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Intraguild predation by shore crabs affects mortality, behavior, growth, and densities of California horn snails

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Abstract. The California horn snail, *Cerithideopsis californica*, and the shore crabs, *Pachygrapsus crassipes* and *Hemigrapsus oregonensis*, compete for epibenthic microalgae, but the crabs also eat snails. Such intraguild predation is common in nature, despite models predicting instability. Using a series of manipulations and field surveys, we examined intraguild predation from several angles, including the effects of stage-dependent predation along with direct consumptive and nonconsumptive predator effects on intraguild prey. In the laboratory, we found that crabs fed on macroalgae, snail eggs, and snails, and the size of consumed snails increased with predator crab size. In field experiments, snails grew less in the presence of crabs partially because snails behaved differently and were buried in the sediment (nonconsumptive effects). Consistent with these results, crab and snail abundances were negatively correlated in three field surveys conducted at three different spatial scales in estuaries of California, Baja California, and Baja California Sur: (1) among 61 sites spanning multiple habitat types in three estuaries, (2) among the habitats of 13 estuaries, and (3) among 34 tidal creek sites in one estuary. These results indicate that shore crabs are intraguild predators on California horn snails that affect snail populations via predation and by influencing snail behavior and performance.

Key words: Baja California; California horn snail; *Cerithidea californica* = *Cerithideopsis californica*; coexistence estuaries; *Hemigrapsus oregonensis*; intertidal; intraguild predation; *Pachygrapsus crassipes*; shore crabs.

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Introduction

Intraguild predation occurs when a predator feeds on a species with which it also competes for food. Although intraguild predation is common in nature (Arim and Marquet 2004, Bascompte and Melian 2005), most mathematical models predict unstable coexistence of intraguild predators and prey (Holt and Polis 1997, Mylius et al. 2001, Tanabe and Namba 2005, Hin et al. 2011). 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 and Polis 1997, Mylius et al. 2001, Hin et al. 2011). Either outcome predicts a strong negative association between

the densities of the intraguild prey and predator. There are several ways an intraguild predator can influence a system. For instance, if the prey is an herbivore, predation can have strong cascading effects on primary productivity (e.g., Estes and Duggins 1995, Silliman and Bertness 2002, Silliman et al. 2004, Kurle et al. 2008). However, predators can also affect their prey in nonconsumptive ways, such as if prey seek refuge in the presence of predators and reduce their own feeding rates (e.g., Trussell et al. 2002, Werner and Peacor 2003, Reynolds and Bruno 2013). Many species have stage-structured life histories, which can complicate predator–prey interactions, and models suggest that the addition of invulnerable stages of prey or an inefficient predator stage can make coexistence more likely (Mylius et al. 2001, Hin et al. 2011).

In California and Baja California estuaries, at least 34 grazing species compete for benthic microalgae (diatoms and cyanobacteria) (Hechinger et al. 2011). The most abundant grazer is the horn snail, *Cerithideopsis californica* (=Cerithidea californica, see Reid and Claremont 2014), which feeds on, and competes intraspecifically for, benthic microalgae (McCloy 1979, Lafferty 1993, Byers 2000, Lorda and Lafferty 2012). The shore crabs *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Grapsidae) also graze on microalgae by scraping them from the sediment (Hiatt 1948, Symons 1964, Kwak and Zedler 1997, Page 1997). In addition, shore crabs use their chelae to handle macroalgae and prey such as snails (Hiatt 1948, Symons 1964, Sousa 1993). Field experiments indicate that *P. crassipes* can reduce benthic microalgal abundance and the growth of California horn snails (Boyer and Fong 2005, Armitage and Fong 2006). Boyer and Fong (2005) found additive reductions in algae when *P. crassipes* and *C. californica* were held together in enclosures compared with enclosures where crabs or snails were alone. Armitage and Fong (2006) reported that crabs would eat up to 70–80% of the snails presented to them and that snails were found buried into the sediment in the presence of crabs, potentially reducing snail feeding and growth rates. Hence, shore crabs are intraguild predators of horn snails. Complicating this food web is that shore crabs have alternative food (macroalgae, carrion, small invertebrates), and predators (larger crabs and birds), whereas snails have additional natural enemies (trematode parasites and birds) (Hechinger et al. 2011).

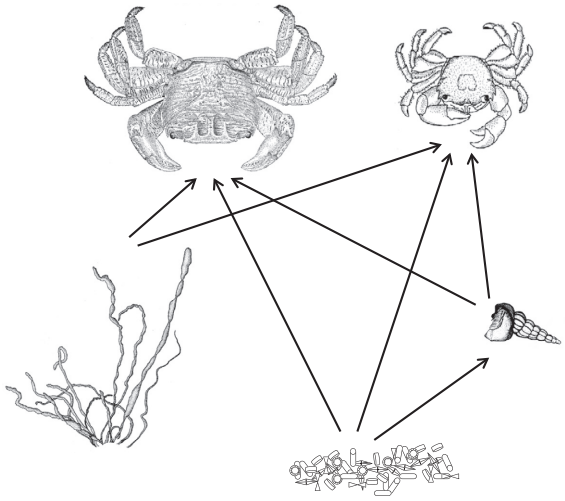

Fig. 1. Trophic pathways among the omnivorous striped shore crab, *Pachygrapsus crassipes* (top left) and yellow shore crab, *Hemigrapsus oregonensis* (top right), the grazing California horn snail, *Cerithideopsis* californica (middle right), and microalgae (diatoms, bottom right) and benthic macroalgae, *Ulva intestinalis* (bottom left). Arrows indicate energy flow from resources to consumers. Crab–crab predation, including cannibalism, was not studied, so these trophic pathways are not included for simplicity. Illustrations taken or modified from Hiatt (1948), Center for Phycological Documentation (2003) and California State Parks (n.d.).

In this study, we investigated the predatory and competitive effects of crabs on snails (Fig. 1), as well as relationships between crab and snail population densities. Our hypothesis was that crabs reduce snail abundance through intraguild predation. We used laboratory experiments to examine differences in predation by different-sized crabs on snail eggs and different-sized snails. We predicted crabs would have high predation rates on the earlier and more vulnerable snail stages with and without alternative food sources (macroalgae). We also did a field experiment to assess how crabs affect the behavior and growth of snails through the combined effects of competition for food and predator avoidance. We predicted crabs would reduce feeding rates, and consequently growth, due to direct competition and nonconsumptive effects. Finally, we explored the ecological relevance of the small-scale laboratory and field experiments by examining the prediction that snail abundance and biomass would decline

with increasing crab abundance within and among several natural populations. The results show that snails and crabs interact via intraguild predation (Fig. 1), with crabs preying primarily on early snail stages and reducing snail growth, leading to a negative effect of crabs on snail abundance, but without completely excluding snails.

Methods

Study sites

We conducted our laboratory experiments at the University of California, Santa Barbara. For the experiments, we collected crabs, algae, snails, and snail egg masses from a channel next to Estero Way in the Carpinteria Salt Marsh Reserve (34.399791°, −119.535337°). The channel was fringed by vegetated marsh dominated by pickleweed, *Salicornia pacifica*, and a road berm. We carried out the field experiments in a 1000 m^2 mudflat surrounded by pickleweed marsh on the western side of Carpinteria Salt Marsh (34.403145°, −119.541740°). We also randomly sampled 16 different salt marsh estuaries open to tidal flow across 10 degrees of latitude (~1110 km) to look for relationships between snail and crab densities (see Table 1 for the locations and names of the estuaries).

Laboratory experiments

To test the predictions that crab predation on snails (*C. californica*) depends on crab (*H. oregonensis and P. crassipes*) size and the presence of alternative food (the macroalgae *Ulva intestinalis)*, we did three laboratory experiments. In the first experiment, we examined crab predation on snail eggs and snails of various sizes, in the second experiment, we added macroalgae as alternative food, and in the third experiment, we used newly settled snails instead of snail eggs. All predation experiments used the same general procedure. We housed each individual crab in a plastic 2-L container filled with 1 L of seawater flowing at approximately 0.017 L/s. We 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 intestinalis*) in each container depending on the experiment (described below). The density of the snails and crabs in the containers (snails = 106–160/m^2 and crabs = 26/m^2) was high, but within the range found in Carpinteria Salt Marsh. Also, we used sizes of snails and crabs found in nature at the time of collection (for this reason, crab and snail sizes differed among the three different experiments). One or 2 d later (standardized among replicates), we scored predation attempts and successful predation events.

Table 1. Estuaries sampled in the United States and México during each survey, arranged North to South.

Estuary	Survey			Latitude	Longitude
	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 de San Quintín‡	X			30.452860°	−116.025592°
Guerrero Negro‡		X		28.007191°	−114.096833°

† Specimens for laboratory and field experiments were collected at this locality.
‡ Estuaries in México.

Predation attempts were indicated by missing pieces of algae and egg mass, and damage to the 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 was measured as the proportion of the food item eaten. We quantified the proportional occurrences of predation attempts and events for each individual crab over six trials. Across all experiments there was less than 5% crab mortality and about 6% of the crabs molted. If a crab died or molted, we replaced it with a crab of similar size. We used male crabs to keep claw size consistent among replicates (males have larger claws than females).

In the first laboratory experiment of the study (summer 2008), we examined crab predation on snail eggs and snails of various sizes. We used three crabs of both species from each of the 10–15, 15–20, and 20–25 mm sizes (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 spire tip to the aperture base). After one or 2 d, we measured the length of the egg mass remaining and calculated the percentage of the egg mass consumed. We also recorded predation attempts and events on snails. After checking the containers, we replaced all snails and egg masses and ran the experiment again, repeating each trial six times for each of the 27 crabs.

To see how an alternative food source affected crab predation on snails and snail eggs, we did a second experiment (summer 2008), where we 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, we put 1 g wet weight of the macroalga *Ulva intestinalis* into each container. We 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 intestinalis* 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.

Finally, we did a third laboratory experiment (fall 2009), where we used macroalgae and the same size classes of snails as in the second experiment but instead of snail egg masses, we 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 snails had hatched from eggs in the late summer-early fall. We 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*. We conducted the experiment using the methods described for the first experiment.

We averaged proportionate predation attempts and successful predation on snails, as well as the proportion of snail 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 replicates in statistical analyses. We 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, we used MANOVAs with the Hotelling–Lawley trace for all prey types, and examined differences in predation attempts and events among crab sizes for single prey types using univariate ANOVAs.

Field experiment

To test the prediction that crabs alter snail behavior, and consequently reduce snail growth, we performed enclosure experiments on mudflats on the northwest side of Carpinteria Salt Marsh in summer 2009 using male *P. crassipes* crabs and *C. californica* snails. We separated the effects of predation from the effects of competition by crabs on snails by using a spatial block design without replication for each treatment within blocks (to account for natural heterogeneity within the study area but without testing for its effect in the statistical model). The three treatments in each of 10 blocks were: (1) cages with no crabs, (2) cages with a crab, and (3) cages with a crab with immobilized claws (i.e., those where the moveable finger

and the fixed finger of each claw were glued together). Immobilized claws allowed crabs to scrape microalgae and feed on macroalgae (Hiatt 1948, Kuris and Mager 1975) but not to handle or feed on snails. We installed bottomless cylindrical-walled cages (~30 cm diameter) made of 0.3 cm Vexar mesh enclosing 10 cm below and 25 cm above the bottom's surface. We 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.

We 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 lip of each shell to calculate subsequent 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 and Jarne 2007, Hechinger 2010). After cage construction, we smoothed the mud bottom of each enclosure by hand to homogenize algal densities, then placed 20 snails and a crab according to treatments inside each enclosure. The densities (286 snails/m^2 and 14 crabs/m^2) 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 this experiment represented the range of natural densities and sizes found in the study area. We 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 attempted dispersal (as in Byers 2000b). We ended the experiment after 2 months, noting the proportions of snails burrowed into 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 laboratory, all snails were measured and checked for parasite infections (which can retard growth), and we calculated snail growth rates by measuring new shell production.

We used general linear models and *post hoc* Tukey's HSD test to determine the effect of treatment on the proportions of snails climbing on cage sides and burrowed into the mud. Both uninfected and infected snails were combined in these analyses because we took these data in the field before dissecting the snails. However, subsequent dissections revealed no differences in parasite prevalence in snails between treatments (ANOVA, $R^2 = 0.007$, df = 2, $F = 0.11$, $P = 0.90$), indicating no effect of trematode infections on snails burrowing and climbing behavior across treatments. On the other hand, to assess the effect of treatment on snail growth, we used data only from uninfected snails because trematode-infected snails have different growth rates than uninfected snails and cannot reproduce (Lafferty 1993, Hechinger 2010). We also excluded dead snails from these analyses. We used a generalized linear model with a Poisson error distribution with a log-link function, given the nonlinear nature of the data, and an overdispersion parameter because the variance was over dispersed for a Poisson distribution.

Field patterns

To test the prediction that crab and snail densities are negatively correlated in the field, we examined the relationship between snail and crab densities using data from three different surveys of wild populations (Table 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 zone of 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 five vegetated marsh, five pan, five mudflat, and eight channel sites. Snail density was determined at each site using ~20 randomly placed 10 × 50 cm quadrats and crab density using five random "core" samples (each consisting of three adjacent 24 cm diameter × 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 in cores by the proportion of habitat containing crab burrows in a plot with maximum dimensions of 10 × 10 m but sometimes limited by channel or pan size. We used average crab and snail abundances at the individual sites in statistical models. With other data collected during this survey, we also calculated the proportions of living snails with

damaged shells (interpreted as unsuccessful crab predation events), across sites and snail 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. 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 chosen in mudflat or vegetated marsh habitats. At each site, the densities of snails and shore crabs were quantified using five, adjacent, large cores (20 cm diameter by 50 cm deep) placed irrespective of the presence of crab burrows. We used average crab and snail abundances in each habitat at each estuary in statistical models.

Lastly, we determined crab burrow and snail densities at 34 sites distributed seaward to landward along three different channels (9, 10, and 15 sites per channel) in Carpinteria Salt Marsh, CA, in 2008. Adjacent sites were 75 m apart. We determined the densities of snails, snail eggs, and crab burrows (as a proxy for crab presence and density) at each site using three randomly placed band transects, each 10 cm in width, stretched across each channel. We used average snail, snail egg, and crab abundances at each site in statistical models.

In all surveys, the density of snails included burrowed 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 length–weight regressions (Kuris et al. 2008). We excluded from all analysis sites where both snails and crabs were absent, because we assumed these sites did not contain suitable habitat for snails or crabs. For this reason, the number of sites sampled in the methods is greater than the sample sizes listed in the results.

From each survey, we calculated the percent overlap 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 crab and snail density (no./m^2) and biomass (g/m^2) for individual sites:

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

where P_{jk} = percent overlap between species j and species k, P_{ij} = proportional density or biomass at site i of all sites where species j was present, P_{ik} = proportional density or 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 across all sites.

We used 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 categorical predictor variables; and distance from the estuary mouth (in the last survey) and crab density and biomass (in all surveys) were used as continuous predictors. All two-way interaction terms were included in initial models, but any nonsignificant ($P > 0.10$) main or interactive effects were dropped. 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. We $\log_{10}$-transformed 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 and Table 3). In the first experiment, crabs of both species attacked and consumed at least five times more snail egg mass than snails (paired *t*-tests and sequential Bonferroni corrections, $P < 0.05$, Table 2 and Fig. 2). On average, *H. oregonensis* attacked more egg masses than *P. crassipes* but there were no significant statistical differences in predation events among crab species and sizes (MANOVAs and univariate ANOVAs, $P > 0.05$, Table 3, Fig. 2). In short, crabs primarily ate snail eggs in this experiment.

In the second experiment where crabs were offered *Ulva intestinalis* as an additional food item, *Hemigrapsus oregonensis* consumed three times

Table 2. Statistics on mean proportions of offered prey attacked (predation attempts) and consumed (predation events) by crabs in the laboratory. Prey items were macroalgae, snail egg masses, and different snail size classes, depending on the experiment, and intraguild predators were *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 indicate significantly different values for different prey types ($P < 0.05$, paired t-tests with sequential Bonferroni corrections).

	1st Experiment	2nd Experiment	3rd Experiment
	Mean (SD)	Mean (SD)	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}

more algae than snail egg mass and did not consume any snails. *Pachygrapsus crassipes* consumed proportionately twice as much algae as snail egg mass and at least 16 times more egg mass than snails (paired *t*-tests and sequential Bonferroni corrections, $P < 0.05$, Table 2 and Fig. 3). On average, there were no significant differences in predation rates among crab species and sizes, and crabs primarily ate macroalgae and snail eggs (Table 3 and Fig. 2).

In the third experiment, the proportions of predation attempts and successful predation events by *H. oregonensis* on macroalgae and 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 Bonfer-

Table 3. MANOVA with Hotelling–Lawley trace 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 laboratory experiments 1, 2, and 3.

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

roni corrections, $P < 0.05$, Table 2 and Fig. 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 the proportion of algae and the smallest snails (0–5 mm) attacked and eaten were not statistically significant (paired *t*-tests with sequential Bonferroni corrections, $P > 0.05$, Table 2 and Fig. 2). The proportions of predation attempts by *P. crassipes* on snails from 0 to 20 mm in length were similar, but successful predation was at least four times higher for the smallest snails (0–10 mm) compared to larger snails (>10 mm) (paired *t*-tests with sequential Bonferroni corrections, $P < 0.05$, Table 2 and Fig. 2). Predation attempts on snails 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 *P. crassipes* (MANOVAs and univariate ANOVAs, $P < 0.05$, Table 3 and Fig. 2). There were no significant differences in predation among crab species and sizes (Table 3 and Fig. 2) and crabs primarily ate macroalgae and small snails (<10 mm).

Field experiment

The mean percentage of snails burrowed into the mud at the end of the experiment was highest for crabs with functional claws, intermediate with crabs with immobilized claws, and lowest without crabs (Fig. 3a). The mean percentage of snails observed climbing on cage walls was three times lower in enclosures with crabs than without crabs (Fig. 3b).

Consistent with the laboratory experiments, we saw few incidents of crab predation on large snails 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 (out of 600 snails total) could not be accounted for and ei-

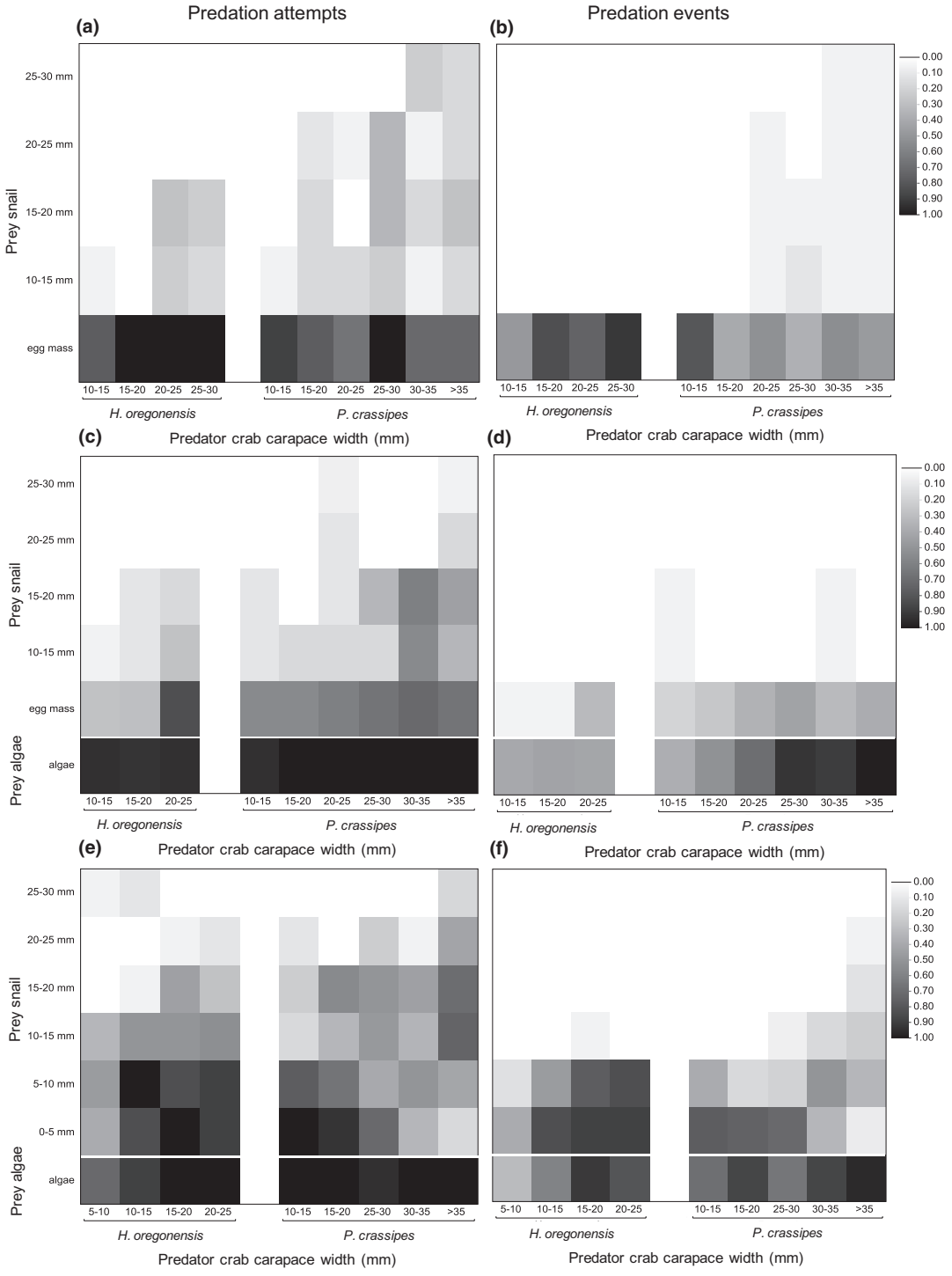

Fig. 2. Mean proportions of predation attempts (figures on the left) and events (figures on the right) on macroalgae, snail egg masses, and/or different snail size classes (length in mm) by different size classes (carapace width in mm) of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* in the laboratory experiments 1 (a and b), 2 (c and d), and 3 (e and f). Shading denotes the proportions of offered prey which were attacked (attempts) or consumed (events) (see code).

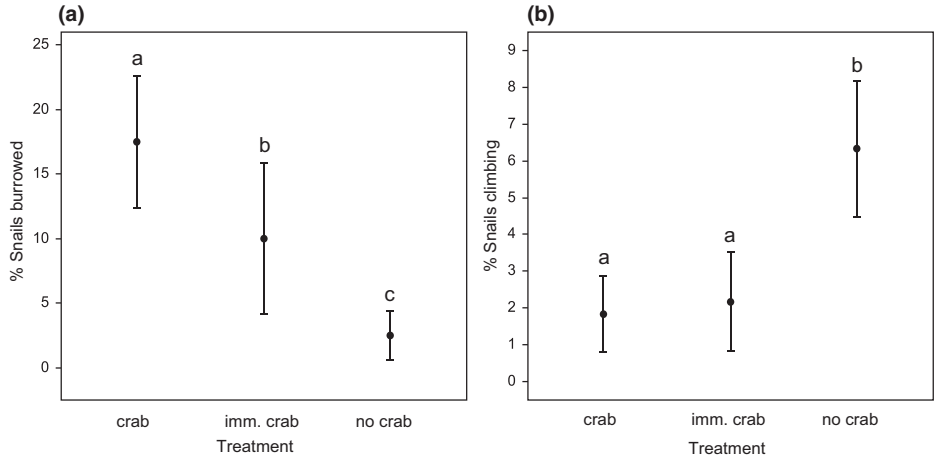

Fig. 3. Mean percentage of snails burrowing (a) at the end of the field experiment across different treatments: crabs, crabs with immobilized claws (imm. crab), and no crabs. Full model: $R^2 = 0.5$, df = 2, $F = 13.5$, $P < 0.001$. Mean percentage of snails climbing on sides of experimental field enclosures (b) across the same treatments. Full model: $R^2 = 0.4$, df = 2, $F = 9.1$, $P = 0.001$. Error bars are 95% confidence intervals and different letters indicate significant ($P < 0.05$) differences among treatments (Tukey's HSD test).

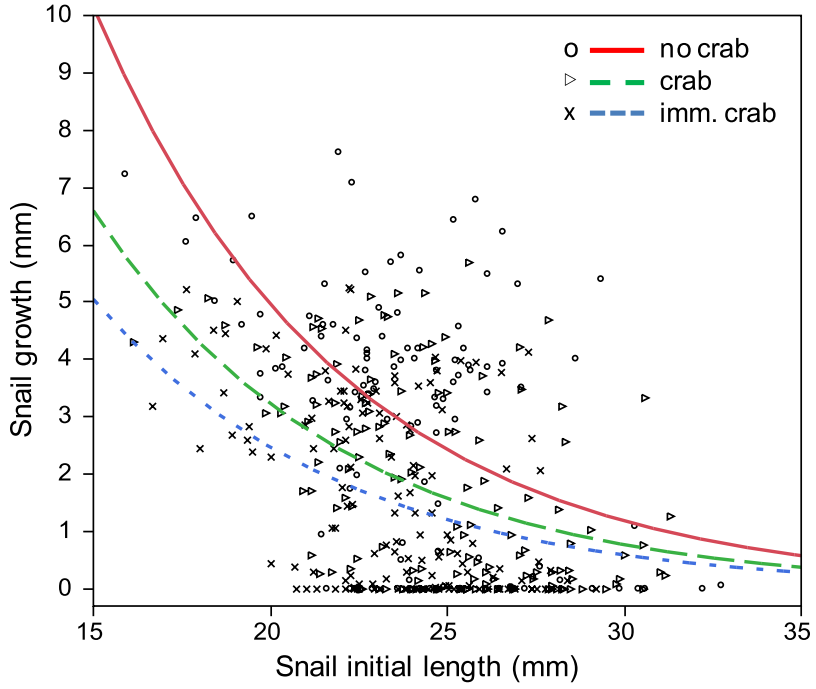

Fig. 4. Snail growth vs. initial snail length across experimental field treatments: no crab: $Y = e^{(4.47 - 0.14 \times X)}$ (red solid curve); crab: $Y = e^{(3.77 - 0.14 \times X)}$ (green dashed curve): and crab with immobilized claws: $Y = e^{(4.03 - 0.14 \times X)}$ (blue dotted curve). Symbols represent the following treatments: open circles = no crabs, triangles = crabs with functional claws, and letter "x" = crabs with immobilized claws. A GzLM analysis showed highly significant effects of treatment (df = 2, $\chi^2 = 53$, $P < 0.0001$) and snail initial length (df = 1, $\chi^2 = 97$, $P < 0.0001$) on snail growth with no interaction effects.

ther 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.

Table 4. Percent overlap and, in parentheses, mean snail, snail egg mass, and crab densities (no./m^2) and biomass (g/m^2) by habitat across three field surveys.

	1st survey	2nd survey	3rd survey†	
	% overlap	% overlap	% overlap	% overlap
Characteristic	(snail/crab)	(snail/crab)	(snail/crab)	(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.

Snails in the enclosures without crabs grew 1.6 times 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 enclosed with crabs that had functional claws grew 1.1 times more than snails in enclosures with crabs with immobilized claws (*post hoc* contrast: df = 1, $\chi^2 = 5.8$, $P < 0.02$) (Fig. 4). As expected, smaller snails grew faster than larger snails (Fig. 4, effect of snail initial length on snail growth: generalized linear model df = 1, $\chi^2 = 97.5$, $P < 0.0001$) (full GzLM statistics, df = 3, $\chi^2 = 114$, $P < 0.0001$, 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 4). The percentage overlap between crabs and snails varied across habitats and surveys, with overlap in density and biomass being the highest in channels and pans, and lowest in vegetated marsh and mudflats, with zero overlap in flats in the 2nd survey (Table 4).

Controlling for estuary, habitat, and distance from the estuary mouth (depending on the survey analyzed), there were negative relationships between snail and crab densities and biomasses (Fig. 5 and Table 5); however, there was considerable unexplained variation in some of the results (Fig. 5 and Table 5). In Survey 2, the interactions between habitat and crab density or biomass accounted for marginally significant ($P < 0.10$) amounts of the variation in snail density or biomass, with negative relationships between snail and crab density and biomass in channel and flat habitats, but little relationship in marsh habitats. We also observed a negative relationship between snail egg mass and crab burrow densities in Carpinteria Salt Marsh channels (Survey 3) (Table 5, Fig. 6). Although creek, distance from the mouth, and crab burrow density all had significant effects on snail density and biomass, and snail egg mass density in Carpinteria Salt Marsh (Survey 3), there were no significant interaction effects of these factors (Table 5).

The proportion of snails with damaged shells in the field was typically low, although there were several "hotspots" where shell damage exceeded 20% (Fig. 7). However, we detected no relationship between the proportion of snails with damaged shells and crab density across

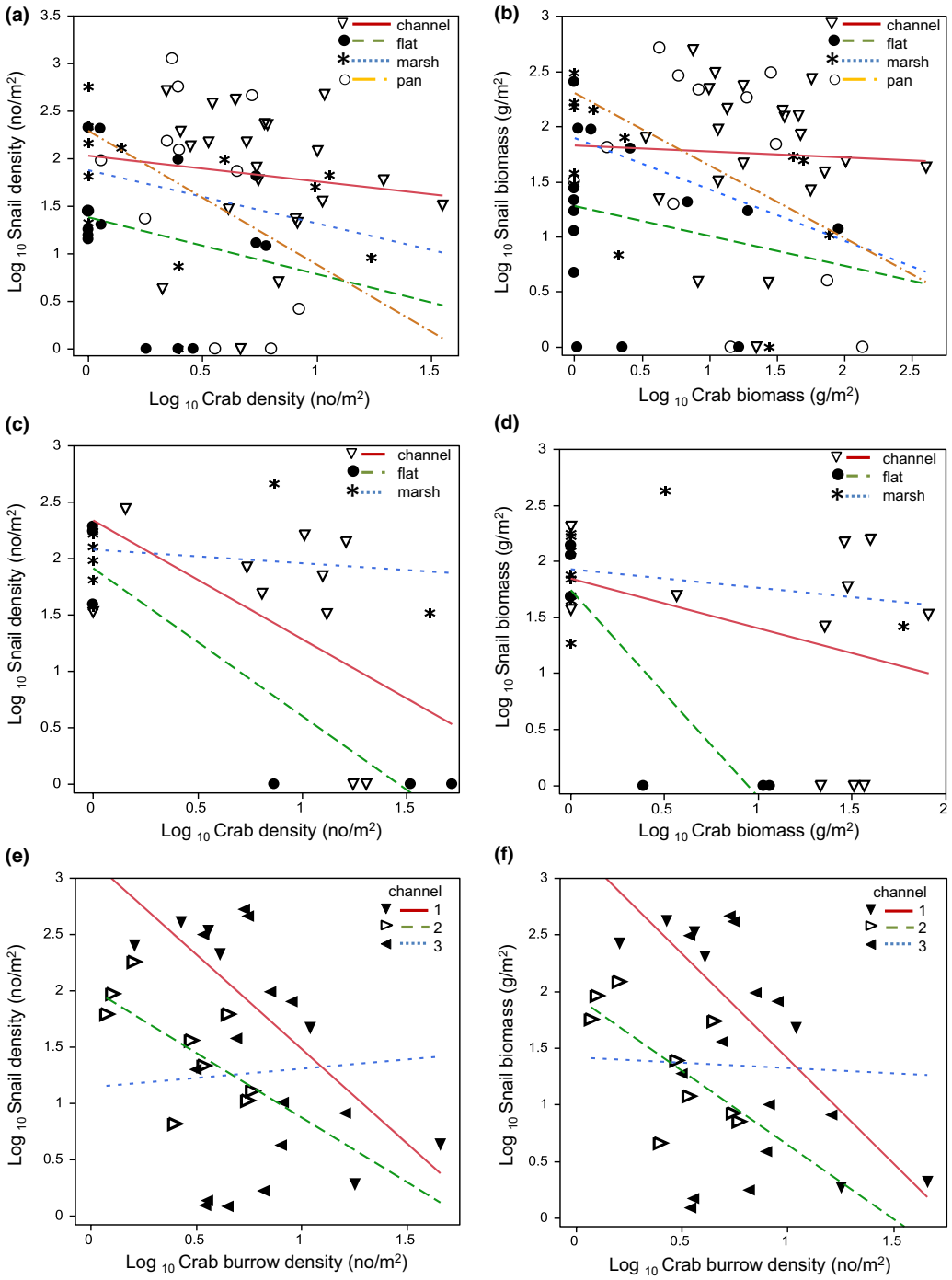

Fig. 5. Relationships between snail and crab densities (figures on the left) and biomasses (figures on the right) in different estuarine habitats. Relationships between snail and crab density and biomass from the first survey (a and b) ($N = 61$ sites from three estuaries). Relationships between snail and crab density and biomass from the second survey (c and d) ($N = 27$ habitat averages from 13 estuaries). Relationships between snail density and biomass and crab burrow density from the third survey (e and f) ($N = 30$ channel sites from three channels in one estuary). Statistical analyses are presented in Table 5.

Table 5. General linear model statistics for 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 × 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	R^2	F	P
Survey 1				
Snail density				
Full Model	4	0.17	2.8	0.03
Habitat	3		5.7	0.02
Crab density	1		2.8	0.02
Snail biomass				
Full Model	4	0.14	1.4	0.07
Habitat	3		3.8	0.06
Crab biomass	1		2.9	0.04
Survey 2				
Snail density				
Full Model	5	0.58	5.9	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	5	0.47	3.7	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	18	0.89	5.2	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	18	0.90	5.0	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	18	0.85	3.4	0.02
Creek	2		8.8	0.005
Distance from mouth	15		3.0	0.04
Crabs burrow density	1		6.4	0.03

snail size classes, although snails of the smallest size classes (<15 mm) with damaged shells were mostly absent except at one site (Fig. 7).

Discussion

Data from laboratory predation trials, a field experiment, and field surveys collectively support the hypothesis that crabs reduce snail abundance via intraguild predation, consuming snail eggs and small snails, 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, although crabs rarely ate adult snails, they did alter snail behavior so that snail growth was reduced. Snails climbed less, burrowed into sediments more, and grew at slower rates in the presence of crabs. Crab and snail populations overlapped in the field, indicating potential for interactions between

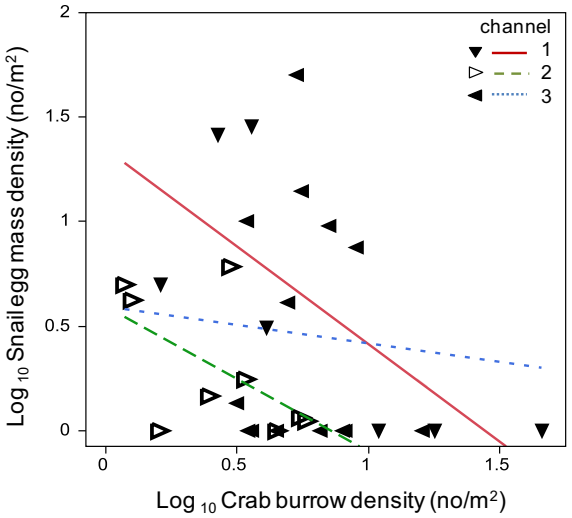

Fig. 6. Relationship between snail egg mass and crab burrow densities among sites in three channels at Carpinteria Salt Marsh (Full model: df = 3, R^2 = 0.23, F = 2.6, P = 0.07; Crab burrow density: df = 1, F = 6.3, P = 0.02; Channel: df = 2, F = 1.4, P = 0.02).

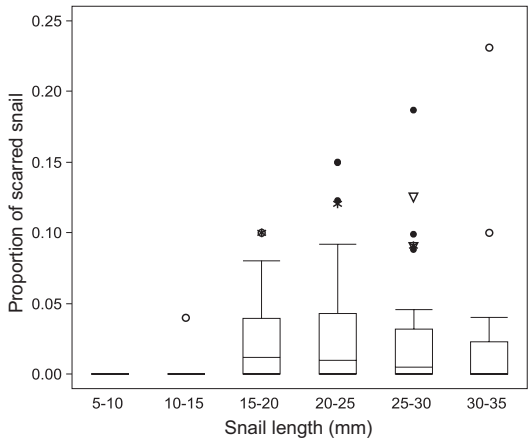

Fig. 7. Proportion of live snails with damaged shells by different snail length size classes. The boxplots show the median and 25% and 75% quartiles. The bars represent the distance of the 75% quartile + 1.5 * the interquartile range and the data points are outliers. The symbols represent different habitats (solid circles = flats, open circles = pans, asterisk = marsh, and triangles = channels). Data are from the first field survey (N = 10,067 snails from 53 sites spread across three estuaries).

them. Interactions between snails and crabs were further confirmed by field observations of large snails with shells showing damage characteristic of failed attacks by crabs. Although crabs often attacked but did not consume small snails in the laboratory (leaving scars), damaged small snails were not observed in the field. Perhaps this occurred because snails quickly grew out of vulnerable stages or because crab attacks on small snails in the field tended to be successful, leaving behind no living snails with damaged shells (Bertness and Cunningham 1981, Sousa 1993). Finally, three surveys conducted at different scales involving 16 estuaries consistently showed negative relationships between snail and crab abundances. Therefore, in part and in sum, the data indicate that crabs have a negative impact on California horn snail populations.

Predator–prey interactions between snails and crabs were stage-structured. As predicted, we found crabs fed more on snail eggs than on snails; however, crabs did feed on small snails, (< 10 mm), which have thinner and weaker shells than larger snails (*personal observations*). These size-structured effects were clear in simple laboratory trials, even though these trial probably underestimated crab predation rates on snails because we presented only one snail per size class to predators in each trial. Using male crabs, on the other hand, might have overestimated crab effects on large snails because male crabs can consume larger snails than comparably sized female crabs because males have larger chelae (Sousa 1993). Regardless, crab predation on snail eggs and the smallest snails seems to 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 as we predicted. Such nonconsumptive effects are important in other systems (e.g., Werner and Peacor 2003, Reynolds and Bruno 2013). Because crabs with functional claws had a stronger effect than crabs with immobilized claws on the percentage of burrowed snails, we suspect that crab handling of snails increases snail burrowing behavior. However, we also found more burrowed snails in cages with crabs with immobilized claws than in cages lacking crabs, suggesting that crabs also elicit snail burrowing responses without handling them. On the other hand, we did not study snail burrow-

ing behavior in detail and it is possible that snail burial is a passive process that occurs simply by crab movement (Jeremy Long and colleagues, unpublished observations). For these reasons, we were not able to disentangle the negative effects of crabs on snail growth as mediated through interspecific competition vs. nonconsumptive effects (burrowing). Armitage and Fong (2006) also found higher burial of snails in enclosures with crabs. We have observed that snails respond to crabs by retreating into their shells and by reducing movement rates (including climbing up cage sides). Other snail species climb onto vegetation or other protruding surfaces to escape from predators (Warren 1985, Vaughn and Fisher 1988), but we observed that lower proportions of snails climbed up the sides of cages in the presence of crabs. In the case of *C. californica*, then, climbing does not appear to be an escape response (see Byers 2000). Burrowing probably reduced the time snails spent feeding, resulting, ultimately, in reduced snail growth rates (as seen in our data). Because fecundity increases with snail size (Hughes 1986), crab effects on snail growth likely reduce snail reproductive output.

Although there were negative associations between crab and snail abundances, these species do coexist. As a consequence, our data support the inference that intraguild predation is common (Arim and Marquet 2004), particularly for herbivorous–detritivorous prey and omnivorous predators, as in our study. Crabs are omnivorous, consuming snails, snail eggs, microalgae, 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. Our results suggest that crabs prefer alternative food sources, such as macroalgae over snails, which could potentially stabilize co-occurring crab and snail populations (Daugherty et al. 2007). Another mechanism that could stabilize crab–snail interactions revolves around the invulnerability of large snails to crab predation, weakening feedbacks between intraguild predators and their prey, thereby promoting their coexistence (e.g., Mylius et al. 2001, Hin et al. 2011). Ironically, a large size refuge might benefit snail parasites more than snails because trematode parasites castrate up to 100% of California horn snails by the time they reach a large size. Finally, other mechanisms promoting stability might include the relative impacts of intra and interspecific competition, additional predators (including crab cannibalism), and parasites (Hechinger et al. 2011) of crabs and snails. These other trophic interactions are not considered in intraguild predation models (e.g., Holt and Polis 1997, Mylius et al. 2001), but might sustain the intraguild sub-web studied here.

In conclusion, the frequency of crab attacks and consumption of snails depended on the life stage and sizes of predators and prey, with most crab size classes attacking and eating snail eggs more than snails and eating small snails more than large snails. In addition, we found that more snails burrowed into the mud, reduced their movements, and slowed their growth in the presence of crabs. These interactions help explain 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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Literature Cited

Arim, M., and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. Ecology Letters 7:557–564.

Armitage, A. R., and P. Fong. 2006. Predation and physical disturbance by crabs reduce the relative

impacts of nutrients in a tidal mudflat. Marine Ecology-Progress Series 313:205–213.

Bascompte, J., and C. J. Melian. 2005. Simple trophic modules for complex food webs. Ecology 86:2868–2873.

Bertness, M. D., and C. Cunningham. 1981. Crab shell-crushing predation and gastropod architectural defense. Journal of Experimental Marine Biology and Ecology 50:213–230.

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

Byers, J. E. 2000. Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. Journal of Experimental Marine Biology and Ecology 248:133–150.

California State Parks. (n.d.). MacKerricher State Park Intertidal Studies. 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. University Herbarium, University of California, Berkeley, Berkeley, California USA.

Daugherty, M. P., J. P. Harmon, and C. J. Briggs. 2007. Trophic supplements to intraguild predation. Oikos 116:662–677.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs 65:75–100.

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

Hechinger, R. F., et al. 2011. Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. Ecology 92:791.

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

Hiatt, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science 2:135–213.

Hin, V., T. Schellekens, L. Persson, and A. M. de Roos. 2011. Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. American Naturalist 178:701–714.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745–764.

Hughes, R. N. 1986. A Functional Biology of Marine Gastropods. Croom Helm, London.

Krebs, C. J. 1999. Chapter 13. page 470 *in* E. Fogarty, V. McDougal, and N. Murray, editors. Ecological Methodology. Addison Wesley Longman, New York.

Kuris, A. M., and M. Mager. 1975. Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. Journal of Experimental Zoology 193:353–360.

Kuris, A. M., et al. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454:515–518.

Kurle, C. M., D. A Croll and B. R. Tershy. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the United States of America 105:3800–3804.

Kwak, T. J., and J. B. Zedler. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110:262–277.

Lafferty, K. D. 1993. Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Marine Ecology-Progress Series 96:229–237.

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.

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, San Diego, California USA.

Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. American Naturalist 158:259–276.

Page, H. M. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California Salt Marsh. Estuarine Coastal and Shelf Science 45:823–834.

Reid, D. G., and M. Claremont. 2014. The genus Cerithideopsis Thiele, 1929 (Gastropoda: Potamididae) in the Indo-West Pacific region. Zootaxa 3779:61–80.

Renkonen, O. 1938. Statisch-okologische Untersuchungen uber die terrestrische Kaferwelt der finnischen Bruchmoore. Archivum Societatis Zoologicae Botanicae Fennicae Vanamo 6.

Reynolds, P. L., and J. F. Bruno. 2013. Multiple predator species alter prey behavior, population growth, and a trophic cascade in a model estuarine food web. Ecological Monographs 83:119–132.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences of the United States of America 99:10500–10505.

Silliman, B. R., C. A. Layman, K. Geyer and J. C. Zieman. 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, W. P. 1993. Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman. Journal of Experimental Marine Biology and Ecology 166:19–37.

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

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

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5:241–245.

Vaughn, C. C., and F. M. Fisher. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: a field test. Journal of Experimental Marine Biology and Ecology 123:163–176.

Warren, J. H. 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). Journal of Experimental Marine Biology and Ecology 89:11–28.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.