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***Successional Processes in the Benthic Invertebrate Communities
at Gray's Reef National Marine Sanctuary***

An Honors Thesis submitted in partial fulfillment of the requirements for Honors in
Department of Biology.

By
Alexis Bivens

Under the mentorship of *Dr. Daniel Gleason*

ABSTRACT

While the process of community development has been studied in terrestrial habitats since the turn of the 20th century, similar information is not as readily available in marine systems. Understanding patterns of community development is essential to predicting recovery potential and to designing effective marine protected areas. In the South Atlantic Bight, invertebrate communities on hard substrata can differ significantly from one rocky outcrop to another, but the factors driving these differences are not well understood. I documented the initial development of the benthic invertebrate community at Gray's Reef National Marine Sanctuary (GRNMS) to address the prediction that this system does not demonstrate a predictable pattern of succession. This prediction was investigated by tracking community development on natural substrate plots (30 x 30 cm) that were cleared of benthic organisms each summer between 2010 and 2015, and in each case were allowed to recover for one year. Comparisons of species richness, diversity, and percent cover showed that one year was not sufficient for the plots to recover to their original composition. While plots cleared in different years did exhibit similar patterns of species richness and diversity after one year of recovery, closer inspection revealed that the particular species present was not consistent across years. In addition, the percent cover varied from year to year. These results indicate that succession models do not apply to the sessile benthic invertebrate community of GRNMS.

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Introduction

According to classical models, ecological succession is a pattern of community development in which a sequence of species, beginning with pioneer species and ending with the climax species, sequentially occupy a habitat after a disturbance (Clements 1916). The definition of ecological succession has been modified over the years. Odum (1969) described incorporated the differences between early and late successional systems. For example, early successional systems tend to have smaller biomass, lower stability, and lower diversity than late successional systems (Odum 1969). Connell and Slatyer (1977) described three different mechanisms by which succession might take place: facilitation (pioneer species promote settlement of other species by altering the environment), inhibition (present species suppress settlement of another species), or tolerance (present species withstand negative effects caused by another species). Although the concept of ecological succession has evolved over the years, the general consensus is that its presence can be verified if community development is both orderly and predictable (Clements 1916, Connell and Slatyer 1977, Odum 1969).

Successional theory was initially developed in terrestrial habitats including moors, dunes, and forests (Clements 1916), but has since been applied to other communities including those in the marine environment (Connell and Slatyer 1977, McDougall 1943, Scheer 1945, Sutherland and Karlson 1977). The succession paradigm has been challenged by many scientists and evidence supporting it is still unclear. In Newport Harbor, California, evidence of sequential patterns of development have been documented within the benthic community (Scheer 1945). Artificial glass and metal plates were cleared and examined for successional patterns in which the first organisms

to colonize were bacteria, algae, and sometimes hydroids, then diatoms, followed by bryozoans, and lastly communities of *Mytilus*, but only in the presence of bryozoans. Although there was evidence supporting the traditional succession models, organisms such as bryozoans, *Ciona*, and *Styela* also exhibited seasonal variation which altered the composition of the community (Scheer 1945).

Other studies have been conducted in which no successional patterns were observed within the marine habitat. Both McDougall (1943) and Sutherland and Karlson (1977) examined the benthic community off the coast of Beaufort, North Carolina, which is located within the South Atlantic Bight (SAB), and consists of sponges, cnidarians, ascidians, and bryozoans. McDougall (1943) determined that the community colonizing pier pilings was short-lived and that most species exhibited seasonal variation. As a result, species died within the winter months and species fluctuated in number which made it difficult to predict the final community composition (McDougall 1943). Like McDougall, Sutherland and Karlson (1977) also discovered that the benthic community off the coast of Beaufort was relatively unpredictable. In some situations, the inhibition model of succession was supported, however, there were dramatic differences in the species richness from year to year. Sutherland and Karlson (1977) proposed that the developmental process in the fouling community of Beaufort, North Carolina was influenced by inconsistencies in recruitment patterns. These observations resulted from three outcomes: 1) variation in the ability to invade occupied substrate (inhibition, unpredictable initial development), 2) variation in resisting larval invasion due to life stage (larvae vs adult), and 3) most adults were short lived (annual mass mortality)

(Sutherland and Karlson 1977). Therefore, the developing community was always changing and unpredictable, so the successional model was not applicable.

In addition to the benthic systems outlined above, other hard substrate communities within the SAB can be found subtidally in Gray's Reef National Marine Sanctuary (GRNMS). This sanctuary is located approximately 34 km off the coast of Sapelo Island, Georgia. It is composed of live bottom reefs with two distinct habitat types: 1) ledges and ridges of rocky surfaces; and 2) sandy bottoms that separate adjacent ledges (Hunt 1974). The percent cover of sessile benthic invertebrates, such as sponges, corals, ascidians, and bryozoans, is high on rocky substrates because of their limited availability (Kendall et al. 2005, 2007).

To determine if traditional succession models apply for the sessile, benthic communities of GRNMS, recolonization patterns were documented on natural substrata each year over the course of five years. If development of the benthic, sessile community at GRNMS is predictable, then plots cleared of benthic organisms in different years should show similar community composition after one year of development. Previous studies conducted within the SAB (Sutherland and Karlson 1977) and at GRNMS (Poirson 2014) provided evidence that traditional successional models may not apply in this system, thus I predicted that benthic plots cleared in different years would demonstrate dissimilarities in community composition after one year of development. The presence or absence of succession was evaluated by comparing species richness, diversity, and percent cover over time.

Methods

I. Study Site and Experimental Design

This study was conducted at Gray's Reef National Marine Sanctuary (GRNMS, 31.3821° N, 80.8655° W) at approximately 18 m below the surface. The sessile benthic community on rocky outcrops at GRNMS is composed of multiple species of invertebrate phyla including representatives of the Porifera, Cnidaria, Bryozoa, Arthropoda, and Chordata (Harding and Henry 1990). To investigate if succession in this community is predictable, diversity and percent cover were analyzed for five years. Beginning in July 2010, 10 plots, 30 x 30 cm (length x width), were established on natural substrate. Plots were marked using 0.5 x 15 cm (diameter x height) stainless steel rods that were embedded into the ground and secured with underwater epoxy. These rods were used as a guide to position a PVC framer allowing photographs to be standardized among sample dates. Plots followed the edge of the rocky outcrop where percent cover and biodiversity were highest. On an annual basis, plots were photographed and then cleared by hand with the aid of a rock hammer.

II. Image Analysis

From 2010 to 2015, photographs of the 30 x 30 cm plots were taken annually in the months of July or August to document the accumulation of sessile invertebrates over the previous 12 months. Either an Olympus SP-320, 7 megapixel camera with an Epoque World Company ES-150 DS strobe (first four years) or an Olympus OM-D, E-M5, 16 megapixel camera with Sea & Sea YS-D1 strobe (last two years) was mounted onto a 30 x 30 x 55 cm (length x width x height) PVC framer.

Images of the biota, including sessile invertebrates and algae, were quantified through Coral Point Count with Excel Extensions (CPCe). One hundred and seventy-five points were randomly distributed across the image within the 30 x 30 cm plot. Organisms

occurring under these points were identified by eye to the lowest possible taxonomic level. The data collected was then processed through the CPCe program in an excel file in which species richness, species diversity, and percent cover were quantified.

III. Statistical Analysis

To determine if development of the sessile invertebrate community at GRNMS proceeds via an orderly successional process species richness, percent cover, and the Shannon-Wiener diversity index were calculated for each year. One-way analysis of variance (ANOVA) was used to test for differences in species richness, diversity, and percent cover between plots photographed prior to clearing and plots cleared annually in 2011, 2012, 2013, 2014, and 2015, as well as the differences between all of the plots cleared annually.

Results

The goal of this study was to determine if development of the benthic, sessile community of GRNMS proceeds by an orderly successional process. Based on previous studies conducted in this region, I predicted that plots cleared of benthic organisms would demonstrate dissimilar patterns of community composition after one year of development. In 2010, the control group was significantly higher for both species richness and diversity than the plots in all other years that were cleared and then allowed to recover for one year (d.f. = 5, 54, $F = 12.3$, $P < 0.05$, one-way ANOVA; Figs. 1 & 2). However, all cleared plots were similar across years for both species richness and diversity. A one-way ANOVA was performed on the annually developing communities to further investigate the composition of the major groups (Coral, Bryozoans, Ascidians, Zoanthids, Macroalgae, Coralline Algae, and Dead H/B Complex). In 2010 and 2011,

even though these two years had similar total percent cover (Fig. 3), major groups such as Coral (d.f. = 1, 18, $F = 5.48$, $P < 0.05$, one-way ANOVA), Sponges (d.f. = 1, 18, $F = 8.86$, $P < 0.05$, one-way ANOVA), Ascidians (d.f. = 1, 18, $F = 33.1$, $P < 0.05$, one-way ANOVA), Macroalgae (d.f. = 1, 18, $F = 13.8$, $P < 0.05$, one-way ANOVA), and Dead H/B Complex (d.f. = 1, 18, $F = 10.8$, $P < 0.05$, one-way ANOVA) were statistically different in 2010 when compared to 2011 (Fig. 4). Similarly, comparisons among the years when plots were cleared (i.e., 2011-2015) demonstrated wide differences in the percent cover of various species groups even though no significant differences in species richness or diversity were detected (Fig. 4). Finally, it was noted that individual species or taxa present after one year of recovery in cleared plots were not consistent. When comparing across years it was found that individual species/taxa either 1) disappeared completely, 2) were present initially but disappeared and reappeared randomly over time, or 3) were not present in the initial group but appeared at random times throughout different years (Table 1).

Discussion

The main objective of this research was to determine if traditional successional models apply to the development of the sessile, benthic community on natural hard bottom substrate at GRNMS. I hypothesized that if succession occurs in this system, plots cleared of sessile benthic invertebrates across a series of years should exhibit similar community composition after one year of re-establishment. The succession model was partially supported because there were no statistical differences in species richness or diversity for plots cleared in five different years and then allowed to recover for one year. However, these results did not provide total verification that succession occurs in this

community because species richness and diversity ignore finer details of the recovery process. Even though these benthic communities may have identical species diversity or percent cover they can be composed of completely different species altogether (Poirson 2014). In fact, this was exactly what was observed. In plots that were cleared annually 54.5% of species/taxa identified either 1) disappeared completely, 2) were present in the initial climax community but disappeared and reappeared randomly over time, or 3) were not present in the initial group but appeared randomly throughout different years. Thus, it is not possible to predict which species/taxa will be present or dominant after one year of recovery.

One observation that was important to note was that within all cleared years, there were fluctuations in the total amount of cover of the major groups, Macroalgae, Ascidians (*Amathia* sp.), other live (*Aglaophenia* sp.). In all cleared years, except 2012, these three major groups made up the majority of the total percent cover each year. Each of these organisms have a similar morphology in which macroalgae and *Amathia* sp. are primarily bush-like and usually form a thick mat on the surface of the substrate. *Aglaophenia* was more rope-like and was usually entangled in *Sargassum* and *Amathia*. Although, the successional model was not supported within one year of development at GRNMS, it is particularly significant that these organisms dominated within four of the five years studied.

With the evidence presented, we can make a number of suggestions as what is influencing the algal-bryozoan blooms. It appears that microalgae and some bryozoans may favor cleared substrate and may have a major impact on the community structure because they are able to occupy large areas of the substrate. These results were similar to

other studies in which algae and bryozoans have been found to be major space occupiers and one of the first organisms to settle within the marine communities in both California and the SAB region (McDougall 1943, Scheer 1945). However, we cannot assume that these blooms will lead to a sequential pattern of development without further investigation. If these blooms do influence the development of the benthic community of GRNMS, managing the live reef would be more attainable. It was found that surfaces covered by algae, hydroids, and sediment are less favorable than clean surfaces for the attachment of other sessile organisms due to the fact that low growing organisms, like some sponges, tunicates, and other encrusting organisms, were smothered by these environmental factors (McDougall 1943). By removing algae and bryozoans from the substrate and increasing available surface area on the substrate, other organisms may be able to inhabit the area. Future projects should consist of extensive surveys to determine what factors are involved in stimulating algae-bryozoan blooms and investigate individual relationships between the blooms and organisms.

Figures and Tables

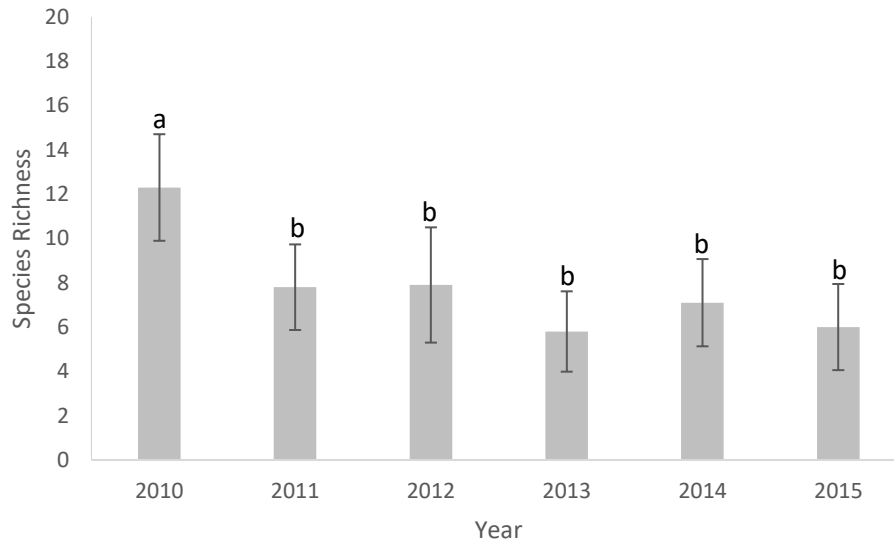


Figure 1. Species richness of the annual developing plots. Error bars represent ± 1 SD. $N = 10$ for each year. A one-way ANOVA identified significant differences among years overall (d.f. = 5, 54, $F = 12.3$, $P < 0.05$), but years with the same letter above the bar were not significantly different.

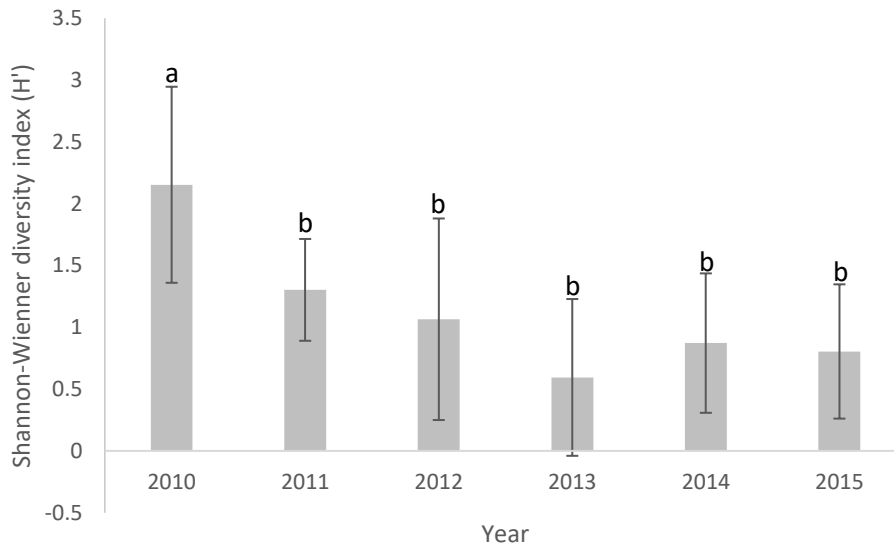


Figure 2. Species diversity of the annual developing plots. Error bars represent ± 1 SD. $N = 10$ for each year. A one-way ANOVA identified significant differences among years overall (d.f. = 5, 54, $F = 7.46$, $P < 0.05$), but years with the same letter above the bar were not significantly different.

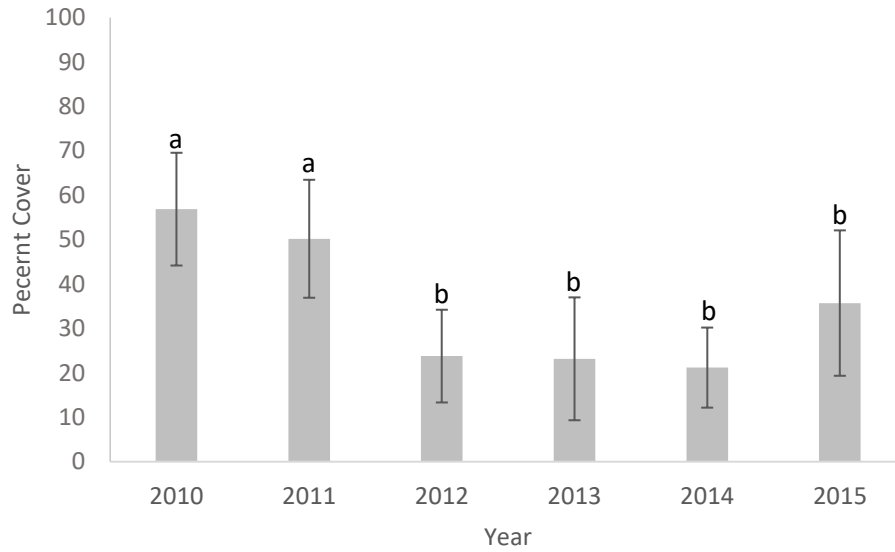


Figure 3. Percent cover of the annual developing plots. Error bars represent ± 1 SD. $N = 10$ for each year. A one-way ANOVA identified significant differences among years overall (d.f. = 5, 54, $F = 14.2$, $P < 0.05$), but years with the same letter above the bar were not significantly different.

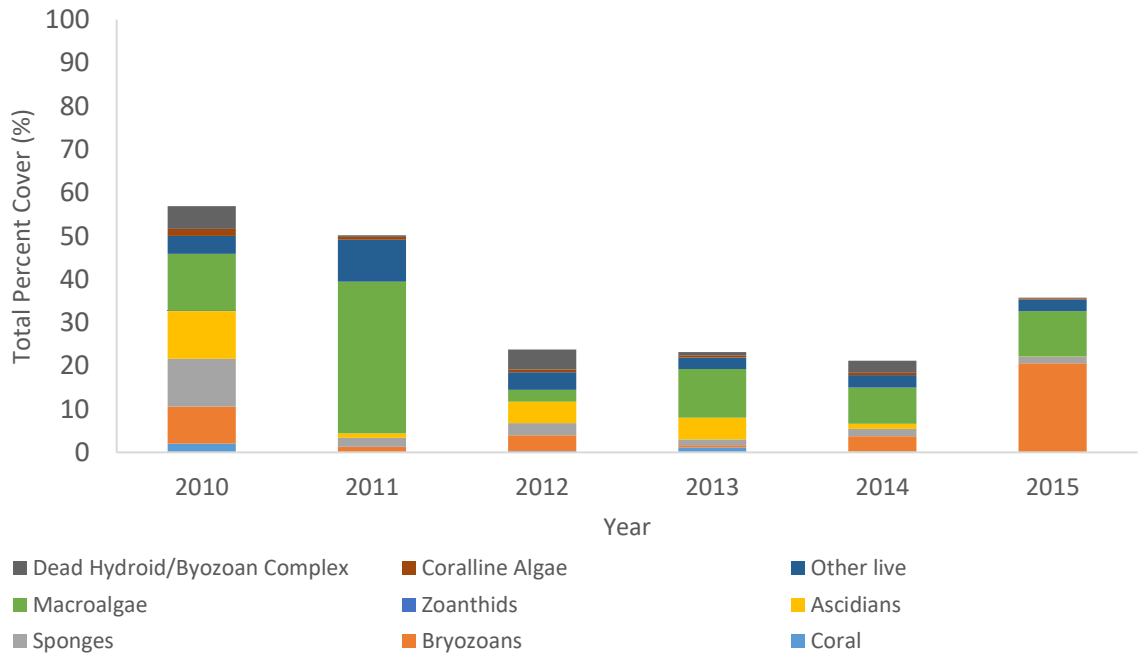


Figure 4. Percent cover of the major groups of organisms in all annually cleared plots.

Table 1. Individual species or taxa present in each year of the study. Table is separated into four sections comprising a) species/taxa present in all years, b) species/taxa that were present in 2010 and then disappeared in subsequent years, c) species/taxa that were present in 2010 and then randomly appeared in subsequent years, and d) species/taxa that were not present in 2010 but then appeared in at least one subsequent year. X represents that the species is present.

Present all years

Species	2010	2011	2012	2013	2014	2015
Other Bryozoan	X	X	X	X	X	X
<i>S. coccinea</i>	X	X	X	X	X	X
Green Algae	X	X	X	X	X	X
Macroalgae	X	X	X	X	X	X
Red Algae	X	X	X	X	X	X
Sargassum	X	X	X	X	X	X
<i>Aglaophenia</i> sp.	X	X	X	X	X	X
<i>Eudendrium</i> sp.	X	X	X	X	X	X
Coraline Algae	X	X	X	X	X	X
Dead Hydroid/Bryozoan Complex	X	X	X	X	X	X

Disappeared

Species	2010	2011	2012	2013	2014	2015
<i>O. arbuscula</i>	X	X				
<i>P. americana</i>	X					
<i>H. violaceus</i>	X					
<i>Didemnum</i> sp.	X	X	X	X	X	
<i>Distaplia</i> sp.	X					
<i>S. plicata</i>	X	X				
<i>S. brakenhielmi</i>	X	X	X	X		
Zoanthid	X					

Random appearance in years

Species	2010	2011	2012	2013	2014	2015
<i>Leptogorgia hebes</i>	X		X	X	X	X
<i>Schizoporella cornuta</i>	X	X	X		X	
<i>Chondrilla nucula</i>	X		X	X	X	X
<i>Ecteinascidia turbinata</i>	X		X			X
<i>Bugula</i> sp.	X		X			
Other Ascidian	X				X	

Not present in initial group

Species	2010	2011	2012	2013	2014	2015
<i>S. floridana</i>					X	
Schizoporella sp.					X	
<i>E. capsulatum</i>					X	
Brown Algae		X	X			
<i>F. implexa</i>				X	X	X
<i>A. fulva</i>		X		X		

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