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The distribution and abundance of the California horn snail at different spatial scales

A dissertation submitted in partial satisfaction of the

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in Ecology, Evolution, and Marine Biology

by

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PUBLICATIONS

Lafferty K. D., R. F. Hechinger, J. Lorda, and L. Soler. 2005. Trematodes associated with mangrove habitat in Puerto Rican salt marshes. Journal of Parasitology 91 (3): 697-699.

Ruiz GM, J. Lorda, A. Arnwine, and. K. Lion. 2006. Shipping Patterns Associated with the Panama Canal: Effects on Biotic Exchange? In: Bridging Divides – Maritime Canals as Invasion Corridors; S. Gollasch, B. Galil, and A. Cohen (eds), Springer, Dordrecht. pp 113-126.

Kuris A. M., R. F. Hechinger, J. C. Shaw, K. L. Whitney, L. Aguirre-Macedo, C. A. Boch, A. P. Dobson, E. J. Dunham, B. L. Fredensborg, T. C. Huspeni, J. Lorda, L. Mababa, F. T. Mancini, A. B. Mora, M. Pickering, N. L. Talhouk, M. E. Torchin, and K. D. Lafferty. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454 (7203): 515-518.

Hechinger R. F., K. D. Lafferty, J. P. McLaughlin, B. L. Fredensborg, T. C. Huspeni, J. Lorda, P. K. Sandhu, J. C. Shaw, M. E. Torchin, K. L. Whitney, and A. M. Kuris. 2011. Food webs including infectious agents, biomass, body sizes, and life-stages, for three estuaries in California and Baja California. Ecology 92 (3):791.

Lorda J. and K. D. Lafferty. 2012. Shading decreases the abundance of the herbivorous California horn snail, *Cerithidea californica*. Journal of Experimental Marine Biology and Ecology 432-433: 148-155.

Bonel N., L. C. Solari and J. Lorda. 2013. Differences in Density, Shell Allometry and Growth Between Two Populations of *Limnoperna fortunei* (Mytilidae) from the Río De La Plata Basin, Argentina. Malacologia 56 (1-2): 43-58.

Hopper J. V., C. White, J. Lorda, S. E. Koch, A. M. Kuris, and R. F. Hechinger. 2014. Reduced parasite diversity and abundance in a marine whelk in its expanded geographical range. Journal of Biogeography 41:9 1674–1684.

Bonel N. and J. Lorda. 2015 (in press). Growth and body weight variability of the invasive mussel *Limnoperna fortunei* (Mytilidae) across habitat and season. Malacologia.

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ABSTRACT

The distribution and abundance of the California horn snail at different spatial scales

by

Julio Lorda Solórzano

The California horn snail (*Cerithidea californica* (Haldeman, 1840) (Potamididae: Prosobranchia) dominates the heterotrophic biomass of the salt marsh estuaries of California, Baja California, and Baja California Sur. Thus, it is an ecologically important species, functioning as a significant grazer and competitor, and host to more than 19 species of trematode parasites that infect many other species of invertebrates, fish, and birds as second, intermediate, and final hosts. Any changes in the distribution and abundance of this snail would likely have strong effects throughout estuarine food webs. Here I present observational and experimental studies performed both in the laboratory and in nature that advance our knowledge about the distribution and abundance of these snails. In the first chapter, I show how snail distribution and abundance was restricted by vascular vegetation, bank orientation in channels, and water depth, due to the negative effects of shading on benthic primary production. Vascular vegetation dominates the

biomass of the estuaries of California and Baja California, any changes in vegetation cover will subsequently have an effect on the abundance and distribution of snails. In chapter two, I present how crabs negatively affected snails through predation and non-lethal effects that changed the behavior and diminished the growth rates of snails. Predation pressure was especially high on eggs and the smallest size classes of snails, which had been overlooked in previous predation studies. Finally, in chapter three I present results on how low temperature seems likely to set the northern extent of the horn snail's range by reducing snail performance. Results also suggest a possible tradeoff between growth and reproduction and highlight that although temperature might be important, several other local variables such as predator abundance and parasitism also have a considerable effects on snail abundance and performance. Understanding what sets the distribution and abundance of horn snails at local and regional scales will allow us to better predict the effects of climate change and other anthropogenic effects on these estuarine ecosystems.

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Chapter 1: Shading decreases the abundance of the herbivorous California horn snail, *Cerithidea californica*

Abstract

Most of the intertidal zone in estuaries of California, USA and Baja California, Mexico is covered with vascular vegetation. Shading by these vascular plants influences abiotic and biotic processes that shape benthic community assemblages. I present data on the effects of shading on the California horn snail, *Cerithidea californica.* This species is important because it is the most common benthic macrofaunal species in these systems and acts as an obligate intermediate host of several species of trematode parasites that infect several other species. Using observational and experimental studies, I found a negative effect of shade on the distribution and abundance of the California horn snail. I hypothesized that shading reduces the abundance of the epipelic diatoms that the snails feeds on, causing snails to leave shaded areas. I observed a negative relationship between vascular plant cover, sub-canopy light levels, and snail density in Mugu Lagoon. Then I experimentally manipulated light regimes, by clipping vegetation and adding shade structures, and found higher snail densities at higher light levels. In Goleta Slough, I isolated the effect of shade from vegetation by documenting a negative relationship between the shade created by two bridges and diatom and snail densities. I also found that snails moved the greatest distances

over shaded channel banks compared to unshaded channel banks. Further, I documented the effect of water depth and channel bank orientation on shading in this system. An additional effect of shading is the reduction of temperature, providing an alternative explanation for some of our results. These results broaden our knowledge of how variation in the light environment influences the ecology of estuarine ecosystems.

Introduction

Sunlight drives most food webs. In addition to providing energy for photosynthesis, it generates warmth necessary for physiological processes. In many ecosystems, sunlight is a limiting resource. Physical factors like season, cloud cover, the aspect and orientation of the substrate relative to the position of the sun, water depth, and turbidity affect the amount of light available to plants (Warren, 2008). Primary producers differentially affect the light environment. For instance, to compete for light, some vascular plants have evolved erect architecture that forms a canopy, shading species below (Schmitt and Wulff, 1993). Variation in the light environment is therefore one of the most obvious factors to consider when trying to understand species distributions.

Estuaries have several distinctive habitats such as channels, pans, and vegetated marsh, and these habitats differ in their light environment. The availability of light varies from exposed mudflats to the periodic shading of steep channel banks (e.g., north-facing banks are often shaded during the

winter) to dimly lit mud under dense canopies of vascular plants (primarily pickleweed and cord grass). Shading can reduce benthic diatom production and alter the structure of benthic communities, with potential indirect effects on upper trophic levels like grazing snails (Whitcraft and Levin, 2007; Kon et al., 2010). In addition, these vascular plants are foundation species, as they provide habitat for some estuarine species. They can have both strong positive and negative effects upon other species by changing the availability of resources as well the environmental conditions (Bertness and Hacker, 1994; Leonard and Luther, 1995; Levin and Talley, 2000; Whitcraft and Levin, 2007)

Epibenthic species often respond to competition and low levels of food with increased movement (Levinton, 1979; Chapperon and Seuront, 2011). McCloy (1979) found that the California horn snails, *Cerithidea californica* (Haldeman, 1840), were more likely to move from high-density areas into low-density areas and that snails moved faster when at high snail densities than at lower snail densities. Byers (2000) found that California horn snails tended to display a greater frequency of climbing behavior when in cages with higher levels of competition (high densities of conspecifics) and lower levels of primary producers (diatom density). Lafferty (1993) experimentally demonstrated that snails depressed the abundance of algae in unshaded plots and grew more slowly at high snail densities, indicating that algae are a limiting resource for snails, even in brightly lit habitats.

The California horn snail is the most abundant grazer on epipelic diatoms within Southern California and Baja California estuaries. Snail density varies considerably within an estuary, perhaps, in part, due to variation in algal productivity. Apart from its importance as a grazer, horn snails are “vectors” of parasites to fishes and invertebrates. Specifically, the snail is the obligate first intermediate host of several species of trematode parasites (Martin, 1972) that parasitize a wide range of other species in these systems (Lafferty et al., 2006). As a result, removal of snails leads to wholesale changes in the estuarine food web (Lafferty and Kuris, 2009).

I predicted that densities of California horn snails would be lower in shaded, less productive areas of estuarine marshes and that snails would move more when relocated to shaded habitats with fewer food resources. To evaluate the role of light in determining California horn snail distributions and densities, I examined (1) the relationship between sunlight and snail abundance, (2) the effect of experimental manipulations of light levels on snail abundance, and (3) the effect of different light regimes on the movement of snails.

Methods

Study sites

I conducted observational and experimental studies to examine the effect of light on the abundance of the California horn snail in two different estuaries

in Southern California. The first site was Mugu Lagoon in the Point Mugu Naval Base Ventura County (34.104152° N and 119.090535° W). The area of study was a large mud flat of about 2 ha, just north of the mouth of the lagoon. The mud flat is surrounded by vegetated marsh dominated by pickleweed, *Sarcocornia pacifica* (formerly *Salicornia virginica*). I choose Mugu Lagoon because snails there inhabit vegetated and unvegetated areas, which facilitated observations and experiments on the relationship between plants and snails. The second site, Goleta Slough (34.417574° N and 119.832553° W) in Santa Barbara County, is located next to the University of California Santa Barbara and the Santa Barbara city airport. The area of study was the Tecolotito/Los Carneros creek about 600 m to the west of the mouth of the slough where two vehicle bridges cross the creek: 1) the Highway 217 Bridge (height = 7 m, width = 14.7 m, orientation = 47 º) and 2) the Sandspit Road Bridge (height = 3 m, width = 10.4 m, orientation = 346 º). The vegetation adjacent to the channel is dominated by pickleweed. This location allowed us to study the effect of shading on snail density in a different habitat (channel) as well as removing the potential effects other than shade by vegetation by using the shade of man-made structures (bridges).

Shading by vascular vegetation

In fall 2006, I studied the effects of shading by vascular vegetation on the distribution and abundance of the California horn snail in Mugu Lagoon. The study area was flat without a strong apparent elevation gradient, so elevation

was not measured. Some areas were covered by pickleweed and other areas were free of vascular vegetation. I set up three parallel 50-meter transects that were 25 meters apart. Half of each transect crossed vegetated areas and the other half crossed open areas. At low tide, within 0.05 m2 quadrats, I recorded snail density and visually estimated the percent cover of vascular vegetation every five meters along each transect. To determine light attenuation by vascular vegetation, I also measured ambient and understory photosynthetic photon flux (PPF) using a Multi-Sensor Quantum Meter (Apogee Instruments). I used linear regression to examine the relationship between percent vegetation cover and light attenuation. I applied a generalized linear model (GzLM) to analyze the effects of transect, distance from the mudflat, and light attenuation on snail densities. Specifically, I used a GzLM with a Poisson distribution, a log-link function, and an overdispersion parameters test because of non-normality, heteroscedasticity, and overdispersion of the variance if assuming a Poisson distribution. In addition, to examine the potential additional effect of parasitic trematodes on snail abundance, I collected all snails along one transect and dissected them under a stereomicroscope to calculate the prevalence of parasite infection. I applied a General linear model (GLM) to analyze the effect of the prevalence of trematode infection, light attenuation, and distance from the mud flat on snail density.

Although these studies provided insights into the distribution of snails with respect to the light environment, it does not let us know if shading by vascular plants is the cause of the low snail densities seen in nature. I experimentally tested the prediction that shaded areas would have lower snail abundances than open areas by manipulating the light regimes on a flat at Mugu Lagoon. I used a randomized block design in contiguous vegetated and mudflat areas with similar elevation. Within the vegetated section of the marsh, each block (N=10) had three treatments separated by 2 meters: 1) a plot where the light regime was increased by clearing vegetation, 2) a plot with cleared vegetation where the light regime was decreased with a plastic shade, and 3) a control plot where the light regime was not altered (control). In the cleared treatments, I clipped all vascular vegetation in a 1.25 by 1.25 m area (note that this clipped area extended beyond the area where I measured snails to avoid edge effects). The shaded treatments were clipped plots, as above, but with a rectangular, dark blue, opaque, plastic shade (0.67 by 0.49 m) set 0.3 m above the sediment supported on each corner by legs buried 0.2 m into the sediment. In addition, within the mudflat section of the marsh, each block (N=10) had two treatments separated by 2 meters: 1) a plot where the light regime was decreased using plastic shades as above and 2) a control where the light regime was not changed (control). I monitored snail densities weekly in each quadrat for 3 weeks before (initial) and 3 weeks after (final) the manipulations. I averaged the initial and final

mean snail densities in each plot over time and then determined the proportionate density change in each treatment by calculating the difference between initial and final mean snail densities and dividing this by initial mean snail densities. Due to the heteroscedasticity of the data, I used a Welch's ANOVA to test for differences among treatments and post hoc pairwise comparisons using a sequential Tukey-Kramer test (habitats analyzed separately).

In a preliminary study from the fall of 2005, I found that our shade structures reduced ambient light by 97.3 ± 0.7 % in the center of the quadrat. In contrast, shade control treatments (an open frame with only leg supports) only reduced light by 4.4 ± 1.3 %. I also found no differences in snail densities between shade control treatments and control treatments (ANOVA, N = 10, df = 1, F = 0.6, P = 0.5). Based on the results from this preliminary study, I did not include shade control treatments in the current experiment.

In a subset of blocks (N = 3 in marsh and N = 3 in the flats) used in the light manipulation experiment, I recorded the temperature of the sediment surface before and after to examine the temperature responses to the manipulations. I deployed temperature data loggers (Maxim iButton, San Jose, CA), which recorded temperature hourly throughout the study in each treatment in three different blocks in both habitats by attaching them at the base of a buried ½ inch PVC pole protruding 10 cm from the ground. I calculated the proportionate temperature change as the difference between

the before and after mean temperatures and dividing this by the before mean temperature in each plot. I used a GLM to analyze the effects of habitat (vegetated vs. mud flat), treatments within habitats, and temperature change on snail density.

Shading by bridges

In the summer of 2007, I investigated the effect of shading on the abundance of the California horn snail by comparing snail densities on channel banks shaded by road bridges crossing the Goleta Slough with those in unshaded nearby areas. The two bridges: 1) the Highway 217 Bridge and 2) the Sandspit Road Bridge are about 200 meters apart. On the north and south facing banks of the estuarine channel, starting beneath the centerline of each bridge (parallel to the roadway), I ran 6 parallel 0.1 meter-wide band transects every two meters in both directions (up and downstream from the bridges). I recorded snail density in each band transect, dividing the band transect vertically into 4 plots corresponding to 0.25 m changes in elevation. For reasons mentioned previously, I used a GzLM to examine the effects of bank (south or north), distance from the centerline of the bridge, and elevation on snail density. I dropped all statistically non-significant interactions in the final GzLM to increase power.

To examine relationships among bridge shading, algal abundance, and the density of snails, I measured the standing stock of benthic diatoms along these transects. I collected sediment samples at every 0.25 m increase in

elevation along all band transects from the downstream side of the south bank of Highway 217. I randomly took 3 sediment cores per quadrat using a 1cm in diameter modified plastic syringe to take 4 mm deep cores. I used the protocol by Byers (2000) to process and estimate diatom densities in these sediment samples and used the formulas from Hillebrand et al. (1999) to calculate the bio volume density of diatoms. This subset of samples were taken across a range of shading regimes from under the middle of the bridge to the open section of the bank that facilitated examination of the influence of shade and elevation on diatom density. I used a GzLM to analyze the relationship between diatom abundance and snail density. In the subset of sites where I sampled sediment for diatoms, I also deployed temperature and light data loggers (onset HOBO) to determine the temperature and light regimes created by the bridge shade and the attenuation of light by the water column over tidal cycles. I attached the loggers to a buried ½ inch PVC pole protruding 10 cm from the ground. The loggers took hourly measurements during the month of August and these data were later averaged.

In the summer of 2007, I also conducted an experimental relocation experiment to examine snail movement in habitats with different light regimes. I collected 50 snails from a wide range of sizes (10-35 mm) from each of three habitats: 1) channel bank shaded by a bridge (Sc), 2) an unshaded channel bank (Uc), and 3) a vegetated marsh (Ma). I cleaned all snails with a toothbrush and rinsed them in fresh water. After the snails were

dry, I painted them with two coats of enamel-based spray-paint and then numbered them individually with small (4 mm^2) plastic tags and glue. These marking techniques apparently do not influence snail performance (Hechinger, 2010; Henry and Jarne, 2007). After marking the snails, I first placed each within 10 cm of a marker located in the middle of its original habitat. At one, two, and three days after placement, I recorded the distances traveled by individual snails. I then relocated the snails to a new habitat with a different light regime and recorded the distances traveled by individual snails for another one, two, and three days; this process was repeated five additional times to obtain an average movement per snail. I calculated the velocity of movement of snails by dividing the distance they moved by the time since they were relocated. After the termination of the experiment, all recaptured snails were dissected to determine if snails where infected by trematodes. This was necessary because snails infected with trematodes grow at different rates (Hechinger, 2010) and might move differently. I used a GLM to analyze the effect of snail size, relocated habitat, original habitat, and parasitism on the log10-transformed mean distance moved by snails.

Results

Shading by vascular vegetation

Snails were less abundant under plants than in the open. I found a strong positive linear relationship between vascular vegetation percent cover and light attenuation (Y = 1.55 + 0.955 * X, where Y = % light attenuation and X = % vegetation cover; N = 30, R^2 = 0.97, *F* = 1021.5, *P* < 0.0001). Using a GzLM (Full model: df = 4, χ^2 = 58.12, *P* < 0.0001, overdispersion = 65.67, P < 0.0001), I found a negative relationship between light attenuation and snail density (df = 1, χ^2 =17.97, *P* < 0.0001), but no effect of transect (df = 2, χ^2 = 1.26, *P* = 0.53), or distance from the open flat (df = 1, χ^2 = 1.38, *P* = 0.24), along the three transects that ran from a vegetated marsh (shaded) area to a conterminous mudflat (open) area in Mugu Lagoon (Fig. 1.1). Light attenuation was the only significant effect (df = 1, *F* = 8.95, *P* = 0.0243) on snail density when examined with distance from the open flat (df = 1, *F* = 0.91, *P* = 0.34) and trematode prevalence (df = 1, *F* = 1.57, *P* = 0.26), using a GLM for the transect for which I had prevalence data (Full model: df = 3, *F* = 7.78, R^2 = 0.796 *P* = 0.0172).

Snail density nearly doubled in the marsh plots after vegetation was removed (before = 138 ± 24 SE vs. after = 244 ± 42 SE snail/m^2) and became significantly higher than the control and shaded treatments (Welch's ANOVA, treatment effect, df = 2, *F* = 8.5, *P* = 0.003) (Fig. 1.2). Snail

densities in the control plots did not change over the course of the experiment (initial = 206 ± 30 vs. final = 204 ± 36 snail/m^2), and, in the experimental shade treatment, snail densities tended to decline, but not significantly (initial = 136 ± 24 vs. final = 76 ± 14 snail/m^2; sequential Tukey-Kramer, t = 1.1, P = 0.14). In the experimental plots in the mudflat habitat, I found that snail density slightly declined in the shade treatment (initial = 348 ± 48 vs. final = 272 ± 40 snail/m^2), and did not change in the control plots over the experiment (initial = 361.6 ± 41.6 vs. final = 384 ± 47 snail/m^2). However, the difference between the shade treatment and the control was not significant (Welch's ANOVA, df = 1, F =1.8, P = 0.21) (Fig. 1.2).

Shading also affected sediment temperature. In the subset of sites with temperature loggers, I found that temperature dropped in all treatments, including the controls, after the experimental manipulations started owing to seasonal changes. Temperatures dropped more in the shaded treatments compared to the controls in both habitats. However, the differences were not statistically significant (Marsh: ANOVA, R^2 = 0.52, F= 3.4, P = 0.10) (Mudflat: ANOVA, R^2 = 0.18, F= 0.64, P = 0.47). In the marsh habitat, seasonal temperature drops in the cleared treatments and controls were similar (Fig. 1.3). A general linear model analysis (Full model, R^2 = 0.76, df = 5, F = 5.82, P = 0.0113) revealed no effects of habitat (df = 1, F = 0.04, P = 0.85) or temperature change (df = 1, F = 0.46, P = 0.55) on snail density, but did

show a significant effect of the shading treatment (df=3, F = 7.66, P = 0.008) on snail density (Fig. 1.3).

Shading by bridges

The Highway 217 bridge and water depth (decreasing with elevation due to submergence time) dramatically affected light environments. The amount of light that reached the channel bank was positively related to the distance from the centerline of the bridge with areas under the bridge centerline receiving only 14.1% ± 4.1 SD of ambient light (Fig. 1.4). Drifting algae completely covered the data logger from the site furthest from the bridge (12 m from the bridge centerline) and, for this reason, this site was not included in our analysis. I also found, as expected, that the amount of light decreased with elevation (Fig. 1.5). Not surprisingly, mean temperature was positively related to the distance from the bridge centerline with sites under the centerline of the bridge being at least 2.0 º C colder than sites in the open channel bank (Fig. 1.6). I observed lower densities of diatoms at lower elevations, which I hypothesize was due a decrease in light due to longer submergence times. I also found lower snail densities at low than high elevations (Figs. 1.7 and 1.8). Bridge shading was associated with lower diatom and snail densities (Figs. 1.7 and 1.8). A GzLM analysis showed that bank orientation (south vs. north facing), distance from the centerline of the bridge, and elevation had significant effects on the abundance of the California horn snail (Table 1.1). The south facing banks of bridges (which

are more exposed to sunlight) had significantly higher densities of snails (Sandspit Road, south facing = 139.7 ± 39.5 vs. north facing = 92.6 ± 31.9; Highway 217, south facing = 119.0 ± 30.7 vs north facing = 103.7 ± 27.3). The density of snails around the Highway 217 bridge site was positively related to diatom density (Fig. 1.9), which supported our prediction that the indirect effect of shading on snail densities was mediated through direct reductions of diatom biomass.

In the relocation experiment, I had an average recapture rate of 86% of snails. A GLM analysis indicated that relocation habitat, original habitat, and snail size affected the movement of snails (Table 1.2). Snails did not move between habitats during our experimental relocations. Snails placed under the bridge moved the most (0.04 ± 0.002 SE m/h), whereas snails relocated to the unshaded channel bank moved less (0.03 ± 0.002 SE m/h) and snails relocated under marsh vegetation moved the least (0.009 ± 0.0020 SE m/h) (contrast analysis: Ma vs Sc, $F = 216$; Ma vs Uc, $F = 135$; Sc vs Uc, $F = 18$, all P's < 0.0001) (Fig. 1.10). In addition, snails originally from the marsh and relocated to the marsh (Ma-Ma) moved less than snails that came from the shaded channel and were relocated to the marsh (Sc-Ma) (Ma-Ma vs Sc-Ma, $F = 60.7$, $P < 0.0001$) (Fig. 1.10). Large snails moved faster than small snails; however, I found no effect of parasitism on the movement of snails (Table 1.2). There were also no significant differences in trematode species diversity (Pearson χ^2, df = 8, $P = 0.57$) or parasite prevalence in experimental

snails in different habitats (Prevalence: Marsh = 9.7%, Shaded channel = 14.3%, Open channel = 16.7%) (Pearson χ^2 = 0.7, df = 2, P = 0.72).

Discussion

Many factors affect the distribution of horn snails. Our results indicated that shading is one of these factors; most snails were found on exposed mudflats or shallow channel banks. Other parts of the estuary had lower light levels owing to shading by vascular plants, inundation by water, and the diminished exposure of northern channel banks, so were less productive environments for epipelic diatoms eaten by horn snails. Snails may search for productive grazing areas, leading to higher densities in more exposed habitats with higher light levels.

The main natural factor driving variation in light environments is the distribution and density of vascular plants, which can cover the majority of the intertidal areas of the estuarine systems I have studied (e.g. Carpinteria Salt Marsh, California 77%, Estero de Punta Banda, Baja California 50%, and Bahia Falsa San Quintin, Baja California 55%). Snails may be completely absent from densely vegetated habitats, such as at Carpinteria Salt Marsh, though they can be common in vegetation at other marshes. There are several potential reasons snails occur in some marsh habitats but not others. Plant species and canopy cover differ with tidal height (Mahall and Park, 1976). Our (unpublished) data for the two most dominant plant

species from 38 estuaries ranging from Tomales Bay, California to Guerrero Negro, Baja California shows that pickleweed forms a dense canopy at high-elevation sites (83.3 % ± 23.8 SD, N=206), but does not extend to lower elevations where California cordgrass, *Spartina foliosa*, dominates with a less dense canopy (60.9 % ± 28.5 SD, N=29). Both plant species, however, vary considerably in canopy density, presumably owing to resources, recruitment, disturbance, and herbivory. For instance, in Carpinteria Salt Marsh and Goleta Slough, the vegetated marsh is dominated by pickleweed (83.7 % ± 21.4 SD, N=30 and 88.9 % ± 21.2 canopy cover, respectively, N = 16), but largely occurs at high elevations rarely inhabited by horn snails. On the other hand, in Estero de Punta Banda and Mission Bay, cordgrass is common in the intertidal zone and both the pickleweed and cordgrass canopies are relatively sparse (58.2 % ± 24.0 SD, N=30, 64.2 % ± 29.2 SD, N=6). As a result, snails are common in the vegetated marsh at both of these locations.

Vegetation cover across a marsh can be patchy. For instance, the parasitic plant dodder, *Cuscuta salina*, can reduce pickleweed cover by up to 63% (Callaway and Pennings, 1998). Large rafts of dead sea grass, *Zostera marina*, and algae, such as *Enteromorpha* sp., transported from low intertidal or subtidal areas into higher elevations by spring tides (Fong, 1996; Thiel and Haye, 2006) can smother and reduce vascular plants (personal observations). Shallow unvegetated pans that contain water during low tides

are common within vegetated marsh habitat. Snails can be abundant in these unshaded pans but do not always recruit to these habitats, and may suffer high mortality from periodic rapid and extreme changes in water quality in high elevation habitats (personal observations).

Although I focused on horn snails, shading can affect other species in these estuaries. Whitcraft and Levin (2007) documented strong effects of shading on the community structure of small benthic infauna in Mission Bay, San Diego, CA. Interestingly, they found no effect of varying light conditions on the abundance of *Assiminea californica*, the only gastropod reported in their study; however, *Assiminea californica* feeds mostly on dead and decaying vascular vegetation, so would not likely be affected by the productivity of epipelic diatoms. Further, Whitcraft (unpublished data, personal communication) found a marginally significant increase in the densities of the California horn snails in cleared treatments compared to vegetated controls in an area dominated by cordgrass in Mission Bay, congruent with our results from Mugu Lagoon.

The shade from our experimental manipulation did not have as strong an effect on snail density as the shade from vegetation and bridges. I believe this lack of an effect occurred because these structures created a small patch of shade surrounded by open habitats with high densities of snails (mudflat, clipped areas in the marsh). Small-scale movements of snails from the open habitats with high densities of snails into the shaded treatment plots

might have obscured the effects of shade treatments so that differences were not statistically significant. It is also possible that the small size of the shades allowed sufficient light into the edges of the plots so that they remained suitable for snails. Finally, it is possible that on hot days the shades provided a thermal refuge for snails that offset the negative effects of reduced resources.

Our observation that snails moved more in less productive habitats (shaded channel bank) than in more productive habitats (unshaded channel bank) is consistent with previous experimental work showing that movement is inversely related to resource availability (McCloy, 1979; Byers, 2000). On the other hand, our results that showed slow snail movement in the vegetated marsh contradicted these results. It is possible that vascular vegetation could create structural barriers to directional movement or that snails remain in vegetation because it protects them from water turbulence, predators, or desiccation. At present, however, I do not have a definitive explanation for limited snail movement in the vegetated marsh.

Many other factors besides light levels affect the abundance and behavior of snails, such as elevation, parasitism, predation, turbulence, salinity, and temperature, and these are the subject of parallel studies. There are possible alternative explanations for the effects of light on snail distributions and abundances, rather than how light affects the snail's food (diatoms). For example, vegetation may provide refuge for snail predators, such as crabs.

However, by isolating the effects of shade from habitat structure, our studies indicated that this is not a fully alternative explanation for the patterns I observed. Our study areas shaded by vegetation, experimental shades, and bridges were cooler than unshaded areas as found in other similar studies (Whitcraft and Levin, 2007; Gedan and Bertness, 2010). Temperature could affect the habitat preferences of snails independently of resource availability. Snails presumably have a thermal optima, and might avoid locations that are too warm or too cool. Because I expected snails to move at faster rates with increasing temperature (at least to a point), our observations that snails moved more in shaded than unshaded channels where diatom densities were lower suggests that snails departed habitats with low resource levels. On the other hand, high summer temperatures may approach snail tolerance limits in southern latitudes. Kon and colleagues (2010) found that *Cerithidea cingulata* in Thailand moved to shaded mangrove areas during the summer, presumably to avoid extreme heat, desiccation, and perhaps extreme rain events. Furthermore, our results only apply to the summer months. Our studies were conducted in the northern section of *Cerithidea californica*'s range, where it burrows and remains dormant in vegetated marsh areas during most of the winter (Sousa, 1983), possibly because burial helps snails avoid extreme cold temperatures and vegetation moderates the effects of disturbances associated with winter storms.

In conclusion, our results emphasize the importance of light and shade in determining the distribution and abundance of a dominant snail grazer and its algal food resources. In this system, artificial structures, vegetation cover, water depth, and the slope and aspect of channel banks affected light levels. Light levels had an effect on diatom density, which, in turn, was positively associated with affect snail densities. Snails moved more in shaded channels, perhaps as an adaptation to find more productive habitats. Snails were less abundant under vegetation, but some snails did occur where the canopy was not too dense. Counter to expectation, these snails moved less, perhaps because vegetation impairs snail movement or because there are other advantages to being under vegetation that I did not measure. Overall, I found that shading has an effect on the distribution and abundance of snails. Changes in light regimes due to natural or anthropogenic perturbations in these estuarine systems would likely have strong effects on the distribution and abundance of the most abundant animal in California and Baja California estuaries.

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References

Bertness, M.D., Hacker, S.D., 1994. Physical stress and positive associations among marsh plants. Am. Nat. 144, 363–372.

Byers, J.E., 2000. Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. J. Exp. Mar. Bio. Ecol. 248, 133–150.

Callaway, R.M., Pennings, S.C., 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia 114, 100–105.

Chapperon, C., Seuront, L., 2011. Variability in the motion behaviour of intertidal gastropods: ecological and evolutionary perspectives. J. Mar. Biol. Assoc. United Kingdom 91, 237–244.

Fong, P., 1996. Salinity stress, nitrogen competition, and facilitation: what controls seasonal succession of two opportunistic green macroalgae? J. Exp. Mar. Bio. Ecol. 206, 203–221.

Gedan, K.B., Bertness, M.D., 2010. How will warming affect the salt marsh foundation species Spartina patens and its ecological role? Oecologia 164, 479–87.

Haldeman, S.S., 1840. A monograph of the Limniades and other freshwater univalve shells of North America. Dobson, J., Philadelphia.

Hechinger, R.F., 2010. Mortality affects adaptive allocation to growth and reproduction: field evidence from a guild of body snatchers. BMC Evol. Biol. 10, 136.

Henry, P.Y., Jarne, P., 2007. Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. Invertebr. Biol. 126, 138–153.

Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.

Kon, K., Kurokura, H., Tongnunui, P., 2010. Effects of the physical structure of mangrove vegetation on a benthic faunal community. J. Exp. Mar. Bio. Ecol. 383, 171–180.

Lafferty, K.D., 1993. Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Mar. Ecol. Ser. 96, 229–237.

Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. Proc. Natl. Acad. Sci. U. S. A. 103, 11211–11216.

Lafferty, K.D., Kuris, A.M., 2009. Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 364, 1659–63.

Leonard, L.A., Luther, M.E., 1995. Flow hydrodynamics in tidal marsh canopies. Limnol. Oceanogr. 40, 1474–1484.

Levin, L.A., Talley, T.S., 2000. Influences of vegetation and abiotic environmental factors on salt marsh benthos., in: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer, Amsterdam, pp. 661–708.

Levinton, J.S., 1979. The effect of density upon deposit-feeding populations: movement , feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). Oecologia 43, 27–39.

Mahall, B.E., Park, R.B., 1976. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt Marshes of Northern San Francisco Bay: I. biomass and production. J. Ecol. 64, 421.

Martin, W.E., 1972. An annotated key to the cercariae that develop in the snail *Cerithidea californica*. Bull. South. Calif. Acad. Sci. 71, 39–43.

McCloy, M.J., 1979. Population regulation in the deposit feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh habitat. M. S. Thesis. San Diego State University.

Schmitt, J., Wulff, R.D., 1993. Light spectral quality, phytochrome and plant competition. Trends Ecol. Evol. 8, 47–51.

Sousa, W.P., 1983. Host life history and the effect of parasitic castration on growth: A field-study of *Cerithidea californica* Haldeman (Gastropoda, Prosobranchia) and its trematode parasites. J. Exp. Mar. Bio. Ecol. 73, 273–296.

Thiel, M., Haye, P.A., 2006. The Ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. Oceanogr. Mar. Biol. An Annu. Rev. 44, 323–429.

Warren, R.J., 2008. Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. Plant Ecol. 198, 297–308.

Whitcraft, C.R., Levin, L.A., 2007. Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. Ecology 88, 904–17.

Tables

Table 1.1

Generalized linear models statistics of the effect of bank, distance from the centerline of the bridge, and elevation over the density of the California horn snail at the Highway 217 and Sandspit Road bridges. The GzLM used a log-link function, Poisson error distribution and overdispersion parameter.

Bridge	Main effect	df	χ^2	*P*
Highway 217				
	Snail density			
	Full model: df = 4, χ^2 = 403.81, $P < 0.0001$, overdispersion = 53.77 ($P < 0.0001$)			
	Bank	1	4.00	0.0456
	Distance from centerline	1	270.29	< 0.0001
	Elevation	1	132.02	< 0.0001
	Bank * Elevation	1	3.38	0.0661
Sandspit Road				
	Snail density			
	Full model: df = 3, χ^2 = 246.78, $P < 0.0001$, overdispersion = 65.98 ($P < 0.0001$)			
	Bank	1	5.25	0.0219
	Distance from centerline[Habitat]	1	161.68	< 0.0001
	Elevation	1	79.85	< 0.0001

Table 1.2

General linear model statistics of the effects of original habitat, relocation habitat, and size of snails on the movement of snails. [Relocation Habitat] denotes the variable is nested within relocation habitat.

Main effect	**df**	**F**	***P***
Snail movement			
Full model: df = 9, F = 56.26, R^2 = 0.323 $P < 0.0001$			
Relocation habitat	2	102.19	< 0.0001
Original habitat [Relocation Habitat]	3	15.03	< 0.0001
Size	1	38.36	< 0.0001
Infected	1	1.76	0.1847

Figures

Figure 1.1. Relationship between light attenuation and snail density ($Y = e^{(6.439 + (-0.017) * X)}$, $R^2 = 0.62$, $F = 44.8$, $P < 0.0001$), along three transects through vegetated marsh (solid circles) and open mudflat (open circles).

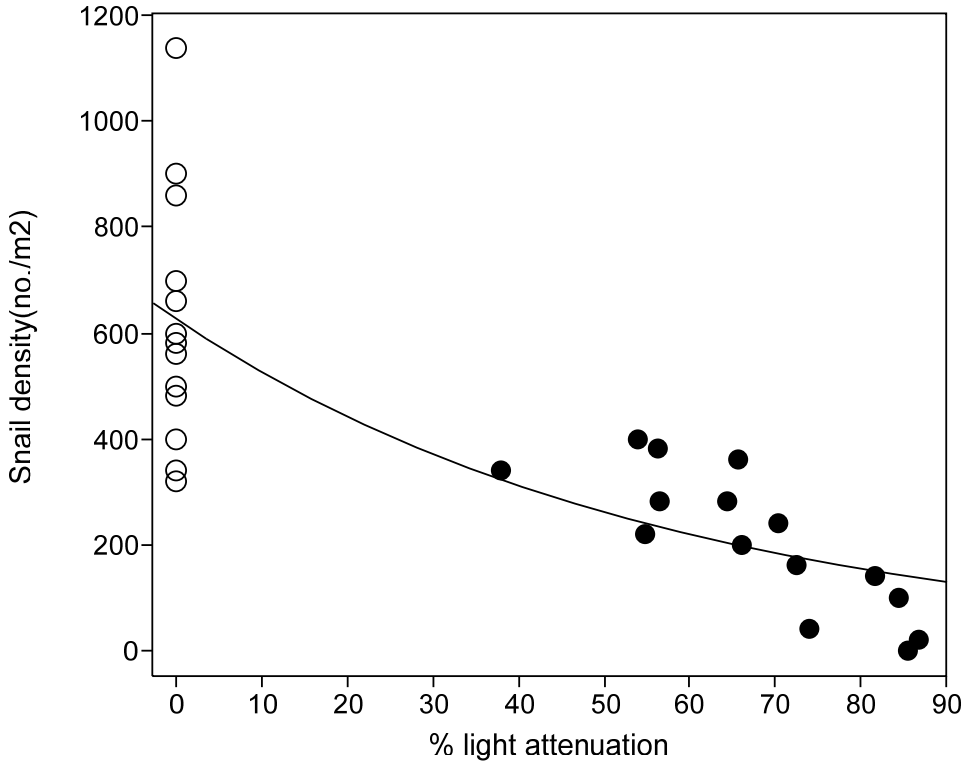


Figure 1.2. Change in snail density after experimental manipulation of light in a) vegetated marsh habitat and b) mudflat habitat. The boxplots show the median and 25% and 75% quantiles and maximum and minimum values. Different letters indicate significance (P<0.05) between groups.

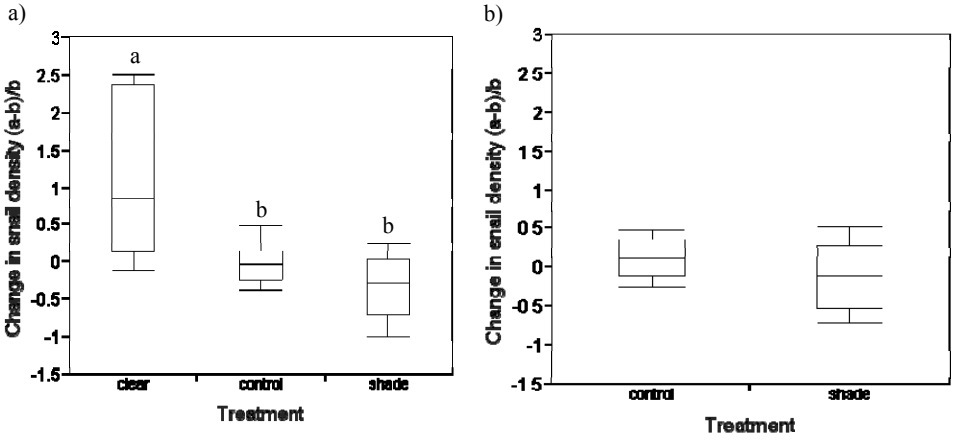


Figure 1.3. Change in temperature after experimental manipulation of light in a) vegetated marsh habitat and b) mudflat habitat. The bars show the mean, standard error, and standard deviation for the different treatments.

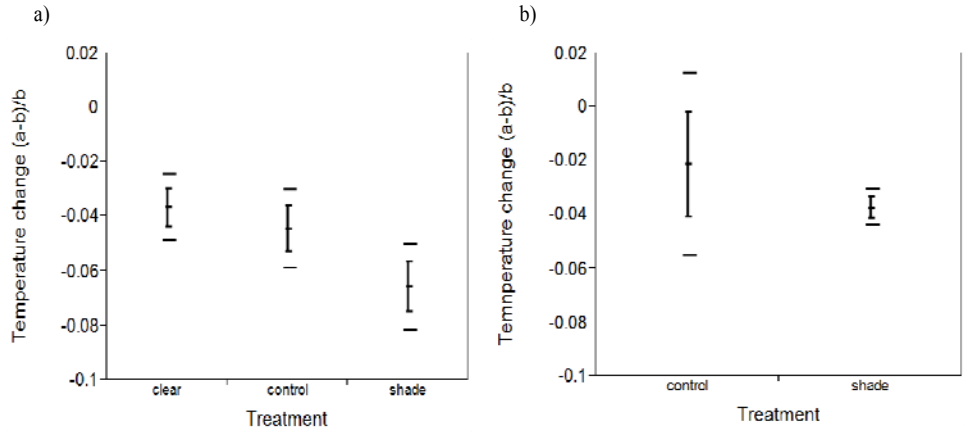


Figure 1.4. Percentage light by distance from the bridge centerline. Solid circles are the sites in the channel bank directly under the bridge and the open circles are the sites in the open channel bank next to the bridge. $Y = e^{(2.42 + 0.18 * X)}$, df = 1, $\chi^2 = 13.46$, $P < 0.0002$, overdispersion = 13.73 ($P < 0.0001$).

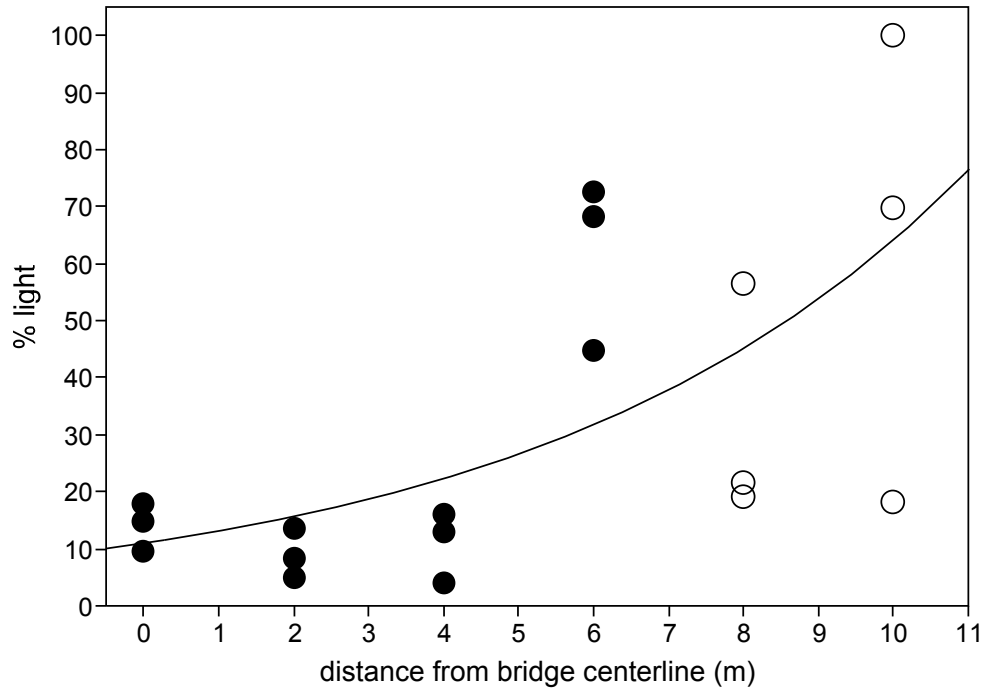


Figure 1.5. One-time measurements of photosynthetically active radiation (PAR) by water depth in Goleta Slough, California, summer 2007.

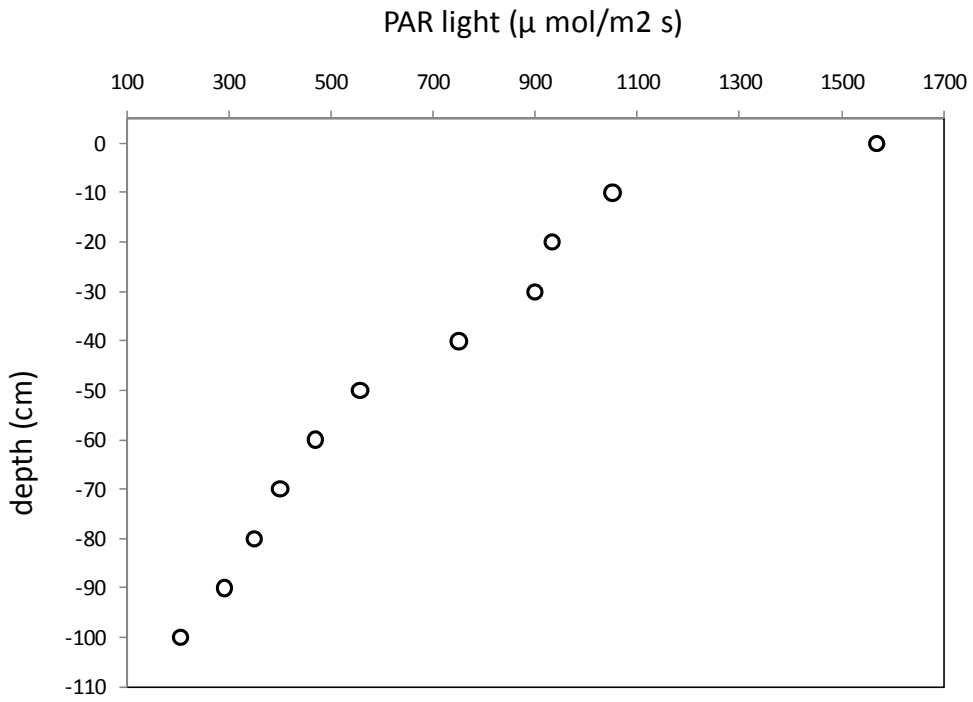


Figure 1.6. Mean temperature by distance from the bridge centerline. Solid circles are the sites in the channel bank directly under the bridge and the open circles are the sites in the open channel bank next to the bridge. Y = 18.55 + 0.28 * X, R^2 = 0.31, *P* < 0.02.

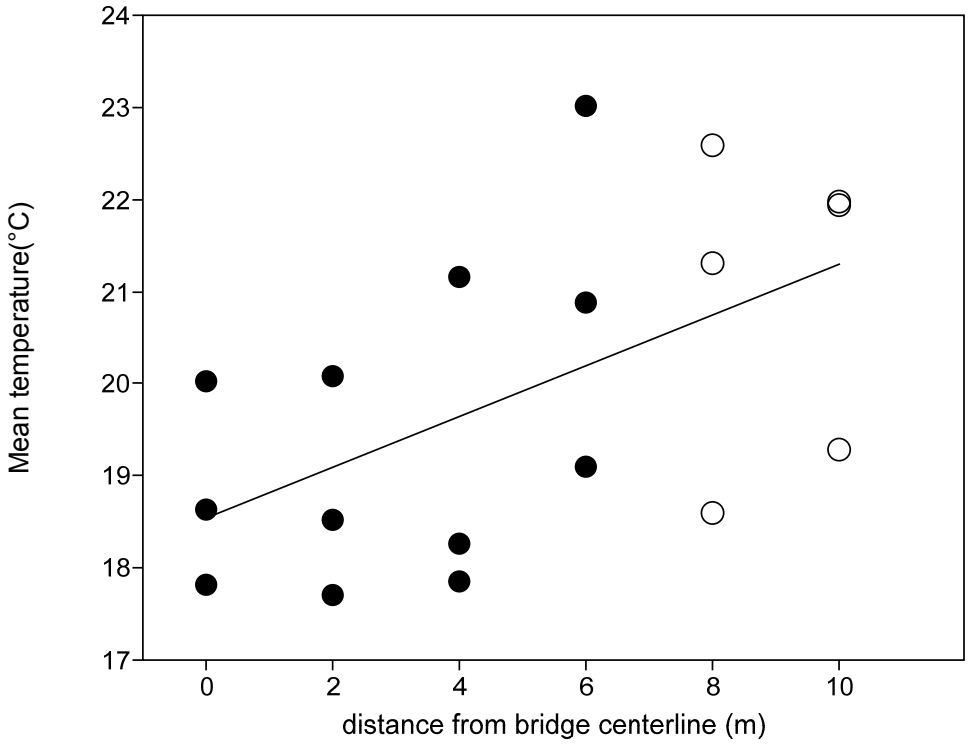


Figure 1.7. Diatom density by distance from the bridge centerline, grouped by elevation (red circles and dash-dotted line = -100 cm: $Y = e^{(-4.59 + 0.051 * X)}$, $R^2 = 0.58$, $P = 0.04740$; green plus signs and dashed line = -75 cm: $Y = e^{(-4.70 + 0.07 * X)}$, $R^2 = 0.47$, $P = 0.0886$; blue diamonds and dotted = -50 cm: $Y = e^{(-4.68 + 0.17*X)}$, $R^2 = 0.91$, $P = 0.0008$; and orange crosses and solid line = -25 m: $Y = e^{(-4.49 + 0.15 * X)}$, $R^2 = 0.96$, $P < 0.0001$). The vertical line that crosses the graph denotes the edge of the bridge, so data points to the left of the line belong to sites under the bridge and the ones to the right of the line belong to sites on the open banks of the channel.

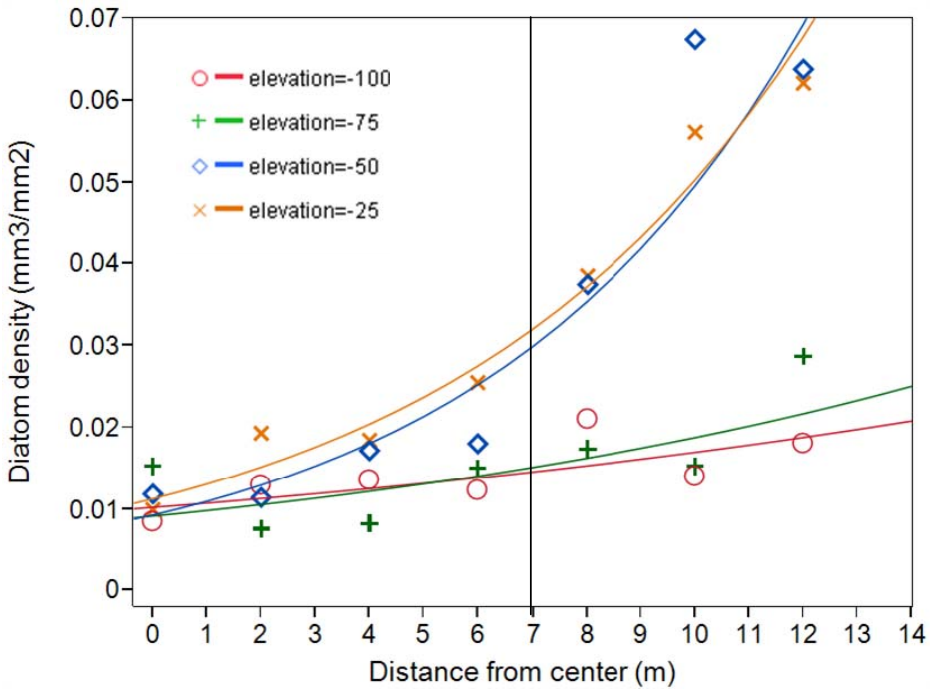


Figure 1.8. Density of snails and the predicted density (curves) of snails from the GzLM by elevation and distance from the centerline of the a) Highway 217 bridge and b) Sandspit Road bridge. The different symbols represent the following elevations: red circles and dash-dotted line = -100cm, green plus signs and dashed line = -75cm, blue diamonds and dotted lines = -50cm, and orange crosses and solid line = -25cm. The vertical line denotes the edge of the bridges, data points to the left of the line belong to sites under the bridge and the ones to the right of the line belong to sites in the open banks of the channel. The prediction curves for Highway 217 bridge: $Y = e^{(2.87+ (0.58 * X)+ (0.032 * Z))}$, and Sandspit Road bridge: $Y = e^{(2.95 + (0.38 * X)+ 0.031* Z)}$, where Y = snail density, X = distance from center, and Z = elevation.

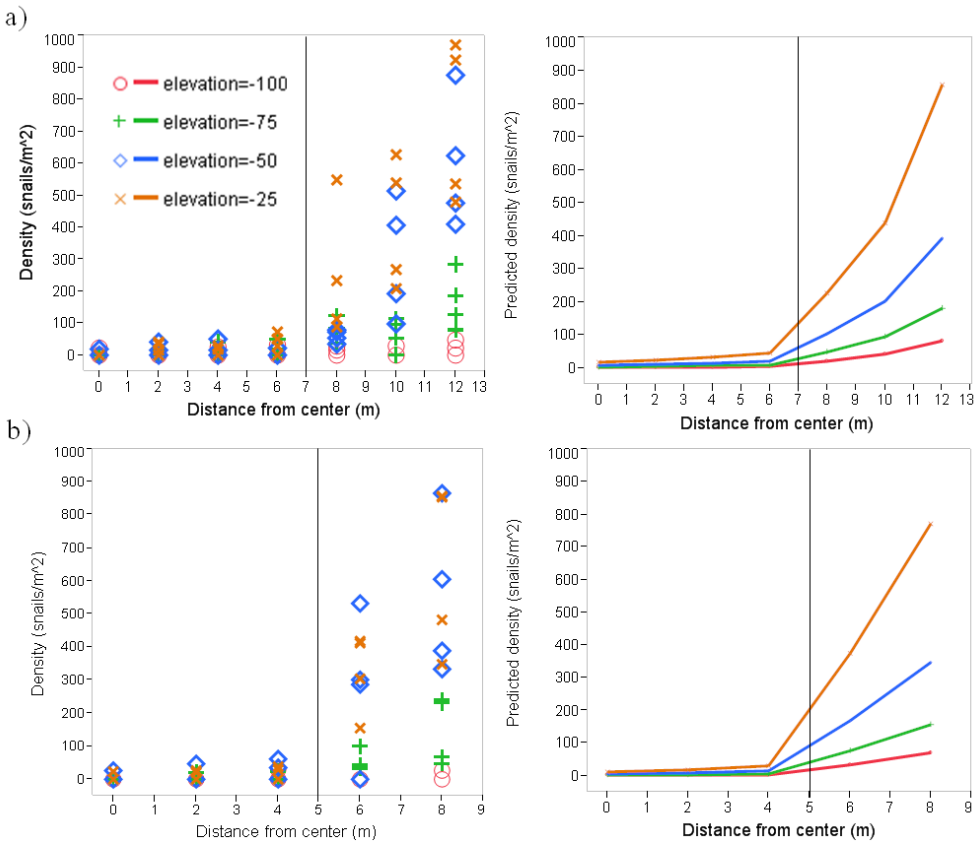

a)
b)
elevation=-100
elevation=-75
elevation=-50
elevation=-25
Density (snails/m^2)
Predicted density (snails/m^2)
Distance from center (m)

Figure 1.9. Relationship between diatom density and snail density. The curve is the predicted snail density calculated from the GzLM [$Y = e^{(1.73 + 68.42 * X}$, df = 1, χ^2 = 73.4, $P < 0.0001$, overdispersion = 62.4 ($P < 0.0001$)]. The different symbols represent the following elevations: red circles = -100cm, green plus = -50cm, blue diamonds = -25cm, and orange cross = -25cm

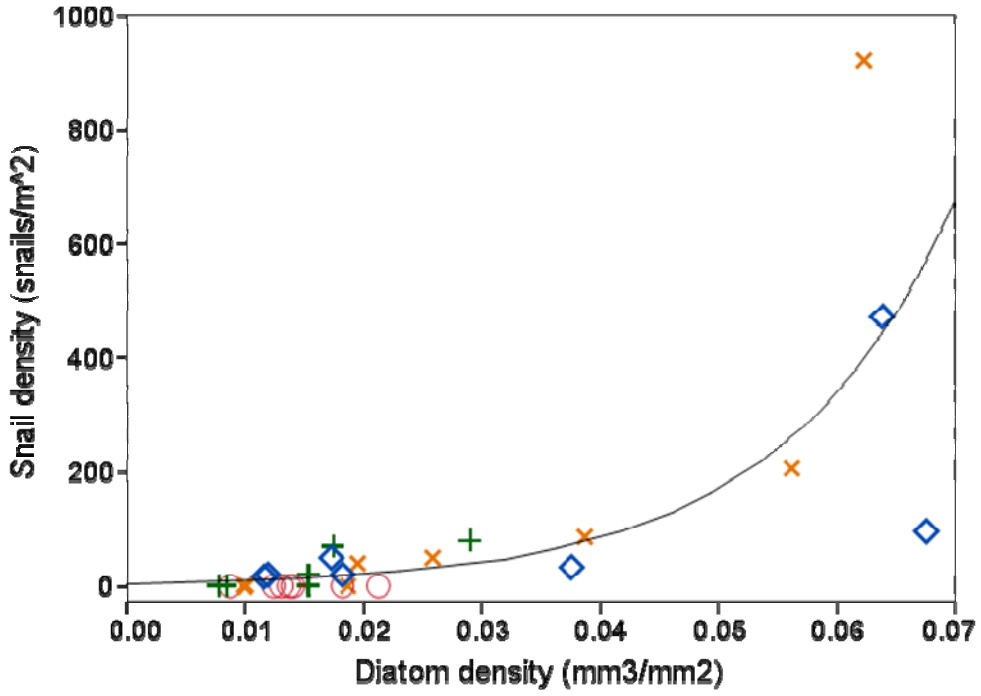
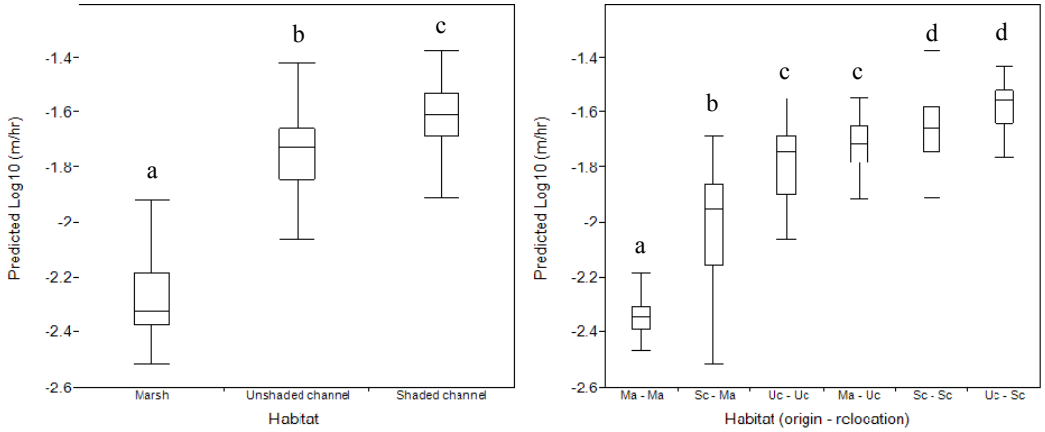


Figure 1.10. The predicted average snail movement calculated from the GLM from Table 1.2 by a) relocated habitats, and b) by original-relocated habitat. The boxes show the median and 25% and 75% quantiles and the bars the maximum and minimum values. Different letters indicate statistically significance ($P < 0.05$) among groups. Ma = vegetated marsh, Sc = channel bank shaded by a bridge, and Uc = unshaded channel bank.



Chapter 2: Shore crabs affect mortality, behavior, growth, and densities of California horn snails (*Cerithidea californica*)

Abstract

The California horn snail, *Cerithidea californica*, and the shore crabs, *Pachygrapsus crassipes* and *Hemigrapsus oregonensis*, are among the most abundant animal species in California and Baja California estuaries. The snail and crabs compete for epibenthic microalgae, whereas crabs also consume snails. Such intraguild predation is common in nature despite models predicting instability. Using laboratory and field experiments as well as field surveys, I documented negative effects of crabs on snails. In the laboratory, I found that crabs preyed on macroalgae, snail eggs and small snails (<15 mm length) more often than on large snails, except for large crabs, which preyed larger snails more than smaller ones. In field experiments, competition with crabs and behavioral responses to perceived predation risk (non-consumptive effects) caused snails to bury in sediment and this reduced snail growth rates. Finally, I found a negative relationship between crab and snail abundances at different scales across up to 16 estuaries in California and Baja California. These results indicate that shore crabs are intraguild predators on California horn snails, and reduce snail populations via predation and by influencing snail behavior and performance.

Introduction

Food webs are often complex, and behavioral interactions among species can have as great an effect on populations as direct consumption (Abrams 1984, Werner & Peacor 2003, Bolker et al. 2013). Intraguild predation, where a predator feeds on a species that it also competes with for food, is an important type of complexity in food webs (Polis et al. 1989). Intraguild predation is common in nature (Arim & Marquet 2004, Bascompte & Melian 2005), however, most mathematical models predict unstable coexistence of intraguild predators and prey, depending on the degree of asymmetry in their use of common resources (e.g. Holt & Polis 1997, Mylius et al. 2001). This is because the intraguild predator either does not have enough resources when competing with its prey or, when resources are high, the predator extirpates the intraguild prey (Holt & Polis 1997, Mylius et al. 2001). These outcomes, lead to a strong negative association between the densities of the intraguild prey and predator at various scales. The effects of predators on their prey could be due to direct consumption, which can have strong cascading effects on the productivity of estuarine systems (e.g. Silliman & Bertness 2002, Silliman et al. 2004). The effects of predators could also occur by non-consumptive interactions, such as if prey seek refuge in the presence of predators, thereby reducing their resource consumption rates (e.g. Trussell et al. 2002; Werner & Peacor 2003; Reynolds & Bruno 2013). Finally, many species have stage-structured life histories, which can complicate predator-

prey interactions, although models suggest that the addition of an invulnerable stage of prey or an inefficient predator stage do not make coexistence more likely (Mylius et al. 2001).

In this study, I investigated the effects of crabs (intraguild predators) on snails (intraguild prey) in Pacific coast estuaries, considering stage-structured direct interactions and non-consumptive effects. In California estuaries, many grazing species consume benthic microalgae (Hechinger et al. 2011). The horn snail, *Cerithidea californica*, competes intraspecifically for benthic microalgae, with snails at high densities reducing algae to lower levels and having lower growth rates than snails at low densities (Lafferty 1993). In addition, snails are more likely to move into areas with low than high snail densities and move faster in areas with high densities and low resource levels (McCloy 1979, Byers 2000b, Lorda & Lafferty 2012). In sum, these studies indicate that benthic microalgae can be a limited resource for snails. The shore crabs *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* feed by scraping microalgae from the sediment with their chelae (Hiatt 1948, Symons 1964). They also use their chelae to handle large macroalgae and larger prey such as snails and their egg masses, although, for snails, they use the chelae to crack or peel the shell open (Hiatt 1948, Symons 1964, Sousa 1993). They also can eat large macroalgae, such as *Ulva* sp., and soft prey, such as egg masses, using only their maxillipeds when missing both chelae (Kuris & Mager 1975). Observations and stable

isotope analyses indicate that the main diet items for these shore crabs are microalgae (e.g., diatoms and cyanobacteria) and green macroalgae (Hiatt 1948, Kwak & Zedler 1997, Page 1997), and both species grow well in the laboratory when fed *Ulva* sp. alone (Kuris & Mager 1975). Also, field experiments indicate that *P. crassipes* can reduce benthic microalgae and the growth of California horn snails (Boyer & Fong 2005, Armitage & Fong 2006). Boyer and Fong (2005) found additive reductions in micro and macroalgae when *P. crassipes* and *C. californica* were held together in enclosures contrasted with enclosures where crabs or snails were present alone. Armitage & Fong (2006) reported that crabs would eat up to 70-80% of the snails presented to them and that crabs also caused snails to burrow into the sediment, potentially reducing snail feeding and growth rates.

In this study, I investigated the predatory and competitive effects of crabs on snails, as well as relationships between the densities of crabs and snails in the field (Fig. 2.1). I used laboratory experiments to examine differences in predation of different sizes of crabs on snail eggs and different sizes of snails. I also did a field experiment to assess the effects of crabs on the behavior and growth of snails through the combined effects of competition for food and predator avoidance behavior by snails. Finally, I explored the relevance of the small-scale laboratory and field experiments for wild populations by examining whether snail abundance and biomass were negatively related to crab abundance. The results show that snails and crabs

interact via intraguild predation (Fig. 2.1), with crabs preying more on early snail stages and reducing snail growth, leading to a negative effect of crabs on snail abundance.

Methods

Study sites

I conducted our laboratory experiments at the Ecological Parasitology Laboratory at UCSB. For the experiments, I collected crabs, algae, snails, and snails' egg masses from a channel next to Estero Street in the Carpinteria Salt Marsh Reserve (34.399791°, -119.535337°). The channel was fringed by vegetated marsh dominated by pickleweed, *Salicornia virginica* (Syn: *Sarcocornia pacifica*) and the road berm. I carried out the field experiments at a mudflat situated on the western side of Carpinteria Salt Marsh (34.403145°, -119.541740°). The mudflat area is about 1000 m^2 and is surrounded by vegetated marsh dominated by pickleweed. I also randomly sampled 16 different salt marsh dominated estuaries open to tidal flow across 10 degrees of latitude (~1110 km), to look for relationships between snail and crab densities and biomass, see Table 2.1 for the location and names of the estuaries.

Laboratory experiments

I did three laboratory experiments to measure predation attempts and predation by shore crabs (*P. crassipes* and *H. oregonensis*) on snail eggs and juvenile/adult snails of a range of sizes (henceforth referred to solely as snail eggs and snails), with and without an alternative food source (adult stage of the alga, *Ulva* sp.= *Enteromorpha* sp.) (Hayden et al. 2003). All predation experiments used the same general procedure. I housed each individual crab in a plastic two-liter container filled with one liter of seawater flowing at ca. 0.017 l/s. I put a single unit of each of the potential prey types (i.e., one snail of each size class, 2 cm of egg mass, 1 mg of *Ulva* sp.) in each container depending on the experiment (described below). The density of the snails and crabs in the containers (snails=106-160/m2 and crabs= 26/m^2) were high, but within the range of densities found in Carpinteria Salt Marsh, California. One or two days later (standardized among replicates), I scored predation attempts and successful predation events. Predation attempts were indicated by missing pieces of algae and egg mass, and damaged shells of live snails. Predation events on snails occurred when crabs extracted the flesh of the snail by cracking the shell. Predation on egg masses and algae were measured as the proportion of the food item eaten. I expressed predation attempts and predation events as the average proportional occurrences for each individual crab over six trials. By calculating the per-crab average, the predation attempt measurements

represent the proportion of prey units that were damaged by crab attacks (in algae and egg mass this is the proportion of prey that was broken in pieces whereas in snails it is shell damage). Predation measurements represent the proportions of prey units eaten (predation on algae and egg masses reflects the average proportions eaten across the six trials whereas, in snails, it represents the proportion of snails eaten by crabs). The crabs and snails used in the experiments encompassed their natural size ranges in Carpinteria Salt Marsh and sizes across experiments varied slightly because of variation in their field availabilities. Across all experiments there was less than 5% crab mortality and about 6% of the crabs molted. If a crab died or molted, I replaced it with a similarly size crab. I used male crabs to keep claw size consistent among replicates (males have larger claws than females).

In summer 2008, I examined crab predation on snail eggs and snails of various sizes. I used three crabs of both species from each of the 10-15, 15-20, and 20-25 mm size classes (maximal carapace width (CW)), as well as three additional size classes of the larger *P. crassipes* (25-30, 30-35, and >35 mm CW). At Carpinteria Salt Marsh, *H. oregonensis* approaches its maximum size at 25 mm CW and *P. crassipes* at 45 mm CW. Each container had one 20 mm long snail egg mass and a snail from each of the following size classes: 10-15, 15-20, 20-25, and 25-30 mm (total length (TL), measured from the tip of the spire to the base of the aperture). After one or two days, I measured the length of the egg mass remaining and calculated

the percentage of egg mass consumed. I also noted successful predation and predation attempts on snails. After checking the containers, I replaced all snails and egg masses and ran the experiment again, repeating each trial six times for all crabs.

I executed a second experiment in the summer of 2009 to consider how an alternative food source affected the way crabs preyed on snails and snail eggs. In this experiment, I used three crabs of each of the following size classes: 10-15, 15-20, 20-25 mm CW for *H. oregonensis* and 10-15, 15-20, 25-30, 30-35, and >35 mm CW for *P. crassipes*. As an alternative food resource for crabs, I put 1 g wet weight of the alga *Ulva* sp. into each container. I also put a 20 mm long snail egg mass and one snail of each of the 10-15, 15-20, 20-25, and 25-30 mm (TL) size classes. The *Ulva* sp. that was not eaten by crabs was recovered and weighed to calculate the percentage of algal mass consumed. Otherwise, procedures were the same as those used in the first experiment.

In the fall of 2009, I did a third experiment where I used algae and the same size classes of snails as in the second experiment but instead of snail egg masses, I included small snails from two additional size classes: 0-5 and 5-10 mm TL. This was intended to reflect available prey for crabs after snail eggs had hatched in the late summer-early fall. I used three crabs of the following size classes: 5-10, 10-15, 15-20, and 20-25 mm CW for *H. oregonensis* and 10-15, 15-20, 25-30, 30-35, and >35 mm CW for *P.*

crassipes. I conducted the experiment using the methods described for the first experiment.

I averaged the predation attempts, successful predation, and proportion of egg mass and/or algae eaten per crab after the six trials and used each crab's angularly-transformed (arcsine square root) average for each prey type as a replicate in statistical analyses. I used paired t-tests adjusted by sequential Bonferroni corrections to examine differences in predation and predation attempts among different prey types for each crab species. To examine differences in predation attempts and rates across prey types among different crab sizes, I used a MANOVA and a multivariate Hottelling-Lawley test for all prey types, and examined differences in predation among crab sizes for single prey types using univariate ANOVAs.

Field experiment

To measure the effects of competition and predation by male *P. crassipes* on *C. californica*, I performed enclosure experiments on mudflats on the northwest side of Carpinteria Salt Marsh in summer 2009. Again, I used male crabs to keep claw size consistent among replicates.

I separated the effects of predation from the effects of competition by crabs on snails by using a spatial block design without replication within blocks (to account for natural heterogeneity within the study area but without testing for its effect in the statistical model) with three treatments in each of

10 blocks: 1) cages with no crabs 2) cages with a crab, 3) and cages with a crab with immobilized claws. Immobilized claws allowed crabs to scrape microalgae and also to feed on macroalgae (Kuris & Mager 1975, Hiatt 1948) but not to handle or feed on snails. I immobilized claws by gluing the moveable finger and the fixed finger of each claw together. I installed bottomless cylindrical-walled enclosures (~30 cm diameter) made of 0.3 cm Vexar mesh measuring 700 cm2 in area with 10 cm below and 25 cm above the bottom's surface. I randomly placed the blocks in the study area and randomly assigned treatments to cages within each block. The enclosures were 1.5 m apart from each other within a block and blocks were at least 3 m apart.

I collected snails for the experiment from the surrounding area, then rinsed and cleaned them with fresh water and painted them with two layers of enamel paint to mark experimental snails as well as the current lip of each shell to calculate growth (change in shell length, where new growth was represented by shell growth below the paint mark). In past studies, this marking technique has not influenced snail movement, growth, or life history traits (Henry & Jarne 2007, Hechinger 2010). After cage construction, I smoothed the mud bottom of each enclosure by hand to homogenize algal densities, and then placed 20 snails and crabs accordingly with the treatments inside each enclosure. The densities (286 snails/m2 and 14 crabs/m2) and sizes (15.9 to 32.8 mm TL for snails and 23.3 to 32.4 mm CW

for crabs) of animals used in the experiment were within the range of natural densities and sizes found in the study area. I checked the cages every week to ensure they were not covered with drift macroalgae, and tracked the proportion of snails that were climbing on cage walls as a measure of dispersal (as in Byers 2000b). I ended the experiment after two months, noting the proportions of snails burrowing in the sediment by hand sifting through underlying mud, checking all enclosures for empty shells remaining after predation, and then collecting all living snails. In the lab, all snails were measured and checked for parasite infections, and their growth rates were calculated.

I used general linear models and post hoc Tukey's HSD test to estimate the effect of treatment on the proportions of snails climbing on cage sides and burrowing into the mud. Both uninfected and infected snails were combined in these analyses because I took these data in the field before dissecting the snails. However, to assess the effect of treatment on snail growth, I used data only from uninfected snails because trematode-infected snails have different growth rates than uninfected snails and cannot reproduce (Lafferty 1993, Hechinger 2010). I also excluded dead snails from these analyses. I used a generalized linear model with a Poisson error distribution with a log-link function, given the non-linear nature of the data, and an overdispersion parameter because the variance was over dispersed for a Poisson distribution.

Field patterns

I examined relationships between snail and crab densities using data from three surveys and 16 estuaries (Table 2.1). In the first survey (Kuris et al. 2008), crabs and snails were sampled from 2002 to 2006 at 23 random sites in the intertidal zones of each of the following three estuaries: Carpinteria Salt Marsh in California, and Estero de Punta Banda and Bahía Falsa in Bahía de San Quintín in Baja California. The 23 random sites in each estuary were stratified by habitat with 5 vegetated marsh, 5 pan, 5 mudflat, and 8 channel sites. Snail density was determined visually at each site using ~20 10 x 50 cm quadrats and crab density by taking five random "core" samples. Each core sample consisted of three adjacent 24 cm diameter by 50 cm deep cores, placed at random within an area with crab burrows. Overall crab density was estimated from these cores by multiplying the density of crabs per core by the proportion of estuarine habitat that had crab burrows in a plot with maximum dimensions of 10 X 10 m but sometimes limited by channel or pan size. With other data collected during this survey, I also calculated the proportions of living snails with damaged shells (assumed to be due to unsuccessful crab predation events), across sites and snail size classes. I only used data from sites and size classes with at least 20 individual snails.

The second survey was conducted in 2007 in the intertidal zones of 13 estuaries ranging from Drakes Estero, California to Guerrero Negro, Baja California (Hechinger et al. unpublished data). Thirty-five sites were sampled

in each estuary, except for two small estuaries where only 20 sites were sampled. The 35 sites at each estuary were stratified by habitat, with 15 sites randomly chosen from channel habitats and 20 randomly selected sites that were not stratified by habitat but which were categorized as mudflat or vegetated marsh sites. At each site, the densities of snails and shore crabs were estimated visually and by hand sifting from five, adjacent, large cores (20 cm diameter by 50 cm deep) placed irrespective of the presence of crab burrows.

Lastly, I calculated crab burrows and snail densities at 34 sites distributed seaward to landward along three different channels (9, 10, 15 sites per channel) in Carpinteria Salt Marsh, CA, in 2008. Sites were 75 m apart within a channel. I determined the densities of snails, snail eggs, and crab burrows (as a proxy for crab presence and density) at each site using three band transects, each 10 cm in width, stretched across each channel.

In all surveys, the density of snails included burrowing snails, which were detected by hand sifting through underlying mud. Burrowed snails are usually within 1-3 mm of the surface and were easily found. Also, in all surveys, snail sizes were measured and snail biomass was calculated using a length-weight regression equation (Kuris et al. 2008). I excluded from all analysis sites where both snails and crabs were absent, because I assumed these sites did not contain suitable habitat for snails or crabs. This explains the

discrepancy between the number of sites sampled in the methods and the tables in the results.

From each survey, I calculated the extent of percent overlap by habitat type between snails and shore crabs (both species combined) for each of the habitats sampled following Krebs (1999) but proposed earlier by Renkonen (1938), using measurements of density and biomass at the site level :

$$P_{jk} = \left[\sum_{i=1}^{n} [\![\left(\text{minimum } P_{ij}, P_{ik} \right)]100]\!] \right.$$

where Pjk = percent overlap between species j and species k

Pij = proportional density/biomass at site i of all sites where species j was present

Pik = proportional density/biomass at site i of all sites where species k was present

n = total number of sites

with values ranging from 0% = no sites with both snails and crabs, to 100% = densities of snails and crabs were proportional in all sites.

I used multi-factorial General Linear Models where snail density and biomass were the response variables; estuary and habitat (in the first survey), habitat (in the second survey), and channel identity (in the third survey) were class independent variables; and distance from the mouth (in the last survey) and crab density and biomass of both crabs (in all surveys) were used as independent covariates. All two-way interaction terms were

included in initial models, but any non-significant (P > 0.10) main or interactive effects were dropped from final models. Replicates in analyses were the data from individual sites in Surveys 1 and 3 and averages for each habitat type from each estuary for Survey 2. I log10-transformed the density and biomass data to meet parametric assumptions (normality and homogeneity of variances).

Results

Laboratory experiments

Crab predation on snails in the laboratory varied with crab size and species and with snail stage and size (Table 2.2 and Table 2.3). In the first experiment, crabs of both species attacked and consumed at least five times more egg masses than they did snails (paired t-tests and sequential Bonferroni corrections, P < 0.05, Table 2.2 and Fig. 2.2). On average, *H. oregonensis* attacked more egg masses than *P. crassipes* but there was no significant statistical difference in predation events among crab species and sizes (MANOVAs and univariate ANOVAs, P < 0.05, Table 2.3, Fig. 2.2).
In the second experiment where crabs were offered *Ulva* sp. as an additional food item, crabs attacked twice as much algae as egg mass and twice as many egg masses as snails. *Hemigrapsus oregonensis* consumed three times as much algae than egg masses and did not consumed any snails. *Pachygrapsus crassipes* consumed twice as much algae as egg masses and

eight times more egg masses than snails (Paired t-tests and sequential Bonferroni corrections, $P < 0.05$, Table 2.4 and Fig. 2.3). On average, there were no significant differences in predation among crab species and sizes (Table 2.3 and Fig. 2.2).

In the third experiment, the proportions of predation attempts and successful predation events by *H. oregonensis* on the smallest snails (< 10 mm) were higher than those for snails larger than 15 mm, which were largely not eaten (paired t-tests with sequential Bonferroni corrections, $P < 0.05$, Table 2.2 and Fig. 2.2). The proportions of predation attempts and successful predation by *P. crassipes* on macroalgae were higher than on small snails (< 10 mm) but differences between algae and the smallest snails (0-5 mm) were not statistically significant (paired t-tests with sequential Bonferroni corrections, $P > 0.05$, Table 2.2 and Fig. 2.2). The proportions of predation attempts by *P. crassipes* were similar for snails from 0 to 20 mm in length, but successful predation was at least four times higher for the smallest snails (0-10 mm) compared to larger snails (paired t-tests with sequential Bonferroni corrections, $P < 0.05$, Table 2.2 and Fig. 2.2).

Predation attempts varied with crab species and size, with *H. oregonensis* showing more attempts on smaller snails than *P. crassipes*, and larger crabs attacking bigger snails, especially for large *P. crassipes* (MANOVAs and univariate ANOVAs, $P < 0.05$, Table 2.3 and Fig. 2.2).

There were no significant differences in predation among crab species and sizes (Table 2.3 and Fig. 2.2).

Field experiment

The mean percentage of snails observed climbing on cage walls was three times lower in enclosures with crabs than in enclosures without crabs (Figure 2.3). The mean percentage of snails burrowed into the mud at the end of the experiment was highest in with crabs with functional claws, intermediate with crabs with immobilized claws, and lowest with crabs absent (Figure 2.3). Consistent with our laboratory experiments, I saw few incidents of predation by crabs on large snails (five cases) in the field experiment, with all five cases occurring in cages containing crabs with functional claws. In addition, two intact snails died in crab enclosures and one died in an enclosure without a crab. Eight snails could not be accounted for and either escaped from enclosures or were eaten but left no remains. One of these snails was from a crab enclosure, three were from different enclosures containing crabs with immobilized claws, and four were from different enclosures with no crabs.

Snails in the enclosures without crabs grew more during the experimental period than did snails from the enclosures with crabs (post hoc contrast: df = 1, $\chi 2 = 47.3$, $P < 0.0001$) and, surprisingly, snails from enclosures with crabs grew more than snails in enclosures with crabs with immobilized claws

(post hoc contrast: df=1, $\chi 2 = 5.8$, $P < 0.02$) (Figure 2.4). As expected, smaller snails grew faster than did larger snails (Figure 2.4, effect of snail initial length on snail growth: generalized linear model □2 = 97, P < 0.0001).(full GzLM statistics, df = 3, □2 = 114, P < 0.0001, overdispersion = 1.48 P<0.0001).

Field patterns

Snails and crabs occurred in all habitat types and their distributions within California and Baja California estuaries overlapped (Table 2.4). The extent of overlap measured as the percentage overlap, varied across habitats and surveys, with overlap in density and biomass being the highest in channels, intermediate in pans, and lowest in vegetated marsh and flats, with zero overlap in flats in the 2nd survey (Table 2.4).

Controlling for estuary, habitat and distance from mouth (depending on the survey analyzed), there were negative relationships between snail and crab densities and biomasses (Figure 2.5 and Table 2.5); however, there was considerable unexplained variation in some of the results (Figure 2.5 and Table 2.5). In Survey 2, the interactions between habitat and crab density or biomass accounted for marginally significant amounts of the variation in snail density or biomass ($P < 0.10$), with negative relationships between snail and crab density and biomass in channel and flat habitats, but little relationship in marsh habitats. I also observed a negative relationship

between snail egg mass and crab burrow densities in Carpinteria Salt Marsh channels (Survey 3), but this relationship was only marginally significant (Figure 2.6).

The proportion of snails with damaged shells was low in the field. I found no relationship between the proportion of snails with damaged shells and crab density across snail size classes; however, snails with damaged shells were absent in the small size classes (0-15 mm), except for at one site (Fig. 2.7).

Discussion

Data from laboratory predation trials, a field experiment, and surveys collectively indicate that crabs reduce snail populations through intraguild predation and by affecting snail behavior with repercussions for snail growth and reproductive output. In laboratory experiments, crabs ate snail eggs and small snails (usually juveniles). The field experiment also indicated that crabs ate adult snails (albeit rarely), but that crabs also altered snail behavior and had negative effects on snail growth. Snails climbed less, burrowed in sediments more, and grew at slower rates in the presence of crabs. Crab and snail populations overlapped in the field, indicating a high potential for interactions between them. Interactions between snails and crabs are further confirmed by field observations of large snails with shells showing the characteristic damage generated by failed attacks by crabs. Although crabs

often unsuccessfully attacked small snails in the laboratory, damaged small snails were not observed in the field, perhaps because they quickly grew out of vulnerable stages or because the short-term laboratory trials did not capture successful crab attacks on snails that had already been damaged (Bertness & Cunningham 1981, Sousa 1993). Finally, surveys conducted at different scales across 16 estuaries showed consistent, negative relationships between snail and crab abundances. Hence, the data suggest that interactions between crabs and snails can reduce local densities of the California horn snail.

Predator-prey interactions between snails and crabs were stage-structured. Crabs fed more on algae and snail eggs than on snails. However, crabs did feed on snails, particularly small ones (< 10 mm), which have thinner and weaker shells than larger snails (personal observations). Although simple laboratory arenas probably did not capture the complexities of habitat, behavior, and alternative prey found in nature, and although predation rates on snails may have been underestimated by the presentation of only 1 individual of each snail size class to predators in each trial, crabs consumed snail eggs even when macroalgae was present and showed higher attack and predation rates on snail eggs than on snails and on small snails than on large snails. The predation patterns I found are likely weaker for female than male crabs, because robust male crabs, which I used, can consume larger snails than comparably-sized female crabs (Sousa 1993).

Hence, crab predation on snail eggs and the smallest snails might be an important, but under-appreciated, source of mortality for horn snail populations.

Shore crabs also appeared to affect horn snail populations by decreasing individual snail activity and growth rates. Such non-consumptive effects are important in other systems (Reynolds and Bruno 2013, Werner and Peacor 2003). Because crabs with functional claws had a stronger effect on snail burrowing behavior than did crabs without functional claws, I suspect that crab handling of snails, increases snail burrowing behavior. However, snails also burrowed more when in cages with crabs with immobilized claws than in cages lacking crabs, suggesting that crabs also elicit snail burrowing responses without handling them. For these reasons, I were not able to disentangle the negative effects of crabs on snail growth as mediated through competition vs. non-consumptive effects (burrowing). Armitage & Fong (2006) also found that snails burrowed more in enclosures with crabs. I also observed that snails responded to crabs by burrowing or retreating into their shells, reducing movement such as climbing. This differs from other snail species that climb onto vegetation or other protruding surfaces in response to predators. In the case of *C. californica*, climbing does not appear to be an escape response (see Byers 2000) as seen in, for example, with Littorina irrorata (Warren 1985, Vaughn & Fisher 1988). Behavioral responses of snails to crabs might have reduced the time snails spent

feeding, resulting, ultimately, in reduced snail growth rates (as seen in our data). Because large snails likely have larger grazing effects on algae than small snails, crabs might have a greater effect on snail populations through their effects on adult snail feeding and growth rates through their harassment of adult snails than via predation on snail eggs and juveniles, although this hypothesis remains to be tested. Because fecundity increases with snail size (Hughes 1986), crab effects on snail growth could also reduce snail reproductive output.

Although there were negative associations between crab and snail abundances, these species coexist. Arim & Marquet (2004) reported that intraguild predation was a common interaction in food webs, particularly for herbivorous-detritivorous prey and omnivorous predators, as in our study. Crabs are omnivorous and eat prey other than snails, snail eggs, and microalgae, including macroalgae, other invertebrates, and carrion (Hiatt 1948, Hechinger et al. 2011). Because crabs are generalists, they can persist under a wide range of resource conditions, even if they drive snails to low levels. Alternative food for crabs and the invulnerability of large snails to crab predation should weaken feedbacks between intraguild predators and prey, but not increase coexistence (Mylius et al. 2001, Tanabe & Namba 2005). Because trematode parasites castrate up to 100% of California horn snails by the time they reach a large size (Sousa 1983, Kuris 1990), any snail size refuges from crab predation will have few snail population

implications because large snails do not produce offspring. Because crabs and snails have many other predators (including crab cannibalism) and parasites (Hechinger et al. 2011), which are not considered in intraguild predation models (e.g. Holt & Polis 1997, Mylius et al. 2001), these other trophic interactions might help maintain the intraguild sub-web studied here. In conclusion, the frequency of crab attacks and consumption of snails depended on the life stage and size of predators and prey, with most crab size classes attacking and eating snail eggs more than snails and small snails more than large snails. In addition, snails responded to crabs by burrowing into the mud, reducing movement, and slowing their growth rates. These interactions can explain the negative associations between crab and snail abundances documented in three separate field surveys. Hence, our results indicate that shore crabs are intraguild predators on horn snails, and reduce horn snail populations through predation and through effects on snail behavior that result in decreased snail growth rates.

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References

Abrams PA (1984) Foraging time optimization and interactions in food webs. Am Nat 124:80–96

Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. Ecol Lett 7:557–564

Armitage AR, Fong P (2006) Predation and physical disturbance by crabs reduce the relative impacts of nutrients in a tidal mudflat. Mar Ecol Ser 313:205–213

Bascompte J, Melian CJ (2005) Simple trophic modules for complex food webs. Ecology 86:2868–2873

Bertness MD, Cunningham C (1981) Crab shell-crushing predation and gastropod architectural defense. J Exp Mar Bio Ecol 50:213–230

Bolker B, Holyoak M, Křivan V, Rowe L, Schmitz O (2013) Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114

Boyer KE, Fong P (2005) Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. Oecologia 143:619–628

Byers JE (2000) Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. J Exp Mar Bio Ecol 248:133–150

California State Parks *Pachygrapsus crassipes* illustration. Mendocino Coast Tidepool Guid http//macpark.mcn.org/lshrcrb.gif

Center for Phycological Documentation (2003) DeCew's Guide to the Seaweeds of British Columbia, Washington, Oregon, and Northern California. http://ucjeps.berkeley.edu/guide/

Hayden HS, Blomster J, Maggs CA, Silva PC, Stanhope MJ, Waaland JR (2003) Linnaeus was right all along : *Ulva* and *Enteromorpha* are not distinct genera. Eur J Phycol 38:277–294

Hechinger RF (2010) Mortality affects adaptive allocation to growth and reproduction: field evidence from a guild of body snatchers. BMC Evol Biol 10:136

Hechinger RF, Lafferty KD, Mclaughlin JP, Huspeni TC, Fredensborg BL, Lorda J, Sandhu PK, Shaw JC, Torchin ME, Whitney KL, Kuris AM (2011) Food webs including parasites, biomass, body sizes, and life stages for three California / Baja California estuaries. Ecology 92:791

Henry PY, Jarne P (2007) Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. Invertebr Biol 126:138–153

Hiatt RW (1948) The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Sci 2:135–213

Holt RD., Polis GA. (1997) A theoretical framework for intraguild predation. Am Nat 149:745–764

Hughes RN (1986) A functional biology of marine gastropods. Croom Helm, London

Krebs CJ (1999) Ecological Methodology (E Fogarty, V McDougal, and N Murray, Eds.). Addison Wesley Longman

Kuris AM (1990) Guild structure of larval trematodes in molluscan hosts: prevalence, dominance and significance in competition. In: Esch GW,

Bush AO, Aho JM (eds) Parasite Communities: Patterns and Processes. Chapman & Hall, p 69–100

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC, Lorda J, Mababa L, Mancini FT, Mora AB, Pickering M, Talhouk NL, Torchin ME, Lafferty KD (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454:515–518

Kuris AM, Mager M (1975) Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. J Exp Zool 193:353–60

Lafferty KD (1993) Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Mar Ecol Ser 96:229–237

Lorda J, Lafferty KD (2012) Shading decreases the abundance of the herbivorous California horn snail, *Cerithidea californica*. J Exp Mar Bio Ecol 432-433:148–155

McCloy MJ (1979) Population regulation in the deposit feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh habitat. M. S. Thesis. San Diego State University

Mylius SD, Klumpers K, Roos AM de, Persson L (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. Am Nat 158:259–276

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Renkonen O (1938) Statisch-okologische Untersuchungen uber die terrestrische Kaferwelt der finnischen Bruchmoore. Arch Soc Zool Bot Fenn Vanamo 6

Reynolds PL, Bruno JF (2013) Multiple predator species alter prey behavior , population growth , and a trophic cascade in a model estuarine food web. Ecol Monogr 83:119–132

Silliman BR, Bertness MD (2002) A trophic cascade regulates salt marsh primary production. Proc Natl Acad Sci U S A 99:10500–5

Silliman BR, Layman C a., Geyer K, Zieman JC (2004) Predation by the black-clawed mud crab,Panopeus herbstii, in Mid-Atlantic salt marshes: Further evidence for top-down control of marsh grass production. Estuaries 27:188–196

Sousa WP (1983) Host life history and the effect of parasitic castration on growth: A field-study of *Cerithidea californica* Haldeman (Gastropoda, Prosobranchia) and its trematode parasites. J Exp Mar Bio Ecol 73:273–296

Sousa WP (1993) Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman. J Exp Mar Bio Ecol 166:19–37

Symons PEK (1964) Behavioral responses of the crab *Hemigrapsus oregonensis* to temperature, diurnal light variation and food stimuli. Ecology 45:580–591

Tanabe K, Namba T (2005) Omnivory creates chaos in simple food web models. Ecology 86:3411–3414

Trussell GC, Ewanchuk PJ, Bertness MD (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecol Lett 5:241–245

Vaughn CC, Fisher FM (1988) Vertical migration as a refuge from predation in intertidal marsh snails: A field test. J Exp Mar Bio Ecol 123:163–176

Warren JH (1985) Climbing as an avoidance behaviour in the-salt marsh periwinkle, Littorina irrorata (Say). J Exp Mar Bio Ecol 89:11–28

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100

Tables

Table 2.1. Estuaries sampled during each survey from North to South.

	Survey			Latitude and longitude
Estuary	1st	2nd	3rd	
Drakes Estero		X		38.055072° / -122.940742°
Bolinas Lagoon		X		37.918782° / -122.679428°
Newark Slough		X		37.508045° / -122.089983°
Morro Bay		X		35.335280° / -120.848593°
Goleta Slough		X		34.417725° / -119.839555°
Carpinteria Salt Marsh	X		X	34.401518° / -119.536947°
Ballona Lagoon		X		33.972082° / -118.459165°
Ballona Wetlands		X		33.967190° / -118.437026°
Golden Shore Wetlands		X		33.763708° / -118.202741°
Salinas de San Pedro Wetland		X		33.714404° / -118.285173°
Santa Margarita River		X		33.234608° / -117.409481°
Los Peñasquitos Lagoon		X		32.930409° / -117.255096°
Mission Bay		X		32.792672° / -117.228989°
Estero de Punta Banda*	X			31.736012° / -116.628797°
Bahía San Quintín*	X			30.452860° / -116.025592°
Guerrero Negro*		X		28.007191° / -114.096833°

* Baja California, México.

Table 2.2. Statistics on predation attempts and events on prey items (macroalgae, snail egg masses, and/or different snail size classes) by *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. In Experiments 1, 2, and 3, the numbers of individual *H. oregonensis* and individual *P. crassipes* used were 12 and 18, 9 and 18, and 12 and 15. Different superscript letters next to □ values indicate significantly different values for different prey types ($p < 0.05$, paired t-tests with sequential Bonferroni corrections).

	Experiment 1 Mean ± SD		Experiment 2 Mean ± SD		Experiment 3 Mean ± SD	
Predation attempts						
H. oregonensis						
Algae			0.94+0.09	A	0.90+0.13	A
Egg mass	0.94+0.11	A	0.47+0.32	B		
0-5 mm					0.78+0.29	AB
5-10 mm					0.80+0.24	A
10-15 mm	0.11+0.13	B	0.15+0.15	C	0.47+0.16	BC
15-20 mm	0.12+0.16	B	0.09+0.12	C	0.19+0.20	CD
20-25 mm	0	C	0	C	0.04+0.08	D
25-30 mm	0	C	0	C	0.04+0.08	D
P. crassipes						
Algae			0.99+0.04	A	0.99+0.04	A
Egg mass	0.80+0.13	A	0.63+0.12	B		
0-5 mm					0.63+0.43	AB
5-10 mm					0.55+0.32	B
10-15 mm	0.14+0.12	B	0.25+0.24	C	0.41+0.30	B
15-20 mm	0.16+0.16	B	0.27+0.28	C	0.48+0.26	B
20-25 mm	0.12+0.15	B	0.05+0.12	D	0.16+0.26	C
25-30 mm	0.06+0.13	B	0.02+0.06	D	0.04+0.10	C
Predation						
H. oregonensis						
Algae			0.41+0.12	A	0.66+0.28	A
Egg mass	0.75+0.18	A	0.14+0.16	B		
0-5 mm					0.75+0.28	A
5-10 mm					0.55+0.33	A
10-15 mm	0	B	0	C	0.01+0.05	B
15-20 mm	0	B	0	C	0	B
20-25 mm	0	B	0	C	0	B
25-30 mm	0	B	0	C	0	B
P. crassipes						
Algae			0.74+0.24	A	0.81+0.15	A
Egg mass	0.52+0.26	A	0.32+0.11	B		
0-5 mm					0.53+0.39	AB
5-10 mm					0.32+0.29	B
10-15 mm	0.05+0.08	B	0.02+0.05	C	0.09+0.21	C
15-20 mm	0.04+0.07	B	0.02+0.05	C	0.02+0.06	C
20-25 mm	0.03+0.06	B	0	C	0.01+0.04	C
25-30 mm	0.02+0.05	B	0	C	0	C

Table 2.3. MANOVA Hotelling-Lawley statistics used to assess differences in the proportions of predation attempts and events on prey items (macroalgae, snail egg masses, and/or different snail size classes) between different species and size classes of crabs in Experiments 1, 2, and 3.

Experiment 1 Main effect	df	F	*P*
Predation attempts			
Full model df = 45, 36.9, F = 3.1, *P* = 0.0003			
Crab species	5, 16	1.5	0.003
Carapace size class [Crab species]	40, 35.8	2.8	0.001
Predation			
Full model df = 45, 36.9, F = 0.9, *P* < 0.64			
Crab species	5,16	1.3	0.32
Carapace size class [Crab species]	40, 35.8	0.9	0.67
Experiment 2 Main effect	df	F	*P*
Predation attempts			
Full model df = 48, 19.8, F = 1.9, *P* = 0.06			
Crab species	6, 10	2.4	0.11
Carapace size class [Crab species]	42, 19.2	1.8	0.08
Predation			
Full model df = 48, 19.8, F = 0.9, *P* < 0.70			
Crab species	6,10	0.7	0.66
Carapace size class [Crab species]	42, 19.2	0.9	0.66
Experiment 3 Main effect	df	F	*P*
Predation attempts			
Full model df = 56, 27.4, F = 6.4, *P* < 0.0001			
Crab species	7, 12	20.9	<0.001
Carapace size class [Crab species]	49, 26.3	4.6	<0.001
Predation			
Full model df = 56, 27.4, F = 1.4, *P* < 0.17			
Crab species	7, 12	2.7	0.06
Carapace size class [Crab species]	49, 26.3	1.3	0.27

Table 2.4. Percentage overlap, and mean snail, snail egg mass, and crab densities (no/m^2) and biomass (g/m^2) by habitat across 3 surveys.

Survey		1st survey	2nd survey	3rd survey*	
Habitat		% overlap (snail / crab)	% overlap (snail / crab)	% overlap (snail / crab)	% overlap (egg / crab)
channel					
	density	39% (151 / 7)	46% (77 / 10)	63% (110/ 6)	52% (5/6)
	biomass	36% (117 / 45)	53% (64 / 26)	62% (107/ 6)	-
	N	22	11	30	30
flat					
	density	21% (48 / 1)	0% (67 / 14)	-	-
	biomass	9% (42 / 9)	0% (50 / 4)	-	-
	N	15	6		
marsh					
	density	17% (114 /14)	16% (147 / 5)	-	-
	biomass	12% (86 / 16)	6% (116 / 6)	-	-
	N	12	10		
pan					
	density	37% (220 / 3)	-	-	-
	biomass	25% (141 / 27)	-	-	-
	N	12			

*crab burrow density

Table 2.5. General linear model statistics on the effects of habitat (Surveys 1 and 2), crab density, biomass, or burrow density (all surveys), channel (creek) and distance from the estuary mouth (Survey 3), and the habitat X crab density or biomass interaction (Survey 2) on snail densities or biomasses from each of the three surveys. All other unlisted main and interactive effects included in initial models were not significant ($P > 0.10$, see Methods).

	Main effect	df	F	P
Survey 1				
	Snail density			
	Full Model (df = 4, R^2 = 0.17, F = 2.8, P = 0.03)			
	Habitat	3	5.7	0.02
	Crab density	1	2.8	0.02
	Snail biomass			
	Full Model (df = 4, R^2 = 0.14, F = 1.4, P = 0.07)			
	Habitat	3	3.8	0.06
	Crab biomass	1	2.9	0.04
Survey 2				
	Snail density			
	Full Model (df = 5, R^2 = 0.58, F = 5.9, P = 0.002)			
	Habitat	2	3.1	0.07
	Crab density	1	12.6	0.002
	Habitat * Crab density	2	2. 7	0.09
	Snail biomass			
	Full Model (df = 5, R^2 = 0.47, F = 3.7, P = 0.02)			
	Habitat	2	4.9	0.02
	Crab biomass	1	9.3	0.006
	Habitat * Crab density	2	2. 8	0.08
Survey 3				
	Snail density			
	Full Model (df = 18, R^2 = 0.89, F = 5.2, P = 0.004)			
	Creek	2	20.1	0.0002
	Distance from mouth	15	4.5	0.0008
	Crab burrow density	1	5.5	0.04
	Snail biomass			
	Full Model (df =18, R^2 = 0.90 , F = 5.0, P = 0.006)			
	Creek	2	16.8	0.0006
	Distance from mouth	15	4.0	0.02
	Crab burrow density	1	6.5	0.03
	Snail egg mass			
	Full Model (df =18, R^2 = 0.85, F = 3.4, P = 0.02)			
	Creek	2	8.8	0.005
	Distance from mouth	15	3.0	0.04
	Crabs burrow density	1	6.4	0.03

Figures

Figure 2.1. Trophic pathways among predatory shore crabs, *Pachygrapsus crassipes* (top left) and *Hemigrapsus oregonensis* (top right), the grazing California horn snail, C*erithidea californica* (middle right), and benthic macroalgae (bottom left) and microalgae (bottom right). Arrows point from resources to consumers (energy flow). Illustrations taken or modified from Hiatt (1948), Center for Phycological Documentation (2003) and California State Parks.

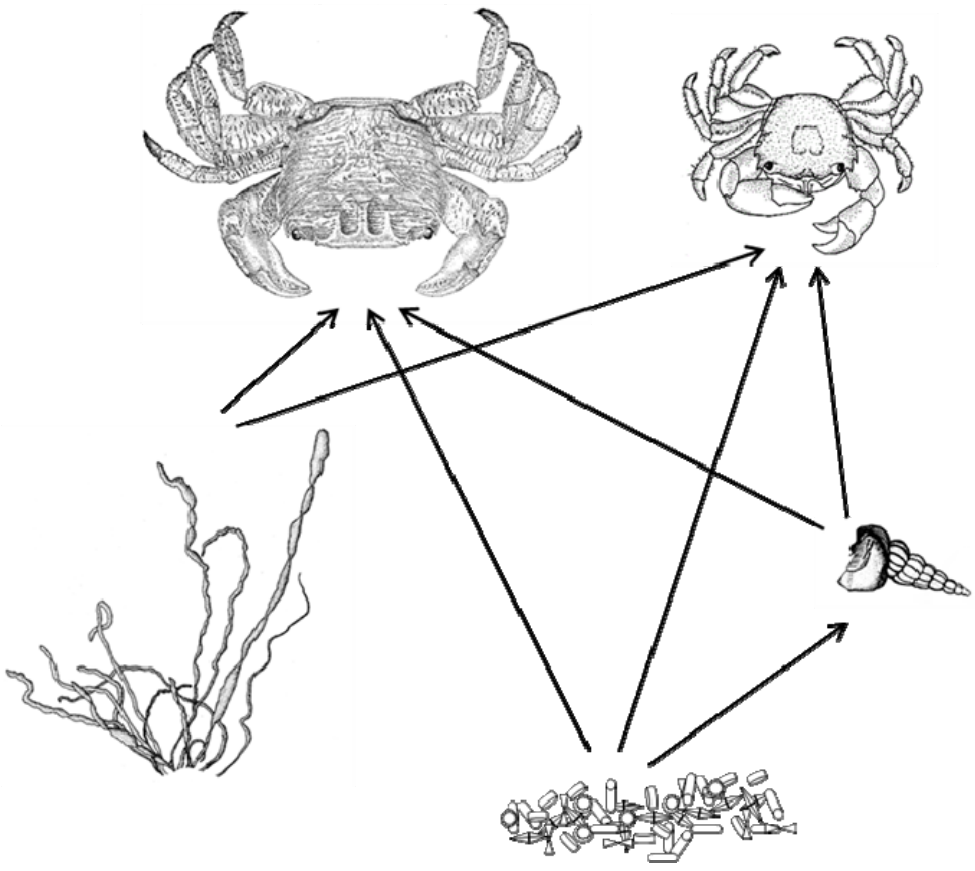


Figure 2.2. Mean proportions of predation attempts (left) and events (right) on macroalgae, snail egg masses, and/or different snail size classes (length in mm) by different size classes (carapace width in mm) of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* in Experiments 1 (top), 2 (middle), and 3 (bottom).

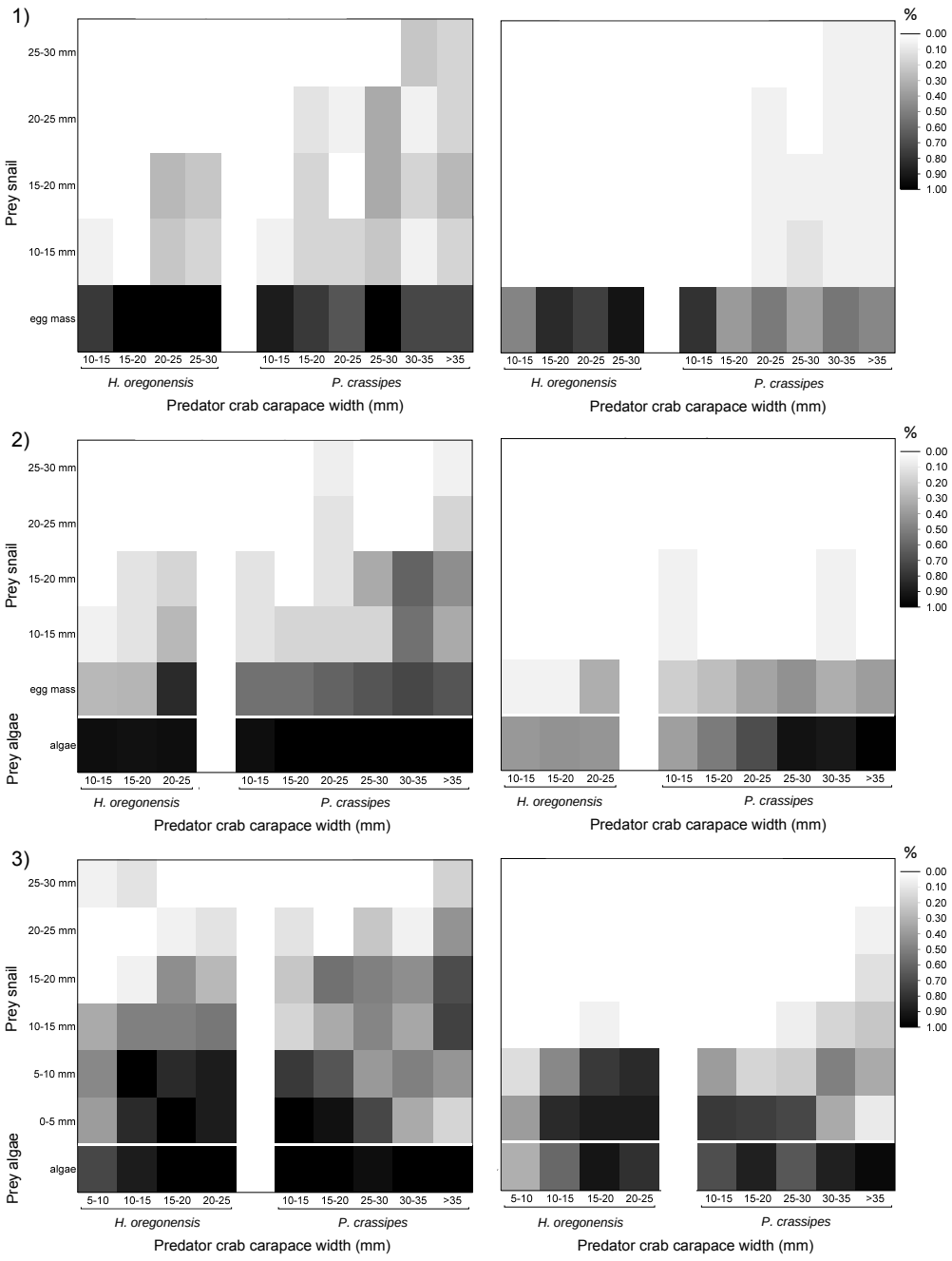
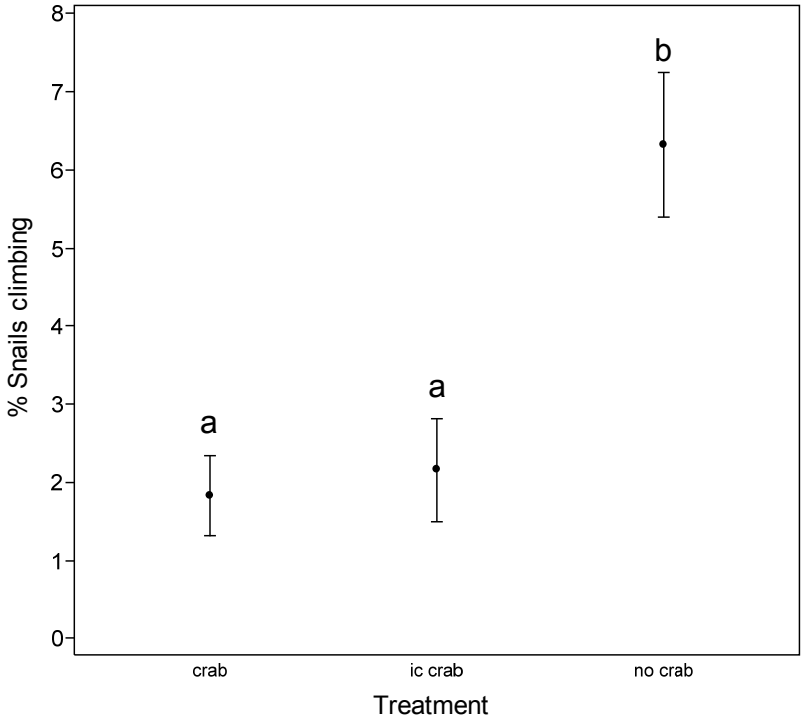

1)
Prey snail
25-30 mm
20-25 mm
15-20 mm
10-15 mm
egg mass
10-15 15-20 20-25 25-30
10-15 15-20 20-25 25-30 30-35 >35
H. oregonensis
P. crassipes
Predator crab carapace width (mm)
%
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
2)
Prey snail
Prey algae
algae
10-15 15-20 20-25
Predator crab carapace width (mm)
3)
5-10 mm
0-5 mm
5-10 10-15 15-20 20-25
10-15 15-20 25-30 30-35 >35

Figure 2.3. Top: Mean percentage of snails climbing on the sides of experimental enclosures throughout the experiment across different treatments: crabs, crabs with immobilized claws (ic crab), and no crabs. Full model: $R^2 = 0.64$, $F = 2.9$, $P = 0.02$. Bottom: Mean percentage of snails which were burrowing at the end of the field experiment across the same treatments. Full model: $R^2 = 0.74$, $F = 4.6$, $P = 0.002$. Error bars are 95% confidence intervals and different letters indicate significant ($P < 0.05$) differences among treatments (Tukey's HSD test).


% Snails climbing
8
7
6
5
4
3
2
1
0
a
a
b
crab
ic crab
no crab
Treatment

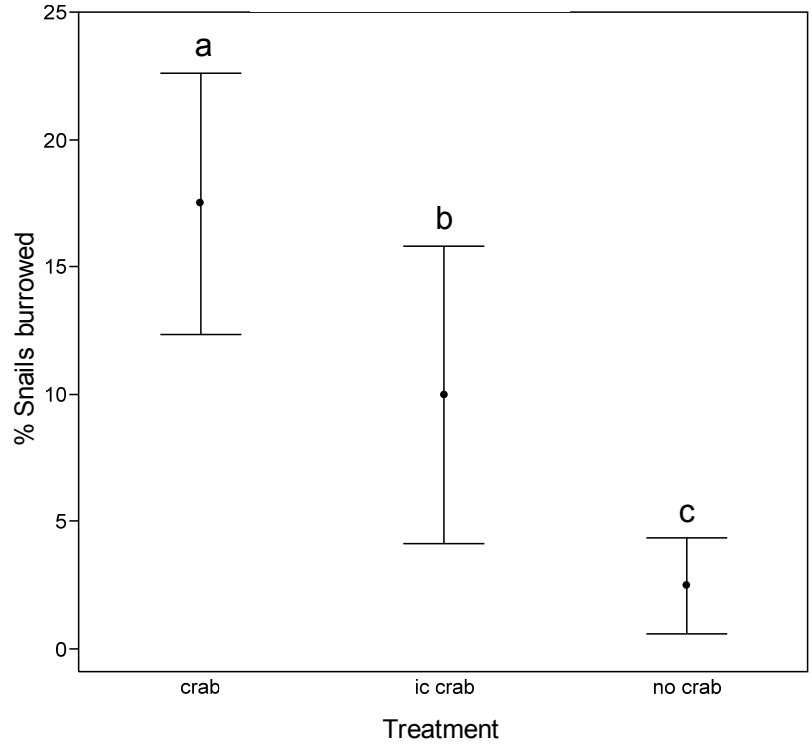

% Snails burrowed
25
20
15
10
5
0
a
b
c
crab
ic crab
no crab
Treatment

Figure 2.4. Snail growth (in mm per 2 months) versus initial snail size (in mm) across experimental treatments: no crab: $Y = e^{(4.47 - 0.14 * X)}$ (red solid curve); crab: $Y = e^{(3.77 - 0.14 * X)}$ (green dotted curve): and crab with immobilized claws: $Y = e^{(4.03 - 0.14 * X)}$ (blue dotted curve). Symbols represent the following treatments: ○ = no crabs, ▷ = crabs with functional claws, and x = crabs with immobilized claws. A GzLM analysis showed highly significant effects of treatment ($\chi^2 = 53$, $P < 0.0001$) and snail initial length ($\chi^2 = 97$, $P < 0.0001$) on snail growth with no interaction effects.

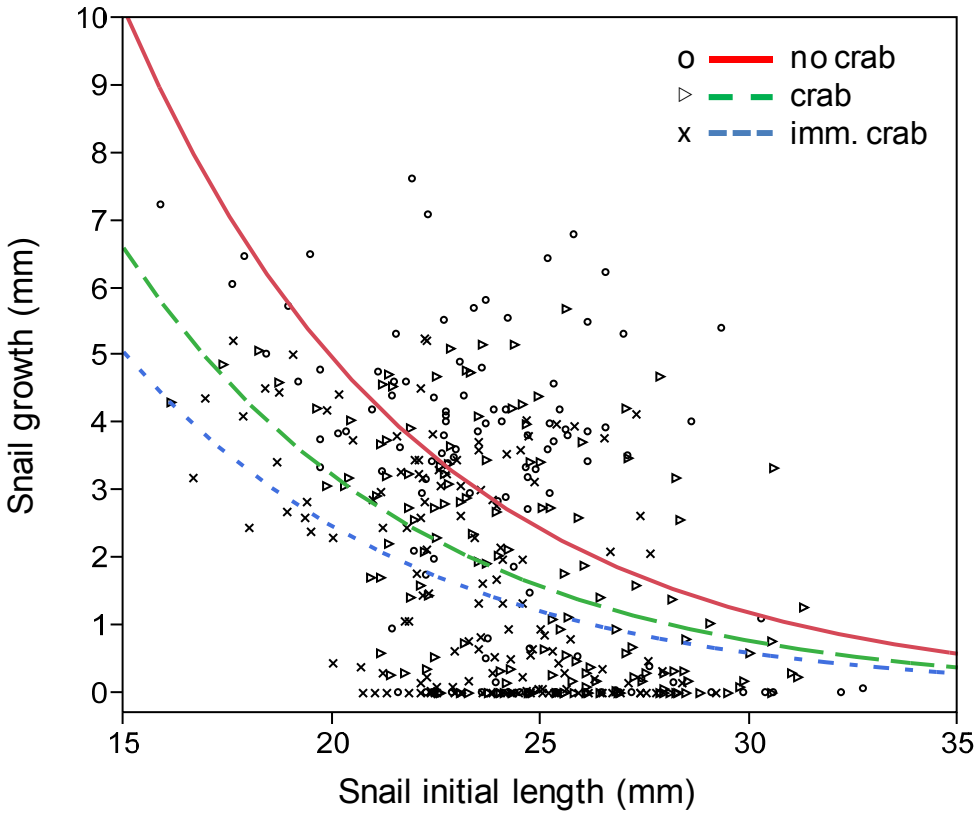


Figure 2.5. Relationships between snail and crab densities (left) and biomasses (right) in different estuarine habitats. a) Relationships between snail and crab density and biomass from the first survey (N=61 sites from 3 estuaries). b) Relationships between snail and crab density and biomass from the second survey (N = 27 habitat averages from 13 estuaries). c) Relationships between snail density and biomass and crab burrow density from the third survey (N = 30 channel sites from 3 channels in 1 estuary).

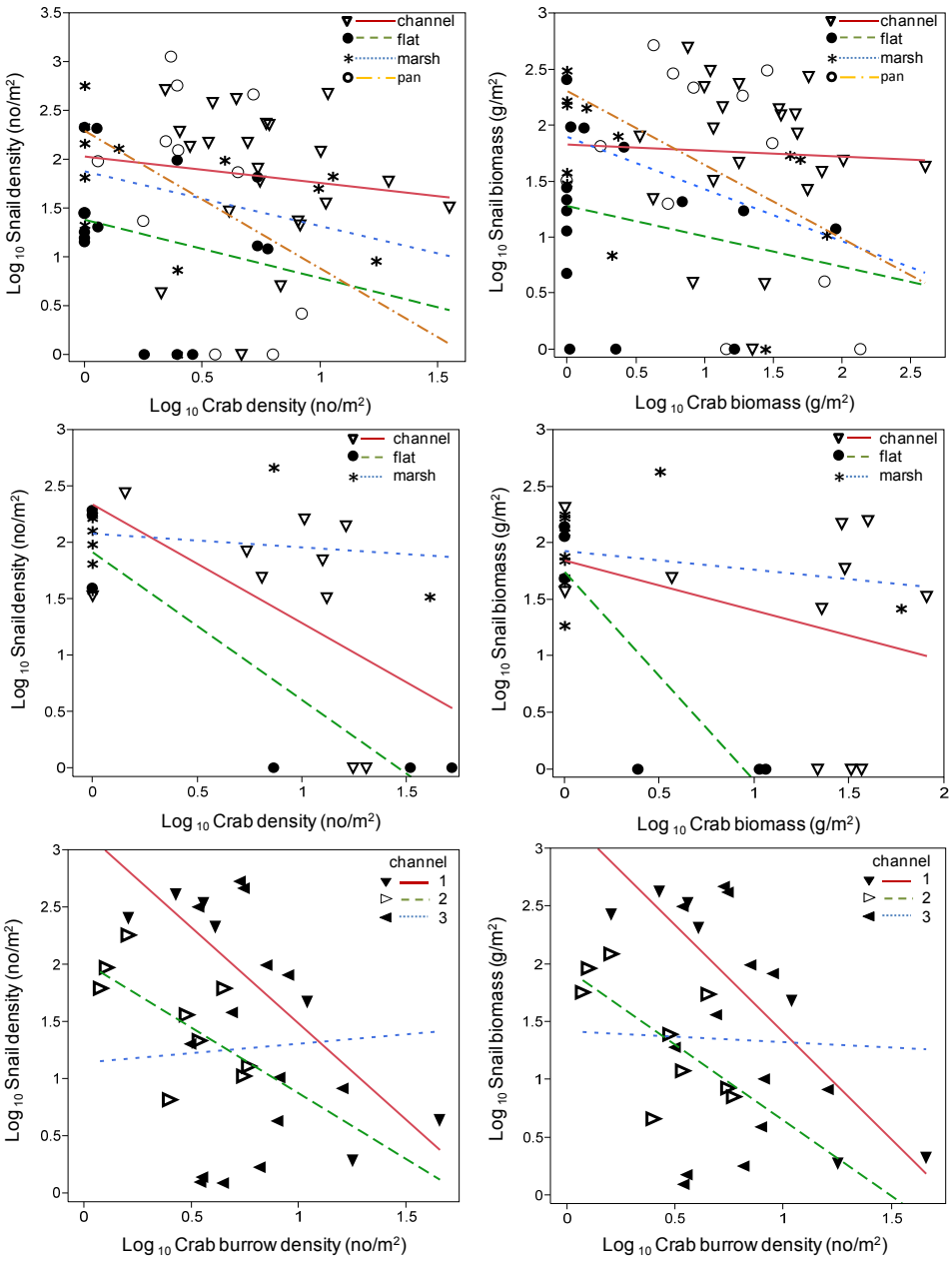

channel
flat
marsh
pan
Log 10 Snail density (no/m2)
Log 10 Crab density (no/m2)
Log 10 Snail biomass (g/m2)
Log 10 Crab biomass (g/m2)
channel
1
2
3
Log 10 Crab burrow density (no/m2)

Figure 2.6. Relationship between snail egg mass and crab burrow densities in three channels at Carpinteria Salt Marsh (Full model: df = 3, R^2 = 0.23, F = 2.6, *P* = 0.07; Crab burrow density: F = 6.3, *P* = 0.02; Channel: *F* = 1.4, *P* = 0.02).

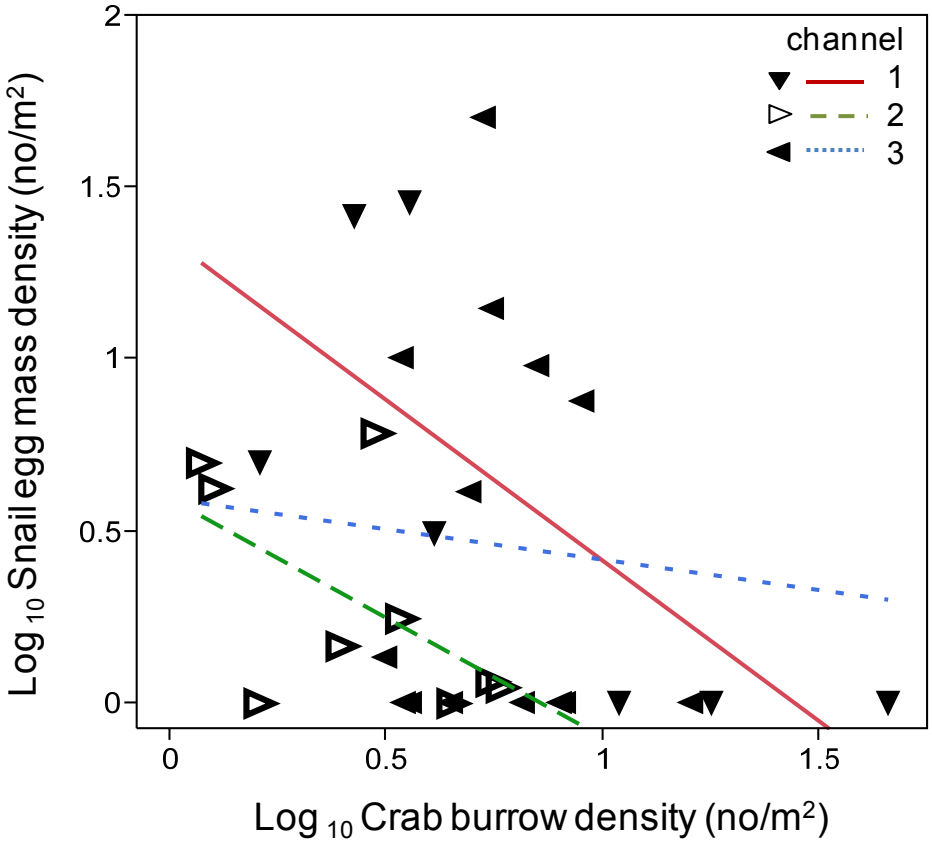
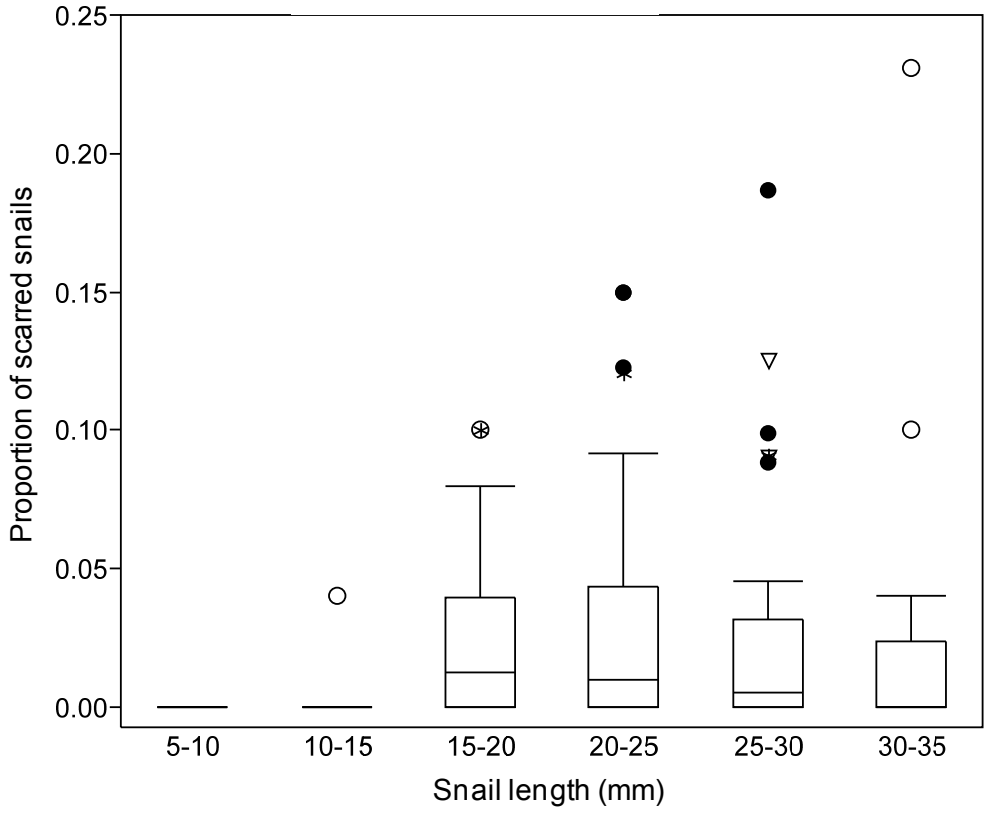


Figure 2.7. Proportion of live snails with damaged shells by different snail length size classes. The box plots show the median and 25% and 75% quartiles. The bars represent the distance of the 75% quartile + 1.5 * the inter-quartile range and the data points are outliers. The symbols represent different habitats (● flats, ○ pans, * marsh, and ▽ channels). Data from the first field survey (N = 10,067 snails from 53 sites spread across three estuaries).



Chapter 3: Growth and reproduction of the intertidal California horn snail, *Cerithidea californica*, throughout its northern geographic range

Abstract

Climate change can influence the distribution and abundance of populations through the effects of temperature on growth and reproduction. However, other factors, such as resources, predation, parasitism, and competition, could override or obscure the effects of temperature. Further, individuals at the edges of species ranges could adapt to local and changing conditions, making them less susceptible to climate change. For these reasons, predictions about the effects of climate change on species distributions should not be inferred solely from laboratory experiments on performance along a thermal gradient. In this study, I examined the effect of temperature, predator density, and parasite prevalence on biomass density of the intertidal California horn snail. I found that biomass density of snails generally increased with temperature and decreased with parasite prevalence, though there were exceptions that were likely due to variation in local productivity. I also measured how growth and reproduction were related to variation in local environmental factors: temperature, predator and competitor densities, parasite prevalence (extrinsic reproductive mortality), and reproduction, after

controlling for habitat, season, sex, and body size. Individual snail growth and reproduction varied significantly among sites and across individual snail sizes. The clearest pattern was that small snails grew fastest at warm sites. The effect of temperature on the growth of medium-sized and large-sized snails depended on the density of crabs and snails. There was a tradeoff between growth and reproduction in small and medium-sized snails when temperatures were low but a positive relationship between growth and reproduction at warmer sites. Overall, these results indicate cold temperatures at the northern part of the range decrease performance as measured by growth. A potential consequence of decreased performance is lower abundance and, ultimately, a range boundary. However, temperature is only part of the story. Interference by crabs, parasitism by trematodes, and unmeasured site characteristics (probably related to food supply) also influenced snail performance.

Introduction

It has become increasingly popular to examine how the physiology and ecology of species vary along latitudinal gradients so that their responses to climate change can be predicted (see Gaston, 2003; Parmesan, 2006). All organisms have an optimal thermal environment where they can maximize growth and reproductive rates (Dell et al., 2011; Savage et al., 2004). However, other factors (e.g., predation, parasitism, and competition) can also

affect individual performance, potentially confounding or masking temperature effects on individuals and populations (Caughley et al., 1988; Gaston, 2003). Several marine biologists have examined how species growth or reproduction varies throughout latitudinal ranges (e.g. Beukema and Meehan, 1985; Defeo and Cardoso, 2002; Dugan et al., 1991; Ebert et al., 1999; Lester et al., 2007; Vaughn and Fisher, 1988), but only a few studies have simultaneously examined both growth and reproduction responses, and the mechanisms for these responses (e.g. Pörtner et al., 2001; Verdelhos et al., 2011). This is important because organisms often must trade-off allocation to growth or reproduction, meaning that performance cannot be measured by one variable without holding the other constant. In this study, I examined how temperature and other local variables affected snail biomass density and quantified how the growth and reproduction of a widely distributed estuarine snail varied across the northern 1,100 km of its geographic range. Further, I examine relationships between growth and reproduction versus possible driving factors, such as temperature, predation, competition, and parasitism.

The California horn snail (*Cerithidea californica* (Haldeman, 1840) (Potamididae: Prosobranchia), including the nominal *C. mazatlanica* and *C. valida* (Miura et al. 2010), inhabits intertidal mud surfaces in Pacific Coast estuaries dominated by salt marsh or mangrove vegetation from Peru to California (Keen, 1963; Race, 1981). The horn snail is a useful species for

studying the impacts of latitudinal temperature gradients on individual performance, because it occurs over a wide latitudinal range, yet has crawl-away larvae and adults with a small home range (Armitage and Fong, 2004a; Lorda and Lafferty, 2012; McCloy, 1979). As a consequence, variables that might influence snail density and individual performance operate at a local (within estuary) scale and are easily measured. The horn snail is also ecologically important because it dominates the biomass of many estuaries, functions as an important grazer and competitor, and hosts more than 19 species of trematode parasites that infect many other species of invertebrates, fish, and birds as second intermediate and final hosts (Armitage and Fong, 2006, 2004; Hechinger et al., 2011, 2007; Lafferty et al., 2006; Kuris et al., 2008; Martin, 1972). Therefore, changes in the distribution and abundance of horn snails at local or regional scales, such as owing to climate change, would likely have strong effects throughout estuarine food webs (Lafferty and Kuris, 2009; Lafferty et al., 2006). As just one example, a shift in the range of *C. californica* would result in a corresponding shift in the range of a dozen or more trematode species, all of which infect other species during their complex life cycles.

Increasing temperatures associated with global warming might influence individual horn snail performance, particularly in the northern part of the species' range. Because a general latitudinal gradient of temperature is expected in estuarine ecosystems, examination of the relationships among

latitude, temperature, snail biomass density, and snail performance might provide data allowing researchers to predict future population responses to temperature increases. However, local variation in tidal heights, exposure, topography, cloud cover, and upwelling may blur the latitudinal temperature gradient (Helmuth et al., 2002). Furthermore, responses to temperature, could be confounded or obscured by other factors (competition, predation, parasitism), so it is important to include these other factors when examining the effect of latitude or temperature on performance (Pulliam, 2000; Sibly and Atkinson, 1994).

We already have some knowledge about the factors that affect performance and density in *C. californica*. Snail (and crab) density increases with benthic diatom productivity (Armitage and Fong, 2004a; Lorda and Lafferty, 2012), which (in addition to temperature) is the result of nutrient levels (e.g. Armitage and Fong, 2004b; Lafferty, 1993a) and light exposure (e.g. Lorda and Lafferty, 2012). This is presumably why pan habitat is more productive than channel or marsh habitat (Hechinger et al. 2008). After controlling for growing conditions, snails grow slower at high densities due to intraspecific competition (Lafferty 1993a). In addition to intraspecific competition, interspecific competition with crabs (Armitage and Fong, 2006, Lorda et al., in review) and snails (Byers and Goldwasser, 2001; Byers, 2000), interference and predation by crabs (Lorda et al., in review), and parasitism (Lafferty 1993a, b) can reduce snail growth and density.

To forecast the effects of climate change on estuarine snail populations, I quantified how the individual growth rates and reproduction of horn snails varied throughout the northern part of its range and how this variation in snail performance was related to temperature and local variables (habitat type (a proxy for productivity), snail and crab densities, parasite prevalence). This effort was motivated, in part, by a previous study by Byers (2005), which surprisingly found no differences in the growth rates of *C. californica* across a wide latitudinal range. However, Byers speculated that the lack of a response was because his study was performed during the peak of the warm growing season when latitudinal differences might be minimized. Furthermore, Byers' measure of growth was averaged across a wide range of snail sizes. Because latitudinal patterns in snail performance might occur during other times of the year and because growth varies substantially with snail size, I conducted this study throughout an entire year and analyzed growth and reproduction separately for different snail sizes.

Methods

Study systems and local variables

I measured growth rates and reproductive indices for horn snails at 22 sites in 14 estuaries in California, Baja California, and Baja California Sur, spanning about 10 degrees of latitude (1,100 km) (Table 3.1). Each site was a 10 m transect of channel or pan (bare mud surrounded by marsh

vegetation) or a 10 x 10 m area of vegetated marsh or mud flat. During my first visit to the study sites, I marked each site with a PVC pole.

I calculated local snail density during each site visit by taking the average of all snails counted in three 0.25-m belt transects across the width of a channel or pan or the average of snail counts in three 1 X 0.25 m quadrats in a marsh or mud flat site. Sampling methods detected both surface and burrowing horn snails, the latter often found 1 to 3 mm under the surface in the winter, but being readily detected by probing with fingers. For crab densities, I used the estuary average crab density of the grapsid shore crabs *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* for the same habitat type (channel, pan, mud flat, marsh) where snails were censused (See Chapter 2 for methodology). Parasite prevalence for snails 20-25 mm in length (a proxy for infection risk) was calculated for each site from the dissections of snails as described in the Growth section below.

Temperature gradients do not always align with latitude in the intertidal zone due to differences in the exposure of the intertidal areas, and timing and height of low tides (Helmuth et al., 2002). During my initial site visits in fall 2007, I deployed a temperature data logger (Onset Hobo Pendant ®) at each site, which subsequently recorded temperature every hour for the duration of the study. Loggers were placed on the surface of the mud (attached to a ¼-inch PVC pole) to record temperatures experienced by horn snails (Table 3.2).

Biomass density

Snail density should reflect the population-level outcome of snail performance at a site. All else being equal, density should be highest where temperatures are optimal for growth and reproduction. However, other variables such intraguild predator abundance and parasite prevalence can affect snail abundance (Armitage and Fong, 2006; Lafferty, 1993a; Lorda and Lafferty, 2012). To examine the combined effects of temperature, crab abundance, and parasite prevalence on snail density, I calculated biomass density for each site (using biomass instead of counts to control for variation in size structure among sites) as the dependent variable .I used General Linear Models (GLMs) which included all main effects and all two-way interactions and backwards stepwise elimination techniques using Akaike information Criterion (AIC) values to select the most parsimonious models (Akaike, 1974; Burnham and Anderson, 2004).

Growth

I marked and recaptured snails to measure their individual growth rates. In fall 2007, I collected 700 snails from each site (~15,200 snails in total), except for Estero de Punta Banda and Bahia San Quintin, where I collected snails in spring 2008. After collection, I cleaned snail shells with fresh water and a toothbrush, permitted the shells to dry, then painted them with two layers of enamel paint to mark the current lip of the shell to establish initial

size. After the paint dried, I returned snails to their collection sites. The cleaning and painting process took place over two days at each site. This marking technique has been used without any effect on snail growth or snail life history traits (Henry & Jarne 2007; Hechinger 2010). I returned to each site in fall 2008 to collect marked snails, then measured snails to calculate growth as the change in shell length. After quantifying individual growth, I used a dissecting microscope to determine snail sex and the presence of trematode parasites from dissected snails (and calculated parasite prevalence as describe above). I only included uninfected snails in the analyses because infected snails cannot reproduce and grow at different rates than uninfected snails (Hechinger, 2010). In spring 2009, I returned to the study sites to capture snails missed in fall 2008, and measured and dissected any additional snails that were collected.

I used a generalized linear model (GzLM) to determine individual growth rates after controlling for the effects of habitat, site, season collected, sex and snail length. I did not test the effect of estuary since I only sampled one or two sites per estuary. In the initial analysis, sites were nested within habitat and two and three-way interaction effects were included. I then examined the effects of snail reproduction (as calculated in the Reproduction section below), temperature, parasite prevalence, snail density, and crab density on the snail growth rates estimated above. I used General Linear Models (GLMs), which included all main effects and all two-way interactions,

and backwards stepwise elimination techniques using Akaike information Criterion (AIC) values to select the most parsimonious models (Akaike, 1974; Burnham and Anderson, 2004). The response variables for the GLMs were the growth rates for each of four snail lengths: 10, 15, 20, and 25 mm, values derived from the GzLMs for individual growth at each site. I calculated growth for the different snail sizes because the allocation to growth and the effect of independent variables likely varies with snail size. I excluded four sites from the analyses because I found less than 30 uninfected snails (Table 3.2). Snail growth is highly variable across sizes as reported by Hechinger (2010), so small sample sizes can yield imprecise relationships. Therefore, I weighted the statistical models with the number of uninfected snails per site.

Reproduction

The gonadosomatic index (GSI), is a common metric of reproductive performance in marine invertebrates (e.g. Lester et al., 2007; Pearse et al., 1986). California horn snail gonads, however, are not readily isolated, because they are integrated with the digestive gland. Fortunately, the entire gonad-digestive gland complex is easily isolated, so I used the “gonad-digestive gland-somatic index” (GDSI) to reflect reproductive performance, after confirming that this index was tightly correlated with the GSI in uninfected snails. To assess the validity of this index, I calculated the GSI and GDSI after Hechinger et al., (2008), for 17 uninfected snails from

Carpinteria Salt Marsh in spring 2007. After collecting 30 snails, I cracked their shells and fixed them in 10% formalin. In the laboratory, I transferred snails to 70% ethanol and dissected them a month later. I removed the shells and weighed the snail's body without shells and its separated gonad-digestive gland. To estimate gonad weight, I took photographs of five cross sections of the gonad-digestive gland complex, then used the image processing software ImageJ to calculate the percent area of gonad and digestive gland for the 17 uninfected snails. GDSI was related to GSI (R2 = 0.86, F = 1,16 = 90.2, P < 0.0001, Fig. 3.1A).

Monthly sampling and quantification of GDSI would have allowed me to estimate seasonality and overall differences in reproductive output in the different populations (Murray et al., 2006). However, due to logistical constraints, I was only able to sample GDSI in fall and spring. Still, by sampling at the beginning and end of the reproduction season, I should have captured differences in GDSI driven by environmental variables like temperature. In fall 2008 and spring 2009, I collected 100 unmarked snails, from the same sites where I measured growth, and measured their GDSI as described above. I used a GzLM to examine the effects of habitat, season, sex, site, and snail weight on GDSI, with sites nested within habitats and two and three-way interaction effects included. As for the growth rate analysis, I calculated GDSI values for snails 10, 15, 20, and 25 mm in length from length-weight relationships determined in the growth dissections and the

GDSI from the individual GDSI estimation from the GzLM. I calculated GDSI for the different snail sizes because allocation to reproduction (e.g. snails mature between 12 - 20 mm, Lafferty (1993b) and Hechinger, unpublished data) and the effect of independent variables likely varies with snail size. This allowed me to evaluate the effect of reproductive effort on growth rates.

Statistical approach

I analyzed the relationship between individual growth rates and GDSI and the response variables using GzLMs. The models used the log of the response variables (log-link), given the non linearity of the relationship between them and snail size and weight. The GzLM used a Poisson distribution and an overdispersion term, given the distribution and overdispersion of the error terms, consistent with previous results (Hechinger, 2010). I multiplied individual growth rates and GDSI by 10 and 1,000 respectively to provide whole number data appropriately modeled using a Poisson distribution. I confirmed the statistical assumptions regarding the distribution of the error terms for the GzLMs by inspecting the predicted values vs. the residual Studentized deviance plots (McCulloch et al., 2008). All post-hoc tests from GzLMs used likelihood-ratio χ^2 statistics or Wald tests in some cases when likelihood-ratio tests were unavailable. For the population-level analyses, I first checked if there were any strong correlations between any of the dependent variables, then entered all two-way

interactions, followed by backwards stepwise selection of the model that explained the greatest amount of variation in the dataset as evaluated by the lowest AIC criteria (Akaike, 1974; Burnham and Anderson, 2004). I ensured statistical assumptions of normality and variance homogeneity were met by inspecting the residual error versus predicted value plots and normal quantile plots with 95% Lilliefors confidence limits curves of the model residuals (Kutner et al., 2005). All *P* values were two-tailed, and all statistical tests were run in JMP ver.11.0.

Results

Site variability

As expected, mean temperature decreased with latitude. The mean temperature varied by as much as 7 °C between northern and southern sites (Fig. 3.1). Although temperature generally decreased with increasing latitude, there was considerable temperature variation even for sites at similar latitudes, probably owing to the local effects of upwelling, fog, or the timing and heights of tides (Helmuth et al., 2002). Because the covariation between temperature and latitude was not strict, I was able to determine temperature effects on snail biomass and performance without some of the potential confounds introduced by other factors (unmeasured) that covary with latitude. The other local parameters, predator and snail density, and

prevalence, also varied from site to site and were not highly correlated with one another (all r < 0.65) (Table 3.2).

Biomass density

Temperature was positively associated with snail biomass density and parasite prevalence was marginally negatively associated with snail biomass density, but this expected relationship was only statistically significant (Full model: R^2 = 0.4, df =1, 16, F = 4.7, P = 0.0276; Temperature: t = 3.06, P =0.0084; Parasite prevalence: t = - 2.0, P = 0.06) when the outlier data point from Newark Slough Cargill was removed (Jackknife distance: 6.0). The excluded site was a pan with an unusually high density of snails (the highest from all sites sampled) and it was located in the northern part of the snails' range, so its annual mean temperature was low. Therefore, although, there was some support for the prediction that temperature constrains snail populations, snails were able to achieve high densities even near the edge of their range under particular circumstances (likely related to unusually high productivity, which is known to aggregate snails).

Growth

Overall, I quantified growth for 1,942 uninfected snails out of 3,436 snails that were recaptured (Table 3.2). Individual growth rates did not differ for snails collected in fall 2008 versus snails collected in spring 2009 (Table 3.3). As expected, big snails grew more slowly than small snails, but the growth-

length relationship varied among sites and habitats (Fig. 3.3, 3.4, and 3.3A, Table 3.3). On average, snail growth rates were 2 – 4 times higher in pans (2.8 ± 0.08 mm/year) than in channels (1.2 ± 0.06 mm/year), marshes (0.9 ± 0.2 mm/year), and flats (0.7 ± 0.1 mm/year) (post-hoc contrast analysis, $\chi 2$ = 8.5, P = 0.003) (Fig 3.2A). Small snails from marshes and channels appeared to grow faster than snails from pans, but this was reversed in bigger snails, and snails collected from flats appeared to grow the least regardless of snail size (Fig 3.3A). There was no main effect of sex on snail growth rates, but there was a sex by site interaction effect (Table 3.3), primarily stemming from sexual differences in growth rates at four sites where females grew faster than males (post-hoc contrast analyses: DEHB χ^2 = 6.7, P = 0.01; GSC χ^2 = 4.3, P = 0.04; EPB χ^2 = 5.8, P = 0.02; BSQC χ^2 = 26.9, P < 0.0001).

The positive effect of temperature on snail growth was context dependent. When examining relationships between the average growth rates of different snail sizes and environmental and biological variables (temperature, snail and crab densities, trematode prevalence and GDSI) across sites, I found that growth rates quadrupled over the measured temperature range for the smallest (10 mm) snails (Table 3.4a, Fig. 3.5). Snail growth tripled in 15 mm snails, but this was only apparent when snail density was high (Table 4b, Fig. 3.6). In medium-sized snails (20 mm), (Table 3.4c, Fig. 3.7), snails only grew more at warm temperatures where

crabs were rare (Table 3.4c, Fig 3.7c and d) or where snail densities were high (Fig. 3.7 a and b). At low snail densities, temperature had an unpredicted negative relationship with growth of medium-sized snails. In the largest snails (25 mm), temperature did not affect growth, however, crab abundance reduced growth rates (Table 3.4d, Fig. 3.8). Finally, for small (15 mm) and medium-sized (20 mm) snails, a tradeoff between growth and reproduction (GDSI) occurred at low temperatures, whereas, at high temperatures, GDSI had an unexpected positive relationship with growth (Fig. 3.9).

Reproduction

Overall, I quantified GDSI for 2,470 uninfected snails out of ~4,400 snails collected (Table 3.2). GDSI increased with snail weight, but slopes for this relationship varied among sites, habitats, and seasons (Table 3.5, Figs.3.10, 3.11, 3.4A, and 3.5A). Snail GDSI was substantially higher in the marshes and pans than in the channels and flats (post-hoc contrast analyses, significant differences (*P*s < 0.03) among all habitats, Fig. 3.4A). Snail GDSI was 11% higher in the spring than in the fall and male GDSI was 7% higher than female GDSI (Table 3.5, Fig 3.5A).

Discussion

Snail density tended to be higher at warmer sites, suggesting that snail performance declines with colder temperatures near the northern limit of the

range. But the predicted positive relationship between performance and temperature was context dependent due to different effects of habitat type, predator and competitor abundance, parasite prevalence and snail size. The positive relationship between growth and temperature found in this study is in concordance with the temperature-size rule, which states that organisms reared in lower temperatures grow more slowly but are larger as adults than individuals reared in warmer conditions (Atkinson, 1994). Further analysis of the data showed that maximum observed size was negatively related to temperature (Fig. 3.6A), confirming the temperature-size rule appeared to apply to the California horn snails in its northern range.

Among the other factors that seemed to influence snail performance was habitat type, with snail growth rates and GDSIs being 66% and 12% higher in pans compared to channels (similar to Hechinger et al 2008). Snails are often restricted to pans in the northern part of the range (Hechinger et al. unpublished data and personal observations). High snail growth rates and GDSIs in pans could have been attributed to the greater exposure to sunlight of pan habitats, which could increase both the snail food supply (benthic diatom production and biomass) and temperature. Hechinger et al. (2008) reported that pans had benthic diatom densities that were 3.4-times higher than those in channels, supporting the idea that differences in food supply drove patterns in snail reproductive and growth performance among habitat types. Further analysis, showed that pan sites were not warmer than channel

sites (GLM controlling for latitude: $F = 1.9$, $P = 0.20$, n = 15), suggesting that just light, or nutrients, or both, drive the pattern seen. Being restricted to the most productive habitat areas in the north should be expected if unfavorable environmental conditions set the northern range limit. Differences in growth rates and GDSI in marsh and flat habitats in this study should be considered cautiously because only a couple sites from each habitat were sampled across the latitudinal gradient. Further unexplained variation in growth rate was probably related to within-habitat variation in productivity not measured in this study.

Why do the other environmental covariates affect snail performance? The negative effect of crabs on the growth rates of medium and large-sized snails is consistent with the results of previous studies that show crabs can compete with large snails and also inhibit snail feeding through harassment (Lorda et al. in review; Armitage and Fong, 2006). The positive association between snail density and growth in medium size snails (15 and 20 mm) could be due to snails aggregating at sites where the productivity is so high that competition does not depress food supply. Controlling for productivity, as in Lafferty (1993a), would have helped clarify the causal relationship between density and performance. The interaction between temperature and GDSI and its effect on growth of small (15 mm) and medium (20 mm) snails hints at the possibility of a tradeoff in energy allocation between growth and reproduction when the temperatures are low (and perhaps where productivity

is low). The positive relationship between GDSI and growth at higher temperatures might occur if higher productivity reduces the resource limitation that leads to life-history tradeoffs.

To summarize, snail density, growth and GDSI varied across sites along a latitudinal gradient, with slower growth of small snails at the colder sites near the edge of the species range. Furthermore, a trade-off between growth and reproduction at colder sites and a positive correlation between growth and reproduction at warmer sites suggests that climate warming could benefit the populations of snails living near the northern range limit. However, several other factors might override this predicted effect of climate change.

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References

Akaike, H., 1974. A new look at the statistical model identification. Autom. Control. IEEE Trans. 19, 716–723.

Armitage, A.R., Fong, P., 2004a. Gastropod colonization of a created coastal wetland: Potential influences of habitat suitability and dispersal ability. Restor. Ecol. 12, 391–400.

Armitage, A.R., Fong, P., 2004b. Upward cascading effects of nutrients: shifts in a benthic microalgal community and a negative herbivore response. Oecologia 139, 560–567.

Armitage, A.R., Fong, P., 2006. Predation and physical disturbance by crabs reduce the relative impacts of nutrients in a tidal mudflat. Mar. Ecol. Ser. 313, 205–213.

Atkinson, D., 1994. Temperature and Organism Size-A Law for Ectotherms? Adv. Ecol. Res. 25, 1–58.

Beukema, J., Meehan, B., 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. Mar. Biol. 33, 27–33.

Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol. Methods Res. 33, 261–304.

Byers, J.E., 2005. Quantifying geographic variation in physiological performance to address the absence of invading species. Ecoscience 12, 358–365.

Caughley, G., Grice, D., Barker, R., Brown, B., 1988. The edge of the range. J. Anim. Ecol. 57, 771–785.

Defeo, O., Cardoso, R.S., 2002. Macroecology of population dynamics and life history traits of the mole crab *Emerita brasiliensis* in Atlantic sandy beaches of South America 239, 169–179.

Dell, A.I., Pawar, S., Savage, V.M., 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. U. S. A. 108, 10591–6.

Dugan, J., Wenner, A., Hubbard, D., 1991. Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. J. Exp. Mar. Bio. Ecol. 150, 63–81.

Ebert, T., Dixon, J., Schroeter, S., Kalvass, P., Richmond, N., Bradbury, W., Woodby, D., 1999. Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. Mar. Ecol. Prog. Ser. 190, 189–209.

Gaston, K.J., 2003. The Structure and Dynamics of Geographic Ranges, Oxford Series in Ecology and Evolution.

Haldeman, S.S., 1840. A monograph of the Limniades and other freshwater univalve shells of North America. Dobson, J., Philadelphia.

Hechinger, R.F., 2010. Mortality affects adaptive allocation to growth and reproduction: field evidence from a guild of body snatchers. BMC Evol. Biol. 10, 136.

Hechinger, R.F., Lafferty, K.D., Huspeni, T.C., Brooks, A.J., Kuris, A.M., 2007. Can parasites be indicators of free-living diversity? Relationships between species richness and the abundance of larval trematodes and of local benthos and fishes. Oecologia 151, 82–92.

Hechinger, R.F., Lafferty, K.D., Mancini, F.T., Warner, R.R., Kuris, A.M., 2008. How large is the hand in the puppet? Ecological and evolutionary factors affecting body mass of 15 trematode parasitic castrators in their snail host. Evol. Ecol. 23, 651–667.

Hechinger, R.F., Lafferty, K.D., Mclaughlin, J.P., Huspeni, T.C., Fredensborg, B.L., Lorda, J., Sandhu, P.K., Shaw, J.C., Torchin, M.E., Whitney, K.L., Kuris, A.M., 2011. Food webs including parasites, biomass, body sizes, and life stages for three California / Baja California estuaries. Ecology 92, 791.

Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., Blanchette, C. a, 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science 298, 1015–7.

Henry, P.Y., Jarne, P., 2007. Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. Invertebr. Biol. 126, 138–153.

Keen, M., 1963. Marine Molluscan Genera of Western North America: An Illustrated Key. Stanford University.

Kutner, M., Nachtsheim, C., Neter, J., Li, W., 2005. Applied linear statistical models, 5th editio. ed. McGraw-Hill/Irwin, Boston.

Lafferty, K.D., 1993a. Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Mar. Ecol. Ser. 96, 229–237.

Lafferty, K.D., 1993b. The marine snail, *Cerithidea californica*, matures at smaller sizes were parasitism is high. Oikos 68, 3–11.

Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. Proc. Natl. Acad. Sci. U. S. A. 103, 11211–11216.

Lafferty, K.D., Hechinger, R.F., Shaw, J.C., Whitney, K., Kuris, A.M., 2006. Food webs and parasites in a salt marsh ecosystem, in: Collinge, S., Ray, C. (Eds.), Disease Ecology: Community Structure and Pathogen Dynamics. Oxford University Press, Oxford, pp. 119–134.

Lafferty, K.D., Kuris, A.M., 2009. Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 364, 1659–63.

Lester, S.E., Gaines, S.D., Kinlan, B.P., 2007. Reproduction on the edge: large-scale patterns of individual performance in a marine invertebrate. Ecology 88, 2229–39.

Lorda, J., Lafferty, K.D., 2012. Shading decreases the abundance of the herbivorous California horn snail, *Cerithidea californica*. J. Exp. Mar. Bio. Ecol. 432-433, 148–155.

Martin, W.E., 1972. An annotated key to the cercariae that develop in the snail *Cerithidea californica*. Bull. South. Calif. Acad. Sci. 71, 39–43.

McCloy, M.J., 1979. Population regulation in the deposit feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh habitat. M. S. Thesis. San Diego State University.

McCulloch, C., Searle, S., Neuhaus, J., 2008. Generalized linear mixed models, 2nd Editio. ed. John Wiley & Sons, Inc, Hoboken, New Jersey.

Miura, O., Torchin, M.E., Bermingham, E., 2010. Molecular phylogenetics reveals differential divergence of coastal snails separated by the Isthmus of Panama. Mol. Phylogenet. Evol. 56, 40–8.

Murray, S., Ambrose, R., Dethier, M., 2006. Monitoring rocky shores. University of California, Berkeley.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–671.

Pearse, J., Pearse, V., Davis, K., 1986. Photoperiodic regulation of gametogenesis and growth in the sea urchin *Strongylocentrotus purpuratus*. J. Exp. Zool. 118, 107–118.

Pörtner, H., Berdal, B., Blust, R., 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Cont. Shelf Res. 21, 1975–1997.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecol. Lett. 3, 349–361.

Race, M.S., 1981. Field ecology and natural history of *Cerithidea californica* (Gastropoda, Prosobranchia) in San Francisco Bay. Veliger 24, 18–27.

Savage, V.M., Gilloly, J.F., Brown, J.H., Charnov, E.L., 2004. Effects of body size and temperature on population growth. Am. Nat. 163, 429–41. doi:10.1086/381872

Sibly, R., Atkinson, D., 1994. How rearing temperature affects optimal adult size in ectotherms. Funct. Ecol. 8, 486–493.

Vaughn, C.C., Fisher, F.M., 1988. Vertical migration as a refuge from predation in intertidal marsh snails: A field test. J. Exp. Mar. Bio. Ecol. 123, 163–176.

Verdelhos, T., Cardoso, P., Dolbeth, M., Pardal, M., 2011. Latitudinal gradients in *Scrobicularia plana* reproduction patterns, population dynamics, growth, and secondary production. Mar. Ecol. Prog. Ser. 442, 271–283.

Tables

Table 3.1. Site code, estuary, habitat of site, and coordinates of the 22 sample sites, listed from North to South.

Site code	Estuary	habitat	Latitude (°N)	Longitude (°W)
DESB	Drakes Estero Schooner Bay	channel	38.09082	-122.93012
DEHB	Drakes Estero Home Bay	pan	38.07050	-122.91653
BLC	Bolinas Lagoon Creek	pan	37.92307	-122.69234
BLKI	Bolinas Lagoon Kent Island	pan	37.91488	-122.68053
NSLR	Newark Slough La Riviere	pan	37.53333	-122.06546
NSC	Newark Slough Cargill	pan	37.50384	-122.07209
MBP	Morro Bay	pan	35.34303	-120.84064
MBC	Morro Bay	channel	35.34543	-120.83700
GSC	Goleta Slough	channel	34.41791	-119.83432
GSP	Goleta Slough	pan	34.42140	-119.83950
BL	Ballona Lagoon	channel	33.97549	-118.46013
SSPW	Salinas San Pedro Wetlands	channel	33.71503	-118.28490
GSW	Golden Shore Wetlands	channel	33.76434	-118.20306
SMR	Santa Margarita River	flat	33.23100	-117.41277
LPLC	Los Peñasquitos Lagoon	channel	32.93123	-117.24984
LPLP	Los Peñasquitos Lagoon	pan	32.92818	-117.25821
MBKF	Mission Bay - Kendall Frost	marsh	32.79522	-117.22984
EPB	Estero de Punta Banda	channel	31.76225	-116.61748
BSQC	Bahia San Quintín	channel	30.45662	-116.03122
BSQP	Bahia San Quintín	pan	30.45261	-116.03182
GNF	Guerrero Negro Faro	pan	28.03511	-114.11082
GNR	Guerrero Negro Road	flat	28.02266	-114.11199

Table 3.2. Local variable values and sample sizes for each of 22 study sites: mean annual temperature (°C), trematode parasite prevalence, snail and crab density (individuals/m^2), and the number of uninfected snails used in growth and GDSI analyses. Sites are listed from North to South.

Site code	Temp (°C)	Trematode prevalence (20-25mm)	Snail density (snails/m^2)	Crab density (crabs/m^2)	Uninfected snails (n)	
					Growth	GDSI
DESB	13.0	0.02	212	19.3	292	187
DEHB	14.10	0.08	266	0	295	142
BLC	15.5	0	151	0	84	89
BLKI	14.1	0.06	28	0	149	125
NSLR	14.6	0.03	87	0	32	88
NSC	14.7	0.04	1183	0	96	162
MBP	15.1	0.37	144	0	52	131
MBC	14.9	0.29	167	11.5	62	145
GSC	15.6	0.4	30	5.4	46	89
GSP	ND	0	389	0	6	87
BL	16.6	0.37	309	0	88	106
SSPW	16.7	0.83	413	4.4	19	95
GSW	17.7	1	170	0	1	0
SMR	14.3	0.39	83	0	77	91
LPLC	18.2	0.43	490	15.1	94	120
LPLP	18.8	0.21	409	6.4	140	107
MBKF	17.4	0.30	232	12.1	98	89
EPB	17.6	0.80	68	5.5	30	91
BSQC	17.8	0.27	849	4.8	163	118
BSQP	17.7	0.29	719	1.3	113	108
GNF	18.5	0.88	410	19.9	22	77
GNR	19.9	0.86	552	0	31	131

Table 3.3. Generalized linear model statistics for the effects of habitat, site, season collected, snail sex, and snail length on individual growth rates.

Main effect	df	χ^2	*P*
Growth rate			
Full model $df = 109$, $\chi^2 = 3370$, $P < 0.0001$ (overdispersion = 10.8, $P < 0.0001$)			
Habitat	3	30.8	**<0.001**
Site [Habitat]	14	433.7	**<0.001**
Season	1	0.005	0.94
Sex	1	0.05	0.83
Snail length	1	211.3	**<0.001**
Sex * Site [Habitat]	14	43.9	**<0.001**
Season * Site [Habitat]	14	21.1	0.10
Snail length * Habitat	3	33.7	**<0.001**
Snail length * Site [Habitat]	14	62.4	**<0.001**
Snail length * Season	1	0.36	0.55
Snail length * Sex	1	3.54	0.06
Snail length * Sex * Site [Habitat]	14	15.1	0.37
Snail length * Season * Site [Habitat]	14	19.1	0.16
Snail length * Sex * Season * Site [Habitat]	14	9.5	0.80

Table 3.4. General linear models showing relationships between the growth of different snail size classes and independent variables (temperature, snail and crab density, parasite prevalence) remaining after stepwise backwards elimination. Independent variables, AIC values, coefficients of determination, df, and *F* and *P* values are shown for final models. Growth rates for small, medium-sized, and large snails were used as dependent variables.

a. 10 mm snail growth rates

Effects	AIC / ΔAIC	R^2	df	*t*	*P*
Temperature	327, -110	0.34	1	2.9	**0.01**

b. 15 mm snail growth rates

Effects	AIC / ΔAIC	df	*t*	*P*
Full model AIC = 262, ΔAIC = -117, R2 = 0.72, df = 5, 16, *F* = 5.6, P < **0.01**				
Temperature		1	3.3	**0.001**
Snail density		1	2.3	**0.04**
GDSI		1	-0.01	0.99
Temperature * Snail density		1	2.8	**0.02**
Temperature * GDSI		1	2.1	0.06

b. 20 mm snail growth rates

Effects	df	*t*	*P*
Full model AIC = 339, ΔAIC = -71, R^2 = 0.85, df = 9, 16, *F* = 4.5, *P* = **0.03**			
Temperature	1	1.9	0.11
Prevalence	1	-1.2	0.30
Snail density	1	2.4	**0.05**
Crab density	1	-3.8	**0.01**
GDSI	1	-0.2	0.84
Temperature * Prevalence	1	3.0	**0.02**
Temperature * Snail density	1	3.1	**0.02**
Temperature *Predators	1	-2.3	**0.05**
Temperature * GDSI	1	3.2	**0.02**

c. 25 mm snail growth rates

Effects	AIC / ΔAIC	R^2	df	*t*	*P*
Crab density	209, -107	0.27	1	-2.4	**0.03**

Table 3.5. Generalized linear model statistics for the effects of site, season, sex, and snail weight on snail GDSI.

Effects on GSDI	df	χ^2	*P*
Full model df = 130, χ^2 = 1820, *P* < 0.0001 (overdispersion = 5.4, P **< 0.0001**)			
Habitat	3	87.6	**< 0.0001**
Site [Habitat]	17	186.5	**< 0.0001**
Season	1	101.7	**< 0.0001**
Sex	1	169.5	**< 0.0001**
Snail weight	1	105.9	**< 0.0001**
Sex * Site [Habitat]	17	66.8	**< 0.0001**
Season * Site [Habitat]	17	62.7	**< 0.0001**
Snail weight * Habitat	3	22.8	**< 0.0001**
Snail weight * Site [Habitat]	17	39.5	**0.002**
Snail weight * Season	1	9.2	**0.002**
Snail weight * Sex	1	2.7	0.10
Snail weight * Sex * Site [Habitat]	17	34.0	0.08
Snail weight * Season * Site [Habitat]	17	22.7	0.16
Snail weight * Sex * Season * Site [Habitat]	17	25.2	0.10

Figures

Figure 3.1. Relationship between latitude and annual mean temperature for the sampled sites (R^2 = 0.77, N = 21, df = 1, *F* = 59, *P* < 0.0001, mean annual temperature = 33.5 – 0.51 * Latitude). Open circle = pan, solid circles = flat, asterisk = marsh, and solid triangle = channel.

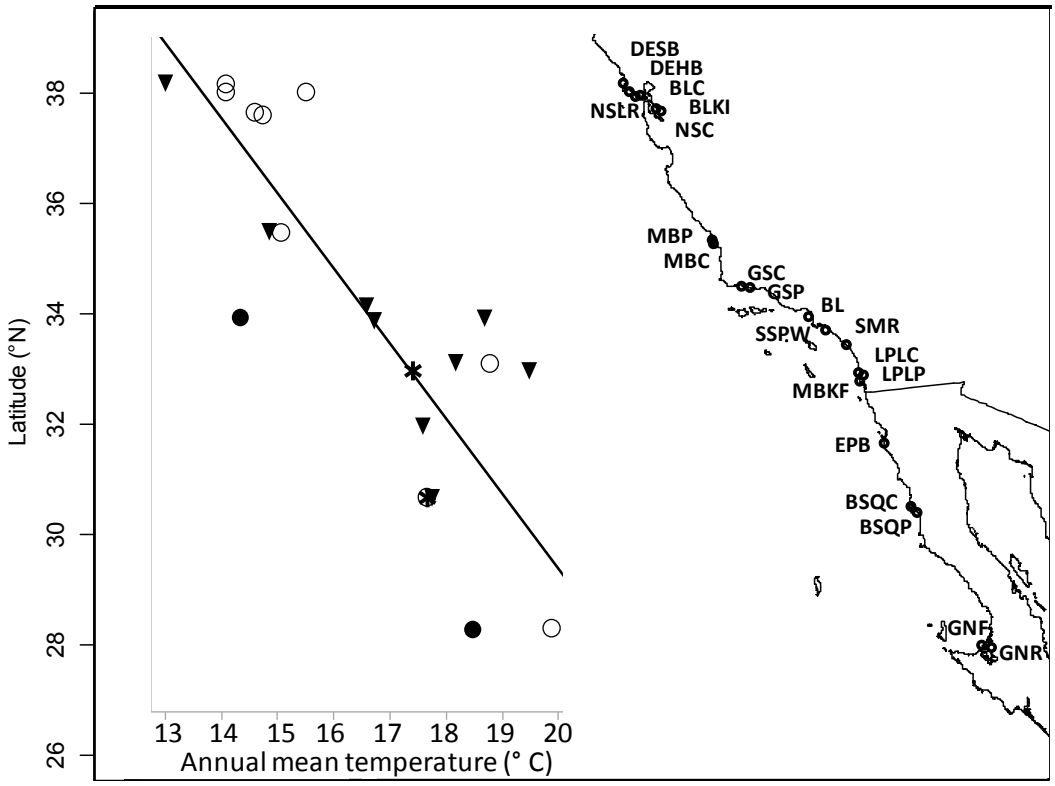


Figure 3.2. Relationship between predicted temperature and snail biomass across sites (biomass density = -135.0 + 12.8 * temperature, R^2 = 0.6, df = 1, 16, *F* = 19.7, *P* = 0.005). Note outlier data point from Newark Slough Cargill included in graph but not in statistical model.

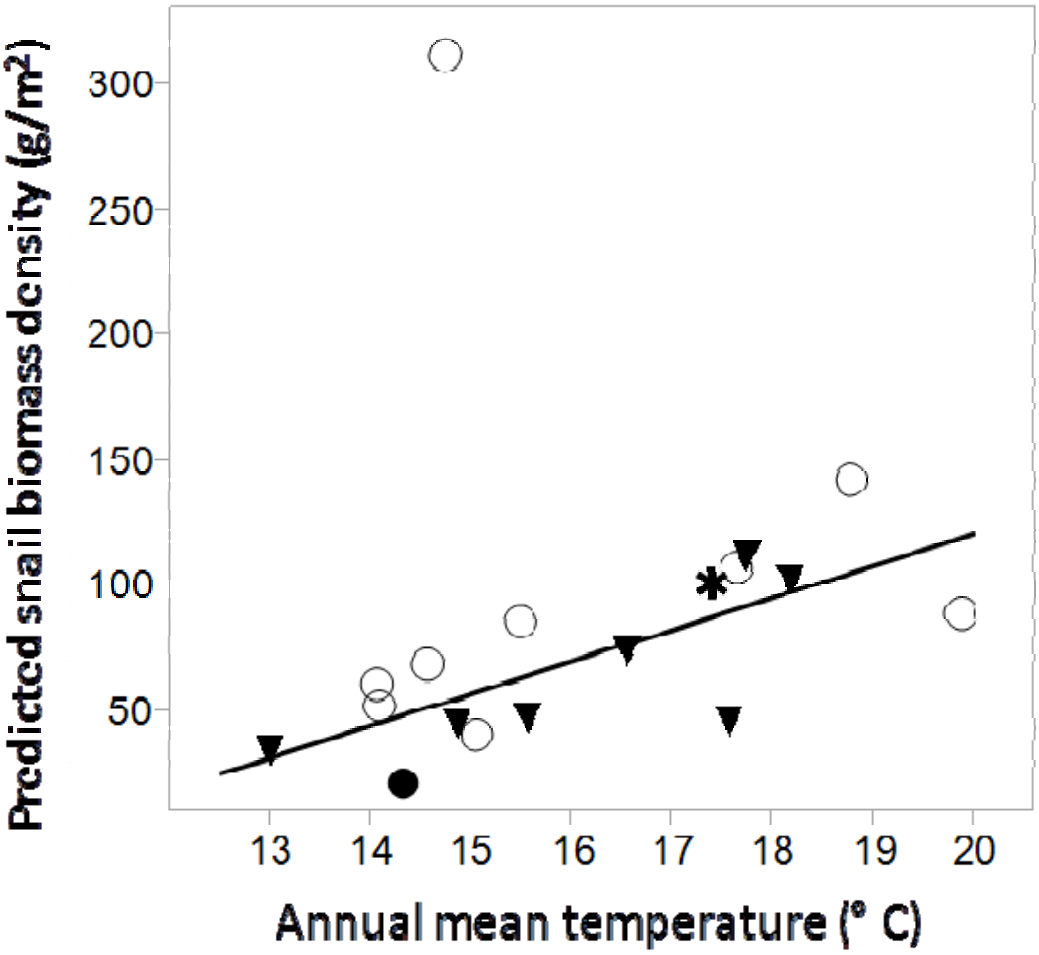


Figure 3.3. Relationship between initial snail length and individual growth rate described by GzLM analysis for each of 18 study sites.

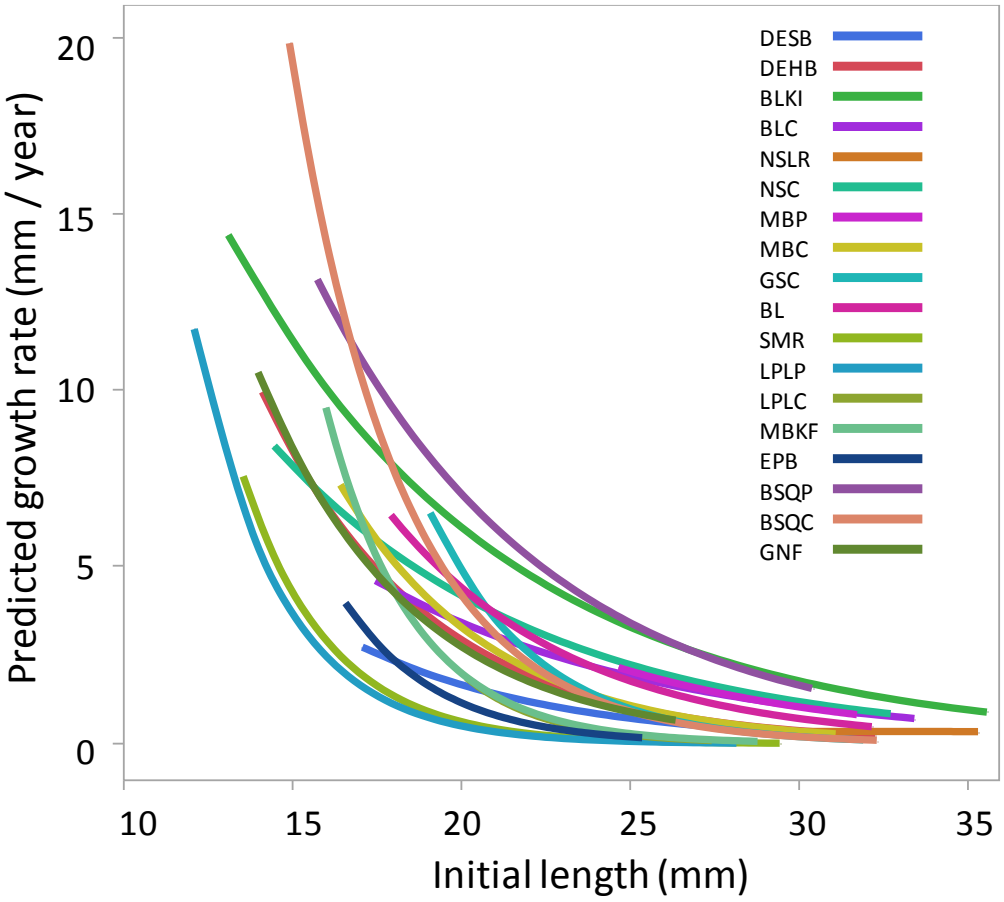


Figure 3.4. Mean growth rates for small 10mm (blue), 15mm (green), medium 20mm (red), and large 25 mm (black) snails across sample sites, which are indicated on the map. Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

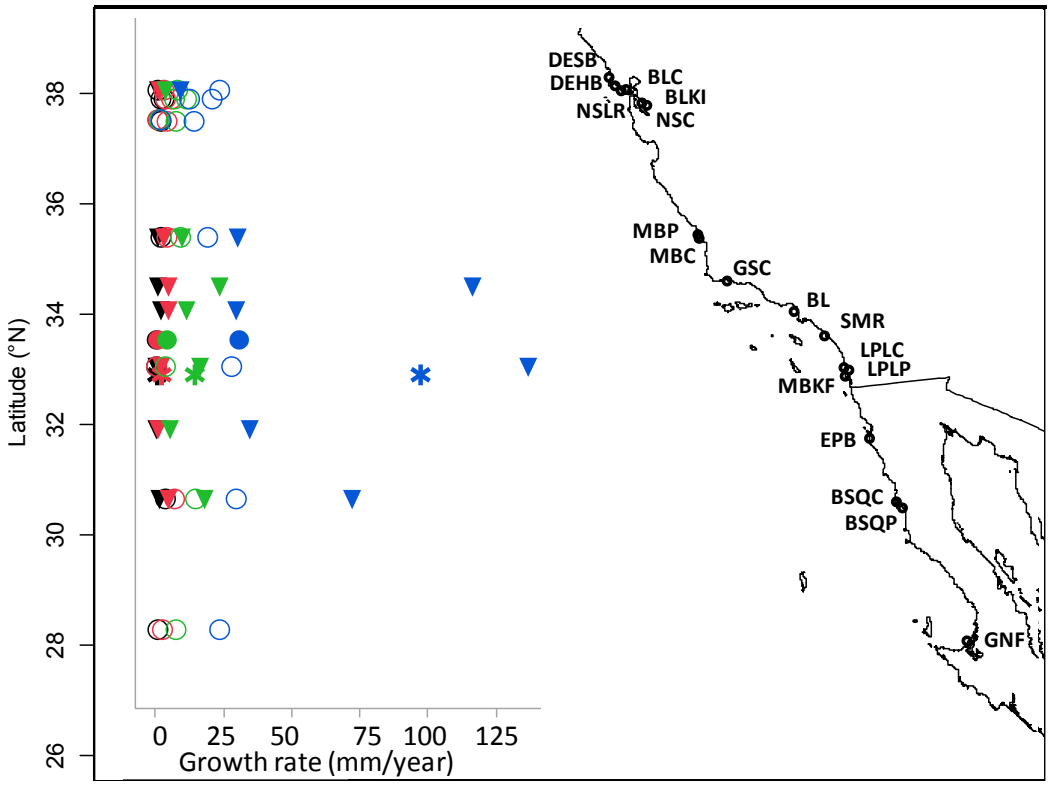


Figure 3.5. Relationship between annual mean temperature (°C) and growth rates of 10 mm length snails at the sampled sites (growth rate = -142 + 12 * temperature, R^2 = 0.34, df = 1, 17, *F* = 8.4, *P* < 0.0106). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

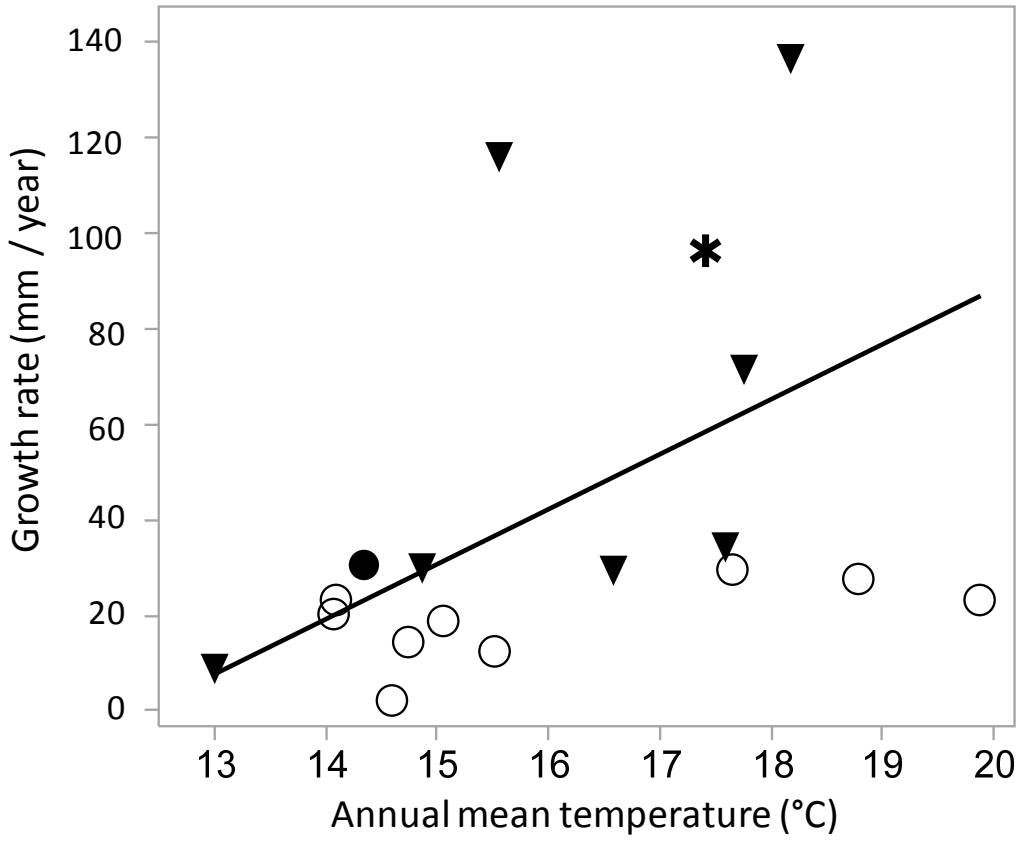


Figure 3.6. Relationship between annual mean temperature (°C) and growth rates of 15 mm length snails at the sampled sites with low snail biomass a) and high snail biomass density b) (growth rate = -25 + 2.2 * temperature, R^2 = 0.79, df = 1, 16, *F* = 57.4, *P* < 0.0001). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

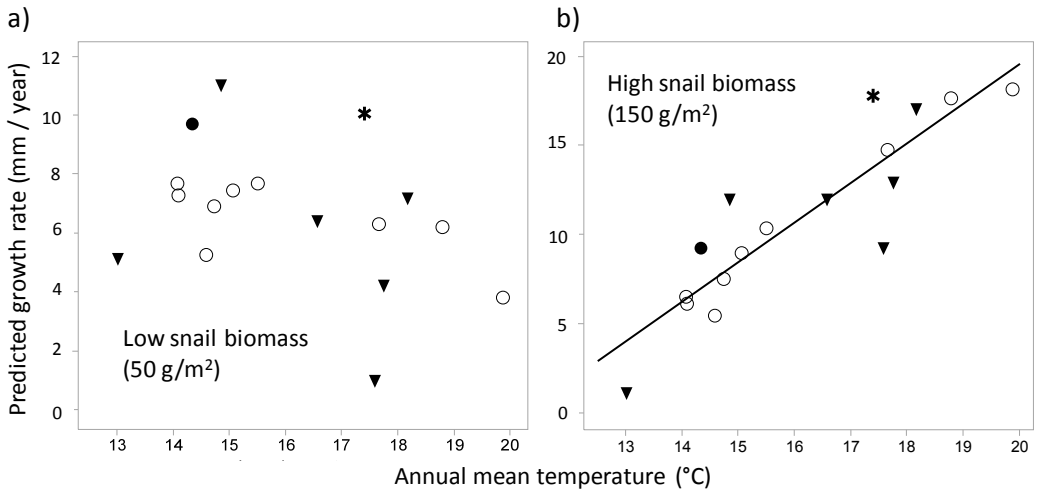


Figure 3.7. Relationship between growth rates of 20 mm snails depending on snail densities a) and b) and crab densities c) and d) across the sampled sites. a) low snail biomass (growth = 10 – 0.5 * temperature, R^2 = 0.4, df = 1, 16, *F* = 10.0, *P* = 0.0062); b) high snail biomass (growth rate = -5.2 + 0.6 0 * temperature, R^2 = 0.5, df = 1, 16, *F* = 12.5, *P* = 0.003); c) low crab density (growth rate = -6.1 + 0.6 * temperature, R^2 = 0.25, df = 1, 16, *F* = 5.0, *P* = 0.0403). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

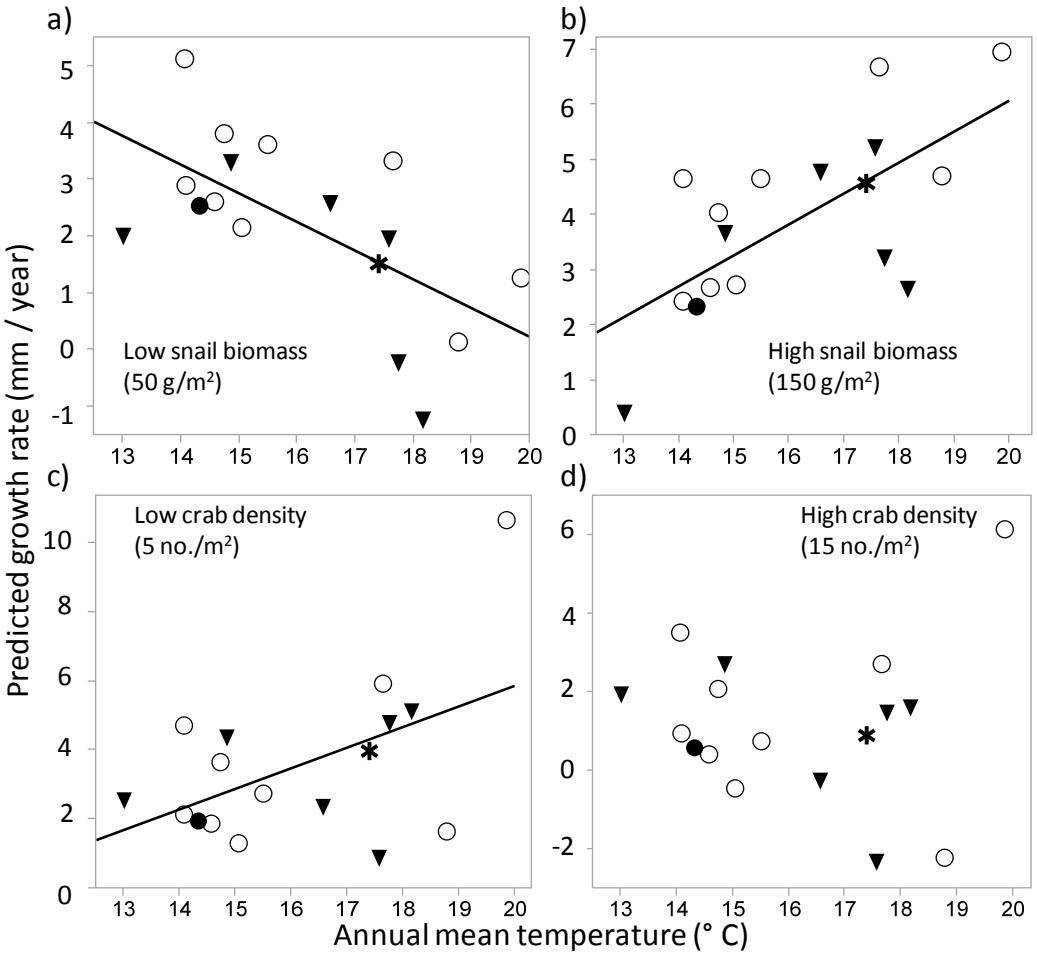


Figure3. 8. Relationship between the growth rates of large 25 mm snails and crab density (growth rate = -0.4 + 0.1 * temperature, R^2 = 0.3, df = 1, 17, *F* = 5.8, *P* = 0.0285). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

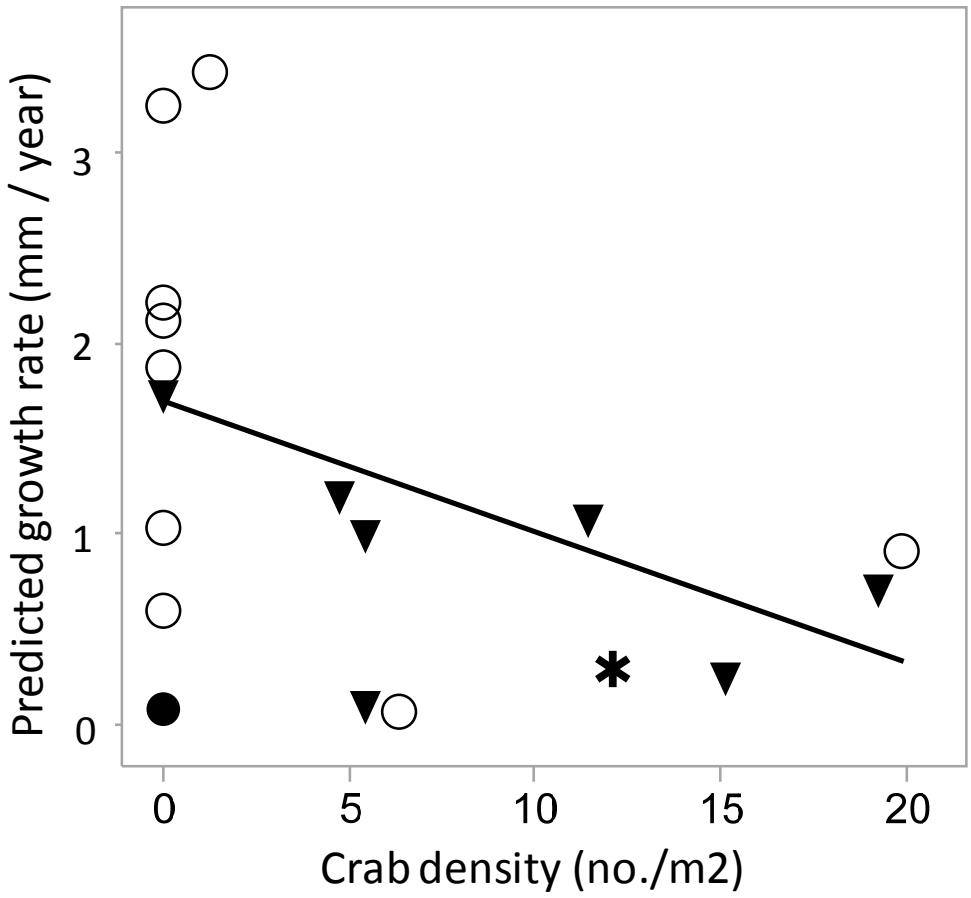


Figure 3.9. Relationship between growth rates of 15 mm (a and b) and 20 mm (c and d) snails and GDSI. Small (15 mm) snails and low temperature a) (growth = 20 – 48 * GDSI, R^2 = 0.5, df = 1, 16, *F* = 13.5, *P* = 0.0023), and high temperature b) (growth rate = -58 + 292 * GDSI, R^2 = 0.4, df = 1, 16, *F* = 9.8, *P* = 0.007). Medium (20 mm) snails and low temperature c) (growth rate = 24 - 92 * GDSI, R^2 = 0.4, df = 1, 16, *F* = 7.8, *P* = 0.0146), and high temperature d) (growth rate = -33 + 152 * GDSI, R^2 = 0.4, df = 1, 16, *F* = 9.0, *P* = 0.0095). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.

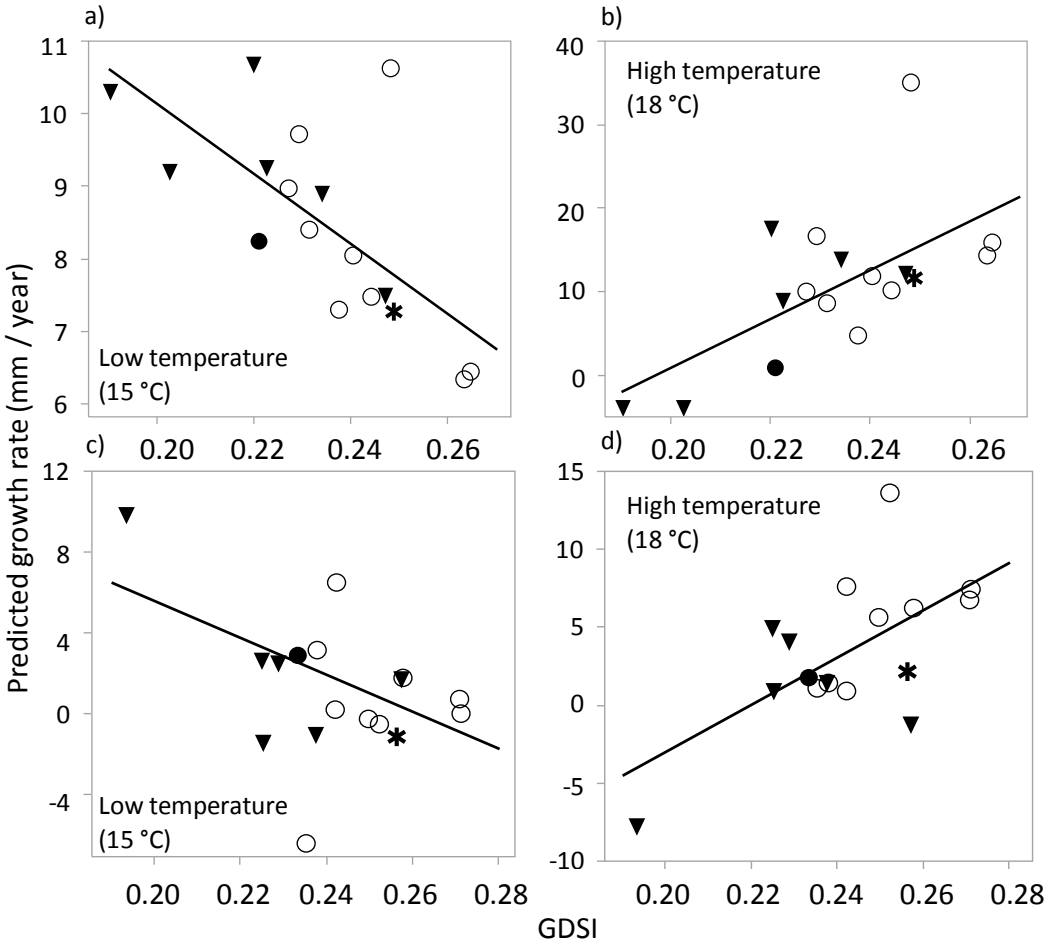

a)
b)
c)
d)
Low temperature
(15 °C)
High temperature
(18 °C)
Predicted growth rate (mm / year)
GDSI

Figure 3.10. Relationships between snail body mass and the gonad-digestive-somatic index (GDSI) for snails at 21 sample sites.

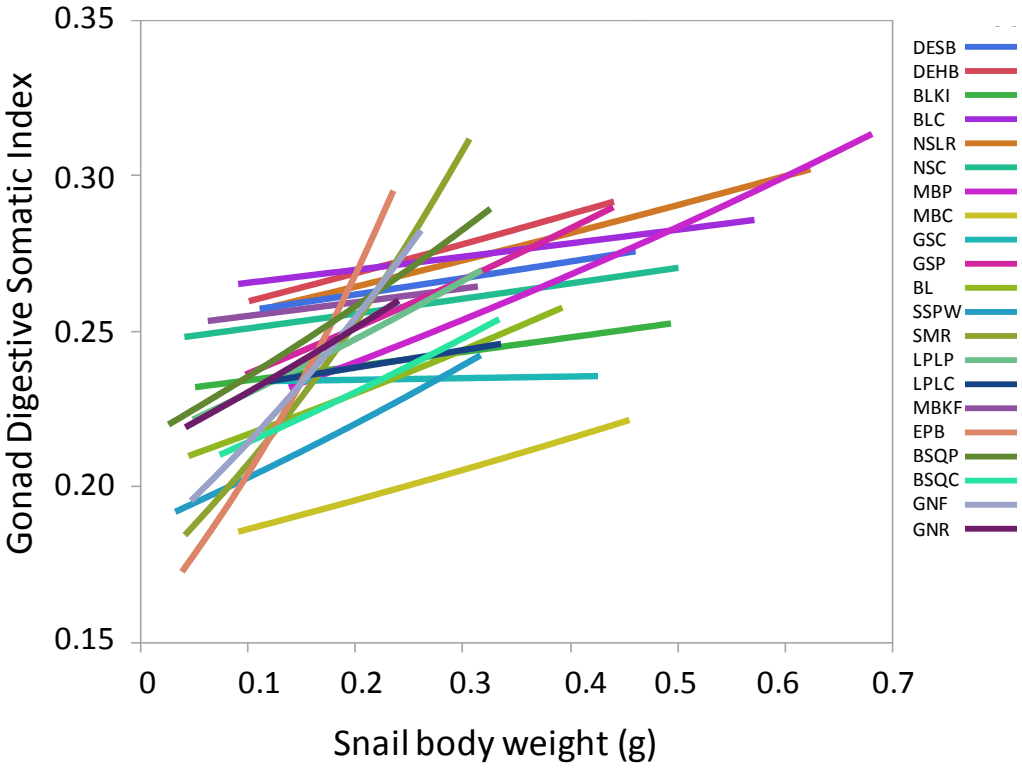
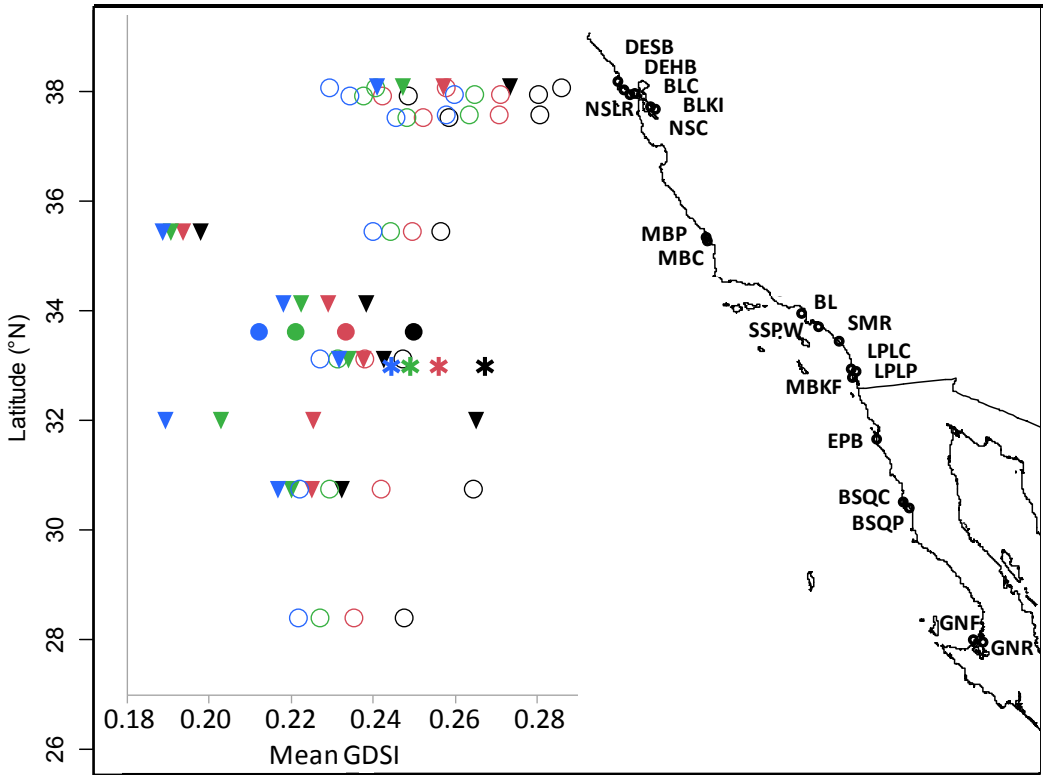


Figure 3.11. Mean GDSI for small 10 mm (blue), 15 mm (green), medium 20 mm (red) and large 25 mm (black) snails at sites at different latitudes. Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.



Chapter 3 Appendix

Figure 3.1A. Relationship between gonado-somatic index GSI and gonado-digestive gland-somatic index (GDSI) for snails from Carpinteria Salt Marsh (GSI= -0.13 + 1.07* GDSI, R^2 = 0.86, df = 1, *F* = 90, *P* < 0.0001, n=17).

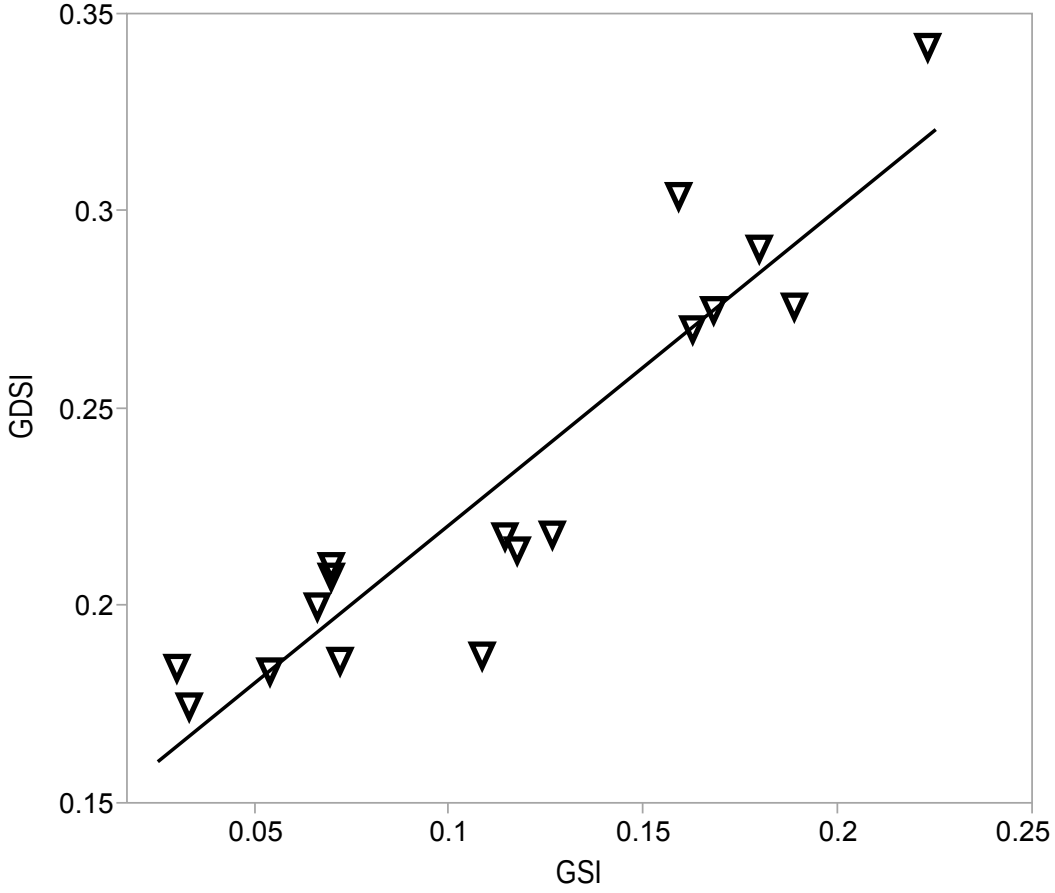


Figure 3.2A. Mean calculated snail growth rates (± standard error) across different habitat types. Habitats not connected by overlying lines represent differences in growth rates that are statistically significant (post-hoc contrast analysis pan vs. channel, χ^2 = 8.5, *P* = 0.003).

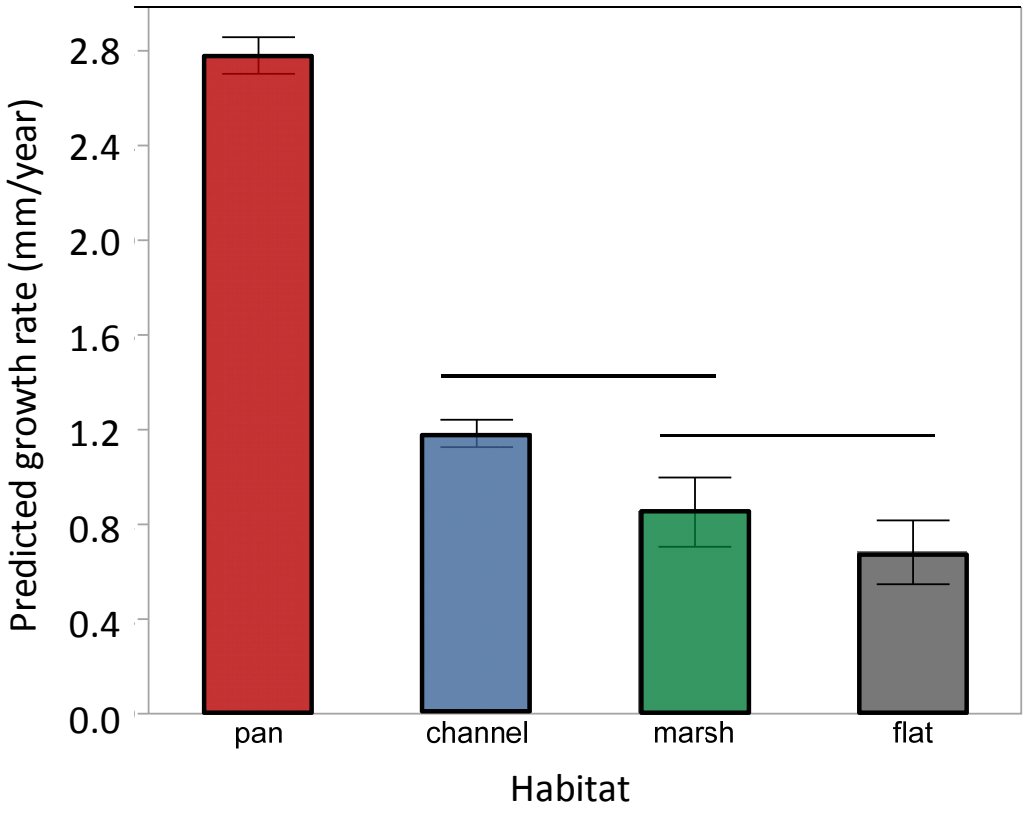


Figure 3.3A. Mean calculated snail growth rate versus initial snail length for the habitats sampled in this study.

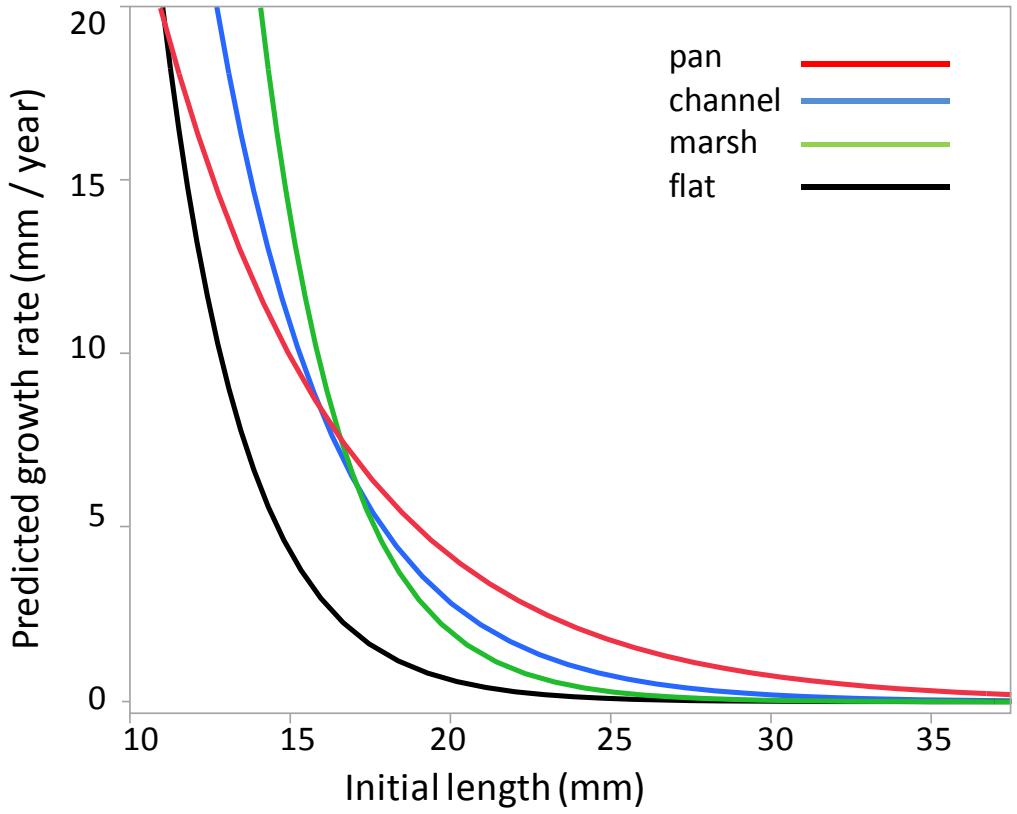


Figure 3.4A. Mean snail GDSI (± standard error) for different estuarine habitats sampled in this study. GDSI values were significantly different across all habitat types (post-hoc contrast analyses, significant differences *P*s < 0.03).

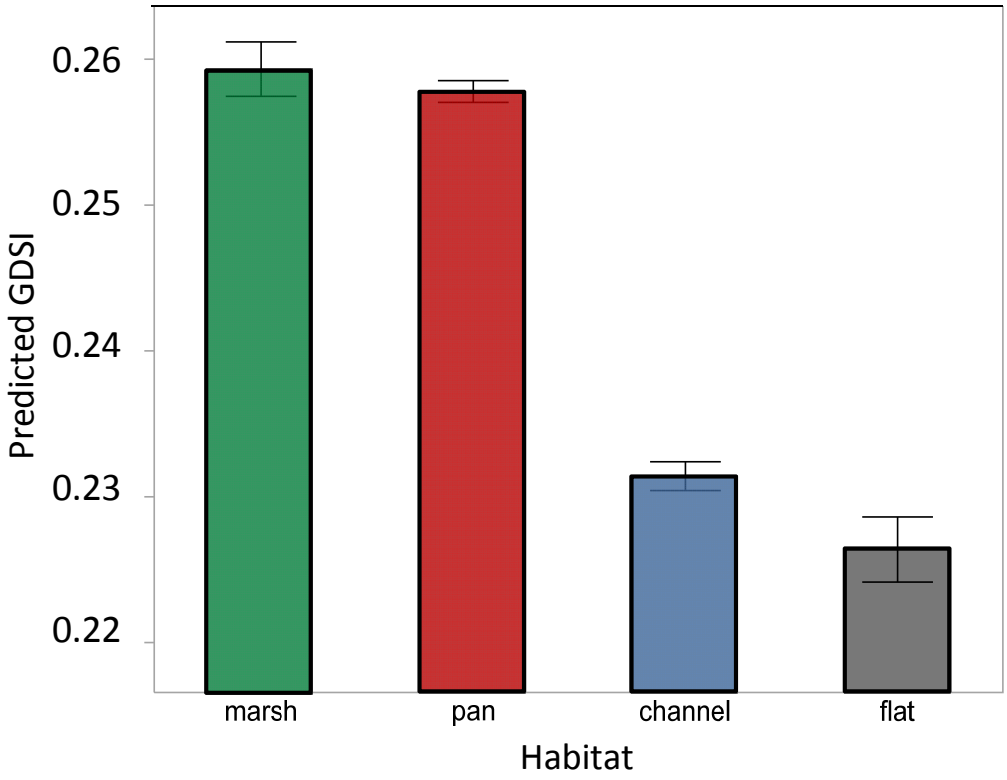


Figure 3.5A. Mean snail GDSI (± standard error) by snail sex and sampling season. GDSI values were significantly different between sexes and seasons (see statistics in table 7).

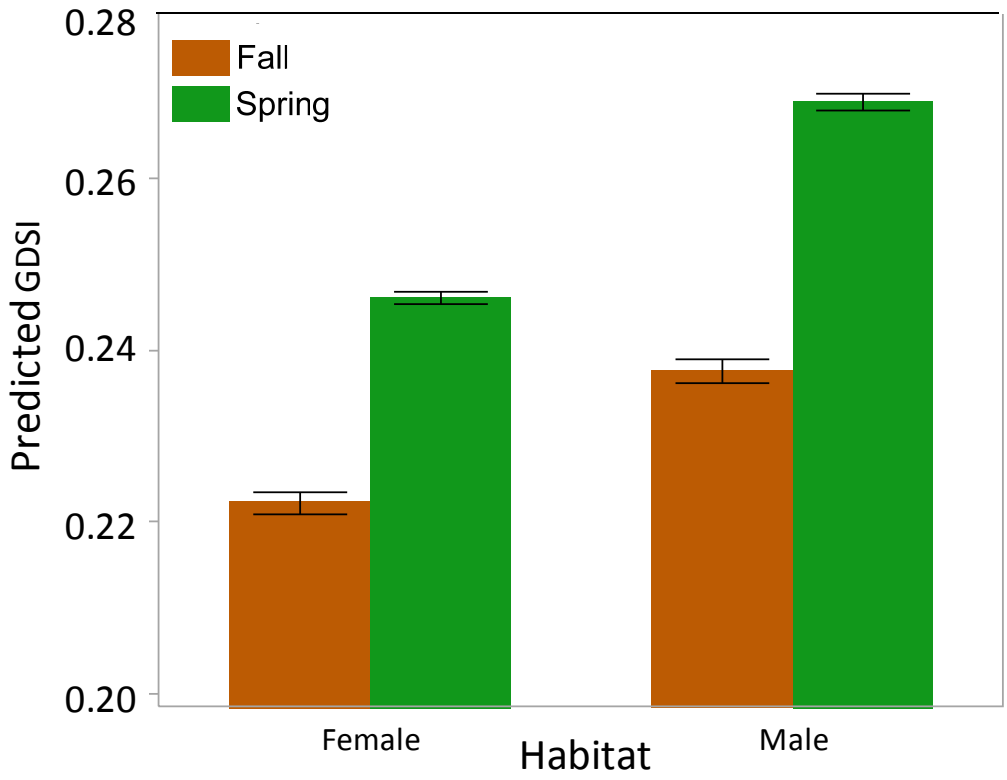


Figure 3.6A. Relationship between temperature and observed maximum length (maximum length = 51.2 – 1.2 * temperature, R^2 = 0.43, df = 1, 17, *F* = 11.9, *P* = 0.032). Open circle = pan, solid circle = flat, asterisk = marsh, and solid triangle = channel.