Fish, algae and coral dynamics from various reefs in southwest Puerto Rico

By

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ABSTRACT

A study composed of three experiments was conducted in 7 reef sites, at 5 and 10 m depth off the southwest coast of Puerto Rico, to examine fish, algae, and coral dynamics. The first experiment employed exclusion cages. Three exclusion cages (0.5 m x 0.5 m x 0.25 m) were placed at each site and depth. Algae and herbivores were removed from these cages to observe algae succession under no grazing pressure after algae removal. Control areas were established in the vicinity of each site to account for natural fluctuations on algae cover. A negative relation between cyanobacteria and coralline algae was observed. Algal development inside the exclusion cages suggests that algae interspecific competition dominates reef population dynamics.

For the second experiment, five 1 m^2 quadrats were marked per site and depth. Algae were removed from inside the quadrats to observe algae development under actual herbivore grazing pressure. The most abundant algae at the studied sites were *Halimeda*, *Dyctiota*, and turf. Algae interspecific competition was observed at most sites, in particular a negative relationship between macroalgae and turf. Shallow mid-shelf reefs and deep inshore reefs showed varying results, and possible explanations for the results are discussed.

The third experiment consisted of fish surveys conducted at each site and depth contour on three different occasions using the stationary plot technique with discrete group sampling. Fish abundance was positively related to macroalgae cover. Turbidity and light intensity affected fish density, possibly because of the effect that these physical factors have on algal growth. Prevailing grazing pressure exerted by scarids, acanthurids, and probably sea urchins, in the mid-shelf at 5 m depth, promotes algal species diversity as predicted by the intermediate disturbance model. Major impact of herbivores on algal cover is thorough their apparent control over

palatable algae. Algal cover is controlled by grazer density only in a spatial scale, since the effect of grazers was only observed at some sites and depths.

RESUMEN

Un estudio compuesto de varios experimentos para evaluar la dinámica poblacional entre peces, algas y corales se llevó a cabo en 7 arrecifes, a 5 y 10 m de profundidad, al suroeste de Puerto Rico. El primer experimento se realizó utilizando jaulas de exclusión, colocándose tres jaulas (0.5 m x 0.5 m x 0.25 m) a 5 y 10 m de profundidad en los 7 arrecifes. Para observar la sucesión de algas en ausencia de herbívoros, las algas y herbívoros dentro de la jaula fueron removidos. Tres áreas circundantes, de igual dimensión, en cada lugar y a las mismas profundidades, se marcaron y monitorearon como control, para tener en consideración la fluctuación natural en cobertura de algas. Se encontró una relación negativa entre cyanobacteria y alga coralina. El desarrollo de algas en las jaulas de exclusión sugiere que la interacción interespecífica entre algas es el componente principal en la dinámica poblacional del arrecife.

En el segundo experimento, se colocaron 5 cuadrantes de 1 m^2 por área y profundidad. Se removieron las algas dentro del cuadrante para observar el desarrollo de éstas bajo presión de herbivoría. Las algas más abundantes fueron *Halimeda*, *Dyctiota* y las algas cespistosas. En la mayoría de los lugares se observó competencia interespecífica entre algas, en particular una relación negativa entre turf y macroalgas. En arrecifes llanos en medio de la plataforma insular y arrecifes profundos cercanos a la costa los resultados variaron por lo que se discutieron posibles explicaciones para los mismos.

El tercer experimento consistió de censos de peces llevados a cabo en cada una de las áreas de estudio, a cada profundidad y en tres ocasiones distintas, utilizando el método de muestreo estacionario con grupos discretos de peces. Se encontró una relación positiva entre la abundancia de peces y la cobertura de macroalgas. La densidad de peces se vio afectada por turbidez e intensidad de luz, probablemente debido al efecto que estos factores físicos tienen

sobre el crecimiento de algas. La intensidad de pastoreo prevaleciente en el arrecife en medio de la plataforma continental a 5 m, ejercida por acantúridos y escáridos, y probablemente erizos, promueve la diversidad de especies según el modelo de disturbios intermedios. Los herbívoros impactan la cobertura de algas en general controlando el crecimiento de algas gustosas. La densidad de herbívoros controla la cobertura de algas sólo en una escala espacial ya que el efecto se observó sólo en ciertos lugares y profundidades.

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CHAPTER 1: INTRODUCTION

Coral reefs are marine ecosystems rich in species diversity. They provide habitat for many commercially valuable invertebrate and fish species (Chabanet *et al.,* 1997). Coral reefs also serve as a buffer zone, protecting the shoreline and mainland from hurricane surge and hazardous weather.

Several factors have detrimental effects on reef ecosystems. These could be classified as natural or anthropogenic (Turgeon *et al.,* 2002), and they could be of long or short term (Done, 1992). Natural factors include hurricanes and diseases among others (Bunkley-Williams and Williams, 1990; Glynn, 1993; Goreau, *et al*., 1998; Hughes, 1994; McClanahan *et al*, 2001b; Peckol *et al.,* 2003; Richardson, 1998; Williams and Bunkley-Williams, 1990). Factors of anthropogenic origin may include: sedimentation; sewage, thermal and, radioactive pollution; hydrodynamic influences; physical disturbance; extractive activities; introductions of exotic species and tourism (Hatcher *et al.,* 1989; Done, 1992; Turgeon *et al.,* 2002; Hudson *et al*., 1994; Tomascik and Sander*,* 1987). Reefs also face long term global threats such as increased water temperatures, ocean acidification and diseases (Connell, 1997; Hoegh-Guldberg, 1999; Jackson, 2001; Jackson *et al*., 2001; Kerr, 2007; McCook, 1999; Pearson, 1981; Williams and Bunkley-Williams, 2000; Williams *et al*., 1999), among others.

Under optimal conditions, reefs may eventually recover from natural disasters, through high coral larval recruitment (Hughes, 1994). Sometimes, even when the threat is removed, as in scenarios of reefs which were under the influence of sewage discharges, corals will not re-establish (Done, 1992; Pearson, 1981). Reef population dynamics and many other aspects of reef ecology are very complex; hence, science still has a long way to go to fully understand coral reef ecosystems.

Despite natural and anthropogenic threats, Caribbean coral reefs were stable marine ecosystems for 125,000 years (Newell, 1971) until they collapsed during the 1980s (Jackson *et al*, 2001). In the last decades, most reefs have gone through a phase shift, characterized by reduced coral cover and an increased algal growth (Done, 1992; Hughes, 1994; McCook, 1999; McClanahan *et al.,* 1999a; Shulman and Robertson, 1996). Coral cover in some reefs has declined from 50% to 1-2% (Hughes, 1994; Jackson *et al*, 2001; Shulman and Robertson, 1996).

Many scientists have tried to identify the cause or chain of events that ended with this observed phase shift in the reefs. The possible scenarios have been classified as bottom-up forces and top-down forces (La Pointe, 1997; 1999; La Pointe *et al*., 1997). Bottom-up forces refer to the effects of an increment in water nutrients, promoting algal growth and affecting corals (Koop *et al.,* 2001; La Pointe, 1997; La Pointe *et al*., 1997). Top-down forces refer to the effects of a reduction in number of algal consuming fishes and invertebrates, resulting in uncontrolled algae growth affecting the corals (Hughes, 1994; Hughes *et al.,* 1999; Jackson, 2001; Sammarco *et al.,* 1974).

In Puerto Rico, reefs are also experiencing this phase shift, showing an increase in algal cover and a decrease in coral cover (Morelock *et al.,* 2001; Turgeon *et al.,* 2002). Unfortunately, no study has been conducted to explore the dynamics of algae, fish, water nutrients and coral cover in this region. Although related research has been conducted in other countries, discrepancies in their results indicate the complexity of this dynamic and how each area should be evaluated separately (Foster, 1987; Hughes *et al.,* 1999; McCook, 1999; Sano, 2001). This information is necessary for adequate management decisions and to guide future studies and restoration programs. The present study provides information on the operating forces in algae-dominated reefs of southwestern Puerto Rico.

1.1 Objectives

The main objective of this research was to study how various reef components (i.e. fishes, algae, corals and water nutrients) interact on the reefs off the southwestern coast of Puerto Rico. This was accomplished through a series of experiments, each trying to assess a different aspect of their interaction. Secondary objectives of this research were:

- to determine the effect of herbivore absence on algal growth,
- to determine herbivore impact on algae cover on the reef,
- to evaluate algal succession on the reef,
- to determine fish abundance and its relation to algal succession,
- and, to evaluate water nutrient levels on the reef and its possible impact on algal growth.

1.2 Literature Review

Coral reefs are non-equilibrium systems whose structure and diversity rely on the frequency and intensity of disturbances (Aronson and Precht, 2000; Connell, 1978; 1997). They survived natural and anthropogenic threats for thousands of years (Jackson, 2001; Newell, 1971). Geographic location, solar irradiance and depth cause local and regional differences between reefs (Coles, 1988; Lesser, 2004; Riegl and Piller, 2003; Van den Hoek *et al.,* 1978). In spite of the expected variations, modern reefs show a dramatic change in species composition or phase shift, being dominated now by algae (Andrews *et al.,* 2004; Connell, 1997; Done, 1992; Donner and Potere, 2007; Hughes, 1994; Williams *et al*., 1999). Increments in the periodicity and intensity of natural reef threats, in addition to global changes and negative anthropogenic effects, have made scientists doubt about the capacity of coral reefs to prevail (Donner and Potere, 2007; Gardner *et al.,* 2003; Hussner, 1994; Kleypas *et al.,* 2001; Pandolfi, 2002; Pandolfi *et al.,* 2003;

2005; Pittock, 1999; Stone, 2007; Williams and Bunkley-Williams 1990). A better knowledge of coral reef response to abiotic and biotic conditions and its dynamics with other reef components would guide management efforts to save and protect coral reefs. Fortunately, scientists worldwide have engaged in this endeavor, although there is still much to learn due to the complexity of reef dynamics.

Various elements have been reported in the literature as responsible for the reef phase shifts from coral-dominated reefs to algae-dominated reefs. These elements include corals, herbivores (sea urchins and fishes), algae and nutrients. Within herbivorous fishes, the literature focuses on three fish families: Acanthuridae (surgeonfish), Scaridae (parrotfish) and Pomacentridae (damselfish).

Parrotfish, surgeonfish, and sea urchins were abundant, conspicuous and important algae consumers on reefs (Ogden, 1976; Ogden and Lobel, 1978). Their density, diversity, high metabolic rates, and need to consume great amounts of low protein algae to acquire the needed nitrogen for growth and reproduction were responsible for their high grazing rates on the reefs (Horn, 1989). Thirty years ago, it was thought they ate food in proportion to its abundance and availability, but that some algae or parts of algae were avoided (Ogden, 1976). Since then, much has been learned about their biology, interspecific interactions, feeding habits and impact on their habitat.

The black sea urchin, *Diadema antillarum*, was conspicuous and abundant in Caribbean reefs until its die-off in 1983-84 (Carpenter, 1985b; Hughes *et al.,* 1987; Vicente and Goenaga, 1984). Increases of algal biomass and changes in algal species composition were attributed to the loss of this herbivore (Carpenter, 1985a; 1985b; 1990; Hay and Taylor, 1985; Shulman and Robertson, 1996). Sammarco *et al.*, (1974) predicted this change in algal cover and species

composition. The subsequent re-establishment of this urchin species and a decrease in algal abundance was documented for Jamaica (Aronson and Precht, 2000; Edmunds and Carpenter, 2001). Nonetheless, many regions still report very low *D. antillarum* densities (Lugo, 2004; Weil, *et al*., 2005; Williams and Polunin, 2001). Haley and Solandt (2001) suggested that another sea urchin species, *Tripneustes ventricosus*, might serve as a successional stage for the re-establishment of *D. antillarum*, by cropping macroalgae to levels easier to be grazed by *Diadema*.

Since the urchin die-off and the increase in algal cover on the reefs, scientists focused on learning more about the grazing impact of *D. antillarum* and its dietary habits and preferences. Turf algae were reported to be the preferred food item of this herbivore (Carpenter, 1981). Various studies documented that its grazing activity promoted growth of low biomass epilithic, endolithic and encrusting turf (Carpenter, 1986). *Diadema* may also feed on calcified algae and algae with unpalatable secondary metabolites, better than other herbivores (Littler *et al.,* 1983; Solandt and Campbell, 2001), as well as on corals (Carpenter, 1981). Studies on its grazing activity reported that its density diminished in heavy wave areas (Foster, 1987), increased with depth (Hay, 1984) and had no impact over algal cover in cryptic areas (Jackson and Kaufmann, 1987).

Many studies documented the increase in herbivorous fishes after the *D. antillarum* die-off (Carpenter, 1985b; Hay, 1984; Hay and Taylor, 1985; Robertson, 1991). This negative relation between sea urchin abundance and herbivorous fish abundance was documented later by other researchers (Carreiro-Silva and McClanahan, 2001; McClanahan *et al*., 1994; 1996; McClanahan and Shafir, 1990).

Scarids are one of the three herbivorous fish groups that have received scientific attention regarding their impact on reef structure (Bruggemann *et al.,* 1996; Choat and Clements, 1983; Lewis, 1986; Mumby, 2006; Overholtzer and Motta, 2000). Choat and Clements (1993) studied the feeding rates of scarids on the Great Barrier Reef. They found low feeding rates in the morning, increasing to higher but variable levels by midday, and variations in daily feeding rate by site. Juvenile stages were reported to feed mainly on *Halimeda* in the Florida Keys (Overholtzer and Motta, 2000). Scarids were also reported to feed on corals, mainly in areas of low skeletal density, with the coral erosion rate inflicted by them increasing with fish size and decreasing with depth (Bruggemann *et al.,* 1996).

Damselfish (Pomacentridae) are another herbivorous fish group that has a great impact on the reef algae community. They cultivate algal lawns that show high algal species richness (Sammarco, 1983; Hinds, 1984; Hixon and Brostoff, 1996), maintained by fish's selective weeding (Ceccarelli *et al.,* 2005; Hata *et al*., 2002). Rhodophytes and cyanophytes dominate in their territory (Hata *et al*., 2002; Sammarco, 1983). It has been suggested that they coexist with unpalatable macroalgae because the later may serve as a possible substratum to grow palatable epiphytes (Ceccarelli *et al.,* 2005). Damselfish feed on algae from their algal lawns in proportion to algae abundance (Hinds, 1984). In eutrophic areas, damselfish nutrient absorption is higher, which is related to grazing on turf with higher nutrient values (Lison de Loma *et al.,* 2000). Damselfish defend their territory through aggressive behavior, preventing other herbivorous fish from feeding on their algal lawn (Overholtzer and Motta, 2000).

Individual studies of surgeonfish, the last of the three major herbivorous fish groups, are not very common in the literature. Of relevance is a study conducted in Florida on their diet preferences (Tilghman *et al.,* 2004). Three species were the target of their study: *Acanthurus*

coerulus, *Acanthurus bahianus* and *Acanthurus chirurgus*. *A. coerulus* showed preference for rhodophytes, phaeophytes and chlorophyes. *A. bahianus* preferred chlorophytes and avoided phaeophytes. *A. chirurgus* chose chlorophytes and sometimes phaeophytes (Tilghman *et al.,* 2004).

Food resources for herbivorous fish are very broad, including: algae, pelagic animal matter, detritus, and sediment (Choat *et al.,* 2002). Their taxonomic relationships do not reflect their diet preferences (Choat *et al.,* 2002). Starch content and digestibility of algae influence their diet choice (Zemke-White and Clements, 1999; Zemke-White *et al.,* 2002).

Spatial distribution of herbivores depends on complex factors including proximity to shelter, predator abundance, density of territorial competitors, and availability of food (Lewis and Wainwright, 1985). Reef substrate characteristics, such as coral abundance and coverage, are also related to fish species richness (Chabanet *et al.,* 1997).

Some scientists believe that overfishing is one of the main factors behind the coral cover decrease and reef phase shift of the last decades (Done, 1992; Hay, 1984; Hughes *et al*, 1987; Jackson, 2001; Jackson *et al*, 2001; McClanahan *et al.,* 1994; 1996; McClanahan and Shafir, 1990). A study conducted at two Fijian reefs after a mass mortality of crustose coralline algae supports this idea (Littler and Littler, 1997). They reported that large herbivores fed on algal turf, opening up substrates for coral recruits, presenting the potential to reverse algae-dominated reef to coral-dominated reef. Contrarily, Ogden and Hodgson (1994) stated that on reefs with similar conditions, those with overfishing and algal overgrowth, decrease in coral cover was not seen. In addition, remote reefs, like the Belize atoll, showed low coral cover and the phase shift, even though it was not subject to overfishing or eutrophication (McClanahan and Muthiga, 1998).

Algae are reported as the dominant group on modern coral reefs (Díaz-Pulido and McCook, 2002; Hughes *et al.,* 1999; McCook *et al.,* 1997; McClanahan *et al.,* 1999a; Williams and Bunkley-Williams, 2000). Many researchers recognize three general reef algal functional groups based on their growth form: turf, macroalgae, and crustose coralline algae (Airoldi, 1998; Phillips *et al*., 1997; Steneck, 1997).

Some algae show seasonality. Seasonal fluctuations on algal community might be driven by temperature, fruiting period, colonization, and spore dispersion (Benayahu and Loya, 1977; Hatcher and Larkum, 1983).

Growth forms are also associated with the physical characteristics of the habitat. Crustose coralline algae prefer areas of high herbivory, high energy, and low nutrients (Belliveau and Paul, 2002). Their abundance is negatively affected by sedimentation (Harrington *et al.,* 2005; Steneck, 1997). Turf, on the contrary, is an herbivore-resistant growth form that traps sediment (Airoldi, 1998; Hackney *et al.,* 1989; Steneck, 1997). It is controlled by disturbances such as abrasion by macroalgae movement and coral rubble tumbling (Cheroske *et al.,* 2000).

Coralline algae have an inverse relationship with turf probably due to the smothering effect that the sediment trapped in the turf has on the former (Steneck, 1997). It can grow under the canopy of macroalgae (Steneck, 1997). Through epithallium sloughing, coralline algae inhibit the settlement of frondose macroalgae (Littler and Littler 1997).

Algae deter herbivore grazing through various mechanisms such as toxins, unpalatable secondary metabolites, calcareous skeleton, and thick textures that impede their consumption and later digestion (Littler *et al*., 1983). There is a relationship between grazing-resistance and algal morphology (Littler *et al.,* 1983). Carpenter (1986) concludes from a study comparing grazing impact between sea urchins and fish that grazing by herbivorous fish promotes the growth of

algae with large biomass (Carpenter, 1986). The turf growth form is energetically expensive, but is advantageous in areas of moderate herbivory or physically stressful habitats, because it loses less biomass to herbivores and suffers less physical damage (Hay, 1981). It has the capacity of branching to compact its structure and avoid further grazing (Hay, 1981). It can also respond rapidly to reduced herbivory with increases in abundance, morphological changes, and altered reproductive status (Lewis, 1986).

Although herbivores are expected to feed on macroalgae, many studies have reported a negative relation between herbivorous fish abundance and macroalgae (Belliveau and Paul, 2002; McClanahan *et al.,* 1999a, 2000, 2002). Conversely, other studies have concluded that the relationship between fish abundance and macroalgae is weak (Chabanet *et al.,* 1997; Sano, 2001).

Lewis (1986) conducted a study on the Belizean barrier reef excluding herbivores to observe their impact on algae composition. Turf and coralline algae were displaced by macroalgae once the herbivores were excluded. In Hawaii, a study conducted by Hixon and Brostoff (1996) reported that crustose and prostrate blue-green mats replaced the early algal succession stage of simple green and brown filaments in areas exposed to parrotfish and surgeonfish schools.

The response of herbivores to macroalgae removal was studied in Belize (McClanahan *et al*., 2000). An increase in herbivore numbers, biomass, and feeding rates was observed. The observation was related to the accessibility of turf, the early algal successional stage, which was considered more palatable. Similarly, an arrest at the early algal successional stage was observed under herbivore presence in a study conducted in Guam (Belliveau and Paul, 2002).

In Belize, on high coral cover reefs, herbivorous fish excluded macroalgae, but on low coral cover reefs the macroalgae overwhelmed the ability of herbivorous fish to crop it down (Williams *et al*., 2001). In Florida, the herbivore abundance was found to control macroalgae, but not to eliminate it from the reef (Paddack *et al.,* 2006).

Many studies have been conducted on algal succession in an effort to understand the operating forces in the reef. Hixon and Brostoff (1996) used exclusion cages to study algae succession under no grazing conditions. They identified three algal successional stages: simple green and brown filaments, thin branched red filaments, and blades and branched thick filaments. Under grazing conditions the succession was different. In areas of intense grazing, crusted and prostrate blue-green mats of low biomass and diversity were observed.

McClanahan (1997) studied successional changes of algae under different herbivore regimes placing experimental coral plates on the reef. He presented an algal succession model based on dominant grazers and sediment accumulation. The model proposed that areas recently disturbed physically are colonized by endolithic algae, followed by epilithic turf-forming algae. The areas dominated by herbivorous fish showed greater algae species diversity and passed through more successional stages. Damselfish concentrated nutrients and promoted fast-growing algae species. In areas dominated by large roaming herbivorous fish, like parrotfish and surgeonfish, algae that overgrew turf-forming algae were promoted (calcareous, fleshy, and coralline). In eutrophic waters algal succession was reversed to turf, promoting algae with high surface to volume ratio (McClanahan, 1997).

Water nutrients are another factor to consider when analyzing algae and coral dynamics on a reef. La Pointe (1997) analyzed the importance of nutrient-limited productivity as part of the algae overgrowth problem in the reef. He gathered available information from other studies,

and conducted a series of water quality analyses at several sites in Jamaica and southeast Florida. In low nutrient environment, macroalgae growth was restricted, as was its ability to compete with corals and algal turf. Herbivory was a significant factor in algal-growth control, but its effect took place on a limited temporal and spatial scale. Water nutrient enrichment was the major factor causing increased productivity and standing crop of macroalgae. Nutrient thresholds for algae overgrowth were determined to occur at 1.0 µM for DIN and 0.1-0.2 µM for Soluble Reactive Phosphorus (La Pointe, 1999).

Algae are one of the major primary producers of the coral reef (Adey and Goertemiller, 1987; Carpenter, 1985a; Morrissey, 1985; Rogers and Salesky, 1981; Wanders, 1976; Williams and Carpenter, 1998). Phosphate and nitrogen have different effects on their growth and productivity, but this could vary among sites (La Pointe, 1997). Phosphate allegedly inhibits the growth of coralline algae (Belliveau and Paul, 2002) while turf is usually limited by nitrogen (Williams and Carpenter, 1998).

Thacker, *et al*. (2001) could not correlate high water nutrient levels with algal overgrowth. They placed exclusion cages on the reef to study the relationship between herbivores, macroalgae, and cyanobacteria growth with nutrient enrichment. They concluded that nutrient enrichment did not have significant impact on algal growth. There were differences between the biomass of macroalgae and cyanobacteria in the exclusion cage treatments. In the caged areas, palatable algae grew; probably due to lack of herbivory. Cyanobacteria cover was negatively correlated with macroalgal cover, and it was speculated that they might compete for space or light (Thacker, *et al*., 2001). A problem with their study was that they could not compensate in the caged treatments for the reduction on light and water flow, which could have stimulated the growth of macroalgae over cyanobacteria.

A different perspective to the cause of reef phase shift was provided by Stimson *et al.* (2001). They studied the abundance of *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. This algal species was responsible of coral displacement in the reef. Its overgrowth was attributed to a sewage plant discharge. The problem persisted after the diversion of the discharge. After studying the abundance and diversity of algae at various sites they proposed two possible explanations. They believed that herbivores preferred grazing on an introduced macroalgae, *Acanthophora spicifera*, which then gives *Dictyosphaeria* an advantage in resource competition. The other explanation was that historical reduction of herbivore biomass was responsible for the low algal growth control observed.

Lack of coral recruitment instead of overfishing or competition with algae, has also been suggested as a possible cause for the reef phase shift observed (McCook *et al.,* 1997; Pearson 1981). Williams and Polunin (2001) studied various reefs in Jamaica, Belize, Grand Cayman, and Cuba. They found that, while herbivores kept macroalgae cover low, there was available space not being colonized by coral; suggesting that a lack of coral recruitment and a decrease in coral cover were the reason for the increase in algae abundance. Coral recruitment has been reported to be enhanced by the presence of refuges (tri-dimensional habitat) and to be more successful under increased grazing pressure (Brock, 1979).

1.3 Study site

The study was conducted at seven reefs on the southwest coast of Puerto Rico. The following five reefs were selected from the insular shelf off La Parguera, Lajas, an area characterized by extensive coral reef development (García *et al.,* 1998; García *et al.,* 2005): Enrique Reef, Mario Reef, Media Luna Reef, Pináculos, and the shelf edge. The other two reefs,

Resuellos and Gallardo, were selected from the western insular shelf off Boquerón, Cabo Rojo. Figure 1 shows the geographical location of all study sites. Table 1 shows the coordinates for each location and their category according to distance from land.

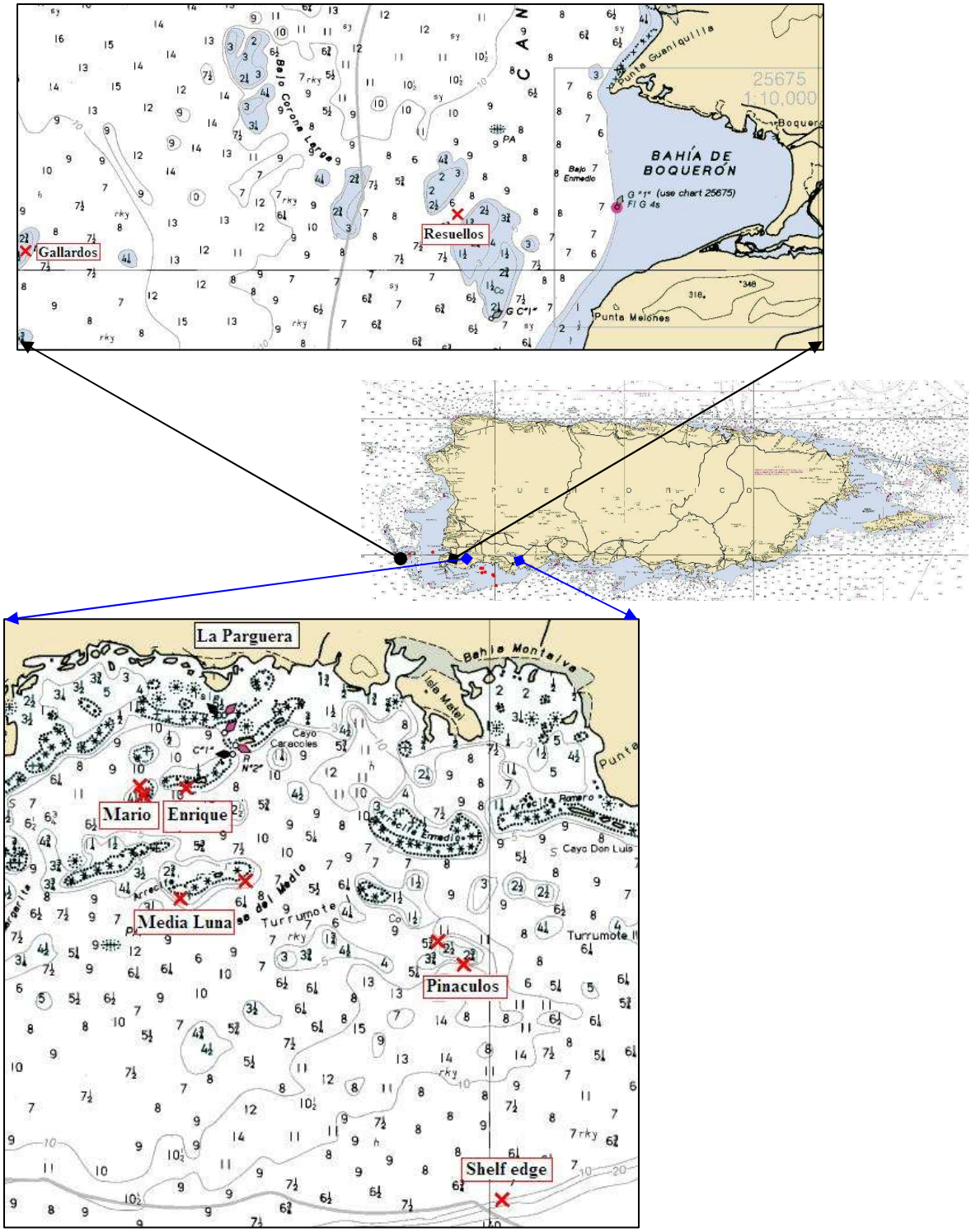

Figure 1.1 Study sites

Table 1.1. Study site information

Site name	Category	Depth (m)	Latitude	Longitude
Mario	Inshore	5	17°57.176'	67°03.416'
Mario	Inshore	10	17°57.088'	67°03.376'
Enrique	Inshore	5	17°57.193'	67°02.953'
Enrique	Inshore	10	17°57.193'	67°02.953'
Media Luna	Mid-shelf	5	17°56.180'	67°03.048'
Media Luna	Mid-shelf	10	17°56.285'	67°02.380'
Pináculos	Mid-shelf	5	17°55.959'	67°00.707'
Pináculos	Mid-shelf	10	17°55.654'	67°00.445'
Resuellos	Inshore	5	18°00.637'	67°14.453'
Resuellos	Inshore	10	18°00.637'	67°14.453'
Gallardo	Offshore	10	18°00.267'	67°19.837'
Shelf edge	Offshore	20	17°53.299'	66°59.868'

GPS System Datum WGS 84

Enrique and Mario reefs are two inshore patch reefs located in the inner shelf of La Parguera, Lajas. The sediments are of mixed grain size and show 10% terrigenous composition (Morelock *et al.,* 2001). The seafloor on these reefs contains loose sediments that are re-suspended with water movement or physical disturbance. Visibility in these reefs during this study was usually poor (~5 m). Previous coral cover reports were 10-30%, dominated mainly by species of massive corals (Morelock *et al.,* 2001). Dominant wave action is of low amplitude (Morelock *et al.,* 1977). Reef zonation used to be marked and similar to that of other Caribbean coral reefs (Morelock *et al.,* 1977). The deeper part of the reef slope is gravelly sand (Morelock *et al.,* 1977).

Media Luna and Pináculos are two mid-shelf reefs off Lajas (Morelock *et al.,* 1977). Sediments are composed of recent and relict deposits (Morelock *et al.,* 1977; 1994). Visibility on these reefs usually exceeded 10 m during this study. Due to their location, they are exposed to greater water movement, mainly due to wind-driven ocean currents and wave action. Zonation is similar to that in other Caribbean coral reefs, with a reef crest dominated by the hydrocoral *Millepora* and limited spur-and-groove formations (Morelock *et al.,* 1977).

The area surveyed at the shelf edge off La Parguera is a spur and groove reef with channels that transport sand (Morelock *et al.,* 1977). Previous studies report coral cover greater than 30%; dominated mainly by species of massive corals (Morelock *et al.,* 2001). The water in this area is usually clear, and it has little no sediment or nutrient load (Morelock *et al.,* 2001). Previous studies report coral cover of 10-30%; dominated mainly by species of massive corals (Morelock *et al.,* 2001). This site was considered an offshore reef.

Resuellos is an inshore reef located near the entrance of Boquerón Bay, Cabo Rojo. Previous coral cover report were less than 10% (Morelock *et al.,* 2001). The slope ends in bare sand. Visibility was usually poor (~5 m) during this study, probably due to land proximity and sedimentation caused mainly by deforestation.

Gallardo is a submerged offshore reef in the center of the western insular platform. It does not have a reef crest. Gallardo is far from land (~ 7 nautical miles), not influenced by nutrient loads or sediments. Water visibility generally exceeded 10 m during this study. It has an *Acropora palmata* zone at approximately 5 m depth. This reef is exposed most of the time to strong wave energy and currents.

CHAPTER 2 : HERBIVORE EXCLUSION

Scleractinian corals are slow growing organisms that provide the primary framework structure for coral reefs (Lesser, 2004). During the last three decades many coral reefs have suffered a phase shift towards domination by fleshy algae (Carpenter, 1990; Done, 1992; Hughes, 1994; McClanahan *et al.,* 1999a; McCook, 1999; Shulman and Robertson, 1996; Tanner, 1995). Various factors, such as reduced herbivory, water eutrophication, hurricanes and diseases, are frequently stated in the literature as responsible for this phase shift (Hughes, 1994; Jackson, 2001; Lesser, 2004; Tomascik and Sander, 1987; Williams and Bunkley-Williams, 1990, 2000). These changes could be reversed depending on the amount of damage and cause that provoked them (Done, 1992).

One of the major factors contributing to this phase shift toward more macroalgae on the reef was the die-off of the herbivorous echinoid *Diadema antillarum*. Studies performed before and after the die-off, manipulating the abundance of this echinoid, suggested that their grazing activity was the principal control of the macroalgae growth (Carpenter, 1981; McClanahan *et al.,* 2000; Sammarco *et al.,* 1974). An increment in abundance of herbivorous fish was observed in some areas after the *D. antillarum* die-off (Carpenter, 1985b; Hay, 1984; Hay and Taylor, 1985; McClanahan *et al.,* 1996; Robertson, 1991). This was attributed to food limitation or competition for food resources between sea urchins and fish (Robertson, 1991). In some areas, the increment in herbivorous fish was related to a decrease in macroalgae cover (Edmunds and Carpenter, 2001; Littler and Littler, 1997). However, in other reefs the increment in herbivorous fish was not observed (Hughes *et al.,* 1987). Another study has reported a negative relation between herbivorous fish and macroalgae abundance (McClanahan *et al.,* 1999b).

The way reef organisms interact could vary with location. The purpose of this experiment was to evaluate the effect of herbivore absence over algal growth in reefs off the southwest coast of Puerto Rico; thus assessing herbivore impact on algae cover in the reef.

2.1 Methodology

Exclusion cages of 0.5 m x 0.5 m x 0.25 m dimensions were built using 1/2" steel rods for the frame, and 1/4” wire mesh to cover the sides and door (Figure 2.1). Cages were placed on the sea floor, considering the cage dimension and the reef relief, so there was no space between the cage and the sea bottom. Each cage was held in place by fastening it with cable ties to four steel rods driven into the substratum. The door on the top was secured to the sides with cable ties after each survey. Three exclusion cages were placed per depth and site (Table 1.1).

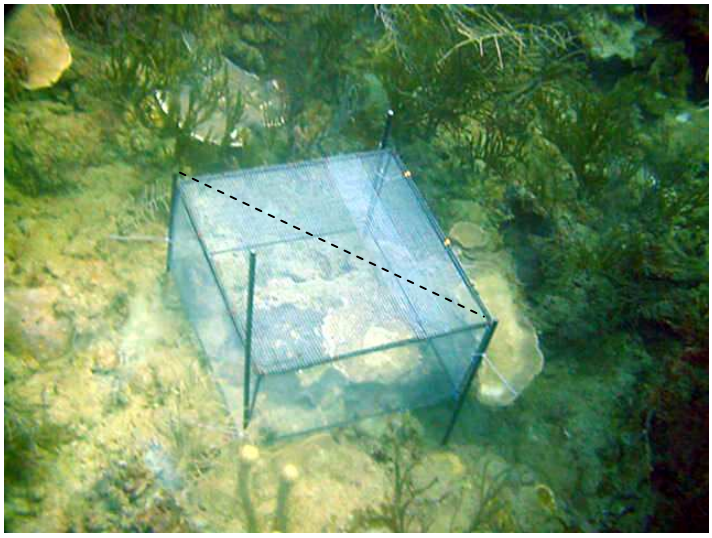

Figure 2.1 Example of an exclusion cage with a line showing the location where the measuring tape was placed once the cage door was opened.

To survey the area inside the cage, the door was opened by cutting the cable ties, and a measuring tape was laid diagonally from corner to corner over the top of the cage (Figure 2.1). Data on substrate type every 5 cm were collected. Categories used for substrate type were: sand, gorgonian, rubble, hard coral, macroalgae, sponge, bare substrate, turf, coralline algae, cyanobacteria, and zoanthids.

Initial baseline surveys were conducted immediately after placing each exclusion cage. Once the baseline data were collected, all algae were carefully removed with wire brushes, avoiding living coral and other invertebrates, following the same procedures of McClanahan *et al.* (1999b). Subsequent surveys were conducted three and six moths after the algae removal. The cages were cleaned on each visit, using scrubbing brushes to avoid reduction of light penetration or water flow due to organisms growing on the cage (Thacker *et al.,* 2001).

Control areas were used to consider the effect of natural variations. Three control areas (no algal removal or herbivore exclusion) of 0.5 m x 0.5 m were established per depth and site, and delimited by steel rods driven into the substratum at each corner. Monitoring of the control areas was done at the same time as the exclusion cage surveys, using the same methodology.

Percent substrate cover data were tabulated for each substrate type. Since the data were not normally distributed because of the small sample size, Kruskal-Wallis nonparametric tests were used for statistical analysis (Lyman, 1993). Data from the exclusion cages and the control areas were analyzed separately. Differences between sites, for each algae substrate type within a particular time period, were analyzed by creating a matrix of interactions and conducting the statistical analysis for each interaction. The same was done to test for differences between depths within each particular time period. Changes over time on percent substrate cover were analyzed within a particular depth. Finally, statistically significant changes on percent substrate cover inside the exclusion cages were compared with changes observed at the control areas.

2.2 Results

Appendix 1 shows the matrix of statistical analysis results generated to test differences between sites in percent algae cover, at 5 m depth, inside exclusion cages. Appendix 2 shows

the matrix of statistical analysis results generated to test differences between sites in percent algae cover, at 10 m depth, inside exclusion cages. Differences between sites for percent algae cover were not statistically significant. The data from Gallardo were included with the data collected at 10 m, although the depth of this study site was 20 m, given that the data were found to be similar to the data from other sites at 10 m depth. Appendix 3 shows the matrix of statistical analysis results to test differences between depths, 5 and 10 m, in percent algae cover inside the exclusion cages. Statistically significant differences with depth were observed for turf ($p<0.01$ at time period 1), coralline algae ($p< 0.05$ at time period 2), and cyanobacteria ($p<0.01$ at time period 2). Based on these results the percent algae cover data inside the exclusion cages were analyzed considering depth and changes with time.

Appendix 4 shows the statistical results for comparisons of percent cover by algal category inside the exclusion cages between time periods at 5 and 10 m depth. At 5 m depth, statistically significant differences were found on percent cover of coralline algae ($p< 0.01$ between time period 1 and 2; $p< 0.05$ between time period 2 and 3), turf ($p< 0.01$ between time period 1 and 2) and cyanobacteria ($p< 0.001$ between time period 2 and 3). Coralline algae cover increased after three months, but decreased after six months. Turf cover decreased after three months and remained low. Cyanobacteria cover increased with time, at three months and six months after algal removal. Macroalgae cover showed no statistically significant changes. Table 2.1 summarizes the average percent cover values for alga categories, at 5 m depth. Figure 2.2 represents the variations with time on percent cover by algal category at 5 m depth inside the exclusion cages.

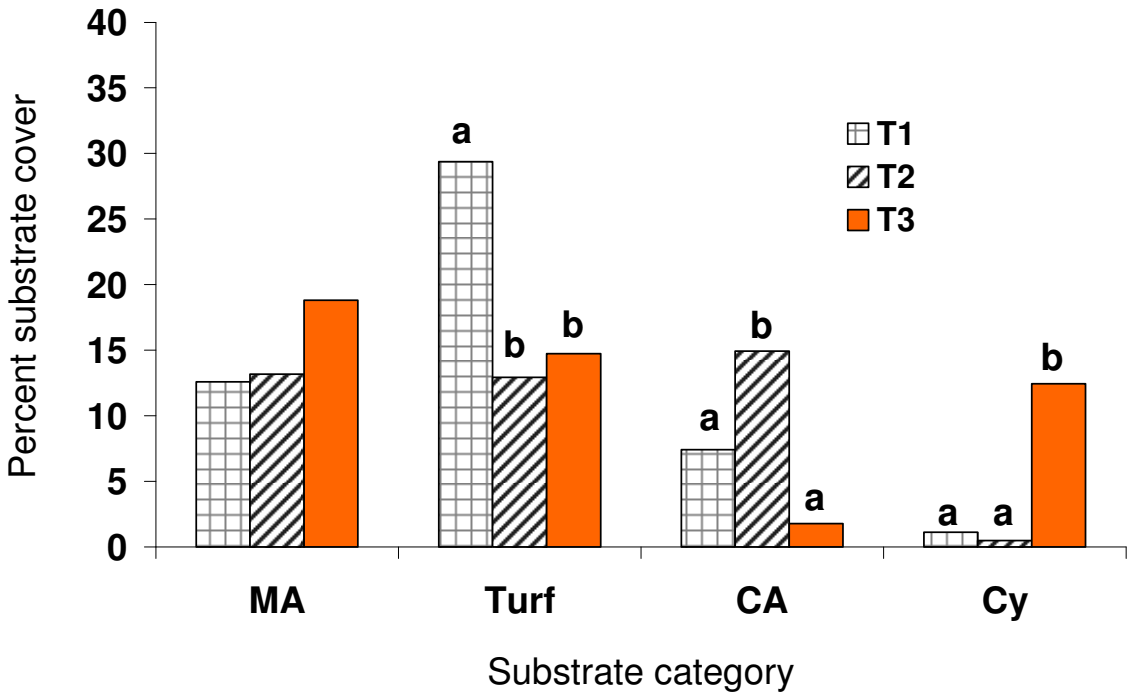

Figure 2.2 Variations of percent cover by algal category in exclusion cages at 5 m.
MA= Macroalgae CA= Coralline algae Cy= Cyanobacteria
T1- Baseline data T2- Three months after algal removal
T3- Six months after algal removal
Small letters indicate statistically significant difference within a category.

Table 2.1 Percent substrate cover inside the exclusion cages at 5 m depth.

Time period	Macroalgae	Turf	Coralline algae	Cyanobacteria
Before algal removal	12.59	36.71	7.42	1.11
Three months after algal removal	13.17	12.94	14.93	0.48
Six months after algal removal	18.81	14.74	1.78	12.46

At 10 m depth statistically significant differences were found on percent cover of macroalgae ($p < 0.05$ between time period 1 and 2) and cyanobacteria ($p < 0.01$ between time period 1 and 2) inside the exclusion cages. Macroalgae cover increased after three months, but started to decrease after six months. Cyanobacteria cover increased throughout the length of the study period. After the algal removal, turf and coralline algae cover showed no statistically significant changes. Table 2.2 shows the average percent cover values for algal categories at 10 m depth. Figure 2.3 shows the variations with time on percent cover by algal category at 10 m depth inside the exclusion cages.

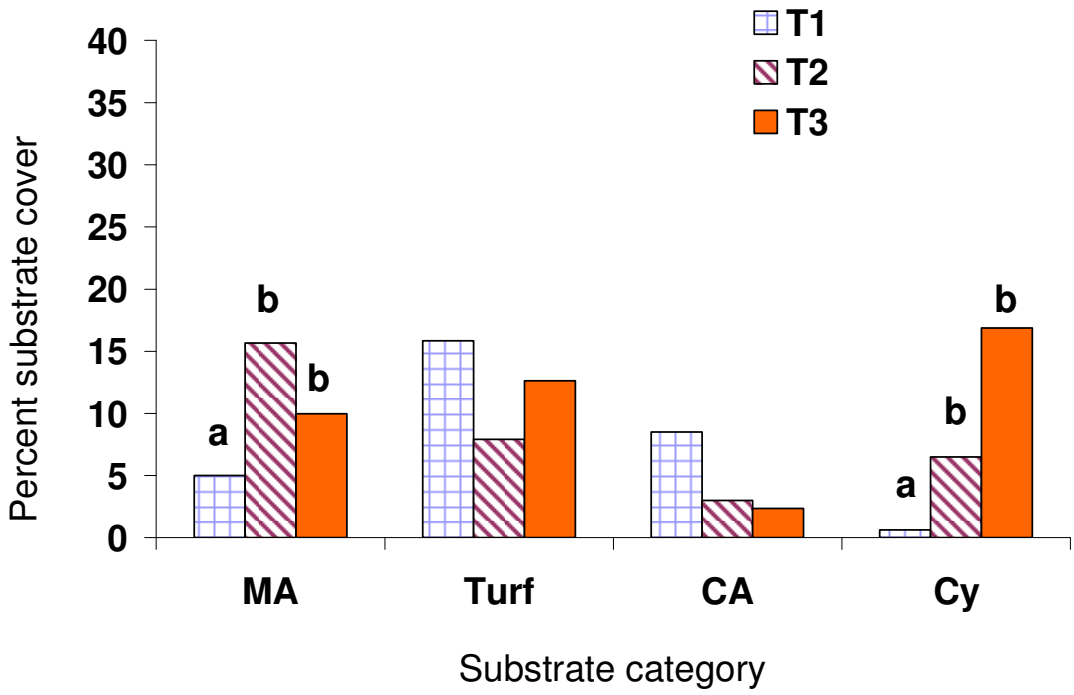

Figure 2.3 Variations of percent cover by algal category in exclusion cages at 10 m.
MA= Macroalgae CA= Coralline algae Cy= Cyanobacteria
T1- Baseline data T2- Three months after algal removal
T3- Six months after algal removal
Small letters indicate statistically significant difference within a category.

Table 2.2 Percent substrate cover inside the exclusion cages at 10 m depth.

Time period	Macroalgae	Turf	Coralline algae	Cyanobacteria
Before algal removal	0.64	0.78	0.71	0.52
Three months after algal removal	0.87	0.71	0.58	0.68
Six months after algal removal	0.74	0.78	0.56	0.82

Appendix 4 shows the statistical results for comparisons of percent cover by algal category in the control areas between time periods at 5 and 10 m depth. Although there were fluctuations on percent cover by algal category at 5 m depth, no statistically significant differences were observed (Figure 2.4). At 10 m depth, statistically significant changes were observed in the control areas for coralline algae ($p < 0.05$) and cyanobacteria ($p < 0.01$) percent cover between time period 1 and 2 (Figure 2.5).

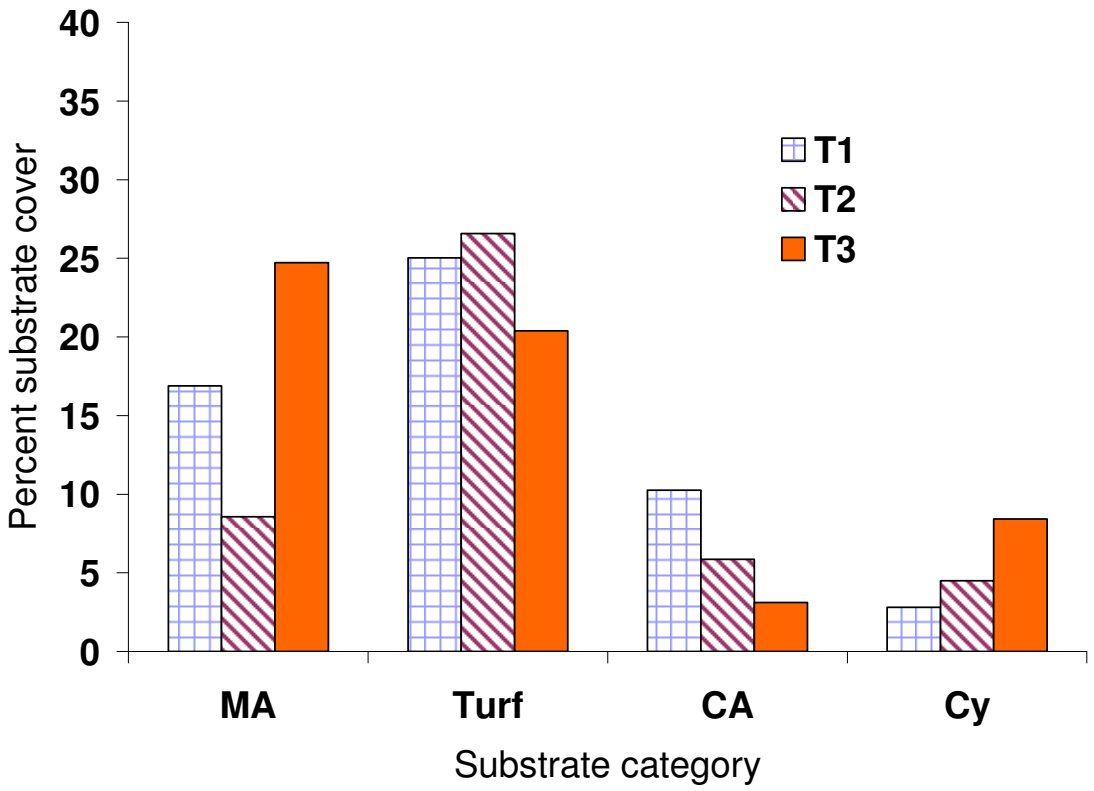

Figure 2.4 Variations of percent cover by algal category in the control areas at 5 m.
MA= Macroalgae CA= Coralline algae Cy= Cyanobacteria
T1- Baseline data T2- Three months after algal removal
T3- Six months after algal removal

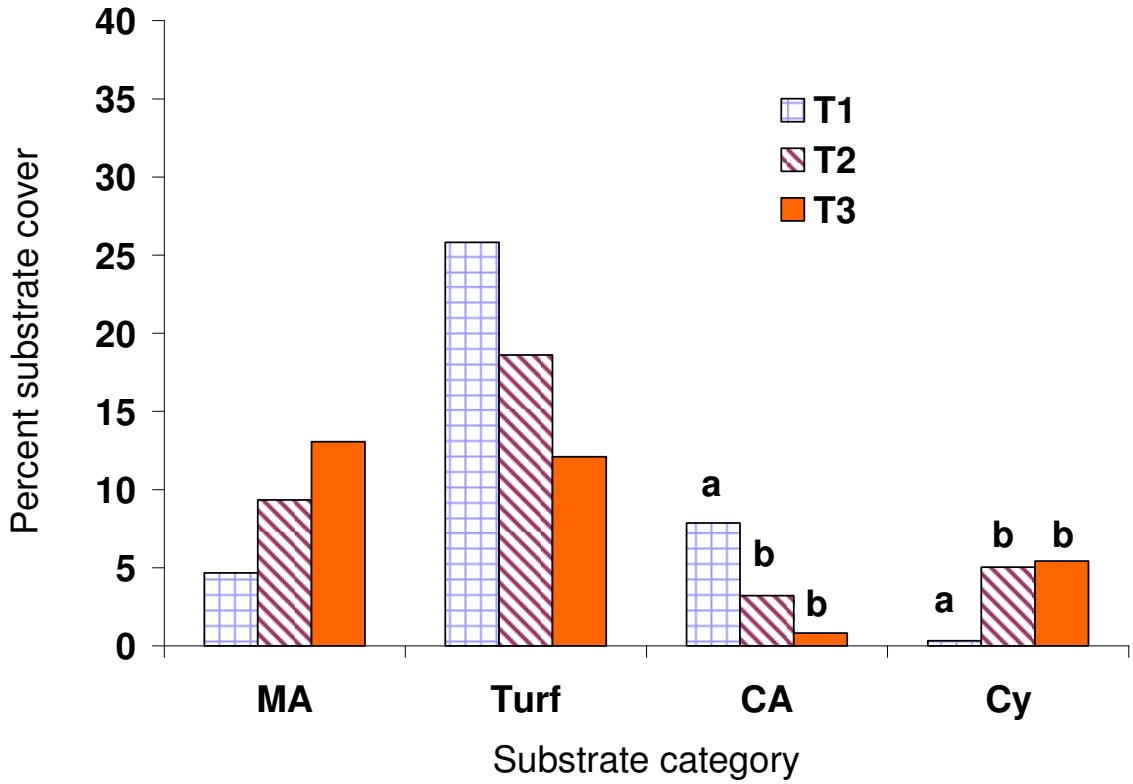

Figure 2.5 Variations of percent cover by algal category in the control areas at 10 m.
MA= Macroalgae CA= Coralline algae Cy= Cyanobacteria
T1- Baseline data T2- Three months after algal removal
T3- Six months after algal removal
Small letters indicate statistically significant difference within a category.

2.3 Discussion

Algae and coral competition for light and space is one of the possible factors influencing coral reef phase shift (Coles, 1988; Costa *et al.,* 2002; Díaz-Pulido and McCook, 2002; Lirman, 2001; McCook *et al.,* 2001; Tanner, 1995). Competition could occur between algae and coral and between different algae species (Díaz-Pulido and McCook, 2004; McCook, 2001). The result from the competition between algae and coral is affected by physical conditions like water nutrients and light availability (Carpenter and Williams, 1993; McCook *et al.,* 2001). It is also affected by biological characteristics like size, form, structure and reproduction mechanisms of both coral and algal species (Lirman, 2001, McCook *et al.,* 2001; Mumby *et al.,* 2005). It has been reported that the turf growth form is not affected by eutrophication and competes for space with corals, although it could not displace them (McCook, 2001). The results from the competition between macroalgae and coral depend on the species involved, both of coral and algae (Lirman, 2001).

The replacement of corals by algae has been suggested to occur after the coral has been subjected to some sort of stress or is dead (Díaz-Pulido and McCook, 2004). During this study, no visible stress was found in the coral colonies, which could be attributed to the experimental manipulation. Thus, increases in algal cover were not related to competition between coral and algae.

Macroalgae, cyanobacteria, and turf have the potential to inhibit coral recruitment (Birrell *et al.,* 2005; Fabricius *et al.,* 2005; Kuffner and Paul, 2004; Kuffner *et al.,* 2006). These are the main components of modern reefs (Done, 1992; Hughes, 1994; McCook, 1999; McClanahan *et al.,* 1999a; Shulman and Robertson, 1996). Still, the available information or evidence of coral

recruitment inhibition is limited, not conclusive or not applicable to all scenarios. It does point out the important role or influences that algal interactions have on coral reefs.

No statistically significant changes were observed in the control areas at 5 m depth. For that reason, the variations observed inside the exclusion cage expeiments were attributed to competition between algae species under no grazing pressure. The initial increase in coralline algae was related to the decrease in turf. This could indicate that coralline algae are limited by space at this depth. The presence of coralline algae has been negatively related to sedimentation (Fabricius and De'ath, 2001; Harrington *et al.,* 2005; McClanahan, 1997). It has been documented that turf smothers coralline algae with the sediment that it traps (Purcell, 2000; Steneck, 1997).

The lack of significant changes in macroalgae cover at 5 m depth, between control and exclusion cages, suggests that herbivores have low impact over macroalgae cover at this depth. The increment in coralline algae after three months supports this argument. The manual removal of algae created the effect of an area subjected to high grazing, which has been documented to promote coralline algae growth (Belliveau and Paul, 2002; Littler and Littler, 1997; Steneck, 1997). In addition, other studies have reported a decrease in grazing activity in shallow areas due to wave stress (Foster, 1987; Korpinen, 2008)

The increase in macroalgae cover at 10 m depth suggests that grazing pressure could be exerting control over macroalgae growth at this depth. Other studies report similar results using exclusion cages (Carpenter, 1981; 1986; Hixon and Brostoff, 1996; Lewis, 1986; Sammarco, 1983). Notwithstanding, another possibility is that algae interspecific competition at this depth is at a stage in which disturbances, like the manual algal removal, give grounds for the dominant species, in this case macroalgae, to take over the available space.

Nitrogen fixation by cyanobacteria has been identified as one of the nutrient sources that support algae high productivity (Adey and Goertemiller, 1987; Adey and Steneck, 1985). While it has been proposed that coralline algae prevail in areas with high nutrient concentration (Littler and Littler, 1984), results of experiments controlling water nutrient concentration suggest otherwise (Belliveau and Paul, 2002). The negative relation between coralline algae and cyanobacteria observed at 5 and 10 m depth in this study could be caused by the nutrient enrichment created by the increase in cyanobacteria. This supports the argument that coralline algae are negatively affected by high nutrient concentrations, contradicting the relative dominance model proposed by Littler and Littler (1984).

Since the decrease in coralline algae was observed at all depths in control areas and exclusion cages, another possible explanation is that some factor, other than the experimental manipulation, affected its cover. The increase in cyanobacteria inside the cages could then be attributed to a decrease in water flow with time, as the wire mesh was covered with fouling organisms despite the cleaning efforts.

In conclusion, the interspecific competition among algae species seems to be the driving force in the reef dynamic. Turf and macroalgae dominate the southwestern reefs of Puerto Rico. Coralline algae cover is limited or negatively affected by turf and cyanobacteria coverage.

The results could be indicating that grazing pressure is higher at 10 m depth than at 5 m depth, implying that herbivores might be controlling macroalgae cover at this depth. Further studies on herbivore density or grazing frequency are needed to address this topic. Additional studies looking closely at algal succession and growth rate would be valuable to corroborate these results and evaluate the effects of other variables, like nutrients and turbidity. Of particular

importance is to study turf species composition and how it could vary under different grazing pressures.

CHAPTER 3: ALGAE REMOVAL

Reef transition from a coral-dominated to an algae-dominated one could be the result of population dynamics, with changes in species composition and abundance as it faces environmental changes, (McCook *et al*., 1997). As plants in terrestrial ecosystems, algae undergo succession on a reef, and are affected by abundance of grazers (Belliveau and Paul, 2002; Connell, 1978; McClanahan *et al.,* 2002). Information on algae succession provides information on grazing and other factors operating reef dynamics.

The dynamics of herbivores and algae have been studied in various localities under different settings, obtaining an array of results. In the Belizean barrier reef, the exclusion of herbivores promoted increases of macroalgae, which displaced turf and coralline algae (Lewis, 1986); and the removal of macroalgae increased herbivore numbers (McClanahan *et al.,* 2000). Also in Belize, herbivorous fish excluded macroalgae in areas of high coral cove,r but not in areas of low coral cover (Williams *et al.,* 2001). In Hawaii, grazing by parrotfish and surgeonfish promoted cyanobacteria growth; and macroalgae replaced turf under conditions of no grazing (Hixon and Brostoff, 1996). In Guam, herbivore presence arrested algal succession in the early stages (Belliveau and Paul, 2002). In Kenya calcareous macroalgae and crustose coralline algae were observed in grazed areas (McClanahan, 1997).

Nutrients and sedimentation also affect reef dynamics. Turf has been reported as the dominant algal group in eutrophic waters or areas subject to high sedimentation (McClanahan, 1997). Coralline algae cover is affected by sedimentation (Fabricius and De'ath, 2001; Harrington *et al.,* 2005; McClanahan, 1997). Macroalgae can also dominate eutrophic areas (Costa *et al.,* 2000; Smith *et al.,* 2001). Light attenuation due to sedimentation or limited water movement is another physical factor determining algae distribution (Van den Hoek *et al.,* 1978).

Some studies have proposed interaction models to predict reef composition under different conditions (Hackney *et al.,* 1989; McClanahan, 1997; Mumby, 2006). Models use parameters based on the acquired knowledge about the organisms' interactions; and how their predictions fit with observations. It is clear that there are many species on a reef. With greater knowledge on the interaction between the species under different circumstances, inductively or by direct experimentation, a better model could be achieved. The following experiment provides information on reef outcome once algae are removed.

3.1 Methodology

Five quadrats (1 x 1 m) were established at 5 and 10 m depth in each site (Table 1.1) (Figure 3.1). Quadrat location was identified with steel rods driven into the sea floor at two opposite corners of the quadrat and identified with flagging tape.

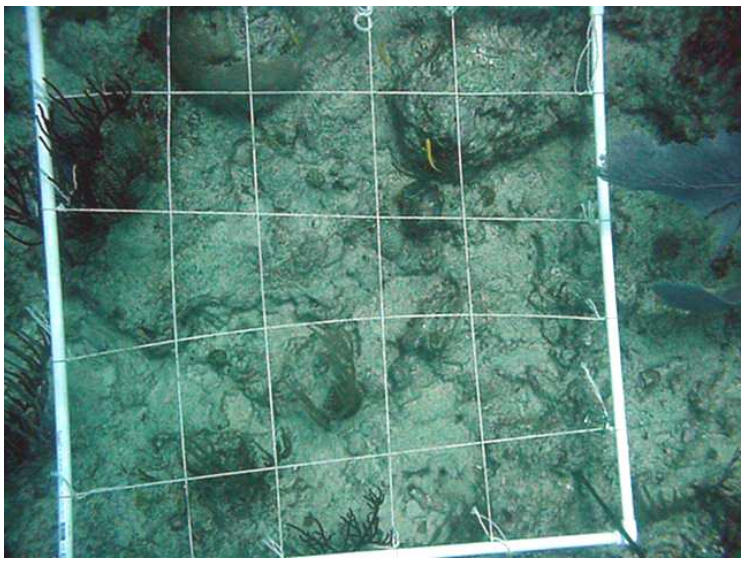

Figure 3.1 Example of a quadrat used to obtain data on substrate cover.

The quadrat had crossing strings, making 36 reference points. To survey the quadrat, substrate type under each reference point was noted (English *et al.*, 1997).

During the first visit, baseline data were collected from all the quadrats. Once the baseline data were collected, all the algae in the quadrat were carefully removed with wire brushes, avoiding living coral and other invertebrates (McClanahan *et al.,* 1999b). Subsequent

monitoring surveys were conducted three months and six moths after the algae removal. Observed algae were classified as macroalgae, turf, or cyanobacteria. Macroalgae present were identified to genus.

Data on percent substrate cover by category were analyzed considering depth (5 m and 10 m) and location (inshore, mid-shelf, and offshore) (Table 1.1). Since the data have small sample size, a nonparametric analysis, Kruskal-Wallis test, was used (Lyman, 1993).

The relative abundance for each alga genus was tabulated to make comparisons among them. The Simpson's Diversity Index was used to analyze changes in macroalgae species diversity by location and depth (Deshmukh, 1986). The results were analyzed using the Kruskal-Wallis test for differences by sites and depth. The equation used for the index was the following:

$$D=1- \{[\sum_{i=1}^{S} n_i (n_i -1)]/[N(N-1)]\}$$

S= Number of macroalgae species

n= Percent cover of a species

N= Total percent of algae cover

3.2 Results

The genera of algae found in the quadrats before and after the algal removal were: *Caulerpa*, *Dictyota*, *Halimeda*, *Penicillus*, *Valonia*, *Udotea*, *Lobophora*, *Hypnea*, and *Laurencia*. The last four were found only at 10 m depth. Appendix 7 shows the relative abundance results by location, depth, and time. The macroalgae most frequently found in the quadrats were *Dictyota* and *Halimeda*. Appendix 7 shows the Simpson's Diversity index values. No statistically significant differences were found in macroalgae species diversity among locations or depth. The time length between surveys was too long for an accurate assessment on algae

succession. Macroalgae, coralline algae, and turf were already settled and erect after the first three month period.

Differences in response to algal removal were found with depth and location (inshore, mid-shelf, and offshore). Appendix 8 shows the results for the statistical analysis. At 5 m depth cyanobacteria cover increased significantly in inshore reefs ($p < 0.001$) but not in mid-shelf reefs (Figures 3.2 and 3.3). A statistically significant increase in macroalgae cover ($p < 0.05$) was observed for inshore reefs (Figure 3.2). A pronounced decline in coralline algae was also observed, but it was not statistically significant. At mid-shelf turf cover showed a decreasing tendency, although not statistically significant (Figure 3.3).

Coralline algae and cyanobacteria cover decreased significantly at 10 m depth in inshore reefs ($p < 0.05$ for coralline algae cover; $p < 0.0001$ for cyanobacteria cover) (Figure 3.4). In mid-shelf reefs, there was a statistically significant increase in macroalgae cover ($p < 0.05$) and a decrease in turf cover ($p < 0.01$) (Figure 3.5). In the offshore reefs, macroalgae cover increased significantly while turf cover decreased ($p < 0.01$ for macroalgae cover; $p < 0.01$ for turf cover) (Figure 3.6). There was a tendency of coralline algae cover to decrease, although it was not statistically significant (Figure 3.6).

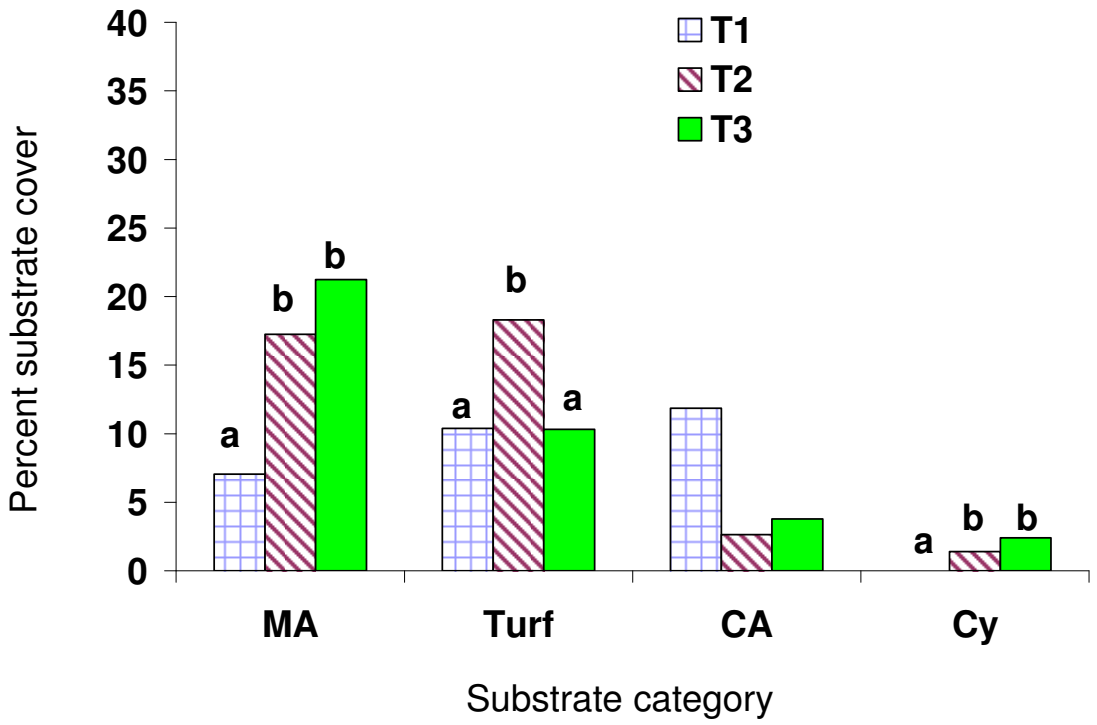

Figure 3.2 Variations in percent substrate cover by algal category at 5 m depth in inshore reefs. T1: Initial survey; T2: Survey after three months; T3: Survey after six months. Small letters indicate statistically significant difference within a category.

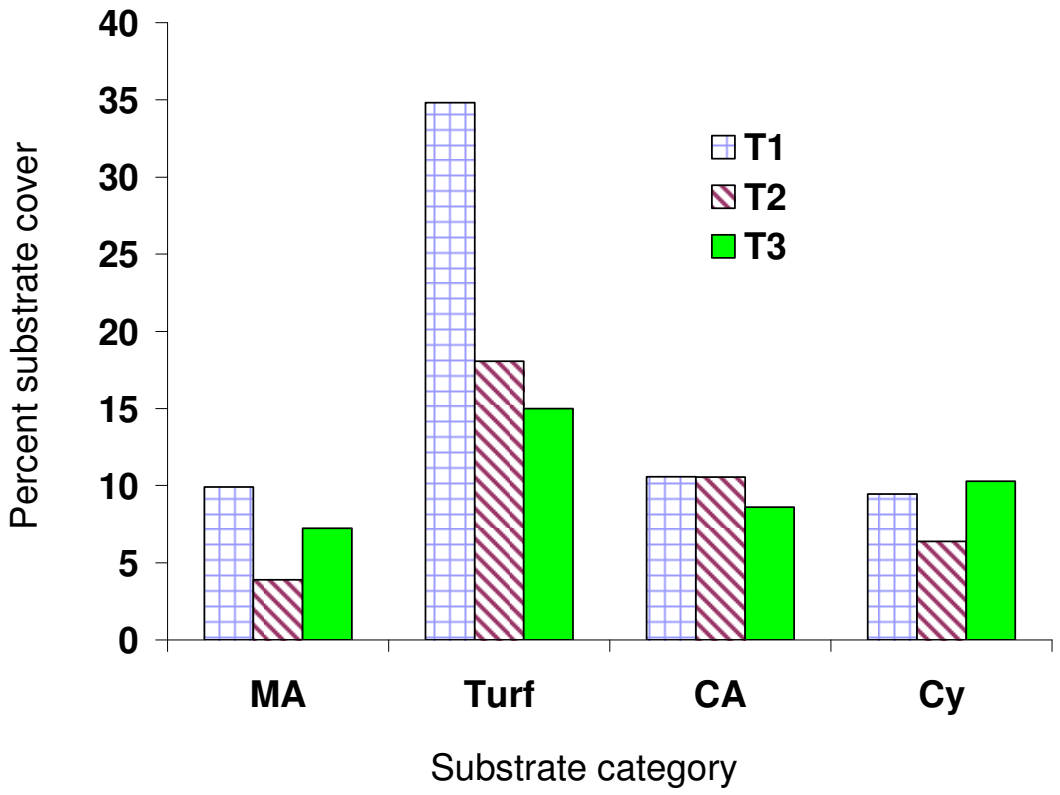

Figure 3.3 Variations in percent substrate cover by algal category at 5 m depth in mid-shelf reefs. T1: Initial survey; T2: Survey after three months; T3: Survey after six months.

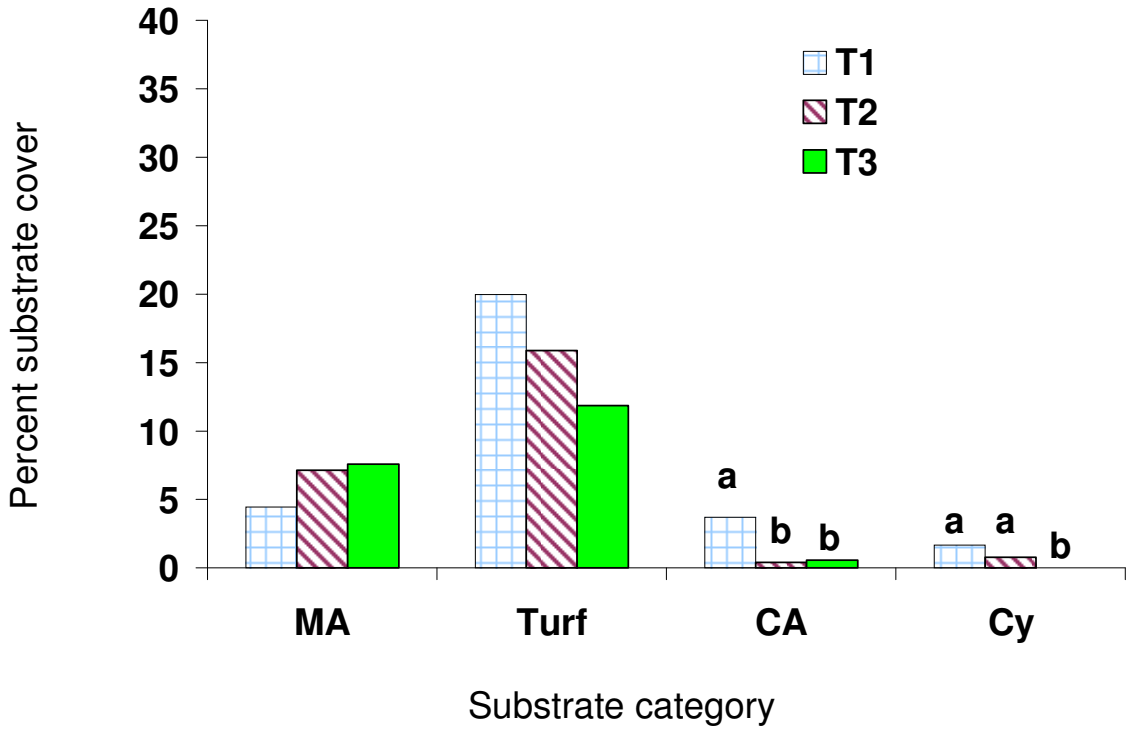

Figure 3.4 Variations in percent substrate cover by algal category at 10 m depth in inshore reefs. T1: Initial survey; T2: Survey after three months; T3: Survey after six months. Small letters indicate statistically significant difference within a category.

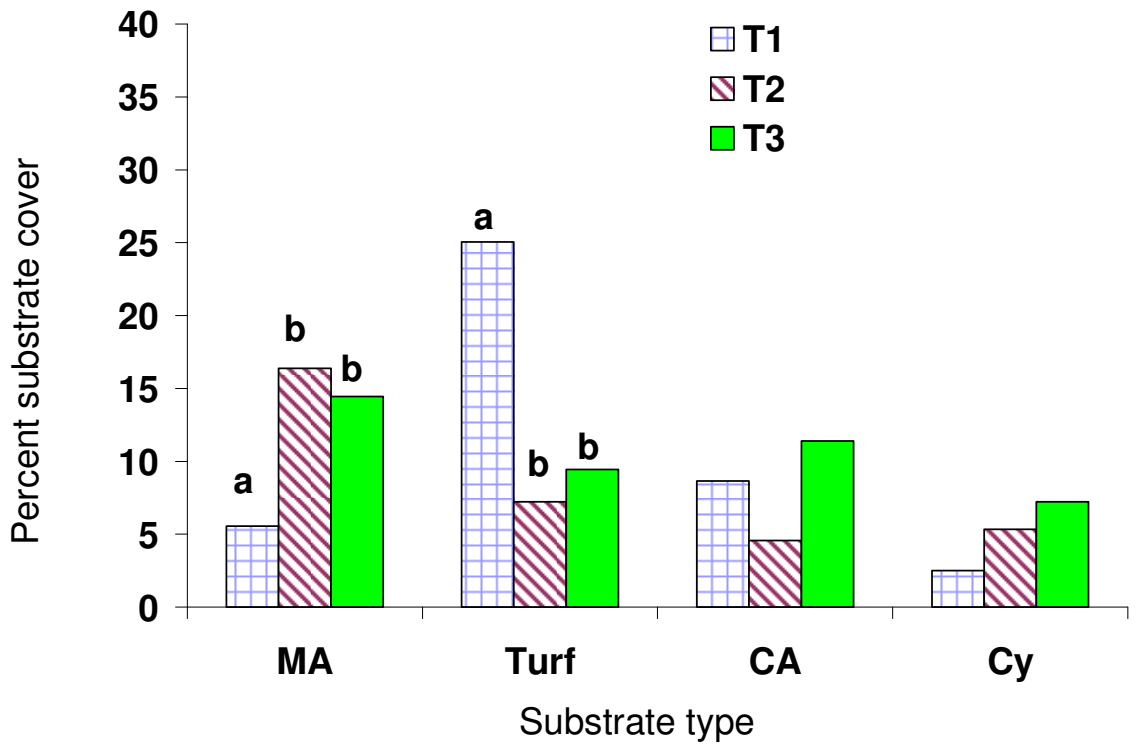

Figure 3.5 Variations in percent substrate cover by algal category at 10 m depth in mid-shelf reefs.
T1: Initial survey; T2: Survey after three months; T3: Survey after six months.
Small letters indicate statistically significant difference within a category.

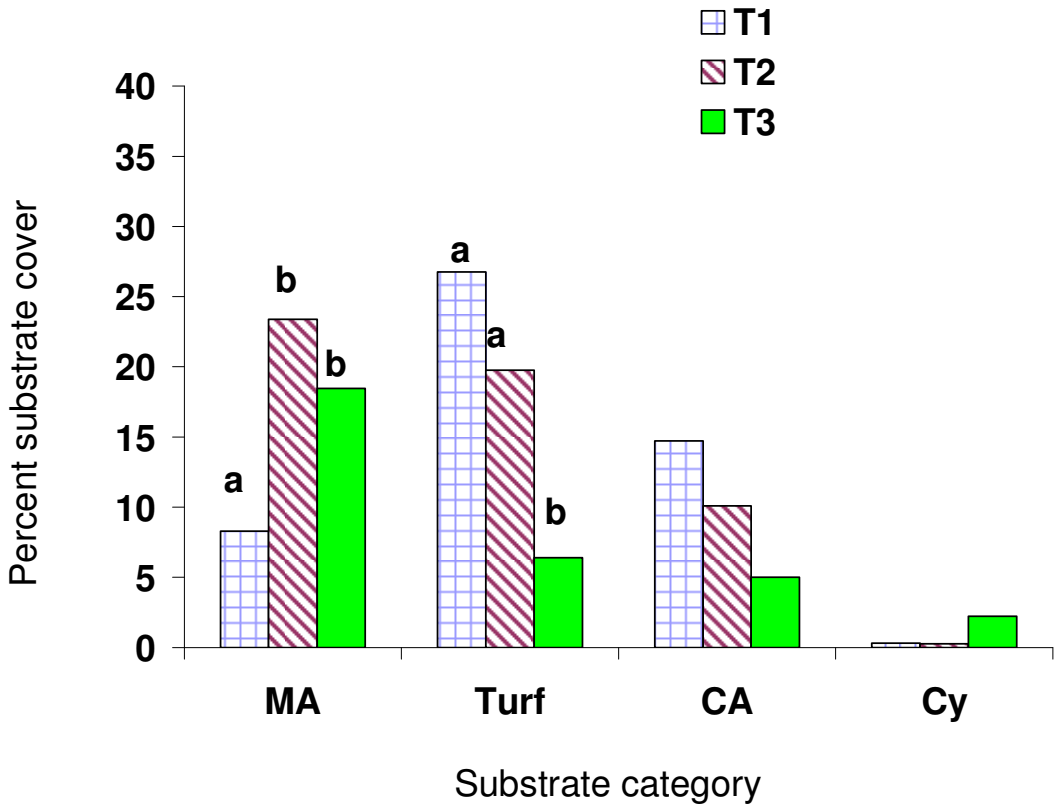

Figure 3.6 Variations in percent substrate cover by algal category at 10 m depth in the offshore reefs.
T1: Initial survey; T2: Survey after three months; T3: Survey after six months.
Small letters indicate statistically significant difference within a category.

3.3 Discussion

The most abundant alga in the quadrats was turf. It was present in 92% of the quadrats. Turf is the major coral reef primary producer (Adey and Goertemiller, 1987; Morrissey, 1985). Production is maintained despite high light intensities and exposure to ultraviolet radiation (Carpenter, 1985a; 1986). This growth form is energetically expensive, but has a better survivor strategy since it looses less biomass when predated upon (Hay, 1981; Lewis, 1986). Turf standing crop is determined by the grazing activity (Carpenter, 1985a). Grazing on the apical portions promotes greater branching of the algae. It has a tendency to decrease from sheltered to highly exposed areas (Crossman *et al.,* 2001). Its structure and morphology also makes it more resistant to physical forces. It has been suggested that the principal grazers of turf are sea urchins (Carpenter, 1981). Notwithstanding, it has been observed dominating areas where *Diadema* was abundant (Carpenter, 1990), which would indicate that *Diadema* were not responsible for controlling that type of algal growth. Macroalgae could have a negative effect on turf development because of the abrasion (Cheroske *et al.,* 2000).

The second alga most frequently found was the genus *Halimeda*. It was present in 43% of the quadrats and showed the highest relative abundance. This calcareous alga is very resistant to grazing. Its caloric value is low because of its inner calcification that makes it hard to digest and decreases the energetic return for the herbivores (Littler *et al.,* 1983). This genus also has a chemical defense against grazers, which makes it highly resistant to sea urchin and fish grazing (Littler *et al.,* 1983). Sammarco (1974) reports that, under low herbivore abundance, *Halimeda* decreases while other algae become more abundant. If the conclusions of that study still hold true, it could be an indicator that herbivore abundance is high in the reefs included in this study.

Another macroalga that was frequently found in the study sites was the genus *Dictyota*. It was present in 36 % of the quadrats. It has been reported to contain secondary metabolites that

deter fish grazing (Littler *et al*., 1983). However, in a study conducted by Littler *et al.* (1983), the genus showed low resistance to sea urchin herbivory.

Cyanobacteria were found in 40 % of the quadrats. They have the potential to hamper coral recruitment (Kuffner *et al.,* 2006). They are known to produce secondary metabolites that deter herbivore grazing (Nagle and Paul, 1999), although this effect could be limited by fish hunger levels and previous feeding experiences (Thacker *et al*., 1997).

The macroalgae frequently found in the quadrats are considered of low palatability for grazers (Littler *et al.,* 1983). The low abundance of palatable macroalgae could suggest that grazing pressure is controlling it (Littler *et al*. 1983) or that some factors limit those algal species recruitment (McCook, 1999). The dominance of turf in the quadrats support the grazing control argument, as it has been related with high density of herbivores population that removes almost all seaweed, except those that are less palatable or physically deter grazing with other mechanisms (Hay, 1997). Turf abundance has also been associated to high grazing pressure on behalf of sea urchins (Aronson and Precht, 2000; Beneyahu and Loya, 1977; Carpenter, 1981; 1986). Since previous results indicate low herbivore grazing pressure, particularly at 5 m depth (see Chapter 2), a possible explanation is that herbivore grazing intensity is enough to keep palatable macroalgae abundance low, but not to exclude macroalgae in general (Paddack, *et al*., 2006). Studies on algal recruitment will be necessary to ascertain if the low abundance of palatable algae is related to factors other than grazing activity (McCook, 1999).

Sediments affect negatively coral and coralline algae growth (Cardona, 2008; Torres, 2001). The areas surveyed in this study are not directly influenced by sedimentation due to river run-off, but are subject to wind-driven resuspension events (Miller *et al.,* 2007). Conditions of low light intensity and high sedimentation are unfavorable for corals; diminishing their growth

rates and leaving them in disadvantage when competing with algae for space (Torres, 2001; Torres and Morelock, 2002). Coralline algae are also negatively affected by sedimentation (Fabricius and De'ath, 2001; Harrington *et al.,* 2005; McClanahan, 1997). Macroalgae and turf, however, have been positively related to sedimentation (Fabricius *et al*., 2005; Purcell, 2000), although there are still debates about the effect of sediments on macroalgae (McCook, 1999). Thus, it is probable that the increase in macroalgae cover observed at 5 m depth in inshore reefs, as well as on mid-shelf and offshore reefs at 10 m depth, respond to a temporal competitive advantage of macroalgae over turf and coralline algae under poor water conditions due to sedimentation, sediment re-suspension or light attenuation with depth (Krause-Hensen *et al*., 2009). In addition, various studies have reported that macroalgae could physically affect turf through abrasion (Cheroske *et al.,* 2000; McCook *et al*, 2001). At 10 m depth, the manual algal removal at the beginning probably opened up space for other macroalgae, like the genus *Lobophora* at the shelf-edge and *Laurencia* in Gallardo, to colonize the area. This could also imply that macroalgae at this depth outcompete the corals.

Cyanobacteria have the potential to lower coral recruitment (Kuffner and Paul, 2004; Kuffner *et al.,* 2006). It is plausible that it also has a negative effect on coralline algae under low light intensity conditions, when competing for space. This would explain the increment in cyanobacteria at 5 m depth in inshore reefs. The relation is evident from the results of the exclusion cages (see Chapter 2), but seems to be affected or altered by herbivores presence.

Various studies have documented the application of the intermediate disturbance model to the effect of herbivore grazing over algal cover in the reef (Hixon and Brostoff, 1996; Sammarco, 1980; 1983). This model predicts greater species diversity under moderate grazing disturbance. At 5 m depth on the mid-shelf reefs, after algal removal, no significant changes

were observed. This could indicate that at this location grazing pressure is enough to promote species diversity, avoiding any particular type of algae to dominate. The last statement assumes that nutrients or water conditions are not a limiting factor in algal growth. The high sea urchin density results for shallow mid-shelf reefs reported by Lugo (2004) could also support this argument. Additional studies on herbivorous fish abundance and their relation to algal cover are needed to corroborate the proposed population dynamic.

On inshore reefs at 10 m depth, there was a decrease in coralline algae and cyanobacteria. This result differed from results obtained in the other study sites, in which interspecific competition seemed to dominate reef dynamics. A study conducted at La Parguera on *D. antillarum* concluded that their density is site dependent, and that small sized urchins increased in density with depth (Lugo, 2004). One of the inshore sites used in that study, Enrique reef, showed higher densities at shallow depth than other sampled sites, which is one of the inshore reefs used in the present study. Although when Lugo's study was conducted urchin densities were low at 10 m depth, densities could have increased during the last six years. If urchin densities are considered high on this site, high sea urchin grazing could explain the observed results. The manual algae removal cropped the canopy to a size more available to be grazed upon by sea urchins, not allowing the macroalgae to increase as observed in the other areas. A similar effect was proposed for the re-establishment of *D. antillarum* in Jamaica, supported by the grazing activity of *Tripneustes ventricosus* (Haley and Solandt, 2001). Under high sea urchin grazing, coralline algae could be affected (Edmund and Carpenter, 2001; Sammarco, 1980), which would explain the observed reduction in inshore reef at 10 m depth.

Additional information on sea urchin density gradient from inshore to offshore reef is needed to evaluate the proposed dynamic for inshore reef at 10 m depth. Other studies should

address nutrient influence on algal growth, palatable algal recruitment, macroalgae interspecific competition and growth rates, and fish abundance to increase knowledge on population dynamics in these reefs.

In conclusion, algae competition for space is one of the main factors influencing reef dynamics on the southwest of Puerto Rico, and it is influenced by grazing intensity, light availability, and sedimentation. Grazing activity controls algal cover in a spatio-temporal scale, promoting species diversity at some sites. Herbivore grazing intensity controls palatable macroalgae but not unpalatable ones in the reefs of southwestern Puerto Rico. Further data on grazing activity are needed to enhance and strengthened our knowledge of reef species interactions.

CHAPTER 4: FISH ABUNDANCE AND NUTRIENTS

Some researchers report that grazing rates in coral reef systems exceeds those for other habitats (Hay, 1997). Evidently, that amount of consumption requires a certain amount of productivity to sustain it. Herbivores are thought to be the natural control for seaweed and other algal groups' growth in the reef (Hay, 1997; Ogden and Lobel, 1978). Fish populations in the tropics, especially herbivores, were thought to be abundant and diverse, promoting diversity in their prey (Hay, 1997; Littler *et al.,* 1983).

For the last two decades, most reefs have undertaken a phase-shift from coral dominated to algae dominated systems (Hughes *et al.,* 1987; Shulman and Robertson, 1996). Many have attributed this change to the *Diadema* die-off in 1983 (Carpenter, 1985b; 1990; Edmunds and Carpenter, 2001; Foster, 1987; Hay and Taylor, 1985; Vicente and Goenaga, 1984) and overfishing (Hay, 1984; Hughes *et al.,* 1987; Jackson *et al.,* 2001; McCook, 1999; Miller *et al.,* 1999; Szmant 1997). Other scientists believe that sedimentation and water nutrients increments have restructured reef community (Hatcher and Larkum, 1983; Hudson *et al.,* 1994; La Pointe, 1997; 1999; La Pointe *et al.,* 1997; McClanahan, 1997; Shulman and Robertson, 1996; Tomascik and Sander, 1987; Torres and Morelock, 2002). It has also been proposed that it is a combination of the removal of both, sea urchins and fish, which have caused this phase-shift in the reef (Hay, 1997).

The objective of this experiment was to determine fish density and abundance in the reef to relate it to the results obtained from the other experiments. This information will increase our knowledge on the interactions between herbivorous fish and algal cover.

4.1 Methodology

Fish surveys were conducted, in three different occasions, at each site and depth, following the stationary plot technique (Bohnsack and Bannerot, 1986). For the surveys, a diver swam randomly to an area of the reef, and stayed motionless close to the bottom. The diver recorded the amount of fish present in a 5 m diameter area. The procedure was done three times, at each site, during each visit, but on different locations within the reef. To survey the 5 m diameter area, the diver rotated at a steady pace recording the number of fish observed within each fish group category. The fish group categories were based on those described by McClanahan *et al*. (1999b) for the discrete group sampling:

a. Group 1→Scaridae (parrotfish), Acanthuridae (surgeonfish)
b. Group 2→Labridae (wrasses)
c. Group 3→Pomacentridae (damselfish)
d. Group 4→Pomacanthidae (angelfish), Chaetodontidae (butterflyfish), Balistidae (triggerfish)

For analysis purposes, density and relative abundance for each fish group were calculated. Relative abundance was calculated considering the total individuals observed during each survey per depth and locality. The density was tabulated using the individuals observed divided by the survey area. Fluctuations within a fish group by locality category (Table 1.1) and depth were analyzed using the Kruskal-Wallis test (Lyman, 1993).

As baseline data to nutrient levels on the reef, analyses were conducted on water collected from each site. Water samples were collected from the surface using 500 ml Nalgene bottles. The water samples were kept in a cooler with ice until delivered to the Laboratory. Water was analyzed for amounts of phosphate and nitrogen at the Oceanographic Chemistry

Laboratory of the Marine Science Department of the University of Puerto Rico. Due to funding constraints, only one sample was collected per site for reference.

4.2 Results

Appendix 9 shows the results for the statistical analysis of density for fish groups by locality and depth. Inshore reefs, at 5 m depth, showed statistically significant lower densities for all fish groups except for Group 2, than at mid-shelf reefs ($p < 0.05$ for Group 1; $p < 0.001$ for Group 3 and $p < 0.05$ for Group 4) (Figure 4.1). Group 4 was significantly lower than the other fish groups in inshore reefs ($p < 0.0001$ between Group 1 and 4; $p < 0.001$ between Group 2 and 4 and $p < 0.0001$ between Group 3 and 4); and significantly lower than Group 1 and 3 in mid-shelf reefs ($p < 0.0001$ between Group 1 and 4; and $p < 0.0001$ between Group 3 and 4). Groups 1 and 3 were significantly higher than 2 and 4 at 5 m depth in mid-shelf reefs ($p < 0.0001$ between Group 1 and 2; $p < 0.0001$ between Group 2 and 3). Table 4.1 summarizes the mean densities tabulated for each fish group at 5 m depth.

Appendix 10 shows the results for the statistical analysis of relative abundance for fish groups by locality and depth. Relative abundances for all fish groups at 5 m depth in inshore reefs were lower, although not statistically significant, than at mid-shelf reefs; except for Group 2 which showed statistical significance ($p < 0.05$) (Figure 4.2). Group 4 was significantly lower than the other fish groups in inshore reefs ($p < 0.0001$ between Group 1 and 4; $p < 0.001$ between Group 2 and 4; $p < 0.0001$ between Group 3 and 4); and significantly lower than Group 1 and 3 in mid-shelf reefs ($p < 0.0001$ between Group 1 and 4; and $p < 0.0001$ between Group 3 and 4). Groups 1 and 3 were significantly higher than 2 and 4 at 5 m depth in mid-shelf reefs ($p < 0.0001$ between Group 1 and 2; $p < 0.0001$ between Group 2 and 3).

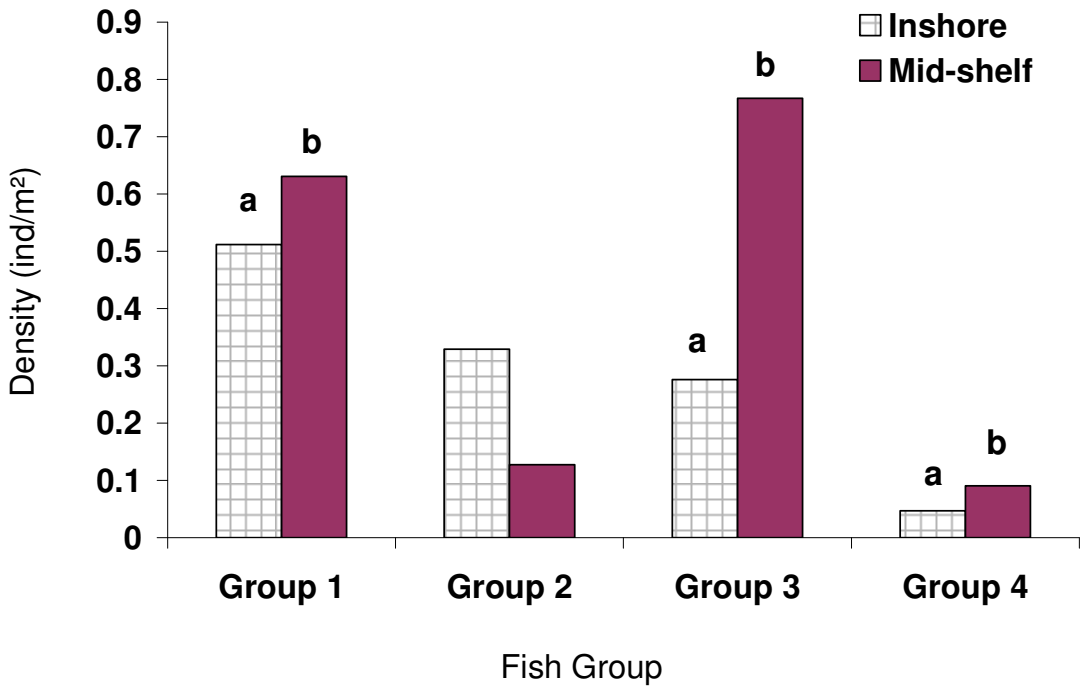

Figure 4.1 Fish group densities at 5 m depth.
Small letters indicate statistically significant difference within a category.

Table 4.1 Mean density for fish groups at 5 m depth (ind/m^2).

	Group 1	Group 2	Group 3	Group 4
In	0.48	0.33	0.28	0.05
M	0.63	0.13	0.77	0.09

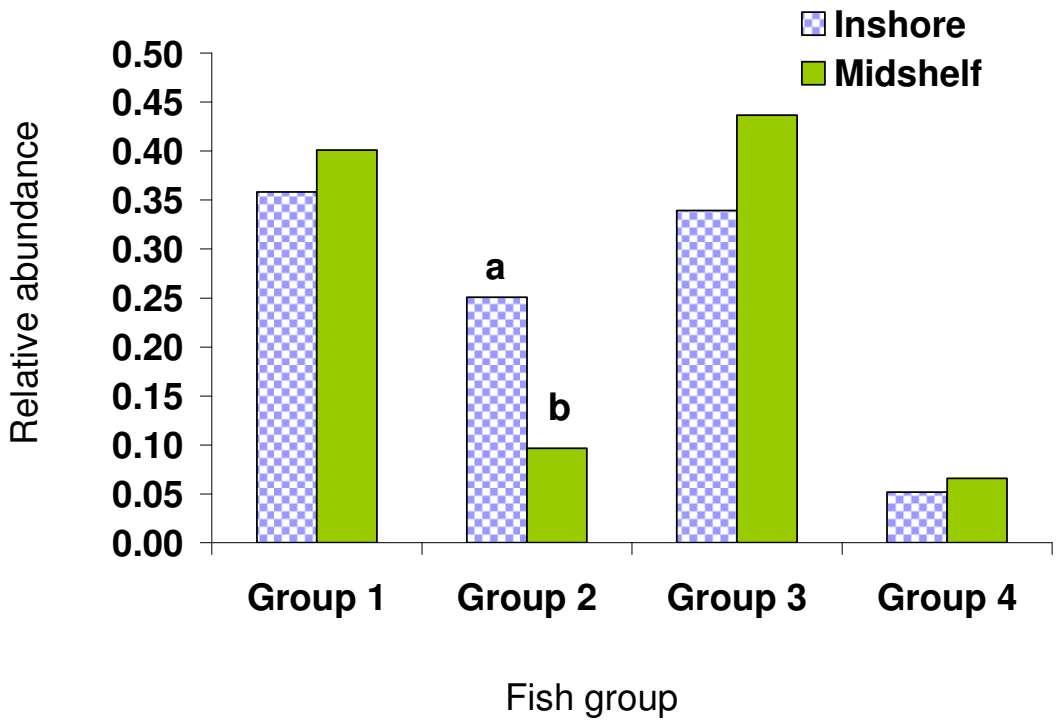

Figure 4.2 Fish group relative abundance at 5 m depth.
Small letters indicate statistically significant difference within a category.

At 10 m depth fish groups showed a pattern of increasing densities from inshore to offshore locations (Figure 4.3). The increment in density was found statistically significant for Group 1 ($p < 0.0001$). Group 1 and 3 dominated in offshore reefs according to density, but statistical significance was observed only between Group 1 and 2 ($p < 0.001$), Group 1 and 4 ($p < 0.01$), and between Group 1 and 3 ($p < 0.001$). In mid-shelf reefs Group 1 had significantly higher density than the other fish groups ($p < 0.01$ between Group 1 and 2; $p < 0.001$ between Group 1 and 3 and $p < 0.001$ between Group 1 and 4). Group 1 had the highest density in inshore reefs, but the differences were not statistically significant. Table 4.2 summarizes the mean densities tabulated for each fish group at 10 m depth.

Relative abundance did not follow the same increasing trend from inshore to offshore as density (Figure 4.4). Group 1 had significantly lower relative abundance in inshore reefs than in mid-shelf or offshore reef ($p < 0.01$ between inshore and mid-shelf reef, and $p < 0.0001$ between inshore and offshore reef). This fish group dominated, according to relative abundance, in mid-shelf ($p < 0.01$ between Group 1 and 2; $p < 0.01$ between Group 1 and 3; $p < 0.0001$ between Group 1 and 4) and offshore reefs ($p < 0.001$ between Group 1 and 2; $p < 0.001$ between Group 1 and 3; $p < 0.0001$ between Group 1 and 4).

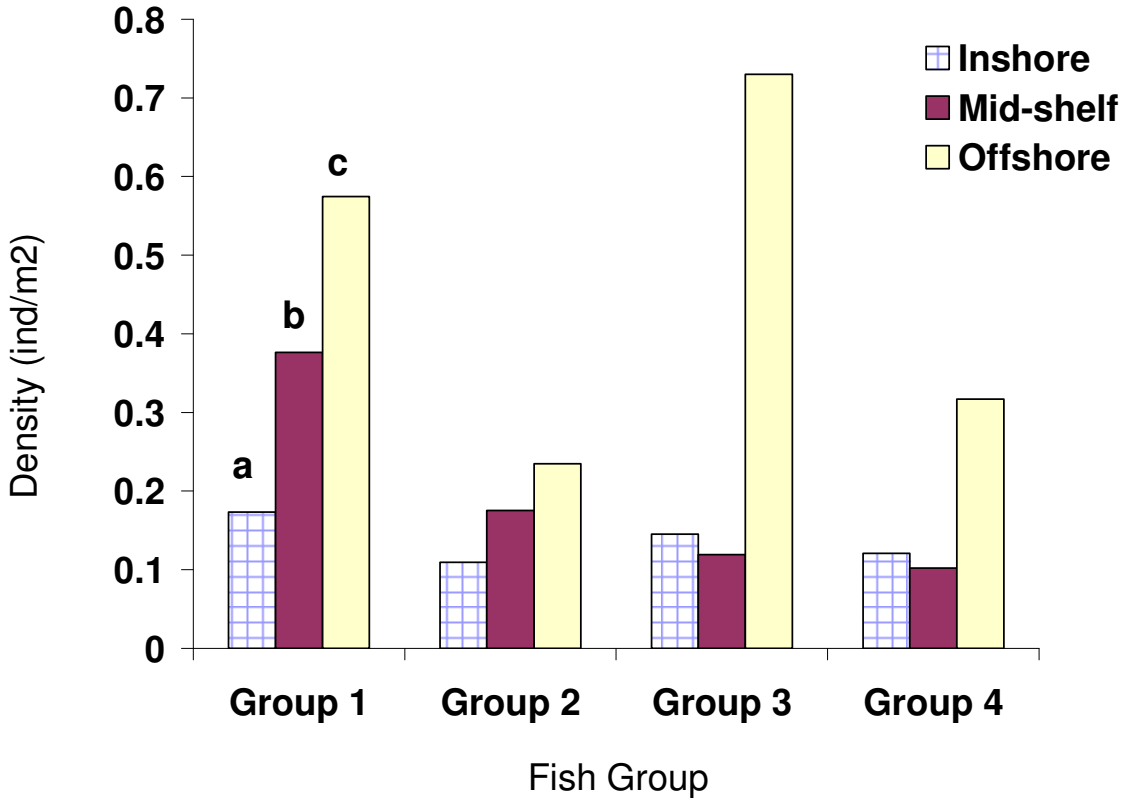

Figure 4.3 Fish group densities at 10 m depth.
Small letters indicate statistically significant difference within a category.

Table 4.2 Mean density for fish groups at 10 m depth.

	Group 1	Group 2	Group 3	Group 4
In	0.17	0.11	0.15	0.12
M	0.38	0.18	0.12	0.10
Off	0.57	0.23	0.73	0.32

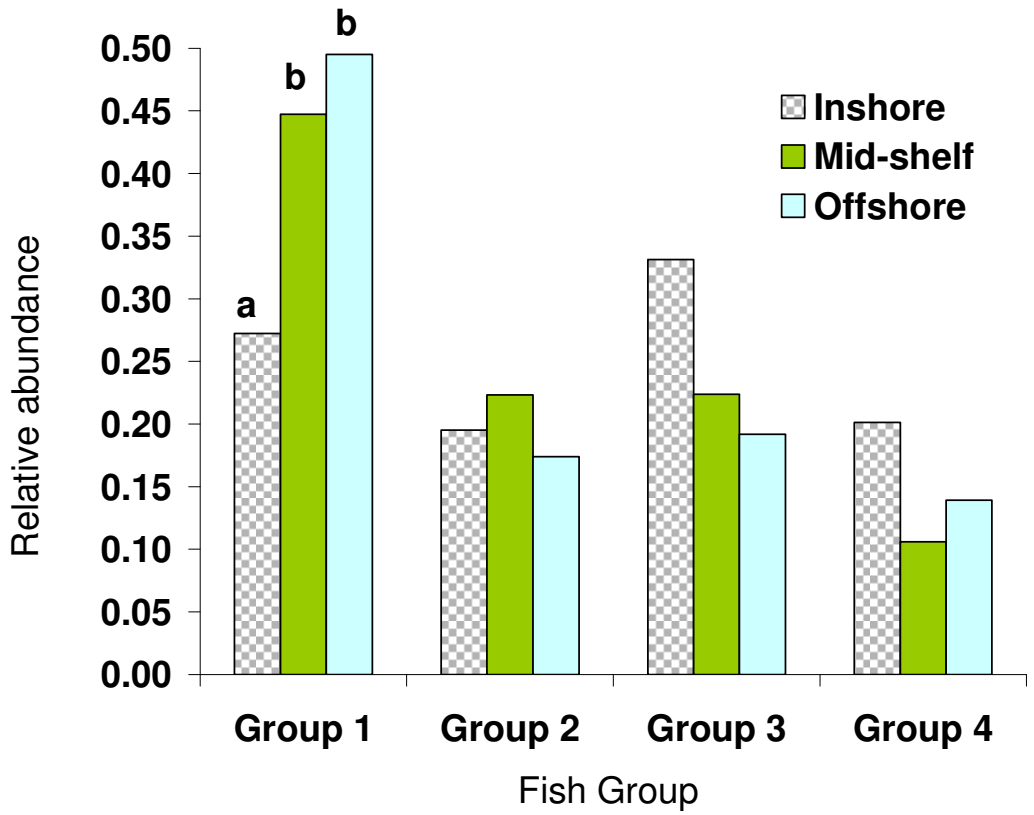

Figure 4.4 Fish group relative abundance at 10 m depth.
Small letters indicate statistically significant difference within a category.

Table 4.3 summarizes the results for nitrates and phosphates at the different sites. The average for nitrates was 0.22 µM. The average for phosphates was 0.03 µM.

Table 4.3 Water nutrient concentrations at different study sites.

Site	NO_2+NO_3 (µM)	PO_4 (µM)
Mario	0.28	0.06
Enrique	0.1	0.03
Resuello	0.18	0.03
Media Luna	0.49	0.1
Pináculos	0.17	0.02
Shelf edge	0.11	0
Gallardo	0.24	0

4.3 Discussion

Herbivores are crucial in structuring reef communities (Mumby, 2006; Ogden and Lobel, 1978). Scarids, acanthurids and sea urchins are usually recognized as the most important consumers of reef algae (Lewis, 1986; Ogden, 1976). As algae dominate coral reefs, the study of the organisms that control algae is important (Hughes *et al.,* 1987).

Sea urchins have been considered one of the key factors in reef phase shift (Hughes *et al.,* 1999). Sea urchin abundance and fishing activities have been found to influence fish abundance and diversity (McClanahan *et al.,* 1996). Parrotfish and wrasses show the greatest response to sea urchin reduction (McClanahan *et al.,* 1994). Possibly the reefs in southwest Puerto Rico are experiencing the same increase in parrotfish and wrasses as a response to sea urchin reduction, since the reported sea urchin densities for the reefs included in these experiments are still very low compared to former levels (Lugo, 2004; Weil *et al.*, 2005), and parrotfish and wrasses had the greatest relative abundance in this study. *Diadema* densities ranged from 3.0 to 13.8 in Puerto Rico before the die off and recent studies reported a range from 0 to 0.83 ind/m^2 (Lugo,

2004). The *Diadema* population is slowly recuperating, but still significantly lower than previous numbers (Lugo, 2004; Weil *et al.*, 2005).

It has been suggested that the increase in macroalgae cover on reefs suppress the abundance of fish as well as coral cover (McClanahan *et al.,* 1999b). Although certain fish groups are more abundant at certain localities, the data do not indicate that fish species richness is affected by algae composition. In this study, macroalgae was not the main component of algae cover, and based on the baseline data, the macroalgae cover had the same trend as fish density. Similar conclusions have been reported in other studies (Chabanet *et al.,* 1997; Foster, 1987; McClanahan *et al.,* 2001; Sano, 2001) showing that the relationship between fish assemblage and macroalgae cover is weak.

Reefs near the coast are exposed to higher sedimentation due to terrestrial run-offs. Fish density results show a general increase from inshore to offshore sites, within a particular depth. Similar results of a negative relation between turbidity and fish density was reported by Bejarano (2006). The inverse was observed with depth, with higher densities at 5 m depth than at 10 m depth. As mentioned before, in this study macroalgae and turf cover followed the same pattern as fish density, suggesting that a combination of turbidity and light attenuation influence fish density due to the effect that these physical factors have on macroalgae growth.

Pomacentrids, acanthurids, and scarids showed the highest density and relative abundance in the studied reefs. Three species that belong to the pomacentrids, two from the acanthurids, and two from the scarids were included within the ten most abundant at these sites in an earlier study on fish assemblage conducted by Kimmel (1985): *Stegastes partitus*, *Stegastes variabilis*, *Stegastes planifrons*, *Acanthurus coerulus*, *Acanthurus chirurgus*, *Scarus iseri* and *Sparisoma viride*. Although damselfish aggressive territorial behavior and maintenance of their

algal lawn could be one of the factors for the general low grazing activity observed (Hinds, 1984; Sammarco, 1983).

The highest density for scarids and acanthurids was in shallow mid-shelf reefs. This result, in addition with the high sea urchin density reported by Lugo (2004) for these sites, indicate that the prevailing grazing pressure exerted by scarids, acanthurids, and sea urchins promote species diversity as predicted by the intermediate disturbance model. This support other researchers that have concluded that sea urchins or herbivorous fish alone could not support high coral cover, but an intermediate grazing pressure by both (Paddack, 2006; Sammarco, 1980; Williams and Polunin, 2001).

The lowest density of herbivorous fish was observed at 10 m depth in inshore reefs. A negative relation between sea urchin and herbivorous fishes has been reported in other areas (Carreiro-Silva and McClanahan, 2001a; McClanahan *et al.,* 1994; 1996; McClanahan and Shafir, 1990). Although establishing sea urchin density was not within the scope of this study, sea urchin grazing was used as a possible explanation for the results from the experiment on algal removal at this site (inshore, 10 m depth). *Diadema antillarum* densities vary between sites (Lugo, 2004), so it would be interesting to verify how its density has change with time at these sites.

The differences between fish groups at all depths within a particular locality indicate that fish distribution within a reef is not homogeneous. Fish distribution varied with depth and for some species, distance from land (Aguilar-Perera, 2004; Lewis and Wainwright, 1985). For scarids, a differential shift in relative abundance towards the outer shelf has been reported previously (Cerveny, 2006). The data obtained in this study support that conclusion. Density and abundance of scarids and acanthurids increased in an inshore-offshore gradient.

The presence of various algae species has been related to herbivore abundance. High herbivore abundance has been related to a decrease in *Halimeda*, while other algae, like *Dictyota*, become more abundant (Sammarco *et al*., 1974). Algal turf has been reported to dominate under moderate to high macrograzing pressure (Hackney *et al.,* 1989). Both, *Halimeda* and *Dictyota*, were the most abundant macroalgae found in the present study. Turf dominated the algae groups observed. Judging from the algae species present and previous studies, it could be inferred that grazing is in a moderate state in southwest reefs of Puerto Rico.

Another factor to consider when analyzing algae and coral dynamics in a reef, is water nutrients (Koop *et al*., 2001; McClanahan *et al.,* 1999; Shulman and Robertson 1996). They could be a major factor causing increase productivity and standing crop of macroalgae (La Pointe, 1997). Macroalgae are limited by nutrients in Jamaica and Florida (La Pointe, 1997). This restricts its ability to compete with corals and algal turf under low nutrient environments (La Pointe, 1997).

Although some studies have concluded that nutrient enrichment has no impact on algal growth (Miller *et al.,* 1999; Thacker *et al.,* 2001), other authors have established nutrient thresholds for algae overgrowth to occur at 1.0 µM for dissolved inorganic nitrogen, and 0.1-0.2 µM for soluble reactive phosphorus (La Pointe, 1999). Under normal nitrogen levels (nitrite and nitrate 0.2µm), turf production rates are in the order of 14g $m^{-2}d^{-1}$ (Adey and Goertemiller, 1987).

Nitrogen fixed by cyanobacteria is a possible important nutrient source maintaining turf high productivity (Adey and Steneck, 1985). The nutrient cycle is enhanced by nutrient flux created by trade winds and cyanobacteria nitrogen fixation (Adey and Goertemiller, 1987).

The water analysis results are below the threshold levels identified in the literature (McCook, 1999). Although there are debates on whether an increase in water nutrients is responsible for the observed reef phase shift, nutrient levels in the studied reefs are too low to be of importance. The reefs may be exposed to short pulsations of higher nutrient flux related to weather or rain, which were not detected by this study.

In Puerto Rico, fecal pollution has been observed in some offshore reefs (Bonkosky *et al*., 2008). It has been suggested that due to the lack of mechanisms to depurate nitrogen and phosphate, the reef systems are not nutrient-limited, thus promoting algae proliferation (Corredor *et al*., 1999). The administration of fertilizers to algae has been reported to promote an increase in algal biomass (Hillebrand *et al*., 2002). For algae to grow, it needs high rates of nutrient advection or access to benthic sources (Larned, 1998). Nutrients should not be underestimated as an important factor in reef dynamics. A study in the Great Barrier Reef concluded that, although an increase in water nutrients could degrade the reef, it would not lead to a phase shift unless coupled with a decrease in herbivory (McCook, 1999).

Reefs in southwest Puerto Rico were not observed to be suffering from great increases in macroalgae cover. Turf, the grazer resistant algal growth form, was the dominant algal type. Interspecific competition was found to be one of the main factors in these reefs population dynamics, with grazing controlling algal cover only in a spatio-temporal scale.

The information obtained with this study gave insight on the interaction of various reef components, on the reefs off southwestern Puerto Rico; establishing the main forces in the population dynamics and the scale at which they operate. There is still much to discover and decipher about species interactions. One of the aspects that need more attention is coral recruitment. Coral survival rates in the Caribbean have decreased in the last decades (Hughes

and Tanner, 2000). Notwithstanding, higher coral recruitment has been reported in areas where grazing by sea urchins has increased and substrate freed from macroalgae (Edmunds and Carpenter, 2001). In Puerto Rico little is known about trends in coral recruitment, so remains unknown if the coral reef phase shift is due to low coral recruitment rates or other factors (Irizarry, 2006).

To manage and protect reef ecosystems it is extremely important to learn how reef species interact and the effect that abiotic factors have on them. Knowing that global climate change is a present threat, we can promote reef resilience through decreasing reef stressors. This can only be achieved through a thorough understanding of reef natural fluctuations and population dynamics.

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APPENDICES

Appendix 1. Statistical analysis to test differences between sites in algae percent substrate covers inside the exclusion cages at 5 m depth.

		Macroalgae				Coralline algae				Turf				Cyanobacteria			
Time period	Station	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
T1	1	N/A	0.82	0.26	0.81	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	2		N/A	N/A	N/A		N/A	N/A	N/A		0.27	0.05	0.26		N/A	N/A	N/A
	3			0.81	0.51			0.27	0.12			0.34	0.50			N/A	N/A
	4				0.50				0.24				0.05				N/A
T2	1	N/A	0.36	0.05	0.50	N/A	0.79	0.26	0.05	0.50	0.26	0.26	N/A	N/A	N/A	N/A	N/A
	2		N/A	N/A	N/A		N/A	N/A	N/A		0.12	0.34	0.50		N/A	N/A	N/A
	3			0.04	0.24			0.50	0.05			0.82	0.26			N/A	N/A
	4				0.50				0.05				0.26				N/A
T3	1	N/A	0.51	0.82	0.50	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	2		N/A	N/A	N/A		N/A	N/A	N/A		N/A	N/A	N/A		0.82	N/A	0.12
	3			0.12	0.05			0.34	N/A			0.51	0.48			N/A	0.07
	4				0.50				N/A				0.36			N/A	N/A

Station 1- Mario
Station 2- Enrique
Station 3- Media Luna
Site 4- Pináculos
Site 5- Resuellos

N/A- No analysis possible because of data limitations

T1- Baseline data
T2- Three months after algae removal
T3- Six months after algae removal

Appendix 2. Statistical analysis to test differences between sites in algae percent substrate covers inside the exclusion cages at 10 m depth.

Time period		Macroalgae						Coralline algae						Turf						Cyanobacteria					
	Station	2	3	4	5	6	7	2	3	4	5	6	7	2	3	4	5	6	7	2	3	4	5	6	7
T1	1	N/A	0.81	0.81	0.81	0.79	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.50	0.50	0.26	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	2		N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A
	3			N/A	0.65	0.48	N/A			0.05	0.05	0.05	0.05			N/A	N/A	N/A	N/A			N/A	N/A	N/A	N/A
	4				0.63	0.23	N/A				0.24	0.24	,24				0.26	0.82	N/A				N/A	N/A	N/A
	5					0.48	N/A					0.79	0.79					0.27	N/A					N/A	N/A
	6						N/A						0.79						N/A						N/A
T2	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.79	0.79	N/A	0.51	0.79	0.81	N/A	0.50	0.79	N/A	0.50	0.26	0.04	0.79	0.79	N/A	N/A
	2		0.12	0.12	0.05	N/A	0.81		N/A	N/A	N/A	N/A	N/A		N/A	0.81	0.48	0.76	0.27		0.26	0.50	0.09	N/A	N/A
	3			0.82	0.51	0.24	0.10			N/A	N/A	N/A	N/A			N/A	N/A	N/A	N/A			0.50	.05	N/A	N/A
	4				0.65	0.24	0.26				N/A	0.81	0.81				0.36	N/A	0.12				0.79	N/A	N/A
	5					0.08	0.05					N/A	N/A					0.51	0.12					N/A	N/A
	6						0.76						0.79						0.56						N/A
T3	1	0.81	N/A	N/A	0.50	N/A	N/A	N/A	N/A	N/A	N/A	0.07	N/A	N/A	0.12	N/A	0.79	N/A	0.23	0.26	0.81	N/A	0.79	N/A	0.50
	2		0.81	N/A	0.50	N/A	0.81		N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A		0.07	N/A	0.05	N/A	0.12
	3			N/A	0.36	N/A	0.82			N/A	N/A	N/A	N/A			N/A	0.12	N/A	0.26			N/A	0.24	N/A	0.82
	4				N/A	N/A	N/A				N/A	N/A	N/A				N/A	N/A	N/A				N/A	N/A	N/A
	5					N/A	0.63					N/A	N/A					N/A	0.45					N/A	0.09
	6						N/A						N/A						N/A						N/A

Station 1- Mario
Station 2- Enrique
Station 3- Media Luna
Site 4- Pináculos
Site 5- Resuellos
Site 6- Gallardo
Site 7- Shelf edge
N/A- No analysis possible because of data limitations

T1- Baseline data
T2- Three months after algae removal
T3- Six months after algae removal

Appendix 3. Statistical analysis to test differences between depths, 5 and 10 m, in algae percent substrate covers inside the exclusion cages.

	Time period		
Substrate type	**T1**	**T2**	**T3**
Macroalgae	0.08	0.79	0.34
Turf	0.009	0.34	0.76
Coralline algae	0.53	0.04	0.91
Cyanobacteria	0.68	0.01	0.8

T1- Baseline data T2- Three months after algae removal T3- Six months after algae removal

Appendix 4. Statistical results for comparisons of percent cover by algal category between time periods.

EXCLUSION CAGES

5 m	T1/T2	T2/T3	10 m	T1/T2	T2/T3
Macroalgae	0.980	0.670	Macroalgae	0.040	0.380
Turf	0.006	0.760	Turf	0.600	0.800
Coralline algae	0.009	0.020	Coralline algae	0.310	0.590
Cyanobacteria	0.820	0.003	Cyanobacteria	0.002	0.260

CONTROL AREAS

5 m	T1/T2	T2/T3	10 m	T1/T2	T2/T3
Macroalgae	0.600	0.140	Macroalgae	0.270	0.310
Turf	0.890	0.500	Turf	0.610	0.060
Coralline algae	0.210	0.330	Coralline algae	0.030	0.900
Cyanobacteria	0.570	0.490	Cyanobacteria	0.010	0.580

T1- Baseline data T2- Three months after algae removal T3- Six months after algae removal

Appendix 5. Statistical analysis to test differences between sites in algae percent substrate covers in the control areas at 5 m depth.

		Macroalgae				Coralline algae				Turf				Cyanobacteria			
Time period	Station	9	10	11	12	9	10	11	12	9	10	11	12	9	10	11	12
T1	8	0.48	0.82	0.48	0.51	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	9		0.48	0.79	0.05		0.26	0.10	0.81		N/A	N/A	N/A		0.06	N/A	N/A
	10			0.48	0.51			0.51	0.12			0.51	0.82			N/A	N/A
	11				0.26				0.12				0.51				N/A
T2	8	0.24	0.82	N/A	0.05	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	9		0.24	N/A	0.05		N/A	N/A	N/A		0.12	0.08	0.65		N/A	N/A	N/A
	10			N/A	0.05			N/A	0.26			N/A	0.27			N/A	N/A
	11				N/A				0.08				0.08				N/A
T3	8	0.07	N/A	0.17	0.37	N/A	N/A	N/A	N/A	0.63	0.48	0.05	N/A	N/A	N/A	N/A	N/A
	9		0.07	0.79	0.05		N/A	N/A	N/A		0.65	0.05	0.63		0.48	N/A	N/A
	10			0.12	0.27			N/A	N/A			0.27	0.48			N/A	0.48
	11				0.05				0.63				0.05				N/A

Station 8- Mario
Station 9- Enrique
Station 10- Media Luna
Site 11- Pináculos
Site 12- Resuellos

N/A- No analysis possible because of data limitations

T1- Baseline data
T2- Three months after algae removal
T3- Six months after algae removal

Appendix 6. Statistical analysis to test differences between sites in percent substrate covers by algal category in the control areas at 10 m depth.

Time period		MA						CA						T						Cy					
	Station	9	10	11	12	13	14	9	10	11	12	13	14	9	10	11	12	13	14	9	10	11	12	13	14
T1	8	0.8	0.55	0.23	0.43	N/A	N/A	0.37	0.56	0.76	N/A	0.07	0.76	N/A	N/A	0.65	0.82	N/A	0.48	N/A	N/A	N/A	N/A	N/A	N/A
	9		0.26	0.82	0.51	0.51	N/A		0.51	0.37	0.51	0.26	0.37		N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A
	10			0.26	0.26	0.26	N/A			0.12	0.51	0.05	0.05			N/A	0.36	N/A	0.23			0.27	N/A	0.05	N/A
	11				0.51	0.51	N/A				0.51	0.05	0.37				N/A	N/A	0.34				N/A	0.24	N/A
	12					0.82	N/A					0.05	0.18					N/A	0.24					N/A	N/A
	13						N/A						0.05						N/A						N/A
T2	8	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.1	0.5	0.05	0.50	0.24	N/A	0.23	0.23	N/A	0.23	N/A	N/A
	9		0.05	0.24	0.24	0.51	0.24		N/A	N/A	N/A	N/A	N/A		0.12	0.27	0.05	0.56	0.51		0.36	N/A	N/A	N/A	N/A
	10			0.12	0.51	0.08	0.07			N/A	N/A	N/A	N/A			0.05	0.50	0.07	0.48			N/A	0.36	N/A	N/A
	11				0.50	0.37	0.65				N/A	N/A	N/A				0.05	N/A	0.27				N/A	N/A	N/A
	12					0.37	0.37					N/A	N/A					0.07	0.82					N/A	N/A
	13						0.76						N/A						0.24						N/A
T3	8	0.5	N/A	N/A	N/A	N/A	0.76	N/A	N/A	N/A	N/A	N/A	N/A	0.76	0.55	N/A	0.23	0.43	0.76	N/A	N/A	N/A	N/A	N/A	N/A
	9		0.12	N/A	0.36	N/A	0.45		N/A	N/A	N/A	N/A	0.79		0.81	N/A	0.48	0.37	N/A		0.79	N/A	0.24	N/A	N/A
	10			N/A	0.18	N/A	0.26			N/A	N/A	N/A	N/A			N/A	0.79	0.55	0.81			N/A	0.81	N/A	N/A
	11				N/A	N/A	N/A				N/A	N/A	N/A				N/A	N/A	N/A				N/A	N/A	N/A
	12					0.32	0.81					N/A	N/A					0.12	0.34		.			N/A	N/A
	13						N/A						N/A						0.37						N/A

Station 8- Mario
Station 9- Enrique
Station 10- Media Luna

Site 11- Pináculos
Site 12- Resuellos
Site 13-Gallardo

Site 14- Shelf edge
N/A- No analysis possible because of data limitations

T1- Baseline data

T2- Three months after algae removal

T3- Six months after algae removal

Appendix 7. Relative abundance for the genera of algae observed in the quadrats.

	Inshore 5 m			**Mid-shelf 5 m**			**Inshore 10 m**			**Mid-shelf 10 m**			**Offshore 10 m**		
Alga genera	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**
Halimeda	0.14	0.20	0.20	0.06	0.00	0.02	0.14	0.28	0.33	0.29	0.12	0.13	0.00	0.00	0.02
Dictyota	0.20	0.18	0.29	0.00	0.00	0.13	0.00	0.00	0.00	0.08	0.36	0.21	0.00	0.09	0.33
Udotea	0.00	0.20	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Penicilus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caulerpa	0.00	0.03	0.16	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lobophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.23
Laurencia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Hypnea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00

Simpson's Diversity Index

Site	**T1**	**T2**	**T3**
Inshore 5 m	0.98	0.93	0.88
Mid-shelf 5 m	1.00	1.00	0.98
Inshore 10 m	0.98	0.92	0.89
Mid-shelf 10 m	0.99	0.86	0.94
Offshore 10 m	1.00	0.95	0.86

T1- Baseline data T2- Three months after algae removal T3- Six months after algae removal

Appendix 8. Statistical results for comparisons of percent cover by algal category between time periods.

Depth	Location	Substrate category			
	Inshore	**Macroalgae**	**Turf**	**Coralline algae**	**Cyanobacteria**
5 M	T1/T2	0.04	0.06	0.07	.0008
	T2/T3	0.55	0.04	0.49	0.12
	Mid-shelf				
	T1/T2	0.17	0.11	0.41	0.79
	T2/T3	0.24	0.3	0.77	0.07
10 M	**Inshore**				
	T1/T2	0.79	0.55	0.02	0.24
	T2/T3	0.81	0.32	0.62	.00004
	Mid-shelf				
	T1/T2	0.03	0.003	0.17	0.36
	T2/T3	n	0.7	0.22	0.84
	Offshore				
	T1/T2	0.01	0.93	0.26	0.93
	T2/T3	0.42	0.01	0.24	0.94

T1- Baseline data T2- Three months after algae removal T3- Six months after algae removal

Appendix 9. Statistical results for comparisons of density by fish groups between locality and depth.

Inshore 5 m	Group 2	Group 3	Group 4
Group 1	0.31	0.52	0.000003
Group 2		0.62	0.001
Group 3			0.000003

Mid-shelf 5 m	Group 2	Group 3	Group 4
Group 1	0.00003	0.96	0.000006
Group 2		0.000007	0.53
Group 3			7.70E-07

Inshore 10 m	Group 2	Group 3	Group 4
Group 1	0.12	0.98	0.48
Group 2		0.05	0.27
Group 3			0.4

Mid-shelf 10 m	Group 2	Group 3	Group 4
Group 1	0.01	0.001	0.004
Group 2		0.38	0.13
Group 3			0.51

Offshore 10	Group 2	Group 3	Group 4
Group 1	0.006	0.001	0.002
Group 2		0.78	0.74
Group 3			0.73

Appendix 10. Statistical results for comparisons of relative abundance by fish groups between locality and depth.

Inshore 5 m	Group 2	Group 3	Group 4
Group 1	0.09	0.60	8.76E-7
Group 2		.28	.0009
Group 3			0.00001

Mid-shelf 5 m	Group 2	Group 3	Group 4
Group 1	0.000001	N/A	0.000005
Group 2		0.000005	0.48
Group 3			9.22E-07

Inshore 10 m	Group 2	Group 3	Group 4
Group 1	0.22	0.34	0.34
Group 2		0.02	0.52
Group 3			0.1

Mid-shelf 10 m	Group 2	Group 3	Group 4
Group 1	0.007	0.01	0.0001
Group 2		0.65	0.06
Group 3			0.21

Offshore 10	Group 2	Group 3	Group 4
Group 1	0.0003	0.001	0.00009
Group 2		0.83	0.65
Group 3			0.48