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

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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. We 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, we found a negative effect of shade on the distribution and abundance of the California horn snail. We hypothesized that shading reduces the abundance of the epipelic diatoms that the snails feeds on, causing snails to leave shaded areas. We observed a negative relationship between vascular plant cover, sub-canopy light levels, and snail density in Mugu Lagoon. Then we experimentally manipulated light regimes, by clipping vegetation and adding shade structures, and found higher snail densities at higher light levels. In Goleta Slough, we isolated the effect of shade from vegetation by documenting a negative relationship between the shade created by two bridges and diatom and snail densities. We also found that snails moved the greatest distances over shaded channel banks compared to unshaded channel banks. Further, we 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.

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1. 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 (Kon et al., 2010; Whitcraft and Levin, 2007). 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 (Chapperon and Seuront, 2011; Levinton, 1979). 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.

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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).

We 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, we 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.

2. Methods

2.1. Study sites

We 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*). We 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°) and 2) the Sandspit Road Bridge (height = 3 m, width = 10.4 m, orientation = 346°). 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).

2.2. Shading by vascular vegetation

In fall 2006, we 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. We set up three parallel 50-meter transects that were 25 m apart. Half of each transect crossed vegetated areas and the other half crossed open areas. At low tide, within 0.05 m^2 quadrats, we recorded snail density and visually estimated the percent cover of vascular vegetation every 5 m along each transect. To determine light attenuation by vascular vegetation, we also measured ambient and understory photosynthetic photon flux (PPF) using a Multi-Sensor Quantum Meter (Apogee Instruments). We used linear regression to examine the relationship between percent vegetation cover and light attenuation. We applied a generalized linear model (GzLM) to analyze the effects of transect, distance from the mudflat, and light attenuation on snail densities. Specifically, we 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, we collected all snails along one transect and dissected them under a stereomicroscope to calculate the prevalence of parasite infection. We 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. We 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. We 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 m: 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, we clipped all vascular vegetation in a 1.25 by 1.25 m area (note that this clipped area extended beyond the area where we 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 m: 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). We monitored snail densities weekly in each quadrat for 3 weeks before (initial) and 3 weeks after (final) the manipulations. We 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, we 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, we 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%. We 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, we 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, we recorded the temperature of the sediment surface before and after to examine the temperature responses to the manipulations. We 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. We 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. We used a GLM to analyze the effects of habitat (vegetated vs. mud flat), treatments within habitats, and temperature change on snail density.

2.3. Shading by bridges

In the summer of 2007, we 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 m apart. On the north and south facing banks of the estuarine channel, starting beneath the centerline of each bridge (parallel to the roadway), we ran 6 parallel 0.1 meter-wide band transects every 2 m in both directions (up and downstream from the bridges). We 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, we used a GzLM to examine the effects of bank (south or north), distance from the centerline of the bridge, and elevation on snail density. We 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, we measured the standing stock of benthic diatoms along these transects. We 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. We randomly took 3 sediment cores per quadrat using a 1 cm in diameter modified plastic syringe to take 4 mm deep cores. We 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. We used a GzLM to analyze the relationship between diatom abundance and snail density. In the subset of sites where we sampled sediment for diatoms, we 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. We attached the loggers to a buried $^1/_2$in. 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, we also conducted an experimental relocation experiment to examine snail movement in habitats with different light regimes. We 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). We cleaned all snails with a toothbrush and rinsed them in fresh water. After the snails were dry, we 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, we 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, we recorded the distances traveled by individual snails. We 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. We 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. We 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.

3. Results

3.1. Shading by vascular vegetation

Snails were less abundant under plants than in the open. We 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, $\chi^2 = 58.12$, P < 0.0001, overdispersion = 65.67, P < 0.0001), we found a negative relationship between light attenuation and snail density (df = 1, $\chi^2 = 17.97$, P < 0.0001), but no effect of transect (df = 2, $\chi^2 = 1.26$, P = 0.53), or distance from the open flat (df = 1, $\chi^2 = 1.38$, 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). 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 we 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. 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, we 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. 2).

Shading also affected sediment temperature. In the subset of sites with temperature loggers, we 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. 3). A general linear model analysis (Full model, df = 5, F = 5.82, $R^2 = 0.76$, 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.

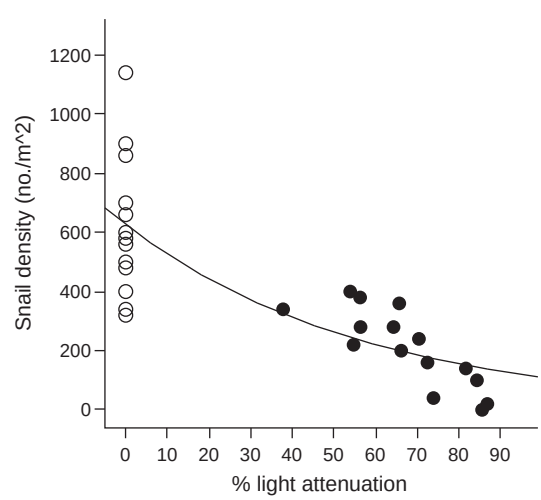

Fig. 1. Relationship between light attenuation and snail density ($Y = e^{(6.439 + (-0.017) * X)}$, $R^2 = 0.62$, F = 44.8, P < 0.0001), along three transects through vegetated marsh (solid circles) and open mudflat (open circles).

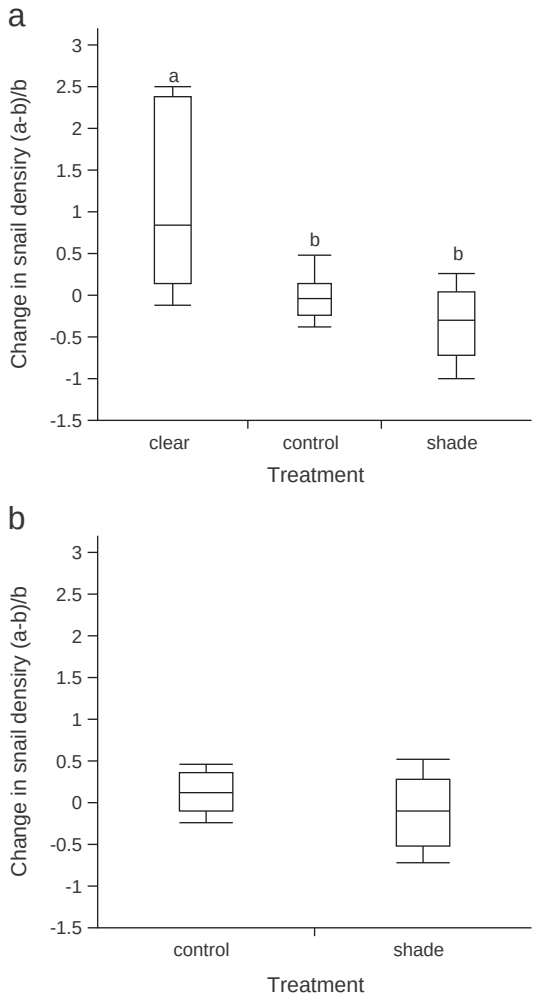

Fig. 2. Change in snail density after experimental manipulation of light in a) vegetated marsh habitat and b) mudflat habitat. The boxplots show the median and 25% and 75% quantiles and maximum and minimum values. Different letters indicate significance (P<0.05) between groups.

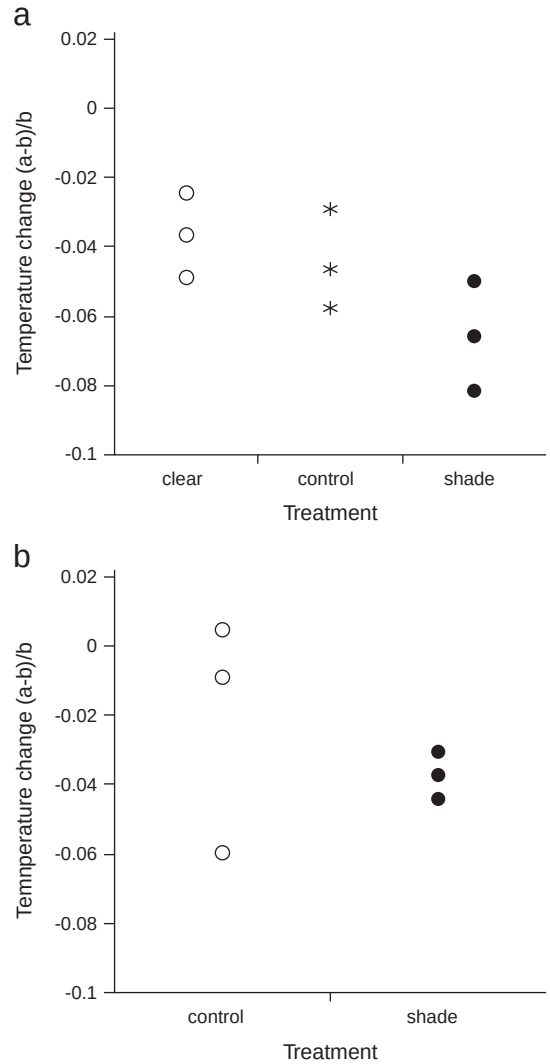

Fig. 3. Change in temperature after experimental manipulation of light in a) vegetated marsh habitat and b) mudflat habitat.

3.2. Shading by bridges

The Highway 217 bridge and water depth 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. 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. We also found, as expected, that the amount of light decreased with water depth (Fig. 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 °C colder than sites in the open channel bank (Fig. 6). We observed lower densities of diatoms at lower elevations, which we hypothesize was due to a decrease in light due to longer submergence times (Fig. 7). We also found lower snail densities at low than high elevations (Fig. 8). Bridge shading was associated with lower diatom and snail densities (Figs. 7 and 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). 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. 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, we 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 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. 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. 10). Large snails moved faster than small snails; however, we found no effect of parasitism on the movement of snails (Table 2). There were also no significant differences in trematode species diversity (Pearson χ^2, df = 8, P = 0.57) or parasite prevalence in

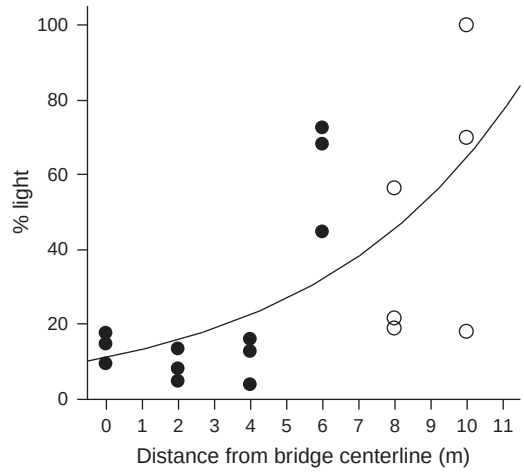

Fig. 4. Percentage light by distance from the bridge centerline. Solid circles are the sites in the channel bank directly under the bridge and the open circles are the sites in the open channel bank next to the bridge. $Y = e^{(2.42+0.18*X)}$, df = 1, $\chi^2 = 13.46$, P<0.0002, overdispersion = 13.73 (P<0.0001).

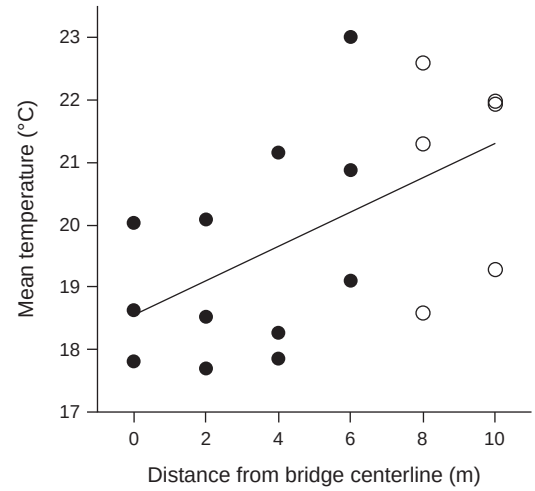

Fig. 6. Mean temperature by distance from the bridge centerline. Solid circles are the sites in the channel bank directly under the bridge and the open circles are the sites in the open channel bank next to the bridge. $Y = 18.55 + 0.28*X$, $R^2 = 0.31$, P<0.02.

experimental snails in different habitats (Prevalence: Marsh = 9.7%, shaded channel = 14.3%, unshaded channel = 16.7%) (Pearson $\chi^2 = 0.7$, df = 2, P = 0.72).

4. 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 we have studied (e.g. Carpinteria Salt Marsh, California 77%, Estero de Punta Banda, Baja California 50%, and Bahia Falsa San Quintin, Baja California 55%).

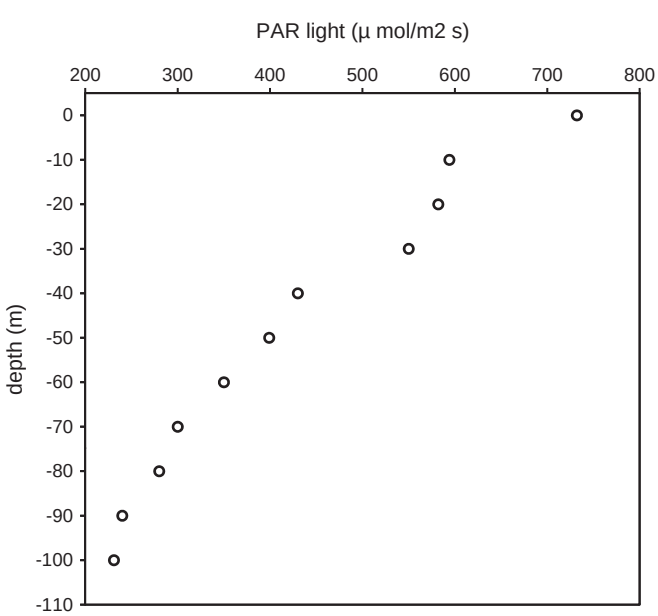

Fig. 5. One-time measurements of photosynthetically active radiation (PAR) by water depth in Goleta Slough, California, summer 2007.

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; Sadro et al., 2007). 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,

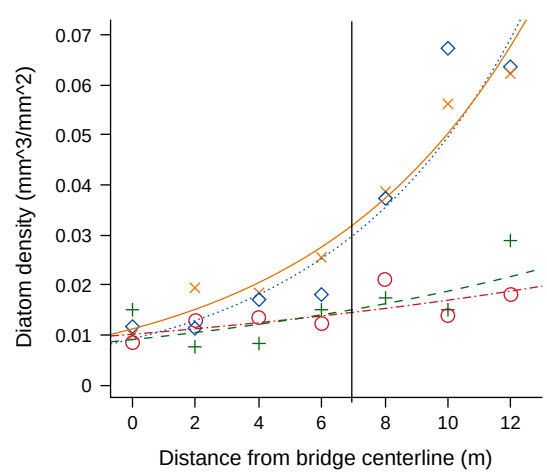

Fig. 7. Diatom density by distance from the bridge centerline, grouped by elevation (red circles and dash-dotted line = −100 cm: $Y = e^{(-4.59+0.051*X)}$, $R^2 = 0.58$, P = 0.04740; green plus signs and dashed line = −75 cm: $Y = e^{(-4.70+0.07*X)}$, $R^2 = 0.47$, P = 0.0886; blue diamonds and dotted = −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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

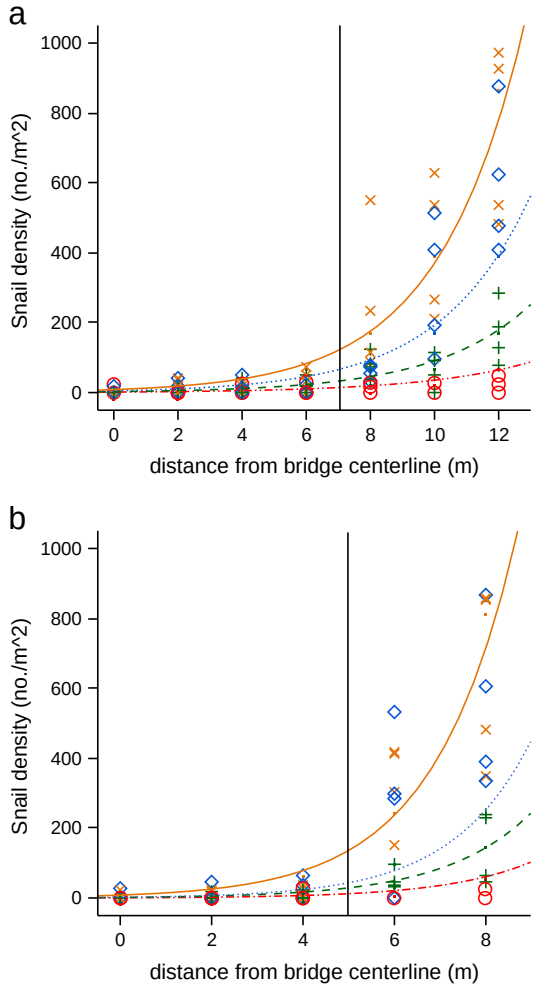

Fig. 8. Density of snails and the predicted density (curves) of snails from the GzLM by elevation and distance from the centerline of the a) Highway 217 bridge and b) Sandspit Road bridge. The different symbols represent the following elevations: red circles and dash-dotted line = −100 cm, green plus signs and dashed line = −75 cm, blue diamonds and dotted lines = −50 cm, and orange crosses and solid line = −25 cm. 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

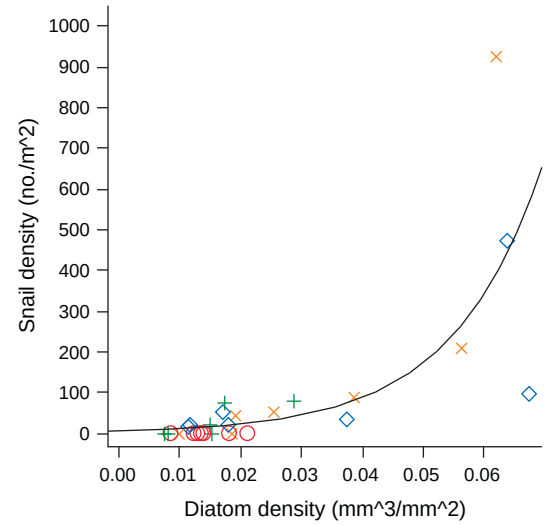

Fig. 9. Relationship between diatom density and snail density. The curve is the predicted snail density calculated from the GzLM [$Y = e^{(1.73 + 68.42 * X}$, df = 1, χ^2 = 73.4, P<0.0001, overdispersion = 62.4 (P<0.0001)]. The different symbols represent the following elevations: red circles = −100 cm, green plus = −50 cm, blue diamonds = −25 cm, and orange cross = −25 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 we 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, *A. 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.

Table 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 2
General linear model statistics of the effects of relocation habitat, original habitat, snail size, and infections status 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
Snail size	1	38.36	<0.0001
Infection status	1	1.76	0.1847

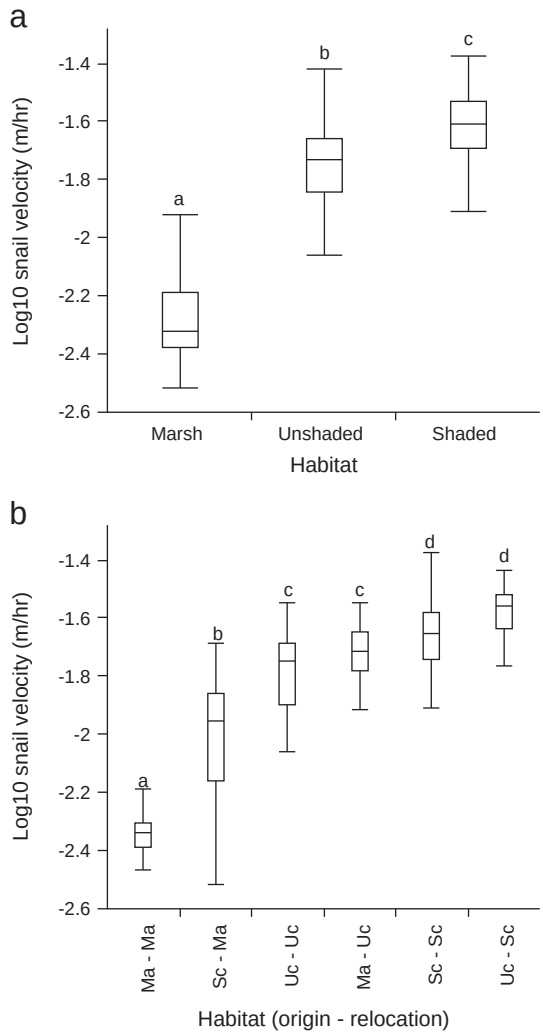

Fig. 10. The predicted average snail movement calculated from the GLM from Table 2 by a) relocated habitats, and b) by original-relocated habitat. The boxes show the median and 25% and 75% quantiles and the bars the maximum and minimum values. Different letters indicate statistically significance ($P<0.05$) among groups. Ma = vegetated marsh, Sc = channel bank shaded by a bridge, and Uc = an unshaded channel bank.

The shade from our experimental manipulation did not have as strong an effect on snail density as the shade from vegetation and bridges. We 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 the previous experimental work showing that movement is inversely related to resource availability (Byers, 2000; McCloy, 1979). 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, we 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 we observed. Our study areas shaded by vegetation, experimental shades, and bridges were cooler than unshaded areas as found in other similar studies (Gedan and Bertness, 2010; Whitcraft and Levin, 2007). Temperature could affect the habitat preferences of snails independently of resource availability. Snails presumably have thermal optima, and might avoid locations that are too warm or too cool. Because we 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 suggest that snails departed habitats with low resource levels. On the other hand, high summer temperatures may approach snail tolerance limits in southern latitudes. Kon et al. (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 *C. 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 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 we did not measure. Overall, we 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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