Population dynamics and community structure of Octocoral species (Coelenterata: Anthozoa: Octocorallia) at Coiba National Park, Pacific Panama

by

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Dedication

A mi familia,

Marcela, Carlos, Juli y Javi

Introduction

Octocoral species are marine sessile invertebrates, considered foundation species with an important ecological role in their community; they increase the complexity of the habitat creating niche spaces and directly host a variety of invertebrates (Bayer 1953; Cantera et al. 1987). Furthermore, some species are recognized as sources of natural products and biochemical compounds with a potential use in pharmaceuticals (e.g. Gutierrez et al. 2005). Octocorals have a wide distributional range, from cold temperate waters to tropical warm water in both deep and shallow environments (Alderslade 1984). However, biological and ecological studies have been almost restricted to species in the Caribbean, Mediterranean and Hawaii, with only a couple of studies in the Tropical Eastern Panacific (TEP), which is recognized as a diversity hot-spot with high levels of endemism (Guzman et al. 2004, 2008). In contrast to octocoral communities in other regions, communities at the TEP are located in very active environments: rocky outcrops and vertical walls exposed to strong swell and currents (Breedy & Guzman 2003).

Due to the lack of studies in the area, this study is the first attempt to examine the basic biology and community structure of shallow octocorals in Coiba National Park (CNP), a recognized octocoral hotspot in the TEP (Guzman et al. 2004). The first chapter reviews the scarce literature available for the TEP and compares biological aspects of TEP species with species in other areas, which occur in a different type of habitat. The aim of this chapter is to compile what is already known about these organisms and suggest future studies. With the literature review as a starting point, chapter two aims to study the population dynamics of 15 common shallow water species at CNP and describe the life history strategy of common species. This study uses fix plots to monitor mapped colonies and quantify recruitment, mortality and growth of common species in four octocoral communities.

Chapter three uses a theoretical approach to evaluate the change in octocoral community structure after two different scenarios. The aim of this last chapter is to compare different ecological community descriptors (Rényi diversity profiles, Rank Abundance Distribution Plots, Abundance Spectrums, and ordination analysis of similarities) to assess changes in the community composition and weather or not this composition is able to recover after a natural population decline, previously reported in chapter 2, and after a anthropogenic punctuated disturbance.

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Abstract

Octocorals (Alcyonacea) are sessile marine foundation species common in very active environments in the Tropical Eastern Pacific (TEP). Although they are a dominant part of the community and have strong interspecific relationships, there have been very few studies of their biology and ecology. This thesis is the first attempt to study the basic biology and community structure of shallow water octocorals present in Coiba National Park in Pacific Panama, a hotspot for species richness and endemism in the TEP. The first chapter reviews the existing scientific literature on octocorals in the TEP and compares this literature to studies in other regions. This Chapter demonstrates the lack of research on these ecologically important communities and suggests future studies. Chapter 2 studies basic population dynamics (recruitment, mortality, and survivorship rates) for 15 shallow water octocoral species in 6 genera, the growth rate of 4 species of different genera, and identifies « r » and « k » selected species. Chapter 2 also reports a significant natural population decline in all study sites. Chapter 3 presents an analysis of the structure of four octocoral communities. This Chapter uses different community ecological descriptors (Rényi diversity profiles, Rank Abundance Distribution Plots (RAD), Abundance Spectrums, and ordination analysis of similarities) to evaluate changes in community structure during the population decline reported in Chapter 2 or after a punctuated anthropogenic disturbance. The population decline was not found to have changed the structure of the community, however, different recovery trajectories were observed after the disturbance. RAD and Rényi plots described the trend of the change, ordination analysis of similarities described the extent of the change, and abundance spectrums described the nature of the change.

Resumé

Les octocoralliaires sont des espèces sessiles marines fondatrices, communes dans des milieux très actifs du Pacifique Est Tropical (PET). Bien qu'elles dominent dans leurs communautés et entretiennent de très fortes relations avec les autres espèces, il existe très peu d'études sur leur biologie et leur écologie. Cette thèse est la première tentative d'étude de la biologie de base et de la structure des communautés octocoralliaires présentes dans la partie panaméenne du PET: le Parc National Coiba, zone chaude d'une grande diversité en espèces endémiques.

Le premier chapitre passe en revue la littérature scientifique sur les octocoralliaires du PET et les compare aux études faites dans d'autres régions. Ce chapitre révèle de manière évidente l'absence d'études sur ces communautés écologiquement importantes et suggère des études futures. Le second chapitre étudie la dynamique de la population de base (naissance, mortalité et survie) de 15 espèces d'eau peu profonde dans 6 genres, le taux de croissance de quatre espèces, et identifie des espèces avec des stratégies écologiques « r » et « k ». Ce chapitre fait également état d'un important déclin de population dans tous les sites étudiés. Le troisième chapitre analyse la structure de quatre communautés octocoralliaires. Différents descripteurs écologiques sont utilisés (Diversité Rényi, distribution d'abondance par rangs, spectre d'abondance et analyse de similitudes par ordre) pour évaluer si la structure de la communauté a changé durant le déclin de population mentionné dans le chapitre deux ou suite à une perturbation anthropogénique aiguë. Le déclin de population n'a changé la structure de la communauté en aucun des sites étudiés. Cependant, après la perturbation, la récupération des communautés s'est effectuée d'une manière différente en chacun de ces sites. Les graphiques RAD et Rényi ont décrit la tendance du changement, l'analyse de similitudes par ordre l'ampleur du changement, et le spectre d'abondance la nature de ce changement.

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Logical order of the thesis

This is a manuscript-based thesis composed of three chapters. Chapter 1 is an introduction to the subject and literature review of relevant scientific publications. Chapter 2 is the first attempt to describe the population dynamics of an octocoral population at Coiba National Park, Pacific-Panama. Chapter 3 studies the community structure in the same location and evaluates changes in the community through common ecological community descriptors.

Contribution of authors

I am the main author of this thesis and all of the manuscripts within it. I prepared the necessary tools and protocols to collect the data, collected the data in the field, analyzed the pictures from which the data was gathered, analyzed the data, wrote the manuscripts, and compiled this thesis. My advisor Hector Guzman contributed to all phases of the development of this research, including thesis proposal, experimental design, fieldwork guidance, data analysis, and the writing of the three chapters of the manuscript. My advisor, Andrew Gonzalez, contributed to data analysis and the writing of the three chapters of the manuscript. Odalisca Breedy, an octocoral taxonomist, identified studied colonies to the species level.

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Chapter 1. Introduction & Literature Review

Octocorallia (Coelenterata) from the Tropical Eastern Pacific: what is known as a starting point for future research

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Introduction

Octocoral species (Coelenterata: Octocorallia: Alcyonacea) are marine sessile invertebrates with high environmental tolerance (Breedy & Guzman 2003a), found in a wide latitudinal and depth gradient (Bayer 1981; Aldersalde 1984). Octocorals are considered foundation species, not only because they host many invertebrates but also because they increase the dimensionality of the habitat and create niche spaces in the community (Cantera et al. 1987). However, octocoral communities are threatened by environmental (water warming events) and anthopogenic (pollution and habitat degradation) disturbances (Guzman et al. 2008). In contrast to reef building hard corals, many octocorals lack the symbiosis relationship with a zooxanthellae algae, therefore they are not restricted to warm shallow water; In addition, their soft body allows them to occupy places with strong current and surge.

Octocorals mostly occur in tropical and subtropical areas (Goh & Chou 1994). Many authors have described them as one of the most characteristic components of tropical seas, particularly the Caribbean (Bayer 1953), the Indo-Pacific (e.g. Cary 1931; Crossland 1938; Bayer 1961; Preston & Preston 1975; Dinesen 1983), the Mediterranean Sea (e.g. Cerrano et al. 2000; Garrabou & Harmelin 2002; Coma et al. 2004; Linares et al. 2008a), and the Tropical Eastern Pacific (Bayer 1953).

While there have been some studies of the octocorals in the Mediterranean, the Caribbean, and Hawaii, the octocorals of the Tropical Eastern Pacific [TEP] have been largely ignored in recent reviews (Cortes 1997; Glynn & Mate 1997; Mate 2003). In 1981, Bayer classified knowledge of the octocorals from the TEP region as ¨poorly known." However, recent efforts have been made to review the taxonomy of the most common genera present in the TEP, including *Pacifigorgia* (Breedy & Guzman 2002), *Leptogorgia* (Breedy & Guzman 2007), *Eugorgia* (Breedy et al. 2009), and *Heterogorgia* (Breedy & Guzman 2011 *in press*). This enormous contribution has resulted in the description of over 20 new shallow water species in less than a decade, which unfolded a new era of octocoral research in molecular systematic, biogeography and ecology across the region.

The Tropical Eastern Pacific region is defined as the area between the Sea of Cortez and the northern coast of Peru (Allen & Robertson 1994; Cortes 1997), and it is divided into 3 biogeographic provinces; Panamic, Cortes, and Ocean Island (Robertson & Kramer 2009). This region has been described as the "smallest natural marine laboratory for the study of coral community structure and function on a regional level" (Cortes 1997). In addition, the region was politically divided for the design of the Marine Conservation Corridor of the Tropical Eastern Pacific (MCCTEP) which includes most of the areas of high octocoral diversity and endemism (Guzman et al. 2008), and lies in the territorial water of four countries: Costa Rica, Panama, Colombia and Ecuador.

Octocorals have a high diversity in the Eastern Pacific region, with eleven genera in four families: Gorgoniidae (*Eugorgia*, *Leptogorgia*, *Pacifigorgia*, *Phycogorgia*); Paramuriceidae (*Heterogorgia*); Plexauridae

(*Muricea*, *Psammogorgia, Thesea, Echinogorgia, Adelogorgia*); and Ellisellidae (*Ellisella*), (Bayer & Deichmann 1960; Breedy & Guzman 2003a) which includes about 94 described species (Annex 1). Many taxonomic problems have arisen within these classifications. Ocotocoral species are described by their morphology and sclerite composition (Bayer 1961) and many existing studies have not included a complete description of the colonies (Breedy & Guzman 2002). An effort to use molecular data for octocoral phylogenetic studies has included DNA (Sanchez et al. 2003), RNA secondary structures (Aguilar & Sanchez 2007; Grajales et al. 2007) and mitochondrial protein-coding sequences (McFadden et al. 2006) analysis. However, due to the very slow rate of mitochondrial gene evolution the resolution of molecular studies is not enough to propose an alternative phylogenic classification to the morphological one that is used today (McFadden et al. 2010). Alternatively, the use of continuous morphological variations was proposed for Octocorallia systematics (Vargas et al. 2010).

Although, the Tropical Eastern Pacific has been described as highly diverse (Bayer 1953) and a "little laboratory" (Cortes 1997), most studies on gorgonians have only examined the variety of active compounds isolated from octocoral tissue that present potential for use in pharmaceuticals and the production of natural products (Rodriguez & Ramírez 1994; Rodriguez 1995; Gutierrez et al. 2005; Gutierrez et al. 2006). There are few studies about the biology and ecology of these organisms, which comprise the major component of rocky habitats in the region (Bayer 1953). Indeed, besides the taxonomic descriptions and phylogenetic studies already mentioned, publications on ocotocorals in the TEP have been limited to four publications on their biology, five on symbiotic relationships in their communities, and two publications on the biogeography. Other studies include the species *Carijoa riisei*, which was previously considered invasive in the TEP (Concepcion et al. 2010).

Grigg (1977) presented the first attempt to describe the life table of *Muricea california* and *Muricea fruticosa* populations in Baja California (Grigg 1977). He also published three more works focused on that region including studies of orientation and water movement (Grigg 1972), growth and periodicity (Grigg 1974), and habitat suitability and stability for *M. californica* (Grigg 1975). Four other studies have examined symbiotic relationships between invertebrates and octocorals (Cantera et al. 1987; Neira et al. 1992; Ramos 1995; Alvarado & Fernandez 2005). In 2005 Van Oppen studied the symbiotic relationship of octocorals with zoozanthellae; 27 species from the TEP were included in the study. Bayer and Deichmann (1960) studied the zoogeography of *Ellisellidae*, and Vargas et al (2008) studied the biogeography of the genus *Pacifigorgia* in the TEP.

TEP octocorals have been ignored for several reasons: the lack of taxonomic reviews; the fact that octocorals are frequently found in environments with exceptionally strong currents and storm-swept reefs (Dai 1991), creating relative inaccessibility to their habitat; the difficulty of identifying recruits (Lasker 1990); and the difficulty of collecting age-specific fecundity and mortality rates (Grigg 1977). The present study reviews the existing literature published in scientific journals on shallow water octocorals (Octocorallia; Alcyonacea) from the TEP. Relevant literature on the subject was identified searching for “octocoral” “Octocorallia”, “soft corals”, “gorgonian” and “Alcyonacea” in the key words, as part of the title and as part of the text, without a time filter. A search for the genera found in the TEP was also performed. Papers where sorted by locations: papers from the Tropical Eastern Pacific where analyzed and papers from other locations where used for comparison. Literature search was performed through ISI Web of Science, Google Scholar and through references cited on relevant papers. This review summarizes the reported species in the TEP, ecological and biological studies on such species, suggests similarities with species from other regions, and possible future studies.

Biogeography

The Tropical Eastern Pacific (TEP) is a relatively new region. Three and a half million years ago, the isthmus of Central America was open, and the marine fauna of what is now the Eastern Pacific was similar to the fauna of the Caribbean (Cortes 1997). With the closure of the isthmus, many oceanographic characteristics changed and marine fauna differentiated (Cortes 1997).

Since the early works of Verrill (1864, 1868a, 1868b) and Bayer (1953), the timeline of gorgonians has been controversial. Addison E. Verrill suggested that the existence of gorgonians in the west part of America began after the raising of the Isthmus of Panama, which separated the Pacific and the Atlantic Oceans. Verrill supported this theory by noting the significant differences between octocorals from the two oceans. Alternately, Frederick Bayer hypothesized that homogenous gorgonian populations existed in the Atlantic and Pacific Oceans before the closure of the Isthmus, with subsequent massive extinctions in the Caribbean due to physical environmental changes and speciation in the Pacific (Bayer 1953). He supported this theory by comparing the distribution of the genus *Leptogorgia*, a species at the lowest level of development and present in both oceans (see Breddy and Guzman 2007), with the distribution of the genus *Pacifigorgi*a, another group of species with a more advanced level of specialization, very diverse in the eastern Pacific and with only one relic species in the Atlantic (see Breddy and Guzman 2002). Ekman (1935,1953) suggested that the fauna of the Eastern Pacific was more closely related to that of the Caribbean than to the fauna of the Western Pacific. Ekman supported this hypothesis by noting the complete absence of the gorgonacean family Ellisellidae in the Eastern Pacific. Bayer and Deichmann (1960) criticized Ekman's theory when the presence of the family Ellisellidae was confirmed in the region. The theory retained some validity, however, because of the restricted distribution of *Psammogorgia* and *Heterogorgia* in the TEP (Table 2).

Recent works have sustained the argument over how this differentiation took place and how closely related the Eastern Pacific corals are to corals from the Atlantic and from the Central Pacific. One hypothesis posits that corals from TEP are more closely related to corals on the Atlantic, and that they have diversified since the closure of the Central American isthmus (Heck and McCoy 1978). Other hypotheses assume that corals present in the TEP are the result of migration from the Central Pacific (Dana 1975), because corals from the TEP are more similar to corals from the Central Pacific than to corals from the Caribbean (Glynn and Wellington 1983; Cortes 1986; Budd 1989; Glynn et al. 1996). This long distance dispersal trespassing the east Pacific filter could be the result of high velocity west to east advection during ENSO events (Glynn & Ault 2000). The first study in the biogeography of *Pacifigorgia* with a track compatibility analysis concluded that the genus *Pacifigorgia* is absent in the Caribbean as a result of ancient absence, rather than as the result of extinction after the closure of the Isthmus (Vargas et al. 2008). However, one *Pacifigorgia* species (*P. elegans*) is present in the Caribbean and considered a relict species that survived the Plio-Pleistocene extinction episode (Vargas et al. 2008).

Based on the distribution of hot spots of endemism for the genus *Pacifigorgia* in the TEP, Vargas et al. (2008) described three distinct biogeographic provinces: Cortez-Mexico, Panamic, and Galapagos. The Central American Gap, an extensive soft-bottom pelagic gap, is considered to be a barrier isolating oceanic gorgonian species. Alternately, stepping stone rocky islands could have prevented the isolation of octocoral species between the Cortez and Mexican areas. Each of these areas is considered an endemicity hotspot for *Pacifigorgia* species: Cortez-Mexican, 6 endemic spp; Panamic, 16 endemic spp; and Galapagos, 4 endemic spp. (Vargas et al. 2008).

Table 1. Distribution of common Octocoral genera present in the Tropical Eastern Pacific (TEP).

Genus	Distribution
Psammogorgia	Restricted to Panamic province (Bayer & Deichman 1960)
Heterogorgia	Restricted to Panamic province (Bayer & Deichman 1960)
Pacifigorgia	Restricted to the Pacific (except for one species) (Breedy & Guzman 2002)
Eugorgia	Restricted to the TEP (Breedy et al. 2009)
Leptogorgia	Panamic Province, Atlantic Ocean, Caribbean, Mediterranean seas, southern Africa and one species in the subantartic (Williams & Lindo 1997; Breedy & Guzman 2007)
Muricea	Bermuda; southern Florida and the Antilles; southern California to Panama (Verrill 1870)

Morphology and Morphological adaptations

Octocoral species occur in a variety of shapes, with primary and secondary fans or branches, and different thickness, sizes and colors (Figure 1). They are composed of different kinds of calcium carbonate sclerites: spindles, capstan, and rods. Similarly, sclerites can have various colors, sizes and shapes, and are used to identify morphospecies. A complete description of a colony and its sclerites is therefore required for traditional taxonomical classification (Breedy & Guzman 2002). Octocorals can establish in very active environments because they have strong holdfasts to attach to the substrate and have flexible colonies to cope with water movement.

Morphological characteristics could vary within a species depending on local conditions. For example, differences in branch diameter and spicule length can help the species tolerate large water forces (Grigg 1972). The direction of the current also plays an important role for colony morphology; Grigg (1972) found that the morphology of two species of *Muricea* (*M. californica* & *M. fruticosa*) varied with current directionality. Colonies in areas with no dominant current direction presented bushy-like appearances, with branches in many directions, while colonies found in bidirectional currents presented branches in a fan-like arrangement. Grigg also related colony orientation with water movement, concluding that branched colonies were oriented at a right angle with respect to the dominant current flow.

This type of relationship was also described for *Eunicella cavolini* (Wainwright and Dillon 1969) and other fan shaped species (Muzik & Wainwright 1977). Colony orientation was thought to be a progressive process related to colony size, with small colonies randomly oriented and large colonies oriented parallel to the current (Theodor and Denizote 1965). It was proposed that colony orientation could also be an adaptation for feeding or an accommodation to hydrodynamic forces (Leversee 1976).

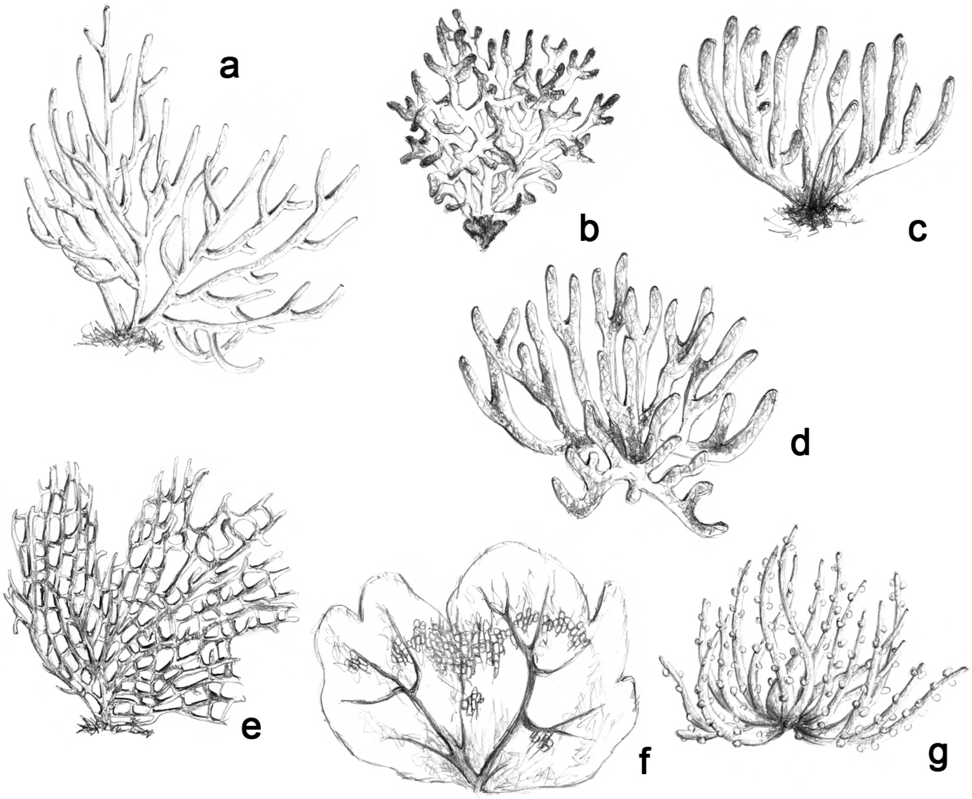

Figure 1. Growth forms of TEP Octocorals (Order Alcyonacea). Branched octocorals can have long and slender branches (a), small branches in many directions (b), thick branches in a fan-like appearance (c) or in many directions (d). Seafans can have a single or multiple fans with an open (e) or closed (f) mesh. Fouling species have a bushy morphology (h).

Growth and age estimates

Octocoral species have different growth forms, including thin or thick branched colonies, with bushy or fan like appearance, as well as seafans composed of closed or open mesh with primary and secondary fans. Growth can happen as an increase in the size of branches or fans as well as the addition of secondary fans and branches. Only the growth rates of three species present in the TEP have been studied.

Carijoa riisei was described as a fast growing octocoral, growing from 0.5-2 cm/week (Kahng et al. 2008), considered a fouling species (Bayer 1961), with rapid vegetative spread after settlement (Kahng & Grigg 2005). Growth and aging was also studied for *Muricea fruticosa* and *Muricea californica.* Grigg (1974) estimated the age of this species by counting annual growth rings in the skeleton of the colonies. Good age estimates were found in young colonies (<30 yrs for *M. californica* and <10 yrs for *M. fruticosa*). Colony growth decreased constantly with colony height. In his study, Grigg formulated an equation to explain the relationship between colony size and age (equation 1), and used the regression method of Bartlett (1949) to fit the data of *M. californica* (equation 2).

Equation 1. $dH/dt= K(H_\infty - H_t)$

Equation 2. $dH/dt= 2.14-0.0274\ H_t$

Where dH/dt is the change in colony height (cm) per year, and K is the slope of the regression of the change against H_t. In this equation, the age estimate error of colonies up to 45 cm high was less than 30%; however, the age estimation for larger colonies (> 50 cm) was very inaccurate (Grigg 1974). By using these equations, Grigg (1974) predicted that a 30 cm colony would be about 20 years old. Other predictions included different factors responsible for high variability in colony growth; like abrasion by algae and predation. It was estimated that around 10-15% of the annual growth of the octocoral was consumed by the predator fish *Hypsypops rubicunda*.

Other aging methods have been proposed for octocorals outside the TEP including repeated photographic records (e.g. Goh & Chou 1995; Cadena & Sanchez 2010; Rossi et al. 2011); counting of annual growth rings in the cold water species *Primnoa pacifica* (Matsumoto 2007) and deep water species *Primnoa resedaeformis* (Andrews et al. 2002); measurement of total branch length to estimate the age of *Eunicella cavolini* (Weinbaurer & Velimirov 1996); and measurement of the stem diameter and colony height to estimate the age of *Leptogorgia caratopjyta* in the Mediterranean Sea (Mistri & Caccherelli 1994).

Diversity and distribution

A total of 94 described species have been reported in the TEP (Annex 1 and Table 2). Most of these species occur in the Panamic region, particularly in recently studied sites in Panama and Costa Rica (Breedy 2001; Breedy & Guzman 2003a,b, 2004, 2005, 2008, 2011; Breedy & Cortes 2008; Guzman & Breedy 2008a,b, 2011; Guzman et al. 2004, 2008) (Table 2). It can be assumed that although Panama and Costa Rica have very high octocoral diversity, the results in Table 2 could be biased by the lack of studies or passivity of coastal surveying in other countries. Two sites have been described as important endemicity and diversity hot-spots: Las Perlas Archipelago, with 38 species (Guzman et al. 2008); Coiba National Park, with 34 species (Guzman et al. 2004), both located in the Republic of Panama; and Isla del Coco in Costa Rica with 12 species (Breedy & Cortes 2008). Robertson and Cramer (2009) proposed that a peak in diversity in marine fauna around Panama was due to the history of the isthmus, which was the last place to be isolated from Caribbean, with a variety of habitats and environmental conditions in abundant continental islands. This could be the reason why there are two hot spots of species richness in Panama; one in the Gulf of Panama (Guzman et al. 2008) in an upwelling area (D'Croz & Mate

2004) and one in the Gulf of Chiriquí (Guzman et al. 2004, 2008) in a non upwelling area (D'Croz & Mate 2004), both of these with a high number of continental islands. However, these hotspots refer only to shallow water communities. Deep-water habitats and species are still to be studied and described.

Out of the eleven genera: Gorgoniidae (*Eugorgia*, *Leptogorgia*, *Pacifigorgia*, *Phycogorgia*); Paramuriceidae (*Heterogorgia*); Plexauridae (*Muricea*, *Psammogorgia, Thesea, Echinogorgia, Adelogorgia*); and Ellisellidae (*Ellisella*), two are described as abundant shallow water (<50m) of the TEP. These are *Pacifigorgia* with 35 valid species (Vargas et al. 2008; Guzman & Breedy 2011), and *Leptogorgia* with about 23 nominal species (Guzman & Breedy 2008b). The Genus *Eugorgia* is the next most abundant with 10 nominal species (Breedy et al. 2009).

Table 2. Octocoral diversity in three distinct regions of the Tropical Eastern Pacific (TEP)

	No. of reported species
Cortez-Mexican Region	**60**
California	8
Baja California	20
Southern Mexico	32
Panamic Region	**132**
Nicaragua	6
El Salvador	9
Costa Rica	32
-Isla del Coco	12
Panama	60
- Coiba National Park	34
- Las Perlas Archipelago	38
Colombia	10
Ecuador (continental)	4
Northern Peru	11
Galapagos	**7**

Habitat

The type of habitat used by octocorals has been described several times. In the Panamic Province, populations are not evenly distributed (Guzman el at. 2004). The octocoral populations are found attached to rocky formations in intertidal areas, vertical walls, or underwater mountains (Breedy & Guzman 2003a). They are located in a wide depth range in high-energy sites with currents and strong and braking surges, clear water, and high particle movement (Bayer 1981) (Figure 2). Octocorals share their substrata with encrusting coralline algae, sponges, bryozoans (Breedy & Guzman 2003a) scleractinian coral (Guzman et al. 2008) and tunicates, and are more diverse in coral communities than in coral reefs (Guzman et al. 2004, 2008).

In the Cortes-Mexican Province, Grigg (1975) looked closely the habitat of *Muricea californica,* found in La Joya, California. He compared populations in different habitats and concluded that the suitability (measured by relative longevity) and stability (low variability between age classes) of the habitat of *Muricea californica* was related to the characteristics of the substratum; the most stable and suitable habitat was composed of firm substrata, sandstone, a few patches of sand, and a rich and dense epifaunal community. On the other hand, the distribution of the octocoral *Carijoa riisei* appears to correlate with low water temperature and low light irradiance (Grigg 2003; Kahng & Grigg 2005). Studies in areas other than the TEP have suggested that gorgonians favor outer and mid-shelf slopes with high water clarity and circulation (Dinesen 1983), have a better tolerance to siltation than scleractinian corals (Preston and Preston 1975), and can be found in higher densities at lower light levels (Weinbauer & Velimirov 1996).

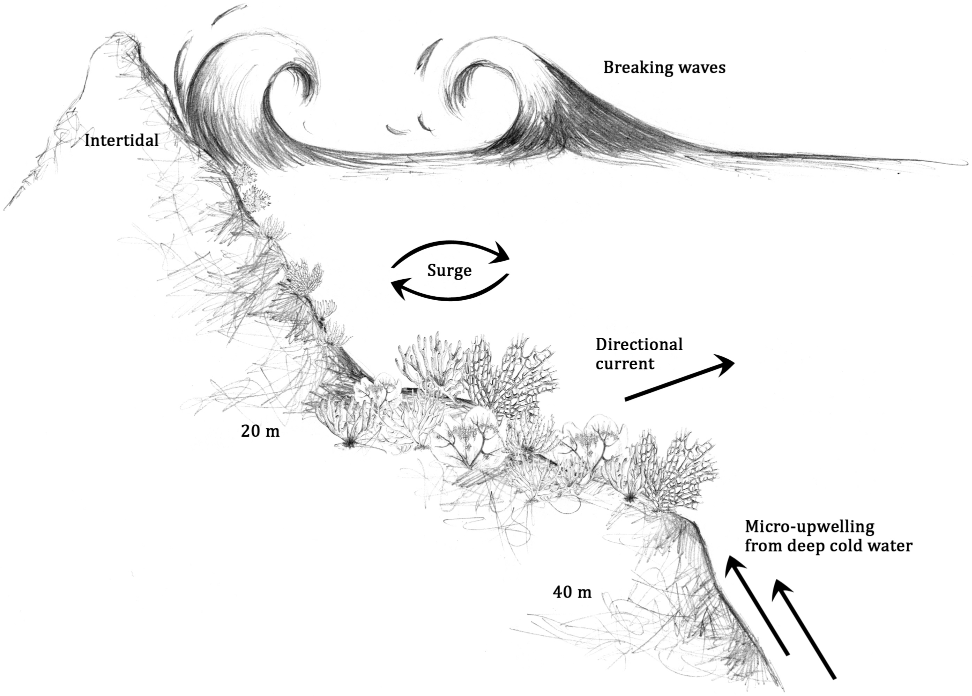

Figure 2. Octocorals at TEP inhabit vertical rocky walls from the intertidal to deep water and are exposed to strong surge and currents.

Reproduction

Sexual and asexual reproduction has been described for octocoral species; maintenance of gorgonian populations, however, may rely on sexual reproduction (Jordán-Dahlgren 2002). About 87% of octocoral species are gonochoric (Kahng et al. 2008), with a low incidence of hermaphroditism (Benayahu & Loya 1984a; McFadden 1991; Coma et al. 1995; Kruger et al. 1998; McFadden et al. 2001; Kahng et al. 2008). Complete reversals in colony sex (between male and female and vice versa) are unknown (Kahng et al. 2008) with a reproductive age of about two years (Grigg 1977; Benayahu and Loya 1983, 1984a,b, 1986; Farrant 1986; Gotelli 1991; Coma et al. 1995a,b; Fitzsimmons-Sosa et al. 2004; Torrents et al. 2005; Kahng et al. 2008). A geographically widespread of a skewed sex ratio biased in favor of males, and synchronous spawning related with the moon cycle is found in octocorals as it is in hard corals (Brazeau & Lasker 1990).

Although sexual reproduction seems to be more common, some octocoral species may rely on asexual reproduction, as it is the case for a *Plexaura* species in the Caribbean (Lasker 1984; Lasker 1990). This species has an adaptive morphology with axis constrictions that facilitate branch fragmentation (Lasker 1984). Due to their original size, fragments have up to 25-fold greater chances of reaching maturity than sexually-produced larvae (Lasker 1990).

Grigg (1977) studied the reproductive biology of two species in the TEP: *Muricea fruticosa* and *Muricea californica* in California. He described the reproductive biology of these species as having an annual cycle and a temperature-dependent peak lasting from two to six months. Grigg also found that the number of eggs produced is related to the number of polyps, which was related to colony weight.

Kahng et al. (2008) described *Carijoa riisei* as a gonochoric brooder, with internal and external fertilization, reaching sexual maturity and beginning gametogenesis within a few months of recruitment, and oogenesis after 6 months or less in large healthy colonies, and with an asynchronous and continuous gametogenesis. Therefore, the aggregation of female and male colonies is required. It has density-dependent sexual reproduction (Kahng et al. 2008) and a fast vegetative spread after settlement (Kahng & Grigg 2005).

Studies outside the TEP of genera present in the TEP include the reproductive features of *Leptogorgia sarmentosa* in the Mediterranean Sea. *L. sarmentosa* is gonochoric without an apparent synchronization with the moon face; as in other gorgonians, the primary sexual effort is from primary branches; in a population with a biased sex ratio toward females, male colonies reache maturity at 21 cm of height and females at 1-10cm (Rossi & Gili 2009). *Muricea atlantica* in Florida is dioecius, with 1:1 sex ratio, an annual reproductive cycle and no evidence of larval brooding (Fitzsimmons-Sosa et al. 2004). However, Rossi and Gili (2009) proposed that the reproductive strategy of octocorals is related with habitat preferences (soft or hard substrata) and biological characteristics such as morphology, feeding and growth.

Recruitment

Different environmental and physical factors have been suggested as influences on octocoral recruitment and distribution. Important factors in determining octocoral distribution include temperature, appropriate water chemistry, and depth (Bayer 1953, 1961), however, the mechanisms by which these factors affect the distribution of octocorals is unclear. Other factors may include level of illumination or sun irradiance (Grigg 1974b; Muzik 1982), some species such as *Carijoa riisei* tent to settle in dark places (Kahng & Grigg 2005), and others such as *Plexaura kuna* in the light (Lasker & Kim 1996) and this could be influenced by the presence and strength of a symbiotic association with a zooxanthellae algae; wave and surge action (Cary 1914; Kinzie 1973; Birkeland 1974; Yoshioka & Yoshioka 1987; Dahlgren 1989), which is related with the flexibility of the colony and the strength of the holdfast attachment, and the movement or accumulation of sediments across the bottom (Yoshioka & Yoshioka 1989); availability of suitable and stable substrata (Bayer 1961; Kinzie 1973; Preston & Preston 1975; Dahlgren 1989; Goh & Chou 1994), with different species inhabiting soft and hard substrata (Lasker & Coffroth 1988); competition (Wahle 1980); predation (Lasker 1985; Harvell & Suchanek 1987); and limitation in ecological connectivity with the availability of functional larvae at the mesoscale, affected by the dynamics of oceanic currents at different scales (Jordan-Dahlgren 2002).

Only Grigg (1977) has studied recruitment of octocoral species in the TEP, where recruitment may be limited by space in *Muricea fruticosa* and *Muricea californica;* these species showed constant recruitment and mortality rates in La Joya, California (Grigg 1977). This space limited settlement regulation in hard substrata has also been described for Caribbean gorgonians (Birkeland 1974).

Feeding

Octocorals are mainly suspension feeders. They have a substantial impact on plankton communities, which are the major contributors of biomass and productivity in the water column (Ribes & Gili 1998). Of the species present in the TEP, only the feeding behaviour of *Carijoa riisei* has been described. However, it is important to note that this study took place in Pernambuco, Brazil. In this Atlantic location, *Carijoa riisei* feeds on 102 phytoplankton (mostly diatoms and cyanophytes) and 25 zooplankton taxa (e.g. crustacean fragments) with a mean prey size of 112.7 μm. Feeding diversity is homogeneous in time and depth and feeding abundance is seasonal with bathymetric variations (Lira et al. 2009).

As in most hard corals, many octocoral species have a symbiotic relationship with zooxanthellae. However, the trophic contribution of the *Symbiodinium* to the energy budget of Octocorlas is lower than in hard corals (Fabricius & Klumpp 1995). The ability to utilize photoautotrophic and heterotrophic food sources has been studied for some species outside the TEP (Gohar 1940; Roushdy and Hansen 1961; Lewis & Smith 1971; Murdock 1978; Lasker 1981; Lasker et al. 1983). Compared to hard corals, it is suggested that on an evolutionary time scale octocorals are able to switch easier from mixotrophy to heterotrophy, which agrees with the lower need of photosynthetic carbon in octocorals (Van Oppen et al. 2005).

The only study including species present in the TEP demonstrated that 27 species (Table 1) did not have a zooxanthellae association (Van Oppen et al. 2005). This study included species in eleven genera (*Eugorgia, Leptogorgia, Pacifigorgia, Psammogorgia, Euplexaura, Heterogorgia, Muricea, Paragorgia, Ellisella, Stylatula, Ptilosarcus and Briareidae*). Of these genera three had an associated zooxanthellae in other regions (*Briareum* in Australia and the Caribbean; *Muricea* in the Caribbean; *Euplexaura* in Australia) and one didn't (*Ellllisella* in Australia). Although there are many other species to be studied in the TEP, with the data available today it can be speculated that there is complete heterotrophy in the area.

Mortality

Different sources of mortality have been described for octocoral species, including incrustation from other species such as the fire coral *Millepora* spp in *Plexaura flexuosa* (Cary 1914; Kinzie 1974), overgrowth (Jeyasuria & Lewis 1987; Esford & Lewis 1990; Weinbauer & Velimirov 1996), detachment from substrata (Kinzie 1973; Yoshioka & Yoshioka 1991), and sedimentation (Dai 1991). Octocorals are known to be predated by fish (Preston & Preston 1975) and invertebrates (Preston and Preston 1975; Lasker & Coffroth et al. 1988). This predation is considered important for tissue removal but not as a cause of mortality (Birkeland 1974; Preston & Preston 1975).

The major sources of mortality reported for TEP species were detachment and abrasion in the *Muricea* species in California (Grigg 1977), where predation and encrustation had a minor effect. *Muricea* colonies were encrusted by the colonial anemone *Corynactis californica* (Grigg 1977) the main diet component of the Garibaldi fish *Hypsypops rubicunda* (Clarke 1970), and the zooanthid coral *Parazoanthus lucificum* and *Epizoanthus induratum,* also found encrusting *Eunicella stricta* colonies (Grigg 1977). Indirect mortality occurred through bioerosion caused by invertebrates such as bivalves, which weakened the basal attachment especially in older colonies (Grigg 1977). In La Joya, California, *M. californica* and *M. fruticosa* had a constant mortality rate in intermediate-age colonies, and there was a mortality rate of more than 99% in larval stages (Grigg 1977).

Other important sources of mortality in soft corals are diseases, such as aspergillosis, gorgonia purple spots, red band disease, black band disease, compromised health, and bleaching (Weil et al. 2009). An increase in water temperature, usually after an ENSO event, has been followed by octocoral bleaching in different locations and times (e.g. Guzman & Guevara 1998; Linares et al. 2005; Weil et al. 2009). It is suggested that the outbreak of a disease can be facilitated in the presence of an already weakened host due to bleaching in zooxanthellae species, as it was the case in *Briareum asbestium* infested by an epizootic disease at Florida Keys (Harvell et al. 2001) and in *Gorgonia ventalina* infected with aspergillosis in Puerto Rico (Flynn & Weil 2009) and throughout the Caribbean (Croquer & Weil 2009).

Although there is still a need to confirm the presence of coral diseases in the TEP (Navas-Camacho et al. 2009), tissue lesions similar to the ones caused by Aspergillous fungi in the Caribbean were reported in a *Pacifigorgia sp*. in the pacific coast of Colombia at Utría Bay (Navas-Camacho et al. 2009). Of the octocoral taxa affected by the bleaching event in 2003 and 2005 in the Caribbean, the genus *Muricea* was the most affected (Prada et al. 2010). However, three of the *Muricea* species present in the TEP do not have a zooxanthellae association, therefore bleaching and bleaching induced diseases don't seem to be a factor for TEP species, at least for the azooxanthellate species reported by Van Oppen et al. (2005).

Interspecific interactions

Octocoral species have been described as facilitators for other species, especially symbiotic invertebrates (Patton 1972; Cantera et al. 1987; Neira et al. 1992; Ramos 1995). Eleven species of mollusks, crustaceans, and equinoderms have been described as strongly associated with the octocoral *Leptogorgia alba* (Table 3). The symbionts are commonly found in the upper parts of the colonies and present behavioral, morphological, and physiological adaptations that cause them to resemble the host colony (Cantera et al. 1987). The association presumably provides protection to the symbiont, which feeds on the octocoral mucus without causing apparent harm to the colony (Cantera et al. 1987). Some symbiotic species do not have such adaptations; they live in the internal part of the colony holdfast and feed on organic detritus (Cantera et al. 1987). These associations, reported in the Colombian Pacific, are equivalent to those reported in the Atlantic *Leptogorgia virgulata* colonies in North Carolina (Patton 1972; Cantera et al. 1987). Besides hosting small invertebrates, octocoral species such as *Muricea* *spp*., form an important part of the community food web, which includes large vertebrates such as sea turtles and fish (Seminoff et al. 2002).

Another reported relationship involves the octocoral *Carijoa riisei,* previously thought to be an invasive species in the TEP due to its aggressive interaction with other corals (Concepcion et al. 2010). In Hawaii, *Carijoa riisei* overgrow 90% of the black coral colonies (*Antipathes dichotoma*, and *Antipathes grandis*) inhabiting some areas of the Au´au Channel. This growth mainly affected mature colonies and had a major impact in depths between 80 m and 105 m (Grigg 2003). *C. riisei* was also described as a facilitator species, which served as a required substratum for the settlement and growth of the Atlantic sponge *Desmapsamma anchorata* in the Indo-Pacifc. In response to the presence of the sponge, *C. riisei* colonies modified their morphology by extending their branches, without an apparent decrease in fitness (Calciani et al. 2004). Another sponge, *Callyspongia sp*., is also known to parasitize *C. riisei* colonies (Kahng et al. 2008). In this case, the sponge stresses the octocoral through overgrowth and mechanistic injury, which was correlated with a decrease in fertility (Kahng et al. 2008). Neves et al. (2007) studied the association between *C. riisei* and brittle stars on the littoral northern coast of Brazil. In this case, it was suggested that the ophiuroids used the habitat created by *C. riisei* as a location for recruitment. This association is thought to be occasional; the octocoral colony serves as growing structure for many sponges, which provide living substrata to ophiuroids (Neves et al. 2007).

In contrast with octocorals in other areas, at least the 27 species that have been studied in the TEP do not present a symbiotic association with zooxanthellae algae (Van Oppen et al. 2005). The absence of this common symbiotic relationship could guide us to questions and conclusions about life history characteristics such as heterotrophy and its impact on the local plankton community, and the evolutionary history of octocoral species at TEP.

Table 3. Ocotocoral symbionts reported for the TEP based on : 1) Neira et al. 1992; 2) Alvarado & Fernandez 2005; 3) Ramos 1995; 4) Cantera et al. 1987

Simbiont	**Octocoral host**	**Observations**	**Reported place**
Echinoderms			
Ophiactis savignyi	*Leptogorgia alba*	Mainly found in the internal part of the branches	Colombia (1) (4)
Ophiothrix spiculata	*Leptogorgia alba*	*	Colombia (1)
Ophiactis mirabilis	*Leptogorgia alba*	Mainly found in the top and peripheral parts.	CostaRica* (2); Colombia (4)
Arthropods			
Neopontoides henryvonprahli	*Muricea robusta* *Leptogorgia alba*	1-6 m deep Adopted the color of its host. Found in the branching points, specially the axial area.	Colombia (3 &4)
Veleronia leavifrons	*Leptogorgia alba*		Colombia (4)
Mollusk			
Simnia rufa	*Leptogorgia alba*	Common. Mainly found in top part of branches. Lays egg mass causing local tissue damage	Colombia (4)
Simnia avena	*Leptogorgia alba*	Found in top branches	Colombia (4)
Coralliophilia (Pseudomurex) costata	*Leptogorgia alba*	Found in the internal part of the holdfast	Colombia (4)
Anachis (Parvanachis) milium	*Leptogorgia alba*	Found in large quantities in the internal part of the holdfast	Colombia (4)
Pteria sterna	*Leptogorgia alba*	Mainly found in top part of branches, with aprox. 25 small (15-20mm) individuals per colony. Also found in other hosts or hard substrata	Colombia (4)
Crustacean			
Veleronia laevifrons	*Leptogorgia alba*	Females found on branching points, males anywhere in the colony	Colombia (4)

* Symbionts that have been reported to cover the entire colony (Alvarado & Fernandez 2005), and 75% of the soft corals in a 2m^2 area hosted this kind these echinoderms (Jimenez 1995).

Heterotrophic octocorals consume important amounts of phytoplankton and zooplankton and have a substantial impact on these communities (Ribes et al. 1998). In a coral community with only heterotrophic octocorals the trophic interaction between octocorals and their prey would be stronger than in a community with heterotrophic and photoautotrophic species. Furthermore, being suspension feeders allows them to have a wide distributional range, not limited to shallow clear water as photoautotrophic species.

Disturbance

The effects of disturbance in octocoral colonies and in community structure have not been studied in the TEP. Studies from the Mediterranean and the Caribbean suggest that disturbances affect species (if rare or common) and class sizes in different ways, depending on the disturbance's temporal and spatial scale, intensity, and nature (Connell 1997). Many octocorals are long-lived structural species, like trees in forests, so forest ecology methods, including size distribution and self-thinning, can be used to study the occurrence of recent or past disturbances in octocoral populations (Linares et al. 2008a).

Environmental disturbances are a common cause of mortality, and can have detrimental effects on octocoral communities. Climate change, warming events in particular is thought to be responsible for the mass mortality event in the NW Mediterranean in 1999 (Linares et al. 2008a). This environmental disturbance had both immediate and delayed negative effects on *Paramuricea clavata* colonies. The effects were felt for at least four years and resulted in a 48% population decline (Linares et al. 2005). This disturbance not only increased adult mortality, but also affected colony reproductive biology, especially in female colonies, and therefore affected the population recovery process (Linares et al. 2008b). The effect of an increase in water temperature varied among taxa in Puerto Rico. Water warming had no effect on *Pseudopterogorgia* colonies but had a severe negative effect in *Muricea* colonies (Prada et al. 2010). Furthermore, weakened colonies affected by bleaching are more sensible to diseases, and this can lead to a disease outbreak in an already decaying community (Harvell et al. 2001; Flynn & Weil 2009).

Smaller scale environmental variations may also have important effects on population and community structure through larval recruitment (Lasker 1990). This was the case in Jamaica, where a winter storm affected the size structure of the hard coral *Agaricia agaricites* population (Hughes 1984).

Anthropogenic disturbances on coral communities are also common. These disturbances can occur directly, through bottom fishing and tourism, or indirectly through sedimentation from coastal development and diseases associated with water pollution. Henry et al. (2003) experimentally tested the effects of bottom trawling and dredging on the cold-water octocoral *Gersemia rubiformis*. Experimental colonies were crushed and rolled over. This disturbance produced colony retraction and a premature release of sexually produced larvae, which experienced high mortality rates (Henry et al. 2003). Octocoral communities are also impacted directly by excessive tourism. Coma et al. (2004) studied the effect of recreational diving on the survivorship of the octocoral *Paramuricea clavata* in the Mediterranean. Recreational activities in a highly visited area did not increase colony injury, but colony death by detachment was found to be four times higher than death by overgrowth and three times higher than death due to natural causes in less visited areas (Coma et al. 2004).

Some species are able to cope with disturbances. Indeed, *Gersemia rubiformis* is thought to be able to cope with frequent bottom fishing and dredging activities, because adult colonies are able to regenerate and replace dead polyps within 30 days after disturbance (Henry et al. 2003). In the Caribbean, *Plexaura kuna,* promotes colony asexual propagation after a disturbance and alters size-frequency distribution among local populations

(Coffroth et al. 1998). In this case, disturbance controls community composition, because it has different effects on the clonal propagation of different species. Therefore, local genotypic diversity is directly related to disturbance level, an effect that is evident until the environment reaches very high levels of disturbance (Coffroth et al. 1998).

Conservation status and threats

Octocorals in different parts of the TEP are being threatened by environmental and anthropological disturbances. Octocoral communities are affected by water warming associated with El Niño Southern Oscillation events, sedimentation, pollution, overfishing, potential coastal development, and tourism (Guzman et al. 2008).

Many octocoral species are long-lived structural organisms with slow dynamics and frequently occur in communities with low species turn-over. These characteristics make octocorals especially vulnerable to disturbance (Coma et al. 2004). For this reason they are an important conservation target for maintaining diversity in marine communities (Linares et al. 2008a). Identified octocoral hotspots of diversity and endemism in the TEP are mostly under protection for different countries. Coiba Island and its surrounding islands were declared a National Park in 2004, protecting the shallow coral communities from trawling activities. Las Perlas Archipelago is also protected from fishing since 2007 (Guzman et al. 2008). Other sites with important populations of soft coral are Cocos Island, Gorgona, Malpelo, and Galapagos, which are also marine protected areas.

Other groups within Octocorallia are protected under international conventions (*sensu* black corals). In 2007, the United States proposed to include the entire genus *Corallium* in the CITES convention. This genus has been historically used for jewelry, with 27 species dispersed in the Pacific, Atlantic, and Indian Oceans and the Mediterranean Sea. Three of these 27 species are in the TEP. The CITES plenary, however, rejected this proposal. Today, the order Anthipatae, with 5 families listed (Antipathidae, Cladopathidae, Leiopathidae, Myriopathidae and Schizopathidae) is protected under the CITES convention Annex II.

Discussion and future research

Octocorals are dominant species in rocky coral communities in the TEP (Bayer 1953; Guzman et al. 2004; Guzman et al. 2008). Studying such foundation species may reflect the environmental suitability and stability of many other associated or dependent species (Grigg 1975). However, not much is known about the biology or ecology of octocoral species in the area. Chemists and microbiologists are studying the potential of octocoral species as sources of active compounds to be used in medicine. The rapid development of the coastal areas leading to sedimentation, the suitability of shallow and deep species to study and monitor climate change, and the pressure from trawling fisheries destroying sessile communities, all create a need for information about soft coral species and communities. Furthermore, it is necessary to review the conservation status of Alcyonacea species, currently unprotected from commercial exploitation.

Early studies by Verill (1868, 1870) and Bayer (1953, 1981, 1960) followed by the studies of Grigg (1974a, 1975, 1977) and the taxonomical reviews of Breedy and Guzman (2002, 2007, 2011) and Breedy et al. (2009) provide excellent starting points for in-depth research about many aspects of these organisms in the Tropical Eastern Pacific, including: 1) the biology of octocoral species in all life stages, including population dynamics, growth, recruitment, and mortality rates; 2) species recruitment, its consequences for connectivity between suitable habitats at different scales, and its implications for conservation and community functioning; 3) coexistence or competition within octocoral communities and between octocorals and other organisms such as mollusks, crustaceans, echinoderms, and possible competition for space with scleractinian corals, algae and sponges; 4) the lack of a symbiotic relationship with a zooxanthellae algae in the TEP, and whether this relationship was lost due to a change in environmental factors or if it has been historically absent, and the implications for species distribution and interaction with plankton communities; 5) diseases affecting populations; 6) the impacts of disturbance on community structure and composition, and the ability of communities to recover from disturbance; 7) the consequences of water warming events and climate change in octocoral at a species and community level; and 8) the study of deep water species and habitats. Nearly 30 years later, one may conclude that the octocoral fauna of the eastern Pacific still is "poorly known" (*sensu* Bayer 1981) compared to our understanding of hard corals and coral reefs (reviewed by Glynn in press).

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Linking statement between Chapter 1 and Chapter 2

Chapter 1 presents a literature review of octocoral fauna in the Tropical Eastern Pacific, demonstrating the lack of existing biological and ecological studies Chapter 2 is an attempt to fill the gap in studies described in Chapter 1. Chapter 2 also attempts to describe basic population dynamics of common species in the area.

Chapter 2

Survival, Growth, and Recruitment of Octocoral Species in Coiba National Park, Pacific Panama

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Abstract

Octocorals (Order Gorgonacea) from the Tropical Eastern Pacific have been largely ignored in coral reef studies until recent taxonomic reviews. This study is the first to examine the population dynamics of 15 shallow water species in six genera (*Leptogorgia, Pacifigorgia, Muricea, Psammogorgia, Heterogorgia* and *Carrijoa*) found in rocky coral communities in Coiba National Park in the Republic of Panama. For a 17-month period, fixed plots at 20m of depth in four coral communities were monitored every four months. A total of 1445 colonies were monitored. Size distribution, survivorship, and recruitment rates were calculated for species present in the study plots. The growth rate was calculated for four species (*Leptogorgia alba, Pacifigorgia irene, Psammogorgia arbuscula and Muricea austera*). Octocorals were found in high densities and patchy distribution, ranging from 77.9 to 11.2 colonies/m^2 between study sites. There was an overall population decline that ranged from 30% to 14% between sites. The species *Leptogorgia alba* was the most common species, abundant in all sites, and described as a weedy ¨r¨ selected species, with high mortality and recruitment rates. The species *Muricea austera* was described as a ¨K¨ selected species with low mortality and recruitment rates. A recruitment or mortality peak was not observed for any of the studied species; this could be due to the effect of El Niño (ENSO) and La Niña (LNSO) events. The high diversity and abundance of octocoral species in the southwestern part of Coiba island could be explained by the strong surges which bring up nutrients from deep cold water, and strong currents which could potentially bring suitable larvae to a stable substrata.

Key Words: Octocoral, Tropical Eastern Pacific, Coiba, rocky coral communities, soft corals

Introduction

Octocorals (Order Gorgonacea) are sessile colonial marine invertebrates found in many kinds of environments, ranging from cold deep oceans to shallow tropical seas (Bayer 1981; Alderslade 1984). Therefore, there is wide variation in the life histories of octocorals due to species-specific symbionts (Mosher & Watling 2009), different growth forms (Breedy 2009), depth ranges, reproductive strategies (e.g. Lasker 1990; Jordán-Dahlgren 2002), and the presence or absence of the zooxanthellae association (Van Open et al. 2005). Most shallow-water octocorals (order Alcyonacea) are poor dispersers relative to scleractinian corals (Concepcion et al. 2010) and are found in an uneven distribution (Guzman et al. 2004).

For many years, humans have exploited gorgonian octocoral species for cosmetic production purposes. Recently, more species, including those in the eastern Pacific, have been recognized as a source for novel natural products and active compounds to be used in medicine (Rodríguez 1995;

Blunt et al. 2004; Mellado et al. 2004; Shen et al. 2004; Gutierrez et al. 2005, 2006; Lin et al. 2008; Berrue & Kerr 2009;) by those seeking to exploit the coral's chemical defense against predators (Epifanio et al. 2000). In addition, human activities have damaged soft coral communities directly through fish trawling and indirectly through sedimentation and habitat degradation (Shester & Ayers 2005).

The biology and ecology of octocoral species have been well studied in the Indo-Pacific, the Caribbean, the Mediterranean, Hawaii, and in the deep ocean. These studies examined symbiotic relationships (e.g. Lewis & Coffroth 2004; Koike et al. 2004; Van Oppen et al. 2005; Mosher & Watling 2009), growth (e.g. Castanaro & Lasker 2003; Lasker et al. 2003; Cadena & Sanchez 2010), sexual reproduction (e.g. Kahng et al. 2008; Linares et al. 2008b; Hellström et al. 2010), asexual reproduction (Lasker 1990), recruitment (Jamison et al. 2008), predation (Lasker & Coffroth 1988), feeding (Lasker et al. 1983), life history (Linares et al. 2007; Linares et al. 2008a), and bleaching (Prada et al. 2010). Knowledge about the species present in the Tropical Eastern Pacific (TEP) however, is mostly restricted to taxonomical reviews and the description of new species, with the exception of a few publications about the life history of two *Muricea* species in the Gulf of California (Grigg 1972, 1974, 1975, 1977), and the biogeography (Vargas et al. 2008) and phylogeny (e.g. Vargas et al. 2010) study of the genus *Pacifigorgia*.

Although octocoral species occur in calm shallow waters in the Caribbean and in the Mediterranean, species present in the TEP are found in very active environments such as seamounts and rocky walls exposed to strong currents, surf, and swells (Breedy & Guzman 2002). These conditions may explain the lack of studies in the area. Unlike octocorals in other locations, none of the 27 species studied by Van Oppen et al. (2005) in the TEP present the zooxanthellae association, meaning an obligate heterotrophism as suspension feeders.

The Tropical Eastern Pacific (TEP) ranges from the Sea of Cortez to the northern part of Peru (Allen & Robertson 1994; Cortes 1997) and includes different octocoral communities from eleven genera in four families with high levels of diversity, abundance, and endemism (Bayer 1953; Guzman et al. 2008). The Gulf of Chriqui in Panama is a biodiversity ¨hot-spot¨ in the TEP with 52 octocoral species in 7 genera (Guzman & Breedy 2008a).

A particularly important ¨hot-spot¨ for octocoral diversity in the Tropical Eastern Pacific is found in Coiba National Park (CNP), the largest marine protected area on the Pacific coast of Panama. CNP, located on the Gulf of Chiriqui, is part of the Marine Conservation Corridor of the Tropical Eastern Pacific (MCCTEP). As part of the Marine Corridor, CNP is included in a multinational initiative to protect highly diverse marine communities and migratory species in five marine protected areas: Cocos Island (Costa Rica), Malpelo and Gorgona (Colombia), Galapagos (Ecuador), and Coiba National Park in Panama.

The most common octocoral genera in CNP are *Pacifigorgia* , *Leptogorgia, Muricea, Psammogorgia*, *Eugorgia*, *Heterogorgia* , and *Carijoa.* There are a total of 35 reported species, many of them endemic to the island (Guzman et al. 2004, Breedy & Guzman 2011). These species are unevenly distributed, occur in a stratified fashion, and on occasion in mono-species patches. At CNP, octocorals share the substratum with encrusting coralline algae, scleractinian corals, algae turf, sponges, and tunicates (personal and peer observation), and have higher species richness in coral communities than in coral reefs, which is also the case for scleractinian corals (Guzman et al. 2004).

Of the 35 species present at CNP, only one, *Carijoa riseii ,* has been studied. Until 2010 *Carijoa riseii,* which inhabits reefs in the Indo-Pacific, Hawaii (Kahng & Grigg 2005; Kahng et al. 2008), Indonesia and Vietnam (Calciani et al. 2004), was wrongly recognized as an invasive species. It is a fast growing azooxanthellate octocoral preferring shaded places (Kahng & Grigg 2005), with density-dependent sexual reproduction (Kahng et al.

2008). *Carijoa riseii* is considered a fouling species (Bayer 1961) able to overgrow other sessile organisms (Grigg 2003).

This study describes the octocoral community composition, survivorship, colonization, and growth rate of common species in monitoring plots located in the Coiba National Park (Pacific Panama) as a first contribution to the natural history of shallow water soft corals from the TEP.

Methods

Study Site

Coiba National Park is the largest marine protected area in the Pacific of Panama covering 270,125 ha, of which 80.2% are marine. The Park, including its Special Zone of Marine Protection, was declared a UNESCO World Heritage site in 2005 because of its high levels of endemism and key ecological interactions both in terrestrial and marine communities (World Heritage Convention, Decision- 29COM 8B.13, 2005). A management plan, designed to protect its highly diverse marine and terrestrial ecosystems took affect in 2009. This plan established a non-take zone of 1.61km around all islands and rocks, and regulated artisanal fishery and tourism activities inside the park (Maté et al. 2009). Guzman et al. (2004) performed a complete description of the distribution and state of coral refs and coral communities covering 1700 ha. This study prioritized three conservation units in the southern and northernmost parts of the CNP as the most important sites for conservation. These conservation units were selected on the basis of their high levels of endangered, rare, and endemic species and populations (Guzman et al. 2004). Marine communities at Coiba are considered special because the island is located in the Gulf of Chiriqui, which has no upwelling process and is therefore protected from the north winds (Glynn & Mate 1997; D´Croz & Mate 2004), while also being influenced by El Niño Southern Oscillation every 2-7 years (Enfield 2001).

Four previously inspected sites were chosen as study sites in a longitudinal gradient (Fig. 1). These sites within Coiba National Park have basaltic rocky substrata inhabited by rocky coral communities, and are exposed to different levels of current and swell.

Frijoles (7°38'59.6" N, 81°43'09.4" W): Small islet located ca. 2.5 km offshore from the northern part of Coiba Island, protected from strong currents and swell. The islet forms a vertical rocky wall from the surface down to 20 meters. Large fish, including the white tip reef shark, aggregate around the island. Encrusting coralline algae, small scleractinian colonies, macroalgae, and sponges cover the substrate. This site is located in a medium-high diversity area for corals and octocorals (Guzman et al. 2004). The octocoral community at this site is not a diverse one however, with the most common species being *Leptogorgia alba*. The coral predator *Acanthaster planci* was frequently seen in the area.

Roca Hacha (7°25'55.0" N, 81°51'29.0" W): Rocky outcrop located ca. 0.7 km offshore from the western side of Coiba Island and exposed to a strong swell. It is located in an area where natural mudslides are common, creating occasional sedimentation events. This area was described as having medium-high diversity of corals and octocorals (Guzman et al. 2004). Roca Hacha forms a vertical rocky wall with a decrease in slope at 20 meters of depth. The substrate is covered by a highly diverse octocoral community (Guzman & Breedy 2008b), which shares the substrata with encrusting coralline algae, macroalgae, algae turf, sponges, tunicates, and small scleractinian corals.

Catedrales (7°13'33.7'' N, 81°49'45.4'' W): Underwater rocky outcrop forming two peaks 10 meters under the surface, located in the southwest region of the National Park, approximately 2.6 km off of Jicarita Island. It is located in one of the four highly diverse areas of corals and octocorals within Coiba National Park (Guzman et al. 2004). Catedrales is exposed to strong currents from different directions and has a rich octocoral community, which shares the substrata with encrusting coralline algae, sponges, tunicates, and small scleractinian corals.

Jicarita (7°12'12.5" N, 81°48'02.3" W): Island located in the southernmost region of the Park (Fig. 1), with a 30 m high cliff which continues vertically down into the water and decreases in slope at 20 meters depth. It is exposed to surf and a strong swell, which brings sediments up from the bottom during a rising tide. Jicarita's rocky substrate is covered by a very diverse octocoral community, which shares the substrata with encrusting coralline algae, algae turf, sponges, and small scleractinian corals. This site is considered the highest coral diversity area in Pacific Panama (Guzman & Breedy 2008b), and like Catedrales, it is located in one of the four highly diverse areas of corals and octocorals within Coiba National Park (Guzman et al. 2004).

Experimental setup, Colony monitoring

With the aid of SCUBA diving equipment, nine 1 m^2 fixed plots were randomly installed at a depth of 20 meters at each site described above. Fixed plots were marked within the octocoral community by installing 2 cm x 2 cm stainless steel square bars into the substrate with underwater cement, arranged parallel to shore and placed 5 m apart from each other. An aluminum 1 m^2 (0.84 m x 1.20 m) quadrat was designed to fit on the fixed stainless steel bars. The quadrat was divided into eight 0.42 m x 0.30 m sections equivalent to a square meter. Each section was photographed using a digital high-resolution Nikon D-80 camera with a wide-angle lens inside an Ikelite underwater case and two external digital strobe flashes. The camera was attached to a stainless steel tripod to maintain a fixed distance (0.80 m) from the quadrat.

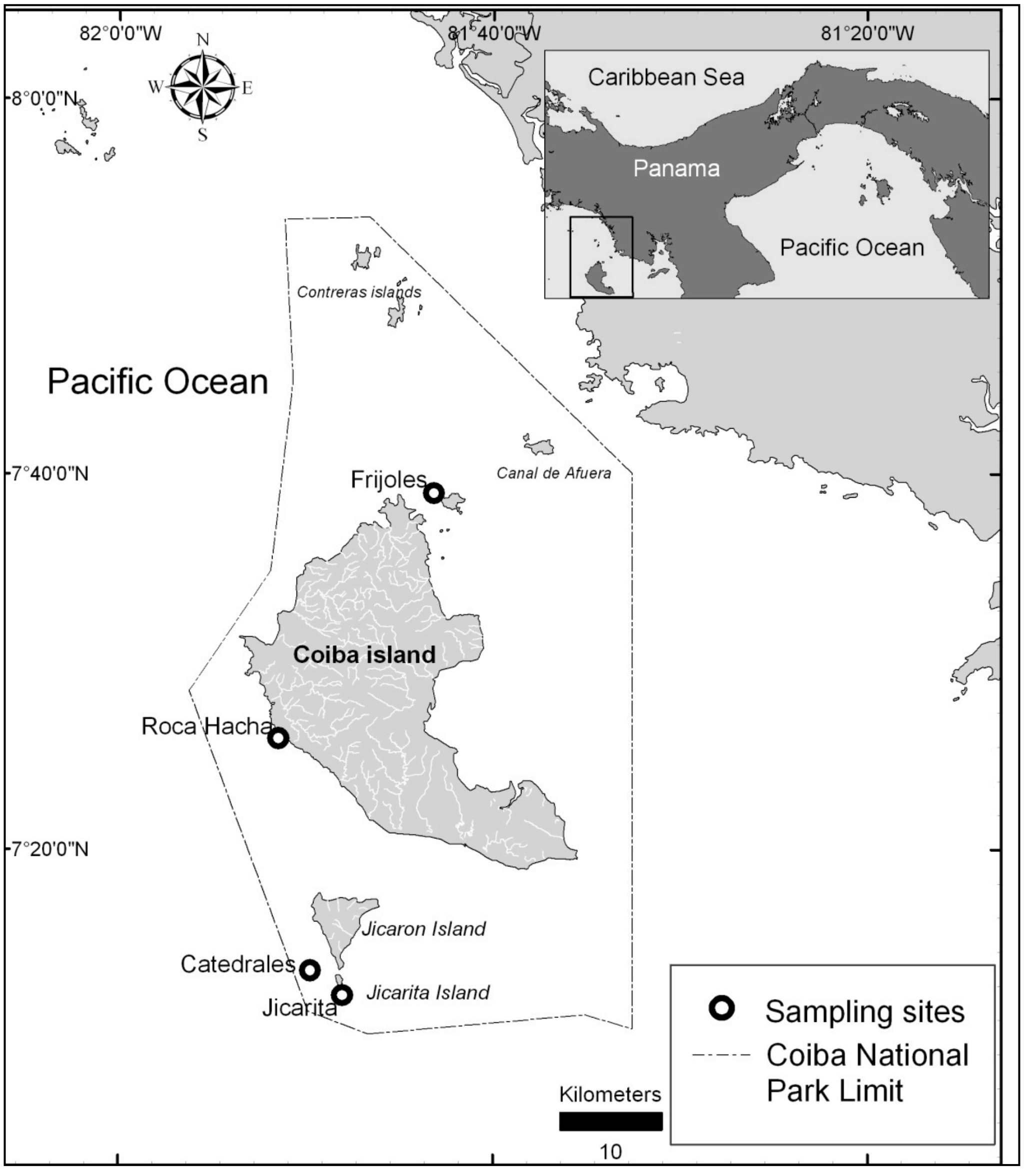

Figure 1. Octocoral sampling sites at Coiba National Park, Gulf of Chiriqui, Republic of Panama, Tropical Eastern Pacific.

Each octocoral colony within the fixed plots was identified to the species level and assigned a unique ID number. The colonies were then manually marked in the pictures using Nikon NX2 and Corel PHOTO-PAINT X3 software. All colonies within the fixed plots were monitored every four months for a 17-month period from July 2009 to December 2010, for a total of five sampling periods (June 20/09, October 20/09, March 28/10, July 21/10, Nov 30/10). Sampling periods 2 and 3 were five months apart due to logistical constraints. Overall species abundance, local diversity, recruitment rates, colony survivorship, damage, and mortality for each sampling period were quantified. In addition, one HOBO temperature recorder (Pro v.2) was installed at each site to monitor water temperature every 30 minutes during the entire study period.

Colonies present since the beginning of the study (sampling period 1) were classified into species specific relative size classes from 1 to 4, where 1 represented recruits; 2: small colonies; 3: branched mid-sized colonies; and 4: the largest colonies in the study plots. Data obtained were analyzed to measure differences in community composition between sites, species-specific survivorship, and recruitment rate.

Colony growth

Colony growth was studied in four species encompassing four different genera within the study sites; *Leptogorgia alba* in Frijoles, *Pacifigorgia irene* in Jicarita, and *Muricea austera* and *Psammogorgia arbuscula*. In Roca Hacha, ten colonies of each species were tagged within the monitoring plots and repeatedly photographed in July, November, and March of 2009 and July and November of 2010. Digital photographs were taken with a reference 1x1 cm grid board. Colonies were later measured to the closest millimeter with the aid of IMAGE-J 64 software (Lasker et al. 2003). Because of the variability of growth forms (e.g., seafan, branching), two kinds of measurements were taken. For the branched species, *Leptogorgia alba* and *Muricea austera*, four measurements were obtained: 1. Colony width: measured between the furthest two points perpendicular to an imaginary Y-axis intercepting the holdfast; 2. Colony height: measured from the holdfast to the furthest point on the Y-axis; 3. Number of branch tips, which included small ($\geq$0.5 cm) growing tips; and 4. Branch growth: ten individual branches were measured at the beginning and end of the study period in five of the ten studied colonies. Only three colonies of *Leptogorgia alba* survived to the end of the study period. For fan-like species, *Pacifigorgia irene* and

Psammogorgia arbuscula, the fan surface-area was measured as well as the maximum width and length.

Data Analyses:

Community composition

Rank Abundance Distribution Plots (RAD) (MacArthur 1957) were used to describe octocoral communities in each site. RADs are common community composition descriptors and provide a graphical mean for comparing the proportion of rare species between communities (McGill et al. 2007).

Survival analysis

The difference in survivorship between species and within species between sampling sites for all size classes (1-4) was analyzed using survival curves. Log Rank Survival Analysis for multiple groups was used to determine a significant difference between survival curves. Its statistics are denominated by an " s. " Analyses were performed using SigmaPlot 11.2 Software. The Log Rank Test is a non-parametric test that uses chi-square statistics to reject the null hypothesis: no difference between survival curves. It assumes equal accuracy between all data at a given time (Systat Software 2009). For the purposes of the analysis, colonies that survived for the entire study period (17 months) were marked as "censored." Colonies that died were marked as "failure" and the survival time was the number of months that the colony remained alive or present in the study plots. For example, a colony that was recorded on sampling t1 and t2 but not seen in t3, t4, t5 had a survival time of 4 months. Overall and partial mortality rates between sampling periods were calculated by dividing the number of dead colonies in t_{n+1} by the total number of colonies in t_n. A significant difference was calculated with repeated measurements analysis of variance. When necessary, data was transformed to achieve normality (ln10 for density and 1+sqr for mortality and recruitment).

Recruitment rate

The number of new colonies present in the study plots during each sampling time was quantified. ANOVA on ranks were performed to test a significant difference between sampling periods and Friedman Repeated Measures of Variance on Ranks were performed to test a significant difference between sampling sites. The statistics of these tests are denominated with a " q. " An overall yearly recruitment rate per m2 was also calculated. Analyses were performed using SigmaPlot 11.2 Software.

Colony growth

The difference in size (height, width, area) between sampling periods and the total difference from the beginning to the end of the study period was calculated for each monitored colony (n=10 per species). When a colony died before completing the study, size differences were calculated only if the colony remained alive for more than 2 sampling periods (≥8 months). The difference in size was divided by the number of months for which the colony was studied and the average monthly growth was calculated for each species. To calculate branch length growth, ten individual branches from a single individual in five *Muricea austera* and three *Leptogorgia alba* individuals were measured to the closest millimeter at the beginning and end of the study, and the differences were divided by the total studied period (17 months).

Results

Site comparisons

Average monthly water temperatures ranged from 25.3 C^o to 28.9 C^o. Monthly standard deviations were relatively high from February to May 2010, up to ± 1.65 C^o. According to NAOOA (2011) Sea Surface Height records, the study period overlapped with an El Niño warming event (ENSO) from June 2009 to April 2010, and a La Niña cooling event (LNSO) from July

2010 until the end of the study (Figure 2). The average monthly water temperature was not significantly different between sites (p=0.195, F=1.622). Sampling period 4 (July-Nov 2010) however, which overlapped with the La Niña event, was significantly different from the rest of the sampling periods after allowing for the effects of differences in sites (p<0.001, F=40.782). There was not a significant interaction between sites and sampling period (p=0.999, F=0.12) (Figure 2). The highest recorded temperatures were 30-30.8 C^{o} during March and April 2010 in all four sites. The coldest temperatures were 20-20.6 C^{o} in Catedrales and Jicarita during November 2010 and in Roca Hacha during March 2009. The lowest temperature at Frijoles was 21.7 C^{o} in October 2010.

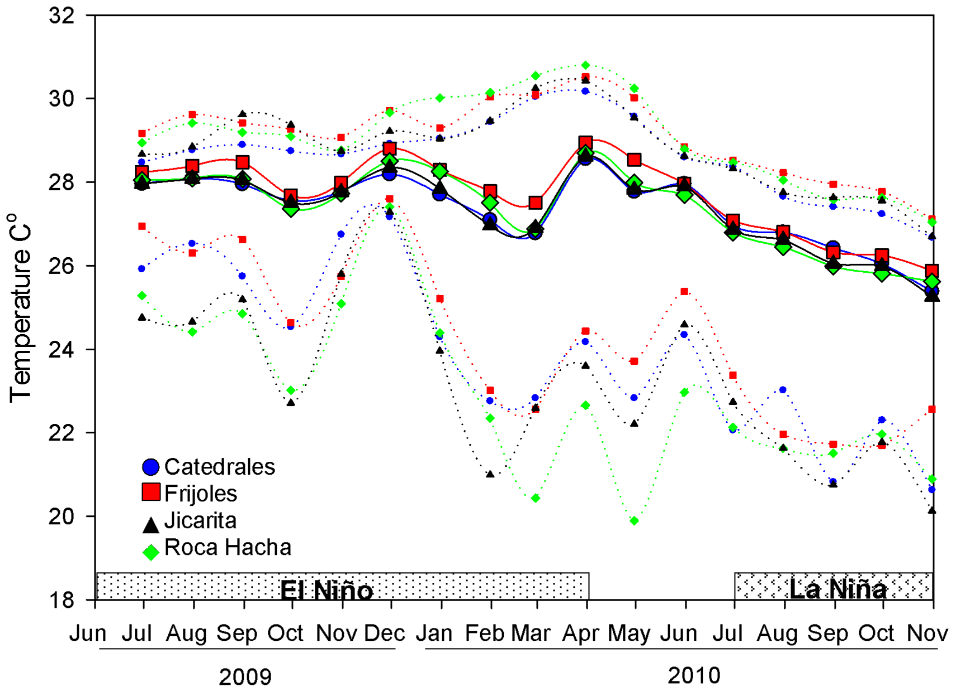

Figure 2. Monthly seawater temperature profiles for studied sites in Coiba National Park, Panama. Average temperature (straight line), maximum and minimum (dotted line) with El Niño (ENSO) and La Niña (LNSO) events overlapping the study period.

Study sites differed in diversity and abundance, with Roca Hacha exhibiting the highest diversity and abundance and Frijoles the lowest. An overall one-year population decline was found in all study sites. Roca Hacha had 14 species with a mean density of 77.6 ± 19 colonies/m^2 and a one year population decline of 17%. Catedrales had with 12 species, a mean density of 44.3 ± 18 colonies/m^2, and a one year population decline of 14%. Jicarita had 12 species with a mean density of 30.3 ± 14 colonies colonies/m^2 and a one-year population decline of 24%. Frijoles had 5 species with a mean density of 11.2 ± 5 colonies/m^2 and a one year population decline of 30%. There was higher species dominance in Frijoles, where *Leptogorgia alba* was the dominant species, and there was a high presence of rare species in Catedrales, Jicarita, and Roca Hacha (Figure 3).

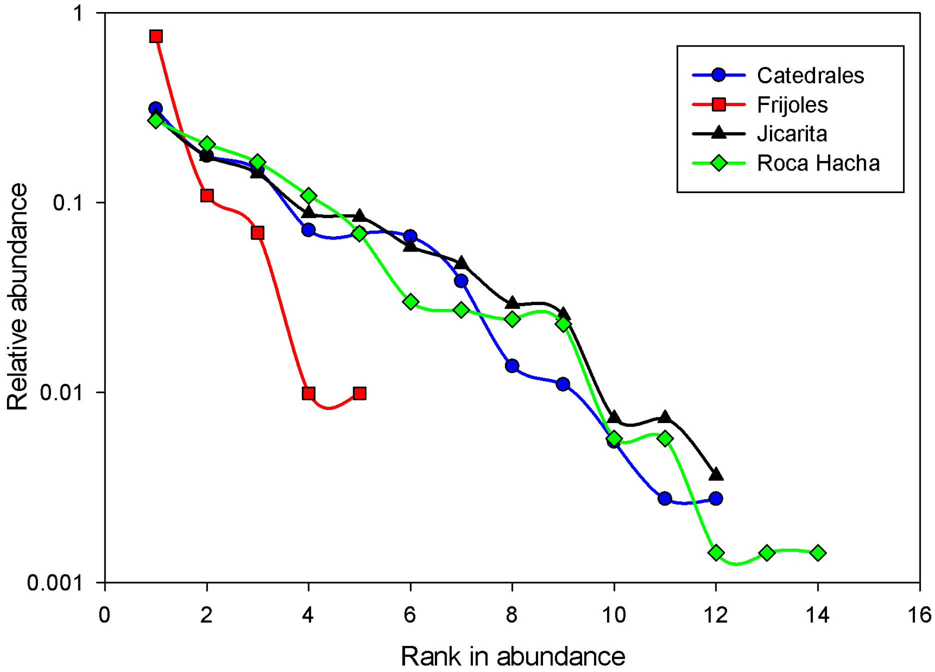

Figure 3. Rank Abundance Distribution (RAD) for each study site during sampling time 1 (June 20, 2009) in Coiba National Park, Panama.

In a site comparison analysis including all species present on each site, there was a positive relationship between local octocoral density and diversity (n=4, $r^2=0.69$), a strong positive relationship between density and yearly mean recruitment (n=4, $r^2=0.99$), and a negative relationship between density and population decline (n=4, $r^2=0.53$). There was a negative relationship between mean recruitment and yearly decline (n=4, $r^2=0.56$). Roca Hacha was the site with the highest density, diversity, and recruitment. It exhibited a correspondingly low population decline. Frijoles was the site with the least octocoral density, diversity, and recruitment and exhibited the highest population decline.

When analyzing local populations at the species level, there was not a significant relationship between local density and recruitment. Similarly, there was not a relationship between recruitment and mortality (p>0.050, Pearson product-moment correlation).

Survival curves

In a global analysis, which included all species in all sites, survival curves were significantly different between colony size groups (p<0.001, s=144.550). Larger sized colonies had a higher survivorship than smaller colonies (Figure 4a). Similarly, survival curves were significantly different between sites (p<0.001, s=17.226) due to low survivorship at Frijoles (Figure 4b). There was a significant difference in survivorship curves between species (p<0.001, s=225.321). *Leptogorgia alba* and *Carijoa riseii* had the lowest survivorship and *Muricea asutera* and *Pacifigorgia rubicunda* the highest (Figure 4c, Table 2). Overall colony mortality was not different between sampling periods after allowing for the effect of differences between sites (p=0.729, F=0.434).

Recruitment

An overall comparison, pooling all species together, showed recruitment peaks differed between sites. Frijoles and Jicarita had a peak during the first sampling period (June-October 2009) with a total of 77 and

81 recruits, Catedrales had a peak during the second (October 2009-March 2010) with a total of 106 recruits, and Roca Hacha had a peak during the last sampling period (July 2010-November 2010) with a total of 184 recruits (Figure 5). Species yearly recruitment rate, as an overall rate for all the sites, was calculated by dividing the total number of recruits into the number of monitored plots. Only *Leptogorgia alba* recruits were divided into 36 m^2 (9 for each site). The number of recruits for the other species was divided into 24 m^2, only calculating recruitment in Catedrales, Roca Hacha and Jicarita. The plots from Frijoles were excluded because these species do not occur or were very rare in this site. *Leptogorgia alba* recruits were the most abundant (3.55 colonies/m^2), followed by *Pacifigorgia rubicunda* and *Pacifigorgia irene* (1.07 and 1.05 colonies/m^2). Recruits from *Muricea austera*, *Pacifigorgia stenobrochis (an* azooxathellate species), and *Leptogoria taboguilla* were not observed during the study period (Table 2).

Species-specific analyses:

Leptogorgia alba Duchassaing & Michelotti 1864

Leptogorgia alba colonies were found in all of the study sites. A total of 607 colonies was monitored. It was a dominant species in Frijoles and very common in the other three sites, with a mean density of 12.6 ± 6.4 colonies/m^2 in Catedrales; 8.4 ± 3.5 colonies/m^2 in Frijoles; 5.3 ± 3.8 colonies/m^2 in Jicarita; and 21 ± 11.4 colonies/m^2 in Roca Hacha. Size classes were not randomly distributed (x^2=33.8, p<0.001); sizes 2 and 3 were the more common on every site (Table 1). Survival curves were significantly different for all size classes (p<0.001, s=44.982); larger colonies had a higher survivorship than smaller colonies, size class 4>3>2>1. When analyzing the population on each site, there a significant difference in survivorship between size classes was only found in Roca Hacha, where all size classes differed (p<0.001, s=26.288), and in Frijoles between size class 1 and 4 (p=0.040, s=8.313). Overall survivorship did not differ between sites but differed between sampling periods (p=0.004); sampling period 2 had a higher mortality than sampling period 5 (p<0.05, q=4.844). However, when analyzing sites separately this difference was only found in Frijoles (p=0.002, F=4.069).

Leptogorgia alba had a year recruitment rate between 0.2 and 0.4 colonies/m^2 (Table 2). There was not an overall significant difference in recruitment between sampling periods or between sites. Recruitment was only significantly higher in Roca Hacha during sampling periods 3 (p=0.001, q=4.389) and 5 (p=0.021, F=3.915). For the growth measurements, only 3 of the 10 colonies that were initially measured and marked to be monitored survived to the end of the study period. The average monthly growth of these three colonies was 0.34 ± 0.14 cm in height and 0.37 ± 0.32 cm in width, with a monthly increase of 1 ± 1.2 for branch tips and an increase in branch length of 0.19 ± 0.02 cm. An increase in branch length was followed by an increase in branch tips (in t4 and t5 respectively). The maximum-recorded monthly growth was an increase in branch length of 0.41 cm (between sampling periods 3 and 4, and an increase of 3.2 new branches between sampling period 4 and 5 (Table 3).

Pacifigorgia rubicunda Breedy & Guzman 2003

P. rubicuanda colonies were common in all the sites except for Frijoles. A total of 332 colonies was monitored. The mean abundance of *P. rubicunda* was 15.8 ± 6.7 colonies/m^2 in Roca Hacha; 8.7 ± 5.7 colonies/m^2 in Jicarita; 7.1 ± 2.4 colonies/m^2 in Catedrales; and 0.8 ± 0.8 colonies/m^2 in Frijoles. Size class 3 was more frequent in Catedrales, Jicarita, and Roca Hacha, and size class 2 was more frequent in Frijoles (Table 1). The survivorship curve was higher in Jicarita (p<0.001, s=13.010) and there was an overall (all sites together) difference in survivorship between size classes (p<0.001, s=18.122) with size 1 having a lower survivorship than sizes 3 and 4, and size 2 lower than size 4. There was a difference in survivorship between sampling periods only in Roca Hacha, where t2 was higher than t5 (p=0.001, q=4.77). Recruitment was different between sampling periods only in Catedrales, where t4 was higher than t5 (p=0.01, q=4.750). Recruitment was not different between sites (Table 2).

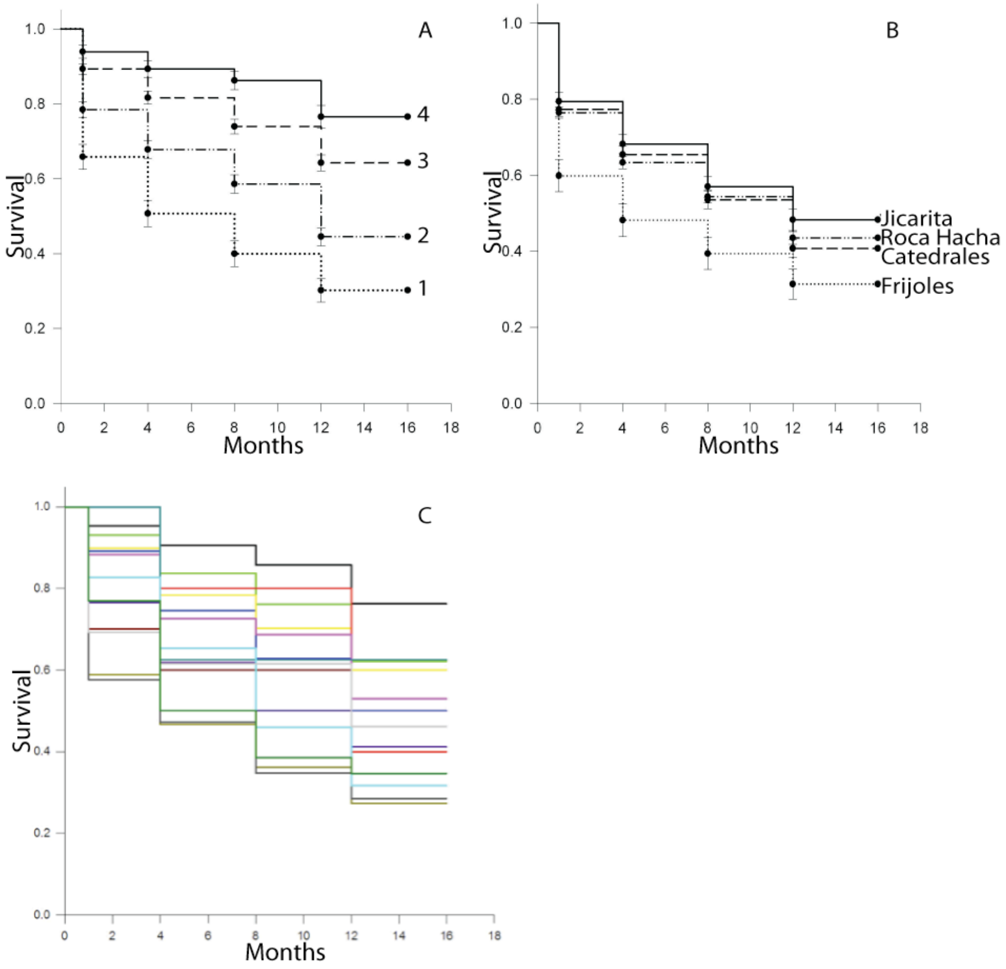

Figure 4. Global Survivorship Curves for ocotocorals in Coiba National Park. A) Between size classes, all species and sites together, larger colonies (4) had an overall higher survivorship than smaller colonies (1). B) Between sites, all species and size classes together, colonies at Frijoles had an overall lower survivorship. C) Between species; each color represents a species, wide variation in curves between species.

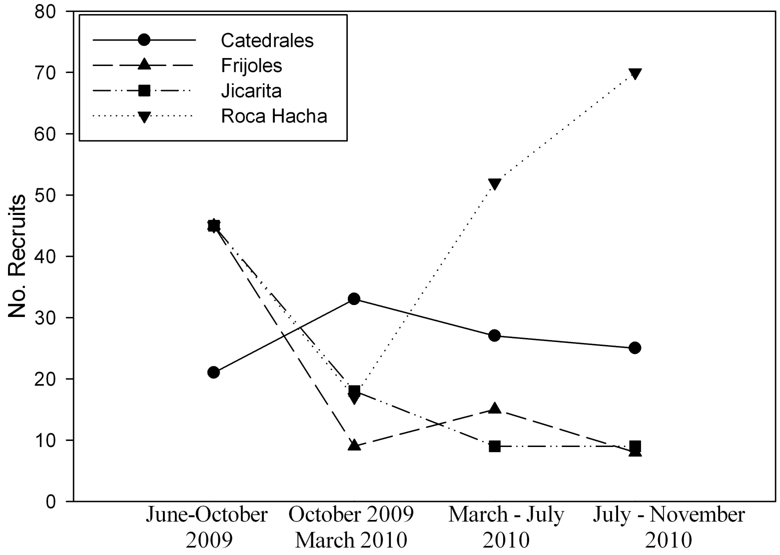

Figure 5. Recruitment rates for each study site in Coiba National Park, Panama. Peaks occurred during different sampling periods.

Pacifigorgia irene Bayer 1951

P. irene colonies were very common in Roca Hacha and common in Jicarita and Catedrales. They were frequently found in mono-species patches with most of the colonies sharing the same orientation. Colonies were frequently damaged with ruptures, but these did not cause colony death. A total of 233 colonies was monitored with a mean abundance of 12.9 ± 5.2 colonies/m^2 in Roca Hacha; 6 ± 2.8 colonies/m^2 in Catedrales; and 2.6 ± 2.3 colonies/m^2 in Jicarita. Size class was not randomly distributed (x^2=16.1, p=0.01). Size 4 was more common in Jicarita and Catedrales, and size 3 more common in Roca Hacha (Table 1). Survival curves were not different between sites or between size classes or sampling periods. Recruitment was relatively low, with 2 recruits in Jicarita, 3 in Catedrales and 8 in Roca Hacha; with non-significant differences between sampling periods and sites (Table 2). Colonies used for growth measurements were in the size classes 3 and 4, from 25 cm^2 to 226 cm^2 in area. There was an average monthly increase in colony area of 0.84 cm^2 ± 5.64 cm^2. Area measurements provided a better growth estimator than height and width because of colony ruptures and uneven growth (Table 3).

Carrijoa riseii Duchassaing & Michelotti 1860

C. riseii colonies were common in Roca Hacha and less common in Jicarita and Catedrales. A total of 144 colonies was monitored, with a mean abundance of 8.4 ± 13.3 colonies/m^2 in Roca Hacha; 2.8 ± 4.3 colonies/m^2 in Catedrales; and 1.8 ± 2.6 colonies/m^2 in Jicarita. Colonies had a rapid growth in which small recruits merged into larger adjacent colonies, making it difficult to distinguish individual colonies. Size classes 1 and 2 were more common than 3 and 4 (Table 1). Survivorship curves differed between sites; colonies at Roca Hacha had higher survivorship than colonies at Catedrales and Frijoles (p=0.001, s=31.678). Survivorship was not different between size classes even when the colonies were grouped in two size categories. Survivorship was different between sampling periods only in Roca Hacha, with higher values during t2. Colonization was not significantly different between sites or sampling periods (Table 2).

Heterogorgia verrucosa Verill 1868

H. verrucosa was more common in Roca Hacha than Catedrales, Frijoles, or Jicarita. A total of 111 colonies was monitored, with a mean abundance of 5.3 ± 2.3 colonies/m^2 in Roca Hacha; 2.9 ± 2.5 colonies/m^2 in Catedrales; 1.2 ± 2.9 colonies/m^2 in Frijoles; and 0.9 ± 1.5 colonies/m^2 in Jicarita. Size classes 1 and 3 were equally abundant in Catedrales, with size 1 being most abundant in Frijoles, and size 2 most abundant in Jicarita and Roca Hacha (Table 1). Survivorship curves were not different between sites, however, they were different between size classes; (p=0.001, s=15.815) size 1 had a lower survivorship than size 3 or size 4. This size class difference in survivorship was not found when analyzing sites separately. Survivorship was different between sampling periods only in Roca Hacha where t2 was higher than t4 ($p<0.05$, q=3.873). There was not a significant difference in recruitment between sites or between sampling periods (Table 2). This species was described as azooxathellate in Isla Tortuga Mexico (Van Oppen et al. 2005).

Leptogorgia cofrini Breedy & Guzman 2005

L. cofrini was very common in Jicarita. A total of 97 *L. cofrini* colonies was monitored, with a mean abundance of 4.3 ± 6.4 colonies/m^2 in Jicarita; 2.7 ± 2.5 colonies/m^2 in Catedrales; and 2.1 ± 1.8 colonies/m^2 in Roca Hacha. Size classes 2 and 3 were the most abundant (Table1). Survivorship curves did not differ between sites, however, they differed between size classes (p=0.030, s=8.948); size 4 had a higher survivorship than size 2. When sites were analyzed separately this difference was only found in Roca Hacha (p=0.019, s=7.9926). Survivorship curves were different between sampling periods only in Jicarita (p=0.023, F=3.826), where t2 was higher than t5. Recruitment was not different between sites or between sampling periods (Table 2).

Pacifigorgia cairnsi Breedy & Guzman 2003

P. cairnsi colonies had similar abundance in Catedrales, Jicarita, and Roca Hacha. A total of 50 colonies was monitored with higher frequencies found in size classes 2 and 3 (Table 1). The mean abundance was 1.4 ± 1 colonies/m^2 in Jicarita; 1.6 ± 1.5 colonies/m^2 in Catedrales; and 1.8 ± 1.7 colonies/m^2 in Roca Hacha. Survivorship curves were different between size classes (p=0.028, s=9.125); size 4 had a higher survivorship than size 2. This difference was not observed, however, when analyzing sites separately. There was no difference in recruitment or survivorship between sites or sampling periods (Table 2).

Leptogorgia rigida Verril 1864

L. rigida was only found at Jicarita, with the exception of one small colony found at Frijoles. A total of 26 colonies was monitored, with a mean abundance of 2.7 ± 4.2 colonies/m^2 in Jicarita, with only one recruit during sampling period 3. *L. rigida* was described as an azooxathellate species in Cabo San Lucas, Mexico (Vann Oppen et al. 2005).

Muricea austera Verrill 1868

Muricea austera was commonly found in Roca Hacha, and rare in Catedrales. A total of 21 colonies was monitored with a mean abundance of 2.3 7 ± 1.7 colonies/m^2 in Roca Hacha, most of them (55%) in size class 4 (Table 1). It had a high survivorship, which did not differ between sampling periods. No recruits were seen during the duration of the study (Table 2). *Muricea austera* colonies had slow growth with a monthly net increment of 0.03 cm ± 0.1 in height, 0.04 cm ± 0.2 in width, and an increase in the number of branch tips of 0.33 cm ± 0.4. The net branch length growth was negative due to bites from possible predators in individual branches (-0.01 ± 0.06 cm). The maximum-recorded monthly growth was an increase of 0.95 cm in height, 1.55 cm in width, 3 new branches, and an increase in branch length of 0.14 cm (Table 3).

Psammogorgia arbuscula Verrill 1866

P. arbuscula was common in Roca Hacha and rare in Jicarita, Frijoles, and Catedrales. A total of 32 colonies was monitored with a mean abundance of 1.9 ± 2.5 colonies/m^2 in Roca Hacha and 0.6 ± 0.8 colonies/m^2 in Catedrales. Size class 4 was the most common in Roca Hacha (59%). There was a significant difference between size class survivorship curves ($p<0.001$, s=18.768) with size 1 lower than sizes 3 and 4 ($p=0.01$ and $p=0.008$, respectively), and size 2 lower than 4 ($p=0.013$). Recruits (n=5) were only observed in Roca Hacha during sampling periods 4 and 5. Measured colonies had a net monthly growth of 0.08 ± 0.17 cm in height and 0.08 ± 0.32 cm in width. The maximum growth reported was an increase of 0.84 cm in height and 0.93 cm in width. Nine of the ten monitored colonies remained alive to the end of the study (Table 3). This species was described as an azooxathellate in California (Vann Oppen et al. 2005).

Table 1. Size class distribution for octocoral species at study sites in Coiba National Park. Relative classes sizes: 1 represents small recruits, 2 small colonies, 3 medium size colonies, and 4 large size colonies. Red ink indicates more common size classes. Species in which the survivorship curves significantly differed between class sizes (*). Catedrales (C), Jicarita (J), Roca Hahca (R), Frijoles (F).

Species	Site	n	1	2	3	4
Carrijoa riseii	C	25	52.0%	12.0%	28.0%	8.0%
	J	16	25.0%	56.3%	18.8%	0.0%
	R	76	37.8%	20.3%	25.7%	16.2%
Heterogorgia verrucosa *	C	26	30.8%	15.4%	30.8%	23.1%
	F	11	54.5%	27.3%	18.2%	0.0%
	J	8	0.0%	57.1%	28.6%	14.3%
	R	48	23.4%	46.8%	23.4%	6.4%
*Leptogorgia alba**	C	113	11.5%	33.7%	34.6%	20.2%
	F	76	25.0%	29.2%	38.9%	6.9%
	J	48	26.1%	39.1%	32.6%	2.2%
	R	189	19.6%	43.5%	33.2%	3.8%
*Leptogorgia cofrini**	C	24	4.5%	27.3%	59.1%	9.1%
	J	39	13.2%	44.7%	34.2%	7.9%
	R	19	5.6%	38.9%	55.6%	0.0%
Muricea austera	R	21	0.0%	15.0%	30.0%	55.0%
*Pacifigorgia cairnsi**	C	14	0.0%	36.4%	36.4%	27.3%
	J	12	0.0%	18.2%	45.5%	36.4%
	R	16	33.3%	26.7%	33.3%	6.7%
Pacifigorgia irene	C	54	11.8%	19.6%	27.5%	41.2%
	J	23	13.0%	8.7%	30.4%	47.8%
	R	116	5.8%	30.8%	42.3%	21.2%
*Pacifigorgia rubicunda**	C	64	1.8%	19.3%	54.4%	24.6%
	F	7	28.6%	71.4%	0.0%	0.0%
	J	78	2.7%	20.0%	58.7%	18.7%
	R	142	6.6%	30.7%	53.3%	9.5%
*Psammogorgia arbuscula**	C	5	0.0%	20.0%	80.0%	0.0%
	R	17	5.9%	23.5%	11.8%	58.8%

Table 2. Mean and standard deviation (m^2/year) density, mortality, and recruitment for species found at study sites. A significant difference between sampling periods is indicated by a (*). A significant difference in survivorship between size classes is indicated by (△). Catedrales (C), Jicarita (J), Roca Hacha (R), Frijoles (F).

Species	**Site**	**n**	**Density**	**sd**	**Mortality**	**sd**	**Recruitment**	**sd**
Carrijoa riseii	C	35	2.8	±4.3	0.6	±0.1	0.3	±0.9
	J	18	1.8	±2.6	0.9	±0.4	0.1	±0.2
	RH	90	8.4	±13.3	0.5*	±0.2	0.06	±0.08
Heterogorgia verrucosa △	C	36	2.9	±2.5	0.1	±0.9	0.9	±0.2
	F	12	1.2	±2.9	0.4	±0.4	0	±0.0
	J	9	0.9	±1.5	0.04	±0.1	0.03	±0.08
	RH	54	5.3	±2.3	0.2*	±0.2	0.07	±0.1
Leptogorgia alba△	C	150	12.6	±6.4	0.4	±0.1	0.3	±0.2
	F	107	8.4	±3.5	0.5 *	±0.3	0.4	±0.3
	J	68	5.3	±3.8	0.5	±0.4	0.2	±0.2
	RH	282	21	±11.4	0.6	±0.3	0.4*	±0.3
Leptogorgia Cofrini △	C	27	2.7	±2.5	0.5	±0.2	0.1	±0.1
	J	44	4.3	±6.4	0.2*	±0.3	0.02	±0.06
	RH△	26	2.1	±1.8	0.3	±0.2	0.2	±0.3
Leptogorgia rigida	F	1	0.1	±0.3				
	J	25	2.7	±4.2	0.4	±0.1	0.01	±0.04
Leptogorgia pumilla	C	1	0.1	±0.3				
	J	7	0.8	±0.8				
	RH	3	0.1	±0.3				
Leptogorgia taboguilla	C	5	0.4	±0.5				
	RH	1	0.1	±0.3				
Muricea austera	C	1	0.1	±0.3				
	RH	21	2.3	±1.7	0.2	±0.3	0.0	±0.0
Pacifigorgia cairnsi △	C	17	1.6	±1.5	0.4	±0.3	0.2	±0.3
	J	15	1.4	±1.0	0.2	±0.3	0.2	±0.5
	RH	18	1.8	±1.7	0.2	±0.3	0.2	±0.3
Pacifigorgia eximia	C	2	0.2	±0.4				
	RH	6	0.4	±0.5				
Pacifigorgia firma	C	1	0.1	±0.3				
	J	4	0.2	±0.4				
	RH	5	0.4	±0.5				
Pacifigorgia irene	C	70	6	±2.8	0.2	±0.2	0.2	±0.2
	J	30	2.6	±2.3	0.04	±0.1	0.2	±0.3
	RH	132	12.9	±5.2	0.2	±0.09	0.1	±0.1
Pacifigorgia rubicunda △	C	83	7.1	±2.4	0.2	±0.2	0.1*	±0.2
	F	9	0.8	±0.8	0.3	±0.4	0.2	±0.3
	J	84	8.7	±5.7	0.05	±0.06	0.04	±0.06
	RH	156	15.8	±6.7	0.2*	±0.05	0.07	±0.05
Psammogorgia arbuscula △	C	6	0.6	±0.8				
	F	1	0.1	±0.3				
	J	3	0.02	±0.4				
	RH	22	1.9	±2.5	0.2	±0.2	0.2	±0.5
Pacifigorgia stenobrochis	J	1	0.1	±0.3				
	RH	1	0.1	±0.3				

Discussion

High octocoral densities (77.6 colonies/m^2) were found at Coiba National Park compared to reported densities in the Caribbean where 25.1 colonies/m^2 were reported in South Florida (Goldberg 1973). Differences in species diversity and abundance between study sites could be the result of an inshore-offshore gradient distribution (Opresko 1973) or a gradient in levels of illumination and irradiance (Grigg 1974; Muzik 1982).

A combination of factors could explain the variation observed among our study sites, previously described as having a high and medium-high diversity. We found low diversity and abundance at Frijoles that may be explained by a number of factors. This inshore location could be linked to a lack of viable larvae. Jordan-Dahlgren (2002) proposed that octocoral distribution was controlled by the availability of functional larvae. Variation in larval viability is affected by the dynamics of ocean and shore currents at large and small scales. Frijoles is less exposed to currents than the other study sites; this could mean that it is exposed to fewer viable larvae carried out by currents. On the other hand, Preston & Preston (1975), Birkeland (1974), and Opresko (1974) hypothesized that octocoral distribution was determined by the availability of substrata. Frijoles had more empty substrata, with less sponge, algae, and hard coral cover than the other three sites. Temperature could be another factor determining local distribution, although there was not a significant difference in the mean monthly temperature profiles between study sites. Frijoles had the highest temperatures all year round and this could have influenced recruitment and mortality rates in these shallow octocoral species. Lastly, the invasive coral predator, Crown-of-Thorns starfish (*Acanthaster planci),* is frequently seen at Frijoles and its predation could decrease the possibility of recruits becoming adults. Interestingly, this selection seems to be directed to species other than

Leptogorgia alba, which was a dominant species at the site and recruitment and mortality rates were not different between sites.

The high standard deviation observed in species densities may reflect the patchy distribution of some species, which had many individuals in one plot and none in others. Similarly, *Pacifigorgia irene* patches were frequently seen around the study plots, most of them sharing the same fan orientation. This synchronized orientation has been described for *Muricea californica* and *M. fruticosa* by Grigg (1972) as a response to water flow direction. *Carrijoa riseii* colonies seemed to merge as they grew, creating mono-species groups. This could be explained by their fast vegetative growth (Kahng et al. 2008).

Over the duration of the study period, there was not an evident peak in recruitment at the species level and levels of recruitment varied greatly between sites. Grigg (1977) proposed that an even recruitment rate for *Muricea californica* and *Muricea fruticosa* was due to a space-limited population, which generated constant recruitment and mortality rates. This could be the case for the studied species, because there were no peaks either in mortality or recruitment. However, it can be speculated that a temperature anomaly due to El Niño and La Niña Southern Oscillation could have caused a decrease in coral reproduction and recruitment, as it does in sclerectinian species (Glynn 2000).

Overall survivorship was different between species: *Pacifigorgia eximia* > *P. stenobrochis* > *P. irene*> *P. rubicunda* > *Psammogorgia arbuscula* > *M. austera* > *P. cairnsi* > *H. verrucosa* >*P. firma* > *L. pumila* > *L. alba* > *L. cofrini* > *L. taboguilla* > *C. riseii*. These results suggest that the genus *Pacifigorgia* has a greater life expectancy than the genus *Leptogorgia*, at least among the studied species. These differences could be due to colony morphology. In general, *Pacifigorgia* species have thicker branches, which create a relatively strong compound or single network which is securely attached to the substratum by a hold fast of different dimensions and forms, and in some cases the colonies are strengthened by midribs (Breedy & Guzman 2002).

Conversely, *Leptogorgia* species have slender and more fragile branches and are attached to the substrate by a single mother branch.

Because the differences in survivorship between sampling periods differed between species, it can be concluded that several factors affect species differently. Otherwise, all the species would be found to have a similar response to environmental changes (e.g. all species presenting a peak in mortality at a specific time or site). Survivorship of *Carrijoa riseii* was higher at Roca Hacha. This species is known to inhabit places with low light irradiance (Kahng & Grigg 2005). During the study period there were more than five moderate mudslides on the coast in front of Roca Hacha, increasing siltation and decreasing light penetration. Moreover, this site is located at ~3.5 km from a river mouth. During the rainy season fresh turbid water covers the marine superficial water, again decreasing light irradiation.

A common cause of death in small colonies (Size class 1 and 2) was overgrowth by macroalgae, sponges, or other octocorals, especially *Carrijoa riseii*. For bigger class sizes (3 and 4) detachment, and to a lesser extent diseases, were the main causes of mortality. Loss of branches, due to breakage or predator bites did not cause colony death. Grigg (1977) explained high mortality rates in *Muricea californica* as being due to bioerosion by bivalves and other invertebrates, which weakened the basal attachment of older colonies. The *Muricea austera* studied here had a relatively low mortality, and in an overall analysis, smaller colonies had a higher mortality than larger colonies. For species that had a significant difference in survivorship between size classes (*H. verrucosa, L. alba, L. cofrini, P. cairnsi, P. rubicunda, Psammogorgia arbuscula.*), it is likely that once a recruit establishes and grows a couple of centimeters, its chances of surviving increase significantly (*sensu* Lasker 1990).

Growth was different between species; *Leptogorgia alba* >> *Psammogorgia arbuscula* > *Muricea austera* > *Pacifigorgia irene*. Net growth measurements reported in this study include negative growth caused by predation. There was an attempt to study the effect of predation on mortality and growth, but unfortunately, the exclusion cages were lost twice from the study site, and it was not possible to collect this type of data. Due to negative growth and further tissue regeneration, measurements of the fan area were a better growth measurement than fan height and width, especially for *Pacifigorgia irene*. Another barrier to studying growth was a high colony mortality rate in *Leptogorgia alba* colonies, with only three out of ten monitored colonies surviving to the end of the study.

The relationship between colony size and colony survivorship appears to be more important in fragile species like *L. alba* than in stiff species such as *P. irene* and *M. austera*. This was evident in a site where the fragile species had low survivorship. In this case, smaller *L. alba* colonies had lower survivorship than larger colonies in Roca Hacha (where the overall *L. alba* survivorship was lower) but not in Jicarita or Catedrales (where the overall *L.alba* survivorship was higher).

In summary, when analyzing all species together for individual sites, there was a relationship between density, recruitment, and mortality rates suggesting that "good sites" had high density associated with high recruitment and low mortality. However, this relationship was not found when analyzing species separately. There seem to be different reasons for Catedrales, Jicarita, and Roca Hacha being "good sites." These sites are located in the western side of Coiba Island, which is exposed to strong currents and surge, and closer to deeper water. The strong surge could create a potential micro upwelling, bringing up nutrients from the deep cold water nearby, which would create a rich environment for octocoral growth and development. Frijoles, conversely, is more protected from strong currents and surge. It is also surrounded by shallower water.

Species-specific trends were more evident in the overall analyses, which pooled the data from all the sites, than in the site-specific analyses. Moreover, the sample size was significantly reduced when analyzing sites separately; e.g. *P. cairnsi, L. cofrini, H. verrucosa*, and *P. rubicunda* all showed differences in survivorship between size classes in an overall analysis (all sites together) but not when the analysis was performed in individual sites.

Octocorals were certainly a dominant species, especially in Roca Hacha, Jicarita, and Catedrales. Because octocorals host many invertebrates and serve as fish aggregation areas, they are recognized as foundation species. Therefore, their age structure may reflect the environmental suitability and stability of the associated taxa (Grigg 1975). *Leptogorgia alba* and *Psamogorgia arbuscula* colonies were frequently seen covered by bridle-star symbionts. The octocoral species had varying mortality rates: *L. alba* had very dynamic populations with lower growth and survivorship, suggesting a similar fate for brittle stars inhabiting *L. alba* colonies, in contrast with a potential higher survivorship of brittle stars inhabiting *Psammogorgia arbuscula* colonies.

There seem to be two life history strategies evident in the sites we studied. *Leptogorgia alba* is abundant and widely distributed in Coiba as well as Cocos Island and mainland Costa Rica (Breedy and Cortés 2008). It has high recruitment rates, low survivorship, and relatively fast growth, with even distribution of size classes. Therefore, *L. alba* can be described as an ¨r¨ selected species. In contrast, *M. austera* is only common at one site, where it has high survivorship, low recruitment, and relatively slow growth, with most of the individuals falling into larger size classes. *M. austera* can be described as a ¨K¨ selected species. Although both of these species have a branched morphology, the branch thickness, size of holdfast, and size of sclerites are very different. *L. alba* has thin and fragile branches (stem is 3 mm and branches are 1-1.5 mm in diameter, small holdfast, and sclerites with a maximum size of 0.18mm (Breedy & Guzman 2007), while *Muricea austera* has thick and resistant branches of about 5 mm in diameter (Verrill 1868), large holdfasts, and thicker sclerites. Due to branch differences, selection from predators could differ, and there could be differences in capacity to overcome overgrowth and stronger resistance to wave action. It is likely that these species may have different reproductive mechanisms, which also alters the distribution and dynamics of each species.

There are many reasons for continuing the study of octocoral species in the Tropical Eastern Pacific. Besides the present study, the ones published by Grigg (1972, 1974, 1975, 1977), and the invasion history of *Carijoa riisei,* there is no other information about the natural history of species present in the TEP. Octocoral species, like many others, face a variety of threats including habitat degradation through anchoring and trawling, water quality degradation through sedimentation and metal contamination, and water temperature changes. Although this study was performed in a protected area, where fishing and extracting activates are prohibited, illegal fishermen were observed on two occasions.

Some of the species present in the area have been identified as sources of active compounds to be used in the generation of natural products and pharmaceuticals including the fast colonizer *Carijoa riisei* (Maia et al. 2000, Reimão et al. 2008), *Leptogorgia alba* (Gutierrez et al. 2005), a " r" selected species, and *Muricea asutera* (Gutierrez et al. 2006), a "K" selected species. Future responsible exploitation of any of these species and successful management for coral communities within and between marine protected areas requires further studies of octocoral reproductive strategies, life cycles, and the effects of physical changes, such as water temperature, on their natural history, and the effect of symbiotic relationships with other invertebrates and microalgae. Further studies are also required on the associated bacteria, which is now the target of many chemical studies; the effect, cause, and distribution of diseases; and the biology and ecology of deep water octocoral communities.

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Linking statement between Chapter 2 and Chapter 3

A significant natural population decline is reported in all study sites in Chapter 2. Chapter 3 studies the consequences of this decline and whether or not it has affected the community structure of each study site. Furthermore, this chapter compares the consequences of the natural decline with the consequences of an anthropogenic-punctuated disturbance, which mimicked the damage caused by a hurricane or by trawling fishing.

CHAPTER 3

Population decline and the effects of disturbance on the structure of octocoral communities in the Tropical Eastern Pacific

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Abstract

Community structure and species composition are frequently studied using common descriptors, which are also used to monitor changes over time after disturbances. This study uses Ranked Abundance Distribution plots (RAD), Rényi entropy plots (Rényi), common theoretical community models, ordination analysis of similarities, and abundance spectra analyses to study the effects of natural population decline and an anthropogenic punctuated disturbance on the structure of octocoral communites located in the Tropical Eastern Pacific (Panama). Over a 17-month study period, no significant change was found in community structure after a natural population decline. After a disturbance, however, different recovery trajectories were observed in the various study sites. Physical and biological reasons are suggested as the cause of such differences and these include exposure to currents and viable larvae, species life history and colony morphology. Differences in community structure among study sites were best interpreted by a combination of community descriptors. Rank abundance distributions, abundance spectra and Rényi plots were useful in determining the changes in octocoral community structure, whilst ANOSIM and cluster analysis allowed determination of the extent of the change.

Keywords: community ecology, soft corals, species relative abundance, disturbance, diversity

Introduction

The causes of the distribution of abundance in a community is a topic of ongoing debate in ecology (McGill et al. 2007). Different patterns have emerged including a few very abundant species and large numbers of rare species, and unimodal distributions with abundant intermediate species (McGill et al. 2007). The distribution of species abundance has been studied graphically with the use of Species Abundance Distribution plots (SAD) (Preston 1948), Ranked Abundance Distribution plots (RAD) (Macarthur 1957), and more common diversity indices that include a spectrum of values with more or less weight given to species evenness, all of them summarized by Rényi (1961) plots.

SADs and RADs are considered useful community composition descriptors (McGill et al. 2007) and have been widely used because they only require basic information from the community (number of species and their abundance). However, there has been ongoing debate over whether these patterns are simply the result of different binning methods in Preston´s plots (see Gray et al. 2006), or the effect of a small sampling scale (McGill 2003). Connolly et al. (2005) examined the community structure of coral reefs and reef fishes using both numerical abundances and biomass and found a significant difference when the data was analyzed at different spatial scales. This phenomenon was explained by arguing that in a small sampling scale (local community) a log-normal shape was truncated due to an under sampling of rare species, and that this distribution was "unveiled" if the data was analyzed on a larger scale (metacommunity).

Diversity indices are also widely used to describe a sampled community. This are non-parametric mathematical functions of relative species abundance which incorporate, with different weights, species richness and evenness (Loreau 2010). The most common indices are: 1) Species Richness (S), which is strictly the number of species present, regardless of their abundance; 2) The Shannon diversity index (H) (Shannon and Weaver 1949), which is more sensitive to abundant species and less to rare species than (S); 3) The Simpson concentration index (λ) (Simpson 1949), which is more sensitive to abundant species and less sensitive to rare species than (H); and 4) the Dominance index (p_1) (Berger and Parker 1970), which is insensitive to rare species. All of these indices can be summarized on a Rényi entropy plot (Rényi 1961), which gives a spectrum of species richness and evenness. In contrast to the diversity indices, the Rényi entropy is a function, rather than a single index, permitting the diversity between communities to be compared; a significant difference in diversity among communities will be represented by non-overlapping Rényi profiles (Loreau 2010).

SADs, RADs, and Rényi plots use the same information to describe, in different ways, how communities are constituted. These plots can be used to compare a community with other communities and with itself after disturbance and recovery. The plots can also be used to evaluate the impact that such processes have on rare and common species. SADs, RADs, and Rényi plots, however, are missing some information; a possible species-turnover process or "reorganization" of abundances will not be reflected in the mechanisms proposed above (MacNally 2007). The rate of change at which a species shifts from rare to common or vice-versa has been described as relatively quick (Hanski 1982), moderate change (Hubbell 2001) or a very slow process of change, taking up to a million years (McGill et al. 2007). For this reason, it is suggested that labeled SADs (Murray et al. 1999) should be used with the Abundance Spectrum introduced by Mac Nally (2007). In the Abundance Spectrum, the rank is species-specific and is plotted against the relative abundance of the species before and after disturbance, or against undisturbed reference communities. With this method each species maintains its position in the rank, making species that changed from rare to common more clearly evident. This method is ideal for habitat-specific analysis but is not as well suited to habitat comparisons, where SADs and RADs are useful.

Disturbances can have different effects on community composition depending on their type (physical or environmental), frequency (chronic or punctuated), strength, and temporal and spatial scale (Connell 1997). The Intermediate Disturbance Hypothesis (IDH) theory states that at intermediate levels of disturbance diversity is maximized; at low levels of disturbance, there is competitive exclusion from the dominant specie, and at high levels of disturbance there is an increase in local extinctions (*sensu* Connell 1978, 1979). After some modifications, the IDH was tested in a marine benthic community (Dial & Roughgarden (1998) and in a coral community (Huston 1985).

Disturbances can alter the composition of species in a community. When the common-monopolizer species is removed, an increase in evenness and *H* diversity is expected (Rogers 1993). Rogers and Zullo (1987) reported this process after a coral reef disturbance created by hurricanes and tropical storms in Jamaica. Other authors, however, have proposed that rare species are likely to be lost faster (Caughley 1994) with a proportional decrease in the remaining species with respect to their initial population (Mac Nally 2007).

After a disturbance, a community recovery can happen in different ways. Connell and Slatyer (1977) identify three major recovery processes: 1) colonizers facilitate the establishment of non-colonizers: 2) colonizers with high-level resource requirements are outcompeted by species with lower requirements; or 3) colonizers inhibit the establishment of other species. All these processes have been supported by empirical evidence from marine communities (Rogers 1993). One example can be found in Svensson et al.

(2009), who reported the rapid decrease of an abundant tunicate and the rapid growth of a colonizer algae as a result of the same disturbance. However, sometimes the hierarchy of very dominant species is not affected even after several population declines (Rogers 1992). Other factors affecting the re-colonization of marine benthic communities is the size of the space to be re-colonized; in relatively small spaces dominant species often colonize through rapid growth. Alternately, larger spaces can be colonized by sexually produced recruits from common or rare species (Rogers 1993).

Because SADs, RADs, and Rényi analyses are useful descriptors of a community, and because community change can vary after a disturbance, these analyses could be used as indicators to evaluate changes in a community and whether or not the original community composition pattern is achieved after a recovery process. Magurran (2007) proposed a comparison between patterns from SADs at various timed intervals to illustrate changes in the composition and structure of a community after natural or anthropogenic changes. In the same way, Gray (1979) proposed the use of RADs to demonstrate the effect of pollution and other major disturbances on communities, and Huston (1985) suggested the use of H′ diversity. With the use of these patterns, Gray (1979) concluded that an increase in the intermediate abundant species, which causes a departure from a log-normal distribution, can be used as an early detectable consequence of pollution in marine benthic communities. Mac Nally (2007) also concluded that in landscapes with major disturbances, original community composition patterns can be expected to change.

This study aims to describe the changes in species composition and structure of an octocoral community through the use of RAD graphs and Rényi entropy plots over time, to determine if a naturally declining community maintains its distribution of species abundance and diversity profile, and if these patterns can be recovered after a punctuated anthropogenic disturbance. In addition, we used ordination analysis of similarities to test and measure differences in community composition and illustrate species turn-over with the use of abundance spectra.

Materials and Methods

Octocorals as study subject

Octocorals (Coelenterata- Anthozoa- Octocorallia) are sessile colonial marine invertebrates inhabiting many diverse environments, including shallow and deep waters in tropical and subtropical regions (Bayer 1981). They are known for being a dominant part of their communities and providing living substrata to a variety of invertebrates (Cantera et al. 1987). Octocorals are also generally unevenly distributed (Guzman et al. 2004) and are poor dispersers compared to reef-building coral species (Concepcion et al. 2010). Octocorals present a variety of growth forms, which increase the tri-dimensionality and heterogeneity of the substrata, creating niche spaces for other taxa.

Study Site

The study took place at Coiba National Park (CNP), the largest marine protected area in Panama, which protects about 2,024.63 km^2 of marine ecosystems. As home to 35 octocorals, CNP is a recognized octocoral diversity hotspot in the Tropical Eastern Pacific, and many of the species are endemic to the island (Guzman et al. 2004, Guzman & Breedy 2008). Octocoral communities at CNP, and in the Tropical Eastern Pacific in general, occur in very active environments where there are vertical rocky walls and underwater pinnacles or seamounts exposed to strong currents and swell. These octocoral communities have not been studied until recently, when efforts were made to describe their basic biology and population dynamics (see Chapter 1 and 2).

Four previously inspected sites in CNP, which had the same depth (20 m) in a longitudinal gradient but were exposed to different levels of water energy, were chosen as study sites: 1) Frijoles islet (7º 38' 59.6" N, 81º 43'

09.4" W), protected from strong currents and swell in the northern part of Coiba Island; 2) Roca Hacha (7º 25' 55.0" N , 81º 51' 29.0" W), a small islet located at the western part of Coiba Island, exposed to swell and occasional sedimentation events; 3) Catedrales (7° 13' 33.7'' N , 81° 49' 45.4'' W) underwater pinnacles, 10 meters from the surface in the southern region of the park and exposed to strong currents; and 4) Jiarita (7º 12' 12.5" , 81º 48' 02.3"), an island with a vertical wall at the furthest southern region of the park, exposed to strong swell and breaking waves (see Chapter 2 for a detailed description).

Experimental set-up

To describe the octocoral community composition and test if this composition changed after a natural population decline, nine 1 m^2 fix plots were installed at 20 m of depth on each study site with the aid of SCUBA equipment. Plots were fixed by installing stainless steel square bars with underwater cement. Each colony present in the study plots was identified to the species level and a unique ID number was assigned to it. Study plots were monitored every four months for a 17 month–period (June 20/09, October 20/09, March 28/10, July 21/10, Nov30/10). For logistical inconveniences surveys three and four were five months apart. Plot monitoring was done through photographic records using a Nikon D-80 camera with a wide-angle lens inside an Ikelite underwater case and two external strobe flashes. The camera was attached to a stainless steel tripod in order to maintain a fixed distance (0.80 m) from an aluminum quadrat, which was attached to the fixed square bar when monitoring. The quadrat was divided into eight equal sections (0.42 m x 0.30 m; equivalent to 1 m^2 plot) to improve resolution in digital photography, resulting in a total of eight pictures per fixed plot. The quality of the pictures was improved by using Nikon NX2 software. Species abundance data was extracted from the pictures for further analysis.

To see the effect of a punctuated disturbance on the distribution of species abundance and determine whether the original distribution was recovered after a 17-month recover period, three $1\ m^2$ plots on each site, adjacent to the monitoring plots described above, were completely cleaned with a wire brush of all sessile organisms, including octocorals, hard corals, sponges, and macroalgae at the beginning of the study. This disturbance mimicked the effect of trawling, hurricanes, or significant mortality due to a drastic change in water physical properties. Clean plots were monitored every four months with the protocol described above. The abundance and diversity of colonies recruiting in the empty space was quantified during each sampling period.

Data analyses

Rank Abundance Distribution Plots

The relative abundance of each species on each site during each sampling period was calculated and ranked from 1 to n, with 1 being the most common species. The relative abundance was plotted on a logarithmic scale against the species rank in abundance, creating a RAD plot. The same procedure was performed for the colonies recruiting in the clean plots. The RAD curves, from both the monitored and cleaned plots, were plotted on the same graph. The null hypothesis was that the curves on each graph would have the same pattern, meaning no difference in community composition between sampling periods or monitored and cleaned plots.

Rényi diversity entropy

Rényi plots were performed by using the Vegan 1.17-6 package (Oksanen et al. 2011) in R64 software (R Development Core Team 2010), function >Rényi(x). This function calculates Rényi diversity of order *a* following equation No.1. Diversity indices can be found in a Rényi diversity profile as Ho=log(S), $H_1 = H'$, $H_2 -\log(\Sigma p^2{}_i)$ and $H\infty = -\log(\max p_i)$.

$$H_a = \frac{1}{1-a} \log \sum_{i=1}^{S} p_i^a$$

Equation No.1. Rényi diversity profile, where p_i is the proportion of species i and S is the number of species.

Best-fit model

By using the function >radfit in the Vegan Package (Oksanen et al. 2011) in the R Software (R Development Core Team 2010), count data for each site was compared with the most common ranked abundance models using the maximum likelihood estimation from the following models: Broken-stick (null hypothesis), Pre-emption, log-normal, Zipf and Zipf-Mandelbrot. This function compared the models by alternately using Akaike´s or Schwartz´s Bayesian information criteria.

Similarity analysis

Similarities were analyzed to test for significant change in community assemblage after a population decline and after a punctuated disturbance. These permutation/randomization tests operated on a Bray-Curtis coefficient resemblance matrix and were performed using PRIMER v6 Software (Clarke & Gorley 2006). Cluster analysis and ANOSIM test (Clarke 1993) were performed with standardized data and the maximum possible permutations. ANOSIM tested the null hypothesis that there was no difference in community composition between treatments. It does not assume a balanced replication so cleaned plots (n=3) could be compared with uncleaned plots (n=9) described in Chapter 2.

Results

There was an overall (all species and sites together) population decline of 31.5% during the study period (17 months) with an initial total abundance of 1304 colonies, representing 15 species. Octocoral communities in the four study sites had differences in diversity and abundance and all showed an important natural population decline. Roca Hacha had the highest species richness and abundance, with 14 species across 655 colonies and population decline of 30.4%. The site at Frijoles had the lowest species richness and abundance, with only 5 species across 56 colonies and a large population decline of 42.5% (Table 1).

Table 1. Baseline octocoral species richness and abundance and their population decline in 9 m^2 at 20 m of depth during a 17-month study period, in each study site within Coiba National Park, Panama.

Site	No. Species	Initial Abundance	Population Decline
Roca Hacha	14	655	30.4%
Catedrales	12	333	26.7%
Jicarita	12	260	31.5%
Frijoles	5	56	42.5%

RAD plots were compared by visual inspection. When comparing plots under a natural population decline (black solid lines in Figure 1), the graph pattern did not show clear differences between sampling periods. However, the RAD pattern did change for plots under a recovery process after a punctuated disturbance (red dotted lines in Figure 1). This change occurred differently between sites. In Catedrales, disturbed plots (red lines) increased in similarity with undisturbed plots (black lines) from sampling period 2 to sampling period 5. At the end of the study, disturbed plots recovered the RAD pattern of undisturbed reference plots, but with three species missing. In contrast, community recovery occurred differently in Roca Hacha and Jicarita, where RAD patterns did not change significantly between sampling periods 3, 4, and 5 and where the community assemblage included more dominant species than in reference plots. When comparing the RAD plot at Frijoles, it can be seen that there was no recovery in cleaned plots, as the red lines are dissimilar to the black lines from reference plots (Figure 1).

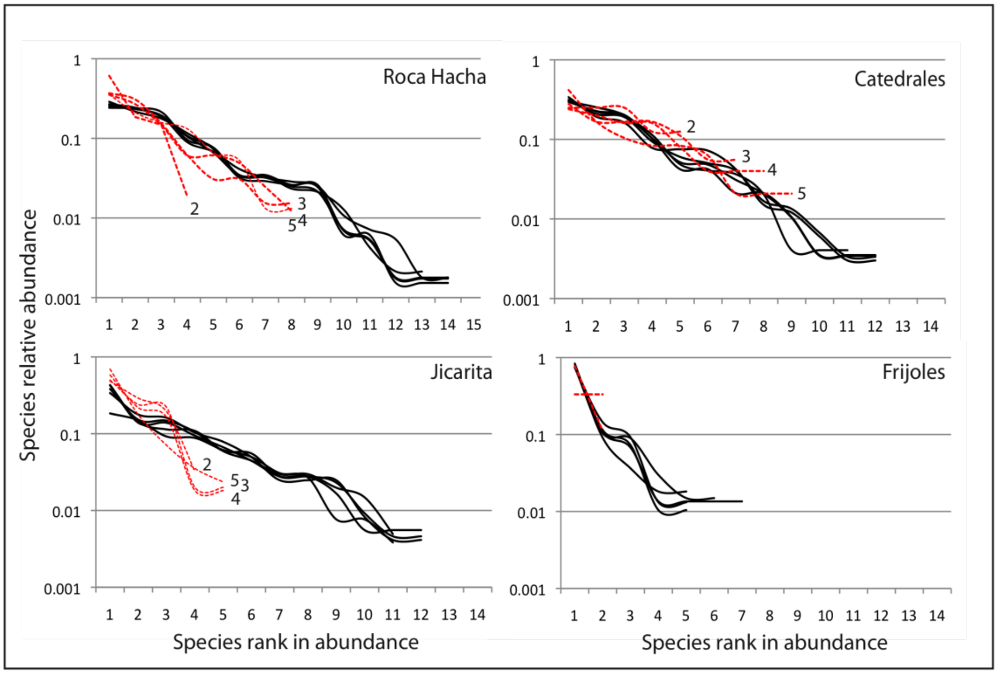

Figure 1. Rank Abundance Distributions (RAD) for each study site during five sampling periods. Black solid lines represent monitoring plots with a natural population decline (n=9). Red dotted lines represent plots under a recovery process after a punctuated disturbance (n=3). Numbers indicate the sampling period, 2=recovery after 4 months of disturbance, 3= 9 months, 4= 13 months and 5=17 months.

A visual inspection of the Rényi diversity profiles showed differences in diversity between study sites. Roca Hacha, Catedrales, and Jicarita demonstrated higher species richness and lower dominance compared to Frijoles, where species richness was lower and dominance was higher (solid lines, Figure 2). Although there was an important population decline in all sites, there was not a notable change in the diversity profiles as can be seen in the overlapping black lines in Figure 2. The diversity profiles for recovering plots changed differently across sites (red dotted lines, Figure 2). Recovery at Roca Hacha occurred by increasing species richness and evenness simultaneously, while never reaching the diversity profiles of reference plots. In contrast, the recovery at Catedrales moved from low richness and high evenness in sampling time 2, to high richness and low evenness in sampling time 5, increasing the similarity of its diversity profile to that of the reference plots as time progressed. In Jicarita species richness showed a relatively small increase while species evenness decreased over time. By looking at the RAD from Frijoles, it can be assumed that a small recovery took place during sampling period 5, reaching a similar species evenness with a lower species richness than in reference plots.

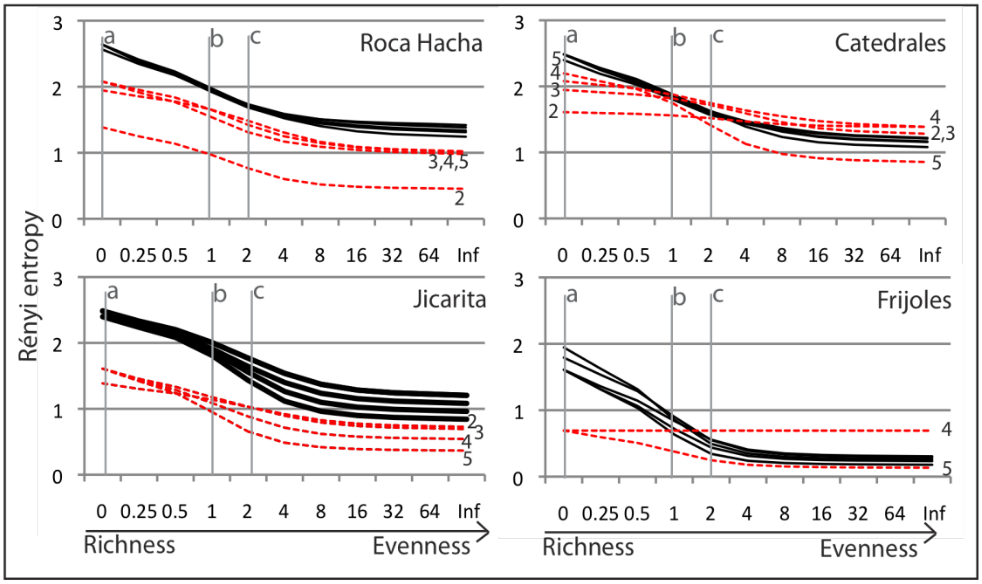

Figure 2. Rényi diversity profiles for each study site during five sampling periods. Black solid lines, mostly overlapping, represent plots with a natural population decline (n=9). Dotted red lines represent plots under a recovery process after a punctuated disturbance (n=3). Letters represent diversity indices: a=Ln S, species richness; b=H, Shannon Weaver; c=-lnλ, Simpson concentration.

Community structure in each site during each sampling period was compared with five different theoretical models: Broken-stick (null hypothesis), Pre-emption, log-normal, Zipf, and Zipf-Mandelbrot (Table 2). In the baseline community, sampling time 1, Catedrales, Jicarita, and Roca Hacha best fit the Preemption model (AICs= 64.9, 58.0, 84.4 respectively) and Frijoles fit best the Zipf model (AIC=24.5). The best-fit model did not change after a population decline in Catedrales, Roca Hacha, or Frijoles, but it did change in Jicarita, where it moved from Preemption to Lognormal (AIC= 58.0, 54.3 respectively). The best-fit model changed to the Null model, representing the broken-stick theory (AIC=31.51) after a disturbance in Catedrales. In Jicarita, the Zipf model had the lower AIC value (AIC=23.84); however, there was a small difference between this model and the Preemption model (AIC=24.47), which was the one that best fit the baseline community. In Roca Hacha the best-fit model did not change over the 17-month recovery process, implying that the community was similarly structured after disturbance. This analysis was not performed for disturbed plots in Frijoles due to its low population size (eight colonies).

The extent of the similarity in community structure between a reference baseline community and the community after a population decline and recovery was analyzed with a Bray-Curtis similarity matrix, tested with an ANOSIM analysis, and plotted as a cluster figure. No significant dissimilarity in community structure was found in any of the study sites (Table 3) between the baseline community and the community after the 17-month population decline. Jicarita had the lowest similarity with less than 80% (Figure 3). The least similarity was found in comparisons between disturbed and undisturbed plots. Community composition was only significantly different, however, in Jicarita (Table 4, Figure 4). The RAD plot for Frijoles suggested no recovery with a significant difference in community composition between disturbed and reference plots, and yet the ANOSIM analysis results showed the opposite pattern, a non-significant difference between disturbed and reference plots (Table 4, Figure 4).

Abundance spectra were plotted to determine if there was species turnover during the population decline or the recovery of disturbed plots. These spectra showed a similar species-specific composition after a population decline and, to a lesser extent, after a disturbance in Catedrales, Roca, and Frijoles. *Leptogorgia alba* was the most common species found in these three sites. This species did not lose its hierarchical rank after the population decline or after disturbance in Catedrales or Frijoles, and it became the second ranked species in Roca Hacha, where *Pacifigoriga rubicunda* became the first. In Catedrales, intermediate species changed in rank after disturbance and there was a significant increase of one rare species (*Leptogorgia rigida*). Jicarita had a species reorganization after disturbance. There, the most common species was *Pacifigorgia rubicunda*, which became rare after disturbance. On the other hand, *Leptogorgia cofrini*, which was third in rank, became the first and dominant species after disturbance (Figure 5). The reorganization of species abundance in Jicarita was expressed by the ANOSIM and Cluster analysis.

Table 2. Best fit model and AIC value for each site and sampling period during a natural population decline and after a 17-month recovery process from a disturbance. n= abundance, S= species richness.
Pree=Preemption. Cat= Catedrales, Jic=Jicarita, Fri=Frijoles, Roca=Roca Hacha

SITE	Base line	Decline n=9m^2				Recover n=3m^2
		4 months	9 months	13 months	17 months	
Cat	Pree	Pree	Pree	Pree	Pree	Null
AIC	64.895	58.452	60.7042	61.858	55.5826	31.5158
n	333	199	291	285	247	47
S	12	12	12	12	11	9
Jic	Pree	Pree	Pree	Log normal	Log normal	Zipf
AIC	58.0438	56.1624	59.5042	54.046	54.329	23.84 Pree 24.47
n	260	242	217	202	180	85
S	12	12	12	11	12	5
Fri	Zipf	Pree	Zipf	Zipf	Zipf	-
AIC	24.4675	23.386 Zipf 24.209	27.2561	25.8655	20.54132	-
n	96	76	74	67	55	8
S	5	5	7	6	5	2
Roca	Pree	Pree	Pree	Pree	Pree	Pree
AIC	84.434	90.617	82.212	82.604	87.572	27.877
n	655	578	561	559	471	75
S	14	14	14	14	13	7

Table 3. ANOSIM results comparing community composition between the baseline survey (June 2009) and after a 17-month population decline (November 2010). None of the results were significant.

Base line vs. 17-month population decline	Catedrales	Frijoles	Jicarita	Roca Hacha
Sample statistics (Global R)	-0.003	-0.046	-0.023	-0.088
Significance level of sample statistics	42.90%	79.10%	58.70%	91.20%
Number of permutations	999	999	999	999
Number of permuted statistics greater than or equal to Global R	428	428	586	911

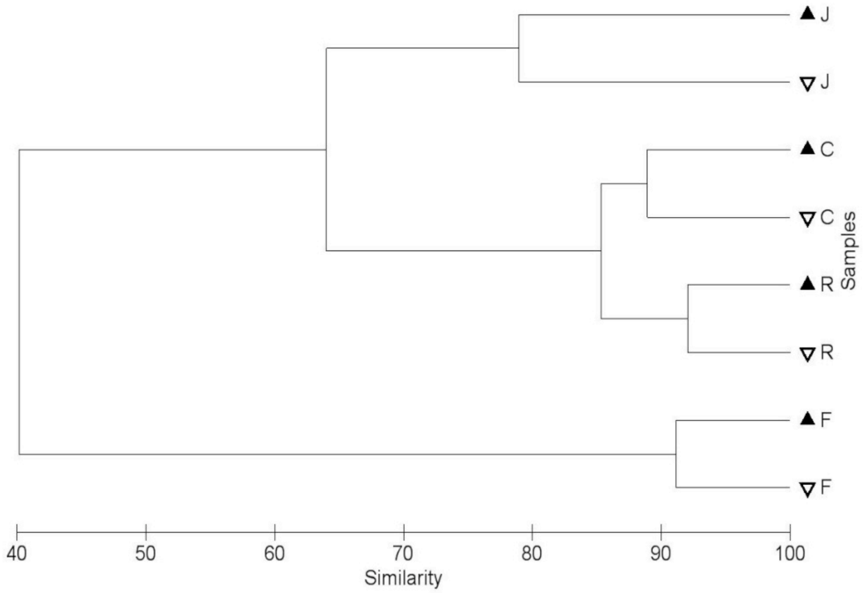

Figure 3. Similarity cluster analysis comparing community structure during the baseline in June 2009 (filled triangles) and after 17 months of population decline in Nov 2010 (empty triangles). C: Catedrales, J: Jicarita, F: Frijoles, R: Roca Hacha.

Table 4. ANOSIM results comparing community composition between reference and disturbed plots. A significant difference is indicated by a (*).

Reference vs. Disturbed plots	Catedrales	Frijoles	Jicarita*	Roca Hacha
Sample statistics (Global R)	0.324	0.358	0.903	0.172
Significance level of sample statistics	10.90%	10.5	0.50%	19.50%
Number of permutations	220	220	220	220
Number of permuted statistics greater than or equal to Global R	24	23	1	43

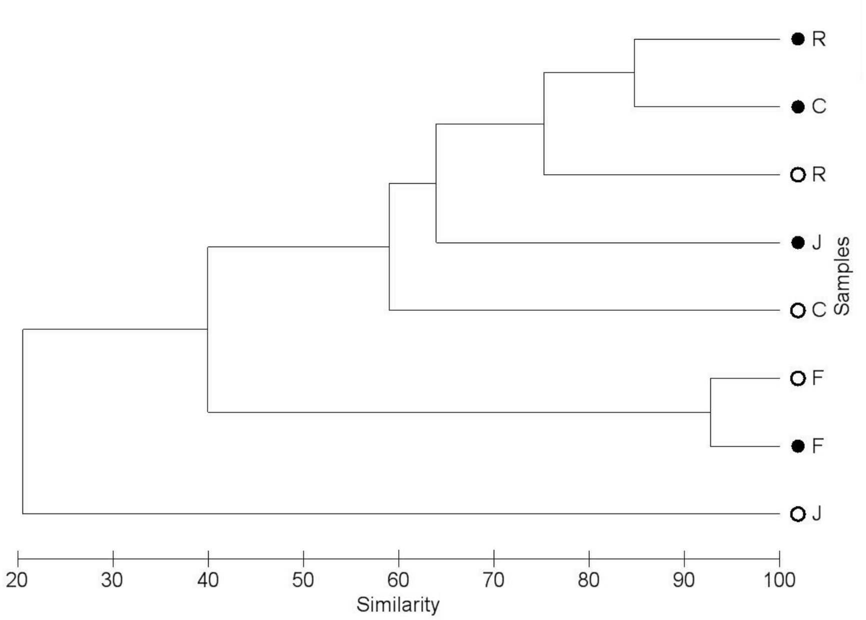

Figure 4. Similarity cluster analysis comparing reference plots (filled circles) with disturbed plots (empty circles) after a 17-month recovery period. C: Catedrales, J: Jicarita, F: Frijoles, R: Roca Hacha.

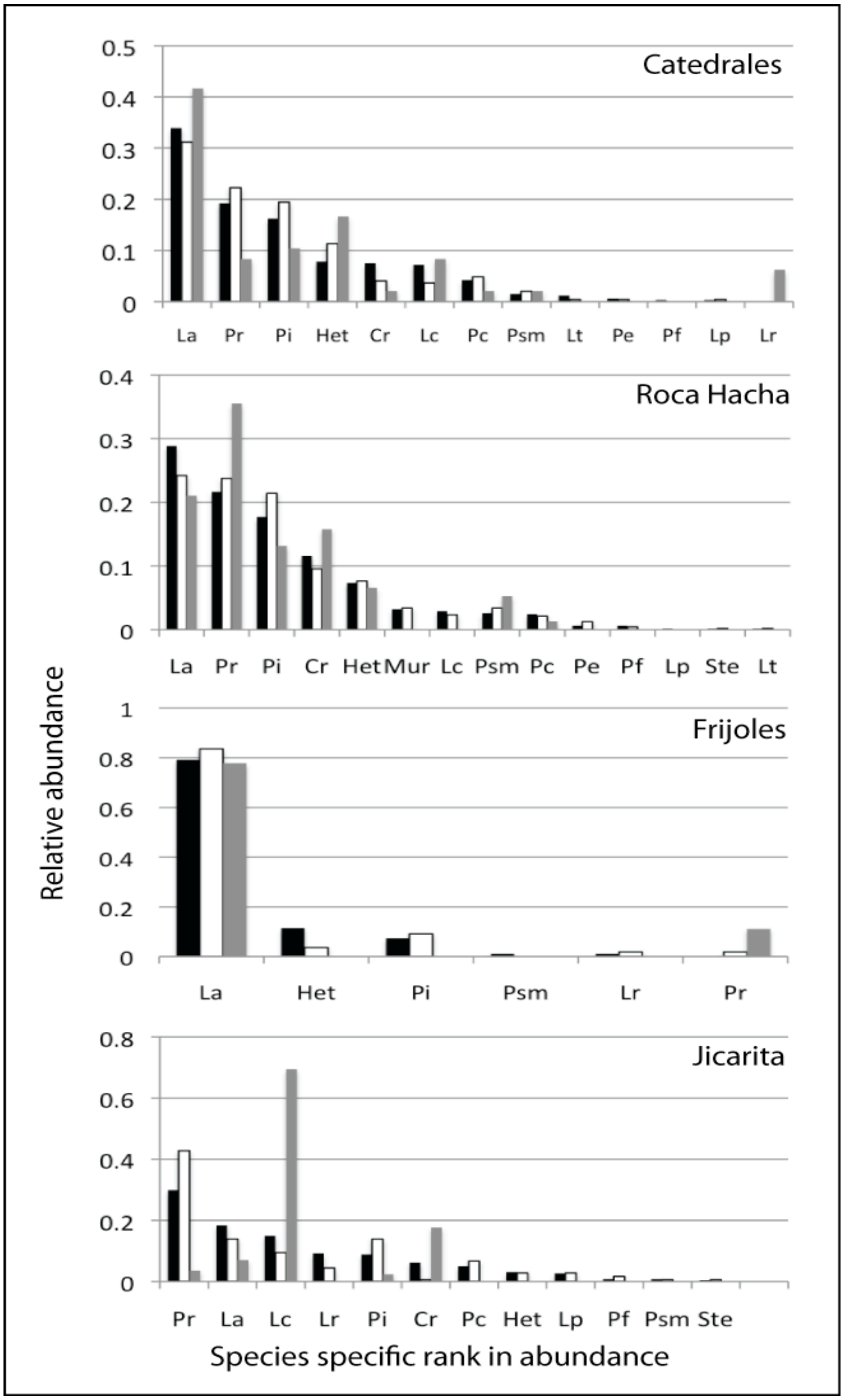

Figure 5. Abundance spectra for octocoral communities in four sites within Coiba National Park, Panama. Black: Base line, community in time 1; grey: community after 17-month population decline; white: community after 17-mothn recovery process from a punctuated anthropogenic disturbance. Cr: *Carrijoa riseii,* Het: *Heterogorgia sp.,* La: *Leptogorgia alba*, Lc: *Leptogorgia cofrini*, Lt: *Leptogorgia taboguilla,* Lp: *Leptogorgia pumilla*, Lr: *Leptogorgia rigida*, Mur: *Muricea austera.*, Pc: *Pacifigorgia cairnsi*, Pr: *Pacifigorgia rubicunda*, Pi: *Pacifigorgia irene*, Psm: *Psamogorgia arbuscula*, Pe: *Pacifigorgia eximia*, Pf: *Pacifigorgia firma*, Ste: *Pacifigorgia stenobrochis*

Discussion

The baseline data from Catedrales, Jicarita, and Roca Hacha best fit the Niche Pre-emption model. This model describes low species evenness, and it is usually seen in highly dominated communities, in resource poor environments, after an environmental disturbance, or in recently colonized environments (Guiller 1984; Fattorini 2005). A non-significant change in community composition in Roca Hacha, Catedrales, and Frijoles after a population decline was described by the RAD graphs and the Rényi plots, and confirmed in the ANOSIM and Cluster analysis. There was therefore no species turnover, and this can be seen in the abundance spectrum. The best-fit model changed for Jicarita, as it switched from Pre-emption to Lognormal, which is related to the Pre-emption model but with a greater number of rare species (Fattorini 2005). This change in best-fit model was supported by the low similarity in the cluster analysis between sampling time 1 and 5 relative to other sites.

Analyzing the effect of disturbance on species diversity, abundance, and community composition is more complex. Recovered plots did not regain the total number of species present in reference plots. As predicted by Mac Nally (2007), rare species were lost in a greater proportion than common species, which also decreased in abundance. The Octocoral community at Frijoles had the lowest initial population size, which could be related to the lack of recovery in cleaned plots shown by the RAD graphs. When the community structure was analyzed with the ANOSIM, however, there was not a significant difference between disturbed and undisturbed plots, and this was reflected in the Cluster graph. As in the other study sites, treated plots at Frijoles still had some species missing after a 17-month recovery process. The absence of these species had a larger effect on community recovery at Frijoles. One explanation could be the initial low species richness and abundance and a strong dominance by *Leptogorgia alba,* in both disturbed and undisturbed plots. In this case, the RAD was more sensitive to rare species than the ANOSIM permutation test, which gives more weight to the presence and hierarchy of the dominant species. This effect becomes clear in the abundance spectrum; the same dominant species is equally present in disturbed and undisturbed plots. In the case of Frijoles, the Rényi plot was a good community descriptor because it predicted the change in species richness and the non-significant change in species evenness after disturbance.

The RAD pattern of recovering plots in Jicarita did not change between sampling periods 3 to 5. This pattern did not resemble the pattern from reference plots, indicating that the community was assembling differently, with less species richness and less evenness as reflected in the Rényi entropy. The difference in community structure after disturbance was confirmed by the ANOSIM analysis. The reason for this significant difference can be seen in the abundance spectrum, which showed that Jicarita recovered with a different species composition, with a non-dominant species (*Leptogorgia cofrini*) becoming dominant after disturbance, and a previously common species (*Pacifigorgia rubicunda*) becoming rare. Jicarita was the site with the lowest similarity (Figure 3) and the only one that changed in best-fit model when comparing the effect of both population decline and disturbance. The fact that the similarity was lower after population decline could indicate that the community structure at Jicarita is more vulnerable to disturbance than the communities found at other study sites. The RADs and Rényi plots showed that there was a change in the community structure at Jicarita; the ANOSIM confirmed the extent of this change.

Although the ANOSIM analysis did not find a significant difference between disturbed and undisturbed plots in Roca Hacha and Catedrales, meaning that the disturbed plots recovered the original community structure, it is interesting to look at the RAD, Rényi, and Cluster graphs. With a simple visual inspection of the RAD and Rényi plots it can be seen that Catedrales had a better recovery process than Roca Hacha; the patterns formed by the red lines, representing disturbed plots, were more similar to the patterns indicated by the black lines, representing the un-disturbed plots. The opposite was shown, however, in the cluster analysis and by the best-fitting model. The cluster showed a higher similarity between disturbed and undisturbed plots in Roca Hacha (>80%) than in Catedrales (60%). In the same way, Roca Hacha fit the preemption model before and after disturbance, as opposed to Catedrales, which switched from Preemption to the Null hypothesis of the broken-stick model. The results from Catedrales are not consistent with Fattorini's (2005) proposal that communities in early stages fit best the niche pre-emption model, eventually shifting to the broken-stick as they changed.

The dominant species in Catedrales and Frijoles was *Leptogorgia alba,* a fast growing branched species with relatively high mortality and recruitment rates (Chapter 2). This species was able to maintain its hierarchical rank even after the punctuated disturbance, which was also the case of the hard coral *Montastrea annularis* in a coral reef community studied by Rogers (1992) after Hurrican Hugo in the Virgin Islands. This was not the case, however, for Roca Hacha, where *Leptogorgia alba* was dominant during the baseline survey, equally dominant with *Pacifigorgia rubicunda* after the population decline, and became second in rank after the disturbance.

Physical and biological reasons could explain the different recoveries across studied communities. Frijoles is located in the northeastern part of Coiba Island. Due to its geographical location, it is less exposed to currents than the other three sites, which are located in the southwestern part of the national park and are exposed to strong currents and swell. In addition, Jicarita, Catedrales and Roca Hacha are surrounded by deep cold water and are subject to local micro-upwelling. Currents, swell and local upwellings could bring viable larvae to a suitable and stable substratum. Therefore, Frijoles could be less exposed to viable larvae. Moreover, the overall natural population decline and the lack of diversity recover in disturbed plots could be due to environmental factors. The study period overlapped with El Niño and La Niña southern oscillation events. These temperature anomalies could cause a decrease in recruitment in octocorals, as reported in hard coral species (Glynn 2000).

The lack of diversity recovery may be explained by the lack of time to quantify slow growing species with infrequent reproductive cycles. Which could include species in the genera *Pacifigorgia* and *Muricea.* In contrast, the weedy species *Leptogorgia alba*, a fast grower with a relative high recruitment, was able to cope with a population decline and was not as severely affected by the disturbance as other species. Species within a genus can have different morphologies, with more or less resistance to disturbance; this can be the case in *Pacifigorgia rubicunda*, which seems more resistant than *Pacifigorgia irene*, and between *Leptogorgia alba* and *L. cofrini* which are more common and occur in patches compare to *L. rigida*. Another factor affecting community recovery at Frijoles could be the presence of the coral predator *Acanthaster planci*, this starfish in known to prey on hard corals (Glynn 1974), but it could also have a potential negative effect on octocoral recruits.

The effect of scale needs to be considered when analyzing the effect of the population decline and the disturbance. This study was done on a relatively small spatial scale. Octocorals occur in a patchy distribution making it difficult to study bigger plots without affecting the entire local community. This is the primary justification for having nine undisturbed monitored plots to study the effect of a natural population decline, and only three plots to study the effect of disturbance. The temporal scale of the study was great enough to see the first part of the recovery process, which interestingly, was different between sites. As a continuation of this study, the plots will be monitored annually to see the change of the entire community and the disturbed plots within it. The effect of spatial scale can be species-specific (Hill 2004) so it will be interesting to observe the behavior of the species present in the study site over a longer duration, and to determine whether there are clear indicator species of disturbance.

Finally, we believe the combination of methods we used were well adapted to quantify change in octocoral structure. Rank abundance distributions, abundance spectra and Rényi plots were useful in determining the changes in octocoral community structure, whilst ANOSIM and cluster analysis allowed determination of the extent of the change. These methods provide useful baseline data for research on the community ecology of octocoral species

Acknowledgements

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General conclusions and contributions to knowledge

Although octocoral communities have been studied in many places of the world, octocorals in the Tropical Estern Pacific (TEP) are exposed to different environmental factors, and this makes them different from species in other locations. Chapter 1 is the first review that compiles the scarce information available for TEP shallow octocoral species, reports the need for more studies, and suggests important topics for future research.

Chapter 2 is the first biological study of the rich octocoral community present in Coiba National Park, a recognized biodiversity hotspot in the TEP. This study reports an important natural population decline in four study sites and hypothesized that it was due to temperature anomalies during the study period (El Niño and La Niña southern oscillation events). This chapter also identifies *Leptogorgia alba* as an "r" selected species and *Muricea Austera* as a "K" selected species, and discuss the dynamics of 12 other species.

In Chapter 3, four different theoretical approaches were used to understand changes in the community structure after disturbance. Rank abundance distributions, abundance spectra, and Rényi plots were useful in determining the changes in octocoral community structure, while ANOSIM and cluster analysis allowed determination of the extent of the change. This chapter also reports that the natural population decline reported in Chapter 2 did not have a significant effect on the structure of the community. The original structure did change, however, after the anthropogenic disturbance.

Findings in chapter 2 and 3 have important consequences for future management of octocoral communities and their associated taxa, especially now, during a climate change period and while they face potential exploitation as sources for natural products.

Annex 1

Octocoral species reported in the Tropical Eastern Pacific

Based on:

1 Arizpe et al.1996
2 Bayer 1951
3 Bayer 1961
4 Baynes 1993
5 Bielschowsky 1929
6 Breedy & Cortes 2008
7 Breedy & Guzman 2002
8 Breedy & Guzman 2003a
9 Breedy & Guzman 2005
10 Breedy & Guzman 2011
11 Breedy & Guzman 2007
12 Breedy & Guzman 2008
13 Breedy 2001
14 Breedy et al. 2009
15 Brusca & Thomson 1975
16 Brusca 1980
17 Duchassaing & Michelotti 1864
18 Grigg 1977
19 Grigg 1974
20 Grigg 1975
21 Guzman et al. 2004
22 Guzman et al. 2008
23 Hickson 1928
24 Horn 1860
25 Prahl et al. 1986
26 Reyes et al. 1997
27 Robinson & Tomson 1991
28 Sincel Duarte 1991
29 Toponce 1973
30 Valenciennes 1846
31 Vann Oppen et al. 2005
32 Verril 1870
33 Verrill 1868
34 Williams & Breedy 2004

Annex 1. Octocoral species reported in the Tropical Eastern Pacific

Species	Ca	Me	Ni	ES	CR	Pa	Co	Go	E-C	Pe
Carijoa riisei						21,22				
Ellisella limbaughi †		31								
Eugorgia alba				14						
Eugorgia ampla		14				21,22				14
Eugorgia aurantiaca †		28, 27, 26, 31				14				
Eugorgia bradleyi					14	14				
Eugorgia daniana	14	14		33, 14	14	21,22,14	25	14	14	14
Eugorgia excelsa		14								
Eugorgia multifida		14								
Eugorgia nobilis		14	14		14	14				14
Eugorgia panamensis						14				
Eugorgia purpurascens			33			33				33
Eugorgia quercifomis				11						
Eugorgia rubens	11	11			14	21,22				11
Euplexaura nuttingi †		31								
Fungia curvata		16								
Heterogorgia cf. papillosa						22				
Heterogorgia verrucosa †		31				22	25			
Leptogorgia aequatorialis									5	
Leptogorgia alba		11		5	5, 6,12	17,5,21,22	25	11	5	
Leptogorgia californica		33								

* not found recently

† Reported as azooxanthelate

California (Ca), Mexico (Me), El Salvador (ES), Costa Rica (CR), Isla del Coco (IC), Panama (Pa), Colombia (Co), Galapagos(Go), Ecuador continental (EC), Peru (Pe)

Annex 1. Octocoral species reported in the Tropical Eastern Pacific, continuation

Species	Ca	Me	Ni	ES	CR	Pa	Co	Go	E-C	Pe
Leptogorgia chilensis	11									
Leptogorgia carva										
Leptogorgia cf. ramulus						21				
Leptogorgia christiae						22				
Leptogorgia clavata		24 *								
Leptogorgia cofrini					9	9, 22				
Leptogorgia cuspidata	11	32		32	11	11, 21,22				
Leptogorgia diffusa	11			11	11	11, 22	25			
Leptogorgia exigua		32	32		32	32				32
Leptogorgia flexis	11			11		11				
Leptogorgia florae						11				
Leptogorgia fruticosa						11				
Leptogorgia ignita					12					
Leptogorgia labiata		11				11 *				
Leptogorgia laxa		11			11	23, 11				
Leptogorgia obscura		11							11	
Leptogorgia parva						11*				
Leptogorgia peruviana										11
Leptogorgia pumila		11			11	11,22				11
Leptogorgia ramulus			11	32	11	11 *	25			11

* not found recently

† Reported as azooxanthelate

California (Ca), Mexico (Me), El Salvador (ES), Costa Rica (CR), Isla del Coco (IC), Panama (Pa), Colombia (Co), Galapagos(Go), Ecuador continental (EC), Peru (Pe)

Annex 1. Octocoral species reported in the Tropical Eastern Pacific, continuation

Species	Ca	Me	Ni	ES	CR	Pa	Co	Go	E-C	Pe
Leptogorgia ramulus (pink morph)						11				11
Leptogorgia regis					11	11, 22				
Leptogorgia rigida †		28,4, 26,31, 11		11	11	11				
Leptogorgia taboguilla					11	11				
Muricea appressa						22				
Muricea austera		28, 26				22				
*Muricea californica **	18,19,20	27, 26								
Muricea cf. appressa						21				
Muricea cf. austera										
Muricea cf. crassa						21				
Muricea cf. hispida						21				
Muricea crassa						22				
Muricea diffusa						22				
Muricea fruticosa †	19,20					21,22				
Muricea herbes		28,1,26								
Muricea purpurea						22				
Muricea rubusta							25			
Muricea squarrosa						22	25			

* not found recently

† Reported as azooxanthelate

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Annex 1. Octocoral species reported in the Tropical Eastern Pacific, continuation

Species	Ca	Me	Ni	ES	CR	Pa	Co	Go	E-C	Pe
Pacifigorgia adamsii		32,29, 15, 281, 26	32, 7		32, 7, 8	32, 7				32, 7
Pacifigorgia agassizii	7	32, 4, 26				32	25			
Pacifigorgia arenata		34								
Pacifigorgia bayeri					23, 8	13, 21,22				
Pacifigorgia cairnsi					8	9, 21				
Pacifigorgia catedralensis						21				
Pacifigorgia cribrum		34								
Pacifigorgia curta					6,8					
Pacifigorgia dampieri								34		
Pacifigorgia darwinii								23, 34		7
Pacifigorgia douglasii								23, 34		7
Pacifigorgia engelmanni		24, 32								
Pacifigorgia exilis	32	32, 34								
Pacifigorgia eximia					7,8	33,21,22	25			
Pacifigorgia ferruginea						21,22				
Pacifigorgia firma					8	21,22,9				
Pacifigorgia flavimaculata					8					
Pacifigorgia gracilis †	7	32, 31				32				

* not found recently

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Annex 1. Octocoral species reported in the Tropical Eastern Pacific, continuation

Species	**Ca**	**Me**	**Ni**	**ES**	**CR**	**Pa**	**Co**	**Go**	**E-C**	**Pe**
Pacifigorgia irene					3, 7,8	2, 21,22				
Pacifigorgia Lacerata					8					
Pacifigorgia media	7	33	33				25			
Pacifigorgia pulchra	7	32, 28, 26				7				
Pacifigorgia rubicunda					8	21,22				
Pacifigorgia rubinoffi						8				
Pacifigorgia rubripunctata								34		
Pacifigorgia rutila	7	33								
Pacifigorgia samarensis					8					
Pacifigorgia sculpta						22				
Pacifigorgia senta					8	21				
Pacifigorgia simbiotica								34		
Pacifigorgia smithsoniana						22				
Pacifigorgia stenobrochis †		32, 31	32		32, 7,8	30, 21,22				32
Pacifigorgia tabogae						23				
Pacifigorgia tupperi					8					
Pacifigoriga marviva						10				
Psammogorgia arbuscula †	31					21				
Psammogorgia arbuscula dowii †		31								
Psammogorgia teres †		31								

* not found recently

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Annex 1. Octocoral species reported in the Tropical Eastern Pacific, continuation

Species	Ca	Me	Ni	ES	CR	Pa	Co	Go	E-C	Pe
Psammogorgia variabilis					6					
Ptilosarcus longate					6					
Ptilosarcus undulates †		31								
Stylatula cf. longate					6					

* not found recently

† Reported as azooxanthelate

California (Ca), Mexico (Me), El Salvador (ES), Costa Rica (CR), Isla del Coco (IC), Panama (Pa), Colombia (Co), Galapagos(Go), Ecuador continental (EC), Peru (Pe)