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Sessile Invertebrate Colonization on Rocky Outcrops at Gray's Reef National Marine Sanctuary

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SESSILE INVERTEBRATE COLONIZATION ON ROCKY OUTCROPS AT GRAY'S REEF NATIONAL MARINE SANCTUARY

by

BRITTANY NICOLE POIRSON

(Under the Direction of Daniel F. Gleason)

ABSTRACT

Documenting patterns of sessile invertebrate community development is important for predicting recovery patterns after disturbance and designing effective marine reserves. In the South Atlantic Bight, invertebrate assemblages can differ significantly from one rocky outcrop to another, but the factors driving these differences are not well understood. I tracked community development for fourteen months at four rocky outcrops at Gray's Reef National Marine Sanctuary (GRNMS) to address the predictions that (i) developing sessile invertebrate communities in this system do not exhibit a predictable pattern of succession and (ii) recolonization patterns for small patches of open space that become available are influenced by the composition of the invertebrate community in the immediate vicinity. Community development was followed for 14 months on paving tiles (30 x 30 cm) deployed in July 2012 by photographing these tiles, along with the adjacent natural community, each month through September 2013. Species composition, percent cover, and diversity were determined each month.

Sessile invertebrate taxa colonizing tiles were similar across all four sites in the first three months after deployment, but diverged over time. At all sites, developing communities exhibited lower percent cover and diversity than their adjacent existing communities over the fourteen months of the study, but analyses of similarities (ANOSIM) did provide evidence of convergence over the long term. These results indicate that succession of sessile invertebrates is not a

predictable process in this system and that the extant community plays a role in deciding the final outcome of species re-establishment. Thus, differences in invertebrate community structure among rocky outcrops likely persist in this system because the extant community influences recruitment.

INDEX WORDS: Community ecology, Succession, Recruitment, Benthic invertebrates, Gray's Reef National Marine Sanctuary

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GRAY'S REEF NATIONAL MARINE SANCTUARY

by

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B.S. Western Washington University, 2007

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MASTER OF SCIENCE

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SESSILE INVERTEBRATE COLONIZATION ON ROCKY OUTCROPS AT
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BRITTANY NICOLE POIRSON

Major Professor: Daniel F. Gleason
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DEDICATION

I dedicate this work to my parents, Judith and James Poirson for always stressing the importance of an education and an interest in the natural world. My brother Evan inspired me to work extremely hard by being my biggest competition in scholastics. Evan, thank you for being intelligent and introspective and a generally awesome human.

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CHAPTER 1

LITERATURE REVIEW

Community Structure and Function

Sessile invertebrates in the benthos provide energy and habitat for fish and mobile invertebrates (Sale et al. 2010, Burt et al. 2011). Complex live-bottom areas increase biodiversity by providing ample microhabitats for many species to co-exist (Wenner et al. 1983). Large sponge species such as *Ircinia campana, Ircinia felix,* and *Cliona celata* are especially important for creating habitat in temperate ecosystems and protecting organisms from predation (Wenner et al. 1983). Popular sessile invertebrate prey items for fish and mobile invertebrates include barnacles (Connell 1961), a variety of sponges (Ruzicka and Gleason 2009), and the ascidian *Botryllus* sp. (Osman and Whitlatch 2004). The availability of food and habitat relate to the function of a community, thus, the function of an ecological community is related to the organisms within the community (deGroot et al. 2002).

A resilient community is one where the densities of species in the system remain relatively constant and can return to the original state quickly after a disturbance (Berlow 1997, Tilman 1999, Chesson 2000, Gleason 2010). Resilient ecosystems can retain community function better than those that do not recover as quickly. It has been suggested that higher biodiversity in an area leads to redundancy within an ecosystem, which makes communities more resilient to stress (Berlow 1997, Covich et al. 2004). Resilience in marine communities is extremely important for ecosystem function, especially as stressors such as habitat destruction and storm frequency increase with global climate change (Gleason 2010).

The composition of an ecological community is determined by the interaction between physical and biological factors (Menge and Sutherland 1987, McGill et al. 2006). Abiotic factors influencing sessile invertebrate community structure in subtidal marine systems include sedimentation, light penetration, substrata type, and temporal changes in water temperature. Sedimentation can affect organisms through abrasion, burial, and reduced food capture (Rogers 1990, Gotelli 1998, Divine 2011). Organisms that grow vertically rather than horizontally can escape some detrimental sand scour and survive better in higher sediment environments (Rogers 1990, Gotelli 1998, Divine 2011). For example, Gotelli (1988) found that juvenile gorgonians fared better than new recruits in habitats that were heavily inundated with sediment. Light penetration through seawater affects the distribution of invertebrate species as well. Symbiotic corals need light for intracellular algae, whereas sponges and many tunicate species can survive in lower light habitats (Witman and Dayton 2001). Temporal changes in species abundance are well documented in environments where temperature fluctuates annually (Bram et al. 2005). Colder water temperatures can negatively influence reproduction and settlement success in many species (Osman 1977) whereas warmer water temperatures bring rapid growth, both of which contribute to changes to community composition (Bram et al. 2005).

Biotic interactions between species are as important as abiotic factors in influencing community structure (Bruno et al. 2003). Examples of biotic interactions between species are facilitation and competition. Facilitation occurs when species alter the local environment chemically or physically to favor certain species, deter predation, or create habitat (Stachowicz 2001). Interest in facilitative interactions has risen recently as more evidence supporting its role in influencing communities is gained (Bruno et al. 2003, Yakovis et al. 2008). Facilitation has frequently been documented when the structural aspects of sessile invertebrates positively

influence settlement of other invertebrates (Dean 1981). Corals, seaweeds, and barnacles are all viewed as taxa that facilitate settlement of sessile invertebrates (Stachowicz 2001, Sams and Keough 2012). Negative interactions include competition for food resources and suitable open substrate (Jackson 1977, Connell and Slatyer 1977). Competition is common in sessile marine communities on hard substrata, and can limit where a species resides (Connell 1961). Biotic and abiotic factors that contribute to configuring assemblages of benthic marine invertebrates are also influenced by the various life histories and spawning periods of the invertebrate species that live within the community (Osman 1977). Some taxa such as the ascidians *Styela plicata* and *Botryllus* sp., the bryozoan *Bugula* sp*.,* or the hydroid*, Tubularia* sp. commonly colonize an area during their reproductive peak and subsequently die when environmental conditions become unfavorable (McDougall 1943, Sutherland and Karlson 1977, Grosberg 1988, Sams and Keough 2012).

Life Histories of Benthic Marine Invertebrates

Many sessile invertebrates can reproduce both sexually and asexually (Thorson 1950). These reproductive modes are not mutually exclusive, with many invertebrate species using both mechanisms depending on the time of year or environmental circumstances (Thorson 1950). Asexual reproduction can occur by fission, fragmentation, or budding (Brusca and Brusca 2003, Gleason and Hoffmann 2011). Asexuality allows an organism to quickly take advantage of abundant resources or reproduce in an environment with a paucity of sexual partners (Brusca and Brusca 2003). Conversely, sexual reproduction involves fertilization of gametes to zygotes (Brusca and Brusca 2003). Sexual reproduction can occur by eggs and sperm meeting in the water column, or sperm entering the female body and resulting in brooding of larvae

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(Strathmann and Strathmann 1982, Gleason and Hoffmann 2011). The primary advantage to sexual reproduction is that it maintains genetic diversity in a species (Brusca and Brusca 2003).

Many species of marine benthic invertebrates have a planktonic larval phase that is followed by a sessile adult phase. Larval dispersal distance can vary greatly between species (Grantham et al. 2003, Kinlan and Gaines 2003). Lecithotrophic species spend short times in the plankton, do not feed while dispersing, and therefore must find suitable substrate within a few minutes to a few hours after being released (Pechenik 1999, Nybakken and Bertness 2005). Population genetic studies suggest that some taxa such as barnacles disperse long distances, whereas other taxa such as certain species of ascidians do not (Stoner 1990, Gaines and Bertness 1992). Population differentiation of lecithotrophic species indicates small scale dispersal (<10 km) (Todd 1998). Individual lecithotrophic larvae of the tunicate *Diplosoma similis* disperse 1-4 m from their release point, close enough to allow for divers to follow each larva to settlement (Stoner 1994). In contrast, planktotrophic larvae can disperse hundreds of kilometers and show genetic homogeneity over large distances (Thorson 1950, Todd 1998). Examples of marine invertebrate larvae that have been shown to exhibit long planktonic durations and genetic homogeny over large spatial scales include the mollusk *Littorina littorea* (Shanks et al. 2003, Kinlan and Gaines 2003), and many species of barnacle (Grantham et al. 2003). Larval dispersal is central to a populations' range expansion and gene flow. There are tradeoffs to short and long distance dispersal. The advantages of long distance dispersal include avoidance of competition with conspecifics and withstanding local extinctions (Todd 1998). Disadvantages of dispersal are increased mortality because of greater exposure to predation and environmental stresses (Pechenik 1999, Pineda et al. 2009). The dispersal distances of many marine species are difficult

to determine because larvae are often miniscule and limitations in a researchers time underwater make direct observations difficult (Stoner 1994, Hughes et al. 2000).

The idea of Supply-Side ecology was formulated in the 1980's to explain the link between larval availability and adult marine population dynamics (Lewin 1986). Supply-Side ecology states that fluctuations in larval supply are the major determinant of variation in community structure (Grosberg and Levitan 1992, Caley et al. 1996). Large scale patterns of recruitment can be driven by the distribution and fecundity of sessile adults (Hughes et al. 2000). Variation in recruitment patterns is well documented in subtidal marine habitats (Sutherland and Karlson 1977, Forde and Raimondi 2004, Sams and Keough 2012). Given that the availability of suitable substrate, larval behavior, seasonality of spawning, physical disturbance and other abiotic forces influence dispersing larvae, it follows that recruitment will be more successful closer to the source of larval production (Knowlton 1992, Smale 2012) because longer dispersal distances lead to higher mortality of individual larvae (Pineda et al. 2009). For example, Hughes et al. (2000) found that larvae of fecund coral colonies on the Great Barrier Reef exhibited higher recruitment to nearby open substrate, indicating that settlement occurred most frequently near the parent colony.

Gray's Reef National Marine Sanctuary (GRNMS) is located roughly 34 km off the coast of Georgia, U.S.A. (31°21.45N, 80°55.17W; 31°25.15N, 80°55.17W; 31°25.15N, 80°49.42W; and 31°21.45N, 80°49.42W mark the corners of the sanctuary). At GRNMS rocky outcrops are separated by expanses of sand (Freeman et al. 2007) and communities on rocky outcrops can be characterized as distinct. Larvae of many sessile benthic invertebrate species do not identify sandy substrate as suitable for settlement (Gotelli 1988). Although some rocky outcrops are within close proximity to others (<1 m), and many invertebrates could potentially disperse to the

other outcrops, larval dispersal distances for many organisms are short (Todd 1998), especially at GRNMS. Currents and eddies keep propagules localized (Hare and Walsh 2007) and therefore it is likely that many invertebrates are recruiting locally in this system. The sandy substrates that separate outcrops from one another at GRNMS contribute to the isolation of habitat and further increase the likelihood of local recruitment by creating an area of separation between outcrops. The sandy substrates between outcrops can also function as an agent of disturbance when water currents and wave heights are high and large amounts of sediment are flushed into the water column (Divine 2011). Eventually some of the sediment will be deposited onto the rocky outcrops and can kill many invertebrates (D.F. Gleason unpub. data). Disturbances such as these assist in opening up space for invertebrate colonization.

Successional Theory

Orderly change in species composition over time from bare substratum to a climax community is known as primary succession (Clements 1916, Odum 1969, Connell and Slatyer 1977). Successional theory was originally developed in terrestrial plant communities (Clements 1916, Gleason 1926) but has been applied to marine communities as well (Connell and Slatyer 1977, Bram et al 2005). Succession is important to consider when thinking about the structure of ecological communities. Understanding the mechanisms of ecological succession is fundamental to predicting recovery patterns and restoring increasingly disturbed habitats (Frid et al. 2008, Antoniadou et al. 2010).

Connell and Slatyer (1977) identified three mechanisms that lead to the changes observed in successional sequences: facilitation, inhibition, and tolerance. The facilitation model assumes that only a few early successional species are able to colonize open substrate and therefore facilitation is commonly applied in situations where the substrate has not been previously

inhabited by organisms. This model was supported in two studies where barnacles were the primary colonizers of open substrate and then facilitated settlement of other sessile invertebrates (Yakovis et al. 2008, Sams and Keough 2012). Connell and Slatyer (1977) further predicted any species can colonize to open substrate, but the arriving species change the substrate such that it becomes less suitable for other species to colonize. The result is that the early colonists exclude all subsequent colonists. This inhibition model is supported by two studies that showed that colonial ascidians generally usurp space and inhibit other species from settling (Jackson 1977, Osman and Whitlatch 1995b). Many larvae do not identify colonial invertebrates as suitable settlement habitat (Osman and Whitlatch 1995b). Finally, the tolerance model (Connell and Slatyer 1977) supposes that species that settle on substrate change the environment to become less suitable for later species, but subsequent recruitment still occurs. In the tolerance model, early and later successional species are able to co-exist on the substrate until changes in the physical environment eliminate some species. Tolerance was supported in the intertidal community in California, where succession occurred predictably as a result of secondary colonizers recruiting in to habitats and shading out primary colonizers (Sousa 1979b).

Two competing hypotheses exist on how communities in marine habitats are formed. The first hypothesis is that the community develops following the classical succession model, a predictable sequence of species replacements and occurrences of individuals (Sousa 1979b, Bram et al. 2005, Cifuentes et al. 2010). Predictable community development occurs as a result of foundation species influence, temporal changes in species abundance, and the ability of later colonizers to outcompete earlier colonizers (Odum 1969). A stable climax community results from the classical succession model, however, the existence of a stable climax community has been challenged in some habitats (Sutherland and Karlson 1977, Sams and Keough 2012).

The other hypothesis about how successional processes proceed is that communities form by random chance of larval recruitment and therefore succession is not predictable (Sutherland and Karlson 1977, Smale 2012). These studies found stochastity in the beginning of development and different end-points to the communities. Community development at the Duke University Marine Laboratory dock in Beaufort, N.C. was shown to exhibit no climax community, and unpredictable community development in two separate studies (McDougall 1943, Sutherland and Karlson 1977). The subtidal hard bottom habitats off the coast of Beaufort, N.C. are encrusted with sponges, cnidarians, ascidians, and bryozoans (McDougall 1943, Sutherland and Karlson 1977, Wenner et al. 1983). The community surveyed by Sutherland and Karlson (1977) supported the inhibition model of succession as many species inhibited other species from settling on adjacent substrate. Subsequent colonizers were different species than previous colonizers and this led to dramatic differences in community structure on the substrata. Pronounced variability in community development was also documented on the temperate coastline of Western Australia (Smale 2012). In this study, PVC panels were placed at three locations, 0, 200 km, and 400 km away from a subtidal rocky outcrop. The differences in development of PVC plates was determined to be due to proximity to source populations. Panels placed closer to the rocky outcrop exhibited higher sessile invertebrate cover and richness overall than those situated around sandy substrata, but high variability in community structure existed on panels submerged centimeters from each other.

It is still unknown if classical successional theory applies to marine communities, as some researchers failed to find true "climax communities" (McDougall 1943, Sutherland and Karlson 1977). It is possible that seasonal shifts in larval supply and growth can complicate successional processes in temperate marine ecosystems or frequent disturbance prohibits some

communities from establishing a stable climax community (Berlow 1997, Antoniadou et al. 2011). Additionally, Osman (1977) outlines five factors that influence variation in community development: larval selectivity for settlement space, seasonal fluctuations, biological interactions, colonizing substrate size, and physical disturbance. For example, Underwood and Chapman (2006) placed nylon pot-scourers at two sites in New South Wales, Australia and found that successional change was confounded by the life history of some organisms that had specific breeding times. The assemblages in the aforementioned study eventually converged after being deployed for six months, but the models of succession were only somewhat successful in explaining the trajectory of species replacement.

Marine reserves are becoming increasingly used for creating sources of fish and invertebrate larvae to supply more degraded habitat (Nigel 2003, Sale et al. 2010). Marine reserves are controlled by regulations that limit anthropogenic disturbances and bolster deteriorating invertebrate and fish communities (ONMS 2011). Understanding how invertebrates repopulate an area after a disturbance can affect how marine preserves or research only areas are constructed (Nigel 2003). If local recruitment predominates, then a higher number of smaller marine reserves are warranted given that small reserves protect species with limited dispersal while allowing maximum areas for fishing and recreation (Grantham et al. 2003). If recruitment patterns indicate longer distance dispersal, then larger marine preserves would be better suited for the area.

Marine subtidal habitats at Gray's Reef National Marine Sanctuary support a diverse array of sessile invertebrate species that impact taxa in higher trophic levels (Wenner et al. 1983, Freeman et al. 2007). Successional processes in GRNMS have not been widely studied, but they are important for assessing patterns of development particularly after a disturbance. In this study

I document patterns of invertebrate colonization on four rocky outcrops along with the changes in extant community structure over fourteen months. This study increases our understanding of community development in a subtidal system by cataloging when new taxa colonize recently available substrata, and if those colonization patterns are consistent among rocky outcrops. These data are useful for determining the stability of extant community structure and recolonization mechanisms present in developing communities at GRNMS, both of which have implications for predicting recovery after large storms and suitable marine reserve design for this area.

CHAPTER 2

SESSILE INVERTEBRATE COLONIZATION AND COMMUNITY DEVELOPMENT AT GRAY'S REEF NATIONAL MARINE SANCTUARY

INTRODUCTION

In biological communities, the change in species composition from open substrate to the climax state is known as succession (Clements 1916, Gleason 1926, Odum 1969, Connell and Slayter 1977). There are competing hypotheses regarding successional processes in ecological communities. One states that there is a predictable sequence of colonization events that leads to a climax community (Dayton 1971, Osman 1977, Sousa 1979b, Bram et al. 2005, Antoniadou et al. 2011). Under this scenario, the patterns of recruitment and mortality can be anticipated and should be consistent among communities of similar types. The predictable change in species colonization is dependent on chemical cues present in the extant community, the influence of primary colonizers, environmental conditions, and the invasion success of later successional species (Sousa 1979b, Pacheco et al. 2011). Evidence from the intertidal zone of California indicates that primary colonizers arrive because of life history characteristics that allow them to take advantage of open substrata after a disturbance, and later colonizers outcompete earlier species once they establish themselves nearby (Sousa 1979b).

The other succession hypothesis states that community development occurs randomly with no stable climax state (Sutherland and Karlson 1977, Sams and Keough 2012, Smale 2012). Random development can occur because of patchiness in larval availability in the water column (Pineda et al. 2010), differential post-settlement mortality (Hunt and Scheibling 1997), or variable microhabitat conditions (Gotelli 1988). The predictability of succession is tied to successful colonization, mortality, and favorable habitat conditions and may not be useful for explaining patterns of colonization everywhere (Sutherland and Karlson 1977).

Established sessile invertebrate communities may exert positive or negative influence on the development of adjacent open space. When new space becomes available in rocky subtidal or intertidal marine communities, larvae can recruit from the plankton or residents surrounding the free substrate can grow into the space (Jackson 1977, Connell and Keough 1985). Connell and Slatyer (1977) identified three mechanisms that drive the changes observed in successional sequences: inhibition, facilitation, and tolerance. These mechanisms can lead to predictable patterns in community development. Examples of these three mechanisms include existing species inhibiting potential colonizers by preying on settling larvae, occupying space, and deterring larvae from settling on available substratum by chemically altering the space (Osman and Whitlatch 1995b). An example of facilitation is that some species enhance recruitment of conspecifics (Hughes et al. 2000, Bram et al. 2005, Smale 2012). High recruitment of conspecifics is especially common for species that settle gregariously or have limited dispersal (Knowlton 1992, Kingsford et al. 2002). The tolerance mechanism of succession is when species increase the likelihood of other species settling nearby and coexisting until one species dominates (Dean 1981, Osman and Whitlatch 1995a). There are positive associations between larval recruitment rates and adult abundances of mussels and barnacles (Osman and Whitlatch 1995a, Broitman et al. 2008), and the tunicates *Molgula sp*., and *Botryllus sp*. (Osman and Whitlatch 1995b).

Gray's Reef National Marine Sanctuary (GRNMS) is located within the South Atlantic Bight (SAB) roughly 34 km off the coast of Georgia, U.S.A. (Figure 1). The bottom composition at GRNMS is typical of the SAB region and is characterized by rocky outcrops of various sizes (5 m to tens of meters in length and 10 cm to over a hundred cm in height) separated by expanses of sand (Harding and Henry 1990). These rocky outcrops are encrusted by a wide array of sessile

marine organisms and extensive bottom surveys conducted within the sanctuary show that sessile invertebrate community composition differs among them (D.F. Gleason unpubl. data). There are a few explanations for how such a pattern could arise. Firstly, if there is a predictable successional sequence, it is possible that the communities are in different stages of development. Such a patchwork of different successional stages could occur if the impacts of disturbance events differ among rocky outcrops. At GRNMS for example, sedimentation resulting from the passage of storms is thought to exert significant negative impacts on the survival of sessile invertebrates (Divine 2011). However, sedimentation rates may vary across rocky outcrops and lead to the different successional stages seen throughout the sanctuary.

Another possibility is that local recruitment is driving the differences among these communities. Contrary to the historical dogma of long distance dispersal, larval transport may be demographically closed on small spatial scales, especially for lecithotrophic and clonal species (Todd 1998, Carlon and Olson 1993). Furthermore, currents and eddies have the ability to facilitate larval retention. For example, satellite drifters released at GRNMS in 2007 remained in the sanctuary boundaries for 60 days (Hare and Walsh 2007). The combination of these eddies and the large numbers of lecithotrophic and clonal species at GRNMS points to short dispersal distance as a mechanism maintaining differences in sessile invertebrate community composition among rocky outcrops.

Multiple stable states have been proposed in some temperate systems to further explain variation in community structure among sites within the same ecosystem (Sutherland 1974). Multiple stable states refers to the phenomenon that more than one stable community can exist in a single environmental regime (Knowlton 1992). Sutherland (1974) classifies a community as stable if it persists for some period of time, and returns to that state after being disturbed.

Maintenance of a stable community is a mixture of successful recruitment and subsequent exclusion of other species. It is possible that multiple stable states exist temporally at GRNMS as a result of cyclical changes in water temperature that drive life history variation of species and result in predictable changes in the composition of invertebrates seasonally.

As opposed to predictable successional sequences, there is also the possibility that colonization of invertebrates within GRNMS is random and that no climax community state exists. The presence of climax communities in marine habitats has been questioned, especially in the South Atlantic Bight (McDougall 1943, Sutherland and Karlson 1977, Fioravanti-Score 1998). Berlow (1997) added to the successional theories of Connell and Slatyer (1977) by introducing the idea of externally driven succession, which occurs when microhabitat variation such as differences in substrate angle, sedimentation, and light availability influences the patterns of recruitment and community development within small spatial scales. Externally driven succession results in seemingly random community development with no climax community (Berlow 1997). This model may describe invertebrate community development in the South Atlantic Bight where variable microhabitat conditions such as fluctuating water currents, which influence dispersal distance (Grantham et al. 2003), different substrate angles, which affect light availability and organisms dependent on photosynthesis (Matterson 2012), and variable sedimentation regimes, which may influence survivorship of some species (Divine 2011) are common.

To obtain a better understanding of the factors driving sessile invertebrate community development at GRNMS, I documented extant community structure on natural substrata and colonizing organisms on artificial substrata at sites within GRNMS over the course of fourteen months. I hypothesized that the surrounding natural community influences the colonization of

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open substrate. Previous studies in temperate habitats have shown that the local community influences colonization of invertebrates (Osman and Whitlatch 1995b, Fioravanti-Score 1998, Smale 2012) and thus I predicted recolonization patterns for small patches of open space that become available are influenced by the composition of the invertebrate community in the immediate vicinity. Additionally, McDougall (1943) and Sutherland and Karlson (1977) showed that colonization of sessile invertebrates did not follow classical succession in the South Atlantic Bight, and therefore I predicted that the successional trajectory would be driven by random processes and would differ among the developing communities at each of the four sites I examined.

METHODS

This study was conducted at Gray's Reef National Marine Sanctuary (31°36.056'N 80°47.431'W) located 34.2 km east of Sapelo Island, GA at depths of 18-20 m (Figure 1). GRNMS encompasses 42.9 km^2 of sand bottom habitat interspersed with sedimentary lithified limestone and sandstone rocky outcrops colonized by invertebrate species from a wide variety of phyla including Porifera, Cnidaria, Bryozoa, Arthropoda, and Chordata (Harding and Henry 1990, Fioravanti-Score 1998).

To establish a baseline for extant sessile invertebrate community structure and select sites for this study, species density and richness were quantified with 0.25 m^2 quadrats on 36 rocky outcrops within GRNMS in June 2011. A non-metric multidimensional scaling (nMDS) plot of community similarity among the sessile invertebrate communities on these rocky outcrops was generated and four sites showing significant separation on the nMDS plot were chosen for the study (Figure 2). Separation on the nMDS graphs indicates disparate community structure among outcrops. I chose sites with dissimilar community structure to determine if extant community

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differences influenced the identity and density of recruiting taxa. Only sites with ledge heights ≥

30cm were considered for inclusion to control for effects of ledge height on species composition.

Of the sites chosen, two were inside and two outside of a research only zone established in

December 2011 within the sanctuary. Inside and outside sites were not compared, but are

important to mention because their location within the sanctuary is reflected in the site names.

Sites were named by the GRNMS staff and in and out designations after the number indicate

whether the site is inside the research only zone or outside of it. Sites selected were 06-in

(31.3732 N, -80.86665 W), 07-out (31.38586 N, -80.83794 W), 30-in (31.3641 N, -80.7085 W),

and 41-out (31.39652 N, -80.89032 W) (Figure 1).

In order to assess invertebrate community development, fifteen paving tiles with a

surface area of $0.089m^2$ were deployed at each of the four sites one meter apart atop the scarp

and no more than 2 m from the edge of the ledge. The scarp refers to the 2-4 m wide area that

parallels the ledge drop off and generally hosts the highest invertebrate biomass (sensu Ruzicka

and Gleason 2009). Tiles were composed of an aggregate calcium carbonate and quartz sand

with iron-oxide (K. Vance, Dept. of Geology and Geography, Georgia Southern University, pers.

comm.). Artificial rather than natural rock was used to standardize habitat structure across

replicates and sites. The tiles have a 0.75 cm deep groove that runs along a diagonal and forks 13

cm from two corners (Figure 3). These grooves created topographic complexity that has been

shown to increase recruitment relative to smooth tiles (Dean 1981, Osman and Whitlatch 1995a,

Bulleri 2005). Invertebrate community development was documented through photographs of the

upper surface of the paving tiles. Tiles were photographed at each site monthly from August

2012 through September 2013 with the exception of site 41-out in December 2012 and February

2013, and site 07-out in February 2013, when adverse sea conditions prevented diving

operations. Photographs were taken using an Olympus C5050 for data captured in August 2012 for 41-out, Olympus SP-320 for data captured at all other sites in August 2012 and all sites in September 2012, and a Canon powershot G12 for all other time periods. Cameras were mounted on a PVC framer (63 cm height x 36 cm width x 36 cm depth) to ensure a constant focal distance of approximately 53 cm above the plots and a similar orientation. Photographs were analyzed with Coral Point Count with Excel Extensions (CPCe) software version 6 (Kohler and Gill 2006). In this computer analysis, 175 random points were overlaid on each photograph and the underlying features were determined at each of the points. The number of points assayed was based on previous work using a similar monitoring protocol (K. O. Matterson and D. F. Gleason, unpubl. data). Organisms were identified to the lowest possible taxonomic level, most often to genera. Serpulid tubeworms (Serpulidae) were classified to family, however, it is likely that only one genus was represented in this study. There was one species of Chordate that could not be identified for this study, here it is referred to as the brain tumor tunicate. Samples have been taken of this species for identification at a later date. Shannon-Wiener diversity indices and percent cover were calculated for each month of data collection to identify additional differences between extant and developing communities over time.

To assess the prediction that recolonization patterns are influenced by the composition of the surrounding invertebrate community at each of the rocky outcrops, surveys were conducted of the extant community at all sites in September 2012 and every month from November 2012 to September 2013. In situ quadrats were used to survey the existing benthic invertebrate communities in September, November, and December 2012. A total of two to eleven quadrats per month ($0.25m^2$) were placed haphazardly between the tiles along the scarp at each site. The organisms within each quadrat were identified to the lowest possible taxonomic level and the

number of 5x5 cm squares each taxa occupied in the subdivided quadrat was recorded to estimate percent cover. Quadrat analysis was admittedly spotty, and is only used in multivariate analysis of extant community structure. Quadrat analysis of percent cover and diversity was removed from the analysis because of low replication in 2012.

Quadrat methods were replaced by photographic monitoring of the benthos starting in January 2013, because dive time limitations made it difficult to achieve enough replication to allow complete characterization of the natural benthic invertebrate community. Sampling was conducted using a Canon G12 digital camera in a waterproof Ikelite housing (Ikelite, Indianapolis, IN). Fifteen photographs (0.093 m^2 area) of the existing community were taken once a month at each site between January and September 2013. Photographs of the extant community were taken along the scarp. Photographs were analyzed using CPCe software as previously described.

Multivariate analyses were used to identify differences in species composition among extant and developing communities over time and between developing communities at all four sites. All multivariate analyses were conducted with PRIMER-E v.6 software (Clarke and Gorley 2006). Non-metric Multi-Dimensional Scaling (nMDS) of Bray-Curtis distances on square root transformed data was used to graphically display the relative dissimilarity between sites and communities. For simplicity, a single point representing the mean abundance of the organisms at a site for each time period sampled is shown on the nMDS. I use the term abundance to mean the number of times specific taxa were identified in the CPCe analysis of a photo plot when discussing data analyzed with PRIMER-E. Analysis of similarity (ANOSIM) was used to test for differences in composition among communities. The test statistic for ANOSIM analysis is an R value, which ranges from -1 to 1, values closer to zero indicate that the communities are more

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similar. Negative R values are a result of having more variability within than among replicates. Composition will be used to describe the specific taxa encountered within replicates and their relative abundances. Similarity Percentages (SIMPER) were used to identify the taxa responsible for differences among communities. In all multivariate analyses, the density of each taxon was scaled to number per m^2 to compare quadrat, tile, and natural bottom photographs by multiplying by 4 for in situ quadrats, 10.75 in photographs, and 11.76 for tiles and then the mean density was calculated. Square root transformation was used for all multivariate analyses to reduce the contribution of the most abundant species in the dissimilarity (Thorne et al. 1999).

To determine if the surrounding invertebrate community influences recolonization patterns, nMDS graphs were generated between the extant and developing communities at each site. ANOSIM and SIMPER tests were also used to assess differences between the extant and developing communities and identify the organisms responsible for these differences. Additionally, the Shannon-Wiener diversity index and percent cover were calculated for the developing and extant communities through time. Diversity and percent cover values were compared with a repeated measures analysis of variance (rmANOVA) for each month sampled. Regression analyses of diversity and percent cover over time were calculated for both extant and developing communities at all sites to assess if values would converge at some time in the future.

SIMPER analyses in PRIMER-E v.6 (Clarke and Gorley 2006) were used to determine Bray-Curtis dissimilarity values between extant and developing communities in 2013. SIMPER analysis compares communities using taxonomic composition within all replicates in a group. Percent similarities between the extant and developing communities were calculated by subtracting dissimilarity values from 100. Only similarity values from January through

September 2013 were calculated due to the low replication of quadrats that were completed for the extant communities in 2012.

To identify the trajectory of the developing communities, MDS and ANOSIM data from all sites were grouped in time blocks (1-3 months, 4-6 months, 7-9 months, 10-12 months, and 13-14 months). Grouping by time blocks was performed to simplify trajectory graphs and to address the second prediction that the successional trajectory would be driven by random processes and would differ among the developing communities at each of the four sites. A rmANOVA was used to test for the effect of site and time on percent cover and species diversity. Univariate statistical tests were run on JMP pro 10 statistical package (SAS Inc., Cary, N.C., USA)

RESULTS

The goal of this study was to assess if the surrounding natural community influences the colonization of open substrate on rocky outcrops at GRNMS and to determine if successional processes are random or directional in this system. I predicted that recolonization patterns are influenced by the composition of the invertebrate community and that the successional trajectory would be driven by random processes and would differ among the developing communities at each site. To assess whether the composition of the invertebrate colonization was influenced by the extant community structure, both extant and developing communities were tracked over time. Community structure between extant and developing communities was different throughout all time periods of this study (Figure 4). ANOSIM analyses confirmed significant differences between the developing and extant communities at all sites and time blocks (Table 1). Extant and developing communities were most similar to each other after tiles had been submerged for 4-6 months, in November-January (Table 1). To assess both successional trajectory and similarity

between extant and developing communities, ANOSIM R values were evaluated for 2-3 month time blocks throughout the study. R values were higher at 13-14 months than at 10-12 months of development indicating more of a difference between extant and developing communities in the last two months of the study. Some of the taxa responsible for significant differences between developing and extant communities were a result of their absence in the developing community (Appendix A, Table A2). Some species missing from the developing communities were represented by the phyla Porifera and Cnidaria (Table 2). Certain species present in high abundances within the extant community exist at relatively low abundances or are absent from developing communities (Table 3). For example, 06-in is dominated by *Eudistoma* sp. and *Distaplia* sp., whereas the developing community contains individuals of these taxa at much lower abundances. The difference in community structure at 30-in and 07-out may be due to a few abundant species in the extant communities that are absent in the developing communities. Site 30-in supports a large tunicate, *Euherdmania gigantea* that did not colonize on the tiles and 07-out has an absence of two Cnidarians in the recruit community that are found in high abundance within the extant community, *Leptogorgia hebes* and *Titandium frauenfeldii*.

Species diversity was higher in the extant than developing community at all four sites throughout 2013 (Figure 5). There was no interaction between month and community type (i.e. extant vs. developing) for 07-out, 30-in, and 41-out (Table 4). The diversity of the developing communities is significantly lower than the extant communities at these three sites. At 06-in, there was a significant interaction between month and community. Regression analyses indicate that diversity in the extant community did not change significantly through 2013, while diversity in developing communities increased (Figure 5). This suggests that developing community diversity will converge on the extant community diversity. Considering that the extant

community diversity did not have a significant slope, the intersection of the extant and developing community diversity was calculated, using the y intercept of the extant community diversity value for 2013. Calculating for the number of months it would take for developing community diversity to converge with the extant community diversity reveals that 06-in species diversity will converge at 17 months after tiles have been submerged, 07-out will converge at 23 months, and 30-in and 41-out diversity will take thousands of years to converge on the diversity of the extant communities.

The percent cover on the paving tiles was low (<25%) at all time periods and sites (Figure 6). Extant and developing communities maintained significantly different percent cover during the study (Table 5). Regression lines of the developing communities explain 31% at 06-in, 86% at 07-out, 76% at 30-in, and 61% at 41-out of the variance. At 30-in, there was a significant interaction between month and community. While diversity and percent cover values may have converged for two sites during the study period, community structure remained significantly different throughout the study (Table 1). Similar to the diversity analysis, percent cover in the extant communities did not change significantly from zero while developing communities exhibited a rise in percent cover throughout the study, which suggests that the percent cover will converge for all communities in the future (Figure 6). Setting regression equations between extant and developing communities equal to each other reveals that 06-in percent cover values will converge after 25 months, 07-out values will converge after 87 months (7 years), and 31-in and 41-out extant and developing communities will essentially never converge (~3400 years after tiles have been submerged).

The percent similarity between developing communities and extant communities did not exceed 40% (Figure 7). Highest similarity values occurred at different times within each site, and

did not rise as expected from January to September 2013 at 06-in, 30-in, and 41-out. Values remained within 10-30% for all sites throughout 2013, and 07-out was the only site to exhibit a positive and significant relationship over time, with 65% of the variation in the data explained by the regression line.

To address the prediction that successional trajectories would be different among sites, developing communities were compared with nMDS and ANOSIM analyses (Figure 8). Mean species abundance in developing communities was calculated for each month with nMDS and compared at 1-3 months, 4-6 months, 7-9 months, 10-12 months and 13-14 months after tiles were submerged. There were significant differences between all sites at all time periods (Table 6). Developing communities appear more similar to each other during earlier (1-3 months) as opposed to later successional stages (13-14 months). Differences among the developing communities became more pronounced as the study progressed (Table 6), primarily a result of differing abundances of similar species (Table 7). The largest contributors to differences between sites were *Balanus sp*. and *Symplegma brakenhelmi* followed closely by serpulid tubeworms, *Didemnum sp*., *Aglaophenia sp*., and *Molgula occidentalis.* The only two species that were present within some of the developing communities and not within others were the tunicate *Eudistoma sp*., found in all communities except 41-out, the sponge *Scopalina reutzleri* which was found in all communities except 30-in, and the tunicate *Molgula occidentalis* which was found in all communities except 41-out. These results are consistent with patterns in the extant communities. *Eudistoma sp*. was found in very low abundance at 41-out in the extant community, as was *Scopalina reutzleri* at 30-in. Both species of *Molgula* were absent from the extant community at 41-out.

Species diversity increased with time in all developing communities (Figure 9). There was no significant interaction effect between month and site in the diversity of developing communities (Table 8), indicating that diversity did not increase similarly at all sites during the study. Percent cover on the tiles also increased with time in the developing communities (Figure 10). There was a significant interaction effect between developing communities at all sites as well (Table 9), suggesting that percent cover did not increase for all sites similarly over time. Percent cover at 07-out increased much more slowly than at other sites, and percent cover at 06-in and 30-in fluctuated between May and September 2013.

The regressions for percent similarity between extant and developing communities were not significantly different from zero for 06-in, 30-in, and 41-out. Calculating the increase of percent similarity in 07-out indicates that the extant and developing community will converge 4.7 years after the tiles had been submerged.

The taxa colonizing the tiles did not follow any predictable patterns after October 2012, three months after tiles had been deployed (Table 10). *Aglaophenia sp., Balanus sp*., Serpulid tubeworms, and *Symplegma sp.* colonized the tiles in almost all of the sites in August 2012. *Didemnum sp.* colonized all of the sites in September 2012, and *Spirastrella coccinea* colonized in October. After October 2012, there were few similarities in the taxa colonizing the tiles. Colonization of new taxa for all of the sites was heaviest in the first three months of the study.

DISCUSSION

The main objective of this research was to assess if the surrounding reference community influences colonization of open substrate at GRNMS and to determine if successional patterns are random or directional in this system. I hypothesized that the surrounding natural community influences the colonization of open substrate. I predicted that the recolonization patterns for

small patches of open substrate that become available are influenced by the composition of the invertebrate community in the immediate vicinity, which was supported after 14 months of community development. Although most of the colonizers to the tiles were found within all four reference communities in this study, many of them have short (<1 km) dispersal distances (Todd 1998), which makes it likely that they are recruiting near the parent colony. I also predicted that successional pattern would be different for developing communities at the four sites examined, which was supported. The successional pattern in the developing community was unpredictable and was consistent with the findings of other studies in this region (Sutherland and Karlson 1977, Van Dolah 1988).

Research in other regions such as Northern Chile (Pacheco et al. 2011) and the Persian Gulf (Burt et al. 2011) suggests that it may take 27 months to ten years for community structure on artificial substrata to match that of reference sites. Additionally, an ongoing study within the South Atlantic Bight indicated that concrete tiles have not converged on the natural community after six years of development (D. F. Gleason unpubl. data). The present study only allows me to predict when percent cover and species diversity will converge between developing and reference communities and does not allow me to predict when they will converge with regard to the presence and density of resident species. Diversity and percent cover convergence do not indicate when the communities converge, as communities may have identical species diversity or percent cover and be composed of completely different species altogether. Regressions from the percent similarity graphs indicated that the percent similarity between extant and developing communities is not significantly different from zero in all sites except 07-out. Therefore, these data do not permit projection of the increase in community similarity for three of the communities; and it is possible that these communities may never achieve full convergence. The

low percent similarity (<40%) between extant and developing communities is most likely a result of early species inhibiting the recruitment of later species on the tiles, as early recruiting species were shown to be a large contributor to differences between developing communities even after one year. Fluctuating abundances of taxa in the developing communities is common in the SAB (McDougall 1943, Sutherland and Karlson 1977), and can also lead to variability in percent similarity between natural and developing communities. Pulses of new recruits were expected in the spring, as seen in other studies in the area (McDougall 1943, Sutherland and Karlson 1977), but seemed to happen irregularly at each site. Six new taxa colonized 30-in in January and 06-in produced six new taxa in March, which indicates patchiness in larval supply at GRNMS. The developing communities also exhibited parallels with another study in the SAB by Van Dolah et al. (1988) who found that developing communities were more similar to each other earlier in development and diverged over time.

It is conceivable that patterns of community development and extant community structure found in this and other studies are the result of sedimentation differences among rocky outcrops in the SAB. Physical differences among ledges may account for some of the variation in extant community structure and community development. At the outset of this study, sites were selected to have at least a 30cm ledge height, however, the ledge at 41-out was ~70 cm higher than other ledges included in this study. Shorter ledge heights likely have higher sedimentation rates (Rogers 1990), which influences the specific organisms that can colonize those areas (Gotelli 1998), and their morphology (Divine 2011). Ledges with high sedimentation often sustain taller or more branching species (Freeman et al. 2007, Divine 2011) because these organisms can escape detrimental sand scour better than encrusting species. Taller branching morphologies allow organisms to allocate energy to growth and reproduction rather than removing sediment

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from their bodies (Divine 2011). Osman (1977) indicates that many factors have effects on the development of a community and physical disturbance arising from differential sedimentation rates is likely one of the driving forces in organism distribution at GRNMS (Freeman et al. 2007).

A possible reason for the failure of extant and developing communities to converge may be a result of using an aggregate substrate instead of one more closely resembling the natural rock substrate at GRNMS. Some studies reveal little effect of using a different substratum composition for the developing community in warm waters of the Persian Gulf and the Mediterranean (Burt et al. 2009, Antoniadou et al. 2010 respectively) and another study indicates that using artificial substrata alters community structure significantly in the shallow waters of Australia (Connell and Glasby 1999). A study by Fioravanti-Score (1998) at GRNMS used rocks from a limestone quarry that were similar in composition to the natural substrata at GRNMS to study colonization of sessile invertebrates. These rocks were placed in wire mesh baskets situated above the sand that occurs between rocky outcrops. Similar species were encountered in my study and the study by Fioravanti-Score, however, the quarry rocks exhibited a higher percent cover of invertebrates by 4 months after deployment, but diversity of colonizing communities was much lower than on my paving tiles because quarried rocks were much smaller than the pavement tiles and were often dominated by one organism. Smaller sized rocks are also more affected by frequent disturbance than larger rocks (Sousa 1979a), because small rocks are easily turned over by currents and tides, which can kill many colonizing organisms. Frequent disturbance affects the progression of succession (Connell 1978).

Future research at GRNMS should include longer term surveys to determine the degree of benthic invertebrate community change temporally and assessing community stability.

Continuing surveys would clarify if multiple stable states occur temporally in this system, or if stable climax communities exist on outcrops at GRNMS. Additionally, tracking abiotic differences among established research sites would add considerably to this study, and would resolve if some outcrops have higher sedimentation than others. Knowing if disturbance regimes are differential within the rocky outcrops would help resolve their role in driving the observed spatial variability in benthic community structure.

The second prediction, that successional patterns would differ for the four communities in this study, was supported. The major difference between the four developing communities is changes in density of similar taxa among sites rather than novel species within sites. However, the sequence with which taxa arrive to these sites was unpredictable after October 2012. These patterns were also found in a study in the South Atlantic Bight in 1988 indicating more similar colonization patterns early in the successional process and trajectories that diverged with time (Van Dolah et al. 1988). Given the unpredictability of colonization after three months of development demonstrated at GRNMS, it is unlikely that succession in the classical sense occurs in this system.

Benthic communities develop over time, creating habitat and storing and cycling materials and nutrients which can benefit higher trophic levels (Covich et al. 2004). If extant and developing communities do not converge on a single end-point, it follows that these differences may translate into bottom-up effects on mobile invertebrates and fish species (Sale et al. 2010, Burt et al. 2011). It is possible that the differences in species assemblage on the tiles can have profound effects on trophic interactions. Given the slow recovery time of benthic communities in the SAB, it is also likely that these altered bottom-up effects may be manifested for years after a disturbance.

Table 1. ANOSIM R values between extant and developing communities at the same site in three month time blocks. All comparisons were significantly different (p<0.0001).

Community	1-3 months	4-6 months	7-9 months	10-12 months	13-14 months
06-in developing community with 06-in extant community	0.522	0.285	0.47	0.352	0.548
07-out developing community with 07-out extant community	0.543	0.335	0.275	0.37	0.452
30-in developing community with 30-in extant community	0.525	0.285	0.607	0.507	0.693
41-out developing community with 41-out extant community	0.623	0.439	0.777	0.661	0.755

Table 2. Taxonomic group present in the (a) extant and (b) developing communities along with the (c) general ecosystem service of the group.

(a.) extant community	(b.) developing community	(c.) ecosystem service
Porifera	**Porifera**	water filtering, habitat forming
Aiolochroia crassa		
Aplysina fulva		
Axinella bookhouti		
Axinella pomponiae		
Axinella waltonsmithi		
Axinyssa ambrosia		
Chondrilla nucula	*Chondrilla nucula*	
Chondrosia collectrix	*Chondrosia collectrix*	
Cinachyrella alloclada		
Clathria prolifera		
Cliona celata	*Cliona celata*	
Coscinoderma lanuga		
Desmapsamma anchorata		
Dysidea fragilis	*Dysidea fragilis*	
Hyrtios violaceus	*Hyrtios violaceus*	
Ircinia campana		
Ircinia felix	*Ircinia felix*	
Lissodendoryx sp.	*Lissodendoryx* sp.	
Ptilocaulis walpersi		
Scopalina reutzleri	*Scopalina reutzleri*	
Smenospongia cerebriformis		
Spirastrella coccinea	*Spirastrella coccinea*	
Cnidaria	**Cnidaria**	habitat forming
Aglaophenia sp.	*Aglaophenia* sp.	
Eudendrium sp.	*Eudendrium* sp.	
Leptogorgia hebes	*Leptogorgia hebes*	
Leptogorgia virgulata		
Oculina arbuscula		
Phyllangia americana		
Telesto sp.		
Titandeum frauenfeldii		
Unidentified anemone	Unidentified anemone	
Arthropoda	**Arthropoda**	habitat forming, facilitate settlement
Balanus sp.	*Balanus* sp.	
Bryozoa	**Bryozoa**	habitat forming, food resource
Bugula sp.	*Bugula* sp.	
Calibugula sp.	*Calibugula* sp.	
Schizoporella cornuta		
Schizoporella floridana	*Schizoporella floridana*	
Schizoporella sp.	*Schizoporella* sp.	
Chordata	**Chordata**	water filtering, food resource
Aplidium constellatum		
Aplidium stellatum	*Aplidium stellatum*	
Aplidium sp.	*Aplidium* sp.	
Botrylloides sp.	*Botrylloides* sp.	
Botryllus sp.	*Botryllus* sp.	
Didemnum sp.	*Didemnum* sp.	
Distaplia sp.	*Distaplia* sp.	
Ecteinascidia turbinata		
Eudistoma sp.	*Eudistoma* sp.	
Euherdmania gigantea	*Euherdmania gigantea*	
Eusenstyela sp.	*Eusenstyela* sp.	
Molgula occidentalis	*Molgula occidentalis*	
	Molgula manhattensis	
Stomozoa roseola		
Styela plicata	*Styela plicata*	
Symplegma brakenhielmi	*Symplegma brakenhielmi*	
Unidentified Chordates	**Unidentified Chordates**	
Brain Tumor Tunicate	Brain Tumor Tunicate	
Other	**Other**	habitat forming, food resource
Serpulid tubeworms	Serpulid tubeworms	
Macroalgae	Macroalgae	
Filograna implexa	*Filograna implexa*	

Table 3. Percentage of individual species or taxa contributing to differences between sites in the extant and developing communities. Mean abundance of a particular group at a site of square root transformed data is shown for each site. Contrib% refers to the contribution of the species or taxon to the overall dissimilarity between sites. Cum.% is a running total of the contribution to the dissimilarity. The top 10 contributors between groups at a site are shown.

06-in developing community with 06-in extant community

Species	Developing Av.Abund	Extant Av.Abund	Contrib%	Cum.%
Distaplia sp.	3.11	6.01	9.05	9.05
Symplegma brakenhielmi	2.98	4.90	8.57	17.62
Balanus sp.	5.78	0.07	8.38	26.00
Eudistoma sp.	1.19	5.68	8.26	34.26
Calibugula sp.	1.29	3.00	5.70	39.96
Aglaophenia sp.	2.97	1.69	5.67	45.63
Didemnum sp.	1.98	2.86	4.80	50.43
Macroalgae	1.03	3.05	4.66	55.09
Serpulid tubeworms	2.42	0.16	3.84	58.94
Spirastrella coccinea	0.34	2.47	3.71	62.64

07-out developing community with 07-out extant community

Species	Developing Av.Abund	Extant Av.Abund	Contrib%	Cum.%
Molgula occidentalis	3.36	4.02	10.67	10.67
Styela plicata	2.64	3.81	9.08	19.75
Titanideum frauenfeldii	0.00	3.16	7.95	27.70
Leptogorgia hebes	0.00	3.82	7.94	35.64
Didemnum sp.	3.92	1.11	7.93	43.58
Distaplia sp.	0.13	2.76	5.35	48.92
Calibugula sp.	1.01	1.52	5.23	54.15
Serpulid tubeworms	1.66	0.11	3.93	58.08
Aglaophenia sp.	0.85	1.20	3.88	61.96
Desmapsamma anchorata	0.00	1.50	3.02	64.98

30-in developing community with 30-in extant community

Species	Developing Av.Abund	Extant Av.Abund	Contrib%	Cum.%
Balanus sp.	8.25	0.15	12.32	12.32
Distaplia sp.	2.14	7.15	10.18	22.50
Macroalgae	1.93	4.34	6.75	29.26
Eudistoma sp.	0.41	4.11	6.51	35.76
Calibugula sp.	0.94	3.55	6.40	42.17
Aglaophenia sp.	1.88	3.09	6.15	48.31
Symplegma brakenhielmi	2.74	3.32	6.13	54.45
Didemnum sp.	2.16	3.28	5.16	59.61
Styela plicata	1.77	2.58	4.84	64.44
Ircinia felix	0.06	2.94	3.94	68.38

41-out developing community with 41-out extant community

Species	Developing Av.Abund	Extant Av.Abund	Contrib%	Cum.%
Chondrilla nucula	0.40	10.27	12.66	12.66
Symplegma brakenhielmi	7.81	10.46	10.27	22.93
Macroalgae	2.15	8.72	10.12	33.05
Spirastrella coccinea	0.53	7.07	8.57	41.62
Balanus sp.	6.48	0.17	7.86	49.48
Ircinia felix	0.20	4.63	5.94	55.42
Oculina arbuscula	0.00	3.55	4.60	60.02
Didemnum sp.	2.72	3.40	4.59	64.61
Leptogorgia hebes	0.19	3.47	4.33	68.94
Scopalina reutzleri	0.73	2.72	3.85	72.78

Table 2. Repeated measures ANOVA results of time and community type on taxonomic diversity at each site for 2013. N=15 for each month in developing and extant communities.

06-in	df	F	p
Month	8	2.7697	0.0061
Community	1	21.5132	<0.0001
Month*Community	8	2.6953	0.0075

07-out	df	F	p
Month	7	5.4109	<0.0001
Community	1	17.3592	0.0003
Month*Community	7	0.3292	0.94

30-in	df	F	p
Month	8	1.8157	0.0753
Community	1	22.7186	<0.0001
Month*Community	8	1.0702	0.385

41-out	df	F	p
Month	7	3.6943	0.0009
Community	1	133.08	<0.0001
Month*Community	7	1.3153	0.2448

Table 3. Repeated measures ANOVA results for 2013 only for percent cover over time in the extant and developing community at each site. N=15 for each month in developing and extant communities.

06-in	df	F	p
Month	8	3.031	0.003
Community	1	13.4958	0.001
Month*Community	8	0.7694	0.6301

07-out			
Month	7	6.3411	<0.0001
Community	1	38.4043	<0.0001
Month*Community	7	1.4751	0.178

30-in			
Month	8	3.0178	0.0031
Community	1	33.0748	<0.0001
Month*Community	8	2.1523	0.0322

41-out			
Month	7	5.9553	<0.0001
Community	1	98.9944	<0.0001
Month*Community	7	0.2601	0.9684

Table 4. ANOSIM R values between developing communities at all time periods. ANOSIM values based on square root transformed data of all replicates. P values are <0.05 for all comparisons of communities and time periods. Refer to Table 4 for sample size information.

Developing Communities	1-3 months	4-6 months	7-9 months	10-12 months	13-14 months
06-in and 07-out	0.166	0.149	0.459	0.497	0.56
06-in and 30-in	0.193	0.054	0.082	0.142	0.172
06-in and 41-out	0.189	0.134	0.178	0.258	0.178
07-out and 30-in	0.131	0.154	0.508	0.568	0.529
07-out and 41-out	0.158	0.153	0.517	0.764	0.78
30-in and 41-out	0.115	0.207	0.289	0.3	0.305

Table 5. Percentage of individual species or taxa contributing to differences between sites in the developing communities. Mean abundance of a particular group at a site of square root transformed data is shown for each site. Contrib% refers to the contribution of the species or taxon to the overall dissimilarity between sites. Cum.% is a running total of the contribution to the dissimilarity. The top 10 contributors between each group of sites are shown.

06-in developing community with 07-out developing community

Species	06-in Av.Abund	07-out Av.Abund	Contrib%	Cum.%
Balanus sp.	5.78	1.23	14.75	14.75
Didemnum sp.	1.98	3.92	11.01	25.76
Aglaophenia sp.	2.97	0.85	9.58	35.35
Serpulid tubeworms	2.42	1.66	8.67	44.02
Distaplia sp.	3.11	0.13	7.98	52.00
Molgula occidentalis	0.02	3.36	7.89	59.89
Symplegma brakenhielmi	2.98	0.52	7.31	67.20
Styela plicata	0.26	2.64	6.74	73.94
Calibugula sp.	1.29	1.01	6.25	80.19
Macroalgae	1.03	0.52	4.00	84.19

06-in developing community with 30-in developing community

Species	06-in Av.Abund	30-in Av.Abund	Contrib%	Cum.%
Balanus sp.	5.78	8.25	19.38	19.38
Aglaophenia sp.	2.97	1.88	10.32	29.71
Symplegma brakenhielmi	2.98	2.74	9.79	39.50
Distaplia sp.	3.11	2.14	9.48	48.98
Serpulid tubeworms	2.42	1.30	7.57	56.54
Didemnum sp.	1.98	2.16	7.29	63.83
Macroalgae	1.03	1.93	6.50	70.34
Calibugula sp.	1.29	0.94	5.32	75.66
Schizoporella sp.	1.02	0.96	4.39	80.05
Bugula sp.	0.81	1.05	4.16	84.20

06-in developing community with 41-out developing community

Species	06-in Av.Abund	41-out Av.Abund	Contrib%	Cum.%
Symplegma brakenhielmi	2.98	7.81	19.14	19.14
Balanus sp.	5.78	6.48	16.90	36.03
Serpulid tubeworms	2.42	2.06	8.64	44.67
Aglaophenia sp.	2.97	0.80	8.40	53.08
Didemnum sp.	1.98	2.72	8.11	61.19
Distaplia sp.	3.11	0.31	7.39	68.59
Macroalgae	1.03	2.15	6.34	74.92
Calibugula sp.	1.29	0.22	3.79	78.71

Species	Av.Abund	Av.Abund	Contrib%	Cum.%
Schizoporella sp.	1.02	0.68	3.59	82.30
Botrylloides sp.	0.50	0.78	2.84	85.14

07-out developing community with 30-in developing community

	07-out	30-in		
Species	Av.Abund	Av.Abund	Contrib%	Cum.%
Balanus sp.	1.23	8.25	21.12	21.12
Didemnum sp.	3.92	2.16	11.08	32.20
Molgula occidentalis	3.36	0.99	9.01	41.21
Styela plicata	2.64	1.77	8.49	49.70
Aglaophenia sp.	0.85	1.88	7.10	56.80
Serpulid tubeworms	1.66	1.30	7.02	63.82
Symplegma brakenhielmi	0.52	2.74	6.97	70.79
Macroalgae	0.52	1.93	6.77	77.56
Calibugula sp.	1.01	0.94	5.57	83.13
Distaplia sp.	0.13	2.14	5.08	88.21

07-out developing community with 41-out developing community

	07-out	41-out		
Species	Av.Abund	Av.Abund	Contrib%	Cum.%
Symplegma brakenhielmi	0.52	7.81	20.19	20.19
Balanus sp.	1.23	6.48	16.31	36.50
Didemnum sp.	3.92	2.72	11.46	47.97
Serpulid tubeworms	1.66	2.06	8.58	56.55
Molgula occidentalis	3.36	0.00	7.72	64.27
Styela plicata	2.64	0.03	6.39	70.67
Macroalgae	0.52	2.15	6.38	77.05
Aglaophenia sp.	0.85	0.80	4.14	81.18
Calibugula sp.	1.01	0.22	3.78	84.97
Botrylloides sp.	0.15	0.78	2.53	87.50

30-in developing community with 41-out developing community

	30-in	41-out		
Species	Av.Abund	Av.Abund	Contrib%	Cum.%
Balanus sp.	8.25	6.48	19.71	19.71
Symplegma brakenhielmi	2.74	7.81	18.92	38.63
Didemnum sp.	2.16	2.72	8.36	46.99
Macroalgae	1.93	2.15	8.06	55.05
Serpuliid tubeworms	1.30	2.06	7.49	62.54
Aglaophenia sp.	1.88	0.80	6.24	68.78
Distaplia sp.	2.14	0.31	5.01	73.79
Schizoporella sp.	0.96	0.68	3.58	77.36
Styela plicata	1.77	0.03	3.47	80.83
Calibugula sp.	0.94	0.22	3.12	83.96

Table 6. Repeated measure ANOVA of the effects of time and site on diversity among developing communities. N=15 for every month at each site.

Diversity	df	F	p
Month	11	28.6325	<0.0001
Site	3	5.7081	0.0018
Month*Site	33	1.6485	0.137

Table 7. Repeated measures ANOVA of the effects of site and time on percent cover in developing communities. N=15 for every month at each site.

Percent Cover	df	F	p
Month	11	25.87	<0.0001
Site	3	4.34	0.008
Month*Site	33	2.27	<0.0001

Table 8. List of the months where taxa were first encountered in the developing communities at each site.

Site	06-in	07-out	30-in	41-out
August 2012	*Aglaophenia* sp. *Balanus* sp. *Bugula* sp. Macroalgae serpulid tubeworms *Symplegma* sp.	*Balanus* sp. Macroalgae serpulid tubeworms	*Aglaophenia* sp. *Balanus* sp. Macroalgae serpulid tubeworms *Symplegma* sp.	*Aglaophenia* sp. *Balanus* sp. serpulid tubeworms *Symplegma* sp.
September 2012	*Calibugula* sp. *Ircinia felix* *Didemnum* sp. *Distaplia* sp. *Schizoporella* sp. *Spirastrella* sp.	*Bugula* sp. *Didemnum* sp.	*Didemnum* sp. *Schizoporella* sp.	*Didemnum* sp. Macroalgae *Schizoporella* sp.
October 2012	*Cliona celata*	*Aglaophenia* sp. *Calibugula* sp. *Distaplia* sp. *Spirastrella* sp.	*Calibugula* sp. *Eudendrium* sp. *Filograna implexa* *Spirastrella coccinea*	*Botrylloides* sp. *Eudendrium* sp. *Ircinia felix* *Scopalina reutzleri* *Spirastrella coccinea*
November 2012		*Symplegma* sp.	*Bugula* sp. *Distaplia* sp.	*Bugula* sp. *Calibugula* sp. *Distaplia* sp. *Filograna implexa*
December 2012	*Euherdmania gigantea*	*Ircinia felix*		N/A
January 2013	*Eudistoma* sp.		*Eudistoma* sp. *Ircinia felix* *Lissodendoryx* sp. *Molgula occidentalis* *Schizoporella floridana* *Styela plicata*	*Chondrilla nucula* *Leptogorgia hebes*
February 2013		N/A		N/A
March 2013	Anemone *Applidium* sp. *Botrylloides* sp. *Molgula manhattensis* *Schizoporella floridana* *Styela plicata*	*Botrylloides* sp. *Molgula occidentalis* *Styela plicata*		
April 2013	Brain tumor tunicate Applidium stellatum	*Molgula manhattensis* *Schizoporella* sp.		*Schizoporella floridana* *Aplysina fulva* *Botryllus* sp.
May 2013	*Chondrilla nucula* *Scopalina reutzleri*	*Botryllus* sp. *Scopalina reutzleri*		
June 2013	*Filograna implexa*	*Eudistoma* sp.		*Dysidea fragilis*
July 2013	*Chondrosia collectrix*		*Molgula* sp.	
August 2013	*Eusenstyela* sp.		*Hyrtios violaceous*	*Styela plicata*
September 2013	*Molgula occidentalis*			

Gray's Reef National Marine Sanctuary
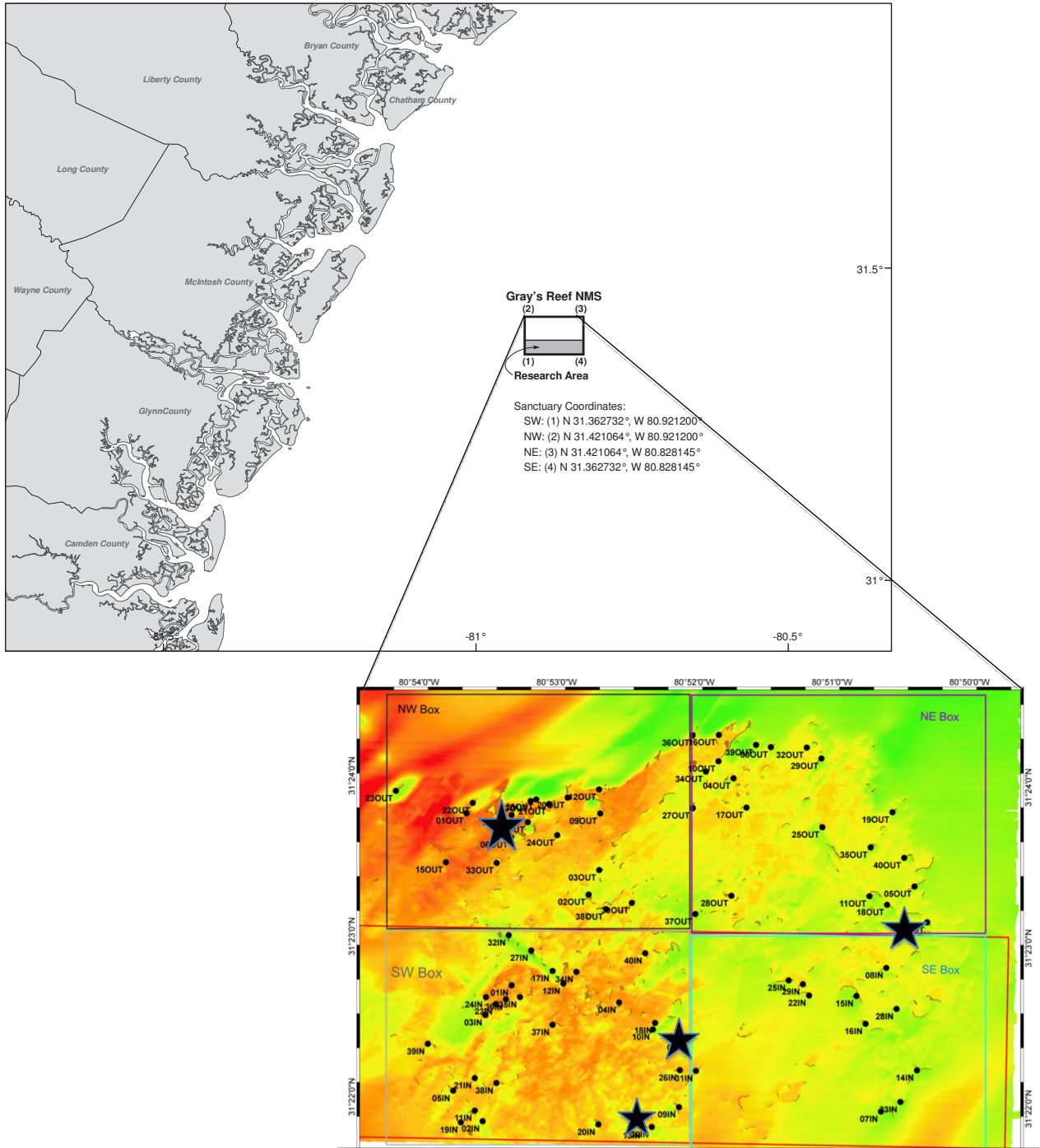
Figure 1. Location of Gray's Reef National Marine Sanctuary off the coast of Georgia, U.S.A. Location of study sites within the sanctuary marked with stars in the multi-beam image at bottom right. (Top image from Skidaway Institute, and multi-beam obtained from GRNMS).
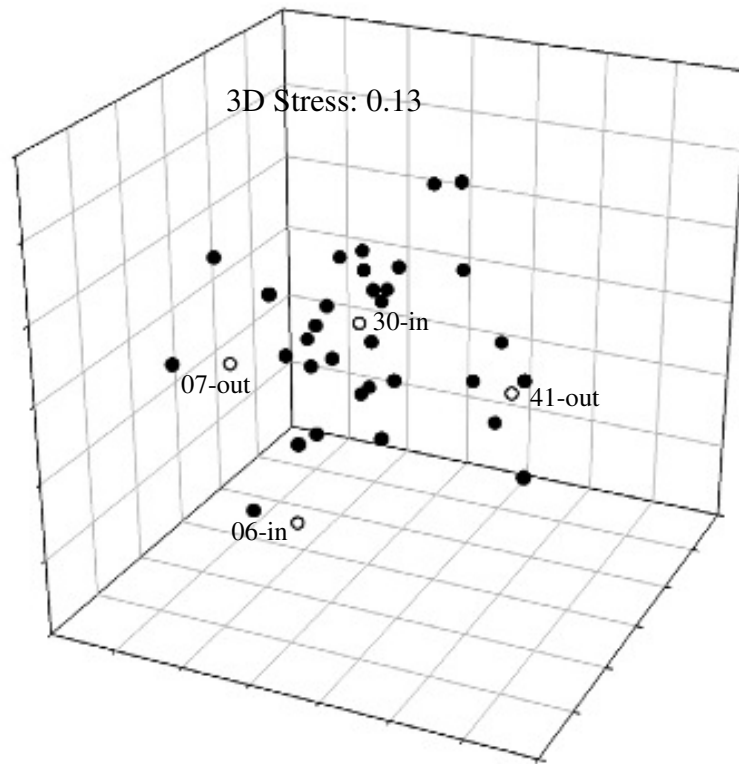
Figure 2. Non-metric multi-dimensional scaling plot depicting the differences in species abundance among sites surveyed on the Nancy Foster research cruise in June 2011. Each circle represents a unique rocky outcrop and unfilled circles labeled with site names were the ones chosen for this study.

Figure 3. Representative 30 x 30 cm paving tile illustrating surface topographic complexity.
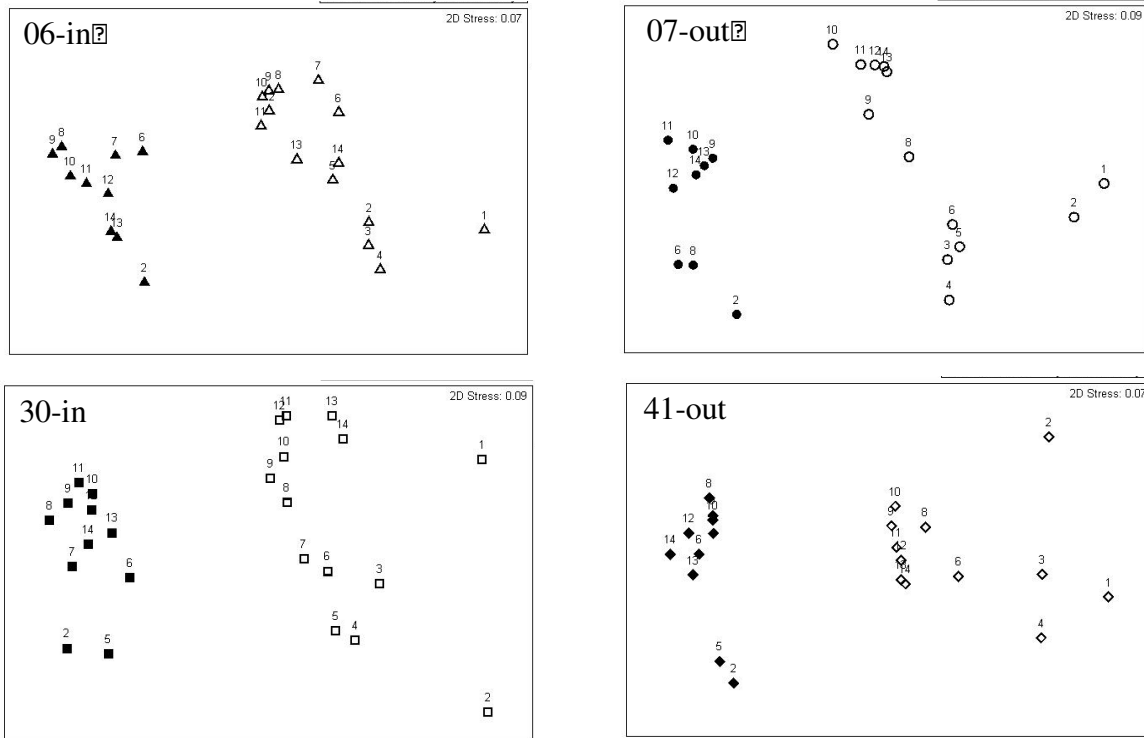
Figure 4. Two dimensional non-metric MDS of taxa in developing and extant communities at all sites during the study period. Each point on the MDS represents the square root transformed data of mean abundance (i.e. centroids) of communities from photographs or quadrats taken for the developing (unfilled symbols) or extant community (filled symbols) during each sampling period. Numbers above points indicate how many months the study had been in effect when the data were taken.
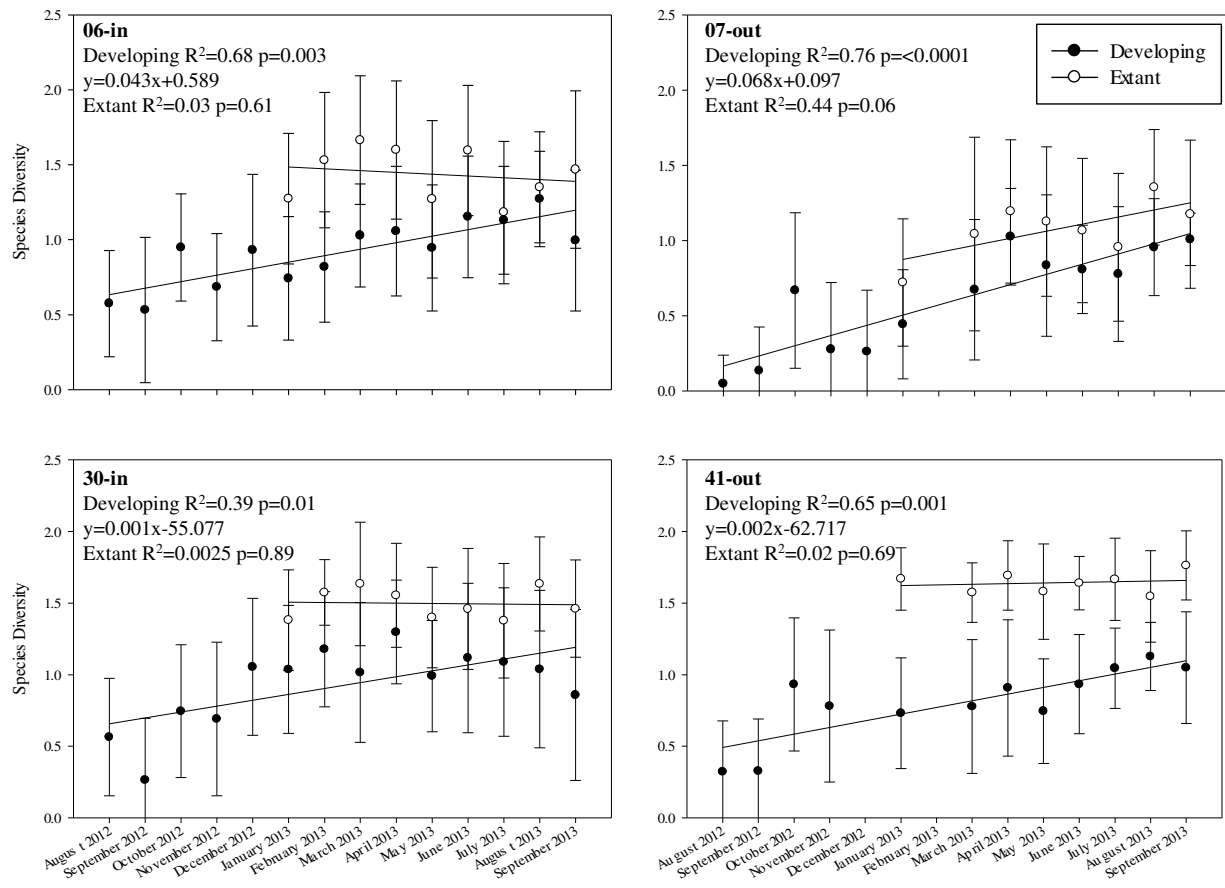
Figure 5. Species diversity between the extant and developing communities at each site over time. Error bars represent ± 1 SD. N=15 for each month in both communities.
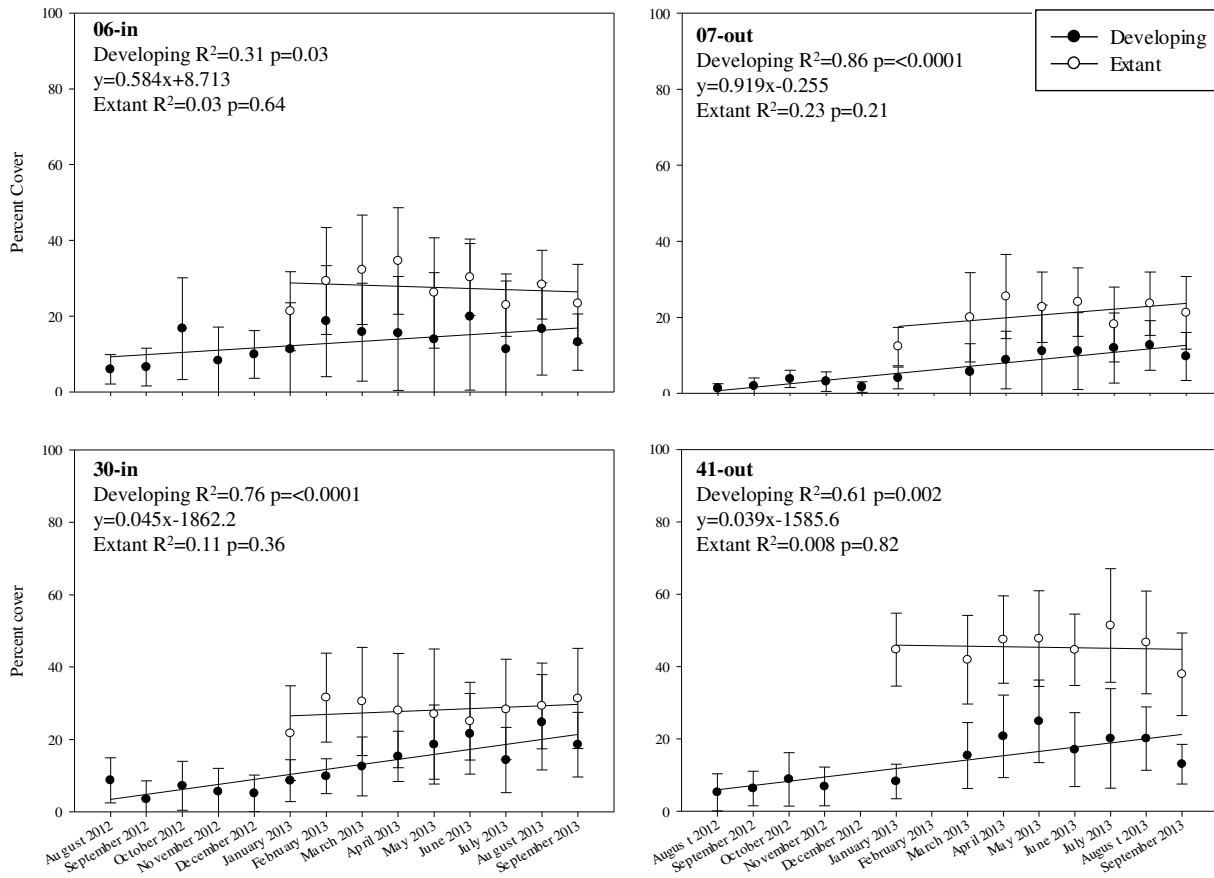
Figure 6. Percent cover in extant and developing communities at each site over time. Error bars represent ± 1 SD. N=15 for each month and each community.
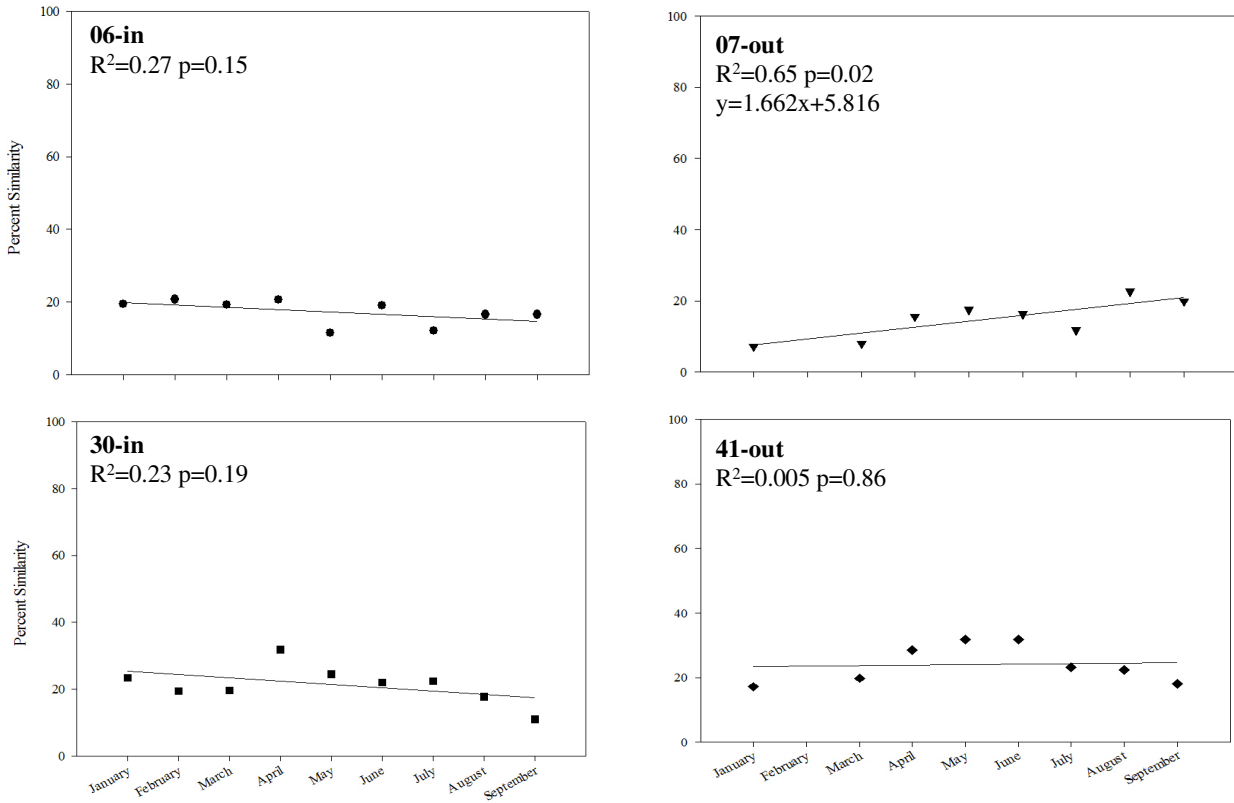
Figure 7. Bray-Curtis similarity between extant and developing communities over the study period. Each line represents the percent similarity of a developing community with its corresponding extant community. Values are based on Bray-Curtis dissimilarity between extant and developing communities from SIMPER analysis each month from January-September 2013. N=15 at each month in developing and extant communities.
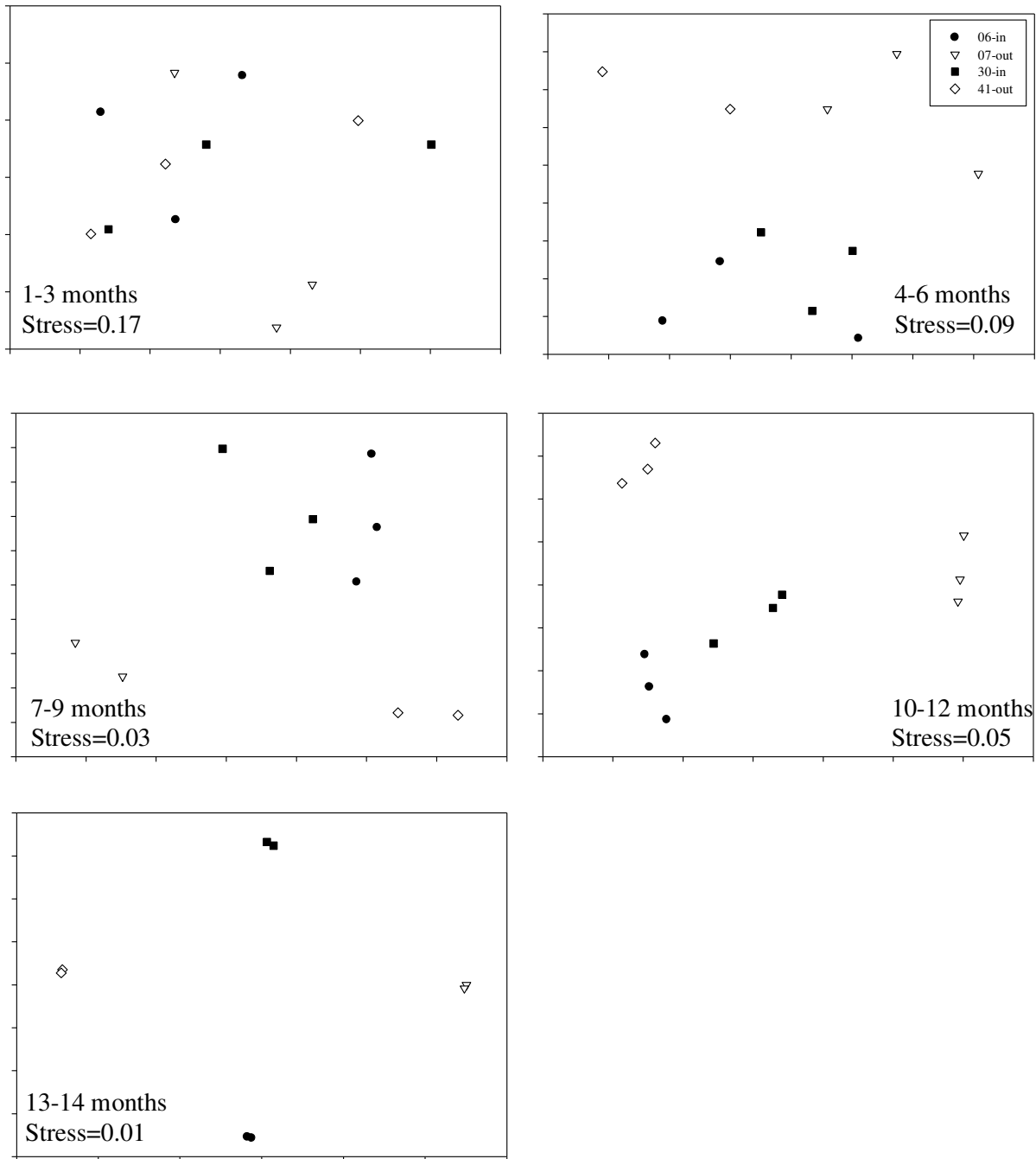
Figure 8. Two dimensional nonmetric multi-dimensional scaling plot of developing communities at each site. Each point represents the square root transformed mean abundance of all organisms on the fifteen replicate tiles for one month of sampling. Plots are grouped by two or three month time blocks.
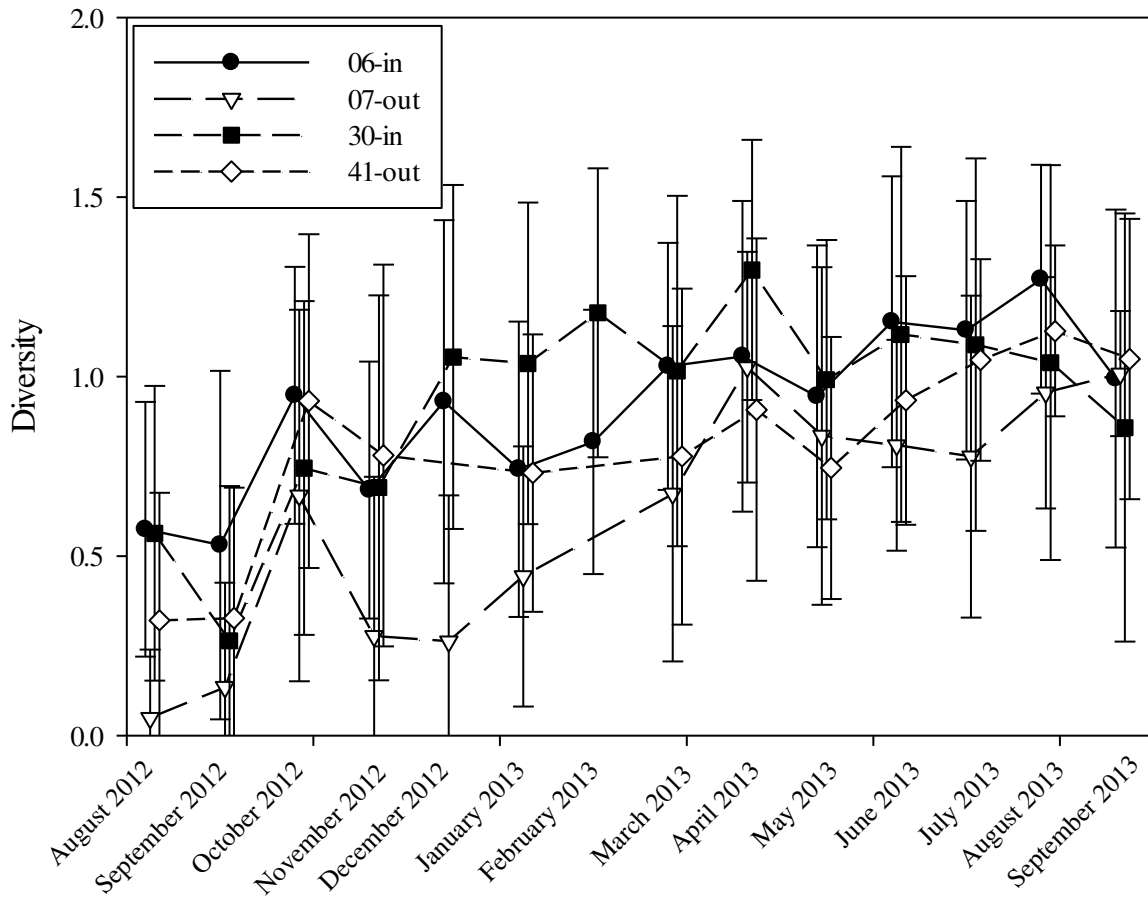
Figure 9. Mean Shannon-Wiener species diversity (± SD) for all developing communities over time. N=15 for all sites.
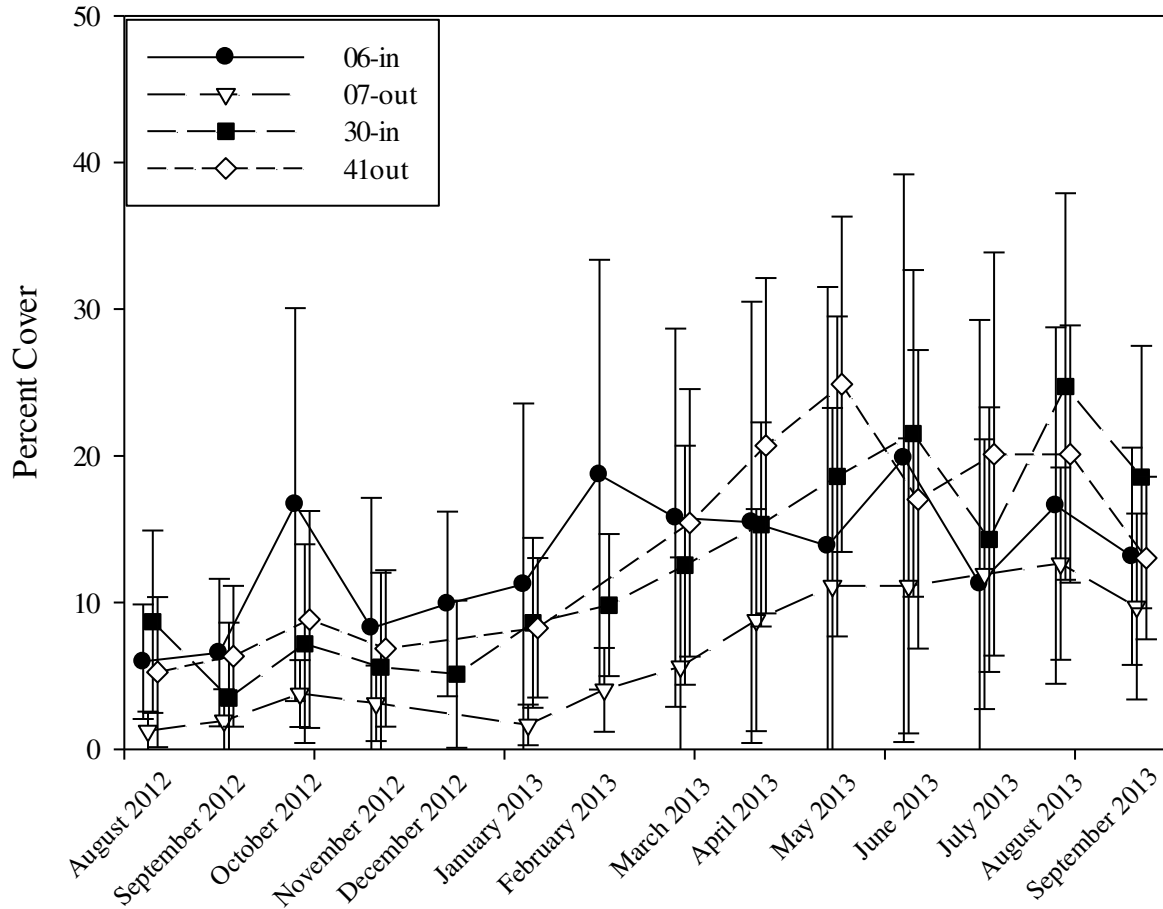
Figure 10. Mean percent cover (± SD) for all developing communities over time. N=15 for all sites.

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APPENDIX A:

SIMPER ANALYSES BETWEEN EXTANT AND DEVELOPING COMMUNITIES EACH MONTH FROM JANUARY TO SEPTEMBER 2013.

Table 9. Percentage of individual species or taxa contributing to the differences between 06-in in the extant and developing communities from January to September 2013. The top 10 contributors between each group of sites are shown.

January 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Distaplia sp.	10.07	7.06	17.15	17.15
Eudistoma sp.	6.33	0.46	11.76	28.91
Symplegma brakenhielmi	3.58	2.24	11.04	39.95
Balanus sp.	0	3.63	7.02	46.97
Didemnum sp.	3.2	0.85	6.56	53.53
Spirastrella coccinea	3.05	0	5.57	59.1
Schizoporella sp.	0.82	2.51	5.15	64.25
Amathia sp.	1.84	0.88	4.39	68.64
Clathria prolifera	2.01	0	3.95	72.58
Aglaophenia sp.	1.18	1.47	3.77	76.35

February 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	9.46	14.37	14.37
Distaplia sp.	10.65	7.72	12.87	27.24
Eudistoma sp.	8.15	1.57	10.49	37.73
Symplegma brakenhielmi	5.12	3.93	8.51	46.24
Macroalgae	4.9	0.55	6.65	52.89
Didemnum sp.	3.81	1.33	5.16	58.05
Serpulid tubeworms	0.22	2.7	4.26	62.3
Schizoporella sp.	1.69	2.32	3.62	65.92
Ircinia felix	2.95	0	3.61	69.53
Spirastrella coccinea	2.32	0	3.19	72.72

March 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	8.3	10.83	10.83
Distaplia sp.	9.36	5.07	10.63	21.46
Eudistoma sp.	8.65	1.87	10.39	31.85
Symplegma brakenhielmi	2.96	6.5	7.75	39.6
Macroalgae	5.76	1.18	6.98	46.58
Spirastrella coccinea	5.26	0.69	6.9	53.47
Didemnum sp.	4.62	1.48	5.84	59.32

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Amathia sp.	1.95	1.14	3.03	62.35
Ircinia felix	1.56	1.01	2.88	65.22
Phyllangia americana	2.16	0	2.6	67.82

April 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Distaplia sp.	10.11	4.77	10.81	10.81
Eudistoma sp.	8.57	2.56	10.62	21.43
Balanus sp.	0	7.48	10.27	31.7
Symplegma brakenhielmi	5.86	5.59	10.09	41.8
Macroalgae	4.64	0.32	5.74	47.54
Didemnum sp.	4.78	3.61	4.47	52.02
Eudendrium sp.	3.09	0	4.39	56.4
Brain tumor tunicate	3.52	0.32	4.38	60.78
Spirastrella coccinea	3.2	0.55	4.3	65.08
Titanideum frauenfeldii	1.33	0	3.17	68.26

May 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	6.61	10.36	10.36
Eudistoma sp.	4.91	2.89	8.54	18.9
Symplegma brakenhielmi	4	3.85	8.14	27.04
Distaplia sp.	4.29	3.16	7.8	34.84
Brain tumor tunicate	3.65	0.79	6.01	40.85
Ircinia felix	3.12	0.69	5.34	46.19
Lissodendoryx sp.	3.07	0	5.19	51.38
Didemnum sp.	2.27	2.05	4.56	55.95
Desmapsamma anchorata	2.25	0	4.37	60.32
Macroalgae	2.11	0.46	3.83	64.15

June 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	9.19	11.56	11.56
Eudistoma sp.	8.8	3.92	10.26	21.82
Symplegma brakenhielmi	6.42	4.38	9.64	31.47
Macroalgae	5.58	3.34	6.18	37.65
Distaplia sp.	4.97	1.31	6.06	43.71
Aglaophenia sp.	2.94	1.28	4.72	48.43
Didemnum sp.	2.48	2.57	4.17	52.6
Botrylloides sp.	0.23	3	3.52	56.12
Eudendrium sp.	2.75	0	3.34	59.47
Phyllangia americana	2.56	0	3.23	62.7

July 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Eudistoma sp.	6.13	2.23	11.04	11.04
Symplegma brakenhielmi	4.6	3.73	9.15	20.2
Amathia sp.	4.33	0	7.72	27.92
Balanus sp.	0	4.63	7.66	35.57
Didemnum sp.	1.03	4.3	7.08	42.65
Distaplia sp.	3.69	2.09	6.32	48.97
Brain tumor tunicate	3.02	0.56	6.04	55.02
Aglaophenia sp.	2.14	1.22	4.54	59.55
Ircinia felix	1.91	0.74	4.28	63.83
Spirastrella coccinea	1.88	0	3.48	67.31

August 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0.66	9.32	11.96	11.96
Amathia sp.	6.96	1.12	9.65	21.61
Ircinia felix	5.48	0.79	7.7	29.32
Schizoporella cornuta	5.33	0	7.39	36.71
Aglaophenia sp.	4.18	2.82	6.72	43.43
Symplegma brakenhielmi	3.22	2.58	5.84	49.27
Serpulid tubeworms	0.44	4.06	5.19	54.46
Macroalgae	1.96	3.3	4.79	59.25
Didemnum sp.	2.76	4.81	4.54	63.79
Lissodendoryx sp.	3.25	0	4.51	68.3

September 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	8.02	10.53	1.44
Amathia sp.	7.33	2.69	9.49	1.19
Aglaophenia sp.	3.28	4.15	6.56	0.93
Symplegma brakenhielmi	5.22	1.8	6.43	1.06
Lissodendoryx sp.	3.93	0	5.5	0.56
Didemnum sp.	3.57	4.25	4.7	1.14
Schizoporella cornuta	3.08	0	3.46	0.6
Ircinia felix	2.29	0.78	3.2	0.64
Schizoporella sp.	0.66	2.35	3.13	0.87
Phyllangia americana	2.5	0	3.01	0.84

Table 10. Percentage of individual species or taxa contributing to the differences between 07-out in the extant and developing communities from January to September 2013. The top 10 contributors between each group of sites are shown.

January 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Titanideum frauenfeldii	3.89	0	14.93	14.93
Aglaophenia sp.	3.39	2.56	12.52	27.45
Didemnum sp.	1.03	2.7	8.79	36.24
Serpulid tubeworms	0	2.02	5.82	42.06
Leptogorgia hebes	2.17	0	5.73	47.79
Amathia sp.	1.11	1.44	5.69	53.48
Symplegma brakenhielmi	0	1.32	4.02	57.5
Eudistoma sp.	1.5	0	3.76	61.26
Spirastrella coccinea	0.76	0.26	3.74	65
Cliona celata	1.17	0	3.72	68.71

March 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Titanideum frauenfeldii	4.44	0	11.03	11.03
Molgula occidentalis	5.03	0	10.15	21.18
Didemnum sp.	2.08	3.17	8.02	29.2
Distaplia sp.	4.4	0.26	7.77	36.97
Aglaophenia sp.	1.9	2.35	6.86	43.84
Ircinia campana	1.97	0	5.15	48.98
Styela plicata	2.06	1.27	4.94	53.92
Symplegma brakenhielmi	0.22	1.61	4.52	58.44
Spirastrella coccinea	1.55	0.79	4.32	62.76
Leptogorgia hebes	2.34	0	3.89	66.65

April 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Molgula occidentalis	9.61	4.03	14.72	14.72
Titanideum frauenfeldii	3.79	0	9.15	23.87
Styela plicata	4.72	3.75	8.97	32.84
Didemnum sp.	0.53	4.91	8.44	41.28
Aglaophenia sp.	2.31	2.52	7.13	48.4
Leptogorgia hebes	3.82	0	6.92	55.33
Distaplia sp.	4.06	0.23	6.38	61.71
Cliona celata	1.76	0	3.09	64.79
Telesto sp.	1.33	0	2.8	67.6
Macroalgae	0.87	0.62	2.73	70.32

May 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Molgula occidentalis	6.06	6.25	14.81	14.81
Leptogorgia hebes	6.13	0	13.18	27.99
Didemnum sp.	1.47	5.39	10.42	38.4
Titanideum frauenfeldii	3.82	0	9.53	47.93
Styela plicata	4.21	4.79	9.18	57.11
Distaplia sp.	4.32	0.4	8.48	65.59
Ecteinascidia turbinata	2.14	0	3.72	69.32
Eudistoma sp.	1.76	0	3.36	72.67
Aglaophenia sp.	1.63	0.23	2.78	75.45
Ircinia felix	1.61	0	2.72	78.17

June 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Molgula occidentalis	6.71	4.97	14.32	14.32
Leptogorgia hebes	5.75	0	12.46	26.77
Styela plicata	5.23	5.44	11.39	38.16
Didemnum sp.	1.45	5.7	9.85	48.01
Titanideum frauenfeldii	3.19	0	7.39	55.4
Distaplia sp.	3.65	0	5.9	61.3
Desmapsamma anchorata	2.05	0	4.43	65.74
Molgula manhattensis	0	1.43	2.83	68.57
Telesto sp.	1.03	0	2.68	71.25
Ecteinascidia turbinata	1.63	0	2.64	73.89

July 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Molgula occidentalis	1.03	8.13	16.2	16.2
Didemnum sp.	0.6	7.81	15.22	31.42
Styela plicata	4.22	4.6	9.86	41.28
Leptogorgia hebes	4.13	0	8.65	49.93
Distaplia sp.	3.24	0.23	6.39	56.32
Cliona celata	2.62	0	5.48	61.81
Titanideum frauenfeldii	2.81	0	5.27	67.07
Desmapsamma anchorata	2.71	0	5.04	72.11
Amathia sp.	1.84	0	4.25	76.36
Cinachyrella alloclada	1.03	0	2.35	78.71

August 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Molgula occidentalis	7.96	8.15	13.61	13.61

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Didemnum sp.	1.87	8.26	12.48	26.08
Styela plicata	4.65	4.41	8.02	34.11
Leptogorgia hebes	4.41	0	7.67	41.78
Titanideum frauenfeldii	3.07	0	5.94	47.72
Balanus sp.	0	2.85	5.09	52.81
Cinachyrella alloclada	2.84	0	4.96	57.78
Desmapsamma anchorata	2.67	0	4.73	62.51
Amathia sp.	1.89	0	3.91	66.42
Ircinia campana	2.23	0	3.71	70.13

September 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Amathia sp.	6.27	0	13.56	13.56
Molgula occidentalis	4.79	6.04	12.37	25.94
Styela plicata	4.63	6.37	10.74	36.68
Didemnum sp.	1.06	5.49	9.84	46.52
Leptogorgia hebes	4.46	0	8.57	55.09
Balanus sp.	0	2.95	5.98	61.07
Titanideum frauenfeldii	2.55	0	5.29	66.37
Desmapsamma anchorata	2.07	0	4.08	70.44
Ircinia felix	2.22	0	3.99	74.44
Oculina arbuscula	1.36	0	2.8	77.24

Table 11. Percentage of individual species or taxa contributing to the differences between 30-in in the extant and developing communities from January to September 2013. The top 10 contributors between each group of sites are shown.

January 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Distaplia sp.	6.69	1.83	13.41	13.41
Amathia sp.	8.58	2.77	13.18	26.59
Balanus sp.	0	6.02	12.24	38.83
Aglaophenia sp.	4.34	5.45	11.64	50.47
Didemnum sp.	4.36	1.92	7.82	58.29
Eudistoma sp.	3.45	0	6.87	65.17
Symplegma brakenhielmi	2.07	2.15	5.43	70.6
Schizoporella sp.	0.84	1.67	3.77	74.37
Serpulid tubeworms	0.58	1.54	3.45	77.82
Oculina arbuscula	2.23	0	3.06	80.88

February 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Eudendrium sp.	10.84	0	15.31	15.31
Distaplia sp.	7.96	3.06	9.84	25.15
Balanus sp.	0	6.31	9.5	34.65
Aglaophenia sp.	4.73	4.24	8.2	42.86
Eudistoma sp.	5.56	0	8.05	50.91
Symplegma brakenhielmi	4.87	1.51	6.57	57.48
Amathia sp.	2.83	2.12	4.96	62.44
Didemnum sp.	4.23	3.07	4.17	66.61
Macroalgae	1.84	2.03	3.87	70.47
Ircinia felix	2.71	0.23	3.75	74.22

March 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	9.02	13.61	13.61
Distaplia sp.	9.7	3.37	10.69	24.3
Eudistoma sp.	4.66	1.25	7.37	31.67
Macroalgae	5.4	0.46	7.25	38.92
Symplegma brakenhielmi	2.85	4.18	6.37	45.29
Aglaophenia sp.	3.63	2.94	6.22	51.5
Didemnum sp.	5.44	3.64	5.9	57.4
Ircinia felix	4.19	0	5.23	62.63
Botryllus sp.	2.91	0	4.25	66.89
Styela plicata	2.87	0.91	4.09	70.97

April 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0.38	9.4	15.37	15.37
Distaplia sp.	10.77	4.75	11.35	26.72
Symplegma brakenhielmi	3.52	7.28	9.51	36.22
Eudistoma sp.	4.44	1.62	7.72	43.94
Macroalgae	6.11	3.46	7.41	51.35
Aglaophenia sp.	2.63	2.72	5.9	57.25
Didemnum sp.	4.71	2.78	5.26	62.51
Styela plicata	2.57	2.52	4.86	67.38
Euherdmania gigantea	3.13	0	4.12	71.49
Schizoporella cornuta	2.3	0	3.71	75.2

May 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0.44	11.35	18.58	18.58
Symplegma brakenhielmi	5.08	7.26	11.66	30.24
Distaplia sp.	9.74	4.05	11.57	41.82
Eudistoma sp.	6.19	1.28	9.74	51.56

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Macroalgae	4.98	1.18	7.88	59.45
Styela plicata	3.09	3.13	5.53	64.97
Didemnum sp.	2.18	1.43	4.26	69.24
Aglaophenia sp.	1.82	1.23	3.99	73.23
Oculina arbuscula	2.39	0	3.99	77.22
Ircinia felix	3.02	0	3.97	81.2

June 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	13.45	20.42	20.42
Distaplia sp.	7.68	2.98	9.56	29.98
Macroalgae	8.24	2.96	9.06	39.03
Eudistoma sp.	5.27	0.69	8.13	47.16
Symplegma brakenhielmi	3.5	5.32	7.56	54.72
Styela plicata	4.5	5.04	7.08	61.8
Molgula occidentalis	0	3.19	4.42	66.22
Ircinia felix	3.2	0.23	4.07	70.29
Didemnum sp.	2.58	1.69	3.97	74.26
Aglaophenia sp.	2.03	0.23	3.57	77.83

July 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0	8.54	13.6	13.6
Distaplia sp.	7.42	3.97	9.96	23.57
Styela plicata	5.2	3.69	8.42	31.99
Eudistoma sp.	4.63	0.69	7.5	39.49
Macroalgae	4.26	3.91	7.49	46.98
Symplegma brakenhielmi	3.38	2.9	6.4	53.38
Amathia sp.	3.49	0.23	6.03	59.41
Didemnum sp.	2.55	2.34	4.79	64.19
Aglaophenia sp.	2.43	0	4.3	68.49
Euherdmania gigantea	3.02	0	4.18	72.67

August 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0.22	15.99	20.07	20.07
Amathia sp.	6.21	0.46	8.16	28.24
Macroalgae	6.84	2.1	7.19	35.42
Styela plicata	3.86	4.34	6.15	41.57
Molgula occidentalis	1.03	4.77	5.59	47.16
Schizoporella cornuta	4.19	0	5.23	52.39
Euherdmania gigantea	4.25	0	5.19	57.58
Distaplia sp.	3.39	2.59	4.5	62.08

	3.45	0	4.17	66.25
Aglaophenia sp.	3.45	0	4.17	66.25
Eudistoma sp.	3.32	0	4.13	70.38

September 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Balanus sp.	0.44	13.47	17.28	17.28
Amathia sp.	7.48	0	9.51	26.79
Aglaophenia sp.	4.97	0.82	6.78	33.57
Styela plicata	2.57	4.2	5.66	39.24
Euherdmania gigantea	4.16	0	5.25	44.49
Didemnum sp.	3.51	1.99	4.42	48.91
Schizoporella cornuta	3.56	0	4.36	53.27
Macroalgae	3.19	1.01	4.25	57.52
Ircinia felix	3.47	0	4.2	61.72
Eudistoma sp.	2.84	0	4.14	65.87

Table 12. Percentage of individual species or taxa contributing to the differences between 41-out in the extant and developing communities from January to September 2013. The top 10 contributors between each group of sites are shown.

January 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Chondrilla nucula	12.26	0.46	15.3	15.3
Symplegma brakenhielmi	13.4	5.31	11.89	27.19
Spirastrella coccinea	9.14	0	11.81	39.01
Balanus sp.	0	5.87	7.4	46.41
Leptogorgia hebes	4.56	0.23	5.77	52.17
Ircinia felix	4.46	0.23	5.67	57.84
Scopalina reutzleri	4.25	0.91	5.33	63.17
Oculina arbuscula	3.71	0	4.76	67.93
Dysidea fragilis	3.6	0	4.48	72.41
Bugula sp.	3.1	0.23	3.89	76.29

March 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Macroalgae	14.73	0.46	18.84	18.84
Spirastrella coccinea	8.5	0	11.22	30.06
Balanus sp.	0	7.77	9.99	40.05
Chondrilla nucula	7.81	0.23	9.55	49.6
Symplegma brakenhielmi	9.4	10.62	9.32	58.92
Eudendrium sp.	3.91	0	5.22	64.14
Didemnum sp.	4.45	3.09	5.19	69.34

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Oculina arbuscula	3.51	0	4.71	74.05
Leptogorgia hebes	2.32	0.32	3.16	77.21
Distaplia sp.	2.16	1.31	3.15	80.35

April 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Macroalgae	14.16	1.31	16.64	16.64
Chondrilla nucula	9.41	0.91	11.01	27.65
Balanus sp.	0	7.84	9.73	37.38
Symplegma brakenhielmi	13.49	13.31	7.93	45.31
Spirastrella coccinea	6.28	1.59	6.82	52.13
Didemnum sp.	5.48	1.31	5.96	58.09
Leptogorgia hebes	4.7	0.32	5.84	63.93
Ircinia felix	4.61	0.23	5.79	69.72
Botrylloides sp.	2.57	3.46	5.64	75.37
Eudendrium sp.	3.67	0	4.64	80.01

May 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Macroalgae	12.47	1.59	15.69	15.69
Chondrilla nucula	10.09	0.23	13.38	29.08
Symplegma brakenhielmi	15.16	16.94	10.9	39.98
Spirastrella coccinea	6.52	1.79	8.24	48.22
Balanus sp.	0.22	4.96	6.59	54.81
Didemnum sp.	3.1	3.8	6.39	61.2
Leptogorgia hebes	4.33	0	5.82	67.02
Botrylloides sp.	3.57	2.75	5.72	72.74
Ircinia felix	2.89	0.74	4.88	77.63
Oculina arbuscula	2.18	0	2.85	80.47

June 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Chondrilla nucula	10.62	0.85	14.7	14.7
Macroalgae	11.79	3.36	12.09	26.79
Balanus sp.	0	7.73	10.83	37.62
Spirastrella coccinea	7.4	0.55	10.29	47.91
Symplegma brakenhielmi	14.04	11.84	9.85	57.77
Didemnum sp.	5.03	2.59	6.08	63.85
Ircinia felix	4.25	0.23	5.86	69.71
Leptogorgia hebes	3.1	0.23	4.44	74.16
Scopalina reutzleri	2.86	0.6	4.32	78.47
Oculina arbuscula	2.72	0	4.15	82.63

July 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Spirastrella coccinea	10.46	0	11.47	11.47
Balanus sp.	0	10.12	11.27	22.75
Chondrilla nucula	10.1	0.55	11.07	33.82
Ircinia felix	9.61	0.23	10.89	44.71
Symplegma brakenhielmi	10.54	9.68	9.23	53.94
Macroalgae	8.42	4.53	6.9	60.84
Oculina arbuscula	4.49	0	5.08	65.93
Didemnum sp.	4.74	3.47	4.73	70.65
Leptogorgia hebes	3.45	0.46	4.11	74.77
Scopalina reutzleri	2.92	1.31	3.73	78.5

August 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Chondrilla nucula	12.26	0.23	14.28	14.28
Balanus sp.	1.27	9.95	10.65	24.94
Lissodendoryx sp.	7.89	0	9.27	34.2
Ircinia felix	7.09	0	9.13	43.33
Macroalgae	8.29	5.89	8.31	51.64
Symplegma brakenhielmi	6.88	7.19	5.99	57.64
Oculina arbuscula	3.72	0	4.29	61.93
Scopalina reutzleri	3.01	1.2	4.02	65.95
Dysidea fragilis	3.09	0.46	3.78	69.73
Leptogorgia hebes	3.01	0.32	3.61	73.34

September 2013

Species	Extant Av.Abund	Developing Av.Abund	Contrib%	Cum.%
Chondrilla nucula	12.85	1.14	14.59	14.59
Balanus sp.	0	8.63	10.54	25.13
Spirastrella coccinea	8.58	0.74	9.6	34.74
Dysidea fragilis	5.71	0.46	6.77	41.51
Symplegma brakenhielmi	5.52	6.29	6.26	47.78
Scopalina reutzleri	5.12	1.67	5.87	53.64
Ircinia felix	4.74	0	5.62	59.27
Leptogorgia hebes	4.46	0.32	5.34	64.61
Oculina arbuscula	4.24	0	5.28	69.88
Macroalgae	3.03	3.96	4.71	74.59