Assessment of coral reef community structure using water optical properties

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ABSTRACT

Measuring and monitoring the underwater light field is essential for coral reef ecological assessments since the health of these communities are affected or influenced by nutrients, sediments, and other materials that are transported from land into the marine environment and affect water quality. Significant changes in the water optical parameters in coral reef areas usually result over large time scales. Therefore, long term monitoring of water optical properties and sediment nutrient loads are required to examine the impact of these factors on community structure, diversity, and health of coral reefs. Although remote sensing technology may be a promising tool for monitoring coral reefs, significant obstacles exist for its implementation; such as the spectral and spatial resolution of sensors and the confounding effect of variable water optical properties and bathymetry. Therefore, we tested an indirect approach to infer coral reef community composition and health based on the characterization of the optical properties of surrounding waters. A total of 31 sampling events that included 19 stations were conducted to measure apparent and inherent water optical properties for the study areas. Regressions were obtained between water transparency, as determined by the diffuse attenuation coefficient of visible light ($K_{d\ (PAR)}$) and coral reef ecological parameters including the percent coral cover ($R= -0.96$, $R^2=0.92$, $p < 0.0001$), the distance of the sites from the shore ($R=-0.66$, $R^2= 0.44$, $p = 0.0020$), the index of diversity (H') ($R=-0.96$, $R^2= 0.92$, $p>0.10$) and the mean rugosity index ($R=--0.46$, $R^2= 0.22$, $p=0.0455$). The vertical attenuation coefficient was also related to secondary parameters including: evenness ($R=0.42$, $R^2= 0.17$, $p>0.10$), richness ($R=-0.47$, $R^2= 0.23$, $p=0.0404$), sponge cover ($R=0.75$, $R^2= 0.56$,

p=0.0002), octocoral cover (R=0.74, R^2= 0.54, p=0.0003), uncolonized substrate cover (R=0.74, R^2= 0.55, p=0.0003), diseased coral cover (R=-0.60, R^2= 0.36, p=0.0065), macroalgae cover (R=-0.52, R^2= 0.28, p=0.0212) and filamentous algae cover (R=0.79, R^2= 0.62, p>0.10). Significance of the relation between percent coral cover and optical depth (R=0.97, R^2= 0.94, p<0.0001), was taken into consideration when dividing the study sites into three optical depth groups. The relationship between the vertical attenuation coefficient (K_d) and the percent coral cover was then reassessed resulting in a stronger relationship (R=-0.9982, R^2= 0.9964, p=0.0384). A strong inverse relationship exists between K_d and the percent coral cover for the areas of Ponce, Guayanilla, La Parguera and Mayagüez Bay. Although weaker, a tendency was also observed relating the vertical attenuation coefficients to the sites' distance from shore. Euphotic zonation was considered a more efficient approach when determining similarities between the study areas. Future work should consider a more detailed evaluation of the specific biological parameters and the construction of a predictive model relating percent coral cover to K_d and optical depth by satellite imagery.

RESUMEN

Las mediciones y el monitoreo del campo lumínico subacuático son de suma importancia para los estudios ecológicos de los arrecifes de coral, debido a que la salud de estas comunidades depende de concentraciones bajas de nutrientes, sedimentos y otros materiales que son acarreados de la tierra hasta el ambiente marino, afectando así la calidad del agua. Esto representa una serie de cambios significativos en los parámetros ópticos del agua que comúnmente se extienden a gran escala temporal y espacial. Por lo tanto, el estudio a largo plazo de las propiedades ópticas del agua y de las descargas de nutrientes, son necesarios para entender el impacto de éstos factores en la estructura, diversidad y salud de las comunidades de arrecife de coral. Aunque la tecnología abarcada por la teledetección resulta ser una herramienta prometedora para el estudio de los arrecifes de coral, existen obstáculos significativos para la implementación de dicha tecnología, tales como la resolución espectral y espacial de diferentes censores y el efecto confuso de la alta variabilidad en las propiedades ópticas del medio acuático y en la batimetría. Por lo tanto, probamos un acercamiento indirecto para deducir la composición y la salud de la comunidad del arrecife coralino basado en la caracterización de las características ópticas de aguas circundantes. Un total de 31 campañas de muestreo a 19 estaciones fueron llevadas a cabo para medir las características ópticas aparentes e inherentes del agua para las áreas del estudio. Se obtuvieron relaciones estadísticas entre la claridad del agua, según lo determinado por el coeficiente de atenuación difuso de luz visible ($K_{d\ (PAR)}$) y parámetros ecológicos del arrecife como por ejemplo el porciento de cobertura de coral vivo ($R= -0.96$, $R^2=0.92$, $p < 0.0001$), la distancia entre las estaciones

y la costa ($R=-0.66$, $R^2= 0.44$, $p = 0.0020$), el índice de diversidad (H') ($R=-0.96$, $R^2= 0.92$, $p>0.10$) y el índice de rugosidad (o relieve vertical) ($R=--0.46$, $R^2= 0.22$, $p=0.0455$). El coeficiente the atenuación vertical (en adelante K_d) también fue relacionado a parametros secundarios en los que se incluyó: la homogeneidad ($R=0.42$, $R^2= 0.17$, $p>0.10$), el número total de especies ($R=-0.47$, $R^2= 0.23$, $p=0.0404$), la cobertura de esponjas ($R=0.75$, $R^2= 0.56$, $p=0.0002$), la cobertura de octocorales ($R=0.74$, $R^2= 0.54$, $p=0.0003$), el por ciento de sustrato no colonizado ($R=0.74$, $R^2= 0.55$, $p=0.0003$), el por ciento de coral enfermo ($R=-0.60$, $R^2= 0.36$, $p=0.0065$), la cobertura de macroalgas ($R=-0.52$, $R^2= 0.28$, $p=0.0212$) y la cobertura de algas filamentosas incrustantes ($R=0.79$, $R^2= 0.62$, $p>0.10$). Luego de determinar que la relación entre el porciento de corbertura de coral vivo y la profundidad óptica fue significativa ($R=0.97$, $R^2= 0.94$, $p<0.0001$), se tomó la determinación de dividir los lugares de estudio en tres grupos ópticos. La relación entre el (K_d) y el por ciento de cobertura de coral vivo fue entonces reconsiderada ($R=-0.9982$, $R^2= 0.9964$, $p=0.0384$) resultando el análisis de ésta en una regresión aún más fuerte. Por lo tanto se determinó la existencia de una fuerte relación inversa entre el K_d y el por ciento de cobertura de coral vivo para las áreas de Ponce, Guayanilla, La Parguera y la Bahía de Mayagüez. Se observó además, que aunque más débil, el K_d estaba inversamente relacionado al incremento de distancia entre los lugares de estudio y la costa. La zonación eufótica fue considerada como el acercamiento más efectivo para la determinación de similitudes biológicas entre las distintas áreas de estudio. La proyección de trabajos futuros debe considerar una evaluación más detallada de ciertos parámetros en el arrecife. En adición, se debe considerar la construcción de modelos predictivos que puedan relacionar el por ciento de cobertura de coral vivo, el K_d y la profundidad óptica con sensores remotos y/o imágenes de satélite.

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INTRODUCTION

Coral reefs are part of an intricate web of marine resources that together serve an important role in the economic, physical protection and environmental structure of many tropical islands. Ecologically, coral reefs serve to generate carbonate material and sand, provide protection from erosion, buffer the impact of natural phenomena, and constitute important habitats for many species (Goreau, 1979; 1959a,b; Hutchings, 1986; Szmant-Froelich, 1973, Ramirez and García, 1997). They are also significant in dispersal, recruitment and replenishment of reefs (Cowen et al., 2000; Roberts, 1997). At present, approximately 75% of the world coral reefs are considered to be deteriorating (Mumby et al., 2004).

It is commonly believed that the health of these communities depend upon low transport of nutrients, sediments and other inanimate materials from the land into the marine environment, and from near shore to offshore areas within the marine realm. Maximum development of coral reefs is considered to occur in oligotrophic areas away from terrestrial inputs. They tend to be affected by high transport of organic and inorganic matter and nutrients (Muscatine and Porter, 1977). In Indonesia, the greatest coral reef development occurs in areas characterized by clear water free from suspended sediments and excessive freshwater runoffs (Tomascik et al., 1993).

Additional factors affecting coral reef communities include natural disturbances and climatic events including hurricanes, and episodes such as the 2005 drastic increase in the sea surface temperature that resulted in numerous storms, major bleaching of coral communities and significant live coral cover decrease for the Caribbean. This occurred between September and late October 2005 (García-Sais et al. 2006, NOAA, 2005).

Disregarding the effects of such events; reefs are continuously being affected and degraded not only by environmental and natural causes but by anthropogenic factors which have accelerated their depletion in the last 30 to 40 years.

Socio-economically, coral reefs are important for their relevance in different industries including local subsistence and commercial fisheries and development of natural products, recreation and tourism. Their visual beauty supports a wide variety of water based activities such as scuba diving, snorkeling, and underwater photography, among others. In addition, growing research on different natural products that are produced by coral reef organisms is giving force to the pharmacological industries which benefit from these resources as well.

Nevertheless, lack of control of commercial and recreational uses of coral reefs together with the lack of education and management plans is causing a dramatic depletion of these resources. In many areas water quality has diminished due to diverse sources of pollution such as petrochemicals and urban waters discharges which lead to the death of mangroves and seagrass beds. Constructions and dredging in coastal areas are only some of the factors increasing the erosion and sediment discharge that results in degradation and eutrophication. Overfishing and the use of high-impact fishing gear, among other fishing methods, negatively affect the coral reef habitat. Irresponsible boating and anchorage practices also cause physical damage to the reefs.

Traditional coral reef survey and monitoring methods can be time consuming, difficult, expensive and result in short temporal and spatial scale assessments (Bohnsack, 1979, Stoddart and Johannes, 1981 and Weinberg, 1981). At the moment there is a need to develop broader methods that could help us assess larger areas more effectively.

One way of addressing this limitation is through the use of remote sensing techniques. Remote sensing can result in more rapid, large-scale assessments of coral reefs since large areas are captured within one image. Although the use of remote sensing from aircrafts and satellites has been proposed as a promising tool for monitoring coral reefs and assessing their health status, there are many limitations in using this technology operationally. The spectral and spatial resolution of existing sensors, the confounding effects of variable water optical properties and bathymetry are significant obstacles for the implementation of this technology.

Water optical properties vary spatially and temporally in most areas and thus cannot be considered uniform. Therefore, besides the effects of anthropogenic activities, the concept of standardized water optical parameters should be reconsidered according to each site and the surrounding ocean being evaluated (Maritorena and Guillocheau, 1996). Some factors affecting water optical properties include sediment run-off, resuspension of bottom sediments resulting from high waves and episodic events, and land-use changes in the drainage basins that affect coastal areas. Since land-use changes occur over large time scales and episodic events can be infrequent, long term monitoring of water optical properties and sediment/ nutrient loads are required to ascertain the impact of these factors in the community structure, diversity and health of coral reefs.

Sediments, nutrient inputs (with the corresponding increases in chlorophyll concentration) and other materials when in the water, help reduce water transparency resulting in less light penetration which in turn affects many photosynthetic benthic organisms including hermatypic corals. Van Den Hoek and Breeman (1978) established the lower limit of growth for hermatypic corals and crustose coralline algae as occurring close to the point where the 0.2% of surface radiation reaches. Data from Indonesia, demonstrated that water transparency, indeed, is a key environmental factor affecting the vertical distribution of corals as well as the maximum depth of a functional coral community (Tomascik et al., 1993).

Although there is a general idea of which factors alter water optical characteristics, very little is known about the patterns and variability of water optical properties in coral reef environments. It is known that water transparency is reduced because of sediment run-off, resuspension, and even water column productivity. This affects directly the photosynthesis / respiration rates causing the organisms to become more susceptible to other factors that may arise, such as the increase in different animal and plant species, algae proliferation, and diseases (Goenaga et al., 1989; Gleason and Wellington, 1993; Reaka-Kudla et al., 1993). Some effects may be observed immediately, while others may be long term as evidenced by cases where even after sewage discharge has ceased, effects continued to be recorded (Coles and Ruddy, 1995). These changes might lead to an increase in coral reef mortality as established by Suhasorno (1990).

Both algae proliferation and diseases, such as the black band disease have been well documented and related to problems with water transparency (Maragos, 1972; Smith et al., 1981; Marszaleck, 1981; Bell, 1992; Williams and Bunkley-Williams, 1990; Porter and Meier, 1992; Peters, 1993, Bruckner and Bruckner, 1998). Other studies have related water transparency to specific motile animal species seen in coral reefs at particular depths, but problems arise since no control can be established on the normal movement of the species during the ongoing study (Schwarz and Hawes, 1997).

However, there is little information on the relationship between the incident spectral flux and the diversity, community composition, and health of coral reefs. There is a need to ascertain how gradual or drastic increases in water attenuation coefficients (K_d), can serve as change indicators for these communities and its predictive value. This coefficient, K_d , expresses logarithmically the rate of change of the downwelling irradiance with variations in depth (Kirk, 1994).

The main objective of this research is to verify the relationships between the vertical attenuation coefficients (K_d) and the percent coral cover of different areas. Also to observe the existence of secondary relationships with coral community parameters and with the sites' distance from shore; and finally to observe how the physical parameters confirm the existence of those relationships.

PREVIOUS WORK

Very little information is available that relates coral reef characterization to water optical parameters. Some studies have compared *in situ* optical and physical measurements with remote sensing data (Mumby et al., 2001). Water clarity and oligotrophy has been addressed as one, if not the most, important characteristics onto which coral success is dependent. The importance of light for coral reefs is due to the symbiotic relationship between the coral polyps and the photosynthetic endosymbiotic zooxanthellae (Yentsch et al., 2002). Even though corals can survive on polyps feeding heterotrophically, the $CaCO_3$ skeleton is dependent upon light from photosynthesis for the production of thick calcium carbonate (aragonite) structures (Rythers, 1956), although some aspects of this relationship are not well known (Maritorena and Guillocheau, 1996).

Most research emphasizes on sediment, nutrients and photosynthesis / respiration rate studies (Ryther, 1956). Yentsch et al. (2002) compared measurements between waters of two optical types. One site was the westernmost reefs of the Florida Keys (Dry Tortugas), classified as clear coastal waters and the others at Lee Stocking Island in the Bahamas, classified as clear oceanic waters. There was a lower percent coral cover for the Dry Tortugas (clear coastal waters) and a higher percent coral cover in the clear oceanic waters of the Bahamas.

Therefore, the common practice of utilizing the maximum depth of corals development as a proxy of water clarity, might result misleading, since this will only be useful when water clarity can be considered constant. Evidence from research by Tomascik et al. (1993) demonstrated that the study of variations of K_d and the relation with coral cover while maintaining constancy on the depth of the study area was a more representative strategy. Results of this study supported the positive relationship between coral cover and water transparency, while lower coral cover resulted in areas of greater turbidity. Results of a study with three species of aquatic plants, from the *Chara* genus, reflected how biomass particularly in shallower depths was related to the attenuation coefficient for downwelling irradiance (K_d) (Schwarz and Hawes, 1997).

Areas of greater turbidity might be influenced by sedimentation due to river discharge, increased growth of phytoplankton in response to nutrient enrichment (Scheffer, 1990) or from inorganic suspended solids (Tanner et al., 1993). Sedimentation affects corals by reducing water transparency and by clogging the polyps, resulting in irreversible damage (Marzalek, 1981). Sedimentation might also result in the proliferation of high-nutrients stimulated green algae, which results in the displacement of corals. This has been documented following the sewage disposal in Kane'ohe Bay, Hawaii (Maragos, 1972; Smith et al., 1981).

Many reef organisms that are adapted to moderate sediment influx are resistant to sediment stress, or depend on browsing and rasping of herbivores and echinoids (Hubbard and Pocock, 1972; Van Den Hoek and Breeman, 1978). However, additional problems arise when this dependency cannot be achieved in a balanced way.

Eutrophication is also believed to be an important cause of coral reef reduction and demise (Loya, 1976). In Barbados, even standard low levels of euthrophication may be enough to significantly restrict the growth and reproduction of damaged reefs (Bell and Tomascik, 1993). These authors report that sites with the lowest chlorophyll values had the most damage recorded. It is apparent that a combination of factors including the amount of radiation reaching the water body, the water column components and finally the ability of light to reach the organisms, are of vital importance when determining the real quality of the ecosystems in the area.

Penetration of photosynthetically active radiation (PAR) into the sea depends on the nature of the light field and the absorbing properties of the water and associated substances. Through the years many mathematical algorithms and simulations have been developed in order to understand and further explain the behavior of light in water. Examples include Gordon et al. (1975), Kirk (1981), Prieur (1976), Morel and Prieur (1977), Bukata et al. (1979), and Platt (1986). However, many aspects of water optics are still poorly documented (Maritorena and Guillocheau, 1996). As Falkowski et al. (1990) mentioned, "There is relatively little information about the spectral nature of the underwater light field, especially on coral reefs".

In 1961, Preisendorfer divided the optical properties of water into two classes: the inherent and the apparent water optical properties (Maritonera and Guillocheau, 1996). The inherent properties are independent of the ambient light field and dependent only upon the nature and the composition of particles and dissolved substances in the medium, but these are difficult to measure. The apparent optical properties depend on the medium but also on the structure of the light field. These are more easily determined although interpretation may be affected by many factors (Maritorena and Guillocheau, 1996; Kirk, 1984; Preisendorfer, 1961). Although attenuation coefficients values are largely a function of water composition and therefore, commonly thought of as properties of the water, their values result from absorption and scattering (two inherent optical properties) (Kirk, 1984). Therefore, the diffuse attenuation coefficient is considered a "quasi-inherent optical property" (Baker and Smith, 1980; Kirk 1984; Gordon, 1989a,b; Kirk, 1993). Depending on the water type, total attenuation can even be divided into several components including water itself, phytoplankton, other particles and dissolved organic matter (Gordon, 1989a,b).

Light extinction in the water column can be mathematically described in terms of the diffuse attenuation coefficient, or K_d. The diffuse attenuation coefficient, which describes qualitatively and quantitatively the decrease of electromagnetic energy with depth (Maritorena and Guillocheau, 1996), is a function of underwater irradiance (Kirk, 1984), and is obtained by recording the downwelling irradiance at two or more depths.

Numerous studies have compared K_d values with estimates of water column primary production. Ryther (1956) described a marine phytoplankton growth model that was applied to autotrophic coral growth. However, most of these models were developed in temperate regions and in places where the water column is stratified (Ryther, 1956; Hawkins and Griffiths, 1986). Therefore, effects of seasonality and of difference in turbidity across the water column have been considerable.

However, in regions where seasonal changes in solar radiation are low and constant, the attenuation coefficient could be more suited as a predictive tool. Delia et al. (1991) has commented on the importance of establishing a monitoring network in the tropics using diverse optical instrumentation, since studies in the tropics eliminate the variability suggested by seasonality.

Comparisons of K_d values to the maximum depth of coral growth have been presented by Yentsch et al. (2002). This kind of relationship is not new to Jakarta Bay in the Indonesian Archipelago ever since the 1930's when Verweys' research demonstrated a strong negative relationship between water transparency and the maximum depth of the living reef. By 1929, not only Verwey's but other authors as well had evidenced that the maximum depth of functional coral reef community were being dramatically reduced (Tomascik et al. 1993; Yentsch et al. 2002; Verstappen, 1953; Verwey's 1931). Relationships between K_d, percent coral cover, and diversity indexes, have been described by Tomascik et al., (1993) for Indonesian reefs. These authors report that very small changes in K_d have represented large changes in percent coral cover. Both coral cover and coral diversity were clearly affected by water transparency. In some cases they recorded a recovery of coral cover to pre-event levels, but that was not the case with diversity indexes. In general, a strong inverse relationship between K_d and a number of coral reef community parameters including coral growth rates were observed. Results showed non-linear relations between K_d, diversity index and percent coral cover. Also, the lower the photosynthesis / respiration rates of corals, the shallower the corals were found (Yentsch et al., 2002).

Percent living coral cover has been considered a good coral reef health indicator, since the most obvious effects are the demise in live coral cover (Mumby et al., 2001). Scleractinian corals have also been considered good indicators of coral reefs status. Such are the cases of the genera *Montastraea* and *Porites* (Mumby et al., 2001; Tomascik and Sanders, 1987). *Montastraea* and *Porites*, represent two important hermatypic corals for the Caribbean for their widely spread distribution and sediment resistance and remotion capabilities and for different studies that establish species dependence on autotrophy instead of heterotrophy (Lesser et al., 2000; Acevedo et al., 1989). Even though these have been good health indicators, especial attention should be given to the present status on coral bleaching, sea surface temperature and the resulting diseases and coral die-offs (Williams and Williams. 1988; Williams et al. 1987; Bruckner and Bruckner, 1998). The year 2005 has been a good marker for what are being considered important stressors to coral reef communities. García-Sais et al. 2006 reported significant decrease in the coral cover of six consistently studied coral areas in Puerto Rico. Therefore, even though this research has focused on luminic stressors attention should be given to possible effects the 2005 climatic event might have had on the coral communities under study, since one of the most affected species was the resilient *Montastraea annularis.*

Another estimator of coral health include the highly negative relationship between suspended particulate matter (within a range of 4.2 to 7.1 mg /L) and coral reef health (Tomascik and Sanders, 1985). In addition, the presence or absence of sponges and coralline algae and replacement of hard coral cover by soft corals, algae and sea grasses might be indicative of healthy or affected communities (Tomascik et al., 1993; Bell and Tomascik, 1993).

Bell and Tomascik (1993) presented a comparison between coral reef health indicators, such as coral cover, growth rate, diversity index, coralline and fleshy algal cover and water quality parameters, such as suspended particulate matter, chl-a, PO_4 and dissolved inorganic nitrogen. Particular interest have been given to chlorophyll-a since there is no definite threshold concentration level that can be generalized to more than one study site. Only an approximation has been proposed by Bell and Tomascik (1993) which showed lower threshold levels that appeared appropriate for places such as Barbados and probably the entire Caribbean Basin. Coles and Ruddy (1995) presented similar results where detection limit for chlorophyll was determined as 30 μg/m^3 for 1 liter of sample water filtered.

STUDY SITES

Mayagüez Bay

Mayagüez Bay covers an approximate area of 100 km^2 and is located in the western coast of Puerto Rico (Figure 1). The bay has a shallow insular shelf of 2 to 6 km with an average shelf break at 15 to 25 m (Morelock et al., 1983). In this bay coral reefs occur sparsely within the shelf. Mayagüez Bay waters are usually turbid with high deposition of fine grained sediments on the coral reefs. These reefs have declined significantly during the past decades (Goenaga, 1988). Three rivers, the Guanajibo, Yagüez and Añasco drain into the bay. In addition, both the Guanajibo and Añasco basins empty large agricultural watersheds.

In this bay, two sites were visited; Manchas Interiores and Escollo Rodríguez. Escollo Rodríguez is mainly a shelf reef located approximately 2 km offshore of Mayagüez Bay. At its shallower areas the reef top may reach the surface during low tide. It is highly influenced by terrigenous sediments from the Guanajibo and Yagüez rivers. Due to the influence of the sediments the majority of the coral cover is found in the upper ten meters of the reef and most of the substrate composition is by terrigenous mud. Resuspension of fine sediments occur during the winter months by large swells approaching from the northwest (Torres and Morelock, 1999).

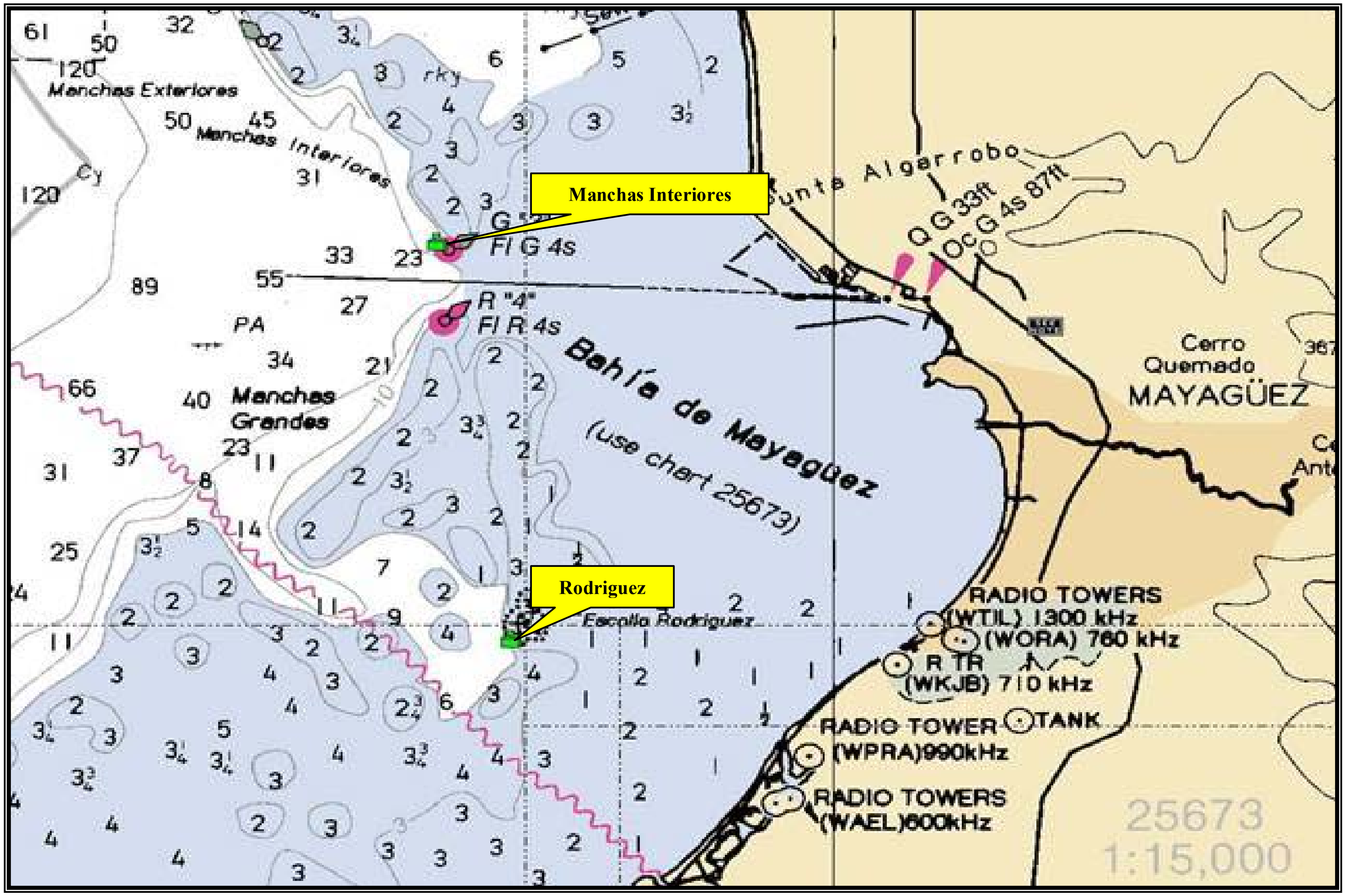

Figure 1. Mayagüez Bay study sites.

From all shelf edge reefs in this area, Manchas Interiores presents the highest coral cover with a 17 percent for the areas studied while only 10 percent coral cover was reported for the other sites (Morelock et al., 2001). Although a more dense gorgonian composition is present in these areas the hermatypic coral community varies mostly between *Montastraea*, *Agaricia, Porites* and *Diploria*. These are all highly sediment tolerant species (Acevedo et al. 1989).

La Parguera

La Parguera is generally considered to have good water transparency due to the absence of rivers in this area. Its sediment composition shows less than ten percent terrigenous influence (Morelock et al., 1994). The coastline is fringed by mangrove channels which trap most run-offs close to shore. However, rapid urbanization and nutrient loading appear to be an increasing problem (Morelock et al., 2001). In both cases changes in water optical properties could be predictive of coral reef degradation.

The southwest coast of Puerto Rico at La Parguera has the best development of emergent and submerged coral reefs in the island (Figure 2).

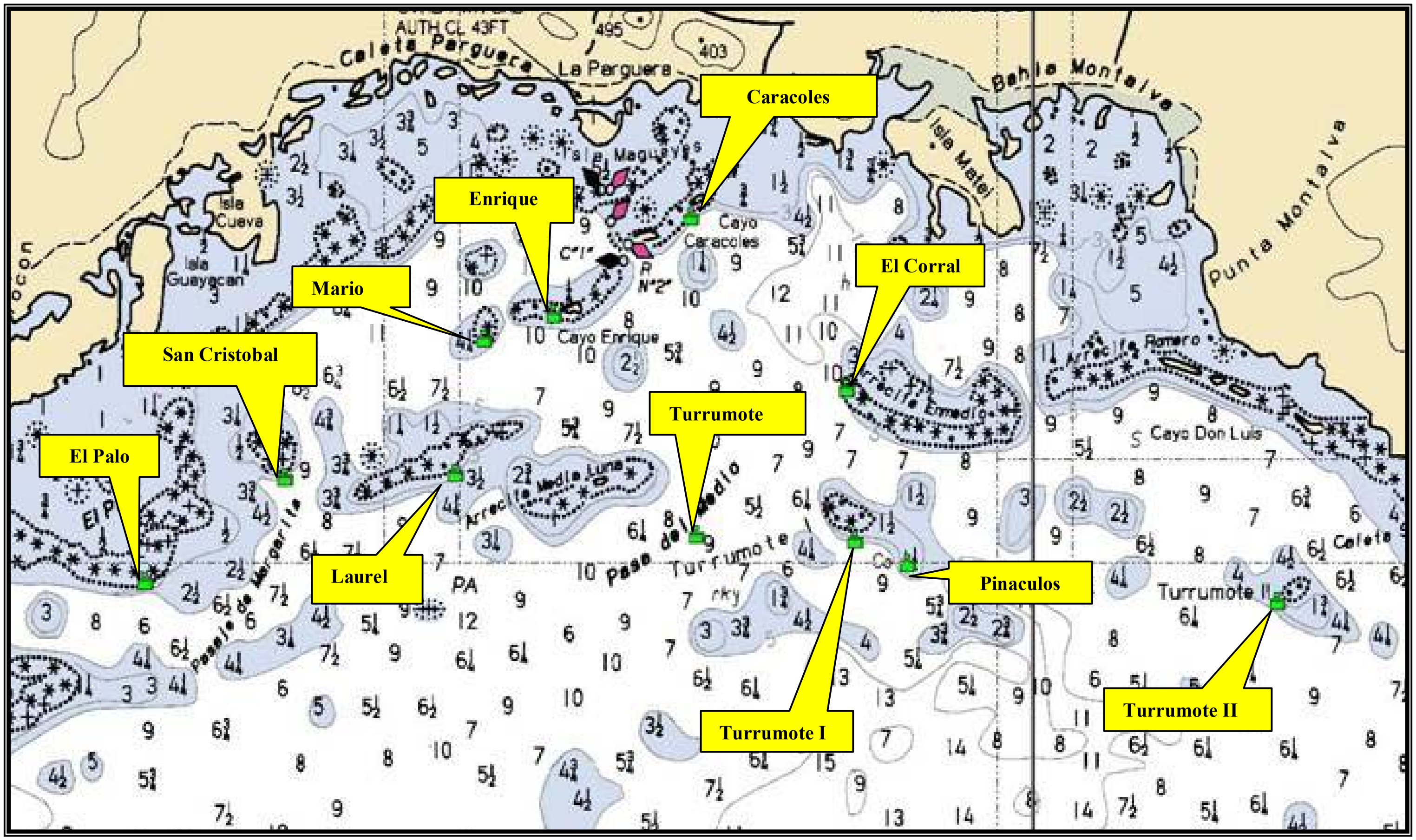

Figure 2. La Parguera study sites.

The absence of rivers in La Parguera creates ideal conditions for coral development. This reef system began to develop between 6,000 and 9,000 ybp, although the modern "coral carpet" is only one to two hundred years old (Morelock et al., 1977; Torres and Morelock, 2002). The reefs are built on topographic "hills", which may represent drowned eolianitic structures deposited parallel to shore during the Wisconsian glacial period (Kaye, 1959; Morelock et al., 1977). Eustatic sea level rise, shallow water, proper water transparency and substrata allowed the development of variable but extensive coral reefs within the shelf.

La Parguera reefs have the highest coral coverage with more than 30% in areas such as the shelf edge. Compared to other sites some of these reefs have been considered a standard of health for reefs in the area (Morelock et al., 2001). This reef system includes both near shore and offshore sites and includes emergent fringing reefs, bank barrier reefs and submerged patch reefs. Most lie on protected sections of the shelf, along a broad carbonate platform that extends up to 15 km offshore, upstream from large riverine discharges (Torres and Morelock, 2002). Reef depth distribution includes shallow environments, from 0-5m, to areas off La Parguera where the reefs start at a depth of about 18m and continues down the shelf slope to depths of at least 30m. (Torres and Morelock, 2002)

Even though La Parguera has been considered an area with high coral diversity, abundance and cover, these ecosystems are confronting many disturbances from both natural and anthropogenic factors. Some examples include coral diseases, hurricanes, and sedimentation; all of which have caused significant changes including local extinctions, competitive displacements of hermatypic corals by sponges, and coral bleaching resulting in a decrease in coral cover and an increase in algal biomass (Vicente, 1993; García-Sais et al. 2006; NOAA, 2005; McWilliams et al., 2005; Whelan et al. 2007; Jeffrey et al., 2005).

A total of eleven sites were characterized at La Parguera with a relatively large range of water quality and coral cover. The selected reefs included Caracoles, Mario, Enrique, Laurel, San Cristobal, El Palo, Media Luna, El Corral, Turrumote, Turrumote II and Pinaculos (Figure 2).

Guayanilla Bay

The reefs of Guayanilla Bay form part of three main sedimentary environments: the bare rocks, reefs and the muddy sediment floor. These reefs have been subjected to high levels of sedimentation and in many places are severely impacted. Most of the sedimentation on this area come either from the inside of the Guayanilla Bay or from Tallaboa Bay where oil refineries and petrochemical facilities were built in the late 1970's (Morelock et al., 2001). Most of the sedimentation may continually be resuspended due to heavy ship traffic in the area. Also, the Tallaboa and Guayanilla rivers discharge directly into this bay. Coral cover depletion in this area has been reported since the above mentioned facilities were built. The substrates at the reef sites are mostly covered by terrigenous muds. Coral cover changes have been described as ranging from few massive coral colonies at the top of the reef in 10 m of water to mostly hardground areas mostly covered by gorgonians. In general these are turbid water areas with poor visibility, and low coral cover. According to the literature, the geomorphology and structure comparison of these reefs present many developmental similarities with reefs at

La Parguera. However, reefs in these areas are technically described as shifted from their actual developmental zone. Their ecology resembles much deeper water assemblages with the characteristic association of grass beds and rubble.

Three sites were sampled in this area (Figure 3): Boya Verde, which is located at the entrance of the navigation channel toward the inside of the bay approximately 1.2 km from shore; Fanduco reef, located at 1.67 km from shore and Cayo Caribe, 2.67 km from shore. Coral cover in these reefs has been reduced close to 5 per cent during the past decade (Torres and Morelock, 1999).

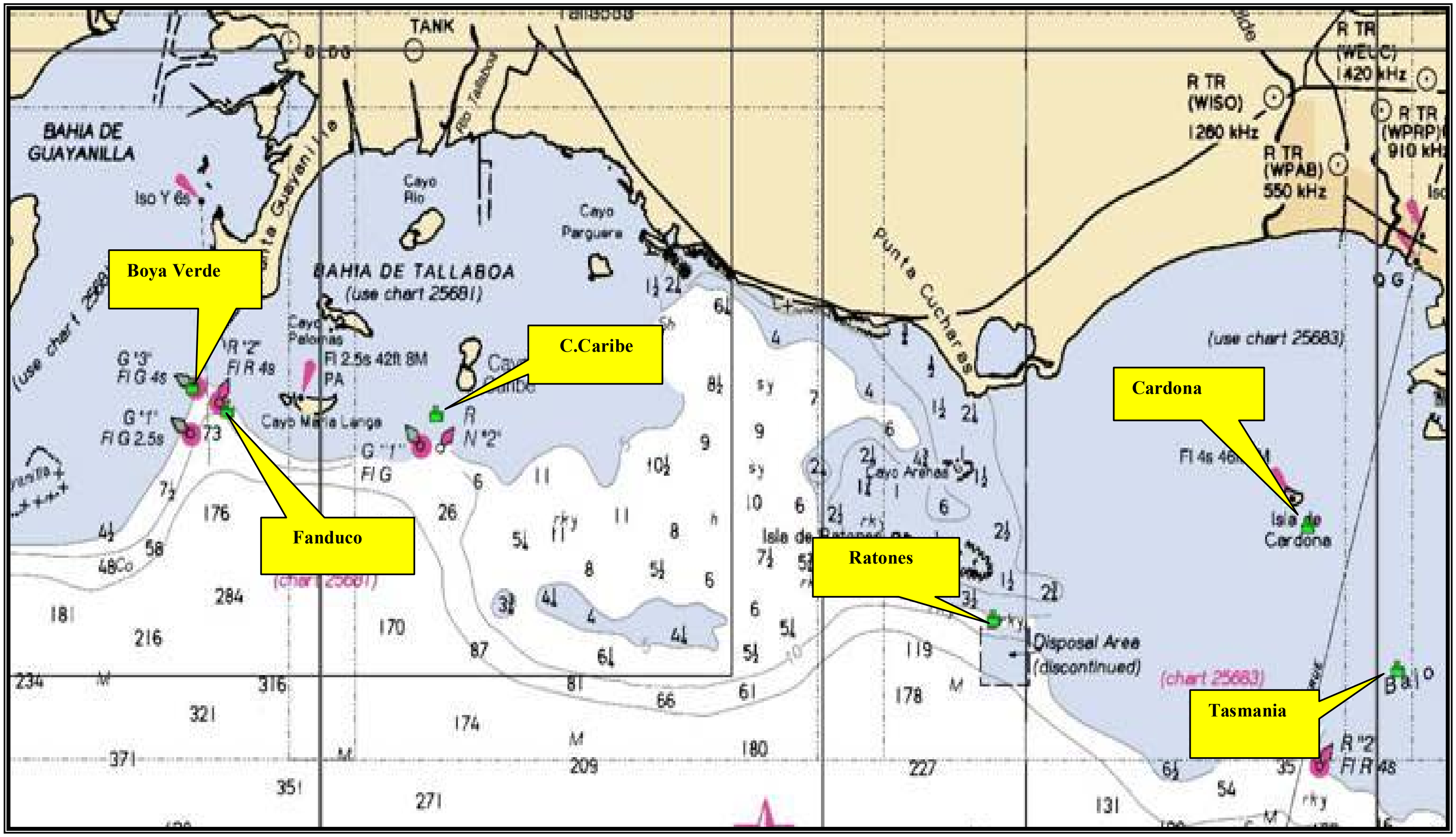

Figure 3. Guayanilla and Ponce Bay study sites.

Ponce Bay

Affected by the influence of Matilde and Portugués Rivers, reef formations in this area are part of a carbonate platform and the Ponce submarine canyon. Shelf edge reefs have the highest percentage of living coral. South of Cayo Cardona and in front of Cayo Ratones rise the only emergent reefs in that area (Acevedo et al., 1989).These sites form part of the Ponce basin where a sediment plume is frequently formed by wave action. This area receives high wave energy which removes some of the fine material that settles as a result of the described sediment plume. The plume characteristically drifts westward reaching both Bajo Tasmania and Cayo Cardona and less frequently, Cayo Ratones.

Sediments in this area are mostly a combination between terrigenous silts and clays, with some carbonate mud and sand (Morelock et al. 2001, Acevedo et al. 1989, Torres and Morelock, 1999). Fine grained sediment is resuspended either by wave action or by ship traffic. A depth shift similar to the one described for Guayanilla also happens here, since a major consequence of the terrigenous influx is the increase in turbidity and the attenuation of light in the water column. Coral species domination shifts appear as well, and are directly related to the tolerances to sediment stress (Hallock and Schlager, 1986). A decrease in total coral cover and a shift to slower growing coral species are some of the visible changes for the reefs between Ponce Canyon and Cayo Ratones.

Three reef sites were characterized in this area west and east of Ponce harbor (see Figure 3). These included Bajo Tasmania (2.41 km from shore), Cayo Cardona (3.09 km from shore) and Cayo Ratones (2.57 km from shore).

METHODOLOGY

The main objective of this research was to establish the relationships between the attenuation coefficients (K_d) of visible light (PAR) with the coral reef parameters of the different areas by testing the following hypotheses:

1. A negative exponential relationship exists between the percent coral cover and the water transparency through the vertical attenuation coefficients (K_d).
2. An inverse relationship exists between the vertical attenuation coefficients (K_d) and the diversity index.
3. An inverse relationship exists between the vertical attenuation coefficients (K_d) and the rugosity index.
4. An inverse relationship exists between the vertical attenuation coefficients (K_d) and the distance from shore.

A total of 19 stations were selected between Mayagüez Bay, La Parguera, Guayanilla and Ponce Bay areas. The locations and coordinates for the 19 sites are presented in Table 1. Eleven stations were sampled in La Parguera, in the southwest of Puerto Rico, and are shown in Figure 2. Six stations were sampled in the south: three in the Guayanilla Bay area and three in Ponce Bay (Figure 3). Finally, two additional stations were sampled in Mayagüez Bay, on the west coast of Puerto Rico (Figure 1).

Distances between the study sites and shore were obtained by establishing the closest straight line of contact between each station and shore contour and were recorded in kilometers (Table 1).

Table 1. Study sites locations and distance from shore in km. Codes refer to the general locations of the study sites; (Gu): Guayanilla Bay, (Po): Ponce Bay, (Pa): La Parguera, (Ma): Mayagüez Bay

Site	Code	Latitude	Longitude	Distance (km)
Boya Verde	**Gu**	17° 58.062'	66° 45.912'	1.20
Tasmania	**Po**	17° 56.513'	66° 37.692'	2.41
Cardona	**Po**	17° 57.260'	66° 37.990'	3.09
Escollo Rodríguez	**Ma**	18° 11.378'	67° 11.528'	2.30
El Corral	**Pa**	17° 56.817'	67° 01.162'	2.32
Cayo Caribe	**Gu**	17° 57.904'	66° 44.180'	2.67
Fanduco	**Gu**	17° 57.925'	66° 45.663'	1.67
Mario	**Pa**	17° 57.071'	67° 03.356'	2.50
Ratones	**Po**	17° 56.733'	66° 40.224'	2.57
Enrique	**Pa**	17° 57.197'	67° 02.928'	2.57
Caracoles	**Pa**	17° 57.694'	67° 02.091'	1.09
El Palo	**Pa**	17° 55.826'	67° 05.435'	3.13
Manchas Interiores	**Ma**	18° 13.448'	67° 11.883'	3.17
San Cristobal	**Pa**	17° 56.362'	67° 04.575'	3.30
Laurel	**Pa**	17° 56.379'	67° 03.529'	3.61
Pináculos	**Pa**	17° 55.920'	67° 00.763'	3.67
Turrumote	**Pa**	17° 56.039'	67° 01.087'	3.54
Turrumote II	**Pa**	17° 55.726'	66° 58.497'	2.46
Turrumote III	**Pa**	17° 56.064'	67° 02.056'	3.87

Coral reef sites where carefully selected to avoid any hardground areas in the analysis. Only well-defined stony coral reefs were included in this study. Stations were selected taking into consideration the geomorphology and history of natural and anthropogenic activities that have affected the water quality and coral reef structure throughout the last few decades.

Variations in water quality were divided into three groups: clear coastal waters, sites of intermediate turbidity, and highly turbid waters. This classification was mostly influenced by Kirk (1994) and is comparable to Preissendorfer's Type I, Type II and the intermediate water's description (Preisendorfer, 1961).

The depth of all stations was maintained constant at ten meters. Control of this variable makes it possible to compensate for the effects of depth-induced fluctuations in the incident light field. As Suhasorno (1990) and Tomascik et al. (1993) recommend, controlling for bathymetry is necessary for better predictions of coral reef parameters based on water optical properties.

Profiles of downwelling irradiance of photosynthetically active radiation ($E_{d\ (PAR)}$) were measured *in situ* using: 1) the submersible cosine corrected underwater quantum sensor (Licor LI-192SA) Model LI-1400 from Licor, Inc.and the Model PMA2132 quantum detector from Solar Light Corporation which measures the photon flux in wavelength range from 400 to 700 nm (PAR) (Figure 4a).

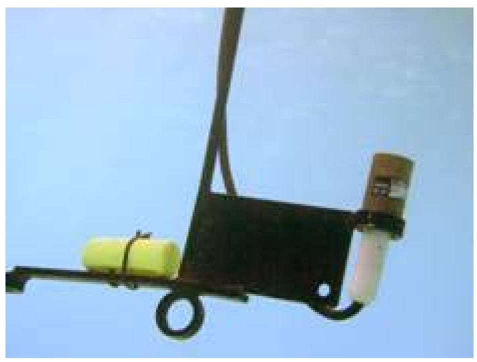

Figure 4a . Licor PAR underwater quantum sensor. LI- 192 in its metal frame.

Figure 4b. Solar Light PAR quantum sensor PMA 2132 inside its underwater metal frame.

Irradiance (E_d) underwater values were corrected using a (Licor LI-190SA) cosine corrected surface sensor. No correction surface sensor was available for the measurements obtained from the Model PMA2132 quantum detector from Solar Light Corporation . Irradiance profiles were developed by recording a total of fifteen measurements of the $E_{d\ PAR}$ value at every meter from 0 to 10 m depth. An average was then calculated for every meter and a profile constructed, for the downwelling irradiance data collected from the previously mentioned handheld radiometers. Irradiance profiles for all study sites are shown in appendix B. Due to the absence of a cloud correction sensor for the Solar Light data, scale differences were observed between both equipments. Therefore, E_d profiles from both equipments are presented separately. Corrected values of E_d were used to calculate the attenuation coefficient, K_d , using two methods: the slope of the log-transformed $E_{d\ PAR}$ profiles and Kirk (1994) formula:

$$K_d = 1/(z_2\text{-}z_1) * \text{Ln } Ed_1/Ed_2 \qquad (1)$$

Since the first few meters of water show high variability in irradiance values due to wave actions, the first five meters of every E_d profile were not considered for K_d calculations. As a result, K_d values were calculated using the formula (1) instead of using the log of the slope from the E_d profiles.

K_d values obtained from both handheld radiometers (Licor and Solar Light) were then compared qualitatively and quantitatively in order to determine the similarity of the results. Since no significant difference was found between the results of both instruments, their measurements were treated as equivalent and averaged.

In order to consider possible temporal variability in K_d calculations and the effect that wet and dry seasons might have on the determination of this coefficient, different measurements through time were obtained and averaged.

Analyses were conducted using SPSS version 15.0 and Statgraphics Plus version 3.1. Kolmogorov-Smirnov and Shapiro Wilks tests resulted in normality compliance for all K_d and biological data as demonstrated by the skewness (S) and kurtosis (K) tests for both K_d values (S:0.841 and K:0.696) and live coral data (S:0.387 and K:0.962). However, since only one visiting campaign was available, sampling restrictions together with skewness and kurtosis values over the limit for normality considerations resulted in the assumption that both the optical and physical data gathered with the bio-optical package were not normally distributed.

Simple and polynomial regression analysis were used to relate $K_{d\ (PAR)}$ to the coral reefs parameters of interest, such as: percent living coral cover, mean rugosity, species richness, index of evenness, index of diversity, percent octocorals, sponge, and uncolonized substrate. Profiles and regressions were also used to relate the different physical properties per site.

In general, attention was given to complying with favorable weather conditions. Measurements were avoided whenever rain, cloud or time of day (between 10:00 hours and 14:00 hours) was not favorable, to restraint from drastic irradiance variations between readings and to restraint whenever possible, from drastic climatic events.

Optical parameters were collected once at each station using an optical instrumentation bio-package with a CTD (Seabird SBE-19 with pump) which measured temperature(C°), salinity(PS) and depth (m). A WetStar fluorometer (from Wet Labs) that measured chlorophyll fluorescence(RU), and an AC 9 meter (from Wet Labs) which measured the beam attenuation coefficient, c (λ), and absorption coefficient, a (λ), in nine wavelengths. Finally, the backscattering coefficient, b_b (λ), at six wavelengths was measured using the Hydroscat-6 (from Hobi Labs). These measurements were obtained in order to establish the inherent optical properties (a, b_b , c) influencing the K_d value at each site (Figure 4c).

Figure 4c. Bio- Optical package containing CTD, fluorometer, AC-9 and a Hydroscat-6.

Both the physical and the inherent optical parameters were gathered between October 2005 and February 2006, with the aforementioned submersible bio-optical package. This offered a glimpse into the oceanographic processes that could have influenced the sampling sites. In general, homogeneity was observed within the water column ($p>0.40$), while heterogeneity was found between the different groups of stations and sites ($p<0.05$). Both relations were statistically tested through analysis of variance using the Kruskal Wallis tests for non parametric data.

Given the observed homogeneity throughout the water column with respect to the absorption, backscattering, and beam attenuation coefficients, as well as with the non-optical physical parameters; an average value was calculated for each of the sites studied. Therefore, the water column was considered as a 10 m thick well mixed layer. This perspective was utilized, since the objective of this study was to elucidate how K_d values varied between study sites and how this variability could be explained through the inherent optical properties and the physical parameters. It was the intention of this research to emulate the integrated upper column estimates provided by satellite images. Therefore, reasoning also took into consideration Kirk's definitions of absorption, scattering and volume scattering coefficients. In other words, the goal here was not to describe possible variations of these optical properties throughout every meter of the water column, but to present the additive effect of these variations as an integration of a 10 m water layer over the corals in areas of interest.

Inherent optical properties data gathered with the Ac-9 were spectrally corrected for temperature and salinity as presented in Pegau et al., (1997) using the ac Meter Protocol Manual from Wet Lab Inc. version from February 2008. For the aforementioned correction it was assumed that the absorption at 715 nm was negligible.

Some seasonal difference was present between the sampling events for the different sites. This was the case for Mayagüez Bay, which was visited during October 2005; while La Parguera, Guayanilla and Ponce were visited between January and February 2006. Such discrepancy is important to consider since: 1) maximum river discharge in Puerto Puerto Rico results from September through November and minimum discharges occur between February and April, 2) significant differences in temperature values could be affected by the wet/dry season mark and 3) the convergence between the drastic rise in sea surface temperature during October 2005 and the sampling visit to Mayagüez Bay stations could be misinterpreted if the afforementioned occurrence is not taken into account.

Importance was also given to the determination of the euphotic zone both at 1% and 10% of the subsurface irradiance values. For practical purposes this will be referred to as optical depths (ζ), following Kirk's definition. Both the 10% and 1% of the irradiance subsurface values were calculated with the following equation.

$$\zeta = (2.3, 4.6) = K_d * (z_m) \tag{2}$$

where Z_m refers to the depth (m) in the water column where E_d becomes either 1% or 10% of the surface value.

Percent coral cover, defined as the total bottom area occupied by living coral colonies, was estimated using photoquadrats (1.0 m^2) constructed out of 1.27 cm pvc material and following the phototransect method described by Bohnsack (1979), Weinberg (1981) and Stoddart (1981). Due to poor water quality, photoquadrats were further subdivided into four areas of 0.5 m^2 in order to obtain better quality digital photographs. Therefore, four photos were obtained per photoquadrat for a total of thirty photoquadrats and 120 photos per site.

A total of three ten meter transects and the best fifteen photoquadrats per site were used as an adequate sample size after analyzing the species-area curve for each study site and considering the minimal area required, which is said to be reached when doubling the sampling area results in a less than 10% increase in the number of species observed (Appendix A) (Kershaw, 1964; Weingberg, 1981 and 1978; Stoddart, 1981).

Transects were parallel to the depth contours. *In situ* identification of the coral species within the photoquadrats was done simultaneously while taking the photos in the field in order to facilitate the coral identification during laboratory analysis particularly for areas of poor visibility. Photoquadrats were photographed at a vertical distance of 1.2 m. Photos were enhanced using Photoshop 7.0 and percent coral cover was determined using the Deneba Canvas 8.0 area measuring tool. All data was entered into an Excel spreadsheet where coral cover, rugosity, index of diversity (3), and evenness (4), were calculated and compared for each site. Rugosity was calculated using the Caricomp (1994) methodology. Ten sets of measurements were obtained by following the contour of the reef every 10m with a 10 m brass chain. A total of 10m were then subtracted to the reading in the reference line according to the respective meter mark.

The Shannon Weaver Diversity Index (*H*') was calculated according to:

$$H' = \sum_{j}^{i} pi \ln(pi) \qquad (3)$$

where *pi* is the number of individuals of an ith species or coral taxon divided by the total number of colonies or individuals in all represented taxons.

The Shannon Evenness index was calculated using the following equation:

$$J' = H' / \ln(S) \qquad (4)$$

where *S* is the number of coral taxa and H' is the Shannon Weaver Diversity Index.

RESULTS

Physical parameters

Temperature

Water temperature in Guayanilla Bay ranged from 26.85 to 27.06 C˚, while Ponce Bay ranged from 26.40 C˚ for Cardona to 26.84 C˚ for Cayo Ratones. Both Guayanilla and Ponce temperature values were obtained during January 2006. In Mayagüez Bay water temperatures were gathered during October 2005 and ranged from 28.98 C˚ to 29.05 C˚. In La Parguera, temperatures ranged from 26.2 C˚ to 26.35 C˚ for all the stations visited during February 2006. Turrumote II, however, was visited on February 2006 and temperature was found to be constant at 26.93 C˚ throughout the entire water column (Figure 5).

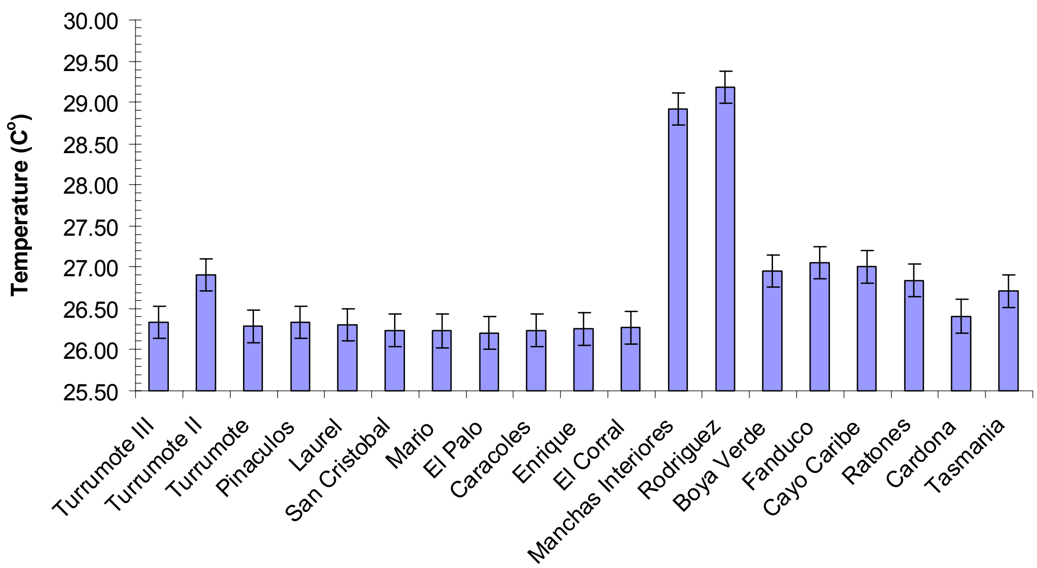

Figure 5. Upper ten meters' average temperature (C°) between October 2005 and February 2006, for all 19 stations.

Salinity

Salinity values present the same time frame as that presented for temperature data. Salinity in La Parguera ranged from 35.45 PS to 35.75 PS. In Guayanilla, salinity was mostly constant at 35.41PS for Cayo Caribe and 35.42 PS for Fanduco. In Boya Verde salinity ranged from 35.39 PS at the surface to 35.44 PS near the bottom.. In Ponce, salinity ranged from 35.32 PS to 35.38 PS. The lowest salinities were recorded in the Mayagüez Bay. Surface salinity at Escollo Rodríguez was the lowest with a 34.6 PS and increased to 35.0 PS from five to six meters depth. In Manchas Interiores a gradual transition was observed throughout the entire profile which started with a salinity of 34.4 PS at the surface and ended with 35.3 PS at the bottom (Figure 6).

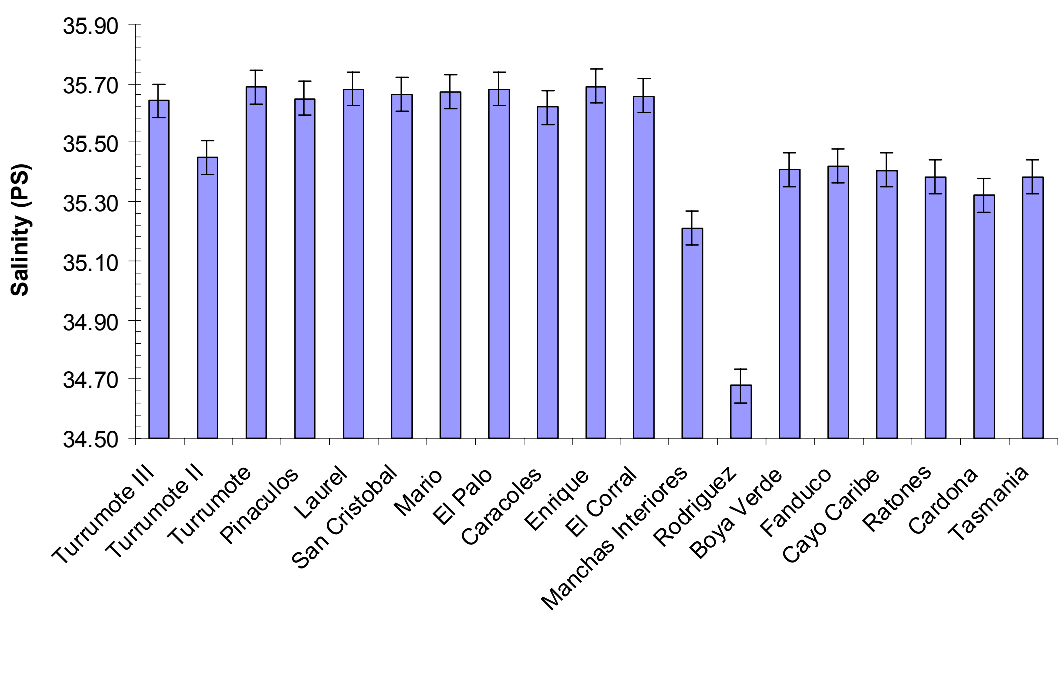

Figure 6. Upper ten meters'average salinity (PS) between October 2005 and February 2006, for all 19 stations.

Chlorophyll fluorescence

Fluorescence was also gathered following the same schedule per area, previously discussed. The highest values were recorded for Manchas Interiores (0.24 RU) and Escollo Rodríguez (0.38 RU). These values were followed by the values found in Cardona (0.20 RU), and Tasmania (0.17 RU). Although little variability was found for La Parguera, the highest values were recorded for Turrumote II (0.16 RU), Pinaculos (0.14 RU), El Corral (0.14 RU) and Enrique (0.14 RU) (Figure 7).

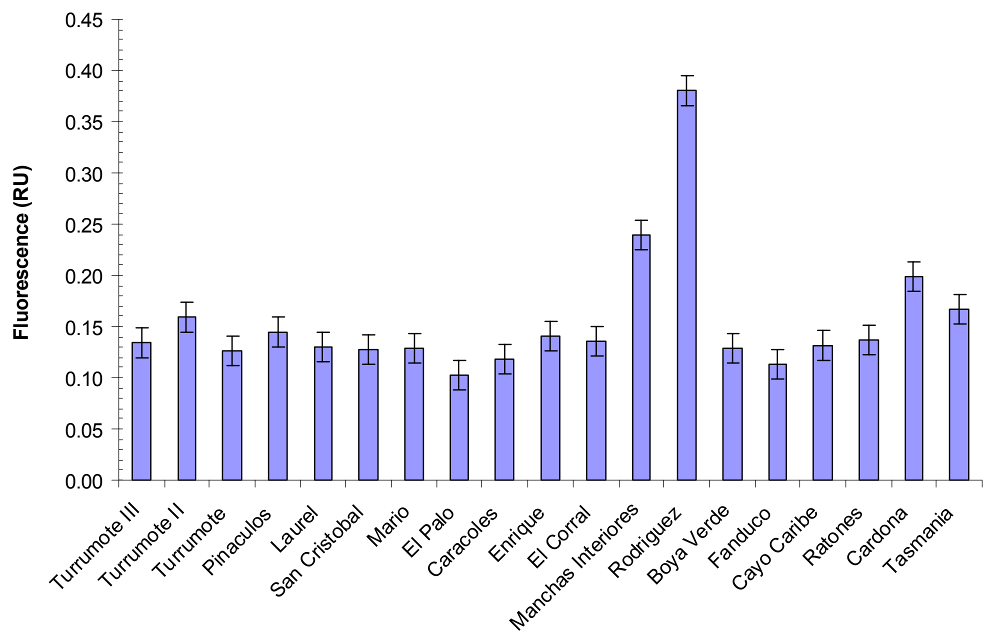

Figure 7. Upper ten meters' average fluorescence (RU) between October 2005 and February 2006 for all 19 stations.

Inherent Optical Properties (IOP's)

Absorption

Although a general similarity was observed between all the wavelengths, absorption was highest at 412 nm and negligible at 715 nm, as expected with the spectral correction. The highest absorption was found at Escollo Rodríguez followed by Cardona, Boya Verde, Manchas Interiores, Enrique, Caracoles, Mario and Turrumote II, respectively (Figure 8).

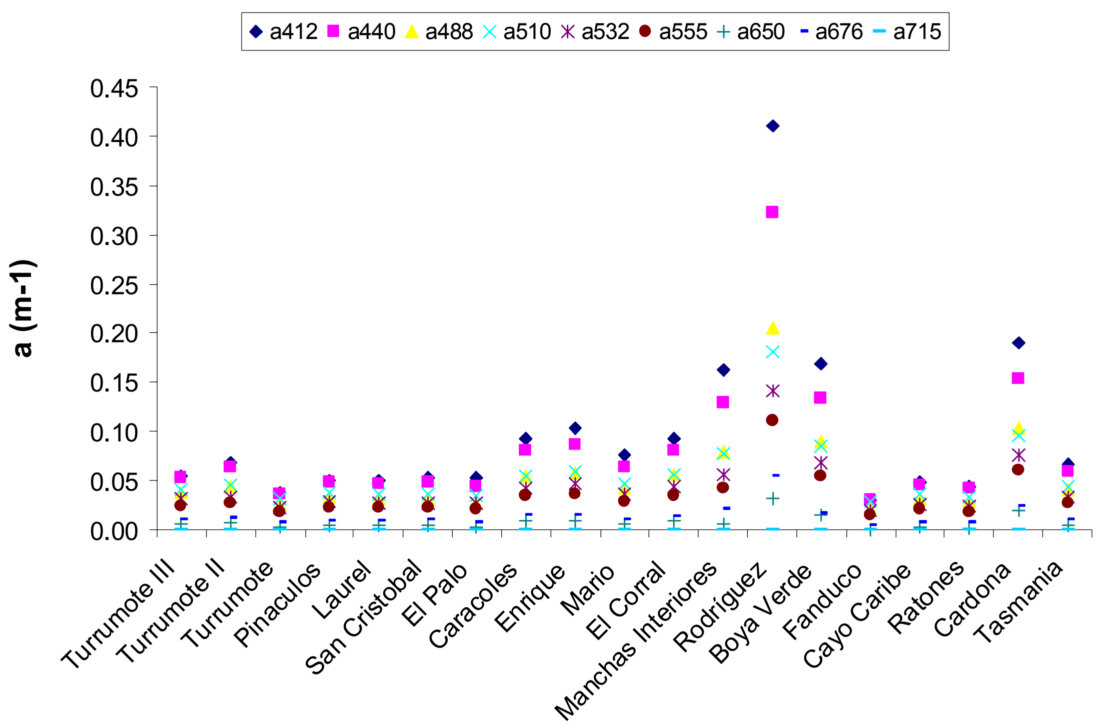

Figure 8. Average absorption per wavelength for 19 stations, between February 2005 and February 2006.

Backscattering

In general, backscattering was highest at 442 nm and lowest at 671 nm although some overlapping could be observed. The highest backscattering was observed at Escollo Rodríguez, similar to the absorption results. This was followed by Cardona, Boya Verde and Enrique, Caracoles, El Corral, Mario, Manchas Interiores and Turrumote II (Figure 9).

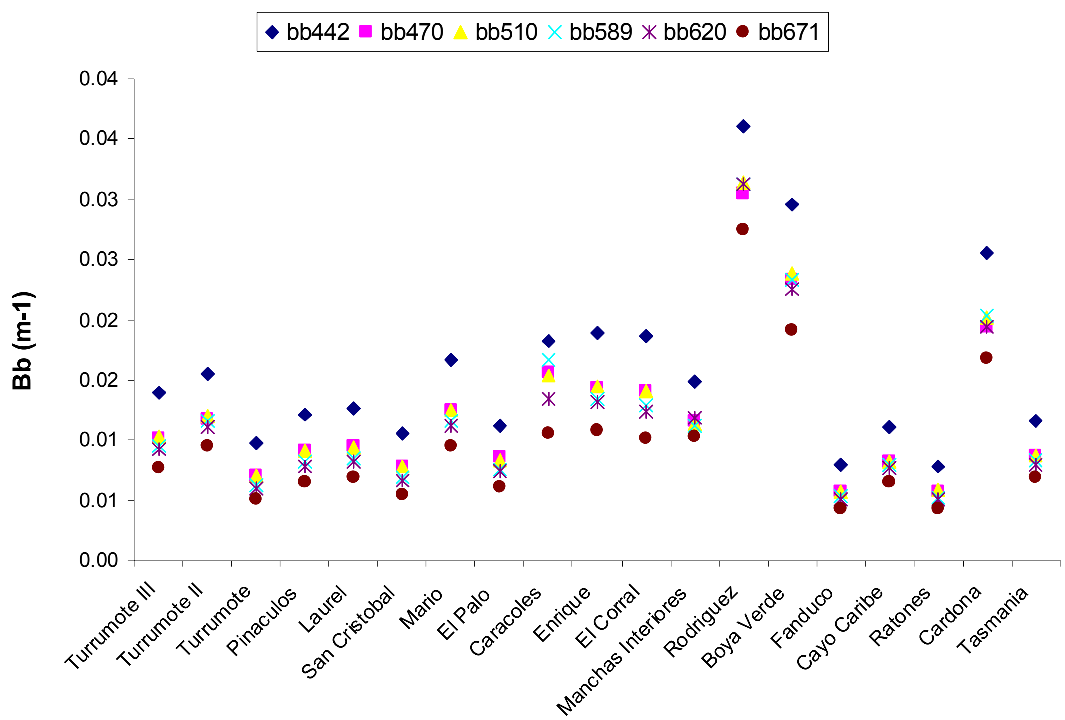

Figure 9. Average backscattering per wavelength for 19 stations, between February 2005 and February 2006.

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Beam attenuation coefficient

The beam attenuation coefficient; since it is the sum of the flux that is absorbed and scattered, highly resembles the one for absorption with a positive shift in the scale, due to the addition of the scattering values into the calculation (Figures 8 and 9). The highest beam attenuation coefficient was observed for Escollo Rodríguez followed by Cardona, Boya Verde, Manchas Interiores, Enrique, Caracoles, El Corral and Mario (Figure 10).

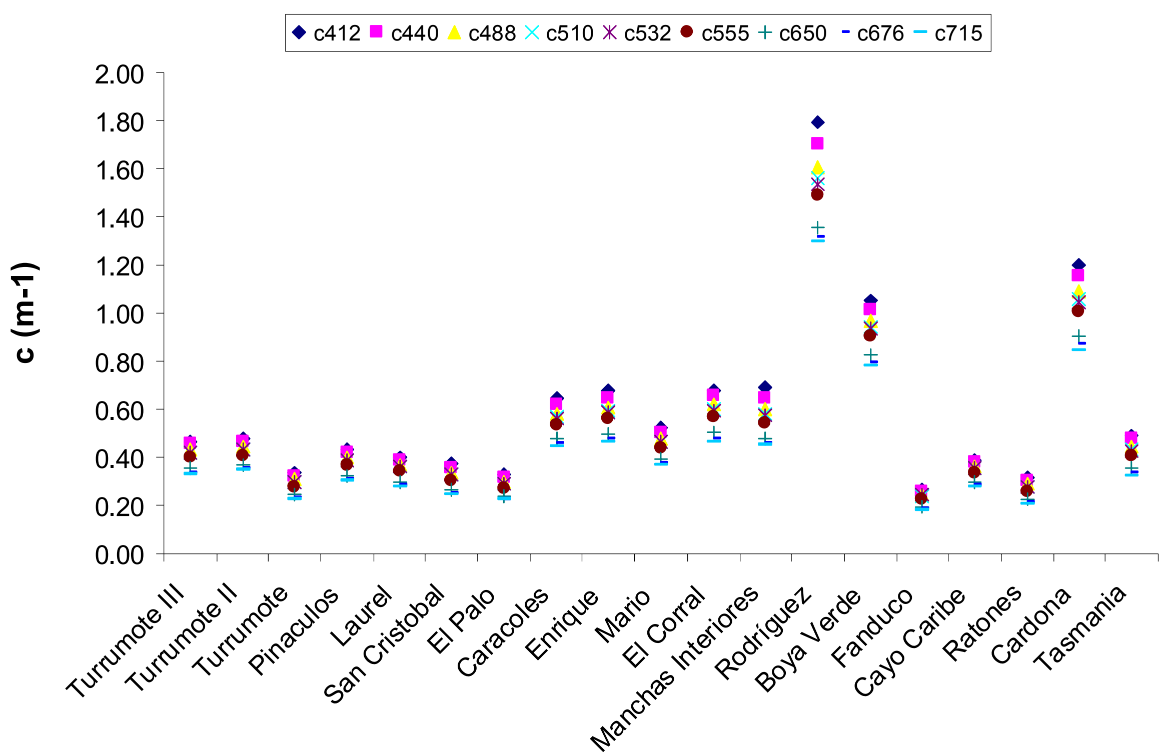


Figure 10. Average beam attenuation coefficient per wavelength for 19 stations, between February 2005 and February 2006.

Irradiance Profiles

Irradiance profiles for all study sites are shown in appendix B. Profiles obtained using the Licor sensor are presented separately from those obtained by the Solar Light sensor.

Apparent Optical Properties

Vertical Attenuation Coefficients

Average vertical attenuation coefficients (K_d) calculated for the study sites after averaging all the visits between December 2000 and February 2006, are shown in Table 2. K_d values ranged from an average maximum of 0.319 and a coral cover of 4.55% for Boya Verde at Guayanilla to an average minimum of 0.142 and a coral cover of 61.43% for Turrumote III. The maximum K_d value for La Parguera was El Corral station with 0.22 and 16.91% live coral cover. The minimum K_d value was Turrumote III with 0.142, while having the maximum live coral cover at 61.43%. This maximum was not only for the area of La Parguera, but overall as well (Table 2).

Table 2. Vertical attenuation coefficients (K_d) and the percent coral cover for 19 study sites.

Site	K_d	%Live coral cover
Turrumote III	0.142	61.43
Turrumote II	0.143	59.34
Turrumote	0.144	59.30
Pinaculos	0.147	51.69
Laurel	0.158	46.10
San Cristobal	0.159	44.79
Manchas Interiores	0.170	29.52
El Palo	0.174	28.97
Caracoles	0.197	27.35
Enrique	0.205	26.36
Ratones	0.206	26.03
Mario	0.209	24.76
Fanduco	0.211	23.60
Cayo Caribe	0.219	19.65
El Corral	0.220	16.91
Rodriguez	0.229	8.12
Cardona	0.253	7.42
Tasmania	0.268	5.46
Boya Verde	0.319	4.55

For Guayanilla the average maximum K_d value was for Boya Verde with a 0.319 and a live coral cover of 4.55%, while the minimum K_d value recorded was 0.211 for Fanduco station with a live coral cover of 23.60%.

In Ponce Bay, the maximum K_d value was for Bajo Tasmania station at 0.268 and live coral cover of 5.46% and the minimum for Cayo Ratones with a K_d value of 0.206 and a live coral cover of 26.03%. Finally, Mayagüez Bay presented a maximum K_d value of 0.229 and 8.12% of live coral cover for Escollo Rodríguez while a K_d of 0.17 and a live coral cover of 29.52% for Manchas Interiores. Simple regressions between K_d and different coral reef parameters are presented in Table 3.

Table 3. Relationships between the vertical attenuation coefficients (K_d) and the coral reef parameters. * levels of significance: *** 99%, ** 95%, * 90% ; w: weak correlation (< 0.5).

Independent variable	Dependent variable	R-coefficient	R^2	Probability	Significance
Kd	Sponge cover	0.7459	0.5563	0.0002	***
Kd	Octocoral cover	0.7361	0.5419	0.0003	***
Kd	Uncolonized substrate cover	0.7390	0.5462	0.0003	***
Kd	Diseased coral cover	-0.6006	0.3607	0.0065	***
Kd	Distance from shore	-0.6615	0.4376	0.0020	***
Kd	Rugosity	-0.4638	0.2151	0.0455	**w
Kd	Macroalgae cover	-0.5245	0.2751	0.0212	**
Kd	Richness	-0.4739	0.2246	0.0404	*w
Kd	Live coral cover	-0.9594	0.9204	0.0000	***

The most significant relationship was between K_d and the percent of live coral cover, which established a negative exponential relationship. Therefore, the live coral cover diminished exponentially as the K_d values increased. The r-squared for this correlation was 0.92 and the correlation coefficient 0.96, meaning that 92% of the variability in coral cover is explained by the K_d variable. With a probability of less than 0.0001 this is a strong and statistically significant relationship (Figure 11).

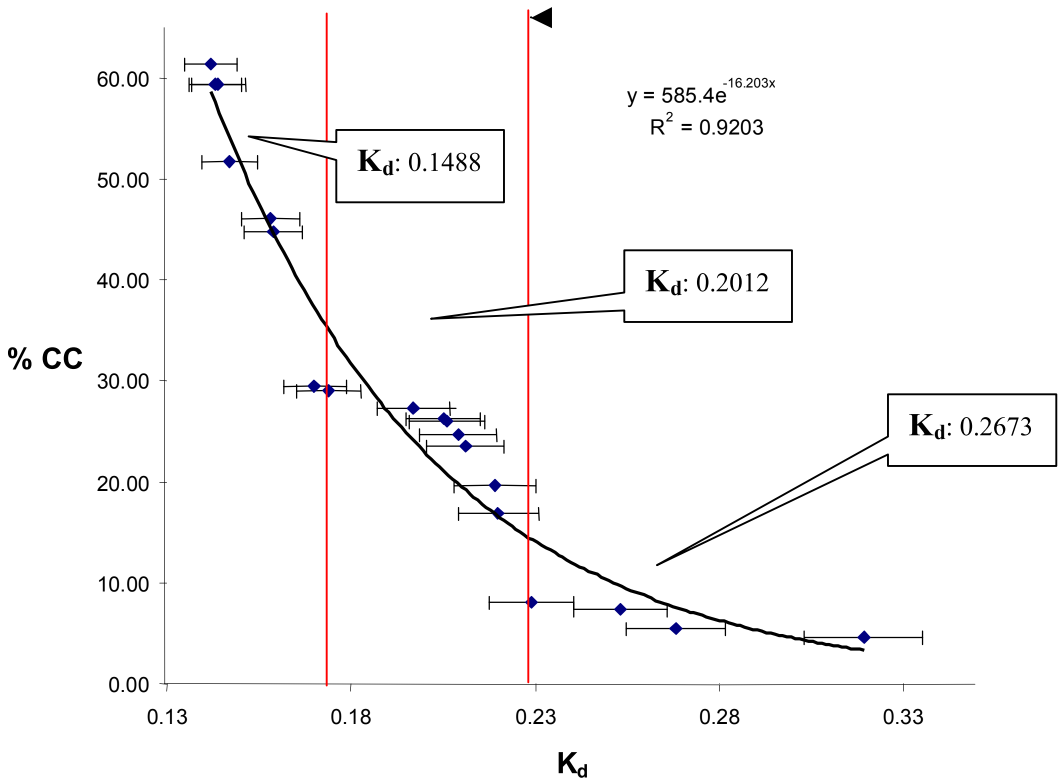


Figure 11. Relationship between the vertical attenuation coefficient (K_d) and the percent living coral cover.

Although not as strong a second relationship was observed between K_d at each site and their distances from shore. Distance from shore can be a potential descriptor of the influx of sediments and other materials which could be affecting water quality in the different areas studied. Therefore, it was hypothesized that an increase in water clarity will be directly related to the distance from shore. This was the case in the sampled areas, where a negative linear regression (R=-0.66; R^2 =0.44, p<0.0020) was found between K_d values and the distance from each site to shore (Table 1-3 and Figure 12).

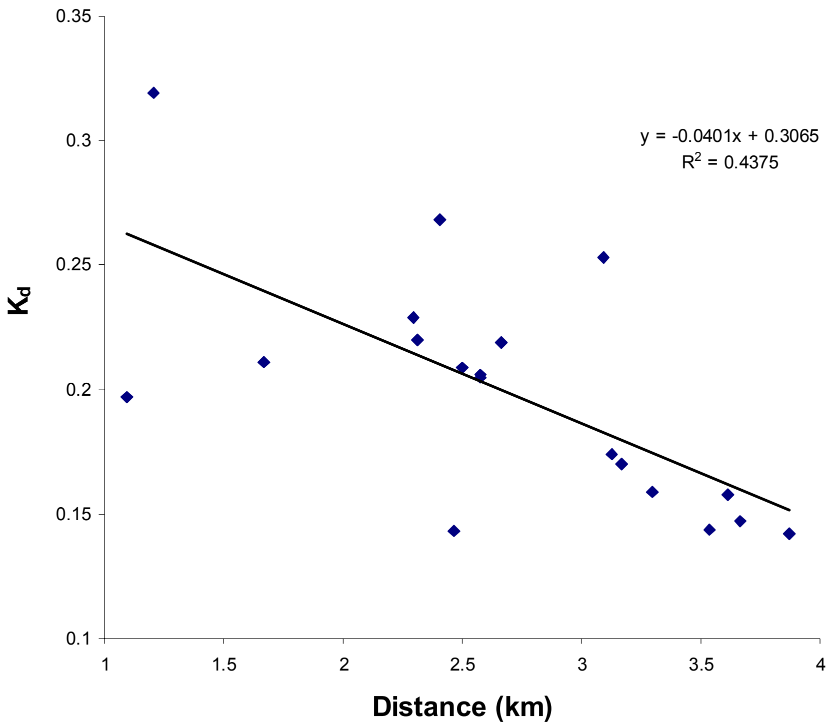


Figure 12. Relationship between the sites distance from the coast (km) and the vertical attenuation coefficient (K_d).

However, careful attention should be rendered since at the moment this model only explains what happens 44% of the time for the study areas visited. Although this relationship seemed more evident in La Parguera because of the greater number of stations and their sparse distribution, Turrumote II seemed to be the only exception to this tendency in the area. It is important to remember that no actual riverine sources are present in this area. Also, at La Parguera, there is a well developed fringe of mangroves that serves as a sediment trap. In addition, precipitation episodes are infrequent. Mean annual precipitation for the south coast of Puerto Rico is 90 cm, and only 30 cm typically occur at La Parguera. Meanwhile, Mayagüez Bay accounts for between 200 and 250 cm of rain per year (Warne et al., 2005).

In Guayanilla and Ponce, although the study sites are more equidistant from shore (Figure 12 and 13) other physical factors, may alter the distance/K_d relationship. In Ponce, for example, not only rivers, but currents and sediment movement has to be taken into consideration, as presented in previous works (e.g. Morelock et al. 2001 ;Torres 1998). The K_d measurements for these areas corroborate previous reports of high persistent turbidity in these waters.

In order to visualize the relationship between turbidity and percent coral cover, with respect to the distance from shore, a GIS image was developed, demostrating the ratio of the percent coral cover to K_d values obtained. Figure 13, shows this distribution through a color gradient that goes from white, for the lowest coral cover and highest K_d values to red, for the highest coral cover and lowest K_d values.

In Mayagüez Bay the sediment input comes from the Yagüez, Guanajibo and Añasco rivers, being the last two the most influential (Warne et al., 2005). Escollo Rodríguez is more directly affected by the influence of the Yagüez river and specially the Guanajibo river, for which the annual discharge is the greatest at $5.5 m^3/s$.

Guayanilla Bay has the influence of three rivers. However, due to the geographic location of the Yauco River and the presence of natural barriers such as the physical structure of Punta Verraco, the main effects are from the Guayanilla and Tallaboa rivers. Sites such as Boya Verde would be also heavily impacted by the high maritime traffic of

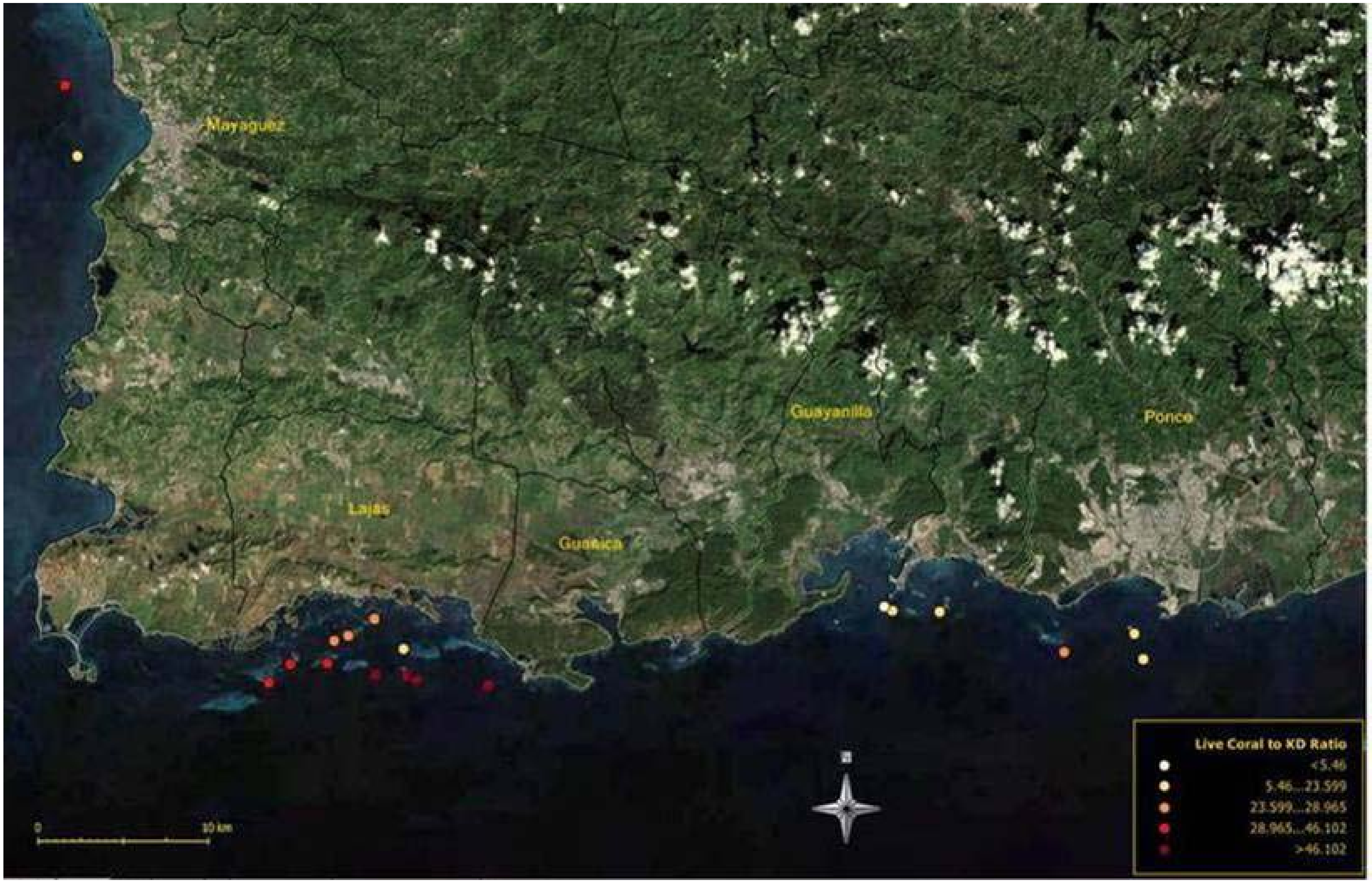


Figure 13. Ratios of the percent of live coral cover to the vertical attenuation coefficient (K_d) for the 19 study sites.

this area. As seen in Figure 13 Boya Verde is clearly the most affected while Fanduco and Cayo Caribe are less impacted.

Finally, Ponce has both natural and anthropogenic hydrographic influences within the Bay. Strong currents and sediment movement along the southeast coast affects the reefs in the Ponce area, with the farthermost station from the bay, Tasmania, being the most affected, followed by Cayo Cardona. Ratones, due to its location, is partially protected from both the western sediment influx and the area's hydrologic sources including the Tallaboa, Matilde and Portugués Rivers. Relationships between distance from shore and other parameters are shown in Table 4.

Table 4. Linear regressions between the sites distance from shore and the coral reef parameters. * Levels of significance:*** 99%,** 95% , * 90% ; w: weak correlation (<0.5); ns: non-significant.

Independent variable	Dependent variable	R-coefficient	R^2	Probability	Significance
Site Distance	OD 1%	0.6814	0.4643	0.0013	***
Site Distance	K_d	-0.6615	0.4376	0.0020	***
Site Distance	Live Coral Cover	0.6101	0.3722	0.0055	***
Site Distance	Diseased coral cover	0.5821	0.3388	0.0089	***
Site Distance	Uncolonized substrate	-0.4805	0.2309	0.0373	**w

Other significant relationships between K_d and the biotic and abiotic parameters are shown in table 3. The positively related included: K_d vs sponge (R=0.75; R^2=0.56;p=0.0002), K_d vs octocorals (R=0.74, R^2=0.54, p=0.0003); K_d vs diseased coral cover (R=-0.60, R^2=0.36, p=0.0065), K_d vs distance from shore, which was previously commented on, and K_d vs uncolonized substrate (R=0.74, R^2=0.55,p=0.0003)(Figures 14-16). Inverse exponential relationships included: K_d vs rugosity R=-.046; R^2=0.22;p<0.0455), K_d vs percent coral cover as previously mentioned, K_d vs richness (R=-0.47, 0.22, p=0.0404) and K_d vs macroalga (R=-0.52, R^2=0.28, p=0.0212) and K_d vs filamentous algae. Relationship between K_d and filamentous algae cover was not found to be statistically significant since the p-value was greater than 0.10 (filamentous R^2: 0.22, R: 0.05).Therefore, it was not included in table 3. Although not significant macroalgae, demonstrated an inverse exponential relationship. It is probable that the relation for macroalgae and filamentous algae were not stronger due to complications with the photoanalysis for the obtention of algae cover percentages.

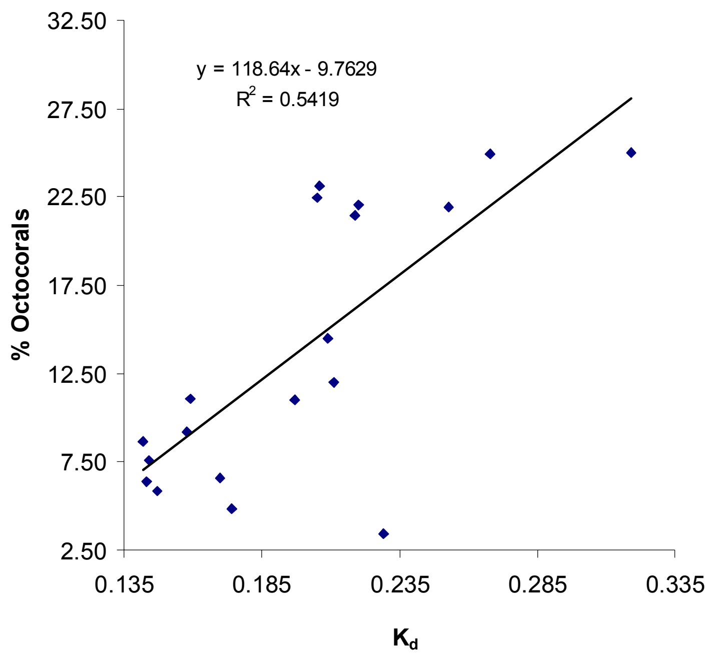


Figure 14. Relationship between vertical attenuation coefficient (K_d) and the percent of octocorals.

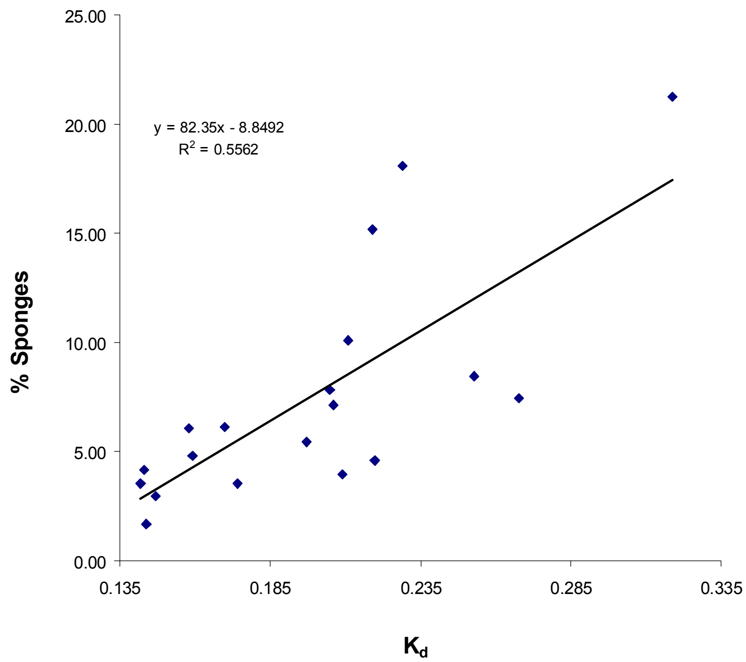


Figure 15. Relationship between vertical attenuation coefficient (K_d) and the percent of sponges.

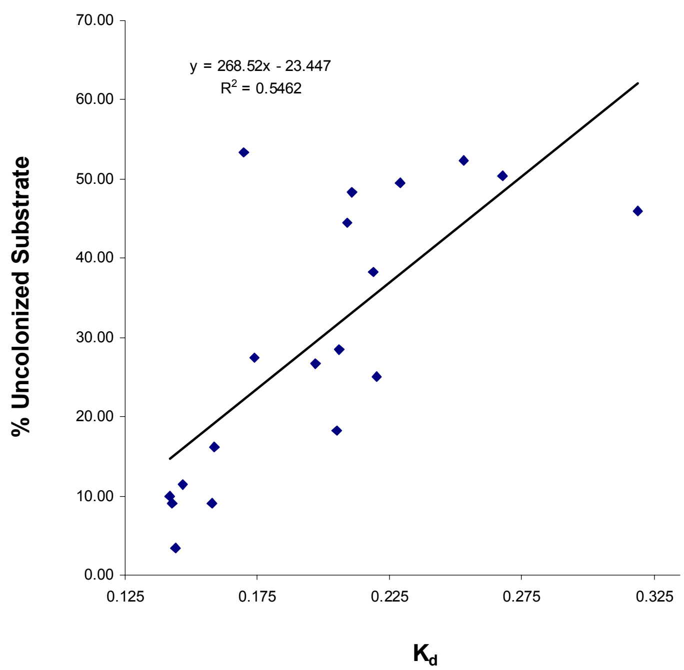


Figure 16. Relationship between the vertical attenuation coefficient (K_d) and the percent of uncolonized substrate.

Euphotic Zonation

Results for the calculations of optical depths at 1% and 10% are shown in table 5. These two represent the points where the surface irradiance is reduced to 10 percent and 1 percent from the subsurface values. They are of interest in terms of primary productivity and are of value in determining the upper (10%) and lower (1%) limit of the euphotic zone for the areas studied. Values of 10% and 1% of the subsurface values were reached at a maximum depth of 16 m and 32 m, respectively, for the clearest waters in the sampled stations.

These were found at Turrumote III, while the most turbid waters of Boya Verde reached the same optical depth at only 7 m and 14 m of depth, respectively. Between the 19 sites visited in this study, a total of 8 different optical depths were found. Optical depths were strongly related to the percent of live coral cover (Figure 17).

This is of utmost interest since it may help to understand the zonations and shifts occurring in coral reef areas, like the one described by Acevedo et al. (1989) for Guayanilla and Ponce Bay. The optical depth provides a more ecologically relevant descriptor for autotrophic benthic communities than the physical depth.

By using the optical depth and the relationship between K_d and the live coral cover for the study sites, a differentiation into three groups was possible (Table 5). These groups provided categorical subdivisions based on the K_d ranges encountered in the study sites.

Group I is a high coral cover group with an average K_d of 0.149. The intermediate group has an average K_d of 0.201 and the low coral cover group has an average K_d of 0.267 (Figure 11).

Table 5. Categorization of 19 study sites into groups as determined by the vertical attenuation coefficient (K_d), the percent live coral cover and the optical depth at 1% and 10% of the subsurface values.

Sites	Group	Kd	Live coral	OD 10%	OD 1%
Turrumote III	I	0.142	61.43	16	32
Turrumote II	I	0.143	59.34	16	32
Turrumote	I	0.144	59.30	16	32
Pináculos	I	0.147	51.69	15	31
Laurel	I	0.158	46.10	14	29
San Cristobal	I	0.159	44.79	14	29
Manchas Interiores	II	0.170	29.52	13	27
El Palo	II	0.174	28.97	13	26
Caracoles	II	0.197	27.35	11	23
Enrique	II	0.205	26.36	11	22
Ratones	II	0.206	26.03	11	22
Mario	II	0.209	24.76	11	22
Fanduco	II	0.211	23.60	11	22
Cayo Caribe	II	0.219	19.65	11	21
El Corral	II	0.220	16.91	11	21
Rodríguez	III	0.229	8.12	10	20
Cardona	III	0.253	7.42	9	18
Tasmania	III	0.268	5.46	9	17
Boya Verde	III	0.319	4.55	7	14

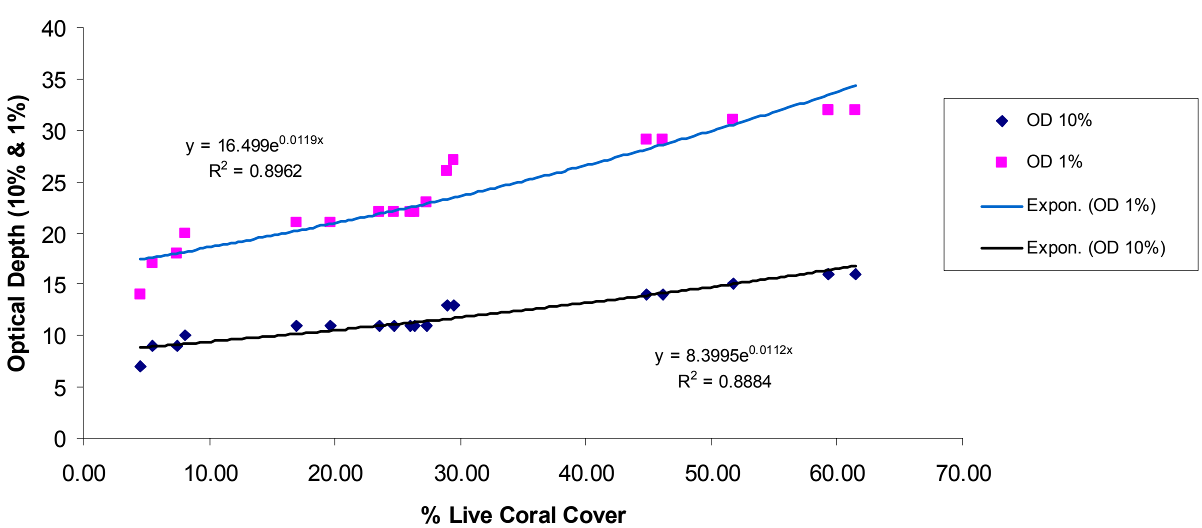


Figure 17. Relationship between the optical depth of 1% and 10% of the subsurface values, and the percent live coral cover.

The high coral cover group, or Group I, included six stations: Turrumote I, II and III; Pinaculos, Laurel and San Cristobal. This group included K_d values between 0.142 and 0.159 and percent coral cover between 61.43% and 44.79%. For these stations, the euphotic zone depths ranged from 16 m to 14 m for optical depth of 10% and from 32 m to 29 m for the optical depths of 1%.

Group II represents an intermediate cover and included nine stations: Manchas Interiores, El Palo, Caracoles, Enrique, Ratones, Mario, Fanduco, Cayo Caribe and El Corral. Vertical attenuation coefficient for this group ranged from 0.170 to 0.220. Live coral cover ranged between 29.52% and 16.91%, respectively. The optical depth at 10% ranged from 13 m to 11 m and between 27 m to 21 m for the 1% subsurface irradiance values.

Finally, Group III had the lowest coral cover and included Escollo Rodríguez, Cardona, Tasmania and Boya Verde. The K_d values ranged between 0.229 and 0.319. The live coral cover for this group ranged from 8.12% to 4.55% . Optical depth for 10% subsurface irradiance values ranged from 7 m to 10 m and from 20 m to 14 m for the optical depth at 1% subsurface values.

Relationships between the optical depth (at 1% and 10%) and biotic and abiotic parameters are presented in table 6.

Similitude between the results from optical depth at 10% and 1%, allowed them to be averaged in one table. There were six linear regressions and two exponential ones. Included were three inverse relations between optical depth and different parameters: OD vs uncolonized substrate ($R=-0.78$, $R^2=0.61$, $p=0.0001$), OD vs sponge cover ($R=-0.71$, $R^2=0.50$, $p=0.0007$) and OD vs octocoral cover ($R=--0.73$,$R^2=0.53$, $p=0.0004$).

Table 6. Relationships between the optical depth (at 10% and 1%) and the coral reef parameters. *Levels of significance: *** 99%, **95%, *90%; ns: non-significant, w: correlation coefficient <0.5.

Independent variable	Dependent variable	R-coefficient	R^2	Probability	Significance
OD	Uncolonized substrate cover	-0.7780	0.6053	0.0001	***
OD	Sponge cover	-0.7089	0.5025	0.0007	***
OD	Octocoral cover	-0.7303	0.5333	0.0004	***
OD	Live coral cover	0.9710	0.9428	0.0000	***
OD	Sites distance from shore	0.6853	0.4696	0.0012	***
OD	Diseased coral cover	0.6276	0.3938	0.0040	***
OD	Macroalgae cover	0.4197	0.1762	0.0736	*w
OD	Richness	0.3980	0.1584	0.0915	*w

The other five were positive relationships including: OD vs diseased coral cover (R=0.63, R^2=0.40, p=0.0040), OD vs sites distance from shore (R= 0.69, R^2=0.47, p=0.0012), OD vs richness (R=0.40, R^2=0.16, p=0.915), OD vs macroalgae (R=0.42, R^2=0.18, p=0.0736) and OD vs live coral cover (R=0.9710, R^2=0.9428, p<0.0001) (Figure 16). Relation between OD and filamentous algae was not significant (R=-0.09, R^2=0.84, p=0.71). Therefore, it was not included in table 6.

Data in Table 7 shows the characterization data collected for each site which included: percent live, unhealthy and dead coral; rubble, octocorals, sponge, macroalgae, filamentous algae, invertebrates and uncolonized substrate. Escollo Rodríguez, in Mayagüez Bay, had the lowest percent of octocorals (3.47%), while Boya Verde had the highest value (25%) as presented in Figure 14. Boya Verde had the highest percent of sponges (21.25%), while the minimum was observed for Turrumote where a 1.70% was recorded (Table 7, Figure 15). Macroalgae, was highest for Caracoles at 20.98%, and lowest for Turrumote III at 0.42%.

Filamentous algae, was highest on Escollo Rodríguez at 19.17%, (Table 7). Although this category was not found to be statistically significant for the regression performed, a qualitative trend could be observed. As mentioned earlier relationships between K_d and filamentous algae cover was not found to be statistically significant since the p-value was greater than 0.10 (filamentous R^2: 0.22, R: 0.05). Relationships between percent coral cover and other coral reef parameters are presented in table 9.

Table 7. Coral community characterized parameters.

Sites	Live coral	Octocorals	Sponge	Macroalgae	Filamentous algae	Invertebrates	Diseased	Uncolonized substrate
Boya Verde	4.55	25.00	21.25	0.76	2.38	0.05	0.00	46.01
Tasmania	5.46	24.90	7.46	0.49	3.29	0.44	0.00	50.39
Cardona	7.42	21.93	8.46	1.05	6.67	1.28	0.00	52.31
Escollo Rodriguez	8.12	3.47	18.07	1.50	19.17	0.16	0.00	49.51
El Corral	16.91	22.07	4.62	2.01	11.54	0.05	1.55	25.07
Cayo Caribe	19.65	21.47	15.19	1.11	3.35	0.00	0.00	38.31
Fanduco	23.60	12.00	10.08	2.97	2.75	0.08	0.00	48.32
Mario	24.76	14.47	3.98	1.14	0.48	0.05	0.51	44.50
Ratones	26.03	23.13	7.16	4.31	7.43	1.60	0.00	28.42
Enrique	26.36	22.47	7.82	8.80	7.50	4.26	0.00	18.26
Caracoles	27.35	11.00	5.45	20.98	3.37	2.11	3.08	26.66
El Palo	28.97	4.87	3.56	9.08	4.29	0.00	7.49	27.43
Manchas Interiores	29.52	6.60	6.15	4.21	0.00	0.18	0.00	53.35
San Cristobal	44.79	11.04	4.82	4.49	0.00	3.11	3.14	16.19
Laurel	46.10	9.20	6.08	2.97	8.80	0.38	7.71	9.09
Pinaculos	51.69	5.87	2.97	6.68	4.91	1.16	11.20	11.42
Turrumote	59.30	7.60	1.70	7.42	9.32	0.00	7.33	3.44
Turrumote II	59.34	6.40	4.19	9.56	4.87	1.03	0.00	8.98
Turrumote III	61.43	8.67	3.55	0.42	4.14	0.90	4.42	9.98

Table 8. Coral reef rugosity, species richness, index of diversity and evenness.

Site	Mean Rugosity	Richness	H'	J'
Boya Verde	0.12	10	2.01	0.87
Tasmania	0.10	7	1.67	0.86
Cardona	0.12	11	1.77	0.74
Rodríguez	0.18	8	1.74	0.84
El Corral	0.19	20	2.20	0.74
Cayo Caribe	0.13	14	1.70	0.64
Fanduco	0.11	14	2.04	0.77
Mario	0.14	21	2.41	0.79
Ratones	0.16	13	1.65	0.64
Enrique	0.16	18	2.18	0.76
Caracoles	0.16	18	2.15	0.75
El Palo	0.15	19	2.25	0.76
Manchas Interiores	0.15	16	2.17	0.78
San Cristobal	0.14	10	2.35	1.02
Laurel	0.14	14	2.05	0.78
Pinaculos	0.16	10	1.54	0.67
Turrumote	0.14	16	2.16	0.78
Turrumote II	0.15	21	2.38	0.78
Turrumote III	0.14	20	2.27	0.76

Coral Reef Sites Characterizations

Coral species richness, diversity index (H'), evenness (J'), and mean rugosity for all the study sites visited are shown in table 8. Although, the experimental design was mainly intended toward the determination of percent coral cover, additional biotic and abiotic parameters were obtained through the photographic analysis.

Coral species richness was highest for Turrumote II (n=21) and lowest for Tasmania (n=7). A significant negative relation was found between K_d and species richness (R=-0.47, R^2=0.22, p=0.0404), while a positive regression described the relation between OD and species richness (R=0.40, R^2=0.16, p=0.0915).

The highest evenness (J') was observed at San Cristobal with 1.02, while Cayo Caribe registered the lowest with 0.64. Although the relations found were always negative as expected, the probabilities were always over 0.10 reason why they were not considered significant.

Diversity index was highest for Mario at 2.41, while the lowest value was for Pinaculos at 1.54; both from La Parguera. No significant relation was observed between H' and K_d or any other parameter.

The lowest vertical relief or rugosity was observed in Tasmania (0.10) and the highest in El Corral (0.19). A negative relation was found between K_d and mean rugosity (R=-0.47, R^2=0.22, p=0.0455), while a posite but non- significant relation was found between rugosity and live coral cover (R=0.29, R^2=0.82, p=0.2334)(Table 8).

Coral species distribution is presented in Appendix C for the 19 study sites. A total of four genera were found to be common at all sites (Table 9).

Table 9. The percent coral cover for the principal four coral genera for the three characterized groups determined by the optical depth and the vertical attenuation coefficient (K_d).

Site	*Agaricia*	*Montastraea*	*Porites*	*Siderastrea*
Turrumote III	3.97	44.04	4.63	2.00
Turrumote II	3.75	39.07	12.84	0.37
Turrumote	0.96	49.65	4.95	1.93
Pinaculos	1.02	45.64	2.60	0.72
Laurel	4.17	1.23	2.32	1.83
San Cristobal	7.43	14.52	6.86	3.28
Group I	**3.55**	**32.36**	**5.70**	**1.69**
Manchas Inter	5.84	11.24	7.21	0.57
El Palo	2.41	15.23	2.14	3.29
Caracoles	2.19	7.89	2.12	5.22
Enrique	3.93	7.67	3.56	2.92
Ratones	13.51	6.02	1.40	1.25
Mario	1.52	5.30	3.07	2.93
Fanduco	2.74	12.46	3.52	2.23
Cayo Caribe	11.57	3.26	0.14	2.61
El Corral	0.71	6.24	0.65	4.18
Group II	**4.94**	**8.37**	**2.65**	**2.80**
Rodriguez	0.52	5.99	0.19	0.93
Cardona	1.13	2.00	1.00	2.23
Tasmania	0.50	2.54	0.51	1.05
Boya Verde	0.10	2.46	1.43	0.22
Group III	**0.56**	**3.25**	**0.78**	**1.11**

These included: *Montastraea*, *Porites*, *Agaricia* and *Siderastrea*. *Agaricia* was the least abundant in Boya Verde, with 0.1% and the most abundant in Cayo Ratones with 13.51%. *Montastraea* cover was highest in Turrumote (49.65%) and lowest in Laurel (1.23%). *Porites* cover was highest in Turrumote II (12.84%) and lowest in Cayo Caribe (0.12%). Finally, *Siderastrea* cover was highest in Caracoles (5.22%) and lowest in Boya Verde (0.22%).

Regressions between K_d values and the different coral genera included: K_d vs *Montastraea* (R=-0.71, R^2=0.51, p=0.0006), K_d vs *Porites* (R=-0.60, R^2=0.36, p=0.0062) and K_d vs *Agaricia* (R=-0.21, R^2=0.34, p=0.0087).

The most abundant species at the Ponce and Guayanilla sites were *Montastraea cavernosa* , *Montastraea annularis*, *Siderastrea siderea*, *Porites astreoides,* and *Agaricia sp.*. In the Mayagüez Bay the previous species together with *Colpohyllia natans* and *Porites porites* were present. All these species were also present in La Parguera in addition to *Montastraea franksi*, *Montastraea faveolata*, *Diploria strigosa*, *Diploria clivosa*, and *Acropora cervicornis*. Other species were also present at all study sites, as shown in Appendix C, but their abundance was minimal.

Study sites were further divided into three optical depth groups after taking into consideration the coral species distribution, the percent coral cover, the K_d values and the optical depth values. Consideration of the temperature, salinity and fluorescence (as a proxy of chlorophyll) was also taken into account in order to divide the study sites into three optical depth groups (Table 9).

Temperature was higher for group III. This group included sites that had been affected by 2005 temperature rise, in addition to their freshwater influence and rainfall episodes. Results for salinity and fluorescence also showed that freshwater and nutrient loaded sites presented the lowest salinity and the highest fluorescence recorded. Sampling dates for group III and group II were different in terms of rainfall seasonalities for the tropics and direct influence from the October 2005 climatic episode. Therefore, no special attention was given to these results.

Averages for the absorption, backscattering and beam attenuation coefficient were calculated considering the group division previously proposed (Table 10).

Table 10. Average absorption (a), backscattering (b) and beam attenuation (c) coefficient values for the three characterized groups.

Site	Bb442	bb470	bb510	bb589	bb620	bb671				b(average)
I	0.01	0.01	0.01	0.01	0.01	0.01				**0.01**
II	0.01	0.01	0.01	0.01	0.01	0.01				**0.01**
III	0.03	0.02	0.02	0.02	0.02	0.02				**0.02**
Site	**A412**	**a440**	**a488**	**a510**	**a532**	**a555**	**a650**	**a676**	**a715**	**a(average)**
I	0.05	0.05	0.03	0.04	0.03	0.02	0.00	0.01	0.00	**0.03**
II	0.08	0.07	0.04	0.05	0.04	0.03	0.01	0.01	0.00	**0.04**
III	0.21	0.17	0.11	0.10	0.08	0.06	0.02	0.03	0.00	**0.09**
Site	**C412**	**c440**	**c488**	**c510**	**c532**	**c555**	**c650**	**c676**	**c715**	**c(average)**
I	0.41	0.40	0.38	0.37	0.37	0.35	0.31	0.30	0.29	**0.35**
II	0.50	0.48	0.45	0.44	0.44	0.42	0.37	0.35	0.34	**0.42**
III	1.13	1.09	1.03	1.00	0.98	0.95	0.86	0.83	0.81	**0.96**

Sites in Group I or between Turrumote III and San Cristobal had the lowest average absorption values (Table 10, Figure 8). From Manchas Interiores to El Corral or Group II the intermediate average absorption values were recorded (Table 10, Figure 8). Finally, from Rodríguez to Boya Verde, Group III, the highest average absorption values were encountered (Table 10, Figure 8). Similar results were observed with the average backscattering and beam attenuation coefficients (Table 10, figures 9-10) . Although a difference is not necessarily evident between groups I and II, it was visible between the first two groups and group III. Therefore, these tables were used as a mean to observe trends toward the sites clustering together with Table 11 which showed the characterized coral reef parameters for the three groups.

Group I included the sites with the highest coral cover and the lowest K_d values. This was the most distant group from shore. Coral richness was also high, but not the highest. While being similar in diversity to group II, group I, presented more evenness than group II, therefore a more homogeneous cover was found which is consistent with the higher richness recorded for group II. Mean rugosity was the lowest for Group III and highest for Group II, although difference between Group I and II was minimal. Macroalgae was also lowest for Group III and highest for Group II although as before, difference was minimal. Macroalgae found was mostly coralline algae species, specifically of the genus *Halimeda*. Filamentous algae were also present, and although their abundance was clear to the research group during the dives, their identification was almost impossible through the photoanalysis. Therefore, their abundance could not be well assessed. Sponges, octocorals and uncolonized substrate cover, responded well to the group differentiation (Table 11). The number of invertebrates was observed to decrease from Group I to Group III (Table 11). Most of the invertebrates observed were echinoids. Their abundance was highest for Group I and decreased towards Group III. Diseased corals were highest in Group I and decreased towards Group III also.

Table 11. Average coral reef parameters for the three characterized groups.

Site	**Live coral**	**Richness**	**Rugosity**	**Distance (km)**	**H'**	**J'**
I	53.78	15.17	0.145	3.41	2.13	0.80
II	24.79	17.00	0.146	2.41	2.08	0.74
III	6.39	9.00	0.124	2.25	1.80	0.83
Site	**Kd**	**OD 10%**	**OD 1%**	**Sponge**	**Octocorals**	**Macroalgae**
I	0.15	15.17	30.83	3.89	8.13	5.26
II	0.20	11.44	22.89	7.11	15.34	6.07
III	0.27	8.75	17.25	13.81	18.83	0.95
Site	**Filamentous algae**	**Uncolonized substrate**	**Diseased**	**Invertebrates**	**Chlorophyll Fluorescence**	**Salinity**
I	5.34	9.85	5.63	1.10	0.14	35.63
II	4.52	34.48	1.40	0.93	0.14	35.53
III	7.88	49.56	0.00	0.48	0.22	35.20

Although fluorescence was the same for the first two groups its concentration increased in Group III., implying a larger amount of chlorophyll-a in the area. Absorption was also the highest for this group (Table 10 and 11, Figure 8), and so was the case with backscattering and the resultant beam attenuation coefficient (Table 10, Figures 9-10).

Group II, was considered an intermediate between both extremes. This group is more representative of a community in a transition phase. It had almost half the coral cover of Group I. Its species richness was slightly higher than that of group I, also. However, colonies were not as big and instead smaller colonies of different species were present. Octocorals, sponges, macroalgae and filamentous algae were more abundant in this group with intermediate K_d values. Although *Halimeda* sp. was present, *Dyctiopteris* sp. was also abundant. There was no major difference between the rugosity in Group I and Group II. A more turbid environment likely due to suspended sediments was apparent. The uncolonized substrate cover increased dramatically when compared to group I and a decrease in the amount of diseases was observed.

Group III sites were the closest to shore (Table 1), the more turbid and the most affected as a whole. This group included the sites most influenced currents, river run-offs, sediment plumes, resuspension and heavy commercial traffic. The usually had the most suspended sediments and particulate matter in the water column. The highest K_d values were recorded for these sites (Table 2). They had the lowest coral cover, lowest salinity and highest chlorophyll due to river inputs of suspended sediments and nutrients (Figures 5-10). Study sites within this group had the lowest species richness and diversity (H’), but the highest evenness (J’) probably due to fewer coral species present (Table 11).

Therefore, no major colonization of the area was visible leading to the highest percentage of uncolonized substrate by coral. This group also had the least incidence of diseases observed. Many coral colonies were covered by a mixture of colonizing sponges and sediment together with encrustrating blue-green algae and filamentous algae which were very abundant. Conversely, macroalgae cover was the least observed for all the areas.

Regressions were reconsidered from the three group perspective (Table 12). This resulted in stronger regressions although for most of them their p value was higher than expected (>0.10) for significance considerations.

Table 12. Relationships between the vertical attenuation coefficient (K_d) and the coral reef parameters for the three characterized groups. ns: non-significant; w: weak correlation (<0.5).

Independent variable	Dependent variable	R-coefficient	R^2	Probability	Significance
Kd	Uncolonized Substrate	0.9728	0.9463	0.1489	ns
Kd	Diseased	-0.9293	0.8635	0.2409	ns
Kd	Distance from shore	-0.8814	0.7769	0.3132	ns
Kd	Invertebrates	-0.9874	0.9749	0.1013	ns
Kd	Macroalgae	-0.8390	0.7039	0.3663	ns
Kd	Octocorals	0.9571	0.9160	0.1872	ns
Kd	Richness	-0.7975	0.6359	0.4124	ns
Kd	Filamentous algae	0.7876	0.6203	0.4227	ns
Kd	Mean Rugosity	-0.8925	0.7966	0.2979	ns
Kd	J’	0.4163	0.1733	0.7266	ns
Kd	H’	-0.9592	0.9200	0.1825	ns
Kd	OD	-0.9939	0.9878	0.0705	**
Kd	Live Coral Cover	-0.9982	0.9964	0.0384	**
Kd	Sponge	0.9977	0.9954	0.0434	**

Stronger R-squared and R-coefficients were found between K_d and coral cover (R=-0.99, R^2=0.99), mean rugosity (R=-0.8925, R^2=0.80), diversity index (R=-0.96, R^2=0.92), distance from shore (R=-0.88, R^2=0.78) and optical depth (R=-0.99, R^2=0.99) (Table 12). Additional relationships between grouped data and K_d are presented in Table

12. Some additional relations, considering the three group division, are presented for rugosity in Table 13. As with those presented previously these are mostly statistically non-significant.

Table 13. Relationships between the mean rugosity for the three groups and coral reef parameters. *Level of significance: *** 99%, **95%, * 90%, w: weak relation (<0.5); ns: non-significant.

Independent variable	Dependent variable	R-coefficient	R^2	Probability	Significance
Rugosity	Uncolonized substrate	-0.9809	0.5832	0.4468	ns
Rugosity	Octocoral cover	-0.7235	0.5234	0.4851	ns
Rugosity	Sponge cover	-0.9345	0.8732	0.2317	ns
Rugosity	Diseased coral cover	0.6628	0.4392	0.5388	ns
Rugosity	J’	-0.7817	0.6110	0.4287	ns
Rugosity	Filamentous algae cover	-0.9809	0.9621	0.1248	ns
Rugosity	Macroalgae cover	0.9996	0.9991	0.0186	**
Rugosity	Live Coral Cover	0.9181	0.8429	0.2595	ns
Rugosity	H'	0.9854	0.9711	0.1089	ns
Rugosity	Richness	0.9918	0.9836	0.0818	**
Rugosity	Distance from shore	0.5956	0.3548	0.5938	ns
Rugosity	Invertebrates	0.9730	0.9467	0.1483	ns
Rugosity	OD	0.8372	0.7009	0.3684	ns

In terms of the coral species characterization, the sediment resistant coral genera were found to remain constant along all the visited sites. Four genera were consistently reported throughout all the sites (Table 9). These coral genera were: *Montastraea, Porites, Agaricia and Siderastrea*. Species along group I mostly included *Montastraea faveolata*, *M. annularis*, *Montastraea fraksi* and lower abundance of *M. cavernosa*. It also consisted of *Agaricia* sp., *Colpophyllia natans*, *Porites astreoides*, *P. porites*, and *Siderastrea siderea* Although not as abundant *Acropora cervicornis* was also present

(Figure 18). The presence of *M. franksi* and *M. faveolata* and the lower abundance of *M. cavernosa* were also detected.Although *Agaricia* sp. belongs to a deeper coral zonation their abundance was lower than that observed at group II.

Group II, included a wider range of species. Although *Acropora cervicornis* was present, the percent cover at this intermediate group was lower than in Group I. A higher abundance of *Agaricia sp.*, *Colpohyllia natans* and *Montastraea cavernosa* was found. Corals species more typical of deeper zonations such as *Madracis decactis* were also observed (Figure 19). Other species found in Group III were also characteristic of deeper environments. This was the case of *Madracis decactis* and *Agaricia* sp. present in higher abundance than in group I.

Finally in group III only species with a higher probability of surviving in areas of high sedimentation were found. This included *Montastraea cavernosa*, *Siderastrea siderea*, *Agaricia agaricites* and *Porites astreoides*, among other sediment resistant species (Figure 20).

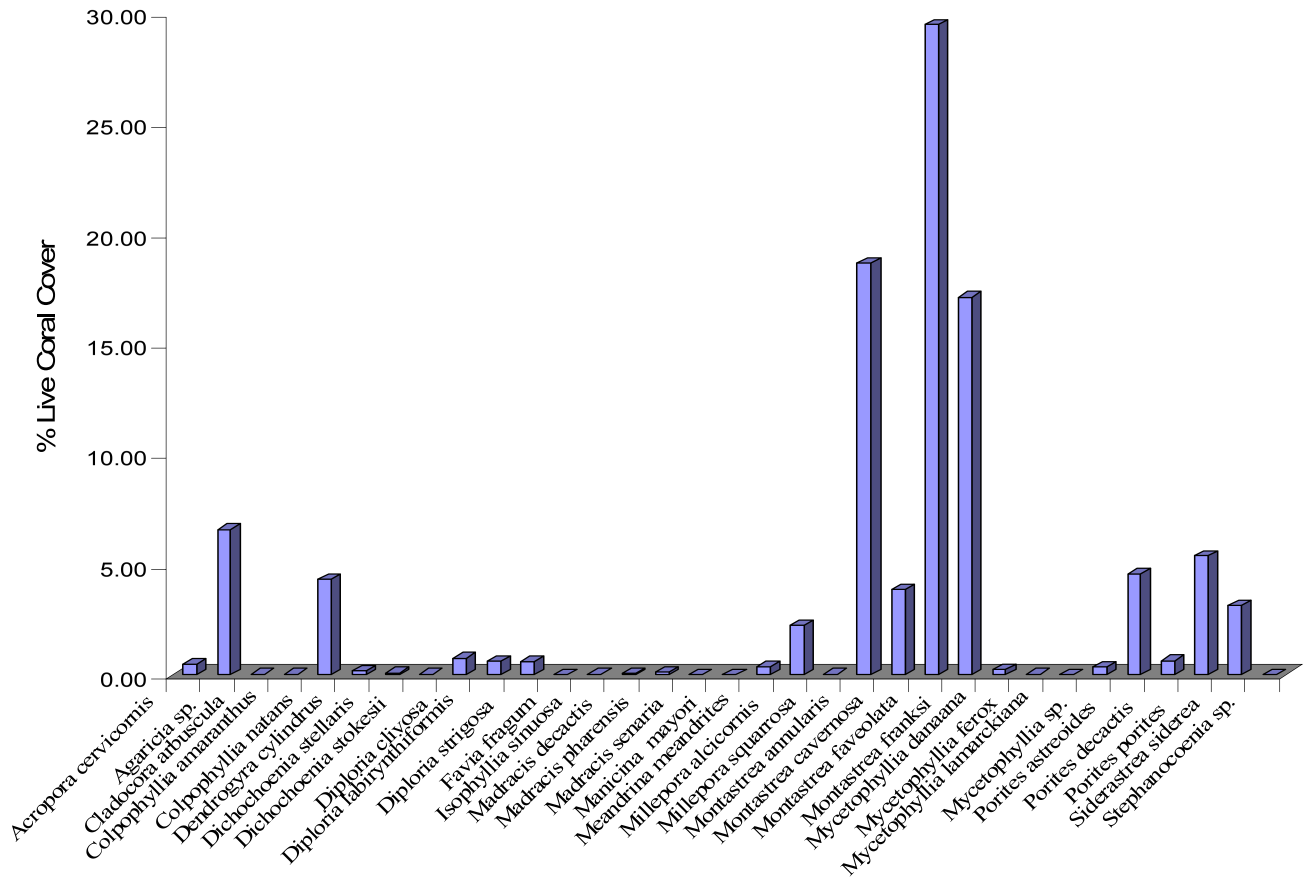


Figure 18. Coral cover species distribution for group I .

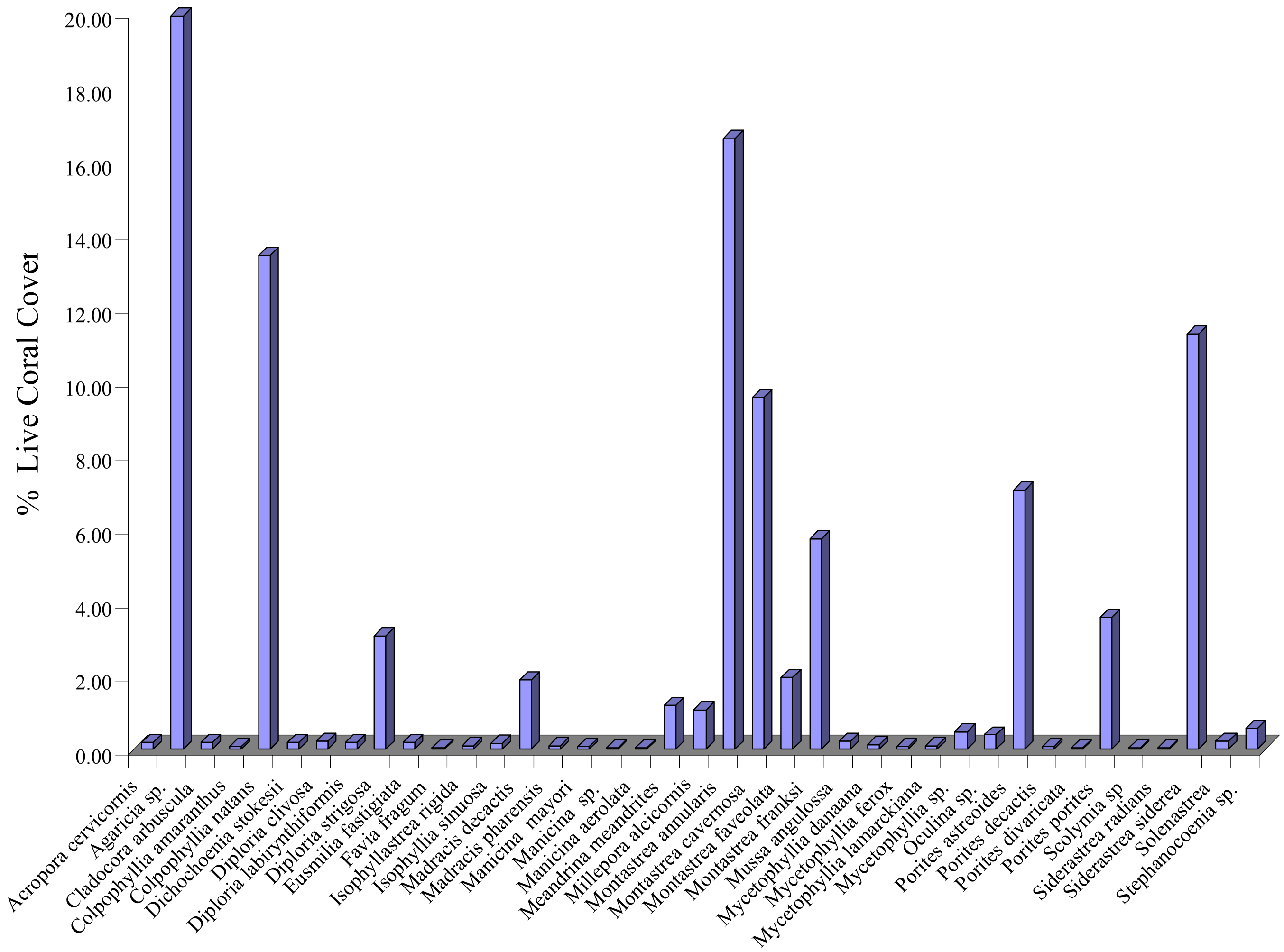


Figure 19. Coral cover species distribution for group II.

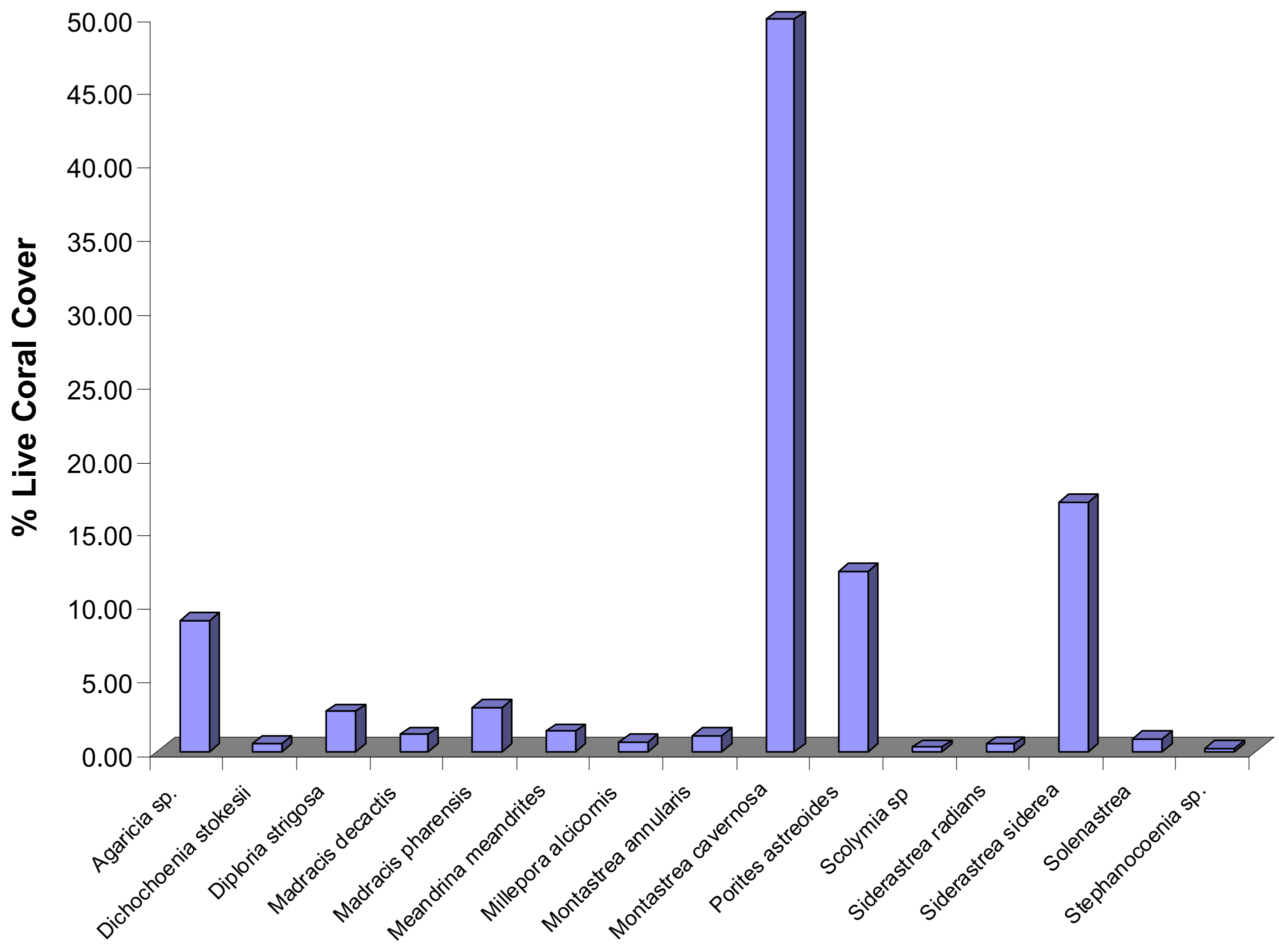


Figure 20. Coral species distribution for group III.

DISCUSSION

Temperature, salinity and chlorophyll fluorescence can be affected by hydrologic aspects such as the seasonal rainfall which affects river discharge, sediment run-off, turbidity, nutrient loads and salinity (Gilbes et al., 1996). As a result, the absorption and backscattering could also show seasonality in their values.

In Puerto Rico, a marine climate is dominant throughout the year. Temperatures tend to decline from October through December, reaching their minimum values between December and March. These values start rising again in April thru May and reach their maximum between August and September (Glynn, 1973). Hydrologically, the highest precipitation prevails from May to November, while the minimum occurs between December and April. The peaks include September and October for the wet season and from February to March for the dry season (Glynn, 1973). Therefore, we observe maximum river discharge from September through November and minimum discharge between February and April (Gilbes et al., 1996; Warne A. G. et al., 2005).

Physical and bio-optical data for the Mayagüez Bay was gathered during October 2005, while all other areas were visited between January and February 2006. Rainfall, indeed affected the Mayagüez Bay (Manchas Interiores and Escollo Rodríguez) area, as predicted by the NOAA weather station one week before October 19, 2005 (date when sampling event occurred). The Weather Station for Puerto Rico had accounted the presence of a long term rainfall event that came from the western Caribbean. Higher runoff from the local rivers affected the sampling area. Riverine sources included the Yagüez, Guanajibo and Añasco Rivers (Glynn, 1973; Gilbes et al. 1996).

Another important aspect taken into account was the September - October 2005 high sea surface temperature event after which a major coral bleaching episode was registered (García-Sais, 2006; NOAA, 2005). Even though maximum temperatures normally occur between August and September, such an event represents an extension to what the affected ecosystems could tolerate (Sammarco et al., 2006; Brown, 1997; Lesser, 2004). High temperature, chlorophyll fluorescence and absorption and the low salinity for the Mayagüez Bay could then be explained as a combination of the previously mentioned factors and events. Since the water physical parameters at this site were only measured once, these data are not necessarily representative of the average conditions for the Mayagüez Bay area.

Mayagüez Bay data, presented the highest temperatures for all the sites visited (Figure 5). Every other station varied between 26.0 and 27.0 C°. Salinity averaged between 35.0 and 35.75 (PS) except for Mayagüez were values ranged between 34.4 and 35.3 (PS) (Figure 6). This could be influenced by the rainfall event and the adjacent riverine inputs. Salinity gradients toward the bottom of the stations, suggest the effect of freshwater influence in the area.

The highest values for chlorophyll fluorescence were also recorded at Mayagüez Bay, followed by Cardona (Figure 7). In Ponce, Cardona was probably the most affected station of the three visited. Natural factors included hydrographic influences, sediment plumes and currents (Acevedo et al. 1989). In addition, anthropogenic influence was also evident at Ponce Bay, since dredging operations were active at that time.

Absorption was highest in Escollo Rodríguez, Mayagüez followed by Cardona, Boya Verde and Manchas Interiores (Figure 8). In Mayagüez Bay, absorption could be divided into several components including the absorption by detritus, phytoplankton and organic matter (Gilbes et al., 1996). Absorption by detritus plays an important role in the total absorption coefficient for the Mayagüez Bay (Armstrong et al., 2001).

Low precipitation occurs in Guayanilla and Ponce where a semi-arid climate prevails (Glynn, 1973). However, both areas are influenced by natural and anthropogenic hydrographic sources including the Guayanilla, Yauco and Tallaboa rivers for the Guayanilla area; and the Matildes and Portugués rivers for the Ponce area (Acevedo et al., 1989). Additionally, ship traffic is common at both areas, while in Ponce westward sediment plumes are very influential (Acevedo et al., 1989). Therefore, in Cardona and Boya Verde, high colored dissolved organic matter, sediment resuspention and input that results from current hydrographic sources and the high commercial traffic explain the high water column absorption, which results in diminished water transparency.

In La Parguera, near optimal water quality conditions for reef development exist due to the absence of river runoff and therefore, sediment and nutrients loading. This area's well developed mangrove fringe serves as an efficient natural sediment trap that protects the adjacent reef sites from terrestrial input. The mean annual precipitation rate for La Parguera is the lowest of all the areas studied, and when combined with a high evaporation rate (Almy and Carrión, 1963; Glynn, 1973; Warne et. al., 2005), results in a stable hydrographic regime.

Backscattering was highest for Rodríguez, Boya Verde and Cardona. This is consistent with the physical and hydrographic data since these are the stations where the most sediment suspension and particulate will be expected to occur (Figure 9 and 13). Results for the beam attenuation coefficient resembled both the absorption and the backscattering results (Figure 8-10). Variation of these water properties became more evident after the study sites were divided into three optical groups (Table 10).

The vertical attenuation coefficient or K_d was considered a good water optics descriptor to use since it is largely determined by the inherent optical properties of the aquatic medium, while not being excessively altered by changes in the radiation field (Kirk, 1994; D'elia et al. 1991, Cooper et al. 2007). Therefore, K_d would be expected to remain the same as long as the composition of the water remains constant. In the tropics, neither seasonality nor water column stratification represent a major source of variability, therefore, it is of ultimate importance to conduct this kind of research (Delia et al., 1991; Ryther, 1956; Hawkins and Griffith, 1986). The range of K_d values obtained was within those presented by Yentsch (2002) for Florida's coastal waters.

La Parguera included a gradient between clear offshore and intermediate turbid coastal waters. Guayanilla and Ponce presented the most turbid waters, while Mayagüez Bay resembled to some degree the conditions found at La Parguera (Table 2, Figure 13).

The most important bio-optical relationship established by this research is summarized in Figure 11 (Table 3). Here, a negative exponential relationship was found between K_d and the percent coral cover for the visited stations. A similar relationship was found by Tomascik (1993) in the Java Sea and Yentsch (2002) and Zaneveld in Florida; in addition to Cooper (2007) and Fabricius (2004 and 2005) in the Great Barrier Reef . Based on this non-linear regression, the visited sites were redistributed into three clusters, based on K_d values and optical depth. The K_d values presented for each section represent the average value for each particular group. For instance, once the K_d values reach 0.159 (the first red line in figure 11) there is a drastic drop in percent coral cover. A second drop in coral cover occurs once K_d values surpass the 0.22 value (second red line in figure 11). This grouping of K_d values, which takes into consideration temporal variability, is important since these are dynamic and not static systems. Therefore, K_d values could also be seen as descriptors of a potential dynamic process of transition. Monitoring K_d values could then offer a predictive tool for the assessment of potential transitional processes. K_d studies can be seen as transparency studies to the infinitesimal level (Yentsch et al, 2002; Cooper et al. 2007; Fabricius, 2005; Fabricius, 2004; Fabricius et al. 2005). However, detection of such small changes in transparency require especialized equipment and measurements that should not be dependant upononly one K_d measurement, but on the constant integration of temporal K_d values. This will allow for the elimination of potential temporal variability. The collocation of permanent probes also allows for the elimination of the upper column variability (Yentsch et al., 2002).

An inverse regression between K_d and distance from shore was observed, although not very strong (Figure 12, Table 3). This tendency has also been observed by Cooper (2007) and Fabricius (2004 and 2005). The subtle nature of this relation probably responds to the coastal nature of all the sampled stations. A stronger relation will be expected when different water types and areas are included and compared. Therefore, attention should be given when classifying them, since approximately 9 categories exist according to their signature composition (Jerlov, 1951). Following Morel and Prieur (1977) our study areas could be summarized into Case-2 waters. This type of waters include in their composition the influence of resuspended sediments, terrigenous particulates, dissolved organic matter, anthropogenic influx, associated debris and living algal cells. In order to visualize this relation a ratio of the percent coral cover to the K_d

was developed and adapted to a GIS image, in order to visualize how the ratio varied with distance from shore. Something similar can be seen with the relation between distance from shore and percent coral cover (Figure 12).

An increase in live coral cover as distance from shore increases was found (Table 4, Figure 17). This relates as well to the expected behavior with the diversity and rugosity indexes. Both were expected to increase with an increase in coral cover and in distance from shore. Therefore, in both cases a weak inverse relationship found. This agrees with the results from deep coral reef habitats, where mostly areas of low relief were encountered (Armstrong et al., 2006; Cooper et al. 2007), since corals will acquire the most perpendicular projection in order to optimize the low incident radiation available.

Other important relationships were those between site distance and the optical depth, where as the distance from shore increased, the euphotic zone and especially the lower limit where only 1% of the downward irradiance reaches, increased as well. Therefore, the optical depth increased with distance since light was able to penetrate deeper into the bottom. The R^2 for both optical depth was approximately 0.94, reinforcing the importance of the euphotic zonation on the adaptation, vulnerability, health and depths shifts of coral communities and individual species (Fabricius, 2004 and 2005; Cooper et al. 2007).

Diseased coral cover was also positively related to optical depth, meaning that disease abundance increased as the light was more available to these communities. The intricate relationship between light and coral diseases has been presented by Bruckner (1999) and Lesser (2004).

Similarily to how vertical attenuation coefficients (K_d) diminished with distance from shore, the amount of uncolonized substrate, sponge cover and octocorals diminished as well (Figure 14-16, Table 11). This was expected since these parameters tend to increase with a decrease in water quality and an increase in the water column suspended particles, phytoplankton and organic matter, among others. Therefore, an increase in the scenario become beneficial for the proliferation of sponges, filter feeders, octocorals and filamentous algae, among others (Fabricius et al. 2005). In this study, only a qualitative trend could be established with filamentous algae, due to the limited capabilities of our experimetal design. This also affected the identification of macroalgae.

However, the relationship with the macroalgae that could be identified was an inverse one. This was expected due to the fact that most of it was coraline algae (*Halimeda* sp.) which benefits from similar conditions as those required by corals. However, in the cases of Rhodophyta and non calcareous Chlorophyta the relation has been directly related (Fabricius et al. 2005).

Relationships between percent coral cover, optical depth and K_d values were critical when clustering sites into three groups (Table 5). Some of the expected relationships were not found when all the sites were considered. However, grouping the sites served to strengthen relationships that otherwise were not found or weak (Table 12-13). Examples included the relationships between rugosity and diversity indices to Kd. Certain reef parameters and even bio-optical data trends were more apparent when treated through this approach. A similar approach was described by Mumby et al. (1999) when he suggested clustering areas by the classification of field data.

Four coral genera were common to all three groups (Table 9), particularly *Montastraea*, the most widespread genus. This probably explains the lower richness for Group I, regardless of their lower K_d values. Group I, comprised the best developed reefs with the highest coral cover and the farthest distance from shore, while having the deepest euphotic zone and the lowest percent of sponges and octocorals. It also included the least amount of uncolonized substrate and the largest percent of diseased colonies. The presence of *M. faveolata*, *M. annularis* and *M. franksi* as well as *M. cavernosa,* but at a lower abundance, serve as an indicator of Group's I highest water transparency (Table 11, Figure 18). Group II was as a transitional group mostly characterized by intermediate values of the above mentioned parameters and by a species shift to deeper reef zones (Figure 19). This coral community was more adversely affected than Group I, but differences between parameters were not obvious in most cases (Figure 19; Tables 10 and 11). Closer to Group I, in terms of similarities, their state was not as irreversible as that seen in Group III. Group III represented the most affected coral areas visited (Figure 20). Low coral cover, richness, rugosity and diversity were observed (Table 11). The most abundant species was *M. cavernosa* (Figure 20). A general consensus of the poor state of these coral communities was reached. Although water temperature was the highest for Group III, this was not considered significant due to the data association with the October 2005 climatological event. However, other parameters such as high absorption, backscattering, and beam attenuation coefficients supported the trends as well (Table 10 - 11).

It is interesting to note that the largest amount of coral species were present in Group II, giving it the highest richness. The other two groups were the extremes. Group I presented lesser number of species, for the sampled areas, but it should be mentioned that the cover was dominant for species such as the *Montastraea annularis* (complex). Therefore, the general impression was that this group had a more even or homogeneous cover, resulting in less richness as well. However, this is probably not the case and it can be seen that diversity was still the highest for Group I. Group III on the other hand, had the least richness and diversity and the highest evenness. Only a few sparse and resistent species were found in these areas, mostly scattered in between sponges, octocorals and even large patches of sediments and uncolonized substrate (Table 11). This group however, had the highest chlorophyll fluorescence, absorption, backscattering and beam attenuation coefficient as would be expected of areas with high turbidity stress (Table 11). Similar results to those achived by our three group division have been achieved by Fabricius (2004) and Fabricius et al. (2005).

Negative relationships between K_d and diseased corals were consistent throughout this study and percentages of diseased colonies were highest within group I (Table 5). Diseased colonies decreased within group II and reached the lowest level in Group III (Table 10). Contrary to general thought, diseases and conditions such as coral bleaching have been demonstrated to amplify detrimental effects in areas of increased light penetration. The work of Bruckner (1999) in Puerto Rico demonstrated that black-band disease decreased its rate of infection as turbidity increased. In the Bahamas, drastic temperatures elevations resulted in exacerbated detrimental effects due to the synergistic role of solar radiation (Lesser, 2004). This could also be the case of low K_d (high water transparency). In cases where thermal stress was considered, a synergistic effect with photoinhibition resulted for coral colonies under the highest water transparency.

It would be interesting to consider this effect in the October 2005 high sea surface temperature and the associated bleaching post-event that resulted in significant coral cover decrease for many well known clear water *Montastraea* spp. communities such as the ones in Mona Island, Isla Desecheo and other shelf edge reef sites (García-Sais et al., 2006).

However, the aforementioned response is not necessarily the case for all diseases scenarios. Other studies have demonstrated the relationship between anthropogenic stressors and turbidity with the compromise of coral species' immunologic systems (Bruckner, 2002). Therefore, the determination for a primary stressor still remains variable and dependent upon the secondary elements that have an additive effect before, during and after such events.

In this study, coastal coral communities with intermediate to low light penetration values could be compromised by a secondary factor, such as sediment runoff and resuspension, pollution, etc. It will be interesting to compare the impacts of coral bleaching events, such as the 2005 episode, in areas with a wide range of K_d values, to oceanic coral reef communities, for which pre and post event data exists. The high, persistent water temperatures of 2005 in the northeastern Caribbean caused widespread coral bleaching, which was followed by coral mortality due to diseases (Jeffrey et al. 2005; Whelan et al. 2007).

We do not imply that coral communities under more turbid environments will be better protected under these circunstances, but that other compromising factors could arise in these ares, since anthropogenic and natural stressors tend to have a negative effect on these communities. Acevedo et al. (1989) described species shifts for

Guayanilla and Ponce Bays. Coral zonation shifts, such as in Group III, are important not only with respect to the specific species that are relocated to a new depth, but also due to the complexity of interactions that may result from the shift. Complex relations between the coral species present and other possible biotic and abiotic factors may influence the success of a species to maintain or re-colonize an area. Some examples include: sediment plumes, wave action, erosion, algal mats, diseases and the capability of eliminating sediment. Greater abundance of filamentous algae, sponges or octocoral, could be observed as well.

The observed trends in our study can help us establish similarities between the different reef sites not only in terms of live coral cover, but in terms of all secondary biotic and abiotic aspects that constitute a functional coral reef. Some similar situations have been already observed in Hawaii and Costa Rica as discussed by Cortés and Risk (1985) where they experienced a species shift due to the sediment stress at shallow depths.

Secondary species could directly influence an area through their presence or absence. This could be the case of fish or invertebrate species which could leave an area only when the conditions have reached a chronic or irreversible status. Invertebrates in our study (although at a minimal scale) were observed to decrease from Group I to Group III (Table 11). Some other studies as those from Cooper et al. (2007) and Fabricius et al.(2005) have encountered relation with fish assemblages in the area.

Traditionally, when the need arises to assess the status of coral reef ecosystems they are usually categorized by depth and/or location. However, these results show that even though different reef sites might be located in the same general area, their specific condition might relate them better to more distant reefs, particularly when dealing with water turbidity (Mumby et al., 1998).

Therefore, K_d and optical depths represent an ecologically relevant descriptor for autotrophic communities that, together with additional physical factors, could explain why sometimes species do not respond to the expected physical depth behavior (Yentsch et al. 2002). This could also mean that species present at a particular depth or light regime could be compromised and therefore, more vulnerable to drastic climatic and/or oceanographic events (Bruckner, 2002). It will then be more difficult for species in such circumstances to survive significant episodes of high temperatures and bleaching. Sammarco et al. (2006) considers that in rising temperature and bleaching events, attention should be given to the coefficient of variation and not as much to the individual rises in temperature, since data shows years of high sea surface temperature where no coral bleaching events, as the one recorded in 2005, have occurred. In Puerto Rico, for example, it is normal to observe maximum temperatures between the months of August and September. However, it is not normal for those periods to intensify and extend, since this will probably prevent ecosystems from reestablishing their balance.

CONCLUSIONS

Through this research an inverse and exponential relationship between the vertical attenuation coefficient (K_d) and the percent living coral cover for the sampled areas of La Parguera, Guayanilla, Ponce and Mayagüez Bays was established. A more subtle negative relationship exists between the sites distance from shore and the corresponding K_d values. This could be influenced by the coastal water classification that limited our site selection criteria. A positive regression described the relationship between percent coral cover and the optical depth for both 10% and 1% of the downward irradiance subsurface values. Therefore, three categories were used, based on their optical depth, to describe the study areas.

Some of the expected relationships with K_d could not be well established through the individual sites analysis. However, reconsideration of those analyses after dividing sites into optical groups resulted in the strengthening of weak or non perceptible relations. This was the case for the rugosity and diversity indices which resulted in stronger negative relationships after such reconsideration.

Secondary biological parameters such as percent cover of octocorals, sponges, algae, invertebrates and uncolonized substrate also supported the existence of these relationships. Diseased coral cover was also found to vary inversely with K_d values. Bio-optical parameters such as chlorophyll fluorescence and inherent optical properties were responsible for the observed K_d values. However, seasonal variability in temperature and salinity were not significant factors in determining the variability of the attenuation coefficients.

These results could be useful for understanding, managing, and assessing coral reef recovery programs and for the development of indicators and models that do not require extensive field work for their implementation. Future work could involve developing a predictive model relating the percent coral cover to K_d and optical depth using satellite imagery.

LITERATURE CITED

Acevedo, R., J. Morelock and R. A. Olivieri. 1989. Modification of coral reef zonation by terrigenous sediment stress. Palaios. 4(1): 92-100.

Almy, C. C. and C. Carrión-Torres. 1963. Shallow water stony corals of Puerto Rico. Caribbean Journal of Science. 3: 133-162.

Armstrong, R. A., J. García and F. Gilbes. 2001. Baseline characterization of bio-optical oceanographic properties and their relation to the diversity and health of coral reef communities. Final Data Report (DNER).

Armstrong, R. A., H. Singh, J. Torres, R. S. Nemeth, A. Can, C. Roman, R. Eustice, L. Riggs and G. García-Moliner. 2006. Characterizing the deep insular shelf coral reef habitat of the Hind Bank marine conservation district (US Virgin Islands) using the Seabed autonomous underwater vehicle. Continental Shelf Research. Vol 26. Pages: 194-205.

Baker, K.S. and R.C. Smith. 1980. Quasi-inherent characteristics of the diffuse attenuation coefficient for irradiance. Proc Soc Photo-Opt Instrum Eng, Ocean OpticsVI 208:60-63.

Bell, P.R.F. 1992. Eutrophication and coral reefs: some examples in the Great Barrier Reef Lagoon. Water Research 26(5): 553-568.

Bell, P.R.F. and T. Tomascik. 1993. The demise of the fringing coral reefs of Barbados and of regions in the Great Barrier Reef Lagoon: impacts of eutrophication. In Ginsburg,R.N., ed. Global Aspects of Coral Reefs (University of Miami Rosenstiel School of Marine and Atmospheric Sciences).304-307

Bohnsack, J.A. 1979. Photographic quantitative sampling of hard-bottom benthic communities. Bulletin of Marine Science. 29(2): 242-252.

Brown, B. E. 1997. Coral bleaching: causes and consequences. Coral Reefs. Vol 16. Suppl: S129-S138.

Bruckner, A.W. and R.J. Bruckner. 1998. Treating coral disease. Coastlines. 8.3:10-11.

Bruckner, A.W. 1999. Black-band disease (BBD) of scleractinian corals: occurrence, impacts and mitigation. Ph.D.Thesis, UMI Dissertation Services, 286 pp.

Bruckner, A. W. 2002. Priority for effective management of coral diseases. NOAA Tech Memorandum. NMFS OPR-22.

Bukata, R.P., J.H. Jerome, J.E. Bruton and S.C. Jain. 1979. Determination of inherent optical properties of Lake Ontario coastal waters. Appl. Opt. 18: 3926-3932.

Caricomp. 1994. Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. Caribbean Coastal Marine Productivity: Data Management Center. Centre for Marine Sciences. U.West Indies. Mona, Kingston, Jamaica and Florida Institute of Oceanography. U. South Florida, USA. 68 p.

Coles, S.L. and L. Ruddy. 1995. Comparison of water quality and reef coral mortality and growth in Southeastern Kane' Ohe Bay, Oahu, Hawaii, 1990 to 1992, with conditions before sewage diversion. Pacific Science. 49(3): 247-265.

Cooper, T.F., S. Uthicke, C. Humphrey and K. Fabricius. 2007. Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Region, central Great Barrier Reef. Estuarine Coastal and Shelf Science. XX: 1-13.

Cortés, J. N. and Risk, M. J. 1985. A reef under siltation stress: Cahuita, Costa Rica: Bulletin of Marine Science. 36: 339-356.

Cowen, R.K., M. Kamazima, M. Lwiza, S. Sponaugle, C.B. Paris and D.B. Olson. 2000. Connectivity of Marine Populations: open or closed? Science. 287:857-859.

D'elia, C., R. Buddemeir and S. Smith (editors). 1991. Workshop on coral bleaching, coral reef ecosystems and global change: Report of Proceedings. Maryland Sea Grant College Publication.

Fabricius, K. E and G. De'ath. 2004. Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications. 14:5. 1448-1465.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin. 50. 125-146.

Fabricius, K. E., G. De'ath, L. McCook, E. Turak, and D. McB. Williams. 2005. Changes in algal, coral, and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin. 51. 384-398.

Falkowski, P.G., P.L. Jokiel, R.A. Kinzie III. 1990. Irradiance and corals. In: Dubinsky (ed). Coral Reefs. Ecosystems of the world, 25. Elsevier Scientific Publishing Co.,Amsterdam, p 89-107.

García-Sais, J. R., R. Castro, J. Sabater Clavell, R. Esteves and M. Carlo. 2006. Monitoring of coral reef communities from Natural Reserves in Puerto Rico,2006:Isla Desecheo, Rincón, Mayaguez Bay, Guanica, Ponce and Isla Caja de Muerto, Final Report(DNER), U. S. Coral Reef National Monitoring Program, NOAA, 146 p.

Gilbes, F., J. M. López and P. M. Yoshioka. 1996. Spatial and temporal variations of phytoplankton chlorophyll a and suspended particulate matter in Mayagüez Bay, Puerto Rico. Journal of Plankton Research. Vol18. No. 1. Pages: 29-43.

Gleason, D.F. and G.M. Wellington. 1993. Ultraviolet radiation and coral bleaching. Nature. 365:836-838.

Glynn, P. W. 1973. Ecology of a Caribbean coral reef – the Porites reef-flat biotope: Part I. Meteorology and hydrography. Mar. Biol. 20:297-318.

Goenaga, C. 1988. The distribution and growth of Montrastrea annularis (Ellis and Solander) in Puerto Rican inshore platform reefs. Ph.D. Thesis, University of Puerto Rico, Mayagüez Campus. 214pp.

Goenaga, C., V.P. Vicente and R.A. Armstrong. 1989. Bleaching induced mortality in reef corals from La Parguera, Puerto Rico: a precursor of change in the community structure of coral reefs? Carib. Jour. Sci. 25(1-2):59-65.

Goreau, T.F. 1959a. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology. 40(1): 67-90.

Goreau, T.F. 1959b. The physiology of skeleton formation in corals. I. A method for Measuring the rate of calcium deposition by corals. Biol. Bull. Mar. Biol. 116: 59-75.

Goreau, T.F., Goreau, N. I. and T. J. Goreau. 1979. Corals and Coral Reefs. Scientific American. 241(2): 124-136.

Gordon, H.R., O.B. Brown and M.M. Jacobs. 1975. Computed relationships between the inherent and apparent optical properties of a flat, homogeneous ocean. Appl. Opt. 14:417-427.

Gordon, H.R. 1989a. Can the Lambert-Beer law be applied to the diffuse attenuation coefficient on ocean water? Limnol. Oceanogr. 34(8):1389-1409.

Gordon, H.R. 1989b. Dependence of the diffuse reflectance of natural waters on the sun angle. Limnol. Oceanogr. 34(8):1484-1489.

Hallock, P. and W. Schlager. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. Palaios. Vol 1: 4. 389-398.

Hawkins, P.R. and D. J. Griffiths. 1986. Light attenuation in a small tropical reservoir (Solomon Dam, North Queensland):seasonal changes and the effects of artificial aeration. Aust. J. Mar. Freshw. Res. 37: 199-208.

Hubbard, J.A.E.B. and Y.P. Pocock. 1972. Sediment rejection by recent scleractinian corals: A key to paleo-environmental reconstruction. Geol. Rundschau 61: 598-626.

Hutchings, P.A. 1986. Biological destruction of coral reefs: A review. Coral Reefs. 4:239-252.

Jeffrey, C. F. G., U. Anlauf, D. Beets, S. Caseau, W. Coles, A. M. Friedlander, S. Herzlieb, H. Starr, M. Kendall, V. Mayor, J. Miller, R. Nemeth, C. Rogers and W. Toller. 2005. The state of coral reef ecosystems of the US Virgin Islands. Interagency Report. http://ccmaserver.nos.noaa.gov/ecosystems/coralreef/coral_report_2005/USVI_Ch4_C.pdf

Jerlov, N. G. 1951. Optical studies of ocean water. Rep. Swedish Deep-See Exped. 3: 1-59.

Kaye, C.A. 1959. Shoreline features and quaternary shoreline changes, Puerto Rico. U.S Geolog. Survey Prof. Paper 3317-B: 49-139.

Kershaw, K.A. 1964. Quantitative and dynamic ecology. Edward Arnold (publishers) Ltd.,London, England. 183pp.

Kirk, J.T.O. 1981. Monte Carlo study of the nature of the underwater light field in, and the relationships between optical properties of, turbid yellow waters. Aust. J. Mar. Freshwater Res. 32:517-532.

Kirk, J.T.O. 1984. Dependence of relationship between inherent and apparent optical properties of water on solar altitude. Limnol. Oceanogr. 29:350-356.

Kirk, J.T.O. 1993. Characteristics of the light field in highly turbid waters: A Monte Carlo study. Limnol. Oceanogr. 39(3): 702-706.

Kirk, J.T.O. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press. 509pp.

Lesser, M. P., C. Mazel, D. A. Phinney, C. S. Yentsch. 2000. Light absorption and utilization by colonies of the congeneric hermatypic coral *Montastraea faveolata* and *Montastraea cavernosa*. Limnol. Oceanogr. 45(1), 76-86.

Lesser M. P. and J. H. Farrell. 2004. Exposure to solar radiation increases damage to both host tissue and algal symbionts of corals during thermal stress. Coral Reefs. Vol 23. Pages: 367-377.

Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. Bull. Mar. Sci. 26(4): 450-466.

Maragos, J.E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. Thesis. University of Hawaii, Honolulu.

Maritorena, S. and N. Guillocheau. 1996. Optical properties of water and spectral light absorption by living and non-living particles and by yellow substances in coral reef waters of French Polynesia. Mar. Ecol. Prog. Ser. 131: 245-255.

Marzaleck, D.S. 1981. Impact of dredging on a subtropical reef community, southeast Florida, U.S.A. Proc. 4th International Coral Reef Symp. Manila. 1: 147-153.

McWilliams, P. J., I. M. Côte, A. J. Gill, W. J. Sutherland and A. R. Watkinson. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology. 8(8): 2055-2060.

Morel, A. and L. Prieur. 1977. Analysis of variations in ocean color. Limnol. Oceanogr. 22: 709-722.

Morelock, J., N. Schneidermann and W. R. Bryant. 1977. Shelf reefs, southwestern Puerto Rico. Reefs and related carbonates ecology and sedimentology. Stud. Geol., 4: 17-25.

Morelock, J., K. Grove and M. L. Hernández. 1983. Oceanography and Patterns of Shelf Sediments Mayagüez, Puerto Rico. Journal of Sedimentary Petrology. 53(2): 0371-0381.

Morelock, J., J. E. Winget, and C. Goenaga. 1994. Marine geology of the Parguera-Guánica quadrangles, Puerto Rico. USGS Misc. Map Series, U.S. Geological Survey, Washington D. C.

Morelock, J., W. Ramírez, A. W. Bruckner and M. Carlo. 2001. Status of coral reefs, Southwest Puerto Rico. Caribbean Journal of Science. Special Publication No.4.

Mumby, P. J., E. P. Green, C.D. Clark and A. J. Edwards. 1998. Digital analysis of multispectral airborne imagery of coral reefs. Coral Reefs. 17(1): 59-69.

Mumby, Peter J. and. Alastair R. Harborne 1999. Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. Biological Conservation. Vol 2:88. Pages 155-163.

Mumby, Peter J. 2001. A bird's eye view of the health of coral reefs. Nature. 413: 36.

Mumby, Peter J., J. R. M. Chisholm, C.D. Clark and J. J. Hedley. 2004. The cover of living and dead corals from airborne remote sensing. Coral Reefs. 23: 171-183.

Muscatine, L. and J.W.J. Porter. 1977. Coral reefs: mutualistic symbiosis adapted to nutrient-poor environments. Bioscience. 27:454-459.

NOAA, 2005. Major coral bleaching event expands across Caribbean, severe in Puerto Rico and the U. S. Virgin Islands. www.noaanews.noaa.gov/stories 2005/s2526.htm

Peters, E.C. 1993. Diseases of other invertebrate phyla: Porifera, Cnidaria, Ctenophora, Annelida, Echinodermata. In: J.A. Couch and J.W. Fournie (Eds.), Pathology of Marine and Estuarine Organisms, CRC Press, Inc. Boca Ratón, FL, 388-444.

Platt, T. 1986. Primary production of the ocean water column as a function of surface light intensity algorithms for remote sensing. Deep Sea Res. 33: 149-163.

Pegau Scott W., D. Gray, J.Ronald and V. Zaneveld. 1997. Absorption and attenuation of visible light in water: dependence on temperature and salinity. Applied Optics. Vol. 36. No. 24. 6035-6046.

Porter, J.W. and O.W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. Amer. Zool. 23:625-640.

Preisendorfer, R.W. 1961. Application of radiative transfer theory to light measurements in the sea. IUGG Monogr. 10. p. 11-29.

Prieur, L. 1976. Transfer radiatif dans les eaux de mer. Application a la determination de parametres optiques caracterisant leur teneur en substances dissoutes et leur contenu en particules. D.S. Thesis. Univ. Pierre et Marie Curie.

Ramírez-Mella, J., and J.R. García. 1997. Taxonomic structure and abundance of larval fishes across a neritic-oceanic gradient off La Parguera, Puerto Rico. Proc. 50th Gulf and Caribbean Fisheries Management Symposium, Merida, Mexico.

Reaka-Kudla, M.L., D.S. O'Connell, J.D. Regan and R.I. Wickland. 1993. Effects of temperature and UV-B on different components of coral reef communities from the Bahamas. In Ginsburg, R. N., ed. Global Aspects of Coral Reefs (University of Miami Rosenstiel School of Marine and Atmospheric Sciences).

Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. Science. 278:1454-1457.

Ryther, J.H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnology and Oceanography. 1: 61-70.

Sammarco W. P., A. Winter and J. C. Stewart. 2006. Coefficient of variation of sea surface temperature (SST) as an indicator of coral bleaching Marine Biology. Volume 49. Number 6. Pages 1337-1344.

Scheffer, M. 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia. 200-201:475-486.

Schwarz, A.M. and I. Hawes. 1997. Effects of changing water clarity on characean biomass and species composition in a large oligotrophic lake. Aquatic Botany. 56: 169-181.

Smith, R.C. and K.S. Baker. 1981. Optical properties of the clearest natural waters (200-800nm). Appl. Optics 20(2):177-184.

Stoddart, D.R. and R.E. Johannes. 1981. (Eds) Coral reefs, research methods. Monograph on oceanographic methodology. UNESCO. Paris.

Suhasorno. 1990. Ecological and physiological implication of coral bleaching at Pari IslandThousand Islands, Indonesia. Ph.D. Thesis. University of Newcastle upon Tyne. 279pp.

Szmant-Froelich, A. 1973. The zonation and ecology of the Jobos Bay coral reefs. In : Aguirre Power Project Environmental Studies 1972 Annual Report. P. R. N.C. 162:174-224.

Tanner, C. C., Clayton, J. S. and R. D. S. Wells. 1993. Effects of suspended solids on the establishment and growth of Egeria densa. Aquatic Botany. 45:299-310.

Tomascik, T. and F. Sander. 1985. Effects of eutrophication on reef building corals. I. Growth rate of the reef building coral *Montastraea annularis*. Mar Biol. 87: 143-155.

Tomascik, T. and F. Sander. 1987. Effects of eutrophication on reef building corals. II. Structrure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Mar Biol. 94: 3-75.

Tomascik, T., Suhasorno and A. Mah. 1993. Case Histories: A historical perspective of the natural and anthropogenic impacts in the Indonesian Archipielago with a focus on the Kepulauan Seribu, Java Sea. In Ginsburg, R. N., ed. Global Aspects of Coral Reefs (University of Miami Rosenstiel School of Marine and Atmospheric Sciences, J26-32).

Torres, J.L. 1998. Effects of sediment influx on the growth rates of *Montastraea annularis* (Ellis and Solander)in southwest, Puerto Rico. M.S. Thesis. University of Puerto Rico, Mayagüez Campus. 133p.

Torres, J. L. and J. Morelock. 1999. Coral cover reduction as a result of high sediment stress in Puerto Rico . Coastal Zone ’99. pp 672-673.

Torres, J. L. and J. Morelock. 2002. Effect of Terrigenous Sediment Influx on Coral Cover and Linear Extension Rates of Three Caribbean Massive Coral Species. Caribbean Journal of Science. Vol 38:3-4. 222-229.

Van Den Hoek, C., A.M. Breeman, R.P.M. Bak and G. Van Buurt. 1978. The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. Aquatic Botany. 5: 1-46.

Verstappen, H.T. 1953. Djakarta Bay, a geomorphological study on shoreline development, Ph.D. Thesis. Utrecht, 101pp.

Verwey, J. 1931. Coral reef studies. II. The depth of coral reefs in relation to their oxygen consumption and the penetration of light in the water. Treubia 13(2): 169-198.

Vicente, V.P. 1993. Structural changes and vulnerability of a coral reef (Cayo Enrique) in La Parguera, Puerto Rico. In Ginsburg, R. N., ed. Global Aspects of Coral Reefs (University of Miami Rosenstiel School of Marine and Atmospheric Sciences).

Warne, G. A. , R. M. Webb and M. C. Larsen. 2005. Water, sediment, and nutrient discharge characteristics of rivers in Puerto Rico, and their potential influence on coral reefs. U.S.G.S. Scientific Investigations Report 2005-5206. 58pp.

Weinberg, S. 1978. The minimal area problem in invertebrate communities of Mediterranean rocky susbstrata. Marine Biology. Vol 49: 1. 33-40.

Weinberg, S. 1981. Acomparison of coral reef survey methods. Bijdragen tot de Dierkunde. 51(2): 199-218.

Whelan, K. R. T., J. Miller, O. Sánchez and M. Patterson. 2007. Impact of the 2005 coral bleaching event on *Porites porites* and *Colpophyllia natans* at Tektite Reef, US Virgin Islands. Coral Reef. Vol 26. Num. 3. 689-693.

Williams, E. H., Goenaga, C., V. P. Vicente. 1987. Mass bleachings on Atlantic coral reefs. Science. 238: 877-878.

Williams, Jr., E. H. and L. B. Williams. 1988. Caribbean marine mass mortalities. Oceanus 30: 69-75.

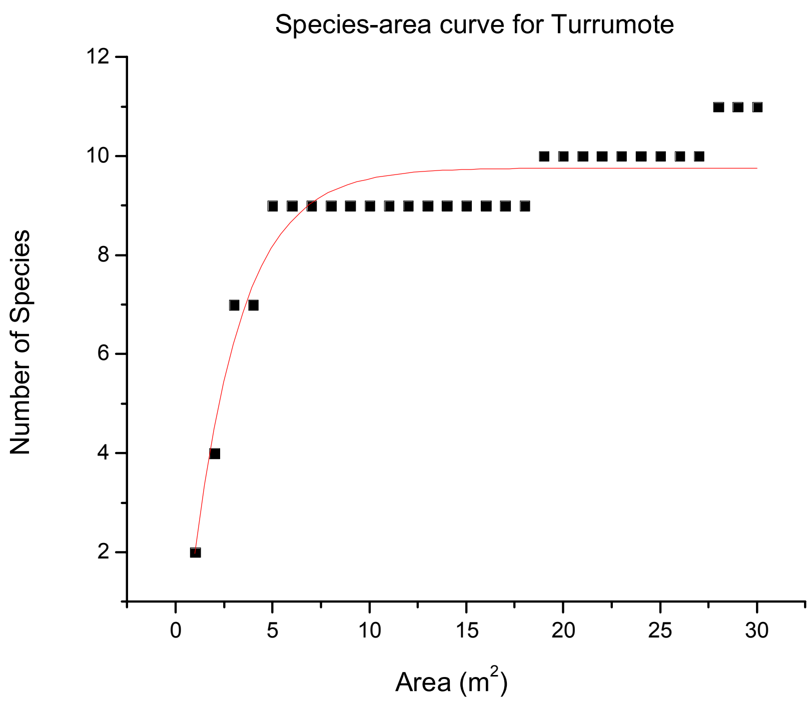
Williams, E. H., Jr. and L. Bunkley-Williams. 1990. The worldwide coral reef bleaching cycle and related sources of coral mortality. Atoll Research Bulletin. No. 335. pp 73.

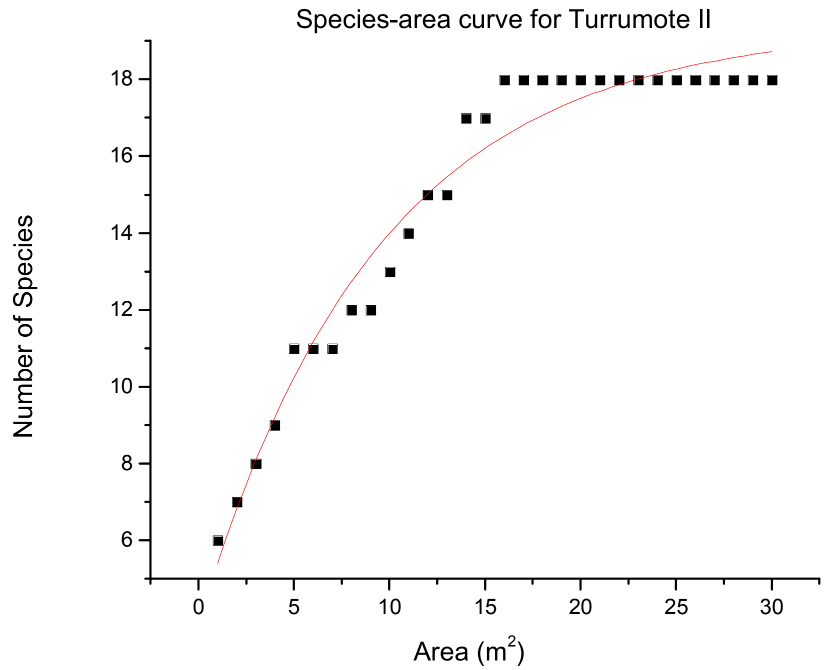
Yentsch, C. S., C.M. Yentsch, J. J. Cullen, B. Lapointe and D. A. Phinney, S. W.

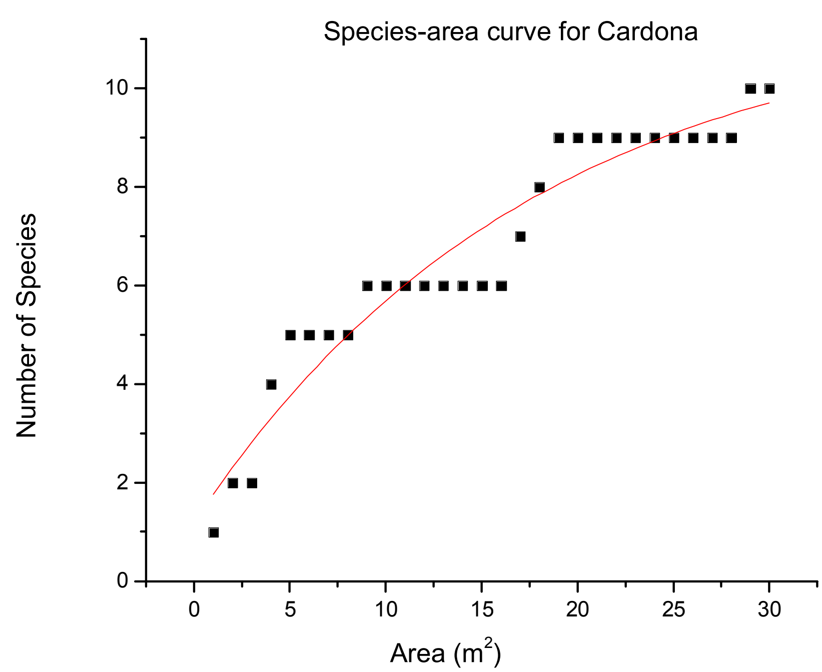
Yentsch. 2002. Sunlight and water transparency: cornerstones in coral research. Journal of Marine Biology and Ecology. 268:171-183.

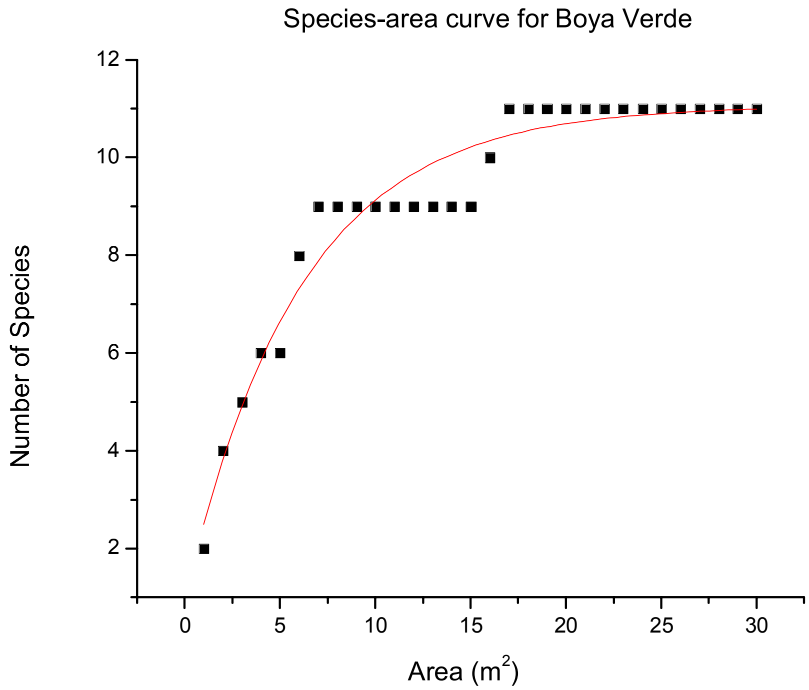
APPENDIX A

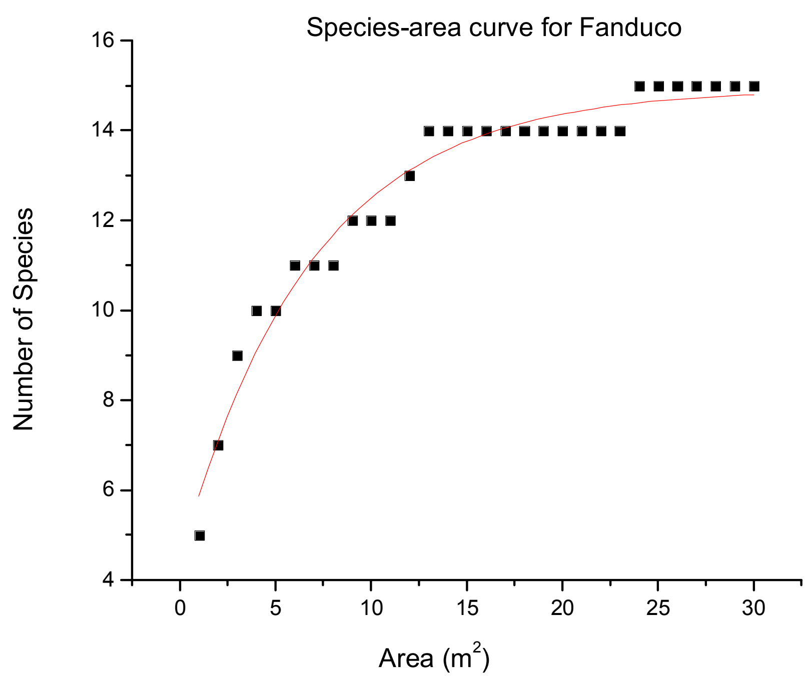
Species-Area Curves for 19 study sites

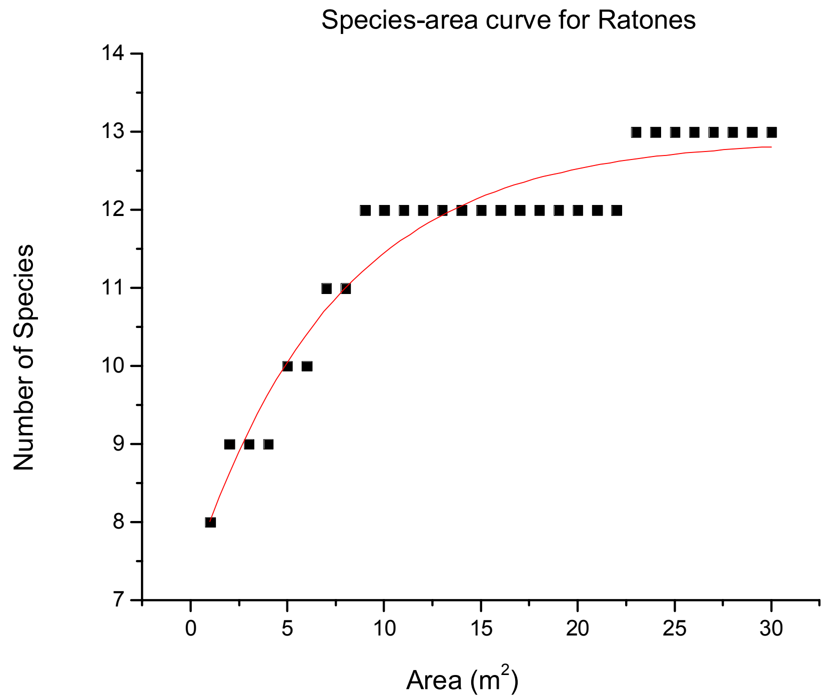


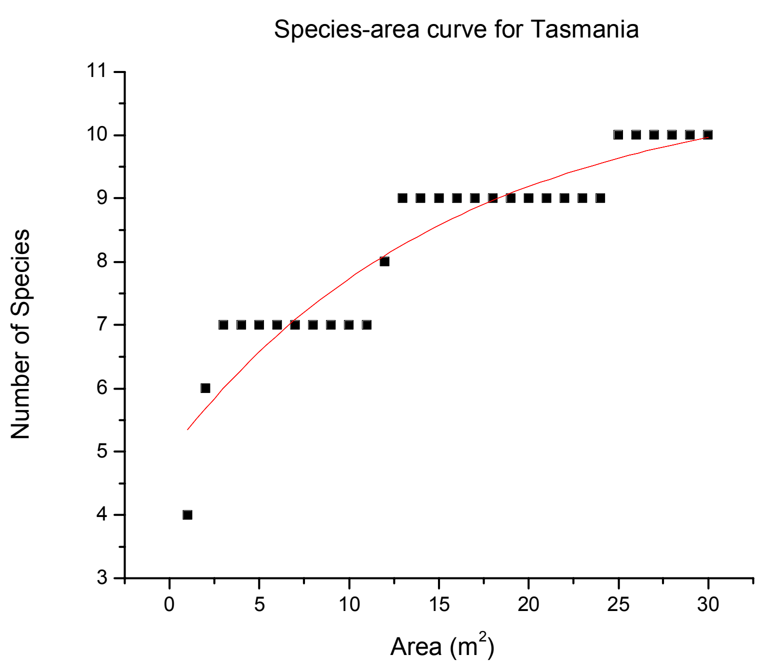

Species-area curve for Turrumote II
Number of Species
6
8
10
12
14
16
18
0
5
10
15
20
25
30
Area (m2)

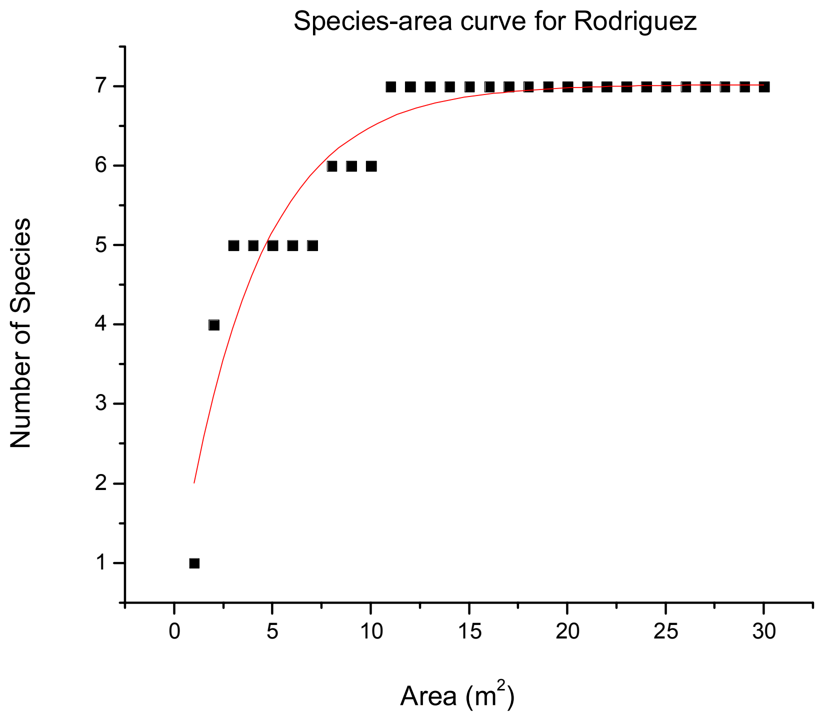

Species-area curve for Cardona
Number of Species
0
2
4
6
8
10
0
5
10
15
20
25
30
Area (m2)


Species-area curve for Boya Verde
Number of Species
Area (m2)
12
10
8
6
4
2
0
5
10
15
20
25
30


Species-area curve for Fanduco
Number of Species
Area (m2)
16
14
12
10
8
6
4
0
5
10
15
20
25
30


Species-area curve for Ratones
Number of Species
Area (m²)
14
13
12
11
10
9
8
7
0
5
10
15
20
25
30


Species-area curve for Tasmania
Number of Species
Area (m²)
11
10
9
8
7
6
5
4
3
0
5
10
15
20
25
30


Species-area curve for Rodriguez
Number of Species
Area (m²)
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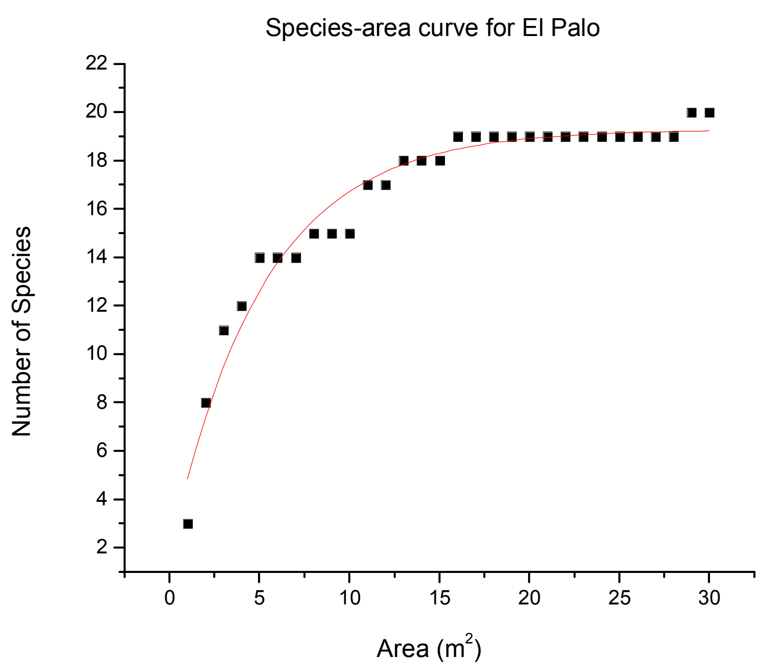
2
3
4
5
6
7
0
5
10
15
20
25
30


Species-area curve for El Palo
Number of Species
Area (m²)
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4
6
8
10
12
14
16
18
20
22
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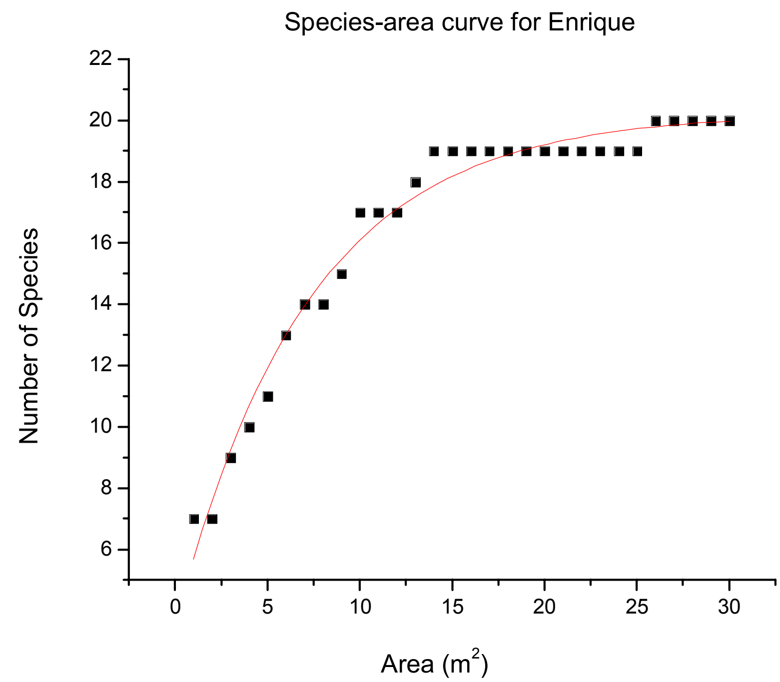
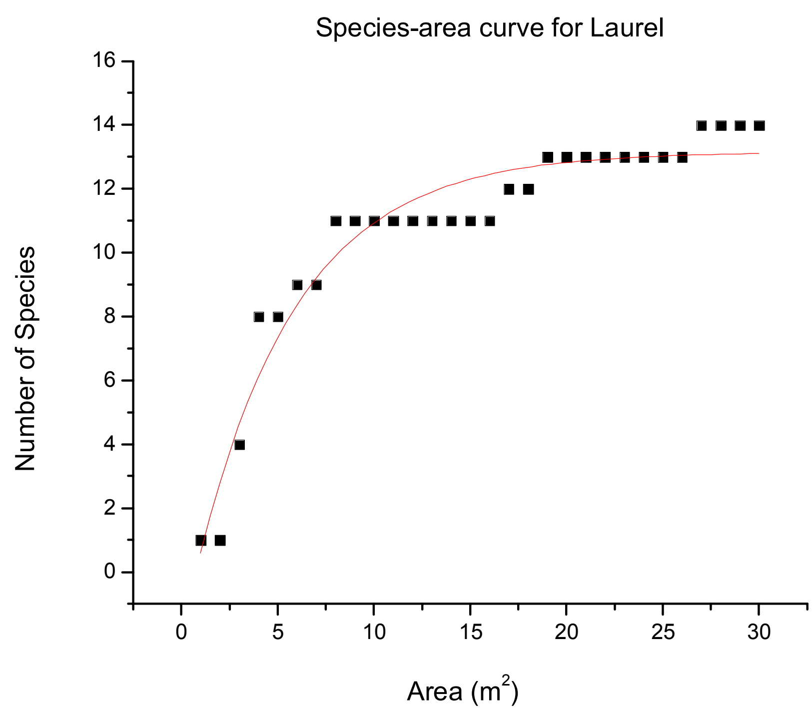
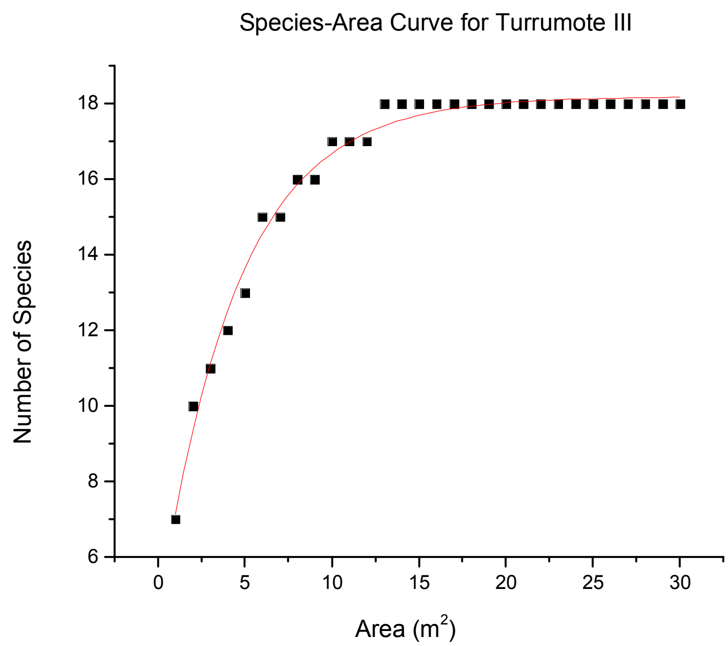
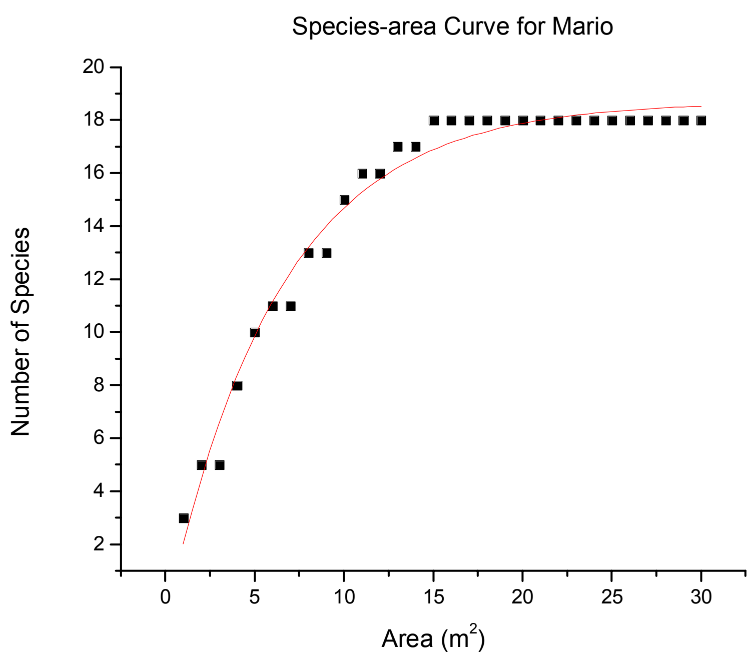
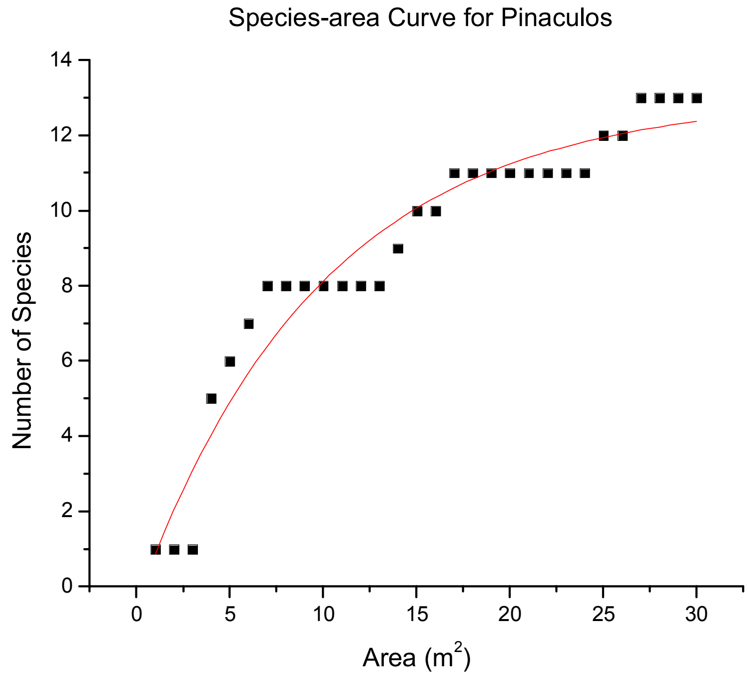
10
15
20
25
30


Species-area curve for Enrique
Number of Species
Area (m2)
22
20
18
16
14
12
10
8
6
0
5
10
15
20
25
30


Species-area curve for Laurel
Number of Species
Area (m2)
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30


Species-Area Curve for Turrumote III
Number of Species
Area (m2)
18
16
14
12
10
8
6
0
5
10
15
20
25
30


Species-area Curve for Mario
Number of Species
Area (m2)
20
18
16
14
12
10
8
6
4
2
0
5
10
15
20
25
30


Species-area Curve for Pinaculos
Number of Species
Area (m²)
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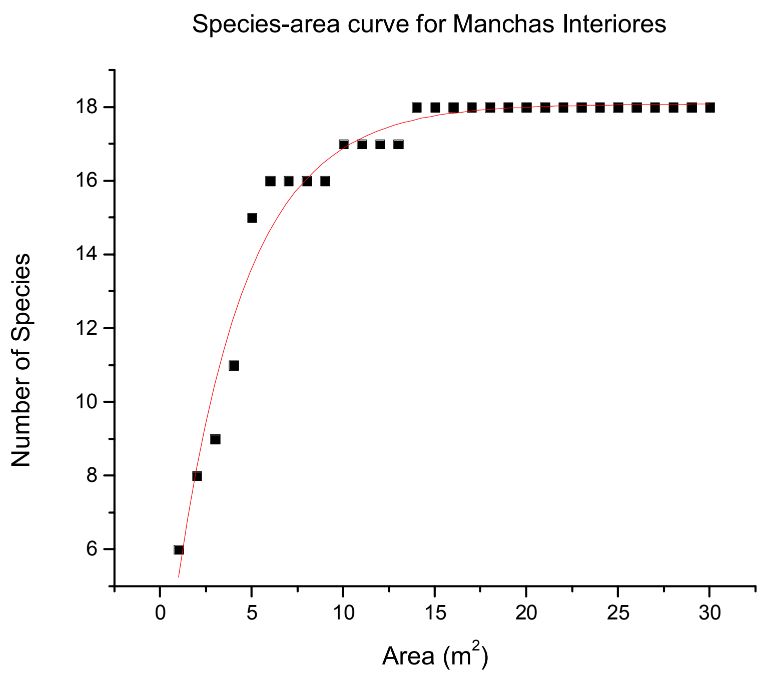
2
4
6
8
10
12
14
0
5
10
15
20
25
30


Species-area curve for Manchas Interiores
Number of Species
Area (m²)
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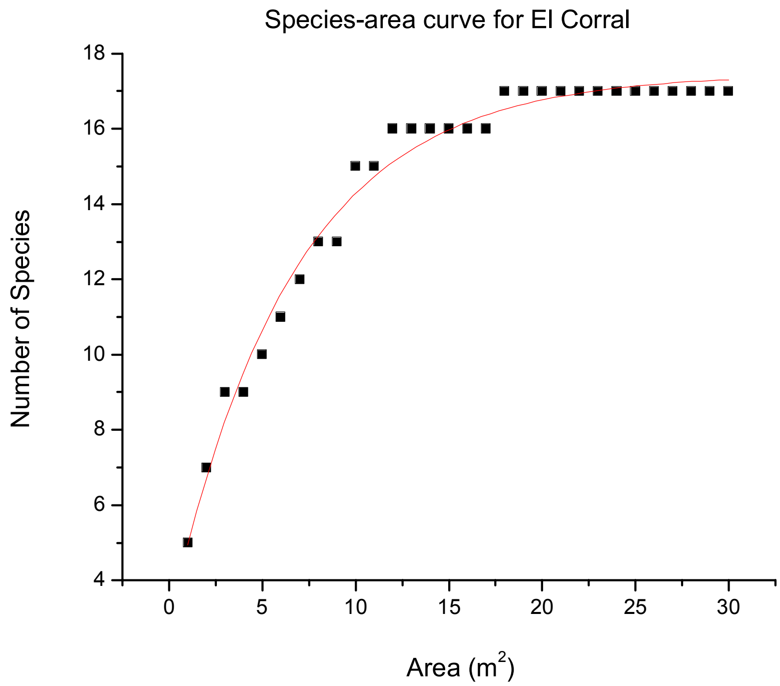
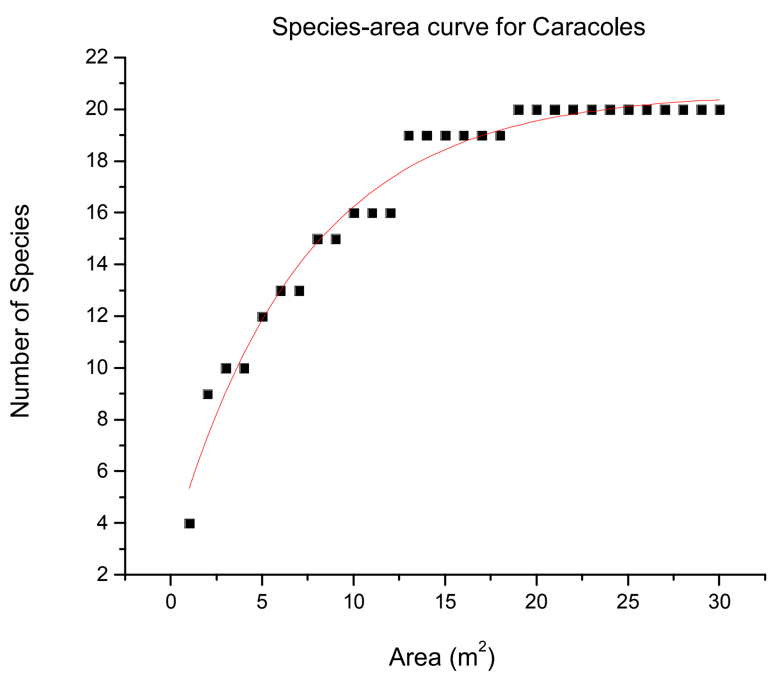
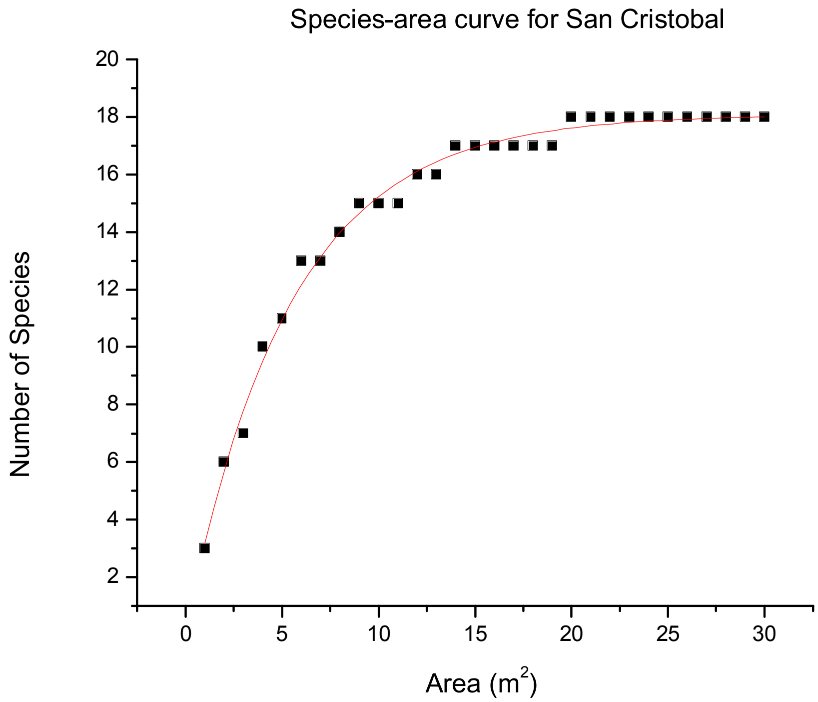
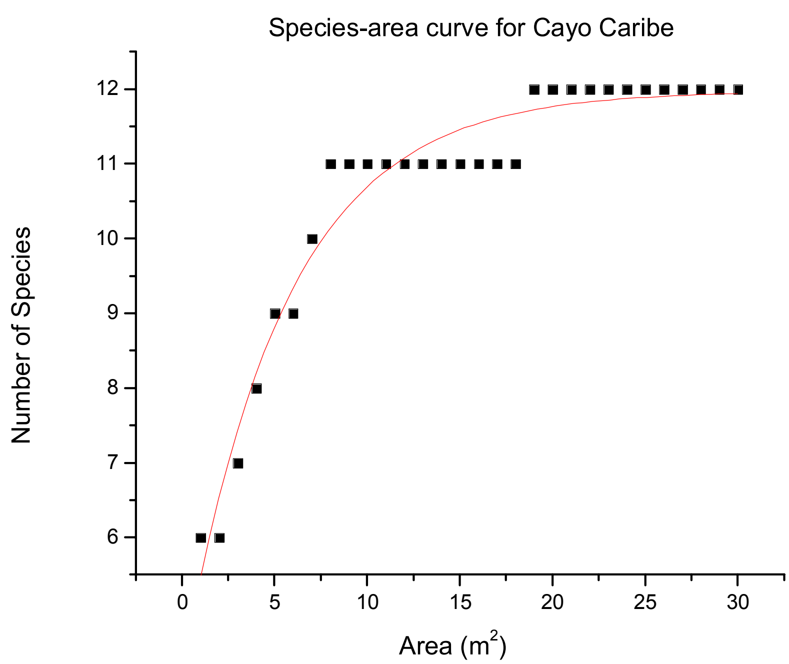
8
10
12
14
16
18
0
5
10
15
20
25
30


Species-area curve for El Corral
Number of Species
Area (m2)
18
16
14
12
10
8
6
4
0
5
10
15
20
25
30


Species-area curve for Caracoles
Number of Species
Area (m2)
22
20
18
16
14
12
10
8
6
4
2
0
5
10
15
20
25
30

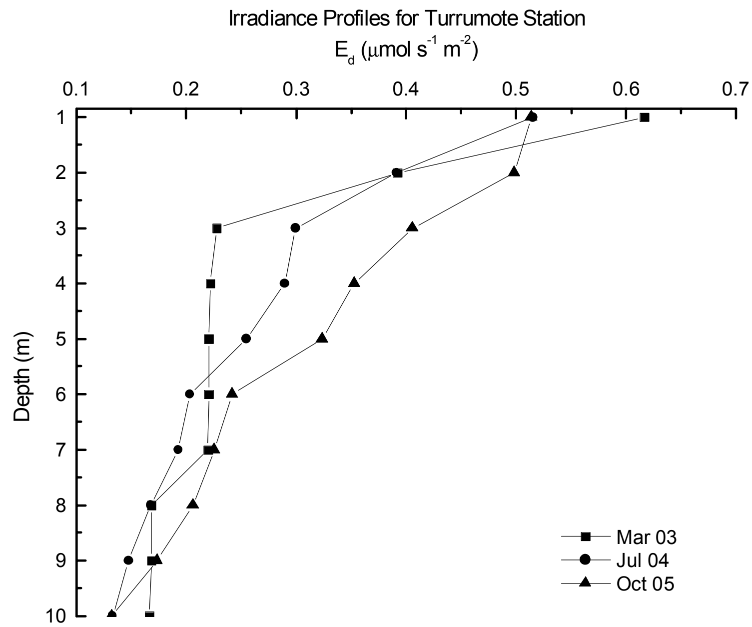

Species-area curve for San Cristobal
Number of Species
Area (m2)
20
18
16
14
12
10
8
6
4
2
0
5
10
15
20
25
30

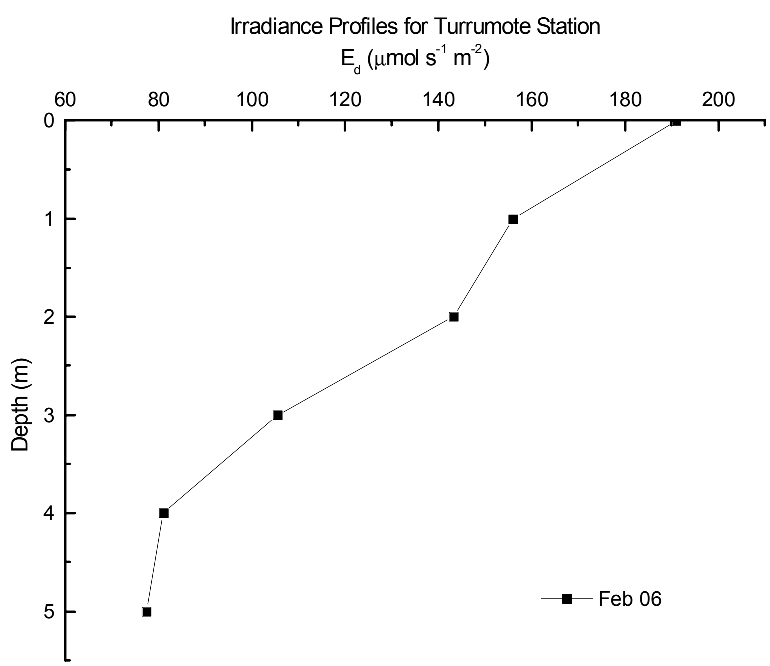

Species-area curve for Cayo Caribe
Number of Species
Area (m2)
12
11
10
9
8
7
6
0
5
10
15
20
25
30

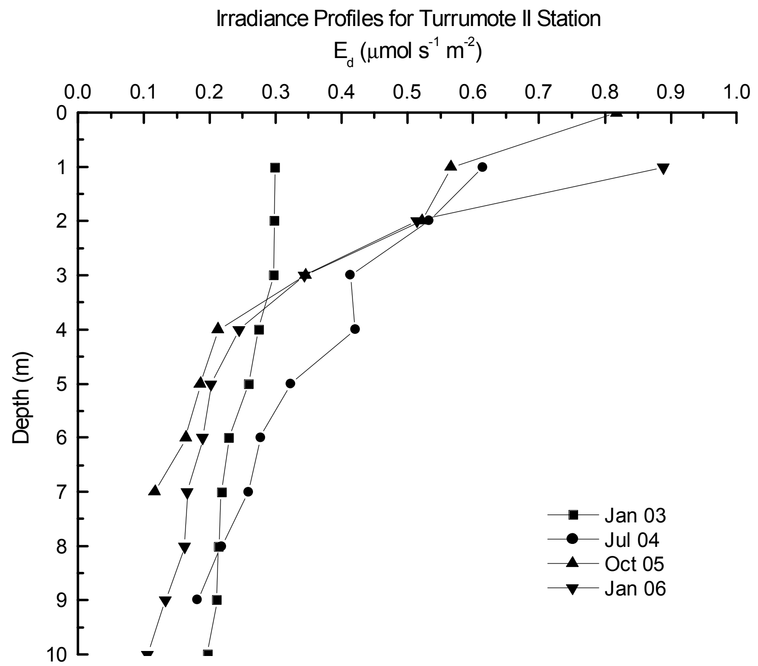
APPENDIX B

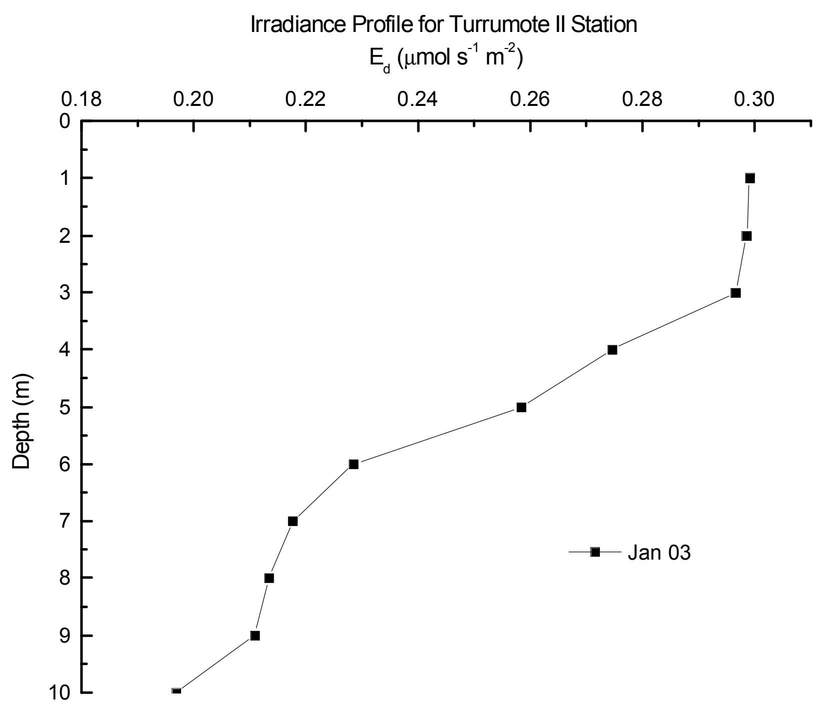
Irradiance profiles for the 19 study sites

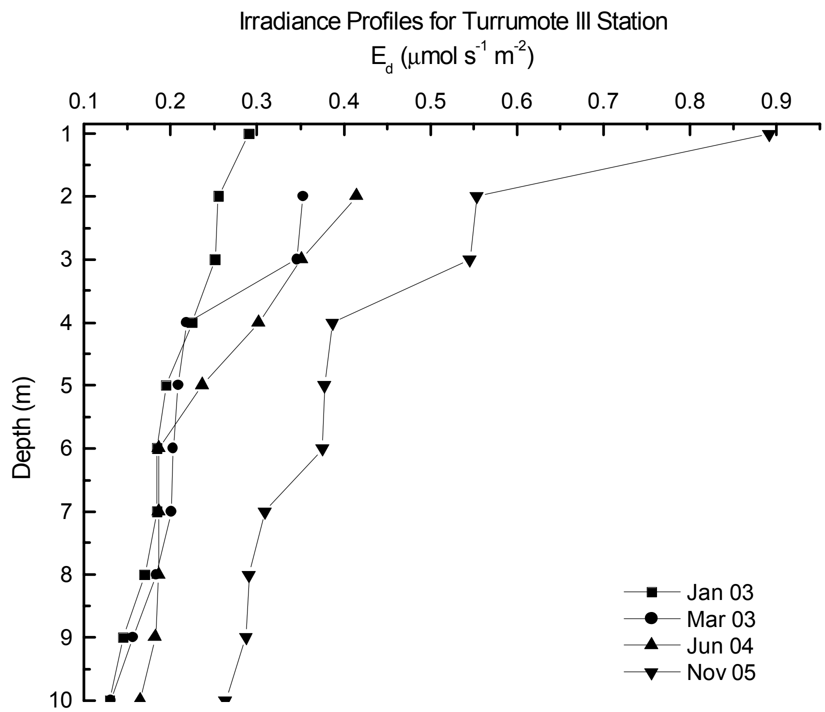
Profiles for E_d

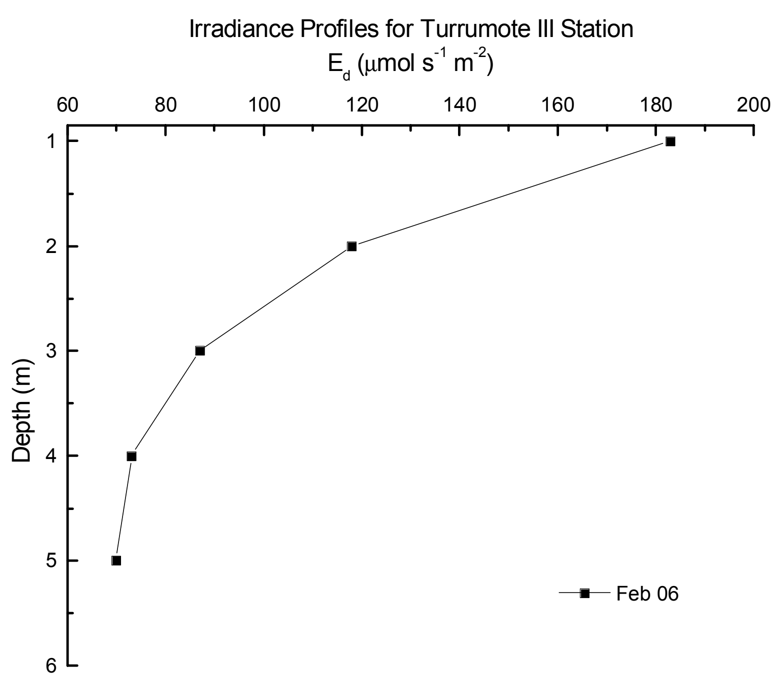

Irradiance Profiles for Turrumote Station
E$_d$ (μmol s^{-1} m^{-2})
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Depth (m)
1
2
3
4
5
6
7
8
9
10
Mar 03
Jul 04
Oct 05

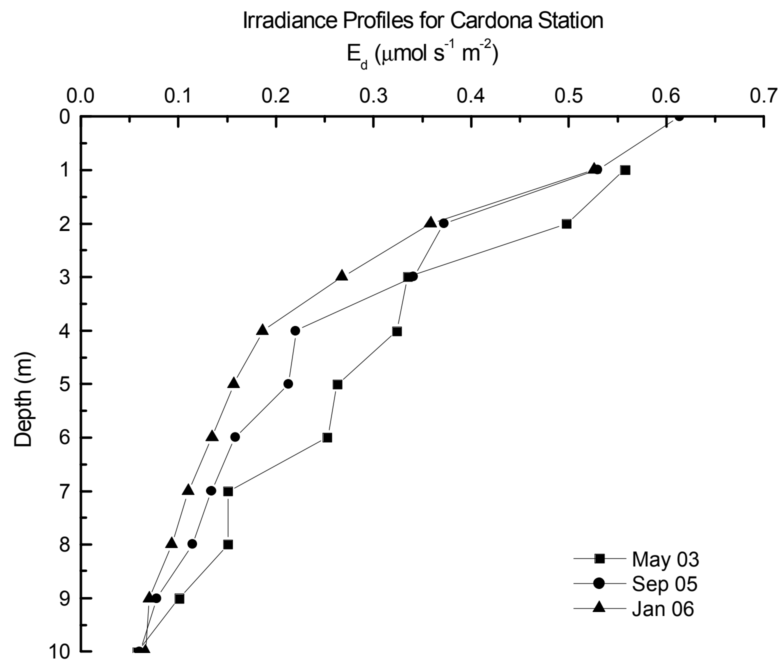

Irradiance Profiles for Turrumote Station
E$_d$ (μmol s^{-1} m^{-2})
60
80
100
120
140
160
180
200
Depth (m)
0
1
2
3
4
5
Feb 06

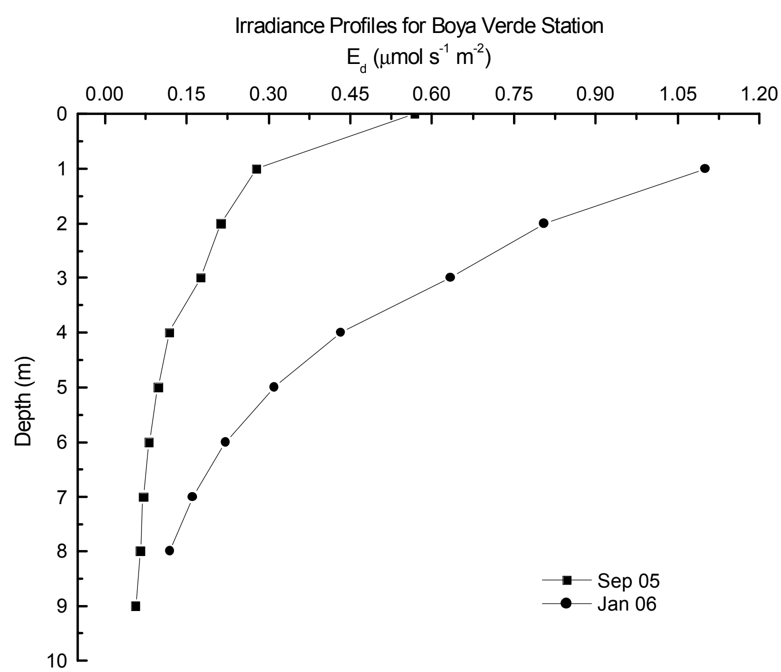

Irradiance Profiles for Turrumote II Station
E_d (μmol s^{-1} m^{-2})
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03
Jul 04
Oct 05
Jan 06

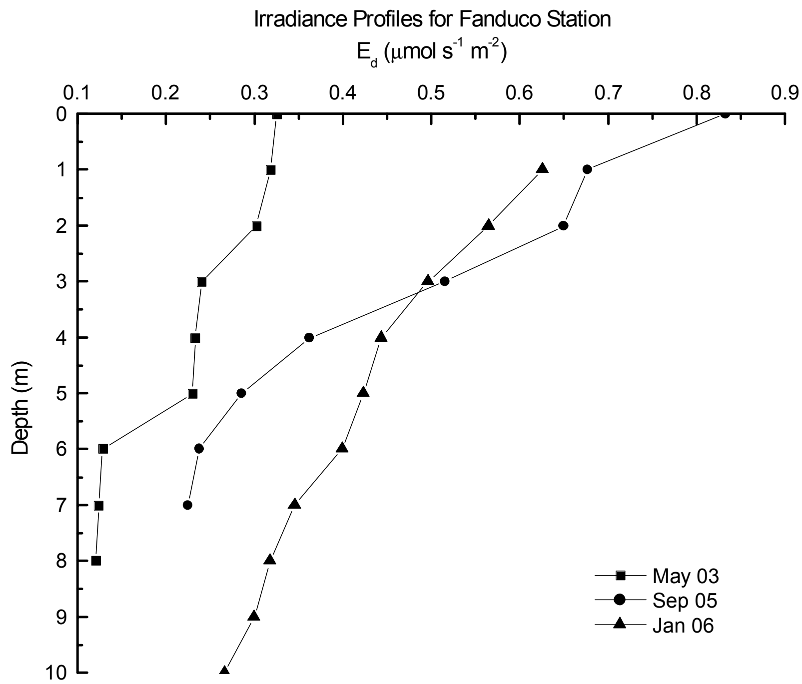

Irradiance Profile for Turrumote II Station
E_d (μmol s^{-1} m^{-2})
0.18
0.20
0.22
0.24
0.26
0.28
0.30
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03

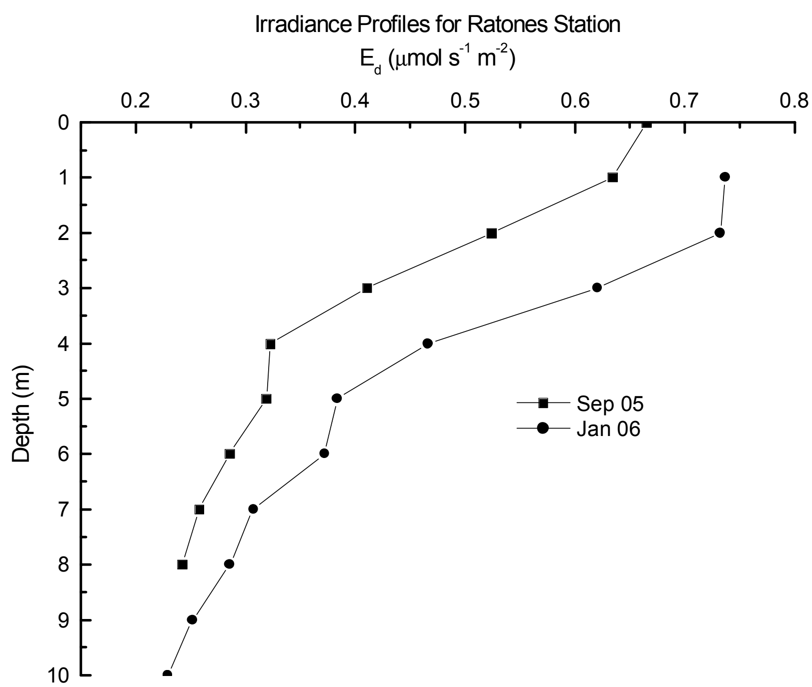

Irradiance Profiles for Turrumote III Station
E_d (μmol s^{-1} m^{-2})
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Depth (m)
1 2 3 4 5 6 7 8 9 10
Jan 03
Mar 03
Jun 04
Nov 05

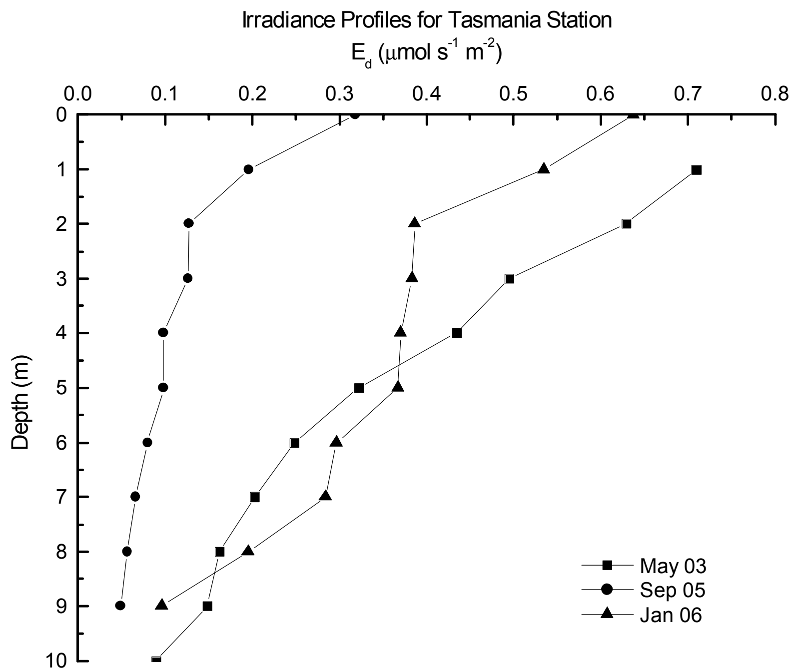

Irradiance Profiles for Turrumote III Station
E_d (μmol s^{-1} m^{-2})
60 80 100 120 140 160 180 200
Depth (m)
1 2 3 4 5 6
Feb 06

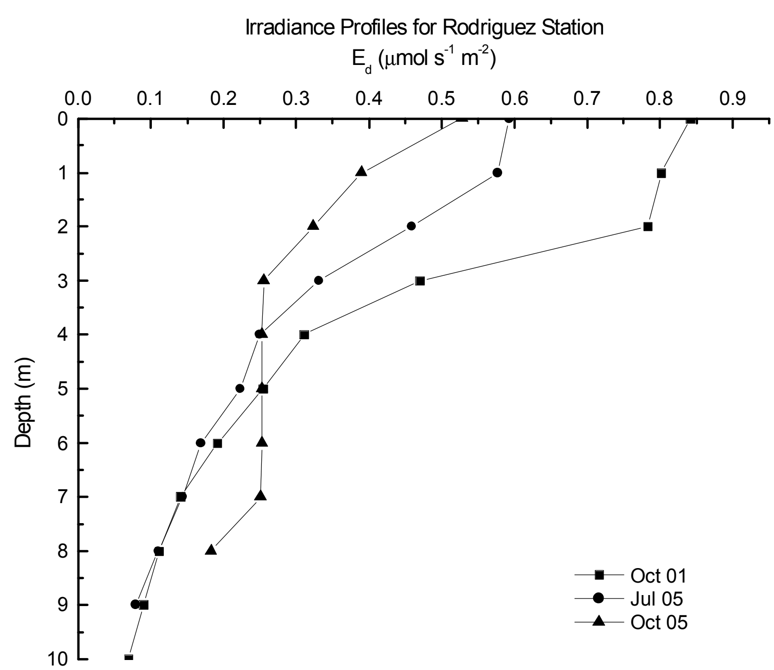

Irradiance Profiles for Cardona Station
E_d (µmol s^-1 m^-2)
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
May 03
Sep 05
Jan 06

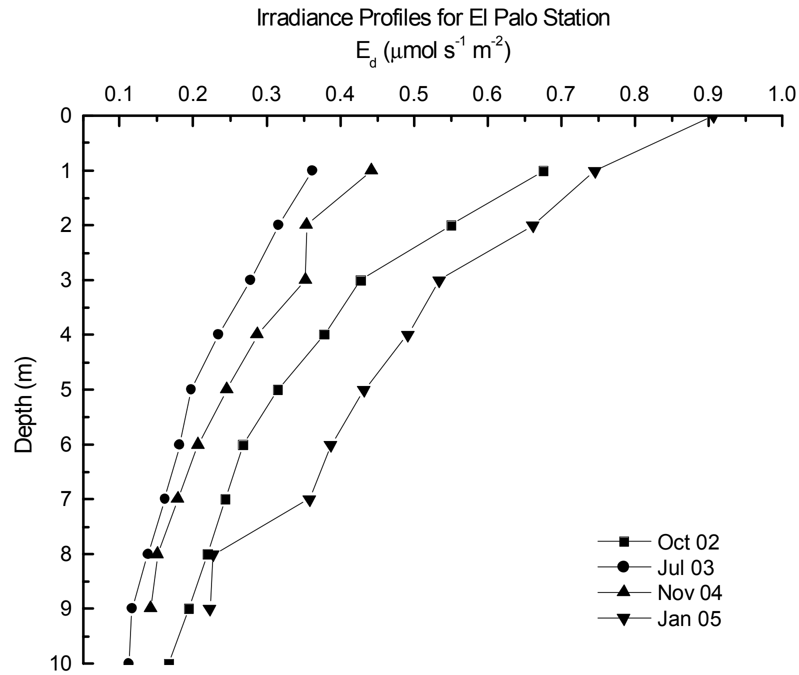

Irradiance Profiles for Boya Verde Station
E_d (µmol s^-1 m^-2)
0.00 0.15 0.30 0.45 0.60 0.75 0.90 1.05 1.20
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
Sep 05
Jan 06


Irradiance Profiles for Fanduco Station
E_d (μmol s^-1 m^-2)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
May 03
Sep 05
Jan 06

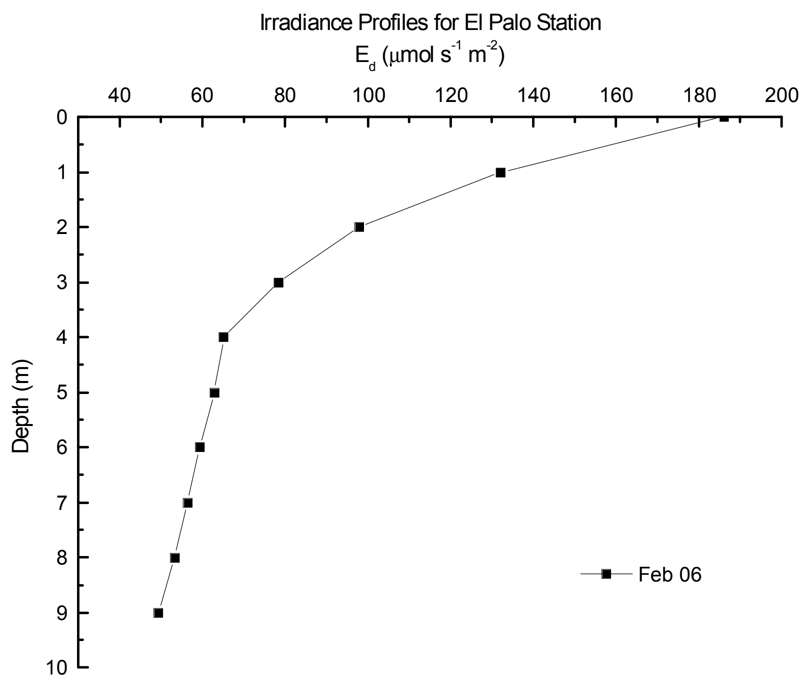

Irradiance Profiles for Ratones Station
E_d (μmol s^-1 m^-2)
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Sep 05
Jan 06


Irradiance Profiles for Tasmania Station
E_d (µmol s^-1 m^-2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
May 03
Sep 05
Jan 06

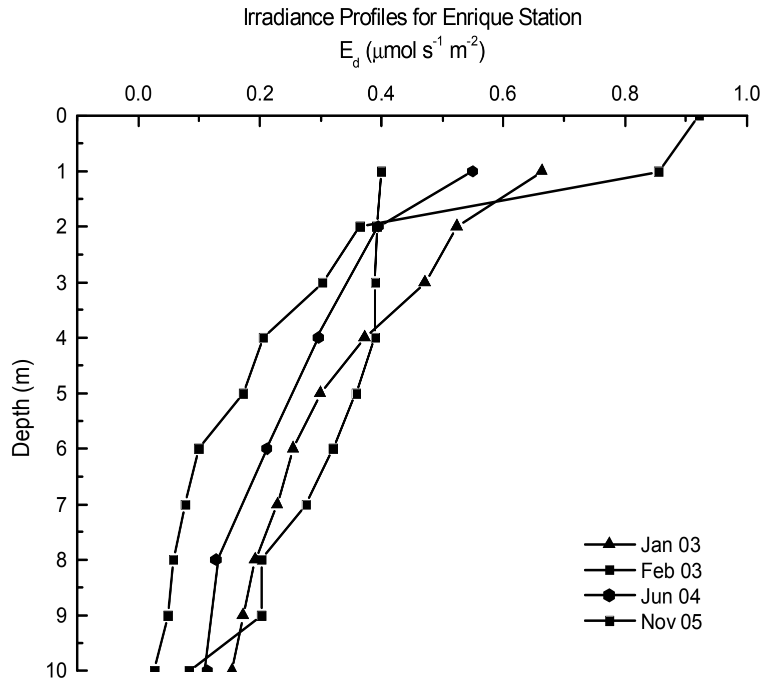

Irradiance Profiles for Rodriguez Station
E_d (µmol s^-1 m^-2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Oct 01
Jul 05
Oct 05

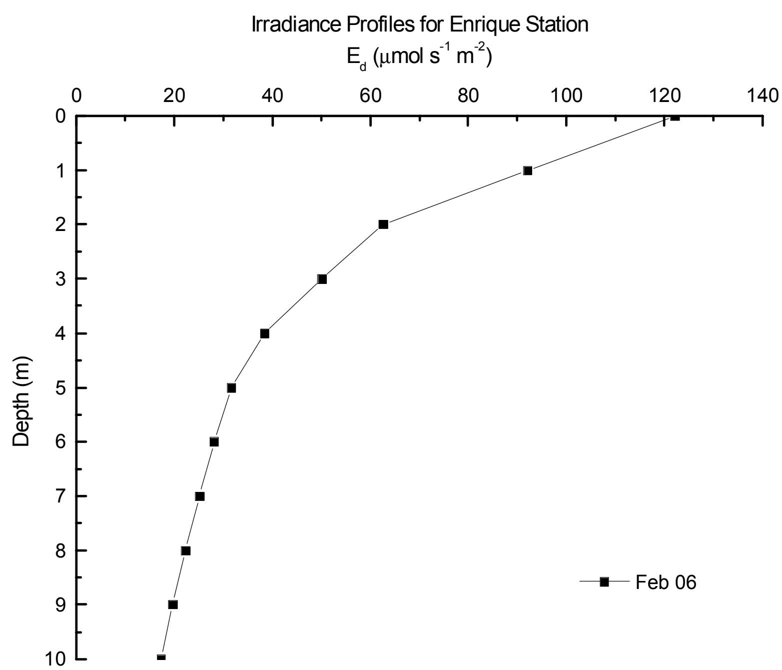


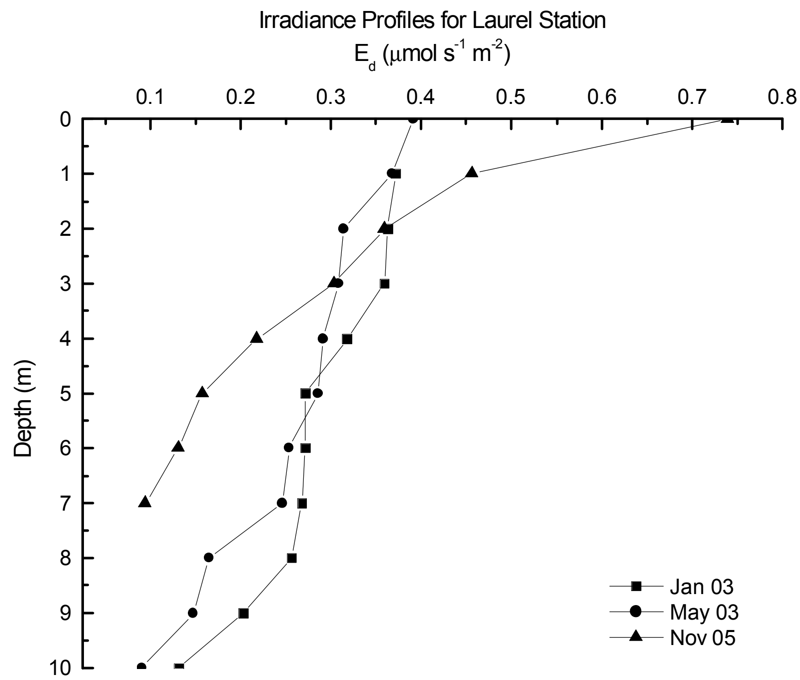
Irradiance Profiles for El Palo Station
E_d (µmol s^-1 m^-2)
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
0 1 2 3 4 5 6 7 8 9 10
Depth (m)
Oct 02
Jul 03
Nov 04
Jan 05

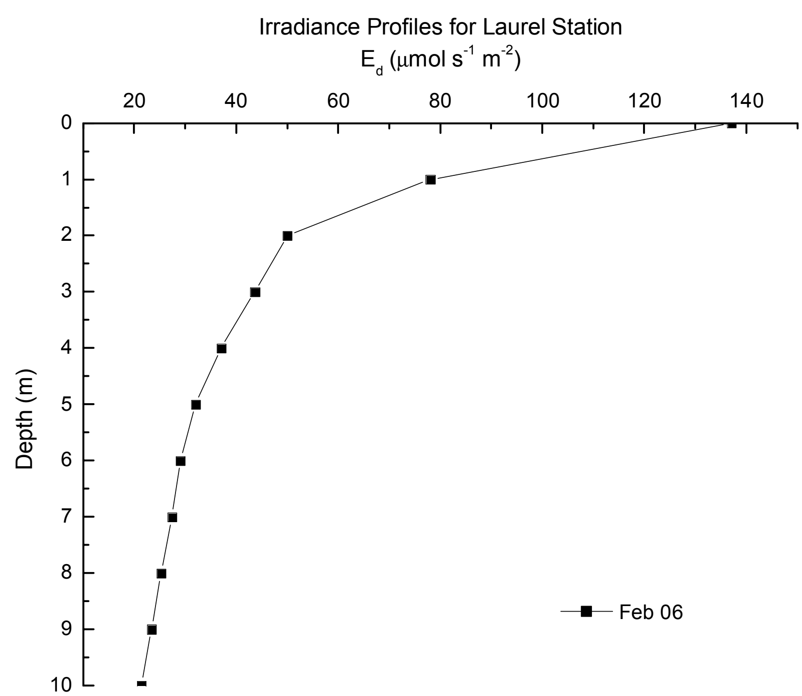


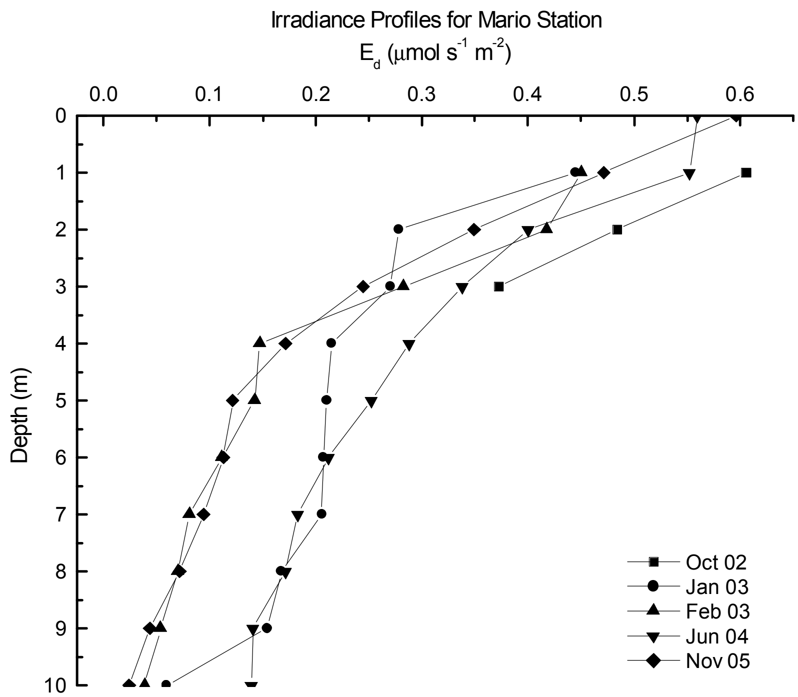
Irradiance Profiles for El Palo Station
E_d (µmol s^-1 m^-2)
40 60 80 100 120 140 160 180 200
0 1 2 3 4 5 6 7 8 9 10
Depth (m)
Feb 06


Irradiance Profiles for Enrique Station
Ed (μmol s-1 m-2)
0.0
0.2
0.4
0.6
0.8
1.0
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03
Feb 03
Jun 04
Nov 05

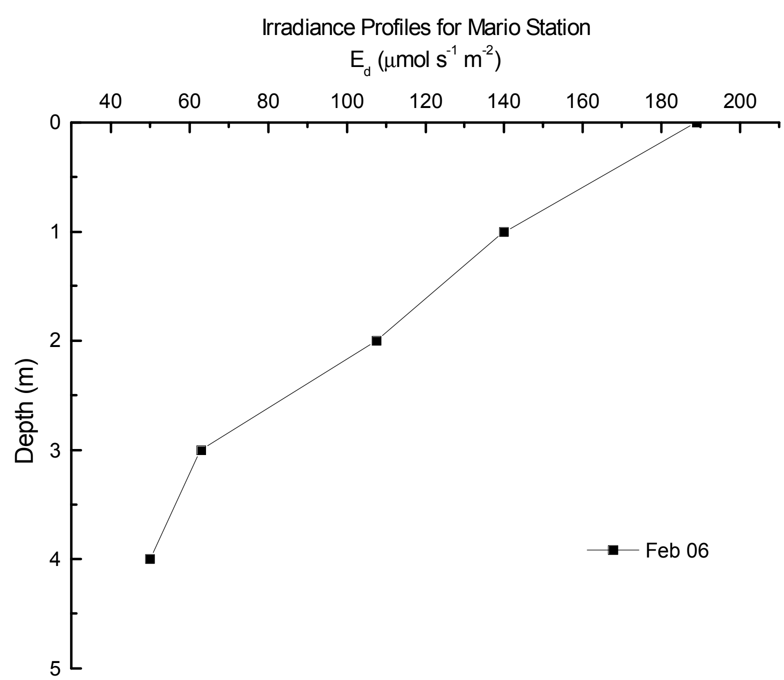

Irradiance Profiles for Enrique Station
Ed (μmol s-1 m-2)
0
20
40
60
80
100
120
140
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Feb 06


Irradiance Profiles for Laurel Station
E_d (μmol s^{-1} m^{-2})
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03
May 03
Nov 05

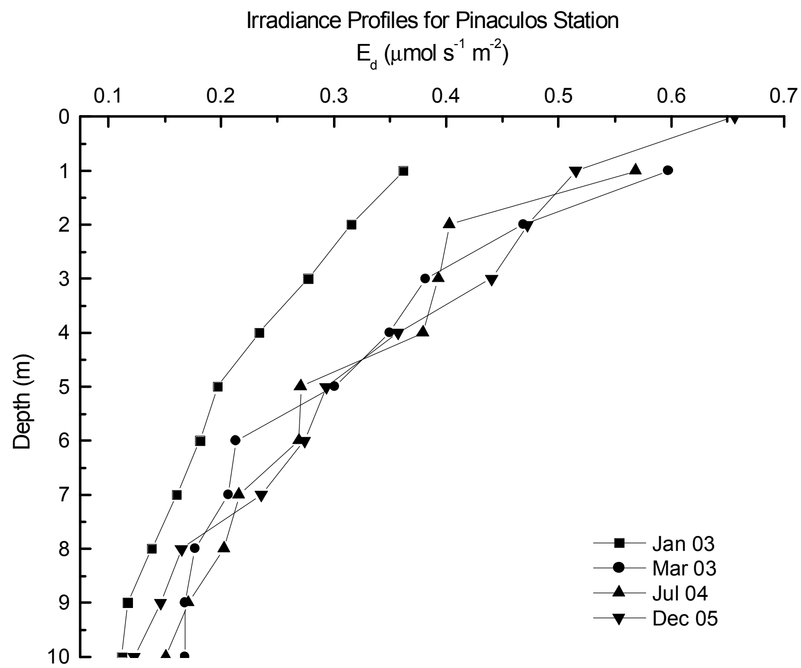

Irradiance Profiles for Laurel Station
E_d (μmol s^{-1} m^{-2})
20
40
60
80
100
120
140
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Feb 06



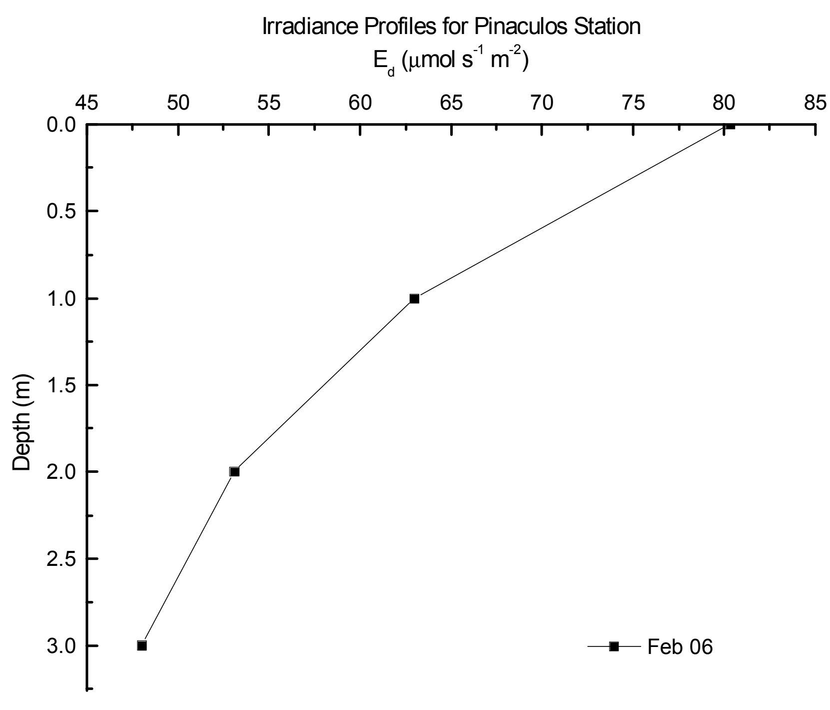
Irradiance Profiles for Mario Station
E_d (μmol s^{-1} m^{-2})
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
1
2
3
4
5
6
7
8
9
10
Depth (m)
Oct 02
Jan 03
Feb 03
Jun 04
Nov 05



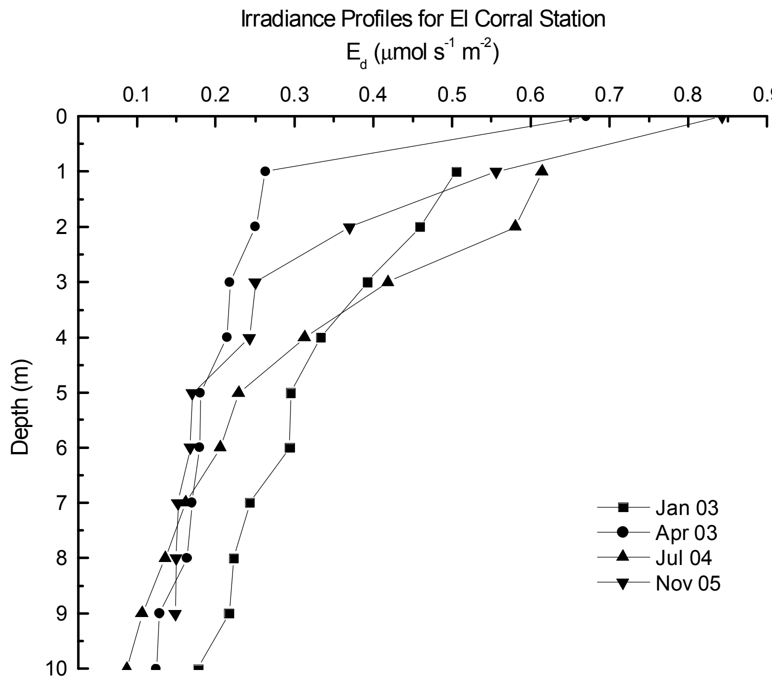
Irradiance Profiles for Mario Station
E_d (μmol s^{-1} m^{-2})
40
60
80
100
120
140
160
180
200
0
1
2
3
4
5
Depth (m)
Feb 06



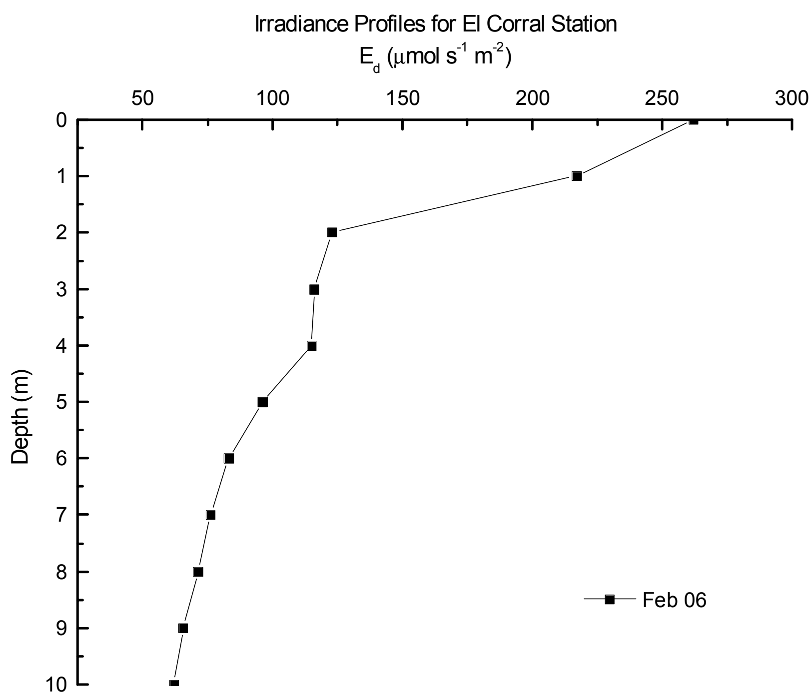
Irradiance Profiles for Pinaculos Station
E_d (μmol s^{-1} m^{-2})
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03
Mar 03
Jul 04
Dec 05



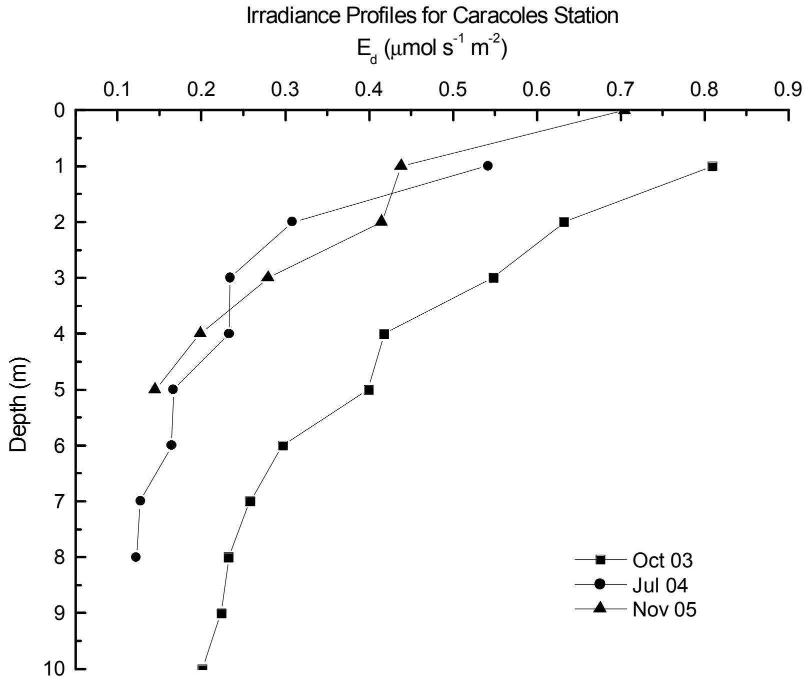
Irradiance Profiles for Pinaculos Station
E_d (μmol s^{-1} m^{-2})
45
50
55
60
65
70
75
80
85
Depth (m)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Feb 06

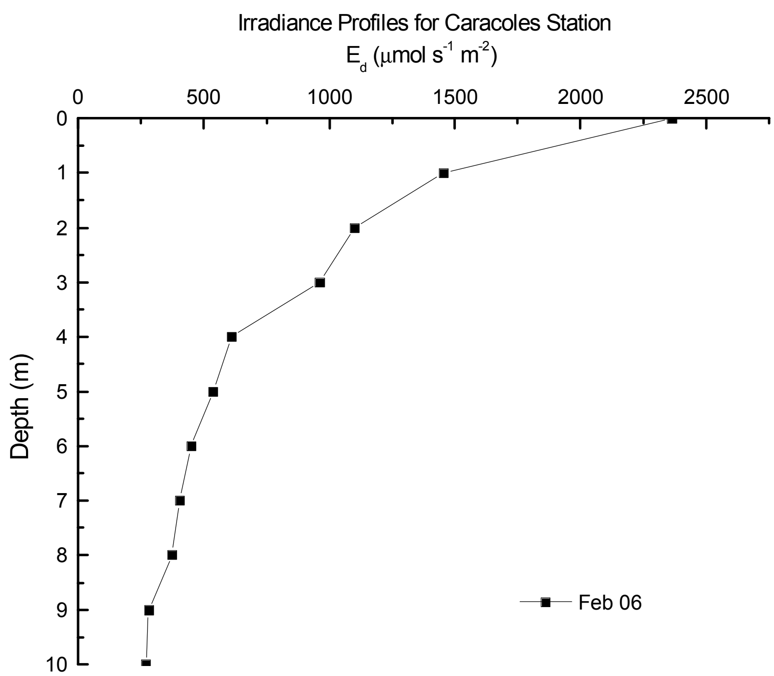


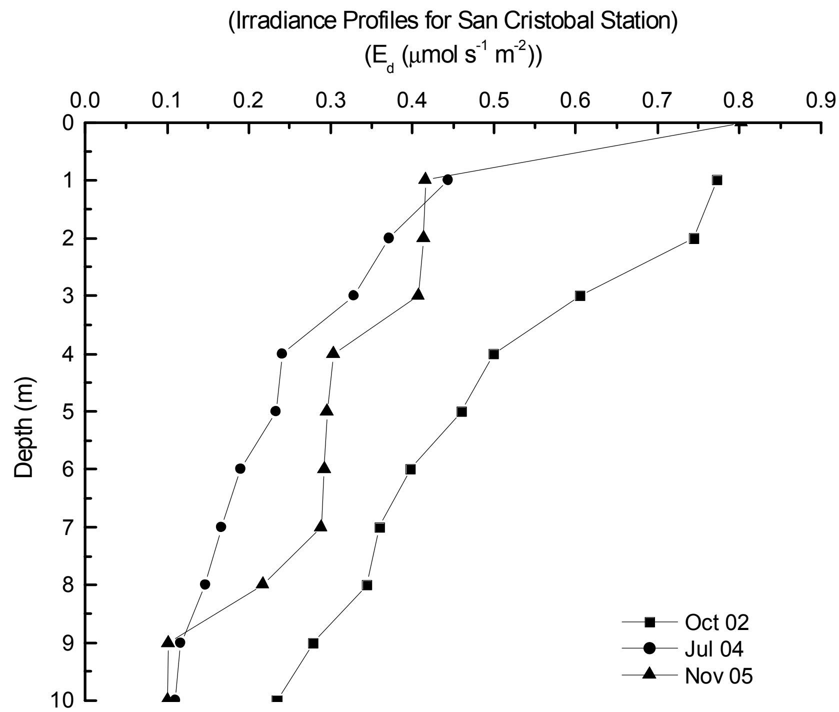
Irradiance Profiles for El Corral Station
E_d (μmol s^{-1} m^{-2})
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Jan 03
Apr 03
Jul 04
Nov 05

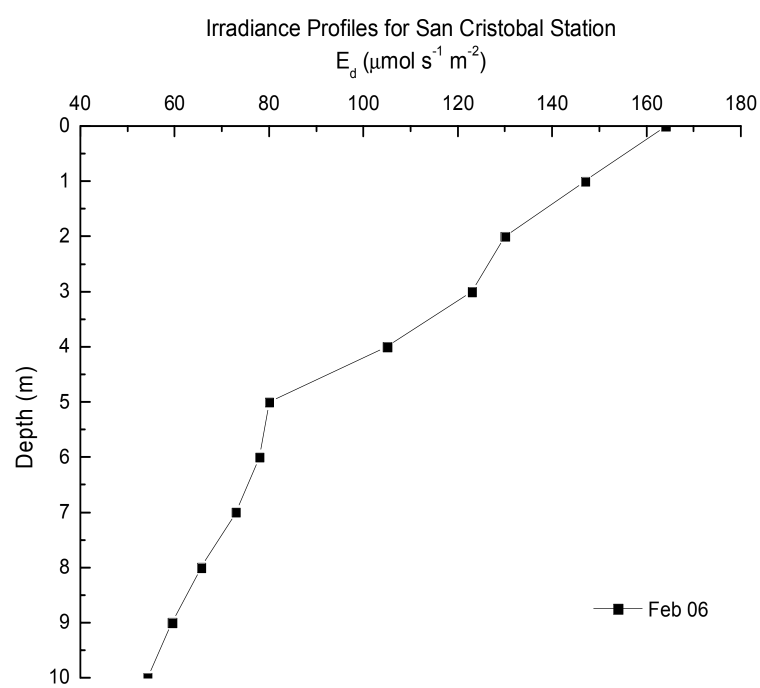


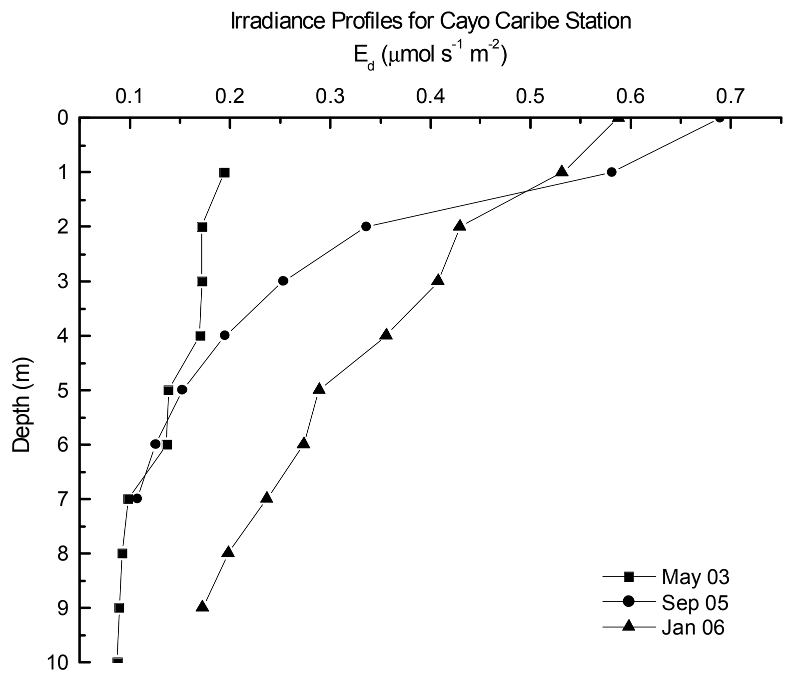
Irradiance Profiles for El Corral Station
E_d (μmol s^{-1} m^{-2})
50
100
150
200
250
300
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Feb 06

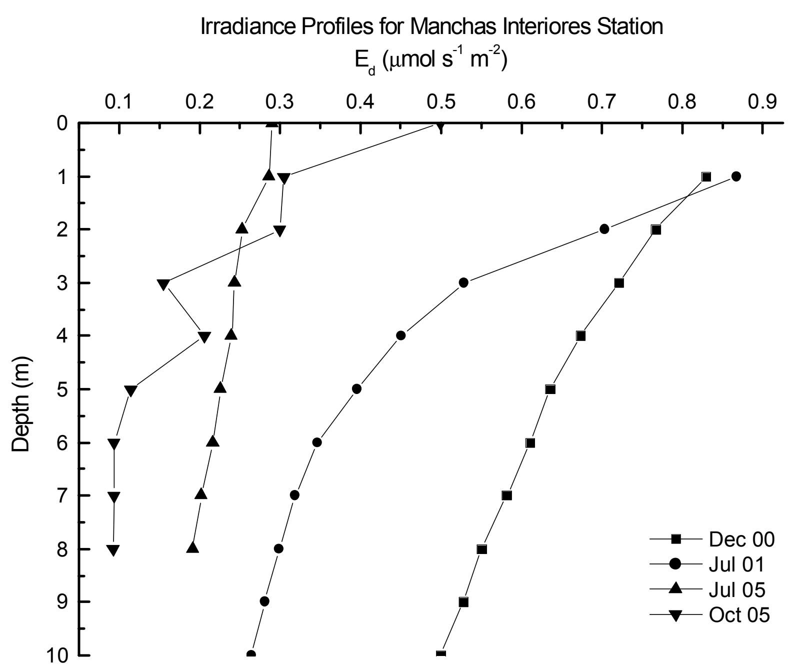

Irradiance Profiles for Caracoles Station
E_d (µmol s^-1 m^-2)
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
Oct 03
Jul 04
Nov 05


Irradiance Profiles for Caracoles Station
E_d (µmol s^-1 m^-2)
0 500 1000 1500 2000 2500
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
Feb 06


(Irradiance Profiles for San Cristobal Station)
(E_d (µmol s^-1 m^-2))
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Oct 02
Jul 04
Nov 05


Irradiance Profiles for San Cristobal Station
E_d (µmol s^-1 m^-2)
40
60
80
100
120
140
160
180
Depth (m)
0
1
2
3
4
5
6
7
8
9
10
Feb 06


Irradiance Profiles for Cayo Caribe Station
E_d (μmol s^{-1} m^{-2})
0.1 0.2 0.3 0.4 0.5 0.6 0.7
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
May 03
Sep 05
Jan 06


Irradiance Profiles for Manchas Interiores Station
E_d (μmol s^{-1} m^{-2})
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Depth (m)
0 1 2 3 4 5 6 7 8 9 10
Dec 00
Jul 01
Jul 05
Oct 05

APPENDIX C

Coral species distribution for the 19 study sites

Coral Species Distribution Tables

Turrumote III

Coral species	**Coral Cover (%)**
Agaricia sp.	3.97
Colpophyllia natans	3.60
Diploria labirynthiformis	1.74
Diploria strigosa	0.44
Isophyllia sinuosa	0.06
Madracis decactis	0.15
Madracis pharensis	0.12
Manicina mayori	0.02
Meandrina meandrites	0.20
Millepora alcicornis	0.11
Montastraea annularis	31.41
Montastraea cavernosa	4.16
Montastraea franksi	8.46
Mycetophyllia danaana	0.18
Mycetophyllia sp.	0.13
Porites astreoides	2.66
Porites decactis	0.17
Porites porites	1.80
Siderastrea siderea	2.00
Stephanocoenia sp.	0.03

Turrumote II

Coral species	**Coral Cover (%)**
Agaricia sp.	3.75
Colpophyllia natans	1.34
Diploria labirynthiformis	0.26
Diploria strigosa	0.41
Dichochoenia stellaris	0.30
Dichochoenia stokesii	0.02
Isophyllia sinuosa	0.06
Madracis decactis	0.04
Madracis senaria	0.02
Manicina mayori	0.02
Millepora alcicornis	0.22
Millepora squarrosa	0.03
Montastraea cavernosa	3.88
Montastraea faveolata	0.14
Montastraea franksi	35.04
Mycetophyllia lamarckiana	0.02
Mycetophyllia sp.	0.57
Porites astreoides	1.33

Porites decactis	1.02
Porites porites	10.50
Siderastrea siderea	0.37

Turrumote

Coral species	**Coral Cover (%)**
Agaricia sp.	0.96
Colpophyllia natans	0.55
Diploria clivosa	0.02
Dichochoenia stokesii	0.05
Madracis pharensis	0.15
Meandrina meandrites	0.30
Millepora alcicornis	0.05
Montastraea annularis	0.17
Montastraea faveolata	49.14
Montastraea franksi	0.34
Mycetophyllia danaana	0.54
Mycetophyllia sp.	0.14
Porites astreoides	1.68
Porites decactis	0.37
Porites porites	2.90
Siderastrea siderea	1.93

Pinaculos

Coral species	**Coral Cover (%)**
Agaricia sp.	1.02
Colpophyllia natans	1.34
Meandrina meandrites	0.03
Millepora alcicornis	0.36
Montastraea cavernosa	0.03
Montastraea faveolata	45.61
Porites astreoides	2.16
Porites decactis	0.11
Porites porites	0.32
Siderastrea siderea	0.72

Laurel

Coral species	**Coral Cover (%)**
Agaricia sp.	4.17
Colpophyllia natans	1.09
Diploria clivosa	0.38
Diploria strigosa	0.60
Meandrina meandrites	0.07
Millepora alcicornis	5.78
Montastraea annularis	28.54
Montastraea cavernosa	0.64

Montastraea franksi	0.59
Mycetophyllia ferox	0.09
Porites astreoides	1.67
Porites decactis	0.26
Porites porites	0.39
Siderastrea siderea	1.83

San Cristobal

Coral species	**Coral Cover (%)**
Acropora cervicornis	1.59
Agaricia sp.	7.43
Cladocora arbuscula	0.13
Colpophyllia amaranthus	0.05
Colpophyllia natans	6.02
Dendrogyra cylindrus	0.54
Diploria clivosa	2.05
Diploria strigosa	0.49
Favia fragum	0.00
Madracis pharensis	0.11
Meandrina meandrites	0.60
Millepora alcicornis	0.75
Millepora squarrosa	0.13
Montastraea cavernosa	3.77
Montastraea faveolata	0.06
Montastraea franksi	10.69
Mycetophyllia sp.	0.25
Porites astreoides	5.17
Porites decactis	0.23
Porites porites	1.46
Siderastrea siderea	3.28

Manchas Interiores

Coral species	**Coral Cover (%)**
Agaricia sp.	5.84
Colpophyllia natans	2.79
Diploria strigosa	0.28
Dichochoenia stokesii	0.04
Isophyllia sinuosa	0.05
Madracis decactis	0.42
Meandrina meandrites	0.61
Millepora alcicornis	0.36
Montastraea annularis	9.26
Montastraea cavernosa	1.98
Porites astreoides	3.46
Porites divaricata	0.02
Porites porites	3.73
Siderastrea siderea	0.57

Scolymia sp.	0.01
Solenastrea sp.	0.12

El Palo

Coral species	**Coral Cover (%)**
Agaricia sp.	2.41
Colpophyllia natans	0.04
Diploria clivosa	0.03
Diploria strigosa	3.80
Dichochoenia stokesii	0.39
Eusmilia fastigiata	0.31
Isophyllia sinuosa	0.07
Madracis decactis	0.01
Manicina aerolata	0.05
Manicina mayori	0.06
Millepora alcicornis	0.03
Montastraea annularis	11.67
Montastraea cavernosa	1.65
Montastraea franksi	1.91
Mycetophyllia danaana	0.15
Porites astreoides	1.34
Porites porites	0.80
Siderastrea siderea	3.29
Stephanocoenia sp.	0.95

Caracoles

Coral species	**Coral Cover (%)**
Agaricia sp.	2.19
Colpophyllia amaranthus	0.07
Colpophyllia natans	7.62
Diploria labirynthiformis	0.04
Diploria strigosa	0.23
Eusmilia fastigiata	0.11
Madracis decactis	0.01
Madracis pharensis	0.15
Meandrina meandrites	0.29
Millepora alcicornis	1.16
Montastraea cavernosa	1.03
Montastraea franksi	6.85
Porites astreoides	1.84
Porites decactis	0.03
Porites porites	0.25
Siderastrea radians	0.07
Siderastrea siderea	5.14
Stephanocoenia sp.	0.24

Enrique

Coral species	Coral Cover (%)
Acropora cervicornis	0.05
Agaricia sp.	3.93
Cladocora arbuscula	0.11
Colpophyllia natans	6.63
Diploria clivosa	0.10
Diploria labirynthiformis	0.04
Isophyllia sinuosa	0.10
Madracis decactis	0.07
Madracis pharensis	0.03
Meandrina meandrites	0.44
Millepora alcicornis	0.26
Montastraea annularis	6.52
Montastraea cavernosa	1.15
Mussa angulossa	0.41
Porites astreoides	2.79
Porites porites	0.77
Siderastrea siderea	2.92
Scolymia sp.	0.01

Ratones

Coral species	Coral Cover (%)
Agaricia sp.	13.51
Isophyllastrea rigida	0.11
Madracis decactis	2.24
Manicina mayori	0.05
Meandrina meandrites	0.46
Millepora alcicornis	0.11
Montastraea annularis	1.55
Montastraea cavernosa	4.47
Mycetophyllia lamarckiana	0.16
Mycetophyllia sp.	0.68
Porites astreoides	1.40
Siderastrea siderea	1.25
Solenastrea sp.	0.05

Mario

Coral species	Coral Cover (%)
Acropora cervicornis	0.36
Agaricia sp.	1.52
Cladocora arbuscula	0.31
Colpophyllia natans	8.85
Diploria clivosa	0.06
Diploria labirynthiformis	0.12
Diploria strigosa	0.65
Favia fragum	0.04

Madracis decactis	0.14
Manicina sp.	0.04
Meandrina meandrites	0.14
Millepora alcicornis	0.26
Montastraea cavernosa	1.37
Montastraea franksi	3.93
Mussa angulossa	0.05
Mycetophyllia lamarckiana	0.04
Oculina sp.	0.86
Porites astreoides	0.67
Porites porites	2.40
Siderastrea siderea	2.93
Scolymia sp.	0.01

Fanduco

Coral species	**Coral Cover (%)**
Agaricia sp.	2.74
Colpophyllia natans	0.37
Diploria clivosa	0.25
Diploria labirynthiformis	0.03
Diploria strigosa	1.53
Isophyllia sinuosa	0.02
Madracis decactis	0.27
Meandrina meandrites	0.10
Millepora alcicornis	0.08
Montastraea annularis	7.45
Montastraea cavernosa	5.01
Porites astreoides	3.52
Siderastrea siderea	2.23
Solenastrea sp.	0.01

Cayo Caribe

Coral species	**Coral Cover (%)**
Agaricia sp.	11.57
Colpophyllia natans	0.17
Diploria strigosa	0.35
Isophyllastrea rigida	0.10
Isophyllia sinuosa	0.07
Madracis decactis	0.83
Meandrina meandrites	0.17
Millepora alcicornis	0.05
Montastraea annularis	0.54
Montastraea cavernosa	2.72
Porites astreoides	0.14
Siderastrea siderea	2.61
Solenastrea sp.	0.29
Stephanocoenia sp.	0.03

El Corral

Coral species	Coral Cover (%)
Agaricia sp.	0.71
Cladocora arbuscula	0.02
Colpophyllia natans	3.47
Colpophyllia amaranthus	0.02
Diploria clivosa	0.05
Diploria labirynthiformis	0.17
Favia fragum	0.01
Madracis decactis	0.23
Meandrina meandrites	0.45
Millepora alcicornis	0.08
Montastraea cavernosa	1.90
Montastraea faveolata	4.31
Montastraea franksi	0.03
Mycetophyllia danaana	0.13
Mycetophyllia ferox	0.11
Mycetophyllia sp.	0.36
Porites astreoides	0.51
Porites decactis	0.10
Porites porites	0.04
Siderastrea siderea	4.18
Stephanocoenia sp.	0.03

Rodriguez

Coral species	Coral Cover (%)
Agaricia sp.	0.52
Diploria strigosa	0.12
Madracis decactis	0.25
Montastraea cavernosa	5.99
Porites astreoides	0.19
Siderastrea siderea	0.93
Scolymia sp.	0.05
Stephanocoenia sp.	0.05

Cardona

Coral species	Coral Cover (%)
Agaricia sp.	1.13
Madracis decactis	0.02
Madracis pharensis	0.75
Meandrina meandrites	0.01
Millepora alcicornis	0.02
Montastraea cavernosa	2.00
Porites astreoides	1.00
Siderastrea radians	0.12

Siderastrea siderea	2.12
Scolymia sp	0.01
Solenastrea sp.	0.23

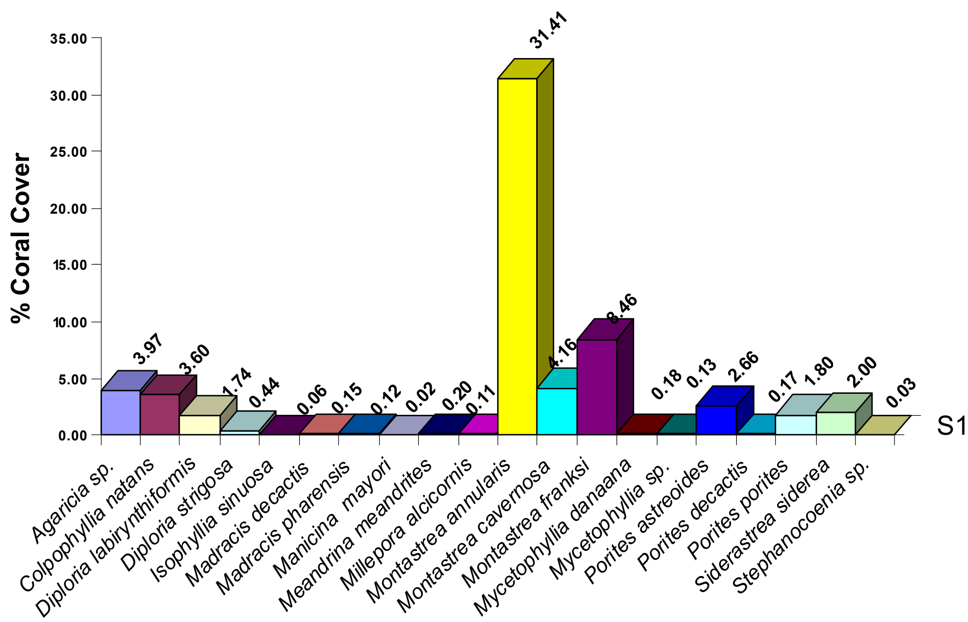
Tasmania

Coral species	**Coral Cover (%)**
Agaricia sp.	0.50
Diploria strigosa	0.52
Dichochoenia stokesii	0.07
Meandrina meandrites	0.28
Montastraea cavernosa	2.54
Porites astreoides	0.51
Siderastrea siderea	1.05

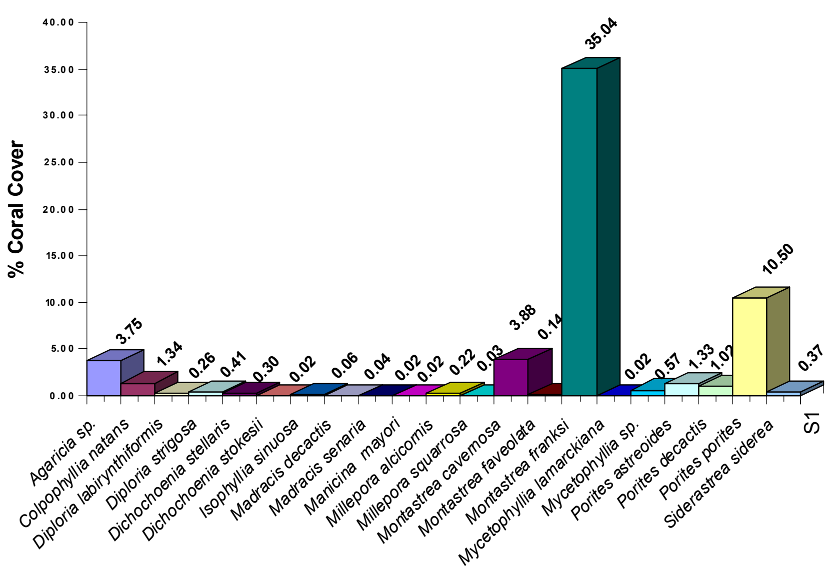
Boya Verde

Coral species	**Coral Cover (%)**
Agaricia sp.	0.10
Diploria strigosa	0.05
Dichochoenia stokesii	0.07
Madracis decactis	0.02
Meandrina meandrites	0.06
Millepora alcicornis	0.15
Montastraea annularis	0.28
Montastraea cavernosa	2.18
Porites astreoides	1.43
Siderastrea siderea	0.22

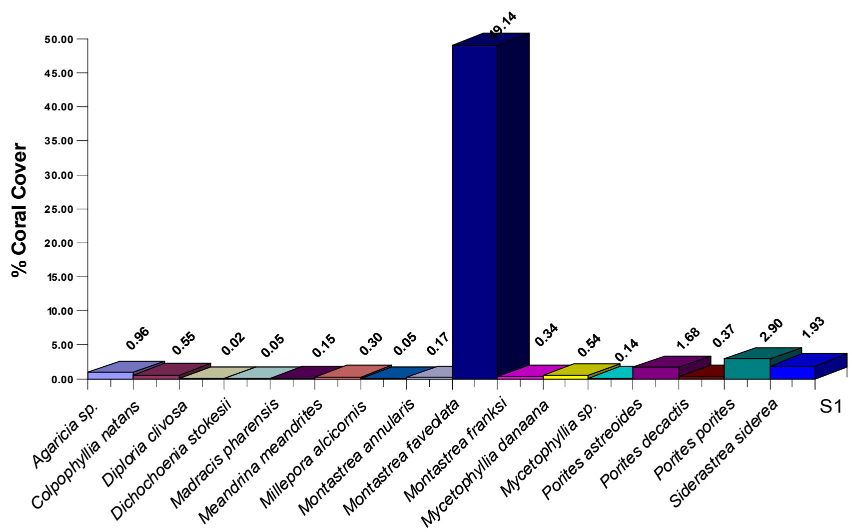
Coral species distribution for Turrumote III



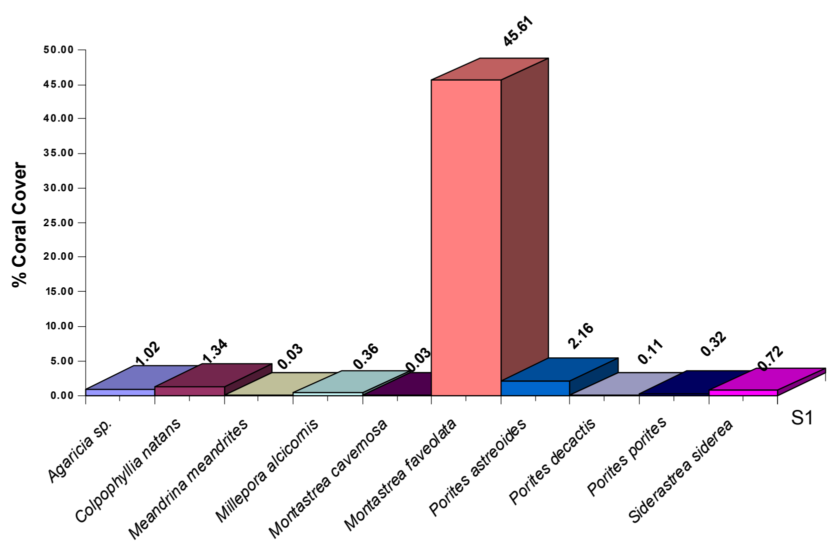
Coral species distribution for Turrumote II



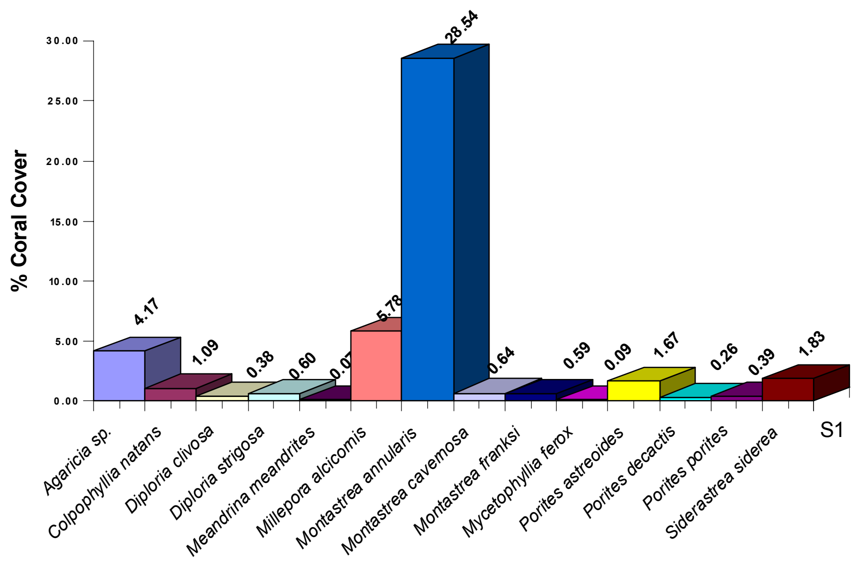
Coral species distribution for Turrumote



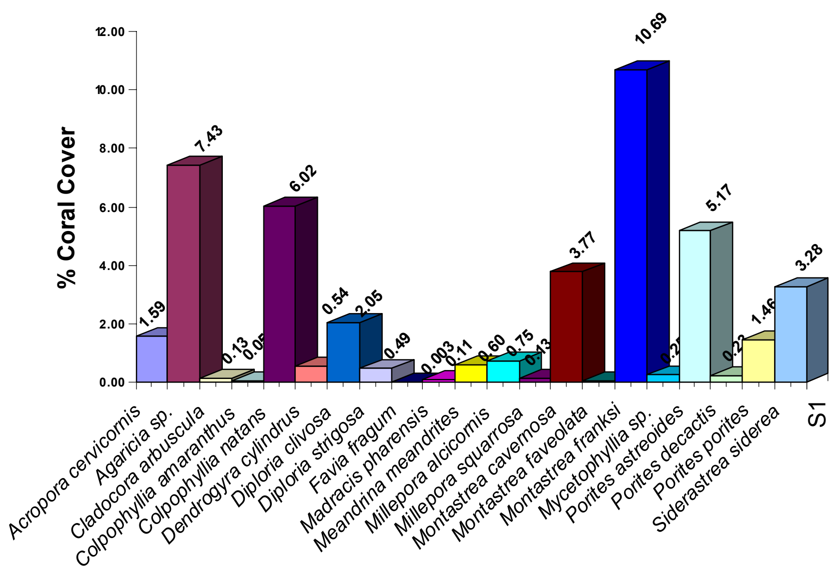
Coral species distribution for Pináculos



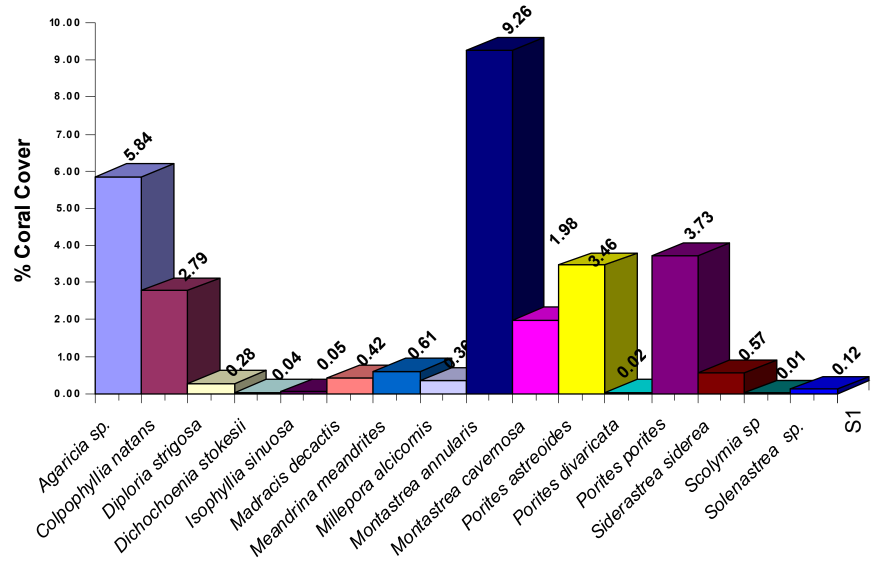
Coral species distribution for Laurel



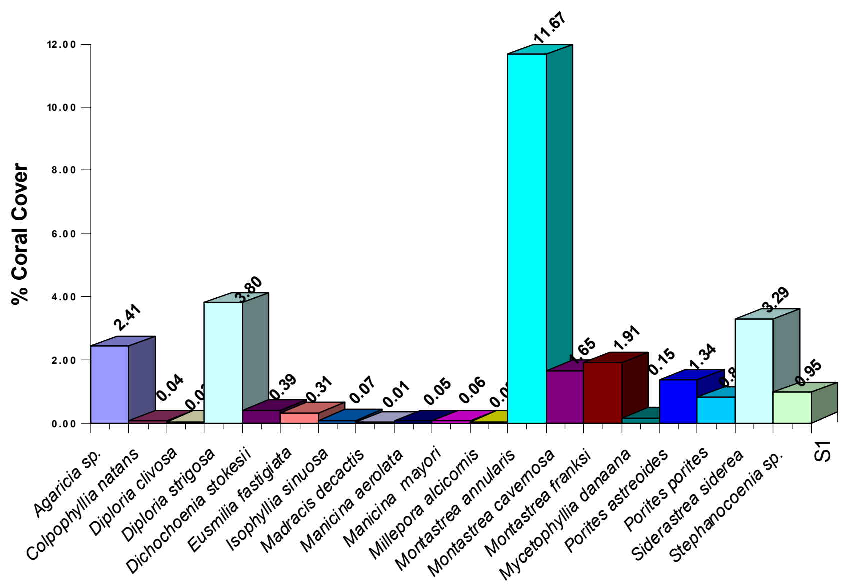
Coral species distribution for San Cristobal



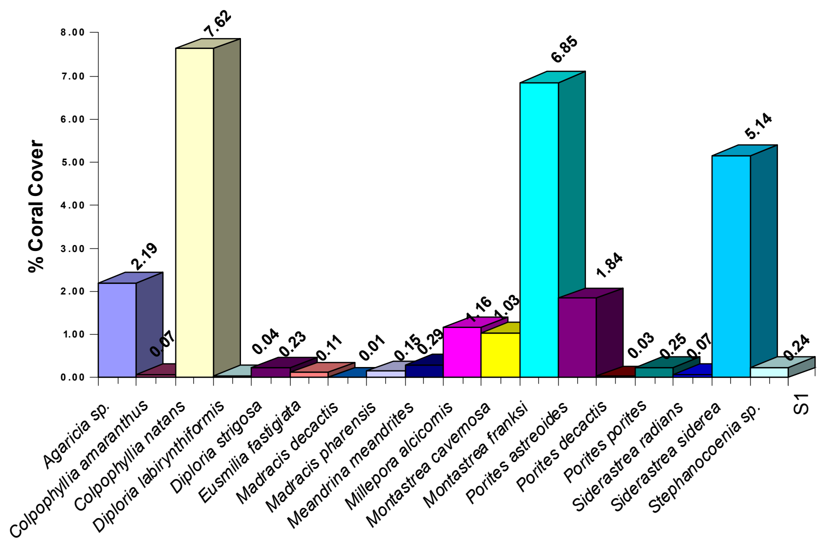
Coral species distribution for Manchas Interiores



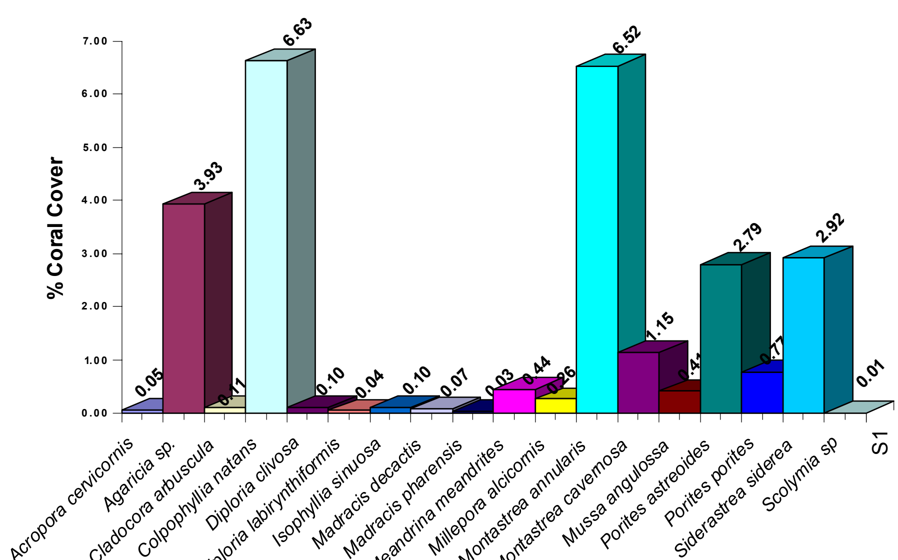
Coral species distribution for El Palo



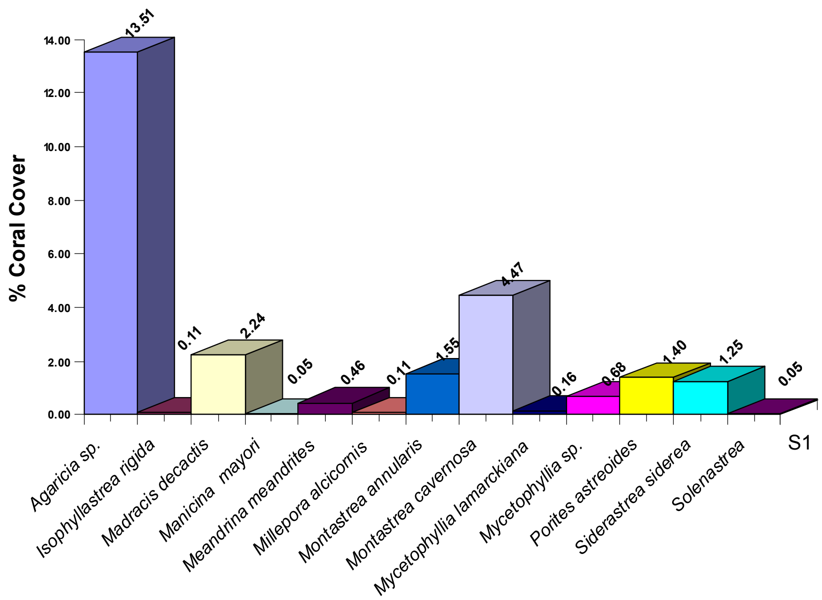
Coral species distribution for Caracoles



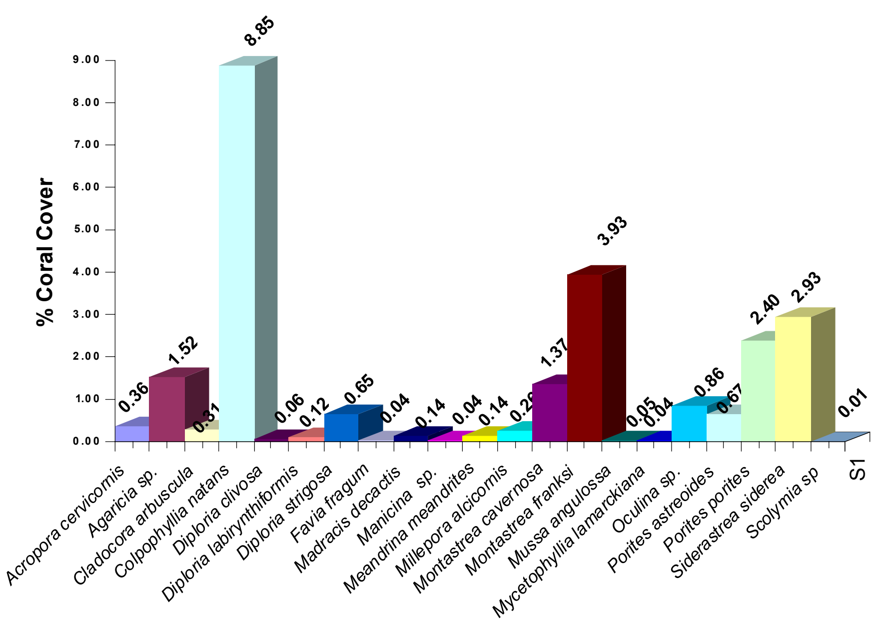
Coral species distribution for Enrique



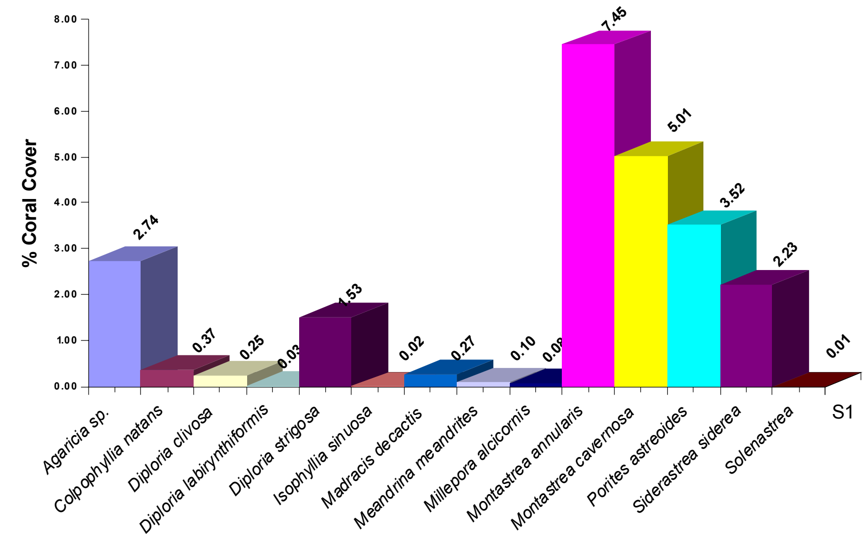
Coral species distribution for Ratones



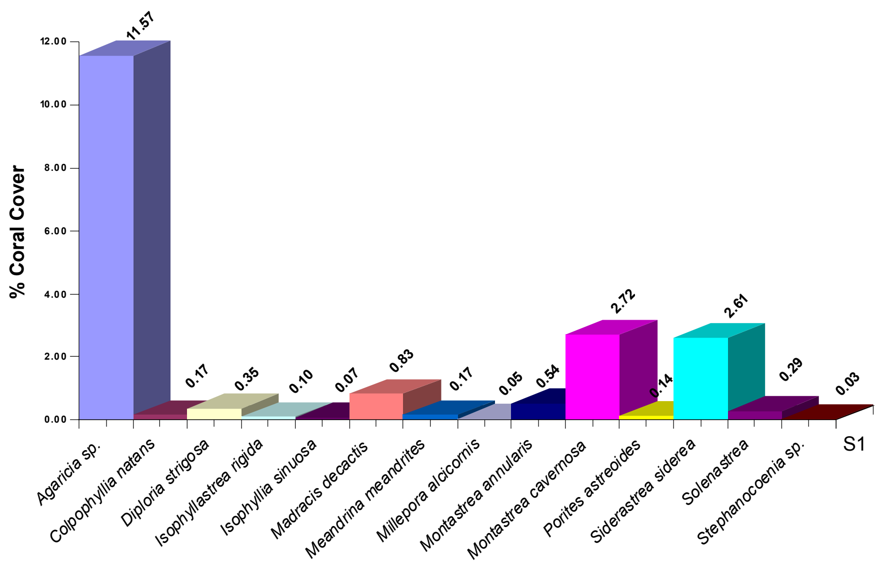
Coral species distribution for Mario



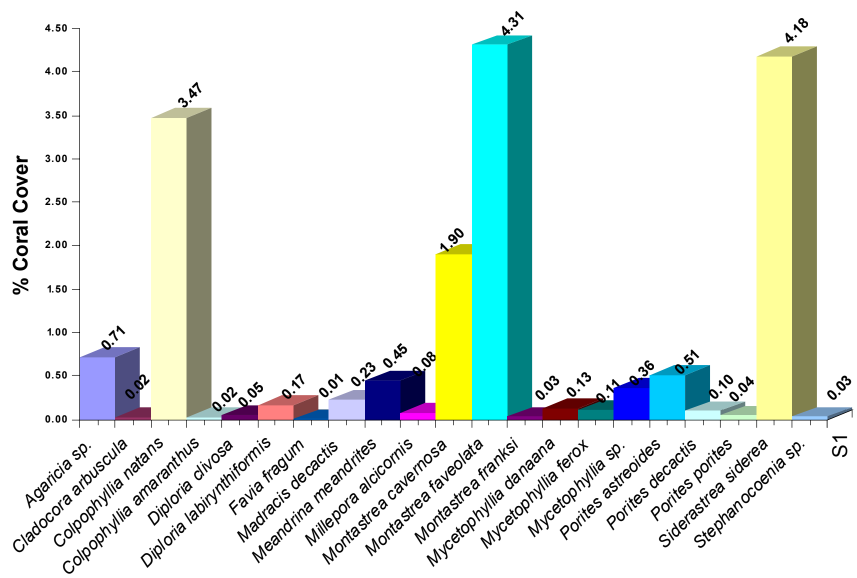
Coral species distribution for Fanduco



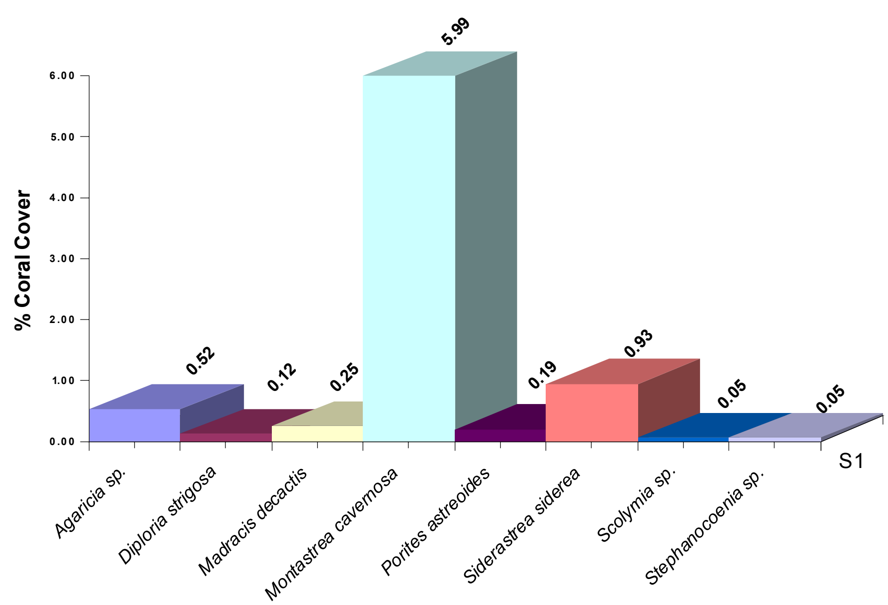
Coral species distribution for Cayo Caribe



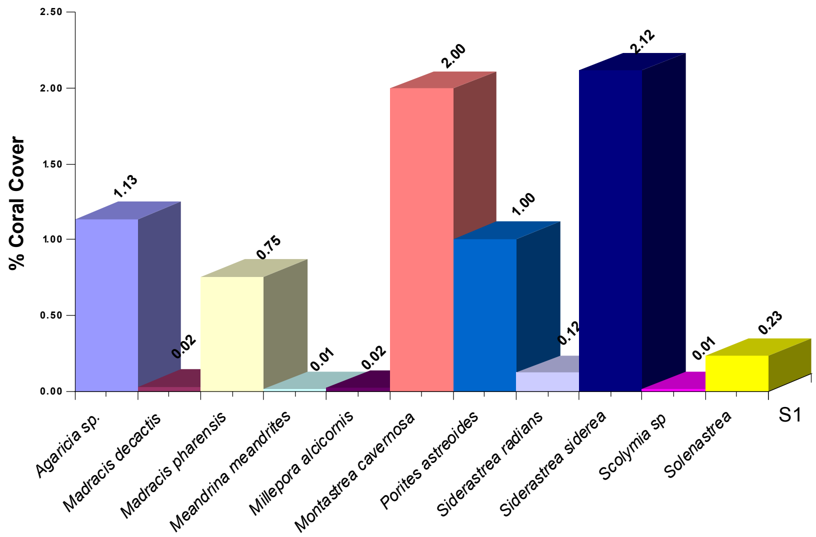
Coral species distribution for El Corral



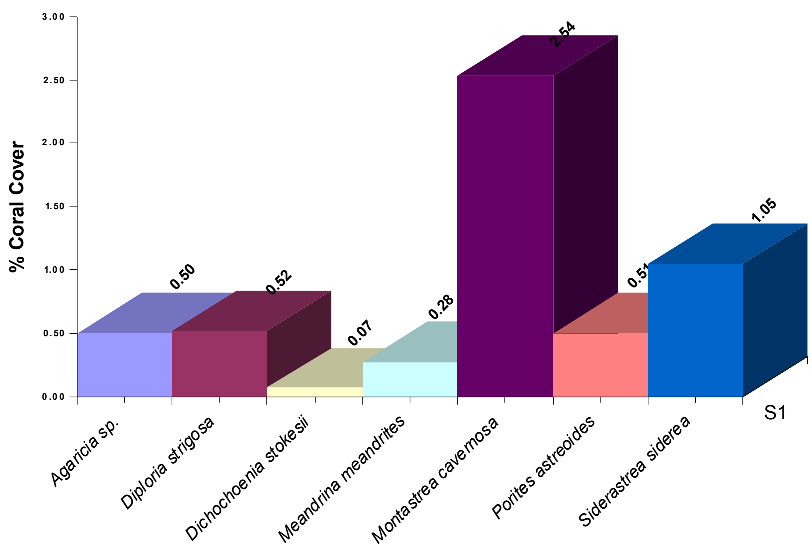
Coral species distribution for Rodriguez

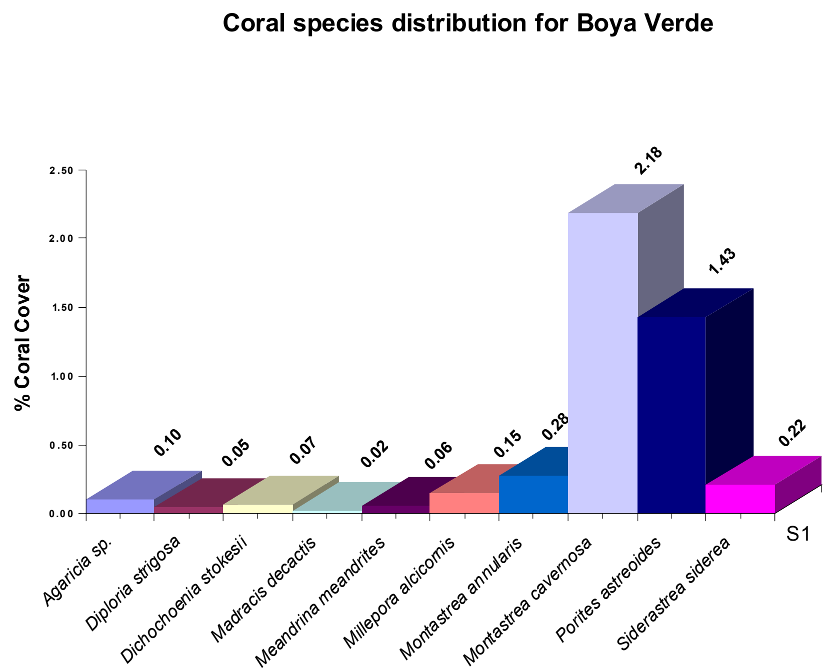


Coral species distribution for Cardona



Coral species distribution for Tasmania





Coral species distribution for Boya Verde
% Coral Cover
2.50
2.00
1.50
1.00
0.50
0.00
0.10
0.05
0.07
0.02
0.06
0.15
0.28
2.18
1.43
0.22
Agaricia sp.
Diploria strigosa
Dichochoenia stokesii
Madracis decactis
Meandrina meandrites
Millepora alcicornis
Montastrea annularis
Montastrea cavernosa
Porites astreoides
Siderastrea siderea
S1

APPENDIX D
Coral Species Distribution for Group I, II and III

Coral Species Distribution Tables

Group I Coral species	Coral Cover (%)
Acropora cervicornis	0.49
Agaricia sp.	6.60
Cladocora arbuscula	0.04
Colpophyllia amaranthus	0.01
Colpophyllia natans	4.32
Dendrogyra cylindrus	0.17
Dichochoenia stellaris	0.09
Dichochoenia stokesii	0.02
Diploria clivosa	0.76
Diploria labirynthiformis	0.62
Diploria strigosa	0.60
Favia fragum	0.00
Isophyllia sinuosa	0.04
Madracis decactis	0.06
Madracis pharensis	0.12
Madracis senaria	0.01
Manicina mayori	0.01
Meandrina meandrites	0.37
Millepora alcicornis	2.25
Millepora squarrosa	0.05
Montastraea annularis	18.63
Montastraea cavernosa	3.87
Montastraea faveolata	29.43
Montastraea franksi	17.08
Mycetophyllia danaana	0.22
Mycetophyllia ferox	0.03
Mycetophyllia lamarckiana	0.01
Mycetophyllia sp.	0.34
Porites astreoides	4.55
Porites decactis	0.67
Porites porites	5.38
Siderastrea siderea	3.14
Stephanocoenia sp.	0.01

Group II ***Coral species***	Coral Cover (%)
Acropora cervicornis	0.19
Agaricia sp.	19.92
Cladocora arbuscula	0.20
Colpophyllia amaranthus	0.04
Colpophyllia natans	13.42

Dichochoenia stokesii	0.19
Diploria clivosa	0.22
Diploria labirynthiformis	0.18
Diploria strigosa	3.06
Eusmilia fastigiata	0.19
Favia fragum	0.02
Isophyllastrea rigida	0.09
Isophyllia sinuosa	0.14
Madracis decactis	1.89
Madracis pharensis	0.08
Manicina mayori	0.05
Manicina sp.	0.02
Manicina aerolata	0.02
Meandrina meandrites	1.19
Millepora alcicornis	1.08
Montastraea annularis	16.58
Montastraea cavernosa	9.54
Montastraea faveolata	1.93
Montastraea franksi	5.70
Mussa angulossa	0.21
Mycetophyllia danaana	0.13
Mycetophyllia ferox	0.05
Mycetophyllia lamarckiana	0.09
Mycetophyllia sp.	0.46
Oculina sp.	0.39
Porites astreoides	7.02
Porites decactis	0.06
Porites divaricata	0.01
Porites porites	3.58
Scolymia sp.	0.01
Siderastrea radians	0.03
Siderastrea siderea	11.26
Solenastrea	0.21
Stephanocoenia sp.	0.56

Group III

Coral Species	**Coral Cover (%)**
Agaricia sp.	8.87
Dichochoenia stokesii	0.54
Diploria strigosa	2.71
Madracis decactis	1.16
Madracis pharensis	2.95
Meandrina meandrites	1.36
Millepora alcicornis	0.66
Montastraea annularis	1.08
Montastraea cavernosa	49.75
Porites astreoides	12.24
Scolymia sp.	0.25

Siderastrea radians	0.46
Siderastrea siderea	16.89
Solenastrea sp.	0.90
Stephanocoenia sp.	0.19