THE EFFECT OF ISLAND BIOGEOGRAPHY ON ISOLATED CORAL HEAD RICHNESS AND ABUNDANCE ON MOOREA, FRENCH POLYNESIA

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Abstract. The oceans are an extremely diverse world, home to thousands of species, many of which are yet to be discovered. Shallow tropical coral reefs are one of the most diverse ecosystems in the ocean, and make home to nearly one third of all marine fish despite accounting for less than 1% of the total ocean area. This study examined the factors that influence the diversity and richness of vertebrates and invertebrates found on isolated coral heads at Temae beach on Moorea, French Polynesia. A detailed map was created to understand the layout and location of the 69 coral heads surveyed. I hypothesized that (1) the size of the coral head, (2) the specific species of coral on the head, and (3) that isolation, as in the theory of island biogeography, would influence the richness and abundance found on each coral head island. The study found that the size of the coral head and the number of different coral species on the head played the strongest role in richness and abundance observed. Isolation, in the context of the theory of island biogeography, was found to play a very minor role in the richness and abundance observed. In some cases, the opposite of the theory was observed, with higher richness further from the defined mainland. As global climate change increases, it is important for conservation efforts in tropical reefs to focus on maintaining a high diversity of corals. It is also important not to neglect isolated reefs in favor of large ones, as the isolated reefs may house unique species. Because corals act as the backbone of one of the most complex ecosystems, their health is paramount to the health of the reef ecosystem as a whole.

Key words: coral; richness; abundance; island biogeography; Moorea, French Polynesia

INTRODUCTION

The ocean is an extremely important natural resource for people around the world. It is used for shipping, power, and food to name just a few of its uses (Corbett et al., 1997; Masutani and Takahashi, 2001; Brander, 2007). As the human population expands and increasingly takes advantage of what the ocean offers, many of the organisms that call it home are becoming threatened. One such marine ecosystem that is particularly impacted by humans is tropical coral reefs (Hughes, 2008). Coral reefs act as key building blocks for shallow marine ecosystems in most of the world's oceans (Connell, 1978). In addition to acting as primary producers with the help of endosymbiotic zooxanthellae, corals also provide habitat for a wide range of vertebrates and invertebrates. Coral reefs provide some of the most diverse ecosystems on earth, and account for a disproportionately high number of taxonomic groups in the world's oceans (McAllister, 1991). With anthropogenic effects such as global warming and ocean acidification increasing (Doney et al., 2012), these delicate and essential ecosystem architects are threatened around the world.

Under normal conditions, coral reefs are in a balance between erosion, both chemical and physical, and growth and calcification of the polyps. As ocean acidification increases, the rate of calcification of coral drops below the rate of erosion and the reef begins to break down (O. Hoegh-Guldberg et al., 2007). As erosion increases, sections of the reef break apart creating fragments of isolated coral heads. When new coral polyps settle, they can also create isolated sections of new reef. This can be accomplished either by colonizing on an already isolated rock, or by settling on the ocean bottom and growing into an isolated coral head. Since newly settled polyps survive better when settling on vertical surfaces or on the bottom of surfaces, it is more likely for new corals to colonize existing rocks (G. Hodgson, 1990). Both reef segmentation and coral growth can create underwater islands, in which richness and abundance can be studied in the context of island biogeography.

When the theory of island biogeography was conceived in 1967, it was used to explain the abundance and richness of organisms found on islands based on their size and distance from a mainland source (MacArthur and Wilson, 1967). Islands closer to a source and larger islands can support higher richness and abundance of organisms. As size decreases or isolation increases, both richness and abundance drop accordingly. Isolated coral heads may act in a similar fashion to the islands studied by MacArthur and Wilson, with the main reef body acting as the mainland or source. Many fish that live on corals rarely leave the safety of their home coral heads and have very limited home ranges (P. F. Sale, 1971; D. L. Kramer and M. R. Chapman, 1998). Fish also look to the isolated coral heads as nurseries for juveniles. Many of these juveniles settle very close to the home coral head on which they were born (G. P. Jones, 2005).

The purpose of this study is to attempt to quantify the effect, if any, that the theory of island biogeography plays on abundance and richness of vertebrates and invertebrates on isolated coral heads. In addition, this study attempts to examine differences of richness and abundance based on species of coral comprising the isolated coral head. I proposed that three factors would play a role in the richness and abundance of fish and invertebrates observed on isolated coral heads: (1) larger coral heads would support higher abundance and richness, and that the abundance of supported organisms will grow exponentially; (2) different coral species and combinations of coral species will support different abundances and diversities. This is because of the different shape and form and the different primary productivity levels of the different coral species; and (3) the theoretical predictions of the theory of island biogeography will hold true for smaller or less mobile fish species and for most invertebrate species. The degree of isolation between coral heads will depend on each organism's ability or preference to swim between heads. The level of isolation will need to be sufficient to prevent organisms from crossing between coral heads. Most fish are able to swim between heads freely, and so the theory of island biogeography should not hold true as well as it does for terrestrial organisms, which are typically hindered by a necessity to cross over large distances of water. However, some fish live their entire lives in a small area and should follow the rule of isolation implicated in the theory of island biogeography.

METHODS

This study examined isolated coral heads at Temae public beach on Moorea, French Polynesia (-17.49, -149.75). Coral head "isolation" was defined as one coral head being at least 2m away from any neighboring coral head. Coral heads less than 2m apart were instead treated as a single island complex, and counted as a single coral head for the purpose of this study. All heads were surveyed beginning from the north east side of the beach and moving south west about 150m. The coral heads ranged from 40m offshore to 120m offshore. This survey of coral heads and associated vertebrate and invertebrate communities was conducted between October 11, 2014 to November 15, 2014.

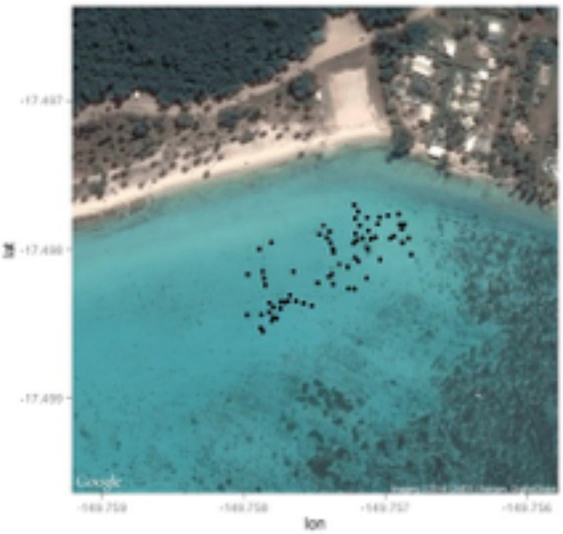

Figure 1: Map of coral heads at Temae beach (-17.498010, -149.757363). Photo courtesy of Google

Mapping Component

As a first step in this project, I created a map of the isolated coral heads at Temae beach to explore the relative isolation among coral heads. To do this, I used Google Earth to determine the location of a starting coral head. From there I swam between all heads, snaking back and forth while swimming west. Some heads were groups of heads, or island complexes (see above). When mapping these island complexes, the largest coral head in the group was used as the map point and all other heads were clumped together into a single volume. Volume was measured as a rectangle, with length and width of the head taken at the base, and depth measured from the base to the highest point. Between each head a compass bearing was taken and the distance measured to the edge of the next head. The diameter of each head was also taken to account for the size of the head when measuring distances. After measuring all heads, geomidpoint.com was used to generate accurate latitude and longitude readouts for all heads. Next, all GPS coordinates were imported into the program R, which I used to produce a map showing the location of all heads on a map from Google Earth (Fig. 1).

The distance to the nearest main coral body was used to calculate isolation, which was necessary to test predictions from the theory of island biogeography. To do this, I swam a measured distance from the furthest north east coral head at a defined heading until I crossed the main reef. The main reef was characterized as having only small patches of sand (<3m across). Once the edge had been reached, it was mapped out in the same fashion as the coral heads were mapped (that is, compass headings were recoded and distances were determined on geomidpoint.com). This process was completed along the same length of reef as was surveyed for the coral heads. Once all points were located, isolation from the main reef could be calculated as the shortest distance between a given coral head and the closest point on the main reef. This allowed a test of H3.

Community survey and coral volume estimates

Once all heads had been identified and mapped, I began the second part of the study: surveys of vertebrates and invertebrates on each coral head as well as finding its volume. Counts were completed to generate measures of richness and abundance. Counting began from a distance in an attempt to not alter the behavior of the fish during the approach and affect the count. Once all visible fish had been counted, I moved closer to the coral head to look for more cryptic fish. This involved swimming several laps around each coral head at sand level to look underneath the head and into nooks and cracks. Once I had confidently counted all fish on the coral head, I next counted the invertebrates. When counting the invertebrates, a few very camouflaged fish were detected and added to the fish count. After counting all organisms, I estimated the volume of the head (or heads in a complex) using a transect tape to measure length, width, and depth, which were then multiplied together to generate an estimate of volume. This allowed a test of H1.

Over the course of this study, I performed two separate surveys for counts at each coral head. The first occurred between 10/3/14 and 10/24/14, and the second occurred between 10/25/14 and 11/12/14. I performed a second round of sampling to explore the influence of migration in altering the richness and abundance observed in the first round. During the second round of sampling, I also identified the coral species present and counted their percent coverage on each head. Coral species that did not meet a 10% coverage minimum were not counted. Percent dead coral or bare rock was also counted assuming it reached the 10% minimum threshold. This was done to test H2

Statistical Analyses

I used regression analysis to analyze the relationship between coral head size to richness and abundance, coral species to richness and abundance, and coral head isolation to richness and abundance. Analyses were run for vertebrates and invertebrates separately, and then both together. The program Numbers was used to graph the data, and the program R was used to preform statistical analyses.

RESULTS

Effect of coral head size on richness and abundance

A strong positive correlation was seen between coral head volume and abundance of vertebrates and invertebrates (Fig. 2). This was expected and confirms H1. Larger coral heads supported higher abundances of organisms, both vertebrate and invertebrate individually. The same is true when looking at richness of vertebrates. Invertebrate richness was only marginally significant (p=0.066).

Effect of coral species on richness and abundance

For each individual coral species, there was no significant correlation seen between percent cover of a single coral species on a

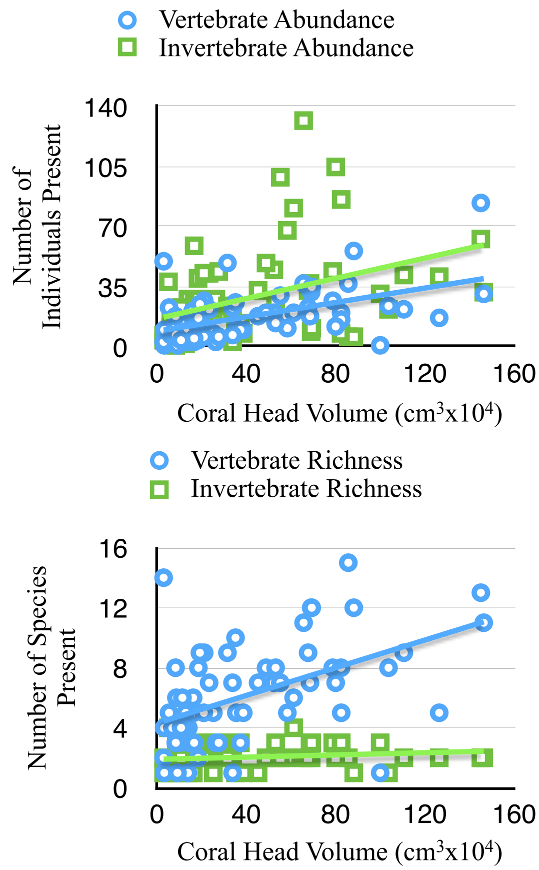

Figure 2: The effect of coral head volume on abundance (above) and richness (below) of vertebrates and invertebrates together. There was a significant effect of volume on vertebrate abundance (Regression, $F_{1,67}$=27.4, p<0.001), invertebrate abundance (Regression, $F_{1,67}$=14.6, p<0.001), and vertebrate richness (Regression, $F_{1,67}$=25.57, p<0.001). Invertebrate richness (Regression, $F_{1,67}$=3.482, p=0.066) was not found to be significant.

head and richness or abundance of vertebrates or invertebrates found on that head. For nearly every coral species, there was a negative correlation seen between percent cover of a single coral species and richness or abundance. The coral *M. mollis* even showed a significant negative correlation between total richness and percent coverage (p-value <.01).

When looking at the number of different coral species present on a single coral head, there was a significant positive correlation

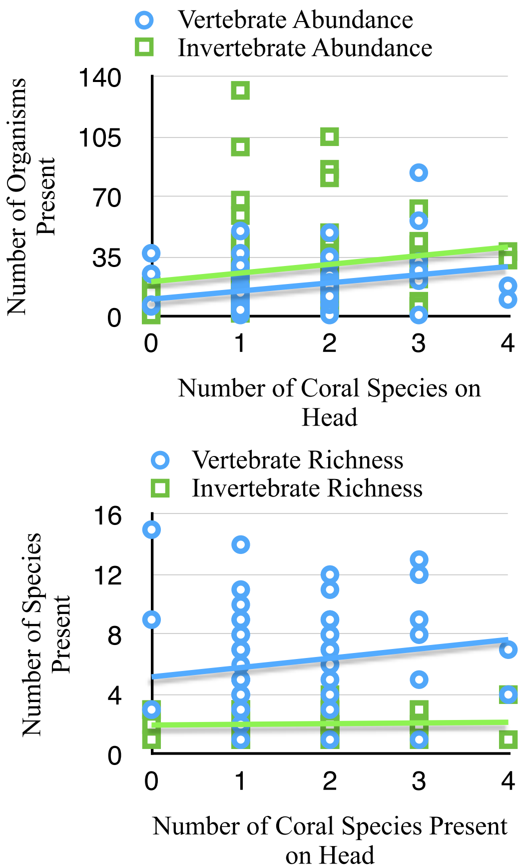

Figure 3: The effect of number of coral species present on abundance (above) and richness (below) of vertebrates and invertebrates together. There was a significant effect of more coral species on vertebrate abundance (Regression, $F_{1,67}$=7.987, p<0.01) and on vertebrate richness (Regression, $F_{1,67}$=3.988, p<0.05). Invertebrate abundance (Regression, $F_{1,67}$=3.095, p=0.083) was not found to be signifiant, nor was invertebrate richness (Regression, $F_{1,67}$=1.767, p=0.188).

seen between the number of coral species present and vertebrate richness as well as vertebrate abundance (Fig. 3). More different species of coral on a head lead to higher richness and abundance of vertebrates.

Effect of isolation on richness and abundance

Isolation in the context of island biogeography was found to have a positive correlation between vertebrate richness and abundance and distance of isolation. That is, marginally significantly higher richness and abundance were observed further from the reef. This is in opposition to the original theory which says that further away islands should carry fewer species. Isolation was found to show a significant effect only on total richness and invertebrate richness. Isolation also played a marginally significant role in total abundance. For all coral heads found within 30m of a large potential source island within the study site, there was no significant effect on the richness or abundance observed. While the island complex consisted of dozens of coral heads, it did not have a different enough population to have any effect.

In the study a second round of richness and abundance counting on vertebrates was done in order to see and understand any migration patterns that may be occurring daily. This second sample found that the population richness and abundance were not significantly different from one round to the other (p=0.622, and p=0.556, respectively).

Discussion

Coral head size

The size of each coral head had a strong positive correlation with richness and abundance of vertebrates, invertebrates, and both together. This applied across all coral species, and was even true of heads that were comprised completely of dead coral and algae. This supports the finding that the amount of available habitat is one of the key factors in supporting organisms. The specific type of habitat is not as important as the amount of total habitat. While specific corals present may be beneficial for corallivorous fish that could benefit from multiple food sources, for fish that simply live on the coral head, there is more benefit from various habitats to gain protection. On each head, there was a variety of different life stages of fish found. With that in mind, having multiple coral species and habitats present would again support increased abundance of fish. Different life stages could require different habitat types and would benefit from a variety of available corals in which to grow.

Coral species

For every coral species sampled, there was a negative correlation seen between percent cover of a single coral species and richness and abundance of vertebrates, invertebrates, and both together. This means that with more complete coverage of each coral species, there was a decrease in richness and abundance. This could indicate that diversity of habitat is the key factor influencing richness and abundance, not the productivity of any given coral species. More different species of coral present could offer benefits for fish. While there was no significant difference between individual coral species present and richness and abundance present, there was a significant link between number of coral species present and total richness and total abundance present, as well as richness and abundance of vertebrates. This suggests that the important factor affecting richness and abundance is not one specific coral or another, but rather a synergistic effect of multiple coral species (Gratwicke and Speight, 2005). Gratwicke and Speight (2005) go on to show that the same benefits of habitat heterogeneity can be seen in many shallow tropic marine ecosystems, including sandy bottoms and seagrass beds. The benefit of heterogeneity is likely due to the variety of habitats provided by each coral species and its growth form. With more different corals present, more potentially available niches are present. This finding supports the hypothesis that combinations of corals will affect richness and abundance, but for a different reason than anticipated. The combination of any specific corals was not affecting richness and abundance, but rather any combination of coral or dead coral habitat.

Coral isolation

Isolation, and island biogeography as a whole, played a very minor role on the richness and abundance or organisms found on the coral heads. Invertebrate richness was the only significant finding, but in a positive correlation with distance (Fig. 4). This tells us that closer to the reef, there is likely more predation on some of the more exposed invertebrates (giant clams, cleaner shrimp). At the further away heads, more species can live without predation. Invertebrate abundance was the only factor that was negatively correlated with distance from the main reef and thus followed the theory of island biogeography (Fig. 4). This is most likely because more of the juveniles of invertebrates reach the closer heads. Invertebrates reproduce via broadcast spawning directly into the water column. They depend on currents and tides to carry their young to settlement locations. It is more likely for them to settle on closer heads than further ones because of this.

Vertebrate richness and abundance were both marginally significant (Fig. 4), but again in a positive correlation. This could be because fish are avoiding some of the larger predatory fish found in the main reef. Another potential explanation is a lack of competition at the further heads. Living in closer heads could come with an inherently larger risk of predation. Either fish are avoiding the closer heads and preferentially choosing the further heads because of increased predators, or their population on the closer heads is being limited by predation. From my own observations, many more sharks, eels, jacks and other large predatory fish were seen in the main reef than around any of the isolated heads in the study. Only 3 small eels were found more than 50 meters from the main reef, and in each case the fish on that head were visibly disturbed.

In the sample area there was a large coral outcropping consisting of dozens of close coral heads. This had the potential of acting as a source population, effecting the coral heads in the local area. However, within a 30m range there was no significant impact on the richness and abundance of vertebrates or invertebrates. This indicates that anything smaller than the main reef as a whole is unlikely to affect local richness and abundance.

When applying the theory of island biogeography to marine ecosystems, it is important to remember the part that mobility plays in the richness and abundance observed. In the original theory of island biogeography, water acts as a barrier to immigration. It is assumed that immigration to the island occurs because of chance events that carry individuals across the barrier via wind or floating debris. In the marine system, there is not a barrier that keeps normal migration from happening between heads. Fish are attracted to different coral heads because of that particular coral head's features. The chance that they will find a suitable head closer to the main reef is independent of that coral head's location. In observations made in the field, fish occasionally swam between heads more than 10m apart, and regularly between heads less than 5m apart. This could be because of local competition and pressure on the coral head, or because the fish saw benefits in another head.

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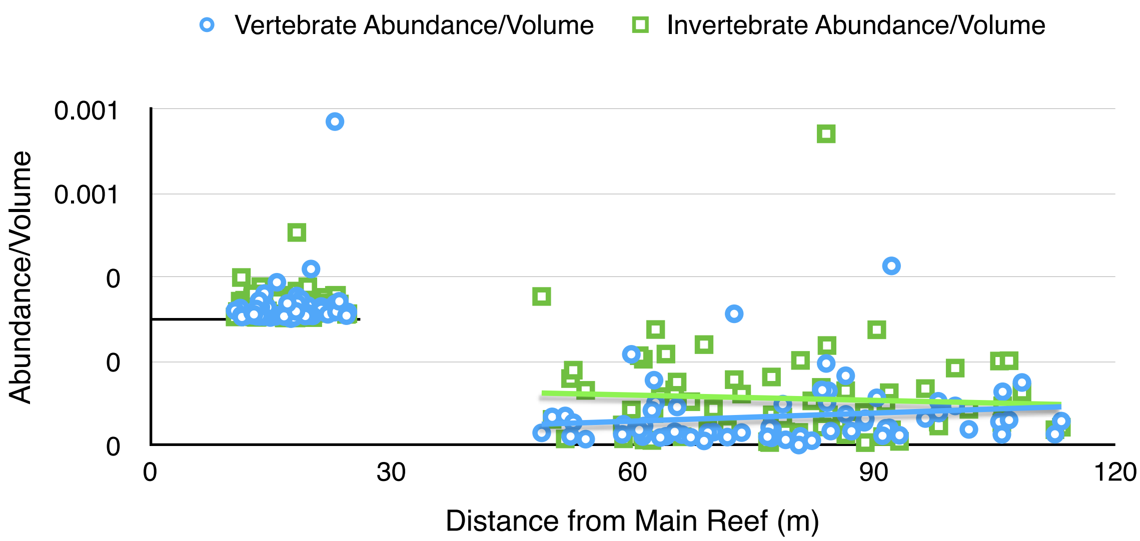
APPENDIX A



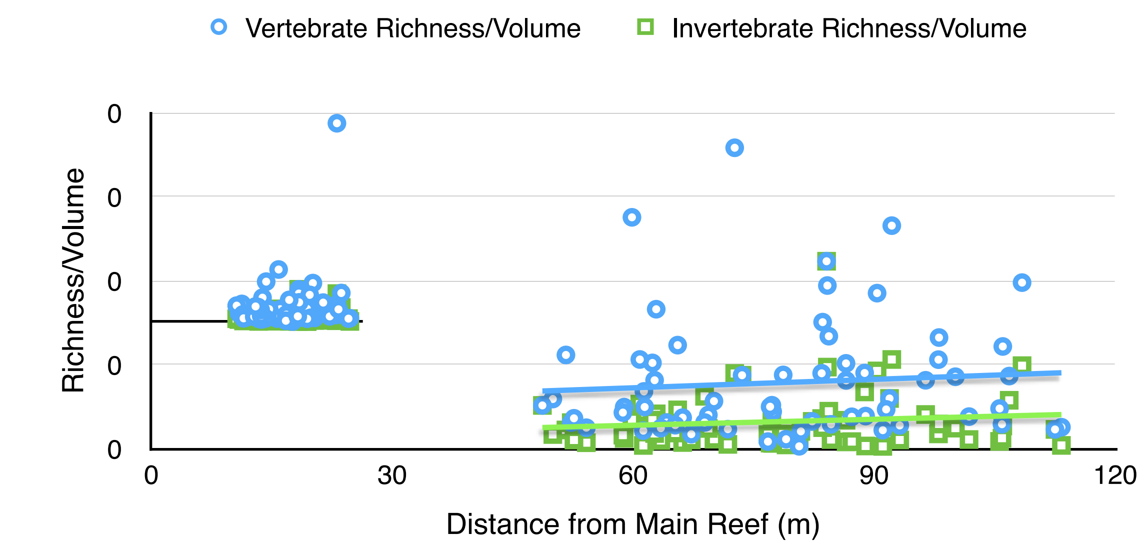


Figure 4: The effect of isolation on abundance (above) and richness (below) of vertebrates and invertebrates together. Vertebrate abundance (Regression, $F_{1,67}$=3.961, p=0.0507) and richness (Regression, $F_{1,67}$=3.817, p=0.0549) were both marginally significant. Invertebrate abundance (Regression, $F_{1,67}$=0.417, p=0.5206) was not significant. Invertebrate richness (Regression, $F_{1,67}$=4.55, p<0.05) was the only significant finding in relation to isolation. Graph in the top left corner of each graph is the graph including outlier point. The point was omitted in the larger graphs to increase clarity.