred substrates by a competitively superior Sp. B. If this were the case COAS could be experiencing lowered growth rates on these substrates, which can in turn have long-term demographic consequences for the population. Controlled experiments in which snails are provided different substrates or plant species would help to determine relative preference and quality.

There also appears to be a temporal partitioning resulting from a trade-off between growth and longevity of COAS and Sp. B: COAS is a slower growing and smaller biennial species and Sp. B is a faster growing and larger annual species. Evidence for this trade-off can be seen in the temporal patterns within each year of both the number of snails captured and the size distribution of snails. The bimodal distribution of Sp. B (Fig. 8B) resulted from a size-dependent detection bias combined with a shifting size distribution of the population due to its annual life cycle (Figs. 9B, 10B) (Ðatkauskienë 2005). The first peak in the distribution represents the cohort that hatched in the previous year. These individuals breed and then die in mid-August, completing their annual life cycle. The low point in the distribution spans the time period when the new cohort of snails are in the egg stage or are recently hatched and thus difficult to detect. The second peak occurs in mid-September as the snails grow and their detectability increases. In mid-October, the numbers decrease again because the snails retreat to their overwintering areas. This pattern was not unique to the years of our study; Aloi (1985) witnessed similar fluctuations in the “gray morph” of COAS, which based on the location in which he found them was likely Sp. B. In contrast, COAS did not exhibit the same patterns of abundance and size distribution as Sp. B, likely owing two its two-year life-cycle. The size distribution and number of snail collected fluctuated but remained more uniform over the course of a year (Figs. 8A, 9A, 10A). The overlapping generations and likely multiple years of breeding allowed the simultaneous attrition of one cohort while the other cohort grew into larger, more detectable size classes, leading to a more uniform distribution of counts and more mixed size structure throughout the summer.

The temporal differences in size distributions resulting from the trade-off between growth and longevity may lead to a less competitive environment for COAS, because at the end of every summer COAS is exposed to a population of Sp. B composed of small snails. This period may allow individuals of COAS to compensate for the lower growth that they likely sustained earlier in the season when the population of Sp. B was composed of large individuals. Our second competition experiment was designed to test the idea that the intensity of competition and thus the effect on growth was less when COAS co-occurred with small (6-10 mm) individuals of Sp. B than with large (> 13 mm) individuals. The experiment supported this prediction at lower densities: COAS growth rates were higher in the presence of small Sp. B. However, at high densities the results were more equivocal. While the treatment with 50 large Sp. B had the greatest negative effect, the treatment with 50 small Sp. B had almost as strong of an effect on COAS growth. This result may have been because small snails can have a higher relative foraging capacity (g plant consumer per g of snail) compared to larger snails. For example, Carlsson and Brönmark (2006) found that the competitive effects of medium-sized and adult snails on neonate snails are weak, whereas the density of neonate snails strongly affected the growth of larger snails. They suggested that depletion of resources was the competitive mechanism because the neonate snails were much more efficient herbivores on the preferred resource. Although we do not have direct measurements of foraging efficiency, in our study small snails tended to grow faster than large snails. Alternatively, if interference competition is functioning (e.g., presence of mucus trails) then the density of snails may be more important then relative size. We found that the *in situ* growth rates of COAS during the periods when the population of Sp. B was composed of large or small individuals did not support our prediction.

We witnessed lower growth rates in late summer when the population of Sp. B was dominated by small individuals (Fig. 14).

Although we did not find strong correlative evidence in favor of coexistence by temporal partitioning due to differences in life history strategies, this mechanism merits further study in this and other systems. In our study, the growth rates may have been low late in the season even without the influence of Sp. B, because temperatures are cooler and plants have begun to senesce. If high densities of large Sp. B were present at this time, the additional influence may have had suppressed the growth of COAS below what we witnessed. Before this mechanism can be ruled out, experiments comparing growth at different densities of Sp. B during early and late summer should be conducted to account for these changing conditions. There is also precedence for this mechanism from other studies. For example, Loreau and Ebenhöh (1994) used a modeling approach to demonstrate that species with complex life cycles (i.e., life cycles in which abrupt ontogenetic transformations and niche shifts occur at the transition between stages) can coexist on the same resources if the various stages of the life cycle use different resources and if they are competitively superior at different life stages. In an empirical study, Veen et al. (2010) witnessed a similar compensatory mechanism with the closely related Collared (*Ficedula albicollis*) and Pied (*Ficedula hypoleuca*) Flycatchers. Both species of flycatchers preferred deciduous forest but the Collared Flycatcher was competitively superior and forced the Pied Flycatcher into territories with more coniferous tree species. The differences in habitat lead to temporal differences in the abundance of an important food resource (i.e., caterpillars). Coniferous tree species exhibited a steady increase in caterpillar abundance through the season, while deciduous tree species showed an early and narrow peak in abundance. Caterpillar biomass decreased more slowly in Pied Flycatcher territories, which helped to increase reproductive success of Pied Flycatchers late in the season. The greater fitness late in the season counteracted the reduction in fitness due to interspecific competition and facilitated coexistence.

Management Implications

From a management perspective, understanding competition and mechanisms of coexistence is particularly important in dealing with established populations of invasive species. As many as 80-90% of established non-indigenous species may have minimal detectable effects on native biota and ecosystem functioning (Williamson 1996). Thus, distinguishing nonnative species with negligible effects from those causing significant damage to native biodiversity, would allow managers to prioritize their efforts and select the most effective strategy for dealing with an invasive species. This knowledge becomes particularly important when there is a legal mandate (e.g., Endangered Species Act) to protect a species and its ecosystem, as is the case with COAS.

When dealing with an established invasive species eradication is an attractive option because it can reverse any impacts and restore the system to its previous state or at least put the ecosystem on a improved trajectory. Further, it does not require the long-term commitment and complex knowledge that is often necessary to effectively and efficiently manage pests using a sustained control strategy (Choquenot and Parkes 2001). However, eradication tends to work best for colonizing populations, limited or patchy populations, and island populations of invasive species (Parkes and Panetta 2009). Sp. B is none of these; it is a cryptic species with a distribution that is widespread but unknown in its extent. As such, widespread methods to eradicate this species will likely be unsuccessful and jeopardize other species within its range, such as COAS. The institution of unachievable eradication efforts can also lead to missed opportunities to act elsewhere as well as increased skepticism, especially among funding agencies (Parkes and Panetta 2009).

When eradication of an established population is not possible, the only options are to control the population or to do nothing. The decision about whether to attempt control or not will depend on: the stage to which the invasion has progressed, the availability of control measures, and the impacts of the invasive species relative to the costs of its control (Grice 2009). A control strategy is most suitable for advanced stages of invasion where the established population is large and extensive. Sp. B fits this criterion. However, as of yet no effective control measures are available. Since 2002, during mark-recapture surveys we have been mechanically removing Sp. B from the area where COAS occurs, with little apparent effect. In fact, the numbers of Sp. B actually increased through mid-summer despite the removal of Sp. B at two week intervals. Moreover, Sp. B is abundant all around the sampling area and we have observed high numbers of Sp. B in the sampling area one day after their removal, suggesting that snails in the surrounding area quickly recolonize the cleared area. If removal is to alleviate competition for COAS in any sort of meaningful way, more work will have to be done to determine the intensity and extent of removal of Sp. B in COAS's range and in the surrounding areas that would be necessary to reduce the population to sufficiently low levels and for a long enough duration. Other options such as the physical removal of COAS and the application of a molluscicide have also been considered but would be subject to the same restrictions.

The final alternative is to do nothing regarding the control of Sp. B, an option that would be warranted should the costs of the control outweigh its benefits for the invaded system. Currently, this option appears to be the most viable for managing Sp. B at the falls. Based on multiple lines of evidence, COAS appears to be stably coexisting with Sp. B, so the removal of Sp. B is unlikely to greatly improve the prospect of long-term persistence of COAS. In fact, removals of Sp. B did not occur in 2006 without leading to apparent changes in the ratios of Sp. B to COAS in 2007-2009 compared to 2002-2005. Although removals of Sp. B may continue as part of the capture-mark-recapture efforts for COAS, more intensive control of Sp. B appears unwarranted at this time.

Monitoring of both COAS and Sp. B populations remains important because, being small, the COAS population is at risk of extinction due to catastrophic events or should the ratio of Sp. B to COAS change 3-6 fold over current levels. Moreover, monitoring provides critical biological data (e.g., population growth rates, survival rates, individual growth rates) used to assess the effects of management actions (e.g., not to remove Sp. B) and adjust them accordingly (i.e., adaptive management), and is necessary to know when recovery goals are met (Campbell et al. 2002). Nevertheless, the time and personnel necessary to sustain monitoring efforts at past levels may be both prohibitive and unnecessary, so we investigated possible ways to reduce sampling efforts while continuing to acquire meaningful information on COAS status.

One possibility is to use total COAS counts over a restricted survey time or space as an index to population size instead of deriving rigorous population estimates. The total number of COAS captured across the summer in any given block (for blocks 7-10 and 14) was highly correlated with the population estimate for that year ($r \geq 0.89$, $P < 0.01$; Fig. 15), suggesting that a subset of these blocks could be surveyed (with or without marking COAS) instead of surveying the full range of the species. Alternatively, the total number of COAS captured across three full-shelf surveys conducted mid-July to mid-August was also strongly correlated with the annual population estimate ($r = 0.96$, $P < 0.01$). And in fact, any single day of a full-shelf survey was strongly correlated with the annual population estimate when conducted in either July (*r* = 0.97, *P* < 0.01) or August (*r* = 0.82, *P* = 0.03). We would favor a multi-day index over any single day index given variation in weather conditions that might strongly influence snail detection on a given day. Also, caution is warranted when choosing to conduct an index instead of a formal population estimate, especially given that these relationships are based on only 5-7 years of data. While an index will allow the detection of trends, the absence of a population estimate would preclude comparisons to estimates of previous years and could compromise recovery efforts because knowledge of population size is a basic requirement for even broad classes of recovery strategy. For example, if the population size is relatively large and stable then continued monitored likely represents the best approach whereas if the population is precariously low then captive breeding may be warranted. For this reason, managers may choose to conduct formal estimates when COAS populations are low (e.g., < 350) and track status by an index when they are more abundant.

Another possibility is to reduce the number of surveys (from bi-weekly to monthly surveys). We divided our survey effort in half and calculated two population estimates each year based on either the even-numbered surveys or odd-numbered surveys, and compared these to the estimate obtained from the full set of data for each year. The monthly surveys produced estimates that were generally on par or lower than the bi-weekly surveys (Table 6), although the decrease in precision for the monthly surveys resulted in only one estimate being statistically lower than the "true" estimate (Fig. 16). Even with the decreased precision, the estimates still allowed us to detect with 95% certainty whether the population fell above a level of about 300 or not, and thus appears useful for continued monitoring purposes.

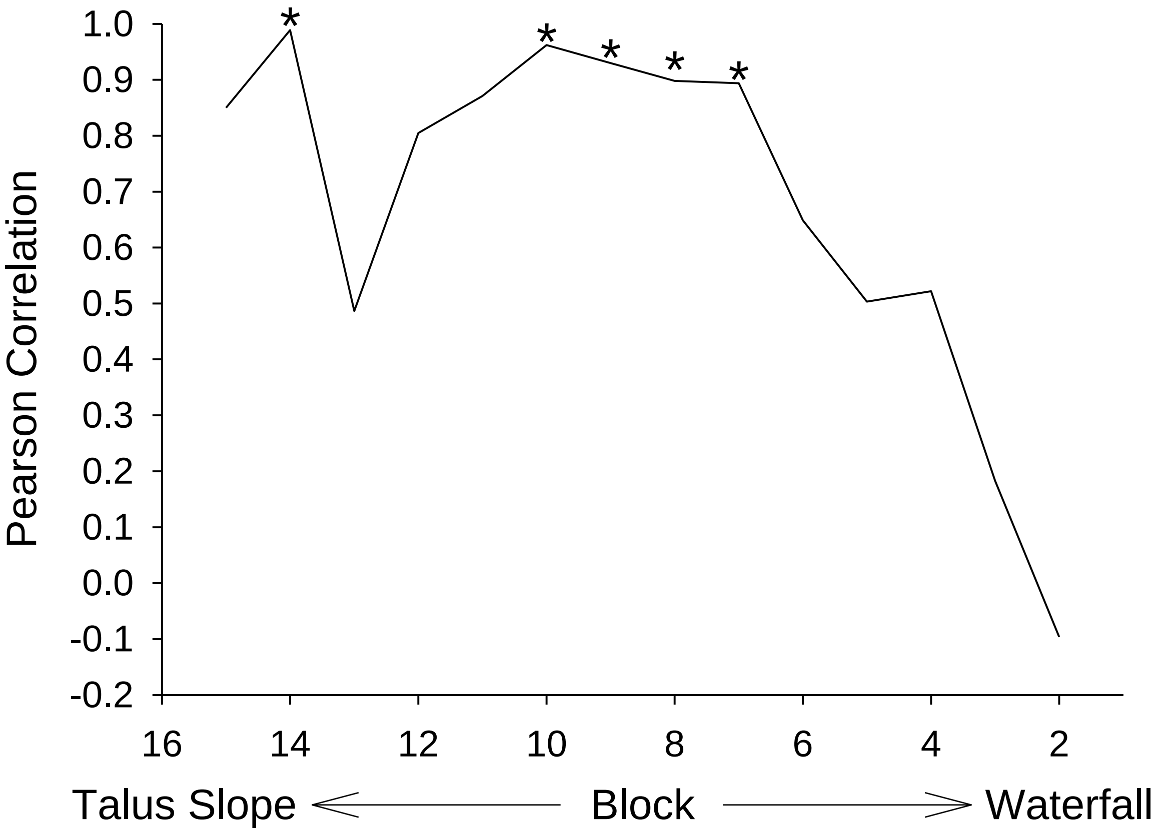

Figure 15. Correlations between the population estimates for each year and the total number of snails captured in each block. Asterisks indicate blocks in which correlation coefficients were statistically significant (0.001 < P-values < 0.01). n = 5 for blocks 2, 10-14, n = 7 for blocks 3-9, and n = 4 for block 15.

Table 6. AIC$_c$-selected best models used to estimate of population size of COAS populations from 2002-2009.

	All Surveys			Odd-numbered Surveys			Even-numbered Surveys		
Year[a]	Best Model[b]	Estimate	SE	Best Model[b]	Estimate	SE	Best Model[b]	Estimate	SE
2002	*p*(.), φ(.), *b*(*t*)	262.4	35.68	*p*(*t*), φ(.), *b*(*t*)	225.5	57.47	*p*(.), φ(.), *b*(*t*)	167.2	55.50
2003	*p*(.), φ(.), *b*(*t*)	225.1	31.76	*p*(.), φ(.), *b*(*t*)	311.1	115.21	*p*(.), φ(.), *b*(*t*)	101.2	68.77
2004	*p*(*t*), φ(.), *b*(*t*)	716.5	68.97	*p*(.), φ(.), *b*(*t*)	599.1	112.23	*p*(.), φ(*t*), *b*(*t*)	419.0	54.38
2005	*p*(.), φ(*t*), *b*(*t*)	784.2	38.10	*p*(.), φ(*t*), *b*(*t*)	688.0	72.03	*p*(.), φ(.), *b*(*t*)	773.3	83.06
2007	*p*(*t*), φ(.), *b*(*t*)	551.1	50.01	*p*(*t*), φ(*t*), *b*(*t*)	595.7	144.37	*p*(.), φ(.), *b*(*t*)	533.7	92.73
2008	*p*(*t*), φ(.), *b*(*t*)	322.6	27.59	*p*(.), φ(.), *b*(*t*)	297.2	64.22	*p*(.), φ(*t*), *b*(*t*)	269.2	43.9
2009	*p*(*t*), φ(.), *b*(*t*)	339.2	52.85	*p*(*t*), φ(*t*), *b*(*t*)	202.7	43.84	*p*(.), φ(*t*), *b*(*t*)	246.8	36.34

[a] In 2006, surveys were curtailed following a rock slide for safety reasons.

[b] Model parameters include probability of capture (*p*), survival (φ), and probability of entering the population (*b*) that vary over sampling occasions within a year (*t*) or are constant (.).

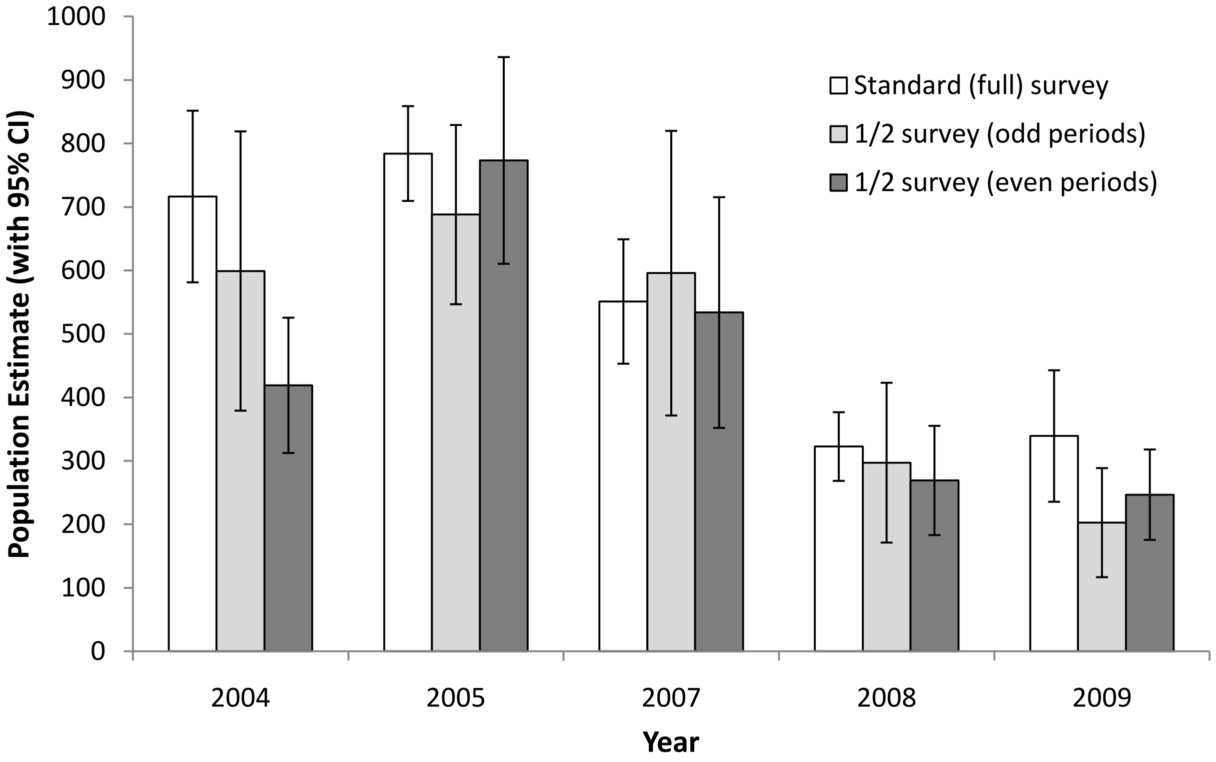

Figure 16. Population estimates for COAS (with 95% CI indicated by error bars) from bi-weekly (white) versus monthly survey designs.

A final possibility is to conduct population surveys every other year instead of annually. Any reduced survey effort should benefit COAS from reduced trampling and site disturbance, and monitoring every two years seems sufficient to pick-up the long-term trends in COAS populations (would have detected both low periods and the peak density observed since 2002). However, given the risk of a catastrophic event going undetected in any given year, we recommend that at least some low level of monitoring be conducted annually with formal population estimates at least every 2-3 years (to ensure the relationship between the index and true population size remains valid).

Finally, we also recommend that a captive breeding program be reinitiated. Although the population is clearly capable of increasing within its range (Fig. 7), the population increase can not lead to a range expansion because the snail is unable to cope with the conditions outside of the spray-zone of the falls. Because the entire population is limited to a single location habitat destruction from rockslides and floods likely pose a larger threat to COAS than Sp. B. A captive breeding program can offset the threat of extinction of the only population at the Chittenango Falls site and serve as a source of founders for new populations at other suitable sites (Molloy 1995). Captive breeding can also generate a pool of individuals for use in additional experiments to gain a more thorough understanding of the ecology of COAS and its interactions with Sp. B.

Acknowledgements

We are extremely grateful for the guidance and oversight of the project provided by Robyn Niver, Jeremy Coleman, and Laury Zicari from the U.S. Fish and Wildlife Service and Al Breisch from the NY Department of Environmental Conservation, as well as their participation in various aspects of the field work. We would especially like to thank Joe Brown from the Rosamond Gifford Zoo who helped with nearly all of the surveys since 2002 and Jeff Wyatt from the Seneca Park Zoo who routinely organized a group of his co-workers to help with the surveys. Stephanie Chapin from Chittenango Falls State Park graciously provided access to the park and on-site support. James Arrigoni conducted mark-recapture surveys in 2002 and Kris Whiteleather ran the mark-recapture surveys from 2003-2005 and again in 2007. Both of them generously shared their data. We gratefully acknowledge the help of Jake Bengeyfield and Brian Stillwell with all aspects of the field work in 2008 and of Carolyn Miller and Ian Trewella with the field work in 2009. Finally, we would like to thank the numerous volunteers who helped conduct the surveys: John Adamski, Kim Allen, Sara Bell, Garret Caulkins, Laura Daley, J. Dallas, Louis DiVincenti, Mike Eackles, Robin English, Kelsey Hostetler, Mark Irwin, Tom Hughes, Cheryl Lowie, Amy Mahar, Christy Martin, Dismus Mwikila, Gary Neuderfer, Wilirk Ngalson, Lily Parkinson, Sheldon Perry, Kristin Randall, Carla Rizzo, Phil Spinelli, Chris Standley, David Stilwell, and Gail Tabone.

Literature Cited

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, New York, NY, USA.

Aloi, M.A. 1985. Population dynamics of a pulmonate snail adjacent to a central New York stream. Master's thesis. State University of New York, College of Environmental Science and Forestry, Syracuse, NY.

Aloi, M.A., and N.H. Ringler. 1982. Population biology and density of *Succinea chittenangoensis*. Final Contract Report to New York State Department of Environmental Conservation under Federal Aid to Endangered Species Project E-1-7.

Alldredge, J. R., and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. Journal of Wildlife Management 70: 337-346.

Baur, B. 1988. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size, and incidence of egg cannibalism. Oecologia 77: 390-394.

Baur, B., and A. Baur. 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. Journal of Animal Ecology 59: 301-315.

Baur, B., and C. Raboud. 1988. Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. Journal of Animal Ecology 57: 71-87.

Branch, G. M. 1984. Competition between marine organisms: ecological and evolutionary implications. Oceanography and Marine Biology Annual Reviews 22: 429-593.

Byers, J. E., and L. Goldwasser. 2001. Exposing the mechanism and timing of impact of nonindigenous species on native species. Ecology 82: 1330-1343.

Byers, J. E., S. Reichard, J. M. Randall, et al. 2002. Directing research to reduce the impacts of non-indigenous species. Conservation Biology 16: 630-640.

Cain, A. J. 1983. Ecology and ecogenetics of terrestrial molluscan populations. Pages 597-647 in W. D. Russell-Hunter. The Mollusca: Ecology, Vol. 6. Academic Press, London, UK.

Campbell, S. P., A. Clark, L. Crampton, A. D. Guerry, L. Hatch, P. R. Hosseini, J. J. Lawler, and R. J. O'Connor. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications 12: 674-681.

Carlsson, N. O. L., and C. Brönmark. 2006. Size-dependent effects of an invasive herbivorous snail (*Pomacea canaliculata*) on macrophytes and periphyton in Asian wetlands. Freshwater Biology 51: 695-704.

Carter, M. A., and M. Ashdown. 1984. Experimental studies on the effects of density, size, and shell colour and banding phenotypes on the fecundity of *Cepaea nemoralis*. Malacologia 25: 291-302.

Chase, J. M., W. G. Wilson, and S. A. Richards. 2001. Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community. Ecology Letters 4: 304-312.

Chesson, P. 1991. A need for niches? Trends in Ecology and Evolution 6: 26-28.

Chesson, P. 2000a. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Chesson, P. 2000b. General theory of competitive coexistence in spatially varying environments. Theoretical Population Biology 58: 211-237.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150: 519-553.

Choquenot, D. and J. Parkes. 2001. Setting thresholds for pest control: how does pest density affect resource viability? Biological Conservation 99: 29-46.

Clout, M. N., and P. A. Williams. 2009. Invasive species management: a handbook of principles and techniques. Oxford University Press Inc., New York, New York, USA.

Cooch, E., and G. White. 2008. Goodness of fit testing. Pages 5.1-5.40 *in* E. Cooch, and G. White, editors. Program MARK: a gentle introduction. Seventh edition. Fort Collins, Colorado, USA.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279: 555-558.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29: 103-107.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

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

Đatkauskienë, I. 2005. Characteristic of lifespan and reproduction period of *Succinea putris* (L.) (Gastopoda: Styllomatophora). Ekologija 3: 28-33.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179: 759-769.

Dudley, T. L., C. M. D'Antonio, and S. D. Cooper. 1990. Mechanisms and consequences of interspecific competition between two stream insects. Journal of Animal Ecology 59: 849-866.

Goodfriend, G. A. 1986. Variation in land-snail shell form and size and its causes: a review. Systematic Zoology 35: 204-223.

Grice, T. 2009. Principles of containment and control of invasive species. Pages 61-76 *in* M. N. Clout and P. A. Williams, editors. Invasive species management: a handbook of principles and techniques. Oxford University Press Inc., New York, New York, USA.

Grimm, F. W. 1981. A review of the Chittenango ovate amber snail, *Succinea chittenangoensis*, Pisbry, 1908 – a Pleistocene relict now greatly restricted in distribution. Contract report to the New York State Department of Environmental Conservation.

Grover, J. P. 1997. Resource Competition. Chapman and Hall, London, UK.

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

Hartley, S., and B. Shorrocks. 2002. A general framework for the aggregation model of coexistence. Journal of Animal Ecology 71: 651-662.

Hairston, N. G. 1951. Interspecies competition and its probable influence upon the vertical distribution of Appalachian salamanders of the genus *Plethodon*. Ecology 32: 266-274.

Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences USA 103: 6067-6072.

Hemphill, N. 1991. Disturbance and variation in competition between two stream insects. Ecology 72: 864-872.

Hiebert, R. D. 1997. Prioritizing invasive plants and planning for management. Pages 195-212 in J.O. Luken and J. W. Theiret, editors. Assessment and Management of Plant Invasions. Springer-Verlag, New York, NY, USA.

Hoagland, K. E., and G. M. Davis. 1987. The Succineid snail fauna of Chittenango Falls, New York: Taxonomic status with comparisons to other relevant taxa. Proceedings of the Academy of Natural Sciences of Philadelphia 139: 465-526.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. American Naturalist 144: 741-777.

Hubbell, S. P. 2001. The Unified Neutral Theory of Species Abundance and Diversity. Princeton University Press, Princeton, NJ, USA.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology 19: 166-172.

Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, history, and the structure of tropical rainforest communities. Pages 314-329 in J. Diamond and T. J. Case. Community Ecology. Harper and Row, New York, NY, USA.

Hubricht, L. 1985. The distributions of the native land mollusks of the Eastern United States. Fieldiana, Zoology, New Series, No. 24: 191 pp.

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

Ives, A. R. 1988. Covariance, coexistence, and the population dynamics of two competitors using a patchy resource. Journal of Theoretical Biology 133: 345-361.

Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7: 69-80.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147: 784-812.

Leisnham, P. T., and S. A. Juliano. 2009. Spatial and temporal patterns of coexistence between competing *Aedes* mosquitoes in urban Florida. Oecologia 160: 343-352.

Lewontin, R. C. 1965. Selection for colonizing ability. Pages 77-91 in H. G. Baker and G. L. Stebbins. The Genetics of Colonizing Species. Academic Press, New York, NY, USA.

Loreau, M., and W. Ebenhöh. 1994. Competitive exclusion and coexistence of species with complex life cycles. Theoretical population biology 46: 58-77.

Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. American Naturalist 154: 427-440.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton, NJ, USA.

Molloy, A. W. 1995. Studies on the endangered Chittenango ovate amber snail (*Novisuccinea chittenangoensis*) and related species of the Chittenango Creek watershed. Master's thesis. State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA.

Molloy, A. W., and R. A. Norton. 1993. Establishment of a captive colony of Chittenango ovate amber snails (*Novisuccinea chittenangoensis*). Interim Technical Report – Department of Environmental Conservation Contract # C002743.

Murphy, G. I. 1968. Pattern in the life history and the environment. American Naturalist 102: 390-404.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.

Oosterhoff, L. M. 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). Netherlands Journal of Zoology 27: 1-132.

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

Parker, I. M., D. Simberloff, W. M. Lonsdale, et al. 1999. Impact: towards a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19.

Parkes, J. P., and F. D. Panetta. 2009. Eradication of invasive species: progress and emerging issues in the 21st century. Pages 47-60 *in* M. N. Clout and P. A. Williams, editors. Invasive species management: a handbook of principles and techniques. Oxford University Press Inc., New York, New York, USA.

Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. Quarterly Review of Biology 64: 393-418.

Pianka, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50: 1012-1030.

Pimentel, D., R. Zuniga, D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273-288.

Sala, O. E., F. S. Chapin III, J. J. Armesto, et al. 2000. Global biodiversity scenarios for the year 2100. 2000. Science 287: 1770-1774.

Schwarz, C. J., and A. N. Arnason. 2008. Jolly-Seber models in MARK. Pages 13.1-13.53 *in* E. Cooch, and G. White, editors. Program MARK: a gentle introduction. Seventh edition. Fort Collins, Colorado, USA.

Simberloff, D. 1981. Community effects of introduced species. Pages 53–81 in M. H. Nitecki, editor. Biotic crises in ecological and evolutionary time. Academic Press, New York, NY, USA.

Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. Pages 3–26 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, NY, USA.

Simon, K. S., and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48: 982-994.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibirum maintenance of species diversity. Ecology 60: 1225-1239.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 535-391.

Stearns, S. C. 1989. Trade-offs in life history evolution. Functional Ecology 3: 259-268.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54: 322-330.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70: 324-336.

Thomee, E.T. 1986. Behavioral ecology of the endangered Chittenango ovate amber snail *Succinea chittenangoensis* and a sympatric introduced succineid. Unpublished Master's thesis. State University of New York, College of Environmental Science and Forestry.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ, USA.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2-16.

Tilman, D. 2000. Causes, consequences, and ethics of biodiversity. Nature 405: 208-211.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 in R. E. Ricklefs and D. Schluter, editors. Species Diversity in Ecological Communities. University of Chicago Press, Chicago, IL, USA.

Underwood, A. J. 1992. Competition and marine plant-animal interactions. Pages 443-475 in D. M. John, S. J. Hawkins, and J. H. Price, editors. Plant-animal interactions in the marine benthos. Systematics Association Special Volume 46, Clarendon Press, Oxford, England.

U.S. Fish and Wildlife Service (USFWS). 2006. Chittenango Ovate Amber Snail *(Novisuccinea chittenangoensis)* Recovery Plan, First Revision. Hadley, MA, USA.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2007. Patterns of relative species abundance in rainforests and coral reefs. Nature 450: 45-49.

Veen, T., B. C. Sheldon, F. J. Weissing, M E. Visser, A. Qvarnström, and G.-P. Sætre. 2010. Temporal differences in food abundance promote coexistence between two congeneric passerines. Oecologia 162: 873-884.

Walker, B. H., and W. Steffen. 1997. An overview of the implications of global climate change for natural and managed terrestrial ecosystems. Conservation Ecology 1(2). Available at http://www.ecologyandsociety.org/vol1/iss2/art2.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, 46: 120–139.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Reviews of the Cambridge Philosophical Society 42: 207-264.

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

Williamson, M. H. 1996. Biological invasions. Chapman and Hall, New York, NY, USA.

Wolda, H. 1963. Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). Archives Néerlandaises de Zoologie 15: 381-471.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130: 1-14.

Zera, A. J., and L. G. Harshman. 2001. The physiology of life history trade-offs in animals. Annual Review of Ecology and Systematics 32: 95-126.

Appendix A. Estimates for the probabilities of survival (*φ*), recapture (*p*), and entering the population (*b*) during each of the sampling occasions and for the overall population (*N*) and the population at each sampling occasion (N_i) from the best models (i.e., models with the lowest AIC_c and $QAIC_c$). Models were fit using the POPAN formulation of Jolly-Seber models in Program MARK.

Year: 2002[a,b]		Model: *p*(.), *φ*(.), *b*(*t*)		
Parameter	Estimate	SE	95%LCI	95%UCI
1: *φ*	0.791	0.033	0.718	0.850
2: *p*	0.129	0.024	0.090	0.183
3: *b*	0.000	0.000	0.000	0.000
4: *b*	0.000	0.000	0.000	0.000
5: *b*	0.277	0.103	0.123	0.513
6: *b*	0.324	0.104	0.159	0.549
7: *b*	0.000	0.000	0.000	0.000
8: *b*	0.000	0.001	0.000	1.000
9: *b*	0.000	0.000	0.000	0.000
10: *b*	0.012	0.058	0.000	0.996
11: *b*	0.000	0.000	0.000	0.000
12: *b*	0.022	0.056	0.000	0.787
13: *b*	0.134	0.056	0.057	0.284
14: *b*	0.000	0.000	0.000	0.000
15: *b*	0.000	0.000	0.000	0.000
16: *b*	0.000	0.000	0.000	0.000
17: *b*	0.000	0.000	0.000	0.000
18: *N*	262.428	35.681	206.602	349.231

[a] Population sizes at each sampling interval (N_i)were inestimable.

[b] Probabilities are based on week intervals between sampling occasions.

Year: 2003		Model: $p(.),\varphi(.), b(t)$		
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.741	0.056	0.619	0.835
2: p	0.179	0.039	0.115	0.269
3: b	0.000	0.000	0.000	0.000
4: b	0.164	0.084	0.055	0.396
5: b	0.156	0.101	0.039	0.455
6: b	0.281	0.098	0.131	0.502
7: b	0.000	0.000	0.00	1.000
8: b	0.054	0.075	0.003	0.503
9: b	0.000	0.000	0.000	0.000
10: b	0.053	0.052	0.007	0.297
11: b	0.000	0.000	0.00	1.000
12: N	225.082	31.764	176.440	303.886
N_1	65.755	18.861	28.786	102.723
N_2	48.744	15.646	18.079	79.410
N_3	73.025	23.096	27.757	118.292
N_4	89.244	26.158	37.975	140.513
N_5	129.416	28.070	74.399	184.433
N_6	95.937	25.230	46.487	145.386
N_7	83.319	18.928	46.220	120.419
N_8	61.765	17.209	28.035	95.495
N_9	57.650	15.202	27.854	87.447
N_{10}	42.736	13.632	16.019	69.454

Year: 2004		Model: $p(t)$, $\varphi(.)$, $b(t)$		
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.900	0.033	0.815	0.949
2: p	0.962	7.821	0.000	1.000
3: p	0.123	0.051	0.052	0.263
4: p	0.255	0.096	0.113	0.480
5: p	0.493	0.091	0.322	0.665
6: p	0.210	0.056	0.121	0.340
7: p	0.201	0.053	0.117	0.324
8: p	0.156	0.029	0.107	0.222
9: p	0.129	0.028	0.084	0.194
10: p	0.074	0.023	0.040	0.133
11: p	0.138	0.033	0.084	0.217
12: p	0.115	0.027	0.072	0.178
13: p	0.042	0.014	0.022	0.078
14: b	0.133	0.149	0.012	0.659
15: b	0.000	0.000	0.000	0.000
16: b	0.015	0.043	0.000	0.849
17: b	0.067	0.041	0.019	0.208
18: b	0.251	0.101	0.104	0.490
19: b	0.242	0.120	0.082	0.535
20: b	0.000	0.000	0.000	0.000
21: b	0.113	0.158	0.006	0.736
22: b	0.146	0.174	0.011	0.726
23: b	0.015	0.136	0.000	1.000
24: b	0.000	0.000	0.000	0.000
25: N	716.462	68.967	603.298	877.002
N_1	13.513	109.917	-201.924	228.951
N_2	105.356	35.676	35.431	175.280
N_3	93.930	32.305	30.611	157.248
N_4	94.936	16.750	62.107	127.765
N_5	132.771	28.941	76.048	189.495
N_6	298.227	71.311	158.457	437.998
N_7	441.224	67.771	308.394	574.054
N_8	393.542	68.072	260.120	526.964
N_9	433.298	112.932	211.951	654.645
N_{10}	494.441	106.367	285.962	702.921
N_{11}	453.068	87.459	281.648	624.488
N_{12}	406.003	89.513	230.557	581.449

Year: 2005		Model: $p(.)$,φ (t), b(t)		
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.995	0.968	0.000	1.000
2: φ	1.000	0.000	0.000	1.000
3: φ	1.000	0.001	0.000	1.000
4: φ	0.767	0.075	0.590	0.883
5: φ	0.929	0.086	0.505	0.994
6: φ	0.886	0.105	0.504	0.983
7: φ	0.702	0.086	0.513	0.84
8: φ	1.000	0.000	1.000	1.000
9: φ	0.543	0.081	0.384	0.693
10: φ	0.469	0.110	0.271	0.677
11: φ	1.000	0. 000	0.000	1.000
12: p	0.22	0.016	0.191	0.252
13: b	0.228	0.039	0.160	0.313
14: b	0.249	0.047	0.169	0.351
15: b	0.000	0.000	0.000	0.000
16: b	0.226	0.045	0.150	0.326
17: b	0.000	0.000	0.000	0.000
18: b	0.041	0.049	0.004	0.331
19: b	0.104	0.047	0.042	0.237
20: b	0.038	0.043	0.004	0.288
21: b	0.000	0.000	0.000	0.000
22: b	0.040	0.023	0.013	0.117
23: b	0.068	0.031	0.028	0.158
24: N	784.216	38.105	718.139	868.398
N_1	4.550	4.558	-4.383	13.483
N_2	181.975	30.911	121.390	242.560
N_3	373.213	34.163	306.254	440.172
N_4	373.212	34.163	306.252	440.172
N_5	463.646	41.223	382.850	544.442
N_6	429.839	42.961	345.636	514.043
N_7	410.266	42.477	327.012	493.521
N_8	365.273	39.437	287.977	442.569
N_9	389.881	35.897	319.522	460.240
N_{10}	203.447	31.052	142.585	264.310
N_{11}	117.962	21.565	75.694	160.229
N_{12}	171.556	26.341	119.928	223.184

Year: 2007[a]	Model: $p(t)$, $\varphi(.)$, $b(t)$			
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.801	0.031	0.734	0.855
2: p	1.000	0.225	0.000	1.000
3: p	0.230	0.071	0.120	0.395
4: p	0.246	0.056	0.153	0.371
5: p	0.232	0.051	0.147	0.348
6: p	0.123	0.029	0.076	0.192
7: p	0.234	0.051	0.149	0.347
8: p	0.094	0.034	0.045	0.186
9: p	0.174	0.050	0.097	0.294
10: p	0.282	0.067	0.171	0.428
11: p	0.175	0.050	0.097	0.295
12: b	0.379	0.124	0.179	0.631
13: b	0.010	0.121	0.000	1.000
14: b	0.103	0.086	0.018	0.415
15: b	0.080	0.074	0.012	0.383
16: b	0.000	0.000	0.000	0.954
17: b	0.189	0.127	0.043	0.543
18: b	0.019	0.125	0.000	1.000
19: b	0.016	0.074	0.000	0.994
20: b	0.121	0.072	0.035	0.342
21: N	551.107	50.007	453.094	649.120
N_1	47.022	12.204	23.102	70.943
N_2	246.301	68.529	111.985	380.618
N_3	202.764	38.014	128.257	277.271
N_4	219.008	39.382	141.820	296.196
N_5	219.724	32.170	156.670	282.777
N_6	176.092	29.334	118.596	233.587
N_7	245.035	72.853	102.243	387.827
N_8	206.624	48.881	110.817	302.430
N_9	174.401	34.764	106.263	242.538
N_{10}	206.185	48.410	111.302	301.068

[a] Probabilities are based on week intervals between sampling occasions.

Year: 2008	Model: $p(t)$, φ (.), $b(t)$			
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.843	0.033	0.766	0.897
2: p	0.999	0.323	0.000	1.000
3: p	0.260	0.118	0.095	0.540
4: p	0.101	0.028	0.058	0.169
5: p	0.166	0.041	0.100	0.263
6: p	0.267	0.064	0.161	0.409
7: p	0.249	0.062	0.147	0.389
8: p	0.112	0.043	0.051	0.226
9: p	0.307	0.073	0.184	0.465
10: p	0.304	0.063	0.196	0.439
11: p	0.113	0.037	0.059	0.207
12: b	0.286	0.139	0.095	0.603
13: b	0.368	0.158	0.133	0.688
14: b	0.000	0.000	0.000	0.974
15: b	0.000	0.022	0.000	1.000
16: b	0.007	0.088	0.000	1.000
17: b	0.076	0.114	0.003	0.665
18: b	0.107	0.112	0.012	0.541
19: b	0.094	0.077	0.017	0.380
20: b	0.000	0.000	0.000	0.996
21: N	322.639	27.593	268.556	376.722
N_1	20.015	7.617	5.086	34.944
N_2	108.168	44.494	20.960	195.376
N_3	208.906	34.768	140.761	277.051
N_4	176.013	30.264	116.696	235.330
N_5	144.936	27.103	91.813	198.059
N_6	121.880	23.167	76.473	167.287
N_7	125.429	34.848	57.127	193.732
N_8	139.508	28.363	83.916	195.099
N_9	147.170	24.673	98.810	195.530
N_{10}	123.155	24.224	75.675	170.634

Year: 2009		Model: $p(t)$, $\varphi(.)$, $b(t)$		
Parameter	Estimate	SE	95%LCI	95%UCI
1: φ	0.845	0.033	0.769	0.900
2: p	1.000	0.143	0.000	1.000
3: p	0.286	0.075	0.163	0.451
4: p	0.197	0.055	0.111	0.327
5: p	0.158	0.036	0.100	0.241
6: p	0.287	0.059	0.186	0.414
7: p	0.180	0.034	0.122	0.258
8: p	0.165	0.037	0.104	0.251
9: p	0.397	0.080	0.256	0.558
10: p	0.018	0.013	0.004	0.072
11: p	0.045	0.026	0.014	0.135
12: b	0.299	0.103	0.140	0.527
13: b	0.058	0.115	0.001	0.789
14: b	0.188	0.104	0.058	0.467
15: b	0.000	0.000	0.000	0.000
16: b	0.202	0.076	0.091	0.390
17: b	0.000	0.000	0.000	0.000
18: b	0.000	0.000	0.000	0.000
19: b	0.000	0.000	0.000	0.000
20: b	0.114	0.134	0.010	0.634
21:N	339.173	52.849	267.240	484.775
N_1	47.015	9.247	28.891	65.139
N_2	140.260	32.343	76.868	203.652
N_3	136.632	30.622	76.613	196.651
N_4	177.545	26.461	125.680	229.409
N_5	150.079	25.099	100.885	199.273
N_6	188.627	22.191	145.133	232.121
N_7	157.757	23.062	112.555	202.958
N_8	133.352	23.741	86.819	179.885
N_9	112.723	23.942	65.796	159.650
N_{10}	132.361	56.126	22.355	242.368