Morphometric Examination of Corallite and Colony Variability in the Caribbean Coral *Montastraea cavernosa*

By

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ABSTRACT

The genus *Montastraea* in the Caribbean was thought to be formed by two species, *M. annularis* and *M. cavernosa*. However, recent research has uncovered two more species in the *M. annularis* complex, and two different morphologies of *M. cavernosa* that commonly co-occur were separated based on polyp size and behavior. A small-polyped form mostly active during the day (diurnal ecomorph), and a large-polyped form only active during the night (nocturnal ecomorph). Nevertheless, no specific taxonomic separation has ever been proposed and most recent studies using this species lumped the two ecomorphs. In this work, a multivariate approach was used to explore the ecological, morphological and behavioral differences between the two behavioral ecomorphs of *M. cavernosa* proposed. Ecological surveys at four different reef localities of Puerto Rico showed that the two behavioral ecomorphs were abundant, but with a differential distribution along the reef profile. Results indicate that 90 % of shallow (6m) *M. cavernosa* colonies were of the diurnal ecomorph, and 60% of the deeper water (20 m) colonies were of the nocturnal ecomorph. High corallite and colony morphometric variability within each behavioral ecomorph across depth gradients support the idea that environmental factors might influence their morphology. Significant morphological differences in 10 micro-morphological characters analyzed in 60 colonies (30 diurnal and 30 nocturnal) from two reefs (Media Luna and Turrumote), and a Stepwise Canonical Discriminant Function Analysis, which separated two distinct groups (with 94.0% of all colonies correctly classified), suggest that the two behavioral ecomorphs are two separate species (sibling species). Reproductive and molecular analyses are now been conducted to support this hypothesis.

RESUMEN

El género *Monstastraea* en el Caribe estaba formado por dos especies: *M. annularis* y *M. cavernosa.* Estudios recientes han descubierto dos especies adicionales en el grupo de *M. annularis* y dos diferentes morfologías en *M. cavernosa* que comúnmente co-existen, estas fueron separadas en base al comportamiento y el tamaño del pólipo. El tamaño pequeño del pólipo esta asociado mayormente con la actividad diurna (ecomorfo diurno) y el tamaño grande del pólipo esta asociado mayormente con la actividad nocturna (ecomorfo nocturno). A pesar de esto, nunca se había propuesto una separación taxonómica específica. En este trabajo se utilizó un enfoque multivariado para explorar las diferencias ecológicas, morfológicas y comportamiento entre los dos ecomorfos de *M. cavernosa*. Estudios ecológicos en cuatro diferentes arrecifes de Puerto Rico evidenciaron que los dos ecomorfos eran abundantes, pero con una distribución marcada entre ambos a través del perfil del arrecife. Los resultados indicaron que un 90% de las colonias de *M. cavernosa* en aguas llanas (6 m) eran ecomorfos diurnos y un 60% de las colonias en aguas profundas (20 m) eran ecomorfos nocturnos. En la morfometría de los coralitos y las colonias se encontró una gran variabilidad, sustentando la idea que factores ambientales pueden influenciar su morfología. Diferencias significativas en la morfología se encontraron en los 10 caracteres micro-morfológicos analizados en 60 colonias (30 diurnas y 30 nocturnas) de los arrecifes Media Luna y Turromote. El análisis discriminatorio multivariado, el cual separó dos grupos distintos (94% de todas las colonias fueron clasificadas correctamente), sugiere que los dos ecomorfos son especies separadas (especies hermanas). Análisis reproductivos y moleculares están siendo realizados para apoyar esta hipótesis.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1 Introduction

Coral reefs are among the most diverse and valuable ecosystems on earth (Cesar et al. 2002). Much of the attention paid to coral reef communities in the past decades has resulted from concerns for the decline and potential loss of biodiversity. However, issues such as patterns of coral reef diversity, ecological interactions and historical relationships, are still not completely resolved, and development of effective conservation and management programs are reliant on the understanding of these issues (Gray 1997). A thorough knowledge of the organisms present in particular habitats is important because it allows a better understanding of the system, its components and their interactions (Knowlton and Jackson 1994; Knowlton 2001), therefore, reliable taxonomy is essential for understanding its biological and ecological roles. Sound conservation and management practices depend in part on the quality of the taxonomy on which they are based (Knowlton and Jackson 1994). In the Caribbean, the numbers of species of corals reported are variable depending on who makes the observations and what criteria are used to discriminate species. Three different concepts of what constitutes a species are commonly used on corals (O'Hara 1994). These are: (a) The Biological Species Concept (Mayr 1940; Paterson 1985); (b) The Evolutionary Species Concept (Simpson 1961); and (c) The Phylogenetic Species Concept (Cracraft 1983; Nixon and Wheeler 1990). The biological species concept defines species as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (Mayr 1940). Species are thus defined in terms of isolating mechanisms to crossbreeding. In corals, which are believed to have high hybridization rates, very few isolating mechanisms are known, hybrid inviability or sterility, short sperm life and gamete chemical recognition are some (Veron 1995). The evolutionary species concept defines species as populations or groups of populations with a common ancestor and evolutionary history (Simpson 1961). Species are held together by developmental, genetic and ecological constrains, not just heredity. This is the nearest of any general species concept that comes close to operational coral taxonomy (Veron 1995). The phylogenetic species concept emphasizes common origin and is a methodical concept where species are the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of characters states in comparable individuals (Nixon and Wheeler 1990; Wheeler and Nixon 1990). This concept, being character based, requires the assumption of a hierarchical taxonomy pattern. Cladistics is not, in Veron’s (1995) view, applicable to corals. Cladograms tend to exclude horizontal transmission of characters by hybridization and dispersion. Each of these concepts has strengths and weaknesses, and each emphasizes slightly different aspects of the evolutionary process and biological characteristics (O'Hara 1994). However, not even the biological species concept or derivations of it, nor most current views of the process of natural selection, seem to be supported by operational coral taxonomy (Veron 1995). This raises problems and confusion on how to define coral species and which characters are important in their definition. For most practical applications of coral taxonomy, species are adequately defined as clearly identifiable morphological discontinuities (Veron 1995). This concept however, breaks down across great geographic distances, is liable to break down in the face of molecular taxonomy, and is demonstrably artificial when dealing with evolutionary processes. Veron (1995) proposed the concept of the “components of species” which is based on the use of spatial variation, local abundance and dispersion information (component of the species) to describe species of coral. Not all species have all these components. A non-varying species endemic to a single location may consist of a single population whereas a widely distributed ‘species complex’ may consist of several tiers of complexity (Veron 1995). To describe these levels systematically and taxonomically in space and time, the terms metaspecies, syngameons, species, races, geographic subspecies, ecomorphs and populations are most useful. These terms are not limited to hierarchical levels having varying morphological and genetic implications, but they are essential to the understanding of biogeography and evolution of species in corals (Veron 1995).

Various studies have regarded morphological variants as different taxa (Emerson and Jacobson 1976) while other have lumped several species into one taxon because they are thought to be ecological variants (Zlatarski and Estallela 1982). Failure to identify cryptic and/or sibling species also contributes to misinterpretations of results in many studies (Weil and Knowlton 1994). Sibling species are those species that are morphologically similar and evolutionary closely related (the product of relative recent speciation). Cryptic species are those that show similar morphologies (coevolution) but are not phylogenetically closely related (species difficult to distinguish *in situ*). In the past, coral researchers have found that sibling species are very difficult or impossible to distinguish based on just morphological characters (Mayr 1963). These problems lead to general confusion, conflicts and inconsistencies in coral identification. From a functional perspective, the first need of a coral taxonomist, irrespective of the methods employed, is to gain an understanding of how species differ from each other *in situ* and how they vary intra-specifically *in situ* (Veron 1995).

There are 110 extant coral genera with approximately 550-700 species of zooxantellate corals described around the World (Veron 1995). Coral diversity in the Caribbean is low compared to the Indo-Pacific, however, it is potentially higher than what is believed today (Weil 2003; Weil 2004). In the Indo-Pacific geographic province, 80 genera composing approximately 600 species have been described compared with 27 genera and 56-80 species in the Atlantic Caribbean providence (Weil 2003). A tendency in coral taxonomy over the past 40 years has been to lump similar taxa into a few, highly variable species or splitting one variable taxon into several species (Brakel 1977). Such a treatment is usually premature and/or incorrect if such taxonomic decisions are based on too few samples and observations, too few characters, insufficient replicates, lack of biological and ecological information, lack of rigorous sampling designs, and lack of statistical analysis (Weil and Knowlton 1994). Some examples of taxonomic problematic species in Caribbean corals include the genera *Agaricia* (Lamark 1801), *Porites* (Link 1807) and *Montastraea* (Blainville 1830). Numerous growth forms (ecomorphs) have been described for *A. agaricites* (Linnaeus 1758) which have not been recognized as different species by most systematists and coral ecologists (Zlatarski and Estallela 1982). However, recent studies have shown specific differences with regard to reproductive traits (Van Morsel 1983; Chornesky 1986; Delvoye 1986) and the degree of larval specificity to a metamorphosis inducer in two ecomorphs (Morse et al. 1988), contradicting the lumping treatment of Zlatarsky and Estellela (1982). There has been a long standing controversy whether or not two ecomorphs of *Porites astreoides* (Lamarck 1816) represent distinct species (Weil 1992b; Potts et al. 1994). Garthwaite and Potts (1994) and Potts *et al* (1994) proposed the existence of two ‘sibling species’ based on electrophoresis. As with non-molecular taxonomy, the collection of samples was guided by the *in situ* co-occurrence of visually distinct colonies. Weil (1992b) however, using a multi-character approach (molecular, ecological, and mophometrics) with populations from a wide geographic area in the Southern Caribbean provided evidence which was contradictory to the separation of the two color-morphotypes of *Porites astreoides* as different species. Weil (1992a, b) also provided diagnostic characters (molecular and morphological) to separate the three branching morphologies of *Porites* into three species.

The genus *Montastraea* belongs in the family Faviidae which contains more genera (24) than any other scleractinian family and is second only to the Acroporidae in number of extant species (approximately 127), as well as overall abundance throughout the Indo-Pacific and Caribbean (Veron 2000). All *Montastraea* species are zooxantellated and colonial (Veron 2000). Two genera, *Favia* (Oken 1815) and *Montastraea* (Blainville 1830) are common to both the Indo-Pacific and Atlantic (Veron 1995). *Montastraea* is distinguished from *Favia* by having extratentacular rather than intratentacular budding (Veron 2000). In *Montastraea* which consists of approximately twelve species, colonies are massive and either flat or dome-shaped. Corallites are monocentric and plocoid. Daughter corallites are predominantly formed by extratentacular budding (from the walls of the parent corallites) and some intratentacular budding may also occur. In the Indo-Pacific, *Montastraea* is a poorly defined genus although it contains mostly distinctive species within a given region (Veron 2000). Based primarily on corallite size, the genus can be divided into three groups: (1) Species with small corallites (less than 7 mm diameter) and no 'groove and tubercle' formation. This group includes *M. serageldini*

(Veron 2000), *M. curta* (Dana 1846), and *M. salebrosa* (Nemenzo 1959) in the Indo-Pacific, and *M. annularis*, *M. faveolata and M. franksi* in the Caribbean; (2) Species with intermediate sized corallites (5-8 mm diameters) and the presence of a groove and tubercle. This group includes *M. colemani* (Veron 2000), *M. annuligera* (Milne Edwards and Haime 1849), and *M. multipunctata* (Hodgson 1985), all in the Indo-Pacific. However, the presence of a groove and tubercle, which have been utilized as taxonomic characters (Veron 2000), has been attributed to polychaetes, thus, its validity now is in doubt. Underwater, they appear as irregular gaps or holes between some or all corallites and when fully developed, the corallites appear detached from each other, (3) Species with large corallites (over 9 mm in diameter) which includes *M. cavernosa* in the Caribbean, and *M. valenciennesi* (Milne Edwards and Haime 1848), and *M. magnistellata* (Chevalier 1971) in the Indo-Pacific. In the geological record, the genus *Montastraea* first appeared in the late Jurasic (150 million years ago)(Wells 1956), although Budd and Coates (1992) argue that the genus appeared later in the Cretaceous (100 millions years ago) in the Tethys. The first record for *Montastraea* in the Caribbean is from the Eocene (51 millions years ago).

In the Caribbean, the genus *Montastraea* is currently the major frame builder of coral reefs (Goreau 1959; Hoffmeister and Multer 1964). For many years it was accepted that *M. annularis* (Ellis and Solander 1786) was the perfect generalist species because of its broad depth and geographical distributions and highly variable colony forms (Goreau 1959; Connell 1978). Most of this variability was though to be due to environmental, depth-dependent gradients which influenced corals directly or indirectly through their zooxanthellae (Dustan 1975; Graus and Macintyre 1976; Foster 1977; Foster 1979;

Foster 1980; Graus and Macintyre 1982; Battey and Porter 1989). However, many of the different morphologies co-occur within the same reef habitat and micro habitat where differences in environmental factors such as light, competition, bioerosion, and wave action appear to be insufficient to explain the extensive variation observed over small spatial scales (Graus and Macintyre 1982; Tomascik 1990; Knowlton et al. 1992; Weil and Knowlton 1994). The problem of coexisting differing colony morphologies led to the use of a multi-character approach to study the *Montastraea annularis* species complex and other problematic genera (Knowlton et al. 1992; Weil 1992a; Knowlton and Jackson 1994). Recognition of consistent significant differences in biochemical, behavioral, physiological and morphological traits among three common, shallow water "ecomorphs" (Knowlton et al. 1992) across a wide geographic area led to the re-description of *M. annularis* and the resurrection of two sibling species, *M. franksi* (Gregory 1985) and *M. faveolata* (Ellis & Solander 1986), (Weil and Knowlton 1994). A similar approach work in Curacao showed that *M. annularis* populations were comprised of at least 3 recognizable morphotypes (Van Veghel 1993). Significant differences were found in allelic frequencies, behavior and morphometric among the three morphotypes, however, because no fixed allelic differences were found, it was concluded there was not enough evidence to separate the morphs into species (Van Veghel and Bak, 1994).

The fourth described species of *Montastraea* in the Caribbean is *M. cavernosa* (Linnaeus 1766). This species also shows different coexisting colony morphologies and a high degree of "intraspecific" variability (Lasker 1976; Lasker 1979; Lasker 1980; Lasker 1981; Foster 1985; Budd 1991). *M. cavernosa* colonies are massive, forming boulders, domes, or flat plates and an important constituent of reefs in the Caribbean.

Corallites are usually conical and exerted, highly variable across habitats and depth gradients. Long and short septa are conspicuously alternated, with both septa joined to the columella. Colony colors are also highly variable with green, brown, grey, blue and red colonies commonly found. It inhabits many different reef environments, particularly lower slopes. Among the characters that display variability, polyp expansion, zooxanthella density, coloration, polyp shape, colony shape, and polyp size are most conspicuous. These characters have been used to separate shallow water (<20m) colonies into two ecomorphs, which are associated with diurnal or nocturnal polyp behavior (Lasker 1976; Lasker 1977; Lasker 1979; Lasker 1980; Lasker 1981). The "**diurnal ecomorph**" has small polyps (<6 mm diameter), which are expanded continuously during the day and also at night (diurnal activity). The other ecomorph has larger corallites (>7 mm diameter) which are only expanded at night (nocturnal activity), this is the "**nocturnal ecomorph**". During the day, these ecomorphs are easily distinguished because the diurnal ecomorph colonies will have most of its polyps expanded and they are mostly small, and the nocturnal ecomorph colonies will have most of its polyps contracted within the larger corallites. The nocturnal morph seems to be a superior predator compared to the diurnal morph because of its substantially longer tentacles (Lasker 1976) and it has greater sensitivity to potential prey items (Porter 1974). *M. cavernosa* is a gonochoric species, with a long (11 month) oogenic cycle, and a shorter (4 month) spermatogenic cycle that ends with the broadcasting of gametes during evening hours, 1 week after the full moon of July to September (Szmant 1986; Soong 1991; Szmant 1991; Wyers et al. 1991; Gittings et al. 1992; Van Veghel 1993; Steiner 1995). In many localities of the Caribbean, a potential third ecomorph with large but loose conical calices (low integration), usually different coloration patterns, has been observed (Weil 2003). Recent research in Colombia, showed reproductive asynchrony in some populations, particularly in male colonies reaching sexual maturity late in the reproduction cycle by November (Acosta and Zea 1997).

All these observations and the coexistence within the same habitat of two or three different ecomorphs, suggest the possibility that there is also a *M. cavernosa* species complex formed by at least two species. Variability can occur in direct response to the environment (phenotypic plasticity), by genetic differentiation, or both (Amaral 1994). The high abundances and wide local and geographic distribution of *M. cavernosa* poses again the question about this species being another "generalists" or, if like in the *M. annularis* case, it turns out that the wide variability is due to a complex of sibling species. Thus, this species is an excellent candidate for a multivariate analyses of morphological character variability to assess the presence of morphological discontinuities, diagnostic characters, and ecological differences useful for discriminating any potential species boundaries in the coexisting ecomorphs. This is the first quantitative attempt to separate the two common behavioral ecomorphs of *M. cavernosa* using a multivariate approach that included polyp behavior, morphometric analyses at the corallite and colony levels and ecological characteristics.

Research focus and questions

The goals of this project were to examine the ecological and morphological variability of the two common behavioral ecomorphs of *M. cavernosa*, the small-polyped diurnal ecomorph (polyps active during the day), and large-polyped nocturnal ecomorph (polyps active only at night). This work explored the taxonomic significance of the distribution of colonies, their behavior, color patterns, shape and size of colonies; and their corallite morphometric variability within and across colonies. Variability of characters was compared across different depths in two coral reefs off La Parguera, on the southwest of Puerto Rico and Carlos Rosario, in Culebra Island on the east coast of Puerto Rico. The following questions were developed to assess the morphological and ecological differentiation and the characterization of potential species boundaries in *M. cavernosa*.

Ecological characters:

1. **What is the variability in colony shape, polyp size, colony and oral disc coloration within and between the two *M. cavernosa* ecomorphs (diurnal activity/nocturnal activity)?**
    - H_{01}: There are no differences in polyp size, colony shape, colony coloration and oral disc coloration within and between the two ecomorphs (diurnal / nocturnal).
    - H_{11}: There are significant differences in polyp size, colony shape, colony coloration and oral disc coloration within and between the two ecomorphs (diurnal / nocturnal).
2. **What is the variability in distribution and abundance of the two ecomorphs of *M. cavernosa* across depth gradients?**
    - H_{02}: There are no significant differences in the distribution and abundances of the two ecomorphs across different depths.

- H_{12}: There are significant differences in the distribution and abundances of the two ecomorphs across different depths.

Morphological characters:

1. **What is the variability of micro-skeletal characters within each behavioral ecomorph?**
    - H_{03}: There are no significant differences in the micro-skeletal characters within colonies of each behavioral ecomorph within and across reefs.
    - H_{13}: There are significant differences in the micro-skeletal characters within colonies of each behavioral ecomorph within and across reefs.

    Across Habitats?

    - H_{04}: There are no significant differences in the micro-skeletal characters among colonies of each behavioral ecomorph across habitats within reefs.
    - H_{14}: There are significant differences in the micro-skeletal characters among colonies of each behavioral ecomorph across habitats within reefs.

2. **How morphologically different are the two *M. cavernosa* behavioral ecomorphs at the corallite and colony level?**
    - H_{05}: There are no significant differences in the micro-skeletal characters at the corallite and colony level between *M. cavernosa* behavioral ecomorphs within and across reefs.

- H_{15}: At least one micro-skeletal character at the corallite and colony level is significantly different between the *M. cavernosa* behavioral ecomorphs within and across reefs.

3. **Is polyp activity a good diagnostic character to separate potentially different species of *Montastraea cavernosa*?**
   - $H_{06:}$ Polyp activity is a good diagnostic character to separate species in *M. cavernosa.*
   - $H_{16:}$ Polyp activity is not a good diagnostic character to separate species in *M. cavernosa.*
4. **Is there more than one species in the morphological complex of *M. cavernosa*?**
   - $H_{07:}$ *M. cavernosa* is single species but it is highly variable (behavioral, morphometric) at the colony and corallite level.
   - H_{17}: *M. cavernosa* is a complex of at least two different species

2 Methodology

2.1 Study Area

Four separated coral reefs localities were surveyed to assess the ecological, behavioral and morphometric differences between different ecomorphs of the coral *M. cavernosa* in Puerto Rico: Media Luna (17’56.096’ N- 67’02.911’ W), Turrumonte (17’56.097’ N- 67’01.130’ W), El Beril (17’53.291’ N- 66’59.871’ W) in La Parguera, southwest coast of Puerto Rico, and Carlos Rosario (18’19.520’ N- 65’19.866’ W) in the island of Culebra on the eastern coast of Puerto Rico (Figure 2.1).

La Parguera is characterized by a dry climate, moderate wave energy and an extensive insular shelf platform (approximately five miles wide)(Almy and Carrion-Torres 1963). The average surface salinity is 35.2 ppt and the mean surface water temperature is 28.4 C° (Garcia et al. 1998). These conditions have allowed the growth and development of scleractinian corals and the development of over thirteen emergent and many submerged coral reefs (Morelock et al. 2001). These reefs are among the best studied of the shallow coral reef systems to a certain extent serving to describe the reefs of the Caribbean region (Glynn et al. 1965; Ballantine et al. 2000). Reefs of La Parguera have a predominately east-west orientation which roughly parallels the coast (Fig. 2.1). The prevailing wind-generated waves are from the south-southeast, establishing unidirectional currents that flow over the reef crests and towards the back reef (Almy and Carrion-Torres 1963). Supra-tidal rubble bars composed primary of storm generated *Acropora palmata* (Lamarck 1816) fragments form small islets on the two reefs studied.

Media Luna (17’56.096’ N- 67’02.911’ W) is located 4 km south of the Isla Magueyes research station (fig. 2.1). This reef is ±1.7 km long and ± 686 meters wide. The back reef is in shallow water and the bottom is dominated by fine-grained sediments which support extensive growth of the marine angiosperm *Thalassia testudinum* (König 1805) and other seagrasses. Coral rubble, scattered coral heads and patches of *Porites* are commonly encountered on the reef flat. Seaward of the reef crest, *Acropora palmata* is a dominant coral. A platform 6 m deep extends approximately 250 meters seaward, on which gorgonians dominate the substratum. Seaward of the platform, the reef slopes breaks at an angle of 45˚ to 60˚ to water depths of 20 meters. All the *M. cavernosa* colonies for the morphological analysis were collected between 6-20 meters in depth (n=30).

Turrumote reef (17’56.097’ N- 67’01.130’ W) is located 4.8 km to the south-east of Magueyes Island and it is roughly 781 meters long by 500 meters wide. The exposed islet is comprised almost entirely of dead pieces of *A. palmata*. Seaward, the shallow platform of consolidated substrata has scattered colonies of live *A. palmata* and *A. cervicornis,* extends approximately 130 meters from the shore. Beyond the *Acropora* zone and at depth up to 15 m, large colonies of *M. faveolata* dominate. From 15 to 20 meters deep, the reef has many species of stony corals and at the base of the reef, an algal plain is present. All of the *M. cavernosa* colonies for the morphological analysis were collected between 6-20 meters in depth (n=30). Wave energy is very strong in this location. The distance between Media Luna and Turrumote is about 3 km.

Culebra Island is located at approximately 28 miles off Fajardo, northeastern Puerto Rico. Carlos Rosario reef is within the Luis Peña Channel Marine Fisheries Reserve at the northwest coast of Culebra. This fringing reef is characterized by clear waters and a 40-50 % of coral coverage. The most dominant species of coral in the reserve is *Montastraea annularis* with 75 % of the coral cover (Hernandez-Delgado 2000).

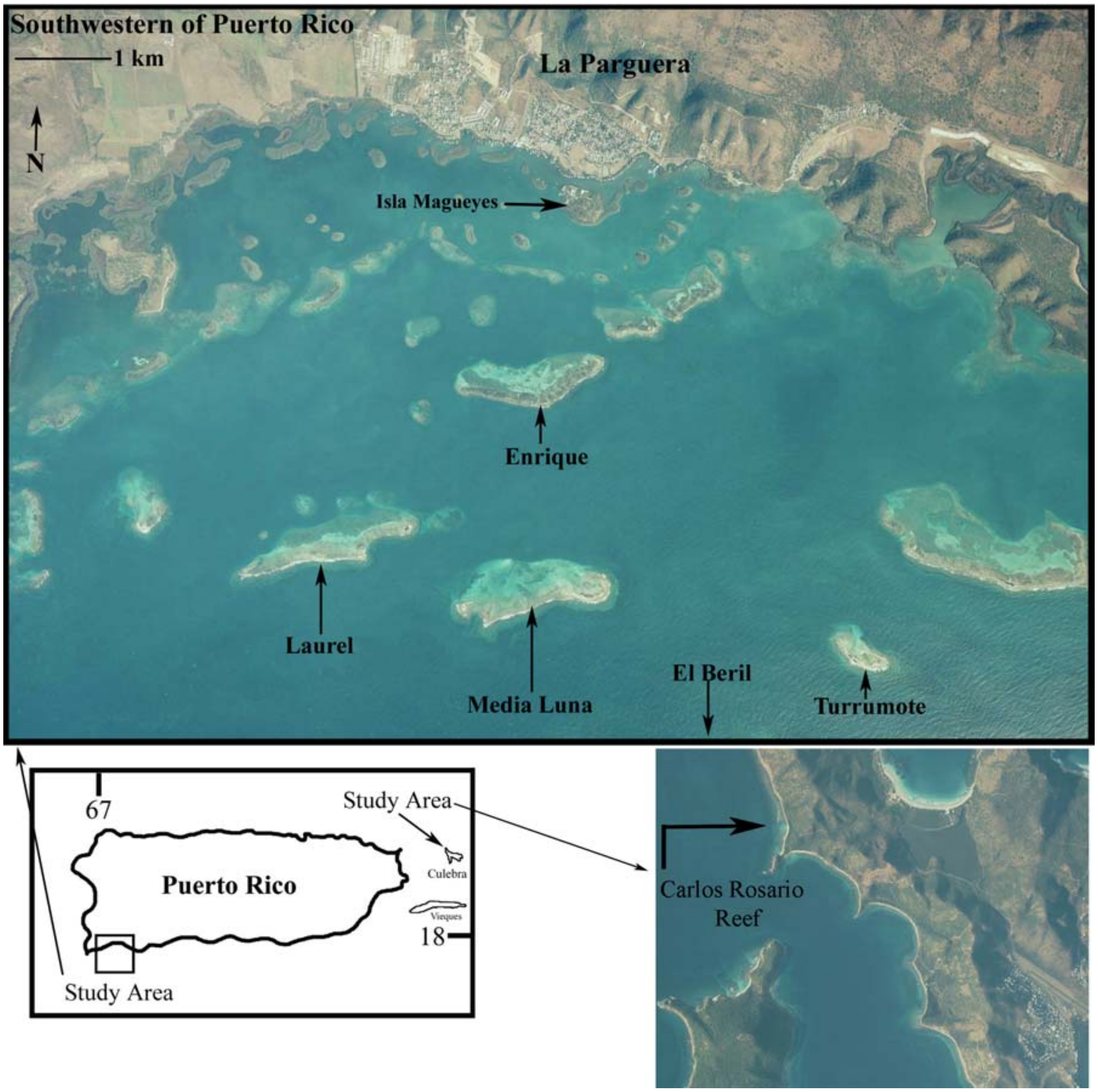

Figure 2.1 Diagram of the Puerto Rico archipelago and aerial photograph of La Parguera, Southwestern of Puerto Rico and Carlos Rosario, Culebra showing the geographical position of the collecting sites (Photo from USNOAA-NOS-NCCOSBP, 2001).

2.2 Distribution of ecomorphs

Each of the four coral reefs was surveyed to check for the distribution and abundance of colonies and variant morphologies in the area. Field surveys were carried out from January 2000 until May 2002. Information about the abundances and ecomorphs, size structure and distribution in the depth gradient was collected using six 40 m^2 band transects (2m wide by 20 m long) haphazardly placed at each of the three different depth intervals from the reef platform to the deepest reef areas (0-7, 8-10, 11-20 meters). Belt transects were placed parallel to the reef crest.

2.3 Size structure of each ecomorph

All colonies of the two behavioral ecomorphs found within the 40 m^2 band transects were measured (maximum length and width) to estimate the size class distribution of each populations. Morphological variants were identified in the field on the basis of colony-level characters (polyp size) and polyp behavior (diurnal or nocturnal) (Figure 2.2). Size class distribution was analyzed following the method used by Bak and Meester (1998). Total live surface area of each colony was estimated by the ellipse formula:

$$A = \pi\, a\, b$$

Where, A = area, a and b are major and minor axis respectively, and π = 3.141516. The surface area was transformed logarithmically ($\log_{10}$) and frequency distribution parameters (mean size, standard error and coefficient of variability) were calculated for each behavioral ecomorph.

2.4 Morphology, behavior and coloration patterns

The morphology, behavior and coloration data of each of the colonies of both behavioral ecomorphs found within each of the 40 m² band transect were recorded *in situ*. In order to characterize the behavioral differences (diurnal and nocturnal) all the colonies were monitored (from 7:00 a.m. to 3:00 p.m.) for daytime expansion behavior. Daytime observations of the behavior of polyps (active, expanded or inactive retracted) were used to develop quantitative criteria to characterize the expansion behavior. The classification distinguished those colonies which were regularly expanded (diurnal) from those which were never expanded during the day (nocturnal). Polyp size, in most cases, was recorded as large or small depending on whether the calical diameter was less than or greater than 6 mm. Polyp size was usually apparent at first observation, since most colonies with large polyps had mean diameter above the 6 mm cutoff. In cases of uncertainty, 5-10 polyps were measured with a ruler and an average determined. Colony color was scored by noting three different ectodermal colors: brown, green and red. The three colors were recorded as being absent or present. The oral disc was usually the same color as the colony, but in some cases had different colors (white, green, brown, red and yellow) which were also noted.

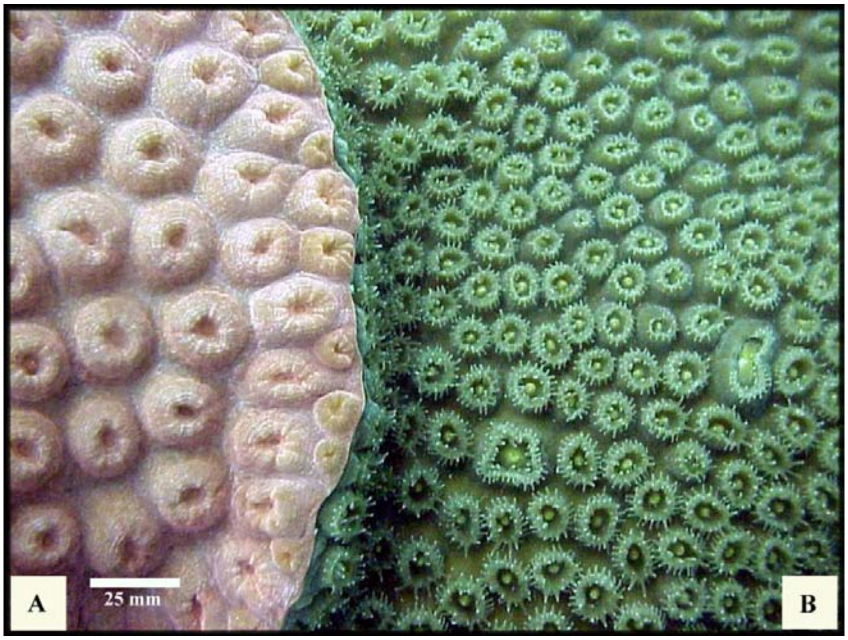

Figure 2.2 Live *in situ* colonies of *Montastraea cavernosa* ecomorphs: A. Nocturnal, B. Diurnal.

2.5 Morphometrics

The work of Amaral (1994) in *M. cavernosa* morphological variation did not separate the two behavioral ecomorphs and this resulted in high variability between colonies, localities and depths on most of the characters measured. In this research, polyp activity was the criteria used to separate the two *M. cavernosa* ecomorphs for the morphometric analyses. Samples were collected from two of the 4 areas surveyed, Media Luna and Turrumote reefs (Figure 2.1). Before collecting the sample, colonies were measured, and their coloration, polyp behavior, habitat, depth and position on the substratum *in situ* were noted. Colonies were tagged and photographed (general view and closed-up with calibration ruler) with a digital camera (Cannon G-2) in an underwater housing (Ikelite® # IK6142). Fifteen representative fragments (10-100 cm^2)

of each of fifteen separated colonies of each behavioral ecomorph of *M. cavernosa* were collected in Media Luna and Turrumonte reefs (Figure 2.3). Samples were collected from May 2002 until August 2003. Within each reef, five samples of each behavioral ecomorph were collected in each of three different depth intervals (0-7, 8-10, 11-20 meters). Fragments were chipped from the basal edge and the center of each colony with a hammer and chisel to minimize damage to the remainder of the colony, labeled, placed in previously labeled 10-gallon zip-locks bags and transported to the lab. Individual fragments were then bleached in 10% sodium hypochlorite in seawater for 24 hours to dissolve the coral tissue without damaging the skeletal elements, rinsed in fresh water, and dried for micro-morphometric measurements. Ten characters (Table 2.1) in each of ten haphazardly chosen corallites from each fragments were measured (Figure 2.4) using digital photographs taken with a DXC-107 Sony video camera system attached to an Olympus SZH-10 stereo microscope and a PVM-1353MD Sony 13' fine pitch high resolution monitor. Measurements were done using SigmaScan (SPSS Inc.) image analysis software on monochromic, high resolution, digital images of each corallite after the corresponding calibration (Figure 2.4). Foster (1985) indicated that a minimum of 5 corallites were necessary to characterize a colony. The characters measured (Table 2.1) were selected based on previous morphological studies of *Montastraea* species (Foster 1985; Amaral 1994; Weil and Knowlton 1994) and includes the most important features used to distinguish species in the family Faviidae (Foster 1985, Table 2.1).

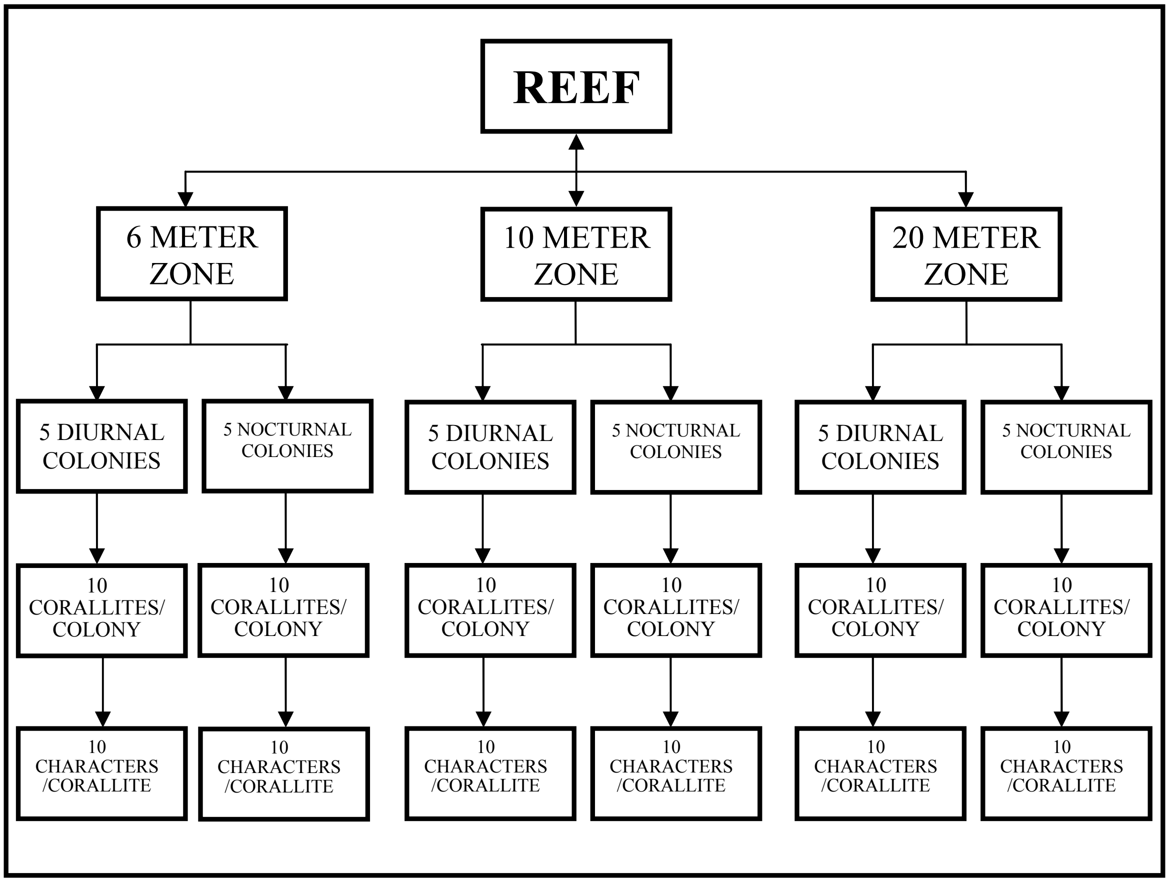

Figure 2.3 A diagram of the experimental design for the morphological analysis of *Montastraea cavernosa* ecomorphs.

2.6 Statistics

The data was analyzed using univariate and multivariate tests with the SPSS + statistical package (v.10, SPSS, Inc, Chicago, licensed to E. Weil). Intra-colony averages for each character were used to analyze the variation at the inter-colony, intra-reef, and inter-reef levels within each ecomorphs. These means were also used to analyze the variations between the two behavioral ecomorphs at the intra-reef (within reef) and intra-regional (within La Parguera) levels. For some micro-skeletal characters, the normality test for the data set failed, so Kruskall-Wallis One Way Analysis of Variance was used to detect significant differences within and across colonies, across depth intervals and reef localities and between behavioral ecomorphs. Then, a Stepwise Canonical Discriminant Function Analysis (SCDFA) (stepwise selection) was used to explore if the previously separated groups (by behavioral and colony-level traits) were mutually exclusive. Selection of characters used in the analysis was based on a stepwise method which minimized Wilk’s lambda.

Table 2.1 List of the micro-characters measured in *Montastraea cavernosa* colonies

Character	Abbreviation	Description
Corallite diameter	CD	Linear measure between theca/corallite cavity margins; average lengths.
Spacing of corallites	CS	Linear measure between theca/corallite wall margins of the nearest neighboring corallites.
Columella width	CW	Linear measure across the columella; average lengths.
Length of first cycle septa	L1S	Linear measure of length of first cycle septa; average.
Thickness of the first cycle septa	T1S	Linear measure of thickness of septa at septum midpoint; average.
Length of the first cycle costae	L1C	Linear measure of costae length from corallite cavity margin to the end of costae; average.
Thickness of the first cycle costae	T1C	Linear measure of costae thickness at mid point; average.
Length of the fourth cycle septa	L4S	Linear measure between columella and corallite cavity margins at the 4 cycle; average.
Length of the fourth cycle costae	L4C	Linear measure between corallite cavity margin and coenosteum margin at the 4 cycle; average.
Thickness of the fourth cycle costae	T4C	Linear measure of costae thickness at L4C; average.

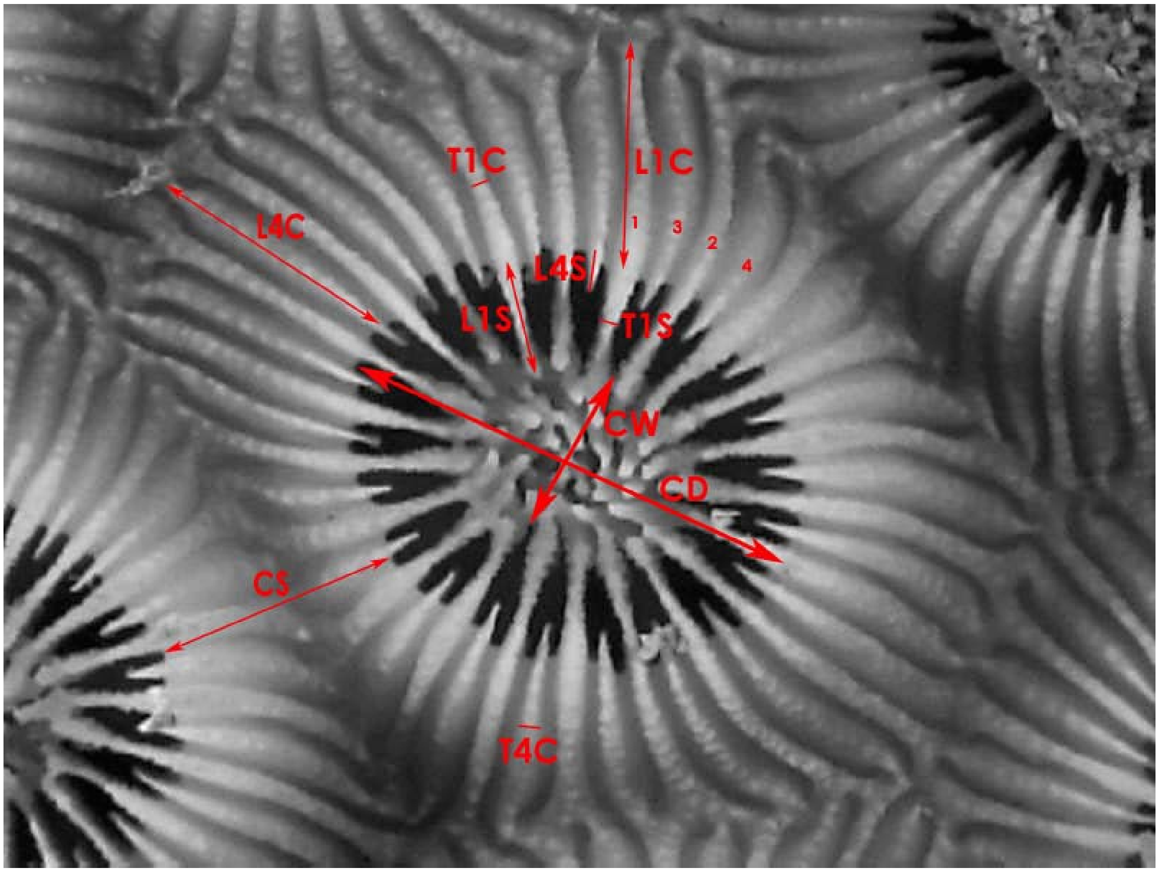

Figure 2.4 Diagram of a corallite from *Montastraea cavernosa* illustrating the measurements done for the morphometric analyses (see Table 1).

3 Results

3.1 Ecology

3.1.1 Behavioral and coloration patterns

The different morphologies (ecomorphs) of *M. cavernosa* were first identified in the field on the basis of their polyp expansion behavior (Lasker, 1980), but they were also distinguishable on the basis of a number other morphological characters, most conspicuously, polyp size which was well correlated with polyp behavior. The diurnal ecomorph was significantly associated with small polyps (≤ 6.5 mm), and were more commonly planar in shape (Table 3.1). The diurnal ecomorph colonies were most commonly associated with brown colony coloration and 43% of the colonies had brilliant green oral discs. Large polyped colonies on the other hand (> 7 mm) had mostly nodular and massive colonies and were only active (expanded polyps) during the night period (nocturnal ecomorph). Colonies of this ecomorph were mostly brown, orange or red. From here on, the behavioral diurnal ecomorphs is the one with small polyps and brownish or green colorations and the nocturnal ecomorph is the one with large polyps and usually orange, red or olive-green coloration.

3.1.2 Distribution and colony size of behavioral ecomorphs

The two behavioral ecomorphs were abundant in three of the reefs surveyed and at intermediate depths (10 meters) they were routinely found together. However, distributional data for the two reefs in Parguera (Fig.3.1) revealed clear distributional differences among the ecomorphs. The diurnal ecomorph was significantly (X^2-test, $p<0.01$) most abundant in shallow-to-intermediate depth habitats (6-10 m) compared to the nocturnal morph. The nocturnal ecomorph was significantly (X^2-test, $p<0.01$) more abundant between 15 and 20 meters with 60 % of all colonies found at this depth belonging to this ecomorph. Observations at other sites generally supported this pattern of distribution for the two behavioral ecomorphs. The raw data was transformed ($\log_{10}$) because the distribution was highly skewed. Colonies of the diurnal ecomorph were significantly (T-test, $p<0.001$) smaller (with an average surface area of 826.60 ± 3.60 cm$^{2)}$ compared to those of the nocturnal morph (1,158.51 ± 3.90 cm^2) (Fig. 3.2). The diurnal *M. cavernosa* ecomorphs showed higher numbers of juvenile and intermediate size colonies. The skewness calculated for the two ecomorphs after the transformation ($\log_{10}$) was negative (-0.27 diurnal and -0.69 nocturnal).

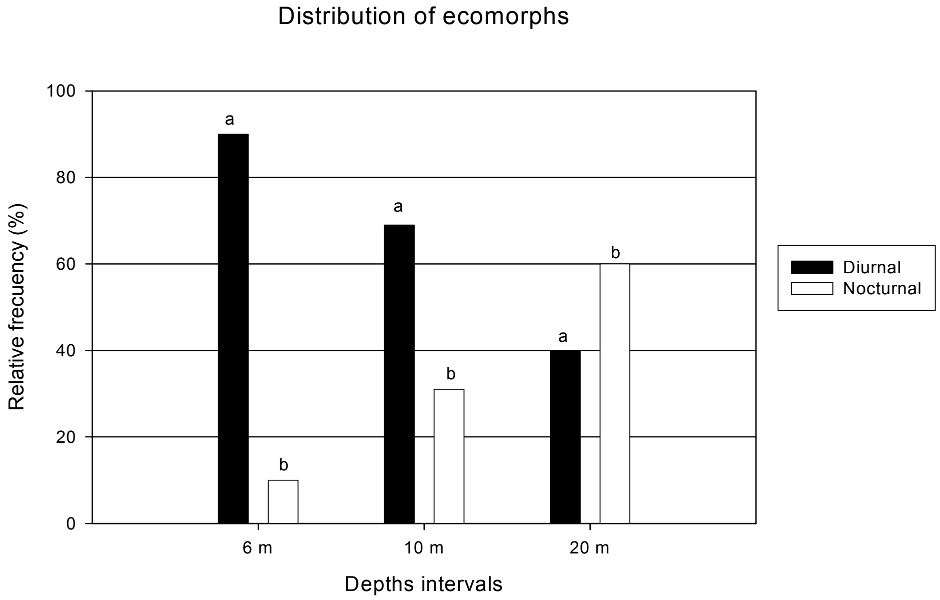

Figure 3.1 Percent of *M. cavernosa* colonies of the diurnal ecomorph (small polyps) and nocturnal ecomorph (large polyps) found in each of the three different depth zones at Media Luna, Turrumote and Carlos Rosario reefs. The distribution is based on observations of 612 colonies.

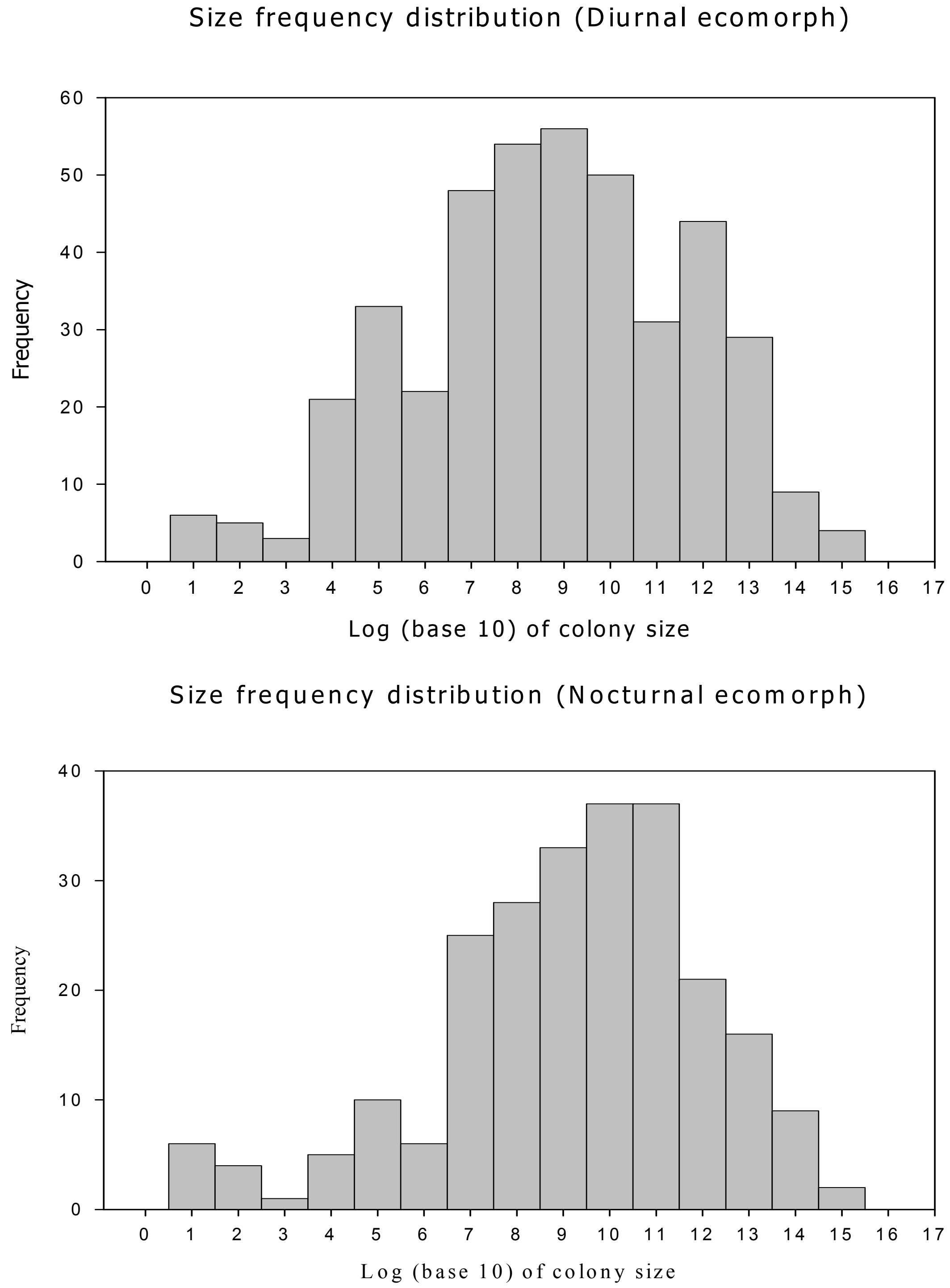

Figure 3.2 Interspecific variation in size class distribution for all of *M. cavernosa* measured in Media Luna, Turrumote, El Beril and Carlos Rosario.

Table 3.1 Contingency tables showing the relationship between daytime polyp expansion and morphological traits among colonies of *M. cavernosa* from reefs along Puerto Rico's Caribbean coast. Contracted (n=274) Expanded (n=287).

		Daytime Polyp expansion		Significance of x^2- test
		contracted (Nocturnal ecomorph)	expanded (Diurnal ecomorph)	
Polyp size	large	218	28	P < 0.001
	small	56	259	
Colony shape	planar	108	225	P < 0.001
	nodular	166	62	
Brown coenosarc pigment	present	176	221	P < 0.005
	absent	98	66	
Green coenosarc pigment	present	28	17	P < 0.01
	absent	246	270	
Red coenosarc pigment	present	67	47	P < 0.025
	absent	207	240	
White oral disc	present	38	67	P < 0.01
	absent	236	220	
Green oral disc	present	83	123	P < 0.005
	absent	191	164	
Brown oral disc	present	87	86	P < 0.95
	absent	187	201	
Red oral disc	present	53	7	P < 0.001
	absent	226	275	
Yellow oral disc	present	12	4	P < 0.1
	absent	262	283	

3.2 Micro-morphometrics

3.2.1 Morphometric variability within habitats in each ecomorph at Media Luna

For colonies collected at 6 m depth in Media Luna Reef, results showed that there were significant differences (Kruskal-Wallis, $p<0.05$) among the colonies of the diurnal ecomorph in eight out of the ten micro-skeletal characters measured. Similar results were obtained for the nocturnal ecomorph with significant differences (Kruskal-Wallis, $p<0.05$) among colonies in the means of eight of the micro-skeletal characters (Table 3.2).

For colonies collected at 10 m depth, significant differences (Kruskal-Wallis, $P<0.05$) were found between the colony means of eight micro-skeletal characters among the colonies of the diurnal ecomorph. The nocturnal ecomorph had fewer characters showing significant inter-colony variability at this depth than the diurnal ecomorph with only six micro-skeletal characters which varied significantly (Kruskal-Wallis, $p<0.05$) among colonies. The only common micro-skeletal character did not vary significantly in each of the two ecomorphs was the thickness of the first cycle septa (Table 3.2).

At 20 m depth, eight micro-skeletal characters varied significantly (Kruskal-Wallis, $p<0.05$) among colonies of the diurnal ecomorph and only six characters varied significantly (Kruskal-Wallis, $p<0.05$) in the nocturnal morph. Of the four micro-skeletal characters that did not varied in the nocturnal ecomorph at this depth, three [corallite diameter (CD), length of the first cycle costae (L1C) and the length of the fourth cycle costae (L4C)] did not vary at 10 m neither (Table 3.2).

3.2.2 Morphometric variability across-habitats (depth) in each ecomorph at Media Luna.

Significant differences (Kruskal-Wallis, $p<0.05$) across the depth intervals were found for all micro-skeletal characters in both the diurnal and nocturnal ecomorphs. Corallite diameter (CD), length of first cycle septa (L1S) and the thickness of the first cycle septa (T1S) were the most variable characters in the diurnal morph. All the characters measured showed a tendency to increase in length with an increase in depth (Table 3.3). This suggests a possible continuous variation along the depth gradient. When all corallite-level characters for all colonies of the diurnal ecomorph collected in Media Luna were included in a Stepwise Canonical Discriminant Function Analysis (SCDFA), three groups (6m, 10m and 20m) were readily separated with 82.7 % of all corallites correctly classified (Figure 3.3). Significant overlap is visible between the three depths classes.

Table 3.2 Probability results of analysis of variance (ANOVA) for all corallite characters between colonies of diurnal (D) and nocturnal (N) ecomorphs of *Montastraea cavernosa* at 6 m, 10 m, 20 m depths in Media Luna reef (P-values). Values in red indicate non significance.

Characters	6 m D	6 m N	10 m D	10 m N	20 m D	20 m N
CD	**0.060**	**0.272**	0.001	**0.439**	0.012	**0.303**
CS	0.001	0.001	0.001	0.001	**0.072**	0.031
CW	0.001	0.002	0.001	0.004	0.002	0.001
L1S	0.022	0.001	0.001	0.001	0.002	**0.719**
T1S	0.001	0.008	**0.080**	**0.244**	**0.226**	0.001
L1C	0.010	0.001	0.001	**0.591**	0.028	**0.430**
T1C	**0.113**	0.001	0.001	0.009	0.021	0.019
L4S	0.001	0.001	**0.708**	0.004	0.001	0.001
L4C	0.019	0.001	0.001	**0.097**	0.017	**0.931**
T 4C	0.008	**0.142**	0.001	0.010	0.013	0.015
n=	5	5	5	5	5	5

* Morphological character abbreviations and explanation in Table 1.

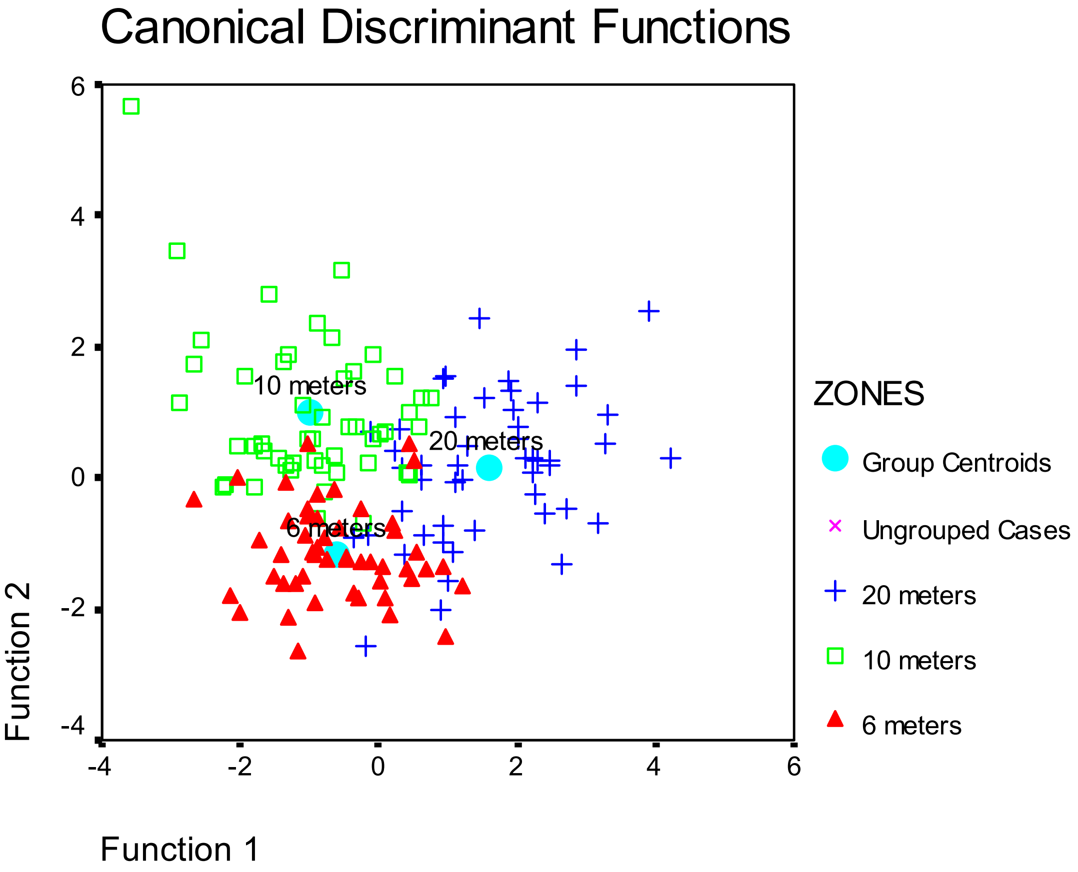

Figure 3.3 Plot of the SCDFA, performed on morphological characters of *Montastraea cavernosa* diurnal ecomorph colonies collected from 6 meters, 10 meters and 20 meters at Media Luna reef (82.7% of all corallites correctly classified). Function 1 characters are CD, L1S and T1S. Function 2 characters are T4C and L4S.

Table 3.3 Means ($\overline{Y}$) and standard deviation (s) for the morphological characters of *Montastraea cavernosa* for each ecomorph (diurnal and nocturnal) at 6 m, 10 m, 20 m depths at Media Luna reef (units in millimeters).

Characters		6 m	6 m	10 m	10 m	20 m	20 m
		Diurnal	Nocturnal	Diurnal	Nocturnal	Diurnal	Nocturnal
CD	$\overline{Y}$	5.160	5.543	5.478	7.318	5.760	8.099
	s	±0.556	±0.527	±0.809	±0.570	±0.584	±0.642
CS	$\overline{Y}$	2.722	3.678	3.710	5.161	4.409	6.281
	s	±0.484	±0.597	±1.135	±0.891	±1.402	±0.993
CW	$\overline{Y}$	2.657	3.078	2.992	3.215	2.980	3.710
	s	±0.393	±0.333	±0.710	±0.605	±0.577	±0.459
L1S	$\overline{Y}$	1.232	1.393	1.335	2.077	1.495	2.306
	s	±0.142	±0.191	±0.243	±0.308	±0.240	±0.167
T1S	$\overline{Y}$	0.235	0.286	0.262	0.308	0.323	0.327
	s	±0.051	±0.052	±0.055	±0.056	±0.050	±0.069
L1C	$\overline{Y}$	1.650	2.234	2.179	2.980	2.369	3.484
	s	±0.306	±0.447	±0.795	±0.622	±0.553	±0.668
T1C	$\overline{Y}$	0.289	0.301	0.326	0.373	0.352	0.412
	s	±0.047	±0.040	±0.068	±0.067	±0.097	±0.064
L4S	$\overline{Y}$	0.436	0.541	0.561	0.760	0.625	0.740
	s	±0.082	±0.074	±0.082	±0.188	±0.139	±0.157
L4C	$\overline{Y}$	1.613	2.152	2.094	2.657	2.010	2.820
	s	±0.326	±0.418	±0.712	±0.663	±0.438	±0.907
T4C	$\overline{Y}$	0.206	0.242	0.296	0.290	0.220	0.243
	s	±0.039	±0.039	±0.064	±0.069	±0.040	±0.044
N		5	5	5	5	5	5

* Mophological characters abbreviations and explanations in Table 2.1

Corallite diameter (CD), length of first cycle septa (L1S), and spacing of corallites (CS) were the most variable characters across the depth intervals in the nocturnal ecomorph. The same trend of increase in length as depth increases was observed in all characters, which again suggest that micro-skeletal characters show continuous variation across the depth intervals (Table 3.3). When corallite-level characters were included in a SCDFA, three distinct groups corresponding to each depth (6m, 10m and 20m) were readily separated with 92 % of all corallites correctly classified (Figure 3.4). Wide overlap occurred between the 10 m and 20 m groups and a slight overlap occurred between the 6 m and 10 m groups. Colonies collected at 6 m showed more cohesiveness with 98 % of the corallites correctly classified, and is isolated from the other two groups (Fig. 3.4).

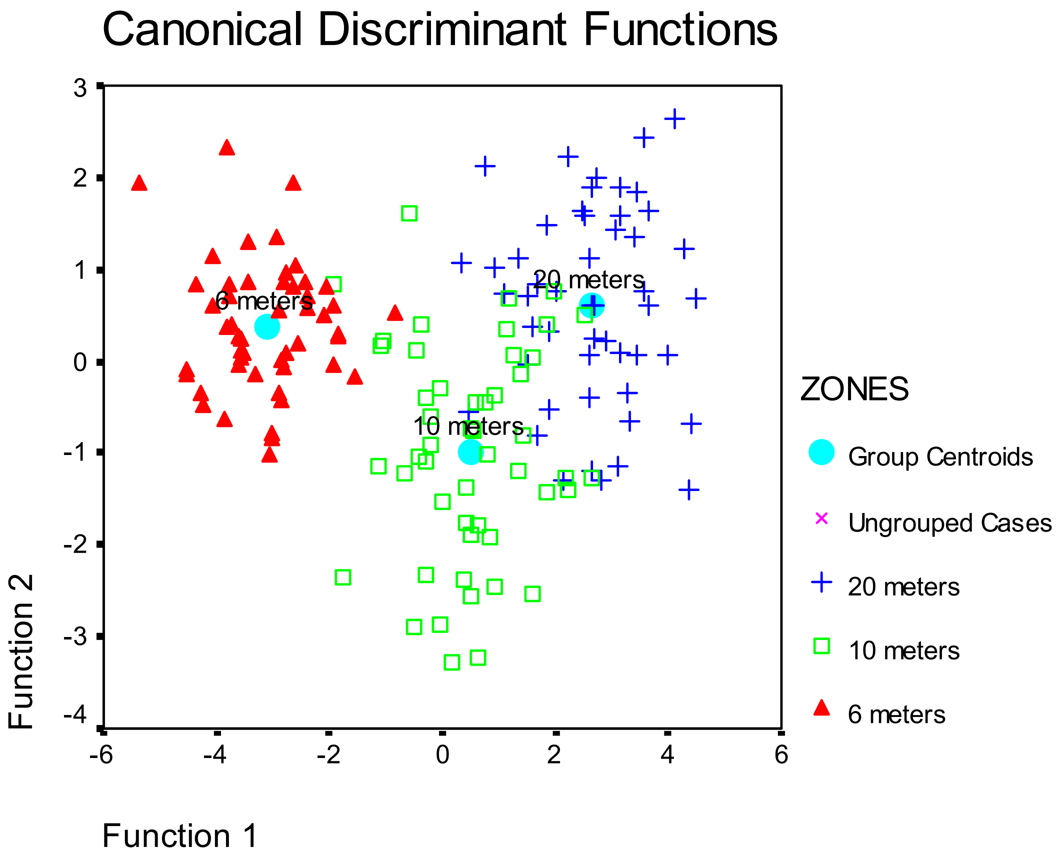

Figure 3.4 Plot of the SCDFA performed on morphological characters of *Montastraea cavernosa* nocturnal ecomorph colonies collected from 6 meters, 10 meters and 20 meters at Media Luna reef (92% of all corallites correctly classified). Function 1 characters are CD, L1S and CS. Function 2 characters are T4C, CW and T1S.

3.2.3 Variance components at Media Luna reef.

A nested analysis of variance of the character measurements for the diurnal and the nocturnal ecomorphs at Media Luna reef indicated that most characters varied widely between colonies within each ecomorph with seven out of the ten characters measured showing a high percentage of inter-colony variation within each depth interval (Tables 3.4 and 3.5) in each ecomorph..

Table 3.4 Proportion of total variation in the diurnal ecomorph (as percentages, in each morphological character examined) at Media Luna reef that is attributable to each nested source of variation, based on measurements of 10 corallites per colony (15 colonies). High percentages are showed in bold.

Source of Variation	df	CD	CS	CW	L1S	T1S	L1C	T1C	L4S	L4C	T4C
Within colonies	135	29.3	15.6	45.7	**45.3**	**42.7**	31.3	46.6	21.8	38.6	36.2
Between colonies	12	**58.3**	**57.6**	**53.3**	27.8	18.7	**50.8**	**48**	**40.2**	**52.6**	17.5
Between depths	2	6.4	26.8	1	26.9	38.6	17.9	5.4	38	8.8	**46.3**
Total	149	100	100	100	100	100	100	100	100	100	100

df = degrees of freedom.

Table 3.5 Proportion of total variation in the nocturnal ecomorph (as percentages, in each morphological character examined) at Media Luna reef that is attributable to each nested source of variation, based on measurements of 10 corallites per colony (15 colonies). High percentages are showed in bold.

Source of Variation	df	CD	CS	CW	L1S	T1S	L1C	T1C	L4S	L4C	T4C
Within colonies	135	11.4	20.4	**38**	15.1	1	37.5	37.6	27.7	**54**	2
Between colonies	12	9.3	11.1	36	8.4	.9	11.7	18.6	**40.3**	33	2
Between depths	2	**79.3**	**68.5**	26	**76.5**	**98.1**	**50.8**	**43.8**	32	13	**96**
Total	149	100	100	100	100	100	100	100	100	100	100

df = degrees of freedom.

3.2.4 Morphometric variability within habitats in each ecomorph at Turrumote.

For colonies collected at 6 m depth in Turrumote, results showed significant differences (Kruskal-Wallis, $p<0.05$) among colonies of the diurnal ecomorph in eight out of the ten micro-skeletal characters measured. Similar results were obtained for the nocturnal ecomorph with significant differences (Kruskal-Wallis, $p<0.05$) among colonies in the means of seven micro-skeletal characters (Table 3.6).

For colonies collected at 10 m depth, significant differences (Kruskal-Wallis, $P<0.05$) were found between colony means of nine micro-skeletal characters among the colonies of the diurnal ecomorph and eight among colonies of the nocturnal ecomorph. At 20 m deep, only five micro-skeletal characters varied significantly (Kruskal-Wallis, $p<0.05$) among colonies of the diurnal ecomorph, seven micro-skeletal characters varied significantly ($p<0.05$) among colonies of the nocturnal morph (Table 3.6).

Table 3.6 Probability results of analysis of variance (ANOVA) for all corallite characters between colonies of diurnal (D) and nocturnal (N) ecomorph of *Montastraea cavernosa* at 6 m, 10 m, 20 m depths at Turrumote reef (p-values). Values in red indicate non significance.

Characters	6 m D	6 m N	10 m D	10 m N	20 m D	20 m N
CD	0.002	0.046	0.009	0.002	0.002	**0.288**
CS	0.001	**0.353**	0.001	0.001	**0.755**	0.001
CW	0.001	0.001	**0.230**	0.001	0.001	0.001
L1S	**0.086**	0.001	0.001	0.001	0.001	**0.276**
T1S	0.001	0.001	0.001	0.007	0.001	0.001
L1C	0.012	0.001	0.001	0.047	**0.282**	0.001
T1C	0.001	0.005	0.001	0.003	0.001	0.001
L4S	0.001	0.035	0.001	0.001	**0.117**	**0.246**
L4C	**0.178**	**0.361**	0.001	**0.147**	**0.453**	0.005
T 4C	0.001	**0.052**	0.001	**0.156**	**0.174**	0.021
n=	5	5	5	5	5	5

* Morphological character abbreviations and explanation in Table 1.

3.2.5 Morphometric variability across-habitats (depth) in each ecomorph at Turrumote

Significant differences (Kruskal-Wallis, $p<0.05$) across the depth intervals were found for the means of all ten corallite-level characters of the diurnal ecomorph at Turrumote reef. Corallite diameter (CD), length of first cycle septa (L1S) and corallite spacing (CS) were the most variable characters. Similarly to Media Luna, all micro-skeletal characters measured had a tendency to get larger/longer as the depth increased (Table 4.7) which could represent a continuous variation along the depth gradient for this ecomorph in Turrumote. When all corallite-level characters were included in a SCDFA, three groups (6m, 10m and 20m) were readily separated with 81.3 % of all corallites correctly classified (Fig. 3.5).

Significant differences (Kruskal-Wallis, $p<0.05$) across the depth intervals were found for the means of all corallite-level characters of the nocturnal ecomorph in Turrumote. When corallite-level characters of the nocturnal ecomorph were included in the SCDFA, three distinct groups (6m, 10m and 20m) were readily separated with 83.3 % of all corallites correctly classified (Fig. 3.6). Some overlap occurs between the 10 m and 20 m groups and a slight overlap occurs between the 6 m and 10 m groups. Like in Media Luna, the 6 m groups showed some cohesiveness and were isolated from the other two groups.

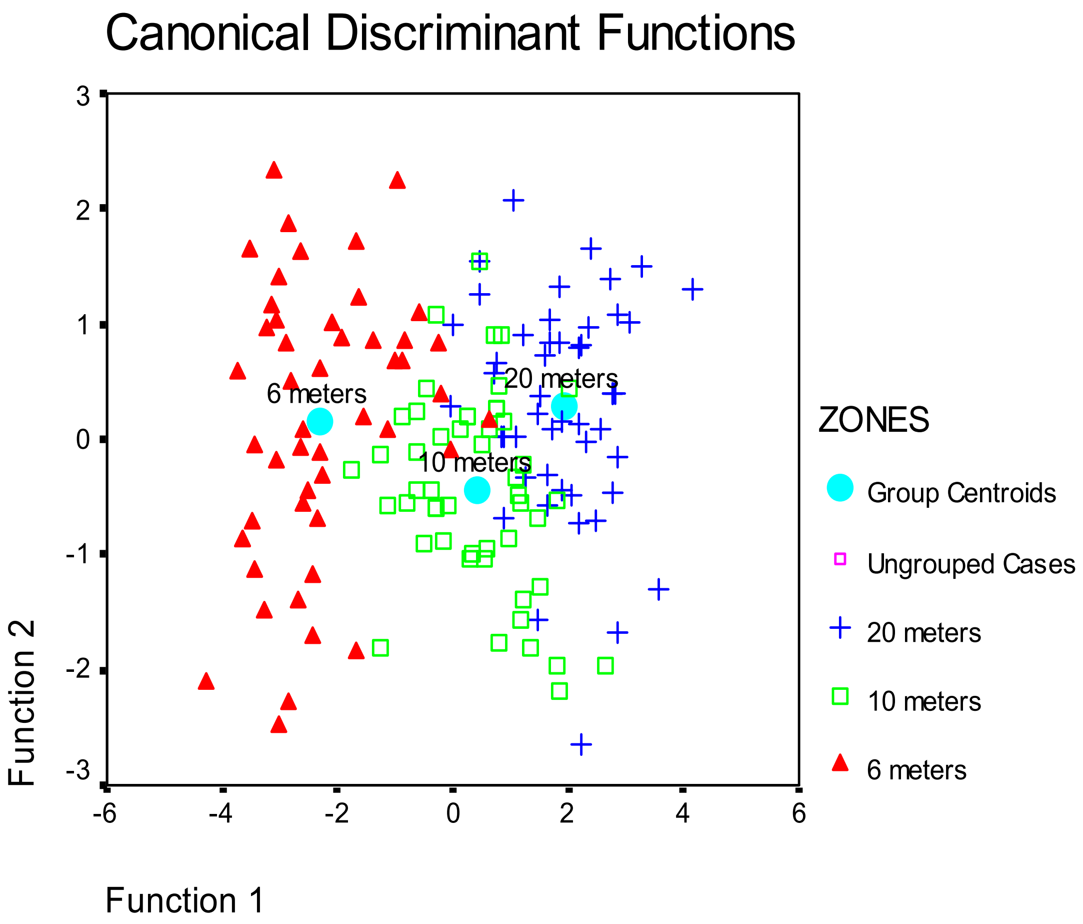

Figure 3.5 Plot of the SDCFA using morphological characters of *Montastraea cavernosa* diurnal ecomorph colonies collected from 6 meters, 10 meters and 20 meters at Turrumote reef (81.3% of all corallites correctly classified). Function 1 characters are CD, CS and L1S. Function 2 character is T1C.

Table 3.7 Means ($\overline{Y}$) and standard deviation (s) for the morphological characters of *Montastraea cavernosa* for each ecomorphs (diurnal and nocturnal) at 6m, 10m, 20m depths at Turrumote reef (units in millimeters).

Characters		6 m Diurnal	6 m Nocturnal	10 m Diurnal	10 m Nocturnal	20 m Diurnal	20 m Nocturnal
CD	$\overline{Y}$	4.830	5.440	5.677	7.353	6.307	8.515
	s	±0.685	±0.426	±0.466	±0.892	±0.408	±1.321
CS	$\overline{Y}$	2.537	3.277	3.766	5.718	4.176	6.823
	s	±0.490	±0.624	±0.748	±1.150	±0.634	±1.774
CW	$\overline{Y}$	2.475	2.810	2.927	3.544	3.357	4.412
	s	±0.293	±0.328	±0.360	±0.583	±0.450	±0.688
L1S	$\overline{Y}$	1.291	1.373	1.451	1.936	1.610	2.241
	s	±0.243	±0.193	±0.237	±0.332	±0.232	±0.486
T1S	$\overline{Y}$	0.240	0.257	0.276	0.375	0.308	0.442
	s	±0.042	±0.050	±0.063	±0.065	±0.050	±0.134
L1C	$\overline{Y}$	1.591	1.933	2.251	3.244	2.447	3.814
	s	±0.324	±0.436	±0.543	±0.624	±0.426	±0.646
T1C	$\overline{Y}$	0.286	0.314	0.321	0.442	0.369	0.546
	s	±0.054	±0.060	±0.060	±0.072	±0.050	±0.143
L4S	$\overline{Y}$	0.540	0.498	0.574	0.737	0.654	0.885
	s	±0.140	±0.106	±0.107	±0.182	±0.110	±0.234
L4C	$\overline{Y}$	1.418	1.853	2.086	2.972	2.358	3.344
	s	±0.312	±0.466	±0.475	±0.628	±0.454	±0.723
T4C	$\overline{Y}$	0.212	0.228	0.249	0.303	0.257	0.376
	s	±0.042	±0.055	±0.062	±0.056	±0.052	±0.105
N		5	5	5	5	5	5

* Mophological characters abbreviations and explanations in Table 2.1

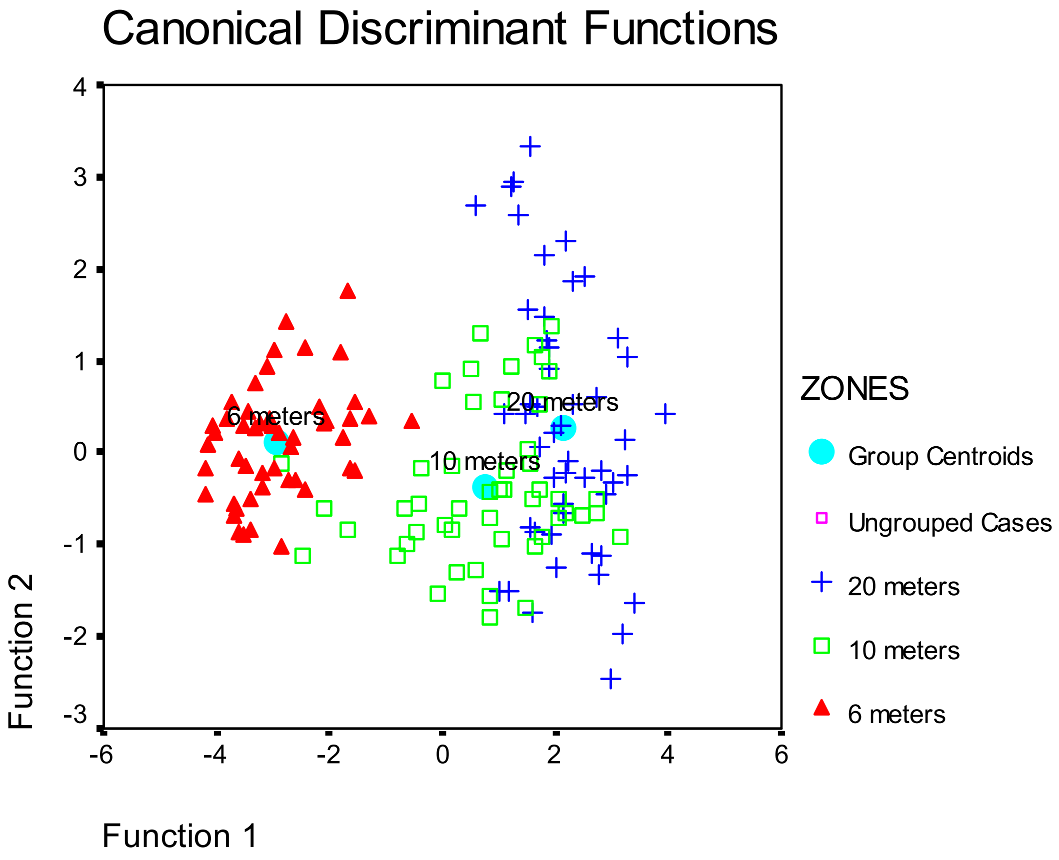

Figure 3.6 Plot of the results of SCDFA using corallite-level characters of *Montastraea cavernosa* nocturnal ecomorph colonies collected from 6 meters, 10 meters and 20 meters at Turrumote reef (83.3% of all corallites correctly classified). Function 1 characters are CD, CS and T4C. Function 2 character is CW.

3.2.6 Components of the variance for the two ecomorphs in Turrumote.

Separated nested ANOVAS of the character measurements for each one of the diurnal and nocturnal ecomorphs from Turrumote reef indicated that most characters varied widely across depths and between colonies. Five out of ten characters measured showed high percentages of between depths variation in the diurnal ecomorph. The other five characters measured showed high percentages of between colony variations (Table 3.8). Nine out of ten characters measured on the nocturnal ecomorph showed high percentages of between depths variation (Table 3.9).

Table 3.8 Proportion of total variation in the diurnal ecomorph (as percentages, in each morphological character examined) at Turrumote reef that is attributable to each nested source of variation, based on measurements of 10 corallites per colony.

Source of Variation	df	CD	CS	CW	L1S	T1S	L1C	T1C	L4S	L4C	T4C
Within colonies	135	16.1	16.5	22.9	33	35.3	26	28.9	41	27.3	42
Between colonies	12	22.4	25.5	27.1	**45.5**	**45.2**	27.7	**43.4**	**50**	8.2	**52**
Between depths	2	**61.5**	**58**	**50**	21.5	19.5	**46.3**	27.7	9	**64.5**	6
Total	149	100	100	100	100	100	100	100	100	100	100

df = degrees of freedom.

Table 3.9 Proportion of total variation in the nocturnal ecomorph (as percentages, in each morphological character examined) at Turrumote reef that is attributable to each nested source of variation, based on measurements of 10 corallites per colony.

Source of Variation	df	CD	CS	CW	L1S	T1S	L1C	T1C	L4S	L4C	T4C
Within colonies	135	6.1	12.4	12.6	13.5	16.1	17.3	14.4	13.4	29.7	29.2
Between colonies	12	26.1	25.4	24.4	32.5	40.5	11.2	34	**48.5**	11.2	27.4
Between depths	2	**67.8**	**62.2**	**64**	**54**	**43.4**	**71.7**	**51.6**	38.1	**59.1**	**43.4**
Total	149	100	100	100	100	100	100	100	100	100	100

df = degrees of freedom.

3.2.7 Inter-population variation across reefs

When morphometric characters were compared across reef localities, only two (length of the first cycle septa and length of the fourth cycle septa) out of the ten characters were significantly different (Kruskal-Wallis, $p<0.05$) between the two populations of the diurnal ecomorph. No significant differences were found for the other eight characters (Table 3.10). Results of SCDFA showed very low variation overall with a high overlap of the corallites of the two groups of the diurnal morph in both reefs indicating that they are mostly similar (Figure 3.7). Only 61% of the original grouped cases were correctly classified.

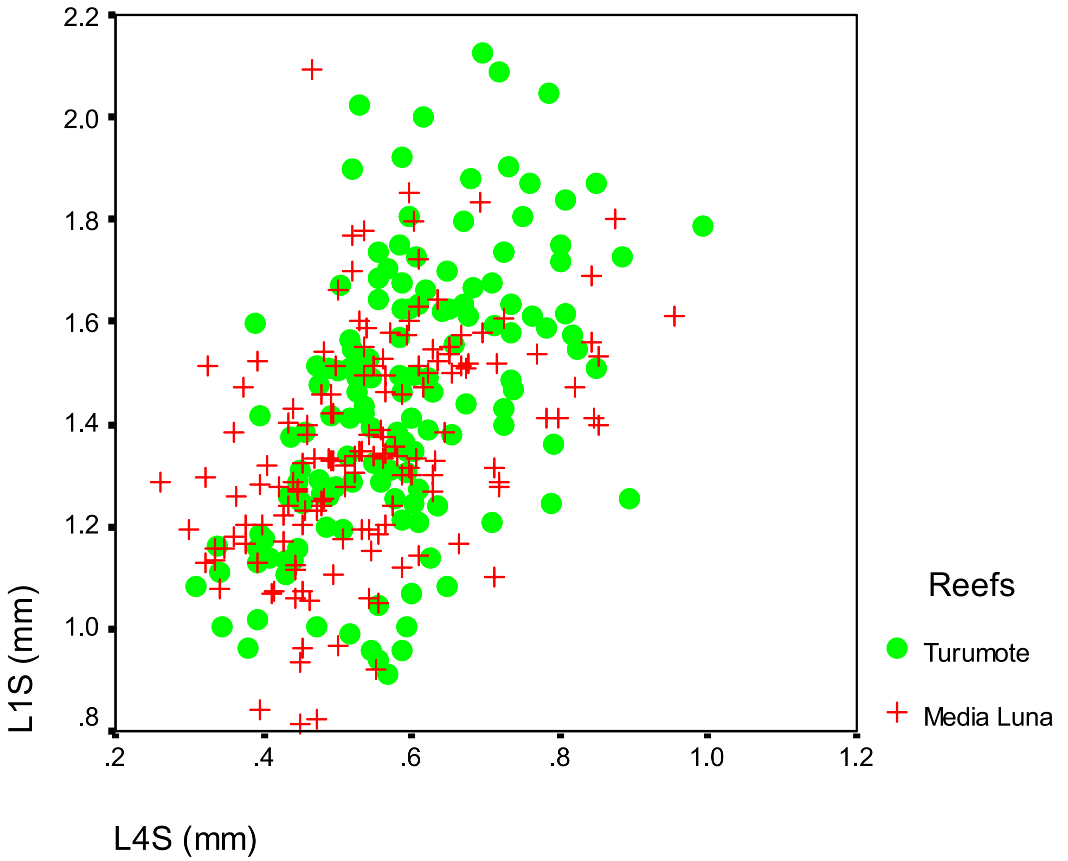

Figure 3.7 Scatterplot (simple) of discriminant variables in the SCDFA of *Montastraea cavernosa* diurnal corallites between localities (Media Luna and Turrumote). L1S= length of the first cycle septa, L4S= length of the fourth cycle septa.

For the nocturnal ecomorph however, five micro-skeletal characters (width columella, the thickness of the first septa, the thickness of the first costae, the length of the fourth cycle costae, and the thickness of the fourth costae) were significantly different

(Kruskal-Wallis, $p<0.05$) between the population of Media Luna and Turrumote. Five morphological characters at the inter-population level did not vary significantly (Table 3.10). Results of SCDFA showed low variation overall however with high overlap between the corallites of the two populations of the nocturnal ecomorph (Fig. 3.8). Only 66% of the original grouped cases were correctly classified.

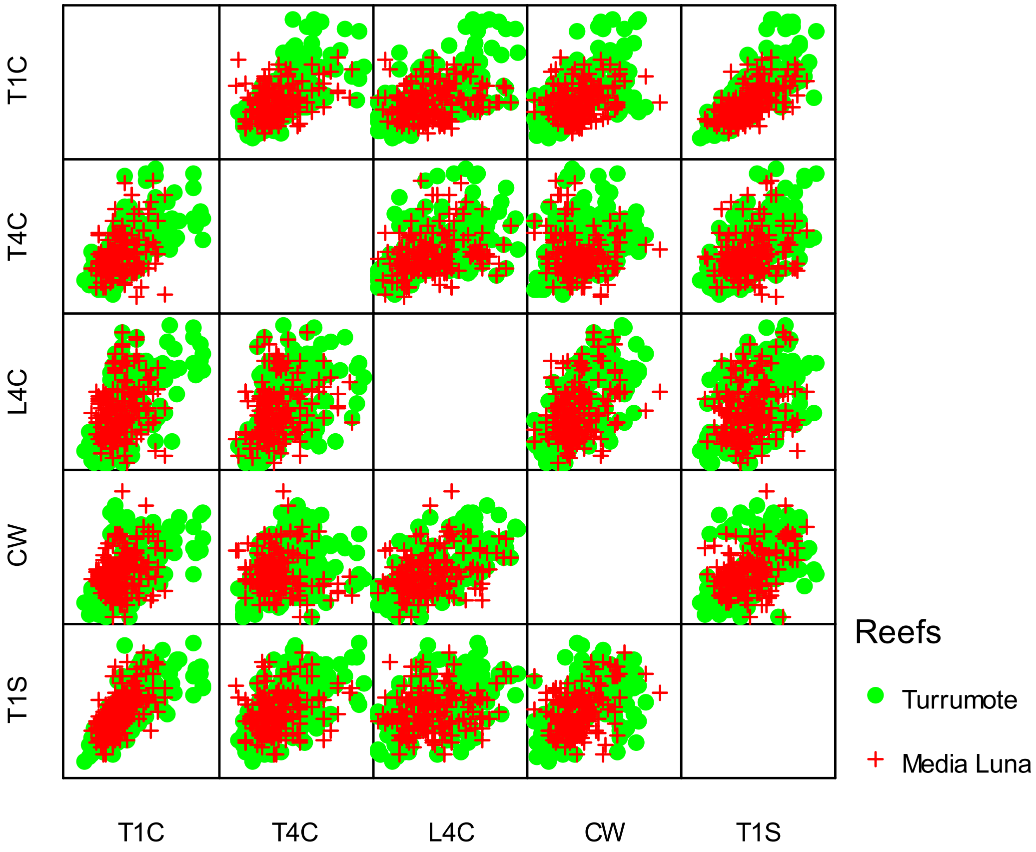

Figure 3.8 Scatterplot (matrix) of discriminant variables in the SCDFA of *Montastraea cavernosa* nocturnal corallites between localities. It showed all significant characters include and the resultant scatter plot of two way combinations of characters for the grouping of the two reefs. T1C= thickness of the first cycle costae, T4C= thickness of the fourth cycle costae, L4C= length of the fourth cycle costae, CW= columella width, T1S= Thickness of the first cycle septa.

Table 3.10 Analysis of variance (ANOVA) of *Montastraea cavernosa* characters (P-values).

Character	Between Localities (Diurnal)	Between Localities (Nocturnal)
CD	0.161	0.792
CS	0.720	0.569
CW	0.627	0.032*
L1S	0.001*	0.069
T1S	0.837	0.036*
L1C	0.255	0.431
T1C	0.316	0.001*
L4S	0.001*	0.622
L4C	0.331	0.029*
T4C	0.889	0.001*
n=	30	30

*Significant at 0.05 level of significance

3.3 Morphometric variability between the two ecomorphs at the corallite level.

3.3.1 Media Luna

All the results presented so far indicate that there is wide variability in the corallite characters within each one of the two ecomorphs when corallites and colonies are compared across habitats (depths) and reefs. When mean corallite characters were compared between the two ecomorphs, significant differences (Kruskal-Wallis, $P<0.05$) were found in nine of ten characters for colonies collected at 6 m and the two ecomorphs were separated by a SCDFA with 87 % of all corallites correctly classified (Figure 3.9). A scatter plot (matrix) of the most heavily weighted characters (most important characters for the classification) from the analysis of corallite level showed some overlap of the two groups (Figure 3.9). Corallite diameter (CD), corallite spacing (CS), width of columella (CW), length of the first cycle costae (L1C), and the length of the fourth cycle septa (L4S) were most heavily weighted characters by the analysis (discriminant characters) (Figure 3.10).

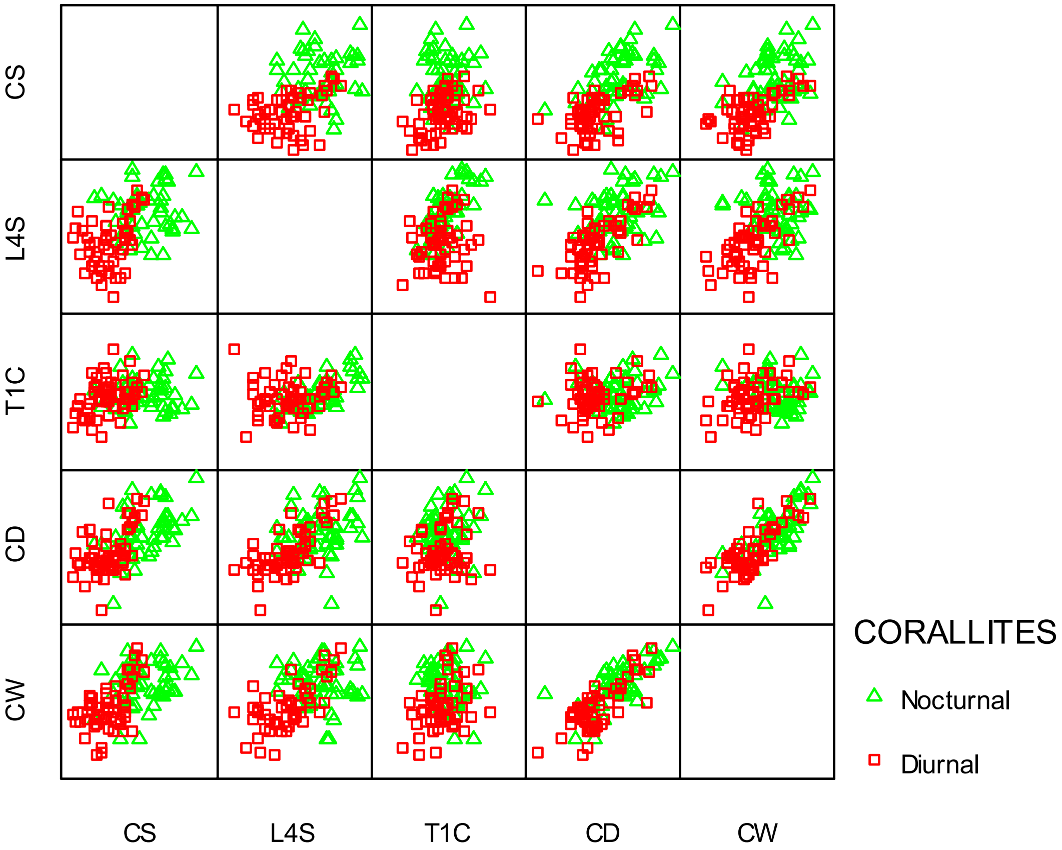

Figure 3.9 Scatterplot (matrix) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Media Luna 6 m. It showed all significant characters included and the resultant scatter plot of a two way combination of characters for the grouping of the two ecomorphs. CD= corallite diameter, CS= spacing of the corallites, CW= width of columella, L1C= length of the first cycle costae, and L4S= length of the fourth cycle septa.

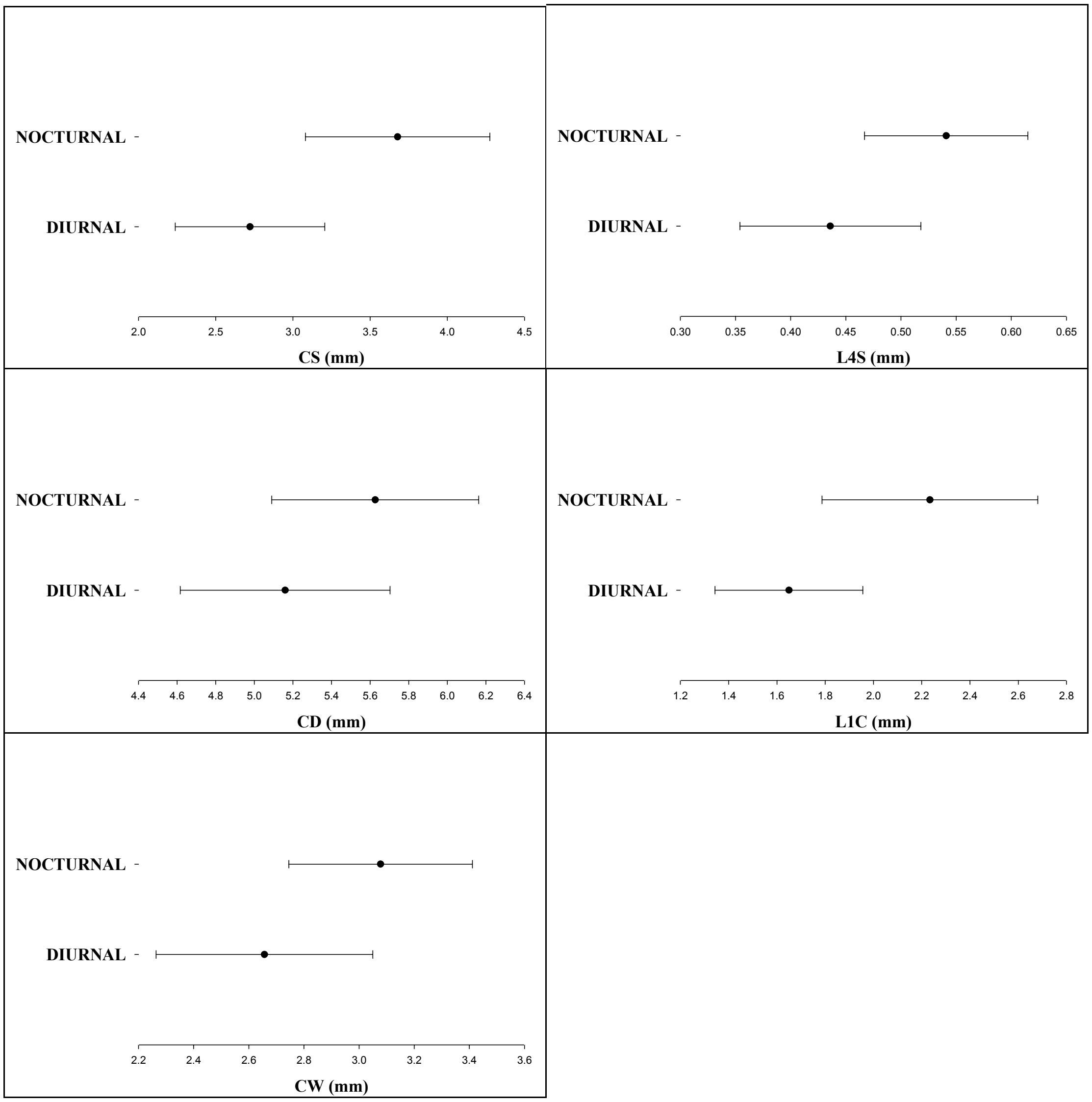

Figure 3.10 Mean and standard deviations of some of the most variable characters of *Montastraea cavernosa* ecomorph at Media Luna reef at 6 meters.). CD= corallite diameter, CS= spacing of the corallites, CW= width of columella, L1C= length of the first cycle costae, and L4S= length of the fourth cycle septa.

Significant differences (Kruskal-Wallis, P<0.05) between the two ecomorphs were found for eight of the ten colony-level characters analyzed at 10 m depth. The two ecomorphs were readily separated by SDCFA when corallite level characters were used in the analysis with 96 % of all corallites correctly classified. A scatter plot of the most heavily weighted characters from the analysis showed almost no overlap of the ecomorph groups (Figure 3.11) indicating that these groups are highly different. A minimum of two characters were necessary to separate the two ecomorphs, corallite diameter (CD) and the length of the first cycle septa (L1S) (Figure 3.12).

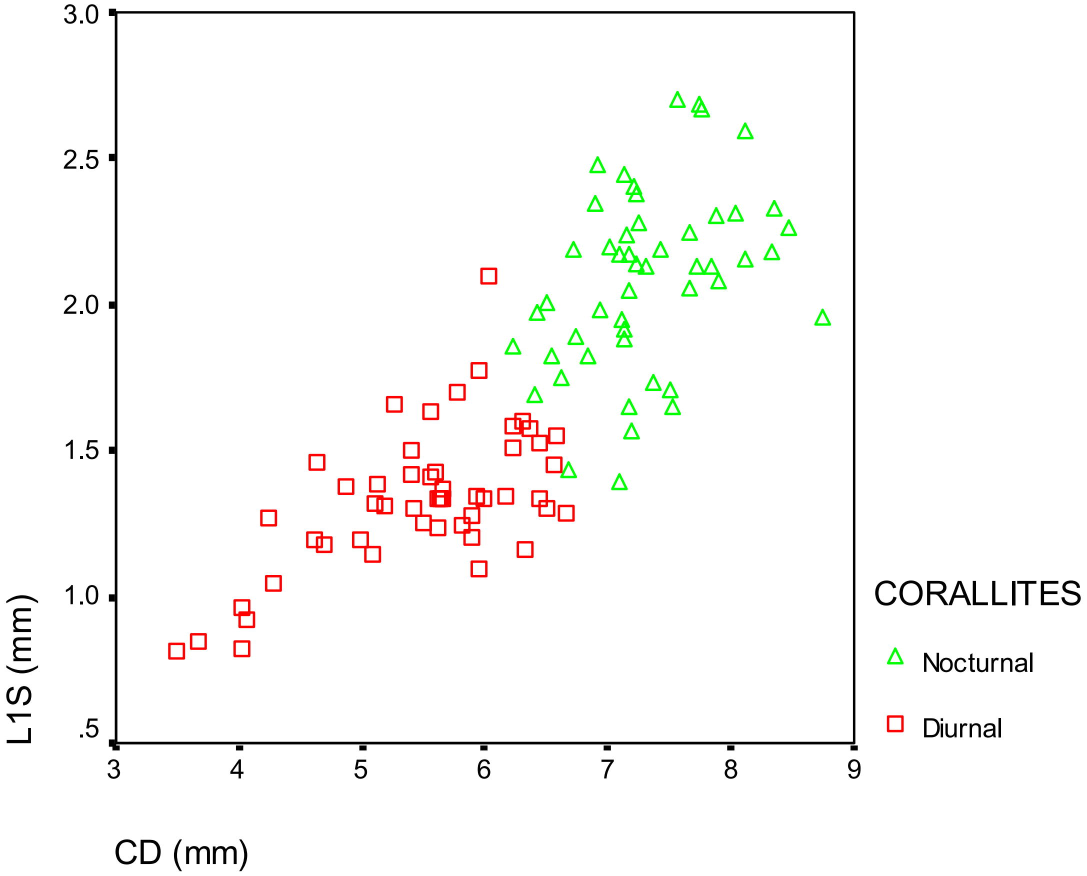

Figure 3.11 Scatterplot (simple) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Media Luna 10 meters. CD= corallite diameter and L1S= length of the first cycle septa.

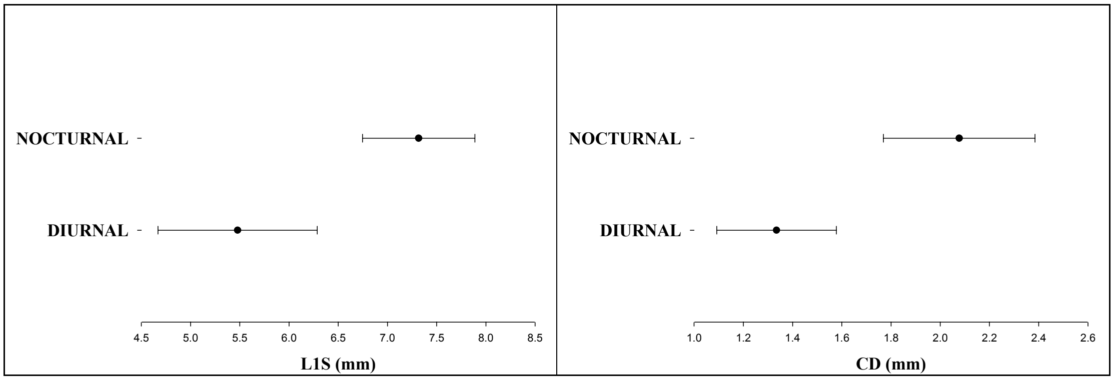

Figure 3.12 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Media Luna reef at 10 meters. CD= corallite diameter and L1S= length of the first cycle septa.

Similar results were found when colonies of the two ecomorphs collected at 20 m depth were compared. Significant differences (Kruskal-Wallis, $P<0.05$).between the two ecomorphs were found in all corallite-level characters analyzed. The two ecomorphs were clearly separated by SCDFA when all corallite level characters were used with 98 % of all corallites correctly classified. A scatter plot (3-D) of the most heavily weighted characters from the analysis of corallite level showed complete separation of the two ecomorphs (no overlap) (Figure 3.13). Corallite diameter (CD), the length of the first cycle septa (L1S), and the length of the fourth septa (L4S) were most heavily weighted by the analysis (Figure 3.14).

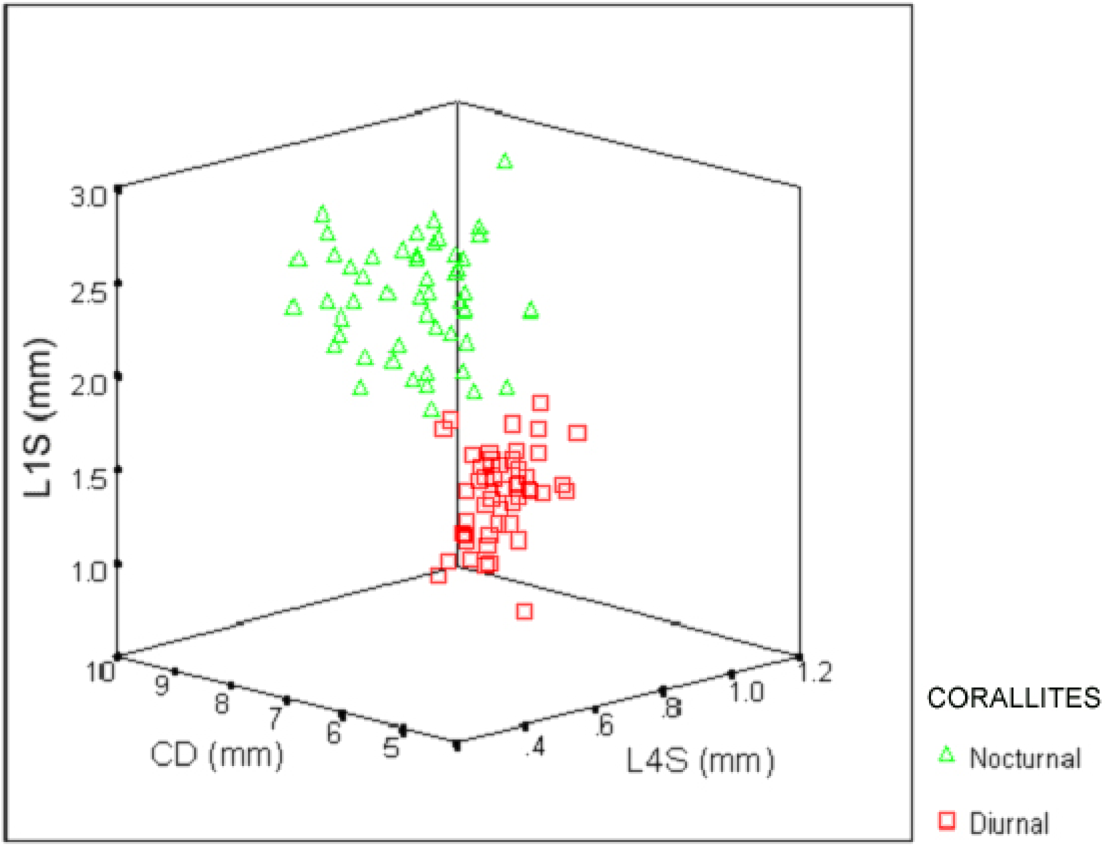

Figure 3.13 Scatterplot (3-D) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Media Luna 20 meters. CD= corallite diameter, L1S= length of the first cycle septa, and L4S= length of the fourth septa.

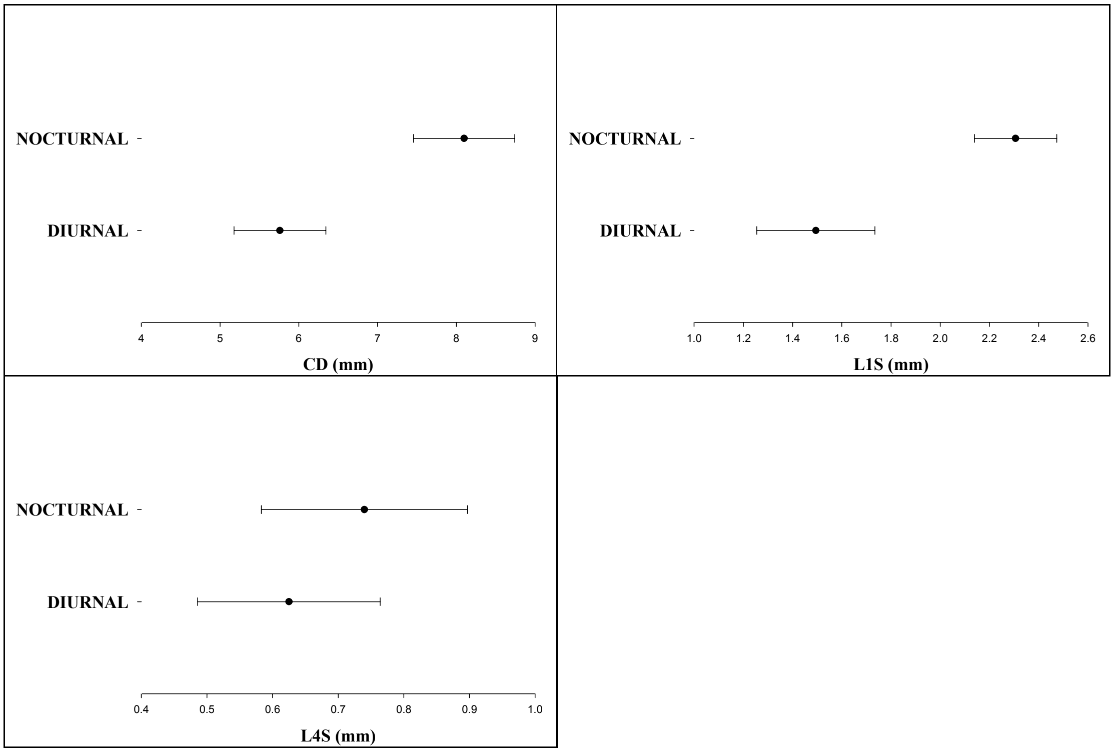

Figure 3.14 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Media Luna reef at 20 meters. CD= corallite diameter, L1S= length of the first cycle septa, and L4S= length of the fourth septa.

When corallite-level characters across depths for all colonies of the two ecomorphs were compared in Media Luna, significant differences (ANOVA, $P<0.05$) between the two ecomorphs were found in all characters analyzed. Two groups were readily separated by SCDFA with 81.7 % of all corallites correctly classified by the analysis. A scatter plot (3-D) of the most heavily weighted characters from the analysis of corallite-level characters however, showed overlap of the ecomorph groups (Fig. 3.15). The length of the first cycle septa (L1S), corallite diameter (CD), the thickness of the first cycle costae (T1C) were most heavily weighted by the analysis (Fig. 3.16).

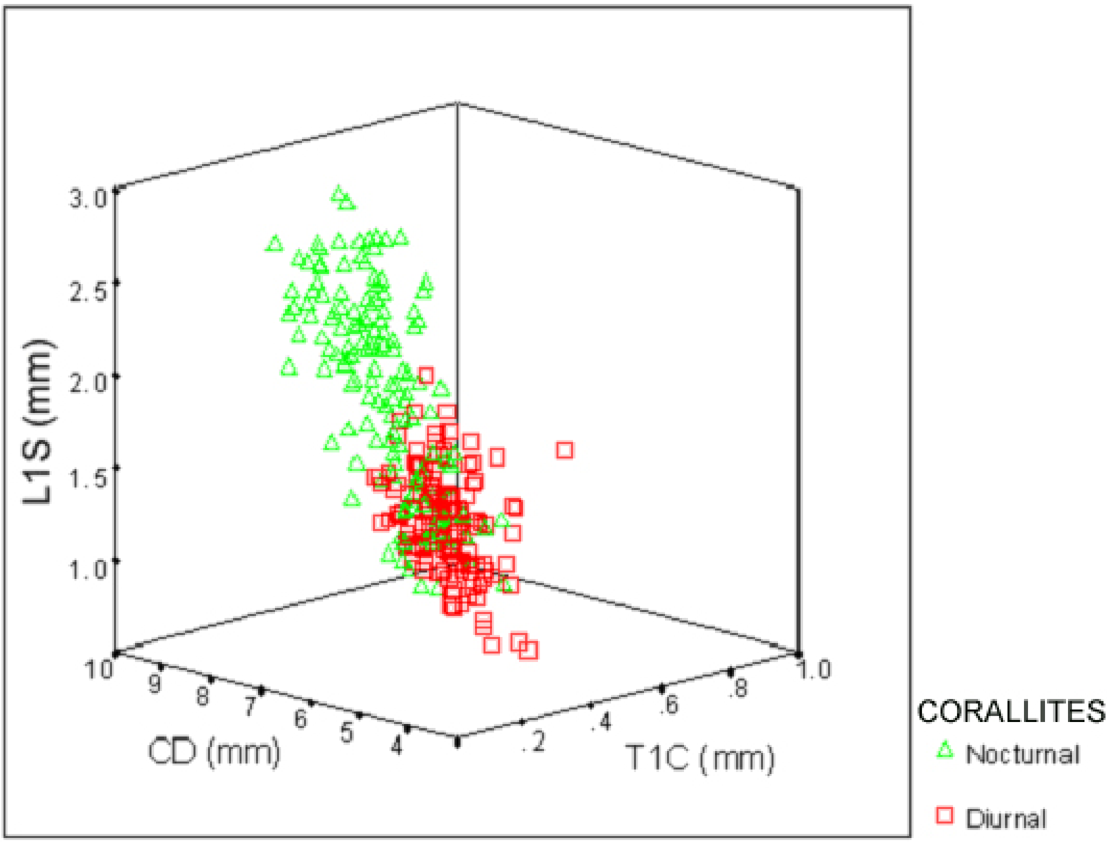

Figure 3.15 Scatterplot (3-D) of discriminat variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Media Luna reef. L1S= length of the first cycle septa, CD= corallite diameter, and T1C= thickness of the first cycle costae.

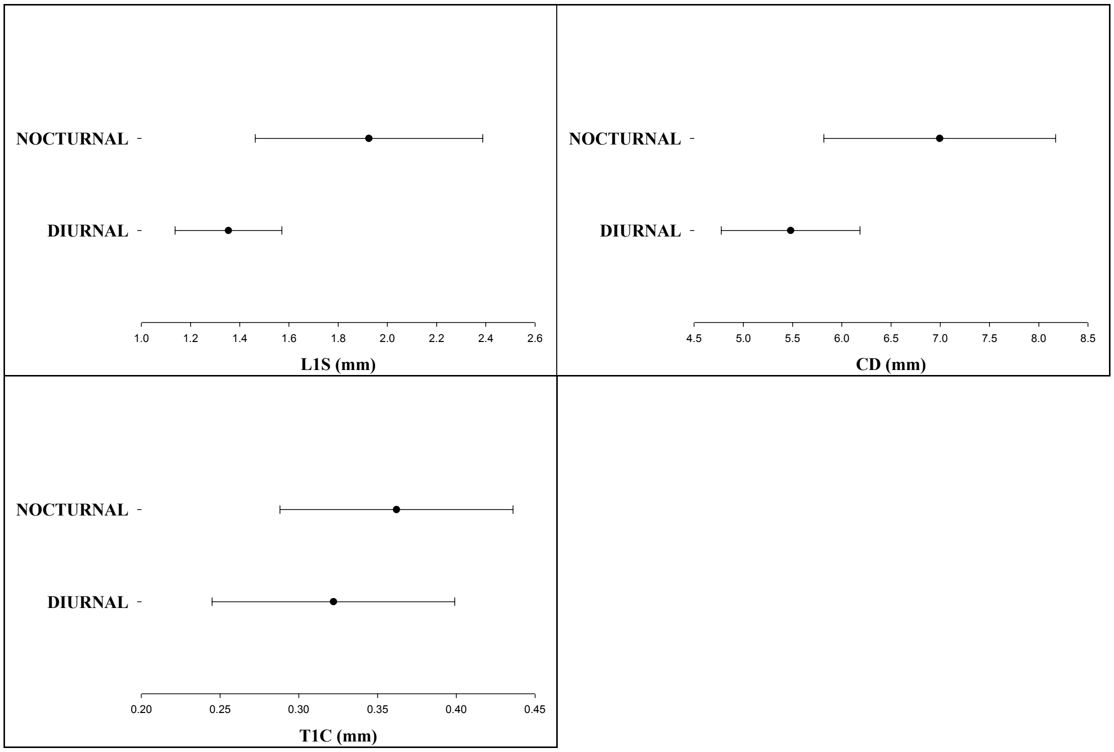

Figure 3.16 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Media Luna reef. L1S= length of the first cycle septa, CD= corallite diameter, and T1C= thickness of the first cycle costae.

3.3.2 Turrumote

Significant differences between the two ecomorphs were found in six of the ten colony-level characters analyzed (ANOVA, P<0.05) for all colonies collected at 6 m. A SCDFA readily separated two groups with only 76 % of all corallites correctly classified when corallite level characters were used in the analysis. A scatter plot (simple) of the most heavily weighted characters from the analysis of corallite level showed high overlap of the ecomorphs groups at this depth (Fig. 3.17). Corallite spacing (CS) and Corallite diameter (CD) were most heavily weighted by the analysis (Fig. 3.18).

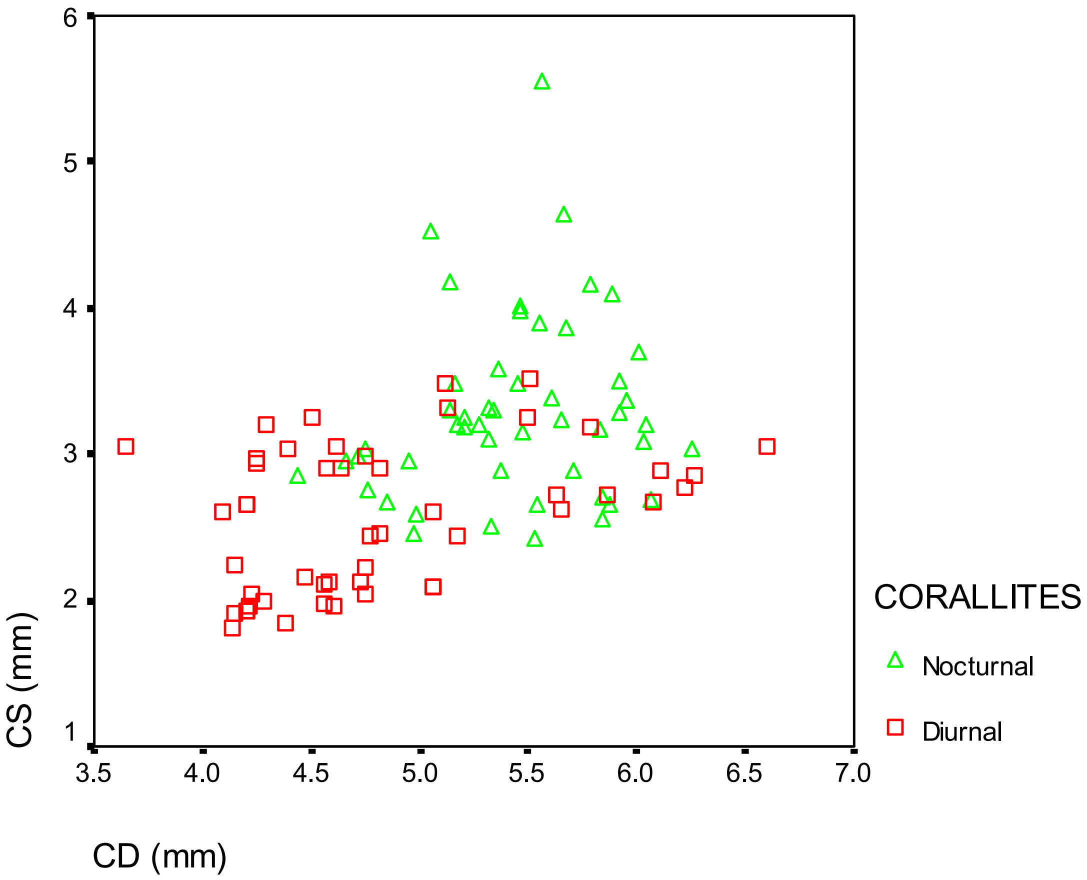

Figure 3.17 Scatterplot (simple) of discriminat variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Turrumote 6 meters. CS= spacing of the corallites and CD= corallite diameter.

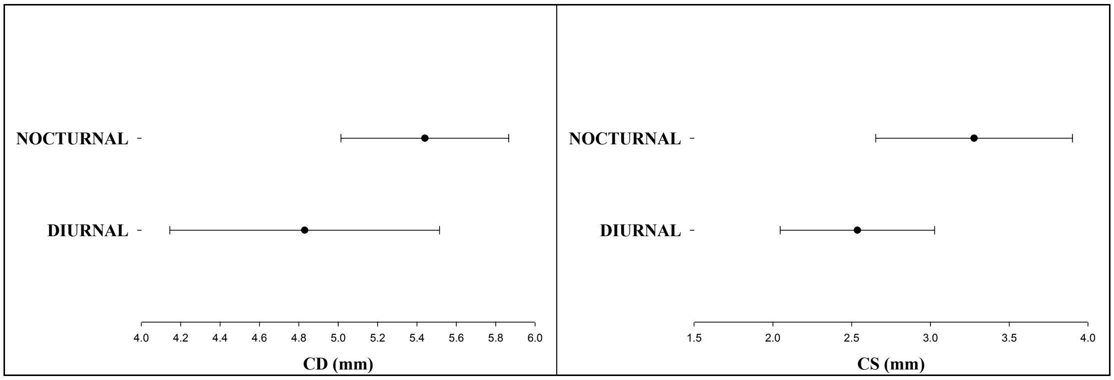

Figure 3.18 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Turrumote reef at 6 meters. CS= spacing of the corallites and CD= corallite diameter.

However, when corallites at 10 m depth were analyzed, significant differences (Kruskal-Wallis, $P<0.05$) between the two ecomorphs were found in all ten corallite-level characters analyzed and the SCDFA readily separated two distinct groups With 91 % of all corallites correctly classified when corallite-level characters were used. A scatter plot (3-D) of the most heavily weighted characters from the analysis of corallite level showed some overlap of the ecomorphs groups (Fig. 3.19). Corallite diameter (CD), the thickness of the fourth cycle costae (T1C), and the thickness of the first cycle septa (T1S) were most heavily weighted by the analysis (Fig 3.20).

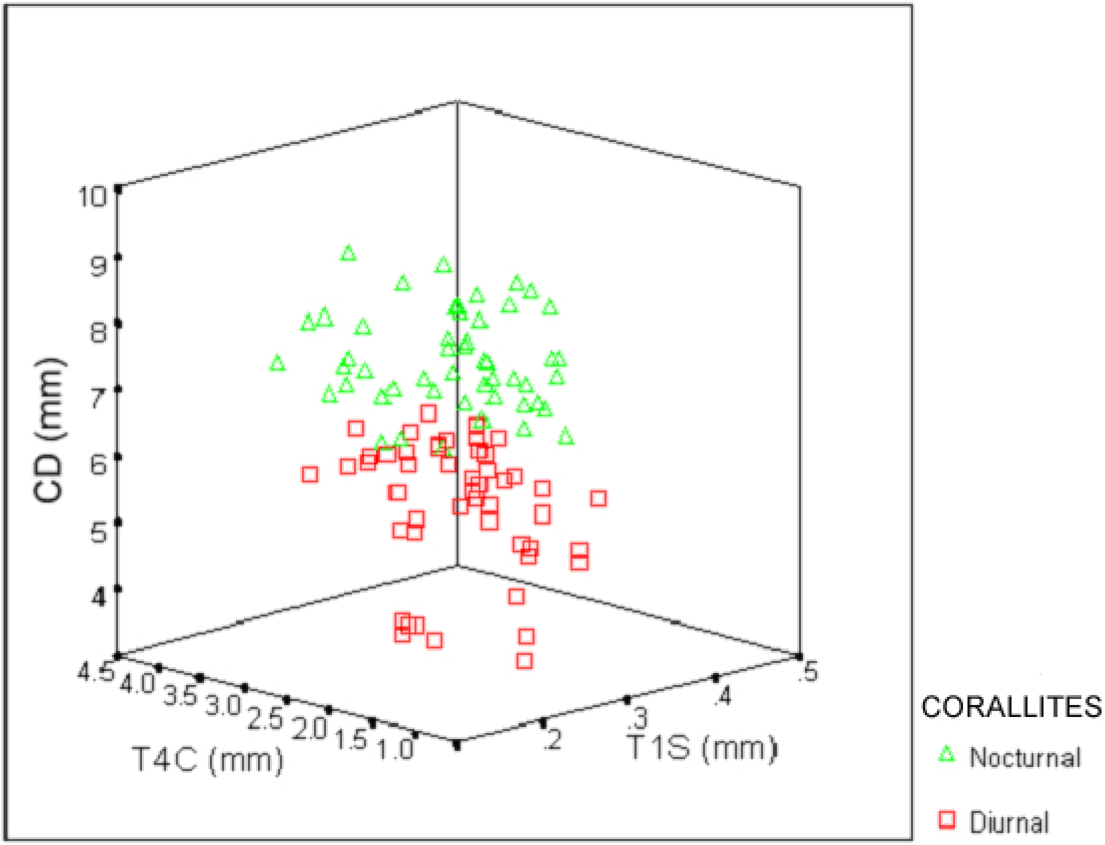

Figure 3.19 Scatterplot (3-D) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Turrumote 10 meters. CD= corallite diameter, T4C= thickness of the fourth cycle costae, and T1S= thickness of the first cycle septa.

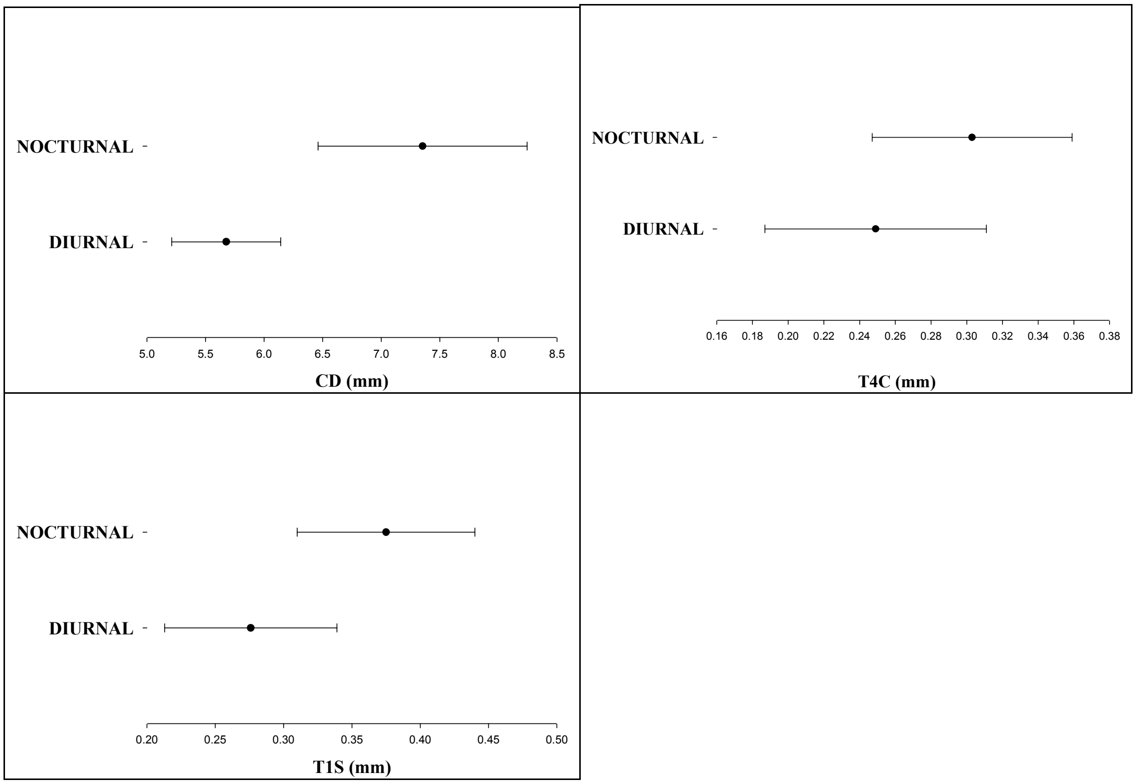

Figure 3.20 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Turrumote reef at 10 meters.). CD= corallite diameter, T4C= thickness of the fourth cycle costae, and T1S= thickness of the first cycle septa.

These differences were even more marked when all colonies of the two ecomorphs from 20 m deep were analyzed. Significant differences between the two ecomorphs were found for all ten corallite-level characters (Kruskal-Wallis, $P<0.05$) and the diurnal and nocturnal ecomorphs were readily separated by the SCDFA with 99 % of all corallites correctly classified in the analysis. A scatter plot (matrix) of the most heavily weighted characters from the analysis of corallite level showed very little overlap of the ecomorphs groups (Figure 3.21). Corallite diameter (CD), corallite spacing (CS), the width of columella (CW), and the thickness of the fourth cycle costae (T4C) were most heavily weighted by the analysis (Fig. 3.22).

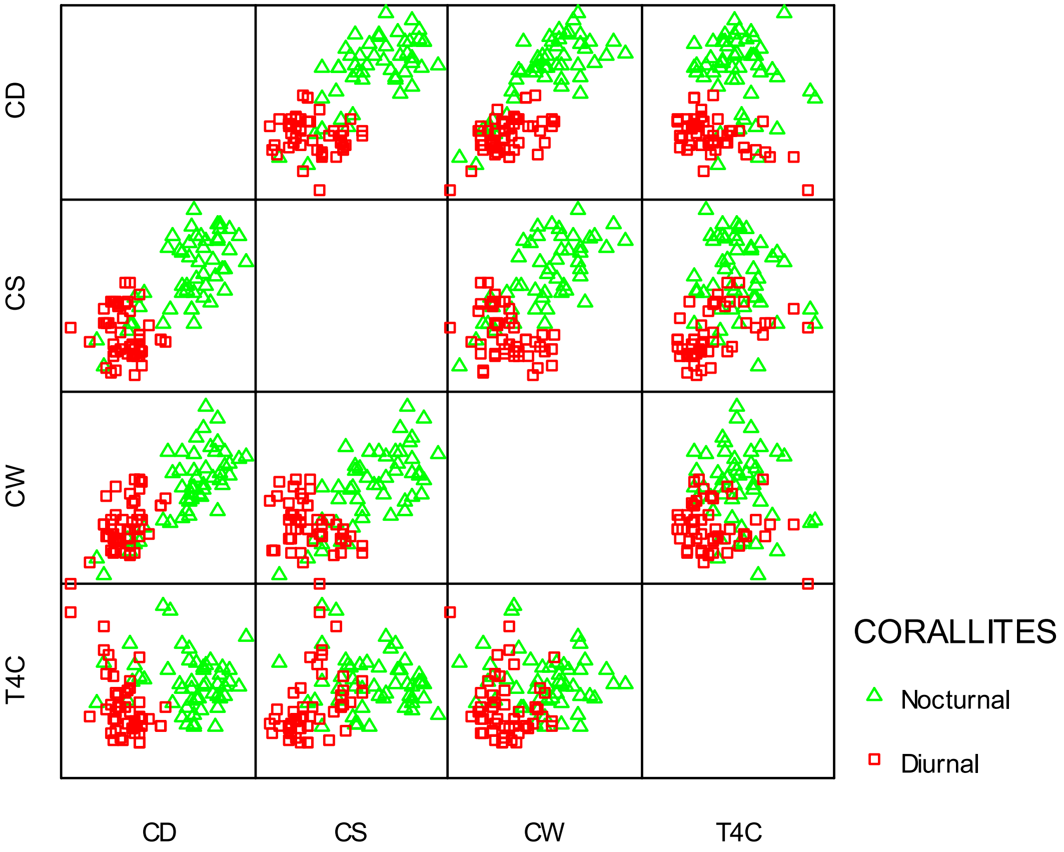

Figure 3.21 Scatter plot (matrix) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs at Turrumote 20 m. It showed all significant characters included and the resultant scatter plot of a two way combination of characters for the grouping of the two ecomorphs. CD= corallite diameter, CS= spacing of corallites, CW= width of columella, and T4C= thickness of the fourth cycle costae.

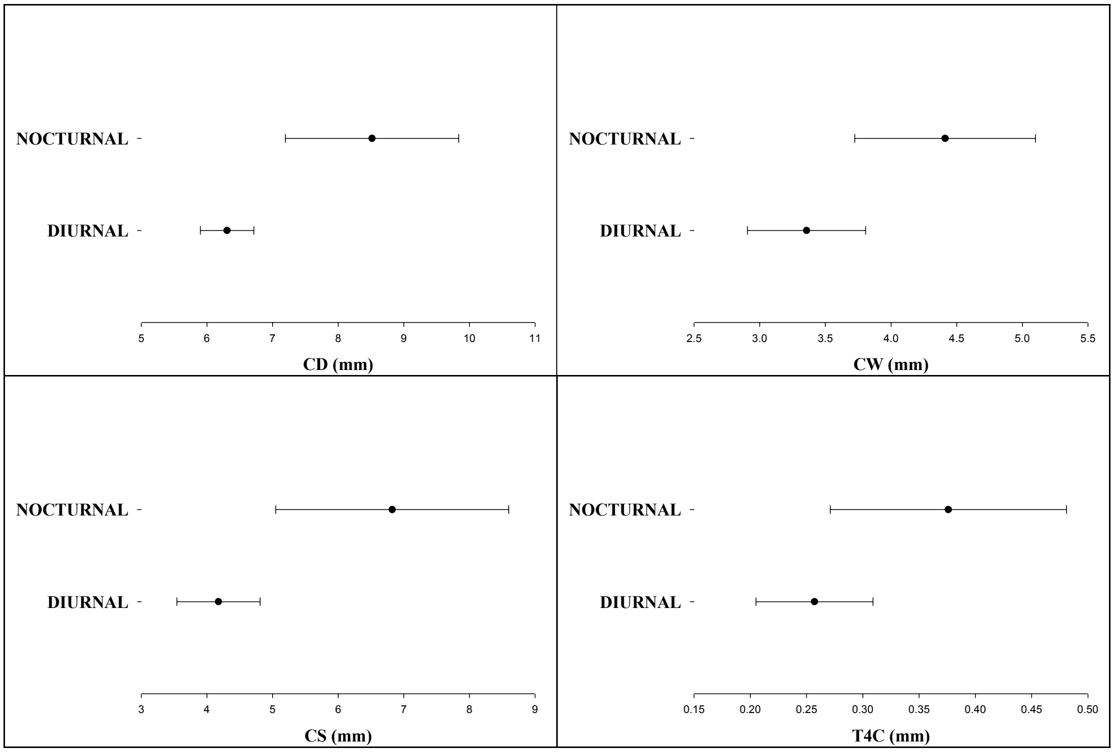

Figure 3.22 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Turrumote reef at 20 meters. CD= corallite diameter, CS= spacing of corallites, CW= width of columella, and T4C= thickness of the fourth cycle costae.

When corallite-level characters across depths for all colonies of the two ecomorphs were compared in Turrumote, significant differences were found for all ten corallite-level characters (ANOVA, $P<0.05$). The two ecomorphs were separated by SCDFA when corallite level characters (70.7 % of all corallites correctly classified) were used in the analysis. A scatter plot (3-D) of the most heavily weighted characters from the analysis of corallite level showed much overlap of the ecomorphs groups (Figure 3.23).

Corallite diameter (CD), the length of the fourth cycle septa (L4S), and spacing of corallites (CS) were most heavily weighted by the analysis (Figure 3.24).

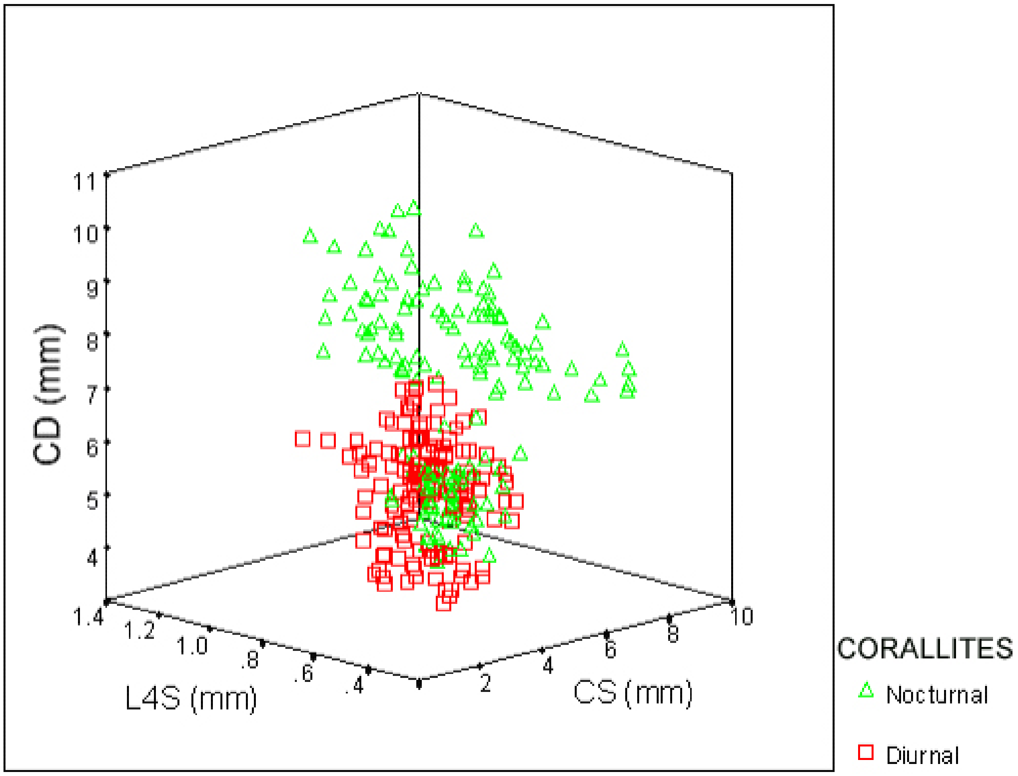

Figure 3.23 Scatterplot (3-D) of discriminant variable in the SCDFA of *Montastraea cavernosa* ecomorphs at Turrumote in general. CD= Corallite diameter, L4S= length of the fourth cycle septa, and CS= spacing of corallites.

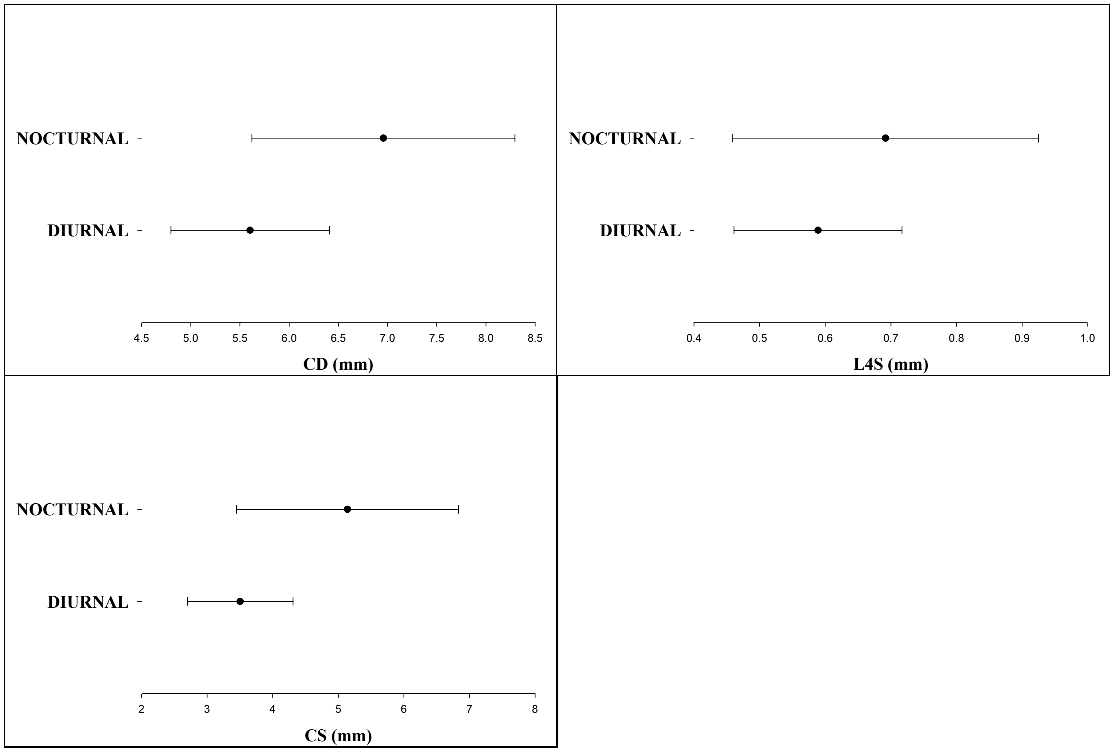

Figure 3.24 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters at Turrumote reef. CD= corallite diameter, L4S= length of the fourth cycle septa, and CS= spacing of corallites.

3.3.3 Comparison of the two ecomorphs across reef localities (regional)

Significant differences between the two ecomorphs were found in all ten corallite-level characters analyzed (Kruskal-Wallis, $P<0.05$) when all corallites from the two reef localities were analyzes. The two ecomorphs were readily separated by SCDFA with 76.8 % of all corallites correctly classified when corallite-level characters were used in the analysis. A scatter plot (matrix) of the most heavily weighted characters showed much overlap of the two ecomorphs (Fig 3.25). Corallite diameter (CD), the length of the fourth cycle septa (L4S), the length of the first cycle septa (L1S), and spacing of corallites (CS) were most heavily weighted by the analysis (Fig. 3.26).cycle septa (L1S), and spacing of corallites (CS) were most heavily weighted by the analysis (Fig. 3.26).

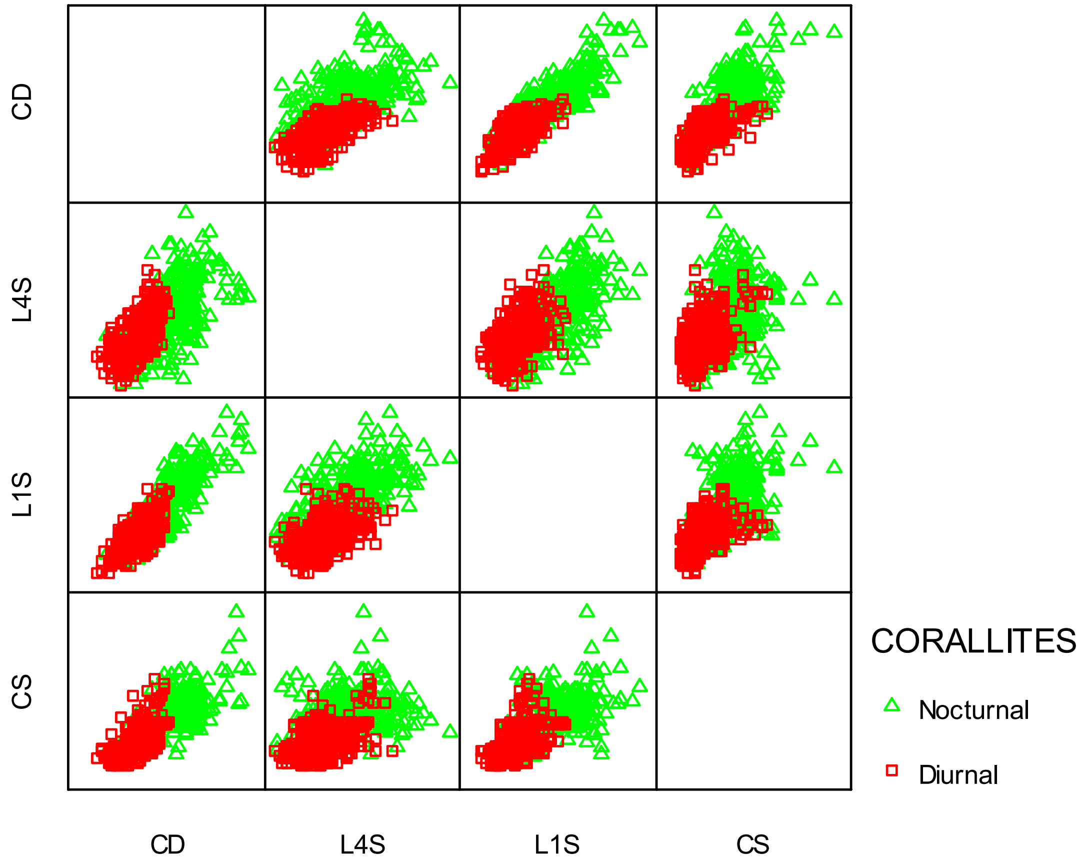

Figure 3.25 Scatter plot (matrix) of discriminant variables in the SCDFA for *Montastraea cavernosa* ecomorphs in general (Media Luna and Turrumote). It showed all significant characters included and the resultant scatter plot of a two way combination of characters for the grouping of the two ecomorphs. CD= corallite diameter, L4S= length of the fourth cycle septa, L1S= length of the first cycle septa, and CS= spacing of corallites.

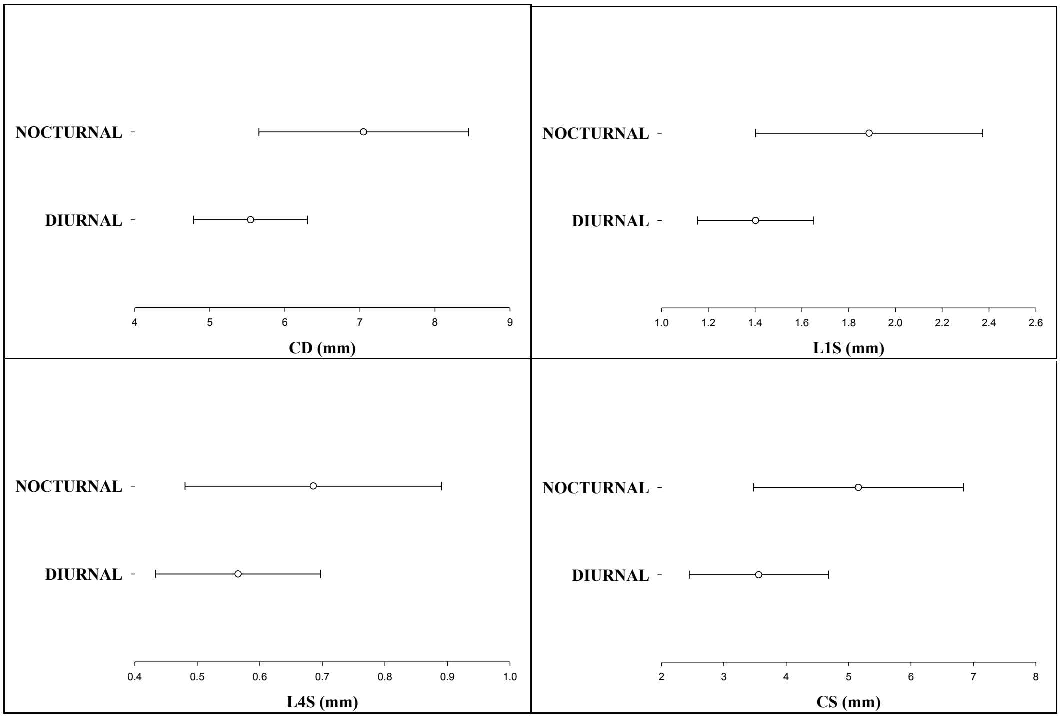

Figure 3.26 Mean and standard deviations of some of the most variable *Montastraea cavernosa* ecomorph characters in general (Media Luna and Turrumote). CD= corallite diameter, L4S= length of the fourth cycle septa, L1S= length of the first cycle septa, and CS= spacing of corallites.

3.4 Morphometric variability between the two ecomorphs at the colony level

3.4.1 Media Luna

Significant differences between the two ecomorphs were found in eight of the ten colony-level characters analyzed (ANOVA, $p<0.05$). Diurnal and nocturnal ecomorphs were readily separated by the SCDFA with 83.3 % of all colonies correctly classified in the analysis. A scatter plot (simple) of the most heavily weighted characters from the analysis showed five overlapping colonies of the nocturnal ecomorphs with the diurnal colonies. These five colonies belong to the 6m depth, which count for a 16.7 % misclassification rate (5 out of 15). All the five colonies showed small polyp size with nocturnal polyp behavior.

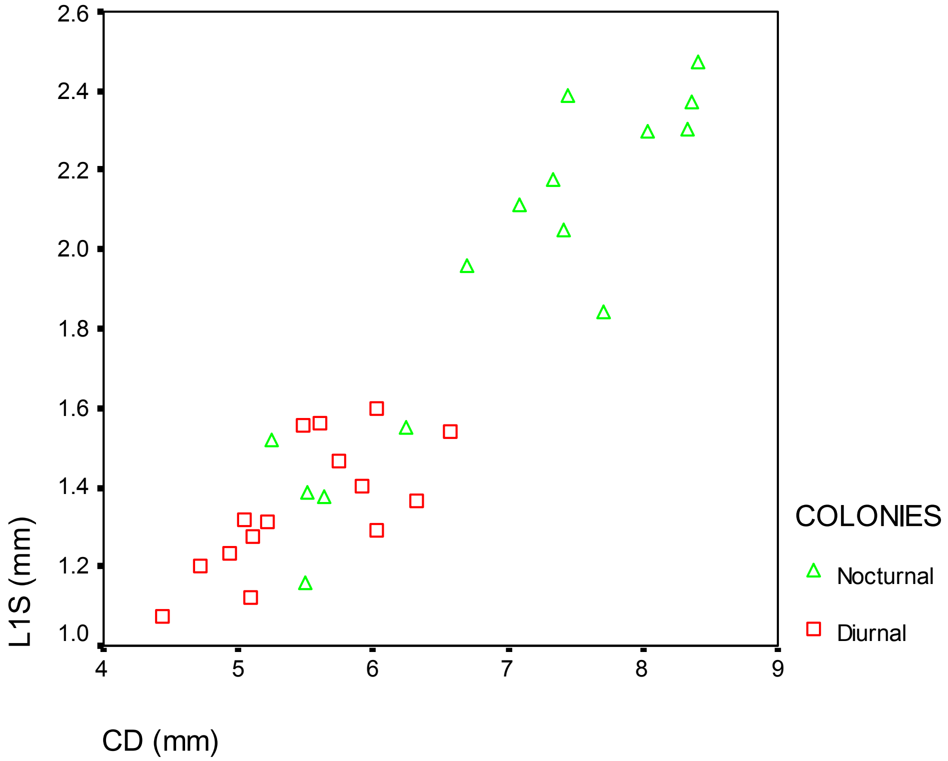

Figure 3.27 Scatterplot (simple) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs colonies at Media Luna. CD= corallite diameter, L1S= length of the first cycle septa.

3.4.2 Turrumote

Significant differences between the two ecomorphs were found in nine of the ten colony-level characters analyzed (ANOVA, p<0.05). Diurnal and nocturnal ecomorphs were readily separated by the SCDFA with 73.3 % of all colonies correctly classified in the analysis. A scatter plot (simple) of the most heavily weighted characters from the analysis showed six (40 % misclassification rate) overlapping colonies of the nocturnal ecomorphs with the diurnal colonies. Of the six colonies in the overlap five of then come from the 6 m depth and one from the 10 m depth (all small polyp and nocturnal polyp behavior). There are also 13.3 % of misclassified diurnal colonies (2 out of 15). These two colonies belong to the 20 m depth level (large polyp size and diurnal polyp behavior).

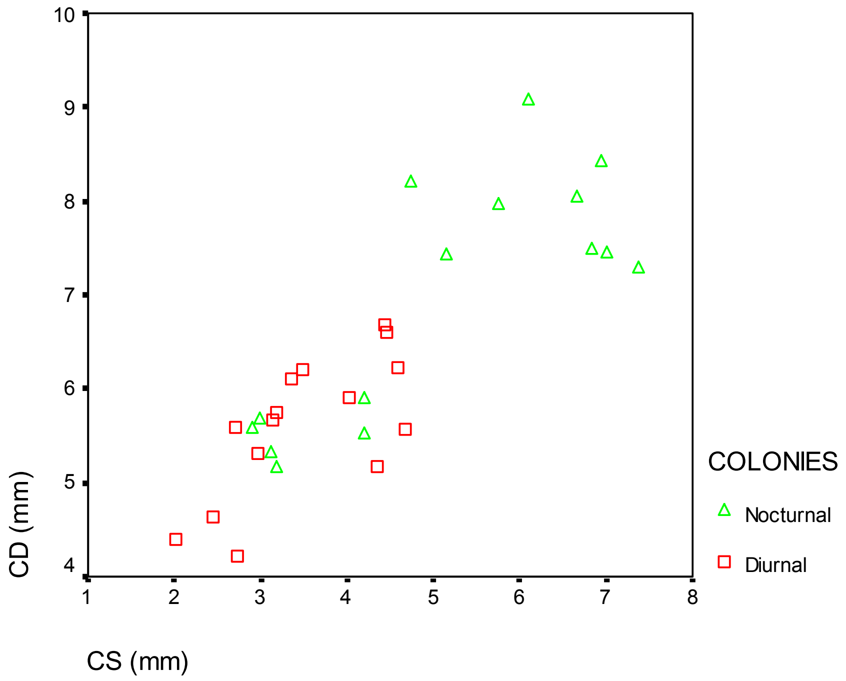

Figure 3.28 Scatterplot (simple) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs colonies at Turrumote. CD= corallite diameter, CS= spacing of the corallites.

3.4.3 Regional variability of *M. cavernosa* ecomorphs colonies (Media Luna and Turrumote)

Significant differences between the two ecomorphs were found in all ten colony-level characters analyzed (ANOVA, $p<0.05$). Diurnal and nocturnal ecomorphs were readily separated by the SCDFA with 75 % of all colonies correctly classified in the analysis. A scatter plot (simple) of the most heavily weighted characters from the analysis showed six (36.7 % misclassification rate) overlapping colonies of the nocturnal ecomorphs with the diurnal colonies. Of the eleven colonies in the overlap ten of then come from the 6 m depth and one from the 10 m depth (all small polyp and nocturnal polyp behavior). There are also 13.3 % of misclassified diurnal colonies (4 out of 30).

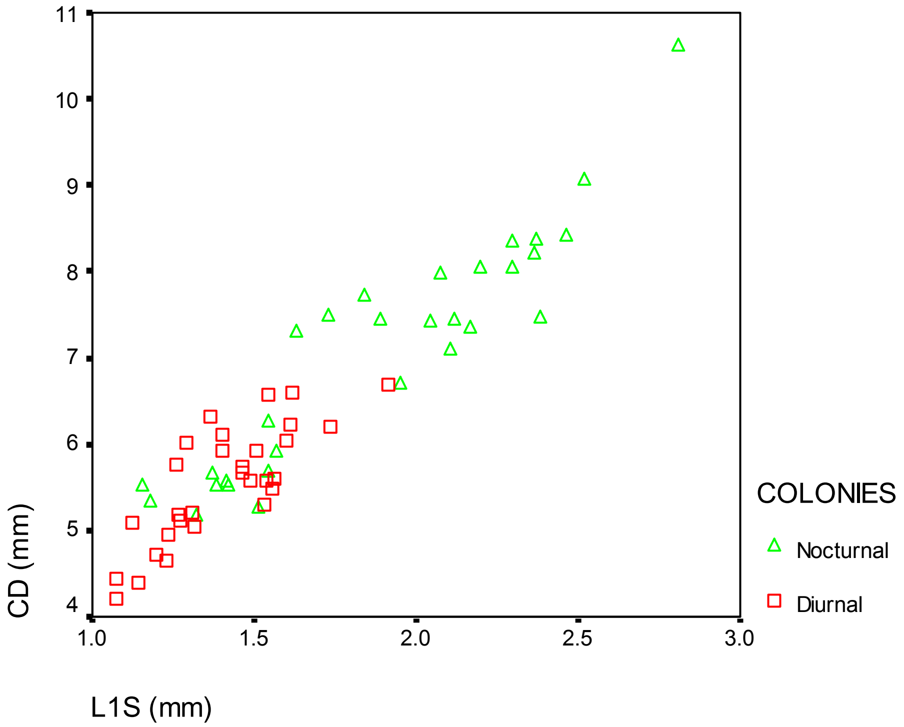

Figure 3.29 Scatterplot (simple) of discriminant variables in the SCDFA of *Montastraea cavernosa* ecomorphs colonies at La Parguera. CD= corallite diameter, L1S=length of the first cycle septa.

A reclassification of the diurnal and nocturnal colonies using the polyp size as a diagnostic character in the SCDFA increases the classification (across Media Luna and Turrumote) percentage to 94 %.

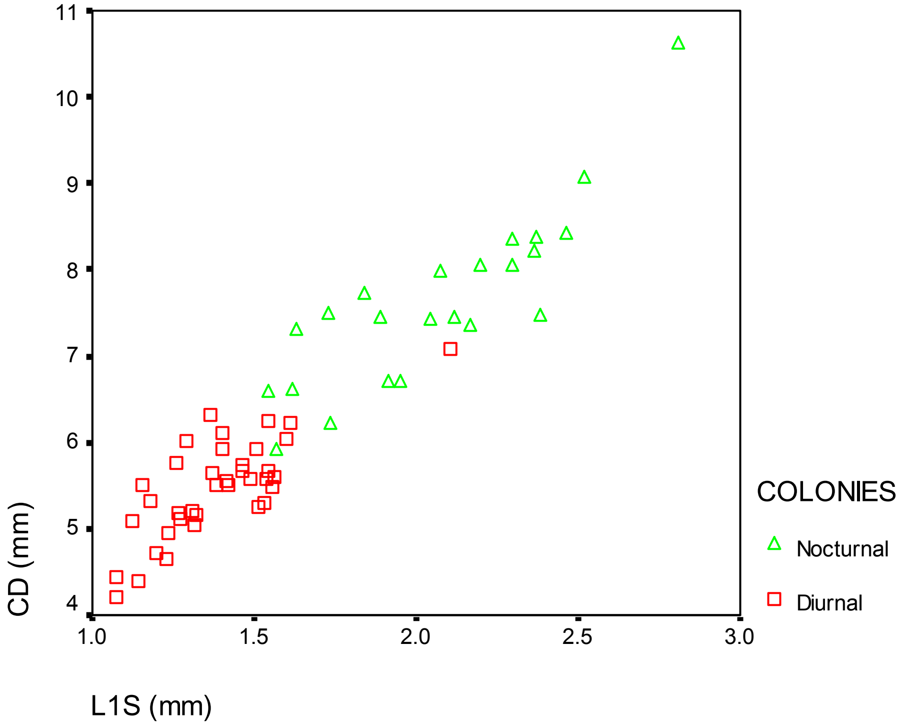

Figure 3.30 Scatterplot (simple) of discriminant variables in the SCDFA of all *Montastraea cavernosa* ecomorphs colonies (Media Luna and Turrumote) using polyp size character for the classification. CD= corallite diameter, L1S=length of the first cycle septa.

4 Discussion

Failure to define and accurately identify coral species prevent us from understanding the role of coral biodiversity in reef dynamics and undermines our ability to make valid statements and predictions in other studies. Increased coral reef deterioration and lack of consensus on the status of many coral species in the Caribbean put us in a compromising situation. Important problems such as assessing loss of biodiversity when we still do not know how many species are in the system or, designing effective resource managing programs for coral reefs areas without reliable information on the species, their biology, biogeography and interactions, will remain partially answered without a clear, alpha-taxonomy (Weil 2003). In the Caribbean for example, species that were considered the best examples of ecological generalists (Goreau and Wells 1967; Connell 1978; Rowan & Powers 1991) are now considered to be complex assemblages of specialists (Weil & Knowlton 1994; Knowlton & Jackson 1994; Rowan & Knowlton 1995). This evidence points to a much more diverse and specialized marine invertebrate fauna than previously believed, challenging widely held theories of the ecology and evolution of coral reef invertebrates (Knowlton 1993) and emphasizing the importance of a clear taxonomy.

In the Caribbean, the taxonomy of many zooxanthellate coral species has been controversial for a long time. Identification problems exist in at least 20 (74 %) of the 27 recognized genera, and one genus, ***Goreaugyra*** *(*Wells, 1973*)*, is still with a doubtful status. Past and present controversies and confusion over coral taxonomy are mostly a consequence of their high morphologic plasticity due to their modular nature (Willis, 1990; Veron, 1995) and the classical, non-quantitative morphological taxonomic approach. These problems are usually compounded by the examination of too few characters from a reduced number of colonies (or pieces of colonies) and the lack of information about the local and geographic variability, distribution, biology, and ecology of most species. Moreover, with the exception of *Montastraea* and *Porites* (Weil 1992a; Weil and Knowlton, 1994), there are no current lists of clearly defined diagnostic characters that can be used by researchers, managers and the public to confidently separate the distinct species (Weil, 2003). Morphological variation in scleractinian corals is generally believed to represent colony response to changing environmental variables (Wijsman-Best 1974; Foster 1979; Foster 1985). Some genera are more variable than others and usually, the more species a particular genera has, and if some of these species are widely distributed across the depth gradient and geographic localities, the higher the morphological variability and the more complicated it is to separate them using few characters. For example, Ross (1967) reported a general relationship between colony shape and environment with rounded, massive, bumpy colonies common in shallow waters and plate like forms abundant in deeper areas for *Porites astreoides*. Also *P. astreoides* has a variable coloration pattern (Weil 1992a) and the green morph was more abundant in shallow waters habitats whereas the brown morph was more abundant at intermediate to deep habitats (5-10 m) (Weil 1992a). These morphs were believed to represent separate species (Garthwhite and Potts, 1994), however after a multivariate study, results did not support the separation of the two color-morphs of *P. astreoides* as different species (Weil 1992a,b). The wide variability in colony morphology of *M. annularis* was also traditionally viewed as a largely phenotypic response to microhabitat differences, competition and bioerosion (Lewis 1960, Dustan 1975, Graus and Macintyre

1982). In this case however, recognition of consistent significant differences in biochemical, behavioral, physiological and morphological traits among the three common ecomorphs led to the re-description of *M. annularis* and the resurrection of two sibling species, *M. franksi* and *M. faveolata* (Weil and Knowlton 1994).

In *Montastraea cavernosa* two morphologies that commonly co-occur were described in the mid 1970's, a small polyped (small calices) form that were mostly active during the day (diurnal ecomorph), and a large polyped (large calices) form that was only active during the night (the nocturnal ecomorph) (Lasker1976, 1977, 1979, 1980,1981). This author argued that primary productivity appears to be a crucial factor affecting the morphology and behavior of *M. cavernosa* colonies. As depth increases, both light and photosynthetic rates decrease, and as the gross photosynthesis of the polyps decrease, so does the advantage of the daytime expansion (Lasker 1977). At some depth however, this value will fall bellow the cost of expansion and the nocturnal behavior will predominate according to Lasker (1977) at deeper habitats. This hypothesis explains the differential distribution of the large and small polyped forms in the depth gradient as a function of deceasing quantity and quality of light affecting photosynthesis, and therefore, available energy to the coral.

The only two studies on the micro-morphological characters of *M. cavernosa* did not take into account the two main ecomorph divisions by Lasker (1977). Results from Brazil showed high morphological variability and polymorphism within populations that could not be explained by the environmental variables (Amaral1994). The other study by Snell (1998) recommended more molecular techniques in order to assess the factors that influence high variability of morphological characters and distinguish populations within *M. Cavernosa*.

In this study *M. cavernosa* ecomorphs were first separated following Lasker's (1977) diurnal and nocturnal classification criteria based on the polyp behavior without considering the morphological polymorphism of the colonies to test if this character alone could separate the two ecomorphs consistently and if the high variability could be then explained by ecological gradients. Additional characters (ecological and morphometric) were measured to test the hypothesis that in reality, these two ecomorphs represent different species.

Ecological surveys in many different reef localities off La Parguera showed that the two behavioral ecomorphs were present and abundant. Results of the quantitative surveys then showed that the diurnal ecomorphs dominate in shallow water to intermediate depth habitats (6-10 m) with a significant reduction in deep waters (20 m) which supports Lasker's findings on the differential distribution of the forms in Panamá (Lasker, 1977, 1978, 1979). The diurnal ecomorph was significantly associated with day time polyp expansion, small polyp diameter, planar colony shape, brown colony color, and green or white oral disc color. However, some colonies also showed nocturnal activity. The nocturnal morph on the other hand, was significantly associated with night time polyp expansion, large polyp diameter, nodular colony shape, red or green colony colors, and red oral disc color. These results are consistent with Lasker's (1976, 1981) description of *M. cavernosa* ecomorphs in Panamá which support the specific distinctness of the two ecomorphs in the study area (Puerto Rico). The generally larger colonies of the nocturnal morph compared to the diurnal morph may be a consequence of the wider area needed for the larger polyps for a more efficient capture of zooplankton.

This study showed that considerable morphologic variations occur within each one of the behavioral ecomorphs, confusing the potential separation into different species. Numerous characters within each one of the ecomorphs were significantly different at the intra-colony and inter-colony level within and across habitats (depths), and across reefs. Variation at the intra-colony level in scleractinians species is generally caused by the environment (Foster 1980). The data collected for the two behavioral ecomorphs of *M. cavernosa* suggested that both respond morphologically to the environment as micro-skeletal characters varied across the depth gradient. However, genetic sources of variation may be responsible for some of the observed morphological variability (Foster 1980) but, most of the variability within and across colonies of the same behavioral ecomorph might be explained by environmental factors (light and sedimentation). Colony variability within each behavioral ecomorph across the three depths support the idea that environmental disturbances, differences in colony position on the substrate, shading, competition and other factors might influence the morphology of theses ecomorphs.

In contemporary, rapidly changing environment, phenotypic plasticity could be advantageous to corals that, due to their long generation time and low-success, sexual reproduction, might not be able to survive through adaptation alone (Potts 1984). Lower variability in the micro-skeletal characters across reefs within each ecomorph suggests that the two populations of each behavioral ecomorph are under similar environmental regimes and therefore, respond similarly.

Significant morphological differences in all ten micro-morphological characters between the diurnal and nocturnal ecomorphs at both locations (Media Luna and Turrumote) at the corallite and colony level suggest that the two ecomorphs might be sibling species. The diurnal ecomorph had smaller micro-skeletal features at every depth in both reefs compared to those of the nocturnal, large polyped morph. The nocturnal ecomorph had significantly larger micro-skeletal characters than the diurnal ecomorph. However, high morphometric variability of the calical characters across the depth gradient for colonies of the nocturnal ecomorph (that presumably supports the environmental influence argument) could be due to a mixing of colonies of the two morphs. It must be clear that when selecting the colonies at the beginning of the study, "polyp activity" was the main criteria used to separate the different ecomorphs. In the shallower habitats many colonies with small calices were not active during the day of the collections and therefore, were collected as "nocturnal ecomorphs" and put together with those colonies with much larger calices, characteristic of the nocturnal morph. Most of the high variability observed in the nocturnal ecomorph and the high overlap of colonies when the two behavioral morphs are compared, is the result of this colony mixing. When these colonies were sorted out of the analyses, variability levels went down and a much clear separation of the two ecomorphs was produced by the SDCFA analyses across reefs, indicating the possible presence of two different species.

The discriminant analyses showed that as colonies were analyzed within each increased depth, the correct classification of colonies within the particular behavioral ecomorphs was higher as depth increased, supporting the observation that in deeper habitats, the behavioral criteria was a better for separating colonies of the true distinct ecomorph (including the morphometric differences) or “species” that in shallower habitats. Almost all of the small polyped colonies were always active in deeper waters compared with shallower habitats, were they might not be active during the day because of the high photosynthetic rates providing enough energy (Lasker, 1978, 1980).

Foster (1980) suggested that scleractinians species must be differentiated on the basis of non-overlapping variation in corallite structures and support the approach in scleractinian taxonomy used by Wijsman-Best (1972, 1974), Veron and Pichon (1976), and Veron et al. (1977) which describes species on the basis of suites of specimens collected in a range of reef environments. No overlap in the stepwise canonical discriminate analysis was showed at 20 m depth at Media Luna and Turrumote reefs clearly indicating the presence of morphological discontinuities between the two ecomorphs. At Media Luna the key characters use in the classification were corallite diameter, length of the first cycle septa, and length of the fourth cycle septa. In Turrumote the key characters were corallite diameter, spacing of corallites, columella width, and thickness of the fourth cycle costae. The only common character for the classification was corallite diameter at this depth zone. In the other two zones (6 meters and 10 meters) the two ecomorphs were separated but with some overlap. This overlap could be caused by misclassification (using the polyp behavior criteria) of the ecomorphs as mentioned above.

Polyp behavior therefore, might be a useful tool in the field for the separation of the two *M. cavernosa* ecomorphs, but other characters must be also used, like polyp size, in order to more accurate classification results, especially in shallow waters (6 m). Results of this study suggest the possibility of two sibling species within *M. cavernosa* and that more research on the genetics and reproduction the different morphological forms *M .cavernosa* is needed to clarify their taxonomic status.

5 Conclusions

1. It is necessary to use more than the daytime expansion of the polyps as a character to separate the diurnal ecomorph of *M. cavernosa.* The most important character is the small polyp size (<6.0 mm). This morph can be active or inactive during the day time, depending on the depth.
2. The most significant characteristic of the nocturnal ecomorph of *M. cavernosa* was the large polyp size and the daytime (active during the night) contraction of the polyps.
3. Variation among colonies of *M. cavernosa* diurnal and nocturnal ecomorphs at both locations (Media Luna and Turrumote) was highly significant, supporting the idea of high morphological plasticity within each of the ecomorphs.
4. Within each ecomorph, even though there was high variability in most of the characters across the depth intervals, there were no significant differences in most of the measured corallite-characters when compared across populations of the two reef localities, suggesting lower genetic-induced variability and similar responses of the two populations to similar environmental conditions.
5. The use of polyp behavior (diurnal and nocturnal) to separate the two *M. cavernosa* morphs could be used as a first step to separation in deeper habitats. In shallow waters, polyp expansion varies in the small polyped forms, which can be active or inactive during day hours.
6. Colony and oral disc coloration are not good diagnostic characters to separate the different ecomorphs of *M. cavernosa*.

7. Overall results support the distinct separation of two ecomorphs (ecologically and morphologically), the small-polyped diurnal ecomorph and the large-polyped nocturnal ecomorph, which suggest the possibility that these could be different species (sibling). More ecological, genetic and reproductive information is needed to support this hypothesis.

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