Sea Urchins on the Move: Distribution Change of Echinometra in Mo'orea French Polynesia

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Abstract

The island of Mo'orea in French Polynesia functions as a model system to study the biological and ecological concept of niche differentiation, whereby two or more species are forced into different habitats so as to avoid competition with each other. In the waters surrounding this island, two species of sea urchin within the genus Echinometra live in distinctly different habitats. Previous studies document Echinometra sp. A located exclusively on the fringing reef and Echinometra mathaei located exclusively on the barrier reef. This study investigated three short-term factors (available space, nutrient supply, and predation) that might be influencing this spatial distribution. None of these factors appear to be causing the separation of E. sp. A and E. mathaei. In fact, they all support the distributional findings of this study that showed non-mutually exclusive distribution data on the two reef types.

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Introduction

Coral reefs consist of a complex habitat wherein a variety of organisms cohabitate, interact, and compete for resources. The reef ecosystem supports a huge number of species from many taxonomic groups and the diversity of organisms thus rivals even tropical rainforests (Connell 1978). This large number of organisms living together in one environment, and often in close proximity, naturally results in inter-species and intra-species competition over available resources. A huge variety of organisms can function peacefully together in an ecosystem for several reasons. One of these reasons is the concept of niche partitioning, an ecological term denoting the natural pressure of the environment that drives two species into separate resource use, resulting in coexistence (Queenborough et al. 2009). The natural pressure might be limited food sources or dwelling spaces, anything essential for an organism's existence that could be sought out by multiple species (Bourguignon 2009).

Inter-species competition can at first be looked at from a conceptual and statistical perspective through the Lotka-Volterra equation. Proposed in the mid-1920s by Alfred J. Lotka and Vito Volterra, the equation describes the interactions between two species as a mathematical function. The growth of a population in time, represented as a derivative, depends on the availability of prey and the pressure of predators on that species. This equation can be extrapolated to show that two competing species can coexist when intra-specific competition is greater than inter-specific competition (Armstrong and McGehee 1980). The Lotka-Volterra equation supports the concept of niche differentiation because as two species are forced into separate niches, the inter-specific competition decreases.

When considering niche partitioning in reality, it is interesting to begin studying inter-species interactions on islands because they can function as model systems for larger, more complex continental habitats (Gillespie and Clague 2009). The waters of the Indo-West Pacific are particularly rich in species diversity and the many islands provide study areas for niche partitioning (Jones 2009). The island of Mo'orea, in the archipelago chain of the Society Islands, is a high, volcanic island located 17 km northwest of Tahiti. A fringing coral reef hugs the shoreline and a deep lagoon channel separates this reef from the barrier reef, a more distal coral habitat that circles the island, like a picture frame (Darwin 1842). There are at least two species of sea urchin within the genus Echinometra living on the island of Mo'orea. (Chris Meyer, pers. com.). These two species are closely related (Hiratsuka and Uehara 2007), which suggests that they require similar nutrient and environmental needs, yet they inhabit the same lagoon without outcompeting one another.

Previous studies of Echinometra distribution indicated mixed conclusions. One study in Mo'orea showed Echinometra distribution to be influenced by elevated levels of carbonate concentrations in the water (Adjeroud 1997). In this study, two places with high levels of carbonates were found- the fringing reef of the lagoon and the barrier reef- and particularly high urchin population densities corresponded to

these two places. Another study in New Caledonia showed the habitat of a different sea urchin, Diadema Savignyi, could be explained by sediment type rather than biotic cover; increasing densities occurred across habitat with larger sediment sizes and decreasing coral complexity/macrophyte cover. In contrast, Echinometra distribution in this study showed no correlation to habitat variables (Dumas et al. 2006).

Sediment type, however, is just one factor influencing Echinometra distribution. Other variables such as nutrient availability play a vital role in determining where these urchins can live. The study by Yuji Hiratsuka and Tsuyoshi Uehara in 2007 showed that, despite the morphological and physiological differences among the four species of Echinometra in Japan, the feeding modes are essentially the same. All four species of Echinometra eat primarily plant material, either by benthic grazing or filter feeding. The four species are, however, found in different places along the coral reef habitat. Echinometra mathaei live in the upper subtidal and lower intertidal areas whereas E. sp. C and E. oblonga live only in the upper intertidal zone.

By feeding on algae, sea urchins control algal overgrowth that, if allowed to proliferate, would cover coral surfaces, smothering and killing the coral. In this way, sea urchins act as important keystone species within an ecosystem. Through their burrowing and feeding behaviors, urchins moderate the balance between coral erosion and algal growth and, in addition, they are generally considered sensitive bio-indicators of various contaminants (Done et al. 1991). Beyond acting as a tool to study general coral reef ecosystem health, Echinometra offer an interesting system for studying niche partitioning in Mo'orea, French Polynesia. The two documented species present in Mo'orea (E. mathaei and E. sp. A) appear to live in distinct habitats. In a previous study, E. mathaei lived primarily on the barrier reef whereas E. sp. A lived along the fringing reef (Collisson 1995). If the two species do truly inhabit separate habitats, the question remains what biotic and abiotic factors influence this spatial differentiation?

This study examined the population densities of E. mathaei and E. sp. A at three different sites on the fringing and barrier reefs of Mo'orea, to address the following questions: Are the urchins displaying classic niche partitioning? What limiting factors in the environment control this partitioning? Can they both live in the same habitat, but one is outcompeted by the other? Are there places where the two species coexist together and, in what way? Do they compete for a food source?

Methods

Although there are many factors that might influence the niche differentiation of Echinometra in Mo'orea, French Polynesia, due to limited time, this project focused on three major factors: nutrient supply, living space, and predation.

Population Distribution

To assess the distribution of Echinometra, this study investigated three sites in Mo'orea, French Polynesia (Fig. 1). Each site was unique and therefore offered a statistically powerful support yet the three were common in the inclusion of a fringing reef and a barrier reef within each site.

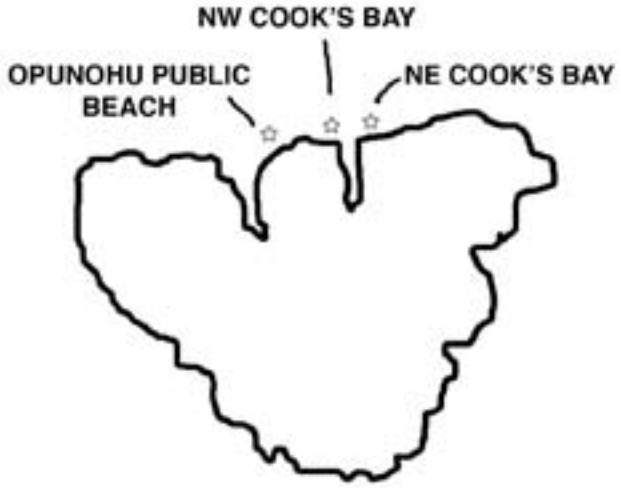

Fig. 1: A map of the island of Mo'orea showing the three study sites. Site A: NE COOK'S BAY; Site B: NW COOK'S BAY; Site C: OPUNOHU PUBLIC BEACH.

Site A. The first site, the northeast side of Cook's Bay, is located on the northern side of the island (17° 29′ 11.71″ S, 149° 49′ 03.52″ W). The fringing reef hugs the shoreline of what was once commercial property but is now abandoned and uninhabited. Very little wave action disturbs this reef that is composed largely of dead Porites russ corals overgrown with turf algae. The water depth is relatively shallow, only 1-2 m in most places. The barrier reef on the northeast side of Cook's Bay is, however, a very turbulent habitat as a result of a strong current and aggressive wave action. Water depth ranges from approximately 5 m to 10 m, in some places. The benthic composition is sandy, punctuated with coral heads spaced roughly 15 m apart. The corals are alive and healthy for the most part.

Site B. The second site, the northwest side of Cook's Bay, is located directly west from the first site, still at the mouth of the bay. (17° 29′ 11.32″ S, 149° 49′ 29.40″ W.) Visibility on the fringing reef is relatively poor in comparison to site A, and the waters contain floating Turbinaria. Several different species of coral populate the ocean floors but many are dead and

covered in turf algae. The barrier reef on the northwest side of Cook's Bay contains many live coral heads, mostly Porites loboda and P. australiensis. The water depth ranges from 1-10 m and, like the first site, the current and wave action are both strong.

Site C. Finally, the third study site is located even further west from the other two sites (17° 29′ 28.34″ S, 149° 51′ 04.23″ W). The shoreline is a public beach, often filled with many people and, perhaps as a result, the fringing reef contains mostly dead P. russ corals. Water movement is minimal and the depth ranges from 1-5 m. The barrier reef at the third study site contains live, healthy P. loboda, P. australiensis, and Pocillopora sp. coral. Wave action is constant and water depth ranges from 2-12 meters.

At each of the three aforementioned sites, I counted urchin population density. Transect lines marked the boundaries of a 10 m x10 m square range--the counting zone. Using a dive slate, I tabulated each E. mathaei and E. sp. A seen during a ten-minute counting period. Then, I repeated this counting process three times in three different, randomly selected, 10 x 10 m zones along the fringing and barrier reefs. Using two-way ANOVA statistical analysis, I determined whether urchin species distribution between the fringing and barrier reefs was non-random. Finally, I qualitatively compared my data with the density values of previous studies.

Habitat Assessment

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Transplant Experiments

I set up exclusion experiments to investigate predation of urchins. The day before the experiment, I sewed cages to cover individual coral heads with 28 kg-strength fishing line and 1 cm-square mesh netting. At the open edge of each cage, I sewed a rope in to cinch tight around the coral heads, thus preventing any predators from getting through the cage and also containing all urchins and other organisms within the cage. I collected a study sample of 30 E. sp. A from the fringing reef on the NW Cook's Bay site. After I removed these urchins from the water, I marked the tips of the spines with yellow nail polish, and allowed them to dry for 5-10 minutes so I could later recognize the individuals in this experiment. Once dry, I placed the urchins back in a 1 m-deep seawater tank overnight to standardize or equilibrate the study sample.

The following morning at 10:30am I transported the urchins to the barrier reef via kayak. I placed three marked urchins, randomly and evenly spread apart, on a coral head that was immediately covered with a mesh cage. I repeated this process five times with five different coral heads separated approximately equidistant along a line extending parallel with the barrier reef crest. In this manner, I therefore covered 15 urchins, three on each of five coral heads, with mesh cages. Likewise, I placed 15 additional urchins, three on each of five coral heads, without mesh cages.

For each urchin placed on coral, I held it in place for 10 seconds, allowing the urchin to attach to the substrate. A yellow ribbon tied around the coral heads without mesh caging (but with marked urchins) indicated the presence of study organisms.

Twenty-four hours later, I returned to the barrier reef site to examine caged and un-caged coral heads for the presence of marked urchins. I analyzed these data by comparing the averages of urchin survival on caged coral and on un-caged coral, using two-way ANOVA.

I repeated this entire exclusion experiment in an identical manner for all controllable factors except that I transplanted the 30 urchins taken from the fringing reef to a different site on the fringing reef, in a caged and un-caged manner. The purpose of this second experiment was as a further control for the predation studies. It was also analyzed by ANOVA. This statistical analysis also provided a mean for comparing the differences in survival rate on the fringing reef compared to on the barrier reef.

Feeding Preference Experiments

In order to assess the feeding preference of E. sp. A, I positioned 21 individuals in the center of separate 1 m square tanks with cycling seawater. Four different species of algae were in each tank, one in every corner. An approximately 7 cm-diameter clump of Halimeda sp. was in the northeast corner of the tank and an equal sized piece of Padina sp. was in the northwest corner of the tank. The southwest corner contained an equal sized clump of Dictyota bartayresiana Lamouroux while the southeast corner contained a 7 cm-diameter chunk of coral overgrown with various microalgae, or other small, filamentous turf algae. I noted the position of the urchin and its activity (that is, whether it was feeding on the algae or not) every hour from 13:00 to 01:00. I later analyzed these data using a $\chi 2$ statistical analysis to investigate whether the urchins fed on different species of algae non-randomly.

Results

	Opunohu Public Beach	NW Cook's Bay	NE Cook's Bay
Fringing Reef	E. mathaei: 0 E. sp. A: 212	E. mathaei: 4 E. sp. A: 220	E. mathaei: 3 E. sp. A: 106
Barrier Reef	E. mathaei: 43	E. mathaei: 48	E. mathaei: 53

Table 1: The total population counts of E. mathaei and E. sp. A on the fringing reef and barrier reef of three independent sites, as measured in three independent samples.

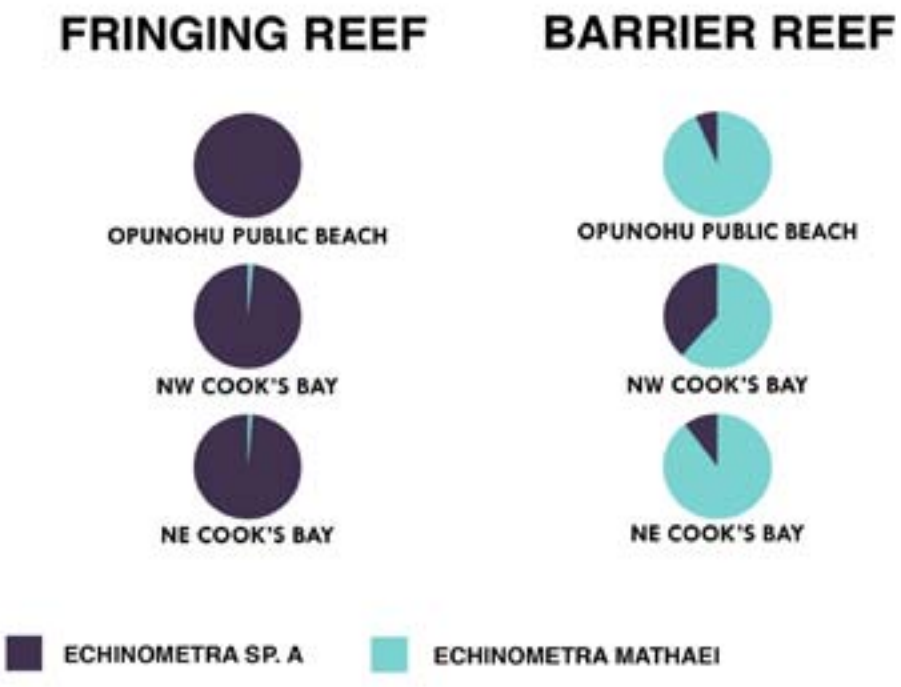

Fig. 2: The distributional findings of E. sp. A and E. mathaei shown in proportion to each other on the fringing and barrier reefs, as studied at three independent sites.

Population Distribution

I counted more E. sp. A individuals on the fringing reef than E. mathaei individuals on the barrier reef, for all three sites (Table 1). E. mathaei populated primarily the barrier reef while E. sp. A populated primarily the fringing reef (Fig. 2). The distributions of the two species overlapped. These non-mutually exclusive distribution data were most evident at the NW Cook's Bay barrier reef where only 62% of the total number of both species were E. mathaei (Fig. 2). However, the trend of non-random distribution between the two reef types was significant (F ratio=234.8, df=5, p<0.0001).

Habitat Assessment

Only E. sp. A inhabited P. russ coral and only E. mathaei inhabited Pocillopora sp. coral (Fig. 3). Both E. sp. A and E. mathaei lived in P. loboda and P. australiensis corals, albeit on different reef types (Fig. 3). The abundances of E. sp. A and E. mathaei were not the same across coral types (x2 value= 124.5, df=3, p<.0001).

Urchins of both types lived in areas with various species of algae, particularly turf algae (Fig. 4). There was significantly greater coverage of Turbinaria ((t-test= -9.34, df=238, p<0.0001), Halimeda (t-test=3.94, df=237, p<0.0001), and encrusting coralline algae (t-test= 6.85, df=237, p<0.0001) on the barrier reef compared to on the fringing reef. There was significantly less coverage of Padina (t-test= 6.25, df=238, p<0.0001) and Amphiroa (t-test= 3.1, df=237, p<0.0021) on the barrier reef compared to on the fringing reef. The percent coverage of both turf algae and algae-free coral on the fringing reef were not significantly different from the percent coverage on the barrier reef (p>0.05).

Transplant Experiment

The average survival rate of urchins placed on caged coral heads was significantly greater than the average survival rate of urchins placed on coral heads with no cages for both the barrier and the fringing reefs (df=1, F ratio= 15.13 p<0.001). In contrast, the differences in the survival rate on the barrier reef compared to the survival rate on the fringing reef were not significantly different (p>0.05). The survival rate of E. sp. A depended on whether the urchin was covered with a cage, but not on which reef the urchin was transplanted to (Fig. 5).

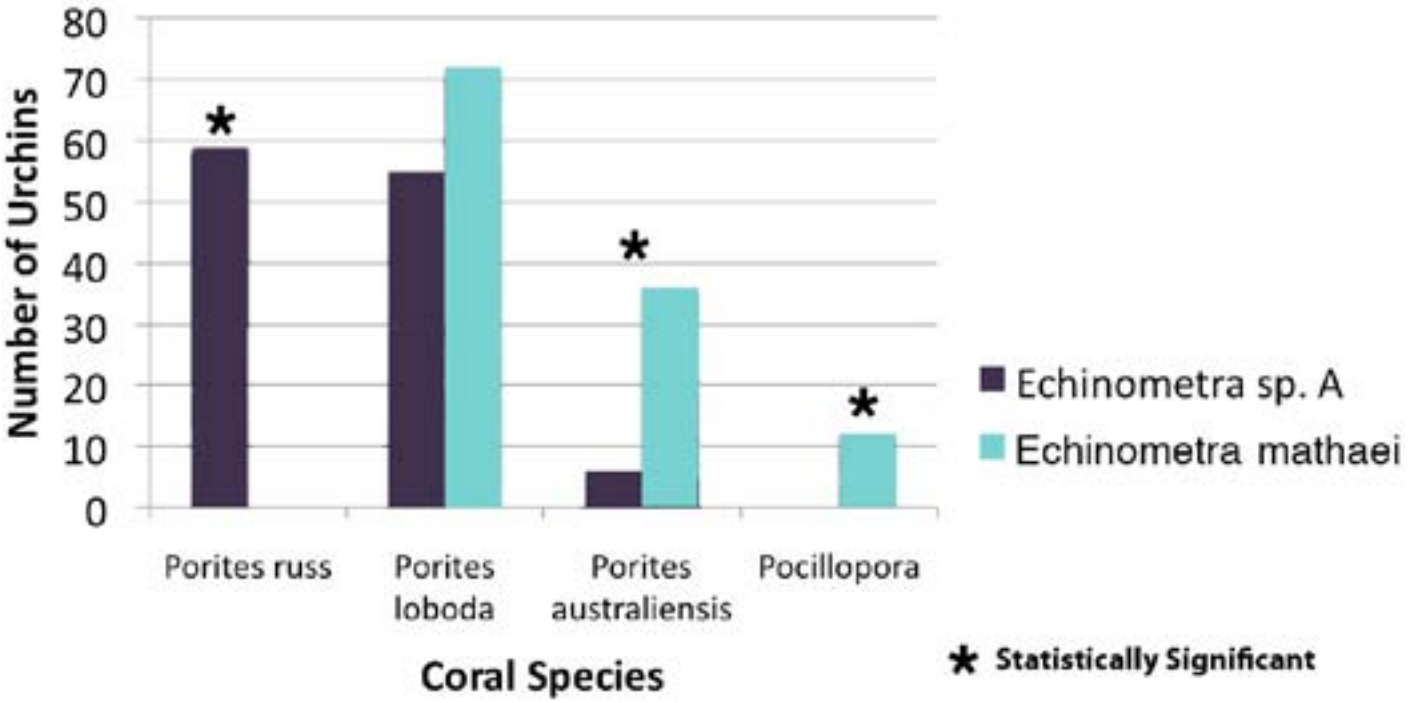

Fig. 3: The number of E. sp. A individuals and the number of E. mathaei individuals inhabiting various species of coral. The bars marked with a * are significantly different from each other (p<0.05).

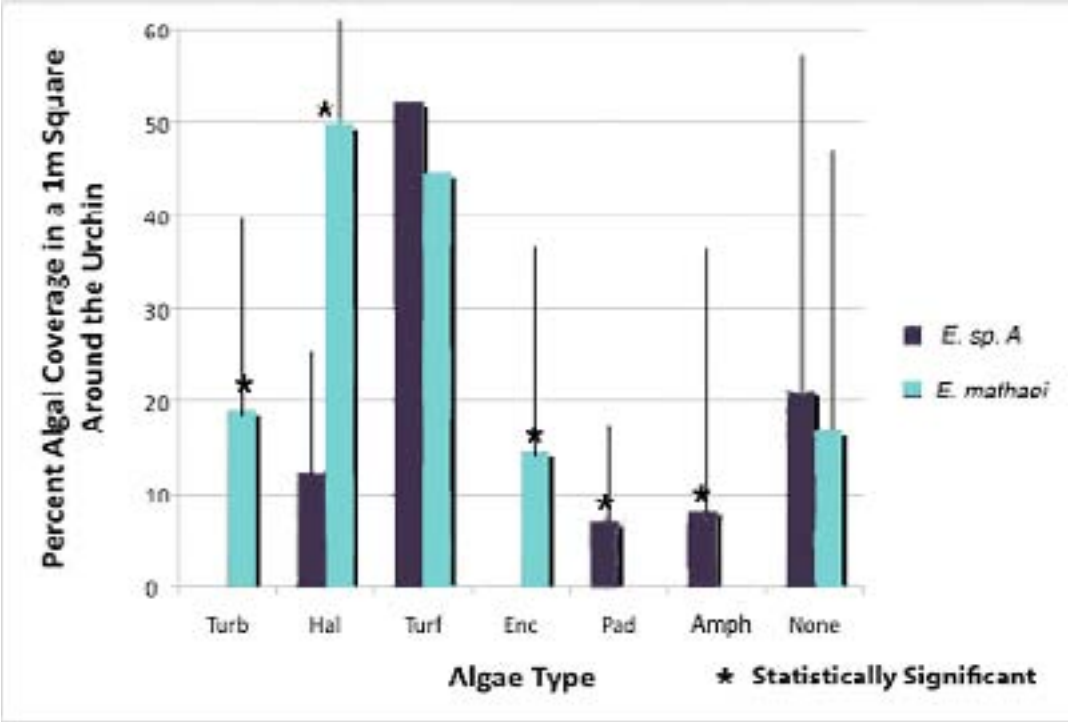

Fig. 4: The relative percent algal coverage within 1 m around Echinometra burrow holes. The bars marked with a * are significantly different from each other ($p<0.05$). Error bars denote +1 standard error. The error bars for turf algae extend to 90% and 80% for E. sp. A and E. mathaei, respectively, but these were not shown to increase readability of small bars on graph.

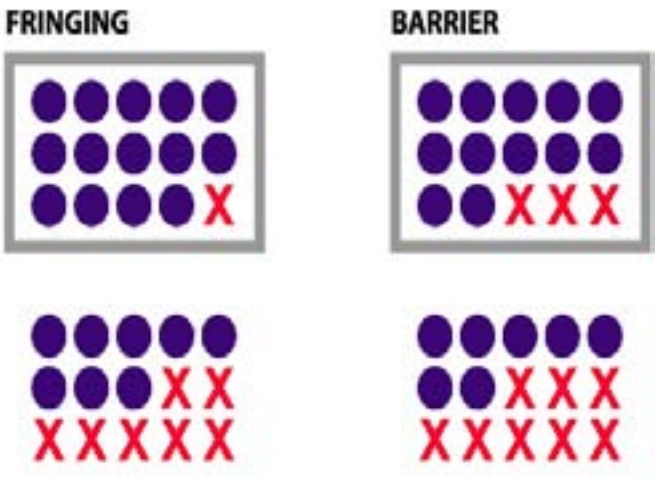

Fig. 5: The 24-hour survival rate of E. sp. A when transplanted to the barrier reef and to the fringing reef. An X indicates urchin death and a box indicates a cage.

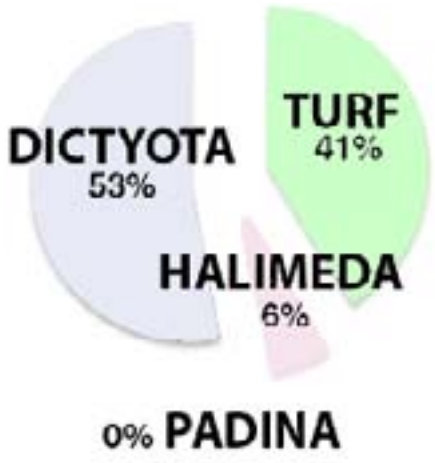

Fig. 6: The percentages of algae eaten by 21 E. sp. A individuals during a seven-night feeding preference experiment.

Feeding Preference Experiment

Urchins fed on Dictyota at a higher frequency than turf, Padina, and Halimeda algae options (Fig. 6). Of the 21 E. sp. A individuals, none fed on algae before the hour of 20:00 (Fig. 7).

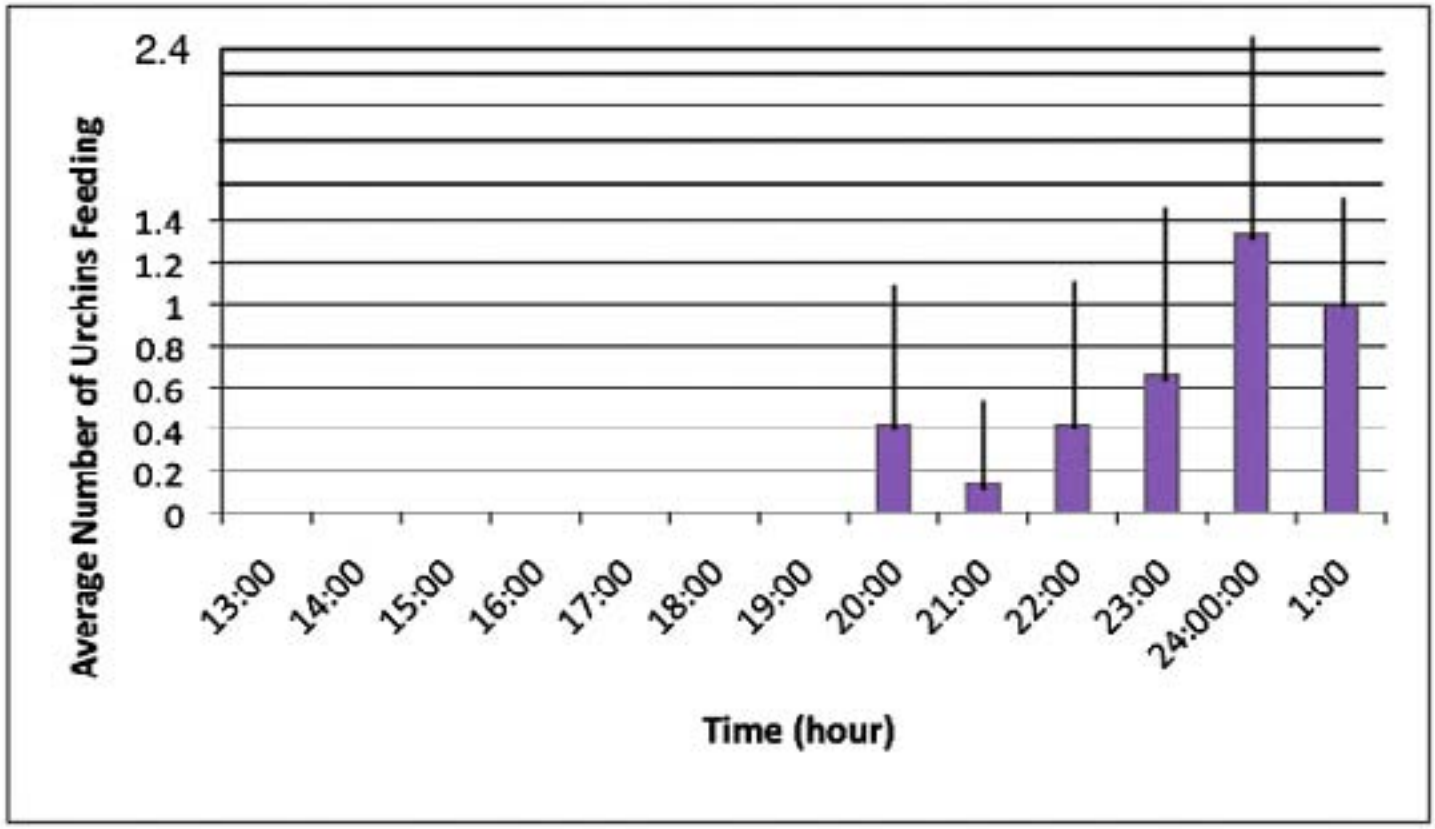

Fig. 7: The average number of E. sp. A individuals that fed on algae during a seven-night feeding preference experiment, at a given hour. Error bars denote +1 standard error.

Discussion

Population Distribution

The distribution of Echinometra was not random; E. sp. A existed primarily on the fringing reef while E. mathaei existed primarily on the barrier reef. This distinction between their distributions on the reefs was not absolute, however. At some sites, both species of sea urchin inhabited the same coral heads. This result stands in contrast to previous studies that showed E. mathaei only on the barrier reef and E. sp. A exclusively on the fringing reef (Collisson 1995). The presence of both species within a single habitat suggests co-inhabitation, without one species out-competing the other. It is possible that the two species of urchin have only recently, since Collisson's 1995 study, moved into one another's habitats. Perhaps in 1995 there was an environmental factor causing the isolation of the two species.

In general, I found a greater number of E. sp. A on the fringing reef than of E. mathaei on the barrier reef. One explanation for this result is E. sp. A might thrive on the high levels of algal coverage present on the fringing reef, as these urchins are known to be active grazers (Peyrot-Clausade 2000). It is also possible that E. mathaei are in fact just as abundant as E. sp. A but that they hide deeper in coral crevices

Habitat Assessment

The habitat of E. sp. A and E. mathaei was generally comparable in that the coral and algae surrounding these two species were quite similar. At first, the presence of Echinometra (of both species) living in P. loboda on both the barrier reef and on the fringing reef suggested that the urchins prefer this coral as a burrowing home. However, the auxiliary data showing E. sp. A inhabiting P. russ, and P. australiensis in addition to P. loboda offered a contrasting explanation that perhaps these sea urchins do not have a coral species preference. It may be that Echinometra only require a specific hole size in which to burrow, rather than an associated coral species (Chris Meyer, pers. com.). From qualitative observation, both species inhabited a high proportion of dead coral, compared to living coral. Algal growth encompassed the dead coral head, except for regions around burrow holes where urchin grazing cleared patches of exposed coral. These data support the theory that the urchins only need a certain burrow size and not a specific type of coral.

Echinometra affinity to specific algal types showed not to be prevalent based on my results. The most common algal species within 1 m-distance of E. sp. A on the fringing reef was turf algae, which ranked second most common near E. mathaei on the barrier reef. This similarity suggests that because E. sp. A and

E. mathaei live near the same types of algae, they both feed on the same species of algae. My results showed primarily turf algae, macroalgae and coralline algae within 1 m-distance of E. sp. A and E. mathaei on both the fringing and the barrier reefs. Many other studies site the majority of Echinometra diet to consist of precisely these three types of algae (Herring 1972, Ogden et al. 1989). Hiratsuka and Uehara (2007) found similar herbivorous feeding habits of Echinometra in Japan through examination of gut contents. Neither coral nor algal association with Echinometra appear to be limiting the distribution of one species to a particular reef type.

Transplant Experiment

The higher survival rate of urchins under cages suggests increased levels of predation when urchins are left exposed on coral heads. This conclusion makes sense; if an urchin is open and available, a predator can prey upon that urchin easily. What is interesting about this conclusion when applied to Echinometra habitat is the idea that one coral head can only support a given number of urchins because of space constraints. That idea would imply that each coral has a maximum carrying capacity of sorts, in terms of the number of burrow holes available, depending on its size.

Another interesting conclusion drawn from the transplant experiment is the repeatability of predation results on the fringing reef. I found results statistically similar to the survival rate on the barrier reef when I repeated the caging experiment on the fringing reef. One possible explanation for the parallel results might be that the same predators prey upon Echinometra on the barrier reef as well as on the fringing reef. Of course, the predation rate appeared to be the same but I cannot conclude if it was indeed the same predators who created this rate. Triggerfish are the main predator for Echinometra and they access the softer mouth side of the urchins by flipping them over and attacking from the ventral direction (Roy Caldwell, pers. com.). Therefore urchins who are exposed on coral heads are thereby accessible to triggerfish, and more easily preyed upon than those urchins deep within coral crevices or burrows. The similar predation rate on the two reef types suggests that E. sp. A can live on both the fringing and the barrier reefs with the same chance of being eaten.

Feeding Preference Experiment

The first, most clearly visible trend among the feeding experiment data is that E. sp. A only fed after a certain hour of the day, or, more accurately, during the dark hours of the night. No urchin fed before the hour 20:00, a time significantly after the sun descended below the horizon. In one case, the urchins did not feed until much later, when the light illuminating the experimental tanks in the wet lab turned off. For the initial few hours of the experiment, the urchins remained sedentary, hiding in one corner of the tank. In contrast, during the dark night hours, the urchins moved around the tank actively, feeding on all the species of algae present, except Padina. This great movement, in combination with the observation of urchin feeding, suggests that Echinometra do indeed feed during the night.

Of the total time spent feeding, E. sp. A fed most commonly on Dictyota algae, but the urchins also fed on two of the other three types of algae. This behavior suggests a generalist habit of feeding. Given the habitat location of an isolated volcanic island, a generalist feeding pattern would be advantageous to any organism hoping to establish a population on Mo'orea. These data further support the distributional findings that both species of Echinometra could colonize and thrive on both the fringing reef and the barrier reef because of generalist feeding habits.

The short-term nature of this study did not allow for following up on some tantalizing suggestions in the data, namely the need to explore the feeding preferences of E. mathaei.

Conclusions

The combined data from this study confirms the initial distributional findings by supporting the idea that the short-term factors of coral habitat, algal nutrient source, and predation are not limiting the urchins' distribution to only one type of reef. In fact, E. mathaei and E. sp. A live in the same types of coral with the same species of algae growing on that coral. Furthermore, the predation rate of E. sp. A is nearly identical on the fringing reef as it is on the barrier reef. These three short-term factors are not causing an isolation of E. sp. A on the fringing reef and E. mathaei on the barrier reef. They do, however, support the idea that the two species of Echinometra can indeed live together on both reef types. All these data align with this study's distribution finding of co-habitation by the two species of Echinometra on Mo'orea, French Polynesia.

Future Research

The nocturnal feeding behavior of other genera of sea urchin, such as Diadema is well documented (Lewis 1964) but the nocturnal feeding of Echinometra is not as commonly studied. Future research might examine nocturnal feeding behavior of these urchins, in a less manipulated, non-laboratory environment. In addition, a feeding preference experiment might be conducted to examine if E. mathaei feed on the

same algal species as E. sp. A. These data would offer greater insight into the niche differentiation of these two urchin species.

Another question that arises from this study relates to the other factors influencing the distribution of Echinometra in Mo'orea—what other short-term and long-term factors might be causing this particular distribution pattern? Will the distribution of E. sp. A and E. mathaei be the same 15 years from now? Will the two species cohabitate both the fringing and the barrier reefs at an even higher percentage? Future research needs to be done to investigate these questions and hypotheses.

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