

THE EFFECT OF ISOLATION ON THE

COLONIZATION OF AN ARTIFICIAL SUBSTRATE

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ABSTRACT:

An experiment was designed to test the prediction of the island biogeographic theory in regard to the relationship between colonization rate and the isolation of an island from potential colonizing sources. Both taxa diversity and abundances as well as individual abundances, were documented for two sites over time. Bottle brushes designed to represent an algal clump, the presumed colonizing source, were placed in an isolated sand patch site and a non-isolated reef crest site on the West Fore Reef at Discovery Bay, Jamaica. Collections over a five day period revealed that the total infauna taxa represented at the sand site appears to reach a maximal value before leveling off, while individual abundances continue to increase over time. No differences in total taxa existed between the isolated and non-isolated substrates after five days. However, the total number of individuals was higher at the non-isolated site than the isolated site after the same time period. The lack of a difference in ~~total~~ total taxa number over time between sites is thought to be due to either, ¹ a storm during the study affecting turbulence on the reef crest, ² a limited number of taxa available from the algal colonizing source, or ³ the equally rapid dispersal capabilities of most of the infaunal organisms. The lower abundance of organisms on the isolated site at the conclusion of our experiment indicates that colonization decreases with substrate isolation from the colonizing source.

INTRODUCTION:

Post studies relating island biogeographic theory to various marine substrates such as sponges or coral heads have dealt primarily with the empirical form of the theory, relating substrate area to species number. (Uebelacker, 1977, Reicher and Baehman, 1979.) However, MacArthur and Wilson's (1963, 1967) equilibrium hypothesis states that there is a dynamic aspect to the theory. They propose that opposing rates of immigration and extinction determine the number of species on an island. A dynamic equilibrium is attained when these rates are equal. Whereas extinction rates are most closely linked to an island's area, which dictates population sizes, the immigration rates are affected by an island's isolation, which determines colonization prospects. Island biogeographic theory predicts that the more isolated an island ^{is from its colonizing source}, the lower the rate of immigration to that island. In the present study, this prediction is tested.

It is difficult to assess absolute immigration rates for to do so involves being aware of all immigrations and extinctions through time. However, it is possible to study colonization through time. Schoener (1974) observed convex colonization curves for her artificial sponge substrates. However, she was unable to detect significant differences between the colonization curves of isolated and non-isolated substrates. This study looked at the colonization process on an artificial algal substrate. Species composition and abundances through time were monitored at two sites in order

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to determine their relationship to substrate isolation from the colonizing source. We also hoped to observe any differences in dispersal abilities between the colonizing species. We hypothesized that the more isolated substrate would show slower colonization in terms of both ^{1) species number and diversity, 2)} and total number of organisms. Further, we speculated that copepods would be the earliest colonizers due to their high abundances in the water column and their diel migration patterns which promote their dispersal.

We were required to make several assumptions in our study. First, we assumed that our bottle brushes were accurate representations of an algal clump and did not exclude or offer preferences to certain species. Our analysis of an algal clump's species composition and relative abundances showed this assumption to be a good one. Second, we assumed that there is a defined source of colonizers, namely algal clumps, and that the two areas chosen don't represent two separate communities altogether. Third, we assumed that the isolated substrate was a great enough distance from the colonizing source to allow for a gradient in dispersal abilities to be observed.

Although the sand patch surrounding the isolated substrate was void of colonizing organisms, not enough is known about algal cryptofauna dispersal to substantiate this assumption. Fourth, extraneous factors such as predation and turbulence were assumed to be similar at both sites. This assumption is questionable due to wave action created at one of the sites during

a storm. Also, one might intuitively expect predation levels to be higher where food abundances are higher at the non-isolated site. Fifth, we assumed that the brush substrates were sufficiently separated such that each brush had an equal probability of colonization. Finally, we assumed that our collections are accurate representations of the cryptofauna colonizing the brush. Most of the organisms are motile and thus possibly exhibit diel patterns. By collecting during the day at a specific hour, we minimized any inconsistencies due to these patterns.

MATERIALS AND METHODS:

The experiment was conducted at two sites on the west fore reef at Discovery Bay, Jamaica, over a five day period beginning February 27, 1984. To simulate isolated and non-isolated island habitats along the reef bottom, two sites were chosen, each within a depth of 2 meters. One was on the reef crest due north of the laboratory boat dock and the second, 30 meters from the crest site in a back reef sand patch. Acropora palmata and Montastrea cavernosa comprised much of the coral substrate on the reef crest. Dense algal clumps covered much of the exposed surface and was assumed to be the source of the colonizing infauna. The second site was located in a large sand patch surrounded by Thalassia beds. This site represented the isolated

island habitat and was 15 meters from potential colonizing sources.

A set of nine bottle brushes, each with a volume of 500 cm^3 , were used as the artificial substrates to be colonized. The brushes were secured in an iron grate and separated by at least 15 cm to eliminate substrate overlap. A single grate was placed at each site.

Collections were to be made on the first, third, and fifth days of exposure at both sites. Severe weather conditions forced the cancellation of the third day collection at the reef crest site. The collections were made using sealed plastic bags, water samples were taken at each site to determine plankton abundances in the area surrounding the brushes. Sediment and algae samples were also collected from the sand and reef crest sites respectively to determine their biotic composition.

In the lab, each bottle brush was thoroughly rinsed with filtered sea water and the resulting rinse water poured through a 75 μm mesh filter. The ~~filtrate~~ ^{filtered material} was preserved in a 10% formalin solution. Dissection scopes were used in examining the samples. The organisms were classified into known taxonomic groupings rather than to species due to our deficiency in identification abilities. As a result, the species number and species diversity values are underestimated.

RESULTS:

Examination of the breeches revealed a very specific trend of colonization for both sites. Each site had a low number of organisms present on the first day with increasing abundance through the study period. (Figure 2) Total organisms present at the conclusion of the study showed that the non-isolated island habitat contained a significantly larger number of organisms than the isolated site. This seems to reflect that differing immigration rates do exist between the two sites due to their relative distances from the immigration source. Copepods compose the largest class of colonizing organism at all times and at both sites, followed by isopods, polychaete worms and amphipods.

A significant increase in the total number of taxonomic groups was seen for both the isolated and non-isolated substrate over the five day period (Figure 1) Total number of taxa did not differ significantly between sites at the conclusion of the experiment. Species diversity, measured by the Shannon-Wiener diversity index, also increased significantly during the study but showed ^{little} difference between sites with time. (Figure 3)

Relative abundance of the four general taxa groups recorded remained constant throughout the study period in all sites and times. (TABLE 1, FIG. 4) One exception was the polychaete worms at the reef crest site, which show a slight rise by the 6th day relative to that of the first day. This rise could be due to a ~~slower~~ ^{somewhat} slower rate of colonization by these worms compared with the other more mobile colonizers. Comparison

of the relative abundances of these taxa with the relative abundances found on an algal sample of Bryothamnion triquetrum collected on the reef crest, showed very similar percentage infauna composition. (Table 2.) This supports our claim that the algal dumps represent our colonization source.

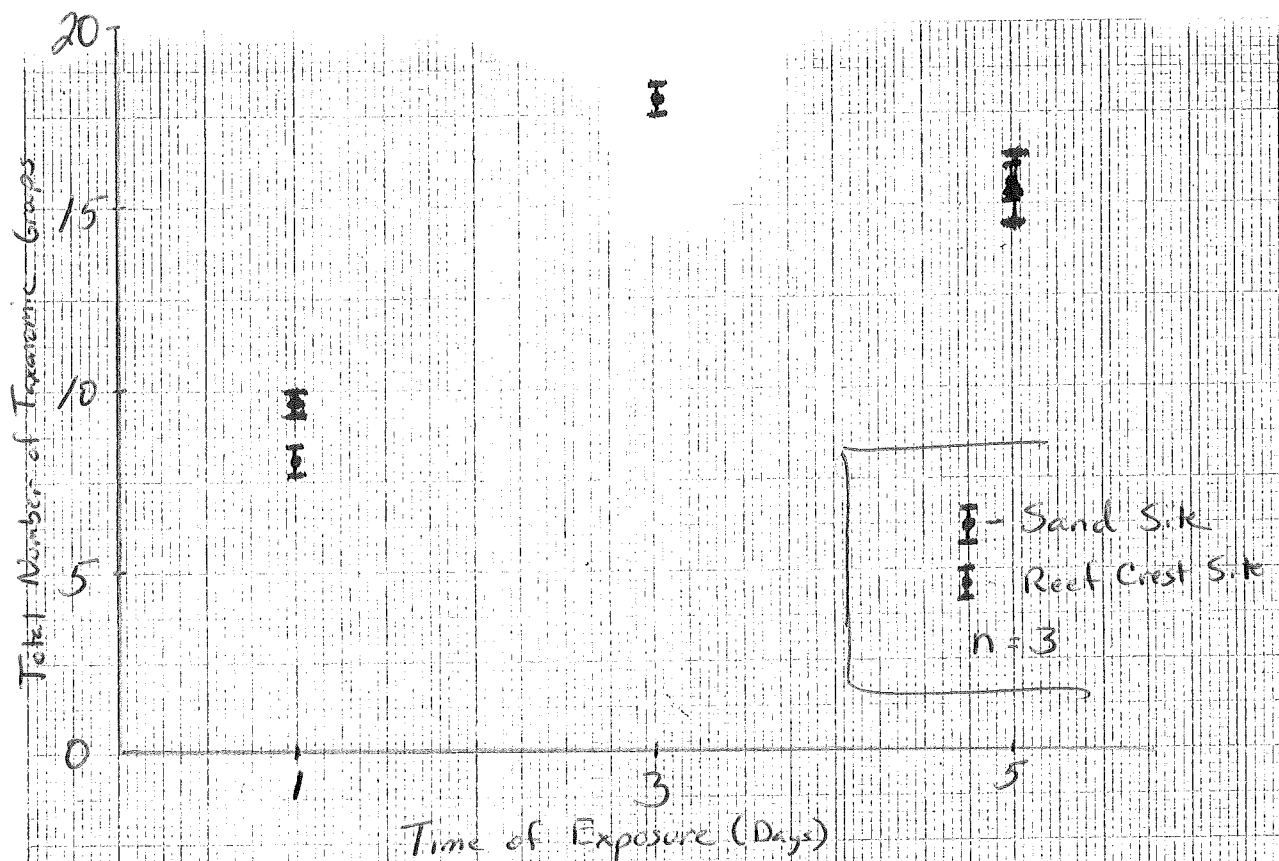


Figure 1 Total number of taxonomic groups found at each site versus the time of exposure to colonists in days (Bars represent standard error)

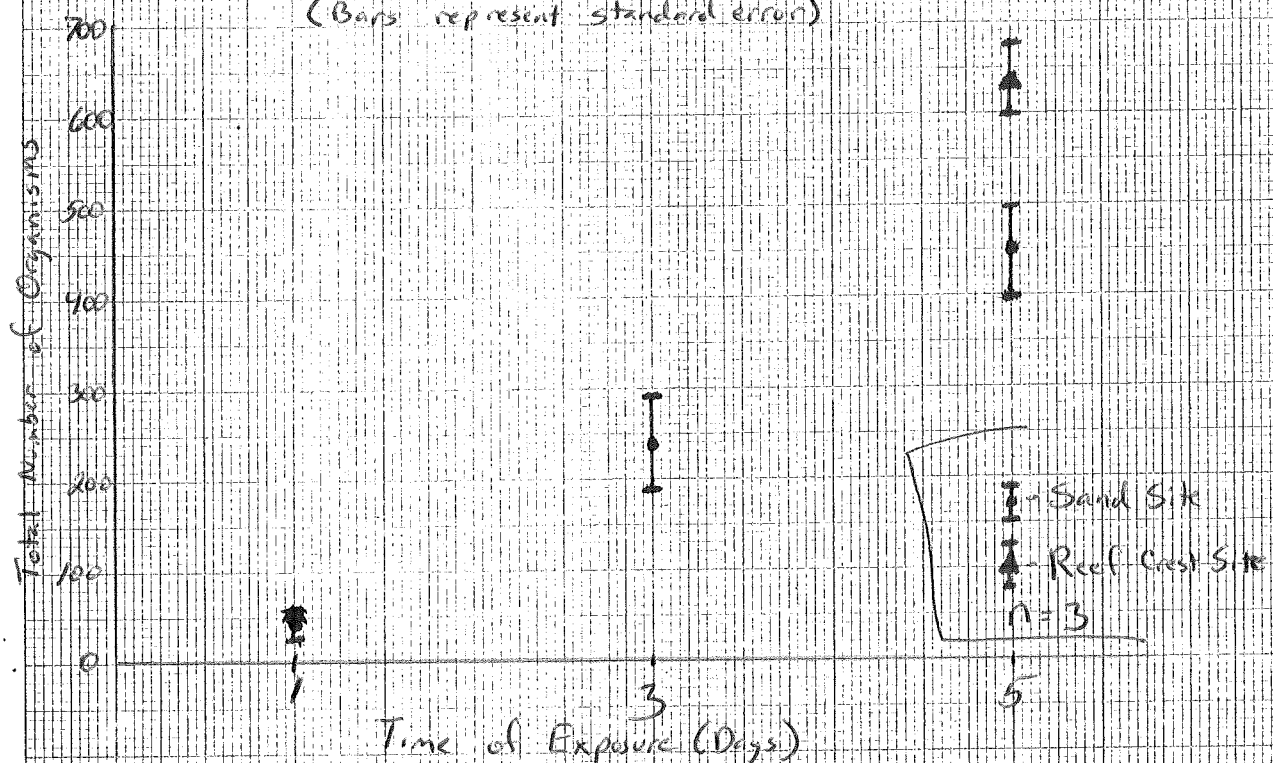


Figure 2 Total number of organisms found versus length of exposure in days (Bars represent standard error)

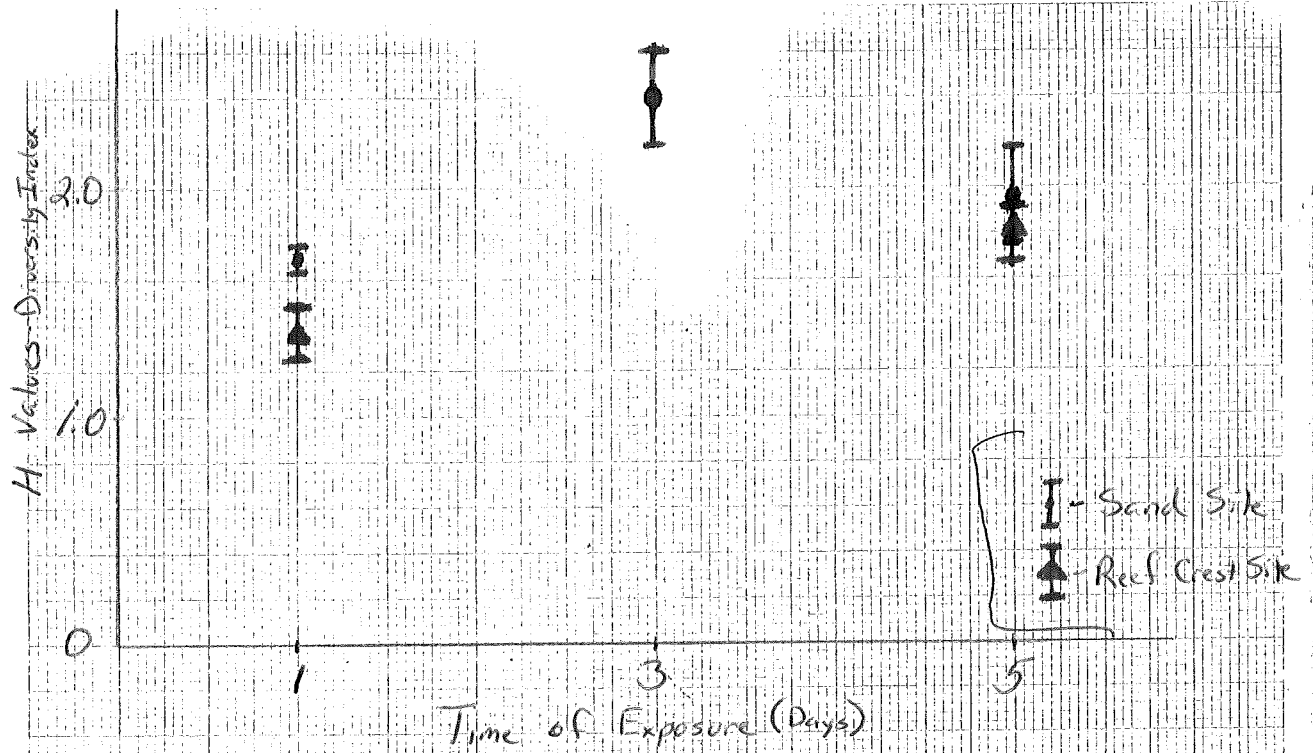


Figure 3. Diversity index values (H) of organisms found versus length of exposure in days at each site (Shannon-Weiner Diversity Index) (Bars represent standard deviation)

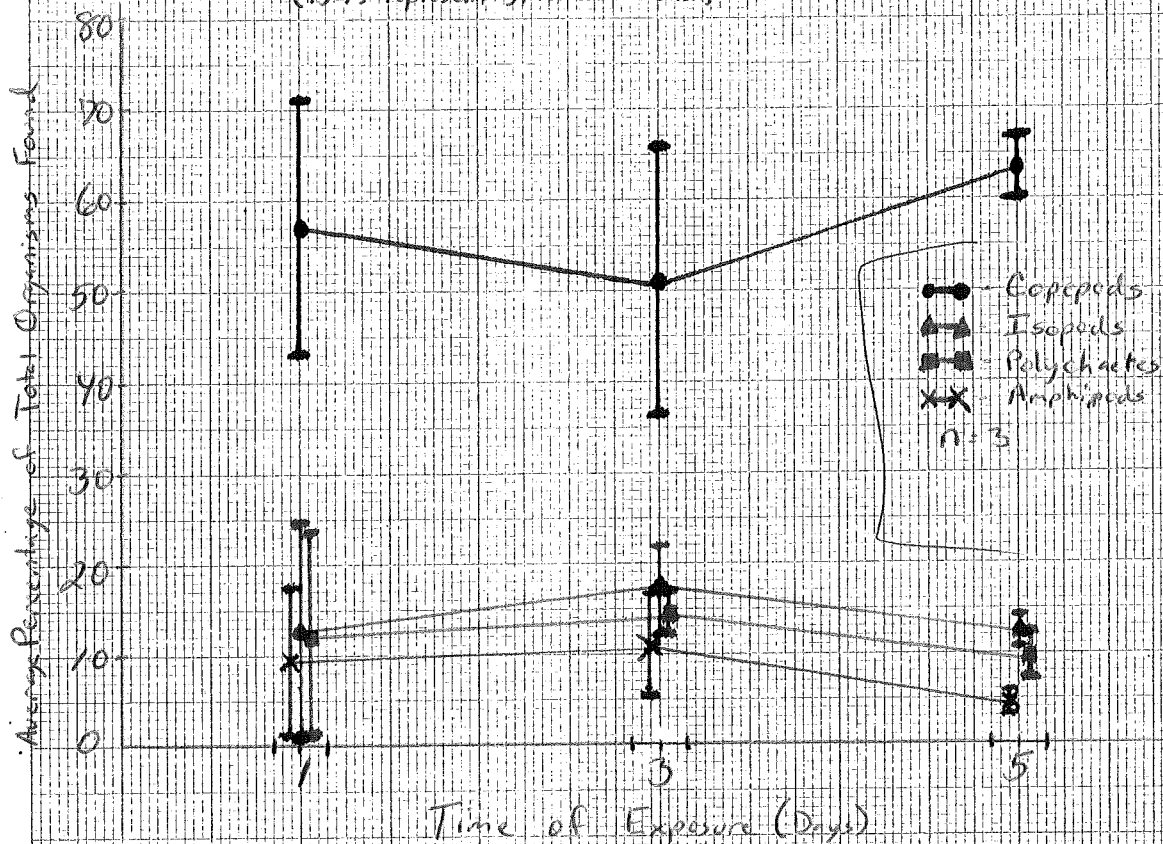


Figure 4. Average percentage of total organisms found versus length of exposure for the isolated sand site (Bars represent standard deviation)

Table 1 Taxa as Percentage of Total Organisms Present at both Study Sites

Taxa	Day 1		Day 3		Day 5	
	Sand	Reef Crest	Sand	Sand	Reef Crest	
Copepods	57.1 ± 14.49	63.8 ± 1.89	51.1 ± 15.47	63.5 ± 3.38	68.1 ± 2.48	
Isopods	12.9 ± 11.91	12.57 ± 7.41	17.6 ± 5.06	12.7 ± 1.78	10.9 ± 2.44	
Polychaetes	12.7 ± 11.01	4.56 ± 3.31	14.4 ± 2.59	9.8 ± 2.16	11.5 ± 3.08	
Amphipods	9.4 ± 8.29	9.77 ± 8.64	10.8 ± 5.72	5.2 ± 1.65	4.1 ± 0.85	

Table 2 Taxa as Percentage of Total Organisms Present in the Algal Species

Bryothamnion triquetrum Collected at the Reef Crest Site

Taxa	Percentage of Total Organisms	
Copepods	76.1%	
Isopods	10.2%	n=1 sample
Polychaetes	6.0%	
Amphipods	5.0%	

DISCUSSION:

Our findings in regard to the relationship between the number of taxonomic groups present with time, and substrate isolation are consistent with those of Schoener (1971). The number of taxa as well as the species diversity were found not to differ significantly at the end of a five day period between the two sites. This is in contradiction to our first hypothesis and to the prediction of island biogeographic theory. However, this contradiction may be superficial. It is possible that heavy wave action at the reef crest site limited the colonization of certain species or groups at that site. This would have explained the fifth days value overlap between sites, but not the first days.

Another possibility is that the infauna of our algal source reflect a limited number of taxa, at least through our classification abilities, and that most of these taxa are represented on both substrates very early in the colonization process. This would produce the asymptotic curve that appear to exist for taxon number in the sand substrate and presumably in the reef crest also, although two points don't allow us to be conclusive on curve shape. A final explanation is that the gradient of dispersal abilities among the infauna is not sharp enough to be reflected in our study. Perhaps the gradient is not well defined, and the infauna are nearly equal in their dispersal capabilities. Another possibility is that the isolation of the sandy substrate brushes was not great enough to allow the gradient in colonizing ability to appear. Most

of the infauna observed were motile and thus very capable of active dispersal. This idea of equal dispersal abilities is supported by the relative abundance data.

The relative abundances of the infauna were found to be fairly consistent across time and substrate isolation. Even the algal colonizing source showed similar relative abundances. This implies that the various infauna taxa possess fairly equal dispersal capabilities, allowing them to arrive in proportions reflecting their relative abundances on other substrates. If dispersal capabilities were to be nearly equal, hence causing the infauna to arrive at a new substrate in temporal proximity, then taxa number would initially increase rapidly and approach an asymptote fairly quickly. This is what appears to happen, at least for the sand substrate for which we have three points. Although most of the taxa may be represented early in the colonization process, the infauna abundances may continue to increase with time.

The trends observed for the number of individuals present with time between the isolated and non-isolated sites supports our second hypothesis. It also provides insight into the overall colonization process. Although the number of taxa appeared to level in time, the number of individuals increased consistently with time, indicating that colonization is continuing to occur through the five day period. These increases could not be accounted for by reproduction alone.

Furthermore, the increase was greatest at the non-isolated site, indicating that the colonization rate was higher there than at the isolated site. Thus, the prediction

of island biogeography regarding isolation is supported by our data.

In summary, we found that colonization does decrease as an island's isolation from the source of colonizers increases. This decrease in colonization is not apparent in terms of taxon number because either, ¹⁾ the heavy wave action at the reef crest inhibited colonization by certain species, ²⁾ there is a limited number of taxon available as colonizers, ³⁾ or the gradient in dispersal abilities was not great enough to be reflected in our study. However, the decrease in colonization at the isolated site is apparent in terms of ^{the} number of colonizing individuals, which showed a significantly lower value at the isolated sand spot after five days. Thus, our data, is in support of the isolation component of the island biogeographic theory.

The findings of our study raise questions that provide areas for further study. The dispersal mechanisms of the cryptofauna taxa are not well known. Studies of their dispersal abilities would reveal a great deal about their specific colonization abilities and would explain many unknowns found in our experiment. Habitat preference, rate of colonization and mode of dispersal are key aspects in determining the colonization process for these organisms.

The algal community appears to be the source of the colonizing invertebrates that we examined. Our single sample analysis revealed a high degree of overlap of taxa between the

we should have quantified this

study site and the algal dump. This overlap is probably observed throughout the algal community on the reef crest but to what extent and in what abundances are these taxa represented. Do the taxa and individual abundances vary between different species of algae even though they are in the same habitat?

Also, a long term study should be conducted to determine if the trends we found are in fact maintained throughout the colonization period or whether other influences such as competition or predation determine the final species composition. Determination of the isolation effect upon equilibrium species diversity should be an essential part of any further study.

Very good study -

References:

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- 2) Diamond, J. 1975. The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves, Biol. Conserv. England, Volume 7, pp 129-146.
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- 7) Schoener, A. 1974. Experimental Zoogeography: Colonization of Marine Mini-Islands. The American Naturalist, Volume 108 No 964. pp. 715-738.

References (continued):

- 8) Uebelacker, J.M. 1977. Cryptofaunal Species/Area Relationship in the Coral Reef Sponge, *Gelliodes Digitalis*. Proceedings, Third International Coral Reef Symposium, University of Miami, Miami, Florida, pp 69-73.
- 9) Westinga, E and P.C. Hoetjes, 1981. The Intrasponge Fauna of *Spheciospongia vesparia* (Porifera, Demospongiae) at Curacao and Bonaire. Marine Biology, Volume 62, pp 139-150.

Appendix:

Table 2 - Infauna Taxa Abundance on Bottle Brushes

Numbers of Individuals Found (standard error indicated) n=3

Organism	Day 1		Day 3		Day 5	
	Sand	Reef Crest	Sand	Sand	Reef Crest	
Copepods	26 ± 15.01	34 ± 2.89	116 ± 16.7	288 ± 32.90	435 ± 29.44	
Cyclopoids	17.7 ± 10.33	32 ± 2.54	67 ± 4.15	187 ± 10.39	227 ± 8.66	
Harpacticoids	7 ± 4.04	0.3 ± 0.33	39.3 ± 10.97	81 ± 19.63	189 ± 17.89	
Calanoids	1.6 ± .66	1.3 ± 0.87	9.3 ± 3.17	20.3 ± 4.91	19 ± 2.89	
Isopods	4.6 ± 2.42	6.6 ± 2.42	116 ± 16.7	57 ± 5.78	70 ± 11.55	
Polychaetes	3.6 ± 1.21	2.3 ± 0.87	35 ± 8.08	46 ± 10.96	73 ± 9.8	
Amphipods	3 ± 0.98	5 ± 2.54	23 ± 4.62	24.7 ± 7.51	27 ± 4.50	
Average Number Individuals Found	41.3 ± 19.05	52.7 ± 3.29	239 ± 52.5	453 ± 54.3	638 ± 39.8	
H Values	1.69 ± 0.05	1.38 ± 0.11	2.42 ± 0.21	1.96 ± 0.2	1.82 ± 0.1	
Total Number Taxa Represented	8.67 ± .88	9.33 ± .67	17.67 ± .88	15.67 ± .88	15.33 ± 1.33	

Table 2 - Organisms found over the five day study period at both sites
Average Numbers Found

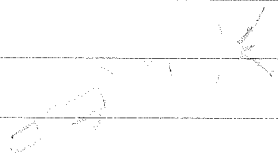
Taxa	Day 1		Day 3		Day 5	
	Sand	Reef Crest	Sand	Sand	Reef Crest	
Copepods-Calanoids	1.6 ± 1.15	1.3 ± 1.5	8.3 ± 5.58	20.3 ± 8.5	19.0 ± 5	
Cyclopoids	17.7 ± 17.9	3.2 ± 4.4	67. ± 57.2	187 ± 18	227 ± 15	
Harpacticoids	70 ± 7	0.3 ± 0.58	39.3 ± 19	81 ± 34	189 ± 31	
Isopods A	4.3 ± 3.8	6.3 ± 3.8	34. ± 14.6	57 ± 10	67 ± 20	
B	0.3 ± 0.58	0.3 ± 0.58	103 ± 14.6	0	3.3 ± 1.5	
Polychaetes A	2 ± 1.7	0.7 ± 1.15	0 ± 0.6	0	1 ± 1.7	
B	0.3 ± 0.58	0	0.3 ± 0.58	2 ± 2	1 ± 1	
C	0.7 ± 0.58	0.7 ± 0.58	0.3 ± 0.58	7.3 ± 6.8	4 ± 3.5	
D	0	0.3 ± 0.58	0.1 ± 1.0	0	1.3 ± 2.3	
E	0.7 ± 1.15	0.3 ± 0.58	11.3 ± 4.9	16.7 ± 6.1	43 ± 12	
F	0	0	13.0 ± 4.9	10 ± 3.6	14 ± 4.6	
G	0	0.3 ± 0.58	4 ± 3.6	0	4.6 ± 4.5	
H	0	0	4.3 ± 6.7	8 ± 2.6	4 ± 3.6	
I	0	0	0	1 ± 1.7	0	
J	0	0	1 ± 1	0.3 ± 0.58	0	
(intermediate) K	0	0	0	0.7 ± 0.58	0	
Amphipods A	3 ± 1.7	4.3 ± 3.2	15.7 ± 6.0	24.7 ± 12.9	27 ± 7.8	
B	0	0.7 ± 1.13	7.3 ± 3.1	0	0	
Decapods	0	0.7 ± 0.58	3.0 ± 0	7.3 ± 0.58	3 ± 2	
Ostracods	2.3 ± 3.2	1.7 ± 1.15	16.6 ± 7	14.7 ± 3.1	23 ± 4.4	
Worm	0	0	4.7 ± 7.2	5.7 ± 1.15	6.3 ± 2.5	
Velliger larvae	0.7 ± 1.15	0	2.7 ± 3.1	0	0	
Nauplius	0	0.3 ± 0.58	1.3 ± 1.5	0	0	
Anenomes	0.7 ± 1.15	0.3 ± 0.58	11.3 ± 5	9.3 ± 2.5	12 ± 2.6	
Chaetognaths	0	0	2.7 ± 3.1	1.3 ± 1.2	0	
Planula	0	1.0 ± 1.7	0	0	0	
Medusae	0	0	0.3 ± 0.58	0	0	
Foraminiferans	0	1.0 ± 1.7	0.3 ± 0.58	0	0	

Polychaete

Size

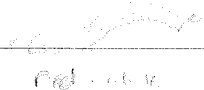
Adult

A



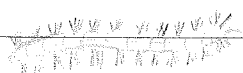
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B



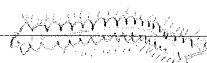
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C



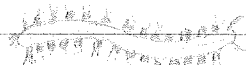
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D



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E



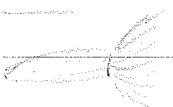
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F



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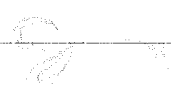
Intermediate



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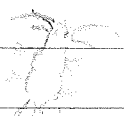
Larvae

G



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H



I

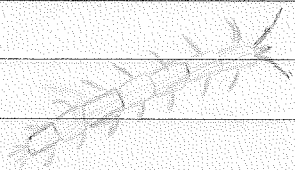
Amphipods →

Polychaete

~ Size

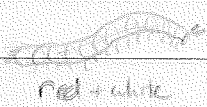
Adult

A -



3mm

B



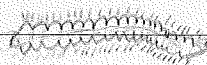
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C



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D



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E



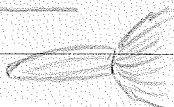
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F



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Intermediate



1.75mm

Larvae

G



1mm

H



Adult

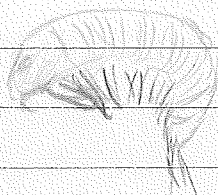
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Amphipods →

Amphipod

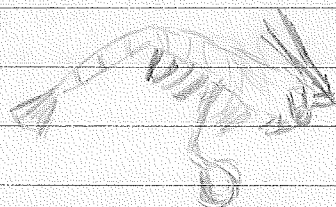
Size

1



.5

2



2 mm