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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

EXPLORING THE POTENTIAL FOR ARTIFICIAL REEFS IN CORAL REEF RESTORATION: RESPONSES AND INTERACTIONS OF ASSOCIATED BIOTA TO VARYING EXPERIMENTAL TREATMENTS IN THE MEXICAN CARIBBEAN

By

Audie Kirk Kilfoyle

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Doctorate of Philosophy

Nova Southeastern University

March 30, 2017

Dissertation of
Audie Kirk Kilfoyle

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Abstract

Coral reefs are being negatively impacted by various causes worldwide, and direct intervention is often warranted following disturbance to restore or replace lost ecosystem structure and function. An experimental coral reef restoration study involving standardized artificial reef modules (Reefballs™) was conducted in Mexico's Yucatan Peninsula in the towns of Puerto Morelos and Akumal. The purpose was to explore the use of artificial structure for restoration and mitigation applications in a highly diverse and dynamic Caribbean coral reef environment by applying and evaluating the performance of select experimental treatments hypothesized to accelerate development of the associated biota. The first treatment consisted of invertebrate enhancing artificial substrate padding material, which provided structurally complex refuge space for mobile epifaunal/infaunal invertebrates and other benthic organisms. The second treatment consisted of coral transplants, intended to provide additional structural complexity and kick-start development of stony coral populations. The third treatment consisted of settlement plates which were intended to provide data on coral recruitment and survival rates. Multiple hypotheses relating to the interactions between experimental treatments and the resulting macroalgal, non-coral invertebrate, stony coral, and coral reef fish assemblages were examined, and comparisons were made between natural and artificial substrates. In Puerto Morelos there were 40 modules; 10 controls and 10 of each of 3 treatments: substrate pads, coral transplants, and settlement plates. In Akumal there were 12 modules; 6 controls and 3 of each of 2 treatments: substrate pads and settlement plates. Following module deployment, 6 biannual monitoring trips were made over the course of three years to assess the development of the biota, with a final 7th trip made six years post-deployment. Divers conducted non-destructive visual surveys to evaluate total abundance, species richness, size class distribution, and assemblage structure of coral reef fishes. Other monitoring work included coral recruit surveys, mobile epifaunal invertebrate collections from substrate pads, and digital imaging of coral transplants, natural reef reference corals, and benthic quadrat areas. Hurricane Dean compromised the Akumal study site during the first year of the study, but Puerto Morelos was unaffected. There the modules developed biotic assemblages that differed from what was found on the natural reef, and the data suggests that the substrate pads may have had an effect on the development of faunal assemblages.

Lobophora variegata macroaglae and *Desmapsamma anchorata* sponge were the major contributors to benthic community composition, and both had significantly greater coverage on the substrate pads treatment modules. *Lobophora* grew rapidly and peaked within the first year, while sponges increased steadily throughout the first three years of the study, surpassing the coverage of macroalgae before the end of the second year, much to the detriment of coral transplants and many coral recruits. By the end of the study, over 75% of the transplants were overgrown by *D. anchorata*, and density of new coral recruits on the Pads treatment modules was lower than the other treatments and controls. Coral recruitment was dominated by *Porites astreoides* on all treatments and controls, and the number of corals increased steadily throughout the study. The controls had consistently greater numbers of corals than the treatments, as well as lower percent coverage of macroalgae and sponges. Total abundance and species richness of reef fishes was generally unaffected by the treatments. However, at the family and species level, several differences were detected, particularly for the substrate pads treatment and to a lesser extent for the coral transplants treatment. For future restoration or mitigation efforts utilizing similar or identical treatments to artificial substrates, this study suggests that, in the absence of routine maintenance, greater success may be achieved after waiting several years post-deployment for the initial wave of unchecked growth by benthic organisms (i.e., macroalgae and sponges) to reach a balance point before a large investment of resources is devoted to coral transplanting. Further recommendations include routine monthly or quarterly on-site maintenance to enhance transplant survival, as well as a longer monitoring window to assess community development in response to experimental treatments. The results of this study suggest that the experimental treatments did indeed have an effect on the biota, but whether or not the effect was beneficial largely depends upon perspective. The Pads treatment in particular had the greatest effect on both reef fish and benthic community development, however, it was not beneficial for stony coral recruitment. Additional research is needed to fully understand the long-term performance and effects of the padding material on biotic assemblage development for future restoration or mitigation projects.

Keywords: restoration, mitigation, coral reef fishes, coral recruitment, coral transplants, benthic community, invertebrates, succession, settlement, competition, artificial substrate, artificial reef, settlement plates

Chapter 1 – Introduction: Coral Reef Restoration

1.1 Background

Coral reefs are one of the most complex, productive, and biologically diverse ecosystems on the planet (Odum and Odum, 1955; Wells, 1957; Veron, 1995; Bowen et al., 2013). They provide extractive goods and ecosystem services that benefit human populations, both directly and indirectly, in the form of fisheries resources, recreational opportunities, storm and coastal erosion protection, and aesthetic and cultural benefits that provide billions to the global economy on an annual basis, many of which are critical to the subsistence of many Caribbean economies (Jameson et al., 1995; Costanza et al., 1997; Moberg and Folke, 1999; Cesar et al., 2003). Despite the importance of these essential benefits, especially to developing countries, coral reefs and other associated tropical nearshore ecosystems have been experiencing world-wide deterioration of health and function over the past three or four decades, mainly as a result of burgeoning human populations and repeated disturbances (Clark and Edwards, 1999; Cesar, 2000; Hoegh-Guldberg et al., 2007; Wilkinson, 2008; Birkeland, 2015).

Coral reefs are dynamic ecosystems that have always been influenced by various forms of natural disturbance. They have an exceptional adaptive capacity to recover from natural stressors under the right conditions, and disturbance is even considered an important driver of their development and for the maintenance of their high levels of biodiversity (Connell, 1978; Pearson, 1981; Sousa, 1984; Nyström and Folke, 2001; Miller, 2015). However, too much disturbance can certainly be detrimental, as it takes time to recover from each successive episode. In many regions, this natural ability to recover is arguably being pushed to the limit and, in many cases, well beyond. The effects of natural disturbance are increasingly compounded by pervasive anthropogenic influences that have resulted in decreases of abundance, diversity, and habitat structure and function (Richmond, 1993; Hughes, 1994; Connell, 1997; Nystrom et al., 2000; Hughes et al., 2003; Pandolfi et al., 2003; Burke and Maidens, 2004; Bellwood et al., 2004; Wilson et al., 2006; Pratchett et al., 2014). Anthropogenic factors are now impacting coral reefs more significantly than the combined forces of most natural factors. Even remote regions that were once considered too distant from civilization to feel its detrimental effects are now showing signs of deterioration (Richmond, 2005; Gilmour et al., 2013; Birkeland, 2015; Miller, 2015). These impacts are increasing in frequency worldwide for a variety of reasons that are generally associated with human population growth, and an explosive increase in coastal development and improvements in technology used to harvest resources. Most coral reef researchers agree that overexploitation, coastal development, poor land management practices, ocean acidification, and climate change are posing the most serious threats, and the combined influence of these disturbances is leading to directional changes in the structure and function of these ecosystems that are effecting the economies of many coral reef-dependent countries (Hughes, 1994; Bryant et al., 1998; Kojis and Quinn, 2001; Moberg and Ronnback, 2003; Bellwood et al., 2004; Wilkinson, 2004; Wilson et al., 2006; Hoegh-Guldberg et al., 2007; Paddack et al., 2009).

Coral reefs require decades to recover from natural disturbances, and it appears that the rate of recovery is related to the intensity of the disturbance (Pearson, 1981; Gilmour et al., 2013). However, in the case of recovery from anthropogenic disturbances, the situation is more uncertain as the environment may have undergone more pervasive or permanent changes and coral reefs may not recover at all or only after an extremely long time from a human perspective (e.g., 100’s of years) (Clark and Edwards, 1995; Edwards and Gomez, 2007). The problems of recovery are further confounded by the great disparity in the amount of knowledge pertaining to 1) the multiple factors responsible for deterioration of coral reef health, 2) how these ecosystems function to recover following a disturbance, and 3) what role intervention or mitigation could play in recovery. Most research has focused on documenting the what, when, and how questions dealing with coral reef deterioration, whereas relatively little research has focused on how to repair it.

Several recent reviews took a comprehensive look at the general health and current stress levels of reefs from a global perspective (Bryant et al., 1998; Pandolfi et al., 2003; Wilkinson, 2008). Collectively the authors estimated that approximately 20% of the world’s coral reefs have been effectively destroyed, and show little or no sign of recovery, and 60% are rated as threatened by human activity (Burke et al., 2011). Additionally, these reviews reported that 24-27% of the world’s reefs are predicted to be under imminent risk of collapse from human pressures, and even more are likely to be affected in the long term. There are reports from the Caribbean that coral cover on most reefs has declined by 80%, and that 75% of reefs in that region are rated as threatened (Wilkinson, 2004; Burke et al., 2011), and many reefs have experienced phase-shifts from coral to algal-dominated benthic communities (Hughes, 1994; Aronson and Precht, 2000; Bellwood et al., 2004; Rogers and Miller, 2006; Mumby, 2009).

An increasing amount of attention has been brought to the plight of the world's coral reefs over the past several decades. Food and sport fish have become smaller and fewer in number (Pauly et al., 2002; McClanachan, 2009; Garcia and Rosenberg, 2010). Coral bleaching events and disease outbreaks have become more frequent and severe (Hoegh-Guldberg, 1999; Baker et al., 2008; Brandt and McManus, 2009; Vega Thurber et al., 2014). Fleshy macroalgae have become more dominant in place of reef-building stony corals in some areas (Hughes, 1994; McClenachan et al., 1999; Bellwood et al., 2004; Hughes et al., 2007; Bruno et al., 2009). Anthropogenic intrusion into the marine environment has continued to increase in step with demographic changes and the increasing demand for resources needed to support them, and reduction of habitat in both quality and quantity is inevitable given current trends of population growth and resource utilization. Precious little progress has been made towards changing societal habits to the degree needed to deal with the root causes of declining reef health and the rate at which they are being destroyed (Cesar et al., 2003; Bellwood et al., 2004; Carpenter et al., 2008).

Disturbances to coral reef ecosystems are classified as either natural or anthropogenic. Anthropogenic impacts to coral reefs can be further split into direct and indirect effects. Direct effects, in which the source of the degradation is obvious and attributable to a specific point-source, include those that result in the damage or destruction of the physical framework of the reef structure itself, such as: ship groundings, anchor damage, propeller scars, cable drags, and destructive fishing practices like trawling and dynamite fishing (Richmond, 1993; Connell et al., 1997; Knowlton and Jackson, 2008). Indirect effects are those disturbances that may not have a specific point-source or that may have origins relatively far-removed from the affected coral reef. Examples of indirect effects include sedimentation generated from deforestation or coastal development that smothers a coral reef, not only killing coral but also removing essential spawning or nursery grounds for reef fishes and other creatures (Spurgeon and Lindahl, 2000; Fabricius, 2005; Bell et al., 2006). Further examples include toxic and thermal pollution, decreased salinity, ocean acidification, eutrophication, and other biotic changes; all of which may be present in conjunction with one another or whose origins may not be directly observable and therefore difficult to pinpoint (Spurgeon and Lindahl, 2000; Hoegh-Guldberg et al., 2007). Some disturbances may fall under both categories, as lines between direct and indirect effects may become blurred and characteristics may be present which apply to both categories. For example, consider the effects of overfishing, in which the targeting and removal of apex predators and herbivores can ultimately end up affecting population levels of multiple other keystone species and, eventually, entire coral reef ecosystems (Dulvy et al., 2004; Hughes et al., 2007). In addition, some seemingly naturally caused disturbances, such as Crown-of-Thorns Starfish (*Acanthaster planci*) outbreaks or coral bleaching, may have actually been encouraged by anthropogenic factors such as nutrient input and global warming (Birkeland and Lucas, 1990; Hoegh-Guldberg et al., 2007; Wooldridge and Brodie, 2015).

In general, the Caribbean has experienced more rapid and severe reef degradation in comparison to the Indo-Pacific and Red Sea (Gardner et al., 2003; Pandolfi et al., 2003; Bellwood et al., 2004). Several attributes have enhanced the speed and severity of regional coral reef decline in response to anthropogenic influences. Geography has long played a significant role in the relatively depressed level of biodiversity that characterizes faunal assemblages from the region. The Caribbean basin has existed in its current state for a shorter length of time than the Indo-Pacific, which has resulted in less time for new species to evolve and radiate (Johnson et al., 1995; Johnson et al., 2008). It is also smaller in area and has limited connectivity to other oceanic basins.

Consider the Long-Spined Sea Urchin (*Diadema antillarum*), once one of the reef's most important herbivores after herbivorous fish populations were depleted, which largely disappeared region-wide due to a rapidly spreading disease that decimated their population in only a few years (Hughes, 1994). The combined grazing pressure exerted on Caribbean coral reefs by other primary herbivores (parrotfishes and surgeonfishes) has not been sufficient to regulate macroalgal populations in the absence of the urchins (Precht and Precht, 2015). However, several areas that have reported some degree of recovery of urchin populations have also shown signs of increased coral recruitment (Lassios, 2016). In addition to the loss of urchins, acroporid corals, Staghorn and Elkhorn (*Acropora cervicornis* and *A. palmata,* respectively), were once among the most dominant reef-building corals throughout the region. These species also suffered massive die-offs due to white band disease and exist now only in small remnant populations (Greenstein et al., 1998; Aronson and Precht, 2000; Gardener et al., 2003; Ballantine et al., 2008; Larson et al., 2014). Both the urchins and corals have the potential to recover, but it serves to illustrate how quickly demographic changes to even a small number of keystone species can affect an entire region.

In some cases, the greatest restoration success may be achieved by allowing natural recovery to run its course or by implementing different forms of passive rehabilitation that reduce stress factors and that in-turn ultimately encourages natural recovery (Woodley and Clark, 1989; Cairns, 1991). Some healthy reefs that have good water quality (low sedimentation, low nutrient loading), high rates of coral recruitment, a high degree of connectivity to other reefs, or a naturally high level of natural resilience, have an increased chance at recovering from anthropogenic impacts (Connell, 1997; Quinn and Kojis, 2006; Gilmour et al., 2013). As long as the natural reef framework is left intact, these reefs, when impacted, have a high likelihood of recovering on their own. However, in most cases, one or more of the key conditions conducive to natural recovery are diminished, or lacking altogether, on impacted or degraded reefs. In such situations, if direct restorative intervention is not applied following an acute disturbance, the reefs may have a higher likelihood of either not recovering or shifting to a less-desirable alternate state (Hughes, 1994; Pratt, 1994; Edwards and Gomez, 2007; Mumby, 2009; Graham et al., 2013). Thus, one of the major debates surrounding ecological restoration is centered on how to decide when, where, and why natural recovery is the best option; and if natural recovery is not the best option, how much and what type of direct intervention is warranted to return a reef to its original state or a more productive approximation thereof. On a practical level, the debate boils down to how best to apply limited resources to manage conservation efforts on coral reefs.

Some critical early actions, such as stabilizing fragmented or shifting sediments and broken reef substrates and rebuilding reef framework, can accelerate the process of natural recovery by creating conditions which are more favorable to settlement and survival of reef-building corals. This recovery in turn makes the area more natural and complex, and eventually more attractive to reef fishes (Jaap, 2000; Rinkevich, 2005). Increasing structural complexity and available refuge space has been shown to have positive effects on species richness, abundance, and size distribution of both reef fish, coral, and invertebrate assemblages (Gittings et al., 1988; Hixon and Beets, 1989; Hixon and Beets, 1993; Edwards and Clark, 1999; Spieler et al., 2001; Sherman et al., 2002; Lindahl, 2003; Jordan et al., 2005; Zimmer, 2006; Walker et al., 2009; Kilfoyle et al., 2015). Coral cover has also been specifically related to abundance of reef fishes, with observed declines in abundance and species richness following loss of live coral cover (Bell and Galzin, 1984; Sale, 1991; Booth and Beretta, 2002; Jones et al., 2004; Wilson et al., 2006; Komyakova et al., 2013). Enhanced structural complexity and heterogeneity of reef substrate can provide a greater variety of ecological opportunities, as well as greater availability of refuge from predation (Duedall and Champ, 1991; Perkol-Finkel et al., 2006; Graham and Nash, 2012).

To combat declining coral reef health, the efficacy and applicability of many different methods of interventive restoration are being developed and tested for use in the marine environment. Restoration, for the purposes of marine resource managers, can be defined as “the return of an ecosystem, in terms of its structure and function, to a close approximation of its condition prior to disturbance” (Precht and Robbart, 2006). However, despite the best of intentions and considerable monetary expenditures, most restoration projects have fallen short of returning damaged areas to their original condition prior to disturbance and have resulted in what may be more appropriately classified as ecologically superficial ‘enhancements’ or ‘rehabilitations’, rather than true ecosystem ‘restoration’ (Moberg and Ronnback, 2003). This is due to the fact that repairing a complex and organically generated ecosystem and entire populations of organisms is inherently challenging, especially in regions where reefs are already struggling from recruitment limitation and multiple anthropogenic influences, but also due, in large part, to the difficulty in defining objectives and successful, or acceptable, outcomes. Given the high degree of variation in the nature and severity of natural disturbances that may occur between years, and that this variation is compounded by anthropogenic influences and fluctuations in benthic community structure as ecological succession progresses, restoration of most marine ecosystems requires acceptance and an understanding that it is extremely difficult to hit a moving target (Richmond, 2005). Artificial reefs factor prominently into the discussion of interventive restoration, as they are often used to mitigate for damage or destruction of marine resources, but are not necessarily ideal for replacing ecosystem services once provided by lost hardbottom or coral reef habitats (Banks et al., 1998; Powers et al., 2003; Goodsell and Chapman, 2009; Pioch et al., 2011; Levrel et al., 2012; Kilfoyle et al., 2013).

Coral reef ecosystems are characterized by extreme complexity at essentially every scale, and as such we still have much to learn about their form and function; further, they exist in a highly dynamic, variable, and often unpredictable environment. Any effort to fully restore such a complex ecosystem to its original state will almost certainly fall short of that lofty goal to some degree. Coral reef restoration is a knowledge and technique driven discipline that is still very much in its developmental stages, and as such there is still much to be learned. Research on the efficacy of both new and existing restoration methods has been increasing in recent years, but significant gaps in our understanding of the processes affecting both still remain.

Although many coral reef restoration projects in the past have dealt with the use of artificial reefs as tools for restoration and rehabilitation or as means of exploring recruitment dynamics and factors affecting community development, their popular use for the purposes of coral reef restoration remains a contentious issue (Clark and Edwards, 1999; Gilliam, 1999; Seaman, 2000; Miller, 2001; Sherman et al., 2001; Spieler et al., 2001; Abelson, 2006; Perkol-Finkel et al., 2006; Jordan, 2010). Many commercially available and mass produced artificial reef designs have acquired what may be considered overstated or unjustifiable reputations as essential tools for successful coral reef restoration. Often these designs have not been subjected to rigorous scientific testing. Obviously, artificial reefs are inherently ‘artificial’, and their use automatically removes true ‘restoration’ from the list of achievable goals under most circumstances. They typically require a conditioning period during which their substrates become more amenable to colonization by corals and other benthic invertebrates and a transitional period where communities go through phases of succession in route to a more advanced state of ecological maturity. And, it is argued that even ‘mature’ artificial reefs cannot fully replicate the function of natural habitats in even the best of circumstances (Pratt, 1994; Edwards and Gomez, 2007).

There is also a disparity between the relative scale of most direct forms of active restoration or mitigation, whose functional influential footprint is usually measured in 10’s to 100’s of square meters, compared to the scale of damage or degradation often inflicted upon coral reef ecosystems that often spans 10’s to 1000’s of square kilometers, depending upon the underlying cause. Most applications of direct intervention have involved sediment stabilization, restoration of structural complexity, and replacement of lost habitat (often with artificial reefs) that has been lost or degraded as the result of ship groundings, anchor damage, storm damage, coastal construction, dredging, sedimentation, beach renourishment, and destructive fishing practices (Banks et al., 1998; Jaap, 2000; Miller, 2000; Miller and Barimo, 2001; Gilliam et al., 2004; Precht and Robbart, 2006; Edwards and Gomez, 2007; Kilfoyle et al., 2013). Direct restorative intervention can be expensive and therefore is best implemented only when natural recovery is expected to be unsatisfactorily slow or altogether unlikely (Spurgeon and Lindahl, 2000; Milon and Dodge, 2001; Moberg and Ronnback, 2003). It is also noteworthy that no amount of restoration effort can repair an ecosystem that is still in the process of being disturbed by one or more degrading influences. It follows that the source of the disturbance must be identified and removed before any form of restoration can be truly effective. Thus, an oft-cited central tenet of ecosystem restoration is it will not be successful unless the original cause of disturbance is identified and removed, regardless of scale or cost of the restoration effort (Richmond, 2005; Edwards and Gomez, 2007).

Particularly in the last few decades, many promising theories have been discussed and new techniques and methodologies field tested for their potential to enhance or accelerate natural recovery following coral reef disturbances. These include development of crustose coralline-algae derived coral-larval ‘fly papers’ to enhance settlement, metamorphosis, and replenishment of coral populations, seeding of coral larvae, and transplanting corals directly onto natural and artificial reefs (Morse, 1990; Morse and Morse, 1991; Morse and Morse, 1996; Heyward and Negri, 1999; Heyward et al., 2002; Monty et al., 2006; Quinn and Kojis, 2006; Quinn, 2009; Boch and Morse, 2011;

Rinkevich, 2014; Cummings et al., 2015; Edwards et al., 2015; Lirman and Schopmeyer, 2016). Some researchers have shown that structurally complex artificial substrates can be used to collect and enhance epifaunal and infaunal invertebrate abundance and species diversity on natural and artificial surfaces. This in-turn assists in the creation of presumably more natural conditions and potentially has positive spill-over effects on biodiversity and abundance of other associated biota (Osman, 1977; Barwick et al., 2004; Zimmerman and Martin, 2004; Rule and Smith, 2005; Rule and Smith, 2007; Robinson et al., 2008). With one notable exception (Robinson et al., 2008; Robinson, in prep), the majority of previously field tested artificial invertebrate enhancing substrate materials has been linked to their use as invertebrate collectors for the purposes of evaluating infaunal community composition. This study, coupled with Robinson (in prep), are apparently the first field studies designed to test an invertebrate enhancing artificial substrate with large surface area (>1 m^2) applied to restoration or mitigation intended artificial reef structures.

Other research has evaluated the efficacy of new coral 'gardening' methods and coral transplantation techniques that can supply a destroyed or denuded area with immediate increase in topographic complexity and species diversity (Rinkevich, 2000; Epstein et al., 2001; Epstein et al., 2003; Rinkevich, 2006; Shafir et al., 2006; Lirman et al., 2010; Johnson et al., 2011). However, a widely-accepted caveat is that transplantation should only be undertaken if natural coral settlement is unlikely to occur on reef surfaces (Edwards and Clark, 1999; Burt et al., 2009; Goodsell and Chapman, 2009). Some researchers have suggested that the addition of coral transplants to otherwise barren substrate may enhance coral recruitment by providing a signal, either chemical or physical, that might serve to attract coral larvae or induce them to settle nearby. The idea is that both the settlement of conspecifics near transplanted adult colonies and settlement of propagules from the brooding transplants would contribute to recruitment density on nearby un-colonized substrates (Harriott and Fisk, 1988; Oren and Benayahu, 1997; Edwards and Clark, 1999; Epstein et al., 2001; Reyes and Yap, 2001; Epstein et al., 2003; Gleason et al., 2003; Zimmer, 2006; Quinn, 2009; Montoya-Maya et al., 2016). Results supporting this hypothesis have been minimal to date and the ability to detect transplant-induced or attributed settlement may be lacking altogether. Nonetheless, it remains a tantalizing concept but more research is needed in order to conclusively substantiate or refute the idea.

Currently, there are no proven and established methods of restoring coral reefs that can be applied with any degree of certainty in every situation, regardless of geographic location or the nature and extent of damage (Spieler et al., 2001; Edwards and Gomez, 2007). Moderate success has been achieved in some localized areas, but methodologies that may appear effective in one region may be completely ineffective in another, and results may even vary within small areas due to the inherent variability of the marine environment (Spieler et al., 2001; Sherman et al., 2001). To eliminate some of the guesswork presently associated with coral reef restoration, continued research is required to build an increasingly comprehensive knowledge base useful for addressing the multiple interacting factors that influence recovery and rehabilitation of these valuable ecosystems (Spieler et al., 2001). The unprecedented decline in global reef health demands that more effort must be made on the part of coral reef researchers and managers to enhance our capacity to make decisions that will have relevant and lasting positive outcomes.

1.2 Significance and Purpose

The outcomes of this project are intended to give resource managers, as well as researchers and others dealing directly with restoration of coral reefs utilizing artificial reef technology, an improved understanding of how multiple variables interact with one another and potential ways to accelerate recovery following a destructive or harmful impact to a coral reef. While many questions will likely never be fully answered and some processes never fully understood, this project is designed to help bridge many of the knowledge gaps that currently exist and hopefully eliminate some of the need for guesswork in future restoration or mitigation projects that involve artificial reefs, coral transplants, and the experimentally novel invertebrate enhancing artificial substrate pads. This study is intended to add another globally applicable, yet regionally specific, tool available to resources managers when making decisions about how and when restoration applications should be utilized should they become necessary, and what potential outcomes might be expected as a result. The science of coral reef restoration is still largely in its developmental stages, and the results of this experimental project help refine some existing methods and hypotheses that may improve future applications of restoration technology in a non-experimental real-world setting.

This study utilizes standardized substrate modules (Reef Balls^{TM}) as experimental platforms to evaluate the efficacy of multiple treatments/restoration interventions applied to their exterior surfaces (artificial substrate padding material, coral transplants, and settlement plates), and describes the development of and competition between major taxonomic groups associated with the modules over the course of six years. While admittedly paralleling and drawing inspiration in some ways from other similar previous and ongoing field manipulations of small concrete artificial reef modules, this project utilizes multiple previously explored techniques and combines them together for experimental field testing in a completely new geographic region. Utilization of concrete pallet balls as an experimental platforms for applying coral transplants, artificial invertebrate enhancing substrate material, and settlement plates, as well as the effects of various fill materials, were examined in separate projects in Broward County (Sherman, 2000; Sherman et al., 2001a; Sherman et al., 2001b; Spieler et al., 2001; Fahy et al., 2006; Quinn, 2009; Robinson, in prep;) and for other experimental purposes in more distant regions – i.e., Indonesia (Bachitiar and Prayoga, 2010), Palau (Edwards et al., 2015), the Philippines (Villanueva et al., 2010), and Tanzania. The Broward County experiments were conducted within an area characterized by low rates of coral recruitment, even by Caribbean standards, and home to a hardbottom coral and gorgonian community, as opposed to an actively accreting coral reef (Goldberg, 1973; Banks et al., 2007; Collier et al., 2008; Riegl and Dodge, 2008).

This project incorporates concrete block fill material, previously shown to increase fish abundance and species richness (Sherman et al., 2002; Quinn, 2009), and functionally serves as a synthesis of methodologies from previous projects, testing them in a region with a highly diverse tropical coral reef ecosystem with higher rates of coral recruitment than southeast Florida. Historically, the utilization of artificial reefs for any purpose has been sparse in Mexico (Baqueiro and Mendez, 1994), and most projects have focused on deploying “casitas” designed to attract Spiny Lobsters (*Panilurus argus*). Artificial reef deployments have increased along the Mayan Riviera of Quintana Roo over the last decade, but almost all of those projects involved construction of breakwaters, snorkeling trails, or artistic endeavors; few have been subjected to routine biological monitoring of their developing faunal assemblages (Encalada, 2010). Therefore, there is a gap in our holistic understanding of how marine assemblages develop on artificial substrates in the Yucatan region, as there are very limited hypothesis-driven projects available for comparison.

This project is ultimately intended to address the debate about whether or not direct intervention is warranted following disturbance or damage to a coral reef. Some researchers are opposed to the idea of using artificial structure of any sort for coral reef restoration, suggesting that artificial reefs will always be too inherently artificial and therefore poor substitutes for the real thing. Additional concerns are centered on the potential for artificial reefs, when used as restoration or mitigation tools, to serve as justification for continued implementation of unsustainable coastal development practices and further coral reef destruction. In reality, there are limited viable options for reef restoration on a relevant and affordable scale, and therefore even a moderately functional approximation of a coral reef habitat is likely better than the alternative given no efforts to restore or mitigate. The results of this project may lend support to either side of this ongoing debate. In addition, this project may also supplement previous recruitment studies and lessons learned here may reinforce or refine established theories on recruitment dynamics of coral reef fishes and associated benthic habitat features (Shulman et al., 1983; Shulman, 1985a; Shulman, 1985b; Doherty and Williams, 1988; Sale, 1991; Caley et al., 1996). Data obtained in this study can also be used to elaborate upon existing sparse reports of recruitment and assemblage structure in the study area.

1.2 Hypotheses

To address the question of what type of, and how much, intervention is warranted, this project examines the development of fish, coral, non-coral invertebrate, and macroalgal communities on standardized concrete artificial reef modules in response to select experimental treatments that were hypothesized to accelerate or enhance aspects of recovery and assemblage development. Invertebrate enhancing artificial substrate padding was added to one treatment group of modules to increase surface complexity and microhabitat resources for invertebrates. Coral transplants were added to a second treatment group to increase surface complexity and provide an early infusion of mature and reproductively viable coral colonies. An equal number of controls with no treatments were incorporated into the sampling design. The response of the biological community to the treatments is also compared to ecological rates and processes on the natural reef. The study is specifically designed to test the following hypotheses:

- Increasing habitat complexity by adding coral transplants to restoration structure will affect (likely enhance) development of coral reef fish assemblages.
- The addition of a novel invertebrate enhancing artificial substrate pads to restoration structure will affect (likely enhance) development of coral reef fish assemblages.
- The addition of coral transplants will affect (likely enhance) coral recruitment rates and kick-start coral populations.
- The addition of novel invertebrate enhancing artificial substrate pads to restoration structure will affect (likely enhance) resulting coral assemblages.
- The addition of novel invertebrate enhancing artificial substrate pads to restoration structure will enhance the return of a “more natural” coral reef ecosystem than simply providing coral settlement structure or coral transplants.
- Comparison of community response to formal treatments applied to the substrate modules (SMs) allows understanding of rates and processes on the artificial structure as compared to the natural reef.

Furthermore, this study presents information on coral settlement rates, species-specific mortality of corals (recruits and transplants), and macroalgal and benthic invertebrate growth rates. These data are critical for contrasting the restoration potential and required interventions at different geographical locations. It is also important to note that comparisons were made between assemblages found on the experimental modules and neighboring natural reef using identical or similar assessment techniques. This study also provides additional insight on the effectiveness of using this particular type of artificial reef design, more than half a million of which have been constructed and deployed worldwide for restoration and other applications.

Chapter 2 - Methodology

2.1 Artificial Reefs and Survey Design

2.1.1 Experimental Design

Multiple studies have shown that concrete can provide a suitable substrate for the settlement of scleractinian corals and other benthic organisms (Fitzhardinge and Bailey-Brock, 1989; Reyes and Yap, 2001; Spieler et al., 2001). To minimize confounding factors due to reef topography and benthic habitat differences, this study utilized standardized artificial reef modules (SMs) of the Reef Ball™ "Pallet Ball" design. Pallet balls are 1.22 m wide and 0.9 m high, weighing 575 kg. The exterior surface area for monitoring (not including the bottom surface), as determined by the aluminum foil technique (Marsh, 1970), is ~2.64 m^2. The selection of this specific artificial reef design was based largely upon a reputation for stability, durability and replicability, and therefore an ability to function as a suitable experimental platform for the purposes of this study and beyond. Reef Balls have been mass-produced and deployed in the marine environment for various uses by the thousands worldwide (breakwaters and shoreline protection, mitigation, research, snorkel trails, etc.) (Barber et al., 2008), with over 550,000 deployed in more than 4,000 projects to date (Reef Ball Foundation website, 2016). Although the modules were identical in basic structure, (i.e. height, number and location of holes, void space), there were minor differences based on, for example, subtle differences in the consistency of the concrete used and random mold-filling pouring effects. For the purposes of this study, such minor differences were considered cosmetic and were not considered to be confounding factors.

A total of 52 pallet balls were constructed as identical replicates and deployed at two separate geographical locations. There were 40 modules deployed at the main study site in Puerto Morelos, Mexico, with ten of each of three treatments (Pads, Coral Transplants, and Settlement Plates) and controls arranged in a randomized grid pattern throughout the deployment site (Figure 2.1). At the secondary study site, Akumal, a total of 12 modules were deployed in a single line, with a random combination of three of each of two treatments, Pads and Settlement Plates, and six Controls (Figure 2.2). No coral transplants were utilized at the secondary study due to a lack of suitable unattached 'corals of opportunity' and no desire to harvest healthy colonies from a nearby reef.

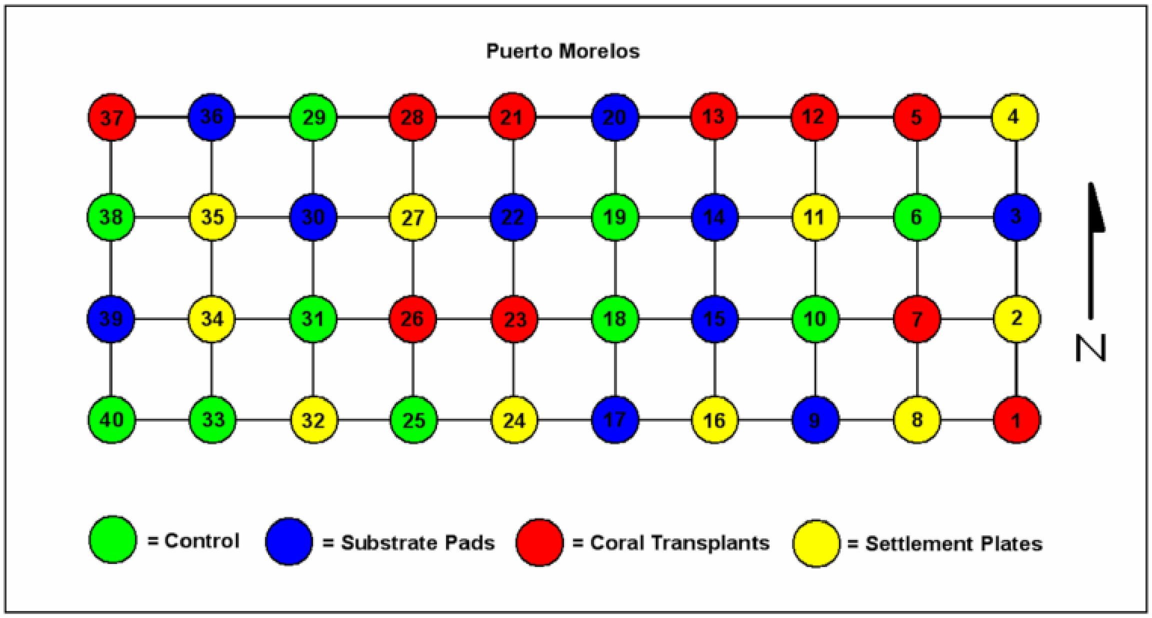


Figure 2.1 Substrate module deployment grid for the main study site in Puerto Morelos, and final randomized design. Numbering was from right to left due to the location of a permanently installed mooring ball near module 1 and the presence of natural reef structure to the south and east of the deployment field.

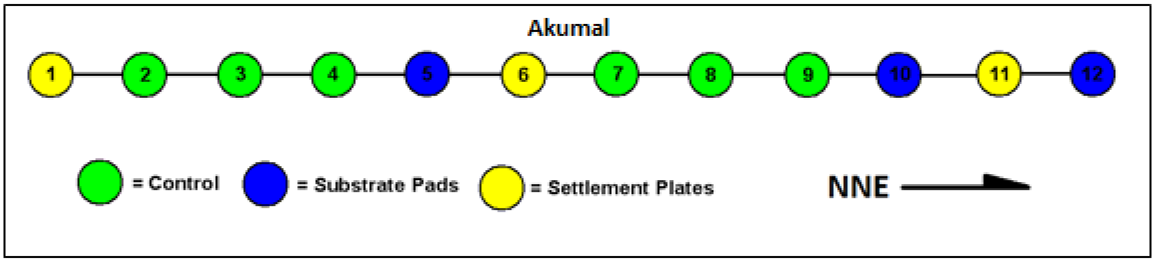


Figure 2.2 Substrate module deployment arrangement at secondary study site in Akumal, and final randomized sampling design.

Other artificial reef studies, similar to this one, in Florida (Gilliam, 1999; Sherman, 2000; Quinn, 2009; Robinson, in prep.) have utilized similar sample sizes and numbers of replicates (Gilliam: 40, Sherman: 20 and 16, Quinn: 40 groups of 4, Robinson: 48), and modules of the same design were utilized in Palau, Philippines, and Tanzania for other similar studies.

The results from previous studies (Sherman et al., 2002; Quinn, 2009) have demonstrated that increased internal complexity, specifically including concrete blocks within pallet balls, has a positive effect on the development of reef fish assemblages in terms of increased abundance and species richness. For this reason, it was decided that implementation of a similar blanket strategy would be employed for this project. Every module within every treatment, at both study sites, had four concrete blocks placed within the interior cavity and identically arranged to enhance internal refuge space and structural complexity while still maintaining replicate uniformity.

After studying community development on sunken vessels in South Carolina, Wendt et al. (1989) suggested that artificial reef communities might still be undergoing succession ten years following deployment. Others have gone further on to state that advanced development of a coral community on artificial reefs likely takes longer than just ten years, even for faster-growing tropical ecosystems with favorable conditions for community development (Perkol-Finkel and Benayahu, 2005; Perkol-Finkel et al., 2005). While it would be informative to examine faunal assemblages on the substrate modules ten years post deployment, this study, as part of a larger research effort designed to provide useful feedback and field tested restoration solutions as soon as possible, was not initially designed with an eye towards finding out how the experimental treatments performed on a decadal scale. It was designed to see if any of the methods implemented here could be applied in the future to facilitate rapid positive changes (within 3-6 years) to developing artificial or recovering natural substrates.

2.1.2 Restoration Interventions

A general overview of each experimental treatment and the controls and the associated monitoring methods is presented here. A fully detailed description of each data collection method and specifics on data analysis are found in section 2.5.

Controls (Natural Recovery) – In Puerto Morelos this consisted of 10 un-altered modules; basic identically constructed pallet balls. This design also served as the foundational unit onto which the experimental treatments, or ‘restoration interventions’, were applied. In Akumal six Control modules were utilized.

Artificial Substrate Pads - Addition of a novel structurally-complex artificial substrate material (3M scrubbing pads) (Robinson and Thomas, 2000; Robinson and Messing, 2009) to the exterior surface of 10 modules in Puerto Morelos was intended to serve as additional refuge space for epifaunal and infaunal invertebrates and hypothesized to possibly accelerate the return of 'more natural' conditions by providing an additional forage base for the developing reef fish community. This material covered approximately 45% of the exterior surface of each of the 10 modules that received this treatment. In Akumal, three Pad-treated modules were utilized.

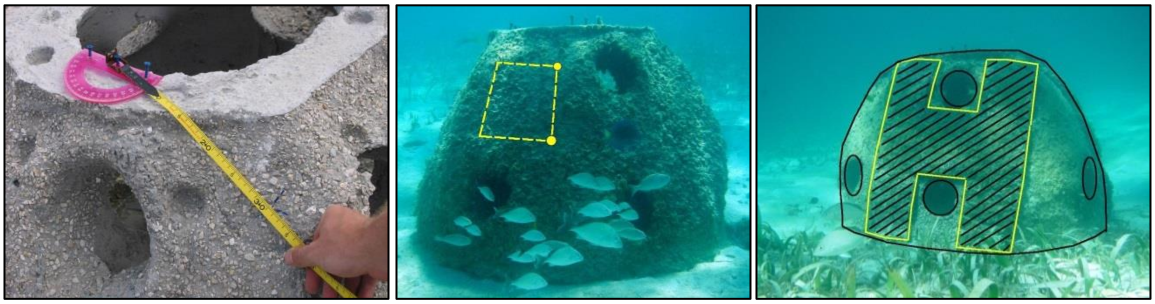
Coral Transplants - A total of six (two colonies x three species) corals were transplanted to the upper surfaces of 10 modules in Puerto Morelos using a cement and plaster mix (60 colonies total). The species used were: *Orbicella annularis*, *Agaricia agaricites*, and *Porites astreoides*. *Orbicella annularis* is a broadcast spawning species, whereas *A. agaricites* and *P. astreoides* are both brooding species. Transplants consisted of healthy "corals of opportunity" of approximately 10 cm diameter (colony width), collected from nearby natural donor reefs that have similar conditions as the deployment site. No Coral Transplant treatments were utilized in Akumal.

Settlement Plates - Both long and short-term coral recruitment to 10 modules (12 plates/module, 120 total) and five natural reef transects (5 plates/transect) in Puerto Morelos were assessed using standardized removable 0.01m^2 fiber-woven concrete settlement plates. Plates were installed on the modules and natural reef transects after a conditioning period of nine months post-deployment, and half of the total were collected six weeks following the regional annual coral spawning event. The remaining half were removed approximately one year following the initial collection, again approximately six weeks after coral spawning. In Akumal, 36 plates were deployed on the modules and 15 on the three natural reef transects.

Natural Reef - Natural processes on a nearby natural "reference" reef were monitored and served as an effective 5th treatment. Five permanent transects, 10 m in length, were established at similar depth to the modules, and 10 quadrat areas were designated and permanently marked on each transect, their selection based on available space for potential new coral recruits and placement of a rigid framer assembly for digital photography. In addition, each transect received three settlement plates, one at the beginning, middle, and end (3 plates/transect, 15 total). Reference corals (N = 10 for each species) of similar size and the same species as those transplanted to the modules were also located within the transect area and marked with metal pins and fluorescent survey tape for repeated monitoring.

2.1.3 Artificial Reef Design and Treatment Applications

A standardized range-and-bearing system was employed on the surface of every module for tracking individual coral recruits over time (Figure 2.3 A). Three masonry screws were permanently installed on the upper lip of side of each module for placement of a plastic protractor and tape measure. In addition, three permanent monitoring areas (25 cm x 25 cm) were established in the same location on each of the three identical surfaces of the modules for digital photography and *in-situ* benthic surveys (Figure 2.3 B). Depending on the treatment, either artificial invertebrate enhancing substrate pad material was applied to the three sides with identical surface area coverage (Figure 2.3 C), coral transplants were attached to the upper edge (Figure 2.4), or settlement plates were arranged in a precise symmetrical pattern on the exterior surface of the modules (Figure 2.5).



A **B** **C**

Figure 2.3 A) Range-and-bearing method of mapping coral recruit locations and tracking individual recruits through time, **B)** Location of permanent markers (yellow dots) and quadrat survey area (dotted line), and **C)** Location of artificial substrate pad material (shaded area).

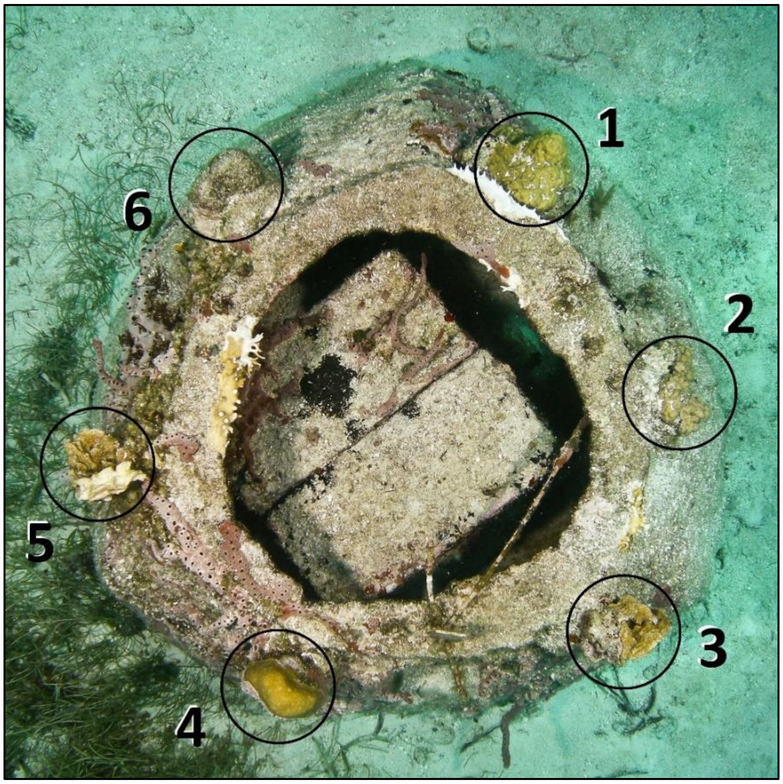


Figure 2.4 Symmetrical clockwise arrangement of the coral transplants: 2 colonies x 3 species = 6 colonies total. Arrangement by species was randomized for each module. On this particular module: *Porites astreoides* (1 and 2), *Agaricia agaricites* (3 and 5), and *Orbicella annularis* (4 and 6).

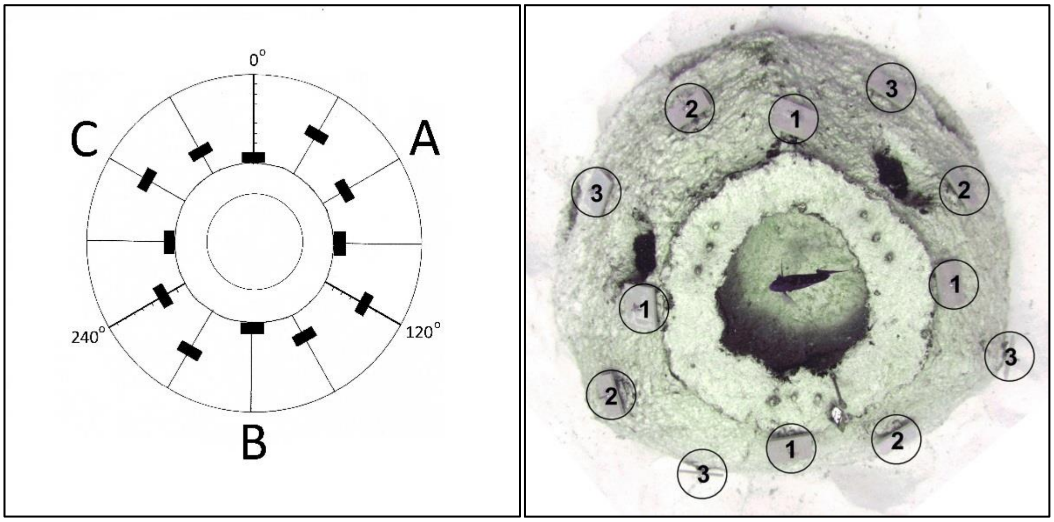


Figure 2.5 Overhead diagram (left) and photo (right) illustrating the symmetrical design of a pallet ball, the 3 identical faces (120° each), and arrangement of settlement plates.

2.1.4 Recovery Assessment

Multiple indicators are available for ecosystem health assessments, many of which have traditionally been heavily reliant upon single species indicators. With single-species methods, the individual response of an alleged indicator, keystone, or flagship species to a disturbance or intervention action may be described (Zacharias and Roff, 2001). However, the direction and magnitude of a single species response is often characterized by a high degree of variability in response to biogeographic range, habitat and environmental variability, and trophic dynamics (Pikitch et al., 2004). As such, single-species indicators may not accurately reflect ecosystem-wide changes and therefore data that reflect ecosystem-wide structure and function often needs to be utilized to better understand observed environmental trends (Sandin and Sala, 2012). This is true for both natural and artificial reefs.

To address the questions posed by the hypotheses (section 1), ecological succession on the substrate modules and the variations in response to the applied experimental treatments (restoration interventions) were studied in great detail. Each of the recovery assessment parameters listed below were monitored semi-annually (twice a year) for a period of three years post-deployment. An opportunistic seventh monitoring trip, six years post-deployment, allowed for collection of an additional dataset and serves as the final data-point for the metrics discussed in this study.

Rates of coral recruitment - The entire exterior surface of each substrate module, along with designated permanent quadrat survey areas on the natural reference reef, was surveyed for the presence of new and previously recorded coral recruits. In addition, the settlement plates were removed at set intervals following local spawning events and returned to the laboratory for microscopic analysis. The use of settlement plates was intended to assist in addressing the question of whether observed rates of coral recruitment were driven by a depauperate larval supply or high post-settlement mortality.

Rates of coral growth - Transplanted corals and new recruits on the substrate modules were monitored, as were adult reference colonies on the natural reef of similar size as the transplants. Greatest and least diameter and height of all colonies was measured and digital quadrat photos were taken.

Rates of coral survival - Appearance, health, and mortality through time of coral transplants and coral recruits were recorded for each species. Coral recruits were mapped and tracked through time to evaluate survival and recruitment density each year, enabling a comparison of the number of recruits that survived between each monitoring trip.

Fish community composition and abundance - All fishes on, inside, under, and within 1m of each substrate module were identified to the lowest possible taxon, counted, and had their estimated total lengths recorded. Coral heads and reef framework of similar size, shape, and complexity as the substrate modules were located on the natural reference reef and all fishes within 1m were recorded using the same method.

Non-coral invertebrate composition and abundance - During each of the six planned monitoring trips, one sacrificial pad section (300 cm^2) was removed to serve as a sub-sample from each of the 10 Pads-treated modules. Analysis consisted of species enumeration and identification to lowest identifiable taxon, and characterization of the resident invertebrate assemblage.

Algal growth and major groupings of algae - Areal coverage of macroalgae in each quadrat on the modules and natural reef transects was recorded with the aid of digital photography and *in-situ* visual surveys. Major functional groupings of algae were determined (visible microalgae, filamentous, foliose, upright corticated foliose, creeping corticated foliose, corticated macrophytes, leathery macrophytes, articulated calcareous, crustose) (Steneck and Dethier, 1994; McCook et al., 2001). This was combined with data from the following recovery parameter.

Diversity and areal coverage of other taxa competing for space - Three areas were designated on the surface of each module for quadrat surveys and digital photography of the benthic community. These images were analyzed with the aid of CPCe (Coral Point Count with Excel extensions) software (Kohler and Gill, 2006) to generate random areas for species identification and estimates of percent coverage, enabling determination of areal coverage of competing taxa, along with species-specific success through time (or lack thereof), and the effect these taxa had on coral recruitment and growth.

Synthesis: interactions and assembly rules - Interactions amongst macroalgal, non-coral invertebrate, coral, and reef fish assemblages were examined by multivariate parametric and non-parametric analysis. Correlation analyses were used to explore the relationships between multiple parameters and the experimental treatments.

2.2 Study Location

2.2.1 Regional Setting, Local Partners, and Site Selection

The choice of study site was dictated by the framework of a large-scale global research initiative known as the Coral Reef Targeted Research (CRTR) and Capacity Building for Management Program (http://www.gefcoral.org). This expansive and ambitious program was funded by the Global Environmental Facility (GEF) and the World Bank, and involves multiple partners from around the world including: the University of Queensland (Australia), the National Oceanic and Atmospheric Administration (NOAA), and approximately 40 additional research institutes and third parties.

Historically, most coral reef research has been conducted by universities, research institutes, and government organizations located in developed countries. However, the majority of the world's coral reef resources are located in countries that are still developing. It is for this reason that the CRTR selected four research institutions in regions which rely heavily upon coral reef-related goods and services and whose reefs are either currently undergoing or are under imminent threat of degradation from various causes. These institutions were designated as Centers of Excellence (COEs) in tropical coral reef studies and were intended to: serve as hubs for targeted research on regional reefs, interface with local management initiatives, and distribute results to other relevant audiences. These regions and their COEs are: Australasia (University of Queensland Center for Marine Studies, Brisbane, Australia), Southeast Asia (University of the Philippines Marine Science Institute, Bolinao, Philippines), East Africa (University of Dar Es Salaam Institute of Marine Sciences, Zanzibar, Tanzania), and Mesoamerica (University of Mexico Institute of Marine Sciences and Limnology, Puerto Morelos, Mexico).

Within the CRTR there were six separate working groups, each tasked with studying factors relevant to a specific research theme that involves coral reef health and exploring new avenues for data collection and managing regional reef resources. These working groups were: Bleaching, Connectivity, Disease, Modeling, Remote Sensing, and

Restoration and Remediation. This dissertation research project falls under the auspices of the Restoration and Remediation working group and was implemented with initial guidance from the Mesoamerican COE in Puerto Morelos, Mexico. Additional experimental restoration projects, some also utilizing standardized modules as done here, were conducted by researchers and students at the other COEs, but each project had its own regionally unique ecological environment to contend with and used experimental methodologies that were designed to address specific local needs.

Puerto Morelos was chosen as the Mesoamerican COE for multiple reasons. Located about 20 km south of the popular resort city of Cancun on Mexico’s Yucatan Peninsula, this small but rapidly growing fishing village (population ~1,000 in 2005, ~9,000 in 2010) (http://en.wikipedia.org/wiki/Puerto_Morelos) has long relied upon the fishing and tourism revenues supported by the fringing coral reef system that lies directly offshore. This reef is part of the greater Mesoamerican Barrier Reef System (MBRS) which is second in size only to Australia’s Great Barrier Reef and extends for >1,000 km from Isla Contoy in Mexico in the north to the Bay Islands of Honduras in the south (Arrivillega and Garcia, 2013). The coral reefs off of the Yucatan Peninsula are influenced by a large and rapidly growing coastal population, short-sighted coastal and urban development, and a seemingly rampant tourism industry. Impacts to local reef ecosystems are exemplified by low densities of carnivores and herbivores, low coral cover, and moderate to high macroalgae cover, with frequent outbreaks of disease and subsequent coral mortality (Kramer, 2003; Roy, 2004; Ortiz-Lozano et al., 2005; Bozec et al., 2008; García-Salgado et al., 2008; Metcalfe et al., 2011). Mexico’s environmental regulatory agency, the Comisión Nacional de Áreas Naturales Protegidas (CONANP), realized the importance to the local economy of reef-generated goods and services and the reef’s proximity to a rapidly developing coastline, particularly in the context of the urbanization and coastal development of nearby Cancun. In 1998, 90 km^2 of fringing coral reef habitat off of Puerto Morelos was designated as a Natural Protected Area. This protected area, known as the Parque Nacional Arrecife de Puerto Morelos (PNAPM), encompasses a 21 km stretch of coastline that includes a mixed array of marine ecosystems and management areas (Figures 2.6 and 2.7).

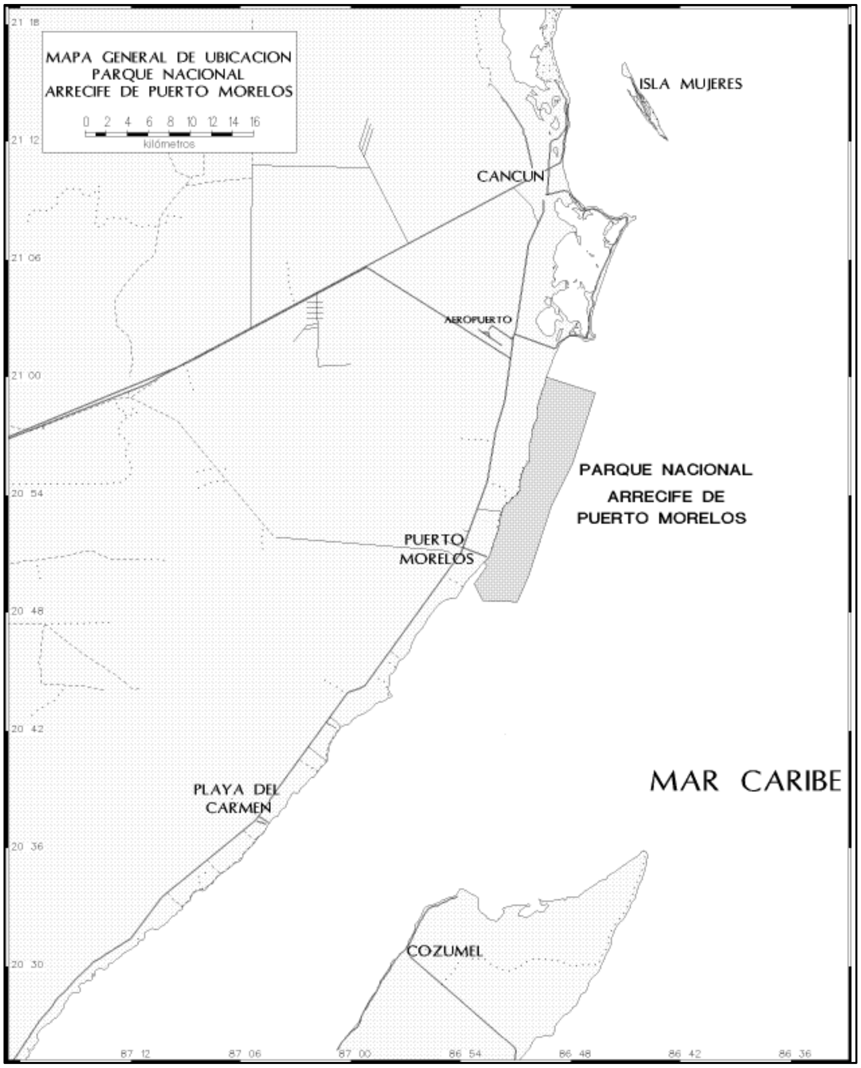


Figure 2.6 The National Park (Parque Nacional Arrecife de Puerto Morelos) boundaries off the coastline of Quintana Roo [Lillo et al., 2000].

The majority of the Yucatan peninsula is characterized as low-relief karstic limestone terrain, and the maritime environment surrounding Puerto Morelos is bounded on the inland side by a Pleistocene berm 10 meters in height that runs parallel to the coast (Ward, 1985). This berm effectively forms a barrier between the fully terrestrial inland habitats and the shallow, semi-enclosed mangrove wetland lagoons that lay behind a 100-200 m wide sand bar that effectively serves as the modern shoreline (Ruíz-Rentería et al., 1998). It is upon this sand bar that most of the town's infrastructure and residential areas have been built. Moving offshore from the sandy shoreline, a shallow lagoon of several hundred meters in width and 3-4 meters in average depth is covered by calcareous sandy sediments, much of which is stabilized by seagrass meadows and rhizophytic algae (Jordán-Dahlgren et al., 1981). The fringing coral reef itself is characterized by back-reef zones that include a loosely connected network of shallow patch reefs and colonized hardbottom pavement, a broad reef crest that becomes partially exposed during low tide in several places, and a gently sloping fore-reef that transitions to a sparsely colonized sand platform at roughly 20-25m depth. Average coastal water temperature stays within a fairly narrow range around 27.7 ^{o}C, with wintertime lows of 26 ^{o}C (February-March) and summertime highs of 29 ^{o}C (July-October) (Merino and Otero, 1991; http://www.worldclimateguide.co.uk/climateguides/mayanriviera/puertomorelos.php).

For over 15 years PNAPM personnel have worked to maintain the health of the area's coral reef ecosystems by monitoring and enforcing the use of designated management areas created for recreation, navigation, commercial and recreational fishing, scientific research, and educational purposes (Figure 2.7). In addition, the PNAPM also serves a key role in educating the local population and visiting tourists about the benefits provided by the reef, the many threats to its existence, and ways the public can help to conserve it. Complementary to the mission of PNAPM, Puerto Morelos is also home to the Universidad Nacional Autonoma de Mexico (UNAM) Marine Science Laboratory (and the Mesoamerican COE), which supports a core group of scientists and visiting researchers, faculty, and graduate students who have long studied factors influencing local reefs. All project objectives, methods, and monitoring schedules used in this study were discussed and approved by PNAPM management. They also generously committed a substantial amount of in-kind logistical support in terms of both personnel and materiel (dive boats, fuel, dive tanks, buoys, weights, etc.) that was essential to successful implementation and execution of this project.

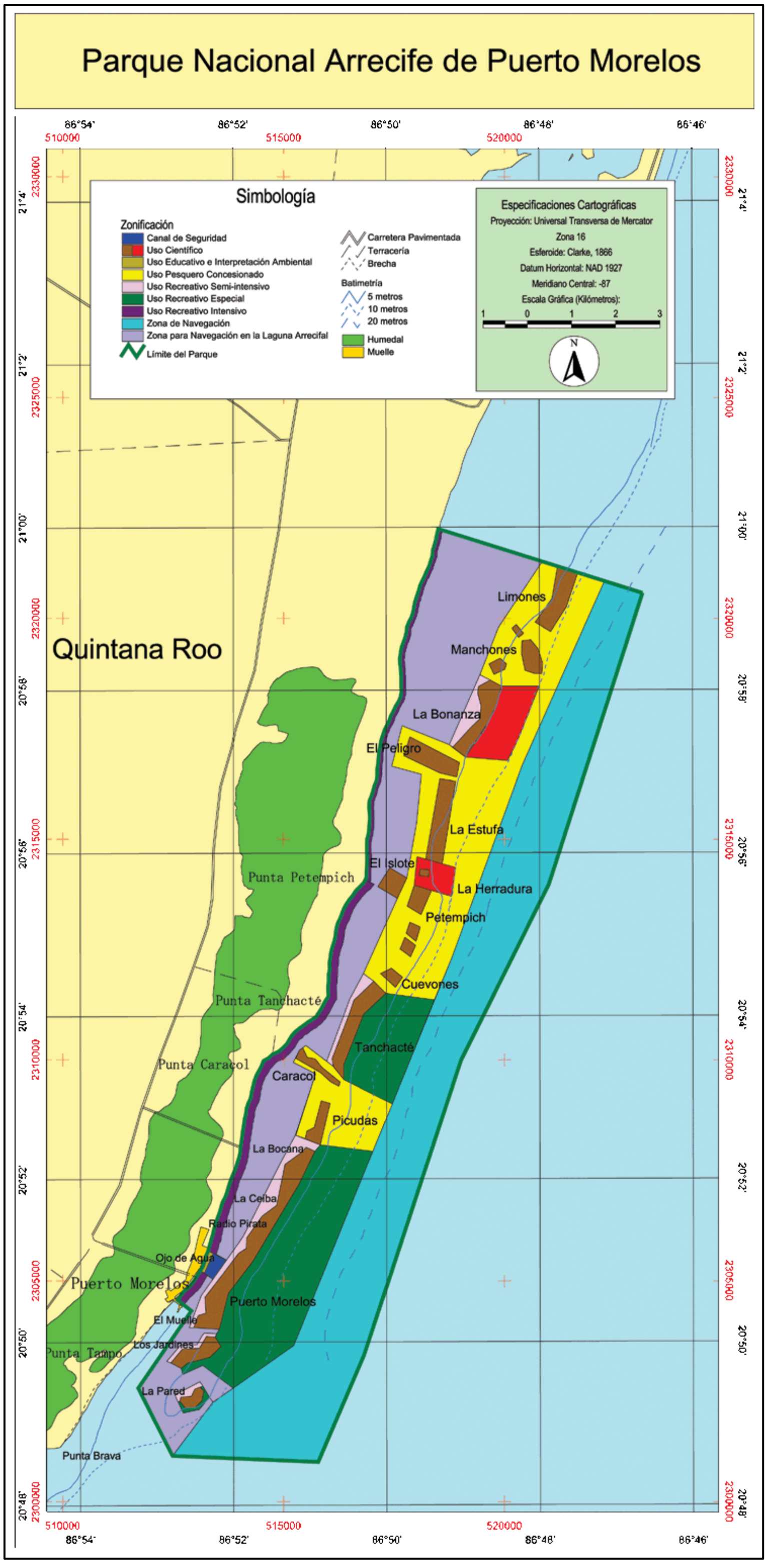


Figure 2.7 Detail of the National Park (PNAPM) and designated usage areas off the coastline of Puerto Morelos [Lillo et al., 2000].

One of the overarching goals of this project was to elucidate the processes influencing natural recovery and restoration at a range of markedly different levels of potential. Therefore, a second study site with similar ecological attributes and areas suitable for deployment of an array of experimental artificial reefs was selected at Akumal 68 km south of Puerto Morelos. The coastline there is characterized by a series of small somewhat protected bays and a mix of barrier and fringing reef structures offshore. A public beach and protected shallow seagrass lagoon attracts many visitors to the area, and an eclectic array of resorts, shops, and restaurants has materialized to capitalize on this attraction. Nestled amongst the dive shops and resorts are the offices of Centro Ecologico Akumal (CEA), a small non-profit private organization established in 1993 that provides environmental initiatives for protection of the coastal marine ecosystems through research, education, outreach, and management recommendations (http://www.ceaakumal.org). Although the reefs of Akumal do not currently have federally protected status like the reefs of PNAPM, CEA works diligently to protect the local coastal and marine ecosystems from unsustainable use and ameliorate the effects of coastal development.

Both PNAPM and CEA provided critical recommendations for module deployment location (see Figure 8 below) based on multiple selection criteria. One of the main factors guiding the selection process was the need for a deployment location that would allow for the placement of multiple artificial reefs (40 in Puerto Morelos, 12 in Akumal) without negatively impacting the surrounding environment in the event that they are moved due to extreme weather-related hydrodynamic forces. This functionally translated into a need for a wide expanse of unconsolidated and largely un-colonized sediment, coral rubble, or sand. This substrate would also serve to achieve project goals by essentially allowing the substrate modules to be placed on a “blank canvas” devoid of anything but rudimentary and sparsely populated pre-existing habitats and their associated inhabitants whose influence on the substrate modules was less likely to confound the results of the study. The water depth at the deployment site also needed to be moderately shallow to provide researchers doing the *in-situ* monitoring on scuba with enough bottom time to conduct multiple repeated time-consuming surveys in a safe, timely, and cost-effective manner.

The spatial footprints of the deployment sites were based on 30m spacing between each module and any nearby natural reef structure. This spacing serves to reduce any confounding influence of neighboring natural or artificial substrate (Gilliam, 1999; Sherman et al., 2001; Spieler et al., 2001; Quinn, 2009), as fishes may be more likely to travel between habitats that are close together (Bohnsack and Sutherland, 1985). It was also preferable that the deployment site be located close to a natural "reference" reef, and an added bonus would be a site that had some degree of protection from heavy wave action that would allow for field work to continue even on days with less than ideal marine conditions. Logistically, a site within range of small boats leaving from shore (i.e. vessels initially used to tow modules from the dockside staging area to the deployment site) was necessary, and having it located within the boundaries of a protected area would allow for the study to proceed with, theoretically, minimal interference by poachers or others. For natural "reference-reef" site selection, a depth range similar to the module deployment site was targeted, along with enough available un-colonized space on the reef framework to allow for attachment of settlement plates and placement of quadrats (see Figure 12 below) without disturbing the established benthic community. The reference reef needed to provide a platform of sufficient breadth to allow for establishment of five parallel monitoring transects 10 m in length, and a sufficient number of isolated healthy coral colonies of the right species needed to be present on a substrate that was conducive to marking and photographing with the framer assembly (see 2.5.5 below).

The sites that were eventually selected for both the module deployment field and natural reference reef had the best combination of as many of those factors as possible that were present within the context of the local seascape and siting recommendations offered by PNAPM and CEA. It is important to note that the placement of artificial reefs in the marine environment for this experimental restoration project was not intended to actively restore the coral reef at the research sites to any particular pre-existing or alternative desirable state.

2.2.2 Substrate Module Deployment Sites and Natural Reference Reefs

a) Puerto Morelos

After assessing multiple potential deployment sites within PNAPM, a large expanse of sand, coral rubble, and sparse seagrass located just east of a popular dive site known locally as "La Pared" (The Wall) was chosen as the deployment site for the Puerto Morelos modules. Spatially, that site provided more than adequate room for the module deployment field with 30-m spacing (see Figure 1 above and Figure 8) and the average depth was 10-11 m, well within practical safe diving limits for the number of repetitive dives that would be needed. Substrate at the deployment site was characterized as a shifting field of sand over low-relief hardbottom, with seagrasses, macroalgae, gorgonians, and small patches of coral rubble found in varying mixes throughout. This was amenable to module placement with minimal collateral affects to the surrounding environment. Great care was taken during the deployment operation to prevent any substrate modules from being placed directly onto seagrass or coral rubble. However, due to the ephemeral nature of the sand-associated benthic communities and tendency for some scouring or under-cutting to take place underneath the large artificial structures over time, by the end of the study period several modules ended up resting directly on coral rubble or hardbottom. In addition, in areas where the sand layer became thicker over time, some of the modules settled and/or were buried to the point where they were temporarily lost to the study.

The current regime at the Puerto Morelos deployment site was variable, from slack to 1-2 kt (0.5-1.0 $m.s^{-1}$), and was heavily influenced by the tides and sea state. This not only had an observable effect on the benthos, whereupon the only benthic organisms present were those that were firmly attached to the hardbottom substrate underneath (seagrasses, macroalgae, gorgonians, sponges, etc.), but it also made *in-situ* monitoring work and underwater navigation challenging during much of the study. During peak flow, it was almost impossible to swim against the current, especially with sampling gear and a camera framer assembly in tow. In addition, the turbulence associated with the strong currents had a tendency to decrease visibility from the typical 15-20 m down to 3-5 m. The temperature fluctuated between seasons, as expected, but on average it was 28 ^{o}C (82 ^{o}F) in the Fall and 25.5 ^{o}C (78 ^{o}F) in the Spring.

As the name suggests, the “La Pared” natural reef adjacent to the substrate module deployment field consisted of a northeast-southwest running vertical wall that varied in height from 3 to 5 meters. Depth gradually increased east of the deployment field, and with the increased depth came greater abundance of coral heads and increasingly large reef structures. For reference, the first substrate module was deployed directly next to a permanently installed mooring buoy. This mooring buoy was frequently visited by recreational dive boats and local fishermen. La Pared is a popular dive site for visiting tourists, and even though it was placed within the boundaries of the national park, the module deployment field also became popular with clandestinely operating lobster fishermen. On multiple occasions damage to the modules in the form of detached coral transplants, gouges on the exterior surfaces, and obvious disturbances to the fouling community was observed. This was presumed to be the result of mooring or anchoring directly on the modules and careless disregard by the poachers while chasing lobsters residing within interior recesses.

The natural reference reef site was chosen at a separate site known locally as "Los Jardines" (The Gardens) (Figure 2.8). This site was shallower and more protected than La Pared, but subject to similar temperature, current, and other physical regimes. The depth at Los Jardines was approximately 4-5 m, and currents could be a factor there as well, although not nearly as strong as those endured at the La Pared site.

There were multiple reasons for choosing this site over one closer geographically and in depth to the module deployment field: 1) Los Jardines had some previously established benthic monitoring transects from other local monitoring and research projects, so our boat drivers were quite familiar with the area and the habitat there; 2) Los Jardines had adequate abundance of the appropriate species and size reference corals that were unobstructed by other organisms and thus amenable to photographing with the framer assembly (see 2.5.5 below), whereas they were more sparsely distributed elsewhere; 3) natural reef habitats at La Pared at the same depth as the modules were too limited for establishment of 5 x 10-m transects and they did not have adequate abundance of reference coral species (see 2.1.2 above), and; 4) other natural reef choices in the La Pared area were either too rugose, too exposed, or too deep.

The difference in depth between the natural 'reference' reef and the module deployment field is admittedly enough to warrant caution when making direct comparisons using data collected from each site. However, as is often the case with field work, finding a perfectly comparable control site was not possible. In the absence of a more suitable alternative, the 'reference' reef evaluated here still provides a solid foundation for large-scale comparisons of benthic community composition and trends between natural and artificial habitat.

Figure 2.8 Puerto Morelos deployment site. The yellow box represents the boundaries of the substrate module deployment site, and the yellow star marks the location of the natural reference reef site. [Photo credit: Google Earth]

Despite local anthropogenic influence and some scattered patches of degraded and heavily trafficked reef, environmental conditions on the coral reef system within the PNAPM boundaries were largely favorable for continued active growth of the reef community. The area's reefs have been subjected to the same trends of degradation common to the rest of the greater Caribbean (bleaching, disease, macroalgae blooms, storm damage, excessive nutrients, overfishing, etc.), but were still characterized by many isolated reef areas that exhibited excellent coral health and thriving communities of reef fishes.

b) Akumal

About 1km north of the town of Akumal and 375m offshore of Half Moon Bay, at 12-14m depth, a continuous 50-60 m wide sand channel that ran parallel to the shoreline in between scattered spur and groove reef structures was chosen for the module deployment site (Figure 9). Although too narrow to accommodate a double row of modules without violating the rules of the 30-m spacing requirement, this channel had more than sufficient length to accommodate a linear deployment array of a dozen modules that would stretch for 360 m end to end (see Figure 2.2 above and Figure 2.9). Underwater visibility in the area was typically excellent, often exceeding 30 m. As was the case with Puerto Morelos, the substrate consisted of hardbottom overlaid with sand of variable depth. However, unlike Puerto Morelos, the sand at the Akumal site was almost completely un-colonized (no seagrass, macroalgae, gorgonians, etc.) and was punctuated only by a sparse scattering of small isolated coral heads.

The natural reef to both the east and west of the sand channel (deeper and shallower, respectively) was characterized by classic spur and groove formations, with dramatic increases in vertical relief (3-5 m) at the reef-sand interface. The natural reference reef monitoring site location for Akumal was conveniently established directly to the east of the northern-most module deployment location and along the top of five evenly-spaced ridges/spurs directly adjacent to the sand channel. Depth at the top of the spurs was 10-11 m, and strong north-south currents were occasionally experienced. Due to the fact that there were no coral transplant treatments applied at the Akumal study site, locating a reference reef with coral colonies of the appropriate species and size was not a selection factor. In general, large portions of the Akumal reef system appeared to be more degraded than the Puerto Morelos reefs. Large formations of dead Elkhorn coral (*Acropora palmata*) and multiple species of *Orbicella* were a testament to the former glory of this reef, which was now dominated by macroalgae; fish and newly recruited corals appeared to be sparse. Subjectively, this degradation was observed to worsen over the course of the study. Temperature on the reef in Akumal was a few degrees colder than in Puerto Morelos, most likely due to the lagoonal conditions of Puerto Morelos and the closer proximity to deeper water in Akumal.

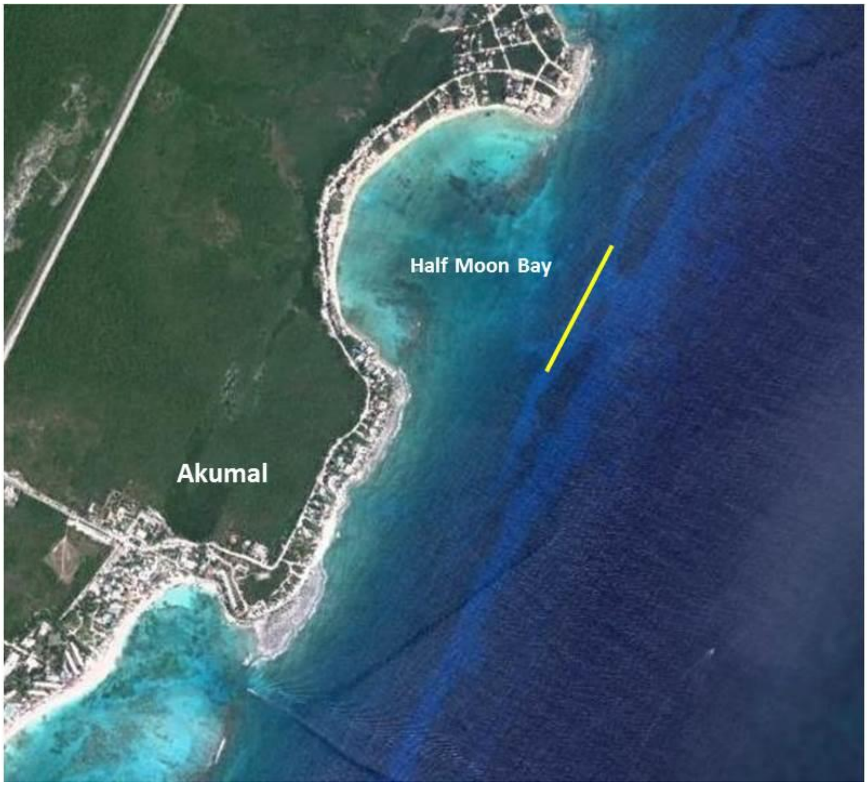


Figure 2.9 Satellite view of Akumal and Half Moon Bay, with a yellow line representing the location of the substrate module deployment field. [Photo credit: Google Earth]

2.3 Project Implementation: AR Construction and Deployment

2.3.1 Laying the Groundwork

Nova Southeastern University became involved with the World Bank funded CRTR-RRWG in 2005. A visit to Quintana Roo prior to the author's involvement had been made by NSU scientists to get acquainted with local key players at CONANP and PNAPM and to go over project goals and objectives. In September 2005, the author, along with multiple members of the thesis committee, embarked on a second mission to meet with local government authorities, academic representatives, and contractors about establishing a timeline including a schedule for officially starting this project. In Puerto Morelos, the NSUOC/NCRI group met with the director and sub-director of PNAPM and discussed project methods, potential site locations, staging areas, transport of the modules through the park, deployment, and the projected logistical schedule for future monitoring trips.

A few months later, in January 2006, a reconnaissance mission to inspect some of the proposed module deployment sites and natural reference reef monitoring sites was organized to take GPS coordinates and determine which areas had the right combination of appropriate substrate, working depth, spatial availability, and adjacent natural reef habitats. While in Puerto Morelos, other options for future procurement of scuba tanks, dive boats and captains, miscellaneous equipment and supplies, and food and lodging were investigated. The group then traveled south to Akumal, where a similarly-themed meeting with CEA took place. Again, the details pertinent to site selection and the deployment operation were discussed, and multiple reconnaissance dives were made to inspect the substrate, working depth, spatial availability, and surrounding natural reef. A similar exploration of the local options for alternate sources of scuba tanks, dive boats, and food and lodging was undertaken.

The final meeting of that January trip was with a local marine construction contractor that had previous artificial reef experience and was familiar with the pallet ball construction we were utilizing for this study. Engineering aspects and custom design specifications for the modules were discussed, along with the construction site and transport logistics, deployment operation, and project timeline.

With the roles of project partners and logistical details solidified, an official construction start date was set and the gathering of equipment and supplies began. Artificial substrate pad material and special concrete additives were ordered, settlement plates and mounting hardware were sent from CRTR-RRWG partners in Australia (Dr. Andrew Heyward), and coral transplanting and underwater concrete mixing training dives were conducted using small limestone rocks and dead coral fragments as live coral surrogates.

The target months of March and September (weather permitting) were agreed upon with local partners for the planned 3-year monitoring period. Subsequently, it was decided that the construction and deployment operations would take place in October 2006. Once deployed in the marine environment, the surfaces of the freshly-minted modules would take several months to “cure”; a process that includes leaching of chemicals from the concrete, stabilization of pH on the module surface, and initial colonization by pioneer settler species (bacteria, cyanobacteria, microalgae, microorganisms, etc.) and important reef stabilizers like crustose coralline algae (CCR) (Glynn, 1997; Spieler et al., 2001; Webster et al., 2004). Coralline algae have also been shown to be one of the main preferred settlement substrates in both natural and laboratory settings (Morse, 1990; Morse and Morse, 1991, 1996; Boch and Morse, 2011). After the initial curing process and establishment of a biofilm on the module surfaces took place, coral recruits were predicted to begin settling and the routine monitoring could begin.

In August 2006, the local contractor constructed some test modules with the Reef Ball^{TM} molds and custom additives (designed to achieve neutral pH) and standard local building materials (cement, sand, gravel). Members of the NSUOC team traveled back to Cancun to inspect the results, give recommendations on how to improve the process, and finalize the date of construction.

2.3.2 Artificial Reef Construction

In October 2006, 52 identically constructed pallet balls were made at a small construction yard north of Cancun. Modules for both the Puerto Morelos and Akumal study sites were constructed there using three pre-fabricated fiberglass molds that had been previously acquired from the Reef Ball company. The author and a graduate student assistant were present for the duration of the pallet ball construction, and determined whether or not each newly-minted substrate module was fit for use. Over a dozen substrate modules had to be re-poured due to various structural flaws. These discarded modules were set aside and later used opportunistically at a satellite/alternate deployment site that was not originally intended as a part of the study (Bonanza, see section 2.5.11).

In addition to evaluating the final products, the NSUOC team also spent many long hours preparing the surface of each module for the experimental treatment applications. This consisted of using a hammer drill to bore 60-70 holes in specific locations on the exterior surface of each of the 10 modules to affix the artificial substrate pad material, installing nine masonry screws along the upper lip of each module for installation of a coral recruit tracking system, and drilling 24 holes for installation of 12 settlement plate mounting plates on 10 modules (approximately 1400 separate holes). In addition, the artificial substrate pad material was assembled and attached to the modules. The finalized pads treatment consisted of 2 x 20cm x 80cm rectangles bound together with zip ties in a double layer, 2 double-bound pads arranged in parallel, and a 20cm x 30cm double bound rectangle in between the two larger pieces to form the shape of a letter “H” and attached to the module surface with plastic anchor pins (Figure 2.10). Total surface area of the padded “H” was 0.38 m^2. Combined in triplicate over the entire surface of the module, the padded surfaces totaled 1.14 m^2. The final pad arrangement left 1.5 m^2 of uncovered available space for studies of benthic colonization and coral recruitment.

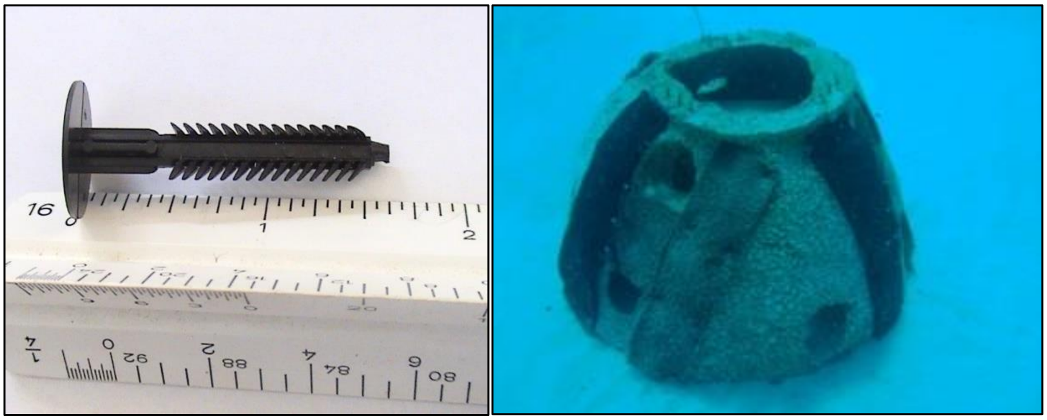


Figure 2.10 Detail of one of the plastic anchor pins used to secure the artificial substrate pad material to the exterior surface of the modules (left), and a freshly deployed module with the Pads treatment (right).

The final task for the NSUOC preparation team was to identify each module with a colored wire marker that corresponded to its experimental treatment group. These would be used by the contractor’s transport and deployment crew to identify which modules to load when, and in what order. At this point, several additional NSUOC personnel traveled to Cancun to assist with the next phase of the operation.

2.3.3 Artificial Reef Deployment

In Puerto Morelos, the contractor made arrangements with the Port Authority to use the city’s loading dock facility as a staging area for the deployment operation. Back at the construction yard, the loading crew used a small trailer-mounted crane to hoist the modules, each weighing 575 kg, one at a time from the ground up onto the trailer and secured them for travel. The loading and transport crew had to make multiple trips to the staging area, as only 12 modules would safely fit on the trailer at one time. Once the transport crew arrived at the staging area, the modules were lowered one at a time directly from the trailer down into the shallow water (~2 m depth) adjacent to the dock (in Puerto Morelos), or onto the beach where a smaller mobile hydraulic lift was used to move the modules one at a time into the water (in Akumal) (Figures 2.11 A and B). From there the rigging crew secured lift bags and buoys in preparation for towing the modules, two at a time, behind a single small boat from the staging area to the deployment site.

At the La Pared deployment site, the NSUOC deployment crew spent several days working from a PNAPM vessel to deploy buoys on specific GPS coordinates for each incoming module. These buoys were color coded to correspond to the colored wire that each module had been marked with, and were held in place by custom made concrete anchors. Both the buoys and the anchors were provided by PNAPM.

Figure 2.11 Modules being offloaded (left) and moved into the water (right) in Akumal.

Back at the loading dock, large deflated buoys had been placed in the interior cavity of each module in preparation for towing. Once inflated, these buoys added a significant amount of buoyancy. However, it still took two large lift bags to provide enough positive buoyancy to make the SMs lift off of the sand. Once floating, the modules were towed behind a small boat, two at a time, single-file through the channel and out to the deployment site. The NSUOC/PNAPM preparatory team was standing by on-site to render both topside and in-water support and supervise final module placement locations. The contractor's deployment crew was tasked with locating the right colored buoy to match the colored wire on the modules they were towing, then deploying divers who would slowly let the air out of the lift bags and escort them during their descent to the bottom. They were to follow the buoy line down to the anchor weight, which had been very carefully placed on specific coordinates and in appropriate substrate/natural habitat by the NSUOC/PNAPM preparatory team. However, due to a combination of moderate currents, a large amount of drag, and a slow descent rate, it was often too difficult to guide the modules to the exact spot on the first try. In addition, many of the contractor's support divers were breathing from a garden hose connected to an air compressor on deck; an arrangement that limited their maneuverability and range of motion (not to mention their safety). Once they reached the bottom, enough additional buoyancy and leverage could be applied to the modules that landed off-target to make them mobile enough to reposition with two people. Without added buoyancy, 3-4 divers could reposition one with great effort.

Although great care was taken to ensure that the final resting place for each module was the requisite 30 m distant from its nearest neighbor and that each was placed along the same lines of latitude and longitude in tidy rows and columns, some slight deviations did occur, and minor course corrections were required when navigating through the module deployment field with a compass. On most days, the visibility at the deployment field was such that multiple modules could be seen from any given location, so slight course deviations were not an issue. However, in stronger currents and reduced visibility, compass navigation when transiting from module to module was relied upon heavily, and it was easy to miss the intended target on the first try. This was exacerbated by the relative lack of unique natural features in the barren low-relief expanse of the deployment field that could otherwise have been used for navigation.

Once the contractor's deployment crew went back for another set of modules (which their shore-side support crew had been preparing/floating while the deployment boat was gone), the NSUOC/PNAPM preparatory team added four concrete blocks to each of the newly settled modules. These cinder blocks were guided from the support vessel to their targets with aid of the buoy ropes and anchors that were already on site. Once the cinder blocks landed, they were removed from the line and stacked carefully in the interior cavity of the module. By the time the cinder blocks were in place, the boat with the next two modules was usually back on site and ready to deploy the next load.

In addition to having to re-position a few modules, several of the artificial substrate pads that had been applied to the exterior of a select number of them had to be repaired on site due to accidental damage incurred during the loading and transport operation. Another task for the NSUOC/PNAPM preparatory team was to install the stainless-steel settlement plate mounting brackets. This was done by finding the pre-drilled holes on the exterior of those select modules and inserting plastic anchors to firmly secure the plates. Settlement plate attachment hardware was not installed prior to deployment because they likely would have been damaged or destroyed during transport.

Deployment operations for all 40 modules in Puerto Morelos were completed in one day. Two days following, the crews traveled to Akumal to repeat the process there. As with the previous operation, the staging area had been approved by the local authorities and was prepared for the arrival of the large tractor-trailer combo and its load of pallet balls. Akumal lacked the infrastructure that Puerto Morelos had, and as such there was no dock to conveniently offload the modules and no road leading all the way down to the beach. To overcome this obstacle, each module had to be off-loaded onto a smaller flatbed truck with a crane, which would then drive down a small path to the public beach. Once at the water's edge, the modules were off-loaded onto the sand and then picked up with a smaller hydraulic hoist that had been mounted onto a frame with large diameter rubber tires (Figures 10 A and B above). Once lifted off of the ground, a 3-4 person team pushed the apparatus through the sand to the beach and into the shallow water. Once in the water, the module was lowered onto the sand and prepared for towing out to the deployment site. Centro Ecologico Akumal was the entity in charge of general oversight for this project, and they were generous enough to lend a boat and some divers for this phase of the deployment operation. The day before the contractor's crew arrived in Akumal, the NSUOC preparatory team had placed marker buoys on precise coordinates throughout the deployment field. Deployment of the 12 modules in Akumal took a full two days.

Once all of the modules had been deployed at both study sites, final approval on placement was given to the contractor and his official role in the project was completed. However, he did donate eight of the rejected modules that did not meet the specific requirements for the project to PNAPM, and generously deployed them at the La Bonanza field site approximately 3 km north of Puerto Morelos (see section 2.5.11). For this operation, the contractor used a private beach at a local resort, and once again had to roll them into the sand and tow them out to the deployment site. The NSUOC/PNAPM preparatory team was once again on-site to render assistance and guide final placement of each module. Logistically, this operation was much simpler than the previous two, as both the distance from the beach to the deployment site and the depth were significantly reduced.

2.4 Coral Transplanting and Settlement Plate Deployment

2.4.1 Coral Collection and Transplantation

In December 2006, just over a month after deployment, the author and a graduate research assistant from NSUOC traveled to the Yucatan to collect corals and attach them to modules to establish the transplant treatment. Even though settlement plates were not installed until the following summer, this finalized the experimental treatments and started the clock on the monitoring schedule. Over the course of two days, 60 coral colonies of three species of approximately 10-15cm diameter (fist-sized) were collected from the natural reef population at multiple sites within a kilometer of the deployment site. On each collection day, the team would begin at the collection sites and harvest as many "corals of opportunity" as could be found until the appropriate number needed for transplanting was collected. This was relatively easy to accomplish for two of the selected transplant species: *Porites astreoides* and *Agaricia agaricites*, as both are considered relatively "weedy" species that recruit to the population through a brooding reproductive strategy (Darling et al., 2012; Alvarez-Filip et al., 2013).

The third species, *Orbicella annularis*, was less abundant and proved far more difficult to find donor colonies that were not firmly attached to the substrate. Eventually, it was agreed that a small number (20) *O. annularis* "potato-heads" would need to be harvested directly from large donor colonies. These corals were carefully detached from their parent colonies with a chisel and hammer. As corals were collected, they were initially cleaned of debris (macroalgae, loose substrate, etc.) and placed in large Tupperware bins for transport. Once full, these bins were brought to the surface and stowed in the shade in a larger bin on the deck of the support vessel, and the boat slowly traveled <1 km back to the deployment site. Great care was taken to minimize the amount of stress experienced by the transplants during transport to the deployment site; transplants were on the boat for less than 1 hour and remained in the shade the entire time. Once on site, the bins were brought down to the modules that were receiving them by divers. When the dive team arrived at a module, they placed two of each of the species (six total) onto the surface of the cinder blocks that had been previously stacked inside until they were ready to be attached to the modules. Collection and transportation of all transplants took place on one day, and the actual transplantation operation took place the following day.

The NSUOC team visited each module sequentially to transplant the corals after all the donor colonies had been collected and distributed to their respective modules. A pre-determined randomized order of arrangement for the coral transplants was used to establish which species would go where on each module. A standard cement-plaster-sand mixture that is recommended for transplanting corals (Jaap, 2000) was measured out and mixed together in 1-gallon Ziploc bags. Thorough shaking and kneading ensured a homogeneous mixture of the dry ingredients.

To attach a coral to a module, the surface that would be receiving the transplant first had to be prepared. As soon as modules were deployed their surfaces began hosting a burgeoning assemblage of benthic organisms. Cyanobacteria, algae, sponges are among the first group of organisms that formed a living biofilm (Spieler et al., 2001; Webster et al., 2004) on the modules' surfaces. This biofilm had to be scrubbed off with a wire brush before the cement mixture was applied to secure attachment of the transplant's cement mixture to the cement surface of the module. Once the site was cleaned of debris, a small amount of seawater was introduced into a bag of cement to activate it. Thorough kneading was necessary to evenly distribute the water throughout the dry cement powder mixture. More water was added as needed until the mixture had reached an appropriate level of viscosity and uniformity. As the appropriate consistency was reached, a chemical reaction fueled by seawater and ingredients in the cement mixture caused heat to be released; the result of an exothermic reaction indicating activation.

As soon as the mixture was deemed ready, it was applied by the handful directly onto the surface of the module, shaped into a basal form, and pressed solidly onto the surface. The coral to be transplanted coral was then gently but firmly embedded in the fresh cement mixture, a procedure which included reinforcing the base of the coral transplant with as much additional concrete as was needed. The cement mixture typically solidified to a sufficient level of hardness (strong enough to hold a coral upright without falling off the module) within five minutes, and was fully cured after several days. This process was repeated for every one of the transplanted corals over a two-day period. After all of the corals were securely attached, each one was photographed as an initial point of reference for studies of their overall health, growth, and survival.

2.4.2 Settlement Plate Deployment

The third experimental treatment application, the settlement plates, was not completed until the summer of 2007. It was decided that they would not be installed during the deployment operation because it was thought they would become too fouled prior to coral spawning. Synchronous coral spawning for the MBRS area had been previously reported to occur approximately one week after the full moon in late August and early September (Van Veghel, 1994; word of mouth from local biologists), which also coincides with the highest sea surface temperature, a factor thought to be the primary trigger for broadcast spawning species (Van Woesik, 2006). Based on recommendations from other studies (A. Heyward, personal communication) a period of 3 months was deemed sufficient time for the newly deployed settlement plates to cure and be ready to serve as an attractive settlement site for coral planulae.

In late June/early July 2007, a small NSUOC dive team led by the author traveled to Puerto Morelos to deploy the settlement plates. Each plate was labeled with permanent marker and covered over with clear epoxy prior to deployment. Once again, the PNAPM field crew provided logistical support in the form of dive boat and captain, and all tiles were installed and securely fastened on the modules and the natural reef transects over the span of one day. The plate was placed over the mounting bolt that was already attached to the bracket and secured tightly with a wingnut (Figures 2.12 A and B). Twelve settlement plates in total were mounted to each of 10 modules (120 plates), and 10 plates were mounted on each of 5 natural reef transects (50 plates). In Akumal, the author chartered a dive boat and, with the NSUOC team, installed all of the plates in two dives. While at the two study sites the team also took advantage of the opportunity to inspect the modules ahead of the next scheduled monitoring trip. Identification tags on each module were cleaned or replaced, pad material was verified to still be securely attached, and health of coral transplants was examined.

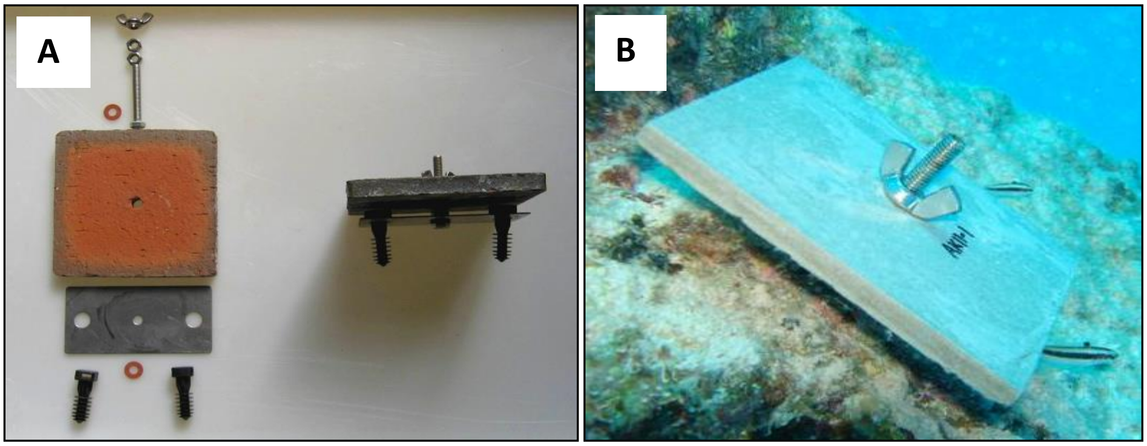


Figure 2.12 Settlement plate with mounting hardware dis-articulated and assembled (**A)** and settlement plate on a substrate module immediately following deployment (**B**).

2.5 Monitoring and Data Collection Methods

2.5.1 Monitoring Schedule and Logistical Planning

Monitoring took place bi-annually (twice a year) and targeted the spring (February/March) and late summer (September/October) seasons. This schedule was advantageous because it avoided the summer hurricane season and winter storm season; both of major concern for a field intensive project. In addition, it allowed for capture of the seasonal variation of the faunal assemblages. Finally, this schedule coincided with at least one off-season travel period (September/October); a time during which travel in the Yucatan is generally more affordable.

The workload for each successive monitoring trip increased steadily throughout the study period. This was mainly due to increasing abundance of coral recruits over the 3-year period, the time that it took to count and measure them, and the time it took to use the range and bearing system to locate survivors from the previous trip and map the location of new recruits. On average, a monitoring trip consisted of 2 travel days, 5-8 field days, 2 weather/rest days, and sometimes an extra day for divers to let any residual dissolved gases metabolize away before flying; usually 10-12 days in total. The first 2-3 trips were completed with only the author and 2 divers, but those trips had no lengthy coral recruit surveys to contend with. Comparatively, the last several trips consisted of the author and 3-5 divers and it took several days just to complete the coral recruit surveys alone. An average day in the field consisted of 3-4 repetitive dives to 30 feet (Puerto Morelos) or 40 feet (Akumal) that were routinely upwards of 90-120 minutes in duration. Working conditions included variable chop, groundswells (0-2 m), currents of variable but usually considerable strength (0-2.5 kt), 3-33m visibility, 25-29 ^{o}C water temperature, and occasional squalls. No sharks were observed by the author, but many large barracuda, turtles, stingrays, eagle rays, and other assorted large pelagic or solitary fishes were commonly encountered.

A detailed description of each of the tasks completed on the monitoring trips follows this section (Table 1). Field team members were selected based on their general level of proficiency with the methods, their schedules and availability, and areas of specific expertise. In general, fish counts and quadrat photos were tasks reserved for the author and other select, experienced members of the fish lab, and coral recruit and quadrat surveys were completed by members of the Coral Reef Restoration, Assessment, and Monitoring (CRRAM) Laboratory who were graciously provided by Dr. Gilliam. Once fish counts and quadrat photos were completed, all team members conducted coral recruit surveys. In addition, special recognition for rendering general assistance in the field and communicating with the locals is due to a Mexican master's student from Veracruz who traveled to Quintana Roo for almost every monitoring trip.

2.5.2 Fish Counts

A customized stationary visual census survey was conducted at each module on every monitoring trip. A team of 2-4 divers would ensure that all of these surveys were done on the same day to minimize any confounding daily differences caused by altered environmental states. These surveys were non-destructive and were not time limited. Survey divers would slowly approach each module and begin counting from a distance of several meters away to increase the likelihood of capturing some of the more reclusive or highly mobile species in the survey before they dispersed or hid. Only fishes that were observed within a distance of 1 m from the edge of and above the modules were counted. During the course of the survey, the diver would move progressively closer and closer to the module, eventually getting close enough to thoroughly inspect the interior cavity and cinder blocks, as well as any protected void spaces underneath. All fishes were identified down to lowest possible taxon (generally species), and total lengths (cm) for every individual were tallied and placed into size bins (0-2, 2-5, 5-10, 10-20, 30-50, +50 cm). Average time of a survey was 5-8 minutes. Each survey produced a measure of total abundance and species richness.

Reef fish surveys on the natural reef were conducted on coral heads or other available reef framework structures that were of approximately equal size as the modules. These sites were ideally separated from other nearby reef structures by several meters or more. In Puerto Morelos, these structures were plentiful in slightly deeper water to the east of the deployment field, although separation from adjacent reef structures was usually lacking. In Akumal there were also plentiful structures of appropriate size, typically consisting of isolated gorgonian-topped heads of *Montastraea cavernosa*, *Orbicella faveolata,* and *Solenastrea bournoni* that were dispersed throughout the Half Moon Bay sand channel and module deployment field. Visual fish surveys along transects on the natural reef were eschewed in favor of the modified point-count method due to the disparity that would have arisen between artificial and natural reef survey areas and the difficulty of finding a way to standardize for rugosity and other habitat differences.

2.5.3 Coral Recruit Surveys

As mentioned earlier (see section 2.1.3) there were 9 masonry screws permanently embedded into the upwards facing concrete lip of each module, positioned in groups of three at the exact mid-points of the symmetrical faces. Each of the three identical faces of each SM was referenced by a letter (A, B, or C) (see Figure 5 A); a task that was aided by the attachment of a large zip tie that was wrapped around the upper lip of the northernmost facing side and tagged with the individual module number. Location of that tag designated it as side A, and sides B and C followed sequentially to the left-hand side of the observer. A coral recruit survey began by first noting what side was being surveyed, and then attaching a flexible soft plastic protractor with 3 pre-drilled holes securely to the 3 masonry

Table 1. Project timeline and general description for each trip.

Date	Accomplishments
September 2005	Meetings w/ PNAPM, CEA, Marenter (contractor).
October 2005	Hurricane Wilma
January 2006	Meetings w/PNAPM, CEA, Mario - Site selection dives, inspection of Hurricane Wilma damage.
May 2006	Palau- Module construction with Surangel & Sons (contractor).
August 2006	Construction site visit, SM inspection, site selection, meetings with PNAPM and CEA. Green light for module production.
Sept/Oct 2006	Module construction and deployment.
December 2006	Coral transplanting
Feb/March 2007	Monitoring I - establishment of natural reef transects, installation of settlement plate mounting hardware.
July 2007	Settlement Plate deployment
August 2007	Hurricane Dean
September 2007	Monitoring II and inspection of damage from Hurricane Dean
November 2007	Settlement Plate Collection I
Feb/March 2008	Monitoring III
July 2008	RRWG-CRTR annual working group meeting, deployment site visit/demo-dive. Guest lecture at MPA course.
October 2008	Monitoring IV + Settlement Plate Collection II
Feb/March 2009	Monitoring V
September 2009	Monitoring VI
September 2012	Monitoring VII

screws. The middle screw, which was positioned at the exact center point, was also used as the point of attachment for a flexible fiberglass tape measure. The tape measure was then used in conjunction with the angle markers on the protractor to record the range and bearing to every coral recruit detected on the module face (See Figure 3 A). This allowed for repeated long-term tracking of individual coral recruits through time for determining survival rate and measuring growth. Each coral recruit was also measured with a small ruler at its widest point (to the nearest mm), identified to lowest possible taxon, and its coordinates recorded on a data sheet. This process was repeated on the other two sides of the module, and then repeated over the entire surface of every module in the deployment field. Coral recruit surveys conducted on modules with artificial substrate pad treatments on their exterior surfaces only surveyed the un-padded concrete surfaces; a fact which was accounted and corrected for in the density (recruits/m^2) calculations for each treatment group. Fire Coral (*Millepora alcicornis*), technically a hermatypic hydrozoan, was present on almost all of the modules but not included in the coral recruit surveys. However, areal coverage of this species was quantified during quadrat surveys and photo analysis along with the other non-coral members of the benthic community.

Coral recruits could be readily detected by the naked eye at a size of 2-3 mm. During initial surveys the divers used magnifying glasses to aid in detection of recruits, but once the eye was trained no additional instruments were needed and the lenses were abandoned in favor of having fewer items to carry in the field. On average, it took a team of 3-4 divers a full 3-4 days to complete all of the coral recruit surveys on every module in the Puerto Morelos deployment field.

2.5.4 Quadrat and Coral Transplant Framer Photos – Substrate Modules

On the first monitoring trip, Aquamend™ epoxy markers with stainless washers or nuts embedded in them were affixed to the same area on each face of each module, or at least as close as the structural components of the module design and externally-applied experimental treatments allowed for (see Figure 3 B). The spacing and placement of the two markers was intended to delineate the upper and lower right-hand corners of a 25 cm x 25 cm quadrat. The majority of these markers were completely overgrown with algae and sponges in between each monitoring trip, but prior knowledge of where they should be located aided in finding them and added confidence to on-site decisions about where each survey should be conducted.

Prior to the first monitoring trip, a custom-built PVC framer assembly was designed and constructed specifically for this project, a task that was aided by availability of several customized strobe and camera housing mounting brackets on reserve from other CCRAM lab projects. Attached to this framer assembly was an Olympus C-5060 digital camera housed in a plastic Ikelite underwater housing. Two Ikelite DS-50 substrobes were then connected via sync cord to the housing and framer assembly. A 12mm wide-angle lens was wet-mounted to the external housing port, which enabled the camera to capture the entire framer assembly in a single frame. The camera was tuned to a pre-programmed setting, the focal distance was locked, and several test photos were always taken to test for functionality and to make adjustments to the positioning of the strobes. Laminated and color coded labels were specifically arranged and affixed to the framer, unobtrusively so as not to obstruct the main body of the image, and used in the processing and analysis of each photo following each dive. Between each successive photo, the diver would change each of the tags as needed in accordance with his/her location in the deployment field and on the module. These tags were bound together according to labeling category, and clipped to the diver's BC during transit between modules.

For each module, there were a minimum of three quadrat photos taken; one for each of the three identical faces of each module. Once the epoxy/stainless reference markers were located, the framer assembly was held flush with the side of the module, and 1-2 photos were taken. Effort on the camera operator diver's part was required to check to make sure each photo was adequately exposed. For those modules that received the coral transplant treatment, an additional six quadrat photos were taken. Coral transplants were photographed from a dorsal view, looking down from directly above to get a whole colony footprint. The framer was held flush with the horizontal upper lip of the module, with the coral transplant positioned directly in the center. Additional effort on the diver's part was needed to hold the framer in the same position relative to the markers and coral transplants for each photo through the entire monitoring period, as well as to not let the framer assembly come into direct contact with the coral transplants.

Under ideal conditions (little or no current with excellent visibility), this task could be accomplished by one thoroughly site familiarized and determined diver (with buddy) in one day. However, it was not uncommon to take 2-3 days to photograph all modules in the entire deployment field. Since the tidally induced currents generally had an east or west component to their movement, efforts were made to deploy divers at down-current locations that would enable them to use the current to their advantage when moving through the deployment field. However, when conducting surveys that resulted in large numbers of modules (>10) being visited on a single dive, this usually meant that at some point the diver(s) had to travel directly against, or at least at an oblique angle to, the current. Certain tasks (i.e., navigating through the 270m long module deployment field while holding the cumbersome and drag-inducing framer, holding the framer in position at odd angles while bracing against the current in a manner that does not damage the colonizing organisms and corals on the module surface, and keeping track of and constantly re-positioning an array of floppy tags, data sheets, and a map), proved to be challenging in the strong currents and low visibility conditions that were commonly encountered. At times the currents were so strong that divers had to pull themselves along the bottom when required to move in any direction opposing the current.

2.5.5 Quadrat and Reference Coral Framer Photos – Natural Reef

On the first monitoring trip, extra time was taken to finalize the location of and establish monitoring transects at the natural reef site of Los Jardines (the Gardens). The methodology of Loya (1972) was followed for this task. Beginning and endpoints for 5 x 10-m transects were marked with pre-sharpened 50cm threaded stainless steel rods that hammered into the substrate with a 10-lb sledgehammer. Further marking of the beginning and endpoints was accomplished by securing a small foam buoy to each of the marker pins. All transects were established at the same depth and in similar habitat. All but four transects were parallel and adjacent to one another, and spaced apart by approximately three meters. Due to space limitations at the monitoring site, the 5th transect had to be located slightly to the east by about six meters. At each transect a flexible tape measure was laid out between the marker pins during surveys. Sites suitable for photo quadrat placement and *in-situ* surveys were selected along and within two meters of each transect. Two small (10 cm) steel pins were hammered into the substrate to mark the corners of each quadrat survey area. In addition, short lengths of florescent plastic survey tape were used to mark the location of each pin.

In addition to the quadrat locations along each transect, naturally occurring healthy colonies of the same species and same general size as those transplanted onto the modules were located and marked for monitoring. Occasionally a colony would be overgrown or overturned, or in some cases just never able to be re-located again for unknown reasons. As a result, over the course of the project multiple colonies were added to the original list of individuals that were photographed each year.

The natural reef substrate was a mix of small narrow sand channels, low-relief (<0.2m) hard-bottom, and isolated patches of higher relief (0.2 - 0.75 m) coral heads and dead coral framework (mainly *Acropora palmata* and *Orbicella annularis*). Interspersed throughout this mixed-relief hardbottom community was a typical Caribbean mix of soft and stony corals, sponges, macroalgae, and other benthic invertebrates. Most corals in the area were of relatively small stature, and competing with an actively growing and advancing macroalgae community that was dominated by *Dictyota*, *Halimeda*, and *Lobophora*. During the course of the study, several individual corals were observed to have been completely overgrown by macroalgae.

On the first monitoring trip a highly detailed and to-scale drawing of the natural reef transects, quadrats, and reference corals and their positions relative to one another was produced (Figure 2.13). This map was updated and improved on the following trip and laminated copies were provided to each diver on every monitoring dive thereafter to aid in setting up the site for quadrat photos and surveys. There were some logistical difficulties unique to the natural reef site; the relatively shallow water made working in surge conditions challenging, especially while taking framer photos of individual reference corals or quadrats located amongst stands of delicate coral branches. For this reason, the calmest day during any given monitoring trip was usually the one selected to visit the NR site. A team of 2-3 divers was usually sufficient to complete all the work at the NR site in one visit.

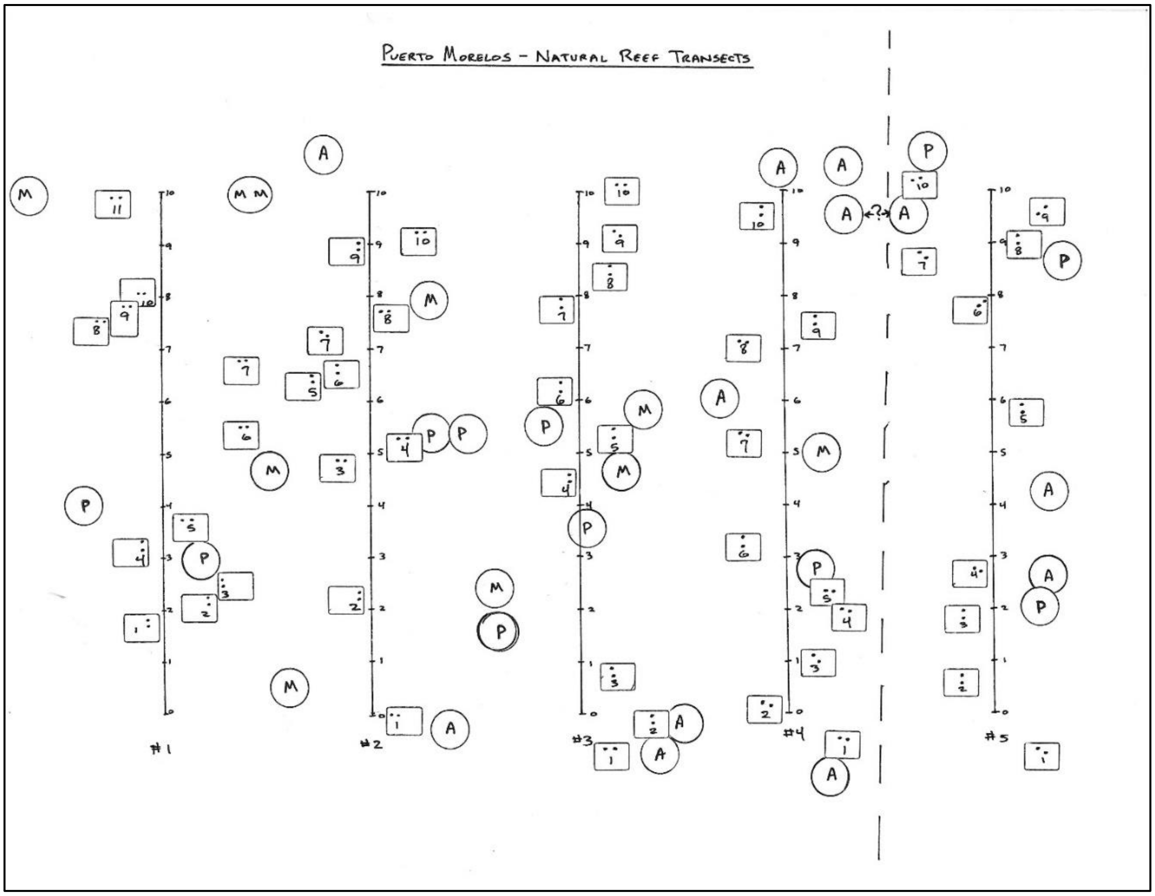


Figure 2.13 Map of natural reef transects, quadrats, and reference corals. Legend: A= *Agaricia agaricites*, M= *Orbicella annularis*, and P= *Porites astreoides*. Transects were labeled left to right, and quadrats along each transect labeled south to north. Within each quadrat two dots indicate the placement of the locator pins.

For each transect, there were at least 10 quadrat photos taken. The framer was positioned according to the location of the pins on the laminated map, and held as flush with the substrate as possible without damaging any corals or other benthic organisms. Reference corals were interspersed throughout the transect field, although in variable numbers. There were multiple corals, of varying number, present in each transect. A total of 30 corals, 10 from each of three corresponding transplant species (*A. agaricites, M. annularis*, and *P. astreoides*), were initially located and photographed. The framer was positioned to get the most dorsally-oriented view of the main axis of lateral growth for each reference coral colony. The framer base was usually, but not always, parallel with the substrate. Due to the complex nature of the habitat, the degree of macroalgal overgrowth, and the relatively short-lived nature of the colored flagging tape, finding and re-flagging each individual reference coral and pin at the beginning of each monitoring session was a challenge and took coordinated teamwork to accomplish.

2.5.6 *In Situ* Quadrat Surveys

In addition to the quadrat framer photos of each marked monitoring patch along the transects, *in-situ* quadrat surveys were also conducted. The quadrat survey diver would carry a 25x25cm PVC square gridded with monofilament line into smaller 5x5cm grid cells. The diver would then find the epoxy and stainless markers (on modules) or flagged pins (on the natural reef) and line the framer up with the markers corresponding to the diagram on the laminated map. A clipboard loaded with multiple waterproof datasheets that had three pictorial representations of each grid (one for each face of the module or for three natural reef quadrats) and some lines for descriptive notes was carried by the diver. He or she would then characterize the occupants of each quadrat in terms of approximate percent cover of major benthic colonizing organisms; each identified to the lowest possible taxon. These survey data were intended to aid in the processing of the quadrat photos that were later analyzed with CPCe software. It was successfully predicted that sometimes an eyewitness account would be useful in steering decisions on identification of complex 3-dimensional organisms when represented in a 1-dimensional digital photo of limited resolution.

2.5.7 Processing and Analysis of Quadrat Photos

Digital photos were labeled, organized, and stored by Collection Date, SM Number, and Treatment. Minor corrections to exposure and contrast were applied as needed during first examination of the photos. After all of the quadrat photos had been taken (after the last monitoring trip), a species list of readily identifiable organisms was generated. This species list was created by examining every framer photo and tallying each species that was documented throughout the span of the entire project. To analyze the photos for space occupancy (percent coverage by benthic organisms), CPCe software was utilized (Kohler and Gill, 2006). This program generated a set of 30 points that were then randomly distributed throughout the 25x25cm framed portion of the photograph. The area directly underneath each randomly generated point was classified according to presence of benthic organism or general state of algal growth. Once all of the photos for one set were point-counted and processed, CPCe generated a summary spreadsheet that detailed the percentages of each organism from each image. This data each module was then combined with data from the other modules belonging to the same treatment or transect during the final analysis.

Photos of the coral transplants and reference corals on the natural reef were also analyzed with the aid of CPCe software, but using the tracing feature of the program. The tracing function enables the user to carefully trace the outline of any feature in a photograph and then calculate its total area based on a standardization/calibration procedure on a reference feature of known size within the photograph. This calibration procedure was performed for each photo. Only living coral tissue was traced for each transplant, and care was taken to exclude areas of sediment or macroalgal growth within the coral skeleton. The total area in cm^2 was recorded for each transplant from each monitoring trip (with exception of September 2012). A database was created to track the sizes for each transplant over time. Net skeletal growth/extension and tissue expansion was documented as increases in total area over time. Tissue loss from disease, sponge overgrowth, or recession from no apparent cause was documented as a decrease in total area over time.

2.5.8 Artificial Substrate Pad Collection

Artificial substrate pad samples were collected on every monitoring trip. One double-thick layer of pre-cut 20 x 15 cm sacrificial pads was randomly chosen from the total original group of six (two on each of three sides) (the centers of the “H”). To remove the pads, a pair of underwater shears was required to cut the zip ties and pad material itself. The cutting process was done with as little disturbance to the pad as possible, and once it was loose the Ziploc bag was quickly placed underneath and around the debris from the pad as it fell away during the detachment process. This was intended to capture as many of the more mobile members of the epifaunal invertebrate community as quickly as possible as they scattered from beneath the pads during collection, as well as to capture any mollusks, echinoderms, or other animals and accumulated debris as it fell during the removal process. Once the bag was securely sealed, a small waterproof label was placed inside with the freshly collected pads. The bag was then double sealed within a second

Ziploc bag, and stored inside a mesh bag. Processing of the collected pad samples began immediately upon return to shore to preserve the animals. Prior to processing, each pad was photographed to document the fouling organisms on the exterior surface. The general workflow for processing of the collected pads proceeded as follows:

1) Remove pads from Ziploc bags, place in Tupperware bin.
2) Pour residual seawater and debris from Ziploc bag through a sieve.
3) Remove large non-organic debris and sediment.
4) Rinse contents of sieve in tap water and place into sample vial.
5) Take note of and carefully remove large macroalgae and other sessile invertebrates from pads (typically sponges, tunicates, bryozoans, and bivalves).
6) Fill plastic bin with tap water, add full strength formalin to make 2-3% solution.
7) Add pads to diluted formalin mixture, submerging completely.
8) Wait for escape response triggered by the addition of the formalin.
9) Remove animals from the solution as they leave the pads.
10) Thoroughly inspect all sides and surfaces of the pads and, carefully remove each remaining invertebrate from the intricate fibers of the pad material.
11) Place all invertebrates into sample vial, add formalin to make 10% solution.
12) Prior to departure, rinse samples of their formalin solutions and top off with 70% EtOH for transport to Florida.
13) Label each vial and seal thoroughly with electrical tape; carefully pack amongst soft items of personal luggage for the return trip to Florida.

The sample vials generally contained a coarse mix of variable grain size sediments and shell fragments, macroalgal pieces, large worms, small crustaceans, assorted echinoderms and mollusks, and a slurry of small crustacean appendages and other invertebrates. Contents from the sample vials were placed into glass dishes for initial sorting. Large specimens were removed first, along with assorted large appendages and pieces of debris. After the preliminary examination was completed, the samples were placed in a petri dish and examined in detail under a dissecting microscope. One by one, each small invertebrate was removed, counted, and placed into an initial classification bracket. Species identifications were aided by multiple taxonomic references and dichotomous keys (Abele and Kim, 1986; Littler et al., 1989; Humann et al., 2013). During the taxonomic sorting and identification process a table of species and their relative abundances for each monitoring trip was constructed and organized by major taxonomic groupings. Species assemblages and abundances were also compared to other trends that were being monitored concurrently using multi-dimensional scaling (MDS) Primer-e software (Clark and Goorley, 2006).

2.5.9 Settlement Plate Collection

In the Caribbean, mass coral spawning events have been well correlated with the warming of the water and phase of the moon over a narrow span of the late summer months. The settlement plates were installed on the modules in July 2007 (deployment procedure described in section 2.4.2), three months prior to the predicted coral spawning. The first group of settlement plates were collected in November 2007, three months after the main local coral spawning event in late August/early September. The first collection harvested 50% of the deployed plates on each module, and took one day in the field. For this collection, 2 divers visited each module that had the settlement plate treatment and removed a pre-determined random assortment of plates from their mounting brackets. Once the wing nuts were removed, the plates slid off of their mounting bolts easily. As each plate was removed, an 50cm section of rigid wire was threaded through the hole in the middle and each plate was separated from the one adjacent with a 3cm spacer section of pre-cut plastic tubing. Each wire collector held six settlement plates, and once filled was closed into a loop and stored in a mesh bag.

When the dive team returned to shore, the freshly collected plates were individually photographed prior to processing. Forceps were then used to remove large macroalgae and/or other select colonizing organisms. Next, the plates were submerged, still on the wire racks for easy handling, in a 10% bleach solution and left to soak for several hours until all of the algae and soft organic material had been dissolved. Afterwards, the plates were dried in the sun and carefully packaged in preparation for the return trip to Florida. The second settlement plate collection trip took place in mid-October 2008 and collected all remaining plates in a similar manner.

During analysis, each plate was thoroughly inspected with both the naked eye and with a dissecting microscope. Coral colonies found on the settlement plates were identified to lowest possible taxon and counted. A measure of recruitment density (recruits/m^2) was obtained from this part of the study, and was used in conjunction with data obtained from the coral recruit surveys for analysis and discussion of coral population recruitment and natural recovery rates.

2.5.10 Other Surveys and Tasks

In order to gain insight on the grazing pressure that was being applied to macroalgae growing on the SM surfaces, herbivory surveys (herbivorous reef fish bites/minute) were conducted on the first two monitoring trips. However, as more coral recruits began to populate the module surfaces, more and more time was required to complete the coral recruit surveys and a decision to sacrifice the herbivory component was made in favor of prioritizing the coral recruitment surveys.

General notes and observations were recorded by the author during each dive. These included: descriptions of coral transplant health and appearance and notes on: species assemblages, items in need of future maintenance, and overall appearance and composition of the module's benthic communities. In addition to the quadrat and coral transplant monitoring photos, a large number of descriptive photos of the modules were taken to document the fishes, corals, and benthic colonizing organisms residing on and in association with them.

Performance of multiple maintenance-related tasks was required through the course of this project. Identification tags and masonry screw protractor mounts (for the coral recruit range-and-bearing surveys) on each module were often completely overgrown with calcareous coralline algae, fire coral, other forms of fleshy macroalgae, and occasionally hydroids, and had to be scraped off with a brush or blade on every trip. The coral transplants turned out to be prone to disease/paling, overgrowth by macroalgae and sponges, meager growth and/or tissue recession, and becoming detached from the module surface. The latter happened four times, likely as the result of disturbance from local fishermen in search of lobsters, who may have used the corals as a hand-hold or the module as a place to moor their boat. Corals that became detached and that were still in good health were re-cemented to the modules on each monitoring trip as needed. During the first two-year monitoring period, corals that died were replaced with newly collected colonies from the nearby natural reef. With the exception of one small *Orbicella annularis* colony, only corals of opportunity, those that were not firmly attached to the substrate, were used to fill this replacement requirement. This was done in order to maintain uniformity of structure and function among the modules that received the coral transplant treatment.

At least two distinct long-term ecological successional features transpired during the course of this study. The first was the appearance and rapid spreading of the fleshy brown algae *Lobophora variegata*. On many of the modules, particularly those with the artificial substrate pad treatment, this species underwent a noteworthy population bloom which resulted in a significant portion of the surface being covered on majority of the modules. On some modules, it appeared to grow thickest on the sides that were in the lee of the predominant current. The boom in *Lobophora* coverage peaked during the September 2007 summer/fall trip (almost 1 full year following deployment) and remained high for the following two monitoring periods for the Controls, Pads, and Coral Transplants treatments. The Settlement Plates treatment did not peak until March 2008. By the end of the third year *L. variegata* had experienced a 6-7 fold decrease on the modules (see Chapter 3, Figure 3.5). This algal species mainly grew along the sides of the modules, and therefore did not directly threaten to overgrow the coral transplants that were all mounted along the upper edge. However, on some modules the algal growth was particularly enthusiastic, and pruning was required to keep the corals from being overwhelmed by shading or abrasion.

The second "event" was the appearance and rapid spreading of an encrusting sponge known as the Lumpy Overgrowing Sponge (*Desmapsamma anchorata*). This fast-growing sponge was seemingly indiscriminate when it came to where it would attach and spread. Unfortunately for the coral transplants, they provided an excellent point of attachment for the upward growing tendrils of the sponge during the 2nd and 3rd years of the study and beyond. On each monitoring trip, coral transplants that were being overgrown had the smothering sponge tissue carefully removed. This was done as delicately and thoroughly as possible, but the basal cells of the sponge on the areas of attachment often remained and new sponge growth was usually visible after a few days of removal. Many coral transplants were smothered completely in between monitoring trips, and the transplant survival rate plunged as a result. Although the destructive influence of the sponge seemed to have peaked around the 2nd and 3rd years, it was apparent that additional coral transplants had been lost over the three-year stretch between Monitoring trips VI and VII. When the first coral transplant to be killed by *D. anchorata* was discovered during

Monitoring trip III, it was replaced by a new healthy colony. However, by Monitoring Trip V it was apparent that many more transplants were going to end up as casualties of sponge overgrowth, and it was decided that no additional efforts would be made to replace deceased transplants.

2.5.11 Bonus Site: La Bonanza

As was briefly described in above, in addition to the Puerto Morelos and Akumal study sites, there was a third module deployment site north of Puerto Morelos called La Bonanza (Spanish for "the Bonanza"). The eight modules deployed there had only the un-modified control and artificial substrate pad treatments, and were not evaluated as routinely or thoroughly as the modules at the other two deployment sites. Surveys conducted there were limited to fish counts and coral recruit surveys. Another way in which this site differed is that the modules were almost completely surrounded by, and in some cases resting directly on top of, a dense seagrass bed consisting of Manatee Grass (*Syringodium filiforme*) and Turtle Grass (*Thalassia testudinium*). The final difference deals with spacing; the Bonanza modules were spaced only 8-10 m apart, as opposed to the 30m spacing present at the other sites. This site was visited several times, but no formal comparisons were made between the Puerto Morelos and Akumal sites and the Bonanza site. It is included here solely as an opportunistic qualitative resource to bolster conclusions discussed in subsequent chapters.

2.5.12 Best Laid Plans - Hurricanes Wilma and Dean

In October 2005, almost exactly a year before the modules were deployed, the Costa Maya (Mayan Riviera) was impacted by Hurricane Wilma (Figure 2.14). This storm made landfall in Quintana Roo on the island of Cozumel with Category 5 winds (217 kph sustained – 273 kph gusts) and waves recorded at 5-8 m. The storm's forward momentum stalled prior to a change in direction that would eventually take it back on a meandering northeast heading to Florida, and during that stall the storm took a full 26 hours to pass from Cozumel to the Yucatan mainland. At the time of the storm's passing, a reconnaissance group from NSUOC was already scheduled to travel to the Yucatan to attend some preliminary project implementation meetings with the directors of PNAPM and CEA, as well as a local marine contractor. Upon arriving in Puerto Morelos in January 2006, almost three months after the storm, the NSUOC team took note of the damage to local maritime and civic infrastructure, vegetation, shorelines, and heard through word of mouth that several previously deployed artificial reefs from other unrelated projects had become dislodged and even rolled completely up onto the shoreline in front of a local resort from a shallow water snorkel trail. Site inspection dives by the author and colleagues conducted on that trip suggested that a deployment depth of 10-12 m would be conducive to module longevity and prevent movement due to disturbance from future severe storm events. Estimations of depth to hard substrate residing beneath the overlying sand layer at potential deployment sites were made. In Akumal, it was noted that hardbottom could be reached after digging only a foot or two into the sandy substrate, whereas in Puerto Morelos the sand layer appeared to be substantially thicker in most places.

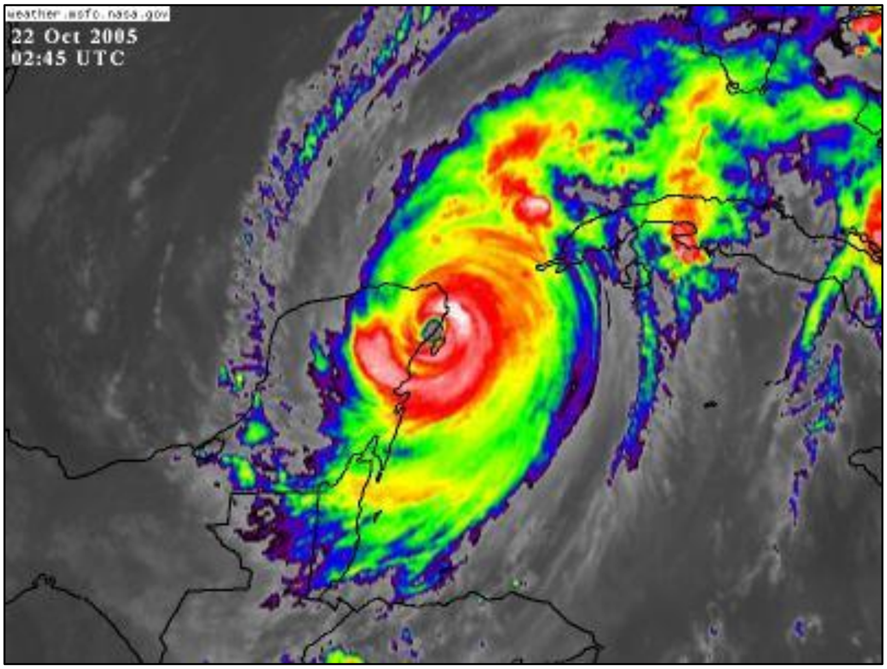


Figure 2.14 Hurricane Wilma passing over the Yucatan peninsula.

In October 2006, the modules were constructed and deployed. Ten months later, on August 21, 2007, Hurricane Dean made landfall as the strongest storm of the 2007 Atlantic hurricane season near the town of Majahual, 193 km south of Akumal (Figure 2.15). This storm came ashore with Category 5 winds topping 280 km/h (176 mph) and storm surge of

4-6 m, but passed well clear of most major population centers and without losing its forward momentum as Hurricane Wilma had done two years prior. However, the coastal and coral reef ecosystems of that region were significantly affected by the storm surge and large crashing waves that battered the shoreline as the massive storm came ashore. Following the storm the coastline from Playa del Carmen to Chetumal was littered with dead fish, dislodged gorgonians and corals, and assorted debris (mangrove roots, palm tree trunks, assorted driftwood and lumber, fishing gear/nets, trash, etc.) (personal communications).

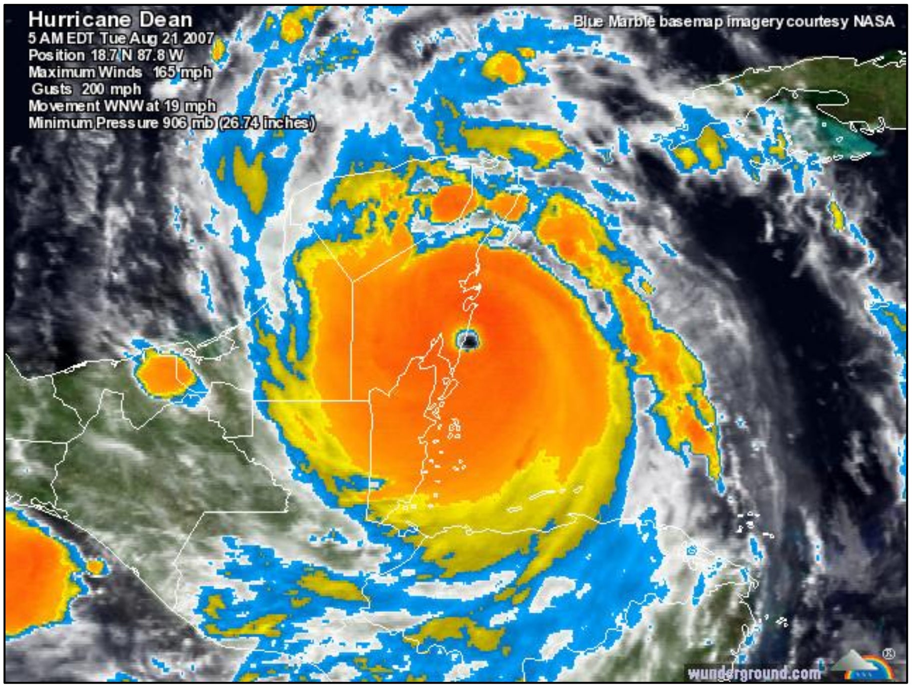


Figure 2.15 Hurricane Dean passing over southern Quintana Roo and Belize.

In September, one month following the hurricane, the NSUOC monitoring team arrived for the second monitoring effort. Upon arrival in Puerto Morelos, it was noted that the pilings holding up the public pier had been partially uprooted out of the sand, and other telltale signs of storm damage were noted around the town. Knowing that the damage would be more severe further south closer to where the storm made landfall, the team immediately decided to do a site inspection dive in Akumal prior to beginning any formal monitoring surveys. A boat was hired from the local dive shop, and the team made the short ride out to the GPS coordinates that marked the location of the first substrate module in the deployment field. The team entered the water, but did not find a module at the original deployment coordinates. After doing a sweep of the entire deployment field, it was discovered that every single one of the modules had been moved to the western edge of the sand channel, towards the shoreline and repositioned near the base of the westward sloping wall of the natural reef. Three substrate modules had been broken up into multiple smaller fragments that could be still found in the sand near the edge of the reef, and one module was missing completely (Figure 2.16 A).

It was concluded that the substrate onto which the modules had been deployed and the artificial reef design both played a key role in the fate of the relocated and destroyed substrate modules. Apparently, there had been enough wave energy, even at the 12-m depth of the deployment field, to apply a significant amount of force on the substrate modules. With enough rocking back and forth in the surge, the modules likely worked their way down to the hard substrate underneath the sand. As a result of the decreased amount of friction on the hardbottom, the modules were able to ‘skate’ along on the underlying hardbottom substrate like hockey pucks with the force of the waves until they reached the foot of the adjacent natural reef. There they were either pushed up against the edge and piled up with other loose reef rubble and assorted debris, or tipped over completely which made it easier for them to be lifted and slammed back down on the hardbottom until they were pulverized. The substrate modules that were disturbed and damaged the least were at the far northern end of the deployment field. From north to south, there is a slight depth gradient, with the bottom getting about two to three meters shallower in the southern end. The modules that had been broken up and lost completely were all from the shallower end of the deployment field. Here, the amount of force the waves were able to apply to the modules was stronger, and was hypothetically enough to have overturned them even with their wide and stable base design. Once overturned, they were much easier to move. Their central cavities, now open to the force of the waves on both ends, may have given the violently rushing water more purchase and allowed them to be repeatedly lifted off of the substrate and dropped back down with each passing wave. The cumulative force of the impacts was likely too great for the relatively thin walls of the modules to withstand, and they broke apart under the wave action.

The team conducted multiple dives and organized search patterns over the natural reef to the west of the deployment field to try and locate the missing module, but no sign of it was ever found. Given the fate of the three destroyed modules that were still present in the sand channel, it is likely that the missing module was also destroyed and its debris was scattered further inshore. It was also noted during the search-and-recovery dives that many large pieces of reef framework and boulders had been overturned, dislodged, and transported a considerable distance from their original locations. One archway and swim-through in the natural reef that had been noticed by the team on a previous visit was completely clogged with foreign material and large chunks of reef rubble. Many of the corals residing low on the substrate displayed obvious signs of sand scouring, and very few fish of any size or species were encountered anywhere. Although the destruction of three ARs adjacent to a sensitive coral reef ecosystem was unfortunate, one possible perspective to consider is that given the size and quantity of naturally occurring reef rubble that was tossed about during the storm, and the comparatively sized and much smaller contribution potentially made by any SM debris, any collateral damage that could be attributed to the substrate modules demise was far overshadowed by the cumulative amount of damage being done as a result of natural processes.

Given the grim scene that the team discovered in Akumal, apprehension was universal as the team traveled back to Puerto Morelos to conduct a similar site inspection dive. However, due to their increased distance from the storm and deployment into a thicker layer of sand, the modules at La Pared were all still in their original locations, and none had any damage. There were some clear signs of a recent disturbance event, with a bit of scouring underneath some modules and gorgonian skeletons and branches lodged in the interior of others (Figure 2.16 B). Also, a few of the modules that were placed in very deep sand had settled a bit; one with the artificial substrate pad treatment settled so considerably that only its top 15% was visible. Burial for this particular module was so extensive that it was removed from routine monitoring for several data collection periods. In the years following the hurricane, the sand continued to shift and this module was mostly uncovered. However, it still resulted in an overall reduction of the sample size for the entire module deployment field for a time (from N =40 to 39), and the number of replicates for the pads treatment (from N=10 to N=9).

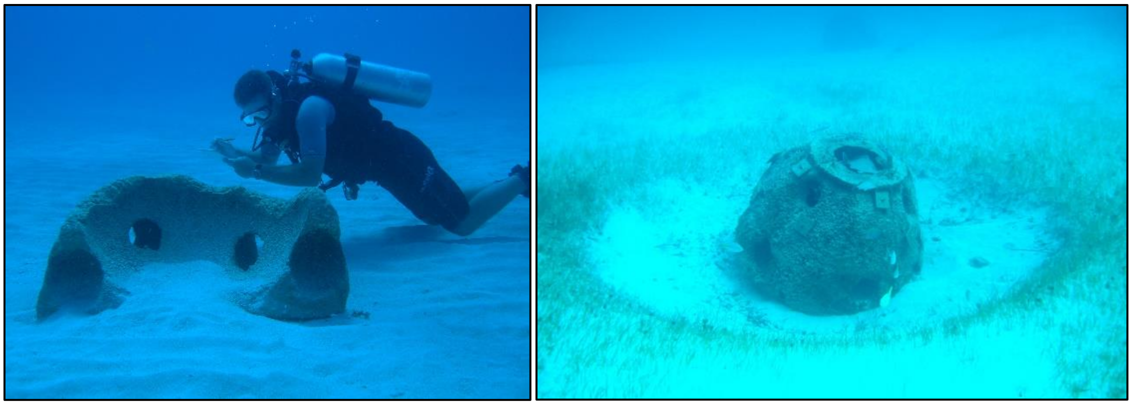


Figure 2.16 Hydrodynamic effects from Hurricane Dean on SM deployment field: left**)** fragments of a broken module in Akumal, and right) scouring around the base of a module in Puerto Morelos.

After monitoring in Puerto Morelos was finished, the team returned to Akumal to salvage what they could from the scattered remnants at the deployment field. During the storm, all of the externally-applied pad material had been ripped off or damaged to the point where it was decided that any remaining material would be removed to prevent further damage to the natural reef. Many of the settlement plates on the modules had also been ripped off, although about half still remained intact. On the natural reef, one plate was missing and all of the flagging tape and most of the pins marking the quadrat areas were absent as well. Another product of the storm was that some of the modules got pushed closer together, in addition to being pushed up against the reef. Thus, the 30-m spacing requirement from adjacent modules and the natural reef was no longer fully met. From that point onward in the study, all of the modules from the Akumal study site were designated as controls, and the natural reef site was abandoned completely. An abridged monitoring regimen was thereafter implemented for this site for the remainder of the study. On every monitoring trip, fish counts and coral recruit surveys would be conducted. In addition, the remaining settlement plates were still collected concurrently with those from the Puerto Morelos site. The list of required monitoring tasks in Akumal had previously taken 3-4 divers 1-2 days to complete. With the abridged workload 2-3 divers could easily finish up in a single day.

A final note about the effect of Hurricane Dennis on the reefs of Akumal: When multiple options for the deployment site were still being considered, the author and crew had a few chances to do a few reconnaissance dives to get a good subjective impression of the local underwater environment. There was a bit of macroalgae growth, the corals were in relatively low abundance as is common elsewhere in the Caribbean, and a seemingly typical community of reef fish was present. In the years following the storm, the entire area in general seemed increasingly depauperate of fishes and corals. Macroalgae became dominant, and fishes of almost every kind appeared to be scarce or altogether absent. The data clearly demonstrates a clear difference in assemblage structure between the Akumal and Puerto Morelos sites (see Chapter 5). This added further support to the decision to severely truncate the data collection effort in this altered study site.

Chapter 3 – Study 1: Development and Interaction of Macroalgal and Benthic Invertebrate Assemblages

3.0 Benthic Community Population Dynamics

Many previous artificial reef studies have focused heavily on development of coral and fish assemblages, either as a basic evaluation of how a particular artificial reef design functions or as a way to evaluate experimental treatments that are designed to enhance or restore one or more key components of a developing or recovering ecosystem (Clark and Edwards, 1999; Gilliam, 1999; Sherman et al., 1999; Sherman, 2000; Spieler et al. 2001; Fahy, 2003; Rinkevich, 2005; Lindberg et al., 2006; Quinn, 2009; Jordan, 2010). However, since the faunal community on an artificial reef consists of much more than just corals and fishes, this study aimed to assess the biological community from a more holistic perspective, beginning with a robust characterization of the succession of macroalgal and benthic invertebrate communities that developed on the substrate modules during the course of the study (Figure 3.1). This chapter examines the floral and faunal assemblages that became established on the exterior surfaces of the substrate modules, how the experimental treatments may have affected them, how they compared to observations from the natural reef, and how the invertebrate assemblage developed on and within the artificial substrate pads.

Figure 3.1. Spatial competition between three key components in benthic community structure: macroalgae (*Halimeda* sp.), sponges (*Desmapsamma anchorata*), and corals (*Porites astreoides*).

At its most fundamental level, a coral reef can be considered a biogenic habitat that has been built over time by the actions and interactions of myriad sedentary encrusting colonial organisms and the associated faunal assemblages they support. The process by which a reef is formed consists of numerous biotic and abiotic components, each contributing at some level to the growth and development of the underlying physical structure and the communities they support. Essentially every part of a coral reef supports life; seemingly barren or un-colonized portions of substrate are covered in a thin biofilm of bacteria and microalgae, and even the interior of the calcareous reef substrate itself supports a large population of bioeroding endolithic algae, fungi, and bacteria, as well as larger invertebrates such as sponges, bivalves, barnacles, sipunculans, and polychaetes (Glynn, 1997). Filamentous turf algae are often one of the first readily visible pioneer settlers on new substrate, and often a major contributor to high productivity on coral reef habitats (Klumpp and McKinnon, 1989; Steneck and Dethier, 1994; Arnold et al., 2010). Macroalgae is another basal and prominent constituent of any reef community and, depending on the health of the entire reef ecosystem and the ambient environment, can become a dominant feature that functionally out-competes corals (Hughes, 1994; Hughes et al., 2007). Macroalgae exists in many calcareous forms, and the remnants of many species can contribute significantly to the amount of unconsolidated sediments on the reef. Crustose coralline algae (CCA) grows on reef substrate and in the process of growing cements unconsolidated sediments and rubble together, contributing significantly to reef accretion (Bak, 1976). In many ways CCA has as much importance as a reef framework builder as scleractinian corals (Goreau, 1963). The presence of CCA, and specifically the chemicals they contain, has been linked to increased settlement of coral recruits and the use of chemically customized substrates has been the subject of much speculation and occasional laboratory based success (Fitzhardinge and Bailey-Brock, 1989; Morse and Morse, 1991; Morse et al., 1994; Morse and Morse, 1996; Heyward and Negri, 1999). However, practical applications of such specialized substrate have yet to succeed on a scale relevant to restoration of degraded reef. In addition to the aforementioned macroalgal constituents, there are also bryozoans, tunicates, sponges, and soft and stony corals that add greater structural complexity and biodiversity to benthic communities.

Whether terrestrial or marine, biological communities are far from static in nature. Dynamic changes to both species composition and community structure occur on seasonal or other long-term time scales. The first organisms to settle on an un-colonized substrate, whether natural or artificial, are not necessarily those that are most well equipped to survive long-term in a highly competitive environment. They frequently belong to a group of species that are considered opportunistic or "weedy" and that are quick to colonize, fast growing, and usually quick to reproduce (R-selected). Once other, typically slower growing but longer-lived (K-selected), species become established, they may effectively out-compete the initial settlers. However, the struggle for resources is fairly continual, and dominance by any one species or group can be temporary or cyclical, especially in the marine environment (Connell and Slayter, 1977; Connell, 1978).

In classical concept, communities change in an orderly, sometimes even predictable fashion over a period of many years until they achieve a self-perpetuating stage that may persist as long as no major disturbance is introduced into the system (Odum, 1969). However, attainment of climax community status is rare or nonexistent in most tropical marine communities (Sousa, 1984; Miller, 2015). Each successive community functionally modifies the environment to some extent and creates favorable conditions for the following community. The physical structure created by biogenic habitats usually changes local environmental conditions and thereby alters biotic interactions among resident organisms (Kelaher, 2002).

The orderly sequence by which each fundamental component of a community becomes established, their relative contribution to overall community structure, and the changes that are brought about through modification of the physical environment are collectively referred to as ecological succession. The terminal, persistent community that is formed once the system has matured is referred to as the climax community, with each intermediate community being defined as a *seres* (Nybakken, 1997). Succession is also defined as a descriptive account of how an assemblage changes over time, or the replacement of populations in a habitat through a regular progression to a stable state (Bohnsack et al., 1991). This basic progression was originally developed for terrestrial plant communities (Clements, 1916; Clements, 1936) and is known as the *Facilitation Model*. However, in the marine environment such a simplistic concept may seldom apply and a true climax community may never truly be achieved, depending on what sort of disturbances it is subjected to and the stability of the surrounding environment (Nystrom et al., 2000).

Another model for succession, the *Inhibition Model* (Egler, 1954), assumes that no single species has competitive superiority over another, and whichever species arrives first will likely prevail over successive settlers, a “first-come = first-served” concept. New settlers will succeed only when resources (space, nutrients, light, etc.) are made available by the previous occupant as the result of either damage, seasonal dormancy, or death. In this scenario, succession is not viewed as a well-ordered and predictable process, and development of community structure through time will likely progress from short-lived to long-lived species. Intermediary to these first two concepts is the *Tolerance Model* (Connell and Slayter, 1977), which assumes that essentially any species can begin the process of succession, and those species that are more tolerant (i.e., able to survive on minimal resources) and/or competitively superior (i.e., most efficient at exploiting resources and investing in growth and reproduction) will eventually become dominant.

There is a greater body of evidence that exists in support of the inhibition and tolerance models being most accurate in describing observed patterns and process of succession in marine habitats (Connell and Slayter, 1977). Following disturbance to benthic communities, new spaces for colonization are typically occupied by those organisms that have a sufficient supply of larvae or propagules that are readily available to settle out of the surrounding environment. Seasonal variations in larval supply for most species apply here, and depending on the timing of disturbance and opportunities for new colonization, different species may be more likely to colonize first. Seaman and Sprauge (1991) stated that “among fouling organisms, species that first occupy available attachment sites may effectively prevent later settlement by other species”. This applies not only to fouling organisms, but reef fishes as well. There is the potential for a priority-effect to come into play in this scenario, wherein the initial occupants may prevent settlement of later successional forms, thereby delaying development of anything that might be considered a mature or climax community (Shulman et al., 1983; Bohnsack et al., 1991; Nybakken, 1997; Hixon, 2015).

Due to the inherent complexity of interactions between biotic and abiotic factors in the coral reef environment, attributing the progression of benthic community development solidly to any one model is a difficult or even impossible goal, and guiding the development of a natural ecosystem towards an alternate and more desirable state following a disturbance is inherently challenging. The processes that influence rates of development in benthic communities growing on natural coral reefs will, of course, affect the biota that grow on artificial reefs in a similar manner. Therefore, it is not surprising that multiple studies have demonstrated that artificial substrates of identical design have faunal communities that display a high degree of spatial and temporal variability, and may be colonized differently even on experimental replicate reefs in the same deployment locality (Schoener, 1982, Shulman, 1985; Sherman et el., 2001; Spieler et al., 2001; Bachtiar and Prayoga, 2010; Villanueva et al., 2010).

This study aims to detect differences in benthic community structure over time in the context of the experimental treatments that were applied to each substrate module. By thoroughly examining the succession of biota on the substrate modules, it is intended that insight into process will be gained and some beneficial and practical outcome of employing the experimental treatments in reef restoration will become apparent. Thus, the results of this study may lead to the generation of useful conclusions on how the techniques used here, or similar ones, might be used in restoration applications on natural reefs following disturbance events or on artificial reefs that are deployed for restoration, rehabilitation, environmental enhancement, or mitigation.

3.1 Macroalgal and Sedentary Invertebrate Community Composition

3.1.1 Methodology and Data Analysis

The methods utilized in this portion of the study primarily involve the collection and analysis of quadrat framer photos and *in-situ* quadrat surveys that were taken on the substrate modules and the natural reef transects. A detailed description of these methods is included in Chapter 2 (sections 2.5.4 – 2.5.6). Section 2.5.7 described the process by which the CPCe software (Kohler and Gill, 2006) was used to process the images and generate the final dataset. Data generated by these methods were summarized in Microsoft Excel and one-way analysis of variance (ANOVA) was performed on log(x+1) transformed data to look for differences among means using Statistica (Statsoft Inc., 2001). Post-hoc analyses utilized Student Newman-Keuls (SNK) to determine homogenous groupings.

3.1.2 Results and Discussion

For each sampling trip, in Puerto Morelos 120 quadrat photos (3 quads/module x 40 SMs) were taken on the modules and 50 (10 quads/transect x 5 transects) were taken on the natural reef transects. In Akumal, during the first monitoring trip 36 quadrat photos were taken on the modules (3 quads/module x 12 SMs) and 50 were taken on the natural reef. Following Hurricane Dean, no quadrat photos were taken in Akumal. During the course of this study, a total of 1,140 quadrat framer photos were taken in Puerto Morelos; 840 on the modules and 300 on the natural reef transects. Those totals also apply to the number of *in-situ* quadrat surveys were conducted as well. No surveys were performed on the natural reef during the last sampling trip (September 2012) due to limited time available and a prioritized need for data collection at the module deployment site.

A total of 57 benthic organisms were documented in the quadrat framer photos from both the substrate modules and the natural reef. These were identified to the lowest readily identifiable taxa and used to create a species list for CPCe analysis (see Appendix 3.1). The the species list consists of: 22 macroalgae species, 6 sponge species, 3 bryozoan species, 4 zoanthid and anemone species, 10 soft coral species, and 11 scleractinian/stony coral species, and 4 tunicate species. Thirty randomly distributed points were overlaid onto each quadrat image during the CPCe point-count procedure (34,200 points in total) to calculate the percent coverages of each organism or taxonomic group. This method is described in greater detail below.

a) Macroalgal Assemblage

In terms of greatest percent coverage, macroalgae was the dominant feature on the exterior surface of the modules and on the natural reef (Figure 3.2). This includes a combination of turf algae, crustose coralline algae, and larger (>10mm height) species of green (Chlorophyta), brown (Phaeophyta), and red (Rhodophyta) macroalgaes that are commonly encountered in the marine environment. Macroalgal coverage was significantly greater on the natural reef than the modules from October 2008 through September 2009 ($p<0.01$). In general, most of the treatments were similar to one another, although the Pads treatment was significantly lower than the Controls and Transplants and Settlement Plates treatments for the last three data collection periods (March 2009 through September 2012)

(ANOVA, p=0.015 and p=0.005, respectively), and the Coral Transplants treatment was a close second in two of those instances. Out of the collective macroalgal group, turf algae comprised by far the greatest percentage of all macroalgae on both the modules and natural reef (Figure 3.3). The term "turf algae" is actually a broadly used term that refers to a multi-species (typically ~30 to 50 co-occuring species) assemblage of small (1-10 mm canopy height), usually filamentous species that are more or less ubiquitous on any otherwise uncolonized surface (Steneck, 1988). This assemblage includes diminutive species that remain small, as well as larger species that have not yet reached their adult sizes. At all study sites, seemingly barren or uncolonized patches were examined and, on close inspection, found to be completely covered by the turf algae mixture. From a distance these "barren" patches were likely to appear as sand-covered concrete (on modules) or sand-covered coral framework (on the natural reef). However, once the sediment was brushed or washed away, a fine verdant carpet underneath was revealed. The filemantous nature of the turf algae is conducive to trapping fine sediments, and at times a majority of the exterior surfaces of many substrate modules seemed to be almost completely covered in sand and other small detrital material. For this reason, when the CPCe point-count analysis was performed, essentially any point that did not overlay a distinct/discernable species of large macroalgae or benthic invertebrate was classified as turf algae. Thus, it makes sense that during the first data collection point, March 2007, turf algae was higher on the modules than it was on the natural reef, and with each successive period, as the modules were colonized, turf algae on the modules was roughly equal with or less than that of the natural reef (Figure 3.3). With the exceptions of September 2007, September 2009, and September 2012, when treatments are compared for each data collection period, the Controls and Transplants treatment shared significance with the two highest peaks and the Pads and Settlement Plate treatments the lowest (ANOVA, SNK, p<0.05). The last two collection points saw the Pads treatment with the lowest amount of turf algae (ANOVA, SNK, p<0.001).

Turf algae excluded, the most dominant types of macroalgae were *Lobophora variegata* and *Dictyota* sp.; *Padina* sp. and *Halimeda* sp. were also among the top contributors, but they made up a relatively small percentage of the total coverage each time.

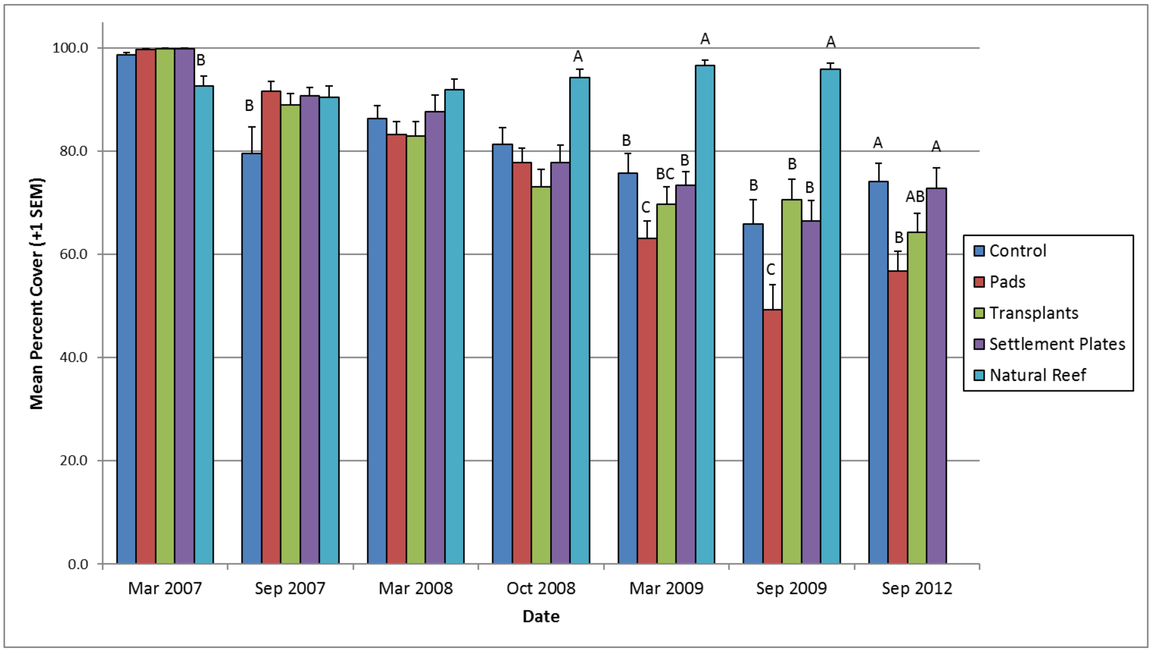


Figure 3.2 Percent coverage of macroalgae, all species combined (including turf algae). Letters indicate significant differences and homogenous groupings within the same time period (SNK, p<0.05).

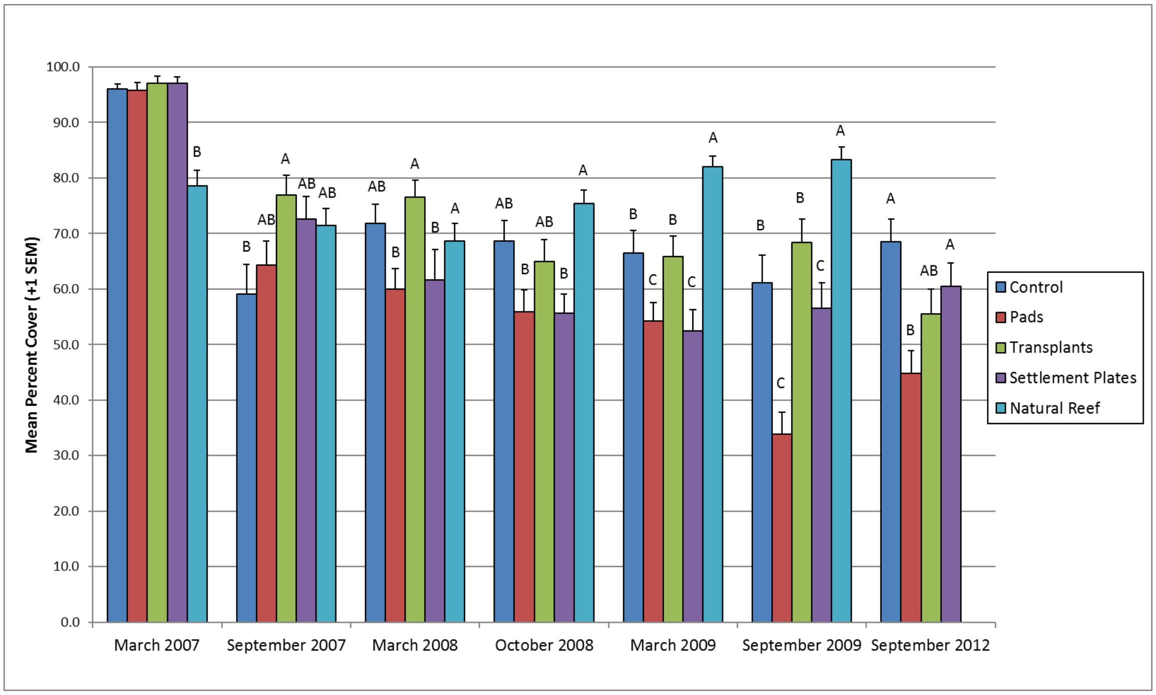


Figure 3.3 Percent coverage of turf algae only. Letters indicate significant differences and homogenous groupings within the same time period (SNK, p<0.05).

It has been well established that heavy sedimentation can have a profoundly negative effect on the health and growth of coral reefs (Ginsburg, 1994; Nugues and Roberts, 2003). Turf algae has the ability to function as a very effective sediment trap (Stewart, 1989). The adverse impacts to coral health brought about by the presence of suspended sediments is accomplished through a variety of different mechanisms that act together to limit coral reef development. First, and most obvious, is the potential for sediments to smother and/or bury corals, which initially results in a reduction of zooxanthellae densities and photosynthetic activity, increased respiration and mucus production, and eventually complete mortality of coral colonies (Aller and Dodge, 1974; Loya, 1976; Riegl, 1995; Riegl and Branch, 1995; Yentsch et al., 2002; Philipp and Fabricius, 2003). Secondly, coral growth can be reduced by the abrasive action of sand grains and the effect of shading (Aller and Dodge, 1974; Loya, 1976; Rogers, 1979). Sedimentation also serves to reduce coral reproductive outputs, settlement of coral larvae, and early survival of coral recruits (Kojis and Quinn, 1984; Hodgson, 1990; Hunte, 1992; Gilmour, 1999). Additional problems and increased coral mortality can be attributed to the ability of filamentous turf algae to trap suspended sediments, which can lead to a dramatic reduction in the percent coverage of the substrata needed for successful settlement of coral larvae, such as coralline algae, and may also facilitate accelerated growth of larger macroalgae that can overgrow, outgrow, and outcompete corals (Birkeland, 1977; Kendrick, 1991; Hughes, 1994; Steneck, 1997; Fabricius and De’ath, 2001; Belliveau and Paul, 2002). Nugues and Roberts (2003) suggested that there is a synergistic relationship between sedimentation and algae that may lead to declines of coral health and survival.

The percent coverage of true macroaglae, which includes the larger (canopy height ≥10 mm), more rigid and anatomically complex forms (Figure 3.4) (Steneck, 1988), does not include turf algae, even though the turf algae may technically include developmental stages of macroalgal species (Scott and Russ, 1987). During the first sampling trip (March 2007) the macroalgal and benthic invertebrate communities were still very much going through their initial developmental stages, and the percent cover of macroalgae was much lower than the following data collections. Throughout the remainder of the first year (March to September 2007), as the water temperature increased during the summer months, macroalgal cover increased considerably. Percent coverage of these species then peaked at the end of the first year but remained high for the following year for the Controls, Pads, and Coral Transplants treatments. It then declined, for the most part, throughout the remainder of the study for all experimental treatments, with the exception of the Settlement Plates treatment, which did not peak until March 2008. The last two data collections, three years apart, showed similar levels of percent coverage. Thus, it appeared that this particular component of benthic community structure showed signs of heading towards a more stable state as time progressed.

The Pads and Transplant treatments both exhibited some minor seasonal oscillation for percent coverage of *L. variegata* (Figure 3.5), particularly during the middle and end of the study. This was in stark contrast to the distinct seasonal oscillation in abundance and species richness that was observed in the coral reef fish assemblage that developed on the substrate modules for every treatment (see Ch.5, Figures 28-30). The difference is likely an artefact of the difference in generational timescales of the two groups; the relatively slow to develop macroalgal community and the relatively quick to develop and constantly fluctuating reef fish assemblage. Changes in specific community structure can take place on a scale of minutes to hours for the fish community, as new individuals either settle or migrate from elsewhere and as individuals are removed from the population due to predation or emigration. In contrast, any given species' appearance and eventual disappearance into and out of the benthic community can be expected to take longer to transpire. Seasonal oscillations in the benthic community should also inherently be harder to detect due to the long-lived and slow to change nature of most of the primary contributors to benthic community structure. If a seasonal fluctuation were there, perhaps it would not show up readily in the data until some point after the community had stabilized to a more steady state of existence.

When the quadrat locations were marked and delineated on the natural reef, they were not cleared of any pre-existing biota. They were chosen for their availability of suitable settlement substrate potentially settling coral recruits, vis-à-vis barren hardbottom with minimal or no macroaglae and/or other benthic invertebrates or corals. However, most of the quadrats had a small amount of prior occupation. Comparisons of the March 2007 macroalgae results to the other data collection periods (Figures 3.2, 3.3, and 3.4**)** demonstrate that macroalgal populations on the natural reef were already at a this preestablished and relatively steady state, as compared to the levels seen on the substrate modules in the beginning of the study.

The main contributors to macroalgal community structure were markedly different between the quadrats evaluated on the modules and the natural reef. The modules were dominated by *L. variegata* (Figures 3.5 and 3.6), which was not recorded at all in the natural reef quadrats, whereas the natural reef was dominated by *Dictyota* sp. which was present almost exlucisvely on the natural reef (ANOVA, $p<0.001$) (Figure 3.7). However, it should be noted that both *L. variegata* and *Dictyota* sp. were present on the natural reference reef, and the natural reef adjacent to the module deployment field, and percent coverage of each as indicated by the quadrat data from the natural reference reef may not be completely representative of that site as a whole (see section 4.3).

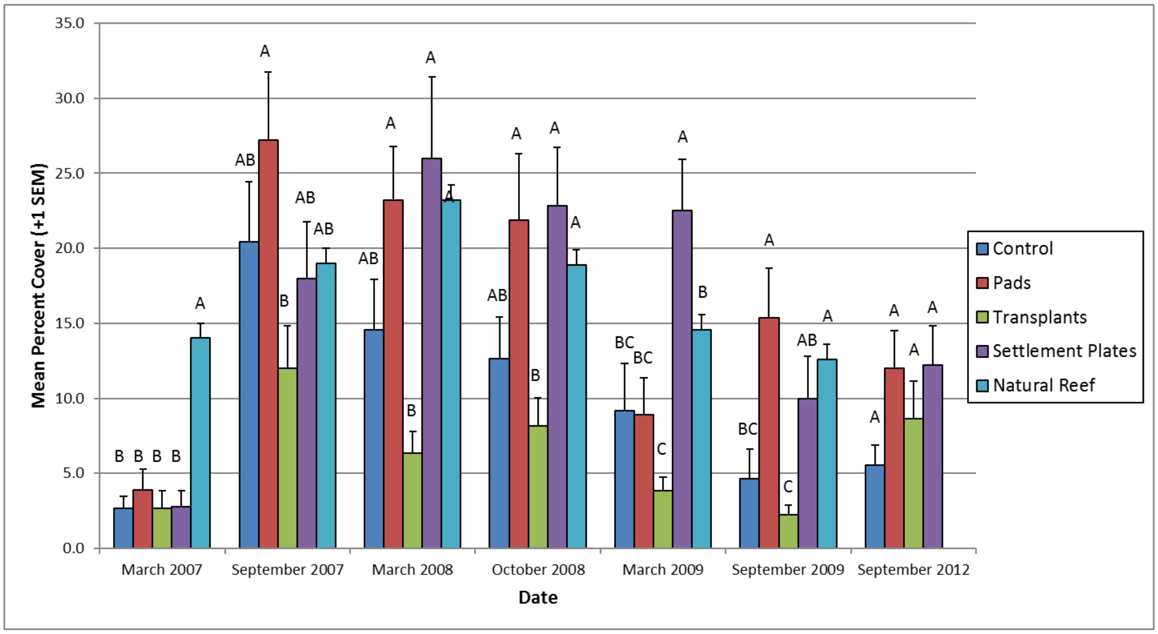


Figure 3.4 Percent coverage of all macroalgae species, excluding turf algae. Letters indicate significant differences and homogenous groupings within the same time period (SNK, $p<0.05$).

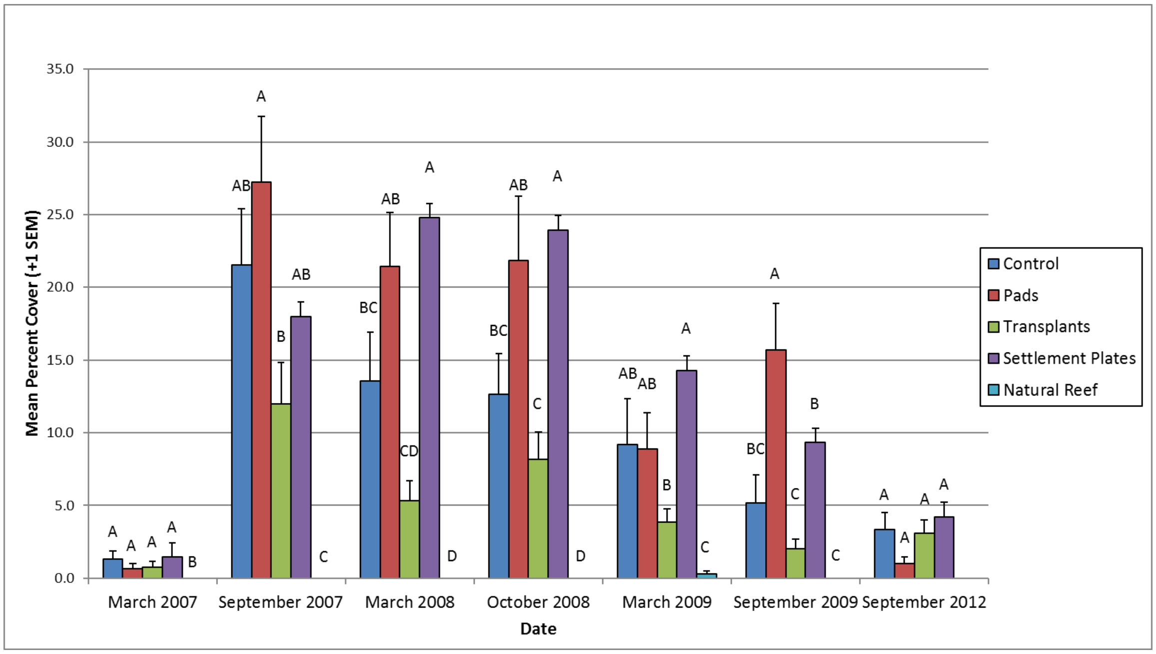


Figure 3.5 Percent coverage of the fleshy brown macroalgae *Lobophora variegata*. Letters indicate significant differences and homogenous groupings within the same time period (SNK, p<0.05).

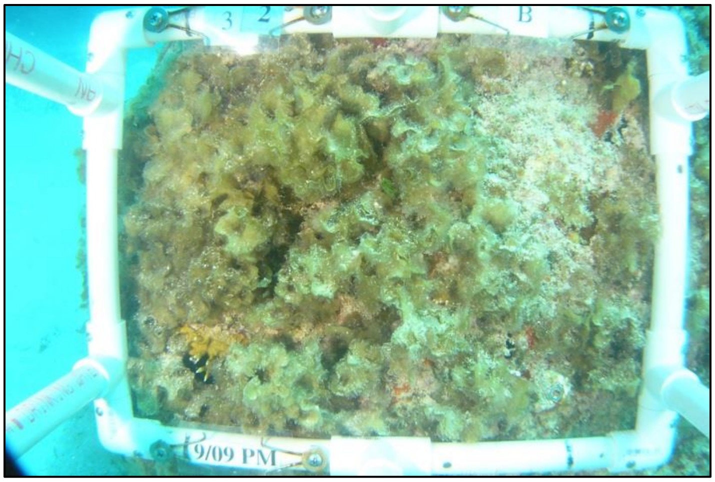


Figure 3.6. A quadrat framer photo centered over a dense patch of *Lobophora variegata* on the surface of a Pad treatment module in September 2009.

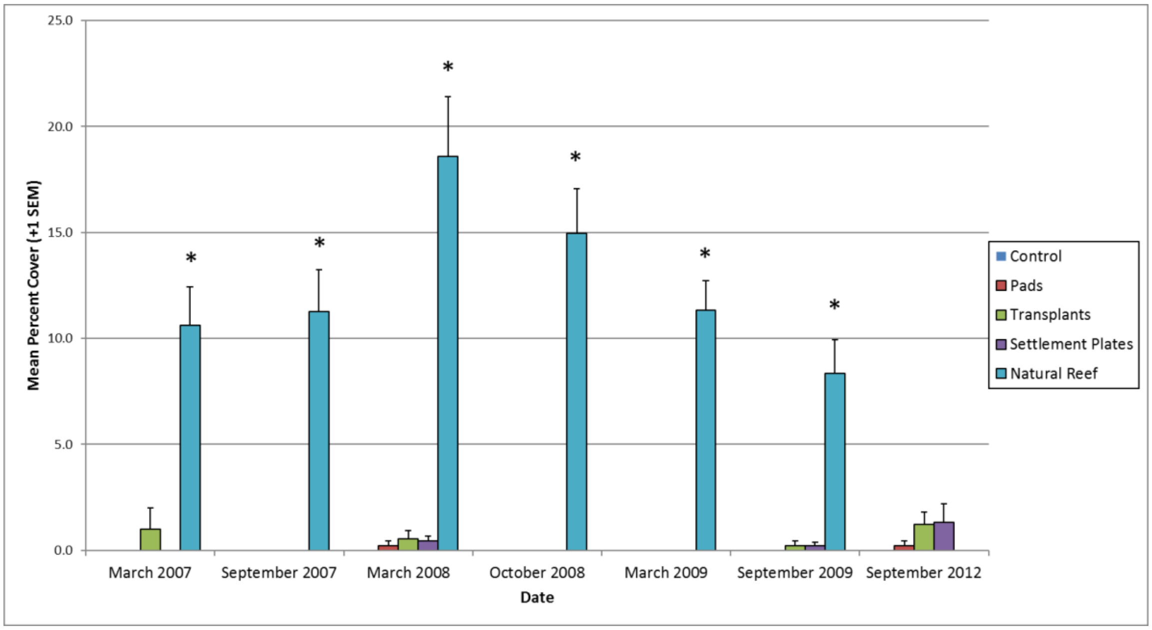


Figure 3.7 Percent coverage of the fleshy brown macroalgae from the *Dictyota* species complex. Letters indicate homogenous groupings within the same time period (SNK, $p<0.05$).

b) Benthic Invertebrate Assemblage

Even though macroalgae was the dominant feature of the benthic community, there were several benthic invertebrates that occurred in numbers great enough to be measured. One species of sponge in particular, the Lumpy Overgrowing Sponge (*Desmapsamma anchorata*), occurred in numbers that well exceeded those of the macroaglal community for a large portion of the study. Benthic invertebrates (excluding sponges and soft and stony corals) that were observed on the substrate modules and the natural reef were mainly ascidians (tunicates) and made up a very small fraction of the total percent coverage each year (<2%). Their appearance in the dataset is sporadic and shows no pattern of affinity towards any of the experimental treatments (Figure 3.8). No ascidians were recorded until the second data collection period, at which point they reached their peak coverage levels. No ascidians were recorded during the following two periods, but they were present in very small numbers in the latter portion of the study. The ascidian species that contributed to this minor assemblage include: a species of flat, encrusting tunicate (*Botrylloides* sp.), likely the Painted or Bulb Tunicate (*Clavelina* sp.), the Mangrove Tunicate (*Ecteinascidia turbinata*), and the Overgrowing Mat Tunicate (*Trididemnum solidum*) (Figure 3.9). A similar early ascidian bloom was observed on artificial reefs in the Maldives (see Clark and Edwards, 1994). Compared to surveys taken later in the study, there was a relatively greater percent contribution of ascidians in September 2007, almost one full year following deployment. Although there are other possible factors, such as disease or weather induced impacts, that may have affected this community, their ephmerality in this dataset may indicate that these species are able to colonize new substrates quickly but are slow-growing and easily out-competed by other more rapidly spreading benthic organisms.

Once the initial wave of rapid *Lobophora variegata* and *Desmapsamma anchorata* growth subsided, the ascidians were once again able to gain a tenuous foothold on surface of the substrate modules. Other non-ascidian benthic invertebrate species were observed by the survey divers, such as bryozoans and zoanthids, but they were present in even smaller numbers and were either not present or not discernable in the quadrat surveys and framer photos.

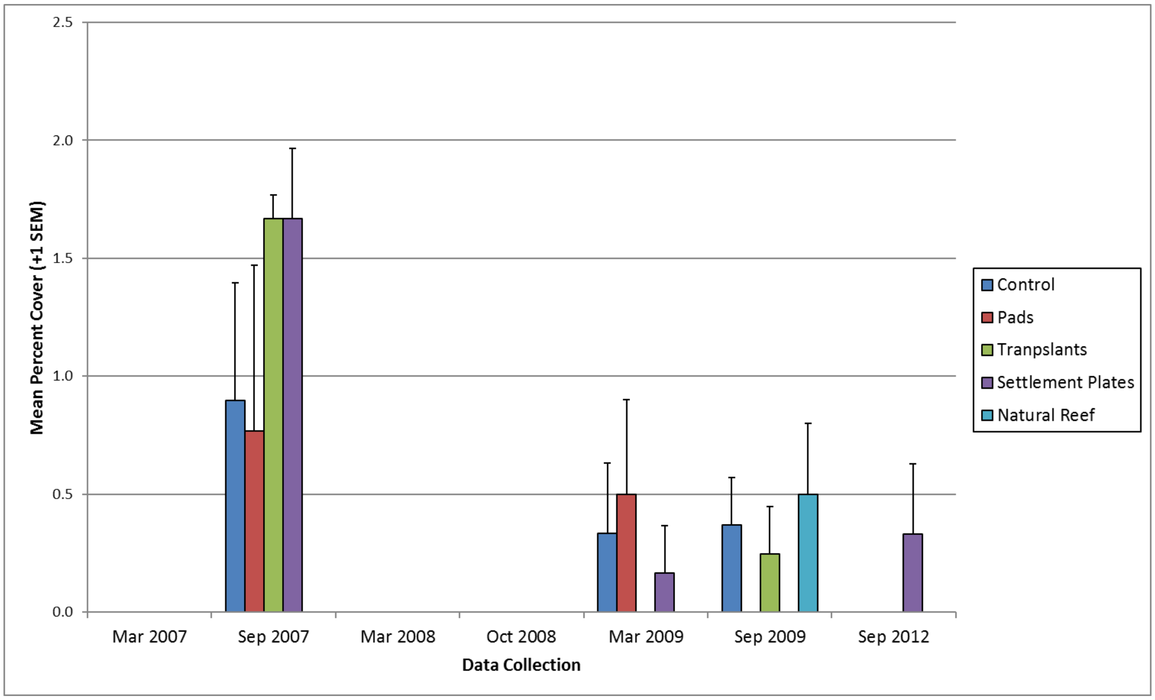


Figure 3.8 Percent coverage of tunicates, all species combined. No significant differences were found (SNK, p>0.05).

Figure 3.9. Mangrove tunicates (*Ecteinascidia turbinata*) (left) and a species of flat, encrusting tunicate (*Botrylloides* sp.) (right) on the modules. Note the juvenile Harlequin Basslet (*Serranus tigrinus*) using the tunicates for refuge in the left-hand photo.

Sponges played a significant role in the development of the benthic invertebrate community on the modules, and, as will be discussed in greater detail in Chapter 4, along with the development of the stony coral community. Multiple sponge species were recorded on the modules, but very few were seen in the natural reef quadrats. Percent coverage for all sponge species (Figure 3.10) displayed a steady increase over the first three years, with indications of stabilizing towards the end of the study. Given the decrease in macroalgal percent coverage following a loosely defined peak during the early and middle portions of the study (Figure 3.4), the steady increase in sponge percent coverage is likely a result of competition between the two groups, with decreasing levels of macroalgae either opening up new space for sponges to colonize or the sponges actively out-competing the macroalgae.

It is notable that the Pads treatment had significantly greater percent coverage of sponges in the last three data collection periods (ANOVA, $p<0.05$). Also noteworthy is the almost complete absence of sponges within the natural reef quadrats, perhaps exemplifying the ephemeral nature of many fast growing and rapidly spreading species.

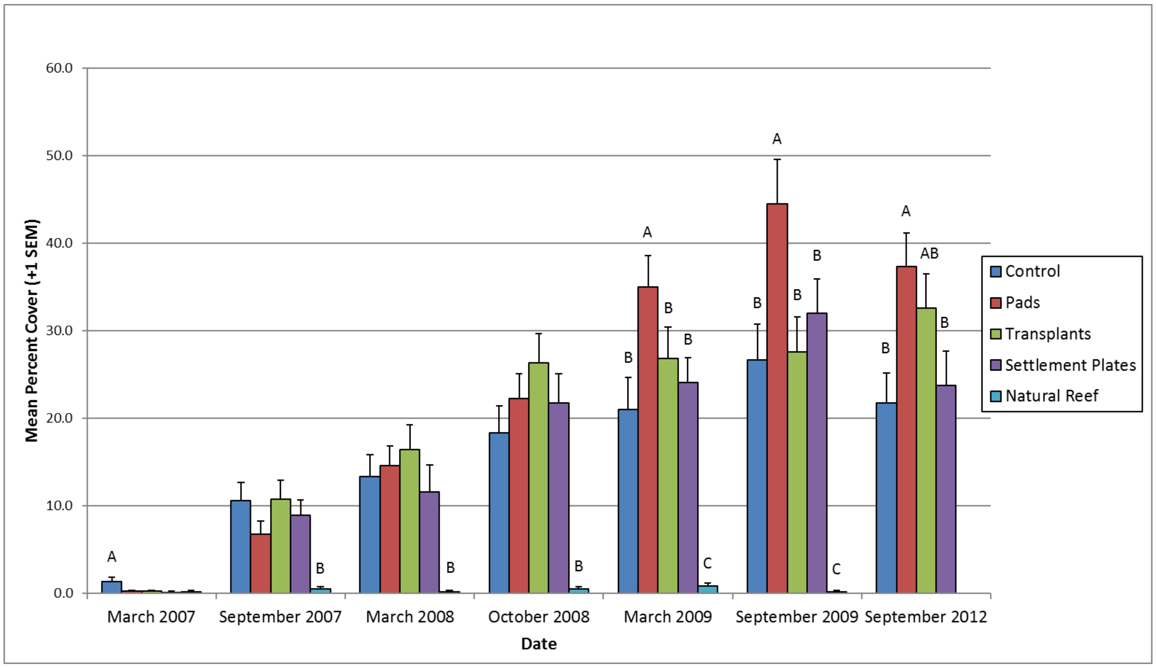


Figure 3.10 Percent coverage of all sponge species combined. Letters indicate significant differences and homogenous groupings within the same time period (SNK, $p<0.05$).

When the sponge assemblage is examined by species, it becomes clear that the trends are almost completely due to the dominance of the Lumpy Overgrowing Sponge (*Desmapsamma anchorata*). This species was responsible for the spikes seen in the Pads treatments, where it seemed to flourish particularly well for the last three data collection periods, and made up at least half to two-thirds of the total percent coverage of all sponges during these periods (Figure 3.11, 3.12). When the remaining group of sponges is examined, the Controls and Transplant treatment had the two greatest amounts of percent cover each time, although they were only significant in March 2009 (ANOVA, $p<0.05$) (Figure 3.12). Comparing the two figures (Figure 3.11 and 3.12), the absence of the *D. anchorata* data is particularly obvious in the decrease in sponge cover on the Pads treatment.

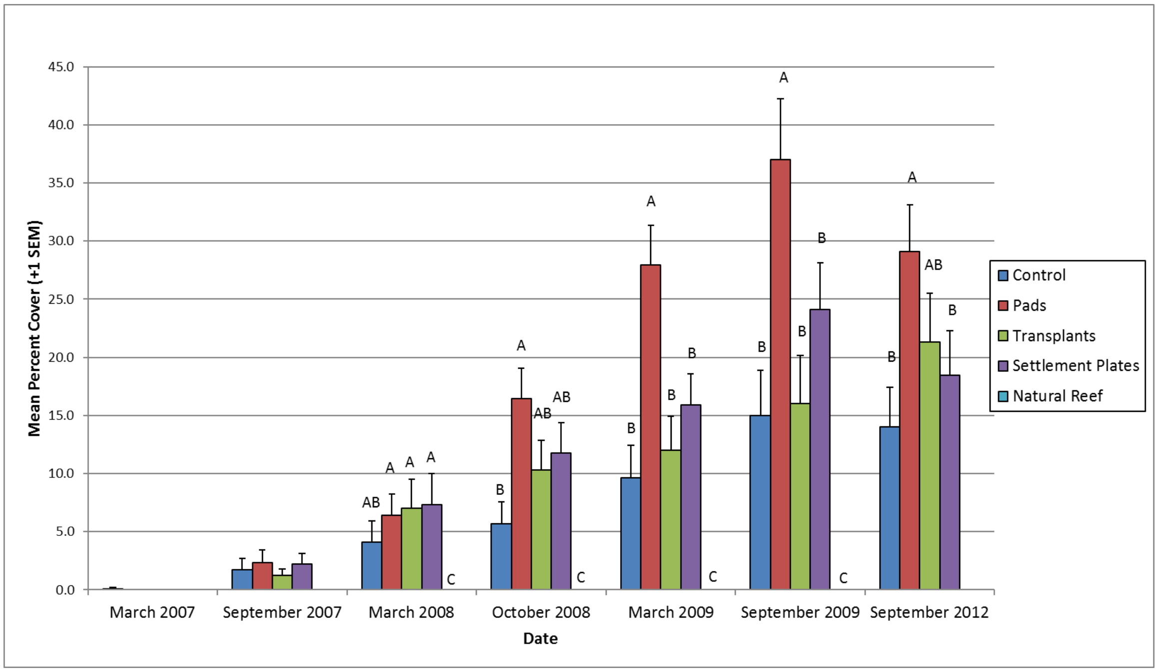


Figure 3.11 Percent coverage of the Lumpy Overgrowing Sponge (*Desmapsamma anchorata*). Letters indicate significant differences and shared groupings (SNK, p<0.05).

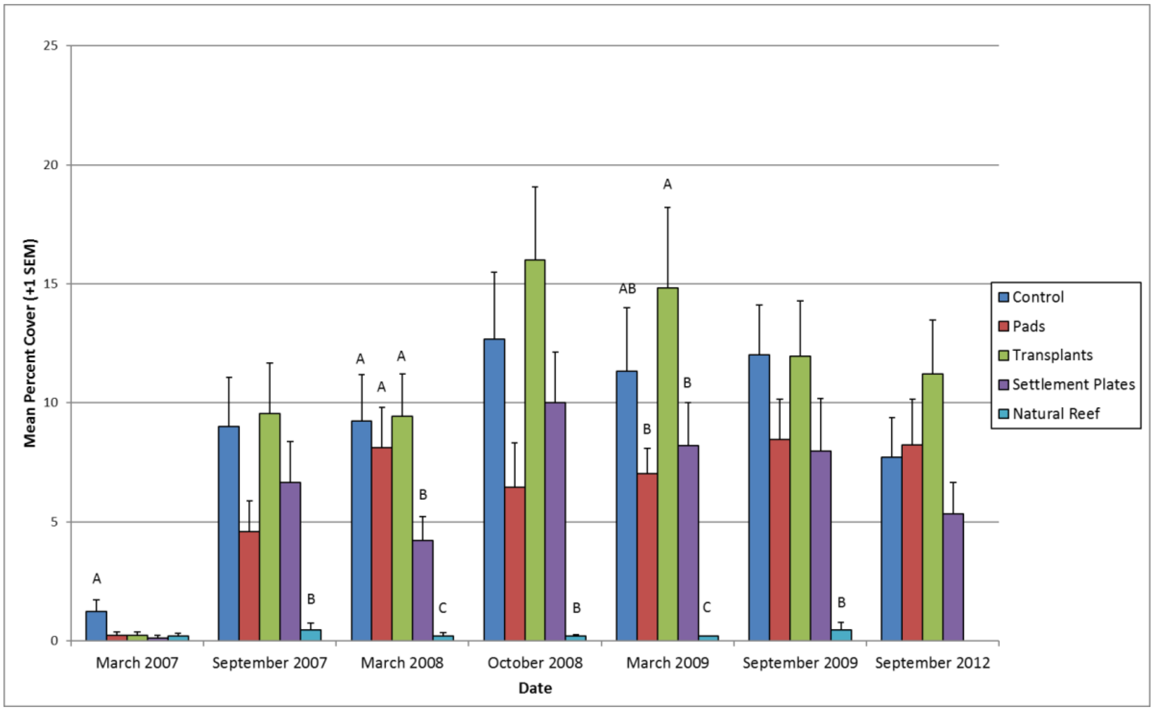


Figure 3.12 Percent coverage of all sponge species combined, with the contribution made by the most dominant species (*Desmapsamma anchorata*) excluded. Letters indicate significant differences between means and homogenous groupings within the same time period (SNK, p<0.05).

c) Coral Assemblage

Soft corals (gorgonians) grew on the exterior surfaces of the modules in every treatement. However, none were observed to have grown within the boundaries of the quadrat survey areas. On the natural reef, gorgonians were present in several quadrat images, but in every case they were individual colonies that were present when the quadrat areas were established at the beginning of the study. Quadrat areas on the natural reef were selected due to their relative absence of pre-existing benthic organisms and the abundance of space to be colonized (Connell et al., 2004). Given the negligible contribution that soft corals made to the overall benthic community within the quadrat areas on both natural and artificial substrates, no analysis was performed on this group. However, some individuals did grow substantially, were never seen to be overgrown or out-competed, and were prominent features on the modules supporting them at the end of the study (Figure 3.13).

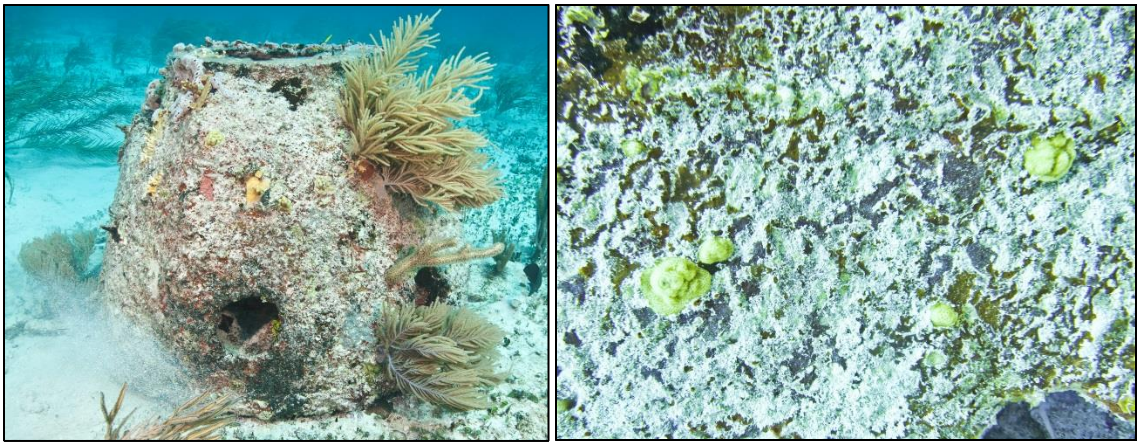


Figure 3.13 Multiple species of gorgonians (left) and Mustard Hill Coral (*Porites astreoides*) (right) growing on the modules.

Stony corals (scleractinians) recruited within the quadrat areas on both natural and artificial substrates (Figure 3.13, right), although they, like the tunicates, contributed a very small mean percentage each year (<3.0%) to overall benthic community composition (Figure 3.14). Coral recruitment on the substrate modules was very sparse and patchy, and coral recruits faced serious competition from macroalgae and sponges over the course of the study. However, there were some colonies that were successful and these had grown to considerable size by the end of the study, many approaching and some exceeding the average size of the coral colonies that had been transplanted (see Chapter 4, Table 4.5).

Very few of the coral recruits recorded during the last monitoring trip were the same individuals recorded during the first few monitoring trips; most were overgrown, but a few did persist through to the end.

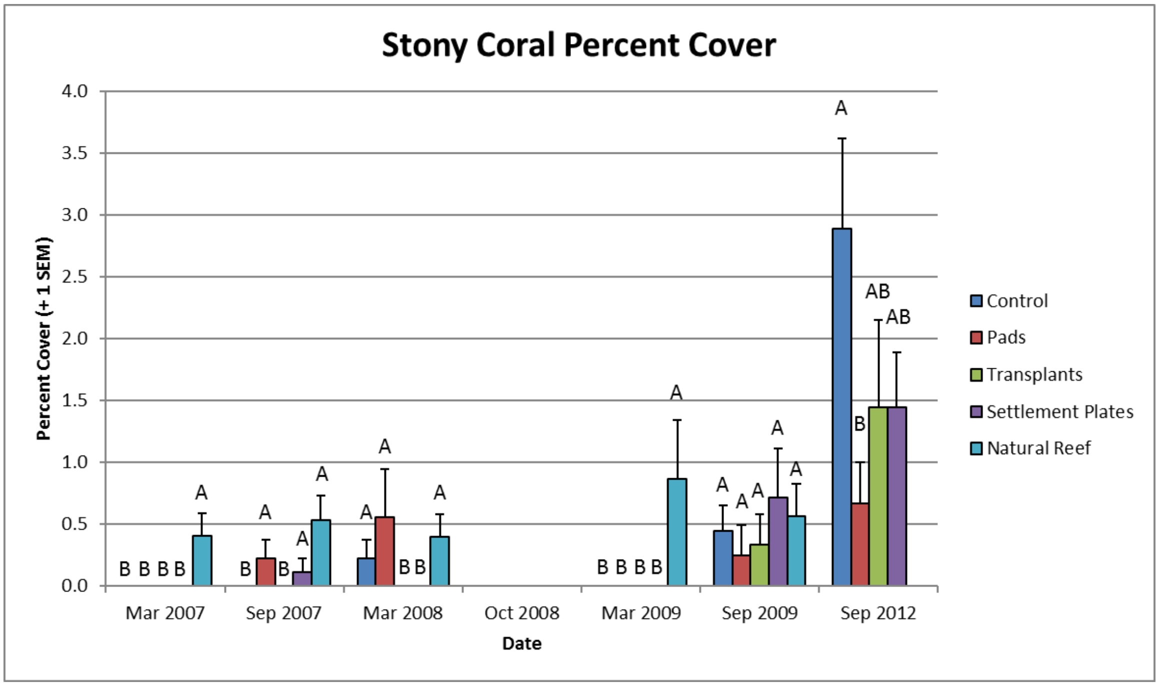


Figure 3.14 Percent coverage of stony coral species. These results are from the CPCe quadrat analysis only. No significant differences were found (ANOVA, p>0.05) until September 2012. Letters indicate significant differences and shared groupings (SNK, p<0.05).

It is noteworthy that a significant difference was found at the six year mark in the study (September 2012), with the percent cover of corals from the Controls being greater than the treatments. Interestingly, Clark and Edwards (1994) also had similar results in the Maldives, with "no treatment" being as effective in the long-term as coral transplantation. This could indicate that the other treatments, with their additional structural complexity, that has been shown to increase the percent cover of the most dominant and rapidly growing competitors, are less suitable in the long term for increasing the number of corals that recruit to the modules. Possibly, presenting a blank substrate may be more conducive to increasing coral cover than adding artificial substrates or transplants. However, this data should be taken in the context of the coral recruitment study outlined in Chapter 4 (Section 4.1.3) which examined the total number of recruits on the entire exterior surface of the modules, and also in consideration of the fact that the CPCe analysis utilized here is not necessarily the ideal method for obtaining accurate quantification of organisms that make up a very small percentage of the total (and thus are unlikely to be selected by the random point generating software) or are too small to be readily identified from the photographs. Further studies of a longer time duration and a methodology yielding a more accurate quatification and a larger sample size are required to examine the value of a blank substrate versus multiple treatments in coral recruitment restoration.

3.2 Infaunal and Epifaunal Invertebrate Community Composition on the Artificial Substrate Pads

Artificial substrate material of various forms has been used as a means of exploring enhancements on artificial reefs on a limited basis, primarily in freshwater applications where piers or other structures had various material added to enhance structural complexity and attract higher numbers of fishes (Barwick et al., 2004). In the marine environment, artificial substrates have primarily been used as a means of collecting or assessing epifaunal invertebrate communities (Edgar, 1991; Zimmerman and Martin, 2004), but seldom used as a specific means of enhancing the invertebrate community for potential positive spillover effects onto higher trophic level communities. While the artificial substrate pads utilized in this study ended up with considerable macroalgae and sessile invertebrate growth on their surfaces (Figure 3.15), this section focuses on the mobile epifaunal invertebrates that were collected within the interior of the bi-annually collected sacrificial pad sections.

3.2.1 Methodology and Data Analysis

Sacrificial artificial substrate pad samples were collected during routine monitoring trips every six months, from March 2007 to September 2009. Section 2.5.8 in the previous chapter outlined the procedure for collection and processing of invertebrates from the sacrificial artificial substrate pads and the analysis of their relative abundances and species assemblage that followed. Although pads were collected twice every year, for the purposes of this study a comparison of samples collected during the very first monitoring trip to those collected three years later at the end of the originally planned monitoring period is sufficient to describe the general trajectory of the mobile and sessile benthic invertebrate assemblage development and the most abundant taxa.

Figure 3.15 One of the 20cm x 15cm sacrificial sections of artificial substrate padding collected in October 2008. *Lobophora variegata* and several species of encrusting sponge were prominent features on the exterior of many substrate pads collected during the study.

3.2.2 Results and Discussion

The benthic invertebrate community living within the artificial substrate pads was mainly composed of members from three phyla: Annelida (primarily Class Polychaeta), Arthropoda (primarily subphylum Crustacea, order Amphipoda), and Echinodermata (primarily class Ophiuroidea). In samples from both 2007 and 2009, amphipods and polychaete worms dominated in abundance by several orders of magnitude (Table 3.1). In March 2007, the mean abundance of amphipods in pads samples outnumbered the polychaetes by a small margin (42.8% to 39.7%, respectively) (ANOVA, p=0.61), but by September 2009 the worms had significantly outpaced the amphipods (49.6% to 30.7%, respectively) (ANOVA, p=0.02). The total number of animals collected from the pads was also greater in the September 2009 sample. This seems a logical outcome given the relatively short period of time (6 months) that the pads had to acquire their species assemblages prior to the first sample being taken. Also, the amount of time that elapsed between the two sample dates allowed for the more dominant and successful members of the species assemblage to establish themselves and grow in both size and number. The majority of the polychaete worms collected in March 2007 were in the range of 10-20 mm in length, while several individuals from the September 2009 samples were >200 mm in length; some actually exceeding the length and width of the pads they were residing in.

Table 3.1 Artificial substrate pad sample invertebrate assemblage summaries for March 2007 and September 2009, ranked in decreasing order of mean abundance, with the percentage of the total for each taxonomic listing. N=9 for both samples.

March 2007			
Taxa	**Totals**	**Means (±SEM)**	**Percent**
Amphipods	1226	153.3 ±29.0	43.6
Polychaetes	1149	123.1 ±20.8	35.0
Pycnogonids	133	19.0 ±12.8	5.4
Crabs	106	11.8 ±3.5	3.4
Isopods	82	10.3 ±1.7	2.9
Snapping Shrimp	52	6.5 ±1.4	1.9
Ostracods	48	6.0 ±1.5	1.7
Hermit Crabs	15	3.0 ±0.7	0.8
Other shrimp	15	2.5 ±0.7	0.7
Starfish	8	2.0 ±0.5	0.6
Gastropods	6	1.5 ±0.2	0.4
Bivalves	6	1.2 ±0.2	0.4
Brittle Stars	4	2.0 ±0.3	0.4
Urchins	3	1.5 ±0.3	0.4
Nudibranchs	3	1.5 ±0.2	0.3
Flatworms	3	1.0 ±0.0	0.3
Chitons	2	1.0 ±0.0	0.3
Holothurians	1	1.0 ±0.0	0.3
Lobsters	1	1.0 ±0.0	0.3
Cumaceans	1	1.0 ±0.0	0.3
Unknown	1	1.0 ±0.0	0.3
Limpets	none	none	none
TOTAL Animals	2865		

September 2009			
Taxa	**Totals**	**Means (±SEM)**	**Percent**
Polychaetes	1943	215.9 ±22.3	49.6
Amphipods	1202	133.6 ±25.7	30.7
Brittle Stars	546	60.7 ±11.2	13.9
Crabs	65	7.2 ±2.7	1.7
Snapping Shrimp	62	6.9 ±1.5	1.6
Isopods	35	5.8 ±1.1	0.9
Cumaceans	16	4.0 ±0.0	0.4
Chitons	10	2.7 ±1.0	0.3
Limpets	8	2.5 ±0.6	0.2
Other Shrimp	6	2.5 ±0.7	0.2
Bivalves	5	2.3 ±0.3	0.1
Nudibranchs	4	2.0 ±0.6	0.1
Ostracods	4	1.5 ±0.2	0.1
Pycnogonids	3	1.5 ±0.2	0.1
Flatworms	3	1.0 ±0.0	0.1
Gastropods	2	1.0 ±0.0	0.1
Urchins	2	1.0 ±0.0	0.1
Hermit Crabs	1	1.0 ±0.0	0.0
Unknown	1	1.0 ±0.0	0.0
Starfish	0	none	n/a
Holothurians	0	none	n/a
Lobsters	0	none	n/a
TOTAL Animals	3918		

Interestingly, pycnogonids (sea spiders) were the third most abundant animal in the March 2007 samples (4.6%) but were only present in negligible amounts in September 2009 (0.1%). This suggests that conditions on the pads earlier in the study were more conducive to their survival, although whether this decline is a function of micro-habitat features and resources changing over time, new predators keeping their population in check, or competition from other members of the benthic invertebrate community is not clear. Decapod crabs were the fourth most abundant animal in the pads samples for both years, and their numbers also declined somewhat over time (3.70% to 1.66%), although not as dramatically as the pycnogonids. Large isopods and *Alpheus* sp. snapping shrimp ranked 5th and 6th with similar abundances in March 2007 (2.8% and 1.8%, respectively), and they remained at similar levels but switched rankings, with snapping shrimp becoming slightly more abundant than the isopods in September 2009 (1.6% and 0.9%, respectively). With the exception of ostracods in March 2007 (1.7%), all other crustaceans (cumaceans, caridean shrimp, hermit crabs and juvenile lobsters) were present in abundances <0.1% for each sample. This group of assorted crustaceans also decreased in abundance over time, with fewer numbers of each taxa present in the September 2007 samples. It is important to note that even though the more highly developed crustaceans were fewer in number compared to polychaete worms and amphipods, they made a similar if not greater contribution to the overall biomass harvested from each pad sample due to their greater size and mass.

One of the most notable population increases is that of the ophiuroids (brittle starfish), especially in relation to the trajectory of all other echinoderms that decreased from the beginning to the end of the study. Brittle stars went from six individuals at 0.2% percent of the total in March 2007 up to 546 individuals at 13.9% of the total and a 3rd place ranking in September 2009. They also contributed a significant portion to the overall amount of invertebrate biomass harvested from the pads for the latter samples. Over time the pads collected quite a bit of loose sediment and detritus, which was, for many samples, more coarsely packed into the interstitial spaces of the pads collected during the September 2009 trip. The space between and underneath the pad sections apparently provides a favorable habitat for the primarily detritus-consuming brittle stars, as the trapped sediment and detritus further enhances these microhabitats.

Mollusks (gastropods and bivalves) and flatworms (platyhelminths) were both present in similar numbers in each sample, although none exceeded 0.5% in either year. In March 2007 this group was loosely distributed throughout the bottom of the list, with the rankings of 12, 14, 15, 17, and 18 out of 22 taxa in total. In the September 2009 samples their rankings all changed, with none of the taxa except gastropods and flatworms ranking below 10th place (Table 1).

It was initially hypothesized that the invertebrate community that developed on and within the artificial substrate pads might provide additional food resources for some members of the coral reef fish assemblages that reside on or near the substrate modules. The reef fish assemblage that developed on the modules primarily consisted of benthic carnivores (similar to natural reefs) (see Chapter 5, Figure 65), so it is possible that there could be some degree of benthic invertebrate/reef fish diet interaction in play that has an effect on the relative abundance of each. For example, small crustaceans and worms are a primary food source for some of the most abundant reef fishes, such as grunts, wrasses, and some damselfishes; all of which were well represented in surveys of fish abundance on substrate modules with the Pads treatment. However, it is also possible that even though the pads support an invertebrate assemblage that includes several dietary items for many of the most highly abundant reef fishes, that potential food resource may be largely inaccessible to the reef fish community. This is due to many of the invertebrates' tendencies to burrow into the interior recesses of the pads and only venture out from sheltered locations to feed under the protection of darkness, if ever at all. These burrowing tendencies are of course the same on natural reefs as they are on the artificial reefs; however, the interwoven fibers of the padding material are far more rigid (and therefore may provide more security for invertebrates) than refuges on the natural reef.

Most of the invertebrate biomass on the pads can be attributed to species that lived either within the interior of the dense pad material or underneath the pads; essentially occupying the space that exists between the inner surface of the pads and the underlying exterior concrete surface of the substrate module. Presumably it would be difficult for any species of reef fish, living in the vicinity of the pads, to capitalize on the invertebrates residing in or under the pad material as a food resource to gain a competitive advantage. The enhanced exterior structural complexity and refuge space provided by sedentary invertebrates, such as sponges and large macroalgal species, may also play a part in the abundance and accessibility of potential prey items that reside on and within the pads.

Many of the pads were packed almost completely with unconsolidated sediments (sand) and detritus, which in turn may have enabled or facilitated the growth of macroalgae and sponges that were present on the exterior surfaces of almost all of the padding material. This sediment packing may have helped the exterior surfaces of the substrate modules with the Pads treatment to achieve a more diverse and dense assemblage of macroalgae and benthic invertebrates, but also one that was not necessarily "reef-associated". For example, there was a greater percentage of species from the Halimedaceae family of macroalgae on the substrate pads-treated modules (Appendix 1). With the exception of some *Halimeda* sp., these species, including *Avrainvillea* sp., *Penicillus* sp., *Rhipocephalus* sp., and *Udotea* sp., are representative of macroalgal assemblages found on muddy or sandy habitats, or sand-covered hardbottom and coral rubble, as opposed to those that would be found on true coral reef habitats. These species have evolved to live in loose, unconsolidated sediments, and have holdfasts that consists of densely packed rhizoids that intertwine with sand grains and rubble that allows them to remain firmly anchored (Littler et al., 1989).

3.3 Conclusions

Substrate colonization can be highly variable on seemingly identical replicate artificial reefs, both between localities and within a single locality. This may be caused by multiple factors, such as temporal fluctuations in availability of settlers, subtle differences in deployment location due to microenvironmental gradients, and interactions with pre-existing biota on surrounding natural substrates (Schoener, 1982; Shulman, 1985; Doherty and Williams, 1988; Anderson et al., 1989) or simple stochastic variation. This study once again confirms the inherent unpredictability surrounding development of benthic communities on artificial substrates, and highlights the importance of pilot studies prior to large scale implementation of new techniques. Without a full assessment of the deployment location and the processes affecting benthic community development there, predicting or guiding the outcome of any intervention or restoration action intended to create positive results is highly questionable.

Space utilization between competing taxa was most exemplified by development of and interaction between a handful of key contributors. As benthic communities matured on the modules, macroalgae decreased on all treatments, finally stabilizing at roughly 10% (6-13%) and generally equivalent with observations on the natural reef. Following the ubiquitous turf algae, the first of the major players to arrive was the macroalgae *Lobophora variegata*, which grew rapidly and colonized a sizeable portion of the available space (12-27%) in a fairly short period of time and remained above 10-15% coverage until the last data collection period (Figure 3.5). Coverage peaked in March 2007, remained fairly high for another year, but then declined gradually throughout the remainder of the study on all of the modules. This species was altogether absent on the natural reef, whereas *Dictyota* sp. was seen almost exclusively on the natural reef (Figure 3.7) and made up the majority of the overall macroalgal contribution there. There was consistently less *Lobophora* present on the Coral Transplant treatment modules, whereas significantly more was present on the Pads treatment during the initial growth outbreak (September 2007), which was then closely matched or exceeded by the Settlement Plate treatment every data collection point following.

In support of the previously mentioned supposition that the sponge out-competed the macroalgae, consider the progression of *Desmapsamma anchorata*, which made the largest contribution to the total percent coverage of all sponges (Figure 3.12**)**. This particular species is characterized by rapidly growing encrusting or tentacle-like growth forms and a tendency to overgrow other organisms; mainly other sponges and gorgonians. It is also quite delicate and relies heavily upon the physical structure of the organisms it encrusts for support. The lack of robust internal architecture allows this species to invest heavily in tissue production; hence the rapid growth rates. However, this is offset by high susceptibility to fragmentation (especially on rigid structures) and a high rate of mortality, which tends to make its prevalence and influence among the benthic community fairly ephemeral (Wulff, 2012; Biggs, 2013). Concordantly, *D. anchorata* was not observed in any of the natural reef quadrats. It was observed, but not quantified, elsewhere on the natural reef transect site and on gorgonians and small coral heads in the vicinity of the substrate module deployment field, but only in very small amounts.

Although *D. anchorata* seemed to be present on natural substrates within the study area at levels that are comparable to reports from the literature (Wulff, 2005; Biggs, 2013), its presence on the substrate modules was not ephemeral. Percent coverage by this species increased steadily following its first appearance, and was still a significant component of the overall benthic invertebrate assemblage at the end of the study. It seemed to grow most readily on modules with the Pads treatment, followed by the Settlement Plates and Coral Transplants treatments. All three of these treatments provided additional external structure, as compared to the Controls, which could vertical growth of the sponge and facilitate its spread on the modules.

Although the Pads treatment had the greatest percent coverage of *D. anchorata*, the effects of this sponge and its overgrowing and smothering tendency was perhaps greatest on the Coral Transplant treatment (Figure 3.16). During the course of the study, this sponge was directly responsible for ≥75% of coral transplant mortality (≥45 out of 60 colonies) on the modules (See Chapter 4, Section 4.2.3). It also affected the three coral transplant species equally, showing no obvious tendency to overgrow one species better than it did on another (Figure 3.16).

Figure 3.16. *Desmapsamma anchorata* in the process of overgrowing Mustard Hill Coral (*Porites astreoides*) (left) and Boulder Star Coral (*Orbicella annularis*) (right) transplants. [Photos taken in September 2009]

Based on the results of this study, careful timing regarding the placement of limited and valuable restoration resources, such as coral transplants, is highly recommended. The fact that coral transplants were killed in significant numbers on every single substrate module onto which they were applied suggests that this was not a chance occurrence nor treatment-specific. Given the majority loss of coral transplants was from overgrowth by *D. anchorata*, and the relatively small contribution this species makes to percent coverage on surrounding natural reef habitats, greater success and higher rates of transplant survival may be realized once the initial wave of rapid and extensive growth of highly competitive, colonizing species such as this have peaked and something more akin to an equilibrium state is achieved. Such an approach might reduce significant losses in future restoration efforts using transplanted corals.

Chapter 4 – Study 2: Coral Assemblage – Recruitment, Growth, Survival, and Transplants

4.0 Coral Population Dynamics

Coral reefs and associated habitats are broadly characterized by a diverse assemblage of benthic flora and fauna that mainly includes: macroalgae, seagrasses, stony corals, gorgonians, sponges, and other colonial invertebrates. Competition for space and resources between colonizing organisms is one of the primary driving factors that determine the relative abundance of each species in a benthic assemblage at any given time. Even on a healthy coral reef, a functional state of equilibrium may seldom, if ever, truly exist amongst members of the benthic community. Constant fluctuations on some scale in abundance and dominance of key species is the norm as biotic and abiotic factors change between seasons or in response to disturbance. Nevertheless, patterns of colonization and competition for space and resources that drive benthic community trends following disturbance or onto newly available or otherwise uncolonized substrates can be studied to address specific research questions by manipulating select variables.

Artificial reefs make ideal experimental platforms for experimental research. Newly deployed artificial reefs undergo a period of initial bacterial and algal biofilm "seeding" which in turn promotes settlement of successive colonizing species (Hadfield, 2010). Following biofilm formation, various forms of macroalgae, turf algae, sponges, bryozoans, and encrusting tunicates begin to appear. One important early settler, particularly for corals, is crustose coralline algae (CCA), which deposits a thin layer of calcareous material as it grows. The chemical signatures of many commonly occurring CCA species are important settlement cues for the planulae larvae of most coral species (Heyward and Negri, 1999; Ritson-Williams et al., 2014; Tebben et al., 2015). In the months immediately following artificial reef deployment, pioneering colonizing organisms are limited only by rate of substrate conditioning and the availability of recruits from either the plankton and/or nearby coral reef habitats and their ability to exploit the resource-limited substrate. Growth may be rapid, as is the case for many species of macroaglae (turf algae, *Lobophora*, *Dictyota*, etc.) and non-coral invertebrates (*Desmapsamma anchorata*), or slow, as is the case for stony corals. Growth and competitive interactions between macroalgae and non-coral invertebrates were previously discussed in Chapter 3.

Coral reefs in the greater Caribbean are typically characterized by relatively low rates of natural stony coral recruitment as compared to the Indo-Pacific and Red Sea (Richmond and Hunter, 1990). Lower rates of recruitment in the Caribbean are due to a variety of interlinked long-standing geographical differences compounded by an increasing number of anthropogenic factors that are negatively affecting coral populations across the entire basin. Coral cover across the region is in decline (Gardener et al., 2003; Green et al., 2008), which results in decreased reproductive output for most key reef-building species. Many Caribbean coral reef ecosystems have slowly but steadily shifted towards macroalgal dominated habitats as a result of the combined effects of: nutrient loading, eutrophication, sedimentation, basin-wide die-off of *Diadema antillarum* (long-spined sea urchin), and overharvesting of parrotfish and other grazing species (Hughes, 1994; Hughes and Tanner, 2000). Out of those that remain, many of their most abundant coral species are relatively fast growing and resilient or “weedy” genera, such as *Agaricia*, *Porites* and some *Siderastrea*, which reproduce gonochoristically by ‘brooding' their larvae internally before releasing them into the surrounding environment (Szmant, 1986; Soong, 1991; Carlon, 1999).

Previous research (Clark and Edwards, 1994; Clark and Edwards, 1995; Fearon and Cameron, 1997; Edwards and Clark, 1999; Vermiji, 2005; Gleason et al., 2009; Ferse et al., 2013) has suggested that there may be a link between the presence of a population of healthy adult coral colonies (and, potentially, coral transplants) and the rate of natural coral recruitment and ecosystem recovery onto nearby barren or otherwise uncolonized surfaces (i.e., physically damaged or degraded habitats, artificial reefs). Chemical cues indicating maturity, quality, and health of reef habitat and suitable settlement substrates are strongly linked to this process (Heyward and Negri, 1999; Puyana, 2009; Dixson et al., 2014). However, evidence supporting the use of coral transplants specifically as a means of increasing coral recruitment onto nearby uncolonized substrates remains sparsely supported by the literature. In a field study Clark and Edwards (1995) reported no significant difference in natural coral recruitment onto artificial reefs with coral transplants. Other studies have shown that the influence of coral transplants on coral recruitment may not always be in a positive direction. A field study by Polachek and Stimson (1994) showed that the survival of small colonies of *Pocillopora meandrina* is reduced when they settle within close proximity or immediately adjacent to a previously established large live colony, and a laboratory study by Fearon and Cameron (1996) showed that the presence of extracts derived from *Goniopora tenuidens* inhibited both larval metahorphosis and post-metamorphic growth of *Pocillopora damicornis*.

The potential for a positive influence of coral transplants on recruitment is expected to apply more specifically to species that employ a brooding reproductive strategy, which may be the predominant mode of reproduction in Caribbean corals (Richmond and Hunter, 1990). Brooders are also considered to be more successful recruiters in the Caribbean, whereas Broadcast spawners are more successful in the Pacific (Szmant-Froelich, 1985; Szmant, 1991). Other studies from Quintana Roo have characterized inshore coral communities as consisting primarily of small, sediment tolerant brooding species (Rodriguez-Martinez et al., 2011). Brooding species produce larvae that are relatively smaller in number, but larger in size, as compared to broadcast spawners with higher fecundity. Brooders are also typically characterized by higher frequency of reproduction. Richmond and Hunter (1990) suggested that the chance of absorbing the negative effects of a single disturbance or catastrophic ecological event on the reproductive success of a species, at both the individual and population level, may be maximized by those species that employ a multiple spawning strategy (same colony spawning multiple times a year). In fact, the larvae of some species, including *Porites astreoides*, have been shown to exhibit various physiological differences that vary temporally (Edmunds et al., 2001), suggesting that larval fitness in this genus, and perhaps others, may vary depending by release date. If this is indeed the case, it implies that the mortality-impacted population structure of the adults may, in turn, be partially regulated by season in which they were spawned and spawning at multiple times during a season could increase the chances of providing healthy recruits.

Spawning of corals is dependent upon a combination of temporal cues, such as temperature, photoperiod, and nocturnal illumination, with temperature providing the seasonal cue and lunar phase providing the most crucial spawning cue (Richmond and Hunter, 1990). For many Caribbean corals, spawning occurs approximately one week after the full moon in August or September. In this study 3 species of hard corals were transplanted. Two out of the three species selected for transplanting were brooding species (*Porites astreoides* and *Agaricia agaricites*) and the third was a broadcast spawner (*Orbicella annularis*). *Agaricia agaricites* is a spring-time spawner (Duerden, 1902; Van Moorsel, 1983), *Porites astreoides* is primarily a May-June spawner (but may also spawn as early as January and as late as September), and *Orbicella annularis* is an August-September spawner (Vaughn, 1910; Szmant-Froelich, 1984; Szmant, 1986).

The artificial reefs utilized in this project provided ample surface area to examine rates of colonization and survival of stony coral recruits. To assess rates of coral recruitment and survival two methods were utilized: coral recruit surveys and settlement plates. The data collected from both method*s was used in tandem to determine whether the observed rates of coral recruitment were the result of low levels of larval supply or high post-settlement mortality (see section 4.1.1 below). Comparison of coral recruitment on the modules enabled testing of the hypothesis that the addition of coral transplants to restoration structure would affect rates of coral recruitment onto the artificial substrate.

4.1 Coral Recruitment

4.1.1 Methodology

A unique recruit location and tracking technique utilized a range and bearing system, allowing for repeated long-term monitoring of individual coral recruits for assessment of recruitment density, growth, and survival (see Ch.2, Figure 2.3A). The total number of coral recruits was evaluated on seven occasions for each module. Settlement plates were collected from both the natural reef and the modules on two separate occasions following expected mass coral spawning events. In November 2007, several months following the predicted coral spawning events of August and September, half of the settlement plates were collected. In October 2008, again following the anticipated spawning events of the late summer, the remaining settlement plates were collected. Settlement plates have long been used for assessing rates of coral recruitment and early survival (Harriott and Fisk, 1987, 1988; Mundy, 2000). Coral colonies found on the modules and on the settlement plates were identified to the lowest possible taxon and counted.

The Akumal study site was heavily damaged by the storm surge and strong currents that swept the area during Hurricane Dean in August 2007. After the storm passed, it was discovered that the study site had suffered extensive damage to both the modules and the natural reef transect site. Almost all of the settlement plates on the modules had been detached or destroyed by the scouring action of the storm (26 missing out of the 36 deployed), as well as one of the plates mounted to the natural reef. From that point onward, quadrat surveys and photos on the natural reef were abandoned, although coral recruit surveys on the remaining modules did continue. The remaining settlement plates were also collected on the same sampling schedule as the plates at the Puerto Morelos study site.

4.1.2 Data Analysis

Data on coral recruitment was obtained from coral recruit surveys and settlement plates. The number of recruits per module was tallied and summarized to create a record of species identifications, total abundance, sizes, and location coordinates for every coral recruit encountered. This allowed for calculation of density (recruits/m^2) by collection date, season, and experimental treatment. Statistical comparisons of means of log(x+1) transformed data were done utilizing ANOVA (SNK), with $p<0.05$ chosen as the threshold for significance. Density data were also collected with the aid of the standardized settlement plates. Size measurements for each colony collected during coral recruit surveys were analyzed to allow for an assessment of growth rates of the coral recruits. CPCe software (Kohler and Gill, 2006) was used for coral transplant growth analysis to calculate changes in surface area of coral transplants and natural reference reef corals between each monitoring trip.

4.1.3 Results and Discussion

a) Coral Recruitment

i) Abundance and Density

During the course of the study, a combined total of 3,683 coral recruits were recorded on the modules; 3521 in Puerto Morelos and 162 in Akumal (Table 4.1). The unstandardized abundance and standardized density of corals per individual module by date are listed in Appendices 4.1 and 4.2. During the first monitoring trip in March 2007, which was just under six months following module deployment, no coral recruits were found. Consequently, the number of corals recorded during the following trip in September 2007 represents only newly recorded corals. From March 2008 through September 2009, each trip total includes every coral that was present during each survey, and is the product of adding the number of new corals that recruited since the previous monitoring trip and those that were confirmed as survivors from the previous trip(s) utilizing the range-and-bearing tracking system. For the September 2012 monitoring trip, due to weather conditions limiting the field work, no effort was made to use the range-and-bearing system to determine which specific coral recruits were survivors that had been previously mapped in September 2009. Corals that had settled during that three-year period were distinguished from older recruits in the analysis based on their size and an estimation of how large they might have reasonably grown during that time.

When considering these totals by date, it is necessary to take into account some of the colonies were counted previously, and thus the totals are composed both of new recruits and previously recorded corals. They are presented here solely as a way of conveying the total number of recruits that were recorded for each date. Out of the 3,521 coral recruits counted in total in Puerto Morelos, >1,900 of those recorded are categorized as new recruits that were recorded for the first time (53.9%), and >1,600 as having been recorded on one or more occasion previously (45.4%). The remaining 0.5% were uncategorized. The proportion of old to new recruits was similar in Akumal. Out of 162 counted there, 83 were estimated to fall into the new recruit category (51%), and the remaining 79 as survivors from previous trips (49%).

Out of the total number of new recruits counted on the modules in Puerto Morelos during the first three years of the study (excluding those that survived from previous monitoring trips), the vast majority were identified as *Porites astreoides* (94.7%), followed by *Agaricia* spp. (1.9%), unknown/unidentified (1.5%), *Siderastrea* spp. (0.8%), *Dichocoenia stokesi* (0.4%), *Manicinia areolata* (0.3%), *Diploria* spp. (0.2%), *Orbicella* spp. (0.2%), and *Porites porites* (0.04%) (Table 4.1). Coral recruitment data from September 2012, six years into the study, revealed a slight increase in the diversity of corals recruiting to the modules. Out of the eight species recorded during that trip, considering only new recruits, *P. astreoides* was still the most numerous but the percentage had decreased to 80.2%, down from the +93% of each previous monitoring trip. Over the six- year timespan, *Siderastrea* sp. increased considerably (7.8%), *Agaricia* spp. remained low (2.4%), *Diploria* spp. and *Orbicella* spp. increased slightly but remained low (3.6% and 1.4%, respectively), and *Dichocoenia* and *Meandrina* remained low (0.6% and 0.2%, respectively). No new recruits of *P. porites* or *M. areolata* were found in September 2012 (Table 4.1).

Table 4.1 The total number of corals present in Puerto Morelos and Akumal by species, with all treatments combined for each monitoring period. Puerto Morelos (N=40 all years); Akumal (N=8, except for Oct. 2008 N=5).

Puerto Morelos Species	**Mar07**	**Sep07**	**Mar08**	**Oct08**	**Mar09**	**Sep09**	**Sep12**
Agaricia spp.	-	-	8	12	16	15	37
Diploria spp.	-	-	3	-	-	2	37
Dichocoenia stokesi	-	-	-	3	3	4	6
Manicinia areolata	-	-	-	2	2	4	-
Meandrina meandrites	-	-	-	-	-	-	2
Orbicella complex	-	-	1	1	1	1	13
Porites astreoides	-	506	422	562	409	622	690
Porites porites	-	-	-	-	-	1	7
Siderastrea spp.	-	-	-	6	3	12	67
Unknown	-	12	6	14	5	3	1
Totals 3,521	0	518	440	600	439	664	860

Akumal Species	**Mar07**	**Sep07**	**Mar08**	**Oct08**	**Mar09**	**Sep09**	**Sep12**
Agaricia spp.	-	-	3	5	5	9	-
Diploria spp.	-	-	-	-	1	4	-
Dichocoenia stokesi	-	-	-	-	-	1	-
Meandrina meandrites	-	-	1	-	-	1	-
Porites astreoides	-	-	19	13	18	40	-
Porites porites	-	-	-	-	-	1	-
Siderastrea spp.	-	-	-	-	-	4	-
Stylaster spp.	-	-	-	-	2	1	-
unknown	-	-	4	2	1	27	-
Totals 162	0	0	27	20	27	88	-

In Akumal, *Porites astreoides* comprised 43-52% of the total number of new recruits, but decreased steadily from October 2008 to September 2009 as more species gained a foothold. *Diploria* sp. increased from none in the beginning to 2% and 4% for the last two collection periods, and *Agaricia* sp. was variable, ranging from 8-20% over time and contributed more to the assemblage in Akumal than in Puerto Morelos. Contributions by additional species were mostly negligible and sometimes consisted of only a single occurrence, but did include: *Meandrina meandrites*, *Porites porites*, *Siderastrea* sp., and *Stylaster* sp., as well as a large cohort of recruits that could not be positively identified in September 2009 (29%).

For almost every treatment, recruitment in Puerto Morelos went down between the Fall and Spring months and increased from Spring to Fall (Table 4.2), although the Pads treatment displayed a slight departure from this pattern during the first three years of the study. The average number of coral recruits on each individual module, with all treatments combined, ranged from 12.9 (±1.5 SEM) to 21.4 (±2.6 SEM) colonies per module over the course of the six-year study period (not including March 2007), and generally increased over time with the exception of the intra-annual seasonal oscillations. In comparison, another study utilizing Reefball^{TM} modules in Indonesia reported highly variable coral recruitment onto the exterior surfaces after three years, ranging from 1-76 colonies per module (Bachtiar and Prayoga, 2010).

There were no experimental treatments in Akumal; all were considered Controls following the impacts from Hurricane Dean in August 2007. Recruit density was lower in Akumal than in Puerto Morelos. Mean recruit density remained fairly low but comparable from March 2008 through March 2009, with 1.2±0.5, 1.5±0.5, and 1.3±0.5 recruits/m^2 (±SEM), respectively, but had tripled by September 2009 (4.3±1.2 SEM). Akumal was not surveyed in September 2012.

Table 4.2 Mean density of coral recruits/m^2 (±SEM) from Puerto Morelos, standardized.

Treatment	Sep 2007	Mar 2008	Oct 2008	Mar 2009	Sep 2009	Sep 2012
Control	15.7 ±2.2	14.9 ±3.6	19.9 ±4.5	10.8 ±1.9	24.9 ±4.5	30.3 ±6.1
Pads	7.7 ±1.0	7.9 ±1.8	9.0 ±1.6	8.0 ±1.7	7.2 ±1.6	10.6 ±2.5
Coral Transplants	16.0 ±4.9	11.6 ±3.4	20.3 ±5.0	12.4 ±2.5	20.8 ±3.6	23.4 ±5.3
Settlement Plates	12.3 ±1.9	10.4 ±2.3	11.4 ±1.6	11.7 ±2.4	18.8 ±3.6	21.3 ±4.6

When the data is standardized for area and all treatments are combined and broken down by monitoring trip, there was still a general pattern of increasing recruit density over time, especially for the last two data collections, as well as the seasonal fluctuation with significantly higher densities in the summer/fall months (ANOVA, p=0.00142) (Figure

4.1). The lack of corals from the first monitoring trip (March 2007) is the result of three factors: 1) once an artificial reef is placed in the marine environment, it takes an initial period of conditioning before its surfaces are conducive to settlement of corals, 2) newly settled corals will not be readily visible until they reach a size of 2-3 mm in diameter, and 3) it is likely there were a small number of newly settled coral recruits present in March 2007, but they were still too small to be detected by the survey divers.

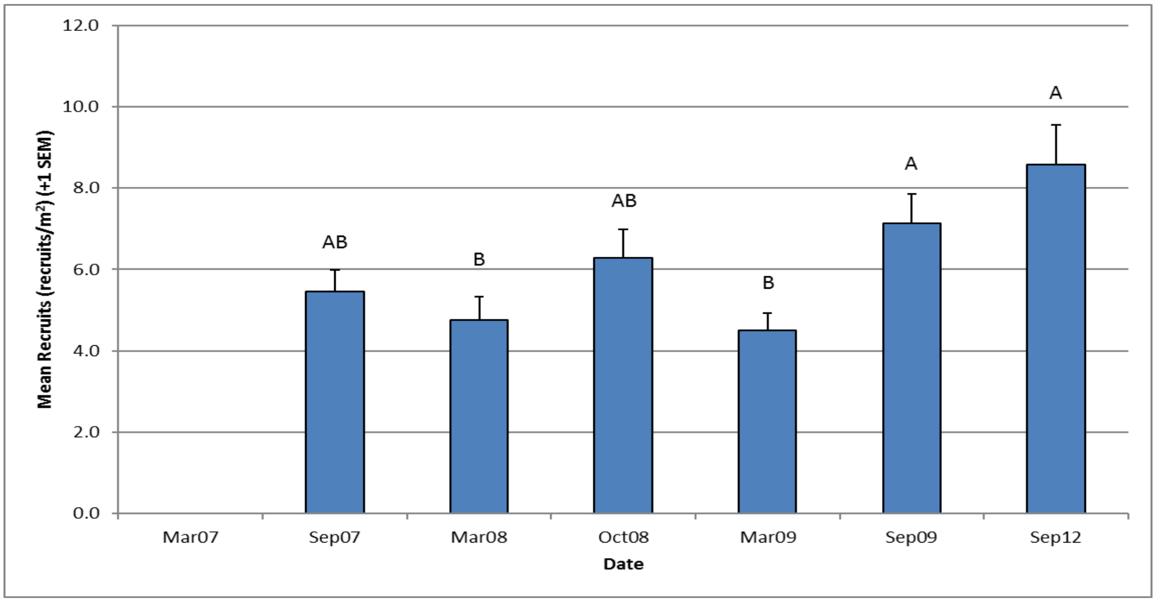


Figure 4.1 Mean coral recruit density on the modules, standardized for area, with all treatments combined for each data collection period. Different letters indicate significant differences between means and homogenous groupings (SNK, <0.05).

When the total number of recruits was standardized by surface area and broken down by experimental treatment (Figure 4.2 and Appendix 4.3), there were no significant differences found between treatments during five out of the six monitoring periods. A general increase in abundance through time is shared by all treatments, with the Controls, Coral Transplants, and Settlement Plates treatments increasing the most and the Pads treatment the least. During the September 2009 surveys, three years post-deployment, there were significantly fewer recruits on the Pads treatment and more on the Control and Coral Transplant treatments (ANOVA, p=.031); Settlement Plates fell in-between but were most similar to the Coral Transplants treatment. Seasonal oscillation was also apparent for almost all treatments, but was most apparent in the Controls and Coral Transplant treatment and more subtle in the Pads and Settlement Plate treatments.

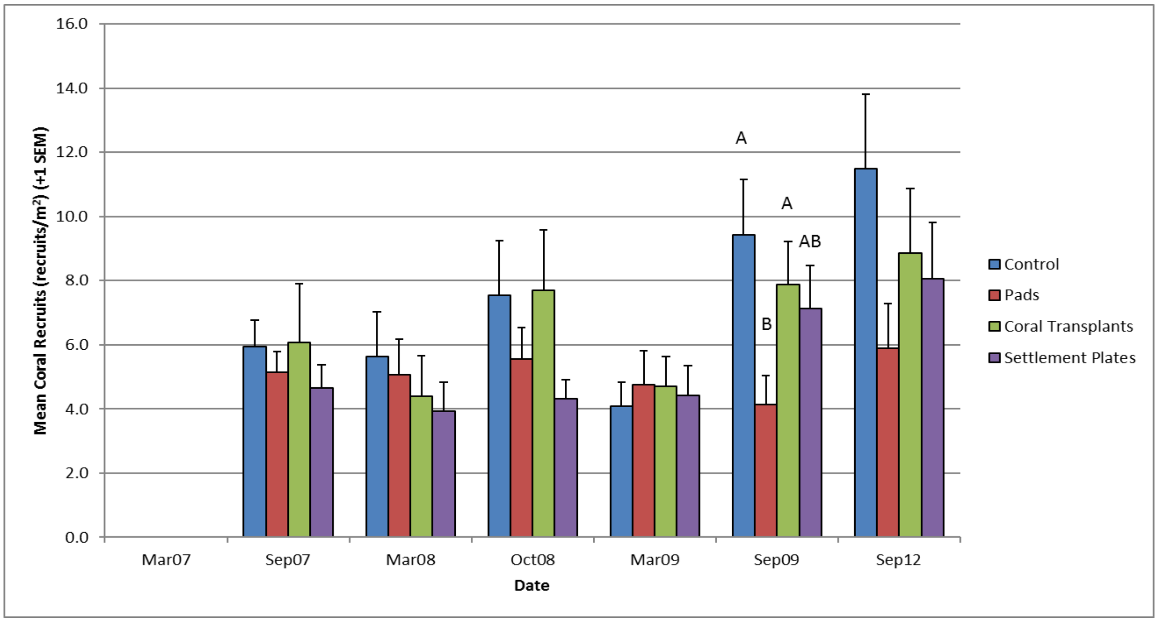


Figure 4.2 Mean coral recruit density, standardized for area, by treatment. Different letters indicate significant differences between means within groups (ANOVA, SNK, $p<0.05$).

An alternate way of examining this data is to look only at the number of new recruits that were recorded during each monitoring trip. The unstandardized and standardized total numbers of new recruits on each module by date are listed in Appendices 4.4 and 4.5. On average, the total number of recruits recorded during each monitoring trip consisted of 44% old recruits and 56% new recruits in Puerto Morelos. However, when this is examined by date there are some noteworthy differences. Early in the study, the percentage of new recruits was higher; for March and October 2008, there were 35% and 33% old recruits, and 65% and 67% new recruits, respectively. In March 2009 that pattern was reversed, with 66% old and 34% new. From there the pattern started gradually returning to what was observed during the earlier part of the study, with 47% old and 53% new in September 2009, and 37% old and 63% new three years later in September 2012. This indicates that during the middle portion of the study there was something influencing either the availability of coral recruits and/or their survival on the module surfaces. This pattern was generally similar among all treatments, however, rebounding percentages of new recruits following the March 2009 trough were most notable on the Control treatment and least notable on the Pads.

When the figure for standardized mean coral recruit density was re-created using only the new recruits (Figure 4.3), the relationships changed somewhat. With all treatments combined, the general trend of increasing density through time is absent. However, the seasonality effect is still obvious with summer/fall dates having significantly greater recruit density than the winter/spring (ANOVA, $p<0.00001$). These results suggest there is either a fair amount of inter-annual variation in the supply of coral recruits, or that the number of new recruits counted was affected by post-settlement processes. A combination of the two is almost certainly responsible for the observed results. It appears that the interval between October 2008 and September 2009 was a particularly unfavorable period for coral recruitment, or a particularly good period for competing members of the benthic community.

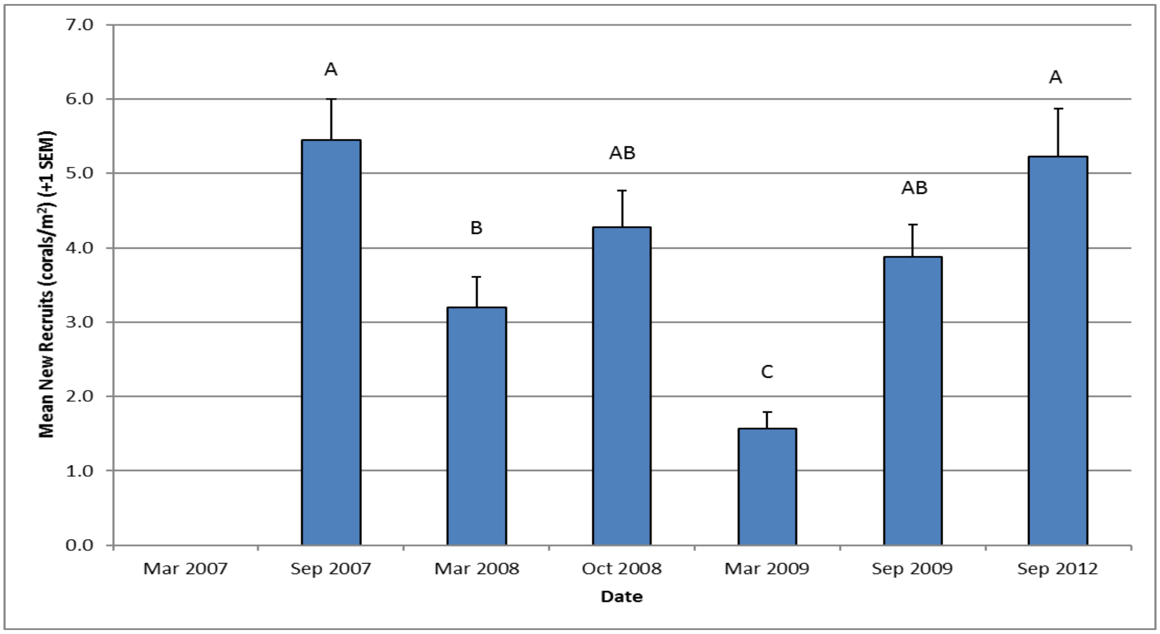


Figure 4.3 Mean new recruit density in Puerto Morelos with all treatments combined, standardized for area. Different letters indicate significant differences between means and homogenous groupings (SNK, $p<0.05$).

When the density of new recruits is examined by treatment (Figure 4.4), once again all treatments were largely similar to one another with no significant differences detected except for September 2009 (ANOVA, $p=0.047$), which displayed the same pattern seen in the data for total coral recruits (Figure 4.2). In October 2008, the Coral Transplants treatment had the greatest number of coral recruits, and in September 2012 the Pads treatment had the least, but in both cases the differences were not significant (p=0.07 and p=0.1, respectively).

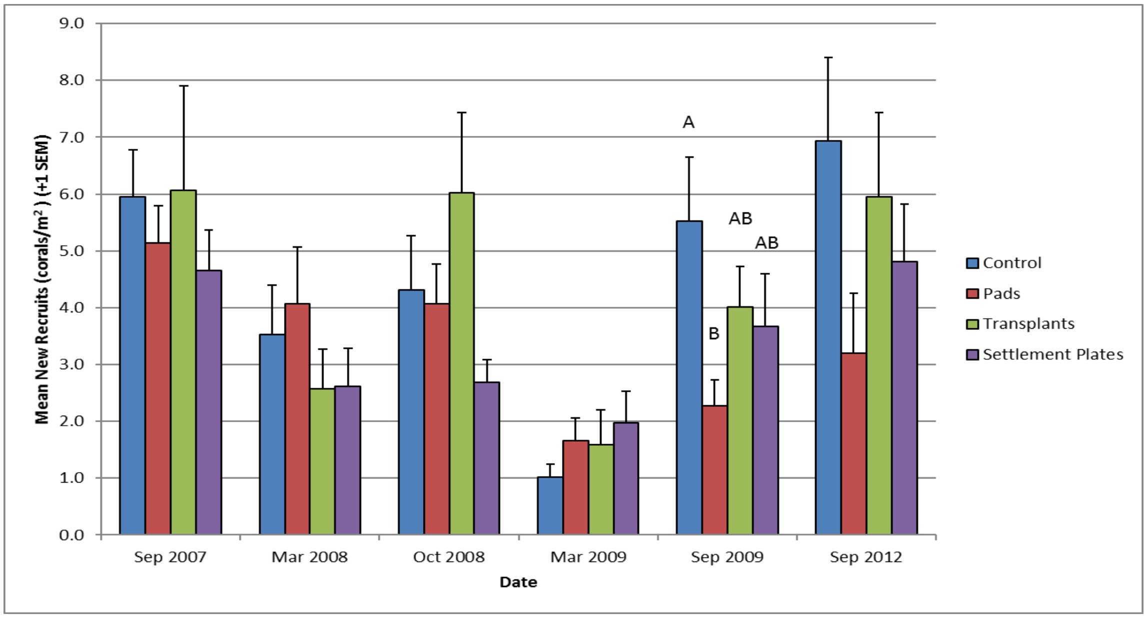


Figure 4.4 Mean new recruit density by treatment, standardized for area. Different letters indicate significant differences between means and homogenous groupings (SNK, $p<0.05$).

The cyclic seasonal shift in density was absent in the macroalgae and benthic invertebrate data (see Chapter 3), but distinctly present in the fish data (see Chapter 5). The date of the last data collection (September 2012) was a full three years following the date of the planned end of the project and the planned final data collection (September 2009). Even though there is a three-year gap in the dataset, it still appears that there is a distinct upward trend of increasing recruit density throughout the study duration, with the final summer observations showing predictably high abundance levels for all treatments. It is possible that the growth of other competing benthic organisms was accelerated during the warmer summer months, thereby killing a significant portion of the newly settled corals and reducing the number available to be counted in surveys in the spring. Due to the relatively slow growth rate of corals, it would take time for the corals to increase their numbers and grow large enough to be counted during a survey. The most dominant form of macroalgae, *Lobophora variegata*, did show some signs of seasonal oscillation (Ch. 3,

Figure 3.5). However, it is unclear as to why the seasonal oscillation was not more apparent in the benthic invertebrate data, particularly the sponges. Perhaps the growth of sponges may have accelerated during the warmer summer and fall months, but due to the continual increase in percent coverage of this species during the first three years the seasonal oscillation signal was obscured. The biennial sampling schedule did not provide the fine-scale temporal resolution needed to fully describe the annual pattern in detail.

When the experimental treatments are ranked in order of decreasing total number of new coral recruits (excluding re-located individuals), using unstandardized abundance data (Figure 4.5), they fall out as such: Control (720), Transplants (692), Plates (539), Pads (306). The pad material was not expected to provide favorable settlement substrate for coral recruits. It was anticipated that the Pads treatment would have fewer total coral recruits on the exterior surface of the module because the pad material took up a significant amount of space, (43% of the total available exterior surface area) and reduced the total area available for settlement, and no coral recruits were found on the pad material during the study.

With all dates combined, the experimental treatments ranked in order of decreasing mean density of new coral recruits per module, using standardized abundance data (Figure 4.6), are: Control Treatment (4.6 recruits/m^2), Coral Transplants (4.4 recruits/m^2), Pads (3.6 recruits/m^2), Settlement Plates (3.4 recruits/m^2). There were no differences detected between the controls and treatments. However, when broken down by date (Figure 4.4 above), the last two dates of data collection (September 2009 and 2012) indicate that the Controls and Coral Transplants treatment had more coral recruits. It is suspected that these results are at least partially due to the added exterior surface complexity of all three of the experimental treatment modules that may have served as more effective anchor points and supports for rapidly growing and spreading benthic organisms, such as *Lobophora variegata* macroalgae and *Desmapsamma anchorata* sponge. Given their extensive coverage on the modules during much of the study (see Ch.3, Figures 3.4-3.6 and 3.10-3.12), it is therefore likely that these species contributed most significantly to a reduction in the number of recruits on all treatments to varying extents, but most severely on the Pads treatment.

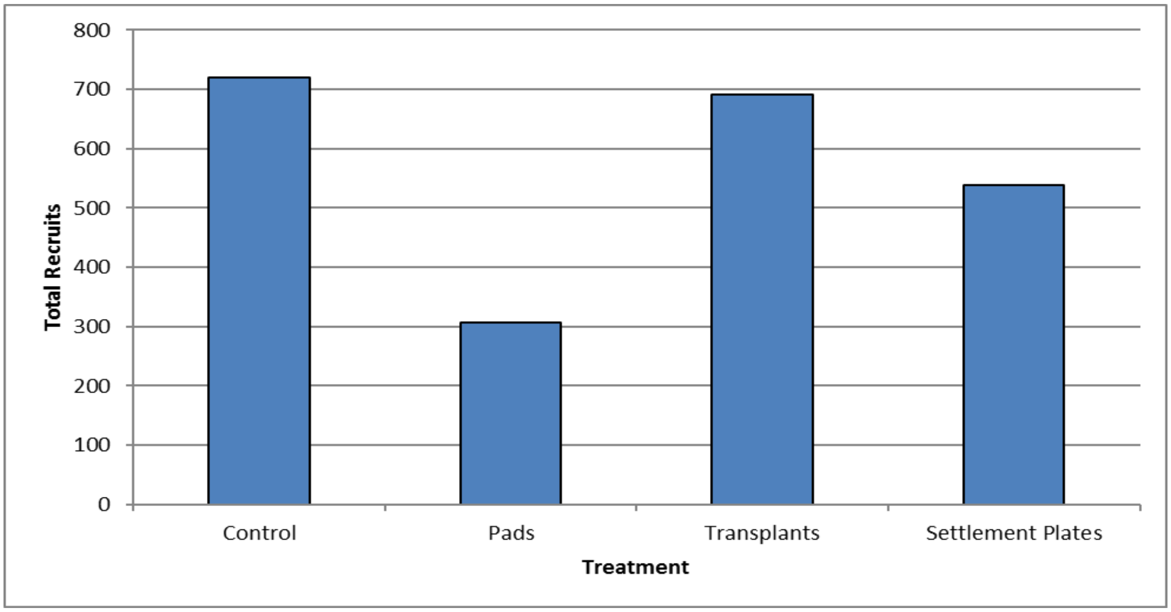


Figure 4.5 The total number of new coral recruits, by treatment, recorded for all dates combined using unstandardized data.

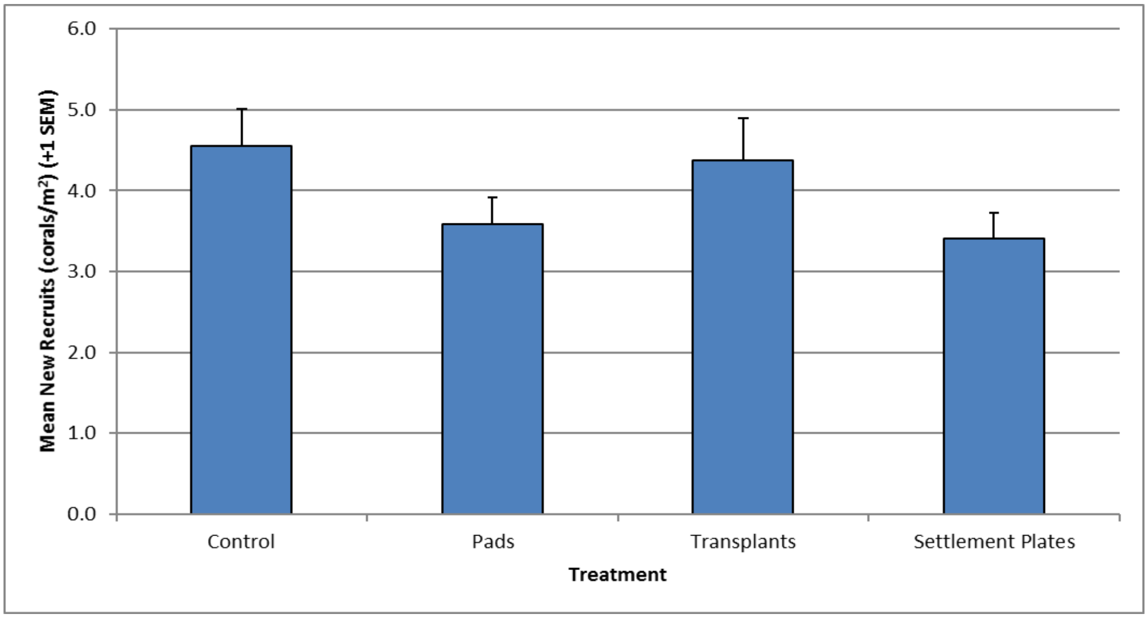


Figure 4.6 The mean number of new recruits to the modules for all dates combined, using standardized data. No significant differences were detected (SNK, $p>0.05$).

ii) Percent Survival

Percent survival was calculated by taking the total number of recruits recorded during one monitoring trip and dividing by the number of “old” recruits that were recorded during the following monitoring trip. The mean number of coral recruits that survived between monitoring trips in Puerto Morelos, with all treatments combined (Figure 4.7), indicates that there was a steady increase in the number of corals that survived over the course of the first three years. The number of survivors increased significantly between each period until leveling off in September 2012 (ANOVA, p<0.0001). March and September 2007 are not present in these figures because there were no recruits located during the March 2007 monitoring trip, and therefore no way to calculate percent survival for recruits located in September 2007.

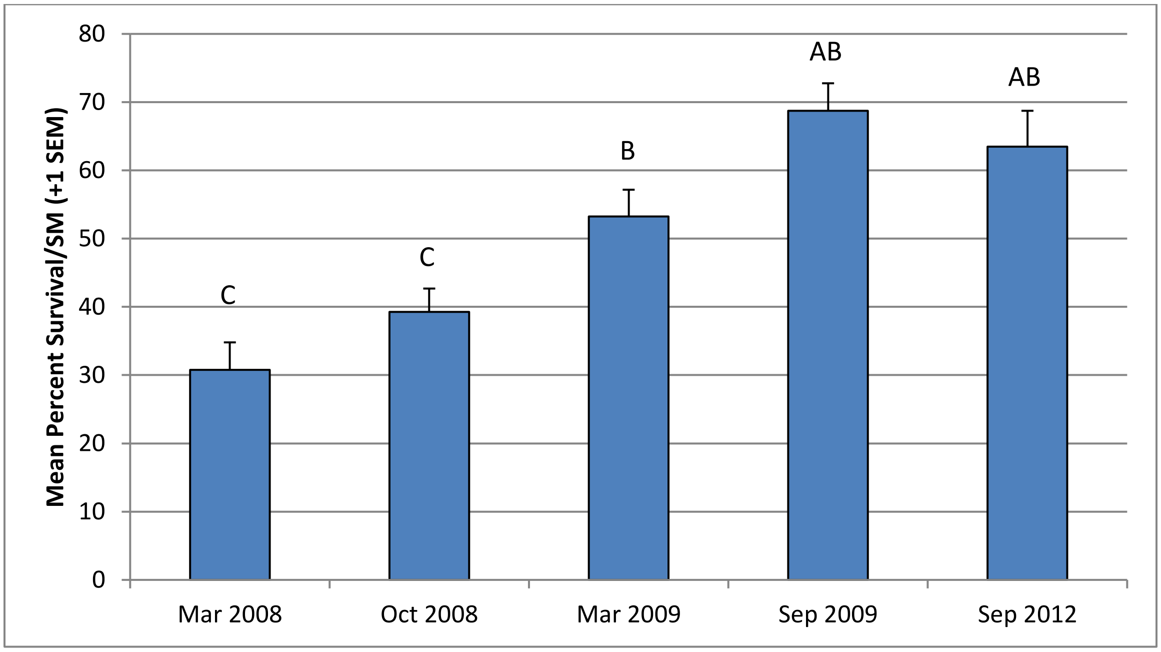


Figure 4.7 The mean percent of coral recruits identified as survivors from the previous monitoring period (6 month intervals) with all treatments combined for each sampling date in Puerto Morelos. Different letters indicate significant differences between means and homogenous groupings (SNK, <0.05).

The similarity in percent survival between September 2009 and September 2012 is difficult to interpret due to the amount of time that elapsed between the two data collection periods. Coral recruits that were recorded in September 2009 and those that settled immediately afterwards were difficult to distinguish. The values represented in the figure are an extrapolation generated by combining those that were obviously present in September 2009 (due to their larger size) and those that could reasonably be included within that group. Without data to fill in the three-year gap between the last two data collection points, it is uncertain exactly how many surviving corals recorded in September 2009 were actually present in September 2012. The data presented here gives a general indication of how many colonies survived, but it is not precise. Therefore, drawing conclusions based on any appearance of stabilization or a gradual tapering off at year six should be done with caution or avoided altogether.

When percent survival of each data collection point was evaluated by treatment (Figure 4.8), no significant differences were detected between treatments within any of the collections with the exception of September 2009. At that point, for reasons that are unclear, the Coral Transplant treatment had significantly lower percent survival than the other treatments (ANOVA, p=0.032). Interestingly, more recruits survived on the Control treatment during the period between March 2008 and October 2008, although the difference was not statistically significant (ANOVA, p=0.065). This time period was one of several that coincided with rapid growth of the macroalgae *Lobophora variegata* and the sponge *Desmapsamma anchorata* (see Chapter 3). This lends some further support to the deduction that increased surface area and reduced topographic complexity on Control modules, as compared to the other treatments, may be linked to higher rates of coral recruitment and survival.

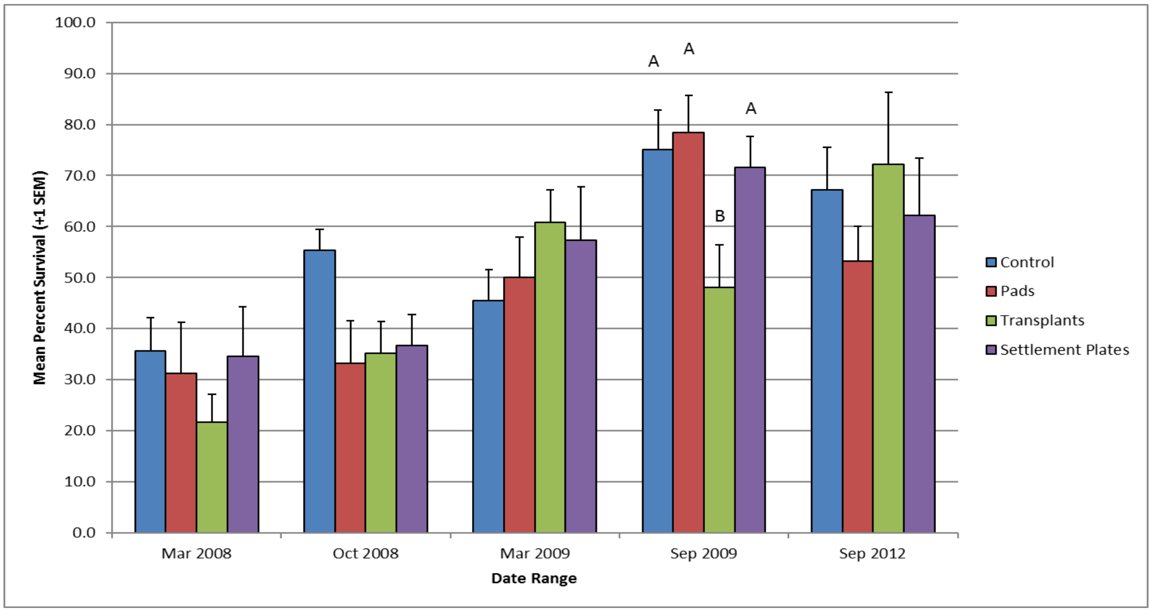


Figure 4.8 The mean percent of coral recruits, by treatment, which survived on each module from one monitoring period to another (6 month intervals). Different letters indicate significant differences within groupings (SNK, <0.05).

The trend of increasing percent survival, combined with the highly variable coral new-recruit data, indicates the number of surviving coral recruits increased over time through the study period. Although it is possible recruit (pelagic larva) availability increased through time it is more likely there was an increased likelihood of survival for corals that settled on the modules after the initial years of rapid benthic community development. As noted above, calculating percent survival using this method essentially introduces a cumulative effect, as individual coral recruits that survive through multiple monitoring trips are counted multiple times. That is to say that if a coral recruit that was recorded in September 2007 survives through to September 2009, it will have been counted multiple times.

ii) Growth and Sizes of Coral Recruits

Due to the small sample size and large variability within the Akumal dataset, only corals studied in Puerto Morelos are discussed here. Size measurements for each colony collected during coral recruit surveys allowed for an assessment of growth rates of the coral recruits. The average size of the coral recruits on the modules increased steadily throughout the duration of the study (Table 4.3), and no significant differences in growth rates were detected between treatments for any of the periods between monitoring trips ($p>0.05$). Between September 2007 and March 2008, the coral recruits on the modules increased in size by an average of 2.5 mm, or 5.0 mm/year (mean radial extension). Between March and October 2008, the corals increased in size by an average of 3.7 mm, or 7.3 mm/year. Between October 2008 and March 2009, the average size of the corals only increased in size by 0.4 mm, or 0.8 mm/year. There was also a notable reduction in the total number of recruits recorded during this time period. Between March and September 2009, the corals increased in size by an average of 1.4 mm, or 2.8 mm/year. Three years later, in September 2012, the average size of the coral recruits was 21.9 mm, having grown at a rate of 7.3 mm/year.

In September 2012, out of the 860 coral recruits recorded, 80% were *Porites astreoides* (Table 4.4). The largest coral recruits recorded were both *Porites* spp. (130 mm), closely followed by *Agaricia agaricites* (128 mm). The largest representatives (>50 mm) for 7 out of 8 species listed here were relatively few in number, with most species exhibiting a size frequency curve resembling that of the two most abundant species, *P. astreoides* and *S. siderea* (Figures 4.9 and 4.10, respectively) (size frequencies for *Agaricia* sp. and *Diploria* sp. located in Appendices 4.8 and 4.9).

Table 4.3 Number and size (±SEM) of coral recruits on the Puerto Morelos modules, with all treatments combined.

	Total Corals	**Average Size**
March 2007	0	0.0
September 2007	516	3.9 ±0.1
March 2008	278	6.4 ±0.3
October 2008	599	10.0 ±0.5
March 2009	440	10.4 ±0.5
September 2009	658	11.8 ±0.5
September 2012	860	21.9 ±0.6

Table 4.4 Total number, mean (±SEM), maximum, and minimum sizes (mm) by species for Puerto Morelos in September 2012 with all treatments combined.

	Total	**Mean Size**	**Max**	**Min**
Agaricia agaricites	37	37.5 ±4.6	128	3
Dichocoenia stokesi	6	26.3 ±6.4	55	9
***Diploria* sp.**	37	23.0 ±2.0	63	4
Meandrina meandrites	2	15.0 ±4.0	19	11
Orbicella sp.	13	31.9 ±6.7	93	7
Porites astreoides	690	20.3 ± 0.6	130	2
Porites porites	7	96.0 ±10.2	130	60
Siderastrea siderea	67	20.0 ±1.7	102	4

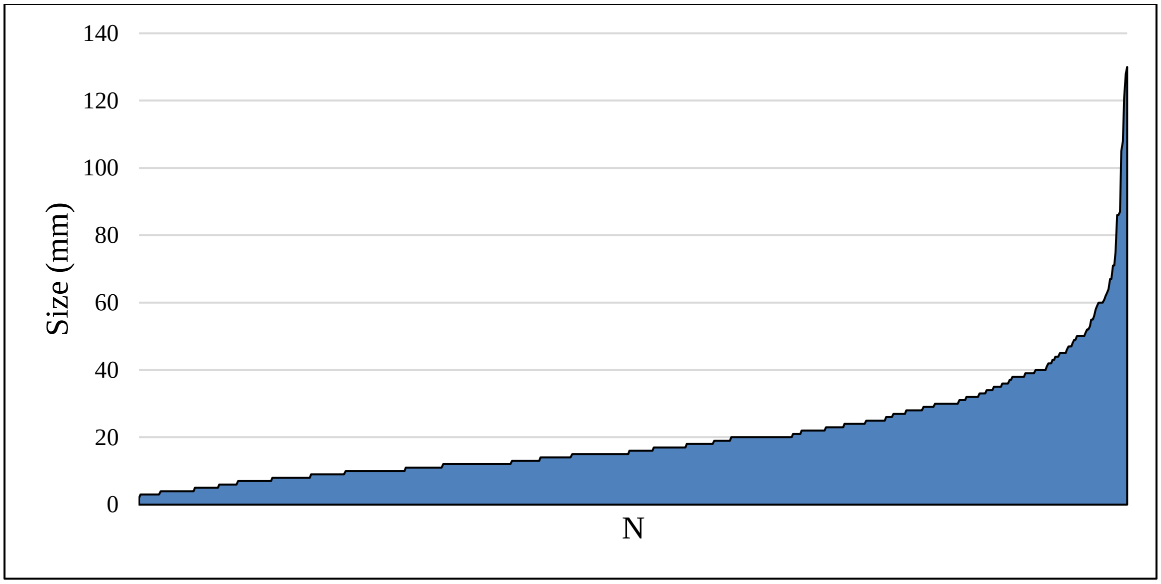


Figure 4.9 Size frequency of *Porites astreoides* for September 2012 (N=860), ordered smallest to largest.

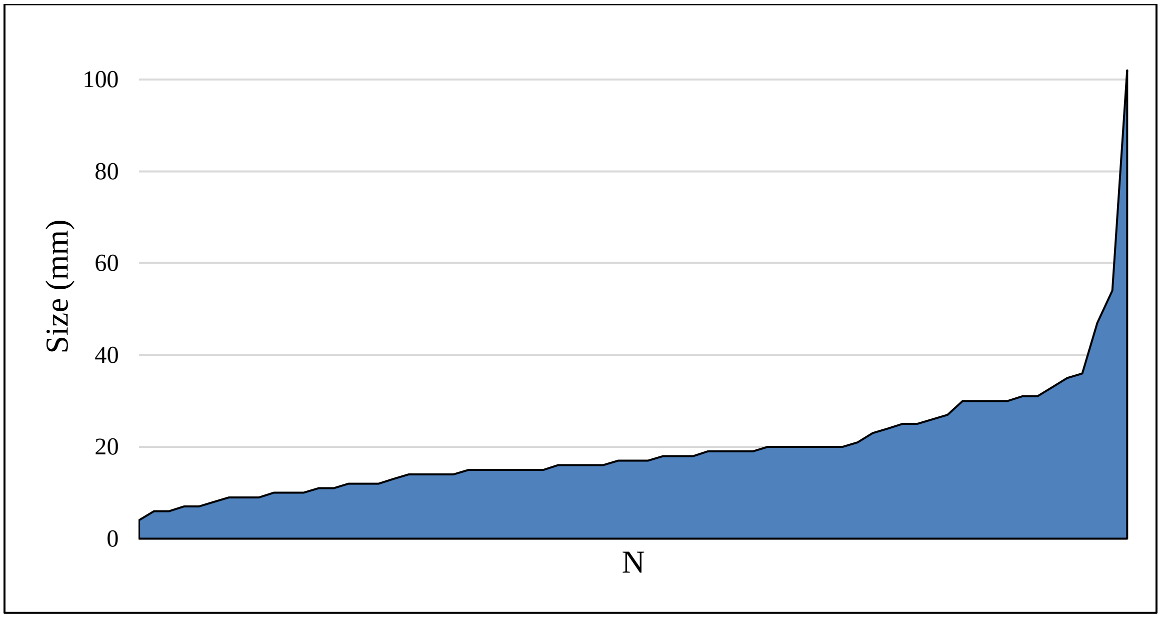


Figure 4.10 Size frequency of *Siderastrea siderea* for September 2012 (N=67), ordered smallest to largest.

When size distributions at the end of the study (September 2012 only) are broken down by individual treatment, a few notable points become apparent. The largest corals were recorded on the Pads and Settlement Plates treatments, followed by Controls and Transplants (Table 4.5). The largest individual colony at the end of the study was *Porites* *astreoides* on each treatment, although it also shared that distinction with *A. agaricites* on the Pads treatment and *P. porites* on the Settlement Plates treatment. Out of the top ten largest corals on each treatment, there were 3 species on the Controls and Pads, 5 on the Transplants, and 4 on the Settlement Plates.

Table 4.5 Sizes in millimeters (mm) of the 10 largest coral recruits by species and treatment, for September 2012 only.

Control		**Pads**		**Transplants**		**Settlement Plates**	
A. agaricites	66	*A. agaricites*	61	*P. astreoides*	45	*Diploria* sp.	52
P. astreoides	67	*A. agaricites*	62	*A. agaricites*	46	*P. astreoides*	53
P. astreoides	71	*Diploria* sp.	63	*P. astreoides*	49	*P. astreoides*	61
P. astreoides	75	*P. astreoides*	63	*P. astreoides*	49	*P. astreoides*	64
P. porites	80	*A. agaricites*	79	*A. agaricites*	51	*P. astreoides*	67
P. astreoides	87	*P. astreoides*	86	*Orbicella* sp.	93	*P. porites*	68
P. astreoides	105	*P. astreoides*	86	*A. agaricites*	95	*P. astreoides*	71
P. porites	111	*A. agaricites*	87	*S. siderea*	102	*A. agaricites*	75
P. porites	120	*A. agaricites*	128	*P. porites*	103	*P. porites*	130
P. astreoides	121	*P. astreoides*	128	*P. astreoides*	108	*P. astreoides*	130

Even though there were more species in the top ten list for the Coral Transplants treatment than the others, that treatment was ranked second behind Controls when the total number of coral recruits from all species recorded in September 2012 are combined and examined by treatment (Figure 4.11). The Pads treatment was ranked last, but the decreased surface area available for settlement on this treatment must be taken into consideration, as these size frequency data are not standardized for area.

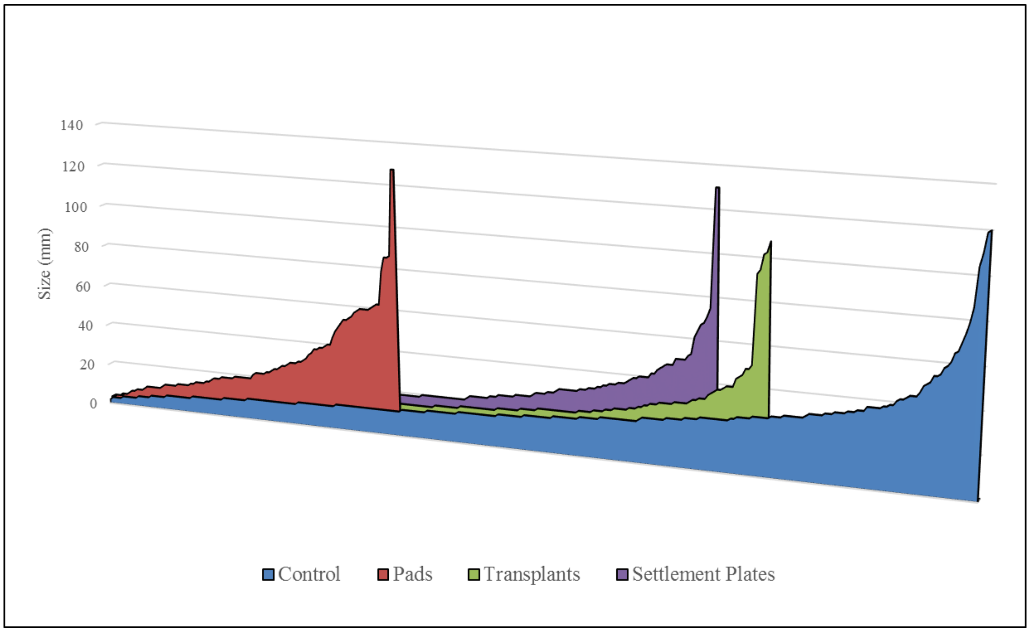


Figure 4.11 Size frequency of coral recruits, all species combined by treatment, for September 2012 (combined N=860).

Given that *Porites astreoides* was responsible for 80% of the total number of coral recruits on the modules at the end of the study, it is not surprising that the size frequency pattern for that species (Figure 4.12) is almost identical to the former one created using all species. However, the Transplants and Settlement Plates treatments were much closer together, giving the Controls a greater lead. When the mean size of *P. astreoides* recruits was examined by treatment (Figure 4.13), the Transplants treatment had significantly lower mean size (ANOVA, p=0.00006).

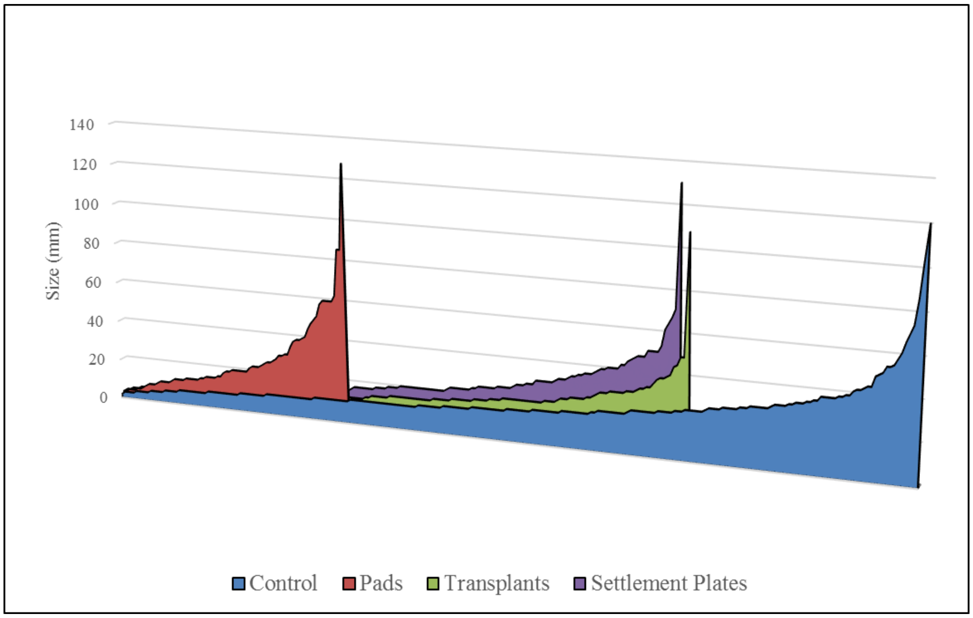


Figure 4.12 Size frequency of *Porites astreoides* coral recruits, by treatment, for September 2012 (combined N=690).

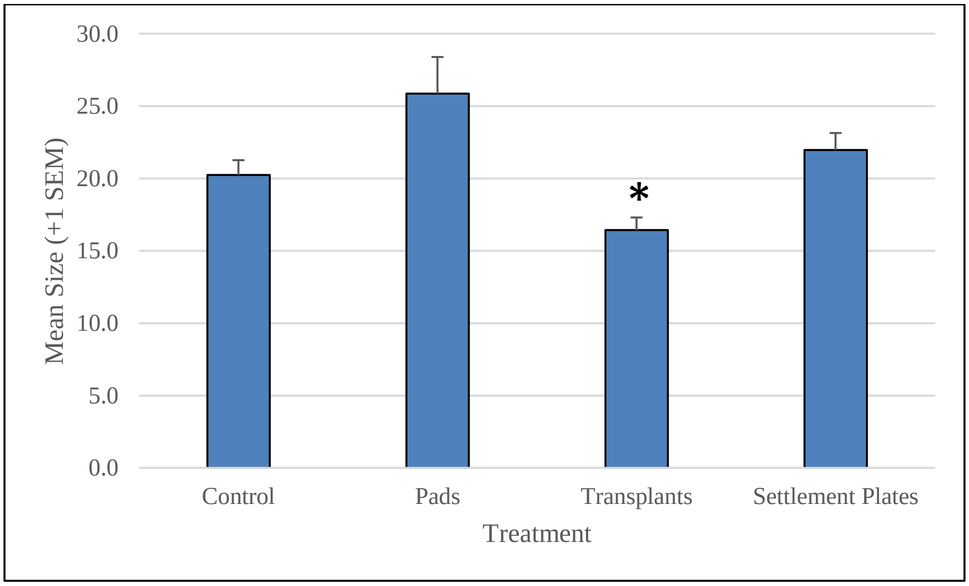


Figure 4.13 Mean size of *Porites astreoides* recruits by treatment in September 2012. The asterisk indicates a significant difference (ANOVA, $p<0.001$).

When the second and third most abundant species recorded at the end of the study is examined by treatment, the pattern is considerably different. For *Siderastrea siderea* (Figure 4.14), there were more recruits on the Transplants treatment, followed by Controls and Settlement Plates, with Pads once again ranking last. In addition, the largest recruits of this species were seen on the Transplants treatment. The Pads treatment had the greatest mean size of *Siderastrea* recruits (Figure 4.15), although the difference was not significant (ANOVA, p=0.6).

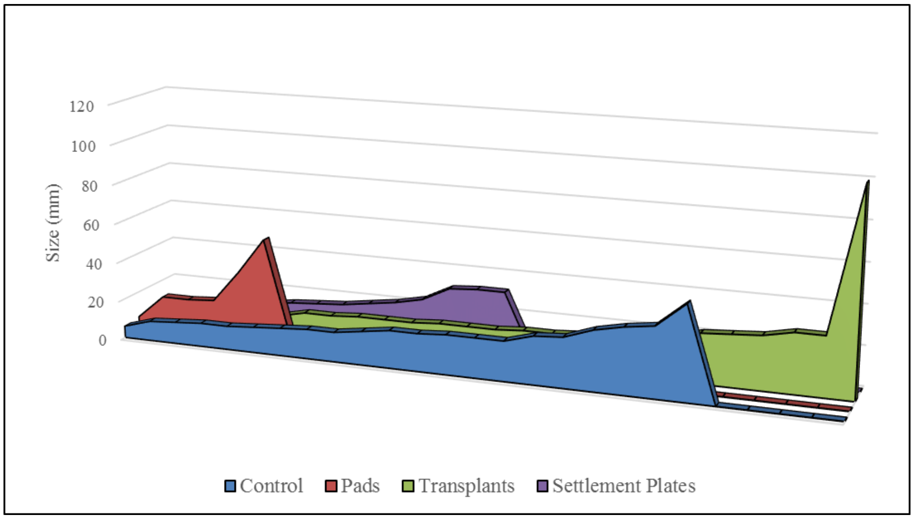


Figure 4.14 Size frequency for *Siderastrea siderea* coral recruits, by treatment, for September 2012 (combined N=67).

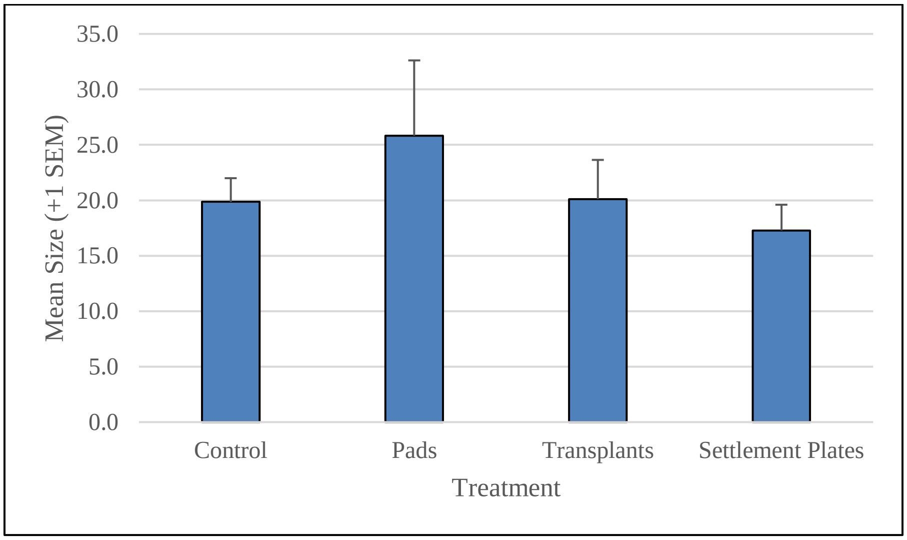


Figure 4.15 Mean size of *Siderastrea siderea* recruits in September 2012.

For *Agaricia* sp. (Figure 4.16), there were far more recruits on the Pads treatment, followed by Transplants and Settlement Plates, with Controls ranked last. The Pads treatment had the largest colonies, as well as the greatest mean size of coral recruits (Figure 4.17); although there were clearly more recruits on the Pads treatment, there was no significant difference found in mean size of *A. agaricites* recruits between treatments (ANOVA, p=0.26).

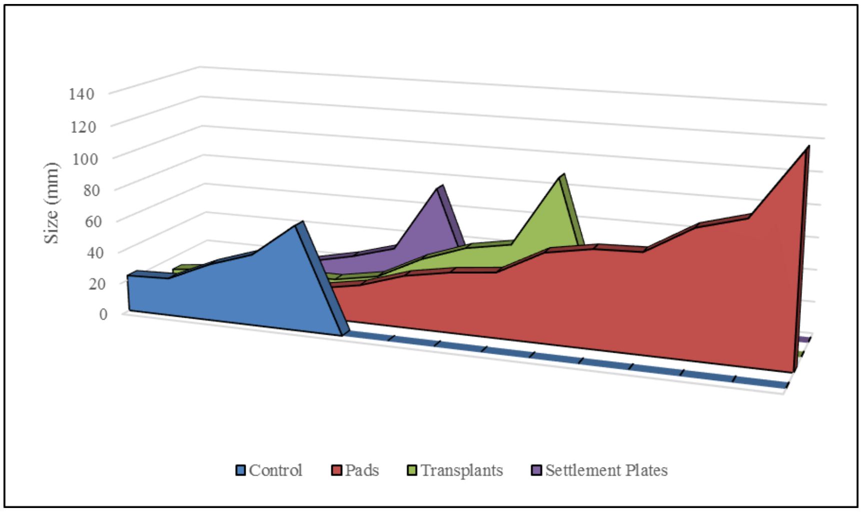


Figure 4.16 Size frequency of *Agaricia* sp. coral recruits, by treatment, for September 2012 (combined N=37).

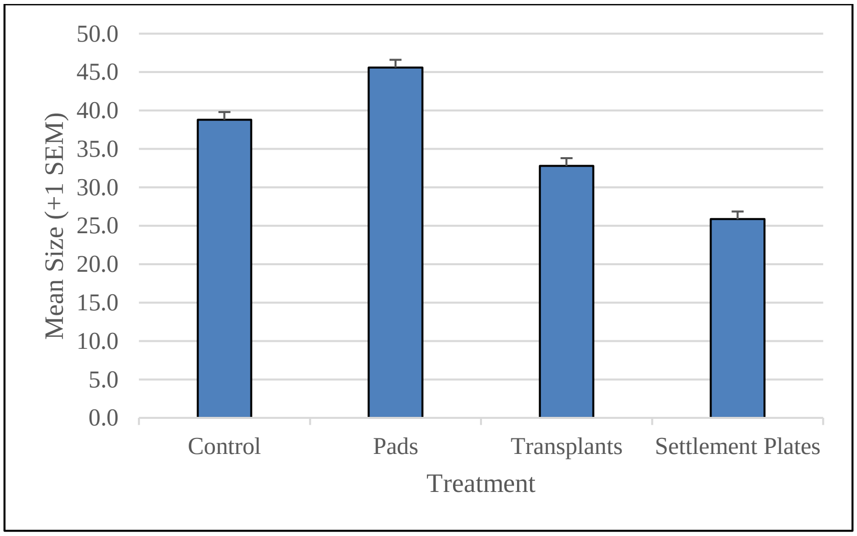


Figure 4.17 Mean size of *Agaricia* sp. recruits in September 2012.

When the fourth most abundant species is examined by treatment, the pattern once again resembles that exhibited by *P. astreoides*. For *Diploria* sp. (Figure 4.18), there were more recruits found on the Control treatment, followed by the Settlement Plates, Transplants, and Pads. The largest individuals were found on the Pads and Settlement Plates treatments, while the smallest were on the Controls. The Pads treatment once again had the greatest mean size of *Diploria* sp. recruits (Figure 4.19), but once again the difference was not significant (ANOVA, p=0.29).

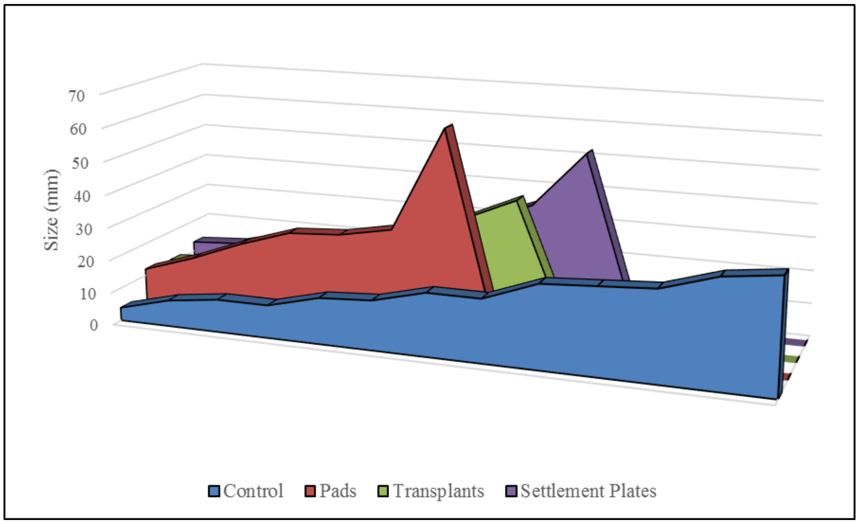


Figure 4.18 Size frequency of *Diploria* sp. coral recruits, by treatment, for September 2012 (combined N=37).

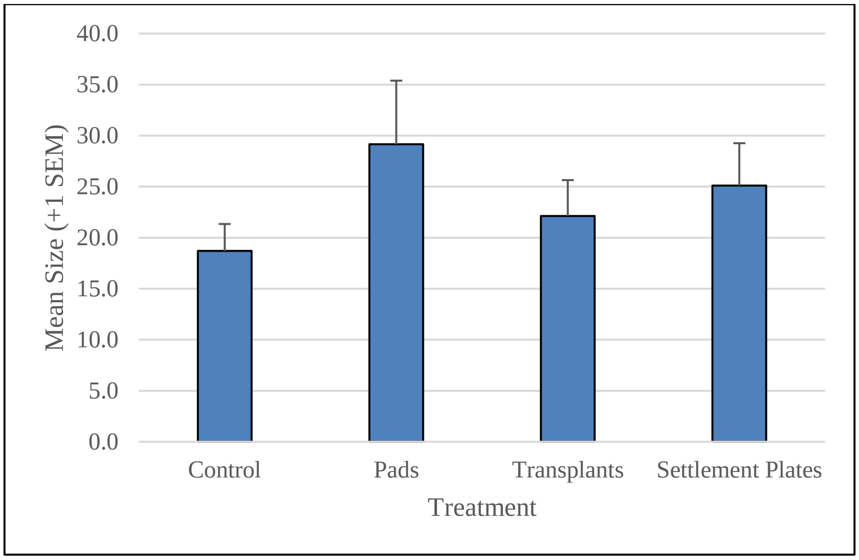


Figure 4.19 Mean size of *Diploria* sp. recruits in September 2012.

b) Settlement Plates

In early November 2007, 2 months after coral spawning was documented on local reefs in Puerto Morelos (full moon Aug. 28; *Acropora palmata* spawning Aug. 31 through Sep. 1, *Orbicella annularis* and *O. faveolata* Spawning Sep. 4) (PNAPM staff, unpublished observations), 60 plates were collected from the Puerto Morelos modules and 12 were collected from the natural reef transects (Table 4.6). In Akumal, 6 plates were collected from the modules and 5 from the natural reef transect site. In mid-October 2008, a full 14 months following the 2007 spawning and 2 months following the anticipated 2008 spawning (full moon Aug. 16 and Sep. 15; no local spawning observations available), the remaining plates were collected (60 from the Puerto Morelos modules and 13 from the natural reef transects). In Akumal, 4 plates were collected from the modules and 9 from the natural reef transect site. Due to assessment error following Hurricane Dean, the number of plates available for collection in 2007 on both the modules and natural reef transect site was miscalculated, resulting in a slightly unequal number of plates collected during each year (Table 4.6).

Table 4.6 Summary and timeline for the number of settlement plates deployed and collected from the modules and natural reef at both study sites.

	Plates Deployed	**Plates Collected**		
Collection Date	**July2007**	**Nov2007**	**Oct2008**	**Total**
Puerto Morelos SMs	120	60	60	120
Puerto Morelos NR	25	12	13	25
Akumal SMs	36	6	4	10
Akumal NR	15	5	9	14
Totals	196	83	86	169

From both collection dates at both study sites, coral recruitment onto the standardized settlement plates was low, with a combined total of 34 identifiable coral recruits collected (Table 4.7). In Puerto Morelos, only 3 coral recruits were recorded from plates deployed on the modules, whereas 21 were recorded from plates deployed on the natural reef transects. In Akumal, only 2 recruits were recorded from the modules, and 8 from the natural reef. At both study locations, there were more recruits recorded from plates collected in October 2008. This was expected considering the longer soak time. In addition, at both study locations there were more recruits recorded from tiles deployed onto the natural reef, although the difference is most apparent in Puerto Morelos.

Each settlement plate had a total area of 0.01m^2 per side, resulting in 0.02m^2 available for coral settlement. When the number of recruits per tile was standardized by area to create a recruit density metric, with both dates combined the mean recruit density on the Puerto Morelos module plates was 1.6 (±1.2 SEM) recruits/m^2 and 41.7 (±22.5 SEM) recruits/m^2 on the natural reef plates. In Akumal, the mean recruit density on the module plates was 9.1 (±6.1 SEM) recruits/m^2 and 28.6 (6.9 ±SEM) recruits/m^2 on the natural reef plates.

Table 4.7 Summary of the total number of coral recruits counted on the settlement plates on both reef types at both study sites from both years, the total number of recruits, the mean number of recruits per tile, the mean density of recruits, and the combined total mean density (±SEM).

Coral Recruits on Settlement Plates	Collection Date	P. Morelos SMs	P. Morelos NR	Akumal SMs	Akumal NR
Total Recruits	**Nov-07**	1	1	1	4
	Oct-08	2	20	1	4
Mean recruits/tile	**Nov-07**	0.02 ±0.02	0.08 ±0.08	0.1 ±0.1	0.8 ±0.2
	Oct-08	0.04 ±0.04	1.7 ±0.8	0.3 ±0.3	0.4 ±0.2
Mean Recruit Density (recruits/m^2)	**Nov-07**	1.0 ±1.0	0.08 ±0.08	7.1 ±7.1	40.0 ±10.0
	Oct-08	2.1 ±2.1	83.3 ±42.3	12.5 ±12.5	22.2 ±8.8
Total Mean Density (recruits/m^2)	**Both Years**	**1.6 ±1.2**	**41.7 ±22.5**	**9.1 ±6.1**	**28.6 ±6.9**

For comparison, the mean recruit densities on the Puerto Morelos modules in November 2007 and October 2008, calculated using the coral recruitment visual survey technique on the entire surface of the modules, were 4.3 and 3.9 recruits/m^2, respectively. This closely matches the recruit density on the November 2007 natural reef settlement plates.

Almost all (91%) of the recruits recorded from the settlement plates were found on the back side of the plates at both study sites. Positive identification of the coral recruits was difficult due to their size and the fact that their living tissues and color had been bleached immediately after collection, and full analysis did not take place until several weeks later (Figure 4.20). Only the remaining calcium carbonate corallite skeletal structures were available to make decisions on species identification. Nevertheless, it is believed that the majority of the recruits were *Porites astreoides* based on their size, corallite structure, and the overwhelming majority of recruits of that species that were identified on the module surfaces (see Table 4.4).

Both of the recruits from Puerto Morelos in November 2007 were <2mm in diameter. In October 2008, sizes ranged from 1.4 mm to 3.7 mm on the substrate module plates (N=2) and from 1.0 mm to 3.7 mm (N=20, mean 2.3 mm) on the natural reef plates. One exception was an 8.5 mm recruit on an October 2008 natural reef plate that was tentatively identified as an *Agaricia* sp. Given these sizes and the timing involved, it is unlikely that any of these recruits were produced by broadcast spawning species during the mass spawning event of late August/early September.

Figure 4.20 Some examples of scleractinian coral recruits collected on settlement plates and bleached for storage, species unknown. Sizes, left to right: 3.0 mm, 4.5 mm, and 7.5 mm.

In November 2007, the difference between the number of recruits on the substrate module tiles and the natural reef tiles was non-existent in Puerto Morelos and negligible in Akumal. However, in October 2008, there was considerable difference between the two in Puerto Morelos, with 10 times more settling on the natural reef tiles. Interestingly, out of the 13 tiles collected from the natural reef, 50% of the recruits were from a single tile, and a further 33% were from another 2 tiles. Given that every single other recruit that settled onto the tiles was a single occurrence at both study sites and in both years, there may have been some unanticipated site-specific microhabitat related factor involved at those plates' precise deployment locations that was responsible for this occurrence, although the specifics remain a mystery.

4.2 Coral Transplants

4.2.1 Methodology

In chapter 2, section 2.4, the procedure for collecting and attaching coral transplants was discussed in great detail. In short, 60 “corals of opportunity” were collected from a nearby natural coral reef, 20 from each of 3 selected species: *Porites astreoides*, *Agaricia agaricites*, and *Orbicella annularis*. Each of 10 modules received 6 coral transplants, two of each species. During each monitoring trip, the health and appearance of each coral transplant was evaluated and quadrat photographs were taken for use in growth calculations. Throughout the course of the study there were occasional signs of physical damage inflicted by local fishermen mooring their boats to the artificial reefs to look for lobsters taking refuge in the modules. During the first three years of the study, any transplanted colonies that had become detached or had died were replaced, and any overgrowing macroalgae or sponges were removed in effort to keep the transplants alive and the transplant-treated modules as identical to one another as possible.

4.2.2 Data Analysis

Growth of coral transplants was calculated by a CPCe analysis of mean radial extension/changes in surface area of coral transplants and natural reference reef corals between each monitoring trip (Kohler and Gill, 2006). Due to an unfortunate data storage issue, the digital framer photographs for October 2008 and March 2009 were lost prior to analysis when the hard drive they were stored on became corrupted. Multiple efforts were made to recover the images, but they were unsuccessful. Therefore, the growth analysis is missing a full year of photo quadrat data. However, the *in situ* quadrat surveys were partially intended to serve as a backup and were used to inform the figures presented here. No quadrat photos of the coral transplants were taken in September 2012. Comparisons of growth between March and September 2007, September 2007 and March 2008, and March 2008 to September 2012 are presented here. Evaluations of transplant survival were unaffected by this issue.

4.2.3 Results and Discussion

Growth was highly variable between the three coral transplant species used in this study, as well as between trips and within species, with many colonies experiencing either growth or tissue recession (Figure 4.21). From March to September 2007, *P. astreoides* had the highest average increase in size with 7.0 (±0.9 SEM) cm^2 per colony, ranging from 0.5 to 14.2 cm^2 and with all colonies showing a positive increase in size (Appendix 4.7).

A. agaricites followed with an average increase of 4.4 (±1.5 SEM) cm^2, ranging from 0.7 to 17.1 cm^2, but with one colony decreasing in size by -15.1 cm^2 (Appendix 4.8). *O. annularis* colonies exhibited the least amount of growth during this time period, with an average increase of 2.6 (±1.5 SEM) cm^2 with a range of 0.5 to 17.1 cm^2. A total of four *O. annularis* colonies decreased in size, ranging from -1.3 to -17.6 cm^2 (Appendix 4.9).

From September 2007 to March 2008 all three transplant species exhibited reduced growth compared to the previous six-month period, which is logical considering seasonal reduction of temperature. *A. agaricites* had the highest growth with an average increase of 1.9 (±1.3 SEM) cm^2, ranging from 0.9 to 10.5 cm^2. A total of five *A. agaricites* colonies decreased in size, ranging from -2.1 to -12.2 cm^2. *P. astreoides* had an average increase of 0.4 (±1.1 SEM) cm^2, ranging from 0.3 to 12.4 cm^2. A total of ten colonies decreased in size, ranging from -0.5 to -7.5 cm^2. The average change in size for *O. annularis* was overall negative, -4.4 (±1.9 SEM) cm^2, with positive values ranging from 0.4 to 8.2 cm^2 and negative values -0.5 to -24.1 cm^2 and a total of 13 colonies decreasing in size. In addition, one *O. annularis* transplant colony died from yellow band disease. It was replaced with a donor colony from the natural reef which was later overgrown by the sponge.

During the 18-month period between March 2008 and September 2009, all three species lost transplants due to overgrowth by the sponge *Desmapsamma anchorata*. Five *A. agaricites* colonies (25%), seven *P. astreoides* colonies (35%), and ten *O. annularis* colonies (50%) were lost. However, positive growth was documented for all but two of the surviving colonies from all three species. Somewhat unexpectedly, *O. annularis* colonies had the greatest average increase in size with 16.0 (±6.9 SEM) cm^2, ranging from 1.7 to 102.1 cm^2. This was followed by *A. agaricites* with an average increase of 13.0 (±4.2 SEM) cm^2, ranging from 6.9 to 30.6 cm^2. Two *A. agaricites* colonies displayed negative growth, ranging from -14.2 to -42.8 cm^2. *Porites astreoides* had an average increase of 10.3 (±1.2 SEM) cm^2, ranging from 1.6 to 21.8 cm^2. In addition, two *A. agaricites* colonies had become dislodged or detached from the modules due to physical means. These two colonies were both later overgrown by the sponge.

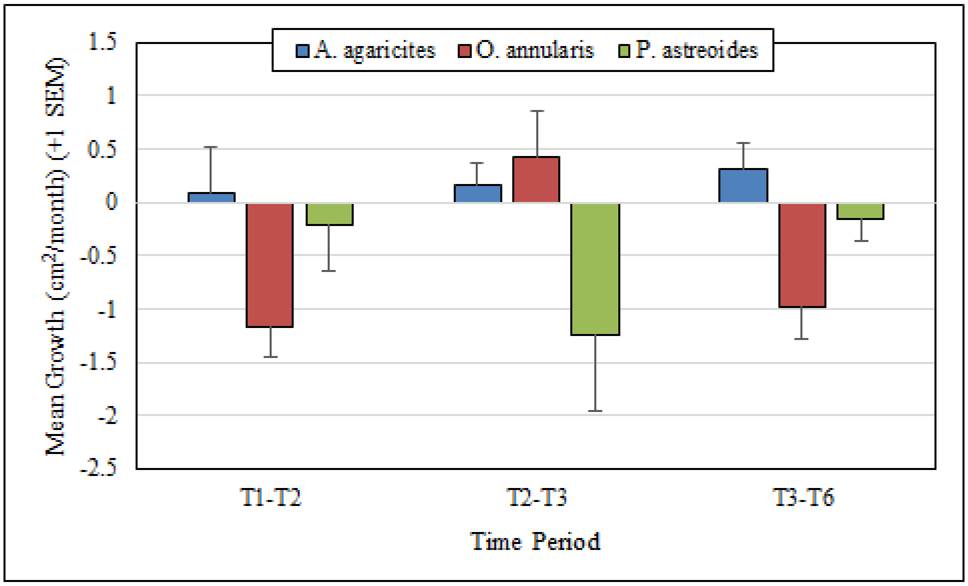


Figure 4.21 Mean growth of coral transplants by species and date (T1-T2 = March 2007 to September 2007, T2-T3 = September 2007 to March 2008, T3-T6 = March 2008 to September 2009).

During the three-year period from September 2009 to September 2012, a further decline in transplant survivorship, almost exclusively due to sponge overgrowth, was observed (Figure 4.22). There were 20 colonies for each species transplanted at the beginning of the study. All but four *A. agaricites* colonies (80%), six *P. astreoides* colonies (70%), and four *O. annularis* colonies (80%) had been overgrown by the sponge; 76.7% of the overall total number of colonies originally transplanted. Of those that survived, the majority (three *A. agaricites*, three *P. astreoides*, two *O. annularis*) were described as having 70-95% overgrowth and/or recent mortality and were on the verge of being smothered completely. However, two *A. agaricites* colonies, two *P. astreoides* colonies, and two *O. annularis* colonies had managed to escape overgrowth, temporarily at least, and were growing well and appeared quite healthy.

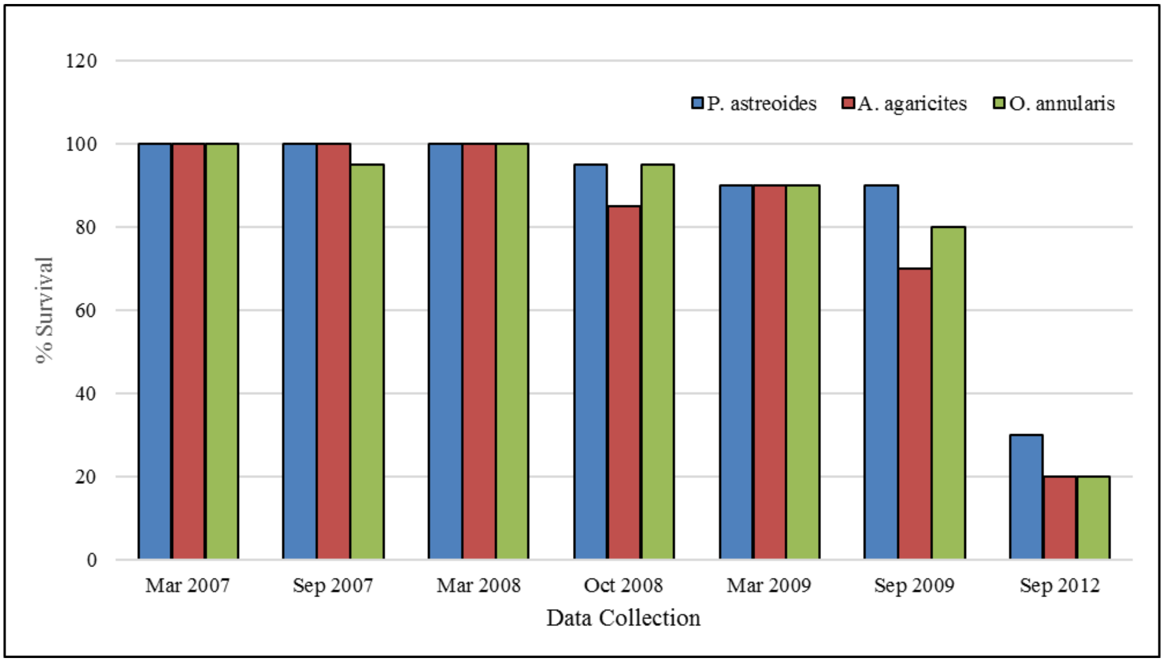


Figure 4.22 Total percent of surviving coral transplants by species and date. Includes transplants added to replace dead colonies during the first three years of the study.

Survival and overall health of the coral transplants was affected not only by sponge overgrowth, but also by disease, tissue recession, and slow or stagnant growth. The general trend in health of the transplants shows a steady decline (Figure 4.23). Although the sponge overgrowth was by far the largest cause of death for all three species, *O. annularis* seemed to suffer from more occurrence of disease and generally lacked the subjective appearance of vigor. *O. annularis* was the first transplant species to lose a transplant, and once the sponge began its rapid overgrowth of the module surfaces it suffered most severely throughout the remainder of the study.

Growth of the natural reef reference corals was also highly variable (Figure 4.24). For *A. agaricites*, from March to September 2007, the mean growth was 0.09 (±0.4 SEM) cm^2/month, ranging from 1.24 to -0.81 cm^2/month, and 50% showed positive growth. From September 2007 to March 2008, mean growth increased to 0.17 (±0.2 SEM) cm^2/month, ranging from 0.90 to -0.93 cm^2/month, and 60% showed positive growth. From March 2008 to September 2012, mean growth once again increased to 0.31 (±0.2 SEM) cm^2/month, ranging from 1.56 to -0.85 cm^2/month, and 64% showed positive growth.

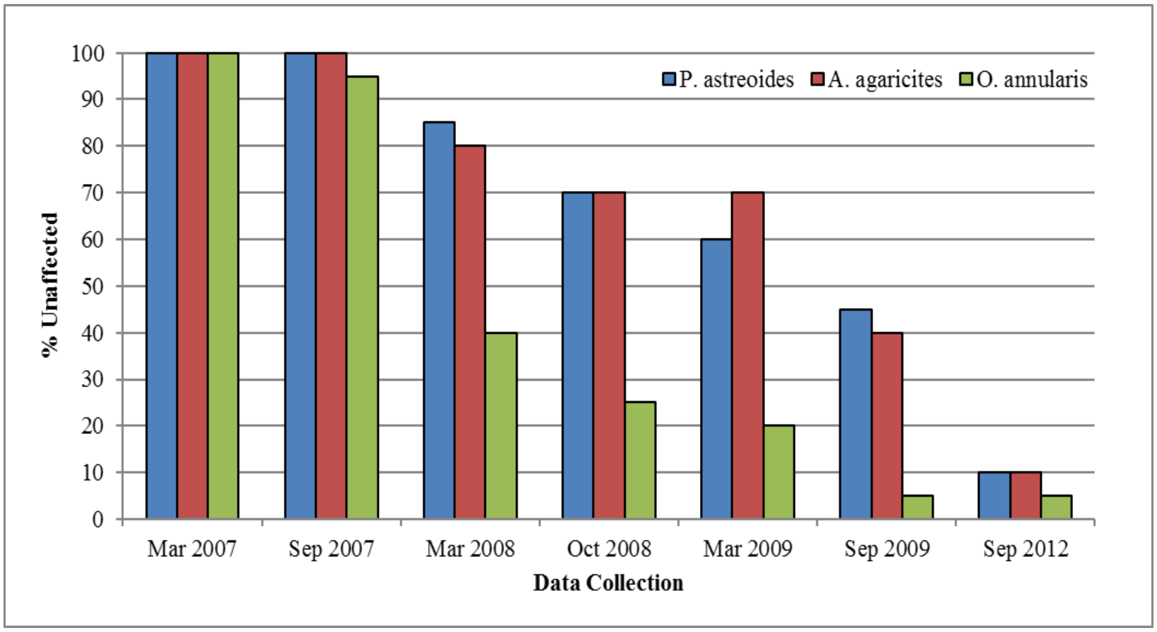


Figure 4.23 Percent of healthy coral transplants by species and date that were unaffected by various maladies that contributed to deteriorating health and/or loss of others, including disease, tissue recession, and overgrowth by the sponge *Desmapsamma anchorata*.

For *O. annularis*, from March to September 2007, the mean growth was -1.17 (±0.3 SEM) cm^2/month, ranging from -0.13 to -2.33 cm^2/month, and all colonies showed negative growth (decreased size due to overgrowth and/or tissue recession). From September 2007 to March 2008, mean growth increased to 0.43 (±0.4 SEM) cm^2/month, ranging from 2.85 to -2.42 cm^2/month, and 64% showed positive growth. From March 2008 to September 2012, mean growth once again decreased to -0.97 (±0.3 SEM) cm^2/month, ranging from 0.67 to -2.67 cm^2/month, and 15% showed positive growth.

For *P. astreoides*, from March to September 2007, the mean growth was -0.21 (±0.4 SEM) cm^2/month, ranging from 2.71 to -2.1 cm^2/month, and 40% showed positive growth. From September 2007 to March 2008, mean growth decreased to -1.24 (±0.7 SEM) cm^2/month, ranging from 3.22 to -6.15 cm^2/month, and 37.5% showed positive growth. From March 2008 to September 2012, mean growth was still negative at -0.16 (±0.2 SEM) cm^2/month, ranging from 0.82 to -1.76 cm^2/month, and 53% showed positive growth.

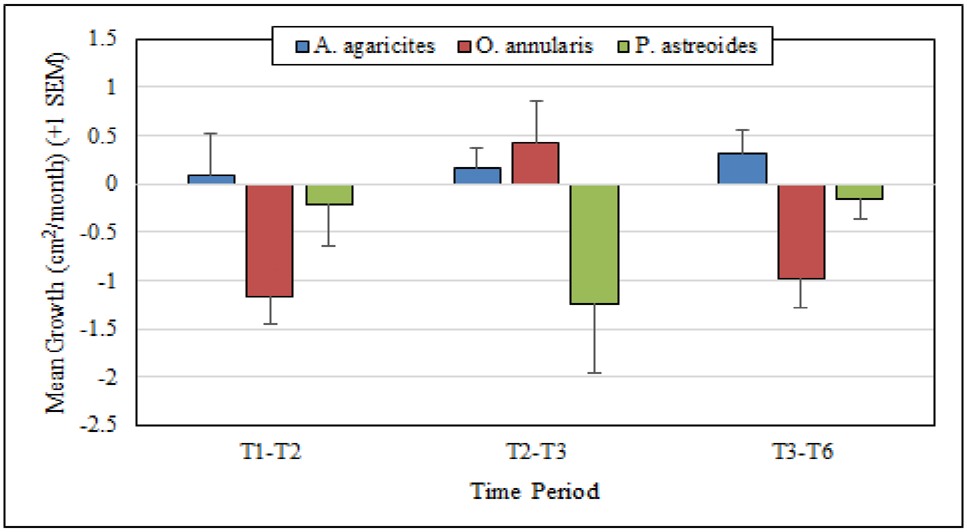


Figure 4.24 Mean monthly growth of natural reference coral colonies by species and date (T1-T2 = March 2007 to September 2007, T2-T3 = September 2007 to March 2008, T3-T6 = March 2008 to September 2009).

The growth trajectories, using mean total area over time, of all natural reference reef corals were highly variable for all species (Figure 4.25), but *Agaricia* had overall positive growth and *Porites* and *Orbicella* had overall negative growth. Tracking individual colonies throughout the entire initial 3-year monitoring period was difficult. Several colonies initially documented and measured during the first monitoring period were unable to be relocated following the passage of Hurricane Dean in August 2007. New colonies were mapped and measured to replace those that were lost, but throughout the remainder of the study several more colonies were lost due to overgrowth by *Dictyota* sp. and *Lobophora variegata* macroalgae. As a result, the sample size for each species ended up being slightly unequal at the end of the study. Trajectories for individual colonies of all three species are displayed in Appendices 4.7-4.9.

There were inconsistencies between the numbers of natural reef reference colonies that were photographed for growth measurements during each monitoring trip. This was due to the loss of several colonies after the first monitoring trip, likely due to the effects of Hurricane Dean in August 2007, as well as difficulty re-locating 100% of the corals after 6 months of overgrowth and routine hydrological or weather related perturbations. To compensate for this loss, as well as potential additional loss and the necessity for obtaining continuous data for as many corals as possible, the number of corals marked for monitoring was increased for all species. Thus, due to the lack of 100% continuity through time for all the reference corals that were included in the growth analysis, no survival figure similar to Figure 4.22 or 4.23 was created for the natural reef corals.

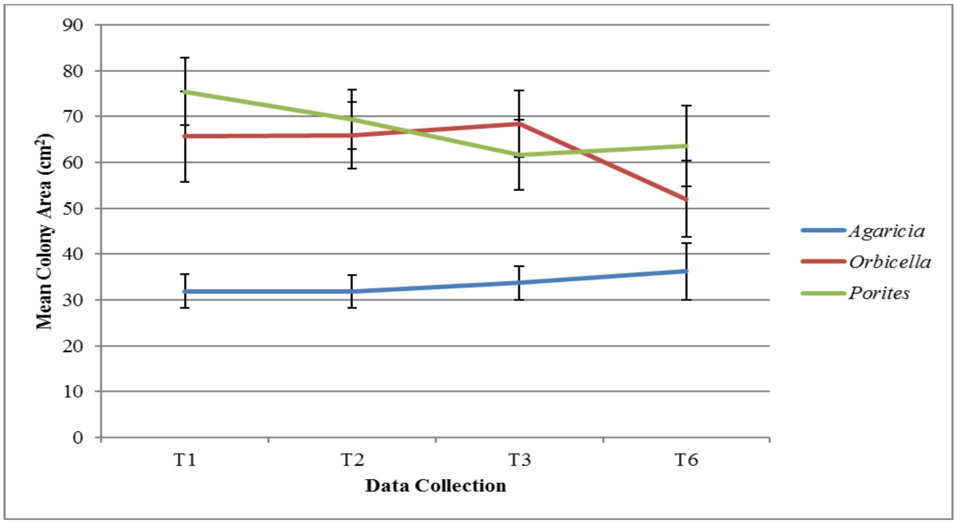


Figure 4.25 Change in the average total colony area over time for coral colonies on the natural reference reef study site.

4.3 Conclusions

Corals recruited to the modules consistently throughout the course of the six-year study, and the number of corals that survived between monitoring trips increased steadily despite a chance of being overgrown by sponges and macroalgae. No coral recruits were found on the natural reef quadrats. In comparison, the results of the *in situ* coral recruitment surveys seem to suggest that coral recruitment on the modules was much higher. This may indeed be the case given the large area of suitable settlement substrate, although the settlement plate results suggest otherwise, showing much higher levels of recruitment onto plates deployed on the natural reef at both the Puerto Morelos and Akumal study sites.

It has been said that coral larvae must run a gauntlet of stressors and bottlenecks as they go through sequential life history stages, and new coral recruits are especially vulnerable when confronted with mature or fully established benthic communities (Vermeij, 2006; Ritson-Williams et al., 2009). This may help to explain the exceptionally low rates of coral recruitment onto the natural reef quadrat areas in Puerto Morelos.

However, there were also other environmental factors, such as sedimentation, that may have contributed to this particular outcome. Even something as ubiquitous as turf algae, with its inherent ability to trap sediments, has been shown to impede settlement of coral larvae (Arnold et al., 2010). The natural reef quadrat survey locations were chosen specifically for their lack of pre-existing benthic biota and perceived area available for settlement of new recruits e.g. the "free space" that important for settling larvae (Gaines and Roughgarden, 1985; Connell, 1997). However, those locations were vacant at the beginning of the study for a good reason. On every monitoring trip, the majority of the quadrat areas were covered with turf algae that trapped fine silt and sand and created a thick layer of smothering sediment that was not conducive to coral settlement. Further, at times there was abundant dead seagrass and macroalgal detritus from *Dictyota* sp. and *Halimeda* sp. on the natural reef, which was more protected from strong currents and heavy seas than the module deployment field. These factors, turf algae and increased protection from currents, likely contributed heavily to the greater sediment buildup at the natural site. There was also usually a fairly solid coating of sediment and small debris on the external surfaces of the modules, increasingly so as their benthic communities and ability to trap sediments developed over time. However, their vertical and near-vertical surfaces and placement in a higher energy environment probably prevented the sediment from packing on as solidly as it did on the natural reef quadrats.

The large number of corals that recruited onto the modules suggest that post-settlement mortality, rather than depauperate larval supply, is largely responsible for shaping community composition on local reefs, at least for brooding species. Since 95% of the corals that recruited to the modules were of a single species, *Porites astreoides*, and the number of corals that recruited onto the settlement plates was very low, drawing conclusions about larval supply and post-settlement mortality for other species is problematic using this dataset. This caveat is especially noteworthy considering that coral assemblages on local natural reefs were much more diverse than what was observed on the modules. Another recruitment study carried out in the northern Mesoamerican Barrier Reef System (MBRS) by Rodriguez-Martinez et al. (2011) suggested that a high density of small colonies was enough evidence to support a conclusion that coral recruitment rates were high, but the probability of surviving to a larger size was low. They suggested that corals that approach or exceed 40cm in diameter have a much greater likelihood of survival. Thus it appears probable that the transplant size (~10cm diameter) that was established at the beginning of the study for transplants, during collection of 'corals of opportunity' from the donor reef, did not convey upon the transplants any significant size advantage that larger colonies would have had.

Overgrowth by the sponge *D. anchorata* was likely the most significant influence affecting development of the coral community on the modules, as well as the fate of the coral transplants. The change in density of new recruits on the modules through time can be described as being inversely parabolic in shape (see Figures 4.3 and 4.4), with greater densities recorded at the beginning and end of the study, a trough in the middle, and seasonal oscillations overlaid throughout. Decreasing density coincided with increasing percent coverage of sponges. In another study in Belize, sponge overgrowth accounted for 50% of coral spat mortality on settlement plates (Arnold and Steneck, 2011). Other studies have shown that the amount of sponge overgrowth and sponge-related mortality affecting corals on natural reefs is more dependent upon coral cover and sponge species composition than it is on the abundance of sponges (Aerts and van Soest, 1997; Aerts, 1998). Although sponges other than *D. anchorata* were present on the modules, that species alone contributed half to two-thirds to the total percent coverage by all sponges, and no other species were observed overgrowing the transplants.

In terms of how the experimental treatments affected the total and new coral recruit density, the results do not indicate a strong influence by any of the treatments, with no significant differences having been found in six out of the seven monitoring trips. It is therefore tempting to conclude that given relatively high rates of coral recruitment, for brooding species at least, that coral transplantation may not have been effective at boosting coral recruitment on the modules. However, the loss of coral transplants through the course of the study effectively reduced the strength of that treatment as a whole and any effect that may be underlying would be more difficult to detect. Nevertheless, there is some evidence indicating the treatments may have been applying a negative influence because the Controls (absence of treatment) had the highest overall recruit density, although only significant on one occasion. The only significant differences were found in September 2009, after the benthic communities on the modules had been developing for a full three years. At that point in the study, the Controls had significantly higher recruitment than the other treatments, and the Pads treatment was significantly lower. Even though no other significant differences were detected, it is worth noting that the Controls and/or Transplants treatments had higher recruitment than the other treatments for four out of five of the other monitoring trips (Figure 4.2), and the pattern of greater density on the Controls and lower density on the Pads treatment was also present at the very last point of data collection in September 2012 after the benthic communities had a full six years to develop and stabilize.

This effect is likely due almost entirely to the decreased likelihood of post-settlement overgrowth related mortality on the un-treated substrate, and therefore completely independent of any actual direct result of structural uniqueness or provision of higher quality settlement area. That is to say, it is possible that the more complex experimental treatments may have actually had higher rates of recruitment due to the treatments or micro-scale hydrodynamic interactions on and around the various external structural features, but more of those recruits would have been overgrown.

In terms of percent survival of coral recruits, there were also no significant differences detected except for in September 2009 when, interestingly, there was significantly lower percent survival of recruits on the Transplants treatment. However, in September 2012 percent survival was greatest on the Transplants, although not significantly so and only by a small margin. Survival on the Transplant treatment modules was only higher than the other treatments for two out of the five periods between monitoring trips, having been the lowest or among the lowest for the other three.

The results of this study support the conclusions made in Chapter 3, which suggest the additional external structure provided by the Pads, Coral Transplants, and Settlement Plates may be conducive to enhancing the growth of the encrusting sponge, *D. anchorata*, and enabling it to persist on the artificial substrates longer than it might have otherwise. The Control treatment often had the greatest or near greatest numbers of coral recruits (even if not statistically significant). This suggests that the lack of structurally complex surface features did not encourage growth of more highly competitive and fast growing benthic biota as it appeared to doon the other treatments, and this left more space available for coral recruits to settle and grow. In addition, the mean size of the coral recruits was greatest on the Control treatment for the most dominant species (*P. astreoides, S. siderea*, *Agaricia* spp., and *Diploria* spp.).

It is logical that given steady recruitment over time that the total number of recruits would gradually increase despite the effects of overgrowth. Once again it seems likely that the initial population explosions of other faster growing benthic organisms (i.e., *L. variegata* and *D. anchorata*) dominated the space available for settlement and growth on the modules, and this effectively served as a hindrance to coral settlement and prevented higher levels of recruitment and survival. Once the competing members of the benthic community reached a more balanced state of existence, levels of coral recruitment and survival increased due to increased availability of suitable settlement substrate and higher survival rates due to decreased chances of overgrowth.

The vast majority of the corals that recruited to the modules were brooding species, dominated mainly by a single species that was also one of the three chosen transplant species that were used. Interestingly, while not statistical significant, the results suggest that the Coral Transplants may actually be providing some level of influence on settlement of new recruits. Mean density of all recruits on the Transplants was tied for highest with the Controls in September 2007 and October 2008, and second highest behind Controls in both September 2009 and 2012. Additionally, mean new recruit density on the Transplant treated modules (Figure 4.4) was tied for highest with Controls in September 2007, higher than all three in October 2008, and second highest behind Controls in both September 2009 and 2012. Even though the additional external structure that was provided by the transplants may have effectively provided an ideal climbing support for the overgrowing sponge that ended up killing 77% of the coral transplants by the end of the sixth year of the study, it is possible that either the direct reproductive output of the transplanted brooding species and/or their ability to provide positive settlement cues for conspecifics and/or other species' larvae enabled slightly increased recruitment rates towards the end of the study as competition for space with macroalgae and sponges gradually became less of a driving factor.

By the end of the study, greater than 90% of the coral transplants had been killed or almost lost completely due to overgrowth and/or disease. *Orbicella annularis* was the first to be affected, while *A. agaricites* and *P. astreoides* both decreased in overall condition at a similar pace. In the end, there were more *P. astreoides* colonies surviving than the other two species, but not by much. Growth of both the coral transplants and natural reef corals was extremely variable. On the natural reef, the *O. annularis* and *P. astreoides* colonies both had a decrease in mean size over the course of the study, and *O. annularis* was still apparently on a downward trajectory at the end; mean size of *A. agaricites* colonies actually increased slightly. Based on the CPCe analysis of surface area, the transplants grew better than the natural reef corals for the very first part of the study (Mar07-Sep07), indeterminate during the second period (Sep07-Mar08), and the surviving transplants were again growing more rapidly than the reference colonies at the 3-year point. *Orbicella annularis* seems to have been the most sensitive species out of the three chosen for this transplantation experiment, but its use in future transplantation efforts could still be warranted.

There are many benefits to using fast growing and structurally complex species, including greater provision of shelter space, food resources, immediate increases in coral cover, and the potential for asexual reproduction through fragmentation (Harriott and Fisk, 1988; Edwards and Clark, 1999; Abelson, 2006). The benefits of using such species, such as those from the genus *Acropora*, on future experimental restoration projects seem obvious. Results here would suggest their use for transplantation should be delayed until the initial waves of macroalgae and encrusting benthic invertebrate growth reach their peaks and reach a more stable state of existence, greater survival and overall success might be achieved. However, Edwards and Clark (1999) suggested that too much focus has been placed on more rapidly growing and structurally complex or branching species. In the Pacific, these corals generally tend to recruit well on their own, but often do not survive the transplantation and relocation effort as well as slower growing massive corals that recruit more slowly. While no branching species were used in this experiment, a logical deduction would be that their more complex physical structure would have been overgrown by the competing sponges just as rapidly, if not more so, as the less-complex transplant species that were employed here.

There are many reasons to sacrifice the immediate and often short-term increase in coral cover that is associated with utilizing rapidly growing branching species in favor of slow growing massive species, provided they can survive long enough to reach a certain size threshold where their chances of overgrowth or smothering from sedimentation is greatly reduced (estimated >40cm diameter for some species) (Rodriguez-Martinez et al., 2011). One of the desired outcomes of the parent CRTR study was a well-informed list of locally applicable restoration strategies that could be utilized by regional reef managers in times of need. Using 'corals of opportunity' that were collected from a donor reef with minimal impact to natural populations will usually be more likely in Puerto Morelos than utilization of donor material that comes from a dedicated coral nursery until an adequate supply of nursery reared propagules ready for out-planting is established nearby.

Consider what a diver/snorkeler might observe while swimming through a low-relief habitat near a coral reef anywhere in southeast Florida or the Caribbean, or anywhere else in the tropics. That habitat may be strewn with small coral rubble and medium sized boulders or coral heads and interspersed with gorgonians and sponges to varying degrees, with the fish scattered loosely throughout the reef matrix. When a large coral head is encountered in the midst of an otherwise structure-limited habitat, it serves as an oasis of sorts, with sharp increases in fish density and species richness as compared to the surrounding area. Large *O. annularis*, *O. faveolata*, and *Montastraea cavernosa* colonies are structurally and ecologically central to supporting large and diverse faunal assemblages and the productivity of the surrounding area (Walker and Klug, 2015). Under better conditions and with more routine maintenance, the mix of *Orbicella annularis*, *Agaricia agaracites,* and *Porites astreoides* transplants, had they survived the onslaught of sponge overgrowth, may have grown to sufficient size to create a fairly functional approximation of a naturally grown and fully-matured coral head, complete with a healthy entourage of coral reef fishes and new coral recruits that would have in turn helped to repopulate neighboring reef habitats following an ecological disturbance. However, without additional routine maintenance to reduce or eliminate the effects of overgrowth by competing benthic organisms, the use of coral transplants of any species or growth form seems an unwise use of precious reef resources, especially when no local coral nurseries are in place to supply a relevant number of outplants.

Chapter 5 – Study 3: Factors Influencing Development of Coral Reef Fish Assemblages on Artificial Reefs

5.1 Introduction

Coral reef fishes are interesting but extremely challenging animals to study for multiple reasons. They are a diverse group characterized by unique body morphologies and color patterns, and they employ many innovative physical and behavioral adaptations that enable them to survive in a highly dynamic environment. Most reef fishes are relatively small (≤10cm TL), which enables a high degree of maneuverability and ability to evade predators by seeking shelter in small spaces (Ansell et al., 1998). Some are cryptic and reclusive, others are highly mobile, fast moving, and/or skittish. There are many species of coral reef fishes, some resident and some transient, some that are strongly associated with one type of habitat and some that have broad distribution throughout adjacent ecosystems (coral reef, seagrass, mangrove, sand, rubble). Their diets and methods of food acquisition can be extremely variable, and they fill essentially every major niche on coral reefs and other adjacent tropical and subtropical ecosystems (Floeter et al., 2008; Rocha and Bowen, 2008). The environment in which reef fishes exist is highly diverse and complex, both in terms of physical structure and the multitude of interacting variables in play at any given time. On a system-wide abiotic scale, reefs are influenced by hydrodynamic forces (tides, currents, wave action, and extreme weather events), terrigenous influences, and large-scale climatic events (i.e., El Niño, global warming, ocean acidification) (Madin and Connolly, 2006; Lowe and Falter, 2015).

Levels of relative abundance and species diversity on any given natural or artificial reef are governed by inherently stochastic biotic factors, such as: settlement and recruitment variability due to spawning seasonality, reproductive status and potential of parent stock, and pulses in larval supply, as well as connectivity with other reef systems, abundance of predators, abundance of previously settled cohorts and competitors (priority effects), and interactions with the benthos (Shulman et al., 1983; Shulman, 1985; Doherty and Sale, 1986; Sale, 1991; Seaman and Sprague, 1991; Almany, 2003; Connolly et al., 2005; Almany, 2006). The often-interdependent relationships and interactions between these factors inherently creates a highly variable system. This makes broadly applicable generalizations about what drives observed trends or population levels problematic, especially on small artificial reefs, where a limited supply of shelter and food resources may affect normal interactions between competitors, and benthic communities may be undergoing changes to community structure or various phases of dominance by one group or another as the communities mature. In addition, the number and species composition of fishes found at artificial reefs may be the result of either attraction and/or production (Bohnsack et al., 1989; Pickering and Whitmarsh, 1996; Osenberg et al., 2002)

Logically, reef fish population dynamics on artificial reefs are influenced by the same factors that influence communities associated with natural reefs. However, they are also subject to various resource limitations not typically encountered by fishes associated with natural reef habitats. This is due to the inherent complexity of natural habitats and availability of refuge on multiple scales, and the limited ability for artificial reefs to provide surrogate habitats of equivalent ecological value (Pratt, 1994; Edwards and Gomez, 2007; Burt et al., 2009). Subtle differences in location of the reefs may also lead to different outcomes (Seaman and Sprague, 1991; Sherman et al., 2001). The true complexity, in both form and function, of a healthy coral reef has never been re-created, and likely never will be, and therefore any usage of artificially created reef substrates, no matter how thoughtfully designed or carefully engineered, can only replace natural habitats in a limited capacity (Abelson, 2006; Perkol-Finkel et al., 2006; Edwards and Gomez, 2007). That being said, there is still much value to be gained by refining existing artificial reef technology for future mitigation and restoration applications, as natural reefs will almost certainly continue to be impacted well into the future as human population and coastal development continue to increase worldwide (Pioch et al., 2011a; Pioch et al., 2011b; Pioch et al., in review). Impacts to marine resources, whether intentional (permitted) or unintentional (collateral), go in lock-step with human progress. Artificial reefs are just one of many tools available to resource managers to help compensate for the inevitable loss of ecological goods and services.

Understanding how reef fishes may respond to future restoration efforts using artificial reefs depends on increased understanding of substrate function and interaction between biotic and abiotic factors, what influences settlement and recruitment, what increases survival rates, what provides the best range of shelter options, and how they develop on a long-term scale. For this reason, pilot studies are valuable for determining what factors may have the most influence, both positive and negative, on the direction of community development on restored natural or artificial reef substrates prior to large scale implementation, especially when novel techniques are being utilized. Continued research endeavors into the subtleties of habitat preference and factors that affect community composition are much needed, as are continued investigations into possible restorative pathways to recovery following population decline. Such research is especially important when preventable or reversible anthropogenic impacts are the root causes and direct intervention is warranted to rehabilitate ecosystem function.

Numerous studies have shown that development of reef fish assemblages on artificial reefs are influenced by shelter availability and structural complexity (Hixon and Beets, 1989; Bohnsack et al., 1994; Gilliam, 1999; Sherman et al., 1999; Sherman et al., 2001; Spieler et al., 2001; Walker et al., 2002; Jordan et al., 2005; Sherman et al., 2005; Freeman, 2007). This study builds upon the progress made by several studies utilizing Reefball™ pallet balls as replicate experimental substrate modules (Sherman et al., 2001; Robinson et al., 2008; Quinn, 2009) and takes it a step further by examining how reef fish assemblages develop in response to the application of two independently tested restoration interventions: invertebrate enhancing substrate pads and coral transplants. Settlement plates were also applied to an equal number of modules and evaluated alongside the other two treatments and controls, but the plates were not expected to serve as a means of influencing development of the reef fish community. This study is an attempt to understand the processes that influenced the rate and direction of reef fish assemblage development over the course of six years, and to determine whether the experimental treatments provided any beneficial stimuli that can be applied to future mitigation and restoration efforts to accelerate the return of a more productive and natural state.

5.2 Data Collection and Analysis

Non-destructive visual censuses of reef fishes collected data on abundance and size class for every species observed in direct association or within 1m of the modules. Visual survey data were first recorded on waterproof paper, then entered into Microsoft Excel and proofed for errors immediately upon collection. Summary statistics were utilized to evaluate mean abundance, density, and species richness, and one-way analysis of variance (ANOVA) was performed on log(x+1) transformed data to look for differences among means. Post-hoc analyses included primarily Student Newman-Keuls (SNK) to determine homogenous groupings. Multi-variate analysis utilized multi-dimensional scaling plots (MDS-plots) generated by Primer-E software (Clark, 1993; Clark and Gorley, 2006) to visually examine relationships between assemblage structure and the experimental treatments (controls, pads, transplants, settlement plates), season, and reef type (natural vs. artificial).

As an additional exploratory measure, the analyses were also performed using two truncated datasets that only included species seen with a ≥10% level of occurrence when combined over the course of the study, and a dataset including the remaining <10% level of occurrence species. The full dataset was also evaluated in terms of juvenile abundance, dominant families, size classes, trophic levels, transients vs. residents, and commercially and recreationally important species.

5.3 Results and Discussion

In Akumal, the sampling regime was impacted by the effects of Hurricane Dean in August 2007. No data were collected in September 2007 due to the recent destruction of four out of 12 substrate modules, storm-surge induced relocation of the remaining eight modules to new locations closer to the reef, and massive disturbance to the entire local reef ecosystem. Data collection on both the modules and natural reef resumed in March 2008. During the first data collection in March 2007, fishes on both the modules and natural reef were counted. The complete loss of the pad material and half of the settlement plates necessitated that all modules effectively served as controls from that point onward. Routine sampling continued through September 2009, but no data was collected in September 2012 due to time and weather constraints. Since no treatments were in effect after the first data collection, continued assessment of the Akumal study site served mainly as a means of comparing reef fishes on the modules to the natural reef. In addition, data from Akumal were compared to data collected in Puerto Morelos in order to compare and contrast the two different study sites.

During the six years of the study, a total of 89 visual surveys were conducted in Akumal, and a combined total of 968 fishes from 22 families and 63 species was recorded. Mean abundance and species richness of reef fishes was significantly greater on the natural reef than on the modules (ANOVA, p<0.00001) (Figure 5.1). A total of 9-15 species were recorded on the modules (pads lowest and controls highest in March 2007), and 45 species were recorded on the natural reef. Multi-variate analysis of this dataset by reef type did not reveal clear separation between the natural reef and the modules (Figure 5.2). However, they were not thoroughly intermingled and the natural reef points were more tightly clustered together amongst themselves, with the modules' points appearing more dispersed and variable.

Abundance of fishes in Akumal was unexpectedly low at all survey sites, given the well-developed spur and groove reef structure and seemingly favorable environmental conditions for coral/benthic invertebrate and reef fish community development. However, the prevalence of macroalgal growth and coral disease were noted increasingly throughout the course of the study, and Hurricane Dean impacted the Mesoamerican Barrier Reef System substantially (García-Salgado et al., 2008). The coastal zone in the Akumal area, much like the rest of the Mayan Riviera, has been undergoing rapid development in the form of new hotels and housing for the local population to support the booming tourist industry, and the general decline in reef health in this area has been closely linked to anthropogenic influences (Roy, 2004; Ortiz-Lozano et al., 2005; Bozec et al., 2008; Metcalfe et al., 2011). In 2007 and 2008, decreases in coral cover and increases of algal cover were reported from all monitored MPAs in Quintana Roo, and surveys in Akumal indicated that the reef there was in 'critical' status with a mean of 10% coral cover and 75% algal cover (García-Salgado et al., 2008). To compound the situation, Akumal is located midway between two of the largest and most rapidly developing cities in Quintana Roo: Playa del Carmen and Tulum.

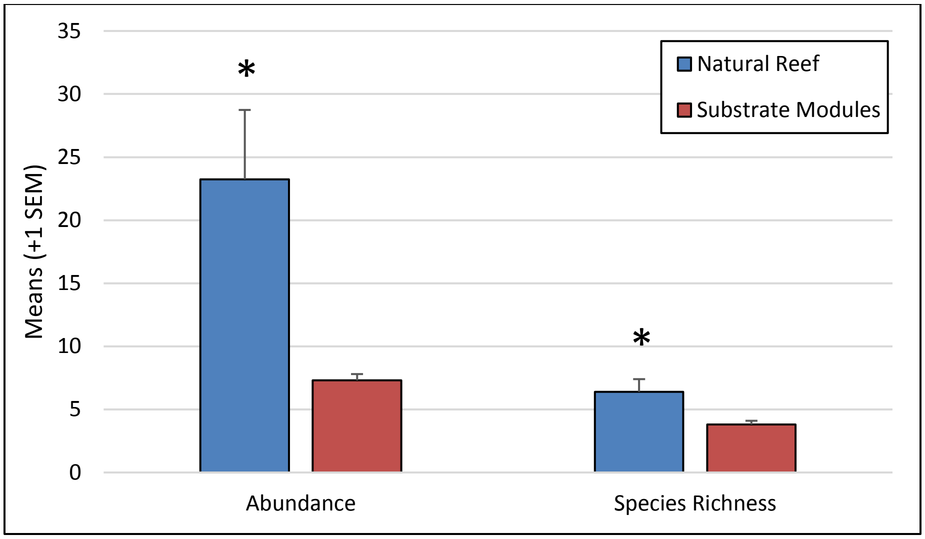


Figure 5.1 Mean abundance and species richness of reef fishes on the natural reef and substrate modules in Akumal, with all years combined. The asterisks indicate significant differences (p<0.00001).

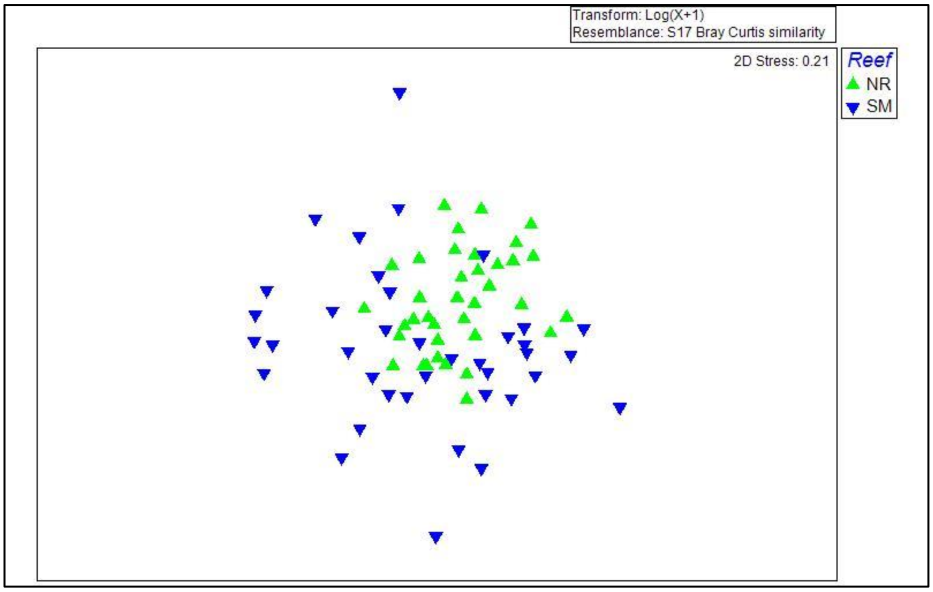


Figure 5.2 MDS-plot of Akumal reef fish abundance data by reef type (natural reef vs. substrate modules).

Following the passage of the hurricane, there was a noticeable decrease in both abundance (Figure 5.3) and species richness (Figure 5.4) on both the natural reef and the modules, although the difference pre- and post-hurricane was not significant when both reef types were combined (ANOVA, mean abundance: p=0.62; mean species richness:

p=0.12). Although neither were statistically significant, when reef types were examined independently from one another, the difference in mean abundance was slightly higher (16.5% higher) on the modules than on the natural reef (ANOVA, p=0.36 and p=0.5, respectively). However, for species richness the difference was higher on the natural reef than the modules (ANOVA, p=0.09 and p=0.91, respectively). Although it was very subtle, there did appear to be an increasing trend in abundance towards the end of the study on both the natural reef and the modules, possibly indicating gradual recovery of local populations towards pre-disturbance/hurricane levels. In addition, multi-variate analysis of the Akumal dataset by date revealed that community structure was slightly different following the hurricane (Figure 5.5). Although there was no distinct clustering present, indicating general similarity between all dates, the majority of the March 2007 (pre-hurricane) points were not as thoroughly intermingled with the others.

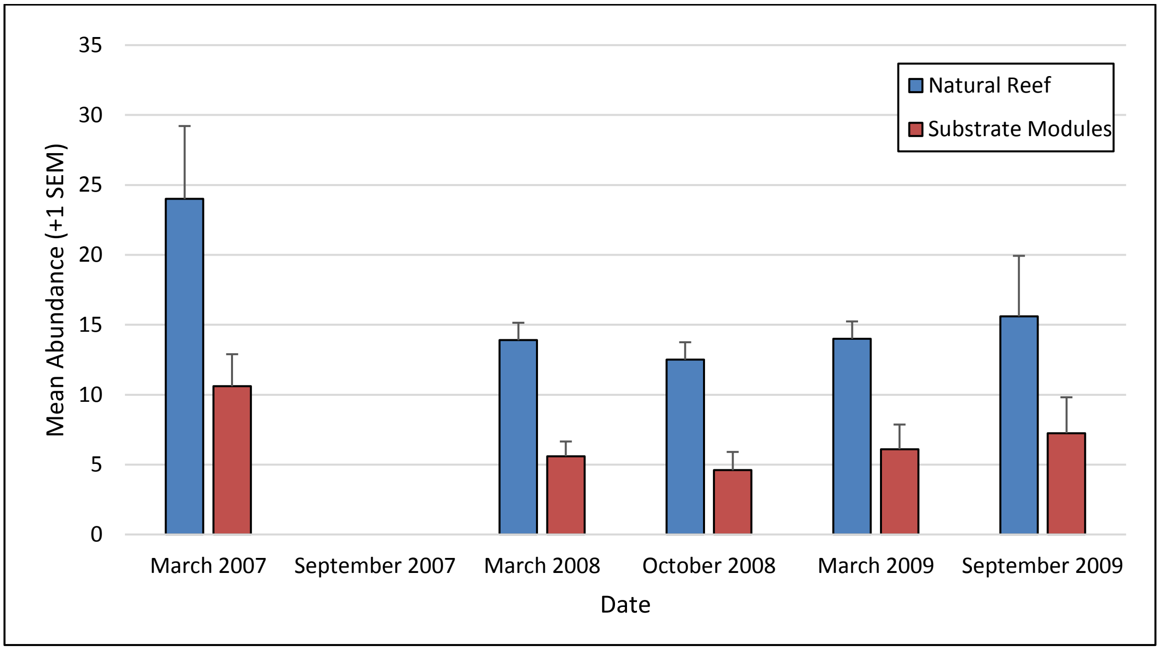


Figure 5.3 Mean abundance of reef fishes on the natural reef and substrate modules in Akumal, by date (natural reef, N=45; substrate modules, N=44). No significant differences were detected (ANOVA, p>0.05).

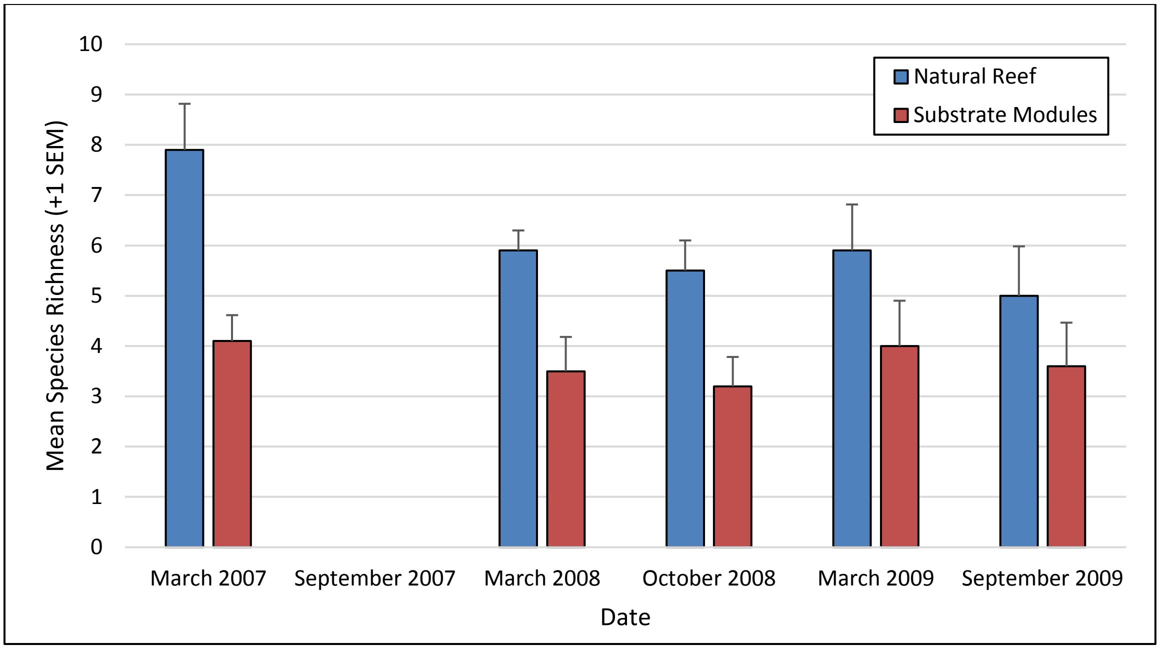


Figure 5.4 Mean species richness of reef fishes for the natural reef and substrate modules in Akumal, by date. No significant differences were detected (ANOVA, p>0.05).

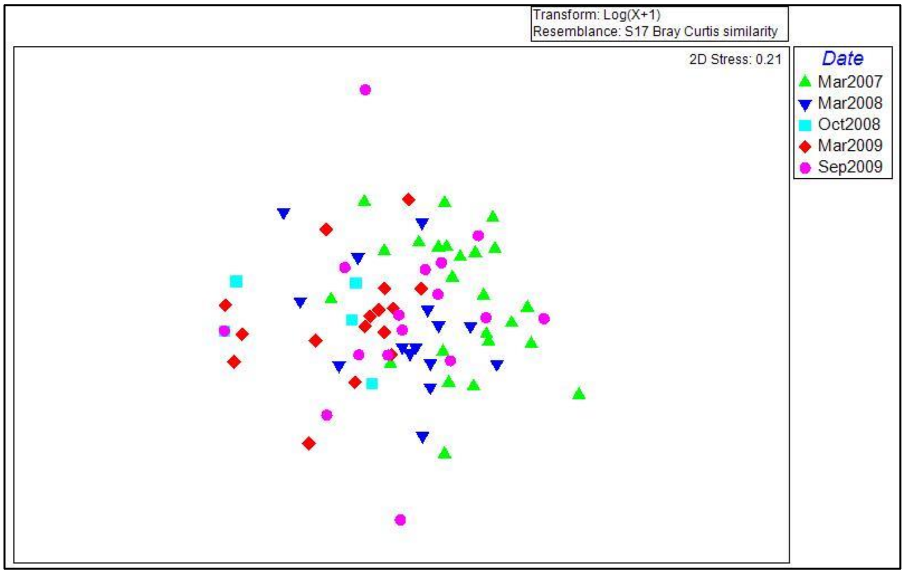


Figure 5.5 MDS-plot of Akumal reef fish abundance data, by date.

In March 2007, when the experimental treatments were still in effect, there were no statistical differences detected for mean abundance (ANOVA, p=0.86), but there were for species richness (ANOVA, p=0.018). Although not statistically significant, both abundance and species richness were higher on the natural reef, and in both cases the Pads and Settlement Plates treatments were greater than the controls (Figure 5.6).

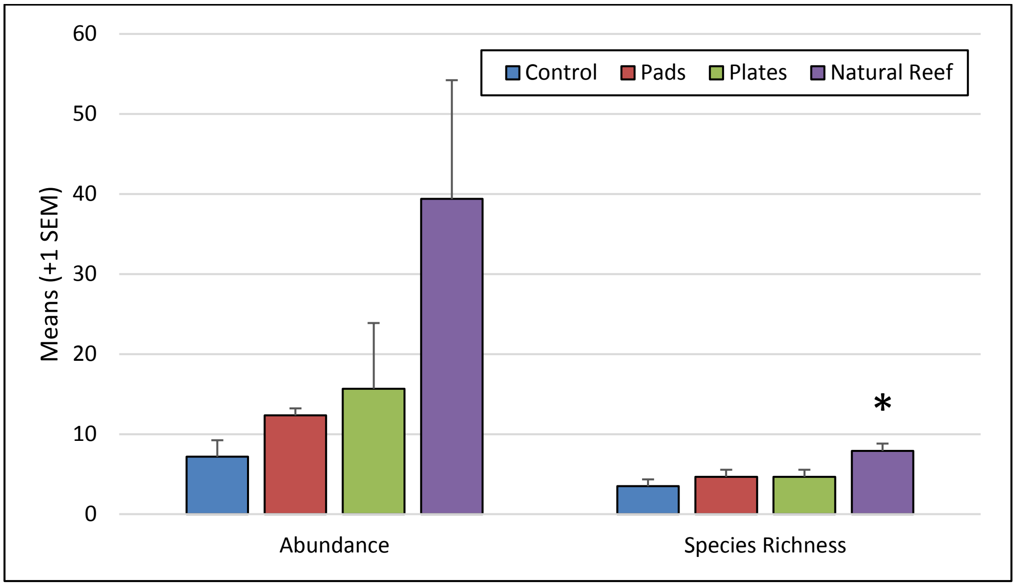


Figure 5.6 Mean abundance and species richness in Akumal for March 2007 only (Control, N=6; Pads, N=3; Plates, N=3). The asterisk indicates a significant difference (ANOVA, p>0.05).

A complete listing of species for Akumal by family, date, and treatment is located in Appendix 5.1. Hurricane Dean made landfall 200 km to the south of Akumal near the city of Chetumal. Although the storm was a powerful Category 5 that affected the entire Yucatan Peninsula, the Puerto Morelos study site was far enough to the north that it was largely unaffected by the storm's passage, and there was no damage to the modules or disruption to the sampling regime. Some minor scouring did occur around the base of some modules, and one was partially buried in sand, but they all remained in place and all of the experimental treatments remained completely intact.

Monitoring of reef fish assemblages on the modules and natural reef in Puerto Morelos took place biannually for a planned period of three years (2007-2009), with one final monitoring trip added at the six-year mark (Sept. 2012). A grand total of 376 visual surveys were conducted over the course of the study, during which a combined total of 10,071 fishes from 34 families and 111 species was recorded. There were some considerable differences in reef fish abundance and species richness between Akumal and

Puerto Morelos (Table 5.1). Mean abundance on the natural reef was greater in Puerto Morelos than in Akumal, although the difference was not significant (ANOVA, p=0.33). Species richness, on the other hand, was significantly greater in Puerto Morelos (ANOVA, p=0.002). On the modules, significant differences were found for both abundance and species richness (ANOVA, p<0.0001 for both), with Puerto Morelos being greater.

Table 5.1 Comparison of mean abundance and species richness of fishes (with standard error) on the natural reef and substrate modules in Akumal and Puerto Morelos, with all dates combined.

	Abundance		**Species Richness**	
Study Site	**NR**	**SMs**	**NR**	**SMs**
Akumal	17.8 ± 2.2	7.3 ± 1.0	6.4 ± 0.5	3.8 ± 0.3
Puerto Morelos	24.0 ± 3.0	31.5 ± 1.6	8.3 ± 0.3	9.1 ± 0.2

5.3.1 Abundance and Species Richness

The remainder of the Results and Discussion section is focused exclusively on the Puerto Morelos dataset unless otherwise noted. None of the experimental treatments were found to produce an assemblage that was consistently greater than the controls in terms of mean abundance or species richness when the dataset was analyzed in its entirety. When the mean abundance values were compared with data from all monitoring trips combined and all species included, no significant differences were found between any of the experimental treatments but the natural reef was significantly lower than the modules (ANOVA, p=0.002) (Figure 5.7). The Pads and Transplants treatments were very similar to the controls with Pads being slightly higher, and the Settlement Plates treatment was situated midway between those and the natural reef. However, the general uniformity in mean abundance between treatments was seldom the case when the data were examined by date.

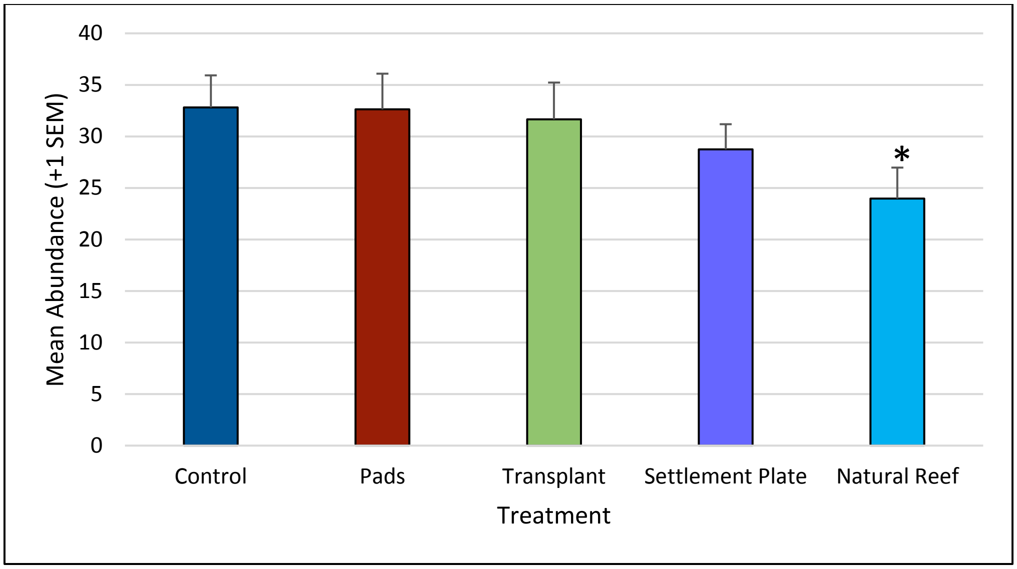


Figure 5.7 Mean abundance for all reef fish species and all years combined, by treatment for substrate modules (N=70) and the natural reef (N=96). The asterisk indicates a significant difference (ANOVA, p<0.05).

Analysis of each separate monitoring trip revealed few significant differences between the treatments (Figure 5.8). There was significant inter- and intra-annual variation documented for all measured parameters, and the treatment(s) with the greatest mean abundance each time fluctuated throughout the course of the study. The Pads treatment had the greatest mean abundance of the module treatments for the first two trips (March and September 2007), although the differences were not significant (ANOVA, p=0.35 and p=0.18, respectively). This may suggest that the padding material was providing some beneficial early influence that enhanced recruitment of fishes. In March 2008, the controls and Settlement Plates treatment were highest, although not significantly (ANOVA, p=0.49). In October 2008, the means for the controls and Settlement Plates treatment were once again higher, although this time significantly (ANOVA, p=0.027). However, even though the ANOVA detected a difference, it was not great enough for the Student Newman-Keuls (SNK) to differentiate between the treatments. In March 2009, the abundances for almost all of the treatments were lower than at any other point in the entire study, similar to or lower than what was observed during the very first monitoring trip. The Transplants treatment and controls were the two highest abundances, although the differences were not significant (ANOVA, p=0.67). The greatest significant differences were found three years into the study in September 2009. Once again, the controls and

Transplants treatment had the greatest mean abundance, and the natural reef was the lowest (ANOVA, p=0.006). Interestingly, three years later in September 2012, the Pads treatment was once again the highest, but the difference was not significant (ANOVA, p=0.62).

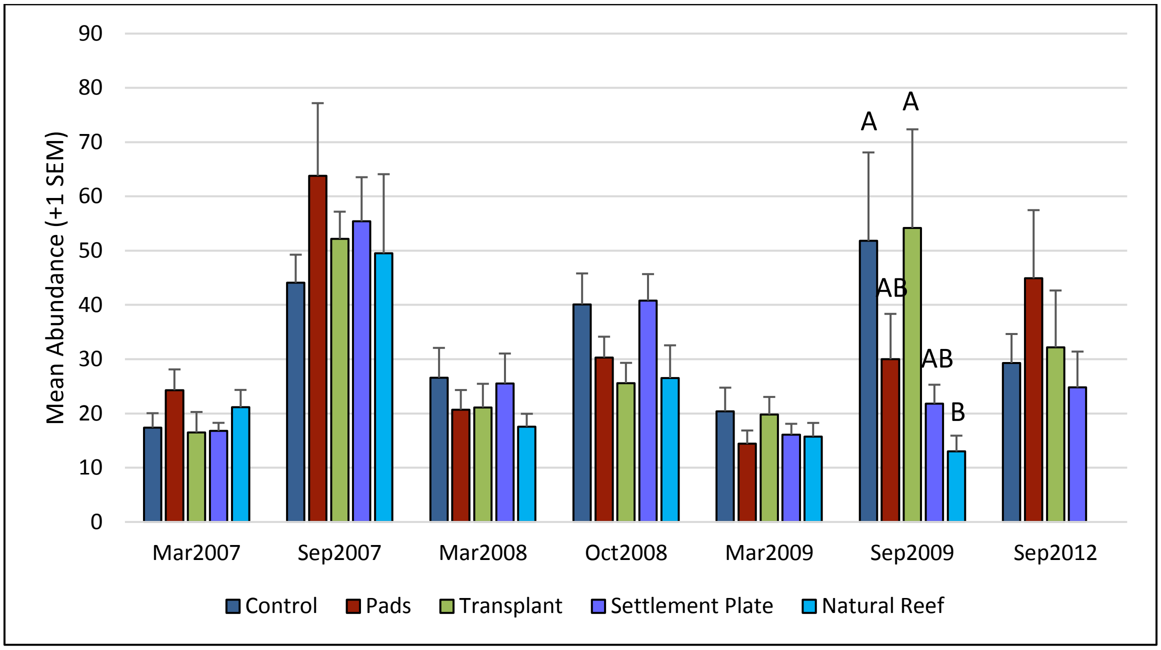


Figure 5.8 Mean abundance of reef fishes by treatment and date. Different letters indicate significant differences between means within groups (SNK, p<0.05). No significant differences were detected except for September 2009; letters have been omitted for clarity.

Reef fish assemblages encountered on the modules in this study were similar to those found on the nearby natural reef and comparable to assemblages documented from previous similar studies of reef fish recruitment to artificial reefs (Quinn, 2009; Jordan, 2010; Kilfoyle et al., 2013) and distribution on natural reef habitats in southeast Florida (Ferro et al., 2003; Baron et al., 2004; Smith et al., 2011; Gilliam et al., 2014; Kilfoyle et al., 2015). A previous study of reef fish populations on natural reefs in the Yucatan (Almada-Villela et al., 2002) reported 225 species, with carnivores being the most abundant and the most important families being Scaridae, Pomacentridae, Labridae, Acanthuridae, Lutjanidae, Haemulidae and Serranidae. Another study in Quintana Roo reported the most abundant species as Bluehead Wrasse (*Thalassoma bifasciatum*), Blue Tang (*Acanthurus coeruleus*), Redband Parrotfish (*Sparisoma aurofrenatum*), and Yellowhead Wrasse (*Halichoeres garnoti*) (Núñez-Lara, 2003).

There were differences in species composition on the modules compared to the natural reef. In Puerto Morelos, the five most abundant species on the modules with all dates, treatments, and controls combined and their percent of the total were: Bluehead Wrasse (18.9%), Blue Tang (8.0%), juvenile Grunts (*Haemulon* spp., 6.0%), Slippery Dick Wrasse (*H. bivitattus*, 5.4%), and Bicolor Damselfish (*Stegastes partitus*, 4.5%). In comparison, the five most abundant species on the natural reef were: Blue Chromis (*Chromis cyanea*, 13.5%), Yellowhead Wrasse (11.6%), Bluehead Wrasse (11.3%), juvenile Grunts (9.8%), and Masked/Glass Gobies (*Coryphopterus hyalinus/personatus*, 9.6%).

Species composition between the Puerto Morelos and Akumal sites was very similar. In Akumal, the top five most abundant species on the modules were: Bluehead Wrasse (24.1%), Slippery Dick Wrasse (12.7%), Sharpnose Pufferfish (*Canthigaster rostrata*, 11.1%), Blackfin Snapper (*Lutjanus buccanella*, 10.1%), and Blue Tang (6.5%). These were closely followed by Ocean Surgeonfish (*A. bahianus*, 5.6%) and Yellowhead Wrasse (3.9%). On the Akumal natural reef, the most abundant species were: Bluehead Wrasse (29.1%), Yellowhead Wrasse (10.3%), Bicolor Damselfish (6.0%), Slippery Dick Wrasse (5.0%), and Sharpnose Pufferfish (3.1%), closely followed by Redband Parrots (2.9%) and Blue Chromis (2.3%).

Mean species richness (Figure 5.9) on the natural reef appeared lower than the modules, although no statistically significant difference was detected (ANOVA, p=0.38). When species richness was examined by date (Figure 5.10), the seasonal pattern of peaks and valleys was also present and very closely aligned with the pattern observed for abundance. For the first data collection, six months post-deployment, richness on the modules appeared lower than the natural reef, although no significant difference was detected (ANOVA, p=0.23). For the following time period, which also coincided with the greatest abundance observed throughout the study, the modules were all higher than the natural reef, although still not significant, but more convincingly (ANOVA, p=0.057). During the following three time periods, there was great similarity of the treatments to one another and to the natural reef (ANOVA, p=0.71; p=0.70; p=0.90, respectively), but at the three-year point (September 2009) the experimental treatments were significantly higher than the natural reef (ANOVA, p=0.039). The difference between the means for September

2009, however, was not great enough for the SNK to differentiate between groups. At the six-year point, September 2012, the treatments were again similar to one another (ANOVA, p=0.81), but the natural reef was not sampled.

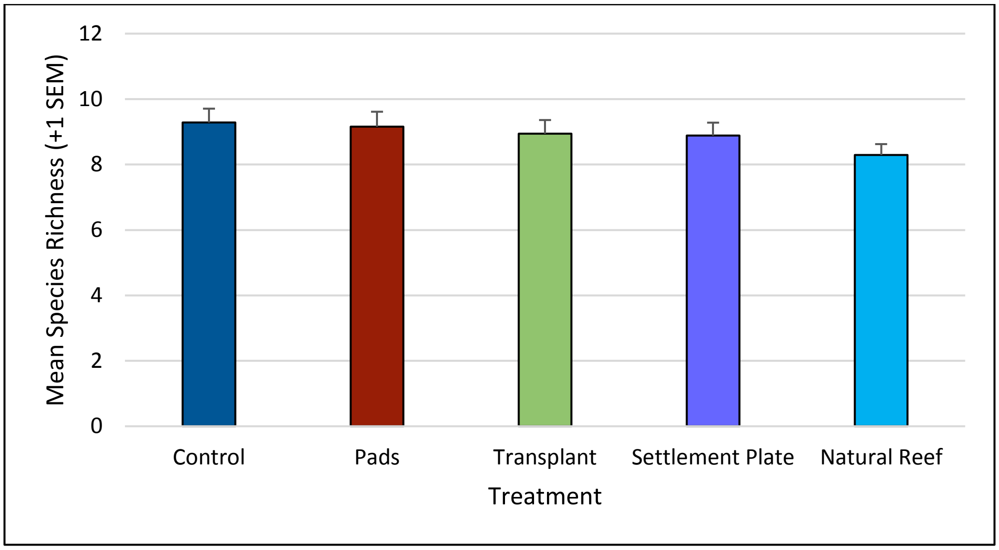


Figure 5.9 Mean species richness of reef fishes for all years combined by treatment (N=70) and natural reef (N=96). No significant differences were detected (ANOVA, p>0.05).

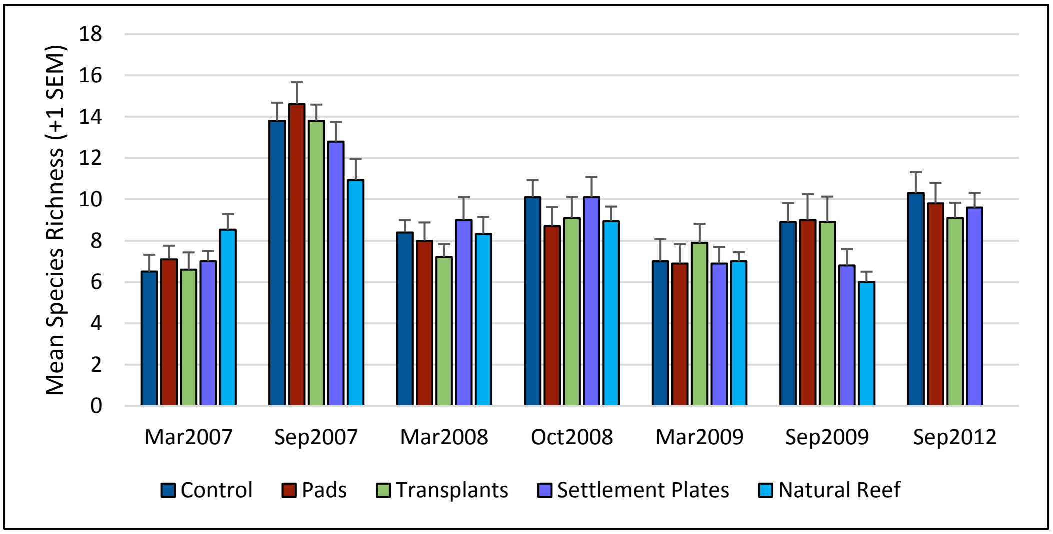


Figure 5.10 Mean species richness for all reef fish species by treatment and date of data collection. There were no significant differences between treatments for any of the sampling dates, with the exception of September 2009 (see text).

When the total number of species encountered on each treatment was compared, there were more total species encountered on the natural reef, and the number of species on the modules was very similar on the treatments and controls (Table 5.2). When the total number of species that had higher abundances within each treatment were compared, the natural reef more than doubly exceeded the treatments and controls (47 species natural reef, 11-17 for the modules). When total abundance from the entire dataset was examined by treatment, there were more total fishes on the Pads treatment than the other experimental treatments, followed by controls, Settlement Plates, and Transplants.

The species assemblages for each treatment were similar to one another in terms of the most abundant species. A full 90% of the total abundance recorded from all treatments and controls combined was represented by only 25 out of 111 total observed species (22.5%), and all shared a top 10 list that included roughly a dozen species present in similar combinations of relative abundance throughout. The following summaries outline the top 10 most abundant species for each treatment.

Control Summary - A total of 1,972 fishes from 24 families and 72 species was recorded from all counts on the controls. The top 10 most abundant species were, in order of decreasing total abundance from all dates: Bluehead Wrasse, Blue Tang, French Grunt (*H. flavolineatum*), Slippery Dick Wrasse, juvenile Grunts, Ocean Surgeonfish (*A. bahianus*), Bicolor Damselfish, White Grunt (*H. plumierii*), Sharpnose Pufferfish, and Cottonwick Grunt (*H. melanurum*).

Treatment Summary: Pads - A total of 2,139 fishes from 23 families and 71 species was recorded from all counts on the Pads treatment modules. The top 10 most abundant species were, in order of decreasing total abundance from all dates: Bluehead Wrasse, juvenile Grunts, Blue Tang, Bicolor Damselfish, Slippery Dick Wrasse, Tomtate (*H. aurolineatum*), Sharpnose Pufferfish, Ocean Surgeonfish, White grunt, and Yellowhead wrasse.

Treatment Summary: Coral Transplants - A total of 1,810 fishes from 20 families and 70 species was recorded from all counts on the Coral Transplants treatment modules. The top 10 most abundant species on the Coral Transplants treatment were, in order of decreasing total abundance with all dates combined: Bluehead Wrasse, Blue Tang, Slippery Dick Wrasse, Bicolor Damselfish, juvenile Grunts, Cottonwick Grunt, Ocean

Table 5.2 Total abundance and percent of the total for each reef fish species recorded in Puerto Morelos by treatment, in decreasing order. Shaded cells had the highest abundance values for each individual species compared to the other treatments. Controls and treatments (N=70), Natural Reef (N=96). Abundance and percent occurrence for each species are organized by family in Appendix 2.

Species List				**Treatments**				
Common Name	**Scientific Name**	**Percent**	**Total**	**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Bluehead Wrasse	*Thalassoma bifasciatum*	21.47	2157	420	473	450	556	258
Blue Tang	*Acanthurus coeruleus*	8.27	831	200	257	169	179	26
juvenile Grunts	*Haemulon* spp.	8.27	831	123	333	111	40	224
Slippery Dick	*Halichoeres bivittatus*	5.68	571	168	126	137	116	24
Bicolor Damselfish	*Stegastes partitus*	5.4	542	92	153	116	89	92
Yellowhead Wrasse	*Halichoeres garnoti*	4.39	441	16	49	70	43	263
French Grunt	*Haemulon flavolineatum*	4.06	408	194	13	55	75	71
Ocean Surgeonfish	*Acanthurus bahianus*	3.6	362	101	62	85	86	28
Blue Chromis	*Chromis cyanea*	3.52	354	7	25	15	1	306
Sharpnose Pufferfish	*Canthigaster rostrata*	3.5	352	52	75	69	84	72
White Grunt	*Haemulon plumierii*	2.69	270	80	55	43	62	30
Tomtate	*Haemulon aurolineatum*	2.61	262	51	115	1	95	-
Glass/Masked Goby	*Coryphopterus hyalinus/personatus*	2.17	218	-	-	-	-	218
Redband Parrotfish	*Sparisoma aurofrenatum*	2.15	216	34	39	37	48	58
Cottonwick	*Haemulon melanurum*	2.03	204	52	6	103	42	1
Rainbow Wrasse	*Halichoeres pictus*	1.83	184	32	34	25	13	80
Yellowtail Snapper	*Ocyurus chrysurus*	1.58	159	33	37	26	32	31
Spotted Goatfish	*Pseudupeneus maculatus*	1.48	149	37	33	39	26	14
Doctorfish	*Acanthurus chirurgus*	1.2	121	26	33	24	18	20
Bluestriped Grunt	*Haemulon sciurus*	0.98	98	26	18	24	13	17
Threespot Damselfish	*Stegastes planifrons*	0.77	77	-	-	1	-	76

Species List				**Treatments**				
Common Name	**Scientific Name**	**Percent**	**Total**	**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Queen Angelfish	*Holacanthus ciliaris*	0.73	73	24	11	20	17	1
Puddingwife	*Halichoeres radiatus*	0.66	66	18	12	15	18	3
Striped Parrotfish	*Scarus iseri*	0.62	62	-	1	-	4	57
Graysby	*Cephalopholis cruentata*	0.55	55	6	15	10	5	19
Clown Wrasse	*Halichoeres maculipinna*	0.48	48	8	6	9	7	18
Sailor's Choice	*Haemulon parra*	0.48	48	9	9	11	19	-
Sergeant Major	*Abudefduf saxatilis*	0.42	42	16	6	3	14	3
Beaugregory	*Stegastes leucostictus*	0.41	41	3	3	1	4	30
Broadstripe Goby	*Elacatinus prochilos*	0.48	48	9	2	7	7	23
Blackfin Snapper	*Lutjanus buccanella*	0.38	38	3	12	11	12	-
Cocoa Damselfish	*Stegastes variabilis*	0.34	34	1	6	3	-	24
Highhat	*Pareques acuminatus*	0.33	33	8	7	12	5	1
Stoplight Parrotfish	*Sparisoma viride*	0.3	30	1	2	3	2	22
Four-eye Butterflyfish	*Chaetodon capistratus*	0.28	28	3	4	5	4	12
Dusky Damselfish	*Stegastes adustus*	0.28	28	2	-	1	1	24
Harlequin Basslet	*Serranus tigrinus*	0.27	27	3	7	6	2	9
Red Lionfish	*Pterois volitans*	0.27	27	8	4	10	5	-
Mutton Snapper	*Lutjanus analis*	0.27	27	8	5	6	8	-
Rock Beauty	*Holacanthus tricolor*	0.26	26	3	8	4	5	6
Goldspot Goby	*Gnatholepis thompsoni*	0.23	23	3	9	3	8	-
Porkfish	*Anisotremus virginicus*	0.23	23	3	4	5	10	1
Yellowtail Parrotfish	*Sparisoma rubripinne*	0.22	22	11	5	3	3	-
Hogfish	*Lachnolaimus maximus*	0.19	19	5	9	2	2	1
Gray Angelfish	*Pomacanthus arcuatus*	0.19	19	8	4	5	2	-
Spotfin Butterflyfish	*Chaetodon ocellatus*	0.19	19	4	4	2	5	4
White Margate	*Haemulon album*	0.17	17	1	1	10	5	-

Species List				Treatments				
Common Name	**Scientific Name**	**Percent**	**Total**	**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Green Razorfish	*Xyrichtys splendens*	0.17	17	1	-	-	1	15
French Angelfish	*Pomacanthus paru*	0.16	16	4	2	5	5	-
Banded Butterflyfish	*Chaetodon striatus*	0.15	15	3	4	4	4	-
Bucktooth Parrotfish	*Sparisoma radians*	0.15	15	-	2	-	6	7
Redfin Parrotfish	*Sparisoma chrysopterum*	0.15	15	6	2	2	3	2
Squirrelfish	*Holocentrus adscensionis*	0.14	14	4	4	3	3	-
Princess Parrotfish	*Scarus taeniopterus*	0.14	14	-	-	-	-	14
Porgy species	*Calamus* sp.	0.13	13	12	1	-	-	-
Red Grouper	*Epinephelus morio*	0.12	12	4	4	2	2	-
Mutton Hamlet	*Alphestes afer*	0.11	11	1	6	1	3	-
Coney	*Cephalopholis fulva*	0.1	10	1	-	-	3	6
Smooth Trunkfish	*Lactophrys triqueter*	0.09	9	1	-	1	3	4
Neon Goby	*Elacatinus oceanops*	0.09	9	1	-	1	2	5
Spotted Moray Eel	*Gymnothorax moringa*	0.07	7	1	1	2	1	2
Bridled Goby	*Coryphopterus glaucofraenum*	0.07	7	-	-	1	3	3
Caesar Grunt	*Haemulon carbonarium*	0.06	6	-	-	4	-	2
Bar Jack	*Carangoides ruber*	0.06	6	-	2	-	1	3
Saddled Blenny	*Malacoctenus triangulatus*	0.06	6	3	3	-	-	-
Longfin Damselfish	*Stegastes diencaeus*	0.06	6	-	1	1	-	4
Lane Snapper	*Lutjanus synagris*	0.06	6	3	1	-	2	-
Brown Chromis	*Chromis multilineata*	0.05	5	1	1	1	1	1
Parrotfish species	*Scaridae* spp.	0.05	5	-	-	1	1	3
Yellowhead Jawfish	*Opistognathus aurifrons*	0.05	5	1	-	-	-	4
Dash Goby	*Ctenogobius saepepallens*	0.04	4	-	1	2	-	1
Yellowfin Grouper	*Mycteroperca venenosa*	0.04	4	1	1	1	-	1
Spanish Hogfish	*Bodianus rufus*	0.04	4	1	-	-	1	2

Species List				Treatments				
Common Name	**Scientific Name**	**Percent**	**Total**	**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Red Hind	*Epinephelus guttatus*	0.04	4	-	1	1	-	2
Saucereye Porgy	*Calamus calamus*	0.04	4	1	-	-	-	3
Sand Tilefish	*Malacanthus plumieri*	0.04	4	2	1	1	-	-
Greenblotch Parrotfish	*Sparisoma atomarium*	0.04	4	2	-	-	1	1
Blackear Wrasse	*Halichoeres poeyi*	0.03	3	-	2	-	1	-
Black Grouper	*Mycteroperca bonaci*	0.03	3	-	1	-	2	-
Great Barracuda	*Sphyraena barracuda*	0.03	3	-	1	-	2	-
Rock Hind	*Epinephelus adscensionis*	0.03	3	-	-	-	-	3
Schoolmaster	*Lutjanus apodus*	0.03	3	-	-	-	-	3
Bluelip Parrotfish	*Cryptotomus roseus*	0.03	3	-	-	3	-	-
Queen Triggerfish	*Balistes vetula*	0.02	2	-	-	2	-	-
Porcupinefish	*Diodon hystrix*	0.02	2	1	1	-	-	-
Green Moray Eel	*Gymnothorax funebris*	0.02	2	1	-	1	-	-
Mahogany Snapper	*Lutjanus mahogoni*	0.02	2	-	-	-	2	-
Spotted Scorpionfish	*Scorpaena plumieri*	0.02	2	1	-	1	-	-
Black Margate	*Anisotremus surinamensis*	0.02	2	-	2	-	-	-
Flamefish	*Apogon maculatus*	0.02	2	-	-	-	2	-
Lofty Triplefin	*Enneanectes boehlkei*	0.03	3	-	-	1	2	-
Vermillion Snapper	*Rhomboplites aurorubens*	0.02	2	-	-	-	-	2
Queen Parrotfish	*Scarus vetula*	0.02	2	-	-	-	-	2
Twospot Cardinalfish	*Apogon pseudomaculatus*	0.01	1	1	-	-	-	-
Blue Angelfish	*Holacanthus bermudensis*	0.01	1	-	1	-	-	-
Spotted Trunkfish	*Lactophrys bicaudalis*	0.01	1	-	-	1	-	-
Redlip Blenny	*Ophioblennius macclurei*	0.01	1	-	1	-	-	-
Lantern Bass	*Serranus baldwini*	0.01	1	1	-	-	-	-
Lizardfish species	*Synodus* sp.	0.01	1	1	-	-	-	-

Species List				**Treatments**				
Common Name	**Scientific Name**	**Percent**	**Total**	**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Scrawled Filefish	*Aluterus scriptus*	0.01	1	-	-	-	-	1
Redspotted Hawkfish	*Amblycirrhites pinos*	0.01	1	-	-	-	-	1
Belted Cardinalfish	*Apogon townsendi*	0.01	1	-	-	-	-	1
Atlantic Trumpetfish	*Aulostomus maculatus*	0.01	1	-	-	-	-	1
Oragespotted Filefish	*Cantherhines pullus*	0.01	1	-	-	-	-	1
Spanish Grunt	*Haemulon macrostomum*	0.01	1	-	-	-	-	1
Butter Hamlet	*Hypoplectrus unicolor*	0.01	1	-	-	-	-	1
Red Goatfish	*Mullus auratus*	0.01	1	-	-	-	-	1
Lesser Electric Ray	*Narcine brasiliensis*	0.01	1	-	-	-	-	1
Rainbow Parrotfish	*Scarus guacamaia*	0.01	1	-	-	-	-	1
Bandtail Pufferfish	*Sphoeroides spengleri*	0.01	1	-	-	-	-	1
Inshore Lizardfish	*Synodus foetens*	0.01	1	-	-	-	-	1
Sand Diver	*Synodus intermedius*	0.01	1	-	-	-	-	1
Yellow Stingray	*Urobatis jamaicensis*	0.01	1	-	-	-	-	1
Total Abundance			**10045**	**1972**	**2139**	**1810**	**1849**	**2275**
Standardized Mean Abundance (fishes per module or count) (±SEM)				**28.2 ±7.6**	**30.6 ±9.3**	**25.9 ±7.5**	**26.4 ±8.7**	**23.7 ±6.5**
Total Species			**113**	**71**	**69**	**69**	**69**	**77**
Highest (excluding NR)				**21**	**20**	**16**	**18**	**-**
Highest (including NR)				**17**	**14**	**11**	**11**	**47**

Surgeonfish, Yellowhead Wrasse, Sharpnose Pufferfish, and French Grunt.

Treatment Summary: Settlement Plates - A total of 1,849 fishes of 20 families and 71 species was recorded from all counts on the Settlement-Plate treatment modules. The top 10 most abundant species on the Settlement-Plates treatment were, in order of decreasing total abundance from all dates: Bluehead Wrasse, Blue Tang, Slippery Dick Wrasse, Tomtate, Bicolor Damselfish, Ocean Surgeonfish, Sharpnose Pufferfish, French Grunt, White Grunt, and Redband Parrotfish.

Natural Reef Summary - A total of 2,301 fishes of 25 families and 77 species was recorded from all counts on the natural reef. The top 10 most abundant species on the Natural Reef were, in order of decreasing total abundance from all dates: Blue Chromis, Yellowhead Wrasse, Bluehead Wrasse, juvenile Grunts, Glass/Masked Goby, Bicolor Damselfish, Rainbow Wrasse (*H. pictus*), Three-spot Damselfish (*S. planifrons*), Sharpnose Pufferfish, and French Grunt (*H. flavolineatum*).

Assemblage structures on the modules and natural reef were similar, but not identical. Out of the 111 species encountered, 20 species from 12 families were found exclusively on the natural reef. In contrast, there were 38 species from 22 families found exclusively on the modules (Table 5.2 and Appendix 5.2). The species that were found exclusively on the natural reef were: Lesser Electric Ray (*Narcine brasiliensis*), Yellow Stingray (*Urolophus jamaicensis*), Inshore Lizardfish and Sand Diver (*Synodus foetens* and *S. intermedius*), Atlantic Trumpetfish (*Aulostomus maculatus*), Rock Hind and Butter Hamlet (*Epinephelus adscenscionis* and *Hypoplectrus unicolor*), Belted Cardinalfish (*Apogon townsendi*), Schoolmaster and Vermillion Snapper (*Lutjanus apodus* and *Rhomboplites aurorubens*), Spanish Grunt (*Haemulon macrostomum*), Red Goatfish (*Mullus auratus*), Redspotted Hawkfish (*Amblycirrhitus pinos*), Rainbow, Princess, and Queen Parrotfishes (*Scarus guacamaia, S. taeniopterus*, and *S. vetula*), Masked/Glass Gobies (*Coryphopterus hyalinus/personatus*), and Scrawled and Orangespotted Filefishes (*Aluterus scriptus* and *Cantherhines pullus*).

Two species were found exclusively on controls: Twospot Cardinalfish (*Apogon pseudomaculatus*) and Lantern Bass (*Serranus baldwini*); three on the Pads: Blue Angelfish (*Holacanthus bermudensis*), Redlip Blenny (*Ophioblennius macclurei*), and Black Margate (*Anisotremus surinamensis*); three on Coral Transplants: Spotted Trunkfish

(*Lactophrys bicaudalis*), Bluelip Parrot (*Cryptotomus roseus*), and Queen Triggerfish (*Balistes vetula*); and two on Settlement Plates: Flamefish (*A. maculatus*) and Mahogany Snapper (*L. mahogani*).

Dorsoventrally compressed benthic predators that are adapted to burying in the sand, such as the stingrays and lizardfishes, are not often found in association with artificial reefs (Quinn, 2009). Although, one large Peacock Flounder (*Bothus lunatus*) was observed at the top of a module eating juvenile grunts (not during a survey). Trumpetfish are often associated with vertical structure that provides them with shelter and camouflage, such as sea fans and gorgonians; commodities that were in relatively short supply on the modules for the majority of the study period. It was, however, interesting that the filefishes, the serranids, the snappers, and the Spanish Grunt were not encountered on the modules, as it stands to reason that all of these species could reasonably be expected to have taken advantage of the structural complexity they provided. However, many were single or low occurrences, and there were many other species of serranids, lutjanids, and haemulids found on the modules. The cardinalfish and hawkfish are both cryptic species and also single occurrences in this study.

Squirrelfish and Porcupine Pufferfish, nocturnal predators that generally stay hidden or near or within protective shelter during the day, were found on the modules in 14 separate occurrences. The triggerfish was possibly a chance occurrence, being a regular inhabitant of the barren and relatively sparsely populated sand and rubble plain of the module deployment field. The same goes for the three Great Barracudas that were encountered, which have wide ranging territories and which on each occasion when the species was recorded followed divers from one module to another. The Saddled Blenny is a species that was likely present on the natural reef as well, but the reef there had greater structural complexity than the modules and more places for a small cryptic species to evade detection.

5.3.2 Community Structure and Multi-Variate Analysis

The results of the multi-variate community level analysis, with Primer-E software (Clark and Gorley, 2006), largely echoed the previously discussed findings of the summary analyses performed on the mean abundance and species richness data. An MDS-plot of each module by treatment revealed that the treatments and controls had thoroughly intermingled distributions, suggesting there was very little difference in community structure and that the controls and experimental treatments all performed similarly to one another (Figure 5.11). As was likewise the case for the abundance and species richness data, multi-variate analyses indicated there was considerable difference in assemblage structure between the modules and the natural reef (Figures 5.11 and 5.12). Differences in assemblage structure between natural and artificial habitats are common (Carr and Hixon, 1995, 1997; Hackradt et al., 2011; Kilfoyle et al., 2013; Kojansow et al., 2013), although it has yet to be documented on artificial reefs deployed in the study area (i.e., the Yucatan peninsula). This is mainly due to the fact that, until this study, no comprehensive evaluation of artificial reef performance had been undertaken there and the use of artificial reefs was relatively limited.

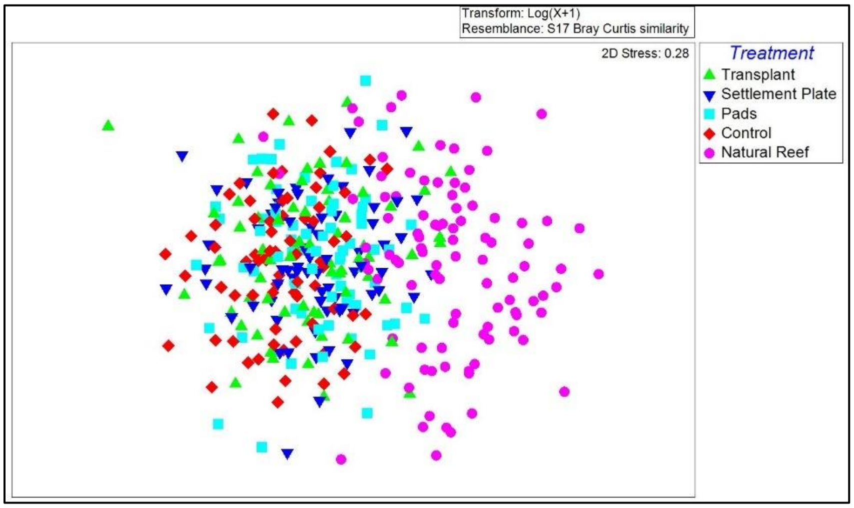


Figure 5.11 MDS-plot reef fish abundance data by treatment, with all dates combined.

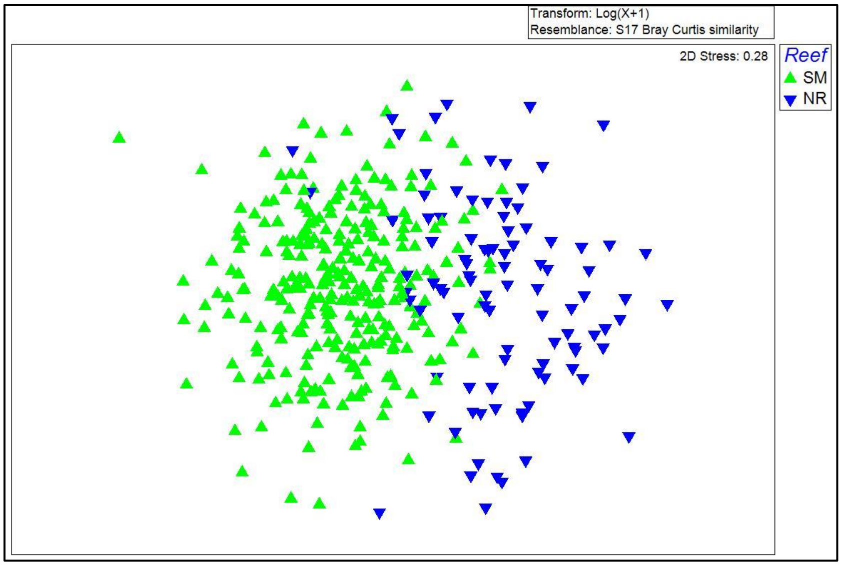


Figure 5.12 MDS-plot of reef fish abundance data by reef type (natural reef vs. substrate modules).

When the cluster analysis and pairwise tests between groups were examined (Figures 5.13 and 5.14), there was the previously mentioned distinction between the natural reef and the modules, but also a closer association of the Pads and Transplants treatments. This lends support to the supposition that these two restoration interventions were having an effect on community structure.

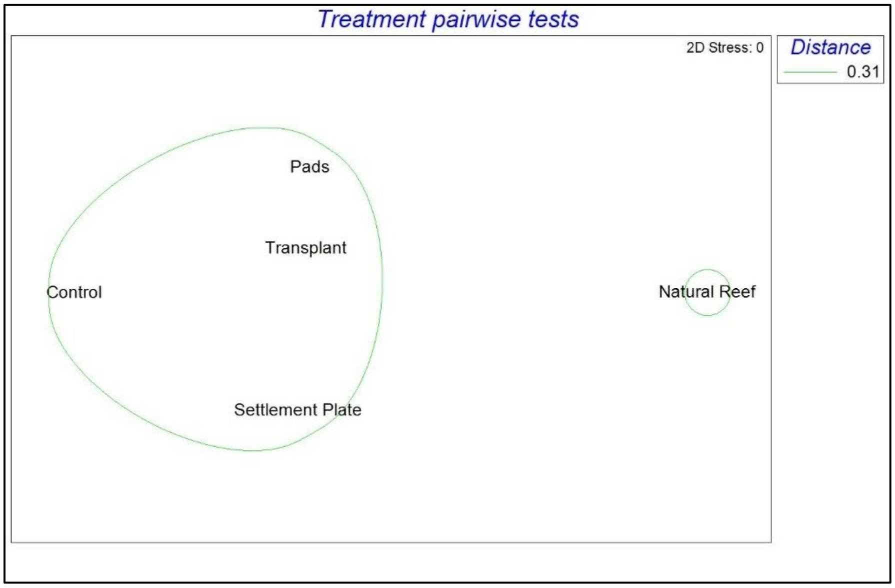


Figure 5.13 Cluster analysis reef fish abundance data by treatment with all dates combined.

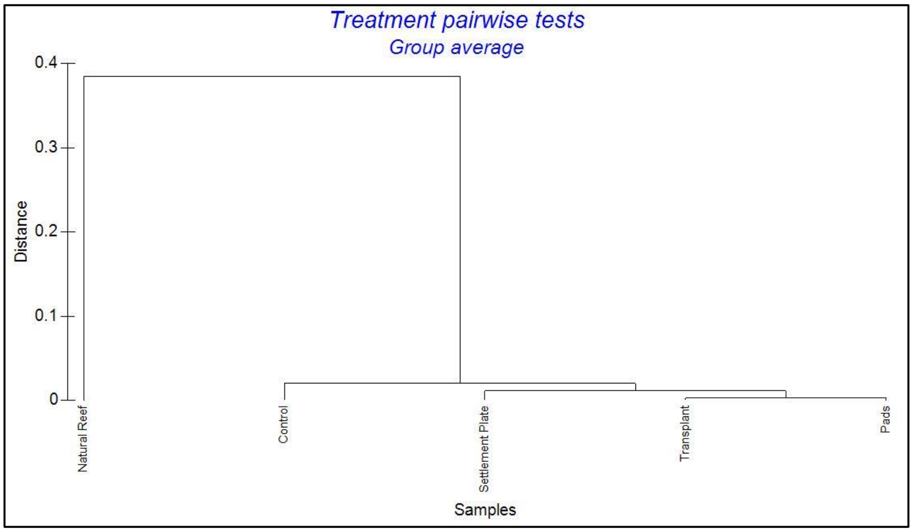


Figure 5.14 Pairwise tests of reef fish abundance data between groups for all years with all species combined.

After it was established that the fish assemblage on the natural reef was dissimilar from the assemblages found on the modules, a more in-depth multi-variate analysis was performed that looked exclusively at the relationships among the controls and experimental treatments with the natural reef completely removed from the analysis. This enabled a more precise examination of the relationships that existed among assemblage structures for the treatments and controls.

A 2Stage multi-variate analysis was performed with the natural reef data removed, which essentially condensed all of the individual samples from each treatment and each monitoring trip into one sample unit, and then compared all of the treatments over time to compare the relationships on a more simplified and streamlined basis (Figure 5.15). Once again, the relationships between treatments were very similar to one another, however the controls were somewhat more spread out, as was the Settlement Plate treatment, and the Transplants and Pads treatments were slightly more condensed and clustered together (Figure 5.16).

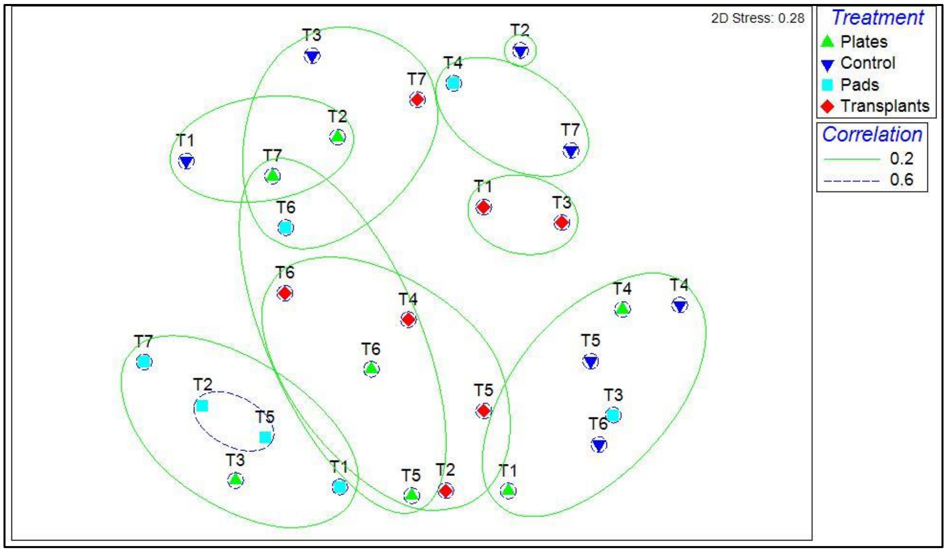


Figure 5.15 3-dimensional view of 2Stage MDS-plot of reef fish abundance data with the natural reef removed and all years combined (T1=March 2007, T2=September 2007, etc.).

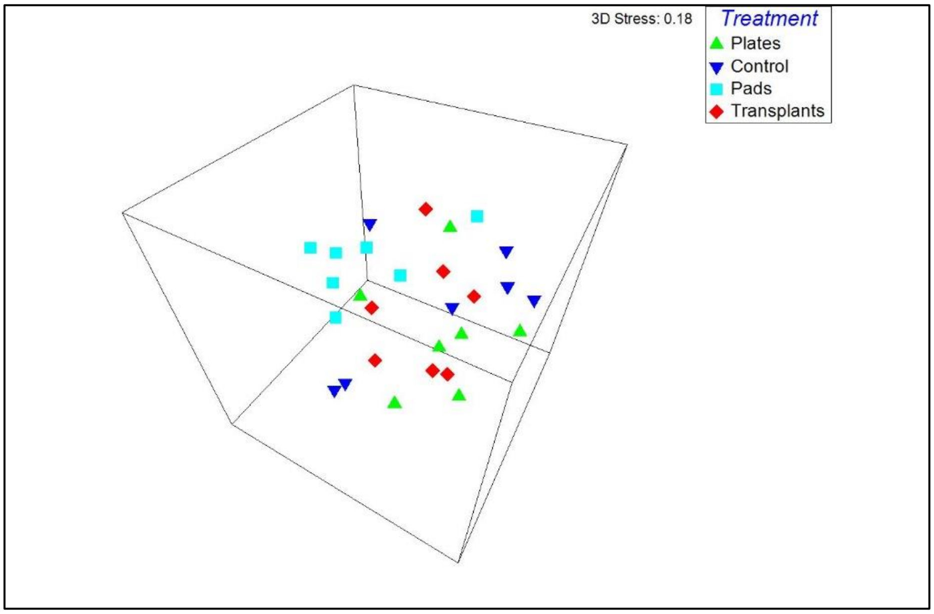


Figure 5.16 3-dimensional view of 2Stage MDS-plot of reef fish abundance data with the natural reef removed and all years combined.

2Stage cluster analyses were also performed for each monitoring trip individually and for all trips combined (Figure 5.17). Assemblage structure for the Pads treatment was different than the others for the first date following module deployment, March 2007 (Figure 5.17-A). Following that, in September 2007 and March 2008 (Figures 5.17-B and

C), the assemblages for three out of four of the treatments were somewhat closely grouped, with the Pads and Settlement Plates slightly more similar and the controls remaining well outside. For the next two sequences in the time series, October 2008 and March 2009 (Figures 5.17-D and E), separation between experimental treatments and the controls was not well defined. This time sequence also happened to coincide with the some of the greatest percent coverage of macroalgae and benthic invertebrates on all treatments (see Chapter 3).

A full three years following deployment, in September 2009 (Figure 5.17-F), three of the experimental treatments once again clustered separately from the controls, with Pads and Settlement Plates treatments being more closely aligned than the Transplants treatment. At the six-year point, in September 2012 (Figure 5.17-G), any sort of long-term pattern is unclear once again, although the Pads and Settlement Plates treatments were clustered together once again and the controls and Transplants treatment were clustered together.

Finally, when all dates were combined (Figure 5.17-H), no distinct trend was apparent, and the Transplants were now further removed from the other treatments, with Pads and Settlement Plates clustered together. This dataset was highly variable, which reduced the power of the multi-variate analyses by masking subtle underlying trends. These results do not present a clear trajectory of assemblage development on any of the treatments, and are difficult to reconcile at this scale.

It is unclear why the Pads and Settlement Plates treatments would have greater similarity to one another than to the Transplants or controls when all dates were combined. MDS-plot spacing of the treatments relative to one another was highly variable within the interim years, but it appeared that as benthic community was maturing (see Ch. 3), the Pads treatment might have been supporting an assemblage that was slightly different than the other treatments when compared along the same timeline. Interestingly, a 3-dimensional representation of the 2Stage analysis from September 2012, at the six-year point in the study, showed that the Pads treatment may have been more dissimilar to the other three experimental treatments (Figure 5.18). However, an MDS plot of the full September 2009 dataset, three years earlier, revealed that the assemblage structure for each experimental treatment was still highly intermingled at that point (Figure 5.19).

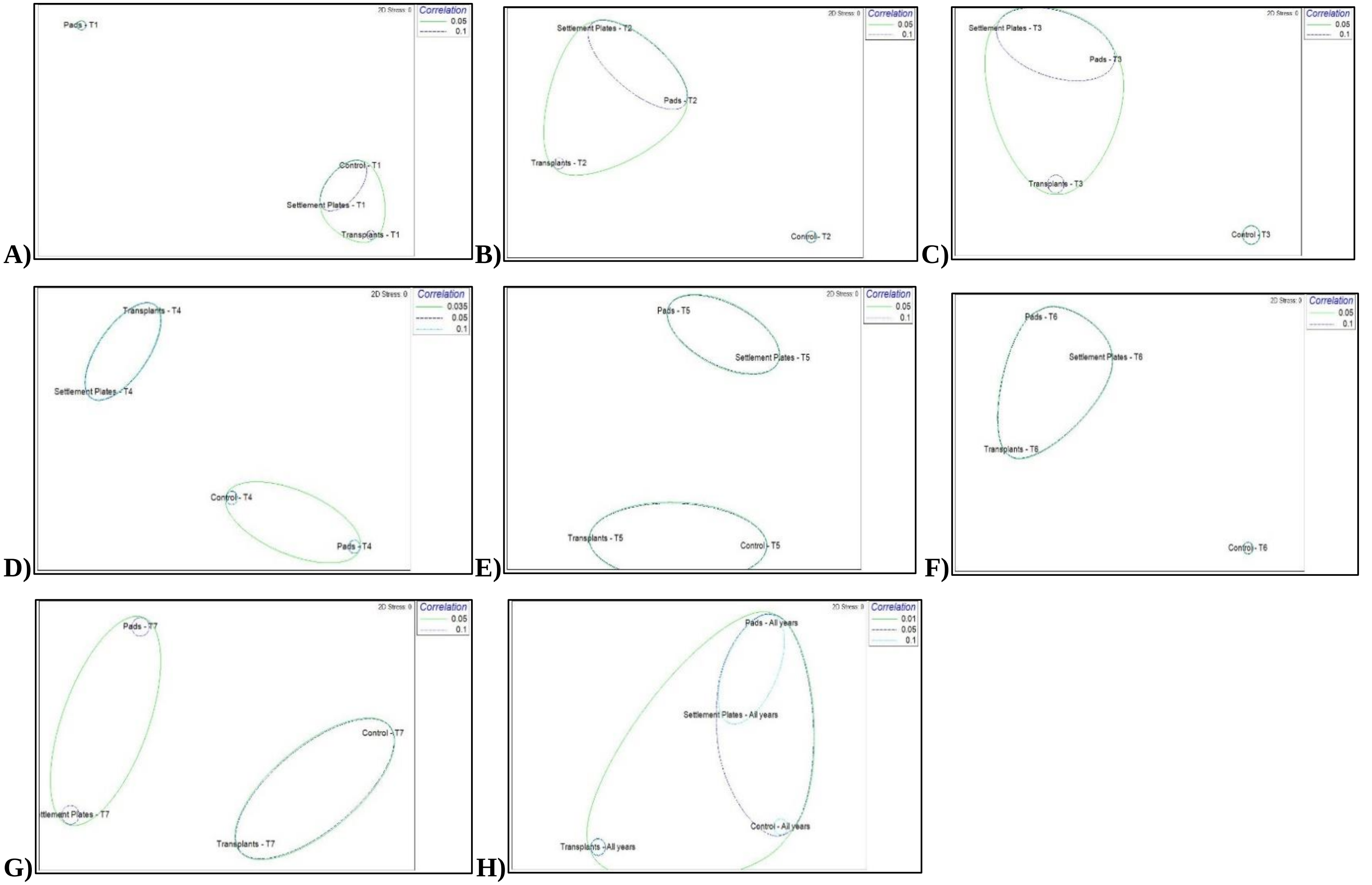


Figure 5.17. 2Stage cluster analyses of reef fish abundance data, by date: **A)** March 2007, **B)** September 2007, **C)** March 2008, **D)** October 2008, **E)** March 2009, **F)** September 2009, **G)** September 2012, **H)** all dates combined.

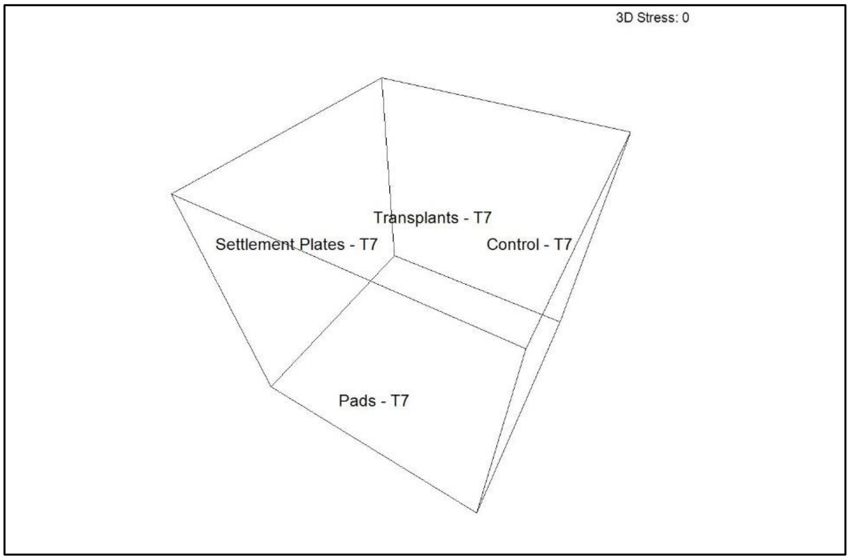


Figure 5.18 3-D MDS-plot of reef fish abundance data by treatment from September 2012, with the natural reef removed.

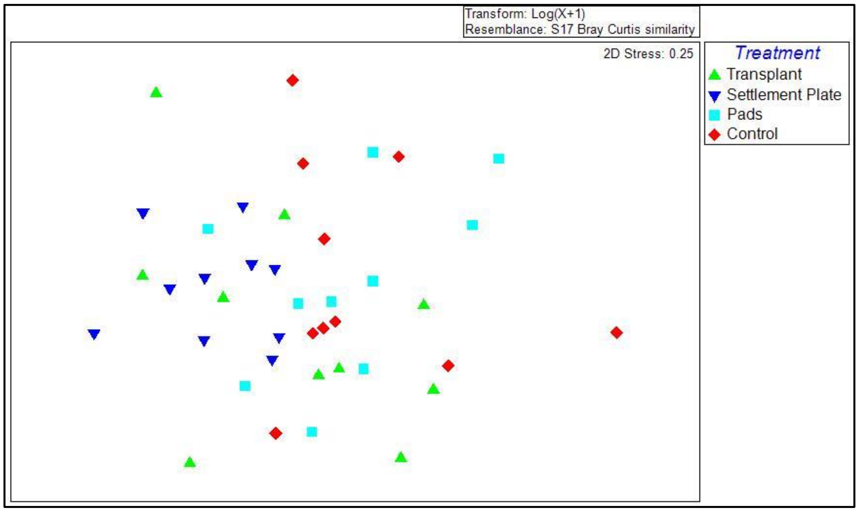


Figure 5.19 MDS-plot of reef fish abundance data for September 2009, with the natural reef removed.

In summary, there was some evidence from the mean abundance and multi-variate analyses supporting a conclusion that some of the experimental treatments were having more of an influence than others on the abundance and assemblage structure of reef fishes on the modules. Even if they were not significantly increasing the overall total or mean number of fishes, one or more treatments may indeed have been supporting assemblages that were developing on a slightly different trajectory than those found on the control modules.

5.3.3 Analysis of Modified Datasets

As an additional exploratory measure, analyses of two truncated versions of the dataset were conducted. The first modified dataset consisted of only species that were present with a percent occurrence (*P*) ≥10%. This enabled a comparison of the experimental treatments using only those species that were most responsible for driving the observed trends and relationships between treatments. Out of the 111 total species recorded during this project, 20 (18.6%) of them had a percent occurrence ≥10%, meaning the majority of the species observed occurred infrequently, as either single digit percent occurrences or less (Table 5.2 and Appendix 5.2). Even though fewer in number, the species within the ≥10% group constituted the bulk of the assemblage, 83.3% of the total number of fishes counted during the entire study, and a truncated dataset of these species was further evaluated for their contribution to overall trends of development in abundance, species richness, and assemblage structure. Specific species included in both modified datasets are listed by treatment in Appendices 5.3-5.7.

The second modified dataset consisted of the remaining species observed with <10% occurrence. This resulted in a group of infrequently and/or rarely encountered species, solitary species, commercially and recreationally important species whose populations may be impacted by local exploitation, pelagic species that may occasionally be associated with coral reefs, small and cryptic species, and in many instances species with highly derived morphologies and specialized feeding strategies.

In general, and not surprisingly as they made up 83.3% of the full dataset, removal of the species with <10% occurrence did little to change the relationship between the experimental treatments as described in Figure 5.7, as the ≥10% dataset results were very similar to those using the entire dataset. No significant differences were detected between controls and treatments for abundance or species richness other than the natural reef (ANOVAs: $p<0.00001$ for abundance; $p=0.00014$ for species richness) (Figures 5.20 and 5.21). With the natural reef removed from the analysis, comparing only the controls and experimental treatments, there was no difference detected between any of the treatments and controls for either abundance or species richness (ANOVA, p=0.84 and p=0.77, respectively).

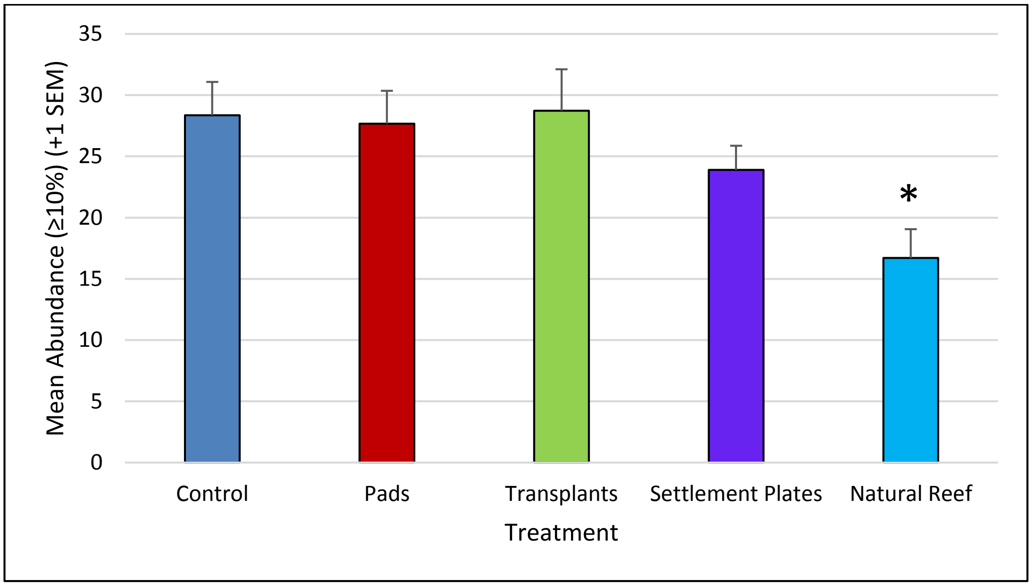


Figure 5.20 Mean abundance of reef fish species with ≥10% occurrence. The asterisk indicates a significant difference (ANOVA, p<0.05).

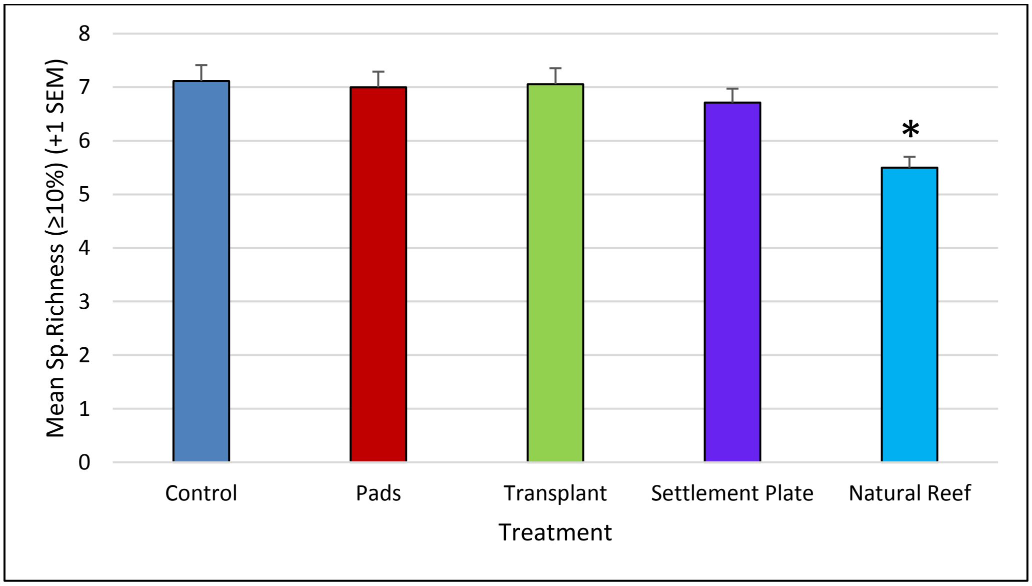


Figure 5.21 Mean species richness of reef fish species with ≥10% occurrence. The asterisk indicates a significant difference (ANOVA, p<0.05).

However, when this modified dataset was examined by date (Figure 5.22), some significant differences were revealed, although, as expected, the patterns were similar to what was seen in the unmodified data (Figure 5.8). In September 2007, there were significantly fewer fishes on the natural reef and all treatments were similar but slightly higher than the controls (ANOVA, p=0.00085). In October 2008, the natural reef was once again lower, and the controls and Settlement Plates treatment were higher (ANOVA, p=0.009). September 2009 was similar in that the natural reef was once again significantly lower (ANOVA, p=0.0025), but the controls and Transplants treatment were the highest.

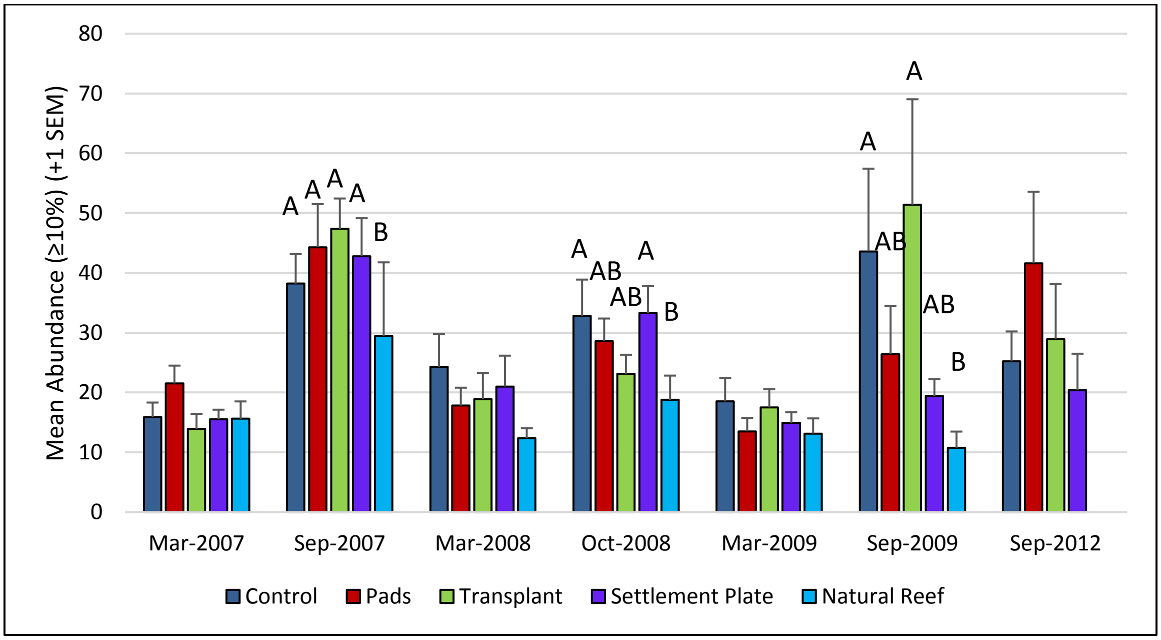


Figure 5.22 Mean abundance of reef fishes by treatment and date, using the ≥10% dataset. Different letters indicate significant differences between means within groups (SNK, p<0.05).

An MDS-plot of the ≥10% data once again reveals a thoroughly intermingled assemblage structure with no clear distinction between controls and treatments (Figure 5.23). Once again, points representing the natural reef are clustered fairly close to one another and poorly intermingled with the other treatments (Figures 5.23 and 5.24), although not quite as distinctly as they were for the MDS-plots created using the entire dataset (Figures 5.11 and 5.12). This indicates that the rarely or uncommonly encountered species that were excluded from the ≥10% analysis were contributing quite a bit to the dissimilarity between the natural reef and the modules.

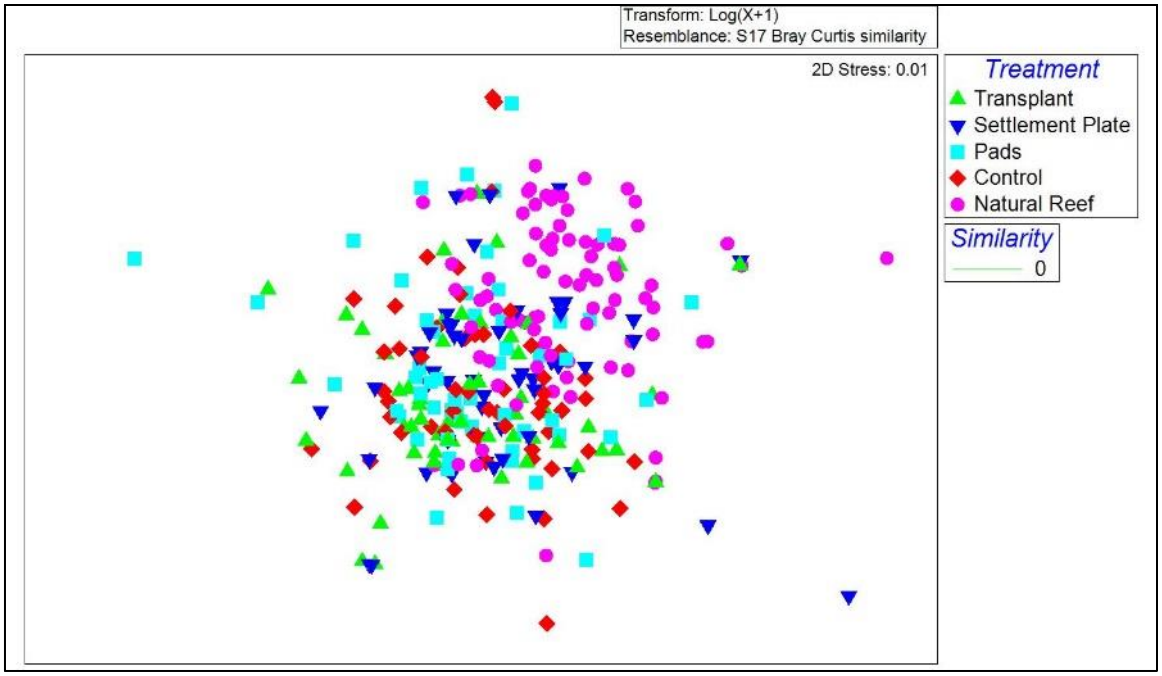


Figure 5.23 MDS-plot of reef fish abundance with all treatments using ≥10% dataset.

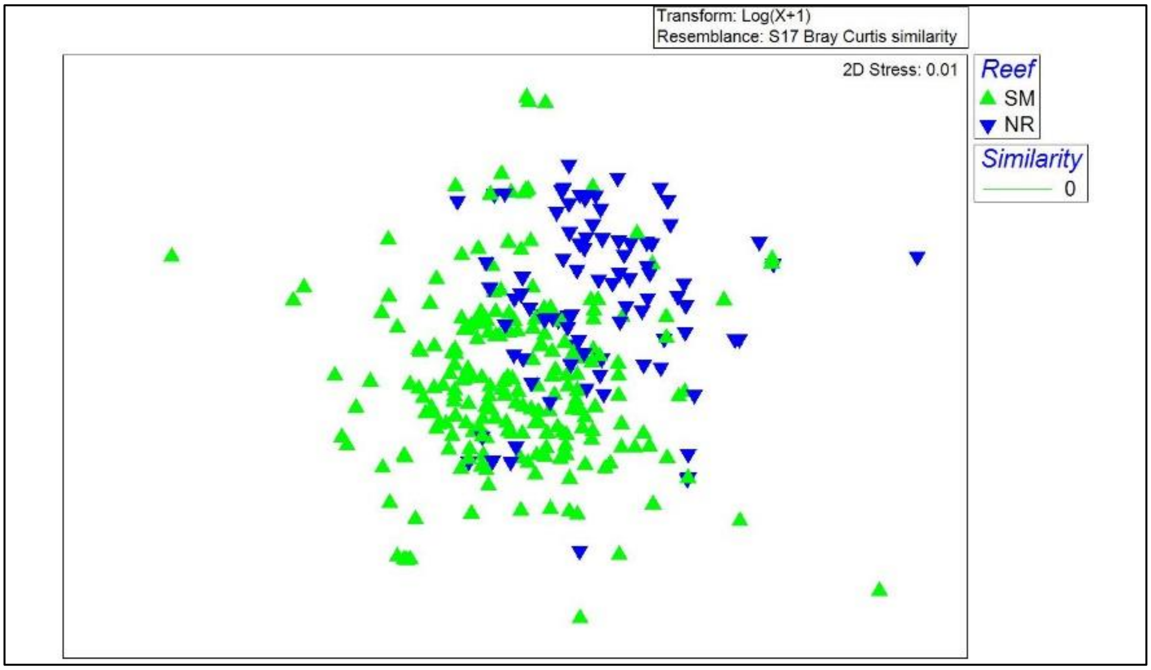


Figure 5.24 MDS-plot of reef fish abundance data by reef type (natural reef vs. substrate modules), using the ≥10% dataset.

The results of the second modified analysis, using only species encountered with <10% occurrence, exhibited quite a departure from the analysis of the entire dataset and the ≥10% version. The natural reef once again stood out from the other experimental treatments, although this time with significantly greater abundance and species richness ($p<0.01$) (Figures 5.25 and 5.26). There were no significant differences between the controls and treatments for abundance (ANOVA, $p=0.75$), although the Pads treatment was higher than the other two treatments and controls, and the transplants was the lowest. For species richness, there were also no differences between the treatments and controls, although the Pads treatment was once again higher but only by a very small margin (ANOVA, $p=0.88$).

The greater values on the natural reef may indicate that the modules were not fully providing the requisite supply of food and shelter resources and were therefore less attractive as potential habitat compared to the natural reef, at least for the specialized species characteristic of the <10% species list.

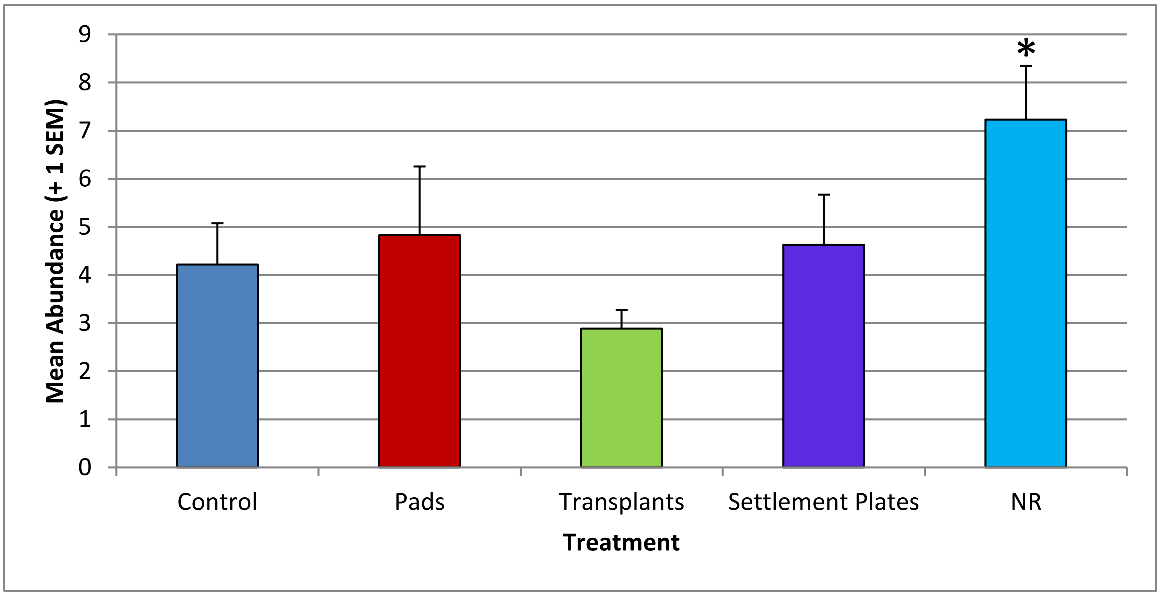


Figure 5.25 Mean abundance of reef fish species with <10% occurrence. The asterisk indicates a significant difference (ANOVA, $p<0.05$).

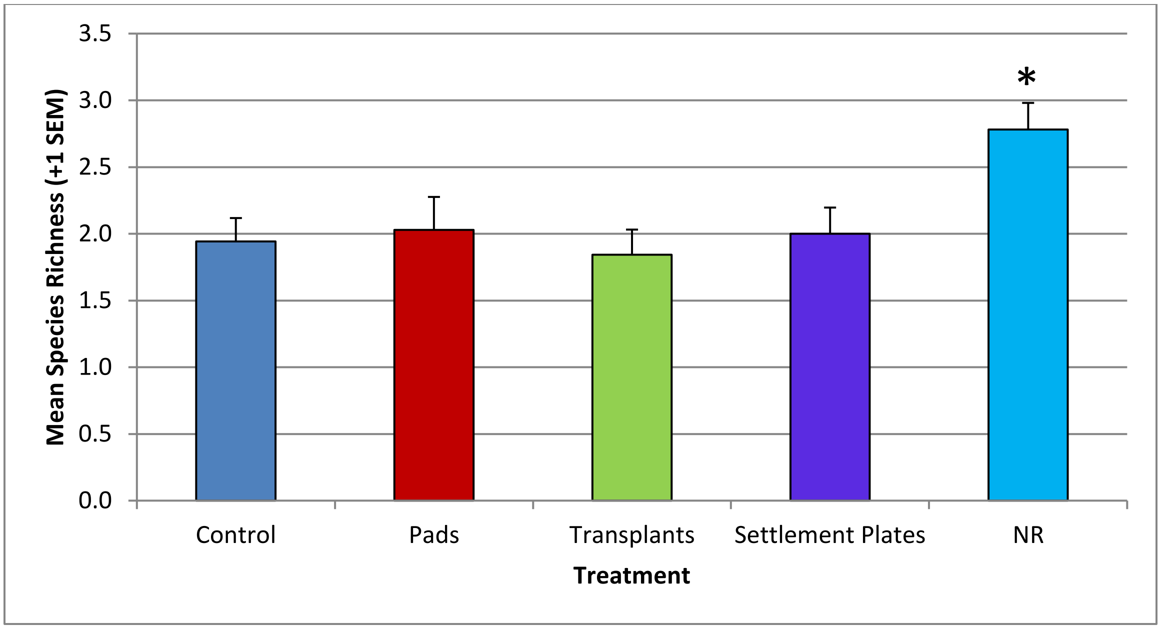


Figure 5.26 Mean species richness of reef fishes with <10% occurrence. The asterisk indicates a significant difference (ANOVA, p<0.05).

Analysis of the <10% occurrence dataset by date resulted in only one significant difference (Figure 5.27). For March 2007, there were significantly more species on the natural reef (ANOVA, p=0.0064). September 2007, March 2008, and October 2008 also had higher numbers for the natural reef, although none were significant (ANOVA, p>0.05). The peaks for September 2007 Pads and Settlement Plates treatments resulted from large numbers of juvenile grunts, and for the natural reef it was from Masked Gobies and Rainbow Wrasse. In October 2008, the peak in the controls was also from juvenile grunts. An MDS-plot was generated for this modified analysis as well, however, due to the extremely high variation within this subset of the data, the results were too highly dispersed and are not included here.

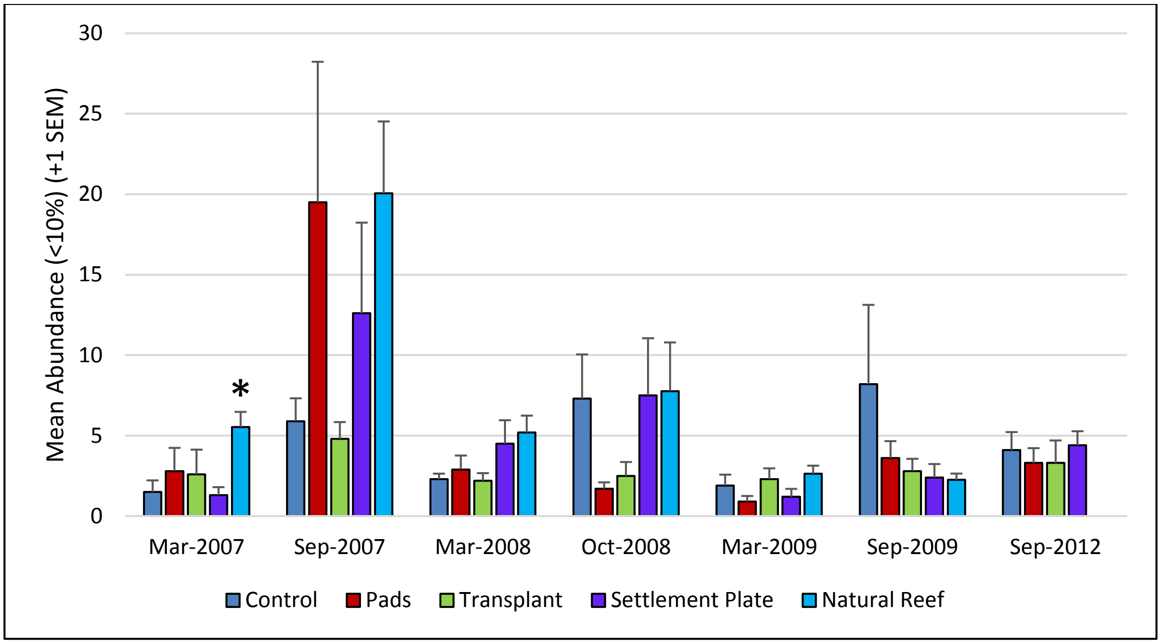


Figure 5.27 Mean abundance of reef fishes by treatment and date, using the <10% dataset. The asterisk denotes a significant difference for March 2007 (ANOVA, $p<0.05$).

5.3.4 Seasonality and Temporal Progression

When mean abundance and species richness were previously examined by treatment and date (Figures 5.8 and 5.10), a seasonal pattern of winter/spring troughs and summer/fall peaks became apparent for all treatments, controls, and the natural reef. This pattern was also detected in the coral recruitment data (see Chapter 4). Seaman and Sprague (1991) stated that although abundance on artificial reefs may fluctuate with season, populations often fluctuate cyclically or seasonally around some average value or within a certain range. Interestingly, although there were some differences, in general mean abundance on the modules was comparable to what was observed on the natural reef from the very first monitoring trip and continued onward throughout the study. This indicates that the modules were colonized to comparable levels as the natural reef within the span of only six months, and assemblages on both the natural and artificial substrates fluctuated in time with one another during seasonal changes.

When all treatments, controls, and the natural reef were combined, the three March data collections were statistically similar to one another and lower than the September/October data collections (ANOVA, $p<0.00001$) (Figure 5.28). MDS-plots by season also exhibit a clear distinction in assemblage structure between the spring and fall (Figures 5.29 and 5.30).

A reduction in total number of fishes and/or number of juveniles and new recruits settling in winter is common to coral reef habitats worldwide likely due to a decrease in larval supply, as spawning typically occurs in the warmer spring and summer months (Russell et al., 1977; Clifton, 1995; Munro et al., 2006; Mitcheson et al., 2008; Mwaluma et al., 2010). In addition, the reduction in larval supply and resultant reduction in numbers of newly settled and juvenile fishes impacts the number of predatory species that normally consume newly settled recruits and juveniles due to a reduction in food availability.

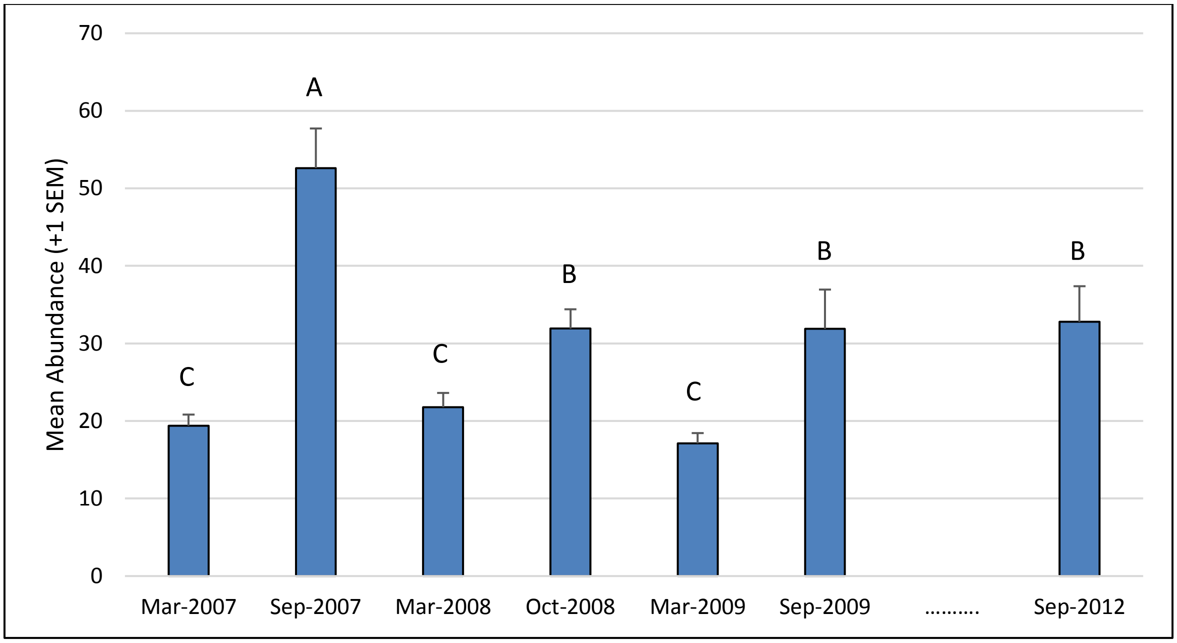


Figure 5.28 Seasonal pattern of peaks and valleys in reef fish abundance data, with all treatments combined. Letters indicate significant differences and shared groupings (SNK, $p<0.05$).

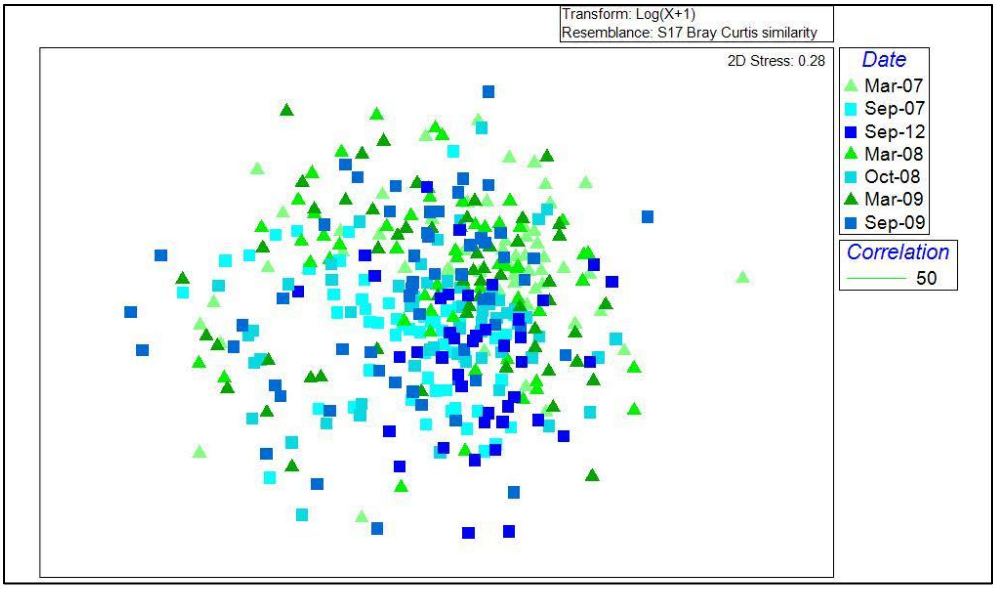


Figure 5.29 MDS-plot of reef fish abundance data by treatment and date. Winter/Spring is green and Summer/Fall is blue.

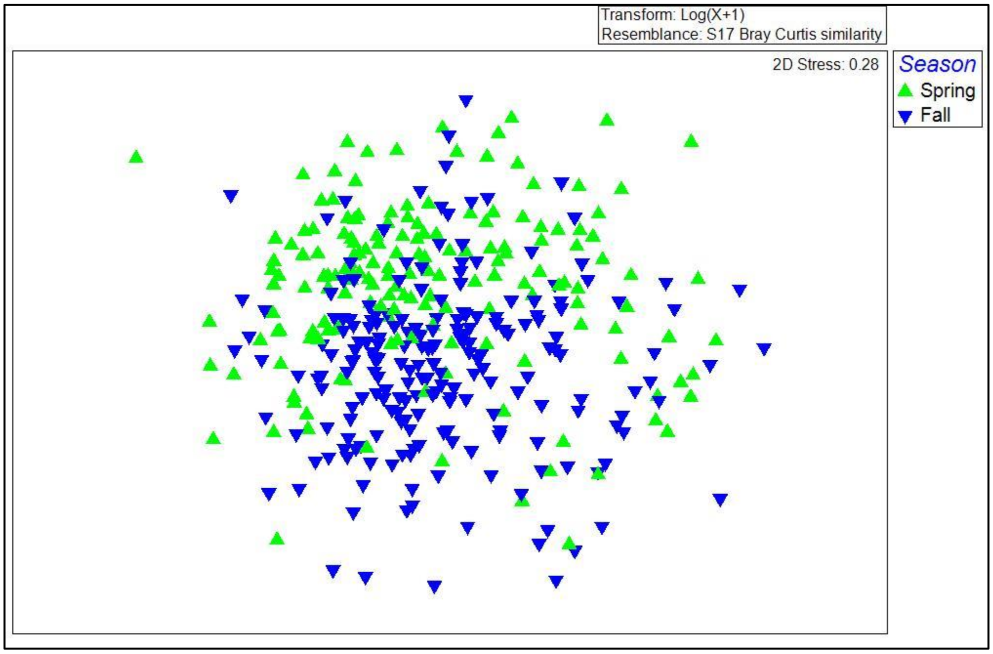


Figure 5.30 MDS-plot of reef fish abundance data by season (Spring vs. Fall), with all treatments and dates combined.

Assemblage structure on the treatments and controls from the first monitoring trip following module deployment was quite similar to what was documented during each successive monitoring effort. That is to say, colonization happened rapidly but the resolution of this dataset was not fine enough to describe the process of assemblage development in the months immediately following deployment or to comment on which species were the first to begin colonizing the modules. It does appear that the seasonal changes affected all species to some extent, and the proportional abundance of the most dominant families remained fairly consistent relative to one another throughout the study regardless of season. However, when the seasonal fluctuations for each of the most dominant families are compared, it becomes clear that Labridae and Haemulidae were responsible for a substantial portion of the observed amplitude in the seasonal abundance (Appendices 5.8 and 5.9).

5.3.5 Dominant Families

Reef fish assemblages are constantly in flux, and using only snapshot surveys taken over a three/six-year period with six months between data collections did not produce a dataset with enough resolution to follow specific cohorts or individual fishes through time. Such is typically the case with long-term fisheries monitoring data and visual survey methodology. However, it is still possible to explore this time series and examine the most dominant families and the most abundant species for each experimental treatment and draw inferences on trends and substrate preferences (or lack thereof).

In Puerto Morelos, the most dominant families across all treatments, controls, and the natural reef were, in order of decreasing mean abundance (Figure 5.31): Labridae (35.1%), Haemulidae (21.6%), Acanthuridae (13.0%), Pomacentridae (11.2%), Scaridae (3.9%), Tetraodontidae (3.5%), Gobiidae (3.0%), Lutjanidae (2.4%), Pomacanthidae (1.3%), and Serranidae (1.3%). Species from these 10 families constitute >96% of the Puerto Morelos dataset. In Akumal, the most dominant families were: Labridae (54.0%), Pomacentridae (11.5%), Acanthuridae (6.8%), Tetraodontidae (6.3%), Haemulidae (4.7%), Lutjanidae (4.5%), Scaridae (3.8%), and Serranidae (2.7%). Together, species from these 8 families comprise >94% of the Akumal dataset.

The eight most-abundant families that both study sites had in common with each other will now be discussed in greater detail, with Gobiidae included due to its relevance in Puerto Morelos. Even though some of these families were present in relatively small numbers, they are still included here due to their contrasting ecological roles and/or economic importance. Since there were no treatments ascribed to the Akumal dataset past March 2007 (all modules served as controls following the hurricane), only the Puerto Morelos data will be utilized for the remainder of the 'dominant families' discussion unless otherwise noted. Total and mean abundances by treatment from Akumal in March 2007 for species within the dominant families discussed here are listed in Appendix 5.10.

For the following size-class figures, means were calculated by taking the overall mean of the individual means for each year. ANOVAs were run for each size class individually. There was considerable variation among the treatments for each family, with no single treatment seeming to produce consistently more fishes. There were a few minor differences between treatments for some species, namely the Pads treatment, but the most common theme was the difference between the abundance of fishes on the modules compared to the natural reef.

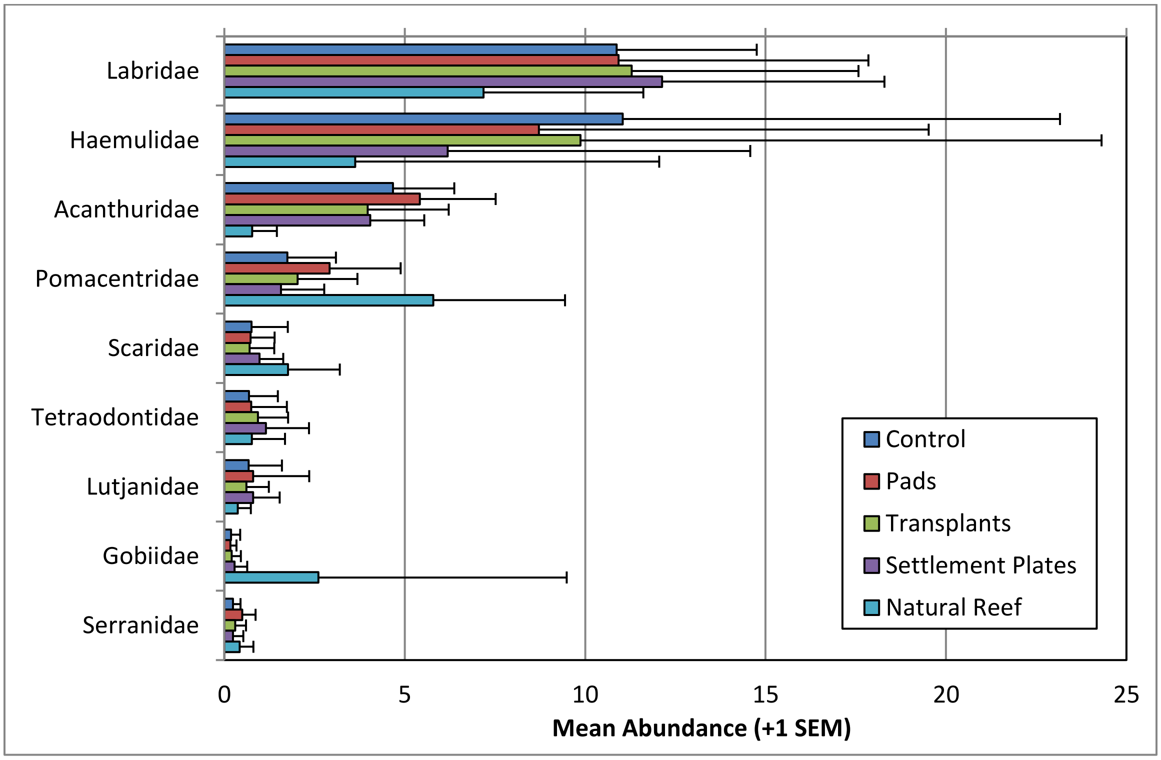


Figure 5.31 Mean abundance of the nine most dominant reef fish families, by treatment with all dates combined.

Labridae

Eleven wrasse species were encountered during this study, with the most abundant being Bluehead Wrasse (64%), Slippery Dick (15%), and Yellowhead Wrasse (12%). All other species contributed <5% (0.05-4.8%) individually to the total number of wrasses: Rainbow, Puddingwife (*Halichoeres radiatus*), Clown (*H. maculipinna*), Hogfish (*Lachnolaimus maximus*), Spanish Hogfish (*Bodianus rufus*), Blackear (*H. poeyi*), Yellowcheek (*H. cyanocephalus*), and Green Razorfish (*Xyrichtys splendens*). Bluehead Wrasse alone contributed 22% of the total abundance of all species (wrasses and all others) for all treatments combined, and was reported as the most abundant species in a previous assessment of Yucatecan coral reefs, while Yellowhead Wrasse as the fourth most abundant (Núñez-Lara et al., 2003). When all wrasse species were combined, they were found in comparable numbers across all experimental treatments and controls; however, mean abundance and species richness were significantly lower on the natural reef (ANOVAs, p<0.001) (Figure 5.32). When the mean abundance of individual species was evaluated (Figures 5.33 and 5.34), there were some notable differences. There were significantly more Bluehead, Slippery Dick, and Puddingwife wrasses on the modules than the natural reef (ANOVAs: p<0.01), although there were no differences between treatments. Conversely, there were more Yellowhead wrasses on the natural reef than the modules (p<0.0001) and more Yellowhead wrasses on the natural reef than Bluehead wrasses. Interestingly, there were significantly more Hogfish on the Pads treatment (p=0.024). Other than that, there were no differences detected for any of the other species. The remaining four species not included in the figures were not present in sufficient numbers to perform meaningful statistical comparisons.

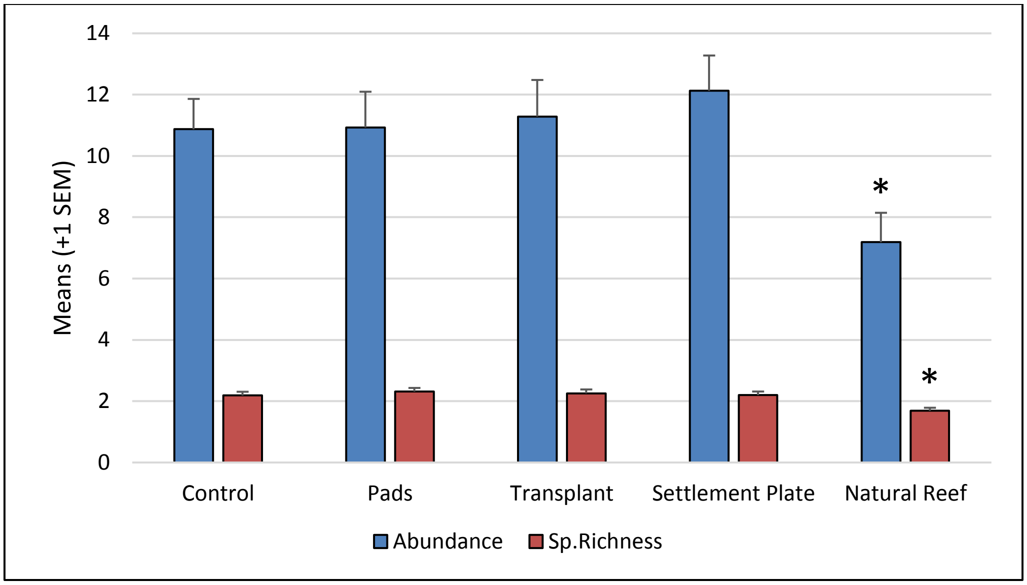


Figure 5.32 Mean abundance and species richness of wrasses. The asterisks indicate a significant difference (ANOVA, p<0.01).

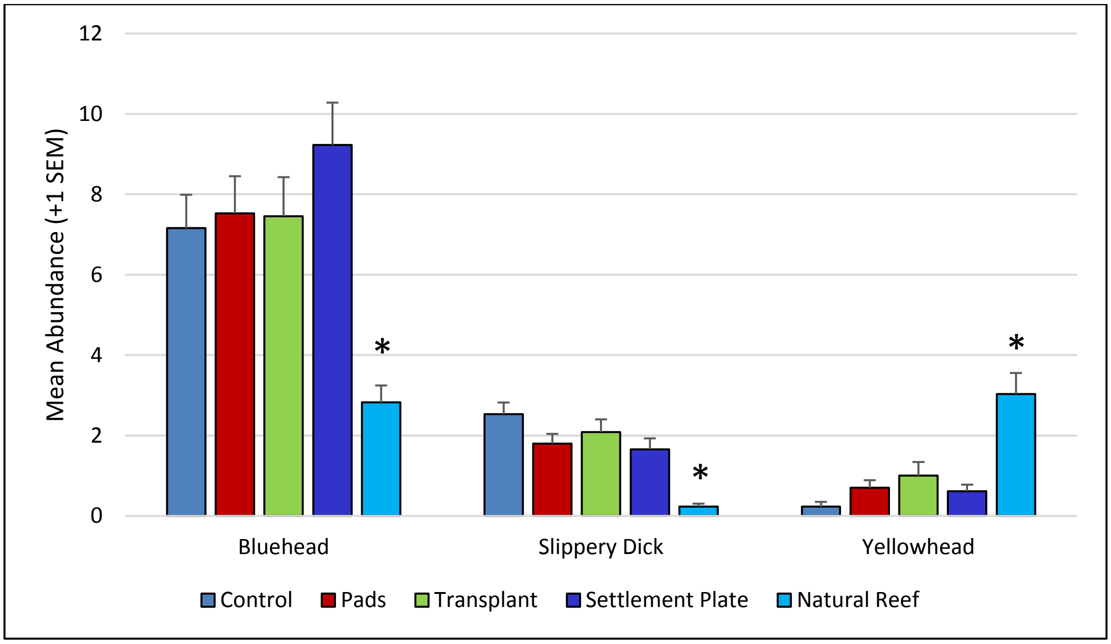


Figure 5.33 The mean abundance of the three most abundance wrasse species, by treatment. The asterisks indicate a significant difference (ANOVA, p<0.0001).

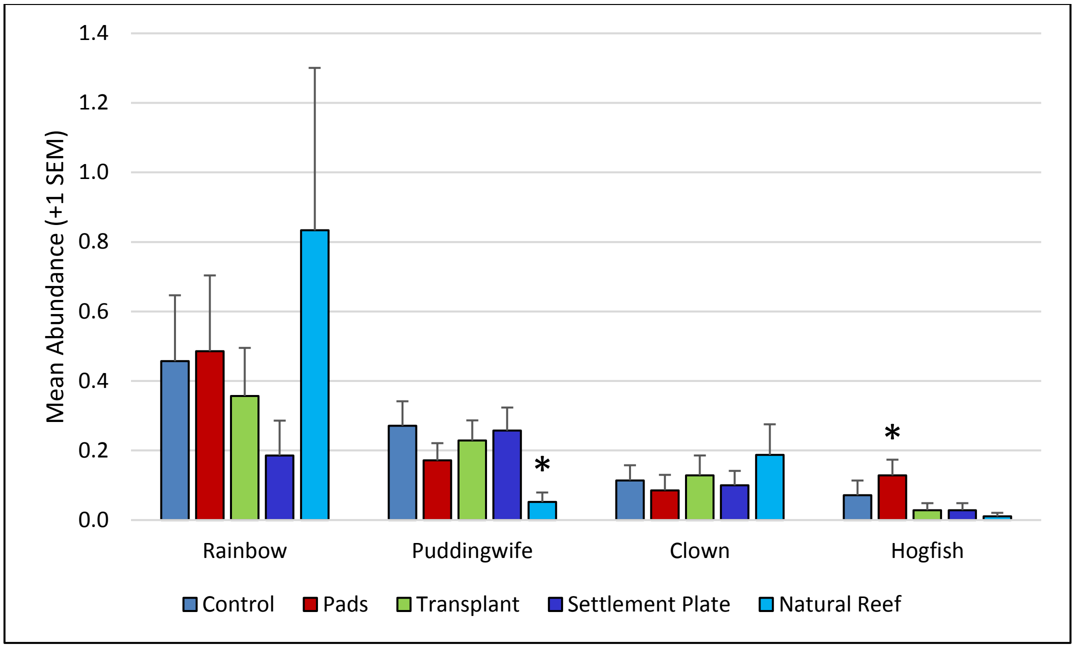


Figure 5.34 Mean abundance of four wrasse species, by treatment. The asterisks indicate a significant difference (ANOVA, p<0.05).

Wrasses in general are relatively small, most with a maximum total length below 15cm (McEachran and Fechhelm, 1998; Nelson, 2006). With the exception of the larger species like Hogfish, Spanish Hogfish, Puddingwife, and Yellowcheek Wrasse, which when combined only contributed 2.5% to the total number of wrasses in this dataset, all of the wrasse species encountered during this study have reported average lengths throughout their range that fall within the 10-20cm size range (Humann and DeLoach, 2014). Examination of mean abundance of all species combined by size class (Figure 5.35) revealed that most were juveniles or sub-adult phases in the 0-2cm and 2-5cm size classes, respectively, followed by the 5-10cm size class. This is not surprising, as a school (or harem) of Blueheads typically consists of numerous females, often accompanied by several intermediate-phase males and one or more terminal-phase males (Warner and Swearer, 1991). However, the large percentage of 0-2cm Blueheads indicates that the modules are suitable juvenile habitat for this species, which are typically more bottom-associated than the adults (Randall, 1967). No significant differences were found between the treatments and controls or the modules and the natural reef for any size class (ANOVAs, p>0.05), although for the 0-2 and 2-5cm size classes there were fewer on the natural reef.

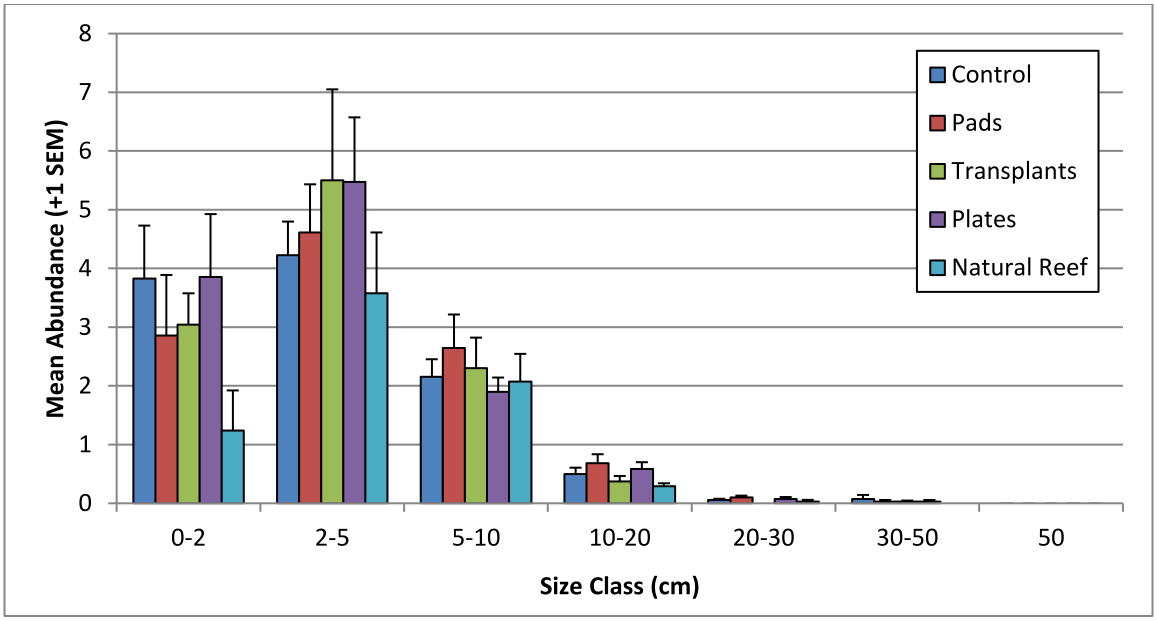


Figure 5.35 Mean abundance of wrasses by size class. No significant differences were detected within any size class (ANOVA, p>0.05).

It is interesting to note that more Yellowhead Wrasse and, to a lesser extent, Clown Wrasse, both members of the same feeding guild commonly found on reef and adjacent habitats (Randall, 1967), were found in greater numbers on the natural reef; whereas the more commonly encountered Slippery Dick Wrasse, also a member of this same feeding guild, was found in greater numbers on the modules. The Slippery Dick is more strongly associated with sand, patch reef, and seagrass habitats, which likely explains this species' prevalence within the module deployment field. In addition, gut content analysis of this species in other studies (Randall, 1967) found a feeding preference for crabs, echinoids, polychaetes, and gastropods. While analysis of the artificial substrate pad samples confirmed the presence of all of these invertebrates (see Ch.3), mean abundance of Slippery Dick on the Pads treatment was actually lower than the other treatments and controls. Even though all the aforementioned taxa were present in the pads samples, the samples were dominated by polychaetes, amphipods, and ophiuroids, with only very small contributions to the total was due to crabs, echinoids, and gastropods. It is therefore more likely that this species was on the modules as the result of the surrounding natural substrate and structure provided by the modules, rather than due to any specific provisioning of food resources by the modules or treatments. The same likely applies for the Puddingwife, which has a similar dietary and habitat preferences as a juvenile to the Slippery Dick. It is, however, unclear as to why the Yellowhead Wrasse was significantly more abundant on the natural reef, as it too has similar dietary and habitat preferences, with similar dentition as the Slippery Dick (Clifton and Motta, 1998). However, Clifton and Motta (1998) also noted that Yellowhead Wrasse consumed slightly less hard-shelled prey items than the Slippery Dick, which may help to explain the difference. Subtle differences in diet may also help to explain the slightly higher numbers of Clown Wrasse on the natural reef, as they have been shown to have higher dietary diversity and prefer soft-bodied prey items such as polychaetes and other crustaceans.

Even though there were significantly more Hogfish on the Pads treatments, given their diet of primarily gastropods and bivalves and the small contribution that these mollusks made to the total number of invertebrates found in the pads samples, the connection is unclear. Out of the total 17 Hogfish encountered during this study, only one was counted on the natural reef and 7 out of 16 were counted on Pads treatment modules. The majority were large mature individuals; 11 were within the 30-50cm size class, followed by 3 from 20-30cm and 2 from 10-20cm. Given their diet, dentition, and large size, it is unlikely that they were feeding directly upon invertebrates living within the pad material, but their elevated presence there does raise the question as to why. Perhaps given the small total number of individuals encountered their presence on the Pads treatment is mere coincidence, but it warrants further study.

Regarding the higher numbers of Bluehead Wrasse on the modules compared to the natural reef, this may be due, in part, to their tendency to congregate over large coral heads and other prominent structural features of the reef as they mature, and the modules provided distinctive vertical relief in the otherwise flat, low-relief deployment field. In addition, as this species matures it experiences shifts in both diet and behavior. Newly settled individuals and very small juveniles (0-2 cm) remained very close to the substrate and were often observed on the down-current side of the modules (personal observations). Feddern (1965) observed schools of juveniles in close association to the bottom while searching for small benthic invertebrates and more mature individuals loosely aggregating higher in the water column consuming zooplankton. Randall (1967) notes that the diet of the sexually mature adults shifts away from zooplankton towards a more varied assortment of benthic invertebrates. Lower numbers on the natural reef for this species may be related to the fact that there were numerous large (>2m vertical relief) coral heads on the natural reef near where the surveys were conducted. Those large coral heads were substantially larger than the ~1m-high module-sized coral heads that were targeted by the natural reef surveys. Therefore, a significant portion of the adult Bluehead Wrasse population on the natural reef may have been missed due to their preference for structures with vertical relief greater than what was present where the natural reef surveys took place. Regarding the juveniles, they may have been more loosely scattered throughout the natural substrate than they were on the isolated modules.

Haemulidae

Ten grunt species were encountered during this study, with the majority being unidentified juveniles (39%), followed by French Grunt (18%), Tomtate (14%), White Grunt (10%), Cottonwick (10%), and Bluestriped Grunt (5%). Sailor’s Choice, Porkfish, White Margate, Caesar Grunt, and Spanish Grunt contributed the remaining 4% to the total. Unidentified juvenile grunts alone contributed 10% of the total abundance of all species (grunts and all others) for all dates and treatments combined. Due to a lack of, or similarity of, visible distinguishing characteristics for newly settled and early juvenile grunts (Courtenay, 1961; Lindeman and Richards, 2005), positive species identification was generally not practicable for the smaller size classes (0-2cm and 2-5cm) with the visual survey methods employed here. In those cases, they were recorded as unidentified *Haemulon* spp., but were likely French, Tomtate, White, and Bluestriped Grunts. These four species were the most abundant in the larger size classes and the other grunt species could be positively identified as juveniles due to their more distinctive color patterns.

When all grunt species were combined, mean abundance was significantly higher on the controls, Transplants, and Pads treatments than the natural reef, with the Settlement Plate treatment situated in between (ANOVA, p=0.0015) (Figure 5.36). There were also significantly more haemulid species counted on the modules as compared to the natural reef (ANOVA, p=0.006).

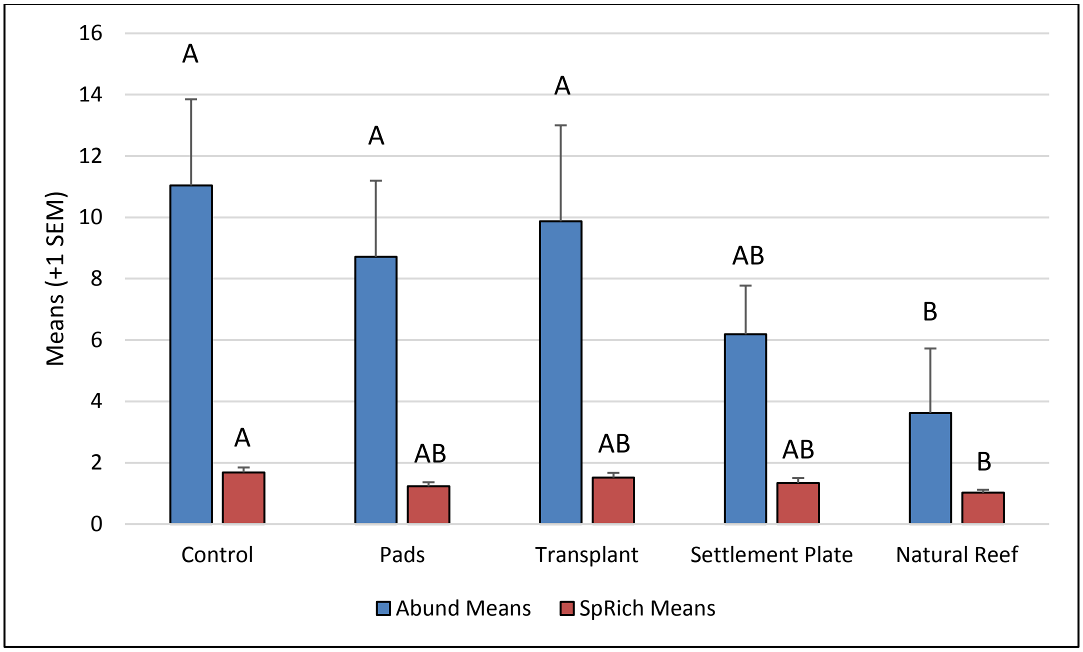


Figure 5.36 Mean abundance and species richness of grunts. Different letters indicate significant differences within groups (SNK, p<0.05).

When the mean abundances of individual species were evaluated (Figure 5.37), there were some subtle differences. Many of the most abundant species (notably unidentified juveniles, Tomtates, French Grunts, and Cottonwicks) exhibited extremely high variation due to their frequent occurrence in large schools. This was particularly true for unidentified juvenile grunts that were counted in schools of 50-200 individuals on many occasions. This variation created difficulty when analyzing the affect, if any, that the experimental treatments may have had on their abundance. However, there were still several significant differences detected during the analysis. More unidentified juveniles were counted on the Pads and Transplants treatments, and there were significantly fewer counted on the Settlement Plates treatment (ANOVA, p=0.02). French Grunts and Cottonwicks, on the other hand, occurred in significantly lower numbers on the Pads treatment (ANOVA, p=0.04 and p=0.0001, respectively), and Tomtates were significantly lower on the Transplants treatment (ANOVA, p=0.01). White Grunts occurred in similar numbers across all treatments and controls, but were lower on the natural reef (ANOVA, p=0.006). There were no significant differences detected for Bluestriped Grunts (ANOVA, p=0.14), although more were seen on the controls.

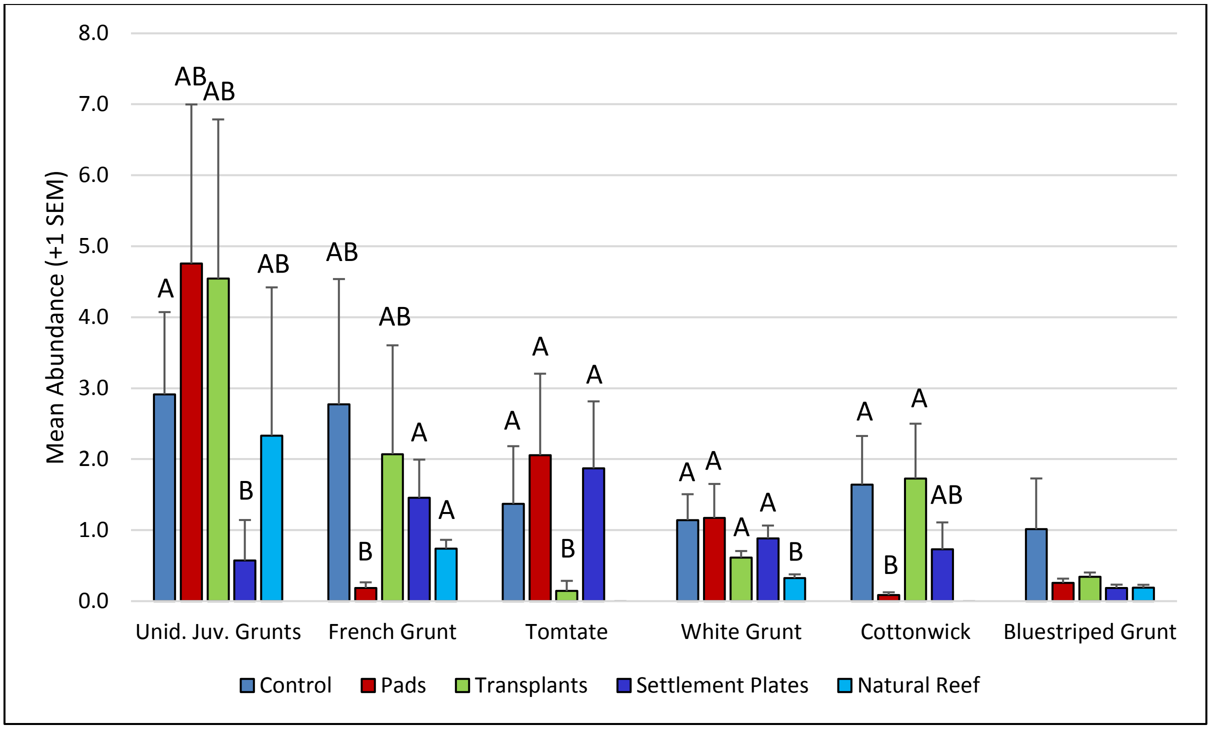


Figure 5.37 Mean abundance for the most abundant grunt species, by treatment. Different letters indicate significant differences between means within groups (SNK, p<0.05).

Grunts from the most abundant species here have documented average sizes that range from 15-30 cm [17cm (French), 18cm (Tomtate), 25cm (Bluestriped and Cottonwick), 30cm (White)] ((McEachran and Fechhelm, 1998; Froese and Pauly, 2016). Grunts in this study were numerically dominated by juveniles from the 0-2cm and 2-5cm size classes (Figure 38), the abudance of which are known to be affected by intense predation pressure (Shulman and Ogden, 1987). Newly settled and juvenile *Haemulon* spp. had stochastic settlement patterns and patchy distribution on both the modules and natural reef (Figure 5.39). It is interesting to note that there were numerically more 0-2cm grunts on the Pads and Transplants treatments, even if the differences were not significant (ANOVA, p=0.85).

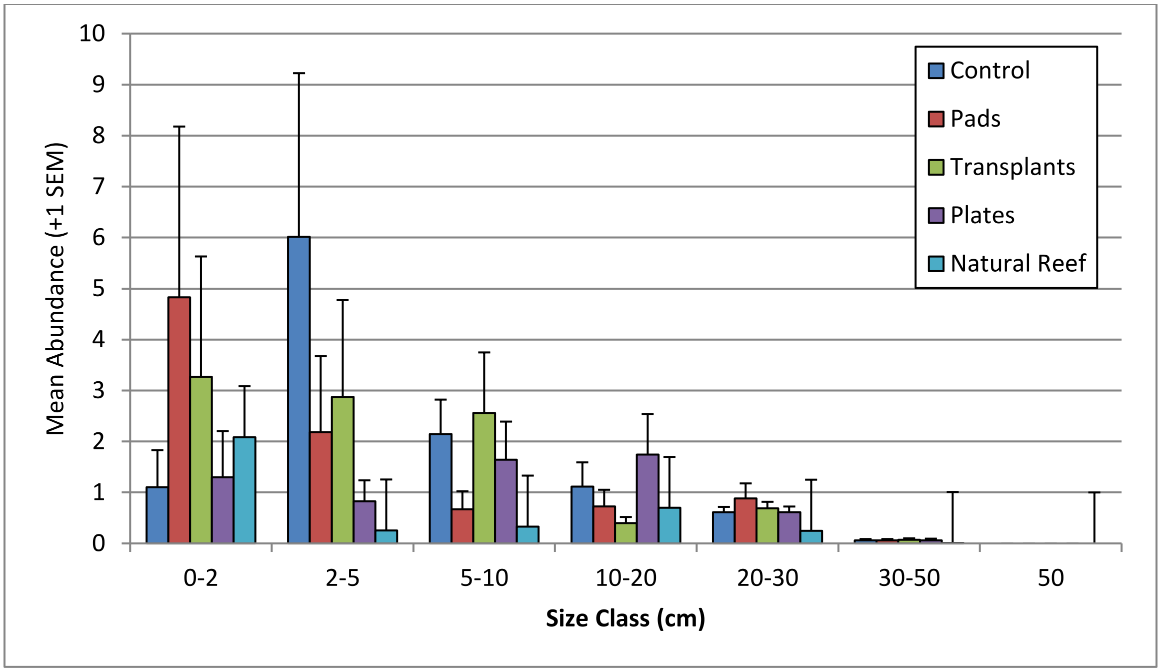


Figure 5.38 Mean abundance of grunts by size class, all species. No significant differences were found within size classes (ANOVA, p>0.05).

Newly settled grunts are mainly planktivorous, with gut content studies reporting high percentages of copepods and tanaidaceans (McFarland, 1980; Shulman and Ogden, 1987; de la Morinière et al., 2003). As they mature, grunt diets shift towards larger, faster, and more heavily armored prey items, such as small fishes and infaunal/epifaunal invertebrates like isopods, amphipods, mysids, gastropods, and bivalves (Lindeman, 1986). As adults, Tomtates consume primarily shrimp, polychaetes, and other small crustaceans; French grunts primarily worms and crabs, and White grunts primarily crabs, worms, and snails (Randall, 1967).

Figure 5.39 A variety of grunt species, mainly Cottonwicks and French Grunts, and size classes on a coral transplant module in September 2012.

Acanthuridae

There were three surgeonfish species encountered during this study, with the majority being Blue Tangs (57%), followed by Ocean Surgeonfish (27%) and Doctorfish (*A. chirurgus*) (16%). Blue Tangs were the second most abundant species previously reported in a study of Yucatecan coral reefs (Núñez-Lara, 2003). Overall there were significantly fewer surgeonfishes on the natural reef (ANOVA, $p<0.0001$) (Figure 5.40), a phenomenon that applied to all three species and almost every size class (Figures 5.41 and 5.42). Among the modules, surgeonfishes were observed in slightly greater numbers on the Pads treatment for every size class with the exception of 5-10cm, and more Blue Tangs and Doctorfishes were found on the Pads treatment. However, none of the differences were significant except for Doctorfish (ANOVA, $p=0.029$). In addition, there were more than twice as many Blue Tangs found on the Pads treatment as on the controls in Akumal in March 2007 (the only trip where the padding material was present at that study site) (Appendix 5.1).

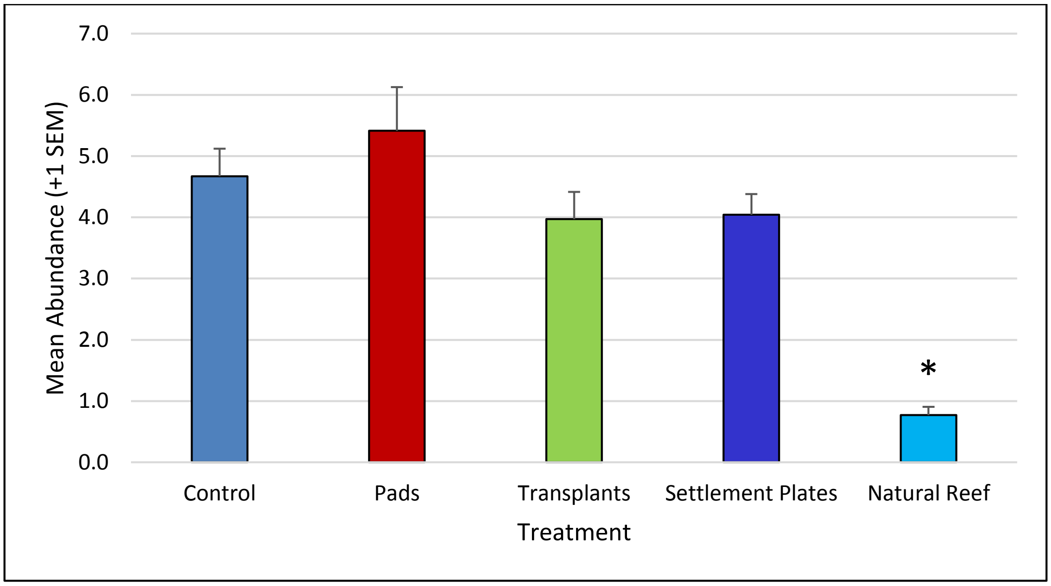


Figure 5.40 Mean abundance of surgeonfishes by treatment. The asterisk indicates a significant difference (ANOVA, p<0.0001).

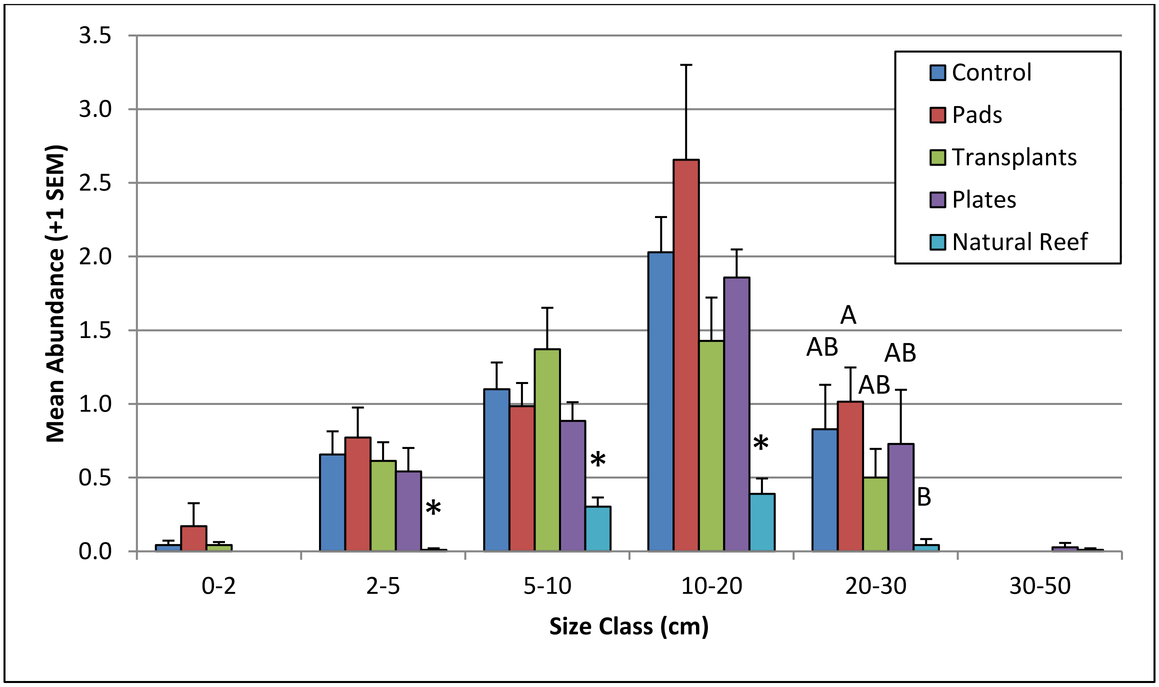


Figure 5.41 Mean abundance of surgeonfishes by size class, all species combined. Asterisks and different letters indicate significant differences between means within groups (SNK, p<0.05).

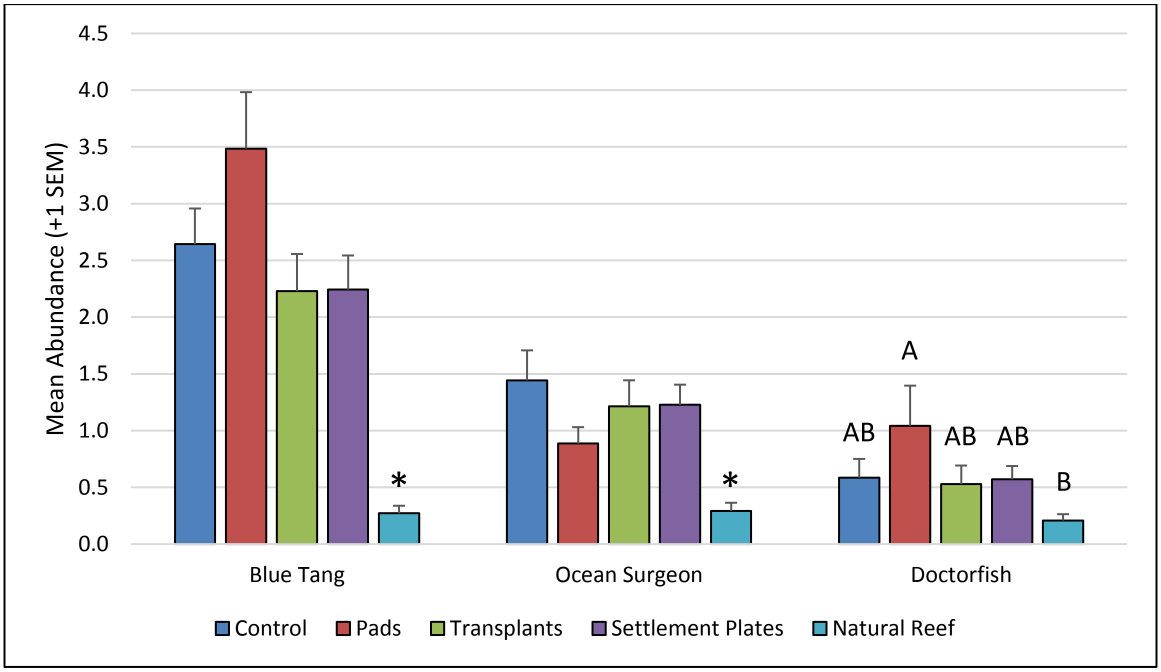


Figure 5.42 Mean abundance surgeonfishes by treatment. Asterisks and different letters indicate significant differences within groups (ANOVA, SNK, p<0.05).

One possible explanation for significantly fewer acanthurids on the natural reef is that fishes on the modules were essentially limited to the interior of the modules or the open sand, rubble, or seagrass habitats of the module deployment field. Based on the author's experience, when a survey diver approached a module, many mobile fishes tended to restrict their movements to the immediate vicinity of the module or remain concealed within the interior unless they were part of a large school that could not all fit inside (Figure 5.43). Fishes have been shown to stay near artificial structures for protection when small, but when larger and less vulnerable to predation, they spend more time away from refuge habitats (Andersen et al., 1989). This was particularly true for acanthurids during this study. Throughout the study, juvenile Blue Tangs were observed in close association with the modules. On multiple occasions when large adults were encountered an entire school was observed to remain near the shelter of a single module, some seeking refuge within and some swimming around closely nearby, and then the entire school would depart to graze on another module after the diver left. In comparison, when a diver conducted a survey on the natural reef, mobile fishes were more willing to disperse towards the shelter and safety of other parts of the reef without apparent hesitation about venturing out into an otherwise refuge-limited open area such as the deployment field.

Although subtle, the results seemed to suggest that surgeonfishes were found more frequently and in slightly higher numbers on modules with the Pads treatment. Interestingly, the same pattern observed for the 10-20cm size class surgeonfishes, which was also the most abundant size class, was observed for percent coverage of *Lobophora variegata* macroalgae (Ch.3, Figures 3.4 and 3.5), with Pads having significantly greater coverage of macroalgae or sharing that distinction with either controls and/or Settlement Plates for five out of the seven monitoring trips. Perhaps it is not simple coincidence that the mean abundance of the two largest size classes of the surgeonfishes, all strictly herbivorous species, was greater on the treatments that were shown to support the most robust community of macroalgae. Caribbean surgeonfishes, most notably Blue Tangs, have been reported to consume *Lobophora* (Randall, 1967; Lewis, 1985; Dias et al., 2001), so they may be targeting that species specifically, as well as the other fleshy macroalgal species or turf. Many other macroalgae species that were found on the modules during this study have also been documented in surgeonfish gut content analyses.

Figure 5.43 A mixed school of surgeonfishes, mainly Blue Tangs and a few Doctorfish, in close association with a Control module.

Pomacentridae

There were nine damselfish species encountered during this study, with the majority being Bicolor (48.5%) and Blue Chromis (31.4%), followed by Three-spot (6.9%), Sergeant Major (*Abudefduf saxatilis*) (3.7%), Beaugregory (*Stegastes leucostictus*) (3.6%), Cocoa (*S. variabilis*) (2.6%), Dusky (*S. adustus*) (2%), Longfin (0.5%), and Brown Chromis (*Chromis multilineata*) (0.4%). Overall, there were significantly more damselfish species and greater abundance on the natural reef than on the module treatments (ANOVA, $p<0.0001$). Among the modules, the Pads' treatment had the greatest abundance (ANOVA, $p<0.000001$) (Figure 5.44). There were significantly more Bicolor Damsels on the Pads treatment (ANOVA, $p=0.00024$), closely followed by the Transplant treatment, and the least on the natural reef (Figure 5.45). For all other species, except for Sergeant Majors, there were significantly more on the natural reef. There were more Sergeant Majors on the modules than the natural reef, but no differences between treatments were detected. The most conspicuous difference between the modules and the natural reef was seen for the

Blue Chromis, which were dramatically more abundant on the natural reef (Figure 5.45). Althoug the Pads and Transplants treatments had more Blue Chromis than the other treatments, the difference was not significant. Nonetheless, these results may indicate that the structure provided by the padding material and coral transplants may be providing preferential habitat for shelter-dependent species such as these (Nemeth, 1998).

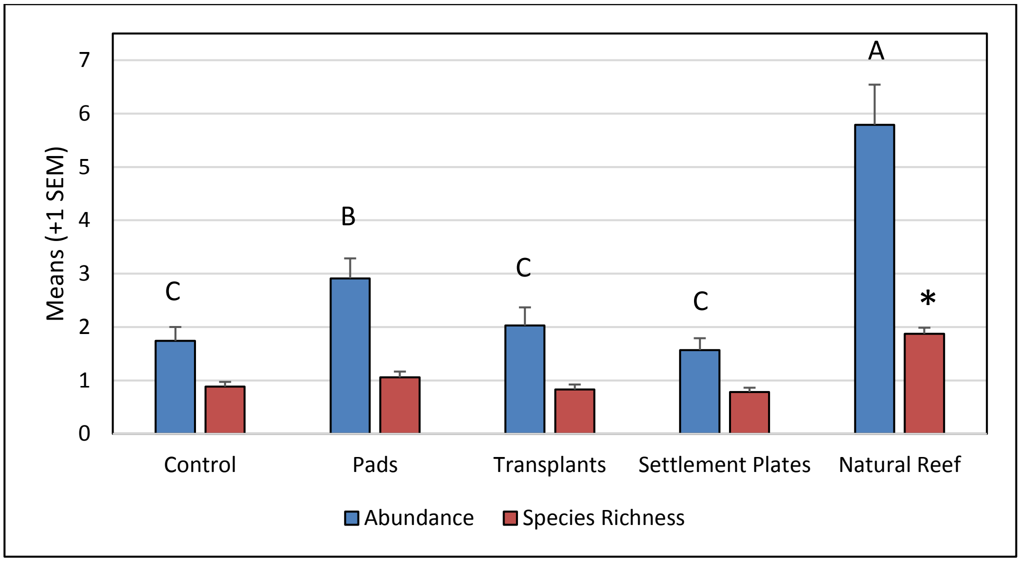


Figure 5.44. Mean abundance of damselfishes. The asterisk and letters indicate significant differences and shared groupings (ANOVA, SNK, p<0.0001).

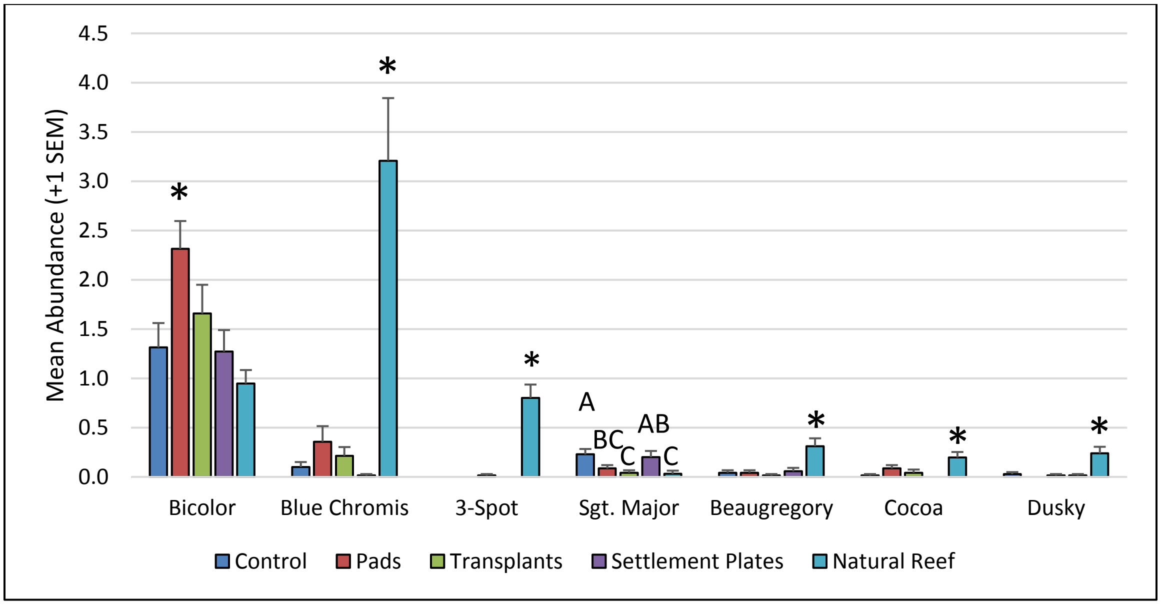


Figure 5.45 Mean abundance of damselfishes by treatment. Asterisks and letters indicate significant differences and shared groupings (ANOVA, SNK, p<0.01).

Mean abundance of damselfishes was significantly greater on the natural reef for the two most abundant size classes, 2-5cm and 5-10cm (ANOVA, $p<0.01$), and greater for the 0-2cm as well, but not significantly (Figure 5.46) (ANOVA, $p=0.37$). Bicolor Damselfish are primarily omniovorous (González-Sansón and Aguilar, 2010) with occasional herbivorous tendencies (Cervigon, 1993), but will also consume small invertebrates. Perhaps this a connection with the greater abundance of this species on the Pads treatment modules. Blue Chromis are strict zooplanktivores (Randall, 1967), targeting primarily copepods, and prefer to station themselves above structures that create hydrologic fronts and have suitable shelter available nearby. Sergeant Majors are known to be extremely diversified in their food habits, consuming both zooplankton and algae, so it is not surprising that they showed no distinct preference for habitat in this study. Low numbers for the other species prevented detailed evaluation of their habitat preferences, although they all have omnivorous diets and similar behavioral traits. Small resident omnivorous keystone species like these (Hixon, 1982; Tanner et al., 1994) may be good indicators of reef health and artificial reef performance. In addition to the aforementioned dietary implications, the results of this study suggest that shelter is a limiting factor on the modules for many small species and juveniles, but the Pads and Transplants treatments may be ameliorating this effect.

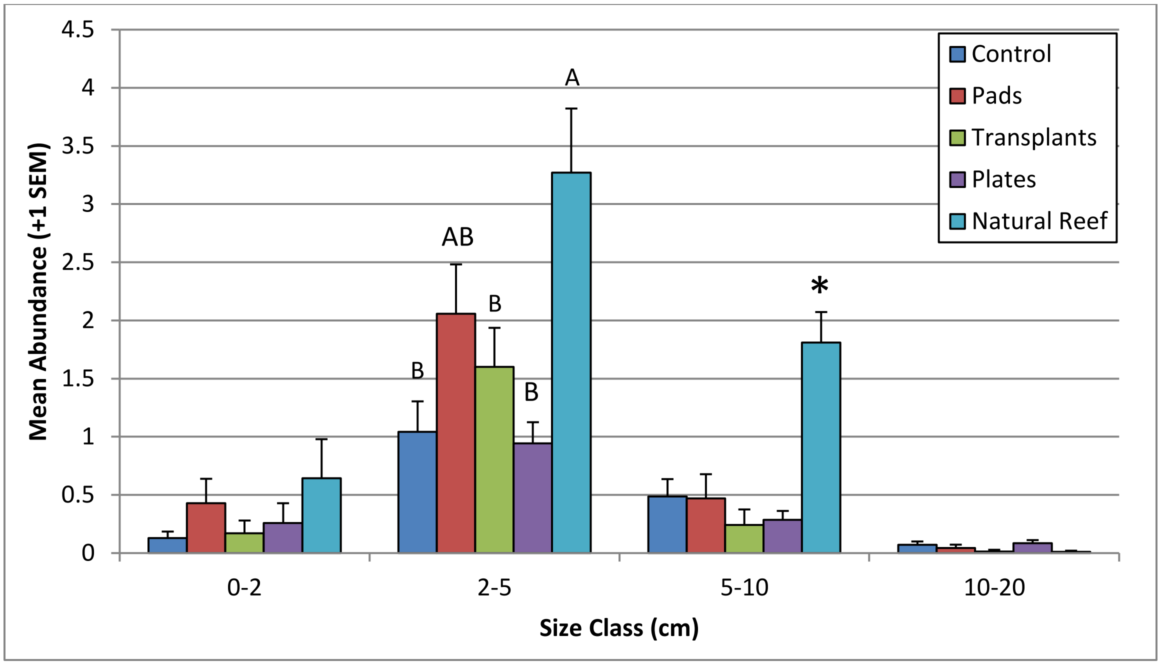


Figure 5.46 Mean abundance of damselfishes by size class and treatment. The asterisk and different letters indicate significant differences within groups (ANOVA, SNK, $p<0.01$).

It is also possible that the disparity in abundance between the modules and natural reef could be the result of predation and competition. Perhaps those juveniles that settled on the modules were either being consumed by resident predators or driven out by the territorial nature of larger conspecifics or other previously established individuals. Lack of sufficient small shelter options may therefore be the limiting factor for damselfishes on the modules, but the Pads and Transplants treatments may be providing enough additional structural complexity to make a difference.

Scaridae

Ten species of parrotfish were recorded in this study. The three most abundant species were Redband (55.6%), followed by Striped (*Scarus iseri*) (12.0%) and Stoplight (*Sparisoma viride*) (8.3%). The other species contributed from 5.4% to 0.5% of the remaining abundance: Yellowtail (*S. rubripinne*), Redfin (*S. chrysopterum*), Bucktooth (*S. radians*), Princess (*S. taeniopterus*), Greenblotch (*S. atomarium*), Bluelip (*Cryptotomus roseus*), Queen (*S. vetula*). Redband Parrotfish were the third most abundant species reported from a previous study of Yucatecan coral reefs (Núñez-Lara, 2003). In this study, overall, mean abundance and species richness were significantly higher on the natural reef than the module treatments (ANOVAs, p<0.00001) (Figure 5.47). They were equally abundant on the treatments and controls at all sizes and for all species (Figures 5.47 and 5.48). There were more parrotfishes present on the natural reef in the 2-5cm, 5-10cm (ANOVA, p=0.04), and 10-20cm size classes (Figure 5.49). The Pads were ranked among the top two highest treatments for two of these size classes, and Settlement Plates were among the highest in every size class, although the differences were not significant.

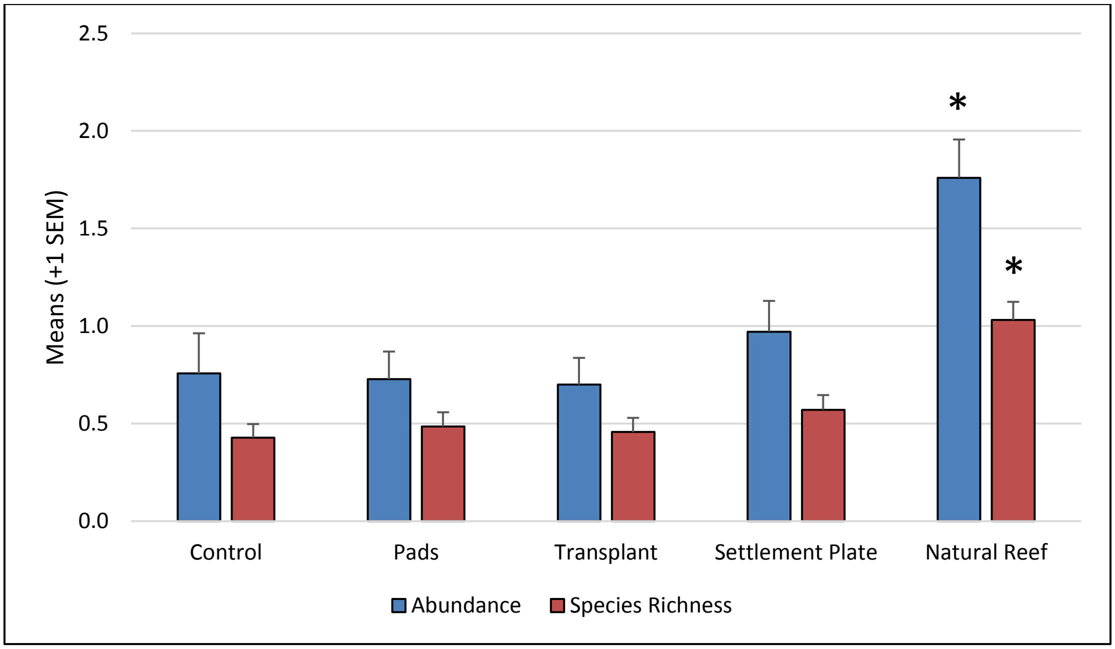


Figure 5.47 Mean abundance and species richness of parrotfishes by treatment. The asterisks indicate significant differences (ANOVAs, p<0.00001).

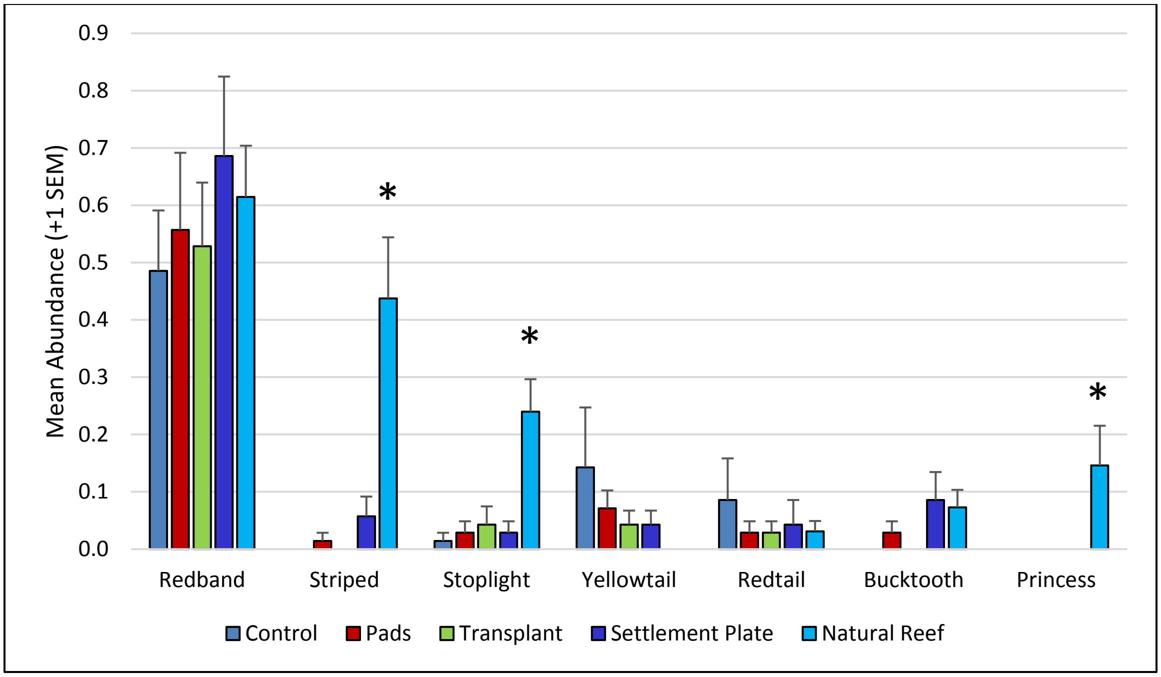


Figure 5.48 Mean abundance of parrotfishes by treatment. Asterisks indicate significant differences (ANOVAs, p<0.001).

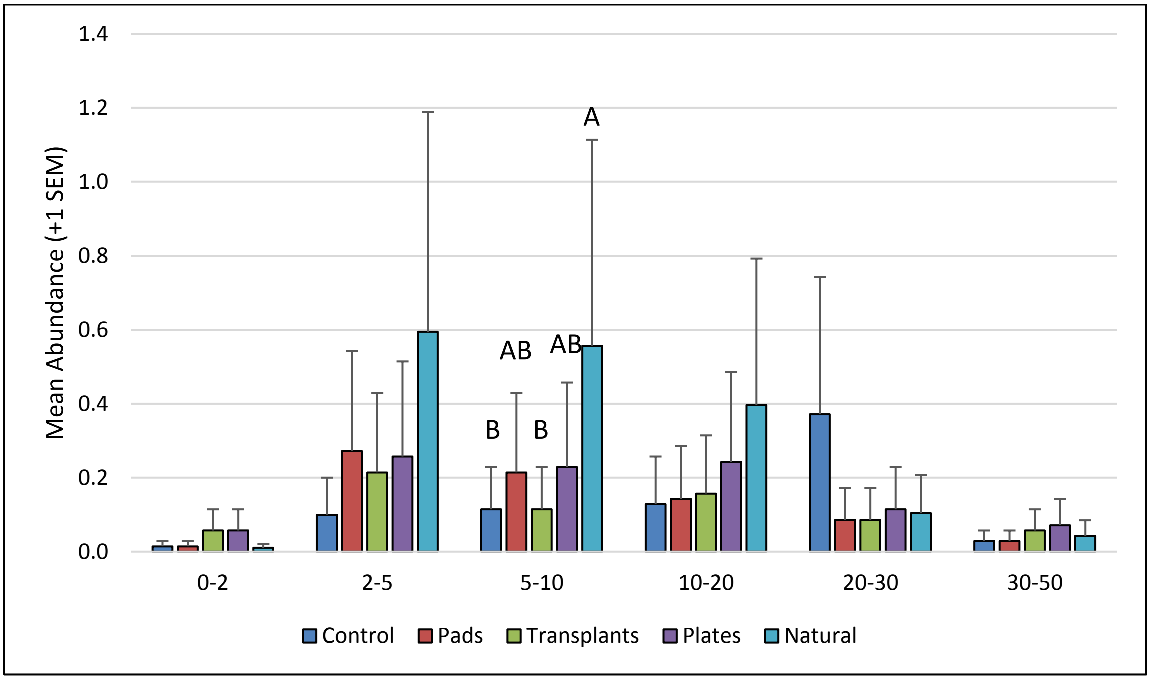


Figure 5.49 Mean abundance of all parrotfishes by size class. Different letters indicate significant differences within groupings (SNK, p<0.05).

The most abundant species, Redband, was equally abundant on both the modules and natural reef, with no distinct preference for any treatment. Striped parrotfishes were completely absent on the Control and Transplant treatments, and significantly more were present on the natural reef (ANOVA, $p<0.00001$). Stoplight and Princess parrotfishes also had significantly greater abundance on the natural reef (ANOVAs, $p=0.00001$ and $p=0.001$, respectively).

In contrast to the herbivorous fishes previously discussed, parrotfishes have dentition specifically adapted for scraping as opposed to grazing or cropping like the surgeonfishes and damselfishes (Ogden and Lobel, 1978). Perhaps some parrotfish species are discouraged from grazing on the artificial concrete substrate. However, the most abundant species found in this study, the Redband, showed no evidence of being deterred.

Tetraodontidae

The sixth most abundant family consisted almost exclusively of a single species, the Sharpnose Pufferfish (99.9%), with a single occurrence of a Bandtail Pufferfish (*Sphoeroides spengleri*). This species is another that is ubiquitous on coral reef habitats region-wide, but as they are typically solitary or found in small groups of 2-3 individuals they do not contribute significantly to the overall number of fishes present. However, as a consistently present omnivore, this species may be another good indicator for comparing performance of the modules to the natural reef. Overall, no significant differences were found between modules and the natural reef (ANOVA, $p=0.23$) (Figure 5.50). However, there were slightly more present on the Settlement Plates, Pads, and Transplants treated modules than the controls and the natural reef.

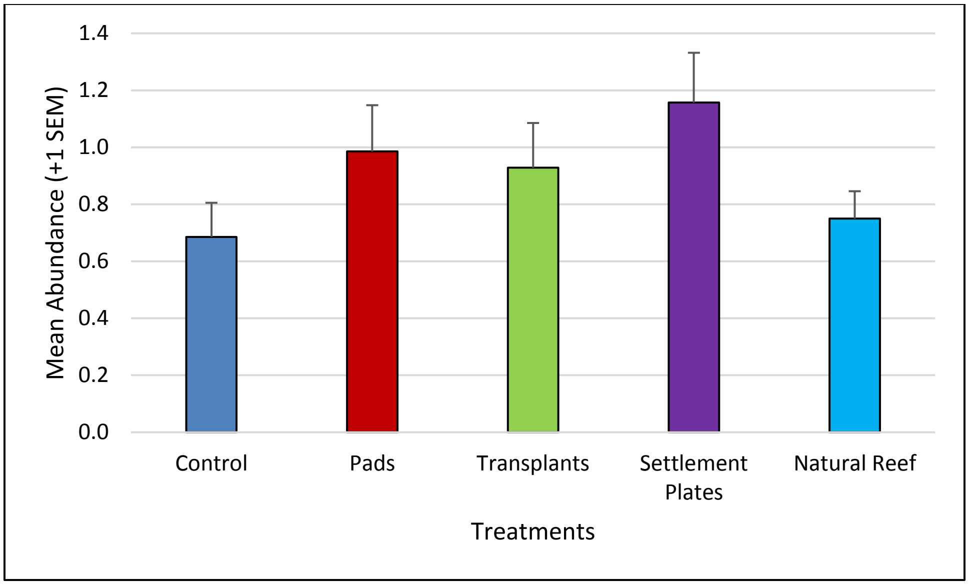


Figure 5.50 Mean abundance of pufferfishes. No significant differences were found (ANOVA, p>0.05).

There were more pufferfishes in the 2-5cm size range, which also made up the bulk of the total (Figure 5.51). Their means were very small and no significant differences were detected (ANOVA, p>0.05), and the largest individuals were found on the natural reef.

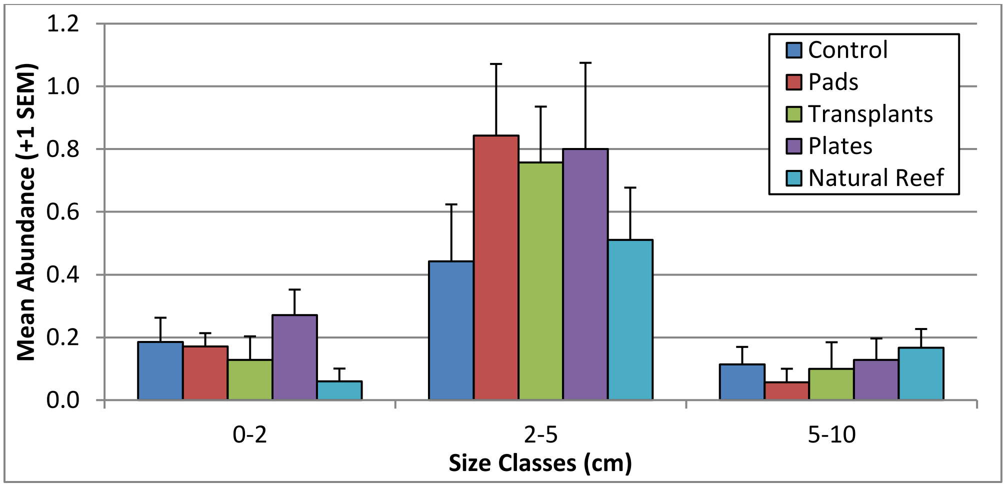


Figure 5.51 Mean abundance of pufferfishes by size class. No significant differences were detected (SNK, p>0.05).

Gobiidae

Five goby species were encountered during this study, with the majority being Masked/Glass Gobies (72%), followed by Broadstripe (*Elacatinus prochilos*) (16%), Goldspot (*Gnatholepis thompsoni*) (7%), Neon (*E. oceanops*) (3%), and Bridled (*Coryphopterus glaucofraenum*) (2%). There were significantly more gobies seen on the natural reef than the modules (ANOVA, p=0.00003), and no differences detected between treatments and controls (Figure 5.52). Given the maximum size of these species, the only size classes recorded were limited to the two smallest (Masked and Broadstripe Goby: 4.0 cm TL) (Lieske and Myers, 1994).

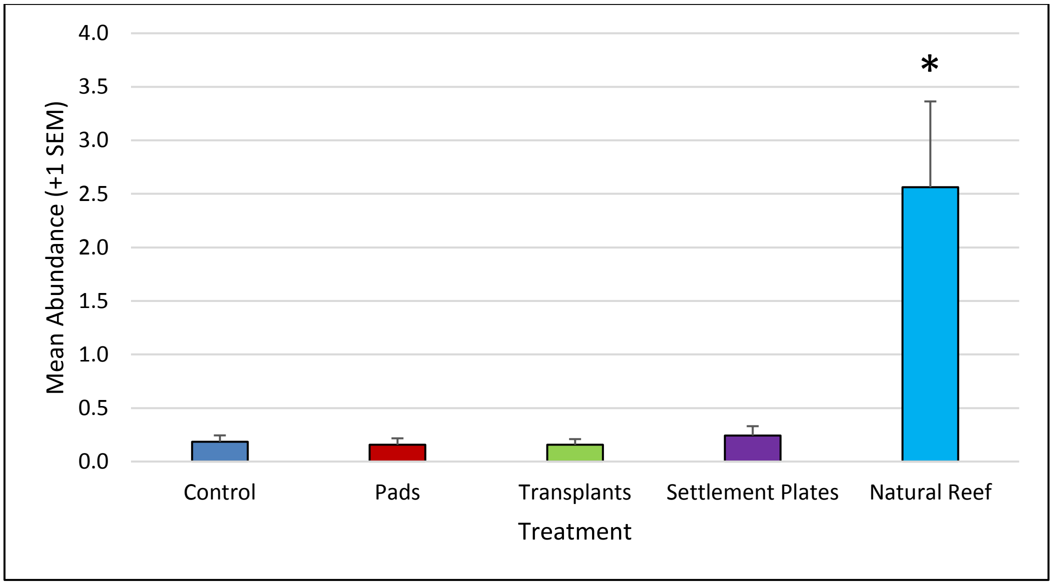


Figure 5.52 Mean abundance of gobies by treatment. The asterisk indicates a significant difference (ANOVA, p<0.0001).

Goby distribution on the modules and natural reef was likely driven by diet and behavior for this family. The planktivorous Masked/Glass Goby was seen exclusively on the natural reef; none were recorded on the modules (Figure 5.53). Out of the other four species recorded, only Broadstripe Gobies showed a tendency towards greater numbers on the natural reef, although the difference was not significant. The rest showed more or less equal abundances for the treatments and controls. On the modules, Broadstripe and Neon Gobies were seen exclusively in the interior cavities.

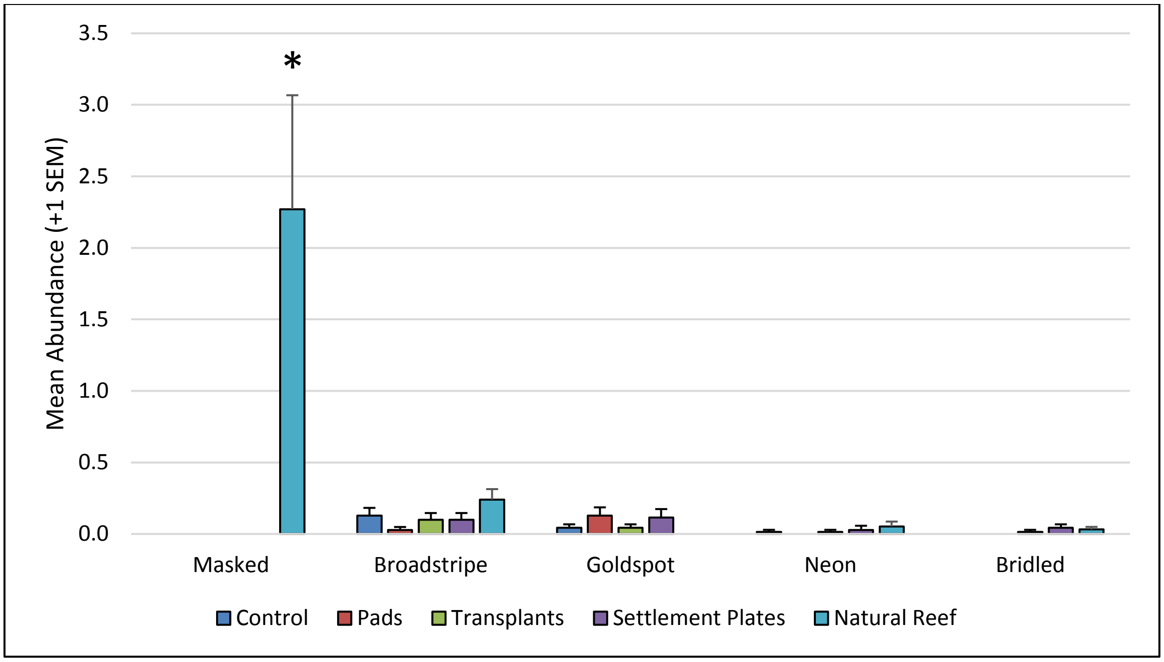


Figure 5.53 Mean abundance of gobies by treatment. The asterisk indicates a significant difference (ANOVA, p<0.000001).

Although Masked/Glass Gobies will also consume algae (Dominici-Arosemena and Wolff, 2005), their primarily planktivorous diet may limit their distribution on the scales evaluated in this study. The planktivorous Blue Chromis was also largely absent on the modules, but it was higher on the Pads treatment (Figure 5.45). The huge disparity between abundance of these species on the modules compared to the natural reef suggests that the module deployment field may be lacking in planktonic food resources necessary to support these species. However, predation may be driving force for the low numbers on the modules as well. On the natural reef, this species frequently occurs in schools of many 10s-100s of individuals which hover above the substrate in protected areas behind large coral heads and other vertical relief (ledges, gorgonians, large sponges, etc.). Given the limited shelter availability for small species on the modules, coupled with this species' tendency to hover visibly in the water column, any Masked/Glass gobies that settled on the modules may have been easy pickings for a variety of resident predatory species.

Serranidae

Ten grouper species were encountered, including a single hamlet. The most numerous were Graysby (*Cephalopholis cruentata*) (42%) followed by Harlequin Basslet (*Serranus tigrinus*) (21%), Red Grouper (*Epinephelus morio*) (9%), Mutton Hamlet (*Alphestes afer*) (8%), and Coney (*E. fulvus*) (8%). The remaining eight species were all present in similar numbers, ranging from 1-3% of the total: Yellowfin (*Mycteroperca venenosa*), Rock Hind (*E. adscenscionis*), Red Hind (*E. guttatus*), Butter Hamlet (*H. unicolor*), Black Grouper (*M. bonaci*), and Lantern Basslet (*S. baldwini*). This family was also very sparsely represented in this dataset, with only 131 individuals counted in total. Even though their abundance was relatively low, there were still some interesting patterns and differences detected. There was significantly greater mean abundance on the Pads treatment, followed closely by the natural reef and Transplants treatment, with controls and Settlement Plates treatment having the least (ANOVA, p=0.024) (Figure 5.54). Interestingly, there were more groupers, although not significantly, seen on the Pads treatment for two of the four size classes (2-5cm and 10-20cm) (Figure 5.55) and more 5-10cm groupers seen on the Transplants treatment.

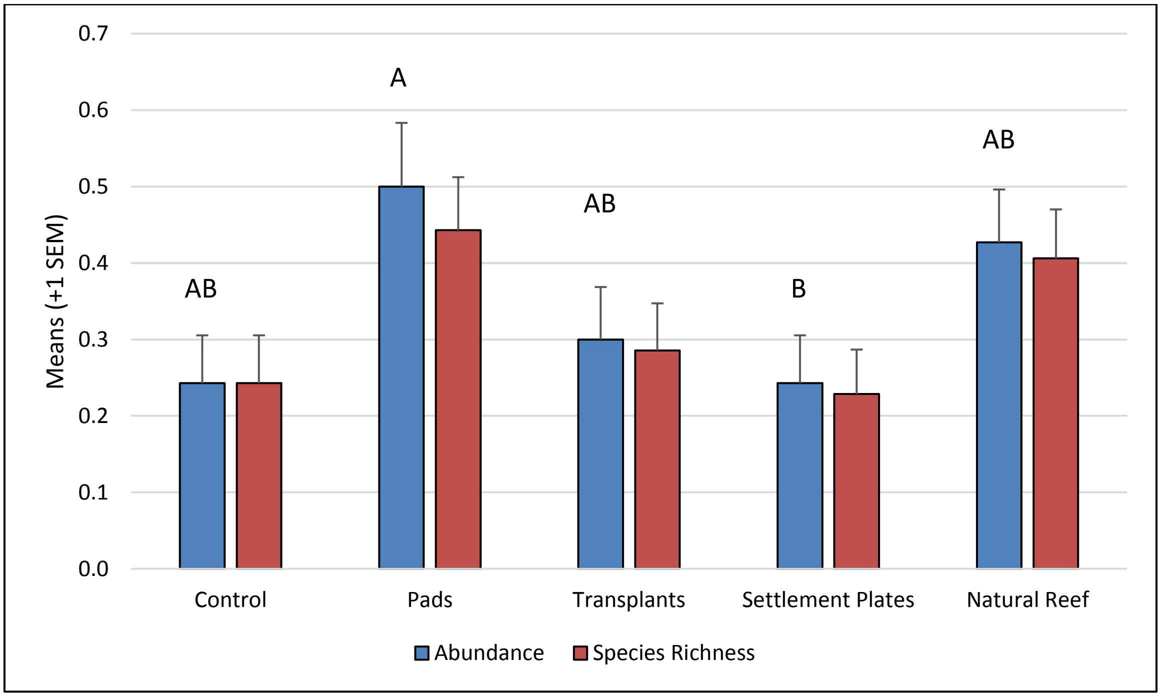


Figure 5.54 Mean abundance of groupers. Different letters indicate significant differences and within groups (SNK, p>0.05).

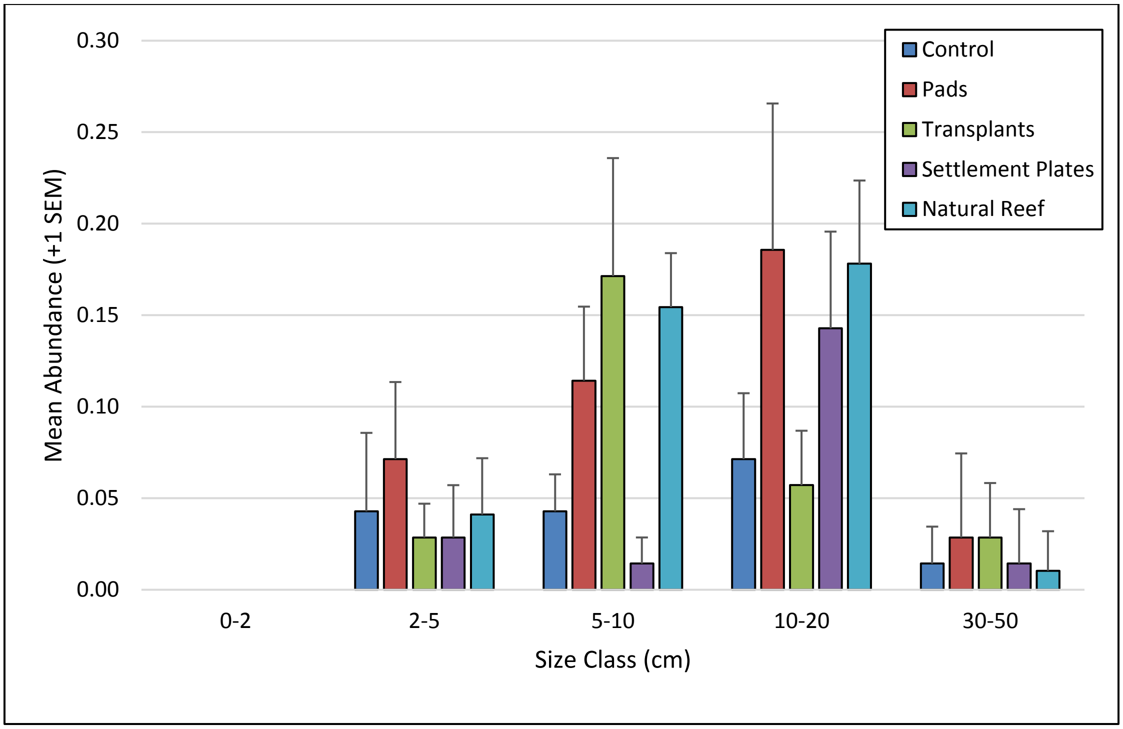


Figure 5.55 Mean abundance of groupers by size class. No significant differences were detected (ANOVA, p>0.05).

The pattern of mean abundance between treatments was identical for both the Graysby and Harlequin Basslet, with more seen on Pads and Transplants than on Control and Settlement Plates (Figure 5.56). However, given the small number of fish in this dataset, when the means were compared no significant differences were found (ANOVA, p=0.42 and p=0.059, respectively). There were also more Mutton Hamlets on the Pads treatment, although again it was not significant (ANOVA, p=0.09). Coneys were only seen on the controls and Settlement Plates, with more (also insignificant) being seen on the natural reef (ANOVA, p=0.66). Once again, the small number of groupers in this dataset prove to be the limiting factor. It is possible though that the Pads treated modules and, to a lesser extent, the Coral Transplants modules, may have been providing more attractive habitat for these small predatory species. Graysbys target a higher dietary percentage of small fishes, while Harlequin Basslets and Mutton Hamlets target more crabs, shrimps, and other small crustaceans (Randall, 1967). Coincidentally or not, there also happened to be more damselfishes and juvenile grunts on the Pads and Transplants treatment modules, as well as more juveniles in general.

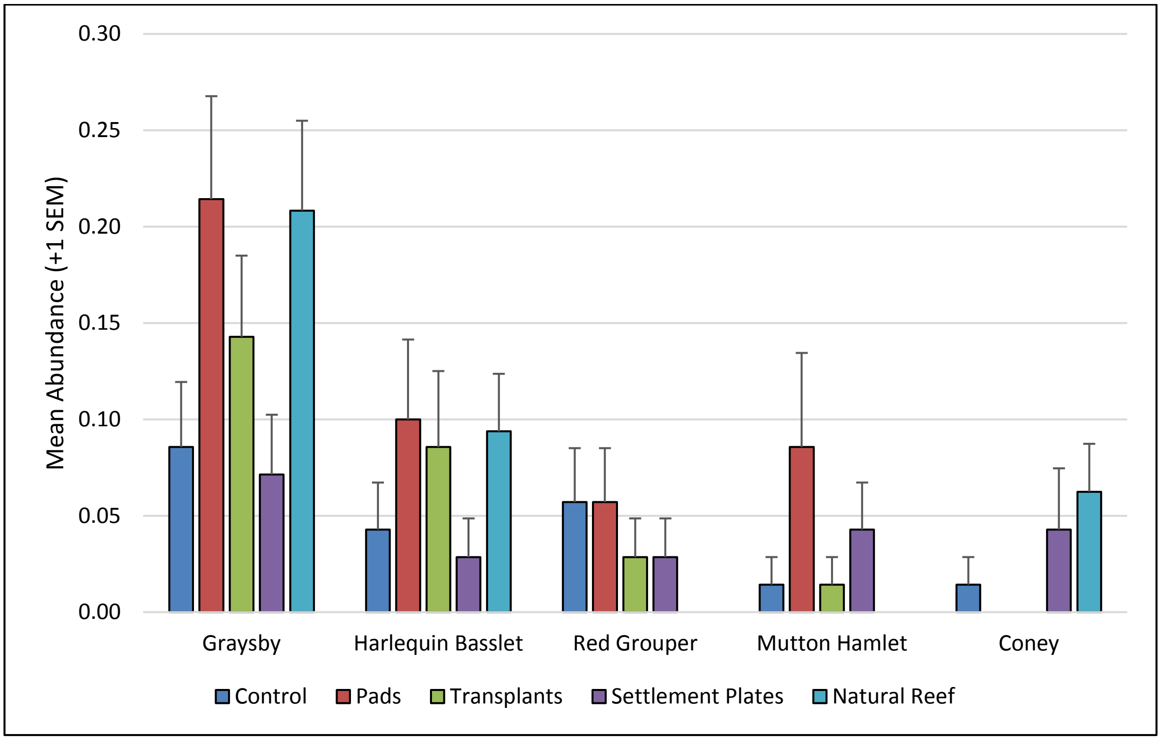


Figure 5.56 Mean abundance of the most abundant groupers by treatment. No significant differences were detected (ANOVA, p>0.05).

Lutjanidae

There were six snapper species encountered during this study, primarily dominated by the Yellowtail Snapper (*Ocyurus chrysurus*) (68%) and followed by Mutton (*Lutjanus analis*) (36%) and Blackfin (16%). The remaining three species, Lane (*L. synagris*), Schoolmaster, and Mahogany, made negligible contributions to the total. Overall there were very few snappers counted during each trip, with a combined total for all species of 76. Over all, there were significantly more snappers and snapper species on the modules than the natural reef (ANOVAs, p=0.01), and slightly more on the Settlement Plates treatment (Figure 5.57).

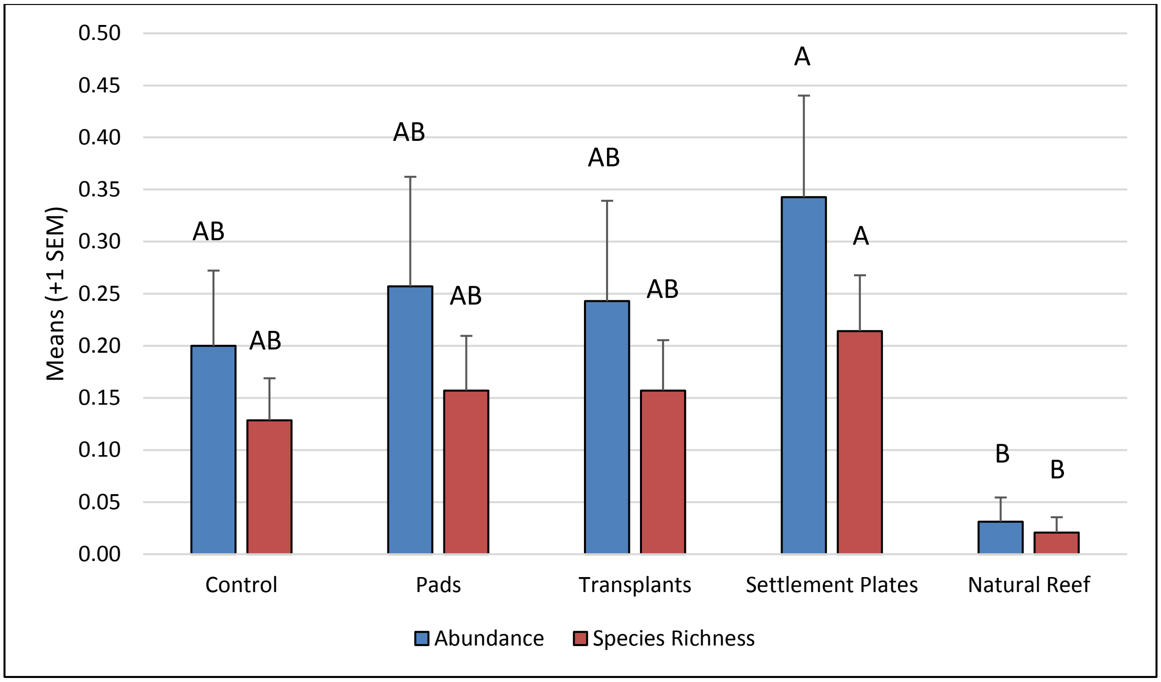


Figure 5.57 Mean abundance of snappers. Different letters indicate significant differences within groups (ANOVA, p<0.01).

No differences were detected between mean abundance for any snapper species (ANOVA, p>0.05), and no consistent pattern was shared between any of the species, except for a slightly higher abundance of Yellowtail and Blackfin Snappers on modules with settlement plates (Figure 5.58). Curiously, there were more Blackfin Snappers on the Settlement Plates treatment in Akumal as well. Possibly, the plates may have provided some sort of baffling affect in heavy currents. Like the groupers, the abundance of species in this family was too low to make solid inferences from the results.

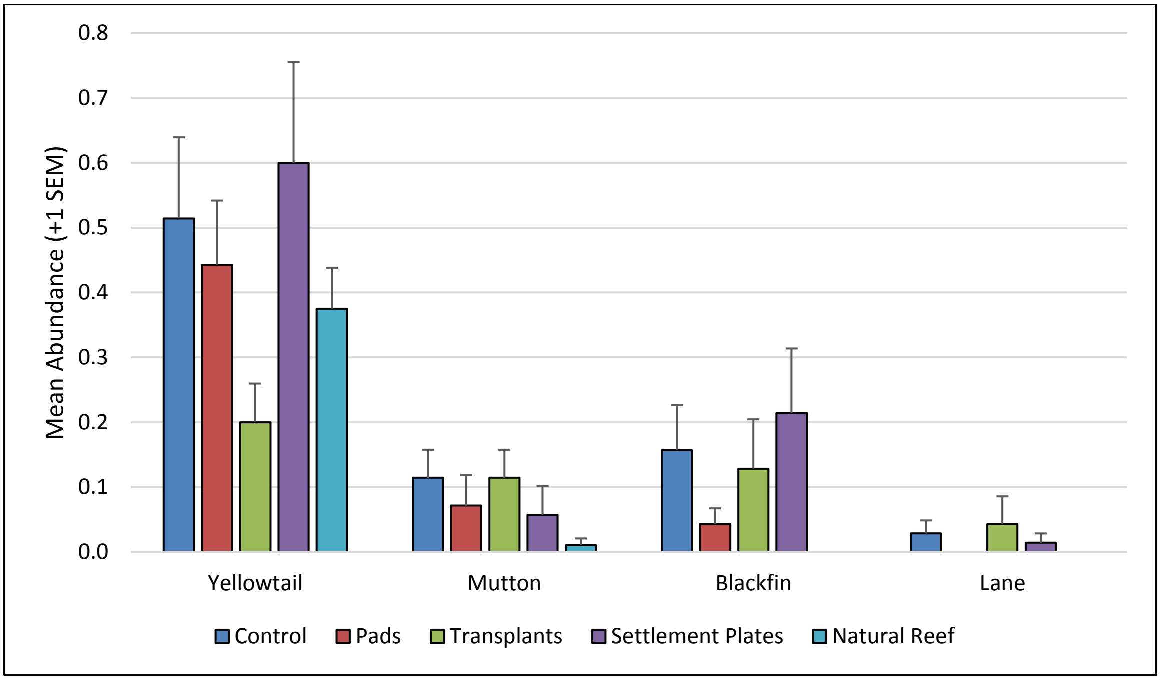


Figure 5.58 Mean abundance of snapper species by treatment. No significant differences were found (ANOVA, p>0.05).

Juveniles accounted for a significant portion of the snappers observed on all treatments (0-2cm through 5-10cm size classes), but the 10-20cm size class was the most numerous (Figure 5.59). Once again, the results were extremely variable, with no clear pattern emerging. There were more seen on the Pads treatment for the 10-20cm size class, although not significantly so. Mutton snappers always occurred as fairly large individuals roaming throughout the module deployment field, and were seldom seen in direct association with any one module for more than a few moments before they swam away.

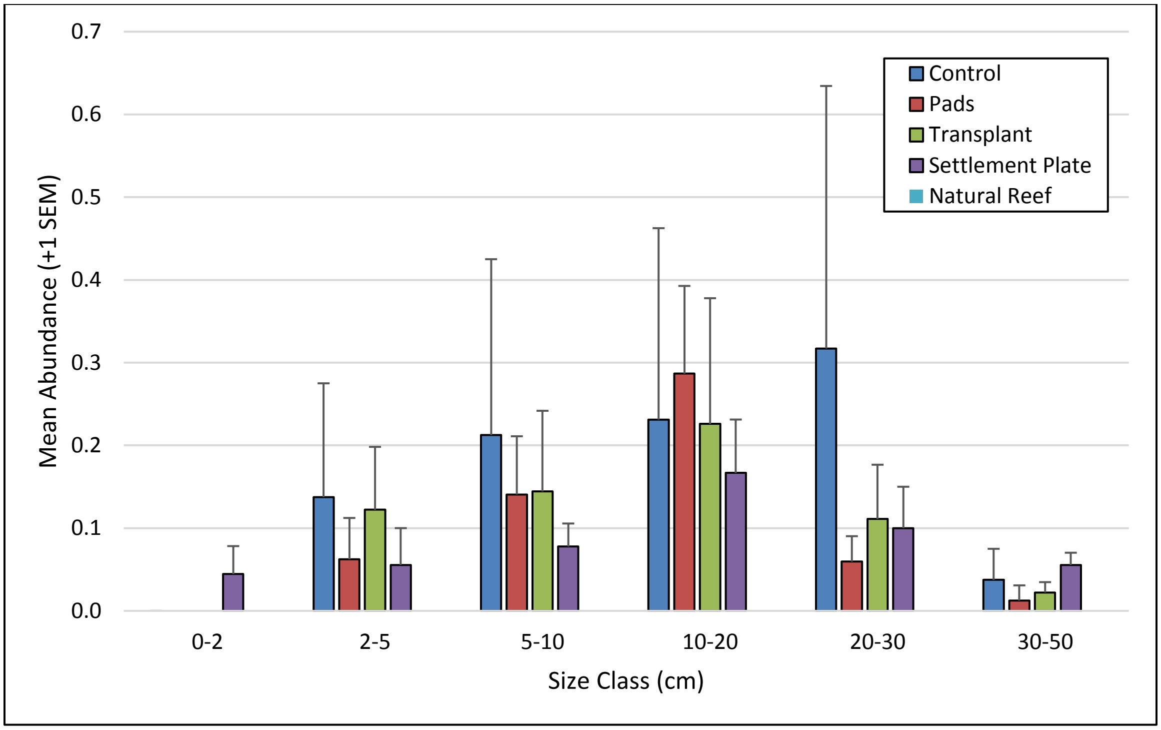


Figure 5.59 Mean abundance of all snappers by size class and treatment. No significant differences were found (ANOVA, p>0.05).

5.3.6 Juvenile Abundance

Other artificial reef studies have reported that in tropical areas, most initial colonization is by juveniles (Russell et al., 1977). Analysis of only those individuals from the 0-2cm and 2-5cm size classes will serve here as an assessment of juvenile abundance. The majority of reef fishes are, as a group, relatively small in body size (≤10cm), and there are several commonly encountered benthic species that do not exceed 5cm in maximum total length. Therefore, inclusion of a species within the 0-5cm size class does not necessarily equate to membership within the newly settled or juvenile age classes, but given the small percentage of these small species in the dataset (gobies, blennies, etc.) the fishes within the 0-5cm range were primarily juveniles.

Juveniles contributed a substantial portion, 64.7%, of the total abundance from all modules and the natural reef combined. In general, there was great similarity between the treatments, although the Pads and Coral Transplants treatments were higher than the natural reef (ANOVA, p=0.047: means were too similar for SNK to differentiate groups) (Figure 5.60). No significant differences between treatments were detected until September 2009, where Transplants had the highest number of juveniles, followed by the controls and Pads (Figure 5.61). However, although not statistically significant, two out of the seven dates had the Pads treatment with the greatest mean abundance, both significant dates; one for being the date with the greatest total number of fishes counted (including both juveniles and adults) (September 2007), and the other for being six years into the study with modules that have had more time to mature (September 2012).

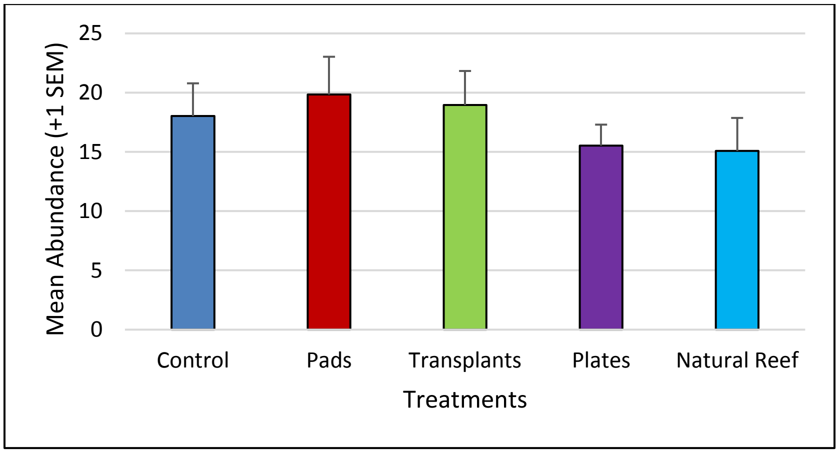


Figure 5.60 Juvenile (0-5cm) mean abundance by treatment. A significant difference was detected, but the SNK did not differentiate between groups (ANOVA, p<0.05) (see text).

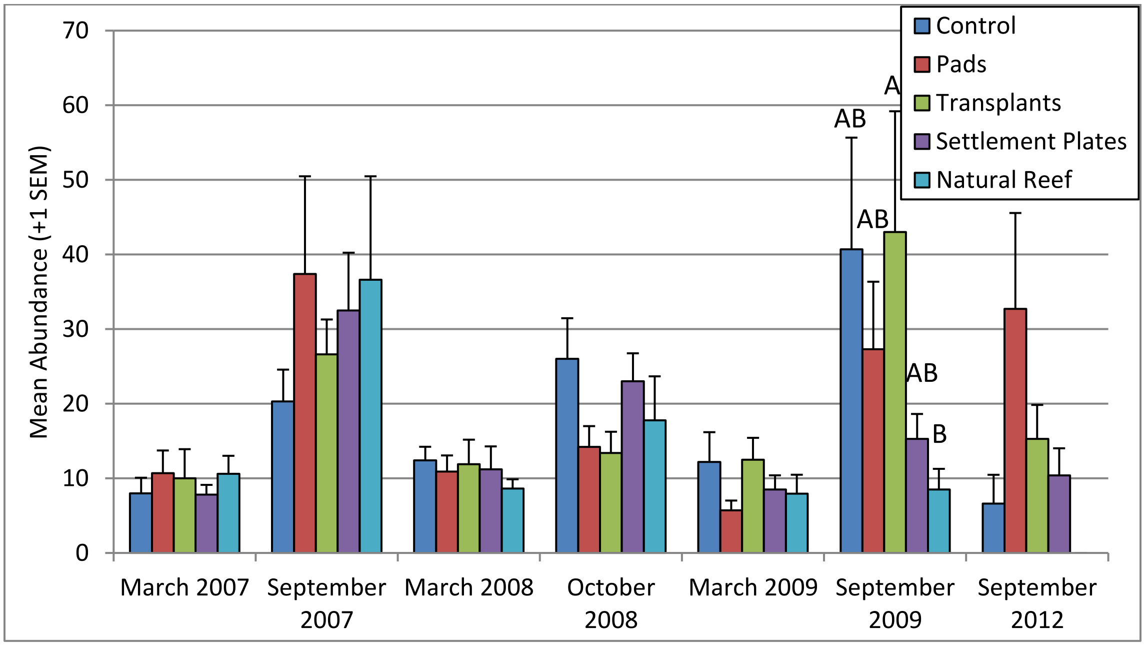


Figure 5.61 Mean abundance of juveniles from the 0-5 cm size class, by date. Different letters indicate significant differences within groups (SNK, p<0.05).

5.3.7 Comparison of Resident and Transient Species

Previous studies (Shulman et al., 1983; Bohnsack, 1991) have reported that resident fishes have been experimentally shown to affect recruitment of other species. This occurs either by active deterrence by territorial species or predation on incoming recruits (Shulman et al., 1983; Bohnsack, 1991; Seaman and Sprague, 1991). Species within this dataset were grouped according to their likelihood of belonging to either the resident population of fishes with strong site fidelity to one module or those more mobile or transient species that had a strong likelihood of being temporary visitors (Belmaker, 2009). In total, 62 species were categorized as residents, whereas 49 were considered transients (Appendix 5.11).

For residents, there were no significant differences detected for mean abundance or species richness among treatments or the natural reef (ANOVAs, p=0.53 and p=0.72, respectively) (Figure 5.62). However, there were numerically more residents seen on the Pads treatment than the others. Given the numerical dominance of this dataset by Bluehead Wrasse and grunts, a secondary resident analysis was performed with Bluehead Wrasse and all grunt species removed. These results were quite different, with significantly more fishes being found on the natural reef (ANOVA, p=0.00037), closely followed by the Pads treatment (Figure 5.63). Following that, all remaining treatments were identical, although there were slightly more on the Transplants treatment.

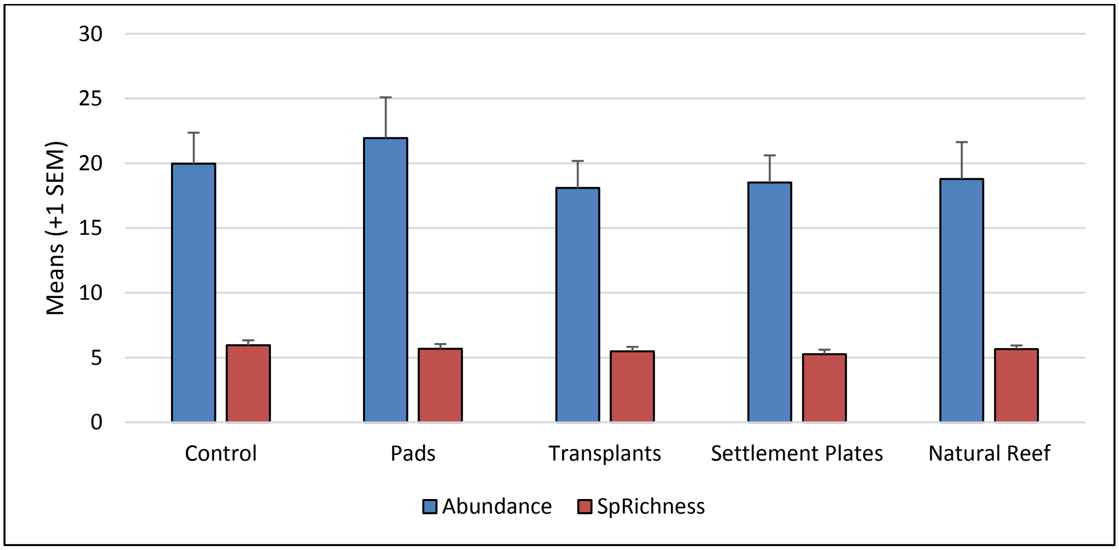


Figure 5.62 Mean abundance of resident species by treatment. No significant differences were detected (ANOVA, p<0.05).

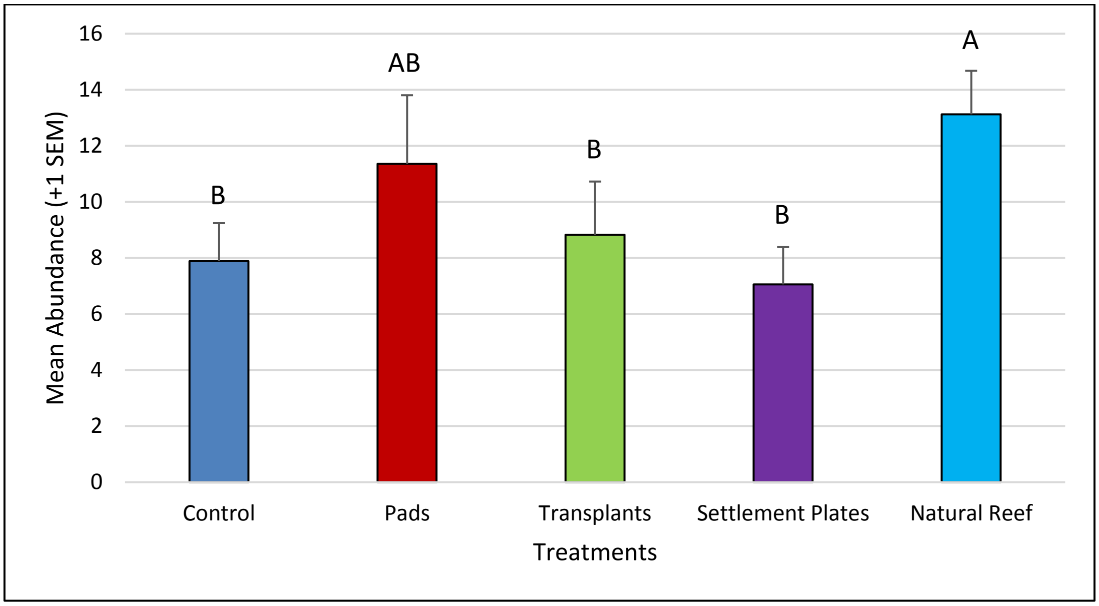


Figure 5.63 Mean abundance of resident species with Bluehead Wrasse and all grunt species removed. Different letters indicate significant differences and shared groupings (SNK, $p<0.05$).

Some examples of the most abundant resident families include wrasses, damselfishes, grunts, gobies, pufferfishes, groupers, butterflyfishes, angelfishes, and moray eels. Greater numbers on the natural reef were mainly due to Blue Chromis, Masked Goby, and Rainbow Wrasse. High numbers on the Pads treatment were due to damselfishes and surgeonfishes.

For transient species, the pattern among treatments and controls was similar to the residents, although there were significantly fewer transients on the natural reef (ANOVA, $p=0.00013$) (Figure 5.64). Examples of the most abundant transient families included: surgeonfishes, parrotfishes, wrasses, snappers, jacks, and boxfishes. Once again there were more on the Pads, although not significantly, mainly due to Blue Tangs.

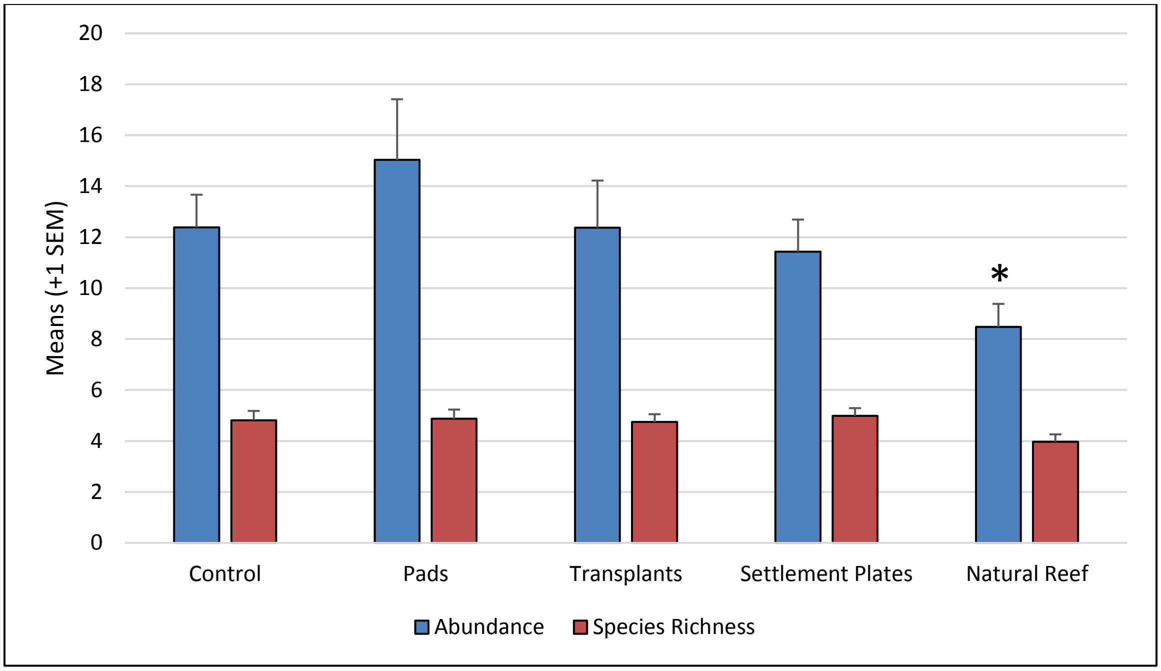


Figure 5.64 Mean abundance and species richness of transient fish species. The asterisk indicates a significant difference (ANOVA, p<0.01).

5.3.8 Trophic Levels

The majority of all reef fishes worldwide are considered generalized carnivores (Randall, 1967) and were the predominant tropic level in this study (Figure 5.65). In other studies, carnivores have dominated in biomass on artificial reefs as well (Brock and Grace, 1987; Kilfoyle et al., 2013), followed by herbivores, planktivores, and omnivores respectively. Here, carnivores were further classified as either benthic carnivores, piscivores, or planktivores. Omnivores included species known to consume both animal and vegetable material intentionally, although most omnivores tend to lean heavily towards one or the other depending upon preference and abundance of local food resources (trophic adaptability) (Gerking, 1994; Gonzalez-Bergonzoni et al., 2012).

Benthic carnivores, such as grunts, butterflyfishes, gobies, goatfishes, wrasses, and some snappers and groupers, were seen in comparable numbers across all treatments and controls, but in lower numbers on the natural reef and in slightly lesser numbers on the Pads and Transplants treatments. Herbivores, such as surgeonfishes and parrotfishes, occurred in significantly lower numbers on the natural reef (ANOVA, p=0.003) and slightly more on the Pads treatment. On average 19.4% of the fishes on each treatment consisted of herbivores (range 18.7% to 20.0%), as compared to the 10.8% found on natural reef. However, it is interesting to note that while the total number of herbivores was lower on the natural reef, parrotfish made a greater contribution to the overall assemblage abundances on the natural compared to the modules. On average 2.9% of the species assemblage consisted of parrotfish (range 2.4% to 3.7%) on the modules, while there were 7.5% on the natural reef. The majority of the parrotfishes that were seen in greater numbers on the natural reef were juvenile and sub-adult Redband, Striped, and Stoplight Parrotfish.

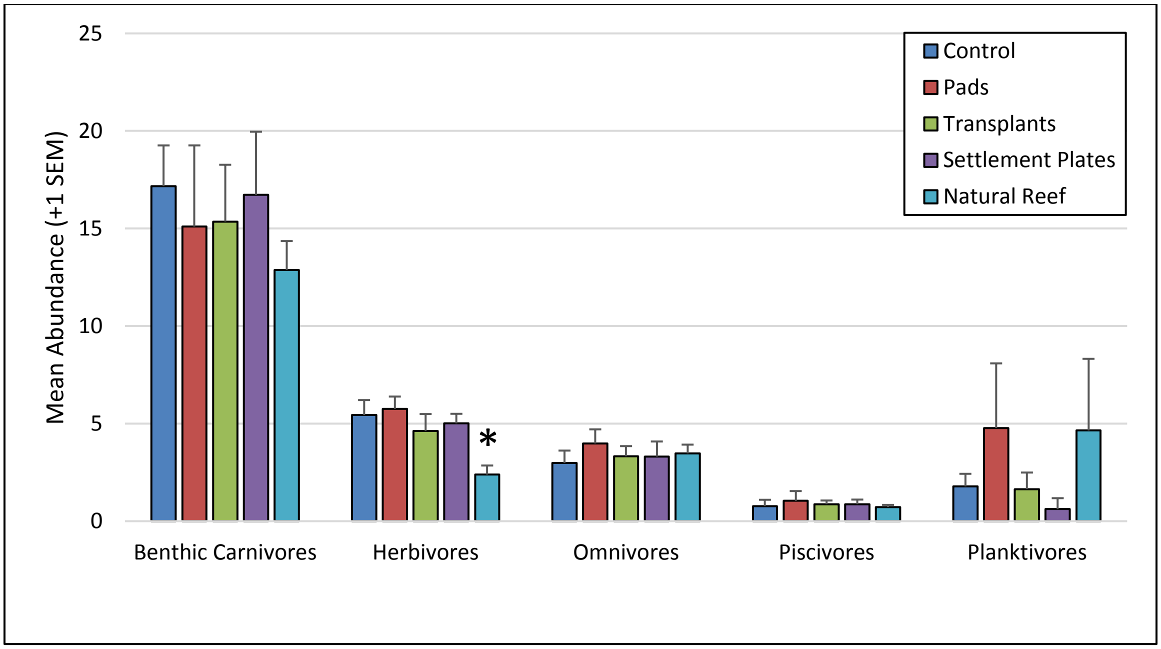


Figure 5.65 Benthic carnivores dominated the assemblage structure of reef fishes for each treatment, followed by herbivores, omnivores, piscivores, and planktivores. There were significantly fewer herbivores on the natural reef (SNK, $p<0.05$).

Williams et al. (2001) suggested macroalgae can be excluded by herbivorous fishes from some reefs with high coral cover, but that on low-cover reefs, algal growth rates may outpace the rate of herbivory. Comparison of surgeonfish, parrotfish, and damselfish abundances revealed that for the most part there were statistically comparable numbers across all experimental treatments and controls, however, slightly more of several species (specifically large Blue Tangs, Doctorfish, and Bicolor damselfish) on the Pads and Settlement Plates modules. Omnivores, such as Chubs, damselfishes, angelfishes, and pufferfishes, were also seen in comparable numbers, but in slightly greater numbers on the

Pads and Settlement Plates treatments. Perhaps not coincidentally, reduced coverage of turf algae data in this study (see Figures 3.2 and 3.3, Chapter 3) coincided with slightly higher abundance of primary herbivores and omnivores on the Pads treated modules. In contrast, fleshy macroalgae (*Lobophora variegata*, specifically) seemed to show the opposite effect, with more being found on the Pads modules (see Figures 3.4 and 3.5, Chapter 3). That might indicate that the higher percentage of herbivores on the Pads is related to the verdant and diverse macroalgal community.

Planktivores such as Blue Chromis, Masked Goby, and juvenile Grunts, were present in higher numbers on the Pads treatment and natural reef, however this difference was not significant when all planktivorous species were combined (ANOVA, p=0.62). The number of strictly piscivorous species found on the modules during this study was relatively low, particularly the large groupers and snappers. However, small piscivores and other benthic carnivores that have been reported to contribute to the overall piscivory on coral reefs were commonly encountered. Hiatt and Strasberg (1960) reported that the cumulative ecological effect of small piscivores may equal or surpass that of other larger predators. It is therefore possible that despite low numbers of piscivores in this dataset, the effect of predation could still be a primary driving factor that determines community structure.

Side-note: Lionfish

Invasive Red Lionfish (*Pterois volitans/miles* complex) were not reported from the Yucatan until 2009 (Schofield, 2010; Bodanoff et al., 2016), and none were recorded as part of this study until September 2012. However, one was seen on a module in September 2009 but it was not during a survey. In September 2012, there were 21 occurrences of lionfish on the modules, 27 in total. There were no differences detected between treatments (ANOVA, p=0.052) (Figure 5.66), but there were more on the Transplants treatment, especially for the 10-20cm size class (Figure 5.67). In the span of three years, abundance of lionfish had increased such that at the end of the study >50% of all modules had one or more lionfish on them. Regretably, no fish counts were done on the natural reef in 2012, so it is not known what their relative abundance there was compared to the modules

Interestingly, there were schools of 10-100 juvenile grunts at 7 out of the 21 modules where one or more lionfish were counted (30%). This was perhaps coincidental, but other studies have reported juvenile grunts as a common prey item for lionfish (Albins and Hixon, 2011; Munoz et al., 2011). In addition, it may also be noteworthy that the mean abundance of wrasses on the modules was seen to decline between March 2009 and September 2009, especially since the previous two summer data collections had reported high numbers of wrasses (Appendix 5.8). Furthermore, wrasse abundance declined even more between September 2009 and September 2012. There was a three-year gap in the dataset between these two points and it is possible that there were once again higher wrasse abundances in the interim summers of 2010 and 2011. Nevertheless, the fact that this decline coincided with an increase in lionfish populations may speak to the detrimental effect that these invasive species are having on community structure in the area.

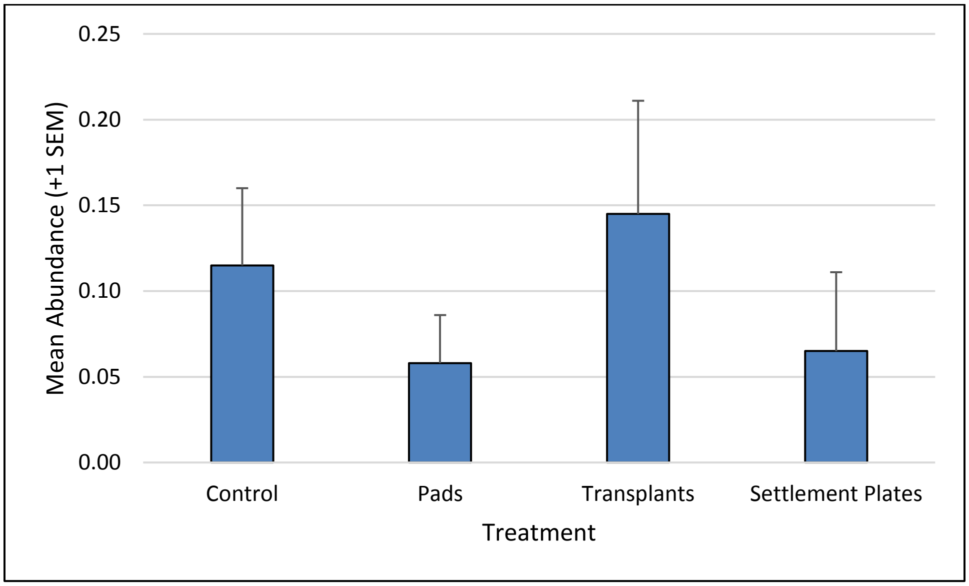


Figure 5.66 Mean abundance of lionfish by treatment. No significant differences were found (ANOVA, p>0.05).

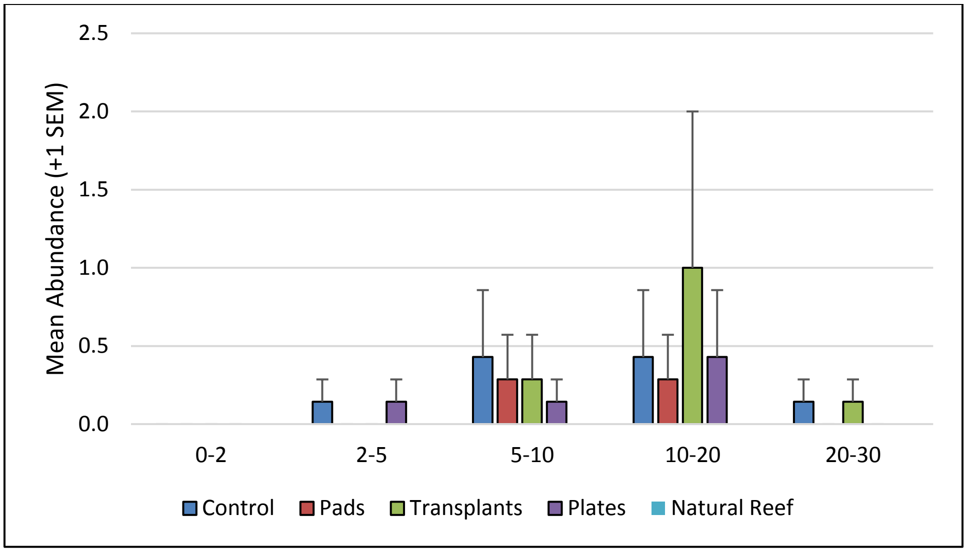


Figure 5.67 Mean abundance of lionfish by treatment. No significant differences were detected (ANOVA, p>0.05).

5.3.9 Commercially and Recreationally Important Species

Out of the 111 species recorded in this study, 13 qualified as important or potentially important to the local economy (Figure 5.68). Yellowtail Snapper, Black Grouper, Red Grouper, Yellowfin Grouper, Great Barracuda, and Hogfish are all targeted by commercial and recreational fishermen, and most are commonly served in local restaurants. The majority of these species were not observed on the natural reef, and the rest occurred in greater numbers on the modules. All occurrences of the grouper species listed here were of large adults, suggesting that they were attracted from nearby natural habitats.

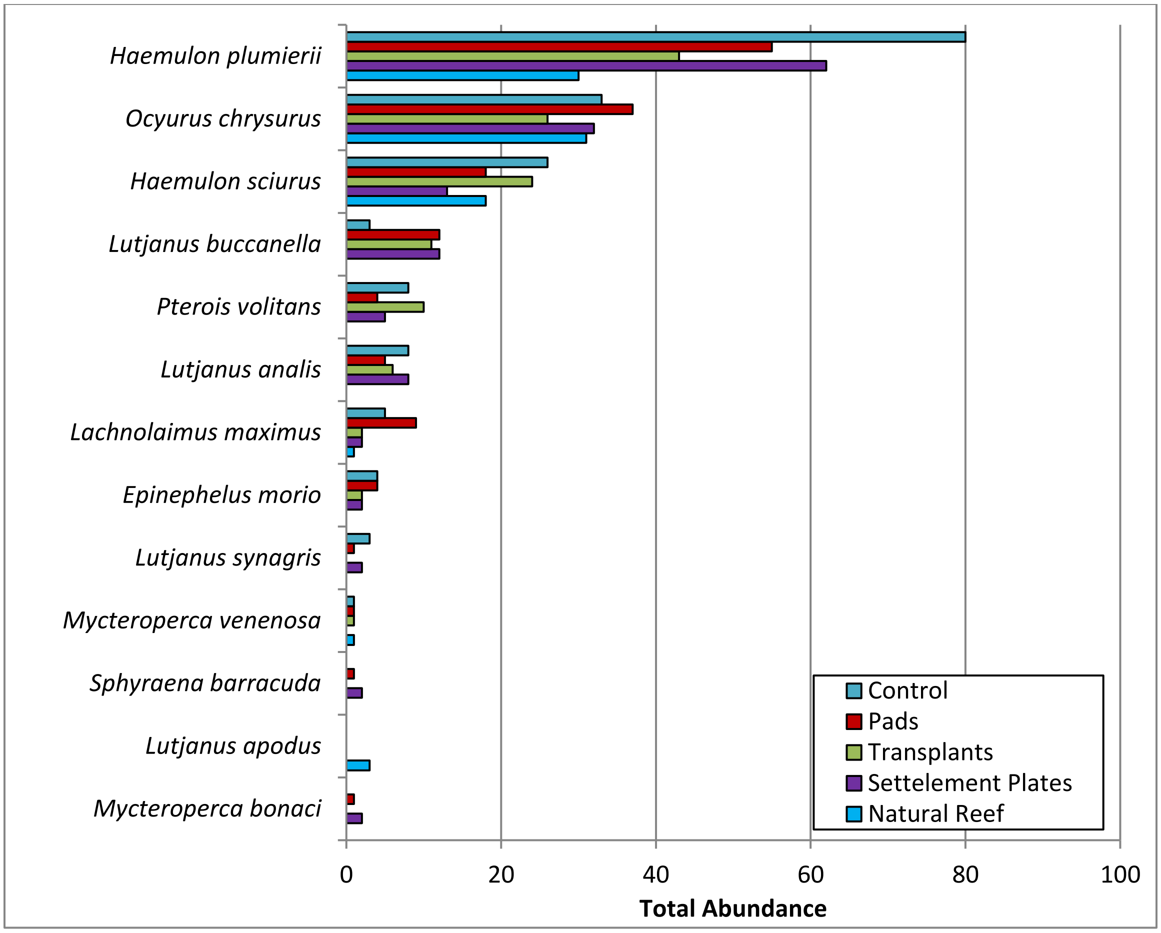


Figure 5.68 Total abundance of commercially/recreationally important fish species, by treatment.

5.3.10 Timeline Summary and Species Highlights

Differences between the treatments, controls, and the natural reef were primarily driven by a handful of species. The following section summarizes notable differences that were found for these dominant species by date (see Appendices 5.12 – 5.20). Only six out of the ten most abundant species on the natural reef were on the top ten lists for the modules. For the first monitoring trip following deployment (March 2007), mean abundance and species richness on the modules was not significantly different than the natural reef (Figures 5.8 and 5.10), but the natural reef still appeared higher, with the exception of the Pads treatment (which actually exceeded the natural reef for abundance due to Bluehead Wrasse, Blue Tang, and Doctorfish). However, after the initial monitoring trip, each of the three treatments and controls had mean abundance and species richness that appeared to be as high as or higher than the natural reef every trip, with one exception of lower abundance on the controls for September 2007. The analyses indicate that the species that contributed most to the differences between the modules and natural reef were: Bluehead, Slippery Dick, Yellowhead, and Clown Wrasses, Surgeonfishes, juvenile Grunts, Damselfishes (Bicolor, Blue Chromis, and Three-Spot Damsel in particular), Sharpnose Pufferfish, most Parrotfishes, and Masked Gobies (see Appendices 5.2 and 5.21).

This group of species primarily, plus a few more, continued to stand out for their consistent presence in higher numbers on the modules or the natural reef. Blue Chromis and Yellowhead Wrasse were higher on the natural reef than the modules all of the six dates of data collection; Damselfishes, with the exception of Bicolor, five out of seven; Parrotfishes four out of seven. Masked Gobies were a strong presence on the natural reef in September 2007 and October 2008, but were completely absent every other visit. Blue Tangs were commonly encountered during the analyses, showing up in greater numbers on the modules, particularly for the Pads treatment (Figure 5.42). Bicolor Damselfish and Blue Chromis also both showed up in higher numbers on the Pads treatment (Figure 5.45), as did most grouper species (Figure 5.54). Yellowhead Wrasses appeared in significantly higher numbers on the natural reef every year (Figure 5.33), and were marginally higher on the Transplants and Pads modules than the Settlement Plates and controls.

In September 2007, mean abundance had more than doubled since the first data collection (Figure 5.8), the first indicator of maturation and potentially of seasonal differences. Once again there were more Blue Chromis and Yellowhead Wrasse on the natural reef; however, juvenile grunts, Masked/Glass Goby, and Rainbow Wrasse made up a larger contribution of the natural reef assemblage than they had six months previously. In addition, there were also more Beaugregory, Three-spot Damsel, and parrotfishes on the natural reef. On the Pads treatment, there were more Tomtates, Blue Tangs, Rainbow Wrasse, White Grunts, Blue Chromis, Yellowtail Snapper, Doctorfish, and Black Margate. Higher abundance in general for all treatments, controls, and the natural reef in September 2007 was primarily the result of an increase in the number of Bluehead Wrasse and juvenile grunts (Appendices 5.8 and 5.9).

In March 2008, levels for all treatments, controls, and the natural reef were back on par with what was originally observed the previous spring (Figure 5.8). Once again on the natural reef there were more Yellowhead Wrasse, Blue Chromis, and Three-spot Damsels, in addition to Dusky Damsels, several parrotfish species, and Sharpnose Pufferfish. The Pads treatment had more Blue Tangs and Yellowhead Wrasse than the other treatments. Juvenile grunts were largely absent in March 2008.

Mean abundance in October 2008 had increased again from the previous trip, but numbers were lower than the previous summer/fall (September 2007). There were fewer juvenile grunts recorded in October 2008 than the previous season. Again, the natural reef had more Blue Chromis, Masked Gobies, Yellowhead Wrasse, Redband Parrots, Three-spot Damsels, and Cocoa Damsels. This time the Pads treatment did not show higher abundances for any particular species.

In March 2009, the seasonal decrease in abundance was apparent, and the levels were as low as or lower than they were at the beginning of the study. There were very few juvenile grunts recorded during this trip, and very few Blue Tangs. Yellowhead Wrasse, Blue Chromis, damsels, and parrotfishes again predictably contributed the most to the difference between the modules and the natural reef. The Pads treatment had more Bicolor Damsels, and Transplants had more Yellowhead Wrasse.

In September 2009, abundances were greater, with higher mean abundance for the Transplants treatment and controls. There were more juvenile grunts, Doctorfish, and Redband Parrotfish on the Transplants modules. Controls also had a large contingent of juvenile grunts. The Pads treatment had more Bicolor Damsels and Blue Chromis than the other treatments again, and there were more Blue Chromis and Yellowhead Wrasse on the natural reef than the modules again.

Six years post-deployment, in September 2012, abundances were still on the upper end of the seasonal swing, with many juvenile grunts recorded. There were more juvenile grunts and Bicolor Damsels on the Pads treatment, and Blue Tangs were found in greater numbers on the Transplants treatment. On the Transplants treatment, there were also many juvenile grunts, Cottonwicks, and slightly more lionfish. The natural reef was not sampled in September 2012.

5.3.11 Treatment Summaries

In an effort to gain an overview of the entire study across the diverse, and often conflicting, results among treatments, years, and metrics, a condensed summary for each of the experimental treatments and controls is provided here, with an attempt to score their overall performance specific to coral reef fishes. All previously discussed parameters (*i.e., mean abundance and species richness, abundance by family, species, and size class, juveniles, residents or transients, trophic level, etc.*) were evaluated by treatment and given a score each time they were ranked or tied for 1st amongst the other treatments (see Appendix 5.21). Statistical significance was not a criterion for inclusion within this scoring system, although the number of significant differences attributed to each treatment was also tabulated seperately.

As ranked by this scoring method, 35% of the analyses had more first place rankings for the Pads treatment as compared to the other treatments (which ranged from 17-22%) (see Appendix 5.21). Out of a total of 14 significant differences detected (of 132 separate analyses) among the experimental treatments alone, eight of those (57% of the total number of differences detected) were from the Pads treatment. Comparatively, there were two differences detected (14%) from each of the Controls, Coral Transplants, and Settlement Plates treatments, and 45% from the natural reef out of the combined total (14 treatments + 17 natural reef) of 31 significant differences.

5.4 Conclusion

The primary goal of this project was to examine the potential for specific restoration interventions to create a more natural assemblage (as compared to natural and unaltered substrate) and kick start recovery on artificial reef substrates. In the process, the study was also intended to evaluate whether or not these treatments could be used for future restoration or rehabilitation applications to compensate for loss of natural reef resources. This chapter examined the interaction of coral reef fishes with the restoration interventions, and analysis of this dataset involved numerous and varied approaches to examine the relationships among variables and detect differences and patterns that would lead to meaningful conclusions. Variation was high within replicates, a feature consistent with other studies of artificial reef fish populations on natural habitats using visual census techniques (Seaman and Sprague, 1991; Smith et al., 2011; Brandt et al., 2009; Lindberg and Seaman, 2011; Kilfoyle et al., 2015). Overall, interpretation of the results revealed that none of the treatments were found to support significantly more fishes by total number than the controls, and two out of the three treatments actually had lower mean abundances than the controls (Transplants and Settlement Plates). In addition, the majority of the individual analyses by date, family, and other metrics revealed very few differences. Although the analyses revealed relatively few significant differences between treatments and controls, several species did demonstrate strong habitat preferences among natural and artificial substrates or the experimental treatments. When the dataset was examined in greater detail it became clear that the Pads treatment, and to a lesser extent, the Coral Transplants treatment, had the greatest effect on reef fish assemblages, and may have been creating conditions that were either different from the other treatments and/or more similar to those found on nearby natural reef.

Despite relatively few statistically significant differences being found, the Pads treatment showed more signs of influence on the reef fish community than the other treatments or controls. The Pads treatment had higher abundance during the first two monitoring trips six months and 12 months post deployment (although not significantly), as well as higher abundance at the final point of data collection at the six-year mark. It is possible that the Pads treatment was providing some sort of benefit to the reef fish community at the beginning of the study, when food and microhabitat resources on the newly deployed modules were limited. More damselfishes, surgeonfishes, and groupers were found on the Pads treatment modules. In addition to providing abundant interstitial habitats for small infaunal and epifaunal invertebrates, the padding material also provided additional surface complexity and vertical relief above the level of the bare concrete surfaces. In another Caribbean study, Nemeth (1998) found that juvenile Bicolor Damselfish experienced greater mortality on *Orbicella annularis* boulder coral than on piles of *Porites porites* coral rubble (a more structurally complex branching species). Over time, the attachment method for the padding material allowed for some loose corners and other occasional gaps between the pads and the surface of the modules, thereby creating additional refuge space for small fishes and additional attachment points for macroalgae and sponges. The greater abundance of Bicolor Damsels and Blue Chromis on Pads and the Transplants treatments could be the result of additional microhabitat complexity, and a simiar situation might explain the higher abundance of Masked Gobies on the natural reef. If this is true, then for small planktivores, the main problem on the control and settlement plate modules may be related to a lack of available refuge space and the resulting condensed community level interactions. The groupers may have been encountered in greater numbers on the Pads treatment due to the increased abundance of juveniles, and other small prey, as well as the additional refuge space. Reef fish assemblages on the Pads showed greater similarity with assemblages recorded on the natural reef. In the Caribbean, many reefs have shifted from being coral dominated to macroalgae dominated (Hughes et al., 1994; Williams et al., 2001, Bellwood et al., 2004), and likewise the coral reefs of Quintana Roo were no exception. Perhaps the greater similarity in assemblage structure between the Pads treatment and the natural reef, as well as a greater abundance of herbivores (damselfishes and surgeonfishes), was linked to the greater percent coverage of macroalgae found on the Pads treated modules (see Chapter 3, Figures 3.4 and 3.5).

Chapter 3 discussed the increase in percent cover by benthic competitors over time and the homogenization effect that resulted from rapid growth and spread of macroalgae and sponges. Towards the end of the study, macroalgae gradually declined in coverage and, concomitantly, influence upon competing members of the benthic community following the initial rapid growth outbreaks decreased. The sponge community also showed signs of reduced or stabilized growth at the end of the study. One potential explanation for the general similarity in reef fish abundances between the treatments, aside from the high variation, is the possibility that the effects of the experimental treatments were dampened due to the homogenizing effect that benthic communities had on the structure and function of the treatments; at least from the perspective of a reef fish.

The biannual snapshot surveys utilized in this study limited the ability to fully investigate interactions between both the restoration interventions and the artificial substrates, and the primary determinents of community structure and abundances on the modules in greater detail. The limited timeframe and opportunities available to evaluate community development on the modules and the resulting coarse resolution of the dataset made it challenging to parse out substantial differences between the treatments and controls, especially as the benthic community and its wide-ranging potential effects on reef fish abundance and assemblage structure was not a consistent variable. Environmental fluctuations and the inherent variability of reef fish communities in general were additional confounding factors. Nonetheless, this study did provide considerable new insight into how the restoration interventions influenced development and structure of reef fish assemblages on the modules, as well as how assemblages on the artificial reefs compared to those found on the natural reef. In addition, this study utilized methods that to date had yet to be employed or evaluated with this level of detail in this particular geographic region.

This project was part of a larger research endeavor designed to examine novel restoration-focused methodologies and their potential for application onto natural and artificial reefs. In this part of the Caribbean, the natural reefs are not dominated by coral cover, and are instead dominated by algae. The Pads treatment arguably did a better job of supporting a reef fish assemblage L }that more closely resembled that of the natural reef. This may be due in part because the natural reef and the Pads both had greater abundances of macroalgae, or, perhaps moremore likely, due to lack of adequate physical structure on the other treatments needed to support a comparatively broader range of species and size classes.

Size dependent mortality, refuge variability, dietary preferences, and seasonal fluctuations in the availability of recruits were no doubt some of the primary driving factors influencing the results of this study. Thus, in terms of enhancing reef fish populations, future recommendations include: increased structural complexity and refuge for juveniles and small species, larger overall artificial reef size and greater provision of hydrologic fronts, and more holes of varying sizes. If used for the purposes of restoring a degraded reef or mitigating for lost natural resources, when used together in larger numbers and with closer spacing the modules might provide a more diverse and abundant reef fish community as compared to a more dispersed and isolated design such as the one utilized here. An extended monitoring window and more frequent survey opportunities are also needed to fully evaluate the performance and true potential of the artificial substrate padding material and coral transplants.

Based on the results of this six-year study, the differences in assemblage structure between the modules and natural reef imply that the modules were performing similarly to one another in terms of overall abundance, but may not have been providing substrate of equivalent ecological value compared to the natural reef. This has important implications if these modules and treatments are to be effectively used as tools for restoration or ecosystem rehabilitation. Artificial reefs can be utilized to support a varied reef fish assemblage and perhaps enhance populations of locally important species, but as mitigation for loss of natural resources, these results suggest that their ability to provide habitat of equitable value is limited and therefore must be taken into consideration when calculating their compensatory value.

Chapter 6 – Synthesis and Conclusions: Interactions between Major Functional Groups and Performance of Restoration Interventions

6.1 Overview

6.1.1 Introduction

The previous three chapters described in detail the developmental trajectories for each of the major functional groups: macroalgae, non-coral benthic invertebrates, stony corals, and coral reef fishes. These groups were evaluated largely independent from one another in response to the experimental treatments that were applied to the modules. However, these groups also co-existed and co-developed on the same artificial substrates over the same time period, and therefore it can be assumed that they were interacting with and influencing each other in multiple ways. This chapter examines these interactions to gain insight into how much overall influence the experimental treatments had on assemblage development on the modules. The overall community perspective utilizing a combination of results from the previous three studies helps identify which group(s) were dominant and how their relative contribution to the overall assemblage structure on the modules changed over time. This perspective also serves as a final assessment of the performance of the restoration interventions in the context of multiple hypotheses tested here and it outlines lessons learned that can be applied to future restoration and mitigation efforts, management strategies, and new artificial reef designs.

6.1.2 Interactions between Major Functional Groups

When treatments and controls were combined and all major groups were compared on the same timeline and vertical scale (Figure 6.11), some interesting relationships between major competitors became apparent and easier to visualize. It should be noted from the outset that this figure is displaying a series of isolated snapshots through time, rather than continuous data. The lines connecting the individual points are an aid to getting a general overview of change through time; they provide a summary of the rate of change in the variable through time and not a constant rate.

Macroalgae was the most frequently enumerated category for benthic cover throughout the study on all treatments and controls (Chapter 3). A general decreasing trend in contribution by turf algae can be explained by considering its ubiquitous status in the marine environment (Steneck, 1988; Arnold et al., 2010) and its presence on all otherwise un-colonized surfaces of the modules as the *de facto* 'blank canvas' condition. Over time, as the larger fleshy macroalgae species and sponges began to occupy an increasing amount of space, obviously, there was less of the blank canvas remaining. Fleshy macroalgae increased rapidly at first, peaking one year after deployment and then gradually declining throughout the remainder of the study. The brown algae *Lobophora variegata* contributed the majority portion of the percent coverage by this group on the modules, but it was almost completely absent on the natural reef. The minority portion of the macroalgae consisted of other common species, such as *Dictyota* spp. and *Halimeda* spp. Regarding performance of the restoration interventions, one year into the study the Pads treatment had significantly more *L. variegata* than the other treatments and controls, where the greatest peak in percent coverage by any treatment throughout the study was observed, and Pads were higher again three years into the study. The Settlement Plates and Pads treatments had greater percent coverage of *L. variegata* in March and October 2008, and Settlement Plates were highest in March 2009. Interestingly, percent coverage of *L. variegata* was significantly lower on the Coral Transplants treatment for almost the entire first three years of the study. At the end of the study, *L. variegata* had a percent coverage that was only contributing an insignificant amount to the total (below 5% on all treatments and controls). Given the small percentage of this species on the natural reef and the trend of decreasing percent coverage over time on the modules for all treatments and controls, it is tempting to consider this as a sign of maturation and perhaps impending stability of the benthic community. There is, however, an alternate possible explanation: the decrease in macroalgae coincided with an increase in percent coverage by sponges, which appeared to be competitively superior to the macroalgae through higher growth rates, more rapid spreading and acquisition of unoccupied space, and direct overgrowth. The sponges therefore may be an important regulator for macroalgal growth on maturing artificial reef modules. As the sponges appeared to be gradually decreasing their overall coverage at the end of the study, macroalgae showed the beginnings of a possible uptick in growth. It may also be noteworthy that this increase in macroalgal growth at the end of the study did not include a significant contribution from *L. variegata*. Considering the amount of available space that was left un-colonized by anything other than turf algae (see Figures 6.14 through 6.17 below), one might surmise that if *L. variegata* was a major long-term competitor on the modules, it would have taken more than partial overgrowth by another competitor (sponges) to regulate its spread. There were more surgeonfishes and damselfishes (herbivores and omnivores, respectively) on the Pads treatment modules, which had the highest level of macroalgae, so grazing by reef fishes was likely not a primary driving factor in the reduction of *L. variegata*. If *L. variegata* was not overgrown or subjected to significant grazing pressure, perhaps the decline of this species is truly an indicator of substrate maturation. However, to what degree the macroalgal community may fluctuate over time in response to changes in environmental variables or in response to competition by other benthic organisms remains to be fully explored.

Sponges increased steadily through the first three years of the study, but the increase was not as rapid as what was observed for macroalgae; it took approximately one year longer for the sponges to reach the same level of mean coverage as the macroalgae on the modules. Coverage by sponges was, however, more extensive, as sponge coverage surpassed that of fleshy macroalgae for the remainder of the study. There were a variety of upright and encrusting sponge species documented on the modules, but the rapidly growing *Desmapsamma anchorata* made the most significant contribution, although not at first. That species was present at the beginning, but it did not contribute the majority portion until March 2008, a year and a half after deployment. From that point onward, the percent coverage by this species increased steadily and it remained the majority contributor through the end of the study. The percent coverage of other sponge species remained relatively stable on the modules.

Regarding the performance of the restoration interventions, the Pads treatment had significantly more *D. anchorata* than the other treatments and controls from October 2008 through the end of the study, with a peak in mean percent coverage in September 2009. On the natural reef, sponges remained at similar levels throughout the duration of the study, never exceeding a mean percent coverage of 2%, and *D. anchorata* made up a minority percentage of that. Given the relatively small contribution made by sponges on the natural reef and the apparent beginnings of a decreasing trend on the modules at the end of the study, perhaps this was another indicator of benthic community maturation and an impending increase in stability (and potentially for increase in coral recruitment and survival rates). However, percent coverage of *D. anchorata* was still rising on the Coral Transplants treatment at the end of the study, and sponges persisted as the main contributors to percent coverage by any major functional group on the Pads treatment. The Controls modules notably had the lowest percent coverage of *D. anchorata* throughout the last five years of the study.

Coral density increased at a slow but steady rate over time relative to observed increases in percent coverage for macroalgae and sponges (Chapter 4). The density of newly recruited corals fluctuated between dates, seemingly aligned in tandem with other observed seasonal changes (i.e. macroalgae and fishes). Mean density of new coral recruits was significantly higher in September 2007 and at the end of the study compared to what was observed during the middle portion. Regarding performance of the restoration interventions, no single treatment was observed to consistently produce a higher density of corals or new coral recruits over time, although in September 2009 and September 2012 observed densities of new recruits and total corals were higher on the Controls than they were on the treatments. In addition, the Pads treatment modules had fewer total corals and new coral recruits recorded on them than the other treatments or controls for the last two collection dates. However, corals were also larger on the Pads treatment modules for most species. No coral recruits were detected within the natural reef quadrat areas. However, those areas also remained largely devoid of anything other than turf algae and sediment for the entire study, thus it can be concluded that this particular quadrat assessment method was insufficient for gaining accurate insight into the true dynamics of coral recruitment and community structure on the natural reef and assumptions about coral recruitment on the natural reef using this data alone should be approached with caution.

The influence that increasing percent coverage of macroalgae and sponges had on coral transplant survival was abundantly clear from both the data and descriptive photos taken of the modules through time. The coral transplants experienced significant losses during this study, mainly due to overgrowth by the sponge *D. anchorata*. This overgrowth effected all three transplant species similarly. However, *O. annularis* had a higher occurrence of colonies that appeared unhealthy (pale color, receding tissue, or disease) and/or dying earlier than the other transplant species in the study.

The influence that the general increase in percent coverage of other benthic organisms had on total coral and new coral recruit density over time is less clearly understood. It may be important that the mean density of new recruits appeared to fall during the middle portion of the study and then gradually rise again at the six-year point, as the middle period of the study also coincided with the steady increase and peak in percent coverage of sponges. However, considering no significant differences were found in the number of new recruits during this period (March 2008 through March 2009), the fluctuations might also be attributed to mere stochastic variability. Regardless of the reason for fluctuations in the number of new coral recruits that were detected on the modules, there were consistently enough survivors from previously recorded recruits to contribute to an overall increase in coral density on all of the treatments throughout the study.

Mean abundance of coral reef fishes (Chapter 5) was highly variable and driven by 111 interacting species. These species created an inherently mercurial assemblage that fluctuated on a more frequent and accelerated basis compared to that of the benthic community, and therefore reef fishes were not included in the combination figure above (Figure 6.11). A subset of 25 of the 111 species comprised 90% of the recorded reef fish abundance. Mean abundance of these species fluctuated seasonally for all treatments and the natural reef (Figures 6.12 and 6.13), but unlike the most dominant members of the benthic community, there was no apparent general increase in mean abundance or species richness of coral reef fishes on the modules over time; at least not on the same multi-year temporal scale. Future observations might reveal whether increasing maturity of the benthic communities leads to an increase in overall abundance and diversity of reef fishes, or if populations on the modules plateaued early on in the study and just fluctuated around some median level, as suggested by Seaman and Sprague (1991). Given the similarities noted here between the modules and natural reef during most of the first three years of the study, it seems that large scale environmental influences and/or natural stochastic variability are responsible for much of the observed fluctuation in reef fish abundance over time.

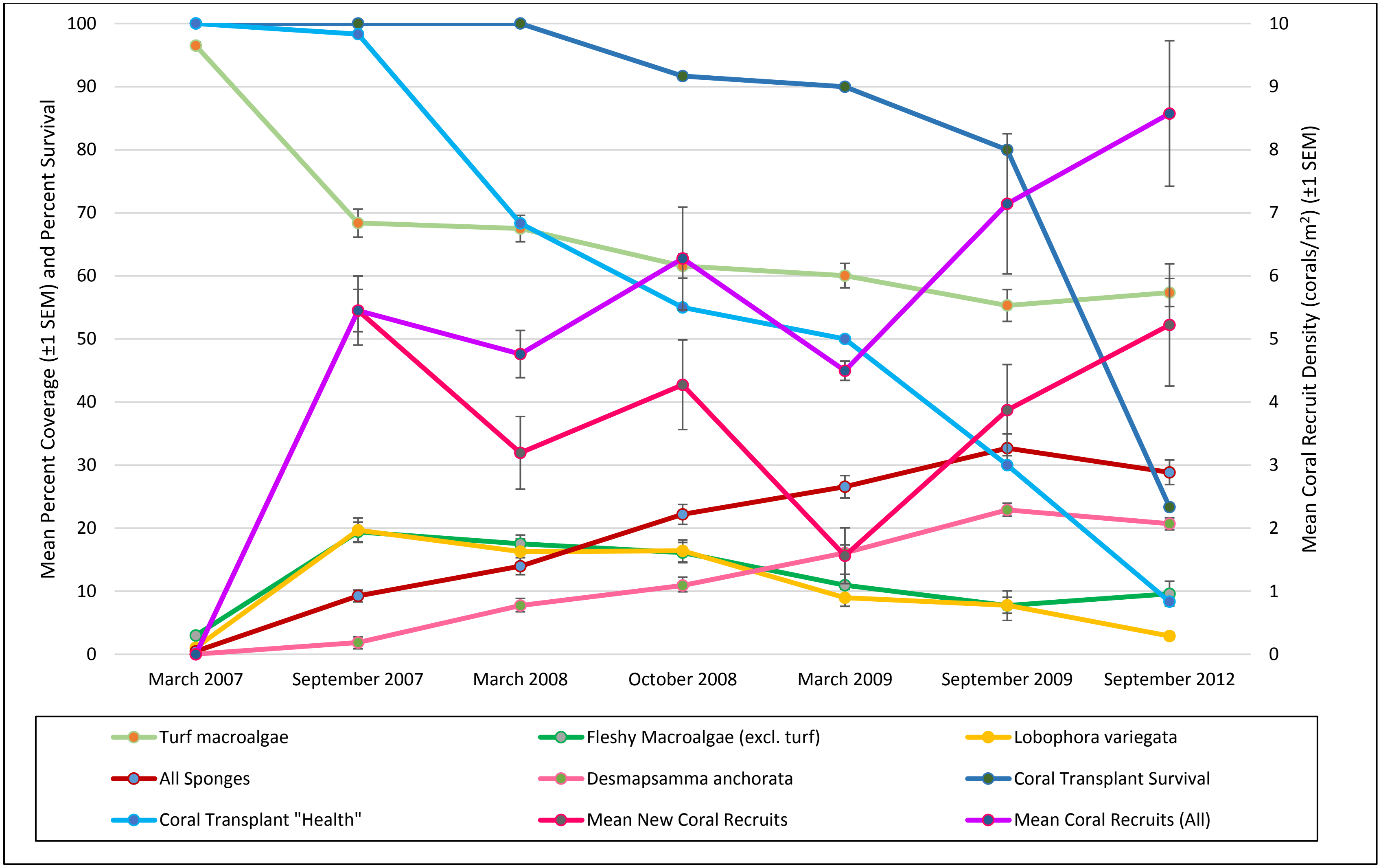


Figure 6.11 Mean percent coverage of all major benthic community components on the modules by date with all treatments combined. Mean coral recruits (in purple) are on the secondary axis. Percent survival of coral transplants and percent of healthy transplants (i.e., not affected by disease, tissue loss, pale coloration, or mortality) is also included on the same primary y-axis (in light and dark blue).

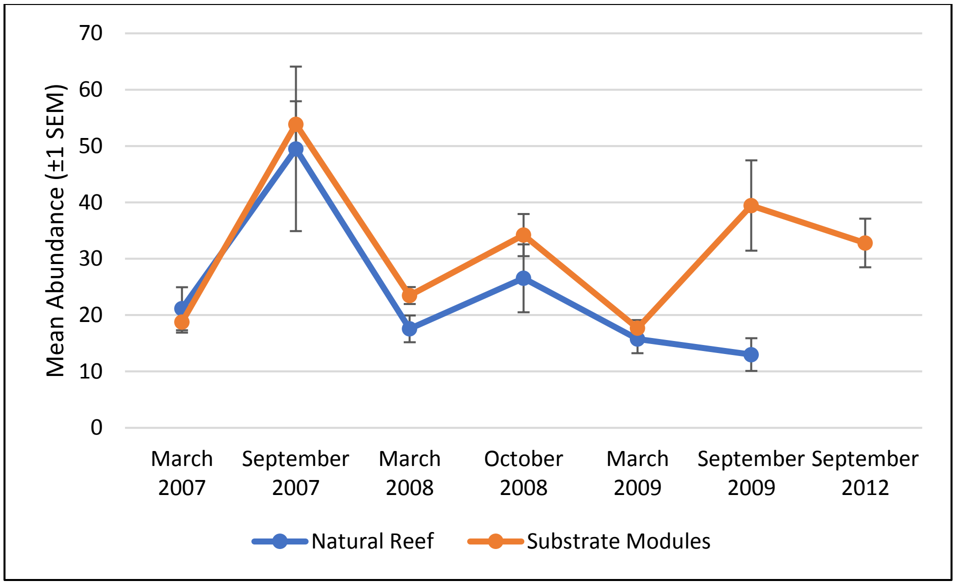


Figure 6.12 Mean abundance of coral reef fishes on the natural reef and modules with all treatments combined by date.

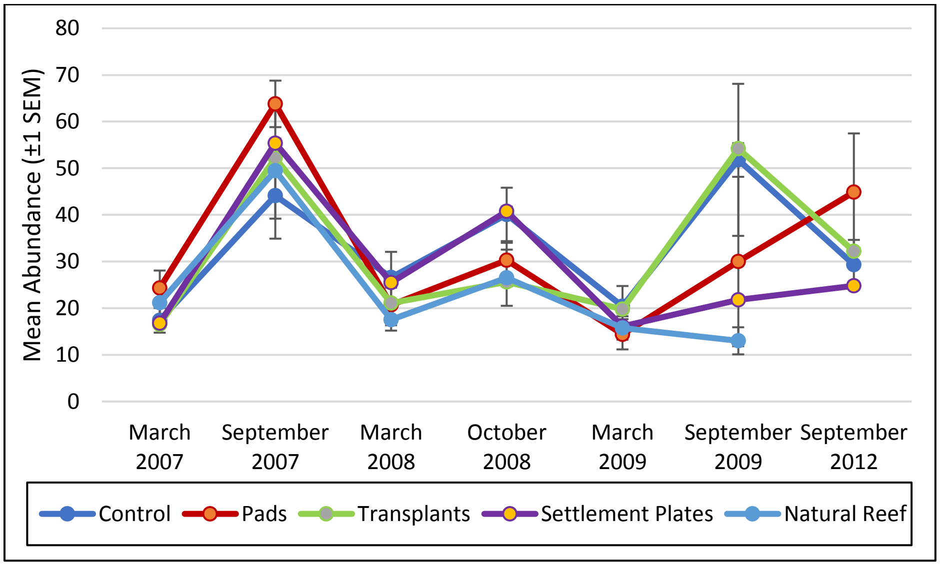


Figure 6.13 Mean abundance of coral reef fishes by treatment and date.

6.1.3 Total Coverage by the Benthic Invertebrate Community

The amount of total space occupied by all members of the benthic community combined (macroalgae, sponges, tunicates, corals – turf algae excluded) was calculated using benthic quadrat data and compared by treatment. With all dates combined, there was significantly more space occupied by the benthic community on the Pads treatment modules (ANOVA, p=0.0001), followed by Settlement Plates, and the Coral Transplants treatment and Controls were even (Figure 6.14). Total percent coverage was significantly lower on the natural reef than all treatments and controls. When coverage was examined by date, the natural reef was initially significantly higher than the modules (March 2007 ANOVA, p<0.0001) (Figure 6.15). From that point onward the modules were equal to or exceeding the natural reef for every treatment. Mean percent coverage was significantly higher on the Pads treatment than the other treatments and controls for three out of seven dates, and significantly higher and/or tied along with the Settlement Plates treatment for another three dates. Total percent coverage on the modules, with all treatments and controls combined by date, increased significantly during the study (ANOVA, p=0.0001) (Figure 6.16)

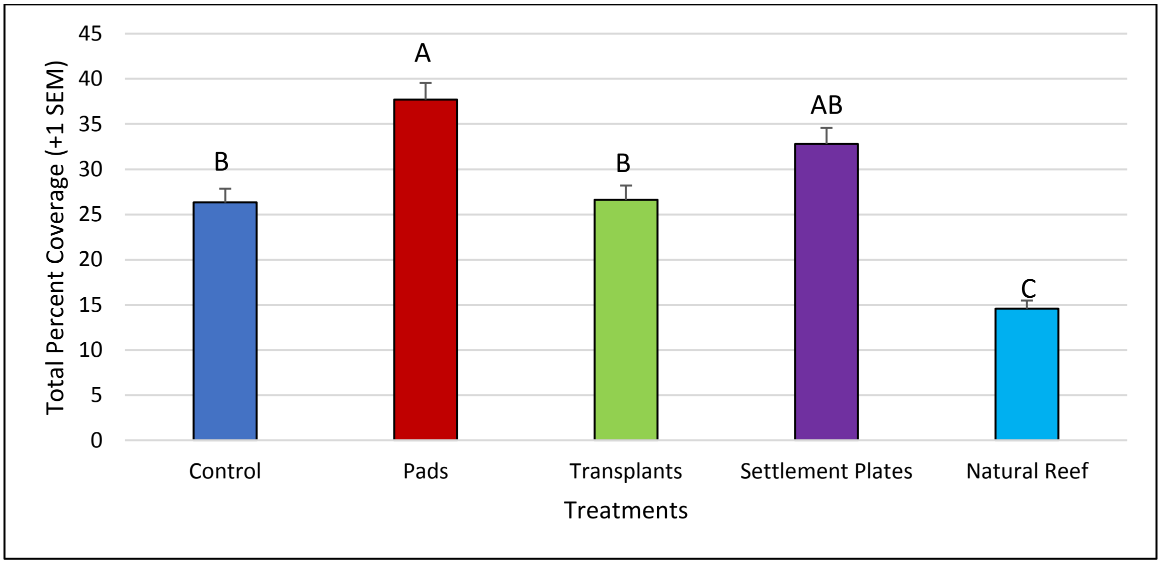


Figure 6.14 Means by treatment for total combined percent coverage for all benthic invertebrates and major macroalgae (not including turf algae) on the modules and natural reef. Different letters indicate significant differences between means (SNK, p<0.05).

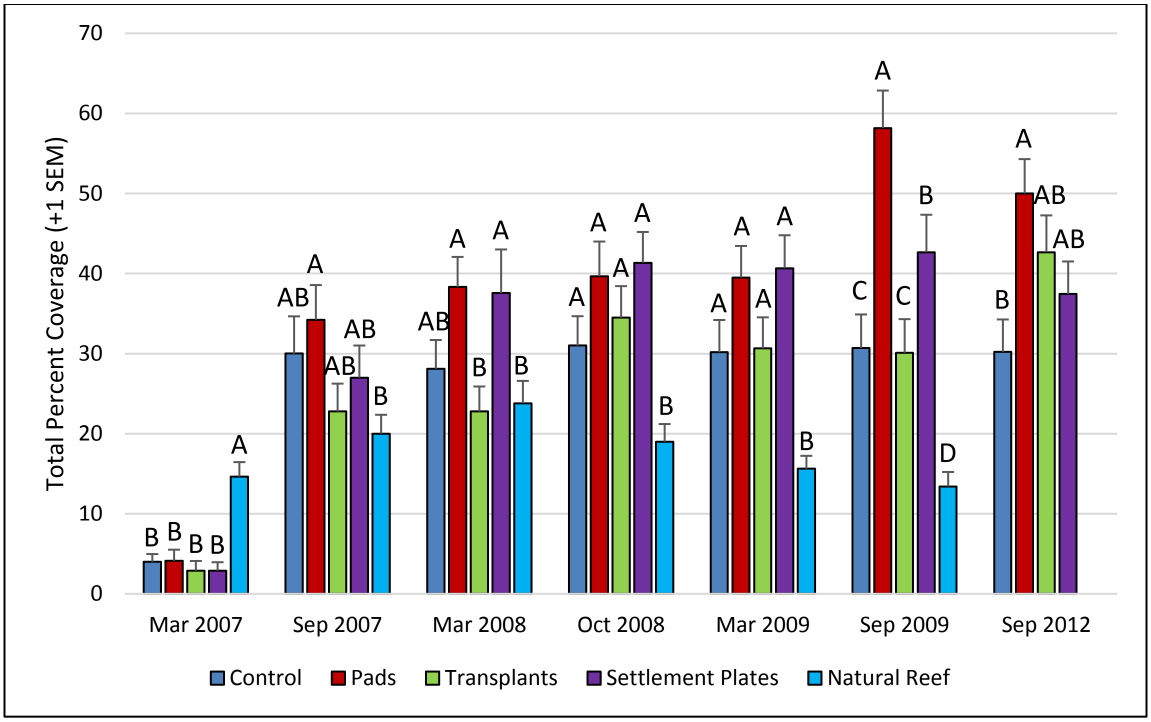


Figure 6.15 Means by treatment and date for total combined percent coverage of all benthic invertebrates and major macroalgae (not including turf algae) on the modules and natural reef. Different letters indicate significant differences between means and shared groupings within each date (SNK, p<0.05).

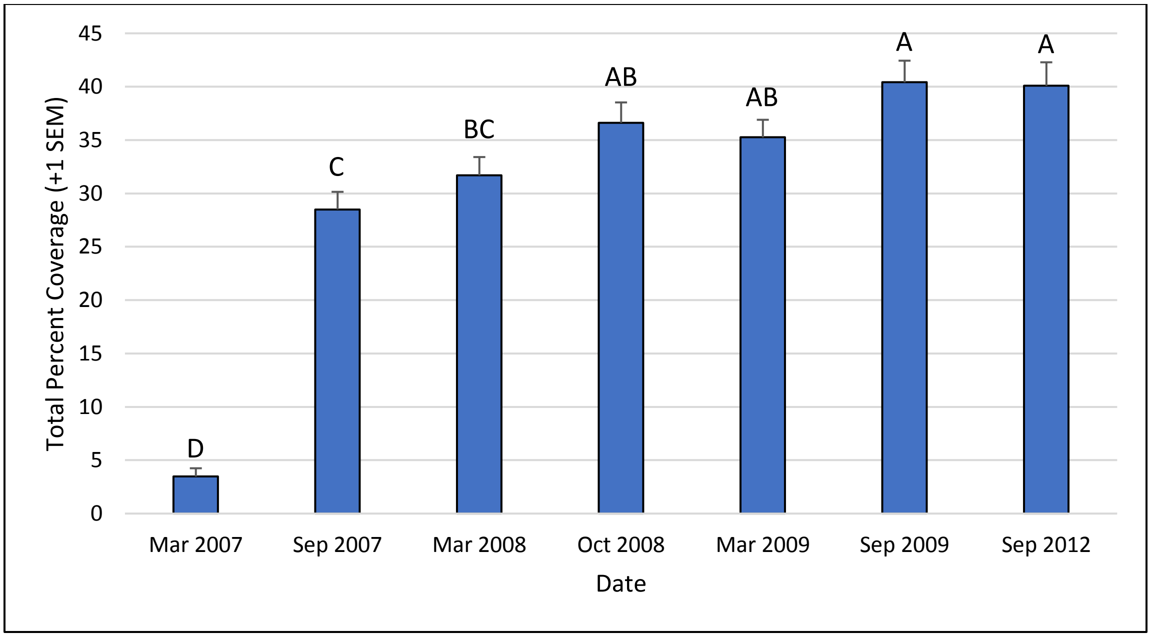


Figure 6.16 Means by date for total combined percent coverage of all benthic invertebrates and major macroalgae (not including turf algae) on the modules. Different letters indicate significant differences between means (SNK, p<0.05).

Despite conflict between major groups, there was still a considerable amount of space left over for colonization at each data collection point (Figure 6.17). The high amount of un-colonized space on the Settlement Plates treatment (ranked second behind Controls) was not surprising considering that by the end of the second year of the study (October 2008) all of the settlement plates had been collected for laboratory analysis (see Ch.4, Table 4.6).

Total percent coverage increased rapidly and steadily throughout the first three years of the study, but then appears to have plateaued given the similarity between the September 2009 and September 2012 (Figures 6.16 and 6.17). Using slope calculated between March 2007 and September 2012, and assuming the same rate of change and no major environmental departures from normal conditions, the modules could be totally covered over approximately 20 years after deployment. However, the similarity between September 2009 and September 2012 casts doubt on the validity of that projection. Once again, a longer study duration is needed to completely answer temporally dependent questions such as these.

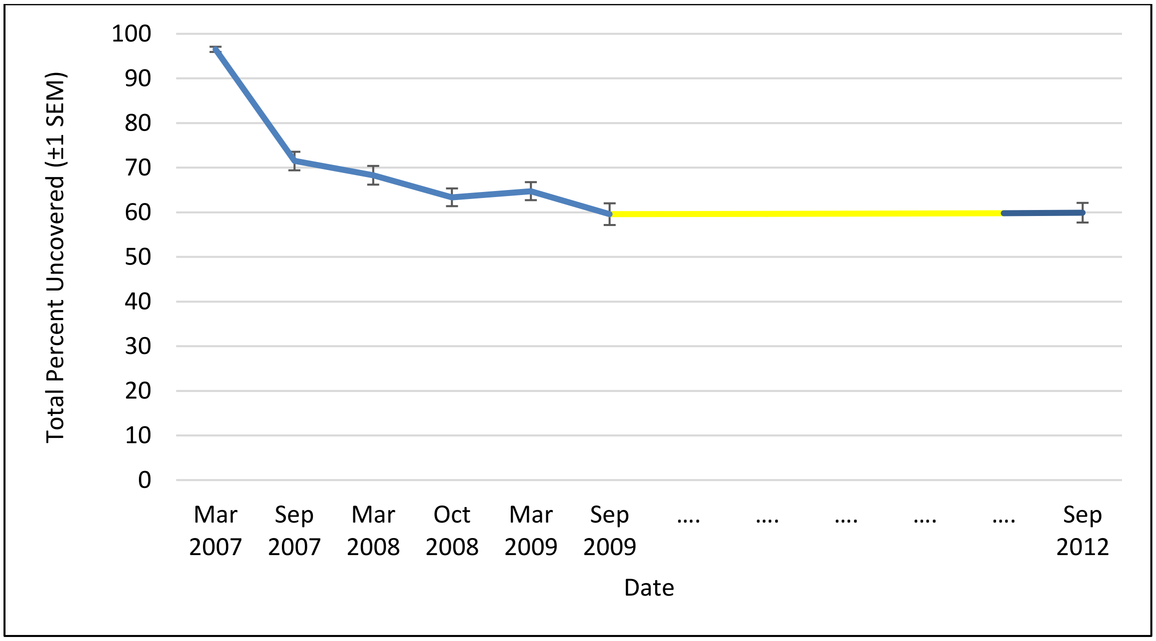


Figure 6.17 Means by date of the remaining un-colonized space on the modules, excluding turf algae. Segments of the line in yellow are an approximation based the percent of uncovered space detected in September 2009 and September 2012.

6.2 Treatment Summaries

Overall, the developmental trajectories for each of the previously discussed major faunal components shared enough similarities among treatments and controls that they appeared to follow generally parallel pathways of development during the study. However, for some treatments these general pathways deviated enough to warrant differential conclusions about the ability of the restoration interventions to influence development of the benthic community on the modules. All three treatments appeared to have more of an effect on community development than the Controls; each provided some degree of additional exterior structural complexity and microhabitat variability that was apparently beneficial to some species. In many instances the differences between treatments and controls were statistically significant, but some treatments appeared to have a stronger effect than others on particular groups of organisms or species and the ability for the treatments to affect the development of benthic communities was not necessarily of benefit to all groups. For example, coral recruitment and survival may have been negatively affected by the rapid growth and increasing levels of coverage of overgrowing macroalgae and sponges. There were more new coral recruits found on Control modules than the treatments in the latter part of the study (significantly for September 2009 but not for September 2012), notably at a time when sponges were at their highest levels of coverage on the treatment modules. There was less *D. anchorata* sponge on the Control modules than the other treatments for four out of seven dates. Furthermore, there was also less fleshy macroalgae (although not statistically significant) on the Control modules at the end of the study in September 2012.

Examples illustrating differences detected between the Controls and Pads are as follows. There was significantly greater coverage of *L. variegata* macroalgae on the Pads treatment modules at the onset of the study and during the highest peak in September 2007. For the following three data collections (March 2008 through March 2009), the Pads treatment had significantly greater coverage of *L. variegata* than the Controls and Coral Transplants treatment, but was ranked second closely behind the Settlement Plates treatment. The Pads treatment also had significantly higher coverage of *L. variegata* than the other treatments and controls in September 2009, and interestingly, the lowest amount of coverage in September 2012 three years later at the end of the study (non-significantly). The percent coverage of fleshy macroalgae other than *L. variegata* was equal for all treatments and controls until the end of the study, when in September 2012 it was higher for the Pads treatment. Thus, even though *L. variegata* diminished on the Pads, other species showed the potential for maintaining a solid macroalgal presence or foothold on the modules. In addition, the overgrowing sponge species *D. anchorata* steadily increased on all treatments and controls throughout the study, and there was significantly greater percent coverage of that species on the Pads treatment modules for the last four collection dates (a full 2/3 of the length of the study). Consequently, the Pads treatment also had significantly lower total coral and new coral recruit density than the other treatments and controls in September 2009, and non-significantly in September 2012. Regarding coral reef fishes, the Pads treatment had more surgeonfishes (Blue Tangs and Doctorfish), juvenile grunts, damselfishes (Bicolor and Blue Chromis), and groupers and basslets (Graysby, Red Hind, Mutton Hamlet, and Harlequin Basslet) than the other treatments. There were also significantly more resident species on the Pads treatment, and more juveniles (non-significantly). These points all lead to a conclusion that the invertebrate enhancing artificial substrate padding material indeed has the ability to affect significant changes to development of benthic and reef fish community structure, and therefore the use of pads, as implemented here, as an integral part of an artificial substrate approach to restoration, warrants additional research.

Fewer differences were detected between the Controls and Coral Transplants treatments, but some were noteworthy. When total coverage of all benthic species was combined (see Figure 6.15) and comparisons were made between treatments, the Controls and Coral Transplant treatments were ranked evenly below the Pads and Settlement Plates treatments when all dates were combined. Furthermore, when broken up by date, the Coral Transplants treatment had the lowest or second lowest total percent coverage for six out of seven collection dates (see Figure 6.16) (a full 92% of the study duration). Of particular note, the Coral Transplants treatment had significantly lower percent coverage of *L. variegata* macroalgae than the other treatments and controls for five out of seven dates, and ranked higher than the controls for total fleshy macroalgae at the end of the study. In addition, the Coral Transplants treatment was ranked lower than the Pads and Settlement

Plates treatments for three out of four dates during the rise in dominance of *D. anchorata* sponge from October 2008 through September 2009. However, interestingly the sponge was still on the rise on the Transplants treatment at the end of the study in September 2012. In addition, the Coral Transplants treatment had the highest abundance of other sponges (excluding *D. anchorata*) for six out of seven collection dates, although the differences were not significant. Thus, it appears that both macroalgae and sponges, *L. variegata* and *D. anchorata* in particular, grew better on the Pads and Settlement Plates treatments than they did on the Coral Transplants treatment. This was likely due to the greater spatial coverage by the other treatments, as well as their greater surface complexity and substrate suitable for attachment of macroalgal holdfasts and climbing support for the overgrowing sponges. It therefore appears, the provision of greater structural complexity is of particular importance for accelerating benthic community development during the early phases of succession, and the resulting increases in diversity and coverage may perhaps lead to advanced maturation and/or may more closely resemble assemblages on nearby natural coral reefs.

New coral recruit density on Coral Transplants modules was higher than the other treatments (but not controls) twice during the first 2 years of the study, in September 2007 and October 2008, and ranked significantly higher than the Pads treatment and even with the Settlement Plates treatment in September 2009, and ranked second behind Controls for September 2009 and September 2012. These results lend tenuous support to claims of brooding coral transplants' potential ability to influence settlement of larvae and recruits onto nearby uncolonized substrates. However, in contrast, the relatively higher numbers of coral recruits on the Coral Transplants treatments may have been merely the result of greater availability of unoccupied settlement area and reduced changes of overgrowth, rather than the presence of the coral transplants themselves.

It is worth noting that the Coral transplant treatment effectiveness was reduced by the loss of live coral tissue that resulted from overgrowth by the sponge *D. anchorata* and the eventual mortality of 70-80% of the coral transplants by the end of the study for each of the transplant species. However, the additional vertical relief and structural complexity provided by the coral transplants' dead skeletons and concrete mounting pedestals remained in effect throughout the duration of the study, and continued to provide anchor points and climbing support for the sponge. This is supported by the fact that *D. anchorata* sponge coverage on the Coral Transplants treatment was still ascending at the end of the study, exceeded only by the Pads treatment and decreasing on all other treatments and controls. Once again, this may be simply due to the presence or absence of additional complex substrate on the exterior surfaces.

The Settlement Plates treatment may have had some influence on biotic assemblages, considering the significantly higher percent coverages of macroalgae in March 2008 through March 2009, and a second-place ranking behind the Pads treatment for two out of the four peak periods for *D. anchorata* sponge growth (March and September 2009). Although the settlement plates were not initially intended to provide any beneficial effects to the biota on the modules, the results of this treatment may warrant exploration of external enhancements that might affect development of biotic assemblages on an artificial reef. Recommending this treatment, or one similar, for use in future experimental or restoration applications at first seems counter-intuitive, especially considering that the associated investment in hardware and labor required to outfit an artificial reef or natural surface with settlment plates at an ecologically relevant scale using the method employed here may be cost prohibitive. In addition, the plates were designed for temporary usage in the marine environment, and were not intended for long-term deployment. However, any added structure, including settlement plates (Perkol-Finkel and Benayahu, 2007), is a potential additional attachment point for benthic organisms and every protrusion of structure into the current may create micro-scale eddies or low pressure areas that might affect behavior/movement and space utilization by reef fishes and settlement of benthic organisms. Additional research into specifically engineered baffles or low-pressure zones, and their potential for facilitating relevant positive change on the modules, would be required to validate this concept fully. Such new designs could incorporate a fin or ridge like structure to provide additional shelter for shoaling reef fishes like grunts and snappers. However, the potential increased drag associated with projecting a flat surface into the current would increase the leverage applied by strong currents and potentially lead to instability, making unwanted movement more likely during severe storm events. Therefore, any protrusions would need incorporate a specifically engineered non-lift-inducing shape.

It is also important to note that the structural complexity provided by the settlement plates themselves was reduced at two points during this study. During the first settlement plate collection on November 2007, half the plates were removed from the modules, effectively reducing the additional surface complexity provided by the plates by 50%. During the second and final plate collection on October 2008, the remaining 50% were removed. With all 12 plates deployed, the amount of additional surface area supplied to each module that received that treatment totaled ($0.01m^2$ x $12 = 0.12m^2$) compared to the total ~$2.64m^2$ of the entire exterior surface of each module (see Ch. 2). This increased the overall surface area by ~4%, a potentially inconsequential appearing amount in terms of surface area. When all of the plates were removed the Settlement Plates treatment modules effectively became equivalent to the Controls, and this control-equivalent condition persisted for the latter two-thirds of the study. When attached to the mounting hardware and secured with a wingnut, the settlement plates protruded no more than 5cm above the surface of the modules. The majority of the coral recruits collected from the settlement plates (80%) were found on the underside of the plates. Therefore, the undersides constituted an important settlement surface for the benthic community, so an additional $0.12m^2$ (the bottom plate surface) can be added, resulting in an ~8% increase in total surface area on the modules. After the plates were collected, all that remained was a single stainless steel bolt protruding from the surface, and the stainless-steel plate mounted flush to the concrete surface and secured by four plastic anchor pins. By time of plate collection, the bolts and plates were completely encrusted by macroalgae, bryozoans, tunicates, and/or sponges on almost every module (personal observations). Perkol-Finkel and Benayahu (2007) reported there were more filter feeders like sponges, tunicates, bryozoans, and bivalves on the artificial reefs than the natural reefs, and most were on the underside of settlement plates. The removal of the plates reduced additional overhanging structure, regardless of how small, and any additional baffling effect that may have subtly influenced settlement preferences or growth of benthic organisms in relation to the prevailing current regime.

6.3 Evaluation of Hypotheses

Chapter 1 presented six alternative hypotheses that this study was designed to investigate. The results as they relate to each alternative hypothesis are summarized as follows:

- ***H_1: Increasing habitat complexity by adding* Coral Transplants *to restoration structure will affect (likely enhance) development of coral reef fish assemblages.*** Did the addition of coral transplants affect the development of coral reef fish assemblages? Yes, according to this dataset, and more so for some species than others. Although, there were relatively fewer occurrences, compared to the other treatments and controls, where mean abundance or species richness of reef fishes was higher on the Coral transplant modules, there was higher abundance on the Coral Transplants modules for March and September 2009 (ANOVA, $p<0.05$) and for the other dates they were ranked higher than the Controls. There were also more juvenile grunts (tied with Pads treatment, ANOVA, $p<0.05$). However, it is not clear whether or not the effect was a beneficial one, an enhancement, as this depends upon perspective. Further assessments after the modules have had more time to develop are needed before this hypothesis can be evaluated with greater confidence, and the loss of the majority of the transplants reduced the overall influence that this treatment may have otherwise provided.
- ***H_2: The addition of a novel invertebrate enhancing artificial substrate* Pads *to restoration structure will affect (likely enhance) development of coral reef fish assemblages.*** There were multiple instances where this alternative hypothesis was supported by the data, with the Pads treatment often having highest ranked mean abundances and species richness, not only for the coral reef fish assemblage as a whole, but for several individual important species as well (such as Blue Tangs, Doctorfish, juvenile grunts, and most groupers). Assemblage structure on the Pads modules was also different than the other treatments and controls. The hypothesis is thus supported as coral reef fishes were definitely affected. Many of the differences detected were not statistically significant, but the frequency of occasions where the Pads treatment was higher than the other treatments and controls does suggest that they were having an effect. Whether the assemblages were ‘enhanced’ or not yet again depends upon

perspective. Did they produce more commercially important species? Yes, groupers (although not significantly) and Hogfish (although N was very low). Was there a more diverse trophic structure associated with this treatment? There were more omnivores and planktivores associated with the Pads treatment, although the differences were not significant. Did the pads provide shelter for more juveniles and small cryptic species that need appropriately sized small refuge spaces? Possibly, as there were more Bicolor Damselfish and Blue Chromis, more juveniles at beginning of the study, and more resident species overall. Did the pads produce an assemblage that was more similar to the natural reef? This is a difficult comparison to make; depth differences between the natural reef and module deployment site confound the issue, and aggregation of fishes due to the effect of isolated structures in an otherwise 'barren' seascape influences species composition and abundance. There is evidence in support of both similarities and differences between the Pads treatment modules and the natural reef, although the differences noted here for reef fishes may be enough to warrant a conclusion that the Pads treatment was more similar to the natural reef than the Coral Transplants or Settlement Plates treatments. However, the natural reef had more Yellowhead Wrasse than the modules, more damselfishes, more parrotfishes, more gobies, more resident species, fewer snappers, fewer transients, and fewer herbivores.

- ***H_3*****: The addition of** **Coral Transplants** ***will affect (likely enhance) coral recruitment rates and kick-start coral populations.*** The effectiveness of this treatment was reduced throughout the course of the study as the majority of the transplanted corals were overgrown and killed by competitors (*i.e., D. anchorata*). Nevertheless, mean density of coral recruits was higher on the Coral Transplants modules than the Pads or Settlement Plates treatments for the majority of the data collection dates (4 out of 6), although it was only significant once (Sep 2009 at end of year 3). Overall, it was actually the Controls modules that performed better in terms of coral recruitment, being higher for 5 out of 6 dates for total coral recruits and 3 out of 6 dates for new coral recruits; two of those being the last two data collections. Perhaps the addition of the coral transplants did less to accelerate and enhance the growth and support of the overgrowing sponge than did the other two treatments. However, it is difficult to determine from this data whether occurrences of higher numbers of coral recruits on the Coral Transplants modules compared to the Pads and Settlement Plates treatments were the result of direct influence by the transplants themselves or the result of slightly less overgrowth by the sponges and macroalgae. Due to the lack of difnintive, significant results, there is not enough evidence to fully support the hypothesis.

- ***H_4: The addition of novel invertebrate enhancing artificial substrate* Pads *to restoration structure will affect (likely enhance) resulting coral assemblages.*** The addition of the padding material significantly increased the growth of both macroalgae and sponges, which were both directly attributed to the overgrowth of coral transplants (significantly more so for sponges) and can also be confidently attributed to overgrowth of coral recruits on the modules as well. Mean density of coral recruits was lower on the Pads modules for the last two dates, significantly in September 2009. However, *Porites astreoides*, *Agaricia* sp., *Siderastrea siderastrea*, and *Diploria* sp. all had larger coral recruits on the Pads treatment, although not by a significant margin. Perhaps there is some other beneficial effect provided by the Pads treatment to the corals that are not overgrown by macroalgae and sponges, and therefore the presence of the padding material may present a trade-off of sorts. It cannot be said with any degree of certainty that this treatment enhanced the resulting coral assemblages. Affected, yes certainly, but whether beneficial or not depends on perspective. Good for increasing numbers of recruits? Not according to this dataset. Therefore, the hypothesis cannot be fully supported at this time.
- ***H_5: The addition of novel invertebrate enhancing artificial substrate* Pads *to restoration structure will enhance the return of a "more natural" coral reef ecosystem than simply providing coral settlement structure or coral transplants.*** There were similarities between certain small shelter-dependent and planktivorous species on Pads and natural reef. There was more macroalgae and sponge on the Pads treatment modules. The padding material appears to promote growth of certain benthic organisms (i.e., *Lobophora* and *Desmapsamma*) much better than the other treatments and controls, presumably due to the depth of the complex surface it provides, the increased sediment and detritus/nutrient levels that accumulate, and the associated epifaunal and infaunal invertebrate communities that develop on and within the padding material over time. Increased growth of rapidly spreading benthic species has

been linked to decreased coral recruitment on the modules, so in terms of enhancing the stony coral assemblage it appears that the padding material is not conducive to success. Artificial reef surfaces take decades to mature, and in the future, coverage on the modules may be dominated by a different suite of species than those that were observed to be successful during the first 3-6 years of the study. More time will be needed to fully evaluate this hypothesis.

- ***H*$_6$*: Comparison of community response to formal treatments applied to the substrate modules allows understanding of rates and processes on the artificial structure as compared to the natural reef.*** There were multiple clear differences detected between the modules and natural reef during this study. Coral reef fish abundance was higher on the modules for the majority of the most dominant species (all treatments and controls), but the opposite for others (Blue Chromis, most damselfishes, gobies). Coral recruitment was significantly higher on the modules and almost altogether absent on the natural reef quadrats. Macroalgae on the natural reef was dominated almost exclusively by *Dictyota* sp., as compared to *L. variegata* on the modules. Sponges on the modules were dominated by *D. anchorata*, which was almost completely absent on the natural reef quadrats throughout the study. This has been reported as a fairly ephemeral species on the natural reef, often relying on other biotic or abiotic structure to support itself and thereby enable greater investment into rapid growth (Wulff, 2012; Biggs, 2013). It would be interesting to see, through an extended monitoring period, how long this particular species maintained its dominance in terms of percent coverage and overgrowth of more desirable competitors, such as stony corals. Or if, alternatively, sponges continued to reduce their percent coverage on the modules, would *L. variegata* or some other species of macroalgae once again rise to prominence? *L. variegata* has been known to serve as important juvenile habitat for the Caribbean Spiny Lobster (*Panilurus argus*) (Briones-Fourzon and Lazone-Alvarez, 2001). Lobsters were frequently encountered during this study, although were not chosen as part of the biota to be quantified. Additional might provide further insight into linkages between *L. variegata* and *P. argus* densities and the padding material.

6.4 Lessons Learned, Recommendations, and Considerations for the Future

There seems to be a recurring pattern in artificial reef research: experimental study designs often involve too many broad questions, too many treatments, too many variables, too few replicates, too little statistical power, and budgets that are often too small to facilitate long-term monitoring and fully explore community development on artificial reefs to adequately answer the most important questions (S. Bortone, personal communication). Dodrill (communication) acknowledged that artificial reef monitoring and evaluation is very much needed but is typically inadequate, and insufficient funding is routinely the reason. This study was a departure from this “business as usual”. The three to six-year study period and biennial snapshot surveys employed in this study were adequate to describe the initial trajectories of the major functional groups in response to the experimental treatments. However, considering benthic communities on artificial reefs develop and mature on a decal scale, the six-year sampling window was a limiting factor when attempting to fully characterize performance of the restoration interventions, especially given the sampling frequency and multitude of variables involved.

Nonetheless, in the process of thoroughly assessing growth and development of the major functional groups on the modules, through routine observation and testing of the experimental treatments in a highly dynamic environment, this study generated multiple useful and practical lessons and recommendations regarding the subtleties of module placement and artificial/restoration structure in the local marine environment. These lessons can be used to guide or enhance the outcomes of future artificial reef deployments and can be applied to future artificial reef designs and up-scaled deployments to hopefully improve their performance and ability to function more similarly to natural coral reef habitats. The information is also intended to benefit resource managers tasked with maintaining complex reef ecosystems. Specific lessons and recommendations include:

1) It is impossible to deploy an artificial reef into any habitat and not have it affect the environment into which it is placed to some extent. Even for artificial reefs that are placed directly onto seemingly barren sand, their presence has been shown to impact the community of benthic invertebrates that are found in the interstices of the sandy substrate

for several meters around the edge of the artificial reef (Ambrose and Anderson, 1990; Guerra, 2015; Hirons et al., 2015; Metallo, 2015). If small artificial reef modules similar to those deployed in this study are to be used, care must be made during the site selection process to minimize impacts to the surrounding habitat. Acknowledging the need to avoid or minimize collateral damage is common practice worldwide, although good intentions, even when implemented are not always effective. Further, the marine environment is highly dynamic and anything placed on the bottom will be subjected to the constant forces of waves and currents and the occasional severe storm or hurricane event. Quinn (2009) and Robinson (in prep) both used Reefball^{TM} pallet ball modules on sandy substrate in different locations in Broward County, Florida, USA. Those modules were routinely affected by hydrodynamic forces of prevailing currents associated with the directional flow of the Florida Current, regularly occurring tidally induced currents, and occasional severe tropical weather events. Within a span of ten years post-deployment, both module arrays experienced partial to complete losses of surface area and structure due to sand burial and settling, likely accelerated by several locally severe hurricane events. In Puerto Morelos, hurricane associated currents scoured sand out from around the bases of some of the modules, and one was partially buried. In Akumal, the effects of the storm were felt much more severely. The combination of hard substrate underneath a thin veneer of sand and extreme hydrodynamic forces from a hurricane resulted in the destruction and complete loss of four out of twelve modules early in the study. The remaining eight modules were all pushed shoreward by wave action until they impacted the leading edge of the natural reef.

2) Site selection must include an awareness of the potentially ephemeral nature of unconsolidated sediments and associated benthic habitats, such as sparsely populated sand, unconsolidated rubble, macroalgae, and seagrass fields. Sand banks were observed to shift at the Puerto Morelos field site, which resulted in several modules that had originally been placed on barren sand being left directly in contact with the underlying hardbottom or large coral rubble pieces after the sand underneath was scoured away. As mentioned above, other modules at that site ended up getting partially or almost completely buried by shifting sand. Seagrass beds were also noted to shift slightly over time with the movement of sand.

3) Seagrass provides essential habitat for numerous species of reef fishes during the early part of their life cycle (Lindeman et al., 2000, Verwij et al., 2008; Luo et al., 2009). Seagrasses were avoided during the deployment operation, but for some modules the seagrass that was located nearby when they were deployed eventually grew to surround them during the six-year study period. Some of those modules were noted to have larger abundances and greater species diversity towards the end of the study, particularly for juvenile grunts, snappers, damsels, and wrasses. Shulman (1985) said that "if seagrasses and algae provide shelter from predation for settling juvenile fishes, recruitment close to a reef may be suppressed by the absence of this shelter. The actual mechanism involved may be either selection by settling juveniles or areas with seagrass and algae or differential survivorship of fishes in areas with and without seagrass and algae". An exploratory analysis evaluating abundance on the modules by their surrounding sub-habitat classification was conducted, but it did not find any immediately obvious statistical differences or links supporting a conclusion of greater abundance of species richness on the modules as a result of seagrass or more complex habitats being located nearby. However, there was no clear boundary between sub-habitats, and this was only done on a preliminary basis without quantitative benthic data to inform decisions about the surrounding habitat classifications.

Although it was not evaluated formally during this study, eight 'bonus' modules were deployed in a shallow seagrass habitat in 3-4m water depth at the "La Bonanza" study site in Puerto Morelos at the request of the national park authorities. Opportunistic visual surveys conducted there by the author and the members of the national park team documented large schools of juvenile grunts (200-500 grunts per module) on almost all of the modules, and many coral recruits on their surfaces. In addition, there was no *D. anchorata* sponge or large percentages of *L. variegata* macroalgae on the modules either. There was also no apparent scouring around the base of the modules or apparent damage to the surrounding seagrass habitat, but it was also further away from the path of the hurricane of 2007, and the Bonanza module array is sited directly behind an exposed fringing reef crest several hundred meters offshore that absorbs the majority of wave energy during storms. This implies that there is a delicate balance between the need to prevent disturbance or damage to the pre-existing natural benthic community and the ability to enhance or focus the population of certain reef fish species by selective placement into habitats that are more productive than ‘barren’ sand, such as seagrass or areas adjacent to natural coral reef habitats. In areas where seagrass habitat availability is not a limiting factor, placing artificial reef modules near or within this habitat appears to be a good method for aggregating some species of reef fishes by providing large structure and shelter in an otherwise barren or monotonous habitat. Although, in a case such as this, the modules would clearly be attracting many fishes, rather than producing them, and to be clear this study is not advocating placing artificial reefs in seagrass beds. However, if creation of replacement habitat for the purposes of mitigation is the goal, perhaps a combination of artificial reefs and transplanted seagrasses established at a previously uncolonized mitigation site would be a beneficial combination worthy of further consideration. The ability for large numbers and/or larger sized artificial reefs to deflect, diminish, or otherwise disrupt water flow might be useful for creating sheltered areas for seagrass transplant deployment. However, seagrass has particular requirements and site selection would need to be very selective. If seagrass is not growing in a particular location, or has not grown there historically, there is probably a good reason for that and efforts to establish a pioneer seagrass population there are may be prone to failure. Establishing a successful seagrass bed using transplants can be difficult, even in areas where they previously flourished (Sheridan et al., 1998).

4) Reef fish abundance and diversity on both natural and artificial reefs appear to be reliant, in large measure, upon availability of size-appropriate shelter that can be accessed quickly and easily (Shulman, 1984; Hixon and Beets, 1993; Friedlander and Parrish, 1998; Sherman et al., 2002; Almany, 2004). For example, coral heads on the natural reef that support large numbers of juvenile fishes and/or other small species seem to have higher abundances when there is a profusion of complex structure that they can be accessed immediately, repeatedly and easily, when the animals are threatened (author unpublished observation). In this study, the average module with no external enhancements to physical complexity initially provided a barren exterior surface with no additional shelter. If shelter-seeking juvenile fishes retreated through the holes to the interior of the module in search of refuge, they would likely encounter a larger predator as they often resided there. Future artificial reef designs might benefit reef fish communities by

incorporating an intermediary shelter somewhere that excludes medium to large sized predators and is immediately accessible to vulnerable juveniles and other small species. An 'attractive' habitat for reef fishes needs to provide ample shelter options for a variety of sizes and age classes. Previous artificial reef studies utilizing plastic mesh for caging or additional structure revealed that such methods can enhance juvenile survival of many species (Fahy et al., 2006; Quinn, 2009; Jordan, 2010). Finding a material and attachment method that is both durable and low-maintenance or maintenance free is an important criterion. For example, adding cinder blocks to the interior void space of Reefball^{TM} modules increased the abundance and richness of juvenile fishes (Sherman, 2000; Sherman et al., 2002). Another option would be adding additional holes and holes of varying sizes on the modules (bearing in mind the need for structural integrity). Stony corals grew particularly well around the undersides of the holes on many modules, so the benefits would not be limited to reef fishes. There was a total of nine holes per module in this study, and twelve holes per module in the Quinn (2009) and Robinson (in prep) studies. However, given the considerable geographical differences in deployment location, comparisons of reef fish assemblages between modules at these two sites would not be completely comparable, and attributing differences to varying numbers of holes would be problematic.

5) Many previous studies on artificial reefs have linked reef fish diversity with larger reef size (Luckhurst and Luckhurst, 1978; Roberts and Orond, 1987; Caselle and Warner, 1996; Quinn, 2009). Small artificial reefs may make it harder for some species to establish populations due to resource limitations and larger reefs with greater availability of food and shelter resources may promote greater stability in population structure. The small modules utilized in this study may be linked to a magnification of competition and predation pressures, resulting in a biased/skewed/altered community structure and resident population size that may not accurately reflect rates and processes as they typically occur on the nearby natural reef. Larger artificial reef modules may support reef fish assemblages that are more diverse than smaller ones. The assemblages on the small modules in this study were temporally always in flux to some degree. Admittedly, much as they were on the small natural reef sites, but perhaps more so than they would have been on larger artificial reefs with greater availability of diverse shelter and concomitant food resources. Also, depending on design, a larger size may yield a larger localized hydrologic front with

more extensive negative pressure zones for fishes to utilize for shelter against prevailing currents, as well as provide enhanced plankton aggregation and thus provide increased potential for larger populations of associated fishes. Thus, if modules as used here, or other similar artificial reef modules, are to be utilized for future restoration or mitigation applications, greater module size and/or deployment densities might produce more favorable outcomes in terms of the resulting population size, stability, and diversity of the reef fish assemblage (but also see Jordan et al., 2005).

6) The attachment method used to secure the artificial substrate padding material to the modules was not sufficient to keep it fully attached to their surfaces during the heavy currents and abrasive onslaught they received during the passage of Hurricane Dean in Akumal. Out of the three modules in Akumal that received the Pads treatment, all were damaged by the storm and had approximately half of their padding torn off, apparently from the strong storm surge and associated battering they received from suspended sediments, loose rubble, and various debris. However, there was still much padding that remained attached indicating that the pins used to attach the pads were basically effective and may have provided adequate holding had they been used in greater numbers.

7) The Pads treatment was associated with a higher percent coverage of sponges and macroalgae. One potential explanation for this is that the padding material accumulates sediment and nutrient containing detritus that are beneficial to the growth of these organisms. However, this came at the cost of reduced rates of coral recruitment. Perhaps future experimental projects utilizing this padding material might consider testing out different variations of pad thickness and percent coverage on the modules exterior surfaces, or if coral recruitment is not the main goal, then an array of extra densely padded modules might further accelerate development of the benthic community than seen here. Or, perhaps thinner strips of padding material or a single layer of thickness could be utilized for comparison. This approach could be particularly useful in future deployments utilizing large numbers of modules of varying treatment types. Treatments could be grouped together to enhance a particular aspect of the community, or mixed thoroughly for a complex but more homogeneous community structure. For replacement or mitigation of large areas of reef or hardbottom, perhaps a trial run of a large-scale patchwork arrangement that consists of a combinations of restoration interventions used in

conjunction with one another, either in mixed applications or in more expansive single-treatment applications, would be an appropriate evolution of this study and could result in these methods performing differently when implemented on larger scales.

8) The coral transplantation portion of this study yielded diverse insights relevant to coral reef restoration. Due to high rates of macroalgae and sponge growth, the majority of the coral transplants had been overgrown and killed by the end of the study. It is also assumed that a significant portion of the survivors suffered the same fate after the study ended. Likewise, the padding material was a favored substrate of the same sponge species (*D. anchorata*) that overgrew the coral transplants. Thus, this study adds strength to the argument that some routine maintenance of reefs can increase the survival rates of coral recruits and transplants as they struggle to become established and reach a critical size that will allow them to effectively compete with potentially overgrowing species. If the modules had been visited once a month and had their surfaces cleared of *L. variegata* and *D. anchorata*, the coral transplants and naturally settling coral recruits may have had a greater chance at survival and may have been able to grow to sufficient size to provide a more naturally functioning habitat structure that attracted and developed a more diverse and/or productive faunal assemblage. Funding entities need to be aware of the level of importance associated with routine maintenance Future mitigation and restoration projects should include in their budgets a provision for routine maintenance of the structure and its nascent assemblages to increase the likelihood of success.

Because of the apparent positive effect the pads had on macroalgae and sponge colonizers, if routine maintenance is not feasible, invertebrate enhancing artificial substrate padding material should be used with caution. If it is used in conjunction with artificial reefs and coral transplants (especially in Quintana Roo), it is recommended that coral transplants should not be affixed until the modules have had several years to mature (depending on local conditions) to avoid the rapidly growing and highly competitive early stages of the macroalgal and benthic invertebrate community and un-checked colonization of the pads. This will enable limited coral transplant resources to have a greater chance of surviving and becoming effective tools for enhancing community structure and overall reef function and productivity. The delay should be adjusted to suit specific site conditions and will help to guide decisions regarding transplant placement and grouping relative to established dense patches of competing benthic organisms or prevailing current effects. There were large differences between the Puerto Morelos and Akumal sites in community structure relative to the differences in depth, deployment habitat, and local environmental conditions. Typically, coral reefs develop on a geological time scale, but can recover from large disturbances (i.e., disease, bleaching, etc.) much more rapidly if conditions are favorable. However, chronic large-scale anthropogenic influences and frequent localized acute disturbances can render these ecosystems unstable and prone to phase-shifts and other forms of degradation on a scale that is measured in decades. If true long-term success is the goal, then five to ten years should not be too long to wait.

9) The combination of insufficient transplant density and choice of transplant species that provided minimal additional structural complexity may also have affected the number of new coral recruits that settled on the Coral Transplants treatment modules. Greater size at transplant has been linked to increased chances of survival in corals (Smith and Hughes, 1999; Meesters et al., 2001), and greater structural complexity has long been associated with greater abundance and species richness of reef fishes. Although the transplants selected for this study did somewhat increase structural complexity and instantly increased coral cover on the modules, the choice of species and low transplant density may have been limiting factors. This study utilized a total of six transplants per module that were harvested from the natural reef and affixed equidistant to each other around the upper surface of the modules. There was abundant space on the modules to accommodate greater transplant densities and/or larger transplants. Structurally complex species, such as *Acropora cervicornis* and *Porites porites*, were not available in sufficient numbers on the natural reef to justify harvest; hence the selection of *Agaricia agaricites, Orbicella annularis*, and *Porites astreoides*. Edwards and Clark (1999) suggested that species with slow-growing massive growth forms (which survive transplantation well but recruit slowly) could be more appropriate for use than fast growing branching species, and that too much emphasis has been placed on transplanting branching forms that recruit well but often do not survive the transplanting operation. However, given the relatively uncommon to rare status of acroporid corals throughout most of the Caribbean, this does not appear to be an option unless there is an established coral nursery nearby.

10) There was no apparent benefit to transplanting *P. astreoides*. This species was responsible for 80% of the corals that were present on the module surfaces at the end of the study. Its brooding reproductive strategy and high reproductive frequency (Chorensky and Peters, 1986; Szmant, 1991) likely led to relatively higher settlement and survival rates as compared to other species recorded on the modules. Additional low-relief growth form brooding species recruited as well, such as *Siderastrea siderea* and *A. agaricities*, the latter of which also performed well as a moderately structurally complex transplant species prior to being overgrown.

11) *Orbicella annularis* appears to be a poor choice for transplant species for several reasons. Since this species exhibits a massive growth form, it provides relatively little additional vertical relief or structural complexity when initially transplanted at small size. Out of the three transplant species chosen for this study, *O. annularis* was the most highly susceptible to disease and bleaching. In addition, because of its massive growth form, it was difficult to find as an unattached 'coral of opportunity' on the natural reef, and obtaining transplant material from the local donor reef involved a fairly intrusive harvesting procedure. Also, *O. annularis* has not proven to be an easy or reliably successful species to propagate in laboratory and field based coral nurseries (Crossett, 2013; Robitaille, 2014). Thus, any short-term benefits to using massive growth forms may be less than what might be achieved with rapidly growing branching species like *A. cervicornis* (providing they survive the transplanting procedure). Most coral nurseries currently operating in Mexico are concentrating on propagation of *A. palmata* (Nava-Martínez et al., 2015). However, the potential use of *O. annularis* in restoration efforts should not be totally discounted and perhaps it will be initiated by local researchers and/or reef managers in Quintana Roo in the future.

12) Nugues and Roberts (2003) suggested that corals have differential abilities to compete against macroalgae, and coral transplant species that are better at competing for space should be investigated. If given a choice, selection of coral species for transplantation that are more readily able to out-compete macroalgae growth may be beneficial, especially as algae are currently becoming more abundant on reefs. However, this study did not produce any specific results providing conclusions regarding specific coral species for transplant other than not recommending *O. annularis*.

13) Temporally continuous *in-situ* environmental data was not incorporated into this study, but it would have been useful in interpreting the results. To truly understand the true nature of the rates and processes on the artificial substrate, a few key site-specific physical parameters should be monitored, such as: prevailing direction and speed of current, tidal influences, salinity, turbidity, and temperature. This could be done *in situ* with electronic recording.

14) In terms of large-scale practicality, on a scale relevant to that of many commonly occurring acute or localized coral reef disturbances, future artificial reef designs may benefit from a basic modular format (along with associated replicability and affordability) that also incorporates some form of linkage to increase stability and prevent the kind of movement noted at the Akumal site. New designs that incorporate some form of anchoring and/or interlocking structure between adjacent modules, i.e., a concrete mat (sensu Clark and Edwards, 1994; Clark and Edwards, 1999; Ebersole, 2001) may be particularly useful for stability during severe storm events Such an interlocking design could hypothetically be deployed with modules in the 10s-100s to create new habitats on a scale similar to that of many small to medium sized patch reefs, hardbottom outcroppings, or ledges.

6.5 Final Conclusion

The emergent characteristics of communities change in predicable ways as they mature (Sandin and Sala, 2012). There are increases in: biomass, mean size of organisms, species richness, number of trophic levels, biomass of higher trophic levels, and three-dimensional biogenic structure. In general, although substrate colonization by key contributors was highly variable in this study, development of benthic communities on the modules during succession incrementally produced increasingly complex states of ecological maturity that were largely comparable among treatments. Macroalgae increased rapidly at first, dominated by *L. variegata*. Sponges took longer to catch up to the macroalgae, but when they did the sponges appear to have outcompeted the macroalgae, especially for the overgrowing species *D. anchorata*. Both *L. variegata* and *D. anchorata* had higher percent coverage on the Pads treatment modules. The natural reef quadrats had negligible amounts of both *L. variegata* and *D. anchorata*, and levels remained comparatively stable at that site throughout the study. Coral density gradually increased over the course of the study. Post-settlement mortality by overgrowth of *D. anchorata* and *L. variegata* was the main driver affecting survival for most coral recruits on the modules. Coral assemblages were dominated by brooding species, particularly *P. astreoides*, followed by *S. siderea* and *A. agaricites*. Based on the minority contribution that massive growth-form species made, there may be limited larval supply for major reef building coral species affecting the local reef system and/or they may be more susceptible to overgrowth by competitors at a small size. There were no coral recruits counted on the natural reef quadrats, but there were more recruits counted on settlement plates from the natural reef than the modules at both the Puerto Morelos and Akumal study sites. There was greater coral density on the Controls modules than the other treatments during the last half of the study, followed by the Coral Transplant treatment, but corals were larger on the Pads treatment modules. The majority of the coral transplants were overgrown by *D. anchorata*, to the point that the transplant effort in this study was considered almost a complete failure. These results suggest implementing a delay between deployment and coral transplantation until after initial wave of sponge growth subsides or stabilizes might be conducive to survival of corals transplanted in this area in the future. However, it is likely that due to the relatively small amounts of additional structural complexity and surface coverage added to the exterior of the modules by the coral transplants, that treatment was inadequate to affect or detect any significant change in either the coral or reef fish assemblage during this study, regardless of the losses due to sponge or macroalgal overgrowth. Implementation of aforementioned recommendations about larger transplant size, greater density, and more structurally complex species should be considered in future experimental or applied coral transplant projects as local transplant resources allow. Neither *P. astreoides* nor *O. annularis* were ideal transplant candidates, but for different reasons. *P. astreoides* recruited so well naturally that transplanting it was totally unnecessary, and *O. annularis* had a higher frequency of unhealthy appearing colonies. However, it cannot be discounted that if the latter had not been overgrown, their presence on the modules might have kick-started the populations of massive growth-form species.

Benthic organisms in general were more abundant on the modules than on the natural reef quadrats. This differential recruitment may have been the result of the combined effect of abiotic and biotic factors, including sedimentation, larval settlement preferences, and current regime. However, it may also have stemmed from the fact that the natural reef quadrats were delineated on an already well-established coral reef habitat that exhibited greater stability than the modules during this study, and barren spots that were chosen as an equivalent to the barren module surfaces were likely that way for a reason, and therefore were not ideal for comparison of succession on the two contrasting substrates.

Abundance of coral reef fishes was also highly variable, and the treatments and controls produced fairly similar results when the entire dataset was combined. When analyzed by date, very few significant differences between treatments were found, but when the overall data was analyzed many differences between the modules and natural reef were detected. When analyzed at the individual family or species level, several species-specific habitat and/or treatment associations became apparent. In general, the Pads treatment appeared to have more of an effect on reef fish assemblage structure than the other treatments, followed by the Coral Transplants treatment. However, these differences were largely attributed to a handful of species. For the remainder of the species observed on the modules, there were very few differences detected between the treatments and controls. The overall similarities between treatments may have been the result of multiple factors. For one, the overgrowing *D. anchorata* sponge covered all of the modules' surfaces, regardless of treatment, by up to 20-30% or more, and killed the majority of the coral transplants by the end of the study. Also, all of the settlement plates were removed two years into the six-year study, and their surfaces were from that point onward functionally equivalent to the controls. Thus, the structure and function provided by the modules had been largely homogenized by the fouling community by the midpoint of the study, and may have made any differences actually resulted from the direct influence of the restoration interventions difficult to distinguish. This could have been largely remedied with routine periodic maintenance. That the Pads treatment was able to stand out amongst the other treatments and controls during these analyses so frequently is a testament to this treatment's ability to affect, both positively and negatively, development of biota on the modules. The use of pads, as implemented here, as an integral part of an artificial substrate approach to restoration, warrants additional research.

The results of this study are heuristic. Taken in the context of other similar studies, it may help to change perceptions about artificial reef use, specifically as it applies to restoration and mitigation applications. This study produced several new insights into artificial reef design, treatment performance, and the processes of succession and assemblage formation on artificial substrates. In addition, it strengthened previously established tenets of restoration and ecosystem rehabilitation, such as careful consideration of artificial reef placement, the potential for high density materials to scour or become buried when placed on soft sediments, the necessity of routine monitoring, and the potential for unexpected results. Obviously, the marine environment is extremely variable and often unpredictable on many scales. This is especially true when working with artificial reefs for restoration. Assemblages on artificial substrates may differ significantly from neighboring natural habitats. Development and maturation of benthic communities on artificial reefs is a process that takes decades to transpire, and a high degree of variation can be expected between replicates at the same location and between different locations (i.e., Puerto Morelos and Akumal).

The outcomes of this project provide resource managers, researchers, and other stakeholders who deal directly with restoration of degraded or damaged coral reef habitats utilizing artificial reefs an improved understanding of how multiple biotic variables may interact with one another and in response to the restoration interventions tested here during the initial phases of benthic community succession. While many questions still remain and many processes are not fully understood, this project helps to bridge many knowledge gaps and reduces the need for guesswork in future restoration or mitigation projects involving artificial reefs, coral transplants, and the invertebrate enhancing artificial substrate pads. It adds another globally applicable, yet regionally specific, set of lessons that resource managers can use when making decisions about how and when restoration applications should be utilized should they become necessary, and how potential outcomes might vary as a result. Multiple recommendations were provided in the previous section but they should not be considered an all-inclusive list. The data set is both large and unique; insightful resource managers will undoubtedly mine others. Currently the science of coral reef restoration is still widely considered to be in its developmental stages, and the results of this project can help refine existing methods and generate new hypotheses that may further improve applications of restoration technology in relevant way. Urban and tourism-related development is applying constant pressure to coastal and marine habitats along the northeastern coast of the Yucatan Peninsula, and artificial reefs deployed there to date have been subjected to limited comprehensive monitoring efforts, when they received any at all. Urban development and population growth in Quintana Roo are not likely to slow down or stop any time soon, and placement of artificial reefs will likely continue. The results of this study can be used to improve the general guidelines under which they are used to follow more ecologically sound principles.

Data obtained during this study can be also be used to bolster existing local reports of coral recruitment rates, coral growth rates, macroalgae and benthic invertebrate growth, and coral reef fish abundance, diversity, and assemblage structure on artificial reefs. However, caution is urged regarding drawing premature conclusions from this limited dataset. Abundance and community structure of coral reef fishes are influenced by many abiotic and biotic variables, including: reef morphology, water chemistry, season, temperature, depth, current regimes, terrestrial influences (i.e. runoff, sedimentation, and nutrient levels), extreme weather events (hurricanes, cold snaps), benthic community composition, stochastic settlement and recruitment dynamics (i.e., larval supply, predation, competition, etc.). Furthermore, many fish populations fluctuate on seasonal or multi-year scales in response to a combination of the aforementioned variables. Because population levels can fluctuate greatly from year to year, understanding of how these biotic and abiotic variables interact with one another and change in response to the restoration interventions would be improved with a locally obtained long-term dataset, similar to routine long-term coral reef fish monitoring done in Florida and elsewhere in the Caribbean (Brandt et al., 2009; Smith et al., 2011; Kilfoyle et al., 2015).

This project also provides substantive reference material for the ongoing debate about whether or not direct intervention in the form of artificial reefs is warranted as a valid option following disturbance or damage to a coral reef or as mitigation for lost habitat. Some resource managers and researchers are opposed to the idea of using artificial structure of any sort for coral reef restoration, suggesting that artificial reefs will always be inherently lacking in sufficient complexity and therefore poor substitutes for the real thing. Additional concerns are centered on the potential for artificial reefs, when used as restoration or mitigation tools, to serve as justification for continued implementation of unsustainable coastal development practices and further coral reef destruction. In reality, there are limited viable options for reef restoration on both a relevant and affordable scale, and even a moderately functional approximation of a coral reef habitat, that does no damage, is arguably better than the alternative in the absence of other efforts to restore habitat or mitigate for loss.

Guiding the development of the benthic community towards a specifically desired outcome or state of existence on an artificial reef or a damaged/degraded natural reef is inherently challenging and can be compared to trying to hit a loosely defined moving target. This is especially applicable in areas where new restoration techniques have been previously untested or thoroughly evaluated with pilot studies. It is clear from the results of this study that application of select treatments onto restoration structure can affect the resulting composition of the resulting biotic assemblages. Whether or not they are considered to be beneficial to overall community development depends upon benchmarks for success and the time at which the evaluations are made. However, even though some aspects relating to coral reef habitat form and function may be replaced or enhanced by artificial reefs, fully replacing the complete suite of ecosystem services (biodiversity and productivity) that are lost when natural habitat is destroyed by building something from scratch is still well beyond the abilities of current restoration technology, and therefore habitat destruction should be avoided at all costs.

The resources provided by an artificial reef that has been placed in an otherwise barren or sparsely populated habitat may be analogous to gathering of competitive species and their subsequent forced interactions at a terrestrial watering hole during the dry season on the African savannah. In many previous studies of artificial reefs that were modified by experimental treatments, it has been common practice to place reef modules in areas that are generally devoid of any pre-existing visible biological community in order to minimize negative impacts to the surrounding ecosystem. Module placement in areas such as these is preferred due to the fact that: 1) many artificial reef installments have been the ultimate product of mitigation compensation, and as such they were deployed areas where they ended up serving as the basis for an off-site “replacement” ecosystem, and 2) most experimental artificial reef projects shared a need to be isolated from as many confounding factors as possible, including other artificial reefs. As such, the majority of data collected on artificial reef studies in the marine environment, including this one, have evaluated structures that serve as effective oases that attract and concentrate fishes that would normally be spread out over a wider area with greater availability of refuge space and different modes of interaction or rates of encounter with other competitors or predators. Thus, studies designed to evaluate the performance of substrate altering or enhancing restoration interventions must take into account that the abundances and interactions of species observed on isolated examples of experimentally treated artificial reefs may not exactly be equivalent to those that would be encountered if the interventions were applied directly to natural reef structure on a larger scale and over a wider area. Many of the resident species observed in this study were perhaps unnaturally influenced by competition (space, shelter, and food) from other species that share the same resources, as well as being subjected to greater chances of predation. It is also possible that the more highly mobile species were encountered on the modules largely due to chance, and their behavior may have been affected by the presence of those species that were already present when they arrived (priority effects).

Replication is widely established as a hallmark of scientific research, although reproducibility of specific results in the highly dynamic marine environment can be challenging. Scientific and technological progress is usually achieved through a combination of numerous small advances and the cumulative effort of many researchers. At its most fundamental level, science is built upon the concept of trial and error. Multiple studies have demonstrated that artificial reef performance and community dynamics are highly variable, even when replicates are located within close proximity to one another, and what may appear effective in one location may be ineffective or perform in a completely different manner elsewhere. Good science is also dependent upon sufficient sample size, which is one thing that has plagued many artificial reef studies. This is one of several in a progression of related projects that were designed to test whether select experimental treatments applied to standardized artificial substrate modules were able to produce any measurable influence on the developmental trajectories of the resulting biological assemblages. Although superficially similar, this project and each of the other previous NSUOC artificial reef-centric projects all added something unique and of distinct value to the science of artificial reef design, function, and practical implementation. However, this study was novel in its own right and stands alone for several reasons. While some of these experimental treatments have been evaluated on a preliminary and highly limited basis in southeast Florida (Quinn, 2009; Robinson, in prep.), never before has a project utilizing the experimental treatments tested here on artificial reef modules been undertaken in the Yucatan region with the explicit goal of routinely monitoring and evaluating their performance for use as tools in future restoration, remediation, and mitigation applications. This project is the first field experiment utilizing standardized artificial reef modules to be conducted in the northern Mesoamerican Barrier Reef System (MBRS), and to date is the first evaluation of the invertebrate enhancing artificial substrate pads have had in a coral reef environment anywhere outside of Florida.

Resource managers must consider multiple options when faced with the prospect of maintaining and repairing ecosystems that are under increasing levels stress. Lessons learned from the collective actions of these projects aid in informing development of future experimental methods and help to refine existing techniques of habitat restoration. Locally obtained knowledge about the rates and processes affecting development of the biological community following either an impact to a natural reef or deployment of an artificial reef is a valuable commodity. The information learned here should be of value to local reef managers in the event artificial concrete reef modules of this or any other design are chosen for use in restoration following destruction of reef resources due to natural or anthropogenic causes. This project not only serves to provide a reference example to be improved upon in future experimental or applied iterations, but may also guide placement of future artificial reef deployments in the area.

Although it was beyond the scope of this study, the data collected and lessons learned here can be used to inform future models of benthic community development, space utilization, and coral recruitment. However, at some point predicting what a natural system will do in response to artificial stimuli starts to resemble something akin to ecological fortune telling, or trying to predict the future, which aligns it with other endeavors like weather forecasting, political outcomes, and the stock market. None of the predictions are ever 100% accurate, and every restoration is different, but over the course of time enough information is learned about each one through the accumulation of various outcomes that a general idea regarding what might happen can be loosely predicted within a range of acceptable error. The goal of projects like this and other similar projects that came before it were to generate data and results from evaluations of novel techniques in a real-world setting to contribute towards the larger body of knowledge that is available for marine resource managers to rely upon for making well-informed management decisions. The goal has always been to learn about potential outcomes while acknowledging that they will be relatively unpredictable in the face of multiple variables.

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Appendices

Appendix 3.1 Comprehensive list of all species documented in quadrat photos and *in-situ* surveys from both the modules and natural reef. Mean percent cover for each species, averaged across the entire study period. Species with “n/a” (not applicable) in their field were seen in the quadrat photos when they were first processed, but not selected by the random points of the CPCe point-count analysis.

Taxonomic Classification		**Treatments**				
Macroalgae		**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Turf Algae	Multiphyletic	73.06	60.57	74.93	69.71	75.51
Caulerpa verticillata	Chlorophyta: Caulerpaceae	0.05	0.86	0.40	0.42	0.49
Dasycladalus vermicularis	Chlorophyta: Dasycladaceae	n/a	n/a	n/a	n/a	n/a
Neomeris annulata	Chlorophyta: Dasycladaceae	0.53	0.98	0.22	0.42	0.00
Avrainvillea sp.	Chlorophyta: Halimedaceae	0.07	0.20	0.02	0.16	0.08
Halimeda sp.	Chlorophyta: Halimedaceae	0.25	0.98	0.40	0.69	2.83
Penicillus sp.	Chlorophyta: Halimedaceae	0.00	0.00	0.00	0.00	0.89
Rhipocephalus phoenix	Chlorophyta: Halimedaceae	0.00	0.05	0.02	0.04	0.28
Udotea sp.	Chlorophyta: Halimedaceae	0.02	0.02	0.00	0.02	0.00
Valonia sp.	Chlorophyta: Valoniaceae	0.02	0.09	0.02	0.07	0.00
Dictyota sp.	Phaeophyta: Dictyotaceae	0.00	0.09	0.60	0.40	12.21
Dictyopteris delicatula	Phaeophyta: Dictyotaceae	n/a	n/a	n/a	n/a	n/a
Lobophora variegata	Phaeophyta: Dictyotaceae	8.91	13.22	4.64	11.56	0.00
Padina boergesenii	Phaeophyta: Dictyotaceae	0.00	0.00	0.04	0.02	0.15
Crustose Coralline Algae	Rhodophyta: Corallinaceae	0.35	0.91	0.64	0.47	0.72
Amphiroa sp.	Rhodophyta: Corallinaceae	0.00	0.05	0.00	0.00	0.10
Galaxaura sp.	Rhodophyta: Chaetangiaceae	0.00	0.00	0.00	0.00	0.17
Coelothrix irregularis	Rhodophyta: Champiaceae	n/a	n/a	n/a	n/a	n/a
Chondria sp.	Rhodophyta: Rhodomelaceae	n/a	n/a	n/a	n/a	n/a
Diatoms	Chrysophyta	0.00	0.00	0.00	0.00	0.02
Schizothrix calicola	Cyanophyta: Oscillatoriaceae	n/a	n/a	n/a	n/a	n/a

Taxonomic Classification		**Treatments**				
Sponges		**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Cinachyra sp.	Porifera: Demospongiae	0.00	0.00	0.00	0.00	0.02
Cliona langae	Porifera: Demospongiae	0.63	0.88	1.44	0.22	0.03
Demospongiae sp.	Porifera: Demospongiae	0.00	0.00	0.00	0.00	0.00
Desmapsamma anchorata	Porifera: Demospongiae	6.99	14.81	9.11	10.42	0.00
Ircinia strobilina	Porifera: Demospongiae	0.07	0.05	0.04	0.62	0.03
Siphonodictyon coralliphagum	Porifera: Demospongiae	0.00	0.00	0.00	0.00	0.02
Bryozoans						
Hippopodina feegeensis	Ectoprocta: Gymnolaemata	0.12	0.09	0.04	0.02	0.13
Hippoporina verrilli	Ectoprocta: Gymnolaemata	n/a	n/a	n/a	n/a	n/a
Schzoporella sp.	Ectoprocta: Gymnolaemata	n/a	n/a	n/a	n/a	n/a
Anemones and Zoanthids						
Epicystis crucifer	Cnidaria: Actiniaria	n/a	n/a	n/a	n/a	n/a
Palythoa caribaeorum	Cnidaria: Zoanthidea	0.00	0.00	0.00	0.00	0.10
Palythoa grandis	Cnidaria: Zoanthidea	n/a	n/a	n/a	n/a	n/a
Zoanthus pulchelus	Cnidaria: Zoanthidea	0.00	0.00	0.00	0.00	0.20
Hydrocorals						
Millepora alcicornis	Hydrozoa: Milliporidae	0.21	0.25	0.22	0.09	0.05
Soft Corals and Gorgonians						
Briareum asbestinum	Octocorallia: Briareidae	n/a	n/a	n/a	n/a	n/a
Erythropodium caribaeorum	Octocorallia: Anthothelidae	0.00	0.00	0.00	0.00	0.72
Eunicia sp.	Octocorallia: Plexauridae	0.00	0.00	0.00	0.00	0.02
Eunicia succinea	Octocorallia: Plexauridae	n/a	n/a	n/a	n/a	n/a
Gorgonia flabellum	Octocorallia: Gorgoniidae	n/a	n/a	n/a	n/a	n/a
Gorgonia ventilana	Octocorallia: Gorgoniidae	0.00	0.02	0.02	0.00	0.12
Muricea sp.	Octocorallia: Plexauridae	0.00	0.00	0.00	0.00	0.18
Plexaura homomalla	Octocorallia: Plexauridae		0.00	0.00	0.00	0.23
Plexaurella sp.	Octocorallia: Plexauridae	0.00	0.00	0.00	0.00	0.02
Pseudopterogorgia americana	Octocorallia: Siderastreidae	0.25	0.00	0.09	0.00	0.13

Taxonomic Classification		**Treatments**				
Stony Corals		**Ctrl.**	**Pads**	**Transp.**	**S. Plates**	**Nat. Reef**
Agaricia tenuifolia	Hexacorallia: Scleractinia: Agaricidae	0.00	0.00	0.00	0.02	0.07
Dichocoenia stokesi	Hexacorallia: Scleractinia: Meandrinidae	0.02	0.02	0.00	0.00	0.02
Diploria strigosa	Hexacorallia: Scleractinia: Faviidae	0.00	0.00	0.00	0.00	0.03
Favia fragum	Hexacorallia: Scleractinia: Faviidae	n/a	n/a	n/a	n/a	n/a
Manicinia areolata	Hexacorallia: Scleractinia: Faviidae	n/a	n/a	n/a	n/a	n/a
Meandrina meandrites	Hexacorallia: Scleractinia: Meandrinidae	n/a	n/a	n/a	n/a	n/a
Orbicella annularis/faveolata complex	Hexacorallia: Scleractinia:Faviidae	0.00	0.00	0.00	0.00	0.02
Porites astreoides	Hexacorallia: Scleractinia: Poritidae	0.42	0.07	0.13	0.33	0.20
Porites porites	Hexacorallia: Scleractinia: Poritidae	n/a	n/a	n/a	n/a	n/a
Siderastrea siderea	Hexacorallia: Scleractinia: Agaricidae	0.09	0.00	0.00	0.00	0.10
Tunicates						
Botrylloides sp.	Chordata: Ascidiacea	0.02	0.00	0.00	0.02	0.00
Clavelina sp.	Chordata: Ascidiacea	0.00	0.02	0.00	0.07	0.00
Ecteinascidia turbinata	Chordata: Ascidiacea	0.00	0.25	0.02	0.07	0.00
Trididemnum solidum	Chordata: Ascidiacea	0.05	0.00	0.00	0.00	0.00

Appendix 4.1 Total number of coral recruits per module within treatment, by date.

Treatment	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	19	13	16	9	21	8
Control	10	8	9	6	4	23
Control	18	15	15	14	36	34
Control	6	6	11	6	16	29
Control	15	6	8	7	14	6
Control	4	6	9	5	11	18
Control	22	10	23	14	34	60
Control	17	29	30	6	36	43
Control	21	15	23	23	26	21
Control	25	41	55	18	51	61
Coral Transplants	15	30	37	25	26	31
Coral Transplants	20	5	26	11	16	9
Coral Transplants	15	8	19	9	20	20
Coral Transplants	6	10	8	13	17	13
Coral Transplants	6	6	12	3	13	10
Coral Transplants	8	2	7	4	13	17
Coral Transplants	9	14	12	12	18	32
Coral Transplants	58	31	56	26	51	66
Coral Transplants	11	2	6	6	16	17
Coral Transplants	12	8	20	15	18	19
Pads	7	13	15	10	12	5
Pads	10	5	0	0	0	1
Pads	11	9	12	13	6	21
Pads	3	3	6	5	2	12
Pads	9	4	3	4	5	0
Pads	5	1	8	6	5	17
Pads	7	10	15	20	16	6
Pads	13	19	13	8	5	7
Pads	4	11	10	9	10	15
Pads	8	4	8	5	11	22
Settlement Plates	16	27	22	18	21	24
Settlement Plates	3	7	10	8	9	6
Settlement Plates	7	5	12	11	14	26
Settlement Plates	10	4	10	17	14	24
Settlement Plates	7	4	5	7	9	7
Settlement Plates	15	4	4	0	4	4
Settlement Plates	23	15	14	25	32	17
Settlement Plates	15	10	13	8	18	18
Settlement Plates	17	16	14	5	40	52
Settlement Plates	10	12	10	18	27	35

Appendix 4.2 Standardized total recruits (corals/m^2) per module within treatment, by date.

Treatment	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	7.2	4.9	6.1	3.4	8.0	3.0
Control	3.8	3.0	3.4	2.3	1.5	8.7
Control	6.8	5.7	5.7	5.3	13.6	12.9
Control	2.3	2.3	4.2	2.3	6.1	11.0
Control	5.7	2.3	3.0	2.7	5.3	2.3
Control	1.5	2.3	3.4	1.9	4.2	6.8
Control	8.3	3.8	8.7	5.3	12.9	22.7
Control	6.4	11.0	11.4	2.3	13.6	16.3
Control	8.0	5.7	8.7	8.7	9.8	8.0
Control	9.5	15.5	20.8	6.8	19.3	23.1
Coral Transplants	5.7	11.4	14.0	9.5	9.8	11.7
Coral Transplants	7.6	1.9	9.8	4.2	6.1	3.4
Coral Transplants	5.7	3.0	7.2	3.4	7.6	7.6
Coral Transplants	2.3	3.8	3.0	4.9	6.4	4.9
Coral Transplants	2.3	2.3	4.5	1.1	4.9	3.8
Coral Transplants	3.0	0.8	2.7	1.5	4.9	6.4
Coral Transplants	3.4	5.3	4.5	4.5	6.8	12.1
Coral Transplants	22.0	11.7	21.2	9.8	19.3	25.0
Coral Transplants	4.2	0.8	2.3	2.3	6.1	6.4
Coral Transplants	4.5	3.0	7.6	5.7	6.8	7.2
Pads	4.7	8.3	9.3	6.0	6.9	2.8
Pads	6.7	3.2	0.0	0.0	0.0	0.6
Pads	7.3	5.8	7.4	7.7	3.4	11.7
Pads	2.0	1.9	3.7	3.0	1.1	6.7
Pads	6.0	2.6	1.9	2.4	2.9	0.0
Pads	3.3	0.6	4.9	3.6	2.9	9.4
Pads	4.7	6.4	9.3	11.9	9.2	3.3
Pads	8.7	12.2	8.0	4.8	2.9	3.9
Pads	2.7	7.1	6.2	5.4	5.7	8.3
Pads	5.3	2.6	4.9	3.0	6.3	12.2
Settlement Plates	6.1	10.2	8.3	6.8	8.0	9.1
Settlement Plates	1.1	2.7	3.8	3.0	3.4	2.3
Settlement Plates	2.7	1.9	4.5	4.2	5.3	9.8
Settlement Plates	3.8	1.5	3.8	6.4	5.3	9.1
Settlement Plates	2.7	1.5	1.9	2.7	3.4	2.7
Settlement Plates	5.7	1.5	1.5	0.0	1.5	1.5
Settlement Plates	8.7	5.7	5.3	9.5	12.1	6.4
Settlement Plates	5.7	3.8	4.9	3.0	6.8	6.8
Settlement Plates	6.4	6.1	5.3	1.9	15.2	19.7
Settlement Plates	3.8	4.5	3.8	6.8	10.2	13.3

Appendix 4.3 Standardized mean coral recruit density (recruits/m^2) by treatment and date (±SEM).

Treatment	Mar07	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	0.0	5.9 ±0.8	5.6 ±1.4	7.5 ±1.7	4.1 ±0.7	9.4 ±1.7	11.5 ±2.3
Pads	0.0	5.1 ±0.7	5.1 ±1.1	5.6 ±1.0	4.8 ±1.0	4.1 ±0.9	5.9 ±1.4
Coral Transplants	0.0	6.1 ±1.8	4.4 ±1.3	7.7 ±1.9	4.7 ±0.9	7.9 ±1.3	8.9 ±2.0
Settlement Plates	0.0	4.7 ±0.7	3.9 ±0.9	4.3 ±0.6	4.4 ±0.9	7.1 ±1.3	8.1 ±1.8

Appendix 4.4 Total number of "new" recruits per module within treatment, by date.

Treatment	Mar07	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	0	19	9	13	5	16	5
Control	0	10	5	5	1	2	18
Control	0	18	11	6	4	13	26
Control	0	6	4	7	0	7	15
Control	0	15	5	5	3	10	4
Control	0	4	4	5	2	8	7
Control	0	22	5	18	2	18	39
Control	0	17	16	11	1	31	26
Control	0	21	7	14	6	12	10
Control	0	25	27	30	3	29	33
Coral Transplants	0	15	18	26	17	15	24
Coral Transplants	0	20	2	23	3	9	4
Coral Transplants	0	15	5	15	1	16	19
Coral Transplants	0	6	10	8	7	9	5
Coral Transplants	0	6	2	10	1	6	9
Coral Transplants	0	8	2	7	0	6	11
Coral Transplants	0	9	7	7	2	8	22
Coral Transplants	0	58	15	43	6	24	45
Coral Transplants	0	11	2	6	1	8	7
Coral Transplants	0	12	5	14	4	5	11
Pads	0	7	11	9	4	6	2
Pads	0	10	4	n/a	n/a	n/a	1
Pads	0	11	5	8	4	4	17
Pads	0	3	3	4	1	0	9
Pads	0	9	3	2	2	3	0
Pads	0	5	1	8	1	3	5
Pads	0	7	6	11	5	3	2
Pads	0	13	16	5	2	3	3
Pads	0	4	10	7	5	6	4
Pads	0	8	2	7	1	6	5
Settlement Plates	0	16	21	10	8	11	20
Settlement Plates	0	3	4	7	3	4	3
Settlement Plates	0	7	4	10	2	7	21
Settlement Plates	0	10	3	10	12	5	15
Settlement Plates	0	7	1	3	2	5	6
Settlement Plates	0	15	4	3	0	3	4
Settlement Plates	0	23	10	6	13	12	8
Settlement Plates	0	15	9	12	2	7	9
Settlement Plates	0	17	7	7	2	29	29
Settlement Plates	0	10	6	3	8	14	12

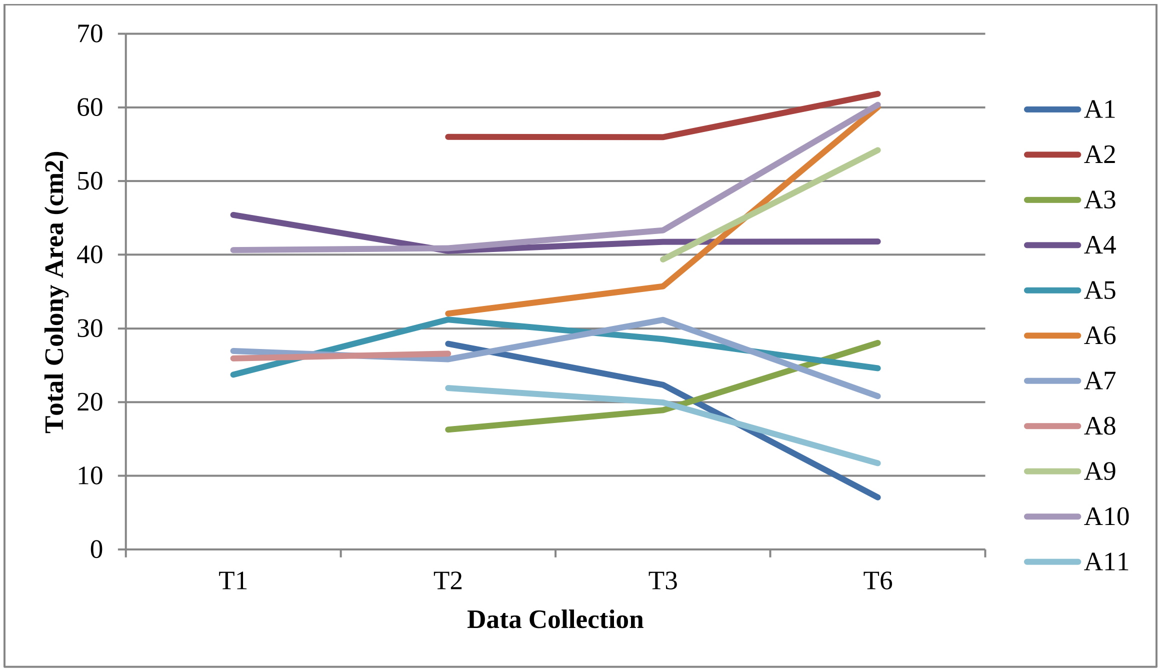
Appendix 4.5 Standardized total “new” recruits (corals/m^2) within treatment, by date.

Treatment	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	7.2	3.4	4.9	1.9	6.1	1.9
Control	3.8	1.9	1.9	0.4	0.8	6.8
Control	6.8	4.2	2.3	1.5	4.9	9.8
Control	2.3	1.5	2.7	0.0	2.7	5.7
Control	5.7	1.9	1.9	1.1	3.8	1.5
Control	1.5	1.5	1.9	0.8	3.0	2.7
Control	8.3	1.9	6.8	0.8	6.8	14.8
Control	6.4	6.1	4.2	0.4	11.7	9.8
Control	8.0	2.7	5.3	2.3	4.5	3.8
Control	9.5	10.2	11.4	1.1	11.0	12.5
Coral Transplants	5.7	6.8	9.8	6.4	5.7	9.1
Coral Transplants	7.6	0.8	8.7	1.1	3.4	1.5
Coral Transplants	5.7	1.9	5.7	0.4	6.1	7.2
Coral Transplants	2.3	3.8	3.0	2.7	3.4	1.9
Coral Transplants	2.3	0.8	3.8	0.4	2.3	3.4
Coral Transplants	3.0	0.8	2.7	0.0	2.3	4.2
Coral Transplants	3.4	2.7	2.7	0.8	3.0	8.3
Coral Transplants	22.0	5.7	16.3	2.3	9.1	17.0
Coral Transplants	4.2	0.8	2.3	0.4	3.0	2.7
Coral Transplants	4.5	1.9	5.3	1.5	1.9	4.2
Pads	4.7	7.3	6.0	2.7	4.0	1.3
Pads	6.7	2.7	n/a	n/a	n/a	0.7
Pads	7.3	3.3	5.3	2.7	2.7	11.3
Pads	2.0	2.0	2.7	0.7	0.0	6.0
Pads	6.0	2.0	1.3	1.3	2.0	0.0
Pads	3.3	0.7	5.3	0.7	2.0	3.3
Pads	4.7	4.0	7.3	3.3	2.0	1.3
Pads	8.7	10.7	3.3	1.3	2.0	2.0
Pads	2.7	6.7	4.7	3.3	4.0	2.7
Pads	5.3	1.3	4.7	0.7	4.0	3.3
Settlement Plates	6.1	8.0	3.8	3.0	4.2	7.6
Settlement Plates	1.1	1.5	2.7	1.1	1.5	1.1
Settlement Plates	2.7	1.5	3.8	0.8	2.7	8.0
Settlement Plates	3.8	1.1	3.8	4.5	1.9	5.7
Settlement Plates	2.7	0.4	1.1	0.8	1.9	2.3
Settlement Plates	5.7	1.5	1.1	0.0	1.1	1.5
Settlement Plates	8.7	3.8	2.3	4.9	4.5	3.0
Settlement Plates	5.7	3.4	4.5	0.8	2.7	3.4
Settlement Plates	6.4	2.7	2.7	0.8	11.0	11.0
Settlement Plates	3.8	2.3	1.1	3.0	5.3	4.5

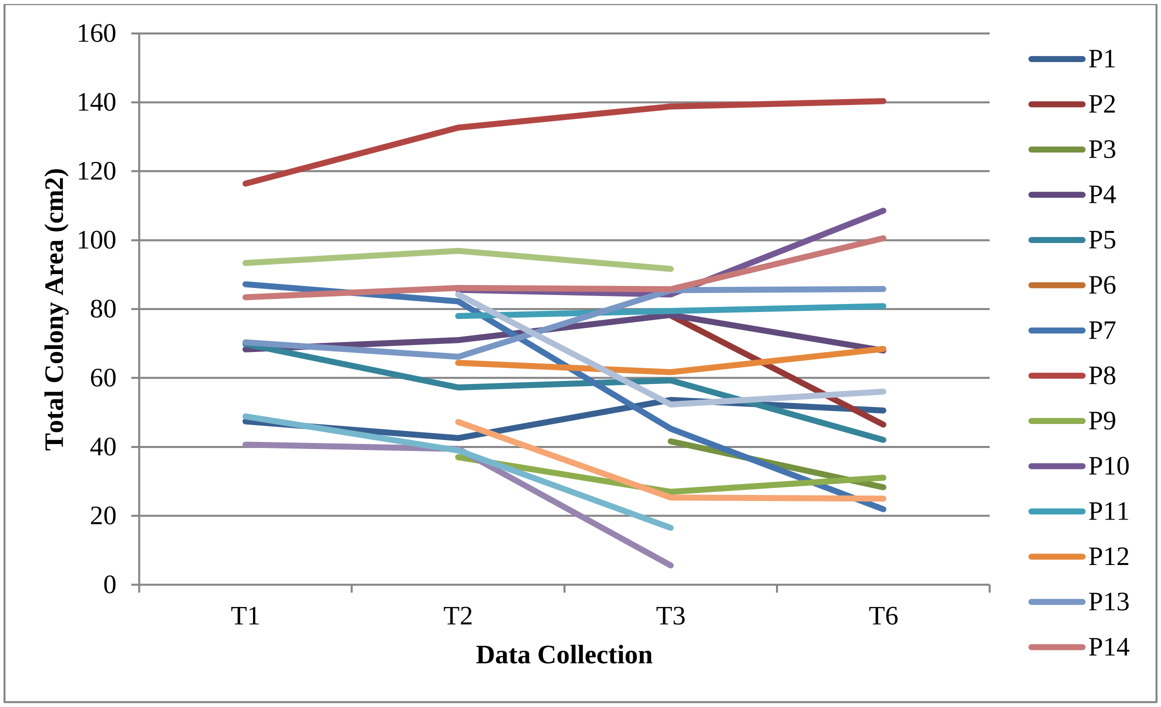
Appendix 4.6 Standardized mean "new" coral recruit density by treatment and date (w/SEM).

Treatment	Mar07	Sep07	Mar08	Oct08	Mar09	Sep09	Sep12
Control	0.0	5.9 ±0.8	3.5 ±0.9	4.3 ±1.0	1.0 ±0.2	5.5 ±1.1	6.9 ±1.5
Pads	0.0	5.1 ±0.7	4.1 ±1.0	4.1 ±0.7	1.7 ±0.4	2.3 ±0.5	3.2 ±1.1
Coral Transplants	0.0	6.1 ±1.8	2.6 ±0.7	6.0 ±1.4	1.6 ±0.6	4.0 ±0.7	5.9 ±1.5
Settlement Plates	0.0	4.7 ±0.7	2.6 ±0.7	2.7 ±0.4	2.0 ±0.6	3.7 ±0.9	4.8 ±1.0

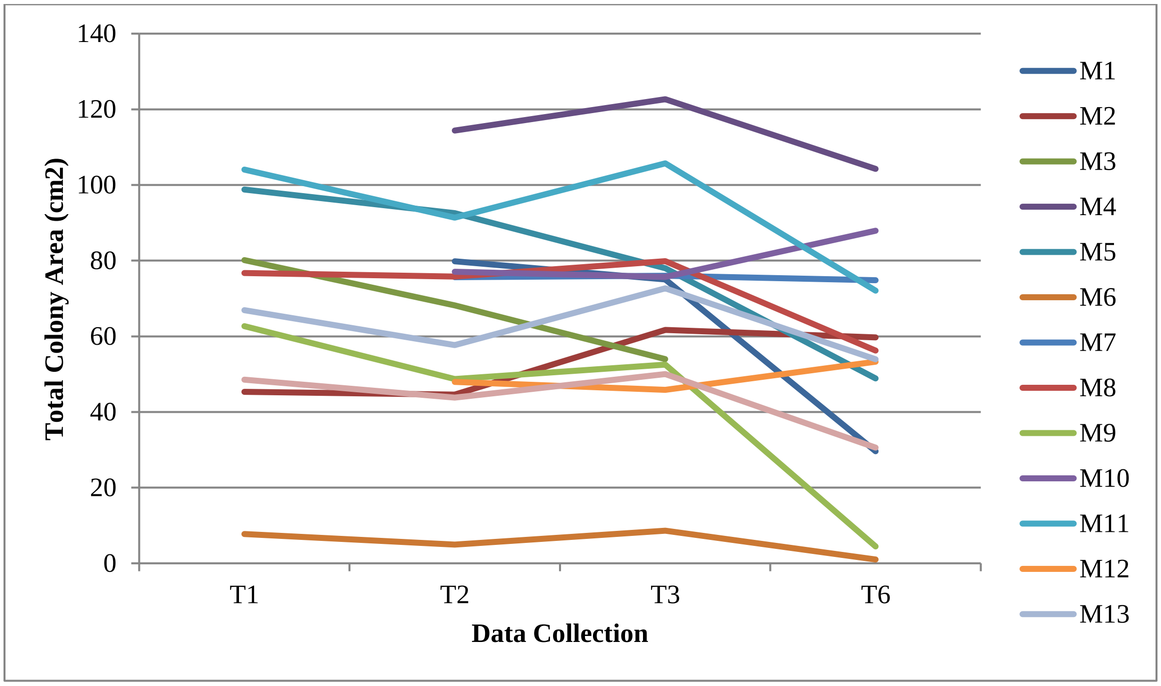
Appendix 4.7 *Agaricia agaricites* transplant growth between sampling periods, by individual colony (T1=March 2007, T2=September 2007, T3=March 2008, T6=September 2009).



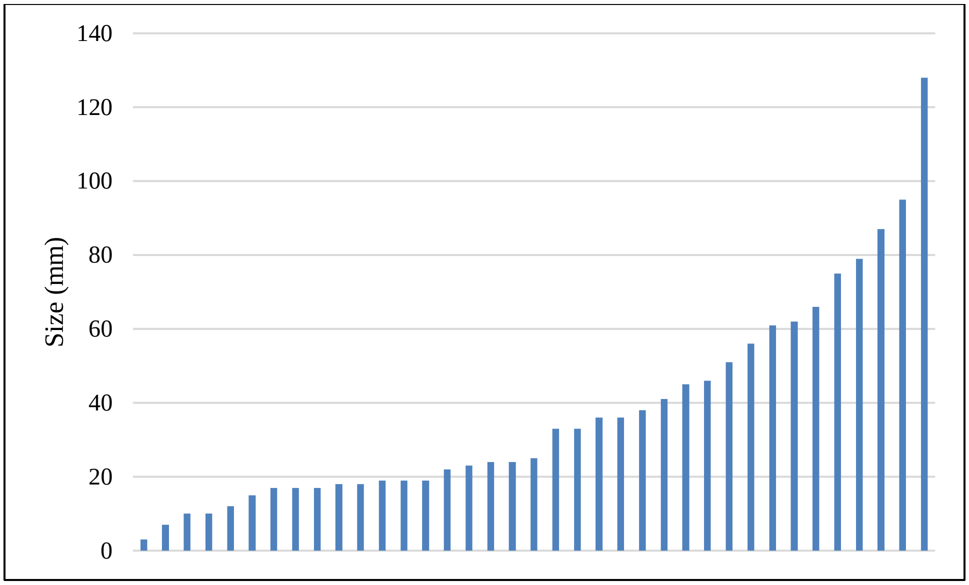
Appendix 4.8 *Porites astreoides* transplant growth between sampling periods, by individual colony (T1=March 2007, T2=September 2007, T3=March 2008, T6=September 2009).



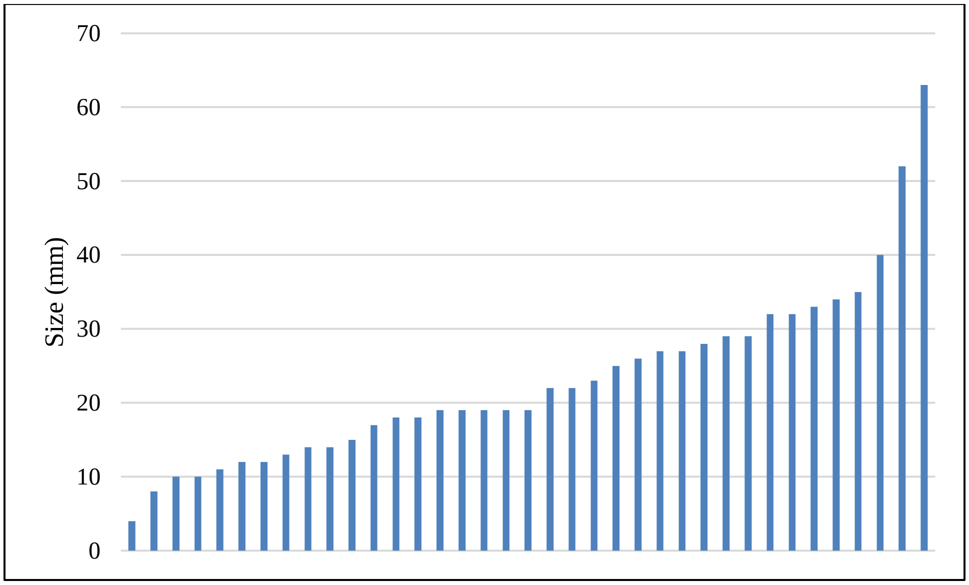
Appendix 4.9 *Orbicella annularis* transplant growth between sampling periods, by individual colony (T1=March 2007, T2=September 2007, T3=March 2008, T6=September 2009).



Appendix 4.10 Size frequency of *Agaricia* sp. recruits for September 2012 (N=37).



Appendix 4.11 Size frequency of *Diploria* sp. recruits for September 2012 (N=37).



Appendix 5.1 Abundance of fishes from Akumal by date and treatment (total/mean).

	Date	Mar 2007				Mar 2008		Oct 2008		Mar 2009		Sept 2009	
Species	**Total**	**Ctrl**	**Pads**	**Plates**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**
Abudefduf saxatilis	11	- / -	- / -	2 / 0.7	3 / 0.2	- / -	- / -	- / -	1 / 0.1	4 / 0.5	2 / 0.3	- / -	- / -
Acanthemblemaria aspera	3	- / -	- / -	- / -	- / -	- / -	1 / 0.1	1 / 0.2	- / -	1 / 0.1	- / -	- / -	- / -
Acanthurus bahianus	31	4 / 0.7	- / -	1 / 0.3	6 / 0.5	2 / 0.3	- / -	1 / 0.2	- / -	6 / 0.8	5 / 0.6	3 / 0.4	3 / 0.4
Acanthurus chirurgus	3	- / -	- / -	- / -	- / -	- / -	3 / 0.4	- / -	- / -	- / -	- / -	- / -	- / -
Acanthurus coeruleus	32	4 / 0.7	10 / 3.3	1 / 0.3	8 / 0.6	2 / 0.3	2 / 0.3	- / -	1 / 0.1	1 / 0.1	1 / 0.1	2 / 0.3	1 / 0.1
Anisotremus virginicus	9	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	9 / 1.1
Aulostomus maculatus	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -
Balistes vetula	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -
Bodianus rufus	3	- / -	- / -	- / -	3 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Canthigaster rostrata	61	1 / 0.2	- / -	- / -	3 / 0.2	6 / 0.8	4 / 0.5	9 / 1.8	6 / 1.4	11 / 1.4	15 / 1.9	7 / 0.9	5 / 0.6
Cephalopholis cruentata	3	1 / 0.2	- / -	- / -	1 / 0.1	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Cephalopholis fulva	17	- / -	1 / 0.3	- / -	6 / 0.5	- / -	- / -	- / -	- / -	1 / 0.1	4 / 0.5	2 / 0.3	3 / 0.4
Chaetodon capistratus	3	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	2 / 0.3	- / -
Chaetodon striatus	2	- / -	- / -	- / -	2 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Chromis cyanea	20	- / -	- / -	- / -	12 / 0.9	- / -	- / -	- / -	- / -	- / -	- / -	- / -	8 / 1.0
Chromis multilineata	2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	1 / 0.1	- / -
Clepticus parrae	2	- / -	- / -	- / -	2 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Coryphopterus glaucofraenum	3	1 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	2 / 0.3	- / -	- / -	- / -
Cryptotomus roseus	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1
Elacatinus oceanops	7	- / -	- / -	1 / 0.3	3 / 0.2	1 / 0.1	- / -	- / -	- / -	- / -	2 / 0.3	- / -	- / -
Elacatinus prochilos	2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	1 / 0.1	- / -	- / -
Gnatholepis thompsoni	3	2 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -
Gramma loreto	5	- / -	- / -	- / -	5 / 0.4	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Gymnothorax miliaris	1	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	- / -

(Appendix 5.1 continued)

	Date	**Mar 2007**				**Mar 2008**		**Oct 2008**		**Mar 2009**		**Sept 2009**	
Species	**Total**	**Ctrl**	**Pads**	**Plates**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**
Haemulon album	1	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Haemulon aurolineatum	1	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.2	- / -	- / -	- / -	- / -	- / -
Haemulon carbonarium	1	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Haemulon flavolineatum	9	- / -	1 / 0.3	- / -	2 / 0.2	- / -	1 / 0.1	2 / 0.4	3 / 0.2	1 / 0.1	2 / 0.3	- / -	- / -
Haemulon plumierii	18	2 / 0.3	3 / 1.0	2 / 0.7	8 / 0.6	1 / 0.1	- / -	1 / 0.2	- / -	- / -	- / -	1 / 0.1	- / -
Haemulon sciurus	6	1 / 0.2	- / -	- / -	2 / 0.2	2 / 0.3	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -
Halichoeres bivittatus	82	7 / 1.2	9 / 3.0	1 / 0.3	- / -	4 / 0.5	27 / 3.4	1 / 0.2	16 / 2.3	4 / 0.5	10 / 1.3	13 / 1.6	6 / 0.8
Halichoeres garnoti	100	3 / 0.5	- / -	1 / 0.3	76 / 5.8	4 / 0.5	8 / 1.0	1 / 0.2	9 / 0.6	1 / 0.1	3 / 0.4	2 / 0.3	1 / 0.1
Halichoeres maculipinna	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -
Halichoeres radiatus	8	- / -	- / -	3 / 1.0	3 / 0.2	2 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Holacanthus tricolor	5	- / -	- / -	- / -	- / -	2 / 0.3	- / -	- / -	- / -	1 / 0.1	- / -	- / -	2 / 0.3
Lachnolaimus maximus	1	- / -	1 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Lactophrys triqueter	2	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -
Lutjanus apodus	2	- / -	1 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -
Lutjanus buccanella	31	- / -	- / -	25 / 8.3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	6 / 0.8	- / -
Lutjanus mahogoni	3	- / -	- / -	- / -	3 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Malacanthus plumieri	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -
Malacoctenus macropus	2	- / -	- / -	- / -	2 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Malacoctenus triangulatus	4	- / -	- / -	- / -	- / -	- / -	2 / 0.3	- / -	1 / 0.1	- / -	1 / 0.1	- / -	1 / 0.1
Microspathodon chrysurus	2	- / -	- / -	- / -	2 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Mulloidichthys martinicus	3	- / -	- / -	- / -	1 / 0.1	- / -	2 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -
Ocyurus chrysurus	7	2 / 0.3	- / -	- / -	5 / 0.4	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Pomacanthus arcuatus	2	- / -	- / -	- / -	- / -	- / -	2 / 0.3	- / -	- / -	- / -	- / -	- / -	- / -
Pomacentridae sp.	3	- / -	- / -	- / -	3 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Pseudupeneus maculatus	1	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -
Rypticus saponaceus	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -
Scorpaena plumieri	1	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -

(Appendix 5.1 continued)

	Date	Mar 2007				Mar 2008		Oct 2008		Mar 2009		Sept 2009	
Species	**Total**	**Ctrl**	**Pads**	**Plates**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**	**Ctrl**	**NR**
Serranus baldwini	1	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -
Serranus tigrinus	5	- / -	- / -	- / -	- / -	1 / 0.1	3 / 0.4	- / -	- / -	- / -	- / -	- / -	1 / 0.1
Sparisoma aurofrenatum	29	- / -	- / -	- / -	6 / 0.5	1 / 0.1	3 / 0.4	- / -	7 / 1.2	- / -	8 / 1.0	3 / 0.4	8 / 1.0
Sparisoma radians	1	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -
Sparisoma rubripinne	2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	2 / 0.3	- / -	- / -	- / -
Sparisoma viride	4	1 / 0.2	- / -	- / -	3 / 0.2	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -
Stegastes adustus	2	- / -	- / -	1 / 0.3	- / -	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	- / -
Stegastes diencaeus	3	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	3 / 0.4	- / -	- / -
Stegastes leucostictus	7	- / -	- / -	- / -	4 / 0.3	- / -	1 / 0.1	- / -	- / -	- / -	- / -	- / -	2 / 0.3
Stegastes partitus	55	- / -	2 / 0.7	- / -	7 / 0.5	1 / 0.1	6 / 0.8	- / -	10 / 0.2	1 / 0.1	12 / 1.5	- / -	26 / 3.3
Stegastes variabilis	8	- / -	- / -	- / -	5 / 0.4	- / -	1 / 0.1	- / -	- / -	- / -	- / -	1 / 0.1	1 / 0.1
Thalassoma bifasciatum	323	14 / 2.3	9 / 3.0	9 / 3.0	124 / 9.5	13 / 1.6	41 / 5.1	6 / 1.2	35 / 5.8	12 / 1.5	37 / 4.6	11 / 1.4	47 / 5.9
Xyrichtys splendens	1	- / -	- / -	- / -	- / -	- / -	- / -	- / -	- / -	1 / 0.1	- / -	- / -	- / -
Totals	965	43	37	47	314	45	111	23	90	53	109	58	125

Appendix 5.2 Full species list, in phylogenetic order and broken down by experimental treatment. Abundance is in terms of total fishes counted across all sampling trips. Occurrence (*O*) refers to the number of times one or more members of each species was observed in a visual survey. Percent Occurrence (*P*) = Occurrence/N * 100. For Controls, Pads, Transplants, and Settlement Plates: N=70. For Natural Reef: N=96. [*Ranked by Decreasing* P *for each treatment in Appendices 5.3-5.7*]

		Control			**Pads**			**Transplants**			**S. Plates**			**Nat. Reef**		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
Narcinidae																
	Narcine brasiliensis													1	1	1.04
Urotrygonidae																
	Urobatis jamaicensis													1	1	1.04
Muraenidae																
	Gymnothorax funebris	1	1	1.43				1	1	1.43						
	Gymnothorax moringa	1	1	1.43	1	1	1.43	2	2	2.86	1	1	1.43	2	2	2.08
Synodontidae																
	Synodus foetens													1	1	1.04
	Synodus intermedius													1	1	1.04
	Synodus sp.	1	1	1.43												
Holocentridae																
	Holocentrus adscensionis	4	4	5.71	4	4	5.71	3	3	4.29	3	3	4.29			
Aulostomidae																
	Aulostomus maculatus													1	1	1.04
Scorpaenidae																
	Scorpaena plumieri	1	1	1.43				1	1	1.43						
	Pterois volitans	8	7	10	4	4	5.71	10	6	8.57	5	4	5.71			
Serranidae																
	Alphestes afer	1	1	1.43	6	4	5.71	1	1	1.43	3	3	4.29			
	Cephalopholis cruentata	6	6	8.57	15	14	20	10	10	14.29	5	5	7.14	19	17	17.71
	Cephalopholis fulva	1	1	1.43							3	2	2.86	6	6	6.25
	Epinephelus adscensionis													3	3	3.13

		Control			Pads			Transplants			S. Plates			Nat. Reef		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
	Epinephelus guttatus				1	1	1.43	1	1	1.43				2	2	2.08
	Epinephelus morio	4	4	5.71	4	4	5.71	2	2	2.86	2	2	2.86			
	Hypoplectrus unicolor													1	1	1.04
	Mycteroperca bonaci				1	1	1.43				2	2	2.86			
	Mycteroperca venenosa	1	1	1.43	1	1	1.43	1	1	1.43				1	1	1.04
	Serranus baldwini	1	1	1.43												
	Serranus tigrinus	3	3	4.29	7	6	8.57	6	5	7.14	2	2	2.86	9	9	9.38
Opistognathidae																
	Opistognathus aurifrons	1	1	1.43										4	1	1.04
Apogonidae																
	Apogon maculatus										2	1	1.43			
	Apogon pseudomaculatus	1	1	1.43												
	Apogon townsendi													1	1	1.04
Malacanthidae																
	Malacanthus plumieri	2	1	1.43	1	1	1.43	1	1	1.43						
Carangidae																
	Caranx ruber				2	2	2.86				1	1	1.43	3	3	3.13
Lutjanidae																
	Lutjanus analis	8	5	7.14	5	5	7.14	6	6	8.57	8	5	7.14			
	Lutjanus apodus													3	2	2.08
	Lutjanus buccanella	3	3	4.29	12	5	7.14	11	5	7.14	12	6	8.57			
	Lutjanus mahogoni										2	2	2.86			
	Lutjanus synagris	3	1	1.43	1	1	1.43				2	2	2.86			
	Ocyurus chrysurus	33	19	27.14	37	19	27.14	26	17	24.29	32	20	28.57	31	26	27.08
	Rhomboplites aurorubens													2	1	1.04
Haemulidae																
	Anisotremus surinamensis				2	1	1.43									
	Anisotremus virginicus	3	2	2.86	4	2	2.86	5	3	4.29	10	7	10	1	1	1.04

		Control			**Pads**			**Transplants**			**S. Plates**			**Nat. Reef**		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
	Haemulon album	1	1	1.43	1	1	1.43	10	1	1.43	5	2	2.86			
	Haemulon aurolineatum	51	7	10	115	6	8.57	1	1	1.43	95	7	10			
	Haemulon carbonarium							4	4	5.71				2	2	2.08
	Haemulon flavolineatum	194	15	21.43	13	9	12.86	55	10	14.29	75	14	20	71	45	46.88
	Haemulon macrostomum													1	1	1.04
	Haemulon melanurum	52	17	24.29	6	5	7.14	103	11	15.71	42	9	12.86	1	1	1.04
	Haemulon parra	9	7	10	9	6	8.57	11	7	10	19	6	8.57			
	Haemulon plumierii	80	36	51.43	55	33	47.14	43	34	48.57	62	35	50	30	27	28.13
	Haemulon sciurus	26	18	25.71	18	16	22.86	24	23	32.86	13	13	18.57	18	17	17.71
	Haemulon spp.	123	15	21.43	333	7	10	111	12	17.14	40	1	1.43	224	4	4.17
Sparidae																
	Calamus calamus	1	1	1.43										3	3	3.13
	Calamus sp.	12	1	1.43	1	1	1.43									
Sciaenidae																
	Pareques acuminatus	8	5	7.14	7	4	5.71	12	7	10	5	4	5.71	1	1	1.04
Mullidae																
	Mullus auratus													1	1	1.04
	Pseudupeneus maculatus	37	17	24.29	33	17	24.29	39	15	21.43	26	13	18.57	14	12	12.5
Chaetodontidae																
	Chaetodon capistratus	3	3	4.29	4	2	2.86	5	3	4.29	4	2	2.86	12	10	10.42
	Chaetodon ocellatus	4	3	4.29	4	2	2.86	2	1	1.43	5	4	5.71	4	3	3.13
	Chaetodon striatus	3	3	4.29	4	3	4.29	4	2	2.86	4	4	5.71			
Pomacanthidae																
	Holacanthus bermudensis				1	1	1.43									
	Holacanthus ciliaris	24	19	27.14	11	10	14.29	20	14	20	17	13	18.57	1	1	1.04
	Holacanthus tricolor	3	3	4.29	8	7	10	4	4	5.71	5	5	7.14	6	6	6.25
	Pomacanthus arcuatus	8	4	5.71	4	3	4.29	5	5	7.14	2	1	1.43			
	Pomacanthus paru	4	4	5.71	2	2	2.86	5	4	5.71	5	5	7.14			

		Control			**Pads**			**Transplants**			**S. Plates**			**Nat. Reef**		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
Amblycirrhitidae																
	Amblycirrhitus pinos													1	1	1.04
Pomacentridae																
	Abudefduf saxatilis	16	15	21.43	6	6	8.57	3	3	4.29	14	11	15.71	3	1	1.04
	Chromis cyanea	7	5	7.14	25	7	10	15	8	11.43	1	1	1.43	308	49	51.04
	Chromis multilineata	1	1	1.43	1	1	1.43	1	1	1.43	1	1	1.43	1	1	1.04
	Stegastes adustus	2	2	2.86				1	1	1.43	1	1	1.43	24	15	15.63
	Stegastes diencaeus				1	1	1.43	1	1	1.43				4	4	4.17
	Stegastes leucostictus	3	3	4.29	3	3	4.29	1	1	1.43	4	3	4.29	30	19	19.79
	Stegastes partitus	92	35	50	153	50	71.43	116	40	57.14	89	38	54.29	92	46	47.92
	Stegastes planifrons							1	1	1.43				76	32	33.33
	Stegastes variabilis	1	1	1.43	6	6	8.57	3	2	2.86				24	14	14.58
Labridae																
	Bodianus rufus	1	1	1.43							1	1	1.43	2	2	2.08
	Halichoeres bivittatus	168	51	72.86	126	42	60	137	44	62.86	116	41	58.57	24	13	13.54
	Halichoeres garnoti	16	8	11.43	49	21	30	70	24	34.29	43	20	28.57	283	71	73.96
	Halichoeres maculipinna	8	7	10	6	4	5.71	9	6	8.57	7	6	8.57	18	7	7.29
	Halichoeres pictus	32	8	11.43	34	9	12.86	25	8	11.43	13	4	5.71	80	8	8.33
	Halichoeres poeyi				2	2	2.86				1	1	1.43			
	Halichoeres radiatus	18	15	21.43	12	11	15.71	15	13	18.57	18	14	20	3	3	3.13
	Lachnolaimus maximus	5	3	4.29	9	8	11.43	2	2	2.86	2	2	2.86	1	1	1.04
	Thalassoma bifasciatum	420	58	82.86	473	65	92.86	450	60	85.71	556	63	90	258	55	57.29
	Xyrichtys splendens	1	1	1.43							1	1	1.43	15	1	1.04
Scaridae																
	Cryptotomus roseus							3	1	1.43						
	Scaridae spp.							1	1	1.43	1	1	1.43	3	1	1.04
	Scarus guacamaia													1	1	1.04
	Scarus iseri				1	1	1.43				4	3	4.29	57	25	26.04

		Control			**Pads**			**Transplants**			**S. Plates**			**Nat. Reef**		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
	Scarus taeniopterus													14	7	7.29
	Scarus vetula													2	1	1.04
	Sparisoma atomarium	2	1	1.43							1	1	1.43	1	1	1.04
	Sparisoma aurofrenatum	34	23	32.86	39	22	31.43	37	23	32.86	48	25	35.71	59	38	39.58
	Sparisoma chrysopterum	6	2	2.86	2	2	2.86	2	2	2.86	3	1	1.43	2	2	2.08
	Sparisoma radians				2	2	2.86				6	4	5.71	7	6	6.25
	Sparisoma rubripinne	11	4	5.71	5	5	7.14	3	3	4.29	3	3	4.29			
	Sparisoma viride	1	1	1.43	2	2	2.86	3	2	2.86	2	2	2.86	23	17	17.71
Enneanectidae																
	Enneanectes boehlkei										2	1	1.43			
	Enneanectes sp.							1	1	1.43						
Blennidae																
	Ophioblennius macclurei				1	1	1.43									
Labrisomidae																
	Malacoctenus triangulatus	3	3	4.29	3	2	2.86									
Gobiidae																
	Coryphopterus glaucofraenum							1	1	1.43	3	3	4.29	3	3	3.13
	Coryphopterus hyalinus/pers.													218	11	11.46
	Ctenogobius saepepallens				1	1	1.43	2	2	2.86				1	1	1.04
	Gnatholepis thompsoni	3	3	4.29	9	6	8.57	3	3	4.29	8	4	5.71			
	Elacatinus oceanops	1	1	1.43				1	1	1.43	2	1	1.43	5	3	3.13
	Elacatinus prochilos	9	7	8.57	1	1	1.43	5	3	4.29	3	3	4.29	23	14	14.58
Acanthuridae																
	Acanthurus bahianus	101	40	57.14	62	33	47.14	85	35	50	86	40	57.14	28	20	20.83
	Acanthurus chirurgus	26	13	18.57	33	13	18.57	24	13	18.57	18	11	15.71	20	15	15.63
	Acanthurus coeruleus	200	61	87.14	257	59	84.29	169	56	80	179	55	78.57	26	19	19.79
Sphyraenidae																

		Control			Pads			Transplants			S. Plates			Nat. Reef		
Familiy	**Scientific Name**	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***	**Abund**	***O***	***P***
	Sphyraena barracuda				1	1	1.43				2	2	2.86			
Balistidae																
	Balistes vetula							2	2	2.86						
Monacanthidae																
	Aluterus scriptus													1	1	1.04
	Cantherhines pullus													1	1	1.04
Ostraciidae																
	Lactophrys bicaudalis							1	1	1.43						
	Lactophrys triqueter	1	1	1.43				1	1	1.43	3	3	4.29	4	4	4.17
Tetraodontidae																
	Canthigaster rostrata	52	31	44.29	75	40	57.14	69	34	48.57	84	42	60	72	46	47.92
	Sphoeroides spengleri													1	1	1.04
Diodontidae																
	Diodon hystrix	1	1	1.43	1	1	1.43									

Appendix 5.3 Species list for ***Controls***, ranked by Percent Occurrence (*P*). Shaded species were present with a *P* of 10% or greater. Species in bold were seen exclusively on the Control treatment. Abundance is in terms of total fishes counted across all monitoring trips. Occurrence refers to the number of times one or more members of each species was observed in a visual survey. N=70. Percent Occurrence = Occurrence/N * 100.

	Abundance	**Occurrence**	**Percent Occurrence**
Acanthurus coeruleus	200	61	87.14
Thalassoma bifasciatum	420	58	82.86
Halichoeres bivittatus	168	51	72.86
Acanthurus bahianus	101	40	57.14
Haemulon plumierii	80	36	51.43
Stegastes partitus	92	35	50.00
Canthigaster rostrata	52	31	44.29
Sparisoma aurofrenatum	34	23	32.86
Holacanthus ciliaris	24	19	27.14
Ocyurus chrysurus	33	19	27.14
Haemulon sciurus	26	18	25.71
Haemulon melanurum	52	17	24.29
Pseudupeneus maculatus	37	17	24.29
Abudefduf saxatilis	16	15	21.43
Haemulon flavolineatum	194	15	21.43
Haemulon spp.	123	15	21.43
Halichoeres radiatus	18	15	21.43
Acanthurus chirurgus	26	13	18.57
Halichoeres garnoti	16	8	11.43
Halichoeres pictus	32	8	11.43
Haemulon aurolineatum	51	7	10.00
Haemulon parra	9	7	10.00
Halichoeres maculipinna	8	7	10.00
Pterois volitans	8	7	10.00
Cephalopholis cruentata	6	6	8.57
Elacatinus prochilos	8	6	8.57
Chromis cyanea	7	5	7.14
Lutjanus analis	8	5	7.14
Pareques acuminatus	8	5	7.14
Epinephelus morio	4	4	5.71
Holocentrus adscensionis	4	4	5.71
Pomacanthus arcuatus	8	4	5.71
Pomacanthus paru	4	4	5.71
Sparisoma rubripinne	11	4	5.71
Chaetodon capistratus	3	3	4.29

Chaetodon ocellatus	4	3	4.29
Chaetodon striatus	3	3	4.29
Gnatholepis thompsoni	3	3	4.29
Holacanthus tricolor	3	3	4.29
Lachnolaimus maximus	5	3	4.29
Lutjanus buccanella	3	3	4.29
Malacoctenus triangulatus	3	3	4.29
Serranus tigrinus	3	3	4.29
Stegastes leucostictus	3	3	4.29
Anisotremus virginicus	3	2	2.86
Sparisoma chrysopterum	6	2	2.86
Stegastes adustus	2	2	2.86
Alphestes afer	1	1	1.43
Apogon pseudomaculatus	1	1	1.43
Bodianus rufus	1	1	1.43
Calamus calamus	1	1	1.43
Calamus sp.	12	1	1.43
Cephalopholis fulva	1	1	1.43
Chromis multilineata	1	1	1.43
Diodon hystrix	1	1	1.43
Elacatinus oceanops	1	1	1.43
Epinephelus prochilos	1	1	1.43
Gymnothorax funebris	1	1	1.43
Gymnothorax moringa	1	1	1.43
Haemulon album	1	1	1.43
Lactophrys triqueter	1	1	1.43
Lutjanus synagris	3	1	1.43
Malacanthus plumieri	2	1	1.43
Mycteroperca venenosa	1	1	1.43
Opistognathus aurifrons	1	1	1.43
Scorpaena plumieri	1	1	1.43
Serranus baldwini	1	1	1.43
Sparisoma atomarium	2	1	1.43
Sparisoma viride	1	1	1.43
Stegastes variabilis	1	1	1.43
Synodus sp.	1	1	1.43
Xyrichtys splendens	1	1	1.43
Aluterus scriptus	0	0	0.00
Amblycirrhitus pinos	0	0	0.00
Anisotremus surinamensis	0	0	0.00
Apogon maculatus	0	0	0.00
Apogon townsendi	0	0	0.00
Aulostomus maculatus	0	0	0.00

Balistes vetula	0	0	0.00
Cantherhines pullus	0	0	0.00
Carangoides ruber	0	0	0.00
Coryphopterus glaucofraenum	0	0	0.00
Coryphopterus hyalinus/personatus	0	0	0.00
Cryptotomus roseus	0	0	0.00
Ctenogobius saepepallens	0	0	0.00
Enneanectes boehlkei	0	0	0.00
Enneanectes sp.	0	0	0.00
Epinephelus adscensionis	0	0	0.00
Epinephelus guttatus	0	0	0.00
Gramma loreto	0	0	0.00
Haemulon carbonarium	0	0	0.00
Haemulon macrostomum	0	0	0.00
Halichoeres poeyi	0	0	0.00
Holacanthus bermudensis	0	0	0.00
Hypoplectrus unicolor	0	0	0.00
Lactophrys bicaudalis	0	0	0.00
Lutjanus apodus	0	0	0.00
Lutjanus mahogoni	0	0	0.00
Microspathodon chrysurus	0	0	0.00
Mullus auratus	0	0	0.00
Mycteroperca bonaci	0	0	0.00
Narcine brasiliensis	0	0	0.00
Ophioblennius macclurei	0	0	0.00
Rhomboplites aurorubens	0	0	0.00
Scaridae spp.	0	0	0.00
Scarus guacamaia	0	0	0.00
Scarus iseri	0	0	0.00
Scarus taeniopterus	0	0	0.00
Scarus vetula	0	0	0.00
Sparisoma radians	0	0	0.00
Sphoeroides spengleri	0	0	0.00
Sphyraena barracuda	0	0	0.00
Stegastes diencaeus	0	0	0.00
Stegastes planifrons	0	0	0.00
Synodus foetens	0	0	0.00
Synodus intermedius	0	0	0.00
Urobatis jamaicensis	0	0	0.00

Appendix 5.4 Species list for ***Pads treatment***, ranked by Percent Occurrence (*P*). Shaded species were present with a *P* of 10% or greater. Species in bold were observed exclusively on the Pads treatment. Abundance is in terms of total fishes counted across all monitoring trips. Occurrence refers to the number of times one or more members of each species was observed in a visual survey. N=70. Percent Occurrence = Occurrence/N * 100.

	Abundance	**Occurrence**	**Percent Occurrence**
Thalassoma bifasciatum	473	65	92.86
Acanthurus coeruleus	257	59	84.29
Stegastes partitus	153	50	71.43
Halichoeres bivittatus	126	42	60.00
Canthigaster rostrata	75	40	57.14
Acanthurus bahianus	62	33	47.14
Haemulon plumierii	55	33	47.14
Sparisoma aurofrenatum	39	22	31.43
Halichoeres garnoti	49	21	30.00
Ocyurus chrysurus	37	19	27.14
Pseudupeneus maculatus	33	17	24.29
Haemulon sciurus	18	16	22.86
Cephalopholis cruentata	15	14	20.00
Acanthurus chirurgus	33	13	18.57
Halichoeres radiatus	12	11	15.71
Holacanthus ciliaris	11	10	14.29
Haemulon flavolineatum	13	9	12.86
Halichoeres pictus	34	9	12.86
Lachnolaimus maximus	9	8	11.43
Chromis cyanea	25	7	10.00
Haemulon spp.	333	7	10.00
Holacanthus tricolor	8	7	10.00
Abudefduf saxatilis	6	6	8.57
Gnatholepis thompsoni	9	6	8.57
Haemulon aurolineatum	115	6	8.57
Haemulon parra	9	6	8.57
Serranus tigrinus	7	6	8.57
Stegastes variabilis	6	6	8.57
Haemulon melanurum	6	5	7.14
Lutjanus analis	5	5	7.14
Lutjanus buccanella	12	5	7.14
Sparisoma rubripinne	5	5	7.14
Alphestes afer	6	4	5.71
Epinephelus morio	4	4	5.71
Halichoeres maculipinna	6	4	5.71

Holocentrus adscensionis	4	4	5.71
Pareques acuminatus	7	4	5.71
Pterois volitans	4	4	5.71
Chaetodon striatus	4	3	4.29
Pomacanthus arcuatus	4	3	4.29
Stegastes leucostictus	3	3	4.29
Anisotremus virginicus	4	2	2.86
Carangoides ruber	2	2	2.86
Chaetodon capistratus	4	2	2.86
Chaetodon ocellatus	4	2	2.86
Halichoeres poeyi	2	2	2.86
Malacoctenus triangulatus	3	2	2.86
Pomacanthus paru	2	2	2.86
Sparisoma chrysopterum	2	2	2.86
Sparisoma radians	2	2	2.86
Sparisoma viride	2	2	2.86
Anisotremus surinamensis	2	1	1.43
Calamus sp.	1	1	1.43
Chromis multilineata	1	1	1.43
Ctenogobius saepepallens	1	1	1.43
Diodon hystrix	1	1	1.43
Elacatinus prochilos	1	1	1.43
Epinephelus guttatus	1	1	1.43
Epinephelus prochilos	1	1	1.43
Gymnothorax moringa	1	1	1.43
Haemulon album	1	1	1.43
Holacanthus bermudensis	1	1	1.43
Lutjanus synagris	1	1	1.43
Malacanthus plumieri	1	1	1.43
Mycteroperca bonaci	1	1	1.43
Mycteroperca venenosa	1	1	1.43
Ophioblennius macclurei	1	1	1.43
Scarus iseri	1	1	1.43
Sphyraena barracuda	1	1	1.43
Stegastes diencaeus	1	1	1.43
Aluterus scriptus	0	0	0.00
Amblycirrhitus pinos	0	0	0.00
Apogon maculatus	0	0	0.00
Apogon pseudomaculatus	0	0	0.00
Apogon townsendi	0	0	0.00
Aulostomus maculatus	0	0	0.00
Balistes vetula	0	0	0.00
Bodianus rufus	0	0	0.00

Calamus calamus	0	0	0.00
Cantherhines pullus	0	0	0.00
Cephalopholis fulva	0	0	0.00
Coryphopterus glaucofraenum	0	0	0.00
Coryphopterus hyalinus/personatus	0	0	0.00
Cryptotomus roseus	0	0	0.00
Elacatinus oceanops	0	0	0.00
Enneanectes boehlkei	0	0	0.00
Enneanectes sp.	0	0	0.00
Epinephelus adscensionis	0	0	0.00
Gramma loreto	0	0	0.00
Gymnothorax funebris	0	0	0.00
Haemulon carbonarium	0	0	0.00
Haemulon macrostomum	0	0	0.00
Hypoplectrus unicolor	0	0	0.00
Lactophrys bicaudalis	0	0	0.00
Lactophrys triqueter	0	0	0.00
Lutjanus apodus	0	0	0.00
Lutjanus mahogoni	0	0	0.00
Microspathodon chrysurus	0	0	0.00
Mullus auratus	0	0	0.00
Narcine brasiliensis	0	0	0.00
Opistognathus aurifrons	0	0	0.00
Rhomboplites aurorubens	0	0	0.00
Scaridae spp.	0	0	0.00
Scarus guacamaia	0	0	0.00
Scarus taeniopterus	0	0	0.00
Scarus vetula	0	0	0.00
Scorpaena plumieri	0	0	0.00
Serranus baldwini	0	0	0.00
Sparisoma atomarium	0	0	0.00
Sphoeroides spengleri	0	0	0.00
Stegastes adustus	0	0	0.00
Stegastes planifrons	0	0	0.00
Synodus foetens	0	0	0.00
Synodus intermedius	0	0	0.00
Synodus sp.	0	0	0.00
Urobatis jamaicensis	0	0	0.00
Xyrichtys splendens	0	0	0.00

Appendix 5.5 Species list for ***Coral Transplant treatment***, ranked by Percent Occurrence (*P*). Shaded species were present with a *P* of 10% or greater. Species in bold were observed exclusively on the Coral Transplant treatment. Abundance is in terms of total fishes counted across all monitoring trips. Occurrence refers to the number of times one or more members of each species was observed in a visual survey. N=70. Percent Occurrence = Occurrence/N * 100.

	Abundance	**Occurrence**	**Percent Occurrence**
Thalassoma bifasciatum	450	60	85.71
Acanthurus coeruleus	169	56	80.00
Halichoeres bivittatus	137	44	62.86
Stegastes partitus	116	40	57.14
Acanthurus bahianus	85	35	50.00
Canthigaster rostrata	69	34	48.57
Haemulon plumierii	43	34	48.57
Halichoeres garnoti	70	24	34.29
Haemulon sciurus	24	23	32.86
Sparisoma aurofrenatum	37	23	32.86
Ocyurus chrysurus	26	17	24.29
Pseudupeneus maculatus	39	15	21.43
Holacanthus ciliaris	20	14	20.00
Acanthurus chirurgus	24	13	18.57
Halichoeres radiatus	15	13	18.57
Haemulon spp.	111	12	17.14
Haemulon melanurum	103	11	15.71
Cephalopholis cruentata	10	10	14.29
Haemulon flavolineatum	55	10	14.29
Chromis cyanea	15	8	11.43
Halichoeres pictus	25	8	11.43
Haemulon parra	11	7	10.00
Pareques acuminatus	12	7	10.00
Halichoeres maculipinna	9	6	8.57
Lutjanus analis	6	6	8.57
Pterois volitans	10	6	8.57
Lutjanus buccanella	11	5	7.14
Pomacanthus arcuatus	5	5	7.14
Serranus tigrinus	6	5	7.14
Haemulon carbonarium	4	4	5.71
Holacanthus tricolor	4	4	5.71
Pomacanthus paru	5	4	5.71
Abudefduf saxatilis	3	3	4.29
Anisotremus virginicus	5	3	4.29

Chaetodon capistratus	5	3	4.29
Elacatinus prochilos	5	3	4.29
Gnatholepis thompsoni	3	3	4.29
Holocentrus adscensionis	3	3	4.29
Sparisoma rubripinne	3	3	4.29
Balistes vetula	2	2	2.86
Chaetodon striatus	4	2	2.86
Ctenogobius saepepallens	2	2	2.86
Epinephelus morio	2	2	2.86
Epinephelus prochilos	2	2	2.86
Gymnothorax moringa	2	2	2.86
Lachnolaimus maximus	2	2	2.86
Sparisoma chrysopterum	2	2	2.86
Sparisoma viride	3	2	2.86
Stegastes variabilis	3	2	2.86
Alphestes afer	1	1	1.43
Chaetodon ocellatus	2	1	1.43
Chromis multilineata	1	1	1.43
Coryphopterus glaucofraenum	1	1	1.43
Cryptotomus roseus	3	1	1.43
Elacatinus oceanops	1	1	1.43
Enneanectes sp.	1	1	1.43
Epinephelus guttatus	1	1	1.43
Gymnothorax funebris	1	1	1.43
Haemulon album	10	1	1.43
Haemulon aurolineatum	1	1	1.43
Lactophrys bicaudalis	1	1	1.43
Lactophrys triqueter	1	1	1.43
Malacanthus plumieri	1	1	1.43
Mycteroperca venenosa	1	1	1.43
Scaridae spp.	1	1	1.43
Scorpaena plumieri	1	1	1.43
Stegastes adustus	1	1	1.43
Stegastes diencaeus	1	1	1.43
Stegastes leucostictus	1	1	1.43
Stegastes planifrons	1	1	1.43
Aluterus scriptus	0	0	0.00
Amblycirrhitus pinos	0	0	0.00
Anisotremus surinamensis	0	0	0.00
Apogon maculatus	0	0	0.00
Apogon pseudomaculatus	0	0	0.00
Apogon townsendi	0	0	0.00
Aulostomus maculatus	0	0	0.00

Bodianus rufus	0	0	0.00
Calamus calamus	0	0	0.00
Calamus sp.	0	0	0.00
Cantherhines pullus	0	0	0.00
Carangoides ruber	0	0	0.00
Cephalopholis fulva	0	0	0.00
Coryphopterus hyalinus/personatus	0	0	0.00
Diodon hystrix	0	0	0.00
Enneanectes boehlkei	0	0	0.00
Epinephelus adscensionis	0	0	0.00
Gramma loreto	0	0	0.00
Haemulon macrostomum	0	0	0.00
Halichoeres poeyi	0	0	0.00
Holacanthus bermudensis	0	0	0.00
Hypoplectrus unicolor	0	0	0.00
Lutjanus apodus	0	0	0.00
Lutjanus mahogoni	0	0	0.00
Lutjanus synagris	0	0	0.00
Malacoctenus triangulatus	0	0	0.00
Microspathodon chrysurus	0	0	0.00
Mullus auratus	0	0	0.00
Mycteroperca bonaci	0	0	0.00
Narcine brasiliensis	0	0	0.00
Ophioblennius macclurei	0	0	0.00
Opistognathus aurifrons	0	0	0.00
Rhomboplites aurorubens	0	0	0.00
Scarus guacamaia	0	0	0.00
Scarus iseri	0	0	0.00
Scarus taeniopterus	0	0	0.00
Scarus vetula	0	0	0.00
Serranus baldwini	0	0	0.00
Sparisoma atomarium	0	0	0.00
Sparisoma radians	0	0	0.00
Sphoeroides spengleri	0	0	0.00
Sphyraena barracuda	0	0	0.00
Synodus foetens	0	0	0.00
Synodus intermedius	0	0	0.00
Synodus sp.	0	0	0.00
Urobatis jamaicensis	0	0	0.00
Xyrichtys splendens	0	0	0.00

Appendix 5.6 Species list for ***Settlement Plate treatment***, ranked by Percent Occurrence (*P*). Shaded species were present with a *P* of 10% or greater. Species in bold were observed exclusively on the Settlement Plate treatment. Abundance is in terms of total fishes counted across all monitoring trips. Occurrence refers to the number of times one or more members of each species was observed in a visual survey. N=70. Percent Occurrence = Occurrence/N * 100.

	Abundance	**Occurrence**	**Percent Occurrence**
Thalassoma bifasciatum	556	63	90.00
Acanthurus coeruleus	179	55	78.57
Canthigaster rostrata	84	42	60.00
Halichoeres bivittatus	116	41	58.57
Acanthurus bahianus	86	40	57.14
Stegastes partitus	89	38	54.29
Haemulon plumierii	62	35	50.00
Sparisoma aurofrenatum	48	25	35.71
Halichoeres garnoti	43	20	28.57
Ocyurus chrysurus	32	20	28.57
Haemulon flavolineatum	75	14	20.00
Halichoeres radiatus	18	14	20.00
Haemulon sciurus	13	13	18.57
Holacanthus ciliaris	17	13	18.57
Pseudupeneus maculatus	26	13	18.57
Abudefduf saxatilis	14	11	15.71
Acanthurus chirurgus	18	11	15.71
Mycteroperca microlepis	10	10	14.29
Haemulon melanurum	42	9	12.86
Anisotremus virginicus	10	7	10.00
Haemulon aurolineatum	95	7	10.00
Haemulon parra	19	6	8.57
Halichoeres maculipinna	7	6	8.57
Lutjanus buccanella	12	6	8.57
Cephalopholis cruentata	5	5	7.14
Holacanthus tricolor	5	5	7.14
Lutjanus analis	8	5	7.14
Pomacanthus paru	5	5	7.14
Chaetodon ocellatus	5	4	5.71
Chaetodon striatus	4	4	5.71
Gnatholepis thompsoni	8	4	5.71
Halichoeres pictus	13	4	5.71
Pareques acuminatus	5	4	5.71
Pterois volitans	5	4	5.71

Sparisoma radians	6	4	5.71
Alphestes afer	3	3	4.29
Coryphopterus glaucofraenum	3	3	4.29
Elacatinus prochilos	3	3	4.29
Holocentrus adscensionis	3	3	4.29
Lactophrys triqueter	3	3	4.29
Scarus iseri	4	3	4.29
Sparisoma rubripinne	3	3	4.29
Stegastes leucostictus	4	3	4.29
Cephalopholis fulva	3	2	2.86
Chaetodon capistratus	4	2	2.86
Epinephelus morio	2	2	2.86
Epinephelus prochilos	4	2	2.86
Haemulon album	5	2	2.86
Lachnolaimus maximus	2	2	2.86
Lutjanus mahogoni	2	2	2.86
Lutjanus synagris	2	2	2.86
Mycteroperca bonaci	2	2	2.86
Serranus tigrinus	2	2	2.86
Sparisoma viride	2	2	2.86
Sphyraena barracuda	2	2	2.86
Apogon maculatus	2	1	1.43
Bodianus rufus	1	1	1.43
Carangoides ruber	1	1	1.43
Chromis cyanea	1	1	1.43
Chromis multilineata	1	1	1.43
Elacatinus oceanops	2	1	1.43
Enneanectes boehlkei	2	1	1.43
Gymnothorax moringa	1	1	1.43
Haemulon spp.	40	1	1.43
Halichoeres poeyi	1	1	1.43
Pomacanthus arcuatus	2	1	1.43
Scaridae spp.	1	1	1.43
Sparisoma atomarium	1	1	1.43
Sparisoma chrysopterum	3	1	1.43
Stegastes adustus	1	1	1.43
Xyrichtys splendens	1	1	1.43
Aluterus scriptus	0	0	0.00
Amblycirrhitus pinos	0	0	0.00
Anisotremus surinamensis	0	0	0.00
Apogon pseudomaculatus	0	0	0.00
Apogon townsendi	0	0	0.00
Aulostomus maculatus	0	0	0.00

Balistes vetula	0	0	0.00
Calamus calamus	0	0	0.00
Calamus sp.	0	0	0.00
Cantherhines pullus	0	0	0.00
Coryphopterus hyalinus/personatus	0	0	0.00
Cryptotomus roseus	0	0	0.00
Ctenogobius saepepallens	0	0	0.00
Diodon hystrix	0	0	0.00
Enneanectes sp.	0	0	0.00
Epinephelus adscensionis	0	0	0.00
Epinephelus guttatus	0	0	0.00
Gramma loreto	0	0	0.00
Gymnothorax funebris	0	0	0.00
Haemulon carbonarium	0	0	0.00
Haemulon macrostomum	0	0	0.00
Holacanthus bermudensis	0	0	0.00
Hypoplectrus unicolor	0	0	0.00
Lactophrys bicaudalis	0	0	0.00
Lutjanus apodus	0	0	0.00
Malacanthus plumieri	0	0	0.00
Malacoctenus triangulatus	0	0	0.00
Microspathodon chrysurus	0	0	0.00
Mullus auratus	0	0	0.00
Mycteroperca venenosa	0	0	0.00
Narcine brasiliensis	0	0	0.00
Ophioblennius macclurei	0	0	0.00
Opistognathus aurifrons	0	0	0.00
Rhomboplites aurorubens	0	0	0.00
Scarus guacamaia	0	0	0.00
Scarus taeniopterus	0	0	0.00
Scarus vetula	0	0	0.00
Scorpaena plumieri	0	0	0.00
Serranus baldwini	0	0	0.00
Sphoeroides spengleri	0	0	0.00
Stegastes diencaeus	0	0	0.00
Stegastes planifrons	0	0	0.00
Stegastes variabilis	0	0	0.00
Synodus foetens	0	0	0.00
Synodus intermedius	0	0	0.00
Synodus sp.	0	0	0.00
Urobatis jamaicensis	0	0	0.00

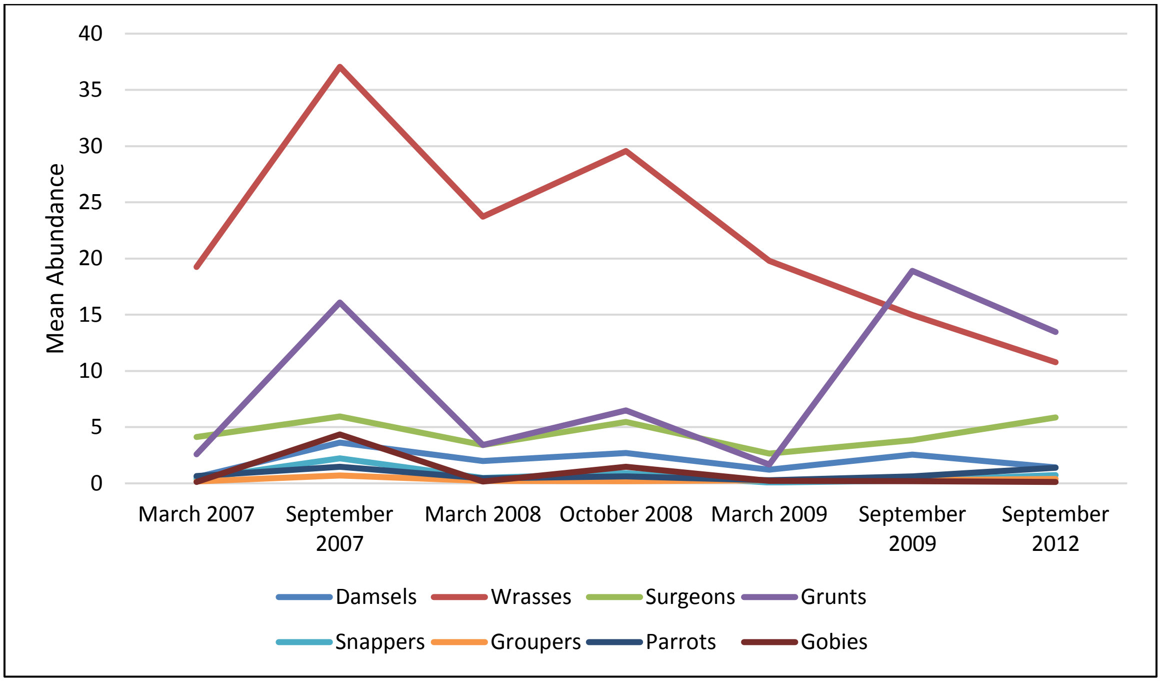
Appendix 5.7 Species list for ***Natural Reef treatment***, ranked by Percent Occurrence (*P*). Shaded species were present with a *P* of 10% or greater. Species in bold were observed exclusively on the Natural Reef. Abundance is in terms of total fishes counted across all monitoring trips. Occurrence refers to the number of times one or more members of each species was observed in a visual survey. N=96. Percent Occurrence = Occurrence/N * 100.

	Abundance	**Occurrence**	**Percent Occurrence**
Halichoeres garnoti	283	71	73.96
Thalassoma bifasciatum	258	55	57.29
Chromis cyanea	308	49	51.04
Canthigaster rostrata	72	46	47.92
Stegastes partitus	92	46	47.92
Haemulon flavolineatum	71	45	46.88
Sparisoma aurofrenatum	59	38	39.58
Stegastes planifrons	76	32	33.33
Haemulon plumierii	30	27	28.13
Ocyurus chrysurus	31	26	27.08
Scarus iseri	57	25	26.04
Acanthurus bahianus	28	20	20.83
Acanthurus coeruleus	26	19	19.79
Stegastes leucostictus	30	19	19.79
Cephalopholis cruentata	19	17	17.71
Haemulon sciurus	18	17	17.71
Sparisoma viride	23	17	17.71
Acanthurus chirurgus	20	15	15.63
Stegastes adustus	24	15	15.63
Elacatinus prochilos	23	14	14.58
Stegastes variabilis	24	14	14.58
Halichoeres bivittatus	24	13	13.54
Pseudupeneus maculatus	14	12	12.50
Coryphopterus hyalinus/personatus	218	11	11.46
Chaetodon capistratus	12	10	10.42
Serranus tigrinus	9	9	9.38
Halichoeres pictus	80	8	8.33
Halichoeres maculipinna	18	7	7.29
Scarus taeniopterus	14	7	7.29
Cephalopholis fulva	6	6	6.25
Holacanthus tricolor	6	6	6.25
Sparisoma radians	7	6	6.25
Haemulon spp.	224	4	4.17
Lactophrys triqueter	4	4	4.17
Stegastes diencaeus	4	4	4.17

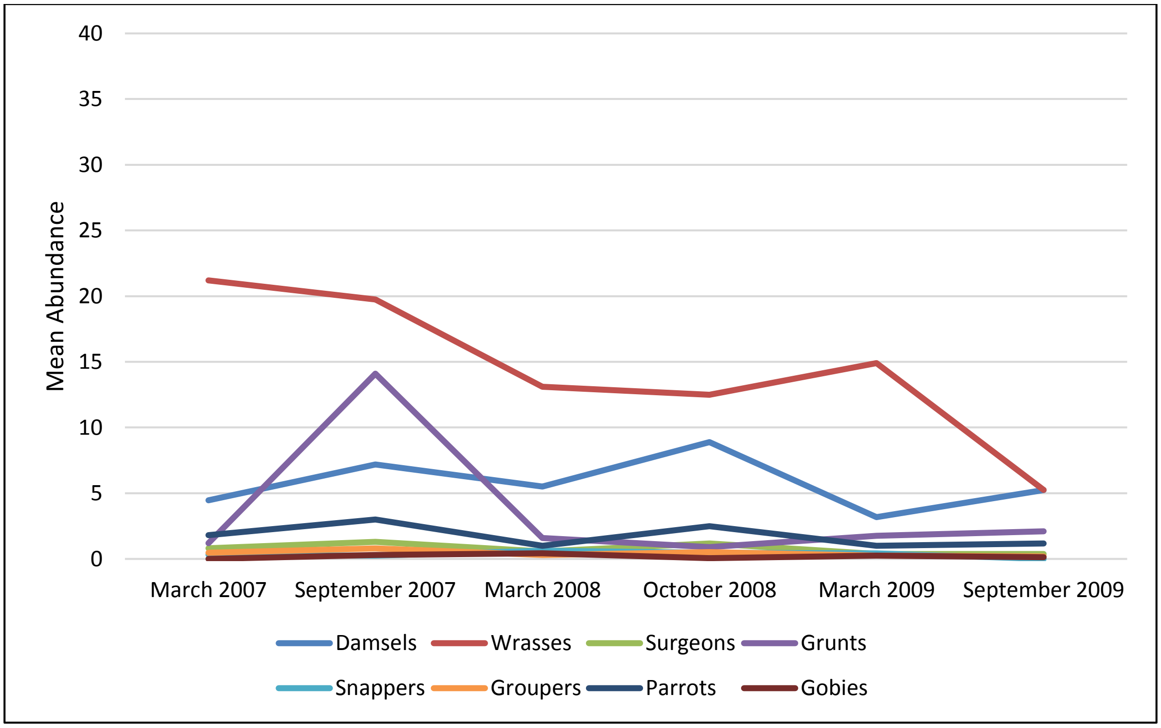
Calamus calamus	3	3	3.13
Carangoides ruber	3	3	3.13
Chaetodon ocellatus	4	3	3.13
Coryphopterus glaucofraenum	3	3	3.13
Elacatinus oceanops	5	3	3.13
Epinephelus adscensionis	3	3	3.13
Halichoeres radiatus	3	3	3.13
Bodianus rufus	2	2	2.08
Epinephelus guttatus	2	2	2.08
Gymnothorax moringa	2	2	2.08
Haemulon carbonarium	2	2	2.08
Lutjanus apodus	3	2	2.08
Sparisoma chrysopterum	2	2	2.08
Abudefduf saxatilis	3	1	1.04
Aluterus scriptus	1	1	1.04
Amblycirrhitus pinos	1	1	1.04
Anisotremus virginicus	1	1	1.04
Apogon townsendi	1	1	1.04
Aulostomus maculatus	1	1	1.04
Cantherhines pullus	1	1	1.04
Chromis multilineata	1	1	1.04
Ctenogobius saepepallens	1	1	1.04
Haemulon macrostomum	1	1	1.04
Haemulon melanurum	1	1	1.04
Holacanthus ciliaris	1	1	1.04
Hypoplectrus unicolor	1	1	1.04
Lachnolaimus maximus	1	1	1.04
Mullus auratus	1	1	1.04
Mycteroperca venenosa	1	1	1.04
Narcine brasiliensis	1	1	1.04
Opistognathus aurifrons	4	1	1.04
Pareques acuminatus	1	1	1.04
Rhomboplites aurorubens	2	1	1.04
Scaridae spp.	3	1	1.04
Scarus guacamaia	1	1	1.04
Scarus vetula	2	1	1.04
Sparisoma atomarium	1	1	1.04
Sphoeroides spengleri	1	1	1.04
Synodus foetens	1	1	1.04
Synodus intermedius	1	1	1.04
Urobatis jamaicensis	1	1	1.04
Xyrichtys splendens	15	1	1.04
Alphestes afer	0	0	0.00

Anisotremus surinamensis	0	0	0.00
Apogon maculatus	0	0	0.00
Apogon pseudomaculatus	0	0	0.00
Balistes vetula	0	0	0.00
Calamus sp.	0	0	0.00
Chaetodon striatus	0	0	0.00
Cryptotomus roseus	0	0	0.00
Diodon hystrix	0	0	0.00
Enneanectes boehlkei	0	0	0.00
Enneanectes sp.	0	0	0.00
Epinephelus morio	0	0	0.00
Epinephelus prochilos	0	0	0.00
Gnatholepis thompsoni	0	0	0.00
Gramma loreto	0	0	0.00
Gymnothorax funebris	0	0	0.00
Haemulon album	0	0	0.00
Haemulon aurolineatum	0	0	0.00
Haemulon parra	0	0	0.00
Halichoeres poeyi	0	0	0.00
Holacanthus bermudensis	0	0	0.00
Holocentrus adscensionis	0	0	0.00
Lactophrys bicaudalis	0	0	0.00
Lutjanus analis	0	0	0.00
Lutjanus buccanella	0	0	0.00
Lutjanus mahogoni	0	0	0.00
Lutjanus synagris	0	0	0.00
Malacanthus plumieri	0	0	0.00
Malacoctenus triangulatus	0	0	0.00
Microspathodon chrysurus	0	0	0.00
Mycteroperca bonaci	0	0	0.00
Mycteroperca microlepis	0	0	0.00
Ophioblennius macclurei	0	0	0.00
Pomacanthus arcuatus	0	0	0.00
Pomacanthus paru	0	0	0.00
Pterois volitans	0	0	0.00
Scorpaena plumieri	0	0	0.00
Serranus baldwini	0	0	0.00
Sparisoma rubripinne	0	0	0.00
Sphyraena barracuda	0	0	0.00
Synodus sp.	0	0	0.00

Appendix 5.8 Seasonal fluctuations on the substrate modules for eight dominant reef fish families.



Appendix 5.9 Seasonal fluctuations on the natural reef for eight dominant reef fish families.



Appendix 5.10 Mean abundance of eight dominant reef fish families in Akumal, by treatment; March 2007 only (N=6, 3, 3, 3, respectively).

Family	Species	NR	Ctrl	Pads	Plates
Acanthuridae	*Acanthurus bahianus*	0.5	0.7	-	0.3
Acanthuridae	*Acanthurus coeruleus*	0.6	0.7	3.3	0.3
Gobiidae	*Coryphopterus glaucofraenum*	-	0.2	-	-
Gobiidae	*Elacatinus oceanops*	0.2	-	-	0.3
Gobiidae	*Gnatholepis thompsoni*	-	0.3	-	-
Haemulidae	*Haemulon album*	0.1	-	-	-
Haemulidae	*Haemulon carbonarium*	0.1	-	-	-
Haemulidae	*Haemulon flavolineatum*	0.2	-	0.3	-
Haemulidae	*Haemulon plumierii*	0.6	0.3	1.0	0.7
Haemulidae	*Haemulon sciurus*	0.2	0.2	-	-
Labridae	*Bodianus rufus*	0.2	-	-	-
Labridae	*Clepticus parrae*	0.2	-	-	-
Labridae	*Halichoeres bivittatus*	-	1.2	3.0	0.3
Labridae	*Halichoeres garnoti*	5.8	0.5	-	0.3
Labridae	*Halichoeres radiatus*	0.2	-	-	1.0
Labridae	*Lachnolaimus maximus*	-	-	0.3	-
Labridae	*Thalassoma bifasciatum*	9.5	2.3	3.0	3.0
Lutjanidae	*Lutjanus apodus*	-	-	0.3	-
Lutjanidae	*Lutjanus buccanella*	-	-	-	8.3
Lutjanidae	*Lutjanus mahogoni*	0.2	-	-	-
Lutjanidae	*Ocyurus chrysurus*	0.4	0.3	-	-
Pomacentridae	*Abudefduf saxatilis*	0.2	-	-	0.7
Pomacentridae	*Chromis cyanea*	0.9	-	-	-
Pomacentridae	*Microspathodon chrysurus*	0.2	-	-	-
Pomacentridae	*Pomacentridae* sp.	0.2	-	-	-
Pomacentridae	*Stegastes adustus*	-	-	-	0.3
Pomacentridae	*Stegastes leucostictus*	0.3	-	-	-
Pomacentridae	*Stegastes partitus*	0.5	-	0.7	-
Pomacentridae	*Stegastes variabilis*	0.4	-	-	-
Scaridae	*Sparisoma aurofrenatum*	0.5	-	-	-
Scaridae	*Sparisoma viride*	0.2	0.2	-	-
Serranidae	*Cephalopholis cruentata*	0.1	0.2	-	-
Serranidae	*Cephalopholis fulva*	0.5	-	0.3	-
Tetraodontidae	*Canthigaster rostrata*	0.2	0.2	-	-

Appendix 5.11 Resident and Transient reef fish species, ranked in descending order by total abundance with all treatments combined.

Residents	Total	Transients	Total
Thalassoma bifasciatum	2157	*Acanthurus coeruleus*	831
Haemulon spp.	831	*Halichoeres bivittatus*	571
Stegastes partitus	542	*Halichoeres garnoti*	461
Haemulon flavolineatum	408	*Acanthurus bahianus*	362
Chromis cyanea	356	*Sparisoma aurofrenatum*	217
Canthigaster rostrata	352	*Ocyurus chrysurus*	159
Haemulon plumierii	270	*Pseudupeneus maculatus*	149
Haemulon aurolineatum	262	*Acanthurus chirurgus*	121
Coryphopterus hyalinus/personatus	218	*Halichoeres radiatus*	66
Haemulon melanurum	204	*Scarus iseri*	62
Halichoeres pictus	184	*Halichoeres maculipinna*	48
Haemulon sciurus	99	*Lutjanus buccanella*	38
Stegastes planifrons	77	*Sparisoma viride*	31
Holacanthus ciliaris	73	*Lutjanus analis*	27
Cephalopholis cruentata	55	*Anisotremus virginicus*	23
Elacatinus prochilos	48	*Sparisoma rubripinne*	22
Haemulon parra	48	*Lachnolaimus maximus*	19
Abudefduf saxatilis	42	*Xyrichtys splendens*	17
Stegastes leucostictus	41	*Sparisoma chrysopterum*	15
Stegastes variabilis	34	*Sparisoma radians*	15
Pareques acuminatus	33	*Scarus taeniopterus*	14
Chaetodon capistratus	28	*Calamus* sp.	13
Stegastes adustus	28	*Lactophrys triqueter*	9
Pterois volitans	27	*Carangoides ruber*	6
Serranus tigrinus	27	*Lutjanus synagris*	6
Holacanthus tricolor	26	*Scaridae* spp.	5
Gnatholepis thompsoni	23	*Calamus calamus*	4
Chaetodon ocellatus	19	*Malacanthus plumieri*	4
Pomacanthus arcuatus	19	*Mycteroperca venenosa*	4
Haemulon album	17	*Sparisoma atomarium*	4
Pomacanthus paru	16	*Cryptotomus roseus*	3
Chaetodon striatus	15	*Halichoeres poeyi*	3
Holocentrus adscensionis	14	*Lutjanus apodus*	3
Epinephelus morio	12	*Mycteroperca bonaci*	3
Alphestes afer	11	*Sphyraena barracuda*	3
Cephalopholis fulva	10	*Balistes vetula*	2
Elacatinus oceanops	9	*Diodon hystrix*	2
Coryphopterus glaucofraenum	7	*Lutjanus mahogoni*	2
Gymnothorax moringa	7	*Rhomboplites aurorubens*	2

Residents	Total	Transients	Total
Haemulon carbonarium	6	*Scarus vetula*	2
Malacoctenus triangulatus	6	*Scorpaena plumieri*	2
Stegastes diencaeus	6	*Aluterus scriptus*	1
Chromis multilineata	5	*Lactophrys bicaudalis*	1
Opistognathus aurifrons	5	*Mullus auratus*	1
Bodianus rufus	4	*Narcine brasiliensis*	1
Ctenogobius saepepallens	4	*Scarus guacamaia*	1
Epinephelus guttatus	4	*Sphoeroides spengleri*	1
Epinephelus adscensionis	3	*Synodus foetens*	1
Anisotremus surinamensis	2	*Synodus intermedius*	1
Apogon maculatus	2	*Synodus* sp.	1
Enneanectes boehlkei	2	*Urobatis jamaicensis*	1
Gymnothorax funebris	2		
Amblycirrhitus pinos	1		
Apogon pseudomaculatus	1		
Apogon townsendi	1		
Aulostomus maculatus	1		
Cantherhines pullus	1		
Enneanectes sp.	1		
Haemulon macrostomum	1		
Holacanthus bermudensis	1		
Hypoplectrus unicolor	1		
Ophioblennius macclurei	1		
Serranus baldwini	1		