Island Biogeography Theory and Protected Area Development
An Intertidal Zone Analysis

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INTRODUCTION

Protected areas are an important tool for conservation of biodiversity, but significant debate exists regarding the influence of size, shape, and distribution in the efficacy of their preservation of species richness. The Theory of Island Biogeography predicts that larger islands, or pockets of habitable land, support a larger number of total species than smaller, more isolated islands (MacArthur & Wilson 1967). Specifically, species richness is thought to be regulated by the combined forces of distance-dependent colonization and area-dependent extinction of species. These regulatory forces have been detected and analyzed in many studies since the initial publication of the theory in 1967, with more recent applications exploring the variable species dynamics between native and non-native species, and the significant roles that colonization and extinction rates play in the regulation of these populations (Gao & Perry 2016).

While this theory has been widely cited and accepted by the scientific community for decades, the potential applications of this theory to conservation practice are still uncertain. Some scientists have suggested that groups of smaller island communities might be able to maintain the same level of species richness as a larger, continuous habitat would (Simberloff & Abele 1976). This claim is often disputed by other researchers who find higher rates of habitat degradation within smaller fragments, with lowered abilities to disperse between these disjointed fragments despite conservation efforts such as corridors (Harrison & Bruna 1999). The rocky intertidal zone provides a compelling setting in which to analyze the relationship between habitat

size, configuration, and the overall species richness of these discrete pools. The many interconnecting and diverse pools can provide reasonable proxies for protected areas of differing sizes and locations.

There are many physical factors that shape the biotic conditions of a particular habitat, but my analysis of species richness will focus on habitat size and connectivity as the primary predictors of richness within these confined areas. I chose these factors because they are the closest analogues to the island size and inter-island distance measurements that are used to analyze the relationship between isolation and relative biodiversity in the Island Biogeography Theory (MacArthur & Wilson 1967).

These factors of habitat size and connectivity can also be used to analyze the habitat fragmentation of the environment, and the impact that varying levels of fragmentation may have on species richness on a larger scale (i.e. larger number of smaller pools vs. smaller number of large pools). Research conducted by Loke et al. in 2019 predicts that an intermediate level of fragmentation can support higher levels of species richness (Loke et al. 2019). In this study, I further explore these intertwined concepts of habitat fragmentation and Island Biogeography through observations in the rocky intertidal zone. Using the rocky intertidal zone as a proxy for large-scale protected areas, I investigate any potential relationships between species richness, pool size, and overall connectivity between disjointed pool habitats.

Adhering to the established predictions of the Island Biogeography Theory, I expect to observe a positive correlation between species richness and both pool size and connectivity. Recent research into this potential relationship has revealed differing results, with alternative drivers of species richness, such as local environmental variation, arising as the potentially dominant driver of observed inter-island variations (Herrera & Laterra 2007). This investigation will attempt to reveal the nature of this size-connectivity-richness relationship, within the context

of intertidal zone habitats, with the ultimate goal of extrapolating the results to the larger context of effective protected area planning and development. If my hypothesis is correct, larger, more interconnected pools will have the highest species richness, while smaller, more isolated pools will have lower richness.

METHODS

This study analyzed a sample of 20 distinct tidal pools, selected from the wave-protected area of the rocky intertidal zone at the Hopkins Marine Station in Monterey, CA. The relative locations and tidal heights relative to mean lower low water (MLLW) of these 20 pools are shown in Figure 1. The selected pools vary in size and location relative to the other sample pools, and are confined to a small sampling area to avoid any potential confounding factors from differences in height, sun exposure, and other variable conditions. The relative species counts between these sampled pools were analyzed in conjunction with surface area and connectivity to analyze any potential relationships between pool structure and biodiversity.
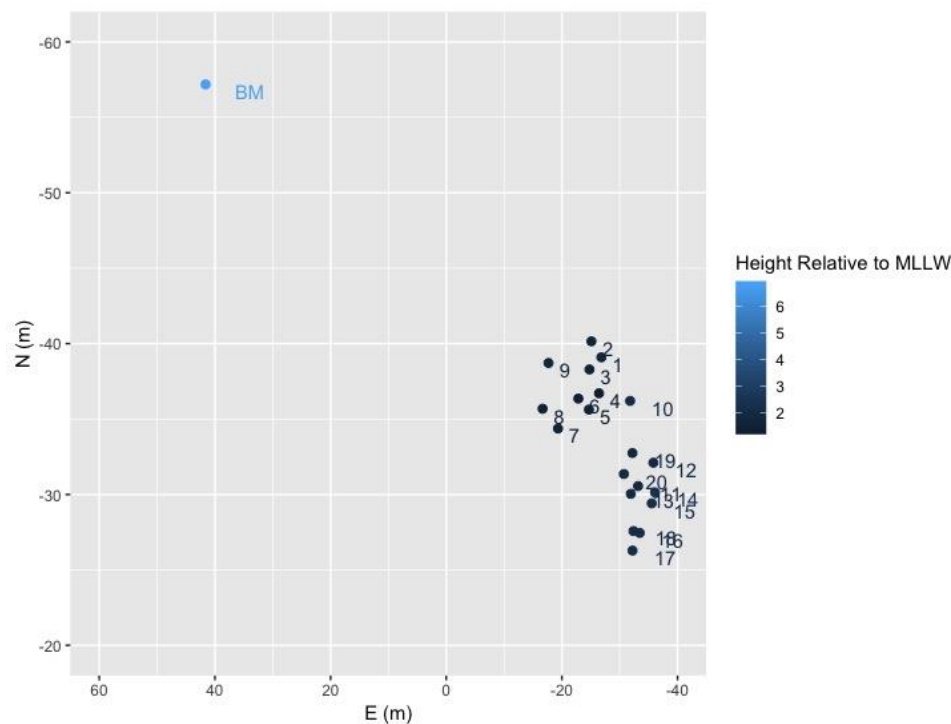
[Figure 1] Relative locations of the 20 pools included in the sample set, graphed based on their North and East locations taken relative to the Benchmark BM(N 36° 37.300, W 121° 54.258).
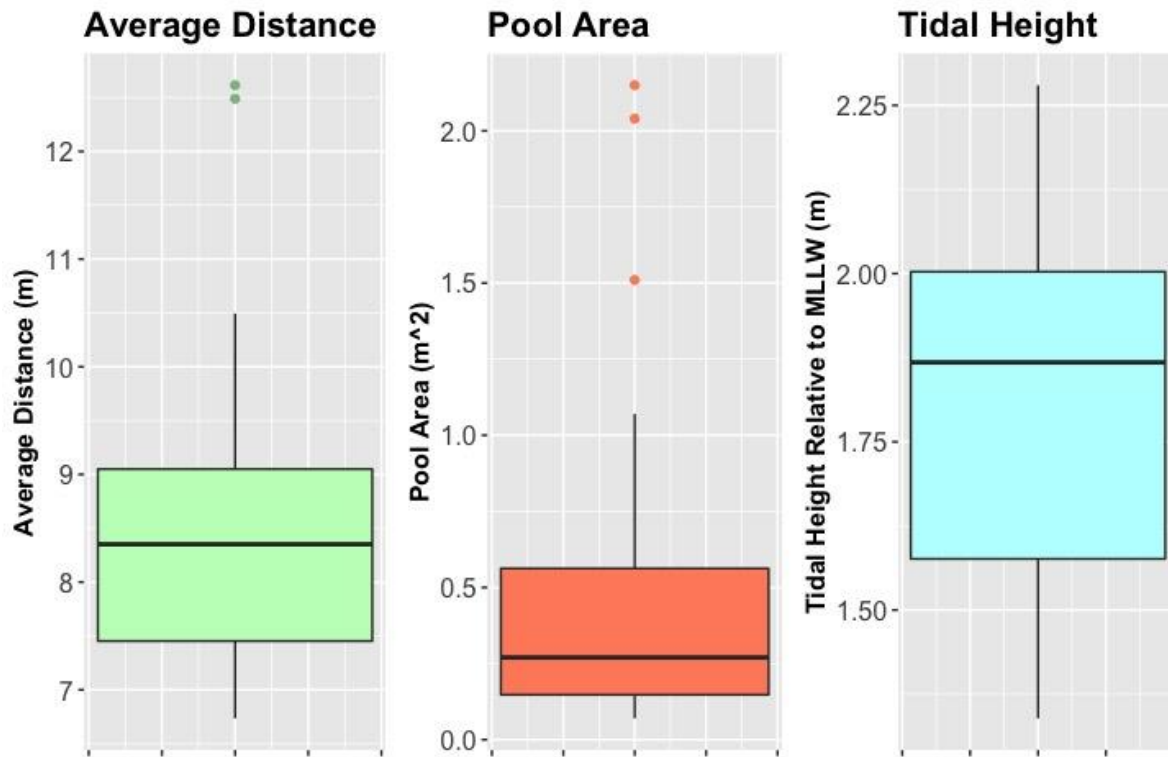
[Figure 2] Summary of the average distances between pools, surface areas, and tidal heights relative to MLLW of the 20 pools in the sample set.

To quantify variation in species richness among distinct pools in the intertidal zone, a variety of metrics focused on revealing the possible relationships between the abiotic (distance and area) and biotic (species richness) characteristics of these habitats were required. Three primary metrics were measured for each individual pool, with the specifics of each metric detailed in the following sections.

Species Richness

The species richness of each pool was measured by counting the number of animal species found within the physical boundaries of each pool habitat. All sessile and motile species were included. Due to the difficulty of identifying algal species, they were not included in my analysis. The raw number of animal species present in each habitat was used as the response

variable in all analyses. Species counts were collected on 05/23/19 during a low tide of -0.9 relative to the mean lower low water level (MLLW).

Pool Area

The surface area of each sample pool was collected using a square quadrat frame, with an overall size of 250 cm^2 and an inlaid grid of 25 x 10 cm^2 to aid in size estimations. The grid was placed over each individual pool, with the number of squares occupied by the water-filled parts of the pool used to estimate the overall surface area. This process was repeated multiple times for pools with a surface area greater than 250 cm^2. While this method of surface area measurement was not very precise, it was adequate in this situation since I was concerned more with relative areas between pools, rather than the exact areas associated with each pool.

Connectivity

The connectivity metric was calculated using a summed function of the distances from the pool of interest (x) to all other pools in the sample set (i). These inter-pool distances (d_i) were measured using a Topcon D total station and a stadia rod, placed at the approximate center point of each pool and divided by the total number of pools (20) to get the average distance from each pool to the others (D_x). Figure 3 illustrates the pool designations and physical measurements taken between pools in the sampling zone, with A_x representing the pool of interest and A_1-A_5 representing the surrounding pools included within the sample set. If the entire sample set were represented in this figure, A_1-A_{19} would be included, with their corresponding distance values of d_1-d_{19}. These distance are then summed and divided by 20 to get the average distance between pools, called D_x, shown in Equation 1. The denominator in this equation is 20, even though there are only 19 distances from the focal pool to the other pools in the sample. This equation is used for ease of coding, and is equivalent to alternative calculation methods that exclude the zero-distance terms from each pool in the sample to itself.
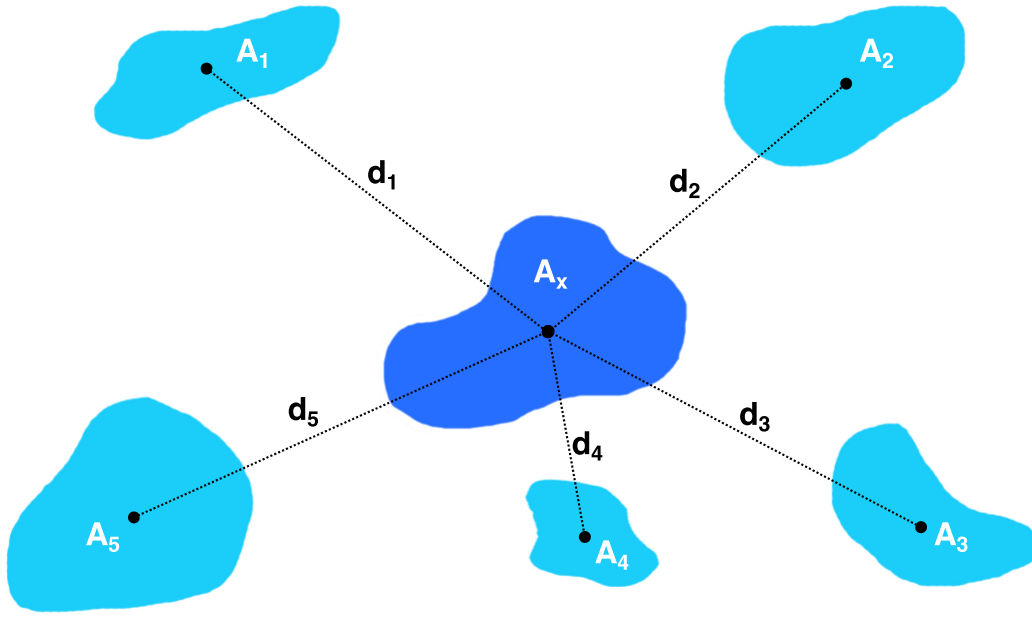
[Figure 3] Visual representation of the method of pool labelling and area measurements for the sample set, with the corresponding distance measurements between pools.

[Equation 1]

$$D_x = \sum_{i=1}^{20} \frac{d_i}{20}$$

The connectivity matrix (C_x) relies on these average distances (D_x), as shown in Equation 2. This calculation takes the inverse of the average distance to other pools, with the connectivity of a pool increasing as the average distances from its center to the centers of all surrounding pools decreases. The x subscript designates the pool of interest for that particular calculation, with i designating the pool numbers of the other 19 pools in the sample, other than the central pool.

[Equation 2]

$$C_x = \frac{1}{D_x}$$

The overall dispersal ability (Q_x) was also calculated, in units of meters^2. This metric takes into account the area of the receiving pool (A_x), the areas of all 19 dispersing pools (A_i), and the distances that the dispersed species must travel, represented by the connectivity metric (C_x). This dispersal metric differs from the basic connectivity metric (C_x) described earlier as it accounts the surface areas of each pool in the analysis, with the dispersal ability increasing as the surface areas of the pools increase. This equation takes into account edge effects, since many species are "edge-intolerant" and do not survive as well at the outer limits of their habitats as they would in the more protected centers (Ries et al. 2004). The distance measurement was also squared in this equation to account for the fact that dispersal of species between pools is nonlinear, and any movement between pools has the potential to travel in any direction away from the focal pool and not just directly towards the satellite pool of interest. Squaring the connectivity metric assumes that dispersal is only two-dimensional between pools, and assumes that any vertical species dispersal is irrelevant.

[Equation 3]

$$Q_x = A_x C_x{}^2 \sum_{i=1}^{19} A_i$$

PRELIMINARY RESULTS

The first analysis compared the average distances between pools and the surface areas of those pools for the entire sample. This analysis was necessary to ensure that there was no correlation between size and relative isolation, which would skew the results of the rest of my analysis and make these two variables dependent. In order to account for the uneven distribution of pool areas in this sample set, the area variable was transformed using a logarithmic operation. A scatterplot of these two variables from the collected data is shown in Figure 4, with no

significant correlation (P = 0.597) between the two variables arising from this analysis. A further analysis using linear regression in R gave an R^2 value of 0.0158, so only about 1.6% of the correlation in the data can be attributed to the best-fitting linear relationship.
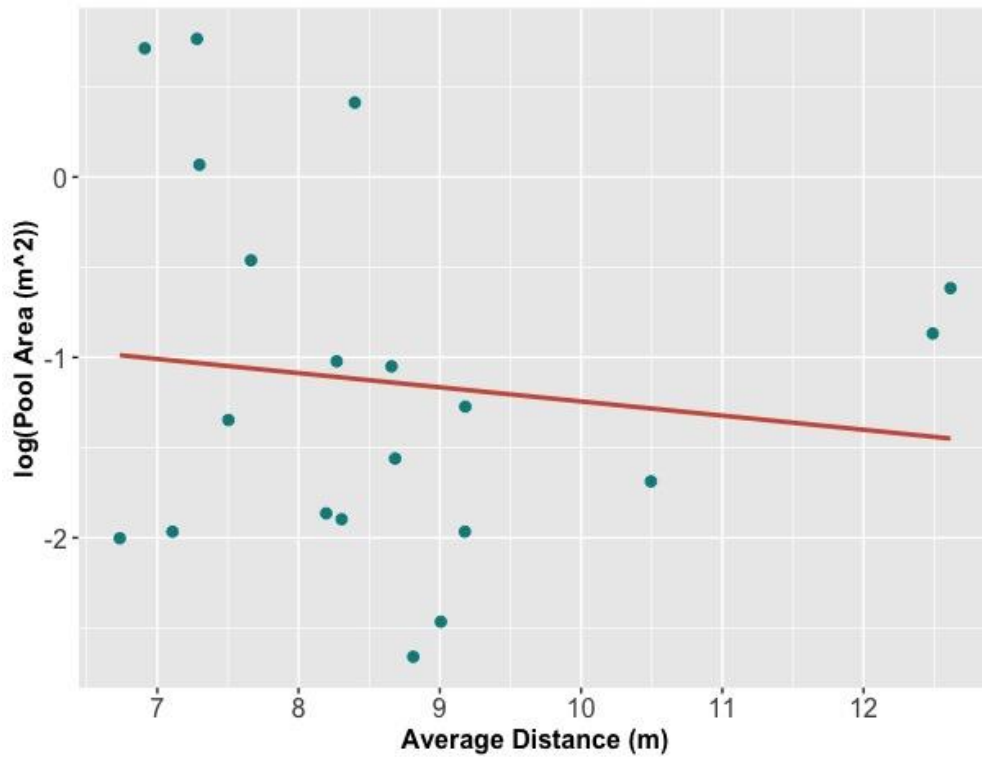
[Figure 4] There is no significant correlation between the log of pool area (m²) and average distance between pools (m), with the linear regression yielding an R^2 value of 0.0158.

Figure 5 plots the transformed area variable ($\log A_x$) against the untransformed connectivity variable ($C_x = \frac{1}{D_x}$). This plot also takes into account the species richness of the pools, with larger points representing the pools with higher observed species richness. There is no significant correlation between connectivity and the log of pool area ($R^2 = 0.0404$, P = 0.396), which is consistent with my previous finding of no correlation between area and the related variable of distance.

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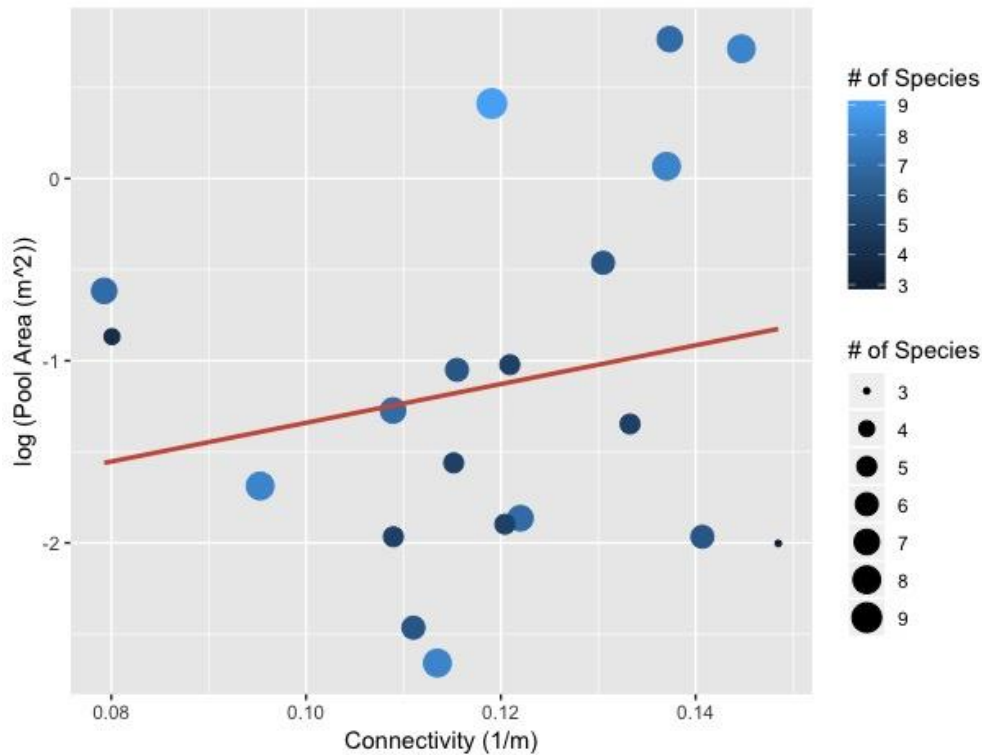
[Figure 5] Plot of the log-transformed pool area (m^2) and connectivity between pools (1/m), with relative sizes of data points representing observed species count for that pool.

With average distance between pools and surface area identified as independent variables, these two explanatory variables were then analyzed for their potential effects on species richness. Figure 6 plots these two main factors of interest against species richness using a linear regression function in R, with pool area transformed using a log transformation. These regressions show a slightly negative association between species richness and connectivity, and a stronger positive association between the log of pool area and species richness. The R^2 and P-values for these analyses are shown in Table 1, with the results of single-regression analyses for the other two variables of average distance (D) and dispersal (Q) also included. The plots for the average distance and dispersal regressions are not included because they are strongly correlated with the primary factors of connectivity and pool area, and thus do not strongly differ from the plots in Figure 6.
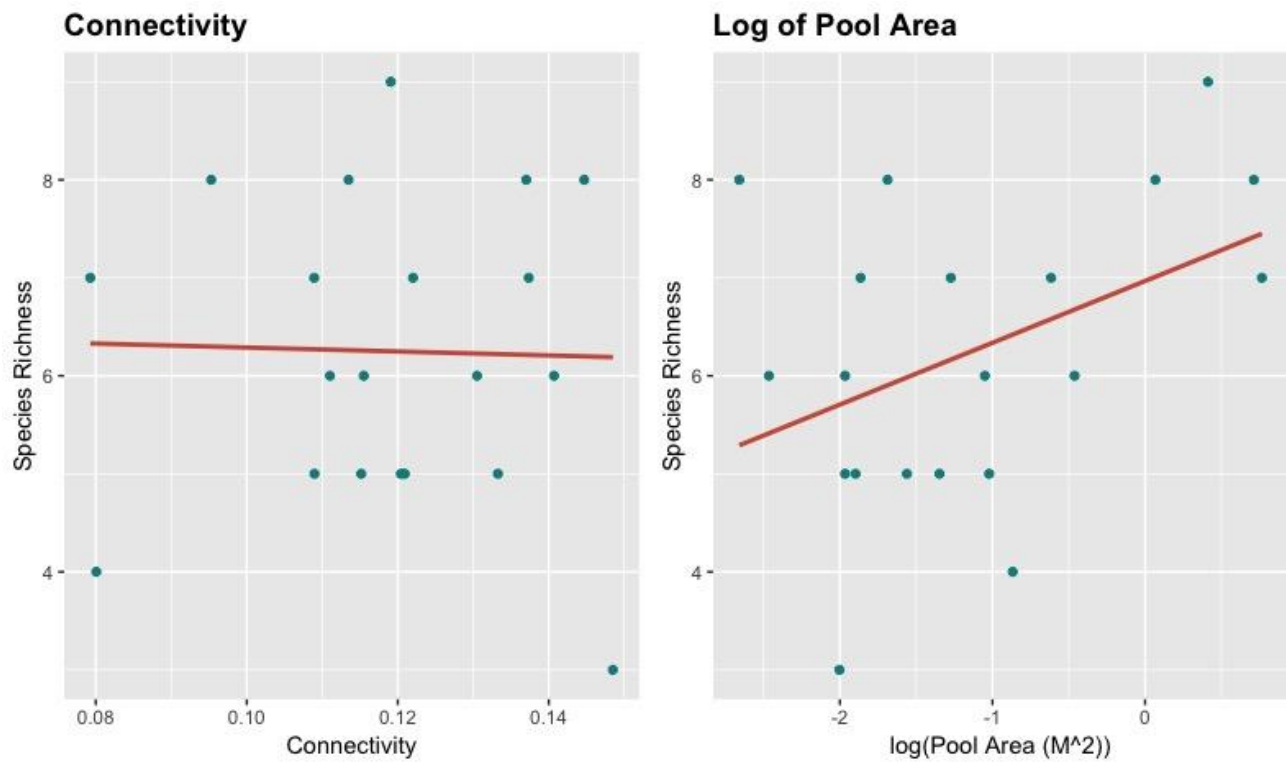
[**Figure 6**] Linear regression plots of species richness as a function of connectivity (C) and the log-transformed values for pool area (logA).

[Table 1]

Single Linear Regression (Species Richness ~ X)			
Factor	Slope	R^2	P-value
log [Pool Area (A)]	0.6305	0.17	0.0708
Connectivity (C)	-2.0200	0.0006	0.9168
Average Distance (D)	-0.01632	0.0003	0.9430
Dispersal (Q)	0.2688	0.2087	**0.0429***

* = significant result

[Table 2]

Multiple Linear Regression (Species Richness ~ $X_1 + X_2$)				
Factor	Estimate	Individual P-value	R^2	Total P-value
log [Pool Area (A)]	0.6650	0.0688	0.1821	0.1810
Connectivity (C)	-9.0901	0.6222		

A multiple regression analysis was also useful in uncovering the relative impacts of connectivity and area on the species richness of the pools. Table 2 shows the results of this analysis, calculated in R with the log-transformation once again applied to area. This analysis reveals a weakly significant (P = 0.0688) positive relationship between the log of pool area and species richness, meaning that increased pool area may be positively correlated with higher species richness in the pools that I sampled. The correlation between connectivity and species richness is negative in this multiple regression, but the P-value is very high (P = 0.6222) so these results are not considered significant.

DISCUSSION

The main goal of this study was to uncover any potential relationships between the size and connectivity of isolated tide pools, and the level of species richness observed within them. I initially hypothesized that larger, more connected tide pools would have higher species richness because of their more abundant habitat options and more centralized locations. Through this investigation, I have found a slight positive association between pool area, dispersal ability, and the overall species richness of isolated pools in the rocky intertidal. A slight negative association was observed between the connectivity metric and species richness, but the p-value is very large so this is not a significant correlation.

Since the dispersal variable is calculated from the surface areas of both the dispersing and receiving pools, and the other two variables of connectivity and distance did not show a significant correlation, we can assume that the main driver of observed changes in species richness is pool area. This is congruent with my initial hypothesis, as well as with the assertions of the Island Biogeography Theory (MacArthur & Wilson 1967) that larger islands are capable of supporting larger and more diverse species compositions.

PROPOSAL FOR FURTHER RESEARCH

My preliminary research has revealed a positive correlation between pool size and species richness in isolated tide pool habitats. The analyses of pool area and the related variable of dispersal both showed slight positive associations, so I propose that further research into this topic focus specifically on these area-related variables. I will extend my analysis to 5 other locations around Monterey Bay, since my analysis has already focused on specific habitats within this relatively-enclosed ecosystem. I can continue my analysis within this environment to avoid any confounding effects that might arise at a substantially different location.

Since there is no clear or unintrusive way to manipulate the sizes of tide pools within a natural setting, I propose an experiment in which I will purposefully select tide pools of specific sizes within each of the 5 new sampling locations. Based on the surface area data gathered in my preliminary study, I propose that this further research focus on 4 distinct pool sizes: 0.5 m^2, 1 m^2, 1.5 m^2, and 2.0 m^2. By selecting tide pools that have surface areas approximately equal to these predetermined values, I can more precisely analyze the direct impact that surface area has on the species richness of tide pools.

This experimental design will also allow me to compare tide pools of similar sizes across all 5 of the new sampling locations. With the 4 distinct size classifications applied to 5 sets of 20 pools, I will be able to calculate the average species richness for each of the 4 groups of 25 similarly-sized pools from the entire data set. I also propose to include species abundance data in further studies of this species-area relationship, since this will allow me to calculate other biodiversity-related metrics that could also be associated with pool size, such as species diversity.

While my proposal for further research focuses specifically on the correlation between species richness and tide pool area, I cannot fully discount the potential role that connectivity

may play in the regulation of biotic factors in tide pool ecosystems. My preliminary analyses showed no discernible correlation between species richness and the two distance-related metrics, but the reason behind this lack of a correlation remains unclear. Further research into this species-connectivity relationship would be an equally important topic for future study, especially since this result is in direct contrast with a component of the Island Biogeography Theory that this study initially sought to investigate.

An expansion of research efforts into the impacts of habitat size on species richness can have major impacts on future establishments of protected areas and other wildlife refuges around the world. A better overall understanding of the relative impacts of habitat fragmentation and size on population dynamics can guide conservation efforts, and aid in the creation of more effective sustainable development plans in the future.

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