COASTAL ECOSYSTEM CONNECTIVITY:

WATERSHED MANAGEMENT, SEDIMENTATION AND THE RESPONSE OF CORAL REEFS

By

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To the memory of my father Miguel A. Otaño Rivera, and to the happiness of my adorable mother Abigail Cruz Hernández

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Abstract

Coral reefs are among the most biologically productive and economically important ecosystem on Earth. Nevertheless, unsustainable coastal development and watershed alteration have increased soil erosion and sediment influx to coastal waters and have been linked to marine habitat degradation. Sedimentation has been identified as a main local threat to coral reefs worldwide. However, there is a lack of information regarding sedimentation dynamics and the potential effects to near-shore coral reefs benthic communities. The goal of this study was to assess spatio-temporal differences in sediment dynamics and sediment characteristics as a function of changing coastal land use patterns, weather, and oceanographic conditions. Also, the benthic community structure response to sedimentation in two reef locations (Bahía Tamarindo (BTA) and Punta Soldado (PSO)) was assessed in the small semi-arid island of Culebra, Puerto Rico. Sediment traps were deployed across a distance gradient from the shore and were monthly replaced from February 2014 to April 2015. Sedimentation rate, sediment texture, and composition were analyzed by dry sieving and loss-on-ignition techniques and were contrasted with environmental variables. Permanent belt transects of $10m^2$ were assessed through high-resolution photo-quadrats by seasons from February 2014 to 2015. There were significant spatio-temporal differences in sedimentation rates over time ($p=0.0001$), and distance from shore ($p=0.0040$). At both sites, time series with increased sedimentation and terrigenous sediment rate were related to meteorological events with high rainfall and wave height. The spatial distribution of silt-clay and terrigenous sediments increased with rainfalls that exceeded 20 mm/hr, and sand resuspension was observed with wave height that exceeded 1.5m. The shallow reef areas, closer to shore were more exposed and vulnerable to sediment stress, suggesting that sediment influx had strong relationship with coastal runoff and changes in land use patterns. Coral diversity changed gradually through seasons as the reef experienced variations in sedimentation patterns. In the other hand, coral recruitment increased through seasons, even though it was lower in PSO zone B, area that received highest amount of terrigenous deposition after coastal watershed deforestation. Coral reef benthic community structure was significantly different among seasons (p=0.0020), site (p=0.0010), and distance zone (p=0.0010). Coral cover was significantly different among sites (pairwise, p=0.0010) with higher percent cover at areas less exposed to terrestrial sediment deposition. Changes in water quality due to stochastic local sediment related stressors are a major factor influencing phase shift towards reefs dominated by macroalgae communities. Sediment dynamics and near-shore coral reefs are highly impacted by rapid transformation of coastal watershed land uses, combined with changes in weather, precipitation patterns and oceanographic hydrodynamics. There is a need of integrating scientific information on the multiple and complex interactions between terrestrial and marine ecosystems that influences sedimentation dynamics and coral reefs response into management and decision-making processes. Ecosystem based management provides an holistic framework that if combined with an inclusive and participatory decision-making process could assist in the identification and implementation of effective management actions that could eliminate local stressors and achieve the conservation of coral reefs worldwide. These processes should take into account future climate scenarios and the need to strengthen coral reef resilience to guarantee human coastal communities livelihoods.

Keywords: benthic community structure, biodiversity, coral abundance, coral recruit, ecosystems interconnectivity, sediment composition, sediment texture, watershed conservation and management

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GENERAL INTRODUCTION

NEAR-SHORE CORAL REEF ECOSYSTEM RESPONSE TO ANTHROPOGENIC STRESS

Introduction

Coral reefs are recognized as the most productive and diverse ecosystem of the World since they provide essential biophysical, ecological, and socio-economic services to human coastal communities (Roberts et al., 2002; Hughes et al., 2010; Barbier et al., 2011; Wild et al., 2011). Shallow water coral reefs have high structural complexity, are mostly dominated by Scleractinian corals, that sustain vital habitats and nursery grounds to a vast amount of fish species and other marine taxa, provide protection and supply calcareous sediments to the shoreline (Bush et al., 1995; Torres and Morelock, 2002; Bellwood et al., 2004; Davidson-Arnott, 2010; Hughes et al., 2010). But coral reefs are showing rapid trends of decline across global scales. Global trends of decline have been mostly associated to a combination of cumulative and synergistic effects of natural disturbances, broad human-induced stressors and global climate change (Hernandez-Delgado et al., 2006; Wild et al., 2011; Ramos-Scharrón et al., 2012; Young et al., 2012). In the tropics, the combined effects of the variation in climatic patterns and the pressure exerted by the consistent alteration of coastal watersheds and land-based source of pollution (LBSP) has increased the vulnerability of near-shore coral reef ecosystems resulting in unprecedented shifts into alternate stable states often dominated by non-reef building taxa, and with profound permanent effects on reef ecosystem functions and services (Huges et al., 1994; Bellwood et al., 2004).

A confounding combination of regional and local stressors has greatly contributed to the variability of coral reef ecological dynamics, thus reducing the overall reef resilience and magnifying the need for urgent ecosystem-based management to prevent further decline (Mumby and Steneck, 2011; Díaz-Ortega and Hernández-

Delgado, 2014). There is still a need to develop and implement an integrated management that aims to restore the environmental conditions needed to recover coral reef ecosystem resilience and to help the reef recover from recurrent severe disturbances. But more information about the disturbance and recovery dynamics, and regarding existing connectivity between the near-shore coral reef ecosystems and its adjacent watersheds through sediment distribution is required to achieve effective conservation and restoration strategies. Therefore, this research aimed to assess spatial and temporal patterns of sedimentation dynamics along two near-shore coral reefs as a function of contrasting land use patterns and variations on meteorological and oceanographic hydrodynamics. Likewise, we also aimed to determine the role of sedimentation on shaping the benthic communities' structure and species composition.

The Caribbean region represents a marine biodiversity hotspot where regional and local threats are reaching the ecosystem tipping point (Miloslavich et al., 2010). With a mean historical net change of live coral cover loss of -20% to -40% from 1970 to 2012, reef sites with the greatest loss where identified at Karpata in Bonaire, Discovery Bay in Jamaica and Flat Cay in St. Thomas (Gardner et al., 2003; Jackson et al., 2014). Among the multiple factors that have impacted the coral reefs, the massive die off of the Caribbean sea urchin *Diadema antillarum* from a disease outbreak in 1983 with an afterward slow and diverged recovery, and a high incidence of white band disease that devastated the *Acropora* spp. populations enabled the regional decline in live coral cover (Mumby et al., 2006; Ruiz-Ramos et al., 2011; Weil and Rogers, 2011; Jackson et al., 2014). The branching coral, *Acropora* spp., used to be one of the most dominant reef-building genus in the Caribbean shallow reefs, and its loss might have reduced the overall reef resilience to further disturbances (Roff and Mumby, 2012; Young et al., 2012). Since the 1980s, events of unprecedented prolonged increase of sea surface temperature (SST), exceeding the bleaching threshold of 29.5°C, has caused recurrent wide-scale bleaching events which resulted in the expulsion of the endosymbiotic zooxanthellae algae from the coral tissue as a thermal stress response (Eakin et al., 2010; Wild et al, 2011; Jackson et al., 2014). In some regions massive bleaching has resulted in afterward mass coral mortality as the potential for incidence of diseases intensified (Wilkinson and Souter, 2008; Weil, 2009; Jackson et al., 2014). Multiple environmental stressors such as ocean acidification, increased light intensity, change in salinity and sedimentation have been identified to also trigger coral bleaching (Nemeth et al., 2001; Wild et al., 2011). The combined synergistic impacts of large-scale factors such as increased SST, massive bleaching, disease outbreaks, and hurricanes, and local factors such as overfishing of key herbivore fish populations, poor water quality, and sedimentation represent a complex combination of stressors that could substantially compromise the rate of the ecosystem recovery from disturbance (McManus and Polsenberg, 2004; Richmond, 2007). Long-term impacts on coral reefs can cause subsequent loss of reproductive success by limited interregional connectivity through larval dispersal, decline in live coral cover and reef structural complexity (Hernandez-Delgado et al., 2006; Alvarez-Filip et al., 2009; Wild et al., 2011). These synergistic effects between regional impacts caused by ocean warming and local stressors represented by overfishing, coastal development and LBSP has produced a widespread cascading effect that has resulted in a mean increase of macroalgal cover from 7% to 23%, or higher, across many Caribbean reefs (Kuffner et al., 2006; Mumby et al., 2006; Bruno et al., 2009; Jackson et al., 2014). This implies that coral reefs have limited recovery ability from such a wide array of recurrent disturbances.

It has been estimated that 75% of the Caribbean coral reefs are threatened by local human activities, mostly from land-based source pollution (Burke et al., 2004). Coastal vegetation assemblages, mangroves, and sea grass communities are ecosystems that undertake essential ecological functions of retaining and reducing pollutant loads and sedimentation to coastal waters (CIEL, 2008; Barbier, et al 2011; Hernandez-Delgado, et al 2012; Maina, 2013). Coastal watersheds under rapid transformation by increased human population settlement, industrialization, and intensification of tourism related development cause fragmentation of coastal buffer zone and foster the decline of essential ecological and socio-economic benefits (Hernández-Delgado et al., 2012). During extreme precipitation events, runoff pulse events typically are accompanied by excessive input of nutrients, bacteriological pollutants, and sediment-laden runoff (primary source of LBSP). In turn, they can result in recurrent runoff pulse events which may cause a substantial water quality decline that degrades coral reefs across local to large spatial scales (Roberts, 1993; Nemeth, 2001; Ortiz-Zayas et al., 2010; Hernández-Delgado et al., 2012, 2014; Diaz-Ortega et al., 2014; Ramos-Scharrón et al., 2015). Chronic discharges of non-point source pollutants (i.e. nitrogen, phosphorous, sewage, sedimentation) result in eutrophic conditions that promote a gradual transformation in the benthic community composition, from a dominance by reef framework-building species towards a system with ephemeral and opportunistic coral species, and increased macroalgal cover (Hughes et al., 1994; Bruno et al., 2009). Water turbidity and sedimentation pulses, have adverse implications into the coral reef, affecting coral growth since photosynthesis processes is impacted as a consequence of reduced light availability (Loya, 1976; Fabricius, 2005). The direct connectivity between coastal watersheds and coral reefs can be significantly affected by changing land uses, management, and by the production and distribution of sediments along both ecosystems (Richmond et al., 2007; Ramos-Scharrón et al., 2012; Maina et al., 2013; Hernández-Delgado, 2014).

Sediment accumulation on coral surfaces can produce negative physiological responses on some coral species by reducing their survival and growth rate, since energy is mostly relocated to sustain higher respiration rates required to achieve sediment rejection, among other responses (Telesnicki, 1995; Woolfe et al., 1999). It has been widely accepted that 10 mg $cm^{-2}d^{-1}$ is the threshold for sedimentation rate; beyond this level it can cause severe reef degradation and significant changes in community structure and composition, in fact this is a main concern worldwide (Rogers, 1990). Reefs exposed to such high levels of sedimentation can experience morphological changes in coral colonies and a reduction in biodiversity while the coral species that are less resistant to sedimentation can be rapidly lost (Cortés and Risk, 1985; Torres and Morelock, 2002). It has also been demonstrated that growth rate of reef building species, such as *Orbicella* spp., *Pseudodiploria* spp., and *Acropora* spp. at reefs which experienced increased loads of terrigenous sedimentation can be significantly affected (Rogers, 1983; Torres and Morelock, 2002). As sediment settles at a high and consistent rate in the reef, it can foster a significant reduction in live coral cover and recruitment success, as available substrate becomes non-favorable for coral larval colonization and development (Rogers, 1990;

Torres and Morelock, 2002; Fabricius 2005). Extreme sedimentation rates can also result in coral abrasion and burial (Loya, 1976).

Sedimentation effects can vary according to the reef historical adaptation to the amount and type of sediment that distributes and accumulates along the reef; the consequences will also differ by the species-specific level of tolerance (Acevedo et al., 1989; Fabricius, 2011; Bégin et al., 2013). In the long-term, sedimentation can cause phase-shift in benthic community composition towards dominance of coral species tolerant to sedimentation, and can result in overall degradation of ecological services provided by coral reef ecosystems (Loya, 1976; Bégin et al., 2013). There is complex spatial and temporal response to sedimentation stress as sediment influx and its distribution along coastal waters are highly dependent on meteorological and local oceanographic hydrodynamics (i.e., wave action, storm swells) (Ogston et al., 2004; Hernandez-Cruz et al., 2009; Fabricius et al., 2013). It can be projected a gradual shift into recurrent chronic events of sedimentation stress as we experience interannual and seasonal variability of the atmospheric circulation induced by climate change, El Niño Southern Oscillation and North Atlantic High. In the Caribbean region it is projected interannual and seasonal climate variability with major impacts on the Tropical Atlantic sea level pressure, surface temperature, sea surface temperature and rainfall patterns and thus resulting a significant reduction in mean precipitation from -10 to -20% with extended periods of drought, however in contrast it should also be expected an increase in frequency of extreme precipitation events (Giannini et al., 2000; Meehl et al., 2007; Campbell et al., 2011; Seneviratne et al., 2012). These fluctuations could intensify sediment yield, as semi-arid coasts become more susceptible to runoff and erosion by drastic changes in climate extreme. Predominantly, these fluctuations will mostly impact highly disturbed and urbanized watersheds where unsustainable development (i.e., unpaved roads, deforested and exposed soils) usually lacks storm-water runoff and erosion control practices, resulting in higher sediment delivery to adjacent coastal waters (Gray, 2008; Ramos-Scharrón et al., 2010, 2012).

Sedimentation complements the multiplicity of regional and local stressors that can contribute to coral reef decline. The lack of attention to address this issue at a local level can produce serious problems on small Caribbean Islands which community-based livelihoods depends on their marine ecosystems. Therefore, sedimentation is considered a main threat to valuable areas that still supports healthy coral reefs with high coral cover and high diversity, such as the Island of Culebra, Puerto Rico (Hernández-Delgado, 2010). Sedimentation also represents a main limitation to the successful implementation of management strategies established to foster coral recovery and resilience through marine protected areas (MPAs) and ecosystem rehabilitation (Bellwood et al., 2004; Keller et al., 2009; McClanahan, 2012; Young, 2012; Hernández-Delgado et al., 2014). Consequently, enforcement of environmental land-use regulations and collaborative actions to conserve and restore ecosystems through integrated management at the watershed and coral reef scales are needed to prevent further degradation of already threatened coral reefs (Hernández-Delgado, 2000; Commonwealth of PR and NOAA, 2010). Integrated terrestrial and marine resource management should aim to achieve community empowerment to guarantee longevity and persistence of holistic conservation and restoration initiatives that aims to booster coral reef resilience (Stoms et al., 2005; Hernández-Delgado et al., 2014).

Coral reefs along the Island of Culebra used to have the highest level of diversity and live coral cover from the whole Puerto Rico archipelago, with live coral cover ranging from 50% to 75% and supporting a high biomass and diversity of fish species (Pagán-Villegas and Hernández-Delgado, 1999; Hernández-Delgado, 2000; Ramos-Scharrón et al. 2012). By 1998, a community effort leaded by Culebra Island Fishers Association with the support of scientific information about the ecological condition of the marine ecosystems achieved the establishment of the first no-take natural reserve in Puerto Rico (CIEL, 2008). The Island has a history of coral degradation due to the past military practices (from 1903 to 1975), unsustainable land use practices, LBSP and ocean warming, reaching a point where human intervention is needed to conserve and restore the long-term integrity of coral reef and *Acropora* spp. populations. The local non-profit organization Sociedad Ambiente Marino, in collaboration with the Culebra Island Fishers Association, and the University of Puerto Rico, developed and established the Community-Based Coral Aquaculture and Reef Rehabilitation Program since 2003. This is a coral farming strategy to restore degraded coral reef ecosystems through the propagation of the threatened Staghorn coral, *Acropora cervicornis,* to restore its population, and the reef's structural complexity and fisheries productivity (Hernández-Delgado et al., 2012; Hernández-Delgado and Suleimán-Ramos, 2014). In the last decade, sedimentation threats to coral reef ecosystems have become a local management priority to conserve Culebra's valuable coral reefs (DNER, 2013). Therefore, it was determined the need to generate a baseline data base to determine the impacts of coastal watershed management and the effects of storm water runoff, erosion and sedimentation pulses into the marine ecosystem (DRNA, 2010; Sturm et al., 2014). After community-based prioritization, in August 2013 it was conducted the first interagency effort to implement best management practices (i.e. bio-filters and reforestation) at Bahía Tamarindo (BTA) to addressed storm water runoff impacts from unpaved parking area (160m^2) as it represents one of the main drainage outlets to the Bay (Viqueira-Ríos et al., 2013; Sturm et al., 2014).

While extensive research has revealed the impact of sedimentation on coral reef degradation, such knowledge regarding the potential synergistic effects of sediment particle properties, weather events and other environmental variables, are needed to better understand the potential harm to near-shore coral reef benthic communities exposed to sedimentation fluxes. This project contributes paramount information for natural resource managers and decision-makers regarding how do semi-arid coastal watersheds affected by rapid human transformation and by climate variability impacts near-shore coral reef benthic community. The goal of this thesis was to i) determine temporal and spatial patterns of sedimentation rate, sediment texture and composition, as a main driver of change across near-shore coral reef ecosystems; ii) identify environmental variables (climatic and oceanographic) that trigger sediment fluxes and the benthic community response; and iii) contrast short-term changes on the coral reef benthic community composition as a response to sediment dynamics.

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CHAPTER 1

EFFECTS OF CHANGING WEATHER, OCEANOGRAPHIC CONDITIONS, AND LAND USES ON SPATIO-TEMPORAL VARIATION OF SEDIMENTATION DYNAMICS ALONG NEAR-SHORE CORAL REEFS

Abstract

Sedimentation is a critical threat to coral reefs worldwide. Major land use alteration at steep, highly erodible semi-arid islands accelerates the potential of soil erosion, runoff, and sedimentation stress to near-shore coral reefs during extreme rainfall events. The goal of this study was to assess spatio-temporal variation of sedimentation dynamics across near-shore coral reefs as a function of land use patterns, weather and oceanographic dynamics, to identify marine ecosystem conservation strategies. Sediment was collected at a distance gradient from shore at Bahia Tamarindo (BTA) and Punta Soldado (PSO) coral reefs at Culebra Island, Puerto Rico. Sediment texture and composition were analyzed by dry sieving and loss-on-ignition techniques, and were contrasted with environmental variables for the research period (February 2014 to April 2015). Rainfall and oceanographic data were analyzed to address their potential role on affecting sediment distribution with BEST BIO-ENV, RELATE correlation, and linear regression analysis. A significant difference in sedimentation rate was observed by time and distance from shore (PERMANOVA, $p<0.0100$), mostly attributed to higher sediment exposure at reef zones closer to shore due to strong relationships with coastal runoff. Sedimentation rate positively correlated with strong rainfall events (Rho= 0.301, $p=0.0400$) associated with storms and rainfall intensity exceeding 15 mm/hr. At BTA, sediment deposited were mostly composed of sand, suggesting a potential influence of resuspension produced by waves and swells. In contrast, PSO sediments were mostly composed of silt-clay and terrigenous material, mainly attributed to a deforestation event that occurred at adjacent steep sub-watershed during the study period. Spatial and temporal variation of sedimentation pulses and terrigenous sediment input implies that coral reefs exposure to sediment stress is determined by local land use patterns, weather, and oceanographic dynamics.

Comprehensive understanding of sediment dynamics and coastal ecosystem interconnectivity is fundamental to implement integrated and adaptive management strategies aimed to promote sustainable development at watershed and island wide-scale to fully mitigate terrigenous sediment impact to marine ecosystems. Furthermore, decision-making processes and policy needs to address sedimentation stress in the context of future climate to reduce land-based threats and strengthen coral reef resilience.

Introduction

Coral reefs are highly productive ecosystems, which provide vital ecological services that sustain human coastal communities' livelihoods (Moberg and Folke, 1999; Roberts et al., 2002; Barbier et al., 2011). Nevertheless, live coral cover decline and coral reef habitat degradation have been documented in the Caribbean region during recent decades (Gardner et al., 2003; Wilkinson et al., 2008; Hughes et al., 2010; Jackson et al., 2014). Coral reef degradation has been mainly attributed to a combination of cumulative and synergistic effects from diverse human-induced stressors, including global climate change (Hughes, 1994; Wild et al., 2011; Hernández-Delgado, 2015). Coastal sediment fluxes produced by sediment-laden runoff have been identified as one of the primary causes of coral reef habitat degradation (Rogers, 1990). Sedimentation is a natural process defined as the distribution of unconsolidated particles (derived from terrestrial or marine sources) through fluvial hydrodynamic means that interconnects the terrestrial, coastal and marine ecosystems (Apitz, 2012). Thus, there is a major concern regarding the potential influence of unsustainable development of arid watersheds and projected climate variability (i.e., increased frequency of extreme rainfall events) on fluvial sediment delivery to nearshore ecosystems of small tropical islands (Brooks et al., 2007; Smith et al., 2008; Hernández-Delgado et al., 2014a).

Trends of unsustainable urban sprawl at sensitive coastal areas, such as arid steep slopes, increase watersheds' vulnerability to erosion during extreme rainfall episodes (Nemeth and Sladek, 2001; Hernández-Delgado et al., 2012, 2014a; Ramos-Scharrón et al., 2012; Gellis, 2013; Edmunds and Gray, 2014). Sediment yield and influx from arid coastal watersheds into marine ecosystems vary in response to the watershed's catchment size, slope, land use patterns, and local rainfall volume and intensity (Rogers, 1990; Ramos-Scharrón and MacDonald, 2007; Rodrigues et al., 2013; Browning et al., 2016). In addition, seasonal meteorological and oceanographic forces, which are related to wind, wave and currents, influence local hydrodynamics, affect sediment distribution along the coastal marine environment (Ogston et al., 2004; Storlazzi et al., 2009). Spatial and temporal sediment dynamics along near-shore coral reefs emphasize existing land-sea and climate interactions. Therefore, to address sediment dynamics it is important to tackle terrestrial impacts, at the watershed scale, of local weather and oceanographic forces.

Elevated suspended sediment loads and accumulation rates have been associated with coral bleaching, partial colony mortality, reduced growth rates, lower coral recruitment rates, declining species diversity, and coral tissue damage (Loya, 1976; Rogers, 1983, 1990; Cortés and Risk, 1985; Richmond, 1997; Torres and Morelock, 2002; Nugues and Roberts, 2003; Fabricius, 2005). Thus, when sedimentation rates abruptly increase, the ecosystem capacity to adapt and cope with ongoing and further change is compromised (Hughes et al., 2010; Fabricius, 2011). Sedimentation impact on coral reef benthic habitat has been related to the sediment accumulation rates, which in turn have been associated with sediment grain size and composition, and have been identified as key factors that determine sediment distribution and the magnitude of influence on coral reefs health (Nugues and Roberts, 2003; Weber et al., 2006; Fabricius, 2011). Thus, there is a major concern about the effects of sedimentation fluxes along near-shore coral reefs in tropical regions. As extreme rainfall events associated with erosion, runoff and sedimentation stress become more recurrent, coral reefs become more susceptible to phase shifts on their benthic community structure favoring dominance of species resistant to sedimentation (Loya, 1976; Hernández-Delgado et al., 2009; Bégin et al., 2013).

Currently, there is a general lack of quantitative information regarding sediment dynamics along near-shore coral reefs surrounding small semi-arid islands. At the same time, there is a need to understand the effects of changing land uses, local weather, and oceanographic conditions on coastal sediment distribution processes. Understanding the spatial and temporal sediment accumulation rates and sediment properties along targeted restoration sites has the potential to enhance management actions effectiveness in order to prevent further coral reef degradation due to local sedimentation stress. This information is of particular importance when it comes to marine conservation because it can provide the foundation for decision-making regarding integrated watershed and coral reef management aimed to reduce land-based source pollution (LBSP) and coral reef decline.

This study assessed and analyzed sediment spatio-temporal dynamics along two near-shore coral reefs of Culebra Island, Puerto Rico, in the northeastern Caribbean Sea. Culebra's coral reef benthic communities have been recognized to possess high biodiversity and benthic assemblages representative of the northeastern Caribbean region (Hernández-Delgado 2000, 2003). The island's tropical semi-arid climate and ephemeral stream flow regime have often-low influence on sediment input to its coastal waters. This historical trend persists when coastal watersheds remain undisturbed, thus providing optimum conditions for the development of healthy coral reefs (Ramos-Scharrón et al., 2012). However, an increasing trend of unsustainable development, alteration of coastal watersheds, and bare soil exposure have increased sediment delivery to Culebra's coastal waters during heavy rainfall events and have caused a live coral cover decline (Ramos-Scharrón et al., 2012; Hernández-Delgado, 2014a). The susceptibility of soil erosion by storm water runoff is aggravated by a general lack of appropriate sediment erosion control practices, the extension of dirt roads network, and the deforestation of coastal buffer zones (Ramos-Scharrón and MacDonald, 2007, Hernández-Delgado et al., 2011, 2012, 2014a; Ramos-Scharrón et al., 2012; Sturm et al., 2014). At the same time, an increase in popularity of Culebra Island beaches and number of visitors has intensified the use of coastal areas by increasing vehicle traffic (Table 1.1) (Hernández-Delgado, 2014a). These combinations of emergent land use activities have resulted in coastal gully erosion, and increase of sediment influx to near-shore coral reef sites. In the last decade, sedimentation threats to coral reef ecosystems have become a local management priority to conserve Culebra's valuable coral reefs (DNER, 2013).

The goal of this study was to assess sedimentation spatio-temporal patterns and dynamics across near-shore coral reef ecosystems as a function of contrasting land use, precipitation, and oceanographic hydrodynamics. Therefore, this study aimed to i) assess spatial and temporal sediment accumulation rates, grain size, and composition, and ii) assess spatial and temporal variability of sedimentation dynamics as a response to meteorological and oceanographic conditions in two near-shore coral reefs in small semi-arid island of Culebra.

Table 1.1 Culebra Island Natural and Social Environment

Culebra Island	*Description*
Natural environment	
Total area[1]	31.6 km^2 (12.2 $miles^2$)
Geology[1, 2]	Extrusive, volcaniclastics, intrusive rocks, and alluvium
Topography[1, 3]	Low elevation and hills with abrupt slopes up to 36 degrees
Maximum elevation[1]	195m, Mount Resaca
Sub-watersheds[4]	37
Climate[3]	Bimodal rainfall, 990mm per year. Temperature 26-27°C
Ecological life zone[1, 5]	Subtropical dry forest
Social environment	
Population[2]	1,478 (2013)
Population density[2]	46.77 people per km^2 (121.1 people per $mile^2$)
Tourism[2]	69,190 visitors per year (mean 2005-2014)
Population working on tourism[2]	98.2% of total working population
Income of population[2]	80.5% income < \$35,000 16.5% income >\$50,000

Sources: [1]Estudios Técnicos, 2004; [2] Estudios Técnicos, 2016; [3]Ramos-Scharrón et al., 2012; [4]Sturm et al., 2014; [5]Ewel and Whitmore, 1973

Methods

Study site

Culebra Island is a mid-shelf semi-arid island located 27 km off the eastern coast of Puerto Rico, in the northeastern Caribbean Sea. The study was conducted from February 2014 to April 2015 across two leeward coral reef locations: Bahía Tamarindo (BTA, 18°18' N, 65°19' W) and Punta Soldado (PSO, 18°16'N, 65°17'W) (Fig. 1.1). In BTA the study was conducted at El Banderote reef, a colonized bedrock with moderate relief reef located within the Canal Luis Peña Natural Reserve (NOAA, 2015). The coastal zone of BTA study site is composed of Tamarindo and Cornelio sub-watersheds that constitute 37.43 and 38.93 ha, respectively, with a total catchment area of 76.36 ha (Appendix 1.1). The dominant soil is mostly Descalabrado, with slopes up to 20 to 40% and high vulnerability to erosion and runoff (Soil Conservation Service, 1977). The BTA sub-watersheds have been influenced by recent tourism development and relatively rapid land use changes characterized by small-scale deforestation events, unsustainable dirt road development, soil destabilization, and bare soil exposure.

In PSO the study was conducted in a linear high relief reef outside the Canal Luis Peña Natural Reserve. The PSO sub-watershed has a total catchment area of 7.37 ha and is characterized as rock land with slopes up to 60 to 70%, also prone to erosion and runoff (Soil Conservation Service, 1977) (Appendix 1.2). The PSO site has a relatively undisturbed sub-watershed and its beach have a limited number of visitors, mostly local residents. Furthermore, the coastal area had an extensive dirt road that lead mainly into the adjacent watershed, which empties to Ensenada Malena, and does not directly influence our study site. The climate in Culebra is tropical semi-arid characterized by a bimodal rainfall pattern and some microclimates due to watersheds topography. Maximum rainfall from May to November is influenced by easterly waves. Maximum rainfall from November to April is predominantly influenced by cold fronts (McGregor and Niewolt, 1998; Daly et al., 2003). Short showers characterize precipitation and its landscape is distinguished by an ephemeral stream flow regime due to the island's constant high temperatures and evapotranspiration. Following Bailey (1979), for the study period (2014-2015), monthly Bailey Moisture Index showed very dry persistent conditions with index values below 0.5 (Appendix 1.3). Dry months showed rainfall anomalies that ranged from -20 to -121mm/mo (Fig. 1.2). However, four strong rainfall episodes with potential impact on surface erosion and runoff were also documented. These documented monthly rainfall peaks differed from historic rainfall averages (Fig. 1.3), with anomalies between +20 and +100mm/mo (Fig. 1.2).

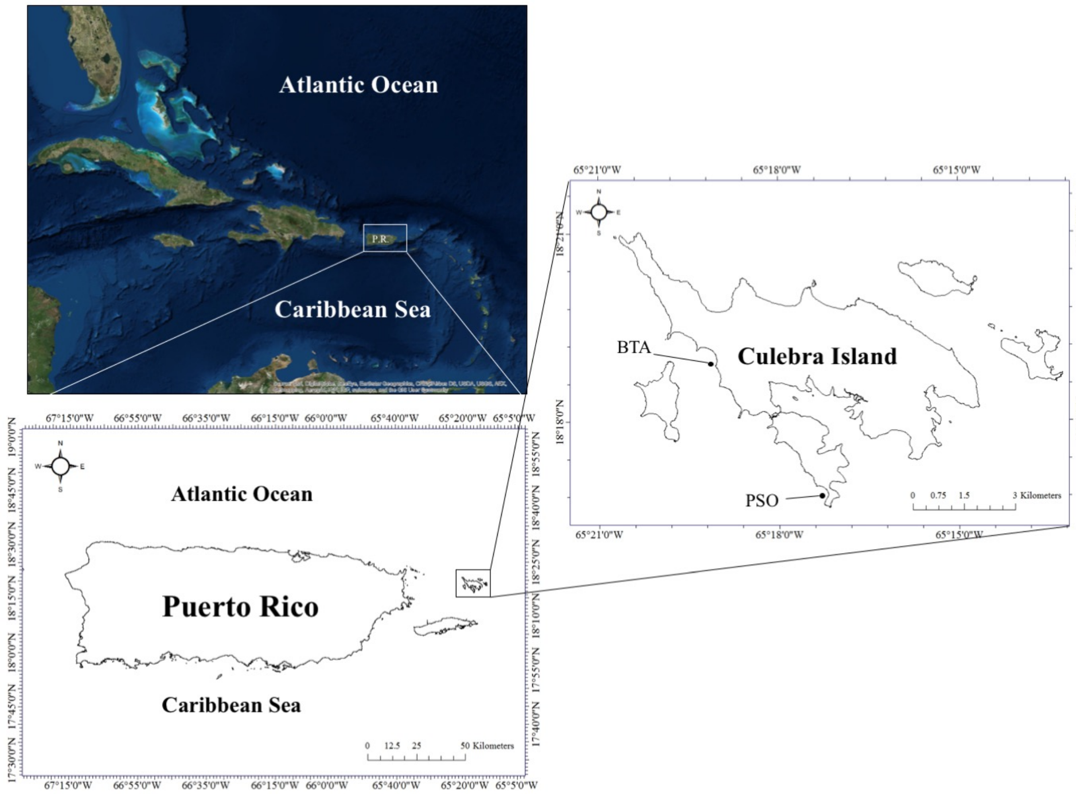

Figure 1.1. Study site at Culebra Island, Puerto Rico. Bahía Tamarindo (BTA) and Punta Soldado (PSO).

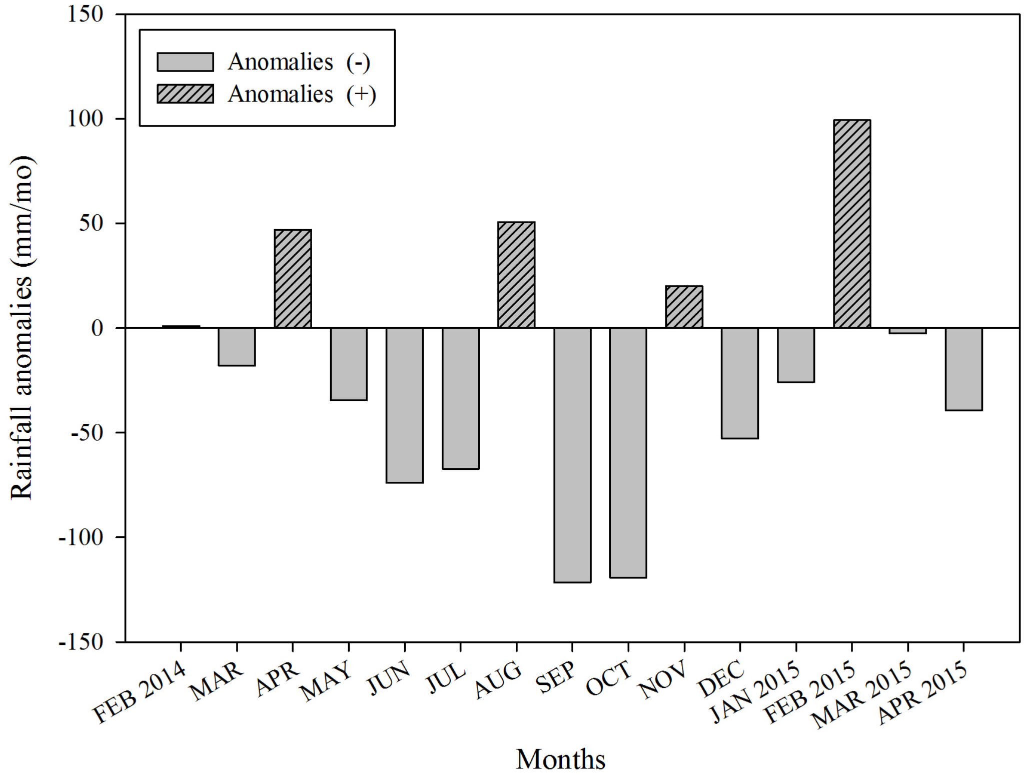

Fig 1.2. Rainfall anomalies from 2014 to 2105 documented at Culebra Island.

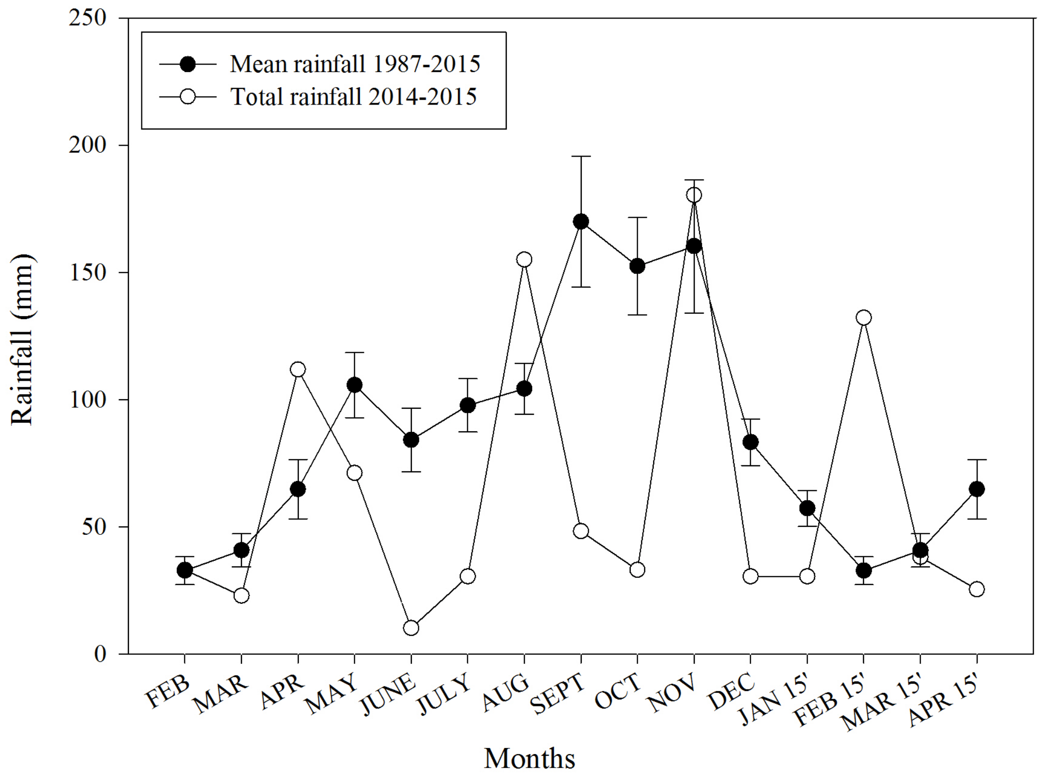

Figure 1.3. Rainfall variability for Culebra Island. Black dots represent mean rainfall by months from 1987 to 2015 (±S.E.) and white dots represent total rainfall for research period from 2014 to 2015. Historical rainfall database obtained from personal rain gauge of community member. Total rainfall 2014-2015 National Weather Service database.

Field sampling design and laboratory analyses

Sediment samples were collected on PVC cylinder sediment traps with a height of 22 cm and circular aperture of 5.5 cm (4:1 height to diameter ratio), following Storlazzi et al. (2009) recommendation for aspect ratio. Sediment traps were deployed 40 cm above sea floor at both sites. The study consisted of 12 sampling periods with an average of 30 days, from February 2014 to April 2015. Sediments deposited on each trap were used to estimate vertical flux of sediment particles as a proxy of sedimentation rate (Smith et al., 2008; Storlazzi et al., 2011). Sampling stations consisted of three replicate traps located across two distance zones from the coastline. Zone A (<60 m from shore) had a depth range from 1.5 m to 3 m, and zone B (>60 m from shore) had a depth range from 3 m to 6 m. In BTA there were three sampling stations along zone A and two along zone B, with a total of 15 sediment traps (Appendix 1.4). In PSO there were a total of two sampling stations along zone A and B, with a total of 12 sediment traps (Appendix 1.5). Traps were capped underwater and placed on a dark environment and laboratory room temperature until analyzed within 72 h.

In the laboratory, supernatant water was siphoned until water reached 2.4 cm on top of sediment deposited on the sediment trap. The remaining water and sediment sample was decanted to centrifuge tubes and processed in a Centrifuge 5810 Eppendorf for 5 minutes at 3,500 rpm. Supernatant water was decanted and sediments were placed in an evaporating dish to oven dry at 60^{o}C for 24 h, or until a constant weight was achieved (Edmunds and Gray, 2014). Total dry sediment weight was recorded on an electronic analytical balance. Sedimentation rate was calculated with the diameter of the sediment trap (r) and days of trap deployment (Rogers et al., 1994; Storlazzi et al., 2009; Edmunds and Gray, 2014).

$$\text{sediment accumulation rate} = \frac{\text{sediment weight (mg)}}{\text{Number of days sediment trap at site} \times \pi \times r^2 \text{ (cm)}}$$

Consolidated dry sediment was disaggregated in a ceramic mortar. Sediment texture was analyzed through dry sieving techniques to classify particles into grain size, silt-clay (<63µm, 4Φ) and sand (>63µm, 4Φ) fractions (Folk, 1974). Silt and clay particles are recognized to originate from terrigenous sources and calcareous sediments are derived from biological sources and processes in the marine environment (Torres and Morelock, 2002; Hernández-Cruz et al., 2009; Edmunds and Gray, 2014).

The organic matter, carbonate, and terrigenous composition of sediment samples were determined stoichiometrically, with a sequential weight loss following the Loss on Ignition (LOI) method (Heiri et al., 2001; Edmunds and Gray, 2014). Subsamples (at least 500 mg) of sand and silt-clay portions were placed on pre-weighed crucibles and were burnt on muffle furnace for 3 hours at 550° C to assess organic carbon composition. Sediment weight loss was recorded and samples were exposed for 3 additional hours at 950° C to assess the carbonate fraction (Bengtsson and Enell, 1986; Heiri et al., 2001; Edmunds and Gray, 2014). Terrigenous sediment proportion (%) was calculated by subtracting the organic and carbonate proportion from sample weight prior to LOI. Afterwards, this proportion was multiplied by the sediment accumulation rate to get the terrigenous sediment accumulation rate (Gray, 2012).

Rainfall intensities were documented with a HOBO RG3 (Onset Computers, Co.) rain gauge located at a coastal watershed adjacent to coral reef study sites. Total monthly rainfall data were acquired from Culebra Hill station of National Weather Service online database (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation), while historical rainfall data were acquired from a local resident rain gauge (W. Kunke, unpub. data). The Simple Daily Intensity Index (Zhang et al. 2011) was calculated as the ratio of total precipitation to number of wet days (mm/day) to assess the relationship with sedimentation dynamics in the coral reef. Other abiotic variables related to oceanographic hydrodynamics, such as wave height, dominant wave period, wind speed and wind gusts were acquired from the Caribbean Integrated Coastal Ocean Observing System (CariCOOS) online database (http://www.caricoos.org/data-download, buoy NDBC 41056 located at Vieques sound.

Statistical analyses

Sediment data were tested using four-way non-parametric permutational analysis of variance (PERMANOVA) and pair-wise comparison for the fixed factors of seasons, time, site and distance from shore (Anderson et al., 2008). Significant relationship was identified by factors that had P values of <0.0500. Ranks ordering of dissimilarities were acquired through Euclidean distance resemblance measure (Clarke et al., 2014). Non-metric multi-dimensional scaling (nMDS) and principal coordinate ordination analysis (PCO) were afterwards tested to acquire a display of the spatial and temporal patterns of variation (Anderson et al., 2008). The nMDS and PCO ordination analysis provided a simple graphical representation in low dimensional space (two or three dimensions), where points represented assessed sediment characteristics, and the distance between points preserved the original rank order of dissimilarities (Anderson et al., 2008; Clarke et al., 2014). Therefore, the nMDS and PCO ordination techniques provide a straightforward interpretation of multivariate data showing how much sediment samples relate to each other, or how much relationship exists between the factors being analyzed (Chariton et al., 2016). The centroids from multivariate sediment data and the Euclidean distance from each pair of centroids were used to create the PCO ordinations plot (Gower, 1966; Anderson et al., 2008). Vectors were superimposed to assess how sediment and environmental factors explained spatio-temporal variation. BEST BIO-ENV and RELATE (Spearman rank) correlations were used to determine the best environmental variables that explained observed sedimentation patterns (Clarke and Ainsworth, 1993). Analyses were conducted in PRIMER v7 and PERMANOVA v1.16 statistical programs (Plymouth Marine Laboratory, UK). Linear regression analysis was conducted on SigmaPlot 11.0 (Systat software Inc.) to determine the relationship between sediment and environmental variables and was also used for graphical representation of data. Sediment variables and environmental data, including weather and oceanographic hydrodynamics data (i.e, precipitation, wave height, dominant wave period, etc.), were $\log_{10}$-transformed prior to analyses to meet assumptions of normality and homogeneity of variances (Smith et al., 2008; Gotelli and Ellison, 2013). All multivariate tests were based in 10,000 permutations (Anderson, 2001; Hernández-Delgado, et al., 2014b).

Results

Sedimentation rate

Sedimentation rate patterns were significantly different among time periods (PERMANOVA, Pseudo F=57.21, p=0.0001), and distance zone from shore (Pseudo F=16.54, p=0.0040) (Table 1). There was also a significant difference among time by distance (Pseudo F=5.94, p=0.0010), and site by distance interactions (Pseudo F=11.18, p=0.0100). Nevertheless, sedimentation rate patterns did not show a significant difference by seasons or sites. Sediment accumulation rate was consistently higher at BTA with 2.42±0.42mg cm^{-2} d^{-1} (mean±standard error) for the whole study period, and 0.47±0.05mg cm^{-2} d^{-1} at PSO. In BTA significant sediment pulses were recorded from December 2014 to February 2015 (Appendix 1.6), and from October to November 2014, corresponding to extreme rainfall and runoff during winter and autumn seasons respectively (Fig. 1.4A). Total rainfall during these two periods was 171.20 and 182.37 mm, respectively. Mean sedimentation rate in BTA during the winter season was 6.84±2.14mg cm^{-2} d^{-1}.

At BTA the highest sediment accumulation occurred at distance zone A (<60m) and for these sampling periods mean total sediment accumulation was 6.80mg cm^{-2} d^{-1} (Oct-Nov) and 21.04mg cm^{-2} d^{-1} (Dec-Feb 2015) (Fig. 1.4B). The highest total rainfall was recorded from October to November, with values up to 171.20 mm. Rainfall reached 182.37 mm from December 2014 to February 2015. Likewise, for these sampling periods with greatest sediment accumulation rate a high frequency of intense wave height (>1m) was also experienced. It can be suggested that coral reefs located at BTA had a higher exposure to sedimentation stress associated with runoff from intense rainfall events. Mean sedimentation rate at BTA during the winter season was 6.84±2.14mg cm^{-2} d^{-1}. The highest sediment pulse (Dec-Feb) had a percent increase of 1,259% from the period with lowest sedimentation rate, recorded from June to July 2014. The second in magnitude (Oct-Nov) had a percent increase of 386%. After a rainfall peak registered in April 2014 an extreme drought event persisted across the wider Caribbean region that lasted until August 2014 (Fig. 1.3), and was related with the period with lowest accumulation rate for both sites (Fig. 1.4A). Sediment accumulation at PSO had an overall lower mean rate and a single sedimentation pulse event was recorded from July to August, with a mean rate of 1.52±0.05mg cm^{-2} d^{-1} (Appendix 1.7). It had a percent increase of 52% from the period with lowest sedimentation rate recorded from February to March 2014. Moreover, sediment accumulation at PSO was non-significant by distance zones (Fig. 1.4C).

Terrigenous sediment accumulation rate showed a significant difference among time, site and distance zones (Table 1). However, difference among seasons was marginally significant (Pseudo F=3.80, p=0.0700). Terrigenous accumulation rate had a similar pattern as sedimentation rate, yet they differed since terrigenous accumulation rate shows the portion of sediment derived from land. At BTA terrigenous sediment accumulation had a total mean of 1.25±0.2mg cm^{-2} d^{-1}, which was significantly higher than at PSO. In PSO the mean terrigenous sediment accumulation was of 0.16±0.2mg cm^{-2} d^{-1}. The highest terrigenous accumulation rate in BTA was documented from December to February 2015, with a mean of 6.35mg cm^{-2} d^{-1} (Fig. 1.4D). There was a great difference from the terrigenous sediment accumulated at BTA between the distance zones (Pair-wise t=3.94, p=0.0050). Closer to shore, zone A, the terrigenous sediment reached accumulation rate of 9.86mg cm^{-2} d^{-1} from December to February

2015 and 3.23 from October to November 2014. Total terrigenous sediment accumulation rate had a mean of 1.25mg cm^{-2} d^{-1}, while zone B had a mean of 0.39 mg cm^{-2} d^{-1}. At PSO, the mean terrigenous sediment accumulation rate also had similar patterns as sedimentation rate. The sampling period with highest accumulation was from July to August, and it was associated with period of intense rainfall after long drought period.

Table 1.2. Results of a permutational analysis of variance (PERMANOVA) sedimentation rate and terrigenous rate

Factors	**Sedimentation rate**			**Terrigenous rate**		
	df	Pseudo *F*	*P* (perm)	df	Pseudo *F*	*P*(perm)
Seasons (Se)	3	1.46	0.2800	3	3.80	0.0700
Time (Ti)	8	57.21	0.0001	7	35.12	0.0001
Site (Si)	1	2.62	0.1500	1	7.38	0.0300
Distance (Di)	1	16.54	0.0040	1	12.07	0.0100
Se x Si	3	0.88	0.4900	3	4.14	0.0600
Se x Di	3	2.12	0.2000	3	3.01	0.0900
Ti x Si	8	39.54	0.0001	7	18.52	0.0001
Ti x Di	8	5.94	0.0010	7	6.93	0.0010
Si x Di	1	11.18	0.0100	1	21.18	0.0030
Se x Si x Di	3	0.25	0.8200	3	2.51	0.1400
Ti x Si x Di	8	5.70	0.0010	7	3.50	0.0300

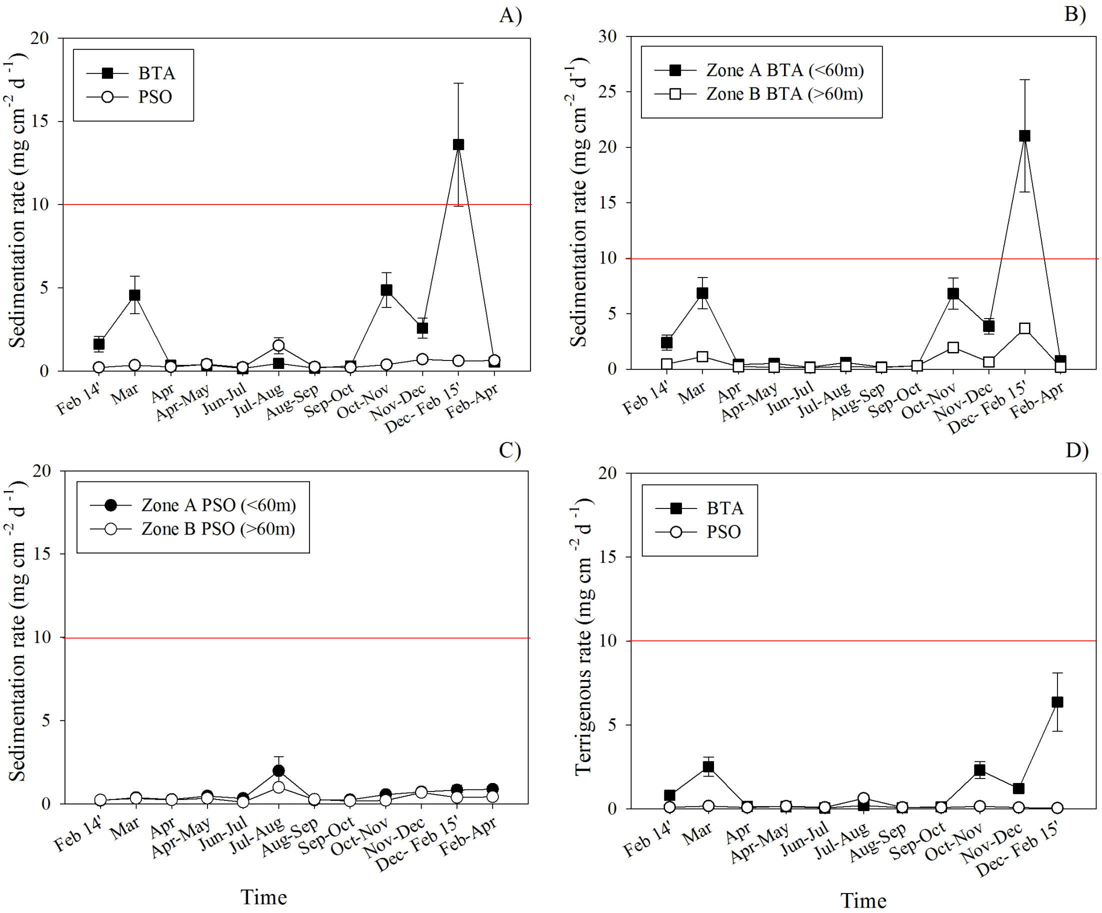

Figure 1.4. Sedimentation rate (±S.E.) for both sites (A), sedimentation rate at BTA by distance zones (B), sedimentation rate at PSO by distance zones (C), terrigenous rate for both sites (D). Red line represents sedimentation threshold of 10 mg cm^{-2} d^{-1} for healthy coral reefs (Rogers, 1990).

Sediment dynamics

Sediment dynamics showed a significant difference between sites (Pseudo F=9.05, p=0.0020) and distance from shore (Pseudo F=10.71, p=0.0030). Also, the interactions of site and distance zone (Pseudo F=7.01, p=0.0060), time and site (Pseudo F=14.20, p=0.0001), time and distance (Pseudo F=2.35, p=0.0020), time and site and distance (Pseudo F=1.87, p=0.0200) were significant. The principal coordinate analysis ordination (PCO) identified three large clusters from the overall sediment patterns by season, sites and distance zone (Fig. 1.5). The farthest cluster was identified by similar sediment dynamics at fall and winter seasons in BTA zone A. It had a strong relationship with major variations in sedimentation rate, terrigenous rate, terrigenous content, and sand. However, sediment dynamics during winter season at zone B was explained by variation in sand grain size. Organic matter was a key factor during summer season at both distance zones, and it might be related to deposition due to lower wave energy. Sediment dynamics in PSO at both distance zones responded predominantly to variations in silt-clay grain size sediment and carbonate content. During winter season there was a critical rainfall event that produced a significant silt-clay input that reached zone B. Nevertheless, zone A had similarity to patterns explained for BTA at spring, fall and winter seasons. The proposed PCO explains 97% of the observed patterns of variation in sedimentation dynamics.

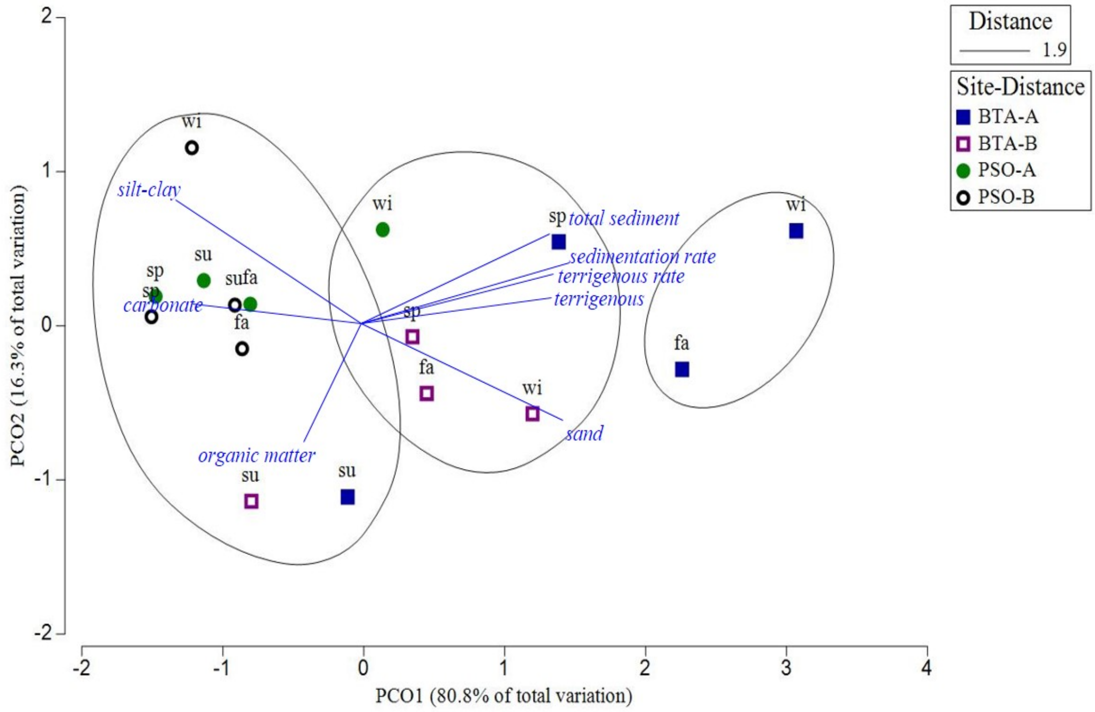

Figure 1.5. Principal component ordination (PCO), analysis of centroids of sedimentation components by seasons, sites and distance zone from shore based on Euclidean assemblage data. Clusters based on a Euclidean distance cutoff level of 1.9. This model explained 97.1% of the observed spatio-temporal variation in sedimentation patterns. Seasons are represented as sp=spring, su=summer, fa=fall, and wi=winter.

Sediment texture

Sediment texture was significantly different among time series (Pseudo F=5.55, p=0.0010), sites (Pseudo F=31.26, p=0.0010), and for the interactions time by site (Pseudo F=8.70, p=0.0001), and site by distance (Pseudo F=5.52, p=0.0300) (Table 2). Sediment grain size categories, sand and silt-clay showed similar spatio-temporal patterns, with significant differences among time series and sites. However, there was no significant difference among seasons or between distance zones. Sediments that accumulated along BTA reef had a major influence of sand particles. The accumulation of the sand, coarser-grained sediments in overall had a mean proportion of 65%, with the highest proportion being recorded at both distances zones from December 2014 to February 2015, with a mean of 83% (Fig. 1.6A) (Appendix 1.8). This period corresponded to winter season (Fig. 1.6B). Similarly, for this sampling period a mean wave height at BTA of 1.16 m was documented, with a dominant wave period or the period with maximum wave energy of 8.45 s, and wind speed ranging from 2.45 to 8.30 m/s (Fig. 1.7A,B,C). It also showed that 45% of days wave height overpassed 1 m and 13% of days waves were higher than 1.5 m. At BTA sand accumulation at sampling stations ranged from 9% to 96% in zone A and from 7% to 90% in zone B. In contrast, silt-clay accumulation had a mean proportion of 30%. The highest accumulation of fine sediments proportion was recorded during sampling period April to May and July to August, with a mean of 40% for both time intervals. These time periods corresponded to spring and summer seasons, respectively, which were characterized by calmer oceanographic conditions. During these seasons, multiple meteorological systems were also experienced (i.e., cold fronts and tropical storms) that produced extreme rainfall at the northeastern Caribbean region.

Table 1.3 Results of a permutational analysis of variance (PERMANOVA) sedimentation texture, sand and silt-clay grain size sediments

Factors	Sediment texture			Sand		Silt-clay	
	df	Pseudo *F*	*P*(perm)	Pseudo *F*	*P(perm)*	Pseudo *F*	*P(perm)*
Season (Se)	3	1.06	0.4100	2.09	0.1900	0.44	0.7200
Time (Ti)	8	5.55	0.0010	4.42	0.0002	6.53	0.0001
Site (Si)	1	31.26	0.0010	31.20	0.0010	31.32	0.0007
Distance (Di)	1	3.08	0.1100	3.80	0.0900	2.57	0.1400
Se x Si	3	0.18	0.9000	0.12	0.9100	0.26	0.8200
Se x Di	3	0.75	0.5500	0.94	0.4600	0.62	0.6100
Ti x Si	8	8.70	0.0001	10.06	0.0001	7.51	0.0001
Ti x Di	8	1.82	0.0800	1.62	0.1400	1.99	0.0700
Si x Di	1	5.52	0.0300	4.66	0.0500	6.38	0.0300
Se x Si x Di	3	1.47	0.3200	1.15	0.4000	1.79	0.2300
Ti x Si x Di	8	1.28	0.2700	1.38	0.2400	1.19	0.3300

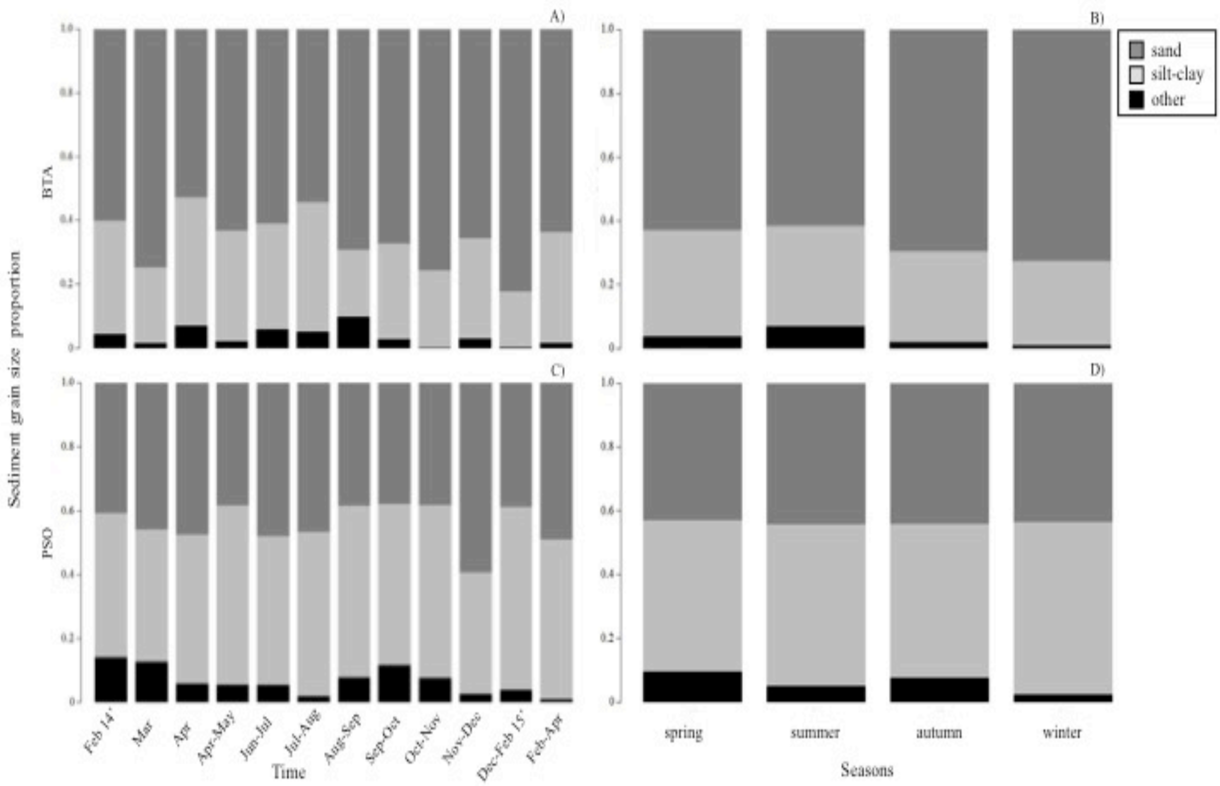

Figure 1.6. Patterns of variation in sediment grain size proportion by time and season at Bahía Tamarindo (BTA) (A-B) and Punta Soldado (PSO) (C-D). Dark gray stacked bar: sand (>63μm), light gray: silt-clay (<63μm), and black: other. The component identified as other represents overall error or missing portion through sediment analysis process.

PSO showed contrasting sediment accumulation patterns, since in overall it had slightly higher proportions of silt-clay grain size sediments (Fig. 1.6C). The fine-grained sediment had a mean proportion percent of 50% and the highest proportion was recorded from December to February 2015, and from April to May, with a mean proportion of 57% for both sampling periods. A significant difference was observed between zones, as a consequence that zone B received higher portion of silt-clay sediments. Silt-clay particles that accumulated along the reef ranged from 18 to 66% in zone A, and from 3 to 94% in zone B, showing drastic variations throughout the study. Subsequent to a massive deforestation event that occurred on April 2014 along the steep coastal watershed of PSO the silt-clay sediment accumulation increased and it was a major contribution to sedimentation fluxes across the coral reef during intense rainfall events (Appendix 1.9). However, sand sediment accumulation in PSO had the highest distribution from November to December, with a mean of 54%. During this sampling period sand accumulation proportion in zone A reached a mean of 62% and a maximum of 85%. However, there was no significant difference for sediment distribution in PSO across seasons (Fig. 1.6D). Documented mean wave height for November to December sampling period was of 1.22 m, dominant wave period of 8.78 s, with 61% of days overpassing a wave height of 1m, and 19% of days the waves were higher than 1.5m (Fig. 1.7A,B).

nMDS analysis showed three distinct clusters of sites and distance zone by time, based on the proportion of sand grain size category distribution (Fig. 1.8A). The farthest cluster includes four events of major sand distribution, predominantly across BTA zone A, suggesting strong recurrent sediment resuspension and bedload transport episodes. These events were associated to a combination of cold fronts and tropical storms that produced extreme rainfall events with significant runoff, surface erosion and swells. Therefore, it can be suggested that sand is transported predominantly through inner coastal areas during periods of active ocean conditions, either by waves or wind-induced turbulence. Besides these extreme events, sand showed a decreasing gradient of effects with similar distribution patterns across most of the remaining events at BTA through zones A and B, evidencing a significant difference between distance zones (Pair-wise, $t=3.09$, $p=0.0100$). The remaining cluster included the majority of events or sampling periods of PSO, with no significant difference between distance zones.

The second nMDS plot shows three distinct clusters of sites and distance zone by time, based on the proportion of silt-clay grain size category distribution (Fig. 1.8B). It shows a gradient of events that distinguished silt-clay distribution from sites. In PSO the majority of the events reached a similar silt-clay distribution between distance zones. However, during two events, there were major silt-clay sediment input and distribution that significantly accumulated or deposited across distance zone B. These events were associated with the tropical trough and cold fronts that produced extreme rainfall, and combined with surface erosion, runoff, and sediment delivery to coastal waters. These events highlighted the ability of fine sediments to remain suspended in the water column long distances and settle far from shore (>60m) on coastal benthic communities during calmer oceanographic conditions. The remaining two clusters indicated significant differences between distance zones at BTA (Pair-wise, $t=2.85$, $p=0.0200$). Both nMDS plots had a very low stress value (0.01), suggesting that the plots are an accurate spatial representation of the sediment grain size differences of distribution and accumulation between time, sites, and zones.

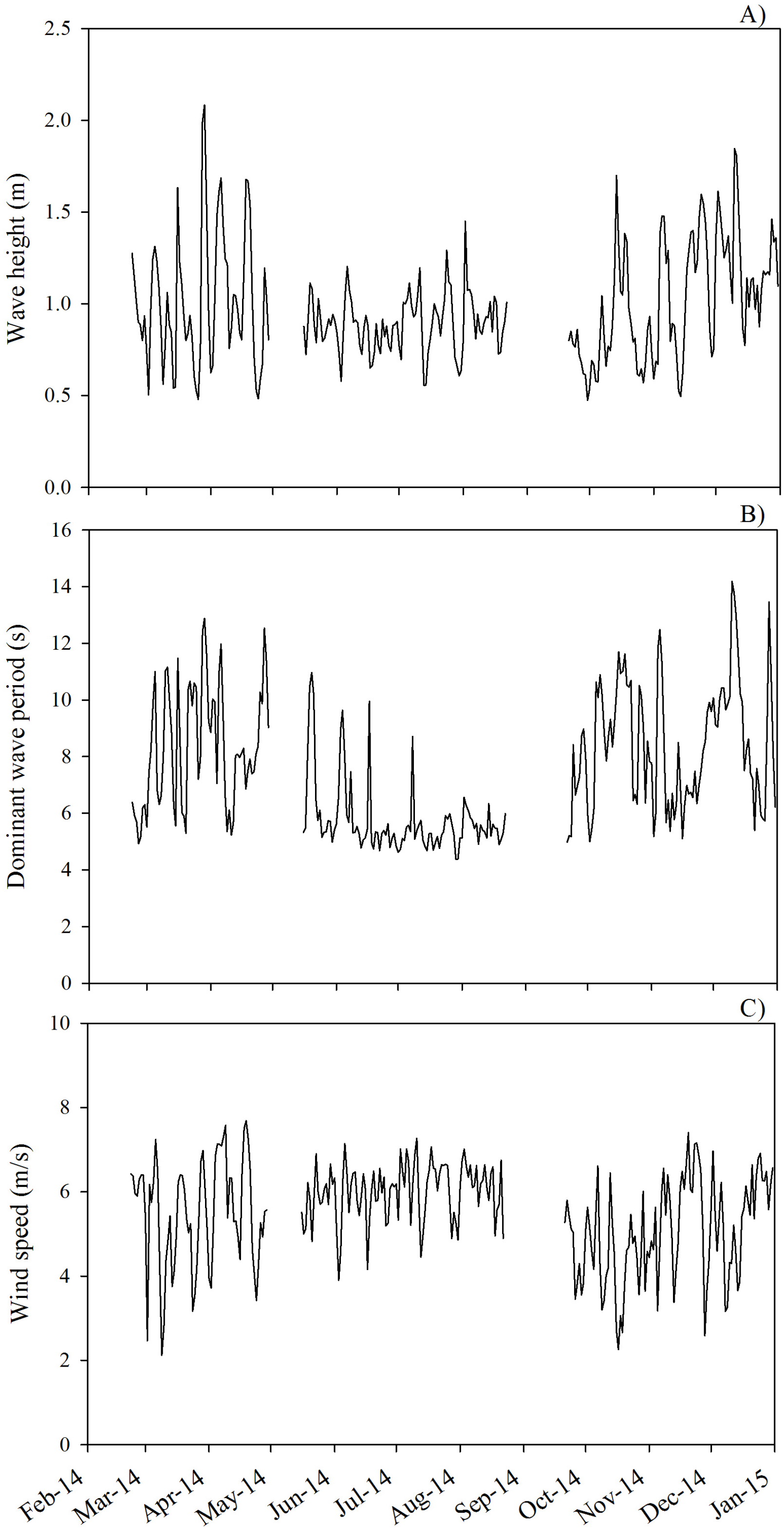

Figure 1.7. Variations of oceanographic environmental data during study period 2014-2015. Wave height (A), dominant wave period (B), and wind speed (C). Data acquired from CARICOOS NDBC 41056 buoy.

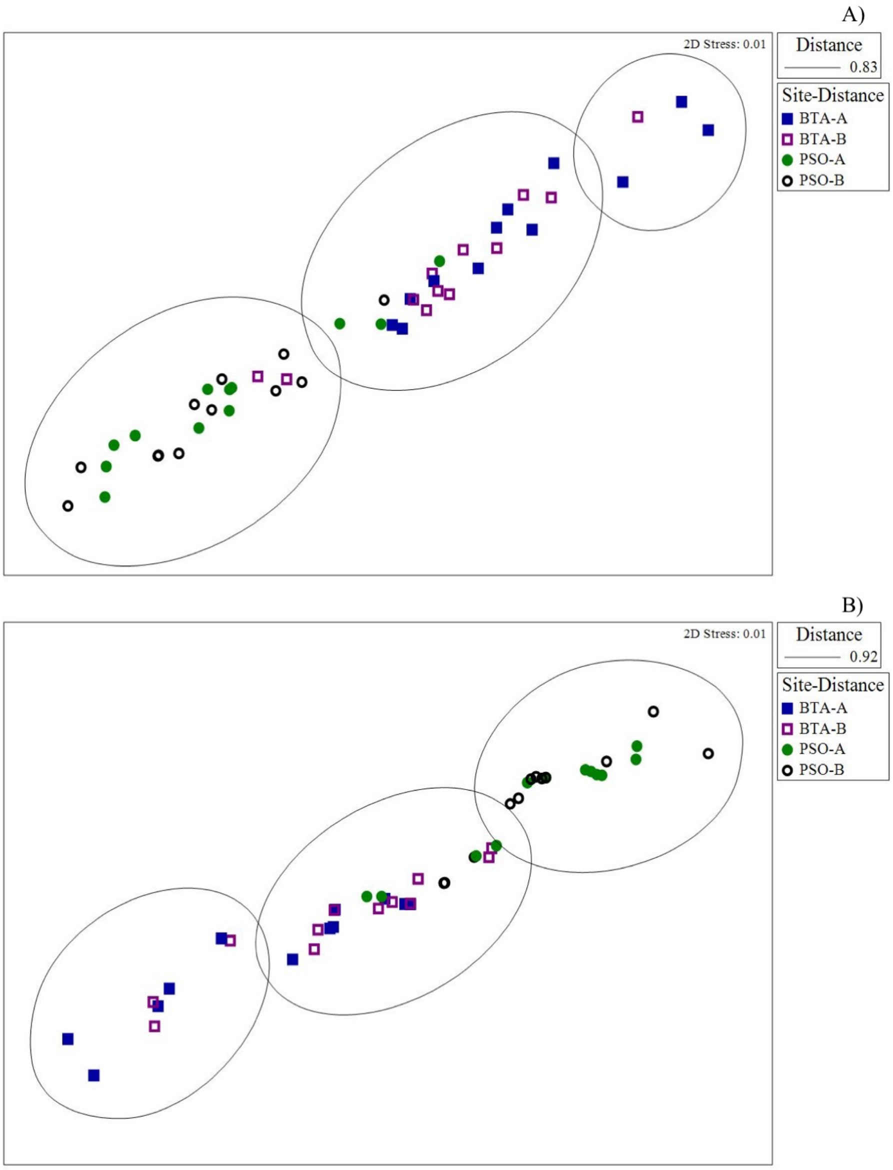

Figure 1.8. Non-metric multidimensional scaling (nMDS) plot for sand grain size (A) and silt-clay (B) by time, site and distance zones. Clusters are based on a Euclidean distance cutoff level of 0.83 (A) and 0.92 (B). Ordination diagram shows sediment particle grain size distribution on first two dimensions, X axis (nMSD1) and Y axis (nMDS2).

Sediment composition

Sediment composition analysis showed a statistically significant difference among time series (Pseudo F=13.58, p=0.0001), between distance zones (Pseudo F=4.15, p=0.0400), and the interaction time series and sites (Pseudo F=11.45, p=0.0001) (Table 3). The largest variation in sediment composition was caused by calcium carbonate ($CaCO_3$) and terrigenous material, as a consequence of the low content of organic matter contributing to less than 10% of sediment assessed for both sites. The average $CaCO_3$ content across BTA reef was 45% (Fig. 1.9A), with the highest $CaCO_3$ content recorded from April to May, and from June to July. The season with the highest $CaCO_3$ proportion was summer, with a mean of 48% (Fig. 1.9B); however there was no significant difference among seasons. Overall, $CaCO_3$ content was similar between distance zones and showed no significant difference. Sediments that accumulated across the reef had mean $CaCO_3$ content ranging from 27 to 84%. There was a similar pattern for terrigenous content with a mean of 45%. The highest terrigenous content was recorded at sediments that accumulated from March to April 2014, corresponding to spring season, at both distance zones. Terrigenous content that accumulated across the reef ranged from 7 to 65%, representing great sediment accumulation along the study period.

Sediments that accumulated across PSO reef had a mean $CaCO_3$ content of 50%, greater than BTA. The highest $CaCO_3$ content was identified from April to May 2014 (Fig. 1.9C), which corresponded to calmer oceanographic conditions and increased fine-grained sediment deposition in the reef. However, there was no significant difference among seasons (Fig. 1.9D). Meanwhile, terrigenous content in PSO had a mean percent of 40%. The highest terrigenous content was identified in sediment that

Table 1.4. Permutational analysis of ANOVA (PERMANOVA) for sediment composition, organic matter, $CaCO_3$ and terrigenous content of sediments.

Factors	**Sediment composition**			**Organic matter**		**$CaCO_3$**		**Terrigenous**	
	df	Pseudo *F*	*P*(perm)	Pseudo *F*	*P*(perm)	Pseudo *F*	*P*(perm)	Pseudo *F*	*P*(perm)
Season (Se)	3	0.17	0.9100	0.55	0.6500	0.13	0.8600	0.31	0.7700
Time (Ti)	7	13.58	0.0001	6.24	0.0001	23.00	0.0001	16.82	0.0001
Site (Si)	1	3.68	0.0800	0.37	0.5800	5.70	0.0500	6.07	0.0500
Distance (Di)	1	4.45	0.0400	4.30	0.0700	3.21	0.1000	5.14	0.0500
Se x Si	3	0.81	0.5600	0.29	0.8200	0.79	0.5500	1.29	0.3400
Se x Di	3	1.09	0.4100	1.55	0.2700	3.33	0.0700	0.70	0.5800
Si x Di	1	1.60	0.2500	8.06	0.0200	0.66	0.4900	1.95	0.1900
Ti x Si	7	11.45	0.0001	8.59	0.0001	18.69	0.0001	9.27	0.0001
Ti x Di	7	1.92	0.0700	1.44	0.1800	1.30	0.2900	2.53	0.0300
Se x Si x Di	3	1.03	0.4400	1.03	0.4400	0.64	0.6100	0.37	0.7800
Ti x Si x Di	7	1.29	0.2900	0.89	0.5200	1.31	0.2800	1.50	0.2000

accumulated from February to March 2014, with a mean percent of 45%, but there was no significant difference between distance zones. However, the highest terrigenous accumulation occurred during fall and winter season with a mean value of 41% for both seasons. Terrigenous sediment that accumulated across the reef ranged from 32 to 43%, representing consistently higher levels.

nMDS plot shows two distinct clusters based on the proportion of marine sediment terrigenous content that mostly distinguished distribution between sites (Fig. 1.10). The plot shows a gradient of events at BTA, indicating that the proportion of terrigenous sediment accumulation experienced variations by seasons and across distance zones. BTA experienced higher terrigenous sediment accumulation during most of the study, except for the summer on distance zone B, while there were calmer meteorological conditions. Overall, terrigenous sediment accumulation was 5% higher in BTA than in PSO. In PSO, most of the seasons received similar terrigenous content within different distance zones. However, the plot shows that for both sites terrigenous content was higher on the distance zone closer to shore on spring, fall and winter. These seasons were associated with cold fronts and frontal boundary events that produced extreme and intense rainfall events and provoked significant soil erosion, runoff and terrigenous sediment influx to inner coral reef areas. The nMDS plots had a very low stress value (0.01), suggesting that it is an accurate spatial representation of the terrigenous sediment differences of distribution and accumulation among sites, and between distance zones by seasons.

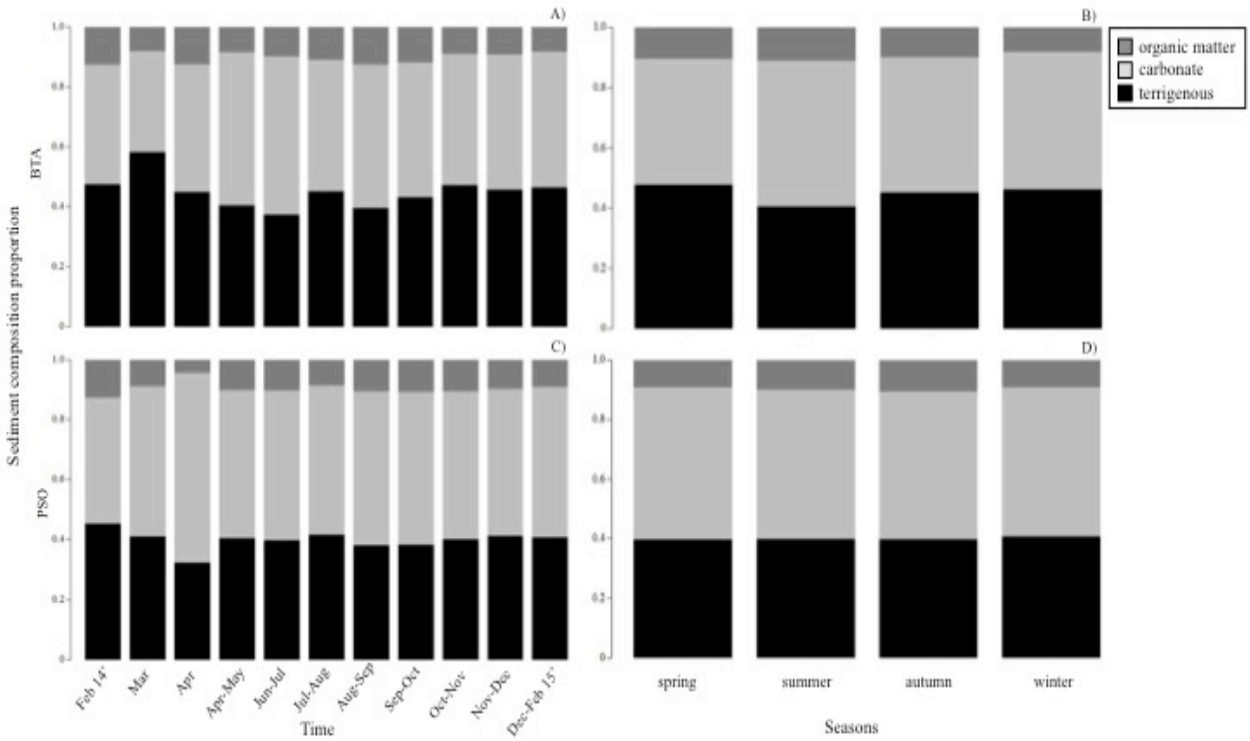

Figure 1.9. Patterns of variation in sediment composition proportion by time (A) and seasons (B) at Bahía Tamarindo (BTA), and Punta Soldado (PSO) (C-D). Dark gray stacked bar: percent organic matter, light gray: percent $CaCO_3$, and black: percent terrigenous.

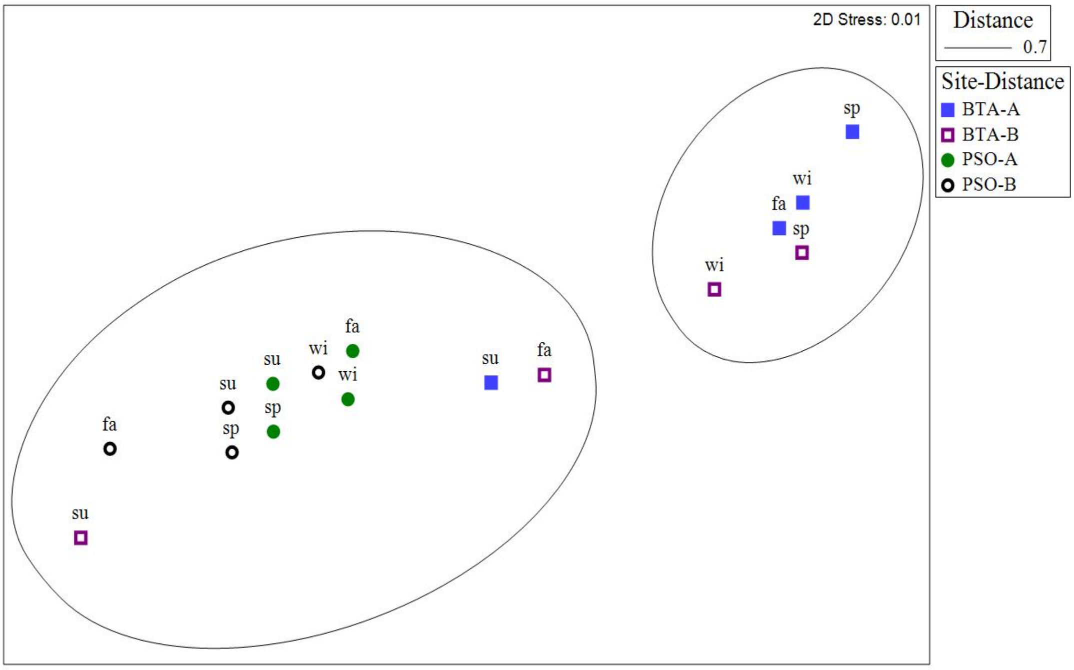

Figure 1.10. Non-metric multidimensional scaling plot (nMDS) plot for terrigenous content by time, sites and distance zone from shore. Clusters based on a Euclidean distance cutoff level of 0.70. Ordination diagram shows terrigenous content on first two dimensions, X axis (nMSD1) and Y axis (nMDS2). Seasons are represented as sp=spring, su=summer, fa=fall, and wi=winter.

Sedimentation patterns and environmental variables

Sedimentation rate, sediment texture and composition responded differently to variations in environmental conditions. Regression analyses indicated that sedimentation rate had a positive marginal linear relationship with wave height in BTA (r^2=0.33, p=0.0511), and a significant relationship with total precipitation in PSO (r^2=0.41, p=0.0240) (Fig. 1.11). At BTA, sedimentation rate also showed a nearly marginal relationship with total precipitation (r^2=0.25, p=0.0986) and a positive linear relationship with dominant wave period (r^2=0.45, p=0.0167), defined as the period with maximum wave energy. The nonparametric correlation BEST BIO-ENV (Spearman rank) analysis demonstrated that terrigenous sedimentation rate had a strong correlation with total precipitation and with dominant wave period (Rho=0.36) by time series. Furthermore, a positive linear relationship between terrigenous rate and total precipitation (r^2=0.40, p=0.0379) was documented at PSO.

There was a significant correlation between sediment texture with total precipitation, wave height, and dominant wave period (Rho=0.20) by time series. Specifically, sand (>63 μm) showed a positive relationship with wave height (r^2=0.42, p=0.0227). These patterns highlight the role of strong waves and swells produced by storms and frontal systems on the resuspension or distribution of coarser sediments along the reef (Fig. 6A,C). However, silt-clay (<63 μm) particle distribution along near-shore coral reefs was mostly associated to periods with higher total rainfall and rainfall intensity (Fig. 1.12).

Sediment composition also correlated with multiple environmental variables, including total precipitation, dominant wave period, simple daily rainfall intensity index (>1mm/day), and sea surface temperature (SST) (BEST BIOENV, Rho=0.48) by time series. At BTA terrigenous content had a strong relationship with dominant wave period (r^2=0.41, p=0.0352). Simple daily rainfall intensity index showed a significant correlation with the accumulated $CaCO_3$ component (Rho=0.308, p=0.0300), and the relationship was marginally significant with terrigenous content (Rho=0.23, p=0.0900). SST showed a strong significant relationship with organic matter content (Rho=0.36, p=0.0060). Variations in SST might have an indirect effect on the amount of $CaCO_3$ available on the coastal marine environment for its distribution along the reef.

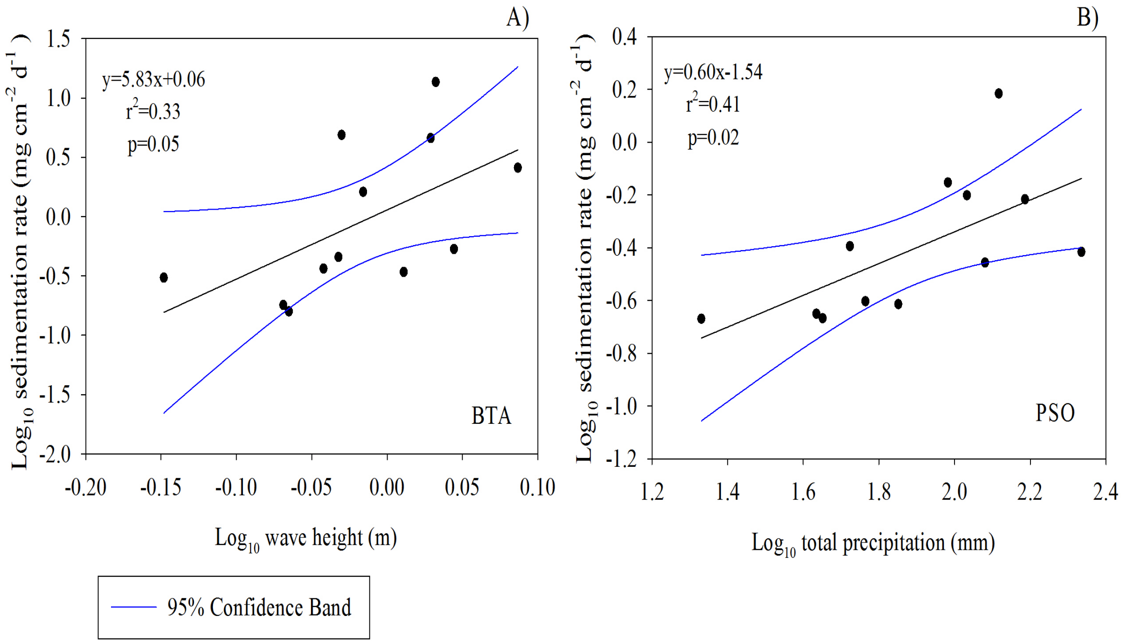

Figure 1.11. Linear regression analysis: sedimentation rate with wave height at Bahía Tamarindo (BTA) (A), and total precipitation at Punta Soldado (PSO) (B). Blue line is 95% confidence interval band.

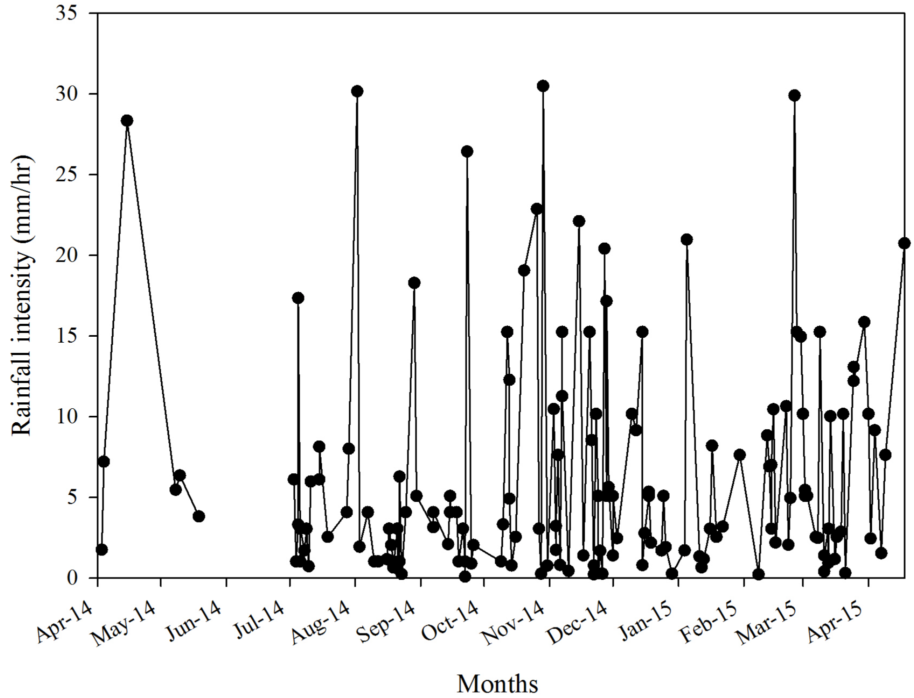

Figure 1.12. Variations of rainfall intensity (mm/hr) in Culebra Island during study period 2014-2015.

Discussion

There was a significant spatial and temporal variation of sedimentation dynamics along near-shore coral reef study sites of Culebra Island. Sedimentation patterns showed significant variation among sampling periods, but not among seasons. These patterns were influenced by local climate variability, characterized by rainfall peaks that differed from historic rainy seasons (Fig. 1.3). Rainfall anomalies (Fig. 1.2) altered stream flow regimes on this semi-arid island, affecting terrestrial sediment influx, and sediment distribution along coastal waters. At near-shore reef spatial scales (120m from shore or less), results from this study reject the null hypothesis that contrasting land use, precipitation patterns, and oceanographic hydrodynamics do not have a significant spatial and temporal impact sedimentation rate, sediment texture, and sediment composition. Our results suggest that the reef zones closer to shore (<60m) were more exposed to sedimentation stress during strong and intense rainfall events. Furthermore, increased intensity of oceanographic conditions (i.e. wind speed, wave height, and dominant wave period) triggered high variation in coastal sedimentation dynamics within our study sites. Shallow inner coral reef zones were more vulnerable to changing sediment dynamics, including terrigenous, fine sediment deposition, coarser sediment resuspension, and bed load transport.

Sediment accumulation rate along near-shore reefs varied from 0.15 to 37mg cm^{-2} d^{-1} throughout the study period of 2014-2015. There were significant differences between distance zones factors and among time series. In both sites, coral reef closer to shore (<60m) had the highest sedimentation and terrigenous accumulation rate. Sedimentation rates documented in Culebra Island were similar to previous field studies carried out in Puerto Rico, ranging from 3 to 30mg cm^{-2} d^{-1} (Rogers, 1983), 3 to 13mg cm^{-2} d^{-1} (Hernández-Cruz et al., 2009), and at St. John (US Virgin Island, sedimentation rates ranged from 1 to 16mg cm^{-2} d^{-1} (Edmunds and Gray, 2014) during normal conditions. Healthy coral reefs have been suggested to have sedimentation rates of less than 10mg cm^{-2} d^{-1}, meanwhile areas exposed to higher rates can have from moderate to severe impacts if they exceeded 50mg cm^{-2} d^{-1} (Pastorok and Bilyard, 1985; Rogers, 1990). Sampling periods with major sediment and terrigenous accumulation rate pulses were associated with meteorological events that produced total rainfall higher than 30mm (Fig. 1.3), and individual rainfall intensity higher than 15mm/hr (Fig. 1.12). Studies conducted on St. John, US Virgin Islands, coastal sedimentary records suggest that runoff and terrigenous sediment input to marine coastal environments runoff were associated to rainfall events that exceed threshold of ~12mm/day (Brooks et al., 2015; Larson et al., 2015). Nevertheless, field studies have also shown that rainfall of just 3 to 5 mm can produce significant runoff and sediment transport from unpaved roads to coastal waters (Ramos-Scharrón and MacDonald, 2007). This suggests that weather conditions and land use patterns, at watershed and sub-watershed spatial scales, can play a significant role in affecting coastal sediment dynamics. During the month of February 2015, a cold front that impacted the Caribbean region produced a total rainfall of 119mm and wave height of up to 2.11m, which generated a high sedimentation rate at BTA (Fig. 1.4) and exceeded the sedimentation rate threshold of 10mg cm^{-2} d^{-1} suggested by Rogers (1990). Rogers (1990) validated the link between this sedimentation threshold and corals reef stress signs. In addition, near-shore coral reef degradation and spatial variation in sedimentation patterns have been widely associated with significant changes in land use at adjacent watersheds (Fabricius, 2005; Smith et al., 2008; Wolanski et al., 2009;

Storlazzi et al., 2009; Risk and Edinger, 2011; Bartley et al., 2014; Hernández-Delgado et al., 2014a; Begin et al., 2016).

The threats associated to unsustainable development of coastal watersheds are prompted by the increasing trend of urban expansion, deforestation, and exposure of bare soil, that increases the potential of soil erosion and sediment-laden runoff during pulse rainfall episodes (López et al, 1998; Fu et al 2010; Ramos-Scharrón et al., 2012, 2015**)**. Other persistent threats are caused by tourism-related activities at sensitive areas and steep slopes, which are highly prone to erosion (Nemeth and Sladek, 2001; Hernández-Delgado et al., 2012, 2014a). In addition, the increasing number of beach visitors and recreational snorkelers could contribute to silt-clay sediment resuspension and impact sensitive coral reef habitats (Webler and Jakubowski, 2016). Throughout the last years, BTA coastal sub-watersheds and its main beach have been subjected to an increase in visitors and at the same time they have become more vulnerable to anthropogenic alteration of coastal areas by deforestation and bare soil exposure (Fig 1.13). In August 2013, watershed best management practices (i.e., bio-filters and reforestation) were implemented in Tamarindo Beach to address storm-water runoff impacts from an unpaved parking area (160 m^2) as it represented one of the main drainage outlets and terrestrial sediment input to BTA (Viqueira-Ríos et al., 2013; Sturm et al., 2014) (Appendix 1.10). Other temporary small-scale mitigation practices (i.e., silt fences) were implemented at upland gully erosion and drainage outlet near to coral reef and seagrass areas, but they had a very limited effect due to their restricted spatial scale and lack of adequate maintenance. The sediments that accumulated along BTA reefs had a proportion of fine, silt-clay (<63 µm) that reached up to 45% during storm seasons. Silt-clay (<63 µm) sediment deposition in BTA reached up to 45%

during storm pulse events. Silt-clay sediment proportion had a significant relationship with total rainfall and rainfall intensity, suggesting that deposition of land-derived sediments is largely affected by local precipitation patterns. It implies that there is a meaningful interconnectivity between watershed condition, land uses, management, and terrestrial sediment impact to near-shore coral reefs largely magnified by pulse events.

A recent study concluded that PSO area had the lowest sediment yield values in Culebra Island (Ramos-Scharrón et al., 2012). However, during the study period the proportion of silt-clay increased (>50%) subsequent to drastic changes in land-based activities and land cover due to an extensive deforestation event (April 2014, Appendix 1.13) of a primary cacti forest located at a steep area for establishing illegal recreational campgrounds, which led to cliff erosion and increased sediment influx to PSO coral reef site (Hernández-Delgado et al., 2014a) (Appendix 1.14, Fig 1.14). During extreme rainfall events, trap accumulation of fine sediments extended to distance zone B (>60m) and silt-clay proportion reached values of up to 94%. These results suggest that significant changes in coastal land use at individual watershed scales can affect delivery of fine sediments and impact coral reefs through large spatial scales (>120m). Fine silts and clays have the ability to remain suspended in the water for prolonged periods of time and can be transported long distances by wind and wave-induced currents (Torres and Morelock, 2002; Hernández-Cruz et al., 2009; Davidson-Arnott, 2010; Fabricius, 2011; Bartley et al., 2014; Edmunds and Gray, 2014). Fine sediments tend to have a major effect on light availability, as they tend to be easily suspended by water turbulence and undergo repeated cycles of deposition and resuspension (Fabricius, 2005). Our results validate the relationship between land

Figure 1.13. Anthropogenic alteration at Bahía Tamarindo coastal sub-watersheds. Installation of road culvert perpendicular to coast line and deforestation of coastal buffer zone in 2012 A); Deforestation along both side of the road due to an increase in vehicle traffic, upland from assessed coral reef site B); Gully erosion and runoff draining from road culvert to assessed near-shore coral reef after acute rainfall event C); and fine silt-clay sediment input close to shore during rainfall event, characterized by superficial sediment distribution produced by differences in salinity as sea water and runoff mix D).

Figure 1.14. Anthropogenic alteration at Punta Soldado coastal watershed. Deforestation event documented in 2014 from assessed near-shore coral reef (zone B, >60m) A); Bare soil exposure and chopped cacti subsequent to deforestation event B); Steep cliff with weathered soil draining towards assessed coral reef site C); and documented additional impact to destabilized and exposed soils by beach visitors with rented vehicles D).

use patterns at the watershed spatial scale, weather and oceanographic conditions on influencing terrestrial-based sediment dynamics.

Our results suggest that changes on the local oceanographic dynamics can also play a significant role on sediment distribution along coastal coral reefs. Overall, wave height and dominant wave period were the main oceanographic forces that combined with rainfall to drive sediment distribution. These patterns were consistent with increased sediment accumulation across the wider Caribbean due to seasonal variation in wave energy by storms and swell events (Edmunds and Gray, 2014). Sediment texture analysis demonstrated that the proportion of sand (>63μm) was greater at BTA reef (>60%) throughout the study period. The statistically significant relationship between sand and wave height (r^2=0.42, p=0.0227) indicates that coarse sediment collected in BTA was mostly influenced by resuspension and bed load transport. Likewise, it suggests that oceanographic dynamics can particularly affect coarse sediment resuspension and bed load transport. Sand sediments and $CaCO_3$ deposit at closer distances to the source, so their transport is mainly driven alongshore and thus resuspension and vertical particle velocities can be limited to periods with strong wave action and swells (Davidson-Arnott, 2010; van der A et al., 2013). Reef bathymetry and depth contour gradient might have also a main role on the generation of wind-induced wave action and near bed shear stress at shallow areas that cause sediment resuspension, as evidenced by differences in sediment texture between sites and distance zones (Ogston et al., 2004; Zou et al., 2006; Storlazzi et al., 2009). Furthermore, this phenomenon is triggered by the ability of fine sediments to deposit between large particles on heterogeneous substrates, since the coarser sediment particles remain more exposed and can be easily resuspended during events of strong water turbulence (Van der A et al., 2013).

In both sites, terrigenous material and CaCO3 caused the largest variation in sediment composition, with a mean proportion of 45% for both constituents. This value is higher than previously documented terrigenous content of 22% from sediment samples collected in coral reefs at southwestern PR (Hernández-Cruz et al., 2009). In contrast, our values were lower than terrigenous content reported from other Caribbean regions, with documented values ranging from 72 to 96% at Saba, from 16 to 87% at St. Lucia (Begin et al., 2013). However, both islands are larger in size, have steeper slopes and larger catchment areas, and rainfall is much higher than in Culebra Island. There is a general trend of decreasing terrigenous material with distance from source. The $CaCO_3$ is a biogenic constituent as it originates from bioerosion of corals and coralline algae, as well as there is direct contribution from organisms with carbonate skeletons, which can be found both in sand and silt-clay grain size fractions (Hubbard et al., 1992; Brooks et al., 2007; Hernández-Cruz et al., 2009;Wolanski et al., 2009). The $CaCO_3$ content on sediments was slightly homogenous along both reefs and it could be hypothesized that near-shore coral reefs may be experiencing similar bioerosion trends at broad spatial scales. Bioerosion might be accelerated by eutrophication (Glynn, 1997; Holmes, 2000). The proximity of coastal reefs to potential eutrophication sources can increase their vulnerability to bioerosion. This is a subject that should be further assessed to understand the reefs $CaCO_3$ production and sinking by component (i.e. coralline algae, coral calcification), and to determine the overall effects of increasing SST and ocean acidification due to climate change on $CaCO_3$ sediment cycling (Hubbard et al., 1992; De Bakker et al., 2016). The organic matter content is the lowest constituent in marine sediment and it has been repeatedly documented (Torres and Morelock, 2002; Brooks et al., 2007; Hernández-Cruz et al., 2009; Begin et al., 2016). Our analysis demonstrated that organic matter represented less than 10% of the total sediment composition. The significant relationship between organic matter and SST can be related to the capability of higher temperature to support organic matter degradation by microbial communities (Arndt et al., 2013).

Sedimentation complements the multiplicity of regional and local stressors that contribute to coral reef decline. It often represents a stochastic stress event and a threat to the health and biodiversity of near-shore coral reefs. This study revealed that even in small tropical semi-arid islands sedimentation associated to rainfall pulses is a recurrent stress, which is linked to local land uses, and to meteorological and oceanographic dynamics. Sedimentation can be identified as a rapidly increasing threat to coral reefs with projected increases in the frequency and severity of extreme weather events, especially intense rainfall after long periods of dry conditions, as a direct consequence of climate change (Giannini et al., 2000; Meehl et al., 2007; Campbell et al., 2011; Beharry et al., 2015). Changing climate trends might also represent an increase in recurrence of terrestrial sediment input to coastal waters, thus leading to chronic states and decline of near-shore coral reefs worldwide. Therefore, as climate variability is projected to continue intensifying across larger spatial and temporal scales (Easterling et al., 2000), there is a need of long-term monitoring of land-sea interactions through coastal-marine sediment distribution to understand the threat it might represent towards endangered coral species, and benthic communities, fostering the long-term degradation of ecosystem functions. Future research could aim to assess sedimentary records through sediment core analyses to identify since when anthropogenic alterations of coastal watersheds have impacted spatial and temporal trends of terrigenous sediment deposition on the marine environment and the combined effects of climatic variation. In addition, assessment of mineralogical composition of surficial marine sediments could assist to identify point sources at the watershed and island-scales and needs further monitoring. Other essential component that needs to be addressed is the assessment of radiological and toxicological content of contaminants, and heavy metals on marine sediments. In the particular case of Culebra and nearby Vieques Island, terrigenous sediments originate from leakage from formerly bombing grounds, which still have a vast amount of unexploded ordnance (UXO). Coral reef habitats impacted by military practices present physical destruction by craters and altered benthic communities with lower coral species diversity and percent coral cover (Hernández-Delgado et al., 2014b). In addition, sediments have high concentration of explosive compounds, such as TNT and chromium (Porter et al., 2011). However, potential toxicological effects on coral reefs still remain unknown.

A possible limitation of the study was the physical and meteorological conditions experienced during study period, which were characterized by an extended period of drought during summer season that altered the original projected sampling time frame, and prevented sampling of more extreme rainfall events. Extreme events were limited to winter and spring season with combined conditions of strong rainfall and wave energy, main forces that produce terrestrial sediment influx to coastal waters followed by resuspension of bottom sediments. These mixed conditions represented a limitation to distinguish the main sources of sedimentation. In Culebra Island there is a lack of permanent meteorological stations to provide easy access to detailed 15-

minute intervals weather conditions, and the existing buoy was more representative of open ocean conditions, since it is located about 10-15 km from the coast. Future research should take into account the need of downscaling local environmental, weather and oceanographic data for accurate analysis, modeling, and to contribute valuable information for coral reef conservation and ecosystem restoration strategies.

The near-shore coral reefs surrounding small islands need an integrated and holistic management approach to conserve and rehabilitate ecosystem resilience and functions, including:

- Long-term commitment of stakeholders (community-based, natural resources managers, academia) to cope with future trends of climate variability, following ecosystem-based management principles.
- Design and implement integrated and adaptive coastal management strategies that address coastal maritime zone and watershed management needs in order to reduce soil erosion and sediment delivery at the watershed and sub-watershed scales, and reduce runoff impacts to adjacent sensitive habitats, such as coral reefs.
- Reduce local stressors that are threatening the viability of coral reef restoration efforts. Strong evidence has already showed that recurrent extreme rainfall events and storm-associated impacts are a major threat for the success of coral farming and reef restoration efforts (Hernández-Delgado et al., 2014a). Efforts need to be taken to reduce or eliminate major sources of soil erosion and sediment delivery stress.
- It is essential to assess sediment fluxes before, during and after implementation of watershed best management and restoration practices in order to be able to

identify the short-term outcomes of erosion control practices along near-shore coral reefs, and to use the generated information to accurately anticipate long-term implications for coral reef benthic communities.

- These holistic approaches also need the support and enforcement of environmental, land-use, and protected area regulations, promote the use and integration of data generated through participatory citizen science and academia into management, decision making processes, and prioritize the need of collaborative actions that promote sustainable restoration and conservation initiatives at the watershed and coral reef scales to prevent further degradation of already threatened coral reefs.

Spatial and temporal sedimentation dynamics along near-shore coral reefs are linked to land-sea and climate interactions. Our results highlight the existing interactions among land use patterns, coastal watershed conservation, and management on its direct influence on sediment supply, distribution and sedimentation stress to near-shore coral reefs. Our results point out five main conclusions: 1) Human alteration of sensitive, highly erodible watersheds adjacent to coastal areas influence the amount, extent and recurrence of terrestrial sediment stress to near-shore coral reefs; 2) Local climate has a significant effect on terrestrial sediment input and distribution, even on semi-arid islands, since total rainfall and intensity, and rainfall pulse events are the main driving forces of sedimentary dynamics at watershed scales; 3) Sediment texture, sand and silt-clay grain size fractions, and sediment composition along near-shore marine environments vary according to local climate and oceanographic conditions. Wave height and dominant wave period determine sediment resuspension and bed load transport; 4) Reef zones closer to shore (<60m) are more exposed to sedimentation stress, and vulnerable to changing sediment dynamics, including fine silt-clay sediments and terrigenous sediment deposition. During doldrum conditions fine sediments tend to remain suspended for prolonged periods of time and it thus may represent broader impact into marine ecosystems across larger spatial scales (>60m), mostly depending on climate and local oceanographic dynamics; and 5) As a consequence, terrestrial sediments were identified as the main constituent of marine sediments, representing a major threat to coral reefs and associated ecosystems at extended spatial and temporal scales. The extent to which climate-related changes influence local weather, which could result in increased frequency and severity of extreme weather events, combined with unsustainable land use practices and the lack of watershed conservation practices, may increase the long-term adverse impacts of sediment delivery to coral reefs. Therefore, the need of implementing a participatory approach, which aims to achieve integrated management of coastal watersheds, coral reefs, and other benthic habitats, is emphasized. This is a fundamental step towards identifying and implementing effective collaborative actions and adaptive management strategies to reduce land-based threats, reverse coral reef decline, and recover ecosystem and structural resilience. Furthermore, decision-making processes should make adequate use of science-based information that advance understanding of terrestrial and marine ecosystem interconnectivity to implement watershed and coral reefs management plans and restore degraded habitats. Integrated ecosystem-based management can provided an adequate framework to implement concerted efforts, such as sustainable land use practices, coastal and marine ecosystem rehabilitation, outreach, and conservation strategies aimed at maximizing ecological integrity and resilience of coral reefs worldwide.

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CHAPTER 2

RESPONSE OF NEAR-SHORE CORAL REEFS BENTHIC COMMUNITIES TO CHANGES OF SEDIMENTATION DYNAMICS AND ENVIRONMENTAL CONDITIONS

Abstract

Coral reefs are facing unprecedented global, regional and local threats that continue to degrade shallow, near-shore habitats. Water quality degradation due to unsustainable development practices at semi-arid watersheds may be one of the greatest threats to coral reefs across multiple spatial and temporal scales. The goal of this study was to assess spatio-temporal variation in coral reef benthic community response to variations in sedimentation patterns, changing land uses, weather, and oceanographic dynamics to assist in the implementation of management strategies that aims to stimulate coral reef recovery and conservation of biodiversity. Our objective was to assess seasonal coral colony density, coral recruit density, and benthic community composition at near-shore coral reefs of Bahía Tamarindo (BTA) and Punta Soldado (PSO) Culebra Island, Puerto Rico. Benthic data were collected at a distance gradient from shore, from February 2014 to 2015, through high-resolution images of $10m^2$ permanent belt transects. Environmental data were assessed and contrasted with changes in benthic assemblages with multivariate BEST BIO-ENV, RELATE correlation, and multiple linear regressions. There was a significant difference in coral species assemblages between seasons, site and distance zones (PERMANOVA, $p<0.0100$). The most conspicuous coral species and coral recruits at near-shore areas were sediment-tolerant *Porites astreoides*, *P. porites* and *Siderastrea radians.* A total of 11 coral recruit species were documented across sites. Benthic species composition implies there is increasing dominance by non-reef building taxa. Mean recruit density was of $1.96m^{-2}$ at BTA and $0.8m^{-2}$ at PSO. Difference in coral density and coral recruits had strong relationship with sediment characteristics ($p<0.0500$). Coral species diversity (H'n) increased at both sites with distance from shore. Coral cover was significantly lower at distance zone more exposed to recurrent sedimentation

stress ($p<0.0100$), it was strongly influenced by sediment texture ($p=0.0060$) and terrestrial sediment content ($p=0.0160$). Benthic components changed in response to sediment stress, especially there was an increased benthic cover by encrusting macroalgae *Ramicrusta textilis,* and invasive sponge *Dyctionella funicularis,* as coral cover decline due to exposure to sedimentation stress. This result highlights the existing link between the coral reef health, land use patterns, coastal watershed conservation and management that determines sediment supply and distribution along near-shore coral reefs. Understanding individual and cumulative factors that produces changes in water quality, sedimentation dynamics, and coral reefs benthic community response is fundamental to implement integrated watershed and coral reef management strategies aimed to reduced local stressors, enhance its recovery, and conservation. Expansion of marine conservation efforts becomes more urgent in context of future climate with projected increase on sea surface temperature, sea level rise, among other global warming-related factors, since it represents serious implications to the resilience of coastal regions. Collaborative and trans-disciplinary efforts based on ecosystem-based management framework have the potential to preserve coral reefs biodiversity and provide an optimistic future for marine species and human communities, which livelihoods and subsistence depends on healthy coral reefs.

Introduction

Coral reefs are affected by a wide array of global, regional and local stressors that has led to habitat degradation worldwide during recent decades (Hughes, 1994; Gardner et al., 2003; Wilkinson, 2008). Global and regional trends of coral decline are associated to anthropogenic stressors combined with climate change-related impacts and natural disturbances (Eakin et al., 2010; Wild et al., 2011; Bozec and Mumby, 2015; Hernández-Delgado, 2015). At a local scale, land-based stressors represent a major threat to near-shore coral reefs in the Caribbean region mostly from increasing trends of land-use changes, coastal urban sprawl and tourism-based activities with direct implications on sediment-laden runoff and sediment distribution along coastal waters (Rogers, 1990; Larsen and Webb, 2009; Hernandez-Delgado et al. 2012; Ramos-Scharrón et al., 2012, 2015; Bégin, et al., 2013). Consistent alterations of coastal watersheds on small tropical semi-arid islands, in combination with changes on local rainfall patterns, have produced alteration of sediment distribution along near-shore coral reef ecosystems (Otaño-Cruz, Chapter 1 M.Sc. Thesis). Intensification of terrestrial sediment delivery to coastal habitats increases coral reef vulnerability and susceptibility to experience phase-shifts favoring dominance of non-reef building taxa and macroalgal assemblages (Bellwood et al., 2008; Dudgeon et al., 2010; Hughes, 2010). Therefore, there is major concern regarding the potential effects of elevated terrestrial sediment delivery to coastal waters and changes in environmental conditions, especially on coral reef habitats adapted to historical low levels of sedimentation, since it can have profound permanent effects on reef ecosystem functions and services (Acevedo et al., 1988; Bellwood et al., 2004; Hughes, 2010).

The short-term response and the spatial extent from local disturbances responds to the frequency, duration, distance from source and sediment characteristics (Fabricius, 2005; Smith et al., 2008; Edmunds and Gray, 2014). Likewise, recurrent environmental disturbances have adverse implications on benthic communities by producing shifts in ecological dynamics and it can have major impact on populations of endangered coral species (Díaz-Ortega and Hernández-Delgado, 2014). It is crucial to understand the short-term response of coral reef benthic community structure and composition to sedimentation stressors to achieve the development of effective and adaptive ecosystem-based management strategies to prevent further decline and enhance coral reef resilience (Rivera-Monroy et al., 2004; Alvarez-Filip et al., 2009; Mumby and Steneck, 2011).

Sedimentation stress has been associated with localized and partial coral mortality, reduced coral growth rate, inhibited larval settlement, and reduced fish grazing (Loya, 1976; Nugues and Roberts, 2003; Fabricius, 2005; Bellwood and Fulton, 2008). Impacted coral reefs have a potential loss of sensitive species, thus reinforcing phase shifts towards sediment-resistant species, algal dominance, and non-reef building taxa (Acevedo et al., 1989; Bellwood et al., 2004; Hughes, 2010; Fabricius, 2005; 2011). Changes on species composition can produce significant changes on structural complexity and functioning by reducing reef accretion and rugosity (Alvarez-Filip et al., 2013). Coral reefs exposed to recurrent sediment pulses and high turbidity levels have also limited ability to recover after chronic disturbances (i.e, bleaching caused by high SST) and increased vulnerability can intensify prevalence of diseases (Cróquer et al., 2002; Toledo-Hernández et al., 2007; Pollock et al., 2014; Stubler et al., 2016). As a result, the implementation of mitigation and restoration projects at watershed and coral reef scale have become a management priority and scientific information related to existing land-sea and climate dynamics becomes critical for the implementation of rapid and effective strategies.

Recent decline in live coral cover across the Caribbean region have been largely attributed to increased sediment delivery to coastal waters after heavy rainfall events due to increasing trends of unsustainable development and alteration of coastal watersheds (Ramos-Scharrón and MacDonald, 2007; Hernández-Delgado et al., 2011, 2012, 2014a; Ramos-Scharrón et al., 2012; Sturm et al., 2014). The combined effects of anthropogenic impacts to coastal habitats and coral reefs due to increasing land-based source of pollution (LBSP), nutrients, declining water quality and the reduction in grazing due to overfishing lead to optimum conditions for macroalgal overgrowth, thus represents unfavorable conditions for coral reef recovery (Hughes et al., 1999; Rogers and Miller, 2006; Jackson et al., 2014 Ennis et al. 2016). Climate related impacts, such as seasonal changes in rainfall patterns, increased SST, and ocean acidification contributes to live coral cover decline and might produce shifts in benthic community species composition (Miller et al., 2009; Hernández-Pacheco et al., 2011; Edmunds 2013). Rapid trends of sea level rise represent a severe threat to coral reefs globally, since corals could drown due to disruption in reef accretion balance, thus making coastal regions more vulnerable to erosion and sediment transport by wave exposure during storms and swells events (Knowlton, 2001; Hoegh-Guldberg et al., 2014).

The goal of this study was to assess if there was a significant spatio-temporal difference in the short-term response of benthic communities to variations in sedimentation patterns and environmental variables. Therefore, this study was aimed to: i) Assess variation in coral reef benthic community structure through species density, diversity, coral recruit density, percent live coral cover, algal functional group, and other benthic components dynamics in a distance gradient from the shore; and ii) Contrast spatio-temporal changes in coral reef benthic community structure with sedimentation patterns, and other environmental variable dynamics.

Methods

Study site

The study was conducted from February 2014 to February 2015 across two shallow near-shore coral reefs at Culebra Island, Puerto Rico: Bahía Tamarindo (BTA) and Punta Soldado (PSO) (Fig. 1.1, Chapter 1). In BTA the study was conducted at El Banderote reef, located within the Canal Luis Peña Natural Reserve, which is colonized bedrock with moderate relief (Appendix 2.1). The BTA reef has low structural complexity with a mean depth of 2 m. In PSO the study was conducted at a linear reef with higher structural complexity (Appendix 2.2). Reef's structural complexity at PSO reef was higher farther from shore, due to the remaining structure of reef-building Columnar star coral *Orbicella annularis,* which used to dominate benthic composition (Hernández-Delgado, 2000; Hernández-Pachecho et al., 2011). Changes in coastal watersheds land use have been prompted in BTA due to increased beach popularity, vehicle traffic, tourist visitation, and sporadic deforestation events that caused soil exposure and destabilization (Hernández-Delgado, 2014a). In contrast, PSO watershed land use experienced a drastic transforming by a deforestation event during study period that increased terrestrial sediment influx to coastal waters (Otaño-Cruz, Chapter 1 M.Sc. Thesis).

Sampling design and analysis

Permanent belt transects of 10 x 1 m (10 m^2), parallel to the coastline, were assessed at seasonal intervals for a period of one year, with a total of ten replicate, one m^2 high-resolution photo-quadrat images per transect. Each monitoring station consisted of triplicate fixed transects. Fixed transects were located within a distance of less than 10m from sediment traps. Benthic assessment in BTA was conducted across a total of three replicate monitoring stations within distance zone A (<60m from shore), with a depth range from 1 to 2 m, and three replicate stations in distance zone B (>60m from shore), with depth range contour from 2 to 3.5m (Appendix 2.3). In PSO there were a total of two monitoring stations within zone A, with a depth range from 1 to 2.5 m, and two stations in zone B, with a depth range contour from 2.5 to 4.5m (Appendix 2.4).

Coral reef benthic community characterization

Scleractinian, hydrocoral and octocorals populations were assessed in each transect to the lowest taxonomic level possible to generate information regarding colony density, species richness (S), species diversity index (H'n) (Shannon & Weaver, 1948), and evenness index (J'n) (Pielou 1966) at each site. Scleractinian coral recruit density was also assessed, specifically for colonies ≤4 cm in diameter for larger species (e.g., *Pseudodiploria* spp., *Siderastrea siderea*), and ≤2 cm for smaller species (e.g., *Porites astreoides*) (Dueñas et al., 2010). Benthic components cover was assessed from high-resolution images by digitally projecting a total of 48 regularly distributed dots over each photo-quadrat image. Benthic components under each dot were identified, including Scleractinian coral, hydrocoral, and octocoral species, sponges, macroalgae, algal turf, coralline algae (CA) (includes erect and crustose calcifying species), cyanobacteria cover and other benthic components (e.g., sand, pavement, rubble). Algal turf was classified as a mix of short algae (<1 cm) and sediments (NOAA, 2015). Data was used to calculate percent benthic component cover and benthic community structure.

Statistical analyses

Benthic components were tested using four-way non-parametric permutational analysis of variance (PERMANOVA) and pairwise comparison for the fixed factors of seasons, time, site and distance from shore (Anderson et al., 2008). Multivariate analysis were performed in Primer v7 and + PERMANOVA v1.16 software (Plymouth Marine Laboratory, UK) to analyze spatio-temporal variation in coral colony density, coral recruit density, and benthic community structure (Clarke et al., 2014; Clarke and Gorley, 2015). Rank order of dissimilarities was calculated through Bray-Curtis resemblance from coral densities, coral recruit density and benthic community matrices. For coral recruitment, a zero-adjusted Bray-Curtis resemblance matrix was calculated, including a "dummy variable" to reduce distortion from absent species by samples (Clarke et al., 2006).

Ordination were performed using non-metric multi-dimensional scaling (nMDS) and principal coordinates ordination (PCO), by calculating the distance among centroids, to display in a three dimensional space the variations in benthic communities and determine which benthic component explained spatio-temporal variation. Vectors were superimposed to assess significance of sediment and environmental variables on influencing benthic coral reef community structure dynamics. Cluster and similarity profile test (SIMPROF) were used to identify groups with similarity differences between samples to test the null hypothesis of no significant spatial and temporal differences on multivariate structure of benthic assemblages. Afterwards a similarity percentage (SIMPER) analysis routine was performed to determine which key taxa contributed most to similarities and spatial variation in the benthic community structure through time, within sites, and distance (Clarke et al., 2014).

Environmental variables were correlated with the biological matrices using non-parametric multivariate correlation routine BEST-BIO ENV (Spearman rank correlation) to determine the best environmental variable that explained differences in coral reef benthic community spatio-temporal variation (Clarke et al., 2014). RELATE routine was used to test the relationship between coral recruit density and percent macroalgal cover, with sedimentation and other abiotic variables. DISTLM was performed for multiple linear regression analysis to assess potential effects of environmental variables on coral colony density, coral recruit density, and benthic cover with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008). The routine is based on a multivariate regression between the response variable (coral recruit density, colony density, percent coral cover) and the predictor variables (sedimentation patterns).

Coral colony density, coral recruit density, and percent benthic community parameters were standardized to balance the contribution of common and rare species and thus represented the relative percentage of species for each sample. Species assemblages were also square root-transformed prior to analysis (Clarke and Warwick, 2001). All multivariate tests were based in 10,000 permutations (Hernandez-Delgado, et al., 2014b). Sediment variables and environmental data, including weather and hydrodynamic data, were $\log_{10}$-transformed prior to analysis to meet assumptions of normality and homogeneity of variance (Smith et al., 2008; Gotelli and Ellison, 2013). Sigma Plot v.11 (Systat Software, Inc.) was used for graphical representation of biological data.

Results

Coral colony density

Overall mean coral density (± 95% confidence interval) at two near-shore coral reefs of Culebra Island was 13.18±0.92m^{-2}. Coral colony density was higher at BTA with a mean 13.77±0.92m^{-2}. The highest coral density value at BTA was documented along distance zone B (>60m from shore), with a mean of 17.95±1.27m^{-2} (Appendix 2.3). Coral density across distance zone B experienced an increase of 15% from spring (16.75m^{-2}) to summer (19.37m^{-2}) season, but afterwards coral colony density decrease 15% from fall to winter season, ending with a coral density of 16.31m^{-2} (Fig. 2.1). The lowest value of coral density at BTA was recorded at distance zone A (<60m from shore), with a mean of 9.59±0.94m^{-2} (Appendix 2.3). Within distance zone A, coral density experienced some variations with an increase from spring (8.72m^{-2}) to fall (9.98m^{-2}), and afterwards a slight decrease towards winter season (9.97m^{-2}). Coral density at BTA was significantly different by distance zones (Pair-wise, t=3.49, p=0.0001). Mean coral density was lowest at PSO with a mean 12.29±1.29m^{-2}. The highest coral density value at PSO was documented along distance zone A, with a mean of 12.78±4.68m^{-2} (Appendix 2.4). Coral density across distance zone B experienced an increase of 13% from spring (10.65m^{-2}) to summer (12.07m^{-2}) season, but afterwards density decrease 5% from summer to fall and stayed stable through, ending with a coral density of 11.58m^{-2}. Coral density at PSO was significantly different by distance zones (t=4.02, p=0.0001). Coral density at both distance zones experienced multiple variations through seasons (Fig. 2.1). The documented patterns showed there were significant differences of coral abundance by seasons (Pseudo F=2.38, p=0.0002), sites (Pseudo F=36.96, p=0.0001), and distance zones (Pseudo F=9.98, p=0.0001) (Table 2.1).

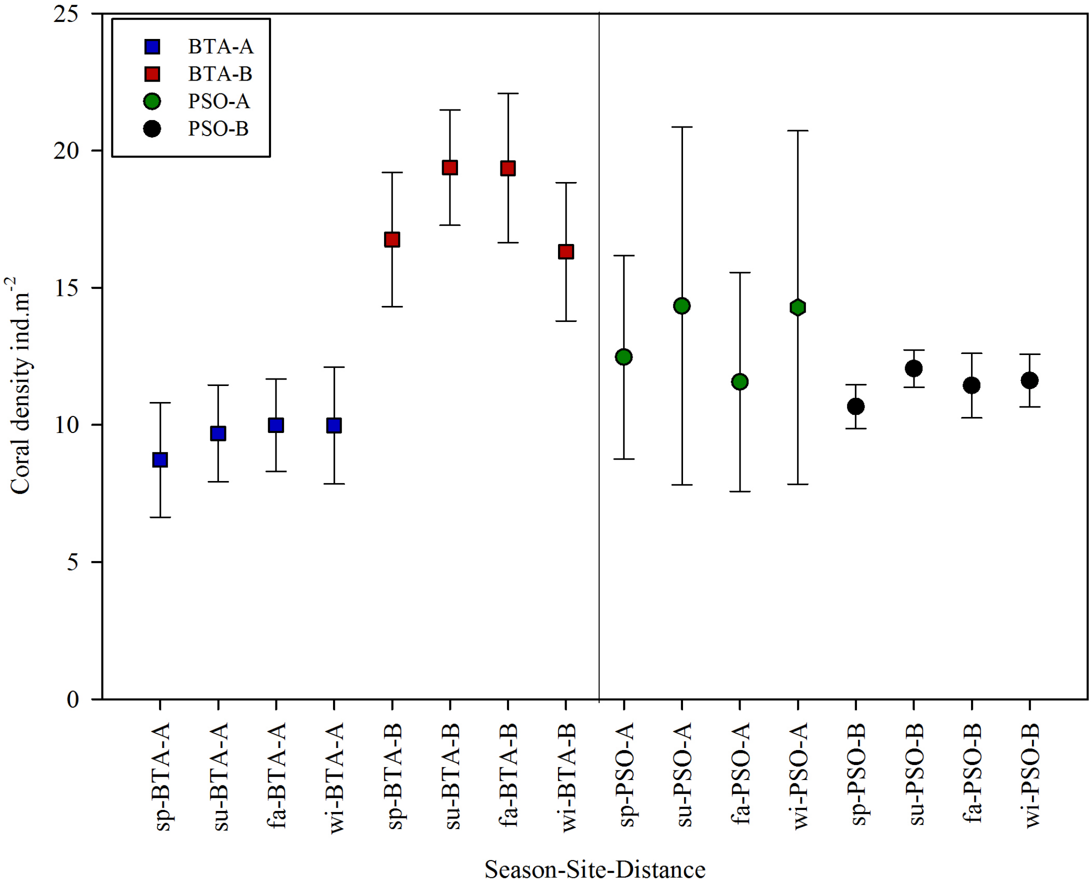

Figure 2.1. Mean coral density by m^2 (mean± 95% CI) by season, site, and distance zone. Coral density includes hard corals, hydrozoans and gorgonians. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.1. Results of permutational analysis of variance (PERMANOVA) coral density

	Coral density		
Factors	df	Pseudo *F*	*P* (perm)
Season (Se)	3	1.71	0.0112
Site (Si)	1	32.09	0.0001
Distance (Di)	1	10.16	0.0001
Se x Si	3	1.35	0.0933
Se x Di	3	0.77	0.8141
Si x Di	1	18.74	0.0001
Se x Si x Di	3	0.75	0.8338

The scleractinian coral species with highest mean relative abundance at BTA were *Porites astreoides* (24.54%), *P. porites* (11.40%), *Acropora cervicornis* (5.84%), *Siderastrea siderea* (5.76%), *Pseudodiploria strigosa* (5.66%), *Diploria labyrinthiformis* (5.03%), S. *radians* (4.59%), *and Agaricia agaricites* (3.48%), representing a total of 66.30% of species contribution. The hydrocorals *Millepora alcicornis* and *M. complanata* had a higher percent relative abundance at BTA with a mean of 16.54% and 2.35%, respectively. The relative abundance of corals *A. cervicornis, D. labyrinthiformis*, *P. strigosa,* and octorcorals *Antillogorgia americana,* and *Plexaura homomalla* decreased from spring to winter seasons at distance zone A and increased through seasons at distance zone B (Fig. 2.2). In contrast, the relative abundance of *O. annularis*, *P. astreoides, S. radians*, *S. siderea*, *M. alcicornis* and *Gorgonia ventalina* decreased trough seasons at both distance zones. The only species that showed a pattern of increased relative abundance through time at both distance zones was *Porites porites.*

At PSO, coral species with the highest mean relative abundance were *P. astreoides* (31.06%), *P. porites* (10.15%), *O. annularis* (10.14%), *S. siderea* (3.30%), *P. strigosa* (2.53%), and representing a total of 57.18%. However, gorgonians had higher relative abundance at PSO with a mean of 11.87% composed by *A. americana*, *Eunicea flexuosa, Gorgonia ventalina*, and *P. homomalla*. In contrast, gorgonians at BTA represented a mean relative abundance of 5.08%. Relative abundance at PSO of corals species *D. labyrinthiformis* and *P. porites* decreased from spring to winter seasons at distance zone A and increased through season at distance zone B (Fig. 2.2). In contrast, the relative abundance of *O. annularis*, *P. strigosa,* and *Gorgonia ventalina* decreased through seasons at both distance zones. The species that showed

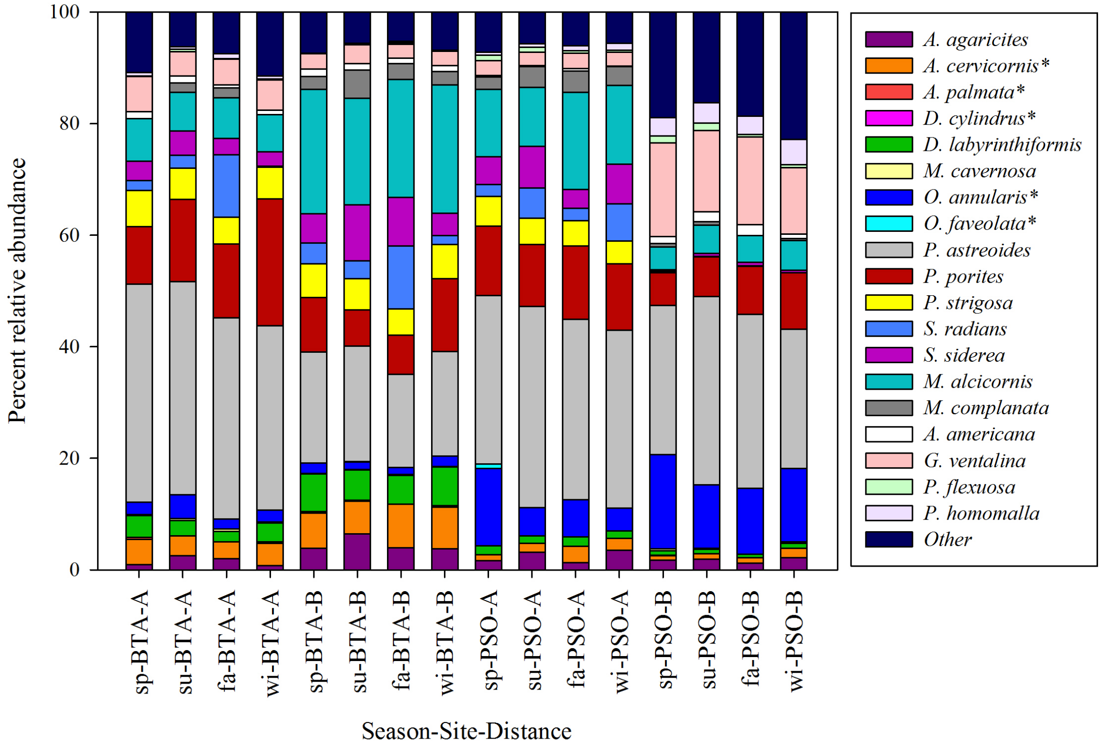

Figure 2.2. Percent relative abundance of scleractinians, octocorals and octocoral species by season, site and distance zones. Colors represent coral species and asterisk identifies coral species listed as threatened under the Endangered Species Act (Federal Register 2014). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

patterns of increased relative abundance through time at PSO at both distance zones were *A. cervicornis, U. agaricites,* and octocoral *P. homomalla.*

The most conspicuous coral species at reef segments exposed to sedimentation stress were *P. astreoides* and *P. porites*, species that dominated coral reefs at BTA and PSO in areas closer to shore (Table 2.2). In contrast, *A. cervicornis*, which is less resistant to environmental stressors, had higher relative abundance at BTA reef segment farther from shore, with a mean value of 6.87% (Table 2.2). At PSO, *A. cervicornis* had higher relative abundance at reef segment closer to shore with a mean value of 1.91%. At both reef sites these are the most active zone of Sociedad Ambiente Marino's *Community-Based Coral Aquaculture and Reef Rehabilitation Program* and its coral reef restoration project conducted since year 2003. Therefore, most part of the living coral colonies were initially transplanted and have successfully attached and grown in areas less impacted by environmental stressors. At PSO the most conspicuous species at reef segment farther from shore were stress resistant *P. astreoides* (29.19%) and *O. annularis* (13.29%).

Table 2.2. Mean percent relative density at sites and site by distance zone

	Percent relative abundance					
Species	**BTA**	**BTA-A**	**BTA-B**	**PSO**	**PSO-A**	**PSO-B**
Acropora cervicornis	5.84	3.78	6.88	1.54	1.92	1.12
Acropora palmata	0.12	0.15	0.10	0	0	0
Agaricia agaricites	3.48	1.55	4.48	2.09	2.38	1.74
Dendrogyra cylindrus	0.05	0	0.07	0.02	0	0.04
Diploria labyrinthiformis	5.03	2.95	6.08	1.15	1.50	0.76
Montastraea cavernosa	0.16	0.31	0.07	0.08	0	0.18
Orbicella annularis	1.93	2.57	1.58	10.14	7.43	13.29
Orbicella faveolata	0.01	0	0.01	0.11	0.20	0
Orbicella franksi	0.01	0	0.01	0	0	0
Porites astreoides	23.53	36.60	19.05	31.06	32.63	29.19
Porites porites	11.40	15.26	9.07	10.15	12.15	7.88
Pseudodiploria clivosa	0.79	1.10	0.60	0.53	0.99	0
Pseudodiploria strigosa	5.66	5.64	5.61	2.53	4.63	0.11
Siderastrea radians	4.59	3.88	4.97	2.25	4.14	0.04
Siderastrea siderea	5.76	3.31	6.99	3.29	5.70	0.47

PCO plot identified four major groups from the coral abundance structure by season, sites, and distance zones (Fig. 2.3). The groups distinguished major variations on coral density patterns between distance zones A and B from both sites. The coral density at BTA distance zone A seemed to differ on winter season and it can be attributed to the increase of coral density from spring to winter. The seasonal variations of coral community within distance zone A had higher similarity between BTA and PSO due to the proximity of both clusters. In contrast, coral community at distance zone B had major difference between both sites with clusters farther apart. The proposed PCO explains 74% of the variation between and within groups.

The SIMPER analysis revealed that the species that mostly contributed to the different patterns of coral density between sites was *O. annularis* (7.45% contribution), *M. alcicornis* (6.41%), and *P. strigosa* (4.86%), *S. radians* (4.83%), totaling 23.55% of the observed variation (Table 2.3). The average dissimilarity between sites was 49.69% and a total of 19 species contributed to explain 70% of total dissimilarity. The species that mostly contributed to explain the differences between distance zones were *M. alcicornis* (7.31%), *P. porites* (5.82%), *P. astreoides* (5.44%), and *Orbicella annularis* (4.92%), totaling 23.49% of the observed variation (Table 2.3). Average dissimilarity between distance zones was 43.70% and a total of 20 species contributed to explain 70% of the total dissimilarity.

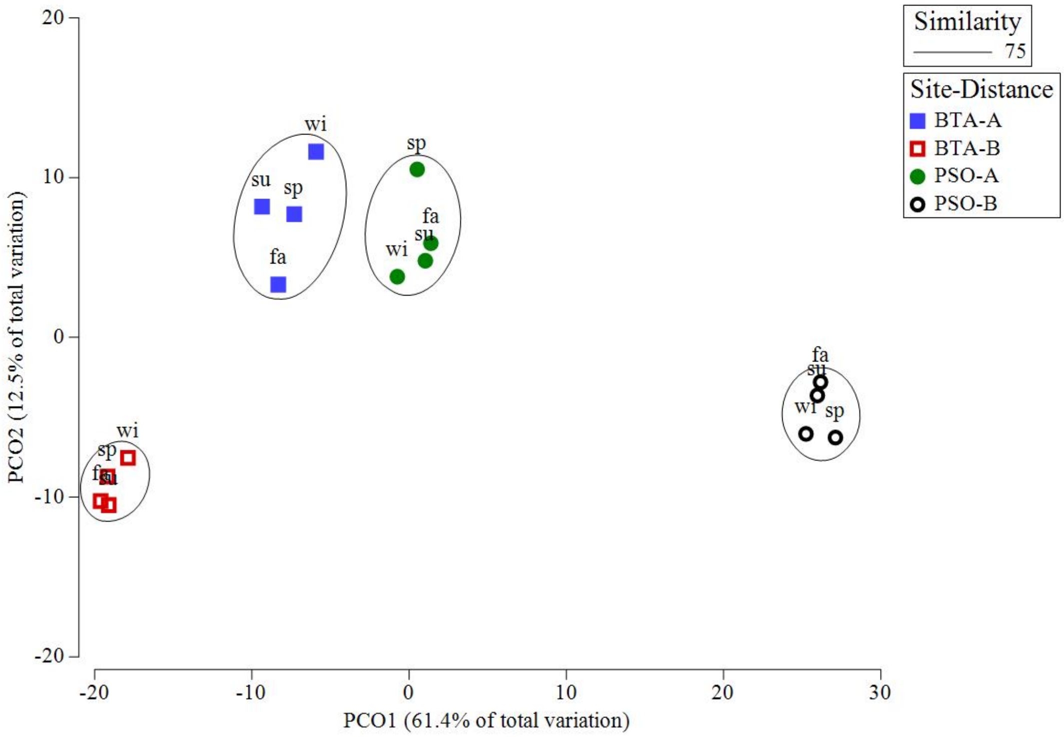

Figure 2.3. Principal coordinates ordination (PCO) plot of distance among centroids of coral colony denisty based on Bray-Curtis similarity matrices performed on a square root-transformed data by seasons-site-distance. Clusters represent groups with 75% similarity. Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.3 Two-way similarity percentage (SIMPER) of coral abundance. Site by distance zones.

Species	Average abundance	Average abundance	Individual contribution (%)	Cumulative contribution (%)
SITE	**BTA**	**PSO**		
Orbicella annularis	1.05	3.1	7.45	7.45
Millepora alcicornis	3.52	2.5	6.41	13.86
Pseudodiploria strigosa	2.18	0.81	4.86	18.72
Siderastrea radians	1.59	0.59	4.83	23.55
Siderastrea siderea	2.08	1.05	4.79	28.34
Gorgonia ventalina	1.94	2.74	4.60	32.95
Acropora cervicornis	1.81	0.69	4.56	37.50
Porites porites	2.97	3.22	4.34	41.84
Eunicea	0.31	1.66	4.32	46.17
Diploria labyrinthiformis	1.85	0.66	4.10	50.26
Porites astreoides	5.11	5.43	3.83	54.10
Millepora complanata	1.02	0.67	3.61	57.71
Plexaura homomalla	0.37	1.25	3.36	61.06
Undaria agaricites	1.45	1.27	2.97	64.03
Eunicea mammosa	0.34	0.99	2.95	66.98
Antillogorgia americana	0.86	0.55	2.28	69.26
Eunicea flexuosa	0.15	0.77	2.21	71.47
Plexaura	0.44	0.5	1.97	73.44
Pseudoplexaura	0.38	0.54	1.96	75.40
DISTANCE	**A**	**B**		
Millepora alcicornis	2.6	3.62	7.31	7.31
Porites porites	3.59	2.55	5.82	13.12
Porites astreoides	5.79	4.69	5.44	18.57
Orbicella annularis	1.63	2.1	4.92	23.49
Siderastrea radians	1.25	1.14	4.83	28.32
Acropora cervicornis	1.29	1.44	4.74	33.06
Gorgonia ventalina	2.02	2.5	4.22	37.28
Siderastrea siderea	1.66	1.67	4.21	41.49
Millepora complanata	0.71	1.06	4.07	45.57
Undaria agaricites	1.13	1.62	3.77	49.34
Pseudodiploria strigosa	1.9	1.37	3.50	52.84
Diploria labyrinthiformis	1.17	1.57	3.49	56.33
Eunicea	0.48	1.21	2.92	59.25
Eunicea mammosa	0.39	0.81	2.71	61.96
Plexaura homomalla	0.57	0.88	2.54	64.50
Antillogorgia americana	0.54	0.93	2.52	67.02
Pseudodiplora clivosa	0.65	0.3	2.31	69.33
Plexaura	0.47	0.47	2.19	71.52
Pseudoplexaura	0.4	0.48	2.08	73.59
Briareum asbestinum	0.5	0.34	2.03	75.62

Species richness, diversity and evenness

A total of 66 species were documented (34 scleractinians, 2 hydrocorals, and 30 octocorals) in both sites. The highest mean coral species richness (S) at BTA was recorded at distance zone B with a mean of 18.11±1.18. The highest mean S at BTA distance zone B was recorded in summer with 18.89±3.36 (Fig 2.4A). Mean S decreased from spring to winter at both distance zones. Overall, the highest total coral species richness between sites was recorded at PSO in distance zone B (>60m from shore) with a mean S of 18.63±1.19 (±CI 95%). The highest S recorded at PSO within distance zone B was in winter season with a mean of 20.60±2.56 (Fig 2.4B). However, species richness at PSO experienced multiple variations through seasons along both distance zones. The lowest values were recorded during fall season, with a mean of 13.83±2.74 at distance zone A, and 16.16±1.63 at distance zone B. Species richness showed significant differences by distance zones (Pseudo F=1.37, p=0.0010), but no difference was recorded between seasons (Pseudo F=1.41, p=0.2300), or sites (Pseudo F=0.91, p=0.3300) (Table 2.4).

Coral species diversity (H'n) showed contrasting patterns by sites. In BTA H'n was higher in distance zone B (Appendix 2.6), with the highest value recorded during the summer with a mean of 2.30±0.14 (Fig. 2.4C). At both distance zones H'n declined gradually from spring 2.11±0.25 to winter season 1.99±0.22, representing a percent change of -5.98%. The highest H'n between sites was recorded at PSO distance zone B with a mean of 2.27±0.07 (Appendix 2.5). At PSO H'n increased from spring to winter at both distance zones (Fig. 2.4D). However, at distance zone B the lowest value of H'n was recorded in fall with a mean 2.16±0.11. The lowest values across distance zone A was documented during the spring with a mean of 1.90±0.24. H'n showed significant differences by distance zones (Pseudo F=32.22, p=0.0010), but no difference was recorded between seasons (Pseudo F=0.44, p=0.7200) or sites (Pseudo F=0.04, p=0.8500) (Table 2.4). Lower H'n values were recorded at both sites along distance zone A, area mostly disturbed by runoff and sedimentation. The evenness (J'n) shows that BTA have higher difference in species dominance between distance zones, with a higher evenness in distance zone B (Fig. 2.4E). J'n at BTA showed a pattern of rapid decline at distance zone A through seasons, reflecting greater changes in species dominance. J'n at PSO had similar patterns of increasing evenness across both distance zones through seasons (Fig. 2.4F). There was significant difference in J'n by distance zones (Pseudo F=12.24, p=0.0020) (Table 2.4), this pattern is mostly attributed to temporal changes in species diversity.

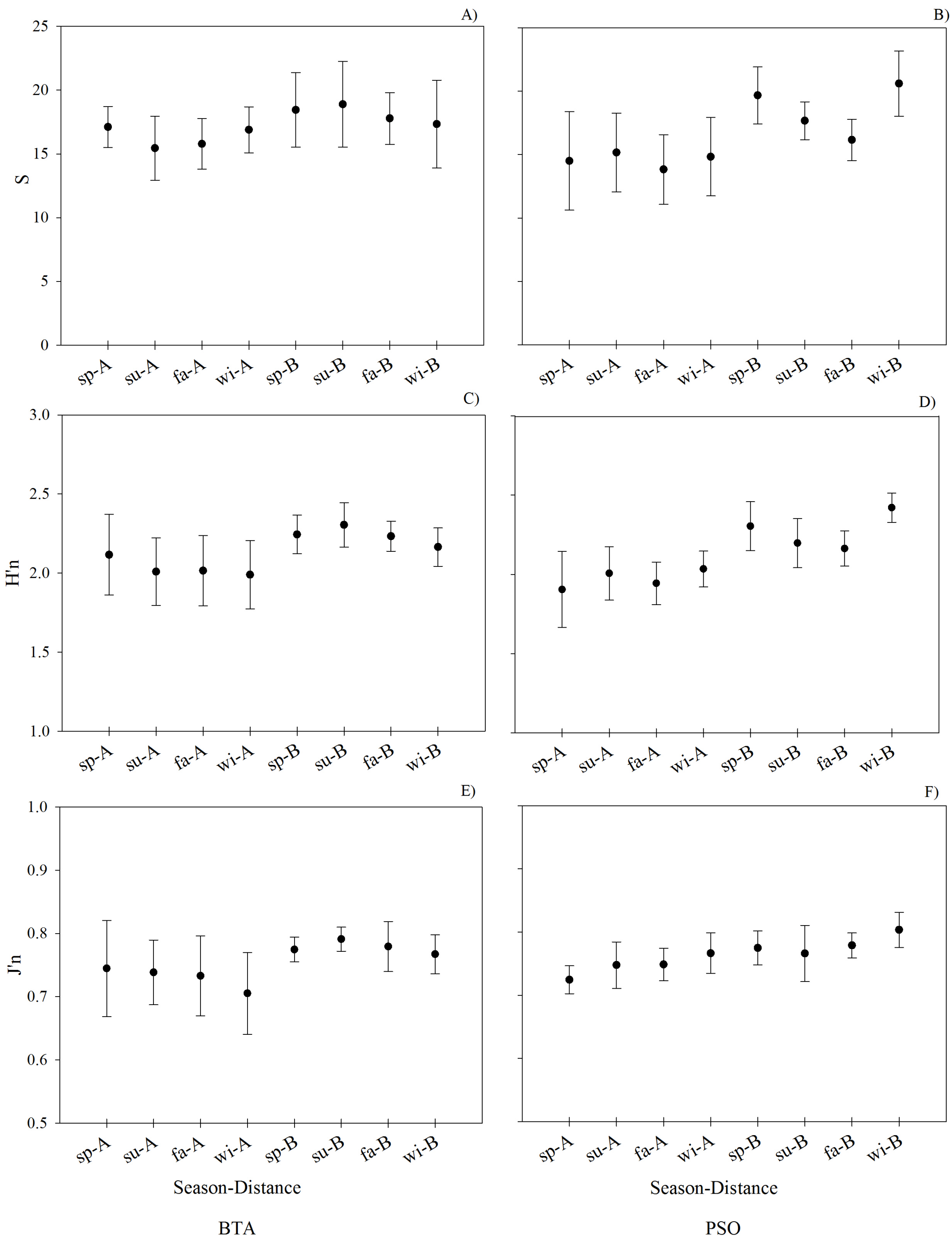

Figure 2.4. Coral species richness (S, A-B), diversity index (H'n, C-D) and evenness (J'n, E-F) by site, season, and distance zones (mean± 95% CI). Left column graphs represent Bahía Tamarindo (BTA) and right column Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.4. Results of permutational analysis of variance (PERMANOVA) on coral species richness (S), species diversity index (H'n) and evenness.

Factors	df	S Pseudo *F*	S P	H'n Pseudo *F*	H'n P	Evenness Pseudo *F*	Evenness P
Season (Se)	3	1.41	0.2260	0.44	0.7240	0.07	0.9790
Site (Si)	1	0.91	0.3330	0.04	0.8540	0.73	0.4190
Distance (Di)	1	21.38	0.0010	32.22	0.0010	12.24	0.0020
Se x Si	3	0.70	0.5500	1.67	0.1960	1.42	0.2420
Se x Di	3	0.17	0.9180	0.13	0.9480	0.08	0.9690
Si x Di	1	3.12	0.0760	1.29	0.2650	0.29	0.6140
Se x Si x Di	3	1.48	0.2410	1.03	0.3760	0.25	0.8640

Coral recruit density

Coral recruit density was higher in BTA with mean of 1.96±0.46m^{-2}. Mean recruit density at BTA increased from 0.88m^{-2} in spring to 2.96m^{-2} in winter. At distance zone A coral recruit increased from 0.28 (spring) to 1.28m^{-2} (winter), and at zone B advanced from 1.47 to 4.63m^{-2} (Fig. 2.5). Therefore, coral recruit density was higher farther from shore, the less exposed reef segment to sedimentation (Appendix 2.7). Meanwhile, in PSO mean recruit density increased from 0.60m^{-2} in spring to 1.38m^{-2} in winter. At zone A coral recruit density increased from 1.13m^{-2} to 2.7m^{-2} (Figure 2.5). In contrast, in zone B recruit density decreased gradually from 0.08 to 0.05m^{-2}. In PSO coral recruit density was higher on reef areas closer to shore (Appendix 2.8). Coral recruit community structure showed statistically significant differences among seasons (Pseudo F=2.72, p=0.0030), site (Pseudo F=23.30, p=0.0001), and distance (Pseudo F=8.00, p=0.0001) (Table 2.5). There were also significant differences between the interactions of seasons by site (Pseudo F=2.25, p=0.0100), and site by distance (Pseudo F=11.29, p=0.0001). Pair-wise comparison showed that coral recruit density was significantly different between sites during summer, fall, and winter. A total of 11 coral species recruited at both study sites and the species with highest percentage relative abundance were *Siderastrea radians* (45.1%), *S. siderea* (23.1%), followed by *Porites astreoides* (19.2%) (Table 2.6). No coral recruits of large reef-building coral species were documented at BTA through the study period.

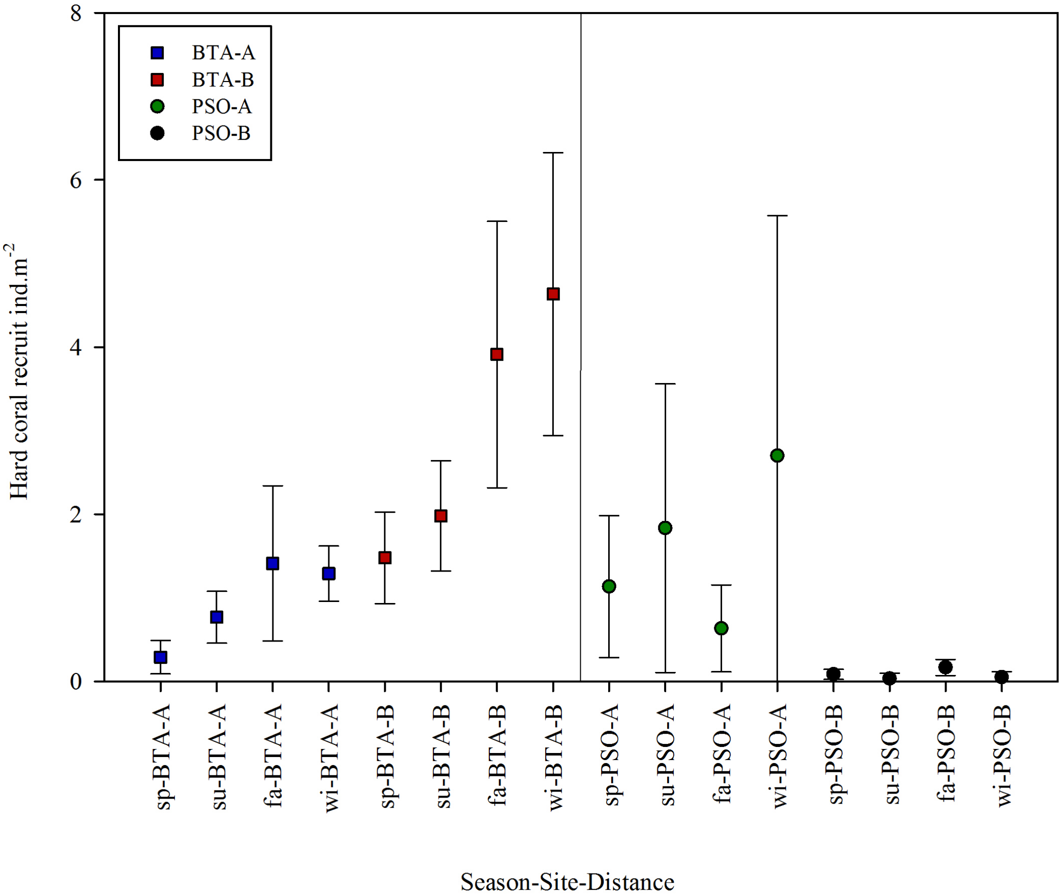

Figure 2.5. Variation in hard coral recruit density (mean± 95% CI) by site, distance zone and seasons. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.5. Results of permutational analysis of variance (PERMANOVA) on coral recruit density.

	Coral recruit density		
Factors	df	Pseudo *F*	*P* (perm)
Season (Se)	3	2.72	0.0030
Site (Si)	1	27.30	0.0001
Distance (Di)	1	8.00	0.0001
Se x Si	3	2.25	0.0100
Se x Di	3	1.47	0.1500
Si x Di	1	11.29	0.0001
Se x Si x Di	3	1.60	0.1100

Table 2.6. Coral recruit species documented and mean percent relative density by site and distance zone.

	Percent relative density			
Species	**BTA-A**	**BTA-B**	**PSO-A**	**PSO-B**
Agaricia agaricites	2.01	9.10	1.04	36.67
Agaricia tenuifolia	0	0	0.36	0
Diploria labyrinthiformis	0	0.12	0	0
Favia fragum	0.72	5.91	0	0
Montastraea cavernosa	0.58	0.19	0	0
Orbicella faveolata	0	0	0.37	0
Porites astreoides	29.67	14.54	23.79	22.50
Porites porites	3.60	2.65	0.31	8.33
Pseudodiploria strigosa	0.72	0.39	0	0
Siderastrea radians	48.19	42.71	23.34	5.00
Siderastrea siderea	14.48	24.39	26.03	27.50

PCO analysis identified two major groups which distinguished different coral recruit density patterns of PSO zone B from distance zone A, and from BTA among all seasons (Fig. 2.6). There was also one outlier event identified for PSO zone B during the summer season, particularly due to a significant reduction recorded with a mean recruit density of $0.4m^{-2}$. However, SIMPROF analysis only identified two distinct groups for coral recruit density. The proposed PCO explains 83.2% of the total variation. According to SIMPER analysis, the three species that contributed to explain 79% of the differences of coral recruit density patterns between sites were *S. radians* (32.41% individual contribution), *P. astreoides* (23.93%) and *S. sider*ea (22.42%) (Table 2.7). The species that contributed to explain 73% of the differences between distance zones were *P. astreoides* (27.83%), *S. siderea* (24.42%) and *S. radians* (21.21%). The average dissimilarity was 49.69 between sites and 61.01 between distance zones.

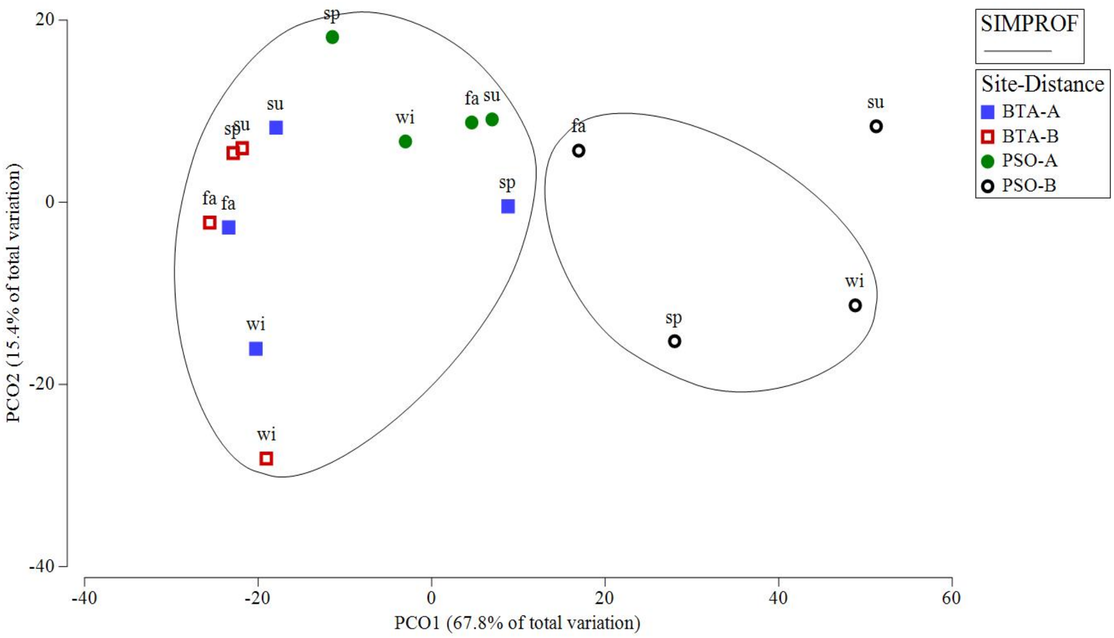

Figure 2.6. PCO plot of distance among centroids of coral recruit density based on Bray-Curtis similarity matrices performed on square root-transformed data by seasons-site-distance clusters. Clusters represent significant SIMPROF groups (~75% similarity within groups). This model explained 83.2% of the observed spatio-temporal variation in sedimentation. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.7 Two-way similarity percentage (SIMPER) of coral recruit by site and distance zone.

	Average abundance	Average abundance	Individual contribution (%)	Cumulative contribution (%)
SITE	**BTA**	**PSO**		
Siderastrea radians	5.82	1.67	32.41	32.41
Porites astreoides	3.81	3.15	23.93	56.35
Siderastrea siderea	3.26	2.26	22.42	78.77
DISTANCE	**A**	**B**		
Porites astreoides	4.37	2.72	27.83	27.83
Siderastrea siderea	3	2.72	24.42	52.25
Siderastrea radians	4.44	3.88	21.21	73.46
Undaria agaricites	0.49	1.98	13.38	86.84

Benthic components percent cover and community structure

Percent coral cover was dominated by scleractinians and hydrocorals. Live coral cover was significantly higher on BTA zone B with a mean percent cover of 17.87±0.67, however it experienced gradual reduction through time series from spring 18.56% to winter season 17.03% (Fig. 2.7A) (Appendix 2.9, 2.10). In contrast, percent coral cover at zone A remained relatively stable through seasons and experienced a slight increase through time, from spring 11.62% to winter season 12.58%. At PSO percent coral cover experienced variations through time (Appendix 2.11, 2.12). At reef zone A percent coral cover decreased from summer 14.38% to fall 12.32% season. In zone B it decreased from spring 9.70% to summer 7.11%, and remained lower during fall season with a percent cover of 6.60%. In overall, PSO zone B had the lowest coral cover. Percent coral cover was significantly different between sites (Pseudo F=25.26, p=0.0010), distance (Pseudo F=13.77, p=0.0010), and the interaction site by distance (Pseudo F=18.82, p=0.001) (Table 2.8).

Stress-tolerant coral species *P. astreoides* and *P. porites* had higher percent relative cover in BTA zone A, with a mean of 4.28% and 2.71%, respectively, this reef segment was more exposed to sediment stress, while in zone B *Millepora alcicornis* had a higher percent cover with a mean of 5.49% (Fig. 2.8). Percent cover of *A. cervicornis* was higher in distance zone B with mean cover of 1.95%. Benthic cover of *A. cervicornis* increased from spring 1.56% to winter 2.35% as branches grew through time. In PSO the coral species with higher percent cover were *O. annularis* and *P. astreoides* with a mean of 3.08% and 2.15%, respectively. *Orbicella annularis* had higher percent cover in distance zone B with a mean of 3.63, while *P. astreoides* was higher on distance zone A, with a mean of 2.51%.

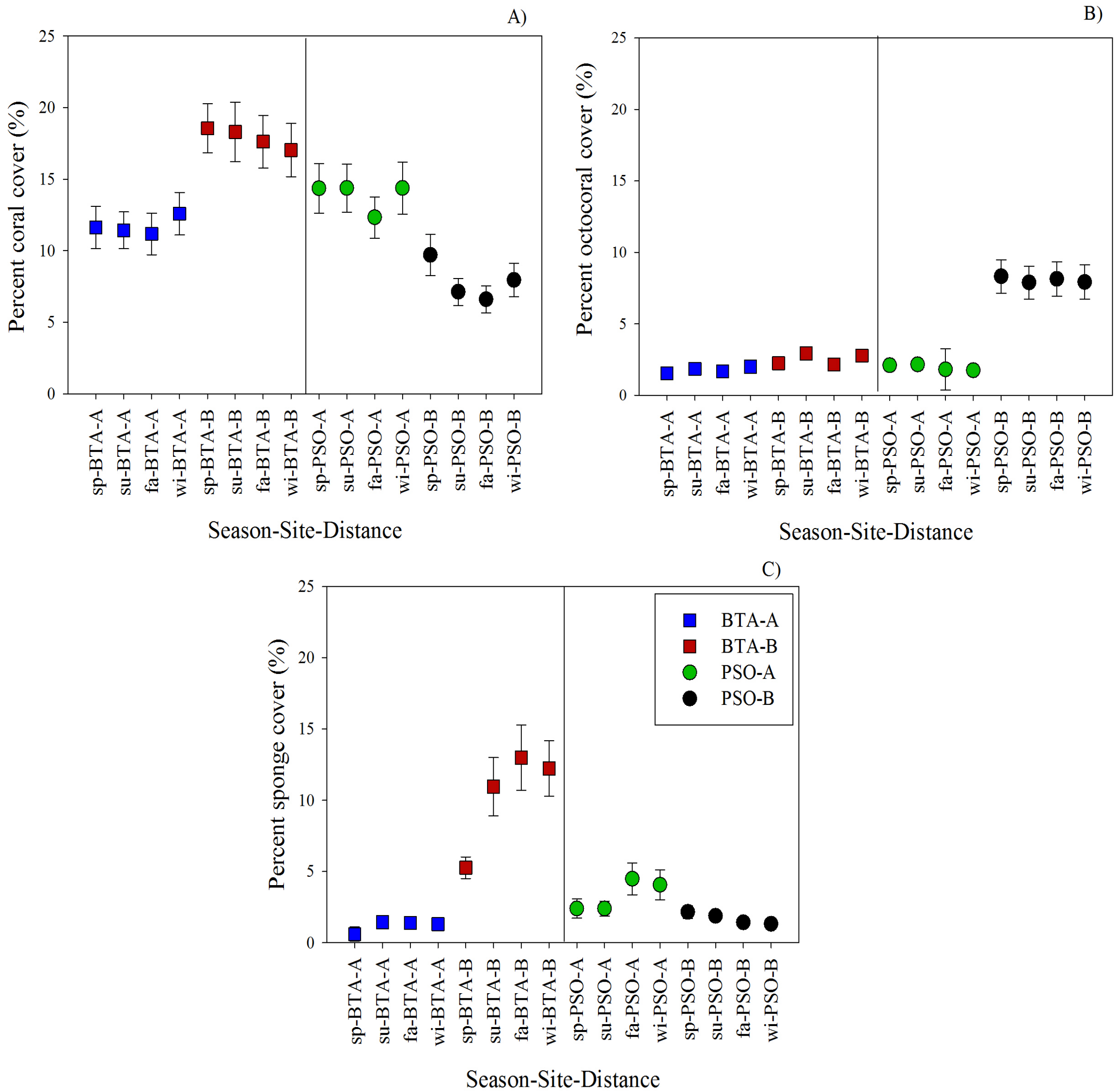

Figure 2.7. Coral reef benthic components cover across a distance gradient from shore and seasons (mean± 95% CI). Percent coral cover (Scleractininas+hydrocorals) (A), octocoral cover (B), and sponge cover (C). Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.8 Results of permutational analysis of variance (PERMANOVA) for benthic cover and benthic components.

Factors		**Coral cover**		**Octocoral cover**		**Sponge**		**Macroalgae**		**Benthic community structure**	
	df	Pseudo F	P	Pseudo F	P	Pseudo F	P	Pseudo F	P	Pseudo F	P
Season (Se)	3	0.59	0.9100	2.24	0.0010	1.53	0.0400	2.69	0.0090	1.96	0.0020
Site (Si)	1	25.26	0.0010	10.43	0.0010	9.68	0.0010	20.26	0.0010	21.00	0.0010
Distance (Di)	1	6.91	0.0010	6.50	0.0010	7.33	0.0010	6.85	0.0020	13.77	0.0010
Se x Si	3	0.76	0.7500	1.03	0.4300	1.02	0.4300	1.27	0.2700	1.95	0.0070
Se x Di	3	0.28	0.9900	0.71	0.8160	1.04	0.3800	1.82	0.0600	0.65	0.9310
Si x Di	1	16.88	0.0010	5.51	0.0010	9.49	0.0010	12.14	0.0010	18.82	0.0010
Se x Si x Di	3	0.68	0.8400	0.68	0.8700	1.80	0.0060	2.54	0.0080	1.84	0.0050

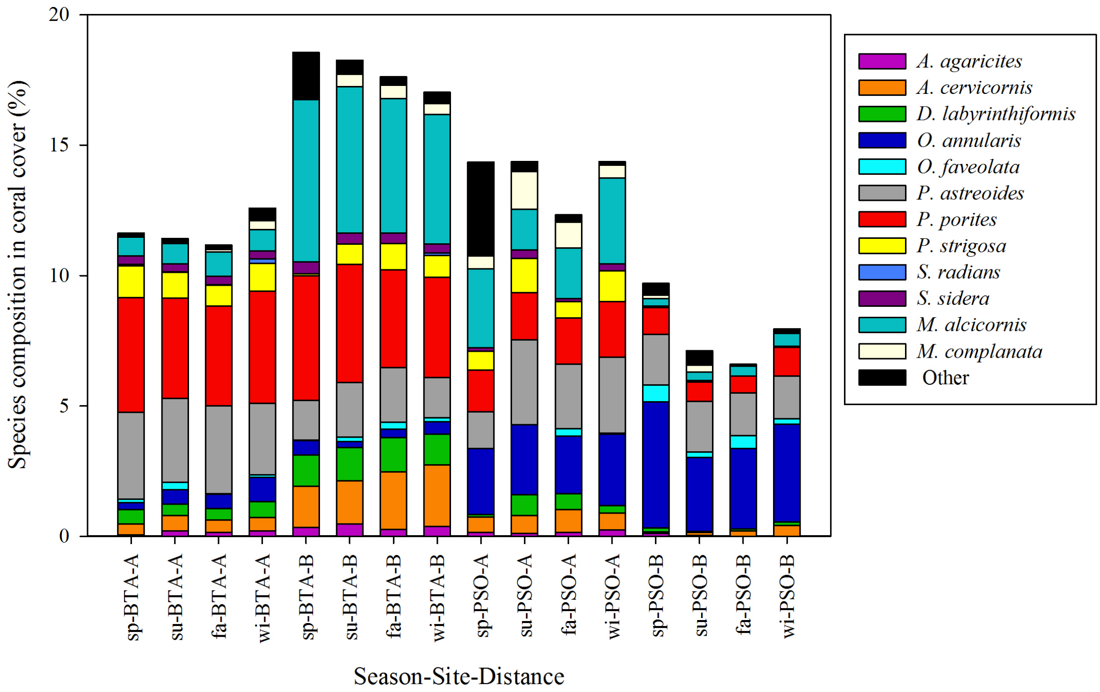

Figure 2.8. Percent species composition of Scleractinian and hydrocoral species. Most dominant species among site, distance zone and seasons identified by colors. Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

The similarity percentage (SIMPER) analysis revealed that there were 8 species that constituted 75% of the observed variations in percent coral cover between sites and distance zones. The species with major contributions to variations between sites were *M. alcicornis* (14.43%, individual contribution), *O. annularis* (13.41%), *P. porites* (11.99%), and *A. cervicornis* (8.63%) (Table 2.7). There was an average dissimilarity between sites of 57.11%. The species with major contributions to variation between distances zones were *M. alcicornis* (15.77%), *P. porites* (13.53%), *A. cervicornis* (9.41%) and *O. annularis* (9.00%). There was an average dissimilarity between distance zones of 49.85.

Percent octocoral cover showed a significant difference among seasons, sites, and distance zones ($p<0.05$) (Table 2.6). They mostly dominated benthic cover at PSO zone B, with higher values up to 8.31% cover in spring season (Fig. 2.8B). In zone A octocorals cover was similar to BTA which had a mean cover of 1.80%, however it experienced a decline from fall 1.80% to winter 1.70%. Sponges had higher percent cover in BTA with a mean of 5.77%. Sponge cover had an evident increasing pattern in BTA zone B, reaching a benthic cover of 12% in fall and winter (Fig. 2.8C). Sponge cover at PSO zone A also experienced an increase from spring 2.39% to fall 4.48% and winter 4.06%. The gray encrusting and invading sponge, *Dictyonella funicularis,* had a significant contribution on sponge dynamics, since it constituted half of total percent sponge cover by season, site and distance zones (Fig. 2.10). This specie was documented overgrowing dead or diseased corals *A. cervicornis* colonies among other benthic components. This sponge had higher percent cover in BTA distance zone B, with a pattern of increasing benthic cover from spring to winter. It reached a percent cover of up to 7.81% in fall season (Fig. 2.10).

Table 2.9. Two-way similarity percentage (SIMPER) of benthic coral cover by site and distance zone.

	Average density	Average density	Individual contribution (%)	Cumulative contribution (%)
SITE	**BTA**	**PSO**		
Millepora alcicornis	0.15	0.09	14.43	14.43
Orbicella annularis	0.05	0.15	13.41	27.84
Porites porites	0.16	0.11	11.99	39.84
Acropora cervicornis	0.08	0.04	8.63	48.47
Pseudodiploria strigosa	0.09	0.03	8.26	56.73
Diploria labyrinthiformis	0.08	0.03	7.07	63.80
Porites astreoides	0.15	0.14	6.07	69.87
Siderastrea siderea	0.05	0.02	5.21	75.07
DISTANCE	**A**	**B**		
Millepora alcicornis	0.10	0.16	15.77	15.77
Porites porites	0.15	0.13	13.53	29.30
Acropora cervicornis	0.06	0.07	9.41	38.71
Orbicella annularis	0.07	0.10	9.00	47.71
Porites astreoides	0.16	0.07	7.65	55.36
Diploria labyrinthiformis	0.05	0.05	6.73	62.09
Pseudodiploria strigosa	0.08	0.03	6.63	68.71
Millepora complanata	0.03	0.04	5.39	74.11
Millepora alcicornis	0.10	0.16	15.77	15.77
Porites porites	0.15	0.13	13.53	29.30
Acropora cervicornis	0.06	0.07	9.41	38.71
Orbicella annularis	0.07	0.10	9.00	47.71

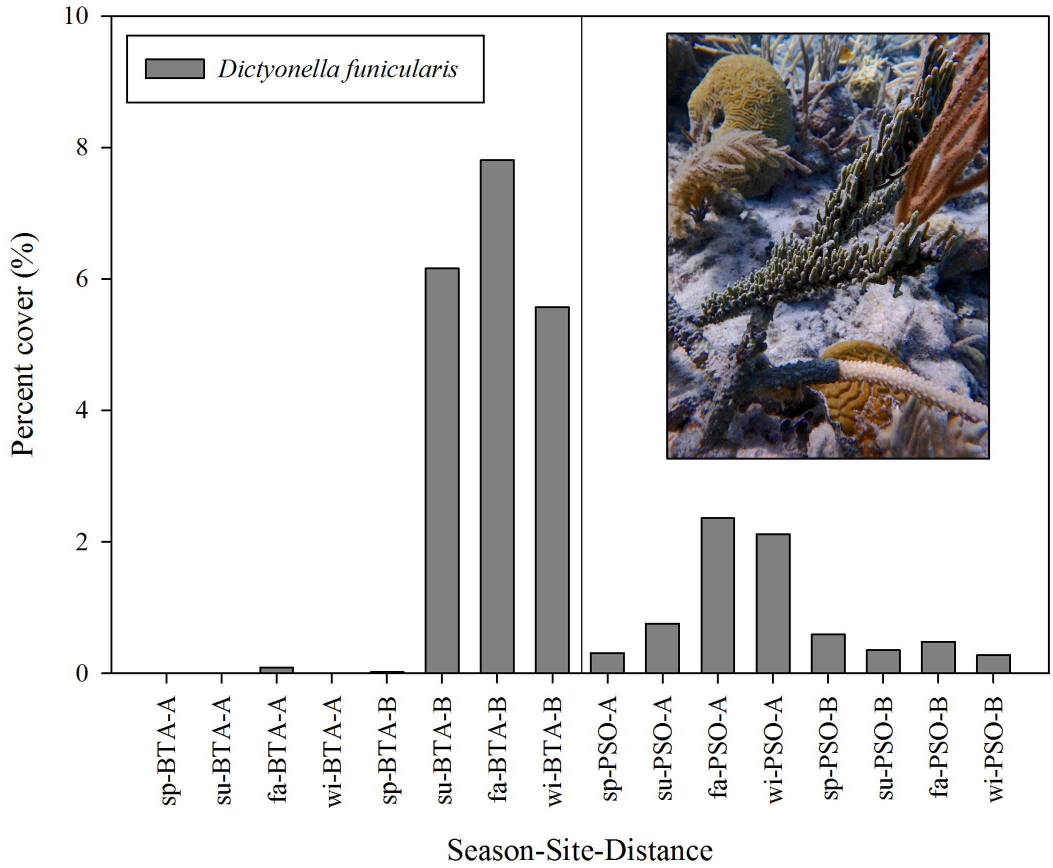

Figure 2.9. Mean percent cover of the gray encrusting and invading sponge *Dictyonella funicularis* by season, site and distance zones. Photo: *Dictyonella funicularis* colonization over dead tissue of outplanted *Acropora cervicornis* at Bahía Tamarindo (BTA). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter

In contrast, *D. funicularis* had higher percent cover in PSO distance zone A, with higher percent cover in fall and winter season with 2.36% and 2.12% respectively. Sponge community had a significant difference between seasons, sites, distance and the interactions site by distance and season by site and distance ($p<0.05$) (Table 2.6).

The benthic component that mostly influenced coral reefs were combined macroalgae and algal turf. Macroalgal assemblages had significant differences among season, sites, distance and the interaction site by distance ($p<0.05$) (Table 2.6). Higher percent cover was recorded at PSO, especially at distance zone B, where it reached up to 35% (Fig. 2.11A). High cover of macroalgae cover was largely caused from the overgrowth of the encrusting, invasive red algae *Ramicrusta textilis,* was overgrowing dead skeletons of the *O. annularis* species complex (Fig. 2.12). Higher percent cover of *R. textilis* was documented at zone B during the summer season. In contrast, at distance zone A *Dictyota* spp. algae had higher percent cover. Macroalgae that had higher influence on benthic community composition on BTA zone A was turf and *Dictyota* spp.*,* which constituted a mean cover of 37.51% and 14.02% respectively. *Dictyota* spp. had the highest percent cover in spring season (Fig. 2.12). Meanwhile on distance zone B the most important algae were turf and crustose coralline algae (CCA) *Porolithon* spp. since these constituted a mean cover of 28.66% and 9.53%. In BTA, turf was significantly higher at BTA zone A, with its highest level recorded during fall season with 51.67% (Fig. 2.11B). The percent cover of CCA increased in zone B through seasons (Fig. 2.11C). The cyanobacteria cover had also an important influence on BTA zone B by increasing its percent benthic cover form spring (3.91%) to summer (6.99%) afterwards percent cover decreased to 1.62% and stayed in low levels during winter season (1.14%) (Fig. 2.11D).

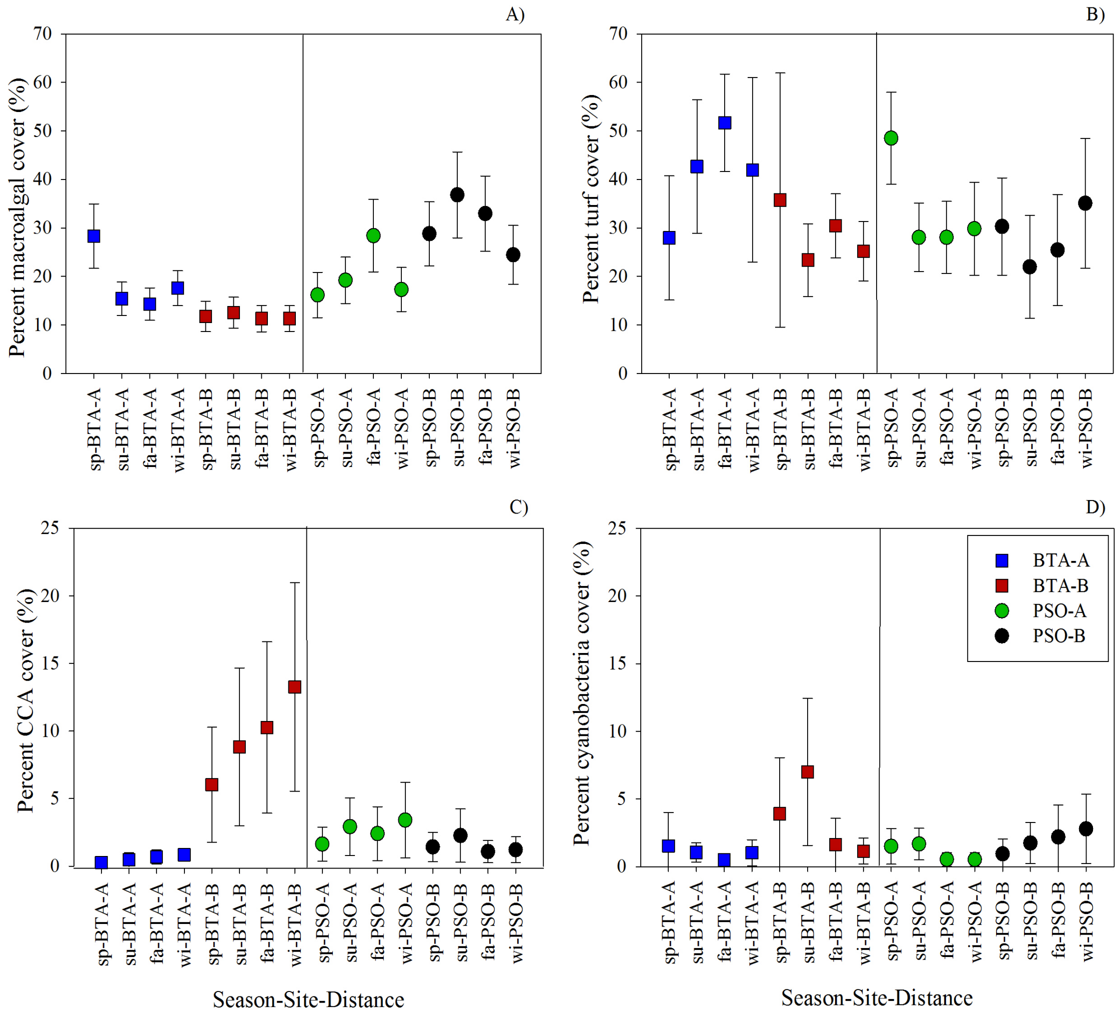

Figure 2.10. Coral reef benthic components cover across a distance gradient from shore, site, and seasons (mean± 95% CI). Percent macroalgal cover (A), turf (B), crustose coralline algae (CCA) (C), and cyanobacteria cover (D). Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

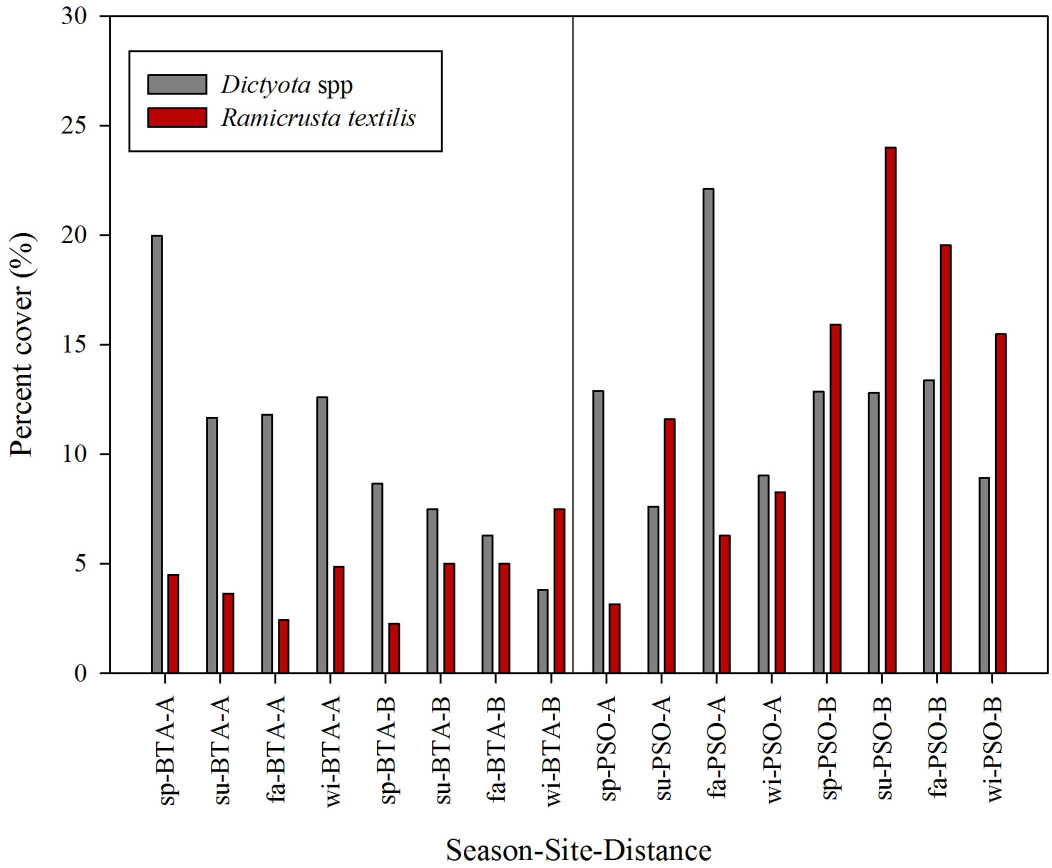

Figure 2.11. Percent macroalgal cover of the common *Dictyota* spp. (blue bar) and encrusting *Ramicrusta textilis* (red bar) by season, site and distance zone 2014-2015. Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Coral reef benthic community structure presented a statistically significant difference among seasons (Pseudo F=1.96, p=0.0020), sites (Pseudo F=21.00, p=0.0010), distance (Pseudo F=13.07, p=0.0010), and within the interactions season by site (Pseudo F=1.95, p=0.0070), site by distance (Pseudo F=18.82, p=0.0010), and season by site by distance (Pseudo F=1.84, p=0.0050) (Table 2.8). PCO analysis identified four major groups that distinguished benthic community structure between sites and distance zone (Fig. 2.12). The benthic community structure at BTA within distance zone A indicates significant difference from spring to summer (Pair-wise, t=1.39, p=0.27), fall (t=1.70, p=0.0010), and winter (t=1.60, p=0.0020). The community structure of BTA within zone B had an outlier during spring season and it was identified with an individual fall (t=1.62, p=0.0460) and winter (t=1.81, p=0.0150). Within distance zone B the community structure at PSO showed differences from spring to summer (t=1.38, p=0.0280), fall (t=1.33, p=0.0480), and winter season. Likewise, there were significant differences on community structure from summer to winter (t=1.40, p=0.0170).

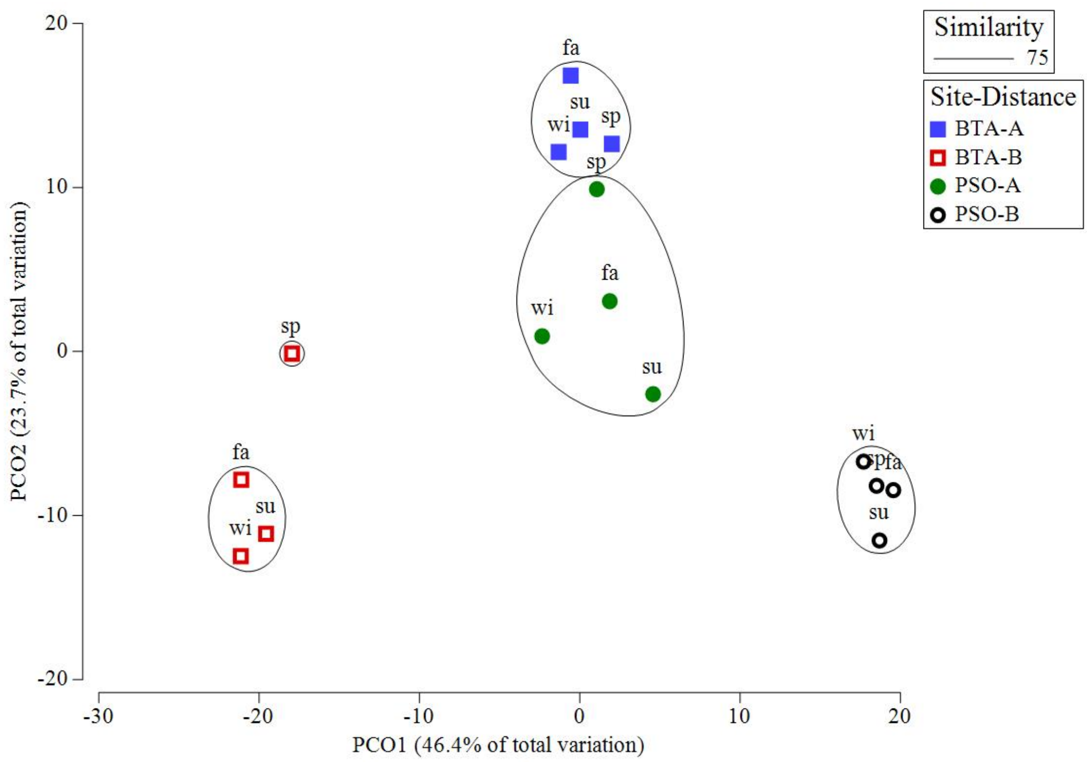

Figure 2.12. Principal coordinates ordination (PCO) plot of benthic community structure on site by distance based on Bray-Curtis similarity matrix. Cluster represent 70% of similarity within groups. This model explained 70% of the observed spatio-temporal variation in benthic cover. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Benthic community structure and environmental variables

Coral colony density had a significant strong relationship with sand (RELATE, Rho= 0.475, p=0.002), silt-clay (Rho= 0.422, p=0.003), carbonate (Rho= 0.263, p=0.026), terrigenous content (Rho= 0.328, p=0.009), and depth (Rho=0.858, p=0.037) (Table 2.8). However, coral density did not show a significant correlation with sedimentation rate, terrigenous rate, and organic matter ($p>0.05$) (Table 2.10). The nMDS bubble plot shows that sand had a higher influence on spatial configuration of coral density at BTA, suggesting stronger influences by bedload sediment resuspension (Fig. 2.13). In contrast, coral density at PSO was influenced by silt-clay due to major runoff pulses from adjacent deforested lands.

From multiple linear regressions, sequential test of coral abundance only showed significance with sand proportion (R^2=0.47, p=0.0110) (Table 2.11). Regression analysis also found significant relationship of coral density with silt-clay, carbonate, and terrigenous sediments. However, sand was the variable that had greater contribution to the coral density variation by season, site and distance zone with 29.15%, followed by sedimentation rate 11.37% and silt-clay 6.46% (Table 2.11). The best model from redundancy analysis between coral density and sediment variables explained 49% of the total multivariate variation of coral density patterns, and four sediment variables that were identified with correlation higher than 0.4 (Fig 2.14). Sedimentation rate is represented as the predictor variable of relative importance that might explain decline in coral abundance at BTA zone A in fall and winter season (Fig. 2.14). In addition, sand sediments is suggested to be responsible for variations in coral density at BTA zone B, and silt-clay is suggested to explain variations of coral density at PSO zone B.

Table 2.10. Summary of RELATE (Spearman rank) correlation matrix for coral colony density, coral recruit density and environmental variables. Averaged by season, site, distance and season by site.

	Coral density	**Coral recruit density**
Season-Site-Distance		
Sedimentation rate	Rho= 0.031, p=0.351	Rho=-0.127, p=0.743
Terrigenous rate	Rho= 0.029, p=0.332	Rho=-0.07, p=0.583
Sand	Rho= 0.475, p=0.002	Rho= 0.225, p=0.017
Silt-clay	Rho= 0.422, p=0.003	Rho= 0.240, p=0.021
Organic matter	Rho= 0.055, p=0.270	Rho= 0.028, p=0.366
Carbonate	Rho= 0.263, p=0.026	Rho=-0.002, p=0.418
Terrigenous	Rho= 0.328, p=0.009	Rho= 0.056, p=0.315
Season-Site		
Total precipitation	Rho=-0.202, p=0.889	Rho=-0.114, p=0.699
Wind speed	Rho=-0.237, p=0.936	Rho=-0249, p=0.891
Wave height	Rho=-0.088, p=0.644	Rho= 0.266, p=0.103
SST	Rho=-0.174, p=0.845	Rho=-0.192, p=0.88
SST max	Rho= 0.001, p=0.461	Rho= 0.026, p=0.444
SST min	Rho=-0.003, p=0.478	Rho= 0.181, p=0.234
Depth	Rho= 0.858, p=0.037	Rho= 0.715, p=0.032

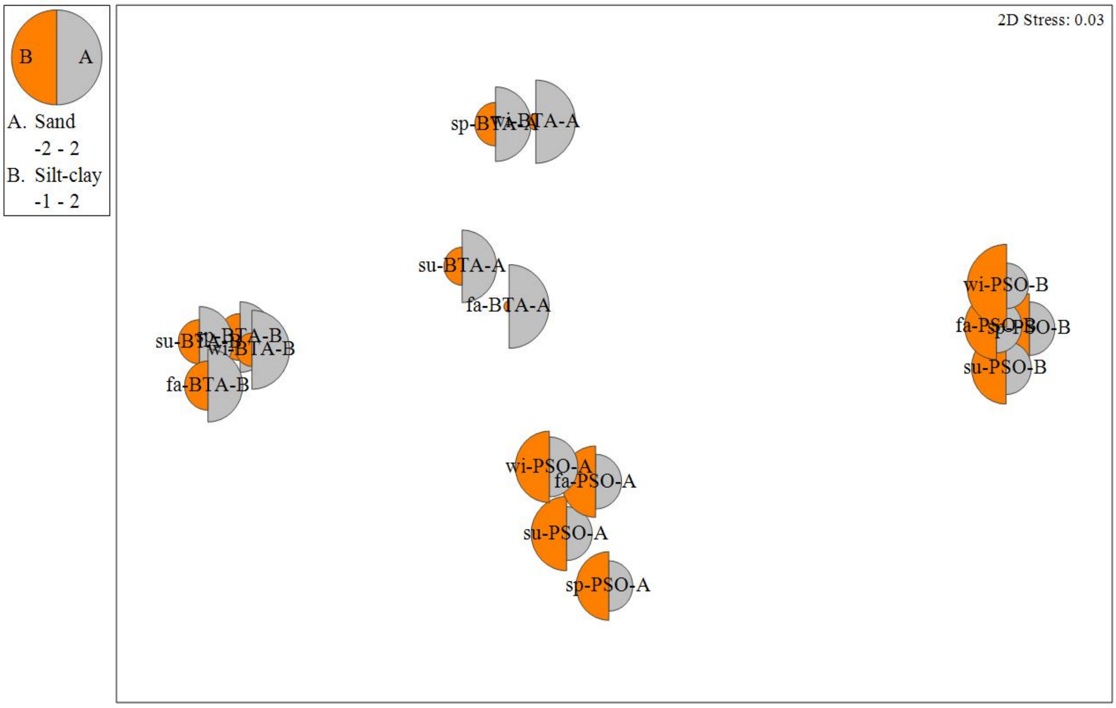

Figure 2.13 nMDS, bubble plot of coral colony density structure at each site by distance based on Bray-Curtis similarity matrices, performed on square root-transformed data. Bubble plot represent sand (gray) and silt-clay (orange). Size represents sediment proportion of each variable at each season by site and distance, based on Euclidean similarity matrices performed on normalized data. Stress=0.03. Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.11. Summary of distance-based linear model (DISTLM) marginal and sequential test, multiple linear regression that examine relationship between coral density and sedimentation variables by the factors of season by site by distance.

Marginal tests

Variable	Pseudo-F	P	Proportion
Sedimentation rate	1.80	0.133	0.113
Terrigenous rate	1.93	0.113	0.121
Sand	7.04	0.001	0.335
Silt-clay	6.74	0.004	0.325
Organic matter	0.92	0.385	0.062
Carbonate	4.97	0.005	0.262
Terrigenous	3.20	0.045	0.186

Sequential tests

Variable	R^2	Pseudo-F	P	Proportion	Cumulative
Sedimentation rate	0.1137	1.796	0.125	0.1137	0.1137
Terrigenous rate	0.1550	0.6357	0.623	0.0413	0.1550
Sand	0.4707	5.777	0.011	0.278	0.4707
Silt-clay	0.5367	1.424	0.209	0.0659	0.5367
Organic matter	0.5548	0.365	0.845	0.0108	0.5555
Carbonate	0.5893	0.6708	0.554	0.0344	0.5893
Terrigenous	0.6136	0.442	0.745	0.0244	0.6137

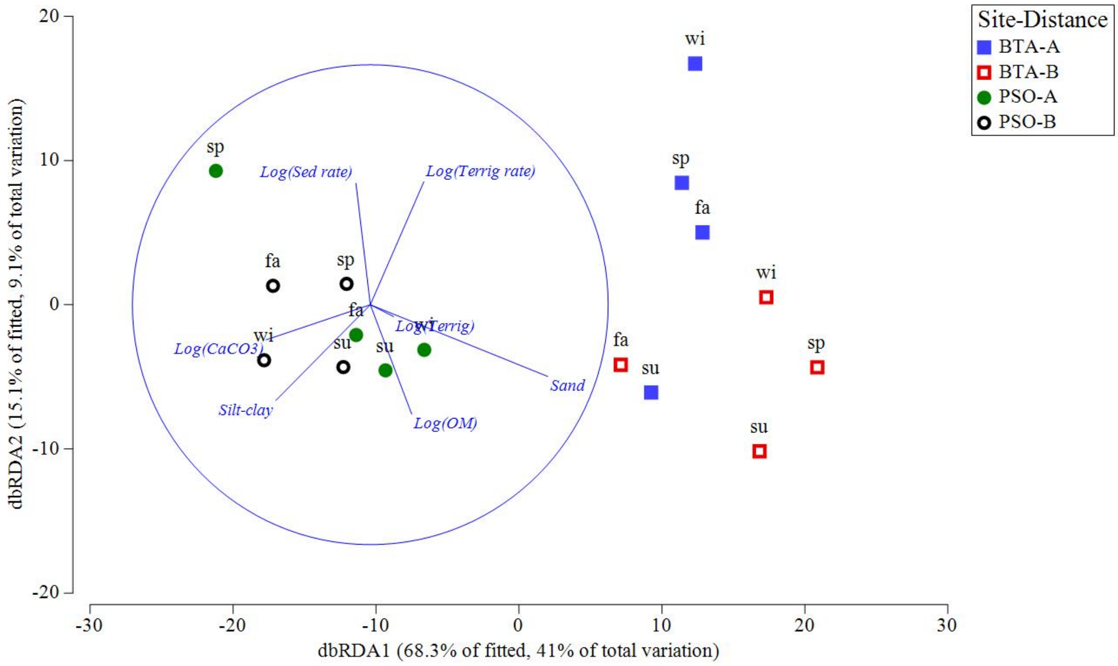

Figure 2.14. Plot of redundancy analysis (dbRDA) of coral colony density. Vectors represent sediment environmental variables with correlation r>0.4 that best explains variation in coral colony density structure by site by distance. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Coral recruit density had a strong significant correlation with sand (RELATE, Rho=0.225, p=0.017) silt-clay (Rho=0.24, p=0.021), and depth (Rho=0.715, p=0.032) (Table 2.8). The vectors overlaying PCO plot showed that coral recruit density was largely impacted by sand sediments (>63 μm) at BTA across distance zone A, the shallow area closer to shore, and as consequence more exposed to sedimentation pulses (Fig. 2.15). The unfavorable impact of sand sediment on coral recruits could be mostly attributed to burial effects experienced after cold front events, climatic events characteristic of winter season that produce significant increase in sedimentation rate by bedload sediment transport and resuspension (Otaño-Cruz, Chapter 1 M.Sc. Thesis). This results contribute to explain the decline in coral recruit density from fall to winter season (-8.66%) across distance zone A. Coral recruit density at BTA zone B was mostly influenced by terrigenous accumulation rate, sediments derived from land (Fig 2.15). In contrast, coral recruit density at PSO was mostly influenced by silt-clay (<63 μm). The vectors show silt-clay sediment had prominent influence across distance zone B, area that experienced a coral recruit density decline from spring to winter season (-40%). Therefore, in PSO coral recruit was largely limited to shallower zones, which had lower silt-clay sediment deposition. The multiple linear regression analysis showed that coral recruit also had a strong significant relationship with wave height (R^2=0.52, p=0.0270) and depth (R^2=0.45, p=0.0250) (Table 2.12). This implies that wave height and depth could have major influence on the combined cycle of sediment deposition and resuspension of silt-clay sands. It was also associated to strong climate events that could led to burial of juvenile corals. There was no significant relationship between coral recruit density and sea surface temperature (R^2=0.71, p=0.37).

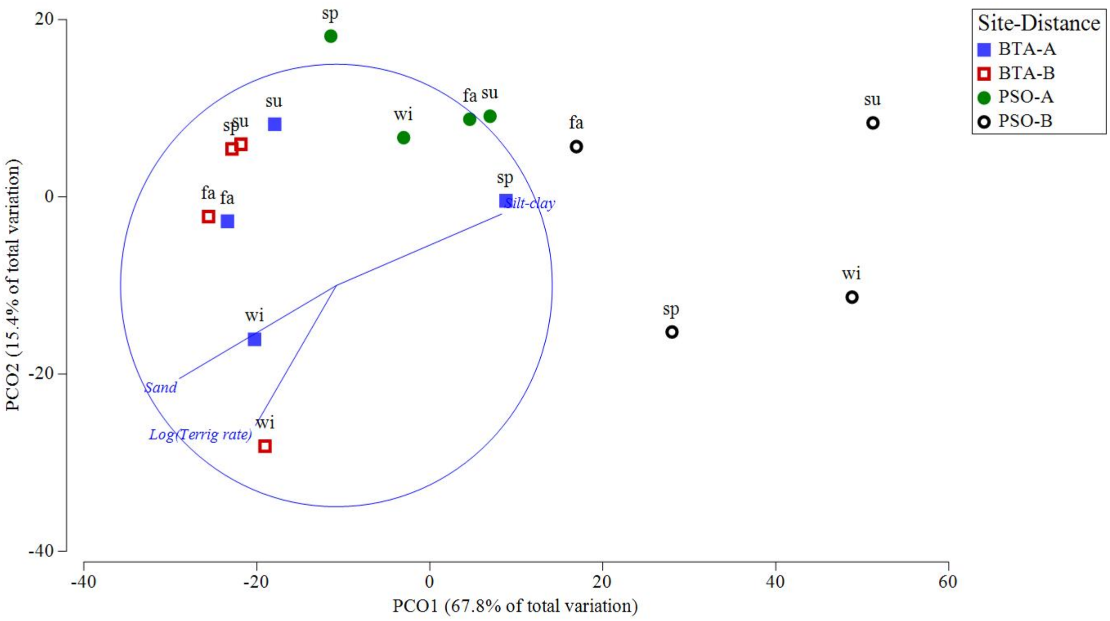

Figure 2.15 Principal coordinates ordination (PCO) plot of coral recruit density based on Bray-Curtis similarity matrices. Vectors represent sediment environmental variables with correlation >0.7. This model explained 83.2% of the observed spatio-temporal variation in coral recruit density. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp=spring, su=summer, fa=fall, and wi=winter.

Table 2.12. Summary of distance-based linear model (DISTLM) marginal and sequential test, step-wise multiple linear regression that examine relationship between coral recruit density and environmental variables by the factors of season by site.

Marginal test			
Variable	Pseudo-F	P	Proportion
Total precipitation	0.809	0.564	0.118
Wind speed	0.230	0.868	0.036
Wave height	2.281	0.113	0.275
SST	0.633	0.635	0.09
Depth	6.675	0.025	0.529

Sequential test					
Variable	R^2	Pseudo-F	P	Proportion	Cumulative
Depth	0.529	6.765	0.025	0.529	0.529
Wave height	0.778	5.620	0.027	0.248	0.778
SST	0.834	1.344	0.386	0.055	0.834
Total precipitation	0.859	0.527	0.586	0.025	0.859

The nonparametric correlation BEST BIOENV (Spearman rank) analyses identified two groups of sediment variables that best correlated with coral reef benthic components, composed by sand and carbonate (Rho=0.42), sand, organic matter, carbonate, and terrigenous (Rho=0.412) (Table 2.13). There was a significant inverse relationship between spatial and temporal changes of in macroalgal cover and coral cover (r^2=0.70, p<0.0001) (Fig 2.16). Changes in percent coral cover through the study period 2014-2015 correlated with variation on sand (Rho=0.38, p=0.006), silt-clay (Rho=0.29, p=0.006), carbonate (Rho=0.255, p=0.03) and terrigenous content (Rho=0.26, p=0.016) on sediment samples (Table 2.14). Coral cover did not show a significant correlation with other environmental variables (Table 2.14). Nevertheless, mean sea surface temperature exceeded mean monthly maximum during fall season (28.5^{o}C) in October 2014, reaching a maximum value up to 30^{o}C, yet it experienced subsequent rapid decline that prevented further impacts to shallow coral communities (Fig. 2.17). Mean sea surface temperature registered from October to November had anomalies of + 1.74^{o}C from historical mean monthly maximum.

Increase of sponge cover was documented at BTA along both distance zone and PSO zone A through seasons, and it had a strong correlation with increased sedimentation rate (Rho=0.43, p=0.002), terrigenous rate (Rho=0.37, p=0.0100), and variations of sand (Rho=0.47, p=0.0010), silt-clay (Rho=0.42, p=0.0020), carbonate (Rho=0.47, p=0.002) and terrigenous content (Rho=0.40, p=0.0020) (Table 2.14). Sponge cover experienced a decline through seasons and showed an inverse response to increase in octocoral cover across PSO zone B (Fig. 2.8).

The RELATE correlation analysis demonstrated that variation in percent macroalgal cover had a significant relationship to changes on grain size by sand (Rho=0.31, p=0.004), silt-clay (Rho=0.26, p=0.014), and changes in sediment composition between carbonate (Rho=0.43, p=0.001) and terrigenous content (Rho=0.21, p=0.028) (Table 2.14). Also, differences in depth (Rho=0.71, p=0.036) between distance zones significantly influenced macroalgal cover between seasons and sites, probably suggesting a combination of wave action or variable herbivory effects not directly addressed in this study. Turf cover had no significant correlation with environmental documented during this study. Changes in percent cover of crustose calcareous algae (CCA) had a significant relationship with multiple environmental variables, including sedimentation rate (Rho=0.25, p=0.042), terrigenous content (Rho=0.29, p=0.016), among others (Table 2.14). It is important to highlight that occurrence of increased cyanobacteria cover during summer season at BTA zone B only, had significant relationship with increased organic matter content (Rho=0.262, p=0.012).

Table 2.13. Summary of Best BIO ENV (spearman rank) correlation analysis between benthic community structure and sediment variable averaged: seasons by site by distance zone.

No. of variables	Correlation	Selected variables
2	0.421	sand, carbonate
4	0.412	sand, organic matter, carbonate, terrigenous
5	0.405	sand, silt-clay, organic matter, carbonate, terrigenous
3	0.405	sand, carbonate, terrigenous
3	0.404	sand, organic matter, carbonate
4	0.392	silt-clay, organic matter, carbonate, terrigenous
3	0.390	silt-clay, carbonate, terrigenous
2	0.387	silt-clay, carbonate
4	0.386	sand, silt-clay, carbonate, terrigenous
4	0.386	sand, silt-clay, organic matter, carbonate

Table 2.14 Relate (Spearman rank) correlation of benthic components and environmental variables. Season by site by distance, and season by site. Bold values represent significant correlations.

Variables	**Coral cover**	**Octocoral**	**Sponge**	**Macroalgae**	**Turf**	**Calcareous Algae**	**Cyanobacteria**
Season-Site-Distance							
Sedimentation rate	Rho=-0.063, p=0.678	Rho=-0.093, p=0.802	**Rho=0.433, p=0.002**	Rho=0.001, p=0.483	Rho=0.077, p=0.259	**Rho=0.256, p=0.042**	Rho=0.156, p=0.10
Terrigenous rate	Rho=-0.073, p=0.661	Rho=-0.06, p=0.686	**Rho=0.371, p=0.001**	Rho=0.021, p=0.447	Rho=0.026, p=0.367	**Rho=0.295, p=0.045**	Rho=0.173, p=0.081
Sand	**Rho=0.38, p=0.006**	**Rho=0.29, p=0.01**	**Rho=0.469, p=0.001**	**Rho=0.308, p=0.004**	Rho=0.086, p=0.156	**Rho=0.285, p=0.013**	Rho=0.038, p=0.281
Silt-clay	**Rho=0.293, p=0.006**	**Rho=0.264, p=0.008**	**Rho=0.421, p=0.002**	**Rho=0.26, p=0.014**	Rho=0.082, p=0.176	**Rho=0.241, p=0.023**	Rho=0.0002, p=0.436
Organic matter	Rho=0.096, p=0.17	Rho=-0.147, p=0.957	**Rho=-0.013, p=0.485**	Rho=-0.07, p=0.748	Rho=-0.012, p=0.52	Rho=0.16, p=0.085	**Rho=0.262, p=0.012**
Carbonate	**Rho=0.255, p=0.03**	**Rho=0.272, p=0.012**	**Rho=0.467, p=0.002**	**Rho=0.425, p=0.001**	Rho=0.065, p=0.239	**Rho=0.303, p=0.021**	Rho=0.065, p=0.251
Terrigenous	**Rho=0.261, p=0.016**	Rho=0.165, p=0.081	**Rho=0.402, p=0.002**	**Rho=0.208, p=0.028**	Rho=0.061, p=0.258	**Rho=0.288, p=0.016**	Rho=0.08, p=0.194
Season-Site							
Total PRCP	Rho=-0.062, p=0.548	Rho=0.048, p=0.330	Rho=0.313, p=0.071	Rho=-0.005, p=0.436	Rho=-0.259, p=0.97	Rho=-0.083, p=0.654	Rho=0.032, p=0.344
WSPD	Rho=-0.197, p=0.859	Rho=-0.194, p=0.871	Rho=-0.152, p=0.748	Rho=-0.067, p=0.562	Rho=0.126, p=0.18	Rho=-0.178, p=0.827	Rho=0.039, p=0.315
WVHT	Rho=-0.27, p=0.943	Rho=-0.124, p=0.714	Rho=-0.073, p=0.606	Rho=-0.276, p=0.923	Rho=-0.131, p=0.636	Rho=-0.035, p=0.541	Rho=-0.048, p=0.524
SST	Rho=-0.151, p=0.794	Rho=-0.189, p=0.879	Rho=0.044, p=0.358	Rho=-0.248, p=0.962	Rho=0.093, p=0.280	Rho=-0.212, p=0.930	Rho=-0.08, p=0.562
SST max	Rho=-0.104, p=0.682	Rho=-0.041, p=0.548	Rho=0.142, p=0.215	Rho=-0.244, p=0.880	Rho=-0.212, p=0.752	Rho=0.226, p=0.157	Rho=0.234, p=0.156
SST min	Rho=-0.186, p=0.853	Rho=-0.014, p=0.486	Rho=0.071, p=0.326	Rho=-0.205, p=0.819	Rho=-0.221, p=0.769	Rho=0.196, p=0.175	Rho=0.059, p=0.32
Depth	**Rho=0.858, p=0.023**	**Rho=0.759, p=0.032**	Rho=0.456, p=0.070	**Rho=0.706, p=0.036**	Rho=-0.009, p=0.557	**Rho=0.759, p=0.036**	Rho=-0.17, p=0.854

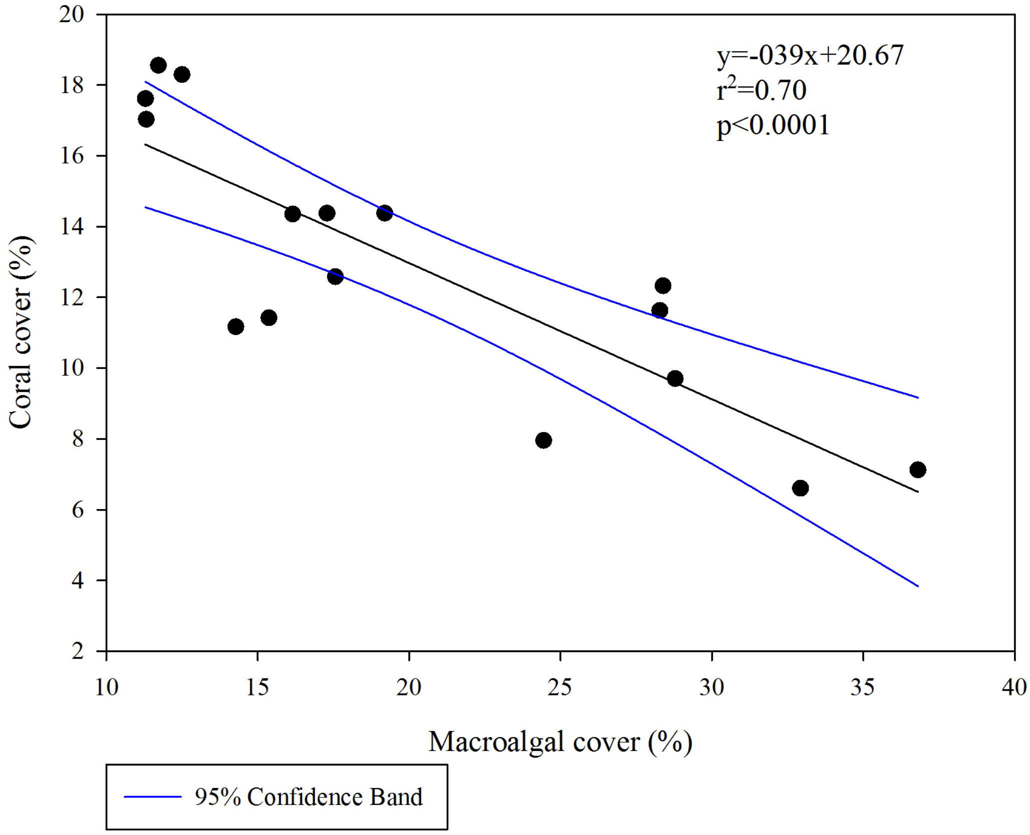

Figure 2.16 Linear regression of percent coral cover with macroalgal cover. Blue line is 95% confidence interval band.

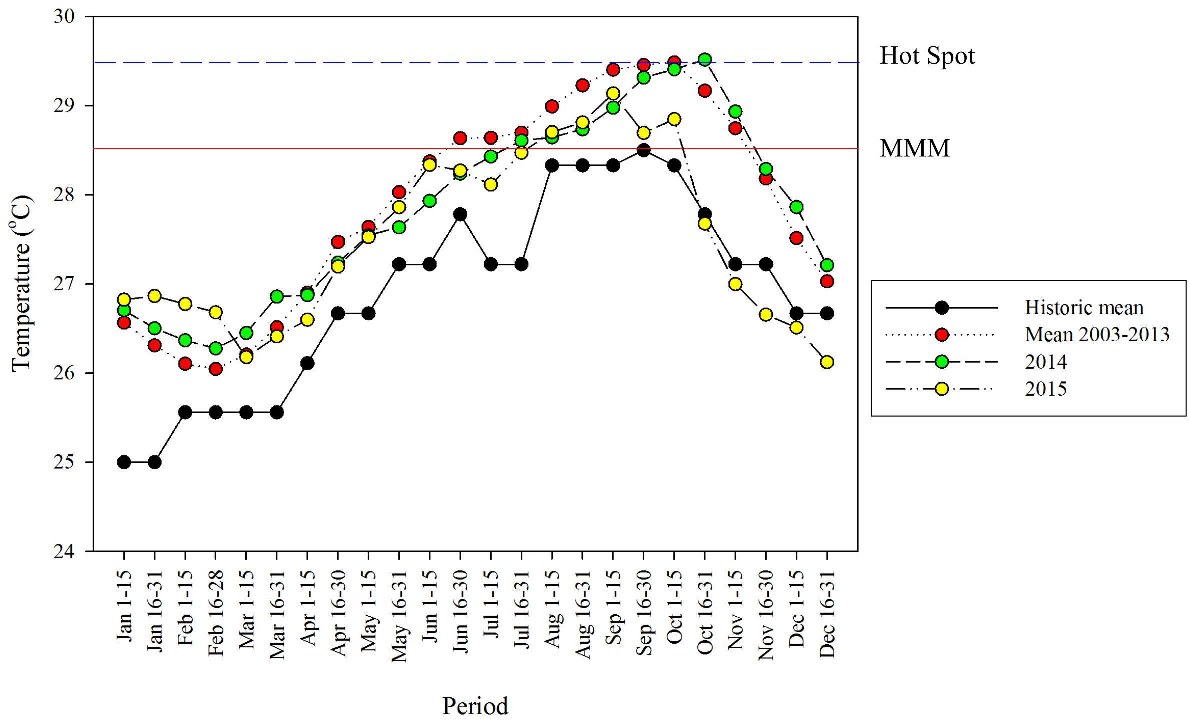

Figure 2.17 Mean sea surface temperature (SST) registered in Culebra Island by periods. Historic mean SST (black dots), mean SST 2003- 2013 (red bots), mean SST 2014 (green dots), and mean SST 2015 (yellow dots). Red line represents mean monthly maximum (MMM) temperature and blue dashed line represents the Host Spot (=+1°C above MMM), the heat threshold for NE Caribbean coral reef ecosystems.

Discussion

Near-shore coral reefs benthic community structure surrounding semi-arid islands are experiencing rapid and significant spatio-temporal ecological responses to degradation of environmental conditions (Table 2.1, 2.6). Changes in benthic communities through temporal (2014-2015) and reef spatial scale (<120m from shore) were strongly associated to variations in sedimentation dynamics. Variables that had an important role on shaping benthic community across a distance gradient from shore were sediment texture, categorized as silt-clay (<63 μm) and sand (>63 μm), and terrigenous sediments (Table 2.8, 2.12). Previous studies have also recognized that sediment dynamics, especially terrigenous-based sediment fluxes associated to runoff, increased human activity, poor land use, and unsustainable development of coastal watershed on small tropical islands have major negative consequences along nearshore coral reefs (Fabricius, 2005; Smith et al., 2008; Risk and Edinger, 2011; Begin et al., 2013). The null hypothesis of no significant spatio-temporal differences at near-shore coral reefs influenced by variation in sedimentation patterns and changes in environmental variables is rejected**.** Therefore, the alternate hypothesis that states spatial and temporal response of near-shore coral reef benthic community structure is significantly related to variations in sedimentation dynamics and environmental conditions was accepted. At the same time, sedimentation dynamics along near-shore coral reefs responds to changing land uses, weather, and oceanographic conditions (Otaño-Cruz, M.Sc. Thesis Chapter 1).

Coral colony density had significant spatial and temporal differences and it was largely associated to sedimentation patterns. Coral density decline during fall and winter season was attributed to extreme weather conditions, since it was evidenced a sequence of acute precipitation events caused by tropical trough and tropical storms from August to November 2014 that prompted sediment-laden runoff and erosion, and were followed by coral decline. Extreme precipitation events have been identified as key a factor that triggers sedimentation pulses and distribution along near-shore coral reefs (Otaño-Cruz, Chapter 1 M.Sc. Thesis). During study period it was documented peak SST that reached up to 30^{o}C, representing anomalies of +1.35^{o}C, might have also negatively impacted coral densities as coral decline followed high SST episodes (Fig, 2.16). Moreover, a regional oceanographic event that increased chlorophyll-*a* concentration due to an extensive influence from a Orinoco river plume was experienced in October 2014, which might have produced coral mortality event that were documented on multiple reefs surrounding Culebra Island and other locations across Puerto Rico (Hernández-Delgado and Vega-Rodriguez, personal communications 2014). Even though coral condition and incidence of diseases was not assessed in this study, it can be suggested that the combined effects of increased SST and nutrient concentration could have combined with other local stressor and triggered adverse environmental conditions with possible implications on coral density decline during fall and winter season. Therefore, it can be argued that coral density mainly responds to environmental stressors that interact synergistically at local and regional scales. This assumption is based on the fact that SST did not showed a significant relationship with coral density patterns (Rho=-0.174, p=0.84) at small spatial and temporal scales (Table 2.8). This result supports the consensus of scientific community that identifies coral colony density as a good indicator of coral reef health in rapidly changing environments (Bruno, 2009; Van Woesik et al., 2011).

A total of 34 scleractinian species were recorded in BTA and PSO shallow reefs, which approximately represent two thirds of the whole total number of species known for the northeastern region of Puerto Rico (Hernández-Delgado, 2000). The most conspicuous species at reef areas under continual sediment stress were *Porites astreoides* and *P. porites*. The *Porites* spp. complex and the *Siderastrea* spp. complex have been recognized as species with high tolerance to sediment by their ability to effectively reject particles, and they are becoming more abundant on shallow reefs throughout the Caribbean (Loya, 1976; Cortes and Risk, 1985; Torres and Morelock, 2002; Green et al., 2008; Ennis et al., 2016). Other common coral species at both study sites were *Acropora cervicornis, Diploria labyrinthiformis, and Orbicella annularis,* generally abundant at reef zones less subject to sedimentation stress (Fig. 3.3). It has been suggested that sediment tolerance and sediment rejection abilities differ between species and coral morphologies, with branching, meandering, and large coral colonies being more tolerant to sediment accumulation (Rogers, 1990; Fabricus, 2005; Sanders, 2005). However, coral species also have different abilities to reject fine particles and thus partial mortality might be a good indicator of stress (Nugues and Roberts, 2003). Coral condition was not assessed in this study and is a component that needs further analysis to determine relationship between coral disease, partial mortality and bleaching with sedimentation patterns and other environmental variables. Also, sedimentation events associated with wide-scale turbidity and light attenuation can have prolonged negative impacts on percent coral cover, species diversity and reef zonation (Loya, 1976; Acevedo et al., 1989). Characteristics of marine sediments deposited across the reef can determine species that will better adapt and dominate reefs subject to experience more recurrent local stressor related to sediment pulses (Pastorok and Bilyard, 1985). Changes in coral reef species composition might have significantly adverse repercussion through reef accretion decline, resulting in increasing vulnerability to sea level rise, one of the main consequences of future climate scenarios (Knowlton, 2001; Edmund, 2010). Degradation of the reef's structural complexity has adverse implications to socio-ecological services provided to coastal communities and as consequence there is an increasing need to address these impacts (Alvarez-Filip et al., 2009; Graham and Nash, 2013; Newman et al., 2015).

Coral species richness and diversity declined through time series, especially at areas subject to recurrent runoff and sedimentation stress. However, in this study there is no data that support the existence of seasonality. Mean species richness decline could be associated to sedimentation pulses documented across BTA reef during fall and winter season, associated to intense rainfall events that reached a total of 279.91 mm and 108.71mm, respectively. Sedimentation rate had its highest levels during these seasons with a mean of 2.58 mg cm^{-2} d^{-1} during fall and 6.84 mg cm^{-2} d^{-1} during winter season (Otaño-Cruz, Chapter 1 M.Sc. Thesis). The PSO reef experienced a reduction in species richness from spring to fall (-12%) and could also be associated to the incidence of high sedimentation pulses and land-based sediment deposition across PSO reef during summer season, produced by intense rainfall events after long drought period with a total precipitation of 242.58 mm (Otaño-Cruz, Chapter 1 M.Sc. Thesis). At PSO reef the peak sedimentation rate was documented from July to August 2014 with a mean of 1.52mg cm^{-2} d^{-1}, and mean terrigenous content that constituted 41% of sediment sample collected across PSO reef (Otaño-Cruz, Chapter 1 M.Sc. Thesis). Similarly, Hernández-Delgado (2000) concluded that in the northeastern region of Puerto Rico coral richness were significantly impacted by sedimentation resulting in the disappearance of rare and sensitive coral species. Over the last decades, multiple Caribbean coral reefs have shown similar trends of increasing coral diversity and coral densities at greater distance from impacted coastal areas and land-based source of pollution (LBSP) (Loya, 1976; Cortés and Risk, 1985; Acevedo et al., 1989; Pastorok and Bilyard, 1985; Lirman et al., 2007; Ennis et al., 2016).

Coral recruit densities has become dominated by sediment-tolerant species, such as *Siderastrea radians*, *S. siderea*, and *Porites astreoides*. The increasing dominance of brooder, non-reef building species recruits has been documented in the wider Caribbean (Lirman et al., 2007; Green et al., 2008; Edmund, 2010; Hernández-Delgado et al., 2014b). This trend might be responsible of the overall shifts in species composition as population growth is skewed towards ephemeral, fast growing, and stress tolerant species as the reef experience a multiplicity of threats and recurrent changes in environmental conditions, thus limiting success of reef-building species recruit settlement, such as *Orbicella annularis* and *Acropora* spp. (Van Woesik et al., 2014; Hernández-Delgado, 2000). Further monitoring of juvenile corals will be required to evaluate long-term implications of changes of species composition of coral recruiting along near-shore coral reefs. In PSO reef, coral recruit density declined on reef zone farthest from shore (>60m) and it had a strong relationship with increased silt-clay sediment deposition after an extensive deforestation event that disturbed coastal watershed. But other factors not addressed in this study might have affected coral recruit density, such as interference out-competition by fast-growing macroalage (Nugues et al., 2014) and cyanobacteria (Fong and Paul, 2014). Macroalgae can proliferate under high nutrient concentrations from runoff (Cloern, 2001), under low herbivory pressure due to lack of recovery of *Diadema antillarum* (Ruíz-Ramos et al., 2011) or overfishing (Hernández-Delgado et al., 2006), or due to a combination of both (Littler et al., 2006). Macroalgae can also interact with corallivory by fireworm *Hermodice carunculata* to accelerate colony mortality (Wollf and Nugues, 2013). This suggest that coral reef trophic condition can be a critical co-factor, in combination with climate change-related impacts, in shaping coral reef benthic assemblages. Coral larvae dispersal patterns can also be affected by climate change and future variations of thermohaline circulation, combined with the possible impacts produced by the occurrence of a positive North Atlantic Oscillation at a mesoscale can result in changes on trade winds, tropical storm activity, currents, gyres direction and forces (O'Hare, 2011; Delworth et al., 2016).

Increased sediment influx and distribution of fine sediments through the reef was documented after strong precipitation events, followed by wind-induced waves and currents that transported fine, land-based sediments until deposited in calmed waters (Otaño-Cruz, Chapter 1 M.Sc. thesis). Previous studies have shown similar patterns where coral reefs exposed to high sedimentation impacts are subject to reduced or inhibited recruitment, since substrate availability is reduced (Pastorok and Bilyard, 1985; Edmunds and Gray, 2014). Coral recruit density showed significant correlation with sand, silt-clay, wave height and depth (Table 2.10). Weather and oceanographic conditions influences wave height and during extreme climate events it is the main driver of sediment resuspension and transport (Hernández-Cruz et al., 2009; Edmunds and Gray, 2014). The unfavorable impact of sand sediment on coral recruits could be mostly attributed to burial effects experienced after cold front events, climatic events characteristic of winter season that produce significant increase in sedimentation rate by bedload sediment transport and resuspension (Otaño-Cruz, Chapter 1 M.Sc. Thesis). The wave height is highly interconnected with light availability and as a result it is a determining factor of recruit density by depth. Other factor contributing to temporal changes of coral recruit density might be related to shifts in benthic dominance from hard coral cover to macroalgae, cyanobacteria and algal turf. It is widely known that algal dominance can inhibit coral larvae settlement, predominantly when combined with deposited sediments, disturbing long-term coral reefs resilience and the ability to recover after disturbance (Birrell et al., 2005; Kuffner, 2006; Vermeij, 2006; Fong and Paul, 2014; Stubler et al., 2016).

Trends of percent live coral cover decline responded to complex local and regional factors (e.g., sedimentation, LBSP, SST) that combined with natural impacts (e.g., hurricanes) and caused percent coral cover decline, the loss of cover by most abundant species (e.g., *Orbicella annularis* complex), and shifts in species composition through the last decades (Pandolfi, 2003; Rogers and Miller, 2006; Knowlton and Jackson, 2008; Miller et al., 2009; Hernández-Pacheco et al., 2010). Differences in percent coral cover at small spatial scales in this study reflected strong relationships with local sedimentation dynamics, largely due to impacts produced by sand and silt-clay sediment deposition. Documented mean live coral cover of 12.82% positions coral reefs study sites below mean coral cover of 16.80% for the Caribbean region (Jackson et al., 2014), and confirms the assumption that corals are not functionally dominant at shallow reefs impacted by recurrent sedimentation pulse stress events (Rogers and Miller, 2006).

Coral cover decline at reef areas subject to higher terrigenous sediment accumulation suggests there is a relationship between local coral reef health, represented by coral cover and species composition, with contemporary changes in coastal watershed management, weather and oceanographic conditions. These are main factors that affect coastal runoff, soil erosion, sediment characteristics, sediment distribution and the level of threat to near-shore coral reefs (Ognston et al., 2004; Hernandez-Cruz et al., 2009; Ennis et al., 2016; Otaño-Cruz, Chapter 1 M.Sc. Thesis). Sediment accumulation on coral surfaces, especially fine sediments, produce significant adverse physiological responses as a consequence of energy relocation, required to achieve rejection of sediment particles through the production of mucus and ciliary action (Acevedo et al., 1989; Telesnicki, 1995; Woolfe et al., 1999; Fabricius, 2011). These processes result in increasing respiration rates and decreasing photosynthesis and calcification rates, consequently, it has negative effects on colony survival and growth rates (Junjie et al., 2014). However, different coral species have varying physiological mechanisms to cope with sediment accumulation, while the same coral species might have similar responses at different locations (Risk and Edinger, 2011). This is the case of the Columnar star coral, *Orbicella annularis*, the most significant reef builder in the Caribbean, where field studies conducted at Costa Rica (Cortes and Risk, 1985) and southwest Puerto Rico (Torres and Morelock, 2002) documented that with increased terrigenous sediments accumulation the coral experimented significant reduction of growth rates and live tissue cover. Similar trends were evidenced in this study at nearshore reefs in Culebra Island, where *O. annularis* had lowest cover; in contrast *Porites astreoides* and *P. porites* had the highest benthic cover. The benthic cover dominance by species that can survive on sub-optimal conditions reflects that these reefs have already experienced changes due to recurrent sedimentation stress.

Other benthic components that responded to terrigenous sediment deposition were macroalgae, calcareous algae, and sponge percent cover. Macroalgae cover increased after high sedimentation events, particularly the fast growing *Dictyota* spp., turf, and encrusting calcareous algae *Ramicrusta textilis* which was documented overgrowing dead coral skeleton. In 2011, *R. textilis* was first documented in Puerto Rico coral reefs (Balletine et al., 2011; Balletine and Ruiz, 2013), and continues to compete and overgrow coral species (Fig 2.18). This encrusting species has been documented overgrowing 14 species of scleractinian corals, gorgonians, hydrocorals and other algae in the Caribbean (Eckrich et al., 2010). A recent new species, *R. monensis*, with similar behavior, was described from Mona Island, Puerto Rico (Ballantine et al., 2016). Therefore, *Ramicrusta* spp. have become a critical factor which can also shape benthic coral reef assemblages across the Caribbean and should be carefully studied.

Bellwood and Fulton (2008) concluded that increased sediment deposition could inhibit fish grazing and promote the growth of macroalgae and filamentous algal turfs. Therefore, reef's trophic state and fish community structure can also influence benthic assemblage dynamics. Throughout the study period a cyanobacteria bloom possibly related to increased deposition of organic matter and SST was documented. These patterns suggest that algal communities are highly dynamic and can respond rapidly to environmental disturbances. In the other hand, the increase in crustose coralline algae at study site far from shore can be suggested to be partly responsible for the increase in coral cover as substrate became available for coral to recruit and grow in area less exposed to sedimentation stress. High levels of sedimentation stress can increase coral reefs susceptibility to degradation and could led to short-term phase-shifts towards the dominance of macroalgae and algal turf. The observed inverse relationship between coral and macroalgal cover at nearshore reefs is a strong ecological indicator of degraded water quality conditions resulting from LBSP and runoff pulse events. Increased extreme rainfall events, as evidenced by Hernández-Delgado et al. (2014a), can have deleterious impacts on corals. Results from this study validated previous studies conducted at the Caribbean region that found adverse consequences on coral cover and coral reef benthic communities from terrigenous sediment dynamics (Acevedo et al., 1989; Begin, 2013*).* According to Bruno et al. (2009) phase-shift index, results from this study also revealed that coral reefs might be experiencing moderate phase shift towards increasing dominance by macroalage. Thus, management intervention is imperative to reduce local stressor and reverse coral reef degradation. This could play an even more critical role under predicted climate change-related impacts.

Sponge cover was the only benthic component to be influenced by sedimentation rate and terrigenous rate, as well as sediment texture and terrigenous content. Increased frequency and severity of sedimentation stress and LBSP that can led to eutrophic states, combined with low grazing rate, can increases competition for space with corals and could favor benthic cover of resistant species, such as encrusting sponges, thus leading to alternate dominant states (Lopez-Victoria et al., 2006; Chadwick and Morrow, 2011; Gonzalez, 2011). The encrusting sponge, *Dictyonella funicularis* was documented aggressively overgrowing dead and diseased corals and it can be classified as an ecological indicator species, since its abundance may directly respond to changes in coral and environmental conditions. Even though this species has been recently reported on Caribbean reefs, its distribution is still unknown (Lang, personal

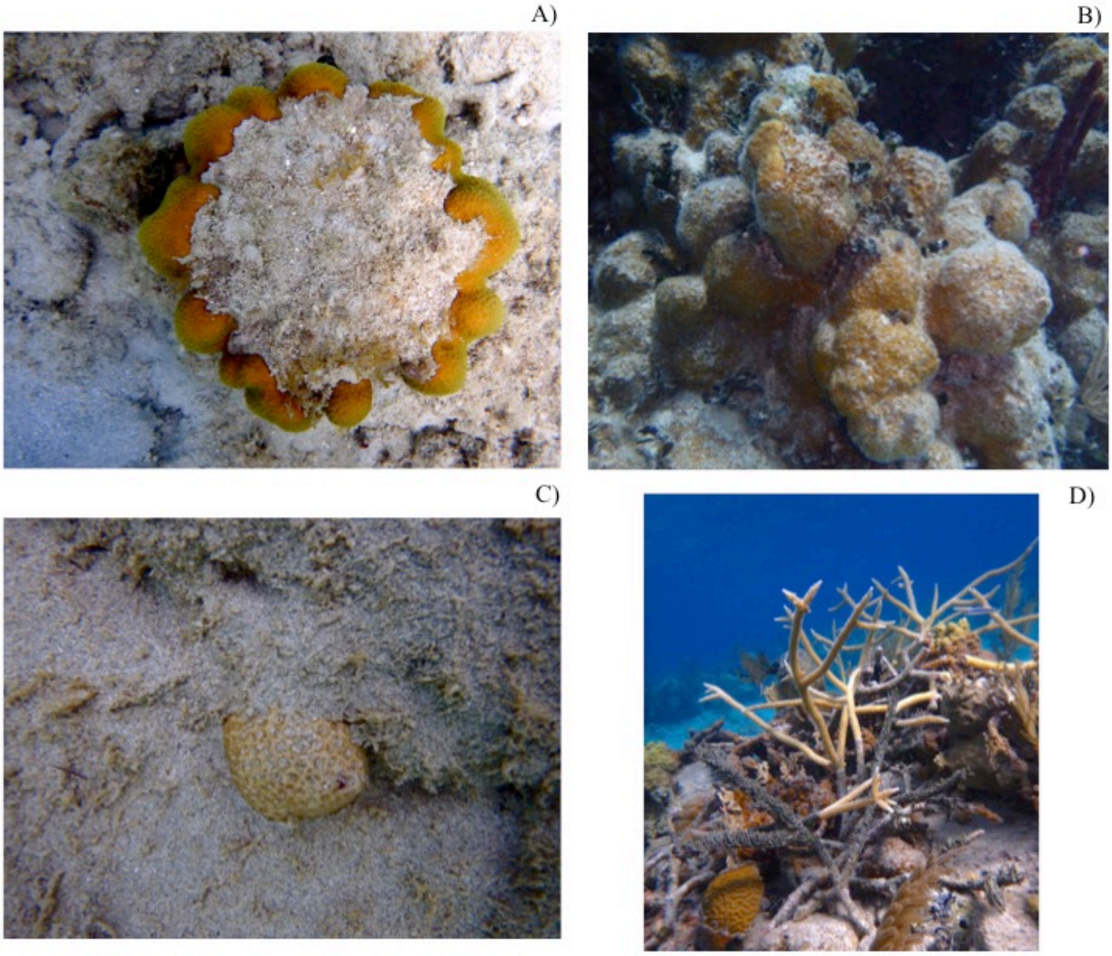

Figure 2.18 Coral *Orbicella annularis* with sand and silt-clay sediment deposited (A), encrusting calcareous algae *Ramicrusta textilis* overgrowing *Orbicella annularis* complex (B), coral recruit *Siderastrea siderea* established in bottom with sand and turf algae cover (C), gray sponge *Dyctionella funicularis* overgrowing *Acropora cervicornis* outplant (D).

communications 2013). The long-term implications of increased sponge dominance and possible shifts into alternate dominate states needs to be assessed in details to prevent neglecting further impacts to coral communities. In addition, it is needed to strengthen local and regional water quality analysis to assess changes in nutrient concentration, and determine other environmental factors that might be benefiting sponge and macroalgae overgrowth.

High octocoral cover was documented in deep areas and farther distance from shore in PSO zone B, a reef segment that was characterized by lower coral recruitment density, low wave energy, and high terrigenous sediment deposition after strong weather events (Otaño-Cruz, M.Sc. Thesis, Chapter 1). Previous studies have shown higher abundance and benthic cover of octocorals at deeper, fore-reef terraces characterized by high bottom relief, medium to low inclination (Sanchez et al., 1997). Octocoral distribution and composition are influenced by bed load sediment transport, which also reduces with depth and at areas with low wave energy (Sanchez et al., 1998; Yoshioka 2009). In addition, dominance by octocoral has been shown to reduce scleractinian coral recruitment, at least in the Great Barrier Reef (Maida et al., 1995). In combination with the known increase in coral recruit mortality with increasing SST (Edmunds, 2004), and adverse impacts by eutrophication (Tomasick, 1991), sediment stress and algal overgrowth (Ruíz-Zárate and Arias-González, 2004; Hoey et al., 2011; Doropoulos et al. 2014), and by hurricanes and bleaching (Mallela and Crabbe, 2009), shifting dominance by octocoral recruitment and growth implies a shift in coral recruit community composition favoring non-reef building species on habitats that were formerly dominated by reef-building scleractinians. This could be an indication of changes associated to climate change-related warming trends, but potentially magnified by local stressors as documented in this study.

A possible limitation of the study was the lack of resources to assess benthic community and environmental variables at a larger spatial scale to contrast various land uses and coastal management strategies and the effects on near-shore coral reefs response. Future research could address larger spatial scales and multiple environmental factors related to water quality, such as nutrient concentrations, to identify which factors exerts greater influence in coral, macroalgae and turf cover at local and regional levels. Furthermore, variations in coral growth rate under contrasting stressors should be addressed, comparing sensitive versus resistant species, and addressing the ability of large reef-building species to tolerate and reject sediment particles. The prevalence of coral diseases and partial mortality as consequence of the direct interactions between coral, macroalgae, algal turfs and sedimentation represents a good indicator of habitat degradation. Likewise, it is imperative to address climate change impacts on local and regional weather since it has the potential to increase frequency of extreme events, including intense storms, wind patterns and wave action, which may influence sediment delivery and resuspension, respectively, to coral reefs and associated ecosystems.

There is a need to develop and implement integrated management strategies aimed at restoring environmental conditions needed to help the reef recover from recurrent, severe disturbances, and to resist unmanageable regional and global human-induced stressors. Since local threats to coral reefs continue to increases there is a need to:

- Promote long-term ecological research of coral reef benthic community structure, reef condition, and benthic response to sedimentation stressors, land-based pollution, among multiple and cumulative stressors to provide scientific information needed for decision- and policy-makers to develop ecosystem based management strategies and reduce local stressors.
- Support low-tech coral reef restoration initiatives across increasing spatial scales, as an essential tool to maintain high diversity, rehabilitate reef functions, enhance coastal habitat protection from wave action, and increase ecosystem resilience. Encourage the propagation of reef-building species, among other coral species that have low recruitment rates.
- Promote the implementation of management plans and emphasize interconnectivity between terrestrial and marine protected areas with high ecological, cultural and economic values for local communities. Reduce tourism stressors to coastal habitats and marine ecosystem by supporting best practices, nature-based tourism, and enforce local regulations.
- Engage coastal communities through education, outreach, and encourage local residents to become advocate for coastal and marine resources that can provide essential socio-economic services to the region. Furthermore, promote the development and implementation of community- and science-based conservation efforts to achieve long-term functioning and broader effectiveness.

Near-shore coral reef benthic community structure are spatially and temporally heterogeneous and subject to confounding combination of regional and local stressors that largely contributes to the variability of coral reef ecological dynamics, thus reducing the overall reef resilience and magnifying the need for urgent ecosystem-based management to prevent further decline (Mumby and Steneck, 2011). Results from this study point out four main conclusions: 1) Coral colony abundance and coral recruits density are affected by local stressors, principally by changes in sedimentation dynamics, sediment texture, and composition. Decline of coral colony densities and shifts on species composition have occurred at reef areas exposed to high rates of silt-clay and terrigenous sediment deposition. 2) Coral species diversity declined through time but increased with greater distance from shore, since stochastic environmental disturbance associated to sediment delivery from adjacent poorly-managed watershed to near-shore areas reduce the occurrence of rare and sensitive species. 3) Local stressors had a highly significant role on shaping benthic community structure and species composition, yet there are complex interactions caused by changes in watershed land use, weather and oceanographic conditions that influences the frequency and extent of sedimentation disturbance to coral reefs. Therefore, coral species relative contribution varied with distance from shore. 4) Coral reefs dynamics even at small spatial and temporal scale experienced evident impacts from variation in sedimentation patterns, sediment texture and composition. Near-shore coral reefs surrounding semi-arid island are exposed to higher sedimentation rate during strong weather events, at the same time can experience rapid shifts towards benthic community structure dominated by macroalgae and other sessile, non-reef building organisms. Individual and cumulative stressors and their impact to coral reefs have become a top research priority for international scientific community due to its significance on identifying how local and regional disturbances affect marine ecosystems and species capacity to adapt and cope upcoming impacts related to to global warming (Rudd, 2014). Sea level rise represents additional threats to coral reefs and human coastal communities as a result of increased exposure to extreme weather events, coastal erosion, sediment influx, sediment influx and distribution, and should be addressed in future studies as well. 5) Severe impacts to land uses and poor governance in implementing existing regulations to protect lands from soil erosion, even at such small spatial and temporal scales such as those documented in Culebra Island in this study, are increasingly detrimental across small tropical islands. Under such small spatial scales, adverse impacts of soil erosion and sediment delivery can be rapidly magnified on deforested steep slopes and dirt roads. Increasing extreme rainfall and runoff episodes can further magnify pulse impacts with rapid, increasing negative impacts on shallow, coastal coral reefs and associated ecosystems. This requires an immediate change in focus and in the implementation of existing watershed restoration plans in order to pay critical attention to areas already shown to be a major roadblock for coral reef conservation and restoration. This is further a concern considering that Culebra Island was designated by NOAA in 2014 a Blueprint Habitat Focus Area, and that adjacent coastal areas are designated critical habitats for the Green turtle, *Chelonia mydas*, and for Acroporid corals.

The potential influence of sedimentation on determining coral reefs trajectories highlights the need of a broader understanding of sedimentation patterns and coral reef response to inform decision- and policy-makers to reduce local stressor and improve water quality. Innovative ecosystem-based management strategies at small islands and developing states need to bridge science, management, and policy-making gaps to achieve adequate planning of coastal watersheds and prevent sediment related local stress. The adoption of inclusive governance structures can provide necessary framework for continuous collaboration among stakeholders, and promote community-based participation, in the extended process of identifying most effective management actions to conserve and restore threatened coral reefs. Therefore, participatory decision-making processes are the most effective way to ensure and sustain long-term socio-ecological benefits while conservation and resilience rehabilitation of coral reefs is encouraged at multiple spatial scales.

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GENERAL CONCLUSIONS

The results of this study demonstrate that near-shore coral reefs surrounding the semi-arid Island of Culebra, Puerto Rico are susceptible to spatial and temporal differences of sediment distribution and accumulation caused by changes in watershed management and environmental conditions. Extreme weather events documented throughout a short-term study period were characterized with short, intense rainfall, and high wave height that produced high terrestrial sediment input, marine sediment transport, and bedload sediment resuspension at small spatial scales (<120m from shore). Coral reefs benthic communities experienced short-term response to variations in sedimentation dynamics and changes in environmental conditions. Spatial and temporal fluctuations in coral density, coral recruit density, percent coral cover and macroalgal cover were related to the amount and characteristics of sediment deposited along the reefs.

Sedimentation assessment presented in Chapter 1 suggests that differences in spatio-temporal sedimentation dynamics are largely influenced by local changes in land uses, weather and oceanographic conditions. Higher sedimentation rates was documented during periods of highest total rainfall and high wave energy, produced by tropical storms or cold fronts. For the study period, rainfall events in Culebra that produced major increments of sedimentation accumulation rate, terrigenous accumulation rate, and silt-clay sediment occurred during periods that exceeded total rainfall of 30 mm and rainfall intensity that exceeds 15 mm/hr. These events had higher impact from terrigenous sediments to reef areas closer to shore; areas exposed to runoff and ephemeral stream outlets. However, sediments also reached reef areas far from their sources. Significant land-use change at PSO watershed by a deforestation event was determinant in facilitating terrigenous sediment influx and distribution along the coral reef. During periods of wave height that exceed 1m it was documented high resuspension of bottom sediments that impacted the whole reef, without distinction of distance zone from shore (<60m, >60m). The magnitudes of impact were dependent on changes in wave and wind dynamics; it can be suggested that reefs bathymetry, depth gradient contour, and reef orientation in relation to wind and wave direction can be an important factor that determines susceptibility of sediment.

Nearshore benthic communities dynamics at small spatial and temporal scales are strongly related with local stressors related to watershed management, characteristics of sediment deposited and other environmental conditions that might affect terrestrial sediment influx and its distribution across the reefs. Coral abundance, coral recruit, benthic cover by functional components, and species composition can be considered good indicators to identify reefs level of stress the reefs by sedimentation disturbances or water quality degradation. Overall, benthic community structure is associated and responds to the amount and characteristics of the sediment influx. The results presented in chapter 2 suggest that sediment texture and composition, predominantly sand, silt-clay, and terrigenous content affect coral species competition and dominance by benthic component. The patterns documented through this study provides an insight of the complex factors that interact and sustains interconnectivity between terrestrial and marine ecosystems and the importance of an integrative management approach of the coastal zone at small arid islands to conserve biodiversity at shallow coral reefs. Land uses and management at sub-watershed spatial scale, physical watershed characteristics, local meteorological conditions, and oceanographic hydrodynamics forces are constantly changing and are altered in a global warming context; affecting the way and time span managers have to observe changes, collect information, interpret, and transform scientific information into a tangible and management effective enough to counteract impacts produce by severe disturbances and stochastic stressors. Therefore, there is a need of an active network of applied research projects that addresses each one of the complex factors and that interacts continuously.

Coral species density and diversity was lowest in reef areas exposed to recurrent episodes of sediment pulses. The most common and abundant coral species at these areas were stress resistant, with low density of reef-building species. The spatial distribution of sensitive coral species and coral recruits also responded to difference in sedimentation disturbance, having the higher densities in reef areas farther from shore (>60m). One main concern of the study is the low number of coral species recruiting on both sites, and the lack of recruits of major reef-building species, such as *Orbicella annularis*. This suggest that coral species composition might be experiencing a shift towards less complex coral reefs as a result of recurrent environmental disturbance, and if present trends of impact persist in the long-term the reef could experience drastic biodiversity and live coral cover decline. This decline would have serious implications in coral accretion rates, reef complexity and elimination of essential functions and services provided, such as habitat for reef-associated species. Thus, local human communities that depend on healthy coral reefs that surround semi-arid islands could experience profound ecological, social and economic impacts. However, coral restoration initiative performed in both reefs is having noticeable positive impacts in mitigating degradation trends by effectively increasing the population of threatened coral specie, *Acropora cervicornis*, on reef areas less subject to sedimentation stress. Changes in coral cover were mostly associated to spatio-temporal variation in sediment texture and terrigenous content. It is suggested that while corals were affected by sediment abrasion and burial it increased vulnerability and competition for space and it made possible colonization and overgrowth of opportunistic, fast-growing and encrusting macroalgae and algal turf. Therefore, it was evident that the coral-algae interactions at both sites had a strong inverse relation in response to sedimentation. Coral reduction also led to the advancement of sponges and there might be a combined performance between both algae and sponge that compete with corals, once affected by sediment accumulation and environmental degradation.

The information generated in this study identifies the main processes that interconnect the coastal and marine ecosystems. The environmental and ecological baseline data generated will be useful to generate models to forecast impacts of sediment influx as the coastal watersheds experience changes in land use and estimate shallow coral reefs benthic communities response in a more useful time frame to be able to implement effective management strategies to prevent impact. The information generated can have significant applications to Culebra Island, Puerto Rico and other small tropical semi-arid islands with similar climatic conditions, ecological characteristics and coastal development trends. Since, there is an increasing need to encourage the adaptation of robust management and conservation strategies to improve environmental conditions needed to boost coral reef resilience and ecosystem recovery from recurrent and severe disturbances. For instance, the main results of this research should support the implementation of collaborative, community-based initiatives, and adaptive management strategies that aims to conserve and restore coral reefs and watersheds.

Sedimentation has been repeatedly identified as a main threat to Caribbean coral reefs, thus it is essential the implementation of adaptive, sustainable development process following best management practices to avoid drastic changes in coastal watershed land uses and to avoid sedimentation impacts to already threatened near-shore coral reefs. One major strategic recommendation would be to develop methodology in collaboration with researchers, natural resources managers, and policy makers to achieve quick coastal and marine ecosystem assessment to detect disturbance events by projects that do not follow local state and federal regulations and needs immediate intervention. This information can be useful to support the enforcement of local regulation for the control of erosion and prevention of sedimentation, also known as Plan CES (by its acronym in Spanish), which is implemented in collaboration by the Puerto Rico Environmental Quality Board and Puerto Rico Department of Natural and Environmental Resources. The Culebra Conservation and Development Act No. 66 (1975) and Culebra Management Plan (1976) similarly provides regulatory framework and tools needed for Culebra Conservation Authority (ACDC) to regulate land use in order to preserve and maintain the ecological integrity of Culebra and its surrounding waters to achieve protection and conservations of coral reefs and associated ecosystems. However, there is a need to improve land use decision making process of Culebra by strengthening and updating existing policies and improving interagency agreements for the control of soil erosion, sedimentation, and non-point source of pollution to achieve optimum water quality and reduce current trends of costal habitat degradation (Johnston, 2004).

Furthermore, there is a need to conduct long-term monitoring efforts of sedimentation dynamics and the near-shore coral reef and associated ecosystems response, such as seagrass, to continually assess the effectiveness of ecosystem management and restoration initiatives, as well as the implementation of existing environmental policies and regulations which purpose is to avoid soil erosion and terrigenous-based sedimentation impacts to Culebra's surrounding marine environment.

There is an increasing need to implement an integrated and adaptive social-ecological governance and ecosystem-based management approach, that incorporates stakeholders, academics, government, and non-government organization into decision making process to maintain long-term biological biodiversity and productivity of coastal and marine ecosystems (Kofinas, et al., 2009). The integrated ecosystem approach should be based on a holistic management philosophy that integrates relevant ecological and ecosystem levels; such as species, habitat, services and functions provide by ecosystems. Also, it must recognize the complex interactions between terrestrial and marine ecosystems and the important role of humans and local community to contribute to reduce habitat degradation by developing and implementation effective management and conservation strategies to enhance coral reef resilience and guarantee the vast number of services, functions and benefits provided by coral reefs to human coastal communities worldwide.

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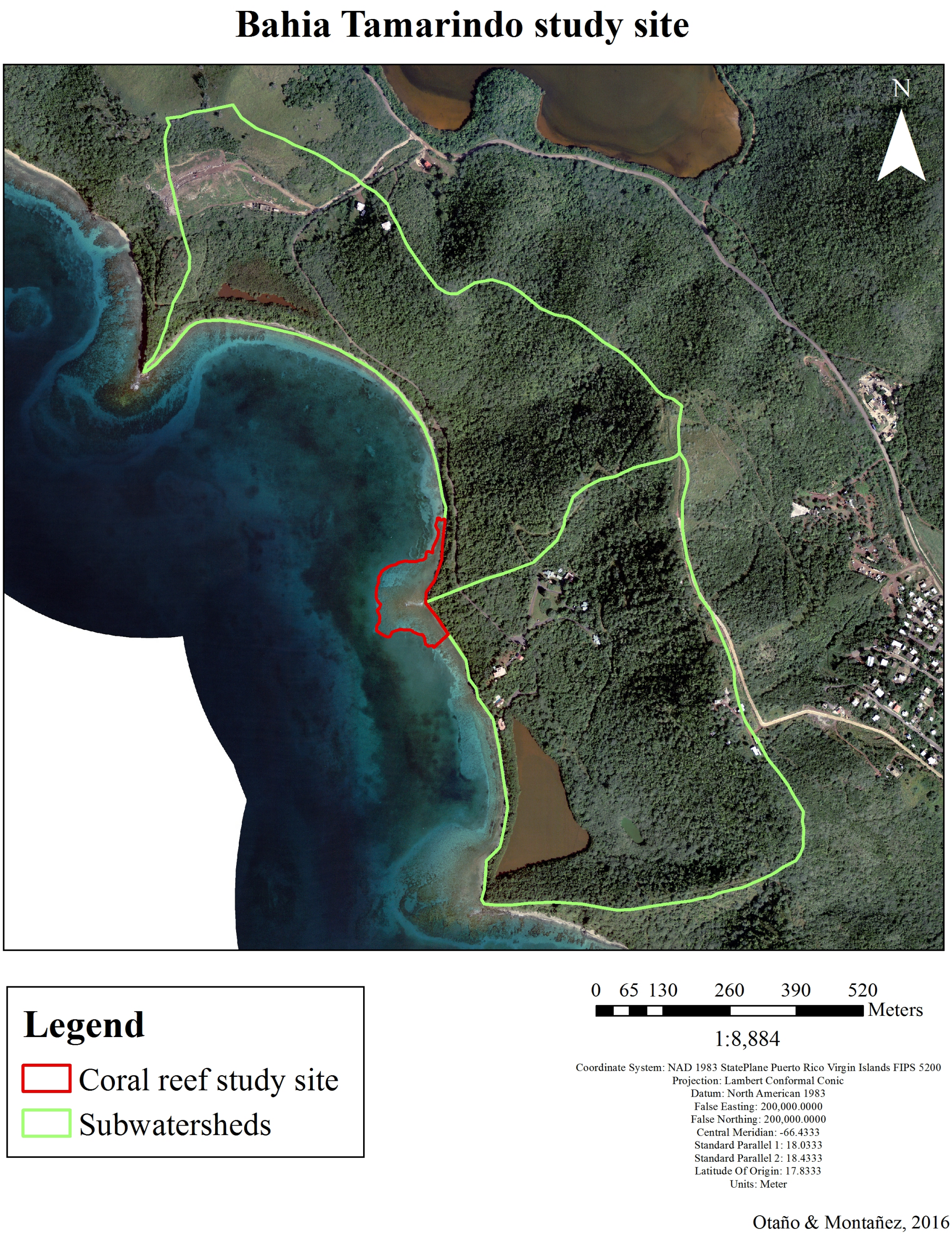
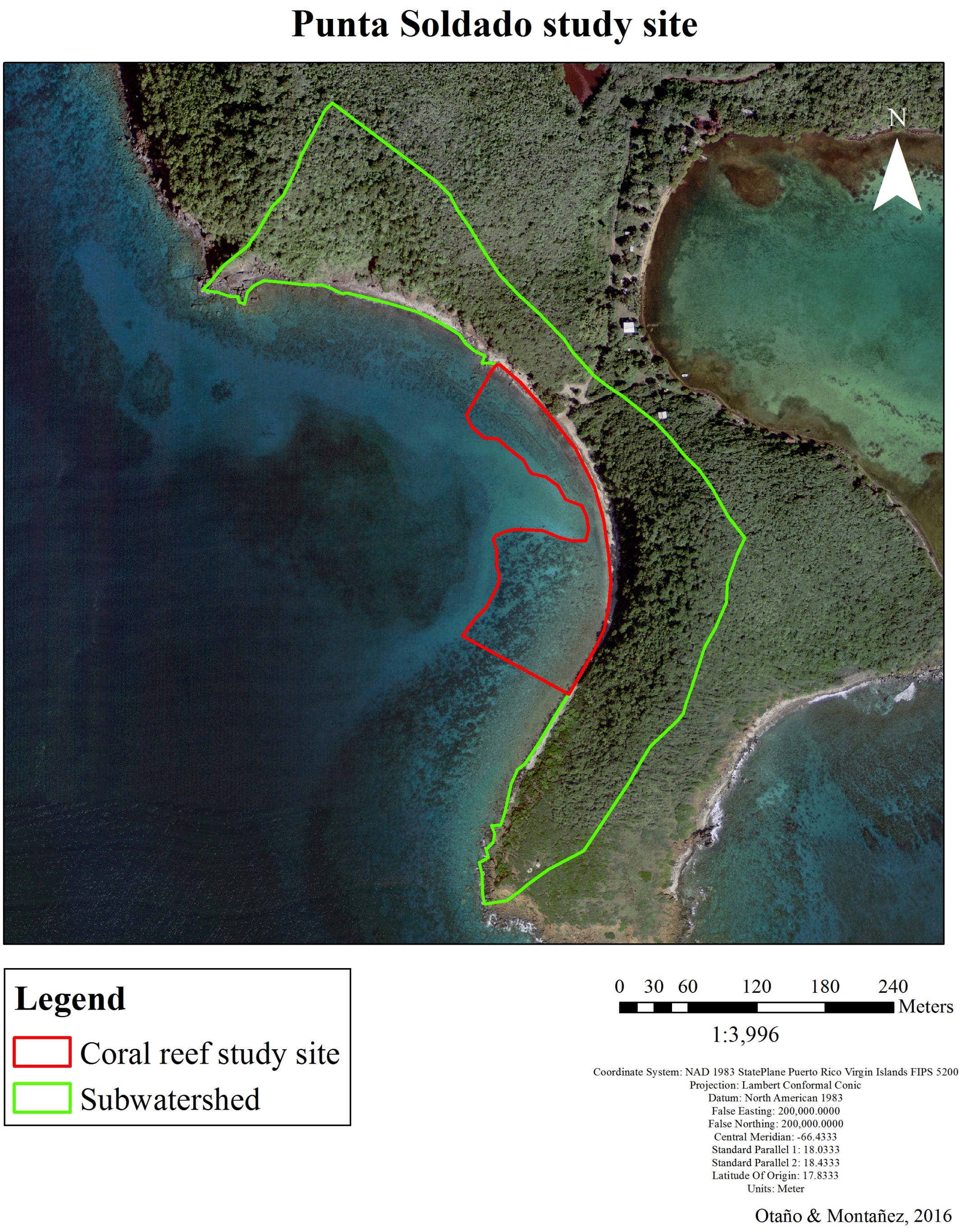
APPENDICES

Appendix 1.1. Bahía Tamarindo (BTA) near-shore coral reef study site and sub-watersheds. The near-shore coral reef site assessed is represented with red polygon. Tamarindo and Cornelio sub-watersheds, adjacent to BTA coral reef study site, are represented with green polygons. Aerial image UPRR, 2010.

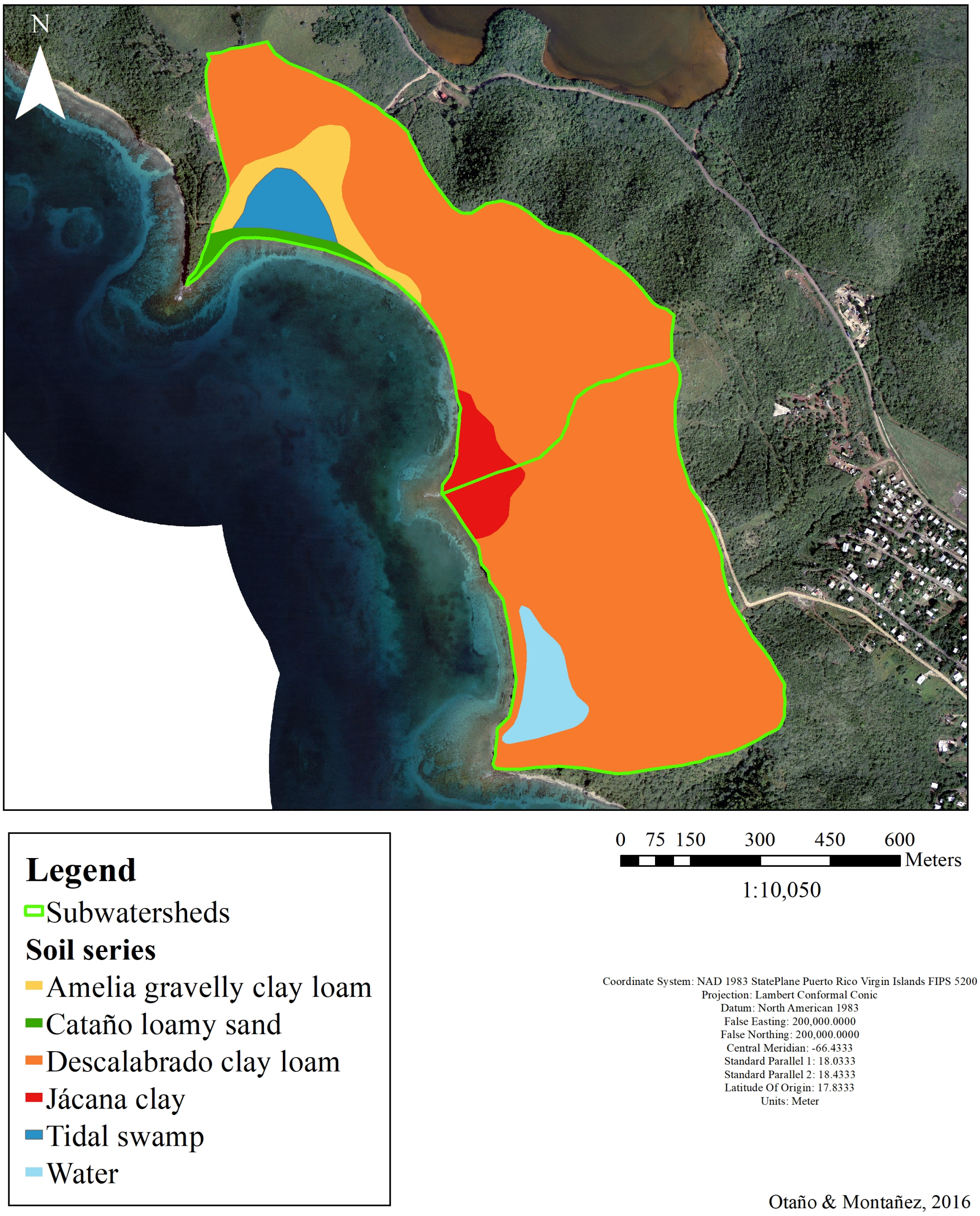


Appendix 1.2. Punta Soldado (PSO) study site.
The near-shore coral reef site assessed is represented with red polygon. PSO sub-watershed is represented with green polygon. Aerial image UPRRP, 2010.



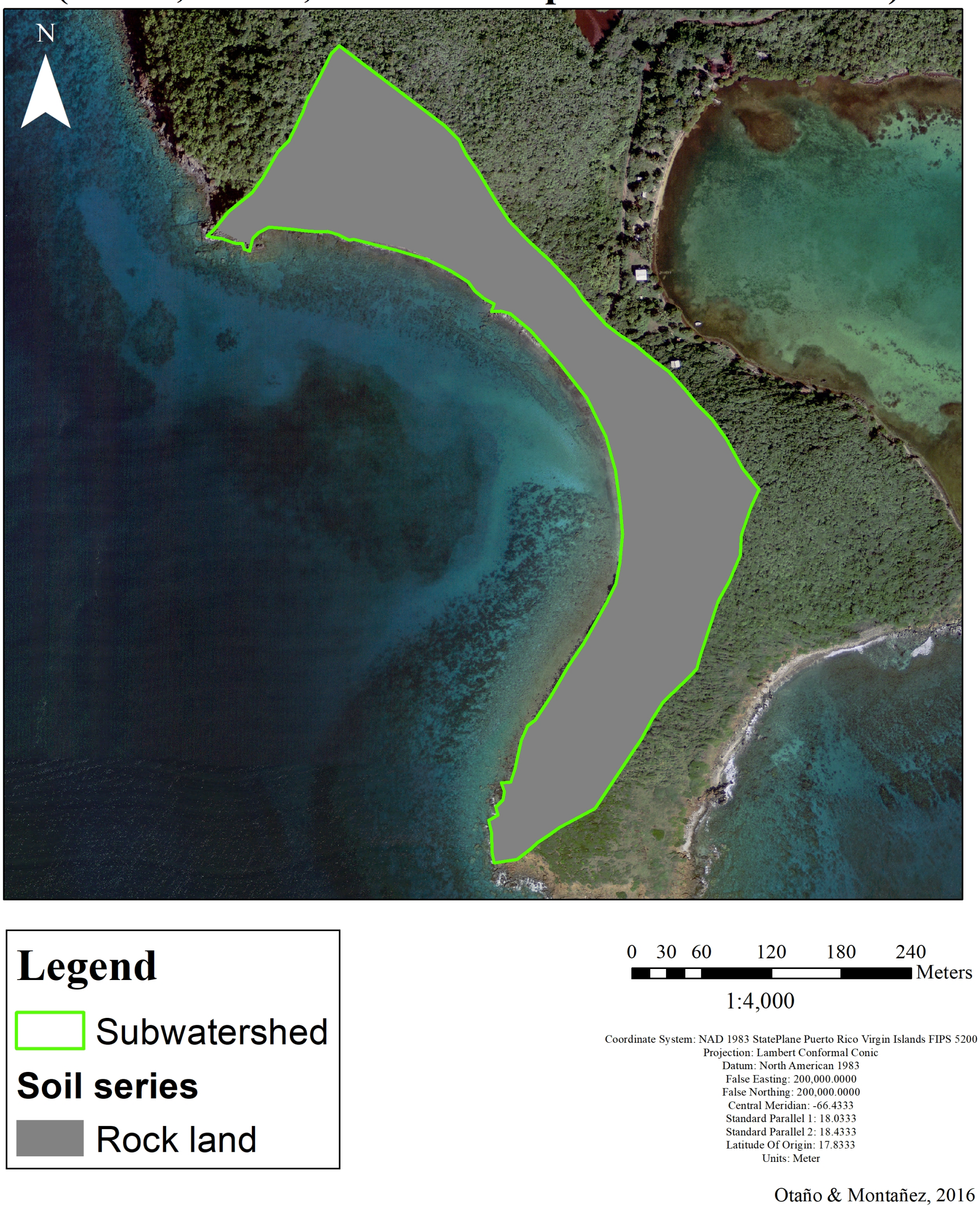
Appendix 1.3. Bahía Tamarindo Soil Series. Tamarindo and Cornelio Sub-watersheds Soil Series (National Cooperative Soil Services).

Bahía Tamarindo Subwatershed Soil Series
(USDA, NRCS, National Soil Service)

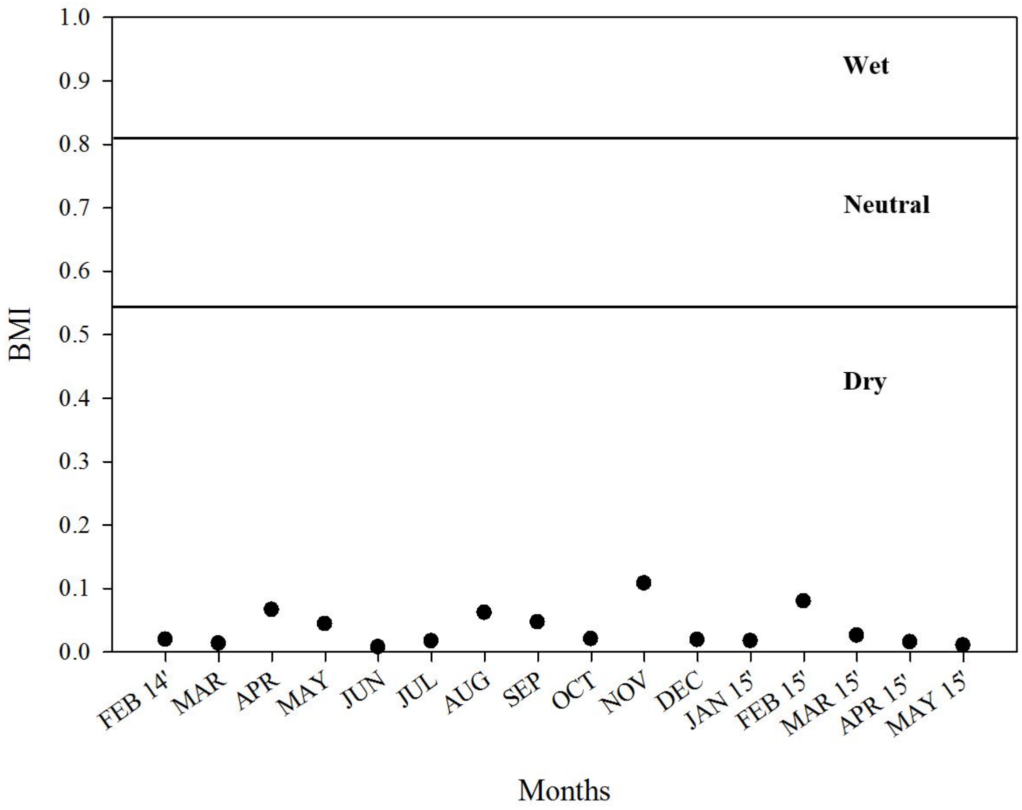


Appendix 1.4. Punta Soldado Sub-watershed Soil Series (National Cooperative Soil Service).

Punta Soldado Subwatershed Soil Series (USDA, NRCS, National Cooperative Soil Service)

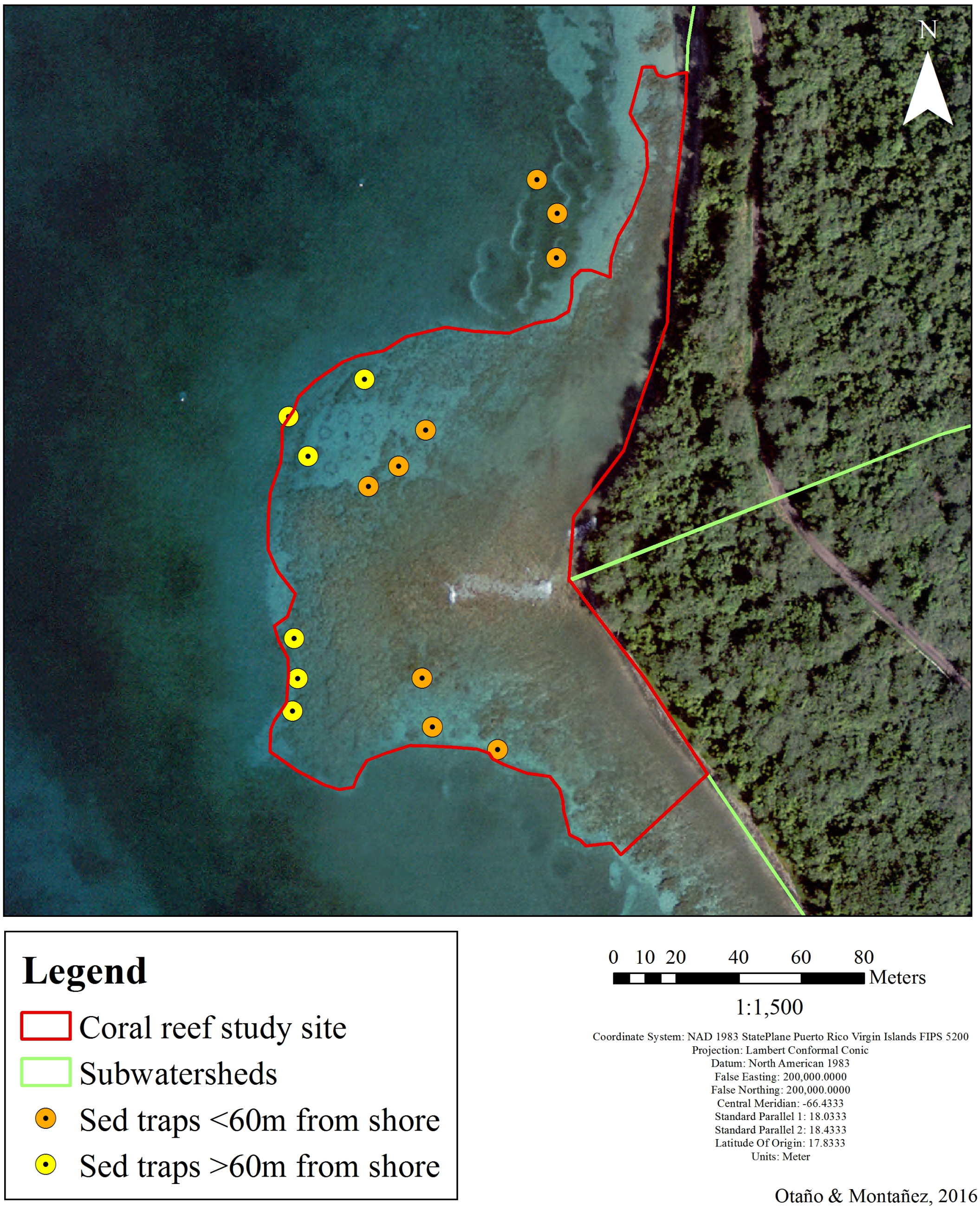


Appendix 1.5. Bailey moisture index at Culebra Island for study period 2014-2015.

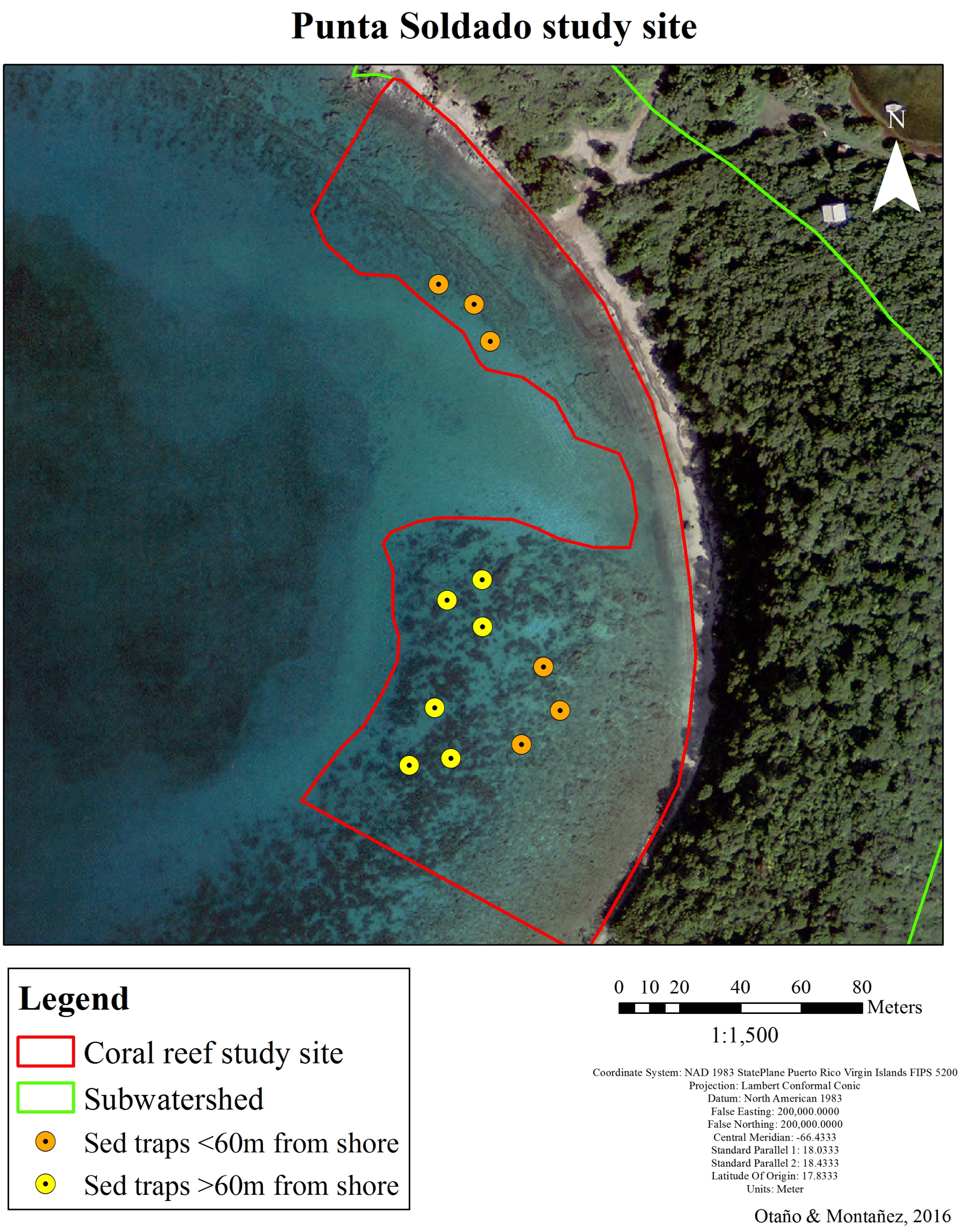


Appendix 1.6. Bahía Tamarindo sediment sampling design by distance zones. Sediment traps deployed at zone A with distance less than 60 m from shore are represented by orange dots. Sediment traps at a zone B with distance greater than 60 m from shoreline are represented with yellow dots. Aerial image UPRRP, 2010.

Bahia Tamarindo study site

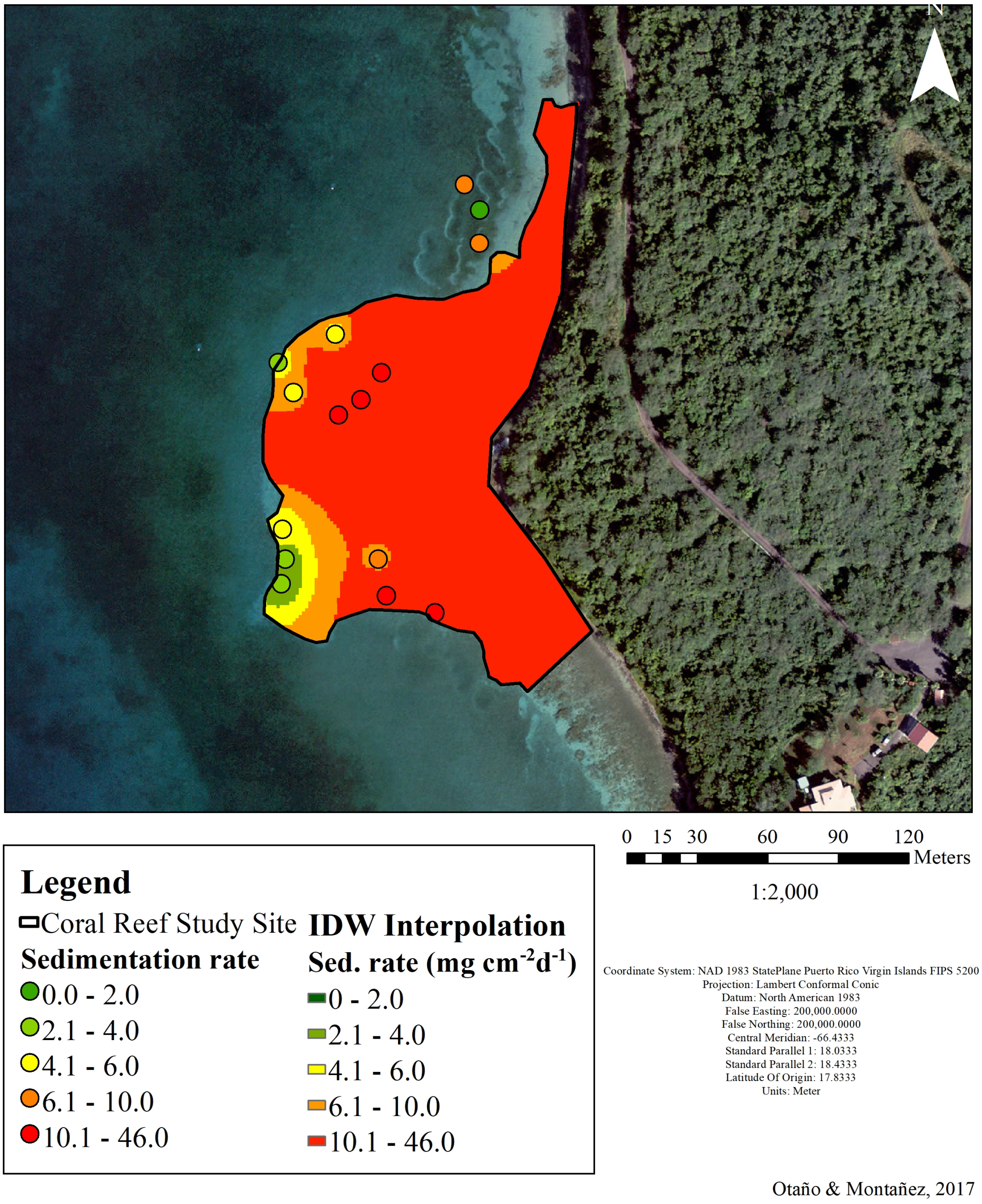


Appendix 1.7. Punta Soldado sediment sampling design by distance zones. Sediment traps deployed at zone A with distance less than 60 m from shore are represented by orange dots. Sediment traps at a zone B with distance greater than 60 m from shoreline are represented with yellow dots. Aerial image UPRRP, 2010.

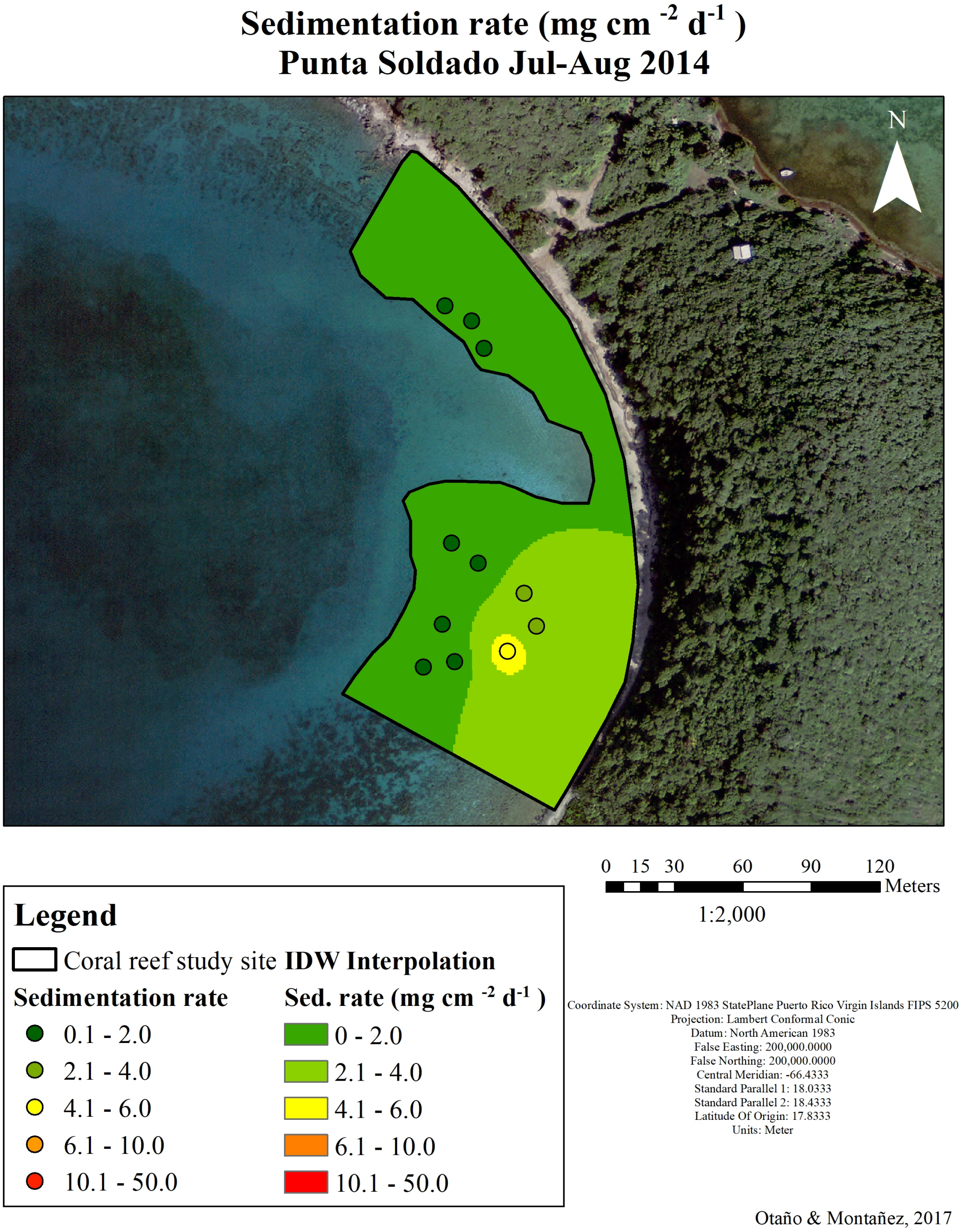


Appendix 1.8. Bahía Tamarindo sedimentation rate (mg cm^{-2} d^{-1}) by sampling period. Sedimentation rate assessed from December 2014 to February 2015 at sediment traps. Inverse Distance Weighting (IDW) interpolation generated with registered sedimentation rates in sampling period. Aerial image UPRRP, 2010.

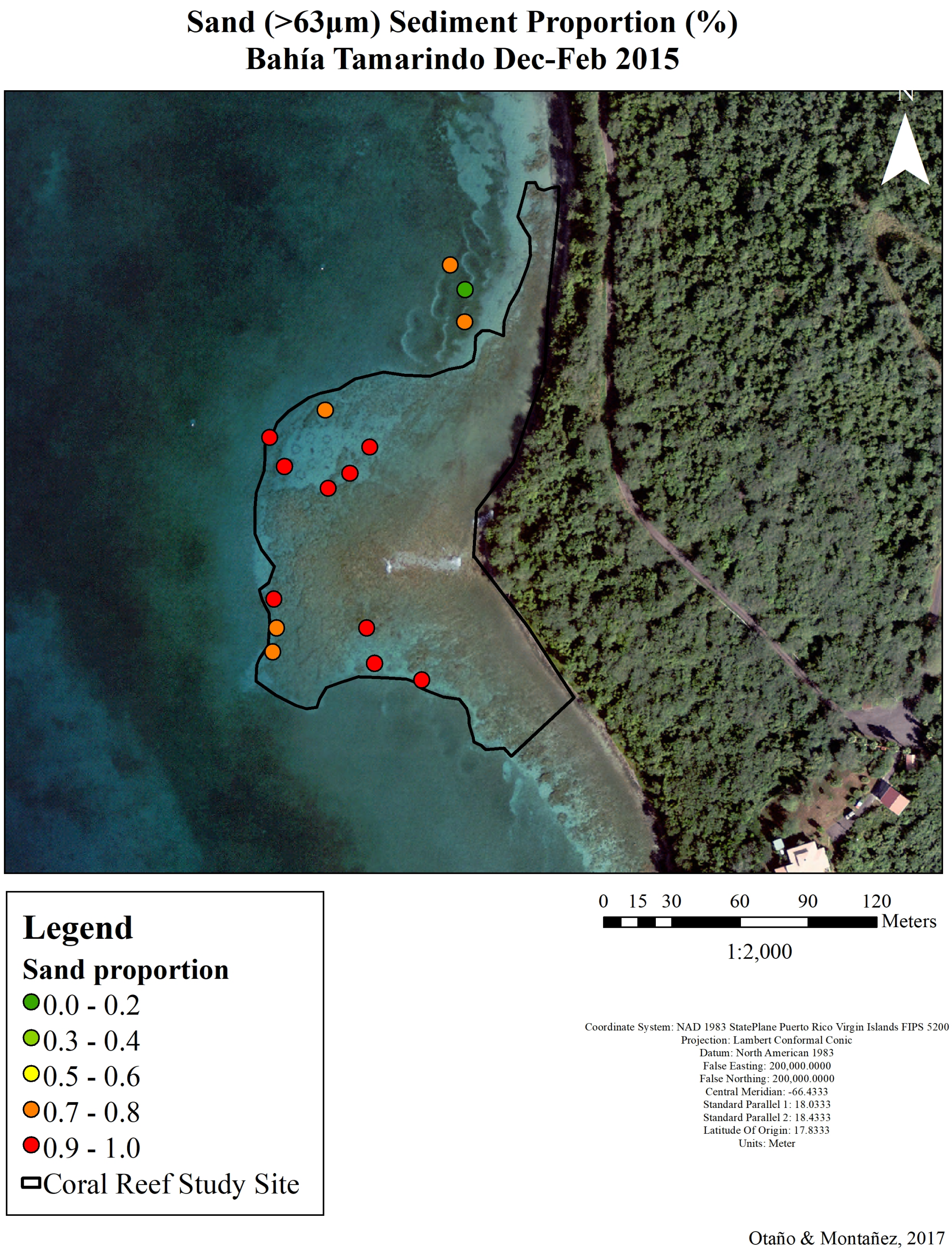
Sedimentation rate (mg $cm^{-2}d^{-1}$)
Bahia Tamarindo Dec-Feb 2015



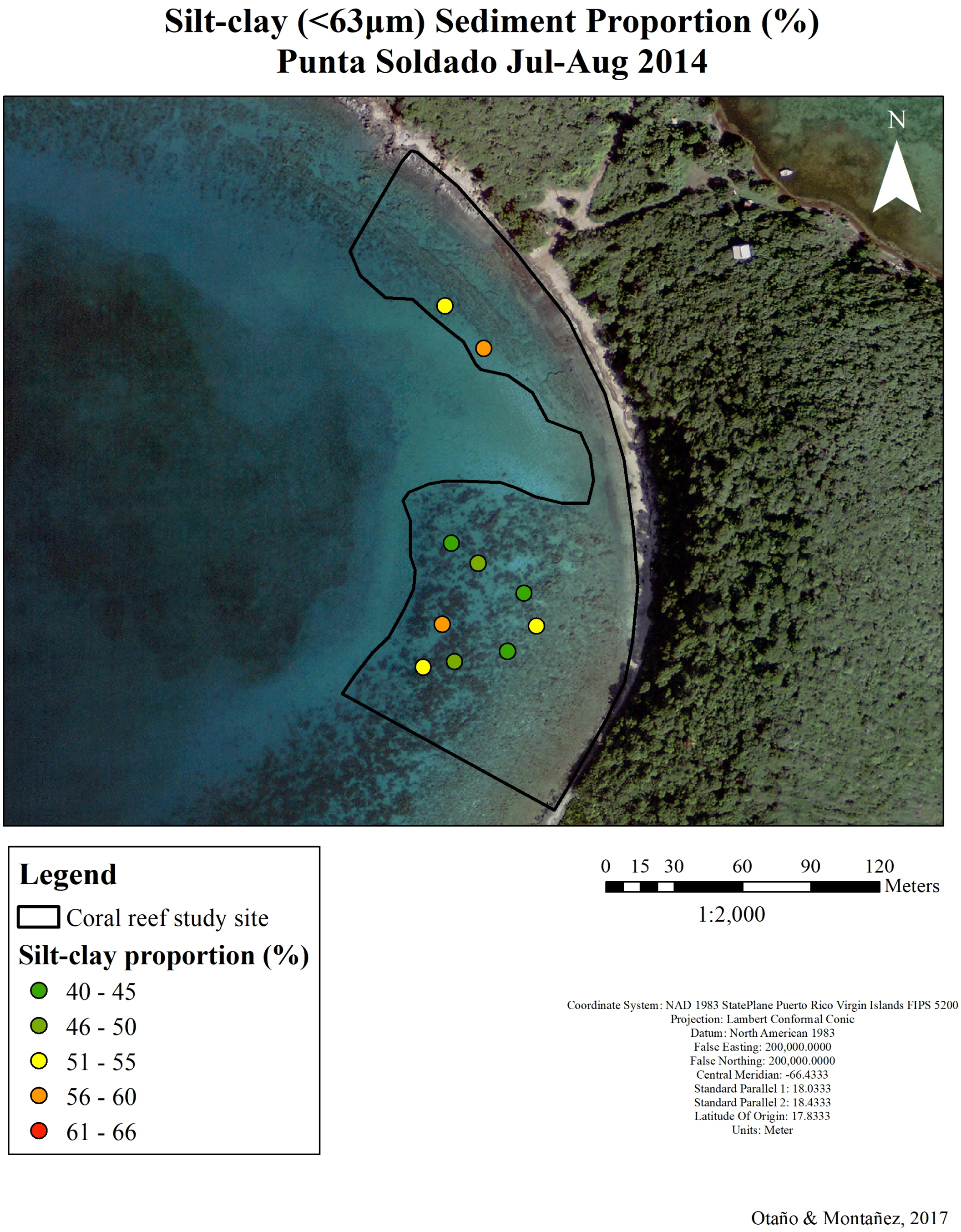
Appendix 1.9. Punta Soldado sedimentation rate (mg cm^{-2} d^{-1}) by sampling period. Sedimentation rate assessed from July to August 2015 at sediment traps. Inverse Distance Weighting (IDW) interpolation generated with register sedimentation rate of sampling period. Aerial image UPRRP, 2010.



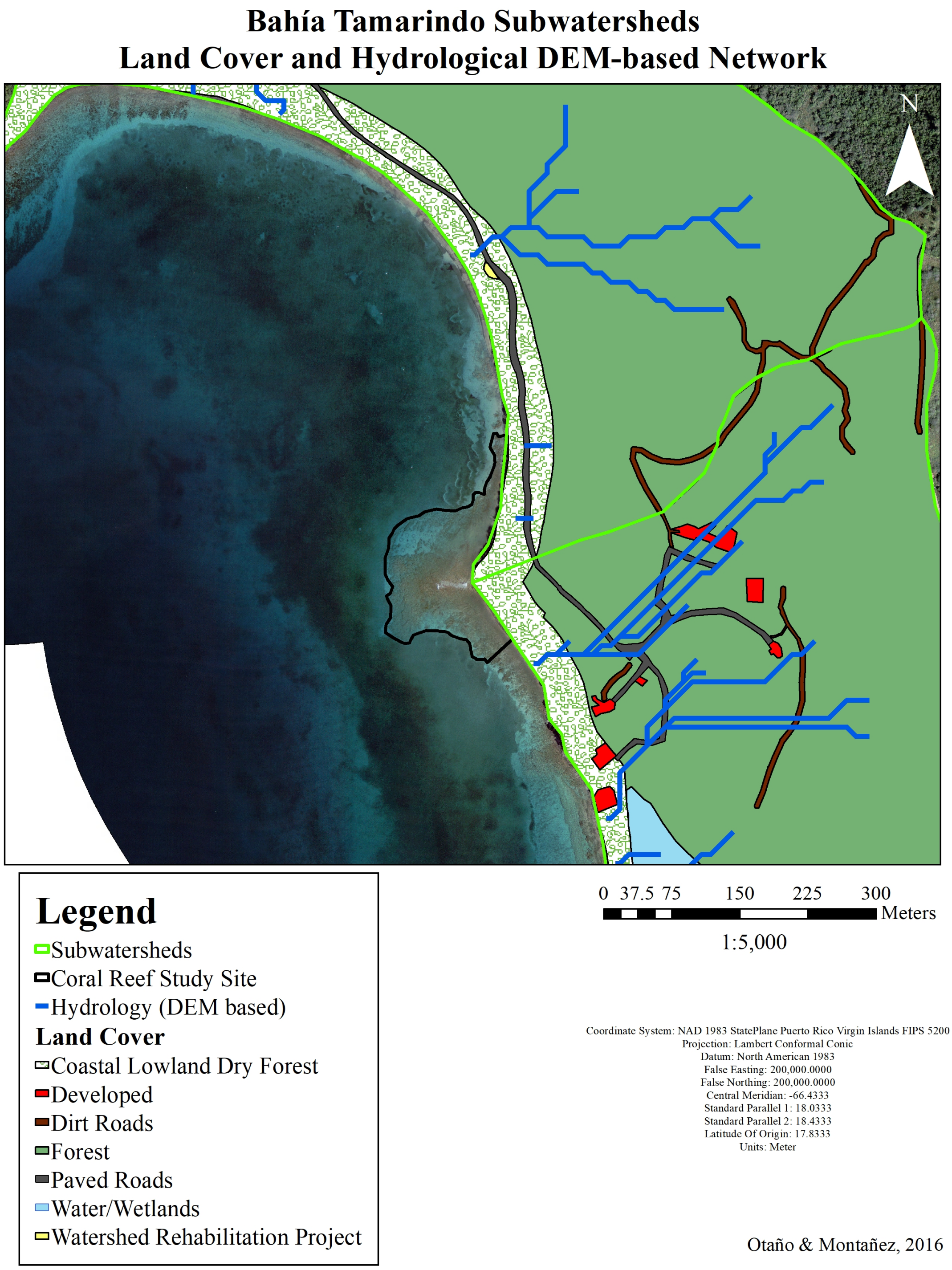
Appendix 1.10. Bahía Tamarindo sand sediment proportion (%) by sampling period. Proportion of sand (>63um) sediment accumulated at traps from December 2014 to February 2015. Coral reef study site represented with black polygon. Aerial image UPRRP, 2010.



Appendix 1.11. Punta Soldado silt-clay sediment proportion (%) by sampling period. Proportion of sand (>63um) sediment accumulated at traps from from July to August 2014. Coral reef study site represented with black polygon. Aerial image UPRRP, 2010.

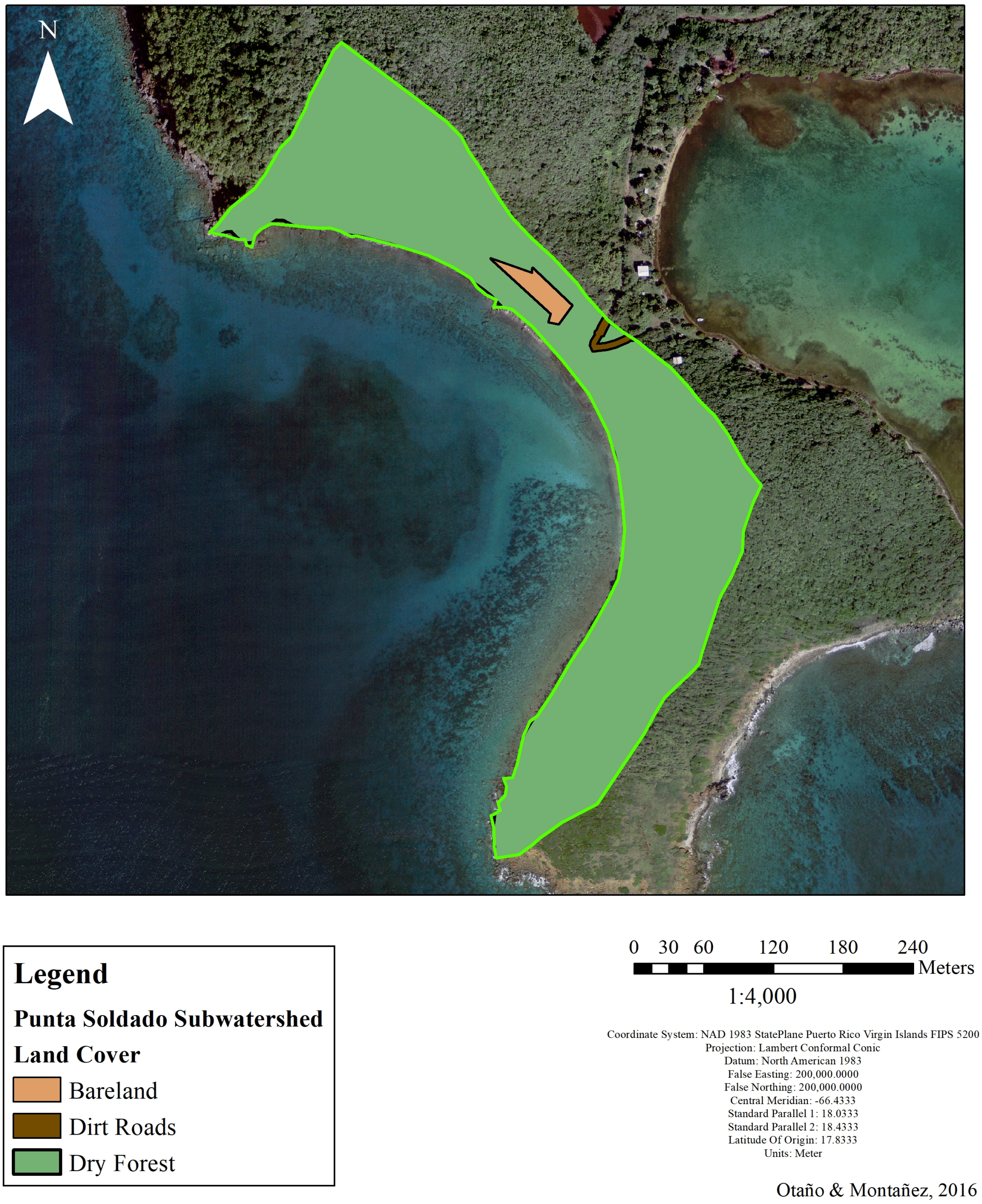


Appendix 1.12. Bahía Tamarindo Sub-watersheds Land Cover and hydrological DEM-based network. Hydrologic drainage outlet represented with blue lines and coastal rehabilitation project represented with yellow polygon. Coral reef study site represented with black polygon. Aerial image UPRRP, 2010.



Appendix 1.13. Punta Soldado Sub-watershed Land Cover.
PSO sub-watershed land cover change after deforestation and soil exposure event documented in April 2014. Aerial image UPRRP, 2010.

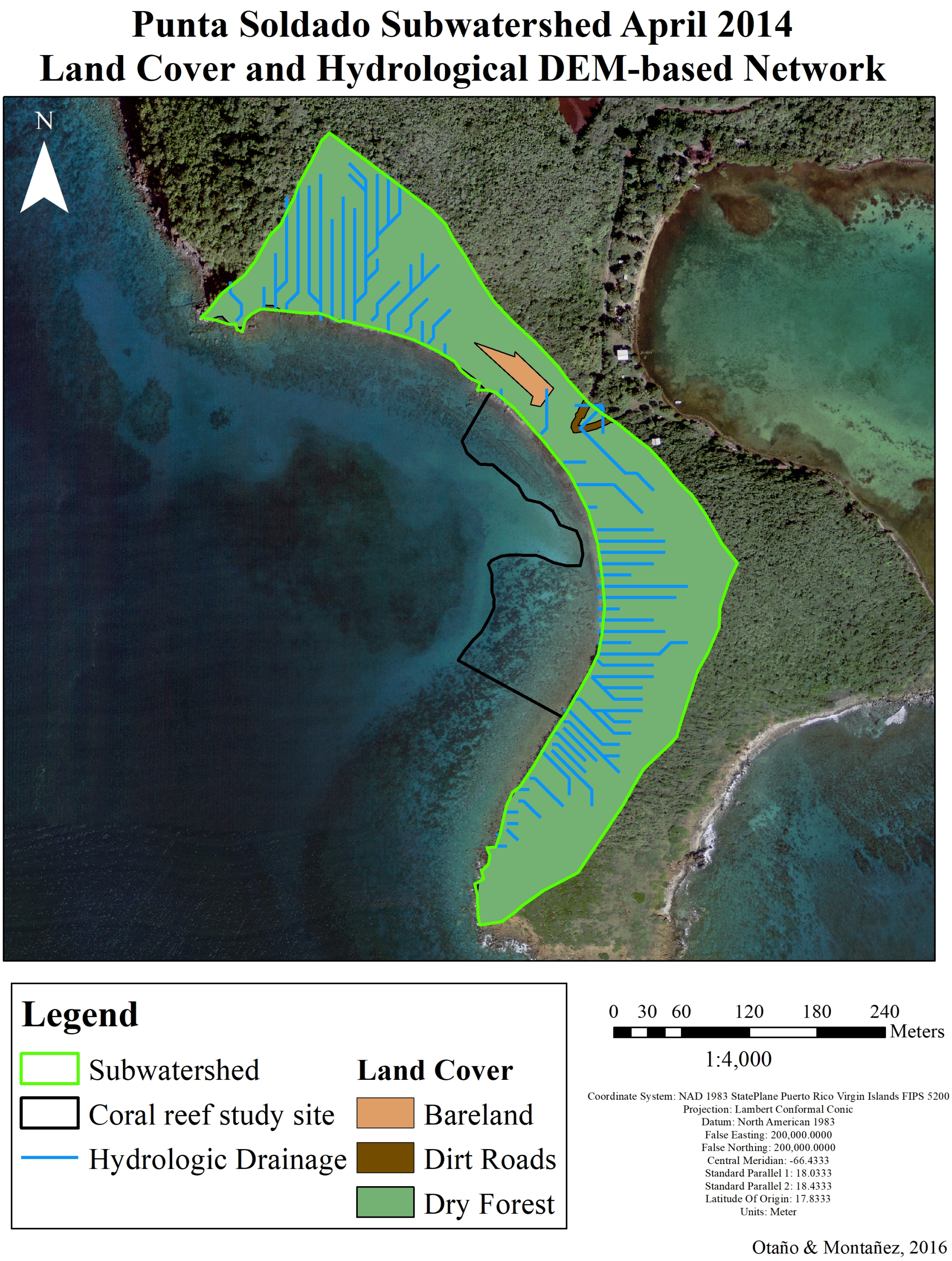
Punta Soldado Subwatershed Land Cover
April 2014



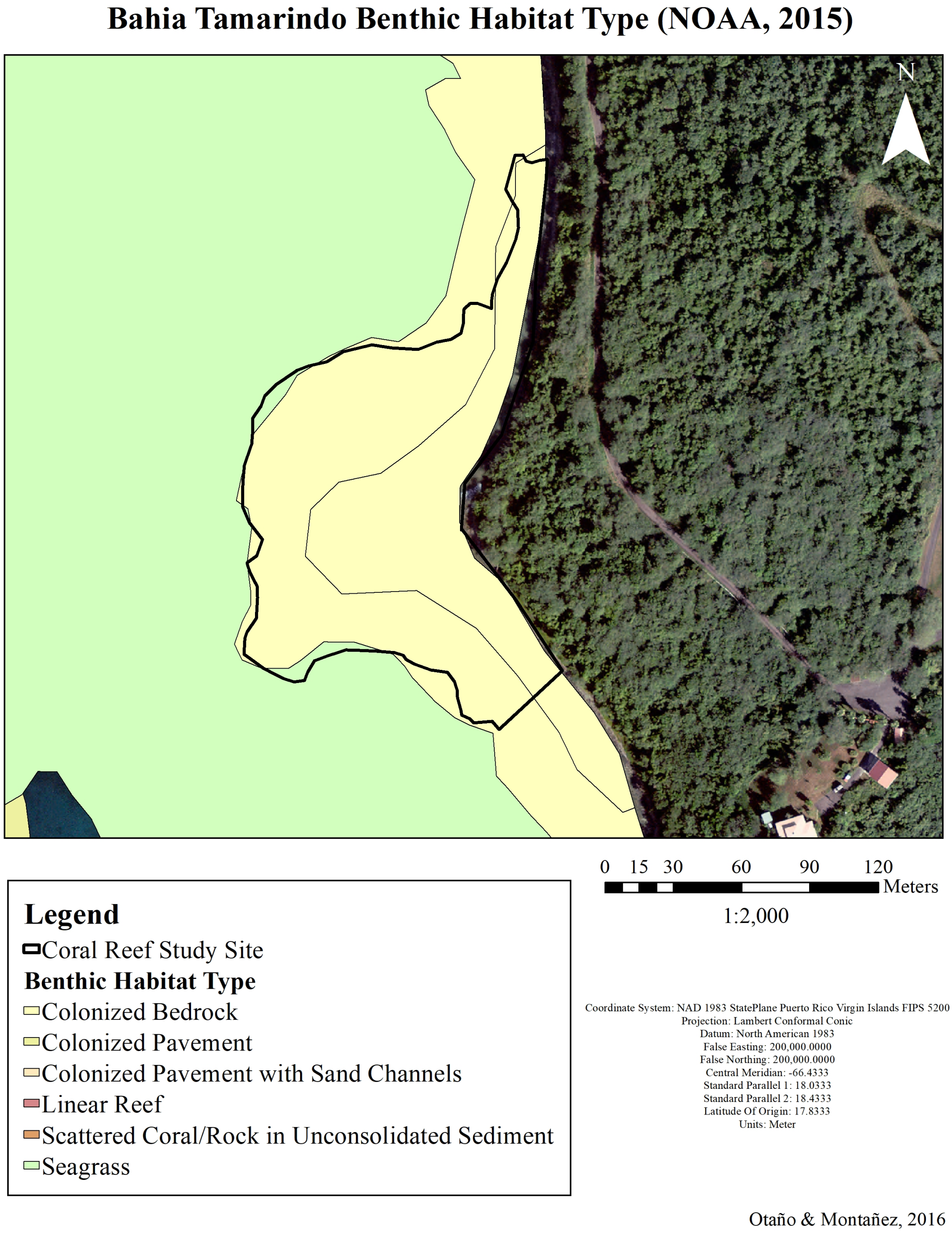
Coordinate System: NAD 1983 StatePlane Puerto Rico Virgin Islands FIPS 5200
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 200,000.0000
False Northing: 200,000.0000
Central Meridian: -66.4333
Standard Parallel 1: 18.0333
Standard Parallel 2: 18.4333
Latitude Of Origin: 17.8333
Units: Meter

Otaño & Montañez, 2016

Appendix 1.14. Punta Soldado Sub-watersheds Land Cover and hydrological DEM-based network. Hydrologic drainage outlet represented with blue lines. Coral reef study site represented with black polygon. Aerial image UPRRP, 2010.

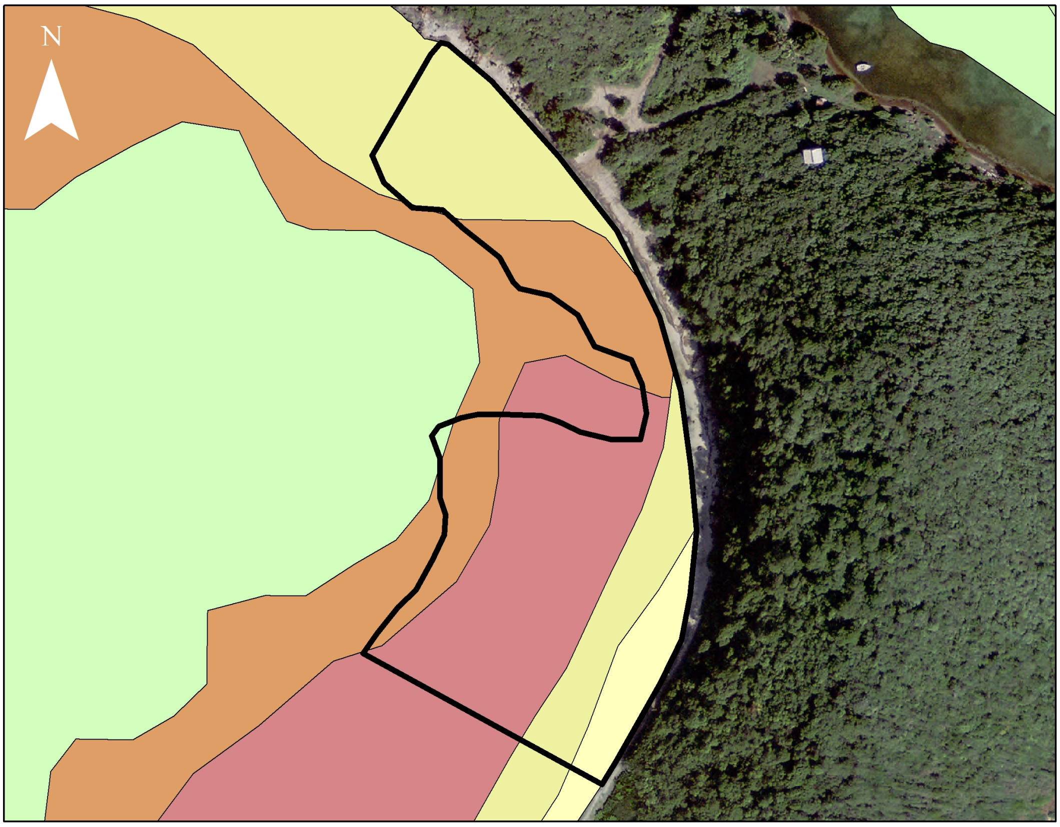


Appendix 2.1. Bahía Tamarindo Benthic Habitat Type (NOAA, 2015).
BTA coral reef study site represented with black polygon. Aerial image UPRRP, 2010.



Appendix 2.2. Punta Soldado Benthic Habitat Type (NOAA, 2015).
Coral reef study site represented with black polygon. Aerial image UPRRP, 2010

Punta Soldado Benthic Habitat Type (NOAA, 2015)



Legend

Coral Reef Study Site

Benthic Habitat Type

- Colonized Bedrock
- Colonized Pavement
- Colonized Pavement with Sand Channels
- Linear Reef
- Scattered Coral/Rock in Unconsolidated Sediment
- Seagrass

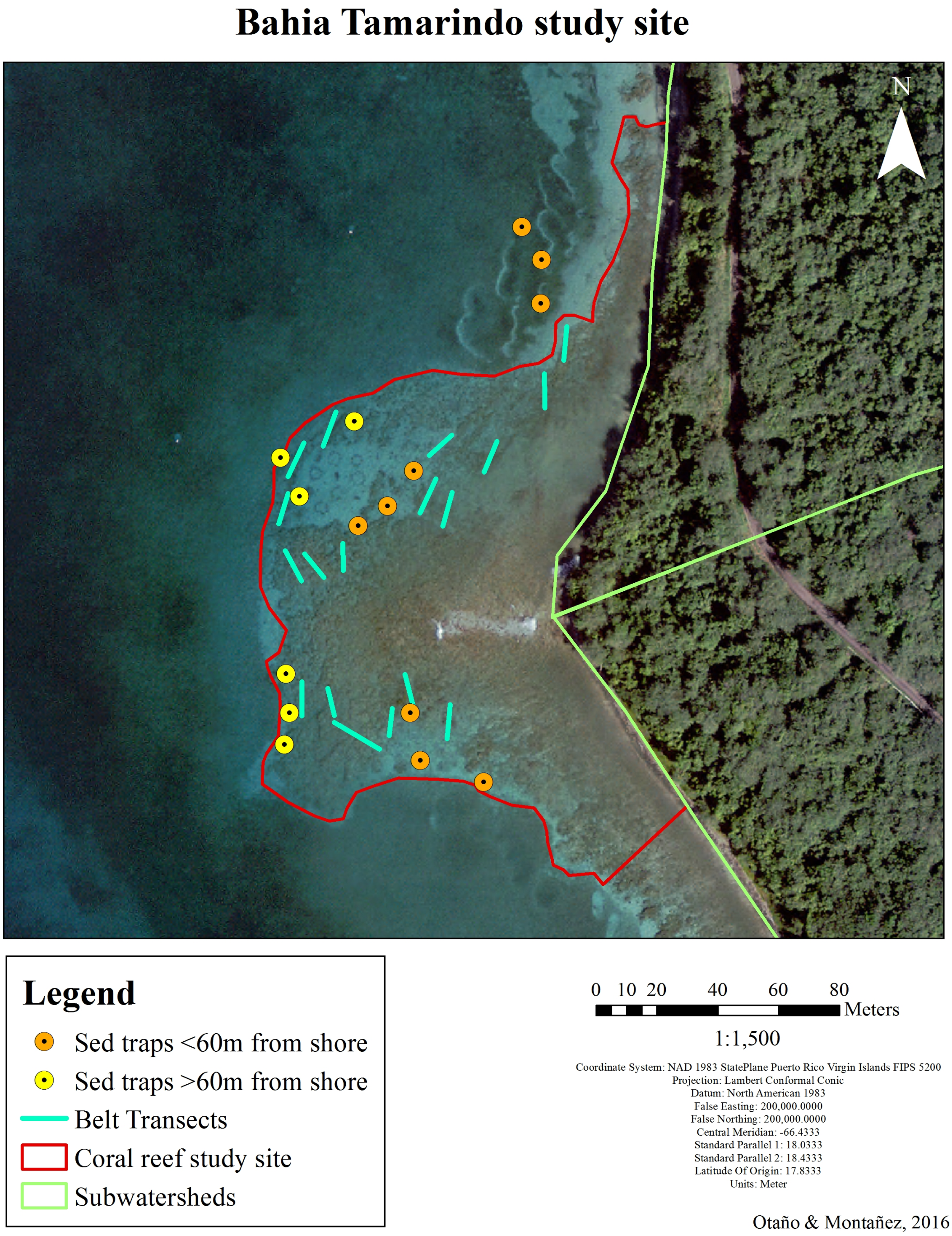
0 15 30 60 90 120 Meters

1:1,989

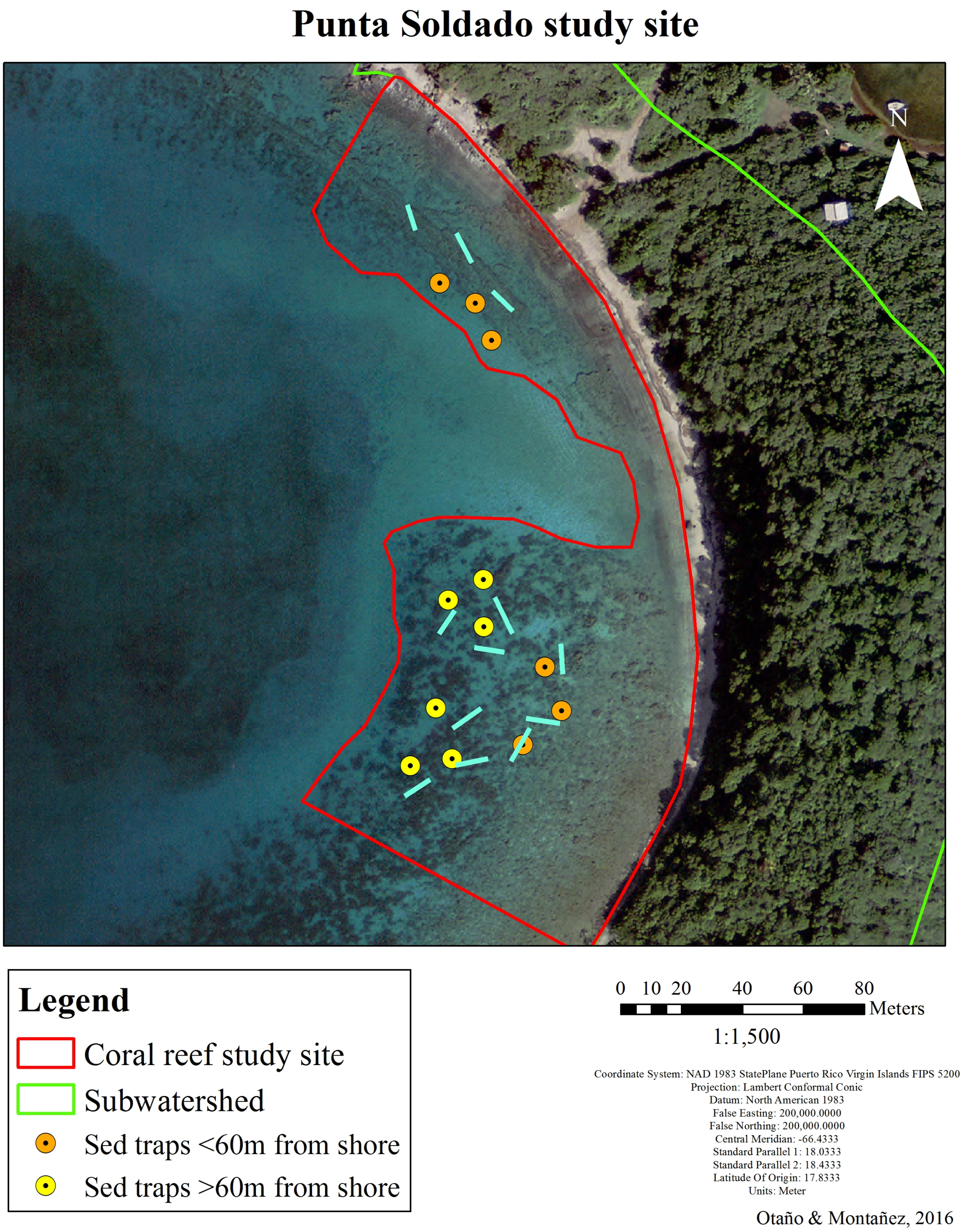
Coordinate System: NAD 1983 StatePlane Puerto Rico Virgin Islands FIPS 5200
Projection: Lambert Conformal Conic
Datum: North American 1983
False Easting: 200,000.0000
False Northing: 200,000.0000
Central Meridian: -66.4333
Standard Parallel 1: 18.0333
Standard Parallel 2: 18.4333
Latitude Of Origin: 17.8333
Units: Meter

Otaño & Montañez, 2017

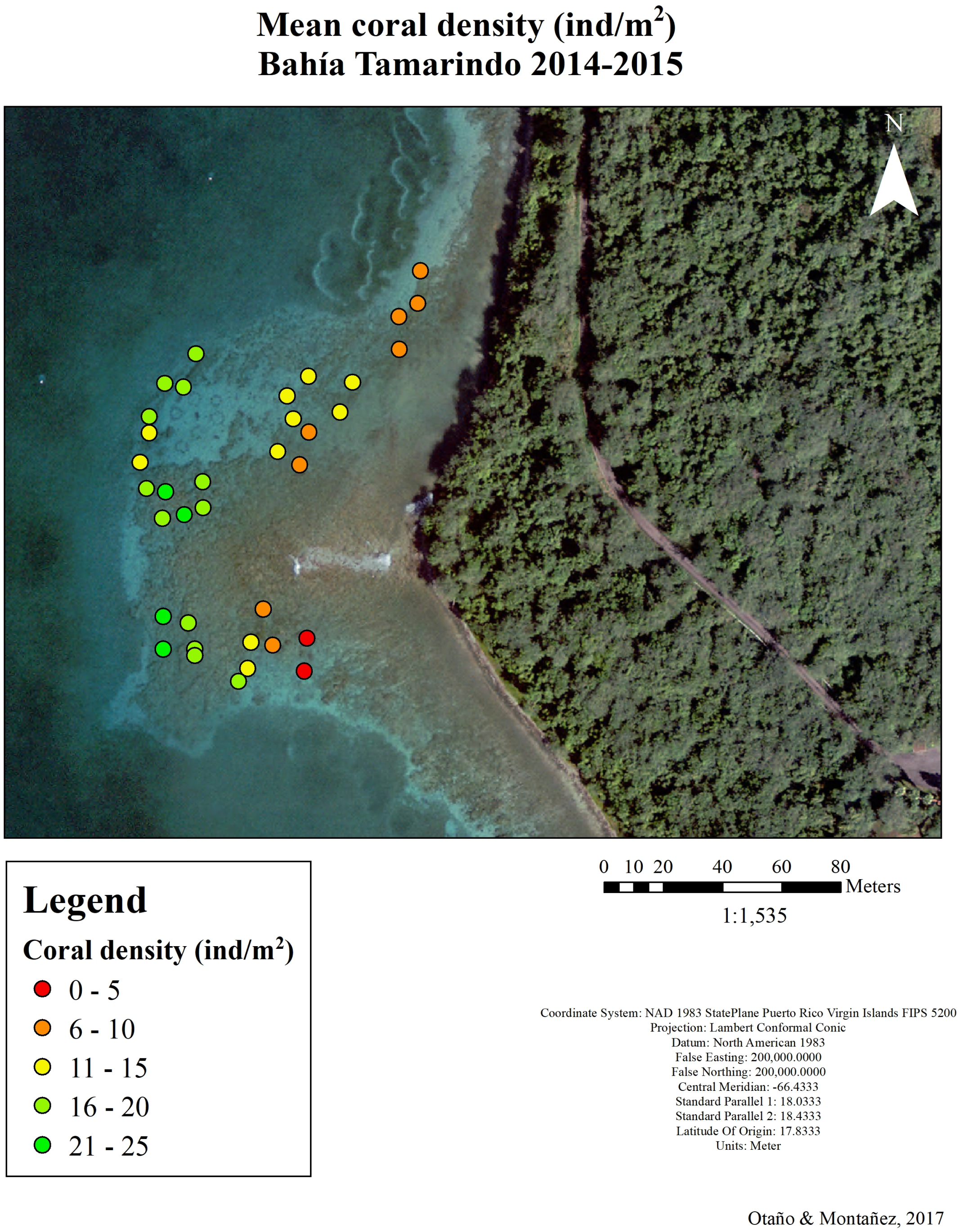
Appendix 2.3. Bahía Tamarindo near-shore coral reef and sediment study design. BTA coral reef delineated with red polygon and permanent belt transects represented with blue lines. Sediment traps by distance zones represented with yellow and orange dotes and adjacent sub-watersheds delineated with green line. Aerial image UPRRP, 2010.



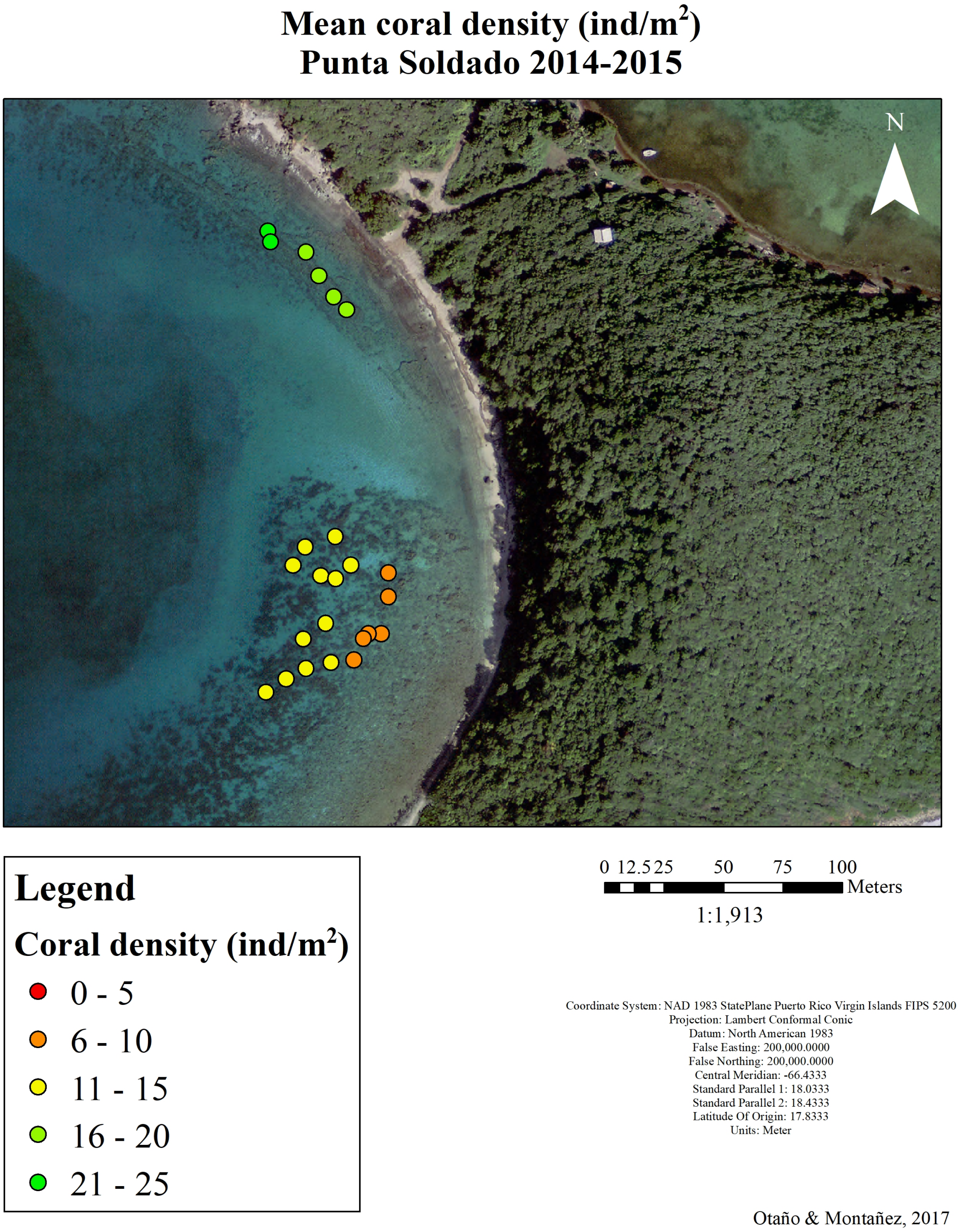
Appendix 2.4. Punta Soldado near-shore coral reef and sediment study design. PSO coral reef delineated with red polygon and permanent belt transects represented with blue lines. Sediment traps by distance zones represented with yellow and orange dotes and adjacent sub-watersheds delineated with green line. Aerial image UPRRP, 2010.



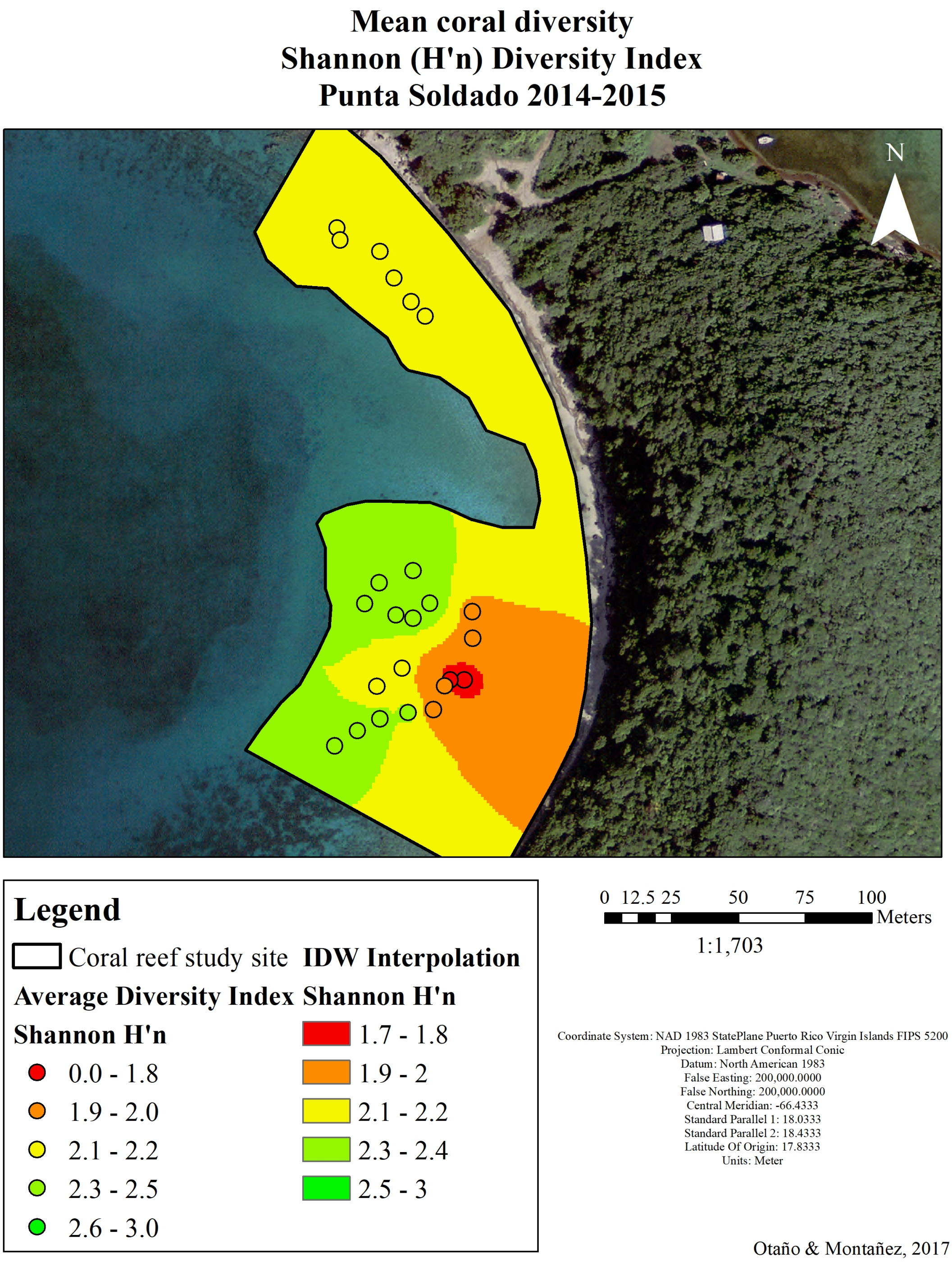
Appendix 2.5. Bahía Tamarindo mean coral density 2014-2015.
BTA mean coral density is represented with color scale, each dots represents limits of permanent belt transects. Aerial image UPRRP, 2010.



Appendix 2.6. Punta Soldado mean coral density 2014-2015.
BTA mean coral density is represented with color scale, each dots represents limits of permanent belt transects. Aerial image UPRRP, 2010.

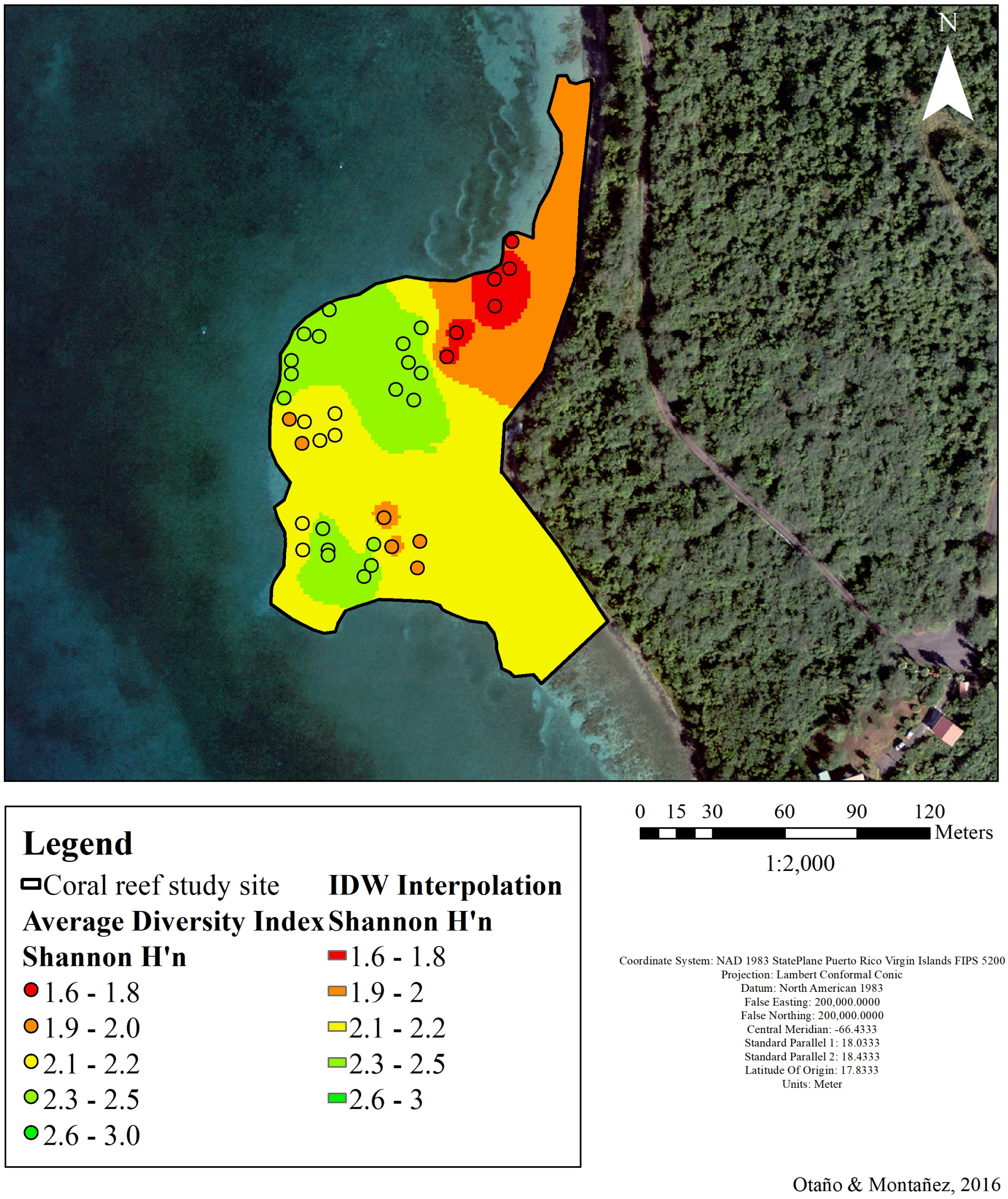


Appendix 2.7. Punta Soldado Mean Coral Diversity (H'n) 2014-2015.
PSO mean coral density for study period is represented with color scale, each dot represents limits of permanent belt transects. Inverse Distance Weighting (IDW) interpolation generated with diversity index by transects. Aerial image UPRRP, 2010.

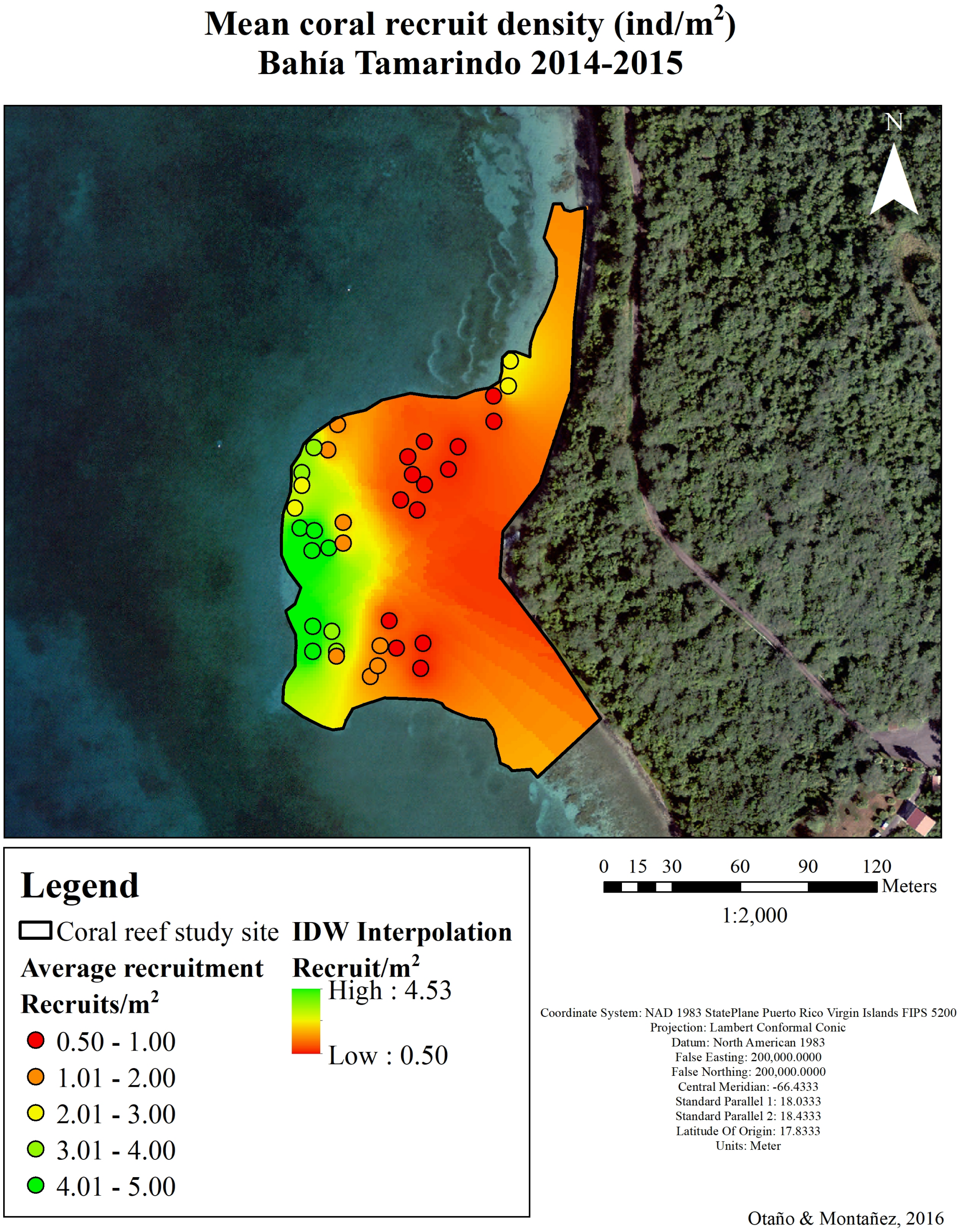


Appendix 2.8. Bahía Tamarindo Mean Coral Diversity (H’n) 2014-2015.
BTA mean coral density for study period is represented with color scale, each dot represents limits of permanent belt transects. Inverse Distance Weighting (IDW) interpolation generated with diversity index by transects. Aerial image UPRRP, 2010.

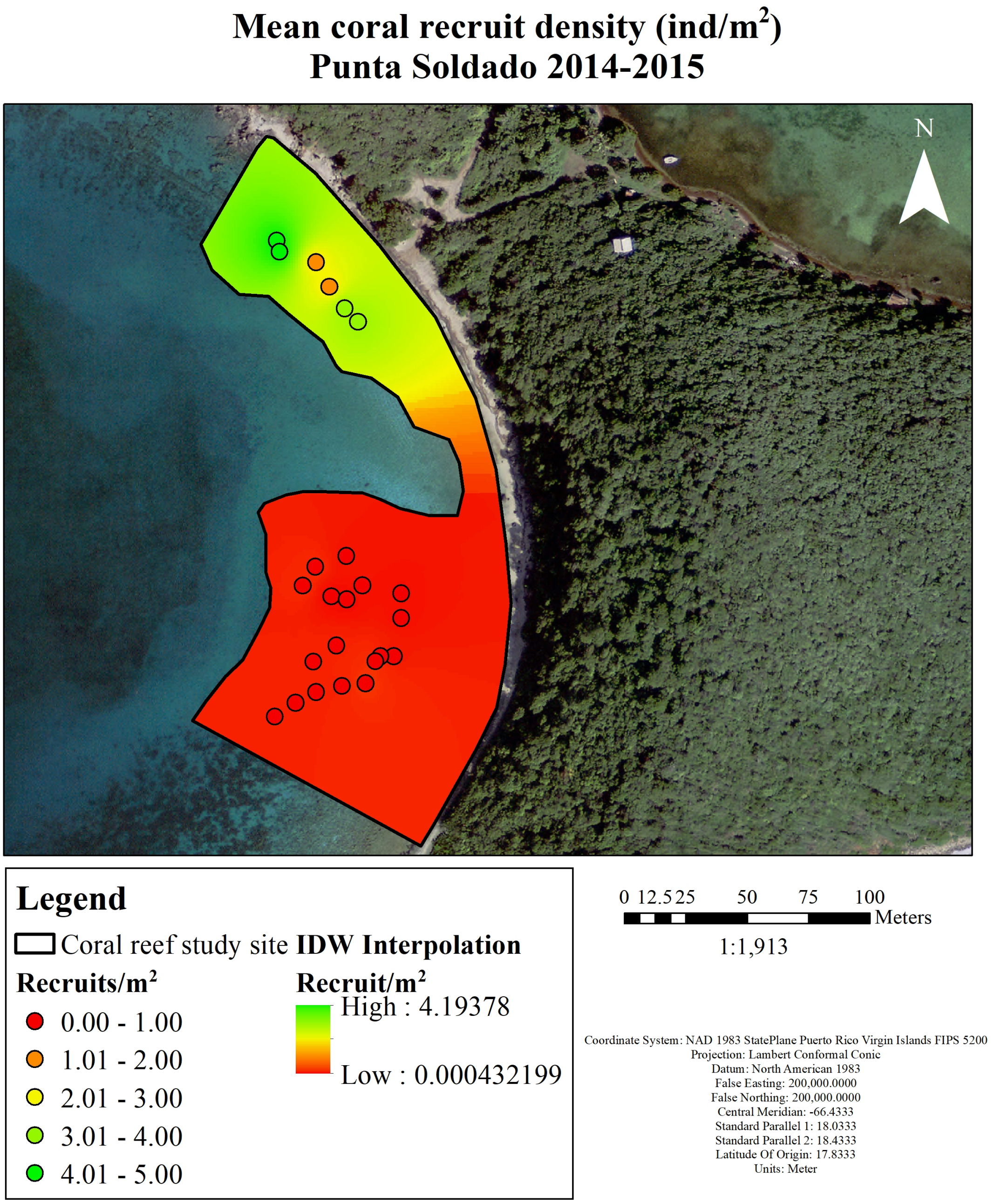
Mean coral diversity
Shannon (H'n) Diversity Index
Bahía Tamarindo 2014-2015



Appendix 2.9. Bahía Tamarindo Mean Coral Recruit Density 2014-2015.
BTA mean coral recruit density for study period is represented with color scale, each dot represents limits of permanent belt transects. Inverse Distance Weighting (IDW) interpolation generated with recruit density by transects. Aerial image UPRRP, 2010.



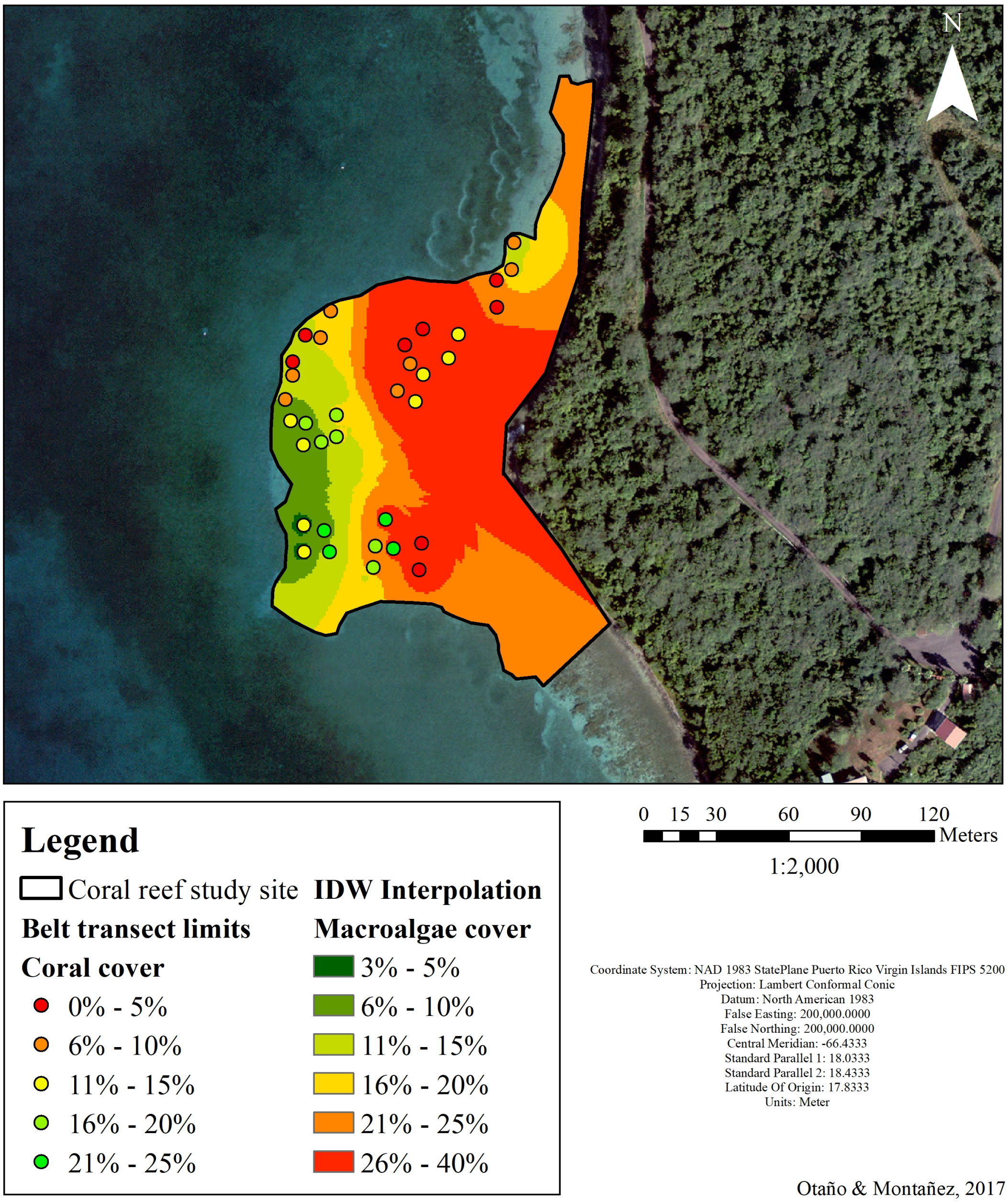
Appendix 2.10. Punta Soldado Mean Coral Recruit Density.
PSO mean coral recruit density for study period is represented with color scale, each dot represents limits of permanent belt transects. Inverse Distance Weighting (IDW) interpolation generated with recruit density by transects. Aerial image UPRRP, 2010.



Otaño & Montañez, 2017

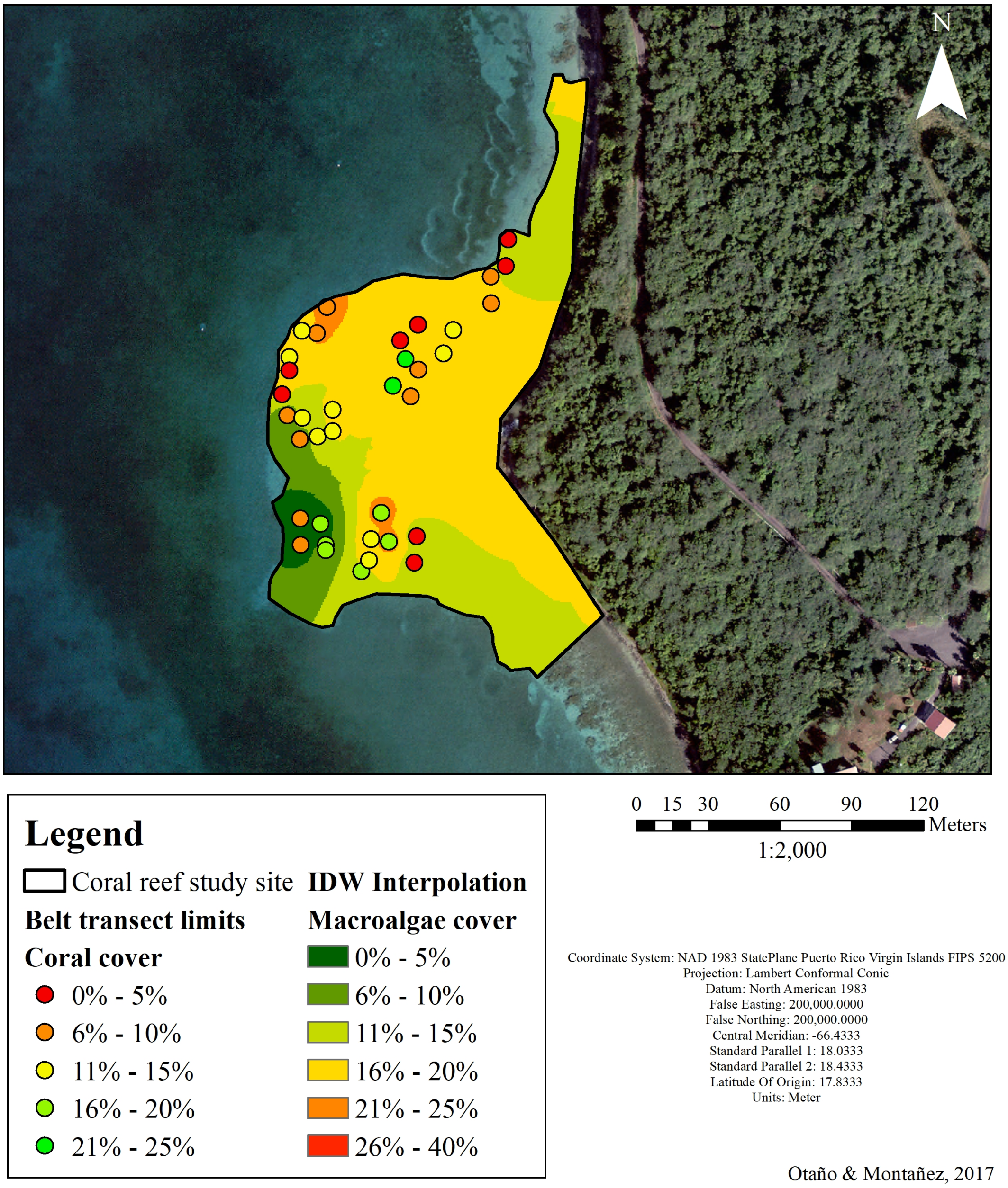
Appendix 2.11. Bahía Tamarindo Percent Coral Cover and Macroalgae Cover. Coral (dots) and macroalgae (IDW interpolation) represents percent benthic cover in spring, 2014. Aerial image UPRRP, 2010.

Percent coral cover vs macroalgae cover
Bahía Tamarindo spring 2014

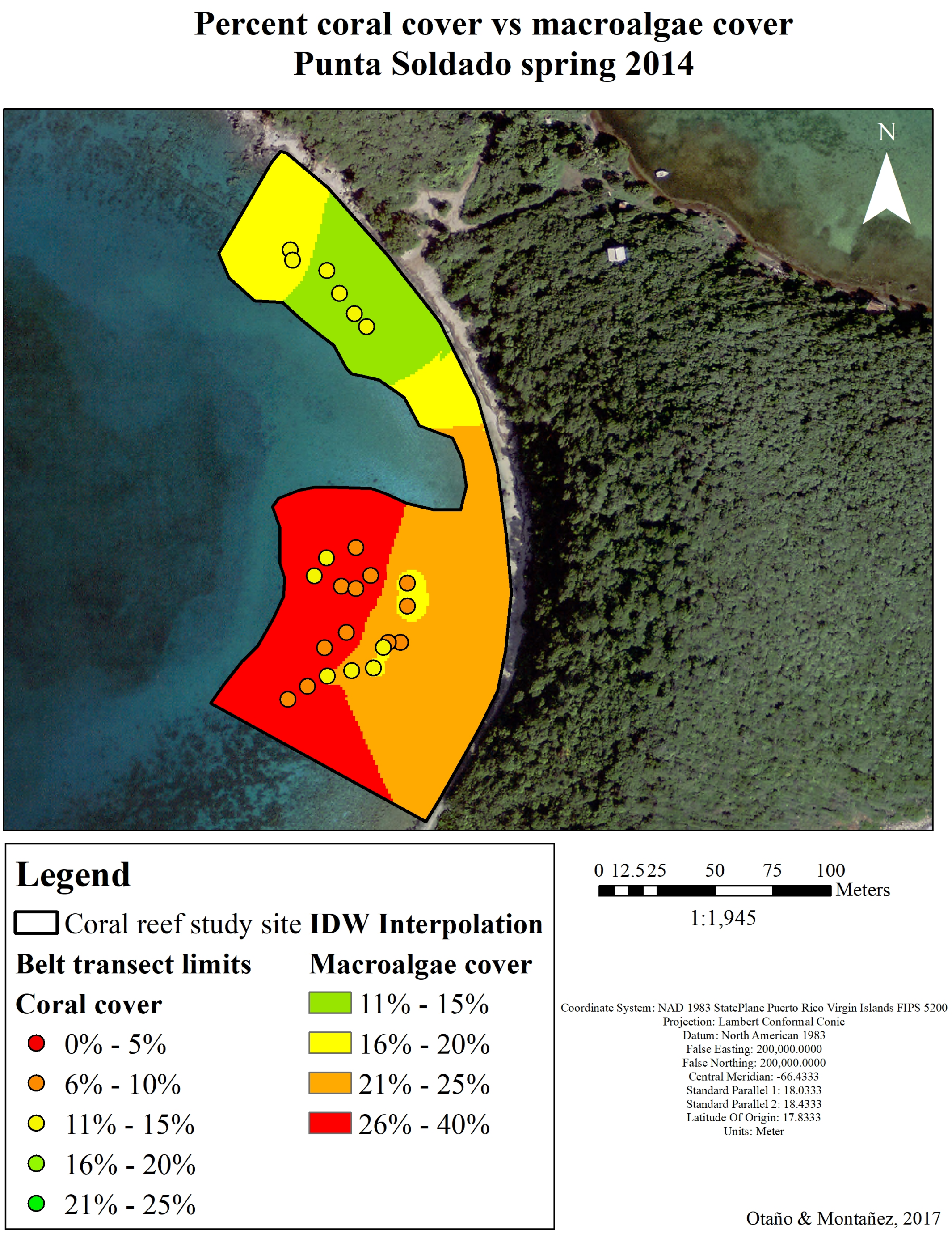


Appendix 2.12. Bahía Tamarindo Percent Coral Cover and Macroalgae Cover. Coral (dots) and macroalgae (IDW interpolation) represent percent benthic cover in winter, 2015. Aerial image UPRRP, 2010.

Percent coral cover vs macroalgae cover
Bahía Tamarindo winter 2015



Appendix 2.13. Punta Soldado Percent Coral and Macroalgae Benthic Cover. Coral (dots) and macroalgae (IDW interpolation) represent percent benthic cover in spring, 2014. Aerial image UPRRP, 2010



Appendix 2.14. Punta Soldado Percent Coral Cover and Macroalgae Cover.
Coral (dots) and macroalgae (IDW interpolation) represent percent benthic cover in winter, 2015. Aerial image UPRRP, 2010.

Percent coral cover vs macroalgae cover
Punta Soldado winter 2015