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Refugia and top-down control of the pencil urchin *Eucidaris galapagensis* in the Galápagos Marine Reserve

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ABSTRACT

Although sea urchins can strongly influence the structure of benthic communities and are abundant in the Galápagos Islands, factors mediating predation on urchins have not been studied experimentally. Here, we examine how habitat structure and behavioral patterns of prey influence predation on the pencil urchin *Eucidaris galapagensis*, an abundant grazer in rocky subtidal habitats. Results indicate that the distribution, abundance and body sizes of *E. galapagensis* vary predictably by habitat in the central Galápagos. Urchins were five times more abundant and significantly smaller in rubble than in exposed ledge habitats. We thus hypothesized that rubble habitats provide a refuge from predation, and conducted tethering manipulations using small and large urchins as prey. Predation by the hogfish, *Bodianus diplotaenia*, triggerfishes, and the sea star *Pentaceraster cumingi*, was significantly higher in exposed than in rubble habitats for small urchins, indicating that rubble habitats represent a refuge. In addition, urchin activity over a 24-hour period indicated that *E. galapagensis* were significantly more abundant on exposed substrate at night than during the day as they emerged from refugia at dusk. Since the fish that prey on *E. galapagensis* are predominantly diurnal, we suggest that the nocturnal activity patterns of the urchins represent a predator avoidance strategy. These results underscore the importance of considering spatial refugia and prey behavior in investigations of top-down control of sea urchins in the Galápagos Marine Reserve.

1. Introduction

Predation can determine the structure of biological communities, though several processes can increase or dampen its influence on communities (Carpenter et al., 1985). Consumers from higher trophic levels regulate lower-food web components through 'top-down' control when predation and herbivory alter the distribution and abundance of prey species either directly or indirectly (Burkepile and Hay, 2008; Guidetti et al., 2005; Pace et al. 1999). Direct consumption reduces prey populations, but predation can also alter species abundances and community structure through trophic cascades when the effects of predation propagate down two or more trophic levels (Hairston et al., 1960; Paine, 1980; Strong, 1992). However, the relative importance of predation as a process that structures communities depends on how efficiently a predator can exploit its prey— necessitating an understanding of the conditions that promote, eliminate, or dampen the effects of top-down control (Power, 1992). Factors that mediate the effects of predation, such as the availability of spatial refugia and prey behavior, play an important role in altering predator–prey dynamics (Byrnes et al., 2006; Duffy and Hay, 2001; Nelson and Vance, 1979; Witman, 1985).

Prey refugia, including any strategy, habitat, or behavior capable of decreasing the risk of predation and preventing overexploitation of prey (Ives and Dobson, 1987; Sih, 1987; Sih et al., 1988) can alter predator–prey dynamics and forestall trophic cascades (Duffy and Hay, 2001; Nelson and Vance, 1979; Witman, 1985). Behavioral responses by prey, such as predator-avoidance strategies, can reduce their risk of mortality and, therefore, dampen the effects of top-down control (Heithaus et al., 2008; Schmitz et al., 1997; Siddon and Witman, 2004). Prey can hide or switch their patterns of habitat usage to areas where their predators are absent, interrupting predator–prey interactions and altering the distribution and foraging patterns of prey (Madin et al., 2010; Sih et al., 1988). In support, theoretical and empirical studies indicate that spatial refugia, such as habitat complexity, are critical for the persistence of prey (Gause, 1934; Huffaker, 1958). For instance, spatial refugia are important for the persistence of sea urchin populations in rocky reefs in the Gulf of Maine (Witman, 1985), in the Mediterranean Sea (Hereu et al., 2005; Sala, 1997), in tropical rocky intertidal habitats (Menge and Lubchenco, 1981), and in Kenyan coral reefs (McClanahan, 1998). In addition to altering their spatial patterns of habitat use to reduce their risk of mortality, prey may alter their patterns of activity

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becoming active when their predators are inactive or absent, potentially representing a temporal refuge from predation (Power, 1992).

The presence of prey refugia and its function in dampening top-down control is particularly important for benthic invertebrates (e.g. sea urchins) in tropical systems like Galápagos Islands where rates of predation are high (Vermeij, 1978). Since urchins can be important prey species and consumers of algae, their addition or removal can cause drastic changes in communities (Paine, 1980). As important grazers, sea urchins can regulate the productivity and structure of benthic algal communities (Brandt et al., in press; Guidetti and Dulcic, 2007; Hereu et al., 2005; Paine and Vadas, 1969; Sala et al., 1998), and at high densities, they can convert foliose algal assemblages to urchin barrens (Hereu et al., 2005; Witman, 1985). For these reasons, understanding the direct and indirect factors – such as predation and availability of prey refugia – that influence the dynamics of sea urchin populations is important.

Eucidaris galapagensis is the most abundant sea urchin species in the central Galápagos archipelago (Brandt and Guarderas, 2002). As an omnivore, *E. galapagensis* consumes algae (Brandt, 2003; Glynn and Wellington, 1983; Irving and Witman, 2009; Ruttenberg, 2001), barnacles (Glynn, 1994) and corals (Glynn et al., 1979), and at high densities it affects benthic community structure (Brandt, 2003; Glynn and Wellington, 1983; Witman et al., *unpublished data*). However, predators may decrease the abundance of *E. galapagensis* and alter its distribution among habitats as it is an important prey for several species, including the slipper lobster *Scyllarides astori,* the spiny lobster *Panulirus penicillatus*, the Mexican hogfish *Bodianus diplotaenia*, and the triggerfishes *Balistes polylepis* and *Pseudobalistes naufragium* (Glynn and Wellington, 1983; Hearn, 2006; Ruttenberg, 2001; Witman et al., *unpublished data*). Recognizing that different types of hard substrate habitats such as rubble rocks and smooth exposed ledges were available to urchins in Galápagos subtidal rocky reefs, we examined the potential for spatial refugia and the ability of urchins to switch habitats (prey behavior) to mediate predation on *E. galapagensis.* Specifically, we addressed four main questions: 1) Do the abundance and the body size of *E. galapagensis* differ among habitats in the rocky subtidal zone? 2) Do rubble habitats provide a refuge from predation for small and large urchins? 3) Do urchins have a size escape from predation? And finally, 4) Does the abundance of *E. galapagensis* on exposed substrate change on a diel basis?

2. Materials and methods

2.1. Study sites

This study was conducted at five subtidal sites in the central Galápagos archipelago, located 965 km off the coast of Ecuador. Situated around Santa Cruz and Floreana Islands, all sites (Baltra, Rocas Gordon, Guy Fawkes, Rocas Beagle, and Champion islands) occur within the Galápagos Marine Reserve. Sites were chosen based on comparable bottom topography and distribution of habitat types (see Fig. 1. of Witman et al., 2010 for site locations). Within each site, research was conducted using SCUBA during May–July 2007, January 2008, and June–July 2008 in three common hard substrate habitats: 1) vertical rock walls ("wall habitat" hereafter), 2) patches of rock rubble on ledges ("rubble habitat" hereafter), and 3) horizontal-gently sloping substrate ("exposed habitat" hereafter).

2.2. Urchin abundance and body size patterns

To ascertain patterns of habitat use, the densities and body sizes of *E. galapagensis* were surveyed at all sites in May–June 2007, January 2008, and June–July 2008 at depths between 6 and 16 m. The sampling procedure consisted of haphazardly placing a 625 cm^2 quadrat on the substrate 7–171 times to quantify the densities and test diameter of urchins in the wall, rubble and exposed habitats. Urchin densities were quantified in rubble and exposed habitats at all five sites, and compared using a two-way ANOVA test, with habitat and site as fixed factors. Urchin body size-frequency distributions were constructed for wall, rubble and exposed habitats; however, in exposed habitats, they were created only at three sites (Baltra, Rocas Gordon and Champion), as urchin densities were too low at the other two sites. Given that sample sizes were low for the exposed habitats, Kolgomorov–Smirnov and T-tests were only applied to compare urchin body size-frequency distributions between rubble and wall habitats within sites.

2.3. Predator abundance

Band transects were conducted to estimate the abundance of potential predators of *Eucidaris galapagensis,* including hogfish (*B. diplotaenia)*, triggerfish (*B. polylepis, P. naufragium)* slipper (*S. astori*) and spiny (*P. penicillatus)* lobsters (Hearn, 2006; Ruttenberg, 2001; Martínez, 2000; Witman et al., 2009; Witman et al., *unpublished data*), and the sea star, *Pentaceraster cumingi* (this study). For predatory fish, one 50×3 m band transect was performed at 6 and 15 m depths at the sites where experiments were conducted (Guy Fawkes, Rocas Beagle and Baltra) in June–July 2008 and again in January 2009 using the methods of Edgar et al. (2004a, 2004b). In addition, fish were counted in eleven 30×5 m band transects at 10 m depth at Baltra, in January 2008. The total numbers of individuals greater than 20 cm were recorded for the entire transect area (150 m^2). Data on the abundance of predatory sea stars at the study sites was taken from an ongoing benthic monitoring program (Witman et al., 2010, *unpublished data*). Sea stars were counted in three replicate 10×1 m band transects at 6 and 15 m depths at each site. Surveys of predator abundance were usually conducted during the same month of the urchin population surveys and predation experiments, and are used as supplemental observations to infer some of the causes of differences in predation between sites.

2.4. Predation experiments

We tested the hypothesis that the rubble habitat functions as a spatial refuge from predation for *E. galapagensis* at 3 sites (Baltra, Rocas Beagle Guy Fawkes), by conducting tethering manipulations using urchins as prey to compare relative predation rates between rubble and exposed habitats (Aronson and Heck, 1995; Aronson et al., 2001; Peterson and Black, 1994). Data from surveys (see Results) revealed that the frequency of test diameters for *E. galapagensis* was bimodal, with modes centered at 2–3 cm and at 5–6 cm. Consequently these two size classes were used in the predation experiments. Small urchins (2–3 cm) were tethered in an experiment that ran ~24 h at each of the three sites, while the experiments with large urchins (5–6 cm) consisted of two 6-day trials at Baltra and one 24-h trial at both Guy Fawkes and Rocas Beagle. For the experiments with large urchins, data from Guy Fawkes and Rocas Beagle were pooled due to the low sample size.

To minimize artifacts in the tethering experiments, each experimental unit used a natural substratum, which consisted of a flat volcanic cobble (approximately 240 cm^2 top surface area) collected from the area. A small eyebolt was attached to the center of the cobble with marine epoxy (Koppers Splash Zone compound). A single urchin was tied to the eyebolt with nylon twine onto its own cobble (Fig. 1). All urchins were collected prior to the experiment and a non-invasive "harness" method was used to tether the urchins. Exploiting the wide interambulacral areas of *E. galapagensis*, the harness was made by tying two loops of twine around interambulacra and secured by a square knot. The use of a standardized substrate and a non-invasive tethering procedure enabled urchins to move around on the top of the cobbles (Fig. 1) and prevented injuries to