NICHE DIVERSIFICATION OF CONIDAE IN MO'OREA, FRENCH POLYNESIA: THE EFFECT OF SUBSTRATE PREFERENCE ON HABITAT SELECTION

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Abstract. This survey examined habitat selection of Conidae in Mo'orea French Polynesia. Three sites were studied for comparison of macrohabitat and microhabitat preferences. The microhabitats were categorized into substrate types, and then a laboratory manipulation was conducted to see if cone snails have substrate preferences in the absence of biotic influences. Results showed that topographically complex environments yield a high abundance, species richness, and species composition of cone snails. In the absence of biotic influences, cone snails show some substrate preferences. As they are predatory organisms, however, prey availability is most likely the factor limiting where cone snails can live and survive in the natural environment. Cone snails forage for prey at night, so in order to accommodate their sedentary life style during the day, sea floor complexity gives them the necessary microhabitats for protection from predation. Minimizing anthropogenic effects on the sea floor makeup sustains these various microhabitats, which enable flexible niche differentiation necessary for cone snail conservation

Key words: Conida; habitat selection; substrate preference; niche differentiation; Mo'orea, French Polynesia

INTRODUCTION

Understanding the niches occupied by species and discerning the biotic and abiotic factors affecting an organisms' place in the environment is essential to ecology. The organisms of individual species occupy habitats based on a range of variables, all of which are based on interactions between the organism and the environment. These interactions are not independent or isolated influences: competition, resources, temperature, substrate, light exposure, and predation are some common examples of limitations on habitat selection (Vandermeer 1972). These influences on niche diversification are categorized into fundamental niche and realized niche. The fundamental niche of a species is where a species can exist given the physical limitations of the environment and its resources. The realized niche is where the species actually exists in the natural environment, including biotic limitations of competition and predation (Holt and Gaines 1992). Differentiating the actual habitats of species, i.e. their "realized niche," allows us to identify the significant limitations on an organisms' survival and the relative importance of ecological demands

(Vandermeer 1972). Moreover, further examination of the physical microhabitats of different species is key to comprehending how organisms of that species interact with various pressures from their surroundings (Pulliam 2000, Kadmon and Allouche 2007).

Niche differentiation in tropical organisms shows the unique ecological limits that determine species habitat selection. This is the case with the tropical land snails in Borneo, whose abundance and species richness decline with increasing elevation (Liew et al. 2009). In the tropics, temperature and area are the main factors that decrease with high elevation, as seasonality does not have as great an effect as in temperate regions. Therefore, the study conducted by Thor-seng Lewis et al. (2009) showed that the low productivity found at high elevations resulted in reduced niche differentiation of tropical land snails. Alexandra Gross et al. (2009) conducted a habitat survey of three tropical species of dolphins, and showed that niche differentiation was the mechanism that allowed these species to coexist despite their competition for resources. Thus niche diversification is a strategy naturally employed to benefit survival of the species. Habitat selection is part of this strategy, and is driven by different variables for different

species. The habitat selection of the tropical organisms belonging to the family Conidae were studied for the purpose of further understanding the effects niche differentiation.

Organisms belonging to the family Conidae are predacious, using a modified radula to inject venom into their prey items. In *Conus*, the radula is a detachable and dart-like tooth utilized mostly as a feeding mechanism and sometimes for defense. Cone snails are active at night and sedentary during the day; although they mostly rely on the "sit and wait" method of predation, *Conus* snails are able to constantly direct water through their body via a siphon. The siphon can often be seen protruding from the sand, and is an anatomical feature enabling water to continually flow into the mantle cavity, passing over the gill and osphradium, and by the anus (Kohn 1956).

Kohn's study (1959) showed that two microhabitats favorable for *Conus* species are subtidal reef platforms and intertidal bench habitats. There is more species diversity in subtidal reef platforms, which have complex substrate such as sand, reef limestone, variable algal cover, dead coral heads in place, coral boulders, coral rubble and living coral. In intertidal bench habitats, however, there is a greater abundance because it houses annelid prey and can support dense populations of invertebrates due to the high rates of primary organic productivity (Kohn and Leviten 1976, Kohn 1983). Sandy substrates in shallow bays are a third microhabitat where *Conus* is found, however, because of the lack of topographical complexity, this setting has the lowest species diversity (Kohn 1967).

This study examined the abiotic influences on niche diversification of Conidae, specifically focusing on their selection of habitat in Mo'orea, French Polynesia. It was expected that cone snails would exhibit preferential habitat selection, existing more densely in topographically complex, rather than uniform, macrohabitats. It was also expected that macrohabitats with the highest abundance would yield the highest species richness of cone snails, as a higher pool of individuals would likely result in a higher chance of finding species diversity. Lastly, it was expected that cone snails would exhibit preferences for specific sea floor substrates, and therefore, would occur in particular microhabitats with different abundance and species richness and composition.

METHODS

Identification

Species of the Conus genus were identified using Salvat and Rive's guidebook *Coquillages de Tahiti* and Kohn and Anderson's Conus Biodiversity Website: Conus Species Account.

Study Site

The study site used for this study was Motu Tiahura, French Polynesia. Motus are conglomerate platforms composed of cemented coral boulders and rubble that form at sea level due to storm surges. Distinct habitats form around these raised landmasses, due to their unique geological formation and positioning with respect to wave action and prevailing winds. Three macrohabitats, were studied, categorized as the Backreef, Lagoon and East Barrier Reef. Microhabitats of cone snails were studied as substrate, with four categories of platform, boulder, rubble and sand.

The back reef is in between the exposed platform and the algal ridge. This area is extremely rocky with some live coral heads, but mostly fossilized coral boulders and coral rubble. The platform protects the leeward, sandier side, providing a habitat supporting live coral, boulders, many fish and macroinvertebrates. Here, the current is swift, and the floor is a sunken platform made of fossilized coral with some sandy patches and coral rubble. The lagoon has a very slow current with a predominantly sandy floor, large, live coral heads and fish. Comparing the species abundance, richness and composition in these three macrohabitats and four microhabitats might explain their niche diversification through substrate preferences.

Habitat survey

Randomized transects were used to quantify abundance and species composition and richness in each of the three macrohabitats and the four microhabitats of the motus (Fig. 1). In the lagoon, five 60-meter transects with a search width of 2-meters on either side of the belt were used. For both the conglomerate platform side of the motu, and the protected sandy beach side of the motu, four 50-meter transects were used with a belt width of 4-meters on either side. A total of

1,600m² was surveyed at each site. Species were identified as well as what substrate they were found on, and this was recorded on a dive slate in the field.

Macrohabitat

Species richness and abundance were surveyed for the three macrohabitats. Analysis of variance and pairwise multiple comparisons tests (Tukey Test) were performed to determine if there were statistically significant differences between cone snail abundance among the three macrohabitats (Backreef, Lagoon, and East Barrier Reef). The same tests were used to determine if there were significant differences between cone snail species richness among the three macrohabitats. The three most common species within each macrohabitat were calculated into percentages of relative abundance and a chi-square test was used to determine if differences in species composition amongst macrohabitats were statistically significant.

Microhabitat

Cone snail abundance and species richness were determined for the four microhabitats found at the Backreef, Lagoon, and East Barrier Reef macrohabitats. Microhabitats were categorized into substrate types: platform, boulder, rubble, and sand. Analysis of variance was used to determine if there were differences between cone snail species richness and abundance across the four microhabitats. Pairwise multiple comparisons tests were used to further test statistical significance in abundance and species richness diversity between the four microhabitats. The three most common species found in this study were calculated into percentages of abundance and a chi-square test was used to determine if there were statistically significant differences in their relative abundance across the four microhabitats.
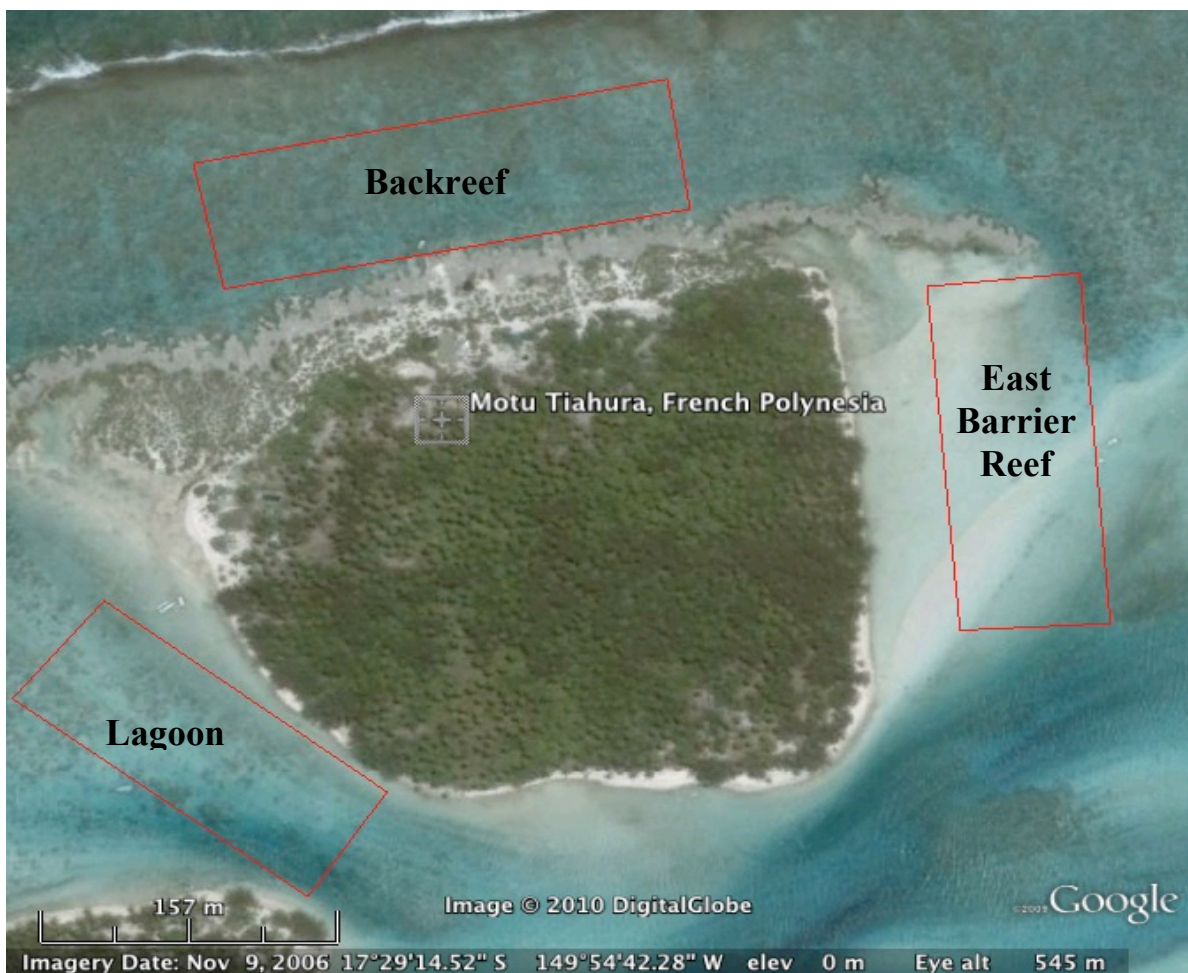

FIG. 1. Satellite image of Motu Tiahura, French Polynesia. Red boxes outline study sites. As indicated by the red boxes, sites surveyed include the Backreef, the Lagoon and the East Barrier Reef of Motu Tiahura, French Polynesia. Image © 2010 DigitalGlobe.

Substrate Preference

In the field, substrate on which each snail was found was categorized as live coral, coral rubble, conglomerate boulder, dead coral or sand. To best manipulate this natural habitat, the aquarium tank was partitioned into three distinct areas: one third filled with sand; one third with coral rubble; and the last third, containing cobble (Fig. 2). As large boulder heads in the field were impossible to reproduce in the lab, cobble was the most suitable intermediate, with an approximate average diameter of ten centimeters. Since the platform microhabitat could not be reproduced in the aquarium, this substrate was not tested in this experiment. All substrates tested were conglomerate coral material collected at the sites surveyed. After acclimatization (present in a tank with no substrate) for up to four days, a cone snail collected from the motu was placed in the center of the tank and left for a 12-hour dark photo-period, starting at 7:15pm and ending at 7:15am. At 7:15am, the tank was checked to see which substrate the snail chose. This was performed a total of twenty times per species, resulting in twenty replicates for each of the two species tested. Results were recorded, and the snails were returned to sites of origin. Chi-square tests were used to determine whether there was a statistically significant difference in the substrate-choice of *C. lividus* and *C. flavidus*.

Study Organisms

The species studied for this portion of the study were *Conus flavidus* (Lamarck, 1810) and *Conus lividus* (Hwass in Bruguiere, 1792). *C. flavidus* is a light brown to orange (sometimes brownish green) with a white to grey foot, the anterior portion often with a black band or mark. This species is 35-75mm and is smooth with the aperture having a purple color. *C. flavidus* feeds on polychaetes and frequently inhabits shallow subtidal reef flats up to 20m. *C. lividus* has a length of 30-81mm and is grayish brown with the aperture having a deep purple color. This species has axial ridges, a white pointed and crown-shaped top as well as a purple to brownish red foot (visible portion of soft body). Like *C. flavidus*, *C. lividus* feeds on polychaetes and inhabits subtidal reef platforms.

RESULTS

Macrohabitat

Abundance and diversity of cone snails greatly varied among the study sites. Cone snail abundance was highest at the East Barrier Reef and lowest at the Lagoon (Fig. 3. A). Difference of abundances across all macrohabitats was statistically significant (ANOVA, D.F.= 2, p= <0.001). As calculated with the Pairwise Multiple Comparison Procedure (Tukey Test), differences between abundance in the Backreef versus East Barrier Reef and the Lagoon versus East Barrier Reef were statistically significant with p-values of 0.020 and <0.001, respectively. The same test showed that there was not a significant difference in abundance between the Backreef and the Lagoon (p= 0.054).

Cone snail diversity was also highest at the East Barrier Reef and lowest at the Lagoon
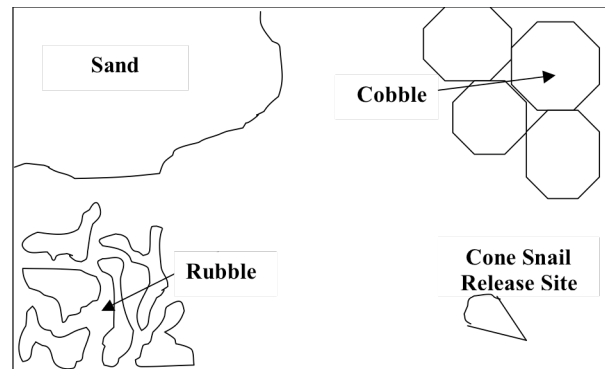

FIG. 2. Substrate layout for laboratory experiments on cone snail substrate preference.

(Fig. 3. B). Differences between species richness across all macrohabitats were statistically significant (ANOVA, D.F.= 2, p= <0.001). As calculated with the Pairwise Multiple Comparison Procedure (Tukey Test), differences between the number of species in the Backreef versus the Lagoon, the Backreef versus the East Barrier Reef and the East Barrier Reef versus the lagoon were all statistically significant with p-values of 0.004, 0.006, and <0.001, respectively.

There was a linear relationship between abundance and species richness across all three macrohabitats (Fig. 4). As diversity, i.e. the number of species, increases, abundance of cone snails also increases. The R^2 value shows that 85% of the data fits the equation of the linear trendline.

Species composition differed considerably amongst the three habitats (Fig. 5). There was

a significant difference in the overall diversity of species at all three habitats (Chi-square value= 91.774, D.F.= 2, p= <0.05). *Conus flavidus* was one of the most abundant species at all three sites. At the Backreef and the East Barrier Reef, the most common species were *Conus lividus* and *Conus flavidus*. Other dominant species, such as *Conus sponsalis* (at the East Barrier Reef) and *Conus frigidus* (at the Backreef), however, were variable. The most common species at the Lagoon was *Conus leopardus*.

Microhabitat

Most snails were found on platform substrate at the East Barrier reef, boulder substrate at the Backreef, and sand substrate at the Lagoon (Fig. 6. A). Differences of abundances across all microhabitats in the Backreef, Lagoon, and East Barrier Reef were statistically significant with p-values of 0.016, 0.001, and 0.013, respectively. At the Backreef, differences between abundance on rubble versus sand and rubble versus boulder were statistically significant with p-values of 0.016 and 0.040, respectively. At the Lagoon, differences between abundance on sand versus platform, sand versus boulder, and sand versus rubble were statistically significant with p-values of 0.003, 0.003, and 0.025, respectively. At the East Barrier Reef, differences between abundance on platform versus boulder, platform versus rubble, and platform versus sand were statistically significant with p-values of 0.030, 0.028, and 0.022, respectively. All other relationships between microhabitats at each macrohabitat were insignificant. The highest number of species was found on platform substrate, and the lowest number of species was found on sand (Fig. 6. B). Species richness, however, was not significantly different between the four microhabitats (Chi-square value=1.788, DF= 3, p= >0.05).

Of the three most abundant species found, percent abundance at each microhabitat varied greatly (Fig. 7). *Conus flavidus* was mostly found on the platform and *Conus leopardus* was mostly found on sand. *Conus lividus* was found nearly equally on platform and boulder substrate. The difference in relative abundance of these three species was statistically significant amongst all microhabitats (Chi-square value= 95.759, DF= 3, p= <0.05).

Substrate

Two species of cone snails, *C. flavidus* and *C. lividus*, were tested for substrate preference in the aquarium (Fig. 8. A). The twenty individuals of *C. flavidus* did not show a significant difference in their choice of substrate, with nearly an even split of six individuals on rubble and seven individuals on both sand and cobble (Chi-square value= 0.010, D.F.= 2, p= >0.05). Of the twenty individuals tested for *C. lividus*, there was a significant difference in substrate choice, with no individuals were found on sand, and most of the individuals were found on rubble (Chi-square= 17.490, D.F.= 2, p= <0.05).

Across all macrohabitats, relative abundance of *Conus flavidus* and *Conus lividus* on substrates boulder, rubble, and sand were calculated (Fig. 8. B). For comparison, percent abundance of each species found on platform was excluded. *Conus flavidus* was found nine times on boulder, five times and one time on sand, yielding an statistically significant difference in abundance on each substrate (Chi-square= 6.4, D.F.= 2, p= <0.05). *Conus lividus* was found sixteen times on boulder, one time on rubble and never on sand, resulting in a statistically significant difference in abundance on each substrate (Chi-square= 28.336, D.F.= 2, p= <0.05).
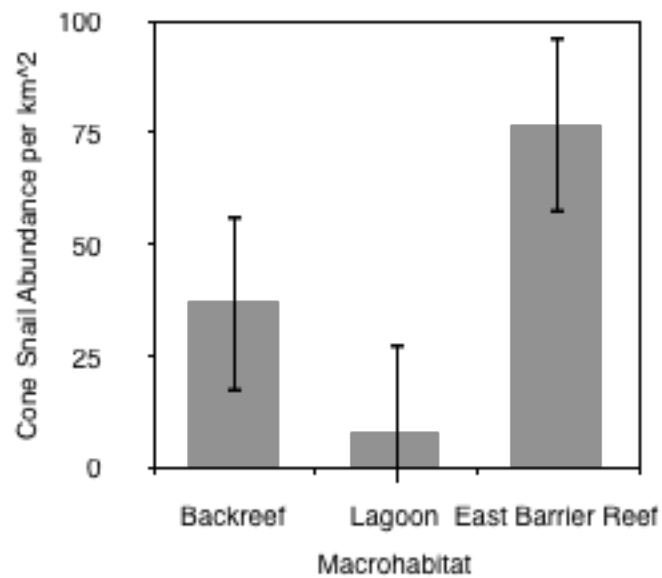
FIG. 3. A. Average cone snail density at each macrohabitat over a total area of 1.6km². Standard deviation was 20.14 snails/km² for the Backreef, 2.97 snails/km² for the Lagoon, and 26.57 snails/ km² for the East Barrier Reef. Bars indicate standard error.
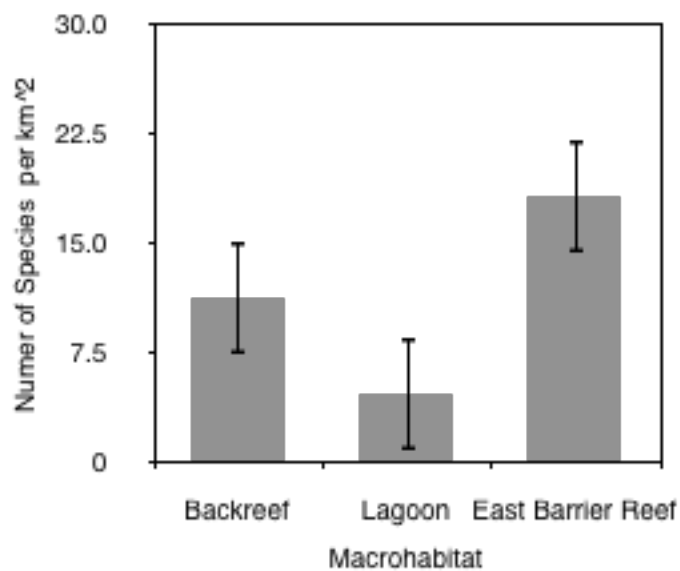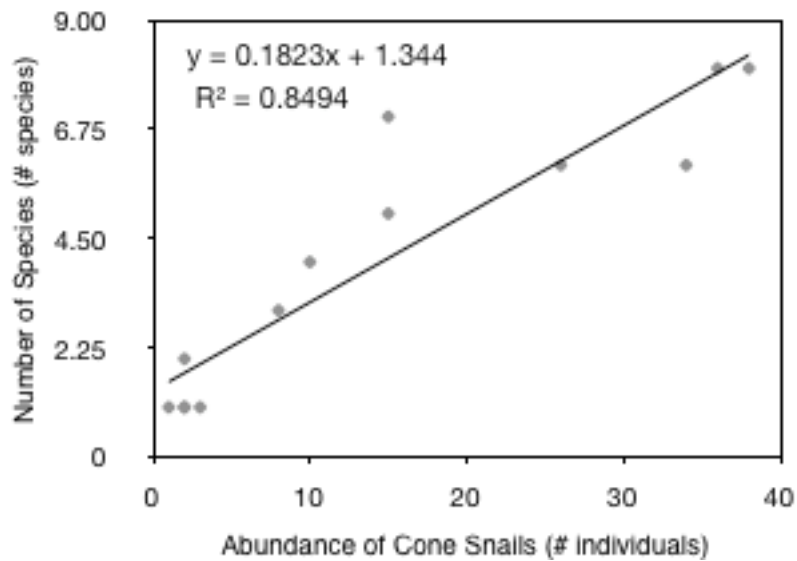

FIG. 3. B. Species Richness at each Macrohabitat over a total area of 1.6km². Standard deviation was 3.23 snails/km² for the Backreef, 1.95 snails/km² for the Lagoon and 2.39 snails/km² for the East Barrier Reef. Bars indicate standard error.

FIG. 4. Cone snail species richness versus abundance across all macrohabitats. The trendline indicates a linear relationship between species richness and abundance.
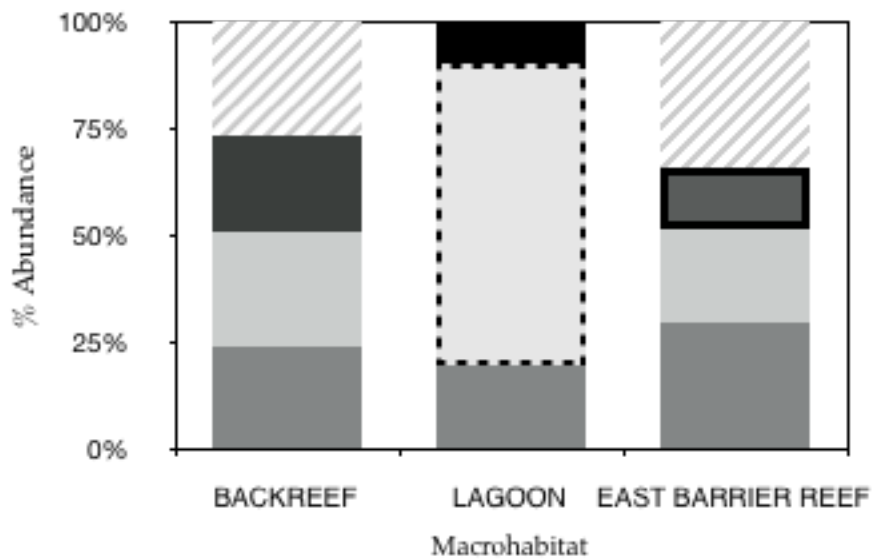
FIG. 5. The percent abundance of the three most common species found at each macroabitat. Medium grey represent *Conus flavidus*, light grey represents *Conus lividus*, dark grey represents *Conus catus*, light grey with thatched outline represents *Conus leopardus*, black represents *Conus pulicarus*, and dark grey with black outline represents *Conus sponsalis*. The white portion with light grey diagonal stripes represents other species.
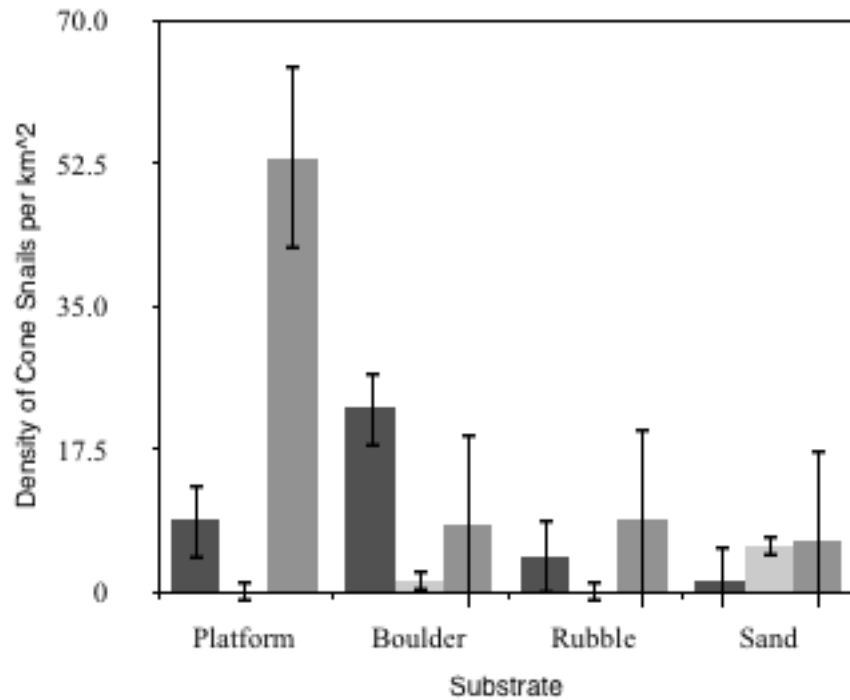
FIG. 6. A. Average cone snail abundance at each microhabitat within the Backreef (dark grey), Lagoon (light grey) and East Barrier Reef (medium grey). At the Backreef, standard deviation was 14.36 snails/km^2 for platform, 2.39 snails/km^2 for boulder, 7.36 snails/km^2 for rubble, and 2.50 snails/km^2 for sand. At the Lagoon, standard deviation was 0 snails/km^2 for platform, 0 snails/km^2 for boulder, 2.15 snails/km^2 for rubble, and 4.26 snails/km^2 for sand. At the East Barrier Reef, standard deviation was 35.02 snails/km^2 for platform, 10.10 snails/km^2 for boulder, 11.43 snails/km^2 for rubble, and 5.20 snails/km^2 for sand. Bars indicate standard error.
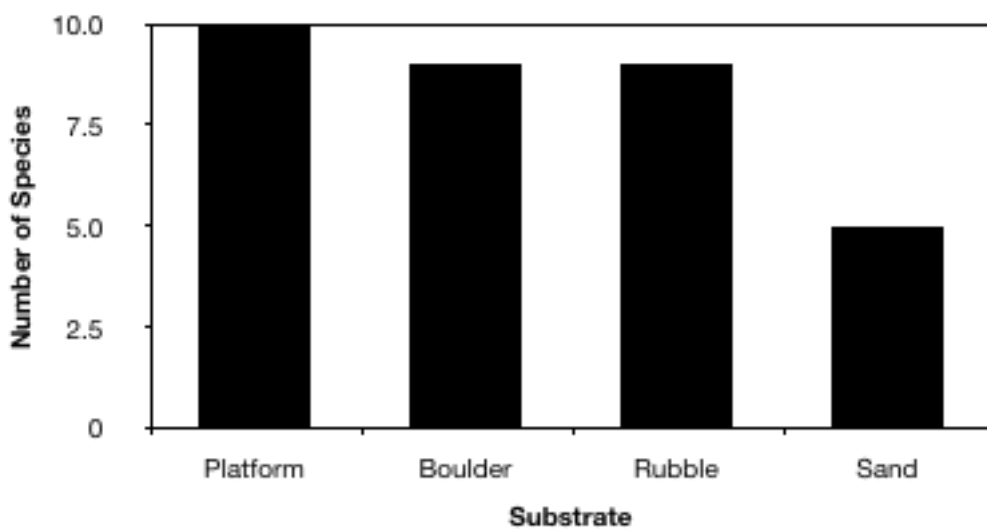

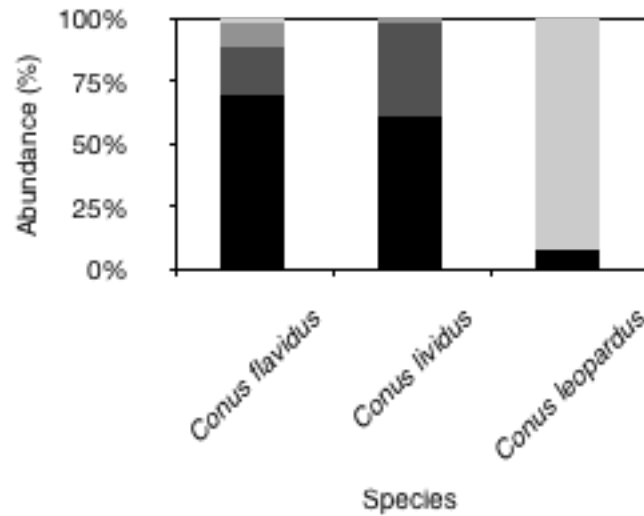FIG. 6. B. Species richness for each microhabitat.

FIG. 7. Percent abundance on four microhabitats for the three most common species. The microhabitat platform is the bar colored black, boulder is dark grey, rubble is medium grey, and sand is light grey.
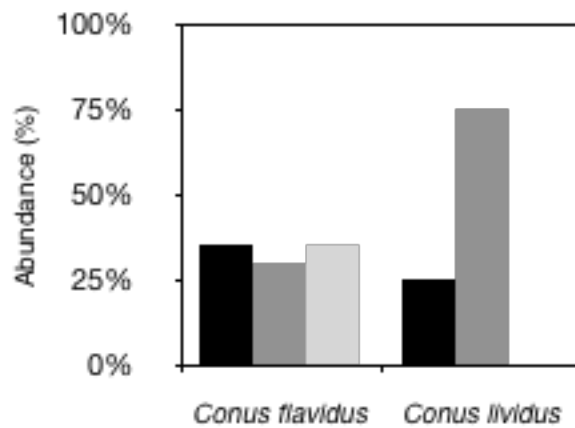

FIG. 8. A. Relative abundance of *Conus flavidus* and *Conus lividus* on substrate in the aquarium. The substrate cobble is represented with black, rubble with medium grey and sand with light grey.
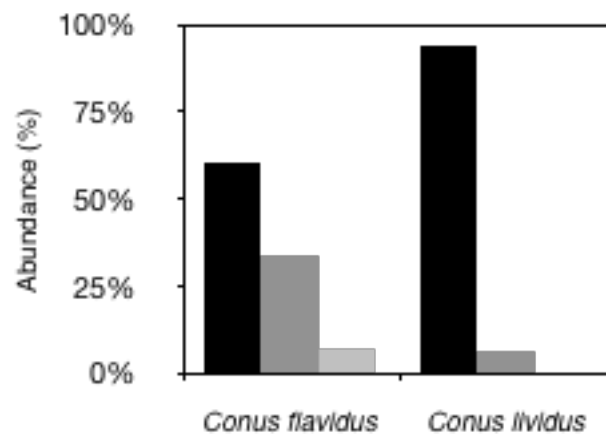

FIG. 8. B. Relative abundance of *Conus flavidus* and *Conus lividus* on substrates across all macrohabitats. Microhabitat of boulder is black, rubble is medium grey, and sand is light grey.

Macrohabitat

The significant differences in abundance, species richness and species composition of cone snails show that organisms belonging to this genus exhibit preferential habitat selection in Mo'orea, French Polynesia. Although other factors play a role in habitat selection, results of this study and other literature show that with topographical complexity come highly abundant and diverse cone snail populations. In this study, the most topographically complex site was the East barrier reef, which had the highest density and diversity of cone snails. The least topographically complex habitat studied was the Lagoon, which had the lowest density and diversity of cone snails.

As results indicate, there was a strong relationship between abundance and diversity across all habitats, and this is probably due to substrate variation. Specifically, the linear regression showed that with greater abundance, the species richness increased. If habitat structure is more varied, that habitat can support a higher number of individuals, inevitably yielding a higher pool for species diversification.

Microhabitat

The variation in species composition, species richness and abundance shows that cone snails distribute according to specific microhabitats within the oceans' bottom floor complex. Since cone snails are predatory animals, prey availability likely plays a large role in where they are located with respect to macrohabitats. Although cone snails are predatory organisms, habitat selection is not based on prey accessibility alone; they also have predators and need protection from them. Cone snails are nocturnal and actively forage for prey at night. During the day they are sedentary, and, therefore, this is when they are the most susceptible to predation.

Thus, as cone snails predate at night and remain inactive during the day, it is likely that microhabitat selection during the day is influenced by predator evasion. They might choose surfaces of the sea floor based on contours and crevices that enable protection from view. Results showed that cones snails were more abundant and diverse in the East Barrier Reef, and the substrate they were most commonly found on in this macrohabitat was platform. They were less abundant and diverse in the lagoon, a habitat, which is largely dominated by sand. These results suggest that microhabitat has an effect on macrohabitat choice. In the field, however, there are confounding biotic factors, such as these predator-prey interactions. Therefore a laboratory set up for substrate choice was used to see if there actually was a preference for a particular substrate, not just a random distribution.

Substrate Preference

The results of my research demonstrate that cone snails exhibit preference for substrate types, which may indicate that ocean topography influence microhabitat selection. The experiment performed showed that while *Conus flavidus* did not exhibit a preference for substrate, *Conus lividus* only chose substrates cobble and rubble and was never found on sand. Within a larger habitat context, cone snails specialize on certain surfaces, and so substrate preferences influence habitat selection.

In their natural environment, however, both species had significantly different abundances on the microhabitats boulder, rubble and sand. Confounding biotic factors, such as prey availability and accessibility, can account for these differences (Underwood et al. 2004). *Conus flavidus* might show such preferences in the field based on prey availability. Furthermore, *Conus flavidus* was mostly found in the field on platform, and second most abundant on boulder, neither of which could be replicated in the laboratory study. So *Conus flavidus* may have substrate preferences, but preferences for substrates that were not available in the substrate-choice experiment.

Conus lividus, however, showed similar patterns in substrate preference both in the field and the lab. *Conus lividus* was never found on sand in both the microhabitat study and the substrate-choice experiment. This demonstrates that *Conus lividus* has a preference against sand substrate. Although *Conus lividus* was most abundant on rubble in the laboratory, this species was more abundant on boulders in the field. Yet boulder substrate could not be perfectly reproduced in the aquarium; the closest manipulation of this microhabitat was cobble. This may explain why *Conus lividus* did not preferentially settle on cobble; whereas rubble offers numerous

crevices and hiding spots. And because prey was unavailable in the substrate-partitioned tanks, *Conus lividus* might have prioritized protection from view alone. Results from the laboratory manipulation indicate that cone snails do have substrate preferences; however, some species (e.g. *Conus lividus*) have stronger inclinations toward or against a particular substrate.

Conclusion

This study demonstrates that cone snails have habitat preferences. Although predator-prey relationships play a large role in determining the habitat of Conidae, abiotic factors are also significant determinants. The outcome of the research conducted in Mo'orea, French Polynesia shows that habitat specialization of predatory organisms, in this case cone snails, is also attributable to microhabitat and substrate preferences. Yet, predator-prey dynamics, especially food attainability often influence microhabitat preferences of predatory animals (Kotler 2001).

For conservation and maintaining biodiversity of cone snails, anthropogenic effects on the sea floor should be minimized. For example, beach raking, boat channels, extraction of limestone, etc. are all human induced changes to geography of the sea floor that could destroy cone snail habitats. Uniformity of sea floor substrate might effect the location of cone snail's prey (e.g. polychaete prey that bores into boulders or mollusk prey that attaches to rubble and inhabits the contours of other solid substrates), subsequently effecting the realized niche of Conidae (Kershner and Lodge 1990, Underwood et al. 2004). Since cone snails forage for prey at night, they utilize complex substrates for habitat and protection during the day. Thus, topographical complexity is important for sustaining cone snail populations and their diversity.

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