

Food webs and fishing affect parasitism of the sea urchin *Eucidaris galapagensis* in the Galápagos

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Abstract. In the Galápagos Islands, two eulimid snails parasitize the common pencil sea urchin, *Eucidaris galapagensis*. Past work in the Galápagos suggests that fishing reduces lobster and fish densities and, due to this relaxation of predation pressure, indirectly increases urchin densities, creating the potential for complex indirect interactions between fishing and parasitic snails. To measure indirect effects of fishing on these parasitic snails, we investigated the spatial relationships among urchins, parasitic snails, commensal crabs, and large urchin predators (hogfish and lobsters). Parasitic snails had higher densities at sites where urchins were abundant, probably due to increased resource availability. Commensal crabs that shelter under urchin spines, particularly the endemic *Mithrax nodosus*, preyed on the parasitic snails in aquaria, and snails were less abundant at field sites where these crabs were common. In aquaria, hogfish and lobsters readily ate crabs, but crabs were protected from predation under urchin spines, leading to a facultative mutualism between commensal crabs and urchins. In the field, fishing appeared to indirectly increase the abundance of urchins and their commensal crabs by reducing predation pressure from fish and lobsters. Fished sites had fewer snails per urchin, probably due to increased predation from commensal crabs. However, because fished sites also tended to have more urchins, there was no significant net effect of fishing on the number of snails per square meter. These results suggest that fishing can have complex indirect effects on parasites by altering food webs.

Key words: common pencil sea urchin; *Eucidaris galapagensis*; eulimid snails; Galápagos Marine Reserve; *Mithrax nodosus*; parasitism; *Pelseneeria* spp.; predation; *Sabinella shaskyi*; trophic cascades.

INTRODUCTION

The Arabian proverb, “the enemy of my enemy is my friend,” is a succinct description of ecological indirect effects. Indirect effects are important in many ecosystems (Wootton 1994b). In the rocky intertidal, indirect effects, such as keystone predation and apparent competition, can account for 40% of community structure (Menge 1995). Although indirect effects make it more difficult to predict outcomes of habitat alterations, extinctions or species introductions (Wootton 1994b), placing interactions in a food-web context can improve the accuracy of predictions and interpretations of existing data (Gotelli and Ellison 2006). A challenge when interpreting species interactions is that habitat variation (including patterns of recruitment) can drive spatial associations among species, and these patterns can then be misinterpreted as species interactions (Lafferty et al. 1994). Therefore, the most powerful way to study indirect effects is through removal experiments (Wootton 1994b). Fishing is a nonexperimental form of removal, and comparing fished and

unfished areas can sometimes reveal indirect effects at scales where experiments would not be practical (Baskett et al. 2007). To investigate the hypothesis that predators would indirectly impact infectious disease of prey, we studied sites in the Galápagos Islands where fishing reduced predator densities and considered the indirect response of eulimid snails that parasitize sea urchins.

Parasites dominate food-web links (Marcogliese and Cone 1997, Lafferty et al. 2006, 2008a) and the diversity of free-living species in food webs can hinder (Keesing et al. 2006) or benefit (Hechinger and Lafferty 2005) parasites. Some evidence for food-web and biodiversity effects on parasites comes from comparisons of fished and unfished areas. Fishing might indirectly increase parasitism of a fished host’s prey. For example, on California rocky reefs, spiny lobsters reduce sea urchin abundance, indirectly reducing the probability of bacterial disease in urchins; at sites where lobsters are fished, outbreaks of bacterial disease are much more frequent (Lafferty 2004). Alternatively, fishing, by reducing free-living biodiversity, might reduce the abundance of parasites that depend on the lost biodiversity; this effect is likely to be strongest for parasites with complex life cycles. For example, on coral

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reefs where sharks and other predators have been overfished, there is a lower diversity of parasites in reef fishes, and, in particular, a lower prevalence of larval cestodes that use sharks as final hosts (Lafferty et al. 2008b). These opposing results demonstrate how food-web linkages can mediate the magnitude and direction of fishing's impact on parasites (Wood et al. 2010).

On Galápagos rocky reefs, two species of eulimid snails, *Sabinella shaskyi* and *Pelseneeria* spp. (Warén 1992, Sonnenholzner and Molina 2005), are ectoparasites of the sea urchin *Eucidaris galapagensis*, which is sometimes called *E. thouarsi*, but is now considered genetically distinct (Fig. 1a, b; see Lessios et al. 1999). *Sabinella shaskyi* creates a hollowed space in the tip of urchin spines and, over time, these galls disintegrate the entire spine (Warén 1983, 1992). *Pelseneeria* spp. lives on the test and can insert its proboscis through the urchin's gonopore to feed on the host's gonad (Warén 1983, 1992). At night, snails occur on the substrate near urchins (J. I. Sonnenholzner, *personal observation*), suggesting that snails can move from urchin to urchin. Despite occasional movement between hosts, eulimids maintain a durable relationship with urchins and we and others view them as parasites (Warén 1983, 1992).

We considered the importance of food-web interactions for eulimid snails in this system by studying direct and indirect associations among species, as well as the indirect effects of fishing and large predators. Pencil urchins are more abundant in areas of the rocky subtidal zone where large predators (lobsters and fishes) are sparse (Sonnenholzner et al. 2009). However, the effect of large predators on urchins varies by habitat, suggesting urchins have effective refuges in some locations and poor recruitment in others (Sonnenholzner et al. 2009). In areas with many large predators, the remaining urchins tend to be fewer and larger, perhaps due to a size refuge from predation. Areas subject to high levels of fishing have fewer large predators (fish and lobsters), more urchins (depending on the habitat), and less algae (Sonnenholzner et al. 2009). In other words, the enemy (fisher) of the urchin's enemies (fish and lobster) is the urchin's friend.

By releasing urchins from predation, fishing should indirectly favor the eulimid snail population due to increased host availability, host survivorship, and parasite transmission rates (because of increased host density). However, closer investigation of this food web reveals crabs (most commonly *Mithrax nodosus*), which shelter in urchin spines (Baeza et al. 2001) and prey on eulimid snails (Fig. 1b, c). The facultative mutualism between crab and urchin complicates our predictions for indirect effects, because trophic and mutualistic networks tend to respond in opposite directions to perturbations (Thebault and Fontaine 2010). Fishing could negatively affect eulimid snails if, by removing large predators, it indirectly facilitates commensal crab survival.

To characterize fishing-associated changes in food-web structure, our study was conducted at multiple

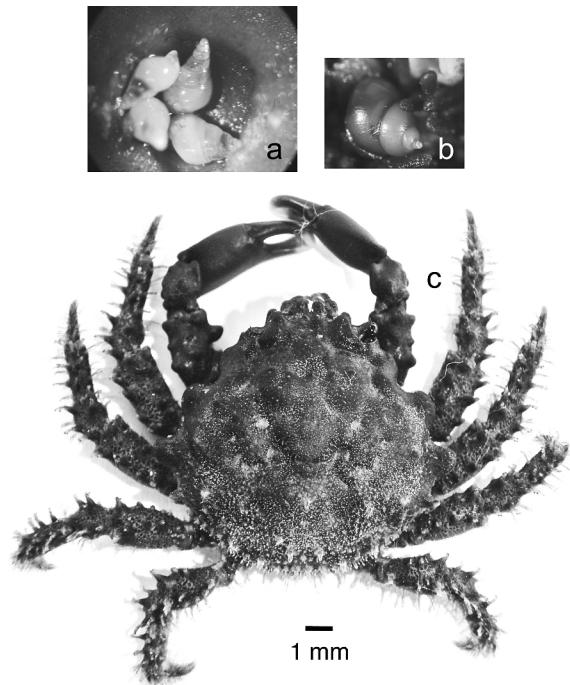


FIG. 1. Eulimid parasites and a commensal crab collected from the slate pencil sea urchin *Eucidaris galapagensis*: (a) four parasites (*Sabinella shaskyi*) found in a swelled primary spine in the interambulacrum 4, (b) one parasite (*Pelseneeria* spp.) positioned on a gonopore, and (c) dorsal view of an adult crab *Mithrax nodosus*. All images share the same scale.

spatial scales. We performed simple observations in aquaria to investigate the potential for trophic interactions among species, followed by field observations of the abundance of snails, crabs, urchins, and large predators at two scales. At the scale traditionally used in epidemiological studies, hosts (urchins) were the unit of replication (e.g., snails per urchin and crabs per urchin). We also considered a broader scale (common to ecological studies), calculating densities of eulimid snails and commensal crabs per unit area and, for the path analyses, counting the average number of snails per urchin and the average number of crabs per urchin, and measuring average urchin size.

METHODS

Study sites and sampling methods

We investigated hypothesized feeding relationships among snails, urchins, crabs, spiny lobsters, slipper lobsters, and hogfish by conducting simple feeding trials with wild-caught individuals held in aquaria. We provided neither refuge for prey nor alternative food for predators (see Appendix A for methods and results).

To describe patterns of association among species in the field, we selected 20 shallow rocky reefs within the southeastern Galápagos Islands at Santiago, Santa Cruz, Baltra, and Seymour Islands (Sonnenholzner et al. 2009). Each of the 20 sites was treated as a single plot

ranging in size from 297 to 333 m² (Sonnenholzner et al. 2009). Ten sites are subject to high levels of fishing, and the remaining 10 are fishing exclusion zones, formally designated in 1998. However, due to uneven compliance with these regulations, we consider the “no-fishing” sites to be subject to low, but undefined, levels of fishing. Scuba divers quantified the density of urchins (band transects), lobsters (nighttime swims over a measured area), and hogfish (video transects), and characterized the habitat at each site (substrate type, location, current speed, wave exposure, island or islet, slope, and temperature; Sonnenholzner et al. 2009). Before collection, all urchins ($n = 3639$) were visually examined for the two eulimid snail species (*Sabinella shaskyi* and *Pelseneeria* spp.) and for commensal crabs. When commensal crabs or eulimid snails were found, they were removed with forceps and stored in labeled tubes assigned to their host urchin. Each urchin was also shaken in a plastic bag with brackish water. The wash was poured into a dish and any additional snails and crabs were counted and attributed to the host urchin. Eulimid snails ($n = 7472$) and crabs ($n = 1211$) were identified. We then examined urchins (diameter measured in centimeters with calipers) with a stereomicroscope for both snail species, as well as for spine epithelial lesions indicative of parasitism by *Sabinella shaskyi*. We dissected urchins to obtain an urchin gonad index ($GI = [G_m/U_m] \times 100$, where G_m was gonad mass and U_m was urchin wet mass). Variables related to individual urchins (gonad index, crab count, snail count, urchin size) were recorded for each urchin and averaged within each site. Variables used in the analyses are described in Appendix B: Table B1.

We used two types of general linear models (GLM). To analyze patterns in the distribution of eulimid snails and commensal crabs from an epidemiological perspective, each urchin was one sampling unit. Site was treated as a random effect in these GLMs. Another set of GLMs was used to describe average values at a site. This allowed us to analyze the standard parasitological measure of mean abundance per site (average number of parasites per host, including uninfected hosts [Bush et al. 1997]) for commensal crabs and each species of eulimid snail. To analyze variation in the ecological density (i.e., density per square meter) of commensal crabs and eulimid snails, we multiplied mean abundance by the density of urchins (resulting in the number of each species of snail and number of commensal crabs per square meter at each site, consistent with our observation that nearly all crabs and snails at a site were associated with urchins). However, because crabs and snails under rocks and in algae would be difficult to detect, we may have underestimated the density of crabs and snails.

In statistical analyses, we attempted to control for environmental variation among sites. As in Sonnenholzner et al. (2009), site variables (substrate, current, latitude, longitude, exposure, island size, slope, mea-

sured temperature at time of collection, average sea surface temperature, and conductivity, temperature, and depth sensor [CTD] temperature) were summarized by principal component analysis (PCA), and we used the first four principal components as covariates in statistical analyses (Appendix B: Tables B1 and B2). When we refer to the environmental effects of the principal components in the results, we note the factors with the highest loadings to provide context, but, because each principal component is an abstract composite of several variables, we refer the reader to Appendix B for the loadings.

We first transformed hogfish and lobster abundances to z scores to scale each equally (Sonnenholzner et al. 2009). Because initial investigations suggested that the effects of fish and lobster were additive (Sonnenholzner et al. 2009), we used the sum of the z scores to represent the density of large predators. This helped to simplify the resulting models, and the results did not differ qualitatively from those obtained when we treated large predators separately.

The similar response of the two eulimid snail species to commensal crabs resulted in a positive association between the abundances of the two snail species. However, given the different effects of the snails on the urchin host, we analyzed the two species of snails separately. Because a single commensal crab had the same effect on snails as several crabs (i.e., for urchins with at least one crab, there was not an effect of crab intensity on snails), the presence or absence of crabs (not the abundance of crabs) on an urchin was used as a factor in those analyses of snail abundance where each urchin was a unit of replication. We did not use MANOVA to test the two snail species simultaneously because the MANOVA contrast matrix (i.e., a comparison of the models for each species) was sometimes significant, suggesting that each species had a different association with at least some factors.

First-order interaction effects were initially entered into each GLM (with the exception of interaction effects between the principal components), but, to improve statistical power (needed for the low number of sites sampled), we discarded nonsignificant interaction and main effects ($P > 0.05$); subsequently, only significant main effects were kept in the model, except for main effects included in a significant interaction effect. For each analysis, we inspected residuals for normality with a normal quantile plot. If residuals were significantly non-normal in distribution, transformations were used (specifically, snails per urchin, crabs per urchin, and gonad index were square-root transformed and urchin density was log₁₀-transformed).

We used a path diagram (Wright 1934, Wootton 1994a) to illustrate our hypotheses about how the average number of parasitic snails per urchin interacted with fishing, large-predator density, urchin density, average crabs per urchin, and environmental factors (see Appendix B for details on path construction).

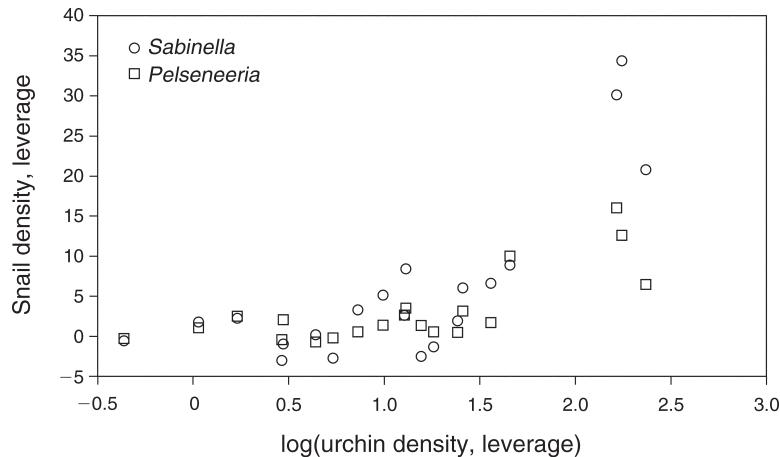


FIG. 2. Snail density increased with the density (measured as individuals/m²) of urchin hosts. Shown are leverage means per site following statistically controlling for crab density (i.e., for this and several other figures, we used leverage plots to account for other factors in the general linear model). See Appendix B (Tables B7 and B8) for statistics.

We report means (with standard errors) in the text. Our redundant approach of testing direct and indirect associations for a crab and two measures of two snails resulted in several similar GLMs. To streamline presentation, Appendix B contains the detailed statistical tables. In all cases, a two-tailed critical alpha of 0.05 was chosen, though we note that most of our predictions were explicitly one-tailed.

RESULTS

Associations between urchins and snails

The two snail species differed in prevalence and mean intensity. Across all sites, *Pelseneeria* snails infected 65% of urchins with an average of 2.5 (range 1–5) snails per infected urchin. In contrast, *Sabinella shaskyi* snails infected 18% of urchins with an average of 6.1 (range 1–63) snails per infected urchin. The number of snails per urchin increased with urchin size (Appendix B: Tables B3–B6), whereas the density of both snail species increased with urchin density (Appendix B: Tables B7 and B8), probably due to greater host availability (Fig. 2).

Eulimid snails had negative effects on infected urchins. Pathology to spines from *S. shaskyi* was associated with the number of snails on an urchin, particularly large female snails. *Sabinella shaskyi* snails (mean length 2.7 ± 0.005 mm) were found in association with severe inflammation, primarily at the top of blunt-tipped primary aboral spines of the interambulacral plates 3, 4, and 5. Infected spines were always shorter (mean = 2.8 ± 0.89 cm, $n = 1916$ infected spines from 522 urchins) than the noninfected neighboring spines (mean = 5.7 ± 0.91 cm, $n = 1916$ uninfected spines from the same 522 urchins). Infected spines also changed color (from dark brown to light purple). In contrast with *S. shaskyi*, *Pelseneeria* spp. (3.4 ± 0.007 mm in length) affected urchin reproduction. The gonad index of an

urchin decreased with the number of *Pelseneeria* spp. on that urchin (Fig. 3) and increased with urchin size and warm water PC 1 (Appendix B: Tables B9 and B10). The maximum of five *Pelseneeria* snails found on an urchin corresponded to the five gonads per urchin, suggesting gonad availability limited snail intensity.

Predation on snails

In the field, 22% of urchins hosted crabs and, for urchins with crabs, there was an average of 1.4 crabs (range 1–7 crabs) per host urchin. In aquaria, large crabs (but not small crabs) readily attacked and ate *Sabinella*

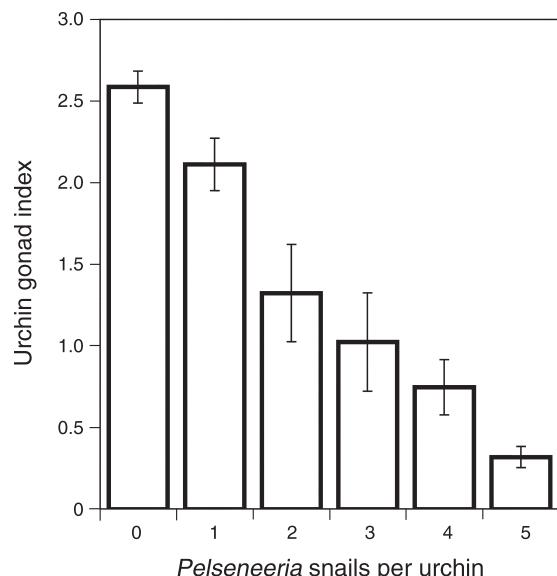


FIG. 3. Urchin gonad index (percentage of relative mass) declined with the abundance of *Pelseneeria* snails on an urchin. Shown are means with 95% confidence intervals over all sites. See Appendix B (Table B10) for statistics. Values plotted are untransformed data.

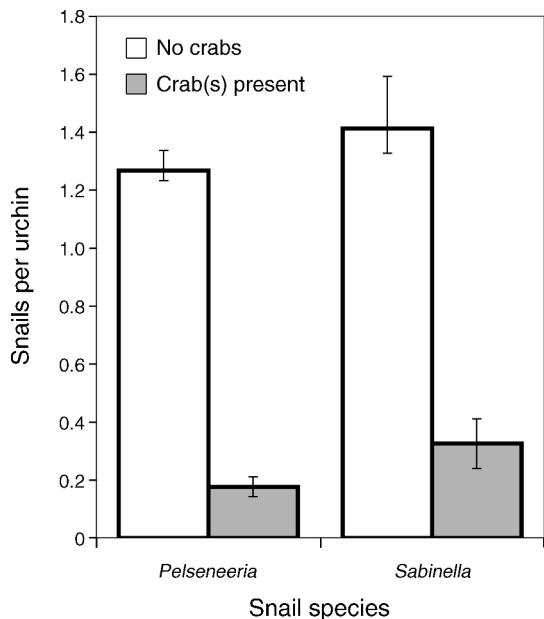


FIG. 4. Snail abundance (both species) declined if a crab was present on an urchin. Shown are means with 95% confidence intervals per site after statistically controlling for urchin size. See Appendix B (Tables B3 and B5) for statistics. Values plotted are untransformed data.

snails, the one species of snail available to us for feeding trials (Appendix A). Because *Pelseneeria* and *Sabinella* snails are similar in size and shell morphology, we conjecture that large crabs also consume *Pelseneeria* snails. Snails were sometimes successful at avoiding predation by fleeing (by floating on the surface of the water, an option not available in nature). In the field, eulimid snails of both species were seen with damaged shells indicative of predation attempts. The abundances of commensal crabs and eulimid snails were negatively

related at the urchin (epidemiological) scale (Fig. 4, Appendix B: Tables B3–B6). Similarly, for both eulimid snail species, density per square meter decreased as the density of commensal crabs per square meter increased (Appendix B: Tables B7 and B8).

Predation on crabs

We observed predation on crabs in aquaria (statistical details in Appendix A). Crabs moved from open ground to shelter, and from shelter to shelter, particularly at night, presumably to avoid predation. Crabs were significantly more likely to shelter under urchins than under rocks of similar size. Captive slipper lobsters, spiny lobsters, and hogfish readily ate large crabs deprived of shelter. Spiny lobsters and hogfish also ate small crabs deprived of shelter. Spiny lobsters and hogfish manipulated urchins to capture the large crabs hiding underneath, though these large predators were less likely to eat small commensal crabs on urchins. Spiny lobsters and hogfish also attacked urchins (thereby putting commensal crabs at risk of incidental predation), but slipper lobsters ignored urchins in the aquaria.

In the field, the average number of crabs per urchin declined with the increasing density of large predators (particularly at exposed, steep slopes, PC 3), was higher on larger urchins, and decreased with increased exposure (PC 4) and warmer water (PC 1; Appendix B: Table B11). The number of commensal crabs per square meter also declined with the increased density of large predators and with increasing exposure (PC 4; Fig. 5; Appendix B: Table B12).

The associations observed between fishing and commensal crabs ran opposite to the indirect associations between commensal crabs and large predators. The number of crabs per urchin was higher at fished sites, and increased with increasing urchin size, and more

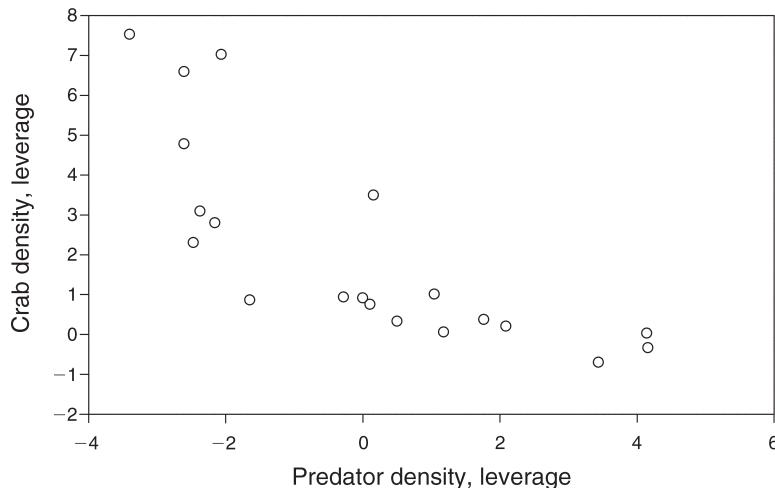


FIG. 5. The density of crabs (measured as individuals/m²) declined with increases in large-predator density (hogfish and lobsters). Shown are leverage means per site after statistically controlling for PC 4 (exposure to waves, southeast region, large rocks and fast currents). For this reason, negative values are possible for abundance. See Appendix B (Table B12) for statistics.

exposed habitats and steeper slopes (PC 3; Appendix B: Table B13). Commensal crab density per square meter was higher at fished sites, particularly at more exposed habitats and steeper slopes PC 3 (Appendix B: Table B14).

Indirect effects of large predators on snails

The number of *Pelseneeria* snails per urchin increased with the density of large predators (Appendix B: Tables B15 and B16), but the number of *Sabinella* snails per urchin increased with large-predator density only at sites with steep slope and high exposure (PC 3; Appendix B: Tables B17 and B18). The density of each snail species increased with large predators only at sites with steep slope and high exposure (PC 3; Appendix B: Tables B19 and B20).

Indirect effects of fishing on snails

Fishing was associated with fewer *Pelseneeria* snails per urchin (Appendix B: Tables B21 and B22), but the number of *Sabinella* snails per urchin declined with fishing only at warm sites (PC 1; Fig. 6; Appendix B: Tables B23 and B24). Interaction effects between habitat and fishing led to a net nonsignificant association between fishing and snail density. The density of *Pelseneeria* snails decreased with fishing only at sites in the northwest and with fast current and protection from waves (high PC 2 and low PC 4; Appendix B: Table B25). The density of *Sabinella* snails was not associated with fishing (Appendix B: Table B26).

The reduction of *Pelseneeria* snails per urchin in fished areas was associated with a higher mean urchin gonad index (Appendix B: Table B27). Multiplying urchin gonad mass by urchin density indicated that total gonad biomass density of the urchin population was three times higher at heavily fished than at lightly fished sites. Multiplying the back-transformed effect of *Pelseneeria* snails on gonad index by the mean abundance of *Pelseneeria* per urchin (Appendix B: Table B21) suggested that snails reduced the average urchin's reproduction by 35% at sites with low fishing pressure compared with only a 7% reduction at sites with high fishing pressure.

The path analysis was internally consistent with the covariance matrix and illustrates our best hypotheses for how fishing and large predators indirectly affect parasitic snails per urchin (Fig. 7; see Appendix B for details). One compound path followed the effect of fishing on large predators, large predators on crabs, and crabs on snails, resulting in a negative association between fishing and snails. In a second compound path, the average number of snails per urchin was positively affected by average urchin size, which was positively affected by large-predator density (presumably due to size-selective predation), which was negatively affected by fishing, leading to another negative compound path between fishing and snails. In a third path, urchin density was associated with the number of *Sabinella*

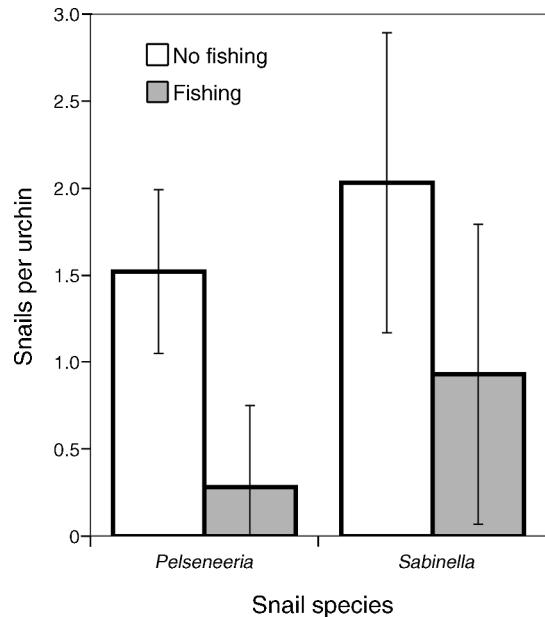


FIG. 6. The mean number of snails per urchin declined with increased fishing (Appendix B: Table B22 and B24). Shown are means with 95% confidence intervals. Values plotted are untransformed data.

snails per urchin, adding a positive path between fishing and *Sabinella* snails. With two negative paths, the average number of *Pelseneeria* snails per urchin was hypothesized to be strongly negatively associated with fishing. With two negative paths and a positive path, the indirect effect of fishing on *Sabinella* snails was hypothesized to be less strongly negative, a prediction consistent with the direct observations (Fig. 6).

DISCUSSION

We found that the enemy (fisher) of the enemies (fish and lobster) of the enemy (crab) of the urchin's enemy (snail) was the urchin's friend. Although this version of the Arabian proverb lacks the symmetry of the original, it effectively illustrates an additional indirect path by which fishing favors urchins. Fishing appears to affect parasitic snails through a series of indirect effects involving urchins, fish, lobsters, and commensal crabs. Where fishing was low, urchin density was relatively low and there were many parasitic snails per urchin. In heavily fished areas, urchin densities were higher and the number of parasites per urchin was lower. This led to a redistribution of the parasitic snail population, but not to a significant net change in the density of snails per square meter (the actual effect varied by habitat). One possible explanation for the results is as follows. Fishing, by removing large predators, indirectly increases the density of urchin hosts and the density of the commensal crabs that prey on snails, leading to many lightly infected urchins. Although fishing indirectly decreases the number of snails per urchin, the parallel increase in

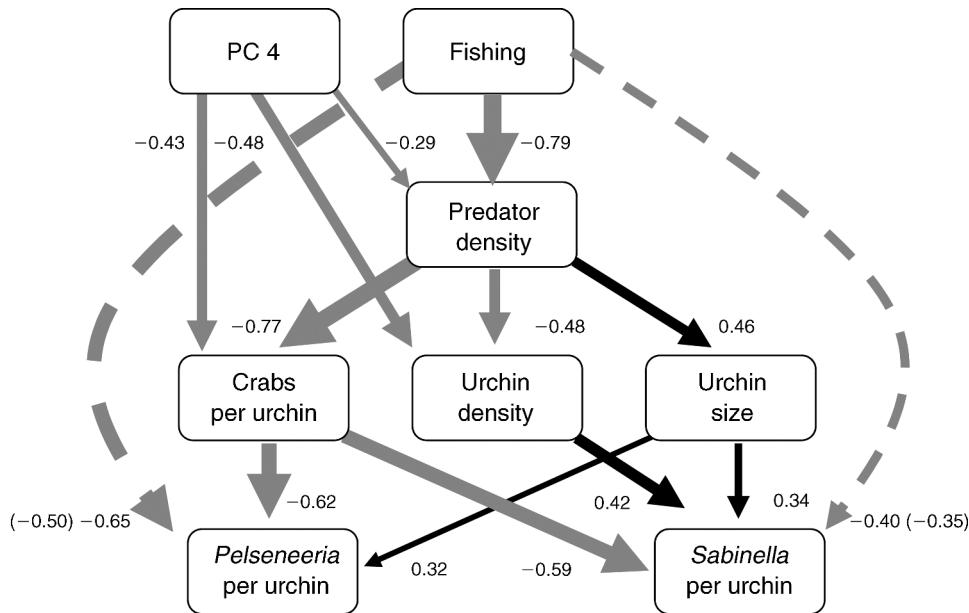


FIG. 7. Path diagram of fishing, large-predator density, pencil urchin density, crabs per urchin, and *Sabinella* and *Pelseneeria* snails per urchin. Black arrows are positive associations; gray arrows are negative associations. Coefficients next to paths are standardized beta weights and correspond to the width of the arrow. Solid arrows indicate direct effects. Dashed arrows indicate the observed indirect association between fishing and snails. Observed correlations between fishing and snails and large predators and snails were consistent with indirect estimates from the compound paths (in parentheses), and a goodness-of-fit test indicated the path was a reasonable hypothesis of the system (See Appendix B).

urchin density means that there are still many snails per square meter.

The correlational nature of our study opens the possibility that variation in the distribution of the species we measured might not be entirely due to trophic interactions as we have suggested. For instance, putative predators and their prey might not recruit to the same sites, so that what appears to be a negative species interaction is simply opposite patterns of spatial heterogeneity in recruitment or habitat use driven by environmental factors (Wieters et al. 2008). Ideally, we would experimentally remove each species from the system and observe the corresponding change in other species (Wootton 1994a, Gotelli and Ellison 2006). Unfortunately, caging, removal, and addition manipulations are difficult to accomplish in this system due to environmental factors. Though habitat and recruitment associations might have led to spurious correlations, they can also obscure patterns. Most notably, fishing effects would be more difficult to detect if habitat or recruitment limits species abundances. For these reasons, we considered environmental covariates in our analyses.

Several environmental factors explained variation in species distributions, helping us better isolate the effect of species interactions. Species interactions can vary in space due to environmental factors that promote or impair predation (Menge and Olson 1990). For example, recruitment limitation might limit prey densities independent of predator densities, prey might have better

access to refuges in some habitats, or disturbance might impair predator success. In our study, the indirect effect of fishing on snail density depended on environmental variables. Certain environmental conditions favored the negative compound path from fishing to snails that went through crabs, making it more likely that fishing would reduce snails on urchins. The indirect effect of fishing on crabs was stronger at exposed sites with steep slopes (PC 3) because the effect of predators on crabs was stronger at these sites (perhaps due to fewer alternative refuges for crabs). This carried over to a stronger indirect effect of predators on snails. Other environmental conditions favored the positive compound path from fishing to snails that went through urchins. The extent that fishing indirectly increased urchin density increased with fast currents (PC 2) and decreased with exposure to waves (PC 4; Sonnenholzner et al. 2009). Strong currents and exposure are known to affect other, similar species interactions in this system (Witman et al. 2010). These are the same sites where fishing did not lead to a reduction in *Pelseneeria* snail density.

Unfortunately, a detailed food web is not available for this system. Although our laboratory experiments point to hogfish and spiny lobsters as potential predators of crabs, there are many other important consumer–resource interactions in the system (Witman et al. 2010). Slipper lobsters might consume urchins in the wild, even though they did not forage actively in our laboratory experiments. Alternatively, hogfish and spiny lobsters might have only eaten crabs in the laboratory

because they were desperately hungry or because the crabs lacked refuges in the aquaria. In addition, crabs might only have eaten snails due to our confining them together in small vials. Observations of predation in aquaria do not guarantee predation rates or preferences in the field, only that these predators are capable of eating the prey offered to them. Still, observations in aquaria were wholly consistent with our limited field observations of trophic interactions in the field.

Although we might expect snails to amplify to high intensities in dense urchin populations, we were not able to measure this effect at the appropriate spatial scale. In marine systems, larval dispersal can obscure relationships between local reproduction and density for both host and parasite (Kuris and Lafferty 1992). The potential for eulimid veliger larvae to disperse broadly could prevent a local build-up by snails on dense urchin populations; this would explain why the number of snails per urchin did not increase with urchin density (though there are many possible explanations for this pattern such as competition among snails or frequency-dependent transmission).

Similarly, although we cannot infer negative effects of eulimid snails on urchin density at the scale of our study, our other observations suggest that eulimid snails could affect urchin populations at larger spatial scales. The reduction in fecundity associated with *Pelseneeria* spp. has obvious fitness consequences for individual urchins with potential population-level effects. However, an effect of reduced fecundity on urchin recruitment would only be observable at broader scales than our sites, because sea urchin larvae disperse over long distances (Lessios et al. 1999, Witman et al. 2010). It is unknown how *S. shaskyi* might affect urchins at the population level, but spine reduction and loss (Metz 1994, Sonnenholzner and Molina 2005) would appear to increase susceptibility to predation and energetic costs for spine repair (Heatfield 1971, Denny and Gaylord 1996).

Many parasites have predators (Johnson et al. 2010). Notably, specialized cleaner symbionts can control ectoparasite populations through predation (Grutter 1999), predators usually consume the parasites of their prey (Lafferty et al. 2006), and predators often eat the free-living stages of parasites (e.g., Kaplan et al. 2009). However, the relative importance of predation vs. host availability for the distribution and abundance of parasites is relatively unknown. Our study provides evidence that predation on parasites can be more important than host availability for determining parasite density. By preying on parasitic snails, the commensal crab engages in a facultative mutualism with its host urchin. Some fishes and invertebrates shelter under urchin spines (Quinn et al. 1993, Hartney and Grorud 2002), but we know of no other example in which the guest “pays its rent” to the urchin. This mutualism is most similar to that seen in the crab *Mithrax sculptus*, which gains shelter from large predators in a branching

coralline alga and repays the algae by eating epiphytes that would otherwise foul the host plant (Stachowicz and Hay 1996).

The field of conservation biology often views infectious organisms as a sign of imbalance in an ecosystem, emphasizing how stressors like fishing (Harvell et al. 1999) and loss of biodiversity (Keasing et al. 2010) decrease ecosystem health by promoting infectious disease. We expected our study might parallel reports that fishing large predators increases infectious diseases in urchin populations (Lafferty 2004), but the complexities inherent even in our simplified path diagram indicate how difficult it is to predict the net effect of fishing on parasitism without an understanding of the food web. If commensal crabs were absent from the system, fishing could have had the positive effects on parasitism we had initially expected. In any case, eulimid snails appear to be a well-adapted, integral part of the Galápagos food web, not an undesirable aberration. Overall, our results are consistent with the perspective that parasites often depend on rich and functioning ecosystems and that perturbations like fishing can make it more difficult for them to persist (Dobson and May 1987, Lafferty 1997, Lafferty and Kuris 1999, Huspeni and Lafferty 2004, Hechinger and Lafferty 2005, Hudson et al. 2006, Wood et al. 2010).

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APPENDIX A

Confirmatory tank predation experiments conducted from 10–20 July 2010, on site at the Charles Darwin Research Station, Isla Santa Cruz, Galápagos Islands, Ecuador (*Ecological Archives* E092-197-A1).

APPENDIX B

Statistical tables describing relationships among species from 20 field sites in the Galápagos (*Ecological Archives* E092-197-A2).