Diversity and stability of coral systems in the Tropical Eastern Pacific

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CHAPTER ONE

CHAPTER TWO

CHAPTER FOUR

Résumé

Les récifs coralliens apportent un grand nombre de services écologiques mais sont en déclin à l'échelle mondiale. Pour assurer leur conservation, il est indispensable de détecter les changements à une échelle locale et de lier ces changements à des facteurs naturels ou anthropiques. De plus, pour prédire les changements de biodiversité dans les communautés marines sessiles, il nous faut étudier davantage les espèces peu connues pouvant pourtant jouer un rôle écologique important. Cette thèse combine des observations de terrain, des données de suivis à long terme, des expériences et de la modélisation pour détecter les changements dans le temps de la biodiversité des coraux durs (formant des récifs), pour mieux comprendre la biologie reproductive d'espèces communes d'octocoraux (coraux mous ne formant pas de récif), pour identifier les facteurs limitant le recrutement des octocoraux et pour estimer la stabilité et la résilience des communautés d'octocoraux selon divers scénarios océanographiques. La thèse se concentre sur le Golfe de Panama (GP) et le Golfe de Chiriquí (GC), tous deux au large de la côte pacifique du Panama. Pour mon premier chapitre, j'utilise des données de suivi provenant de 17 récifs sur une période de 12 ans et montre un déclin significatif de 4% de l'abondance corallienne à l'échelle nationale, du golfe, et du récif, de même que des changements significatifs dans la richesse spécifique et la structure des communautés à différentes échelles spatiales. Les tendances dans la diversité temporelle s'expliquaient par de petites mais fréquentes anomalies positives dans la température de l'eau de même que par sa variation annuelle. Les espèces de coraux sensibles à la chaleur étaient les plus affectées par ces changements. Pour les chapitres deux à quatre, je me concentre sur la biologie et l'écologie des octoraux, ignorés par la science depuis plus d'un siècle. Pour mon deuxième chapitre, j'ai étudié l'efficacité de la reproduction et la chronologie de trois espèces communes. L'efficacité de la reproduction ne corrélait pas avec

les dynamiques de population reportées au préalable; le développement des oocytes et la relâche des oeufs corrélaient avec la température de l'eau, et les espèces différentes relâchaient leurs oeufs à des saisons différentes. Pour mon troisième chapitre, j'utilise des expériences d'élimination à huit sites pour tester si le recrutement des octocoraux est lié à la densité d'adultes et à la disponibilité d'espace. Je montre que le recrutement est lié à la densité mais seulement si l'espace n'est pas limité, ce qui était le cas dans le GC. Pour mon quatrième chapitre, j'ai construit un modèle par chaîne de Markov basé sur les probabilités de transition au sein des colonies d'octocoraux, pour estimer la stabilité et la résilience des communautés des deux golfes. Les communautés du GC étaient trois fois plus stables que celles du GP; néanmoins, elles étaient à l'inverse 1.6 fois moins résilientes, de par le recrutement limité par l'espace seulement présent dans le GC. Cette thèse améliore nos connaissances de deux groupes d'espèces marines fondatrices retrouvés à travers l'Océan Pacifique de l'Est. Nos données serviront aussi de base comparative pour comprendre les tendances futures de la biodiversité marine, par exemple par rapport au fort évènement El Niño en 2015-2016.

Abstract

Coral systems, which serve a great variety of environmental services, are rapidly declining at a global scale. It is therefore essential that we detect changes at the local scale and attribute them to natural or anthropogenic factors. It is also important to increase our knowledge of understudied but ecologically important species in order to be able to explain and predict diversity changes in marine sessile communities. In this thesis I use monitoring, observation, experiments, and modeling to detect temporal diversity changes in scleractinian coral species (reef building corals). I also study the reproductive biology of common octocoral species (non-reef building corals), identify factors that limit octocoral recruitment, and estimate stability and resilience properties of octocoral communities under different oceanographic scenarios in the gulfs of Panama (GP) and Chiriqui (GC) off the Pacific Coast of Panama. In Chapter 1 I analyze coral reef monitoring data gathered from 17 reefs over a twelve year period and detect a significant 4% decline in coral species abundance at the national, gulf, and reef scales, as well as significant changes in species richness and community structure at different spatial scales. Temporal diversity trends were explained by small but frequent positive water temperature anomalies and annual variation. Heat-sensitive coral species were the most important contributors. Chapters 2 through 4 are devoted to studying biological and ecological aspects of octocoral species, which have been ignored by science for over a century. In Chapter 2 I study the reproductive output and timing of three common octocoral species, finding that reproductive output is not correlated to previously reported population dynamics; oocyte development and spawning are instead correlated to water temperature, and different species spawn in different seasons. In Chapter 3 I use clearing experiments conducted in eight sites to test whether octocoral recruitment is related to adult density and space availability. I find that recruitment is related to

adult density but only if space is not a limiting factor, as it is in the Gulf of Chiriqui. In Chapter 4 I create a Markov Chain model based on transition probabilities of octocoral colonies to estimate how stable and resilient octocoral communities are on each of the gulfs. I found that communities in the GC are three times more stable than the ones in the GP, but they are 1.6 times less resilient due to the space-limited recruitment seen only in this gulf. This thesis contributes to the scientific knowledge of the two main marine foundation species found in the Tropical Eastern Pacific. It also serves as a baseline for understanding future diversity trends, especially after the strong El Niño event in 2015-2016.

Preface

Thesis format

This thesis is presented in a manuscript-based style. Each chapter of the thesis corresponds to a manuscript on which I am the lead author. The individual manuscripts have been or will be submitted to scientific journals for publication. The document begins with a general introduction outlining the importance of the study, followed by the chapters. Linking statements explicitly explain the relationships between each chapter. The document finishes with a general conclusion section, which summarizes the context of the study as a whole and the contributions it makes to scientific knowledge. The document is formatted in APA style.

Chapter 1

Gómez, G.G., Gonzalez, G., Guzman, H. M. (Submitted). Multiscale change in reef coral species diversity and composition in the Tropical Eastern Pacific. *Coral Reefs*

Chapter 2

Gómez, G.G., Gonzalez, G., Guzman, H. M. (*Submitted*). Reproductive traits and their relationship with water temperature in three common octocoral (Anthozoa: Octocoralia) species from the Eastern Tropical Pacific. *Bulleting of Marine Science.*

Chapter 3

Gómez, G.G., Gonzalez, G., Guzman, H. M. (*to be Submitted*). The effect of population density, space availability, community composition, and season on octocoral recruitment in Tropical Eastern Pacific communities. *Journal of Experimental marine biology and ecology*

Chapter 4

Gómez, G.G., Guzman, H. M., Gonzalez, G. (*to be Submitted*) Stability and dynamic properties of octocoral communities and the effect of species deletions at different spatial scales. *Marine Ecology Progress Series.*

Contribution of authors

I am the lead author on the four manuscript-based chapters and the thesis itself; I developed the hypotheses, analyzed the data, and wrote the manuscripts. My advisors, Andrew Gonzalez and Hector Guzman (Smithsonian Tropical Research Institute), who co-authored the manuscripts, provided ideas for sampling and analysis, edited manuscripts, and provided research funds for field work.

The coral monitoring data for Chapter 1 was collected from the field by Hector Guzman and Carlos A. Guevara and provided to me by Hector Guzman. I collected data for Chapters 2, 2, and 4 with the assistance of C. Guevara. Based on H. Guzman's experience, I developed the laboratory method and protocol for octocoral dissections in Chapter 2.

Statement of originality

All the work presented in this thesis is original and has not been previously published unless otherwise indicated by references. This thesis integrates monitoring, observation, experiments, and modeling to study the diversity and biological properties of the two main marine foundation species in the Tropical Eastern Pacific, providing new contributions to science in each chapter:

- Using monitoring data, Chapter 1 offers a first description of diversity changes in community composition in a multi-scaled framework at several reefs located in different oceanographic conditions within the Tropical Eastern Pacific.
- Through observation, Chapter 2 provides a first study of the reproductive biology of three common octocoral species in three different genera.
- Through experiments, Chapter 3 provides a first study of demographic and environmental factors limiting octocoral recruitment within the Tropical Eastern Pacific.
- Using a Markov Chain model, Chapter 4 offers a first estimate of the stability and resilience of octocoral communities and the effect of species deletions at different spatial scales.

Ethics statement

All research included in this thesis followed safety regulations imposed by McGill University and the Smithsonian Tropical Research Institute. Research permits were obtained from Panamanian Authorities (Ministerio de Ambiente de Panama, previously known as Autoridad Nacional del Ambiente) permitting us to work in protected areas and collect samples from Las Perlas Archipelago during the entry study.

Acknowledgments

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I'm especially grateful to my advisors, Andrew Gonzalez and Hector Guzman, for all the guidance, ideas, and feedback they provided during the development of my thesis. I also thank my supervisory committee, Frédéric Guichard and Jonathan Davies, for their feedback on the general hypothesis, statistical methods, and interpretation of results.

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Being safe while scuba diving in harsh conditions was possible thanks to the thorough training and equipment provided by Raul de Leon, diving safety officer at STRI, and the optimal conditions provided by Kevan Mantel, technical diver at Dive Base Coiba, while diving in Coiba. I also thank Kevan for sharing his method for installing fix bars with underwater cement and helping Carlos and I during the installation process.

I want to thank Reineldo, Augusto, Alexis, and Chava, who are in charge of research vessel operations at Naos laboratories (STRI), for getting Carlos and I safely to study sites in Las Perlas Archipelago.

Y de todo corazón le agradezco a mi familia, Mami, Papi, Juli y Javi, por tenerme paciencia y apoyarme en cada paso de mi carrera académica. Su constante apoyo fueron la fuerza que necesité para completar cada una de las metas que me permitieron terminar con éxito esta etapa de mi vida. Javi, gracias por lograr que conformáramos un hogar durante esta época de estudio intenso. Juan Abelardo Carles, gracias por apoyar siempre a mi familia y por tenderme una mano en un momento crucial.

No puedo negar que escribir la tesis fue más divertido con la compañía de mi perrita Pacha y mis gatas Siris y Alarmita, que estuvieron a mi lado mientras escribía las más de 200 páginas de este documento. De la misma manera, los momentos de descanso fueron más productivos con la compañía de mis adorados sobrinos, Alejandro, Erik y Martín.

Figure Captions

Chapter 1

Figure 1.1. Location of the 17 monitored reefs in the Pacific Panama (a). (b) *In situ* water temperature C^{o} in the GP (blue) and in the GC (red): mean, maximum (up-pointing triangles) and minimum (down-pointing triangle), number of warm days (> 30 C^{o}), + 1 C^{o} and + 1.5 C^{o} anomalies, and days away from maximum monthly mean (MMM). Mean as solid lines and standard deviation as dashed lines.

Figure 1.2. Expected species richness per year based on species accumulation curves. Individual reef trends in black lines, modeled trend for each gulf in blue lines and red for the entire study region, Pacific Panama. Shaded coloration for model standard error. There was a 2% annual decline in expected species richness in the Gulf of Panama.

Figure 1.3. Temporal trends in species abundance (MAFA). Individual reef trends in black lines, model results for each gulf in thick black lines, modeled trend for each gulf in blue lines and red for the entire study region, Pacific Panama. Shaded coloration shows the model standard error. There was a 4% annual decline in species abundance at the country and at the gulf scales, with variation within individual reefs.

Figure 1.4. Temporal decline in beta diversity indicates significant changes in community structure at all studied scales. Individual reef trends in black lines, model results for each gulf in thick black lines, modeled trend for each gulf in blue lines and red for the entire study region. Shaded coloration shows model standard error.

Figure 1.5. Components of temporal beta diversity. (a) Relative contribution of species replacement and changes in abundance (%) to the total temporal beta diversity for the GC and the GP (b), where most changes were due to a reduction in species abundance. Mean and temporal variation of the contribution of each species to temporal beta diversity changes in the GC (c) and the GP (d). These contributions were correlated between gulfs and not correlated with the species relative abundance. Species full names in Table 1.3.

Figure 1.6. Redundancy analysis of the correlation between changes in diversity metrics (red arrows): MAFA (species abundance), Jaccard (temporal turnover) and Exp.S (Expected species richness) with temperature parameters as explanatory variables (black arrows): a1 (anomalies above 1 ^{o}C), a1.5 (anomalies above 1.5 ^{o}C), dd (degree days), hot (number of days above 30^{o}C), MMM (Maximun Monthly Mean), vc (variation coefficient), mean, maximum and minimum water temperature recorded from *insitu* temperature loggers. Model for the entire study area (a), from five reefs in the Gulf of Chiriqui (b) and from three reefs in the Gulf of Panama (c).

Chapter 2

Figure 2.1. Colony and large oocytes inside gastro vascular cavity of a) *Leptogorgia alba*, b) *Pacifigorgia ferruginea* and c) *Muricea austera* at 15 m of depth in the Gulf of Panama, Tropical Eastern Pacific.

Figure 2.2. Temporal variation of reproductive traits; Colony fecundity (proportion of polyps with oocytes), reproductive output (number of oocytes per polyp), and oocyte size (diameter) for

three common octocoral species off the Pacific coast of Panama: *Leptogorgia alba*, *Pacifigorgia ferruginea* and *Muricea austera.* Notice axis scales are different among species.

Figure 2.3. Reproductive season annual trend (red line) of three common octocoral species off the Pacific coast of Panama. Trend calculated from MAFA (Minimum-Maximum Autocorrelation Factor analysis) taking into account the temporal variation of colony fecundity (proportion of polyps with oocytes), reproductive output (number of oocytes per polyp), and oocyte size (diameter). HOBO water temperature monthly mean (black solid line) and off Elefante Island at 15 m of depth, from March 2015 to February 2016.

Chapter 3

Figure 3.1. General GLM model (pooling all species together) with a significant interaction between number of recruits as a factor of adult density, geographic location (Gulf), and treatment (cleaned or control). The general correlation between recruitment and colony density was found for experimental and control plots in the Gulf of Panama, but was only observed for experimental plots in the gulf of Chiriqui. Space could be more limiting to recruitment in the GC due to higher densities in control plots.

Figure 3.2. Species specific GLM models for the interaction between number of recruits as a factor of mean colony density, geographic location (GC = orange, GP = cyan), and treatment (cleared = solid, control = dashed). There was a significant three-way interaction for *L. alba* and *L. cofrini*. The interaction with treatment and abundance was found for *P. irene*. In *C. riisei*, *P.*

cairnsi, and *P. rubicunda* only the correlation between recruitment and mean colony density was significant.

Figure 3.3. Mean daily temperature timeline during each sampling period. Notice the temperature fluctuations that take please in all the sites from January to June (season 2). Season 3 took place during a strong El Niño event. San Telmo and Elefante are sites in the Gulf of Panama, and Jicarita, Catedrales, Roca Hacha, and Prosper are in the Gulf of Chiriqui. Doted line represents maximum and minimum temperatures.

Figure 3.4. Mean number of recruits per m^2 during each sampling season. *L. alba* had a significant peak from January to June 2015, as did *C.riisei*, but only in the Gulf of Panama. *L. coffrini* had a decline in recruitment during the last season, which coincided with an El niño ENSO event.

Chapter 4

Figure 4.1. Transition probabilities (a), stability properties (b) and predictability (c) of octocoral communities in the Gulf of Panama (GP, cyan) and the Gulf of Chiriqui (GC, orange). In general octocorals in the communities had high persistence rate, with low probabilities of been replace (overgrown) by another octocoral. However, colonization and disturbance rates were higher in the GP (a). These differences made the GC be more stable (greater recurrence time) but less resilient (slower turnover time) (b). The faith of a point randomly taken from the stationary community was more predictable in the Gulf of Chiriqui (c).

Figure 4.2. Species-specific transition probabilities from the community transition matrices of octocoral communities in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Species are displayed in decreasing order of abundance as in Table 4.1. Probability of disturbance, probability of persistence, probability that the species is replaced by another octocoral, and probability that the species replaces another octocoral.

Figure 4.3. Species-specific transition probability of octocoral colonization in spaces previously occupied by sponges (green), crustose coralline algae (magenta) or algae turf (yellow) in communities located in the Gulf of Chiriqui and the Gulf of Panama. Species are displayed in decreasing order of abundance as in Table 4.1.

Figure 4.4. Species-specific dynamic properties of octocorals in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Turnover rate, turnover time, recurrence time and Predictability, quantified by the entropy of the species column in the transition matrix. Species are displayed in decreasing order of abundance as in Table 4.1.

Figure 4.5. Proportional change of community evenness after species removal at three spatial scales: study area, gulfs and individuals reefs. The effect of the removal of each species is displayed in decreasing order of abundance as in Table 4.1.

Supplemental

Supplemental 1.1. Species accumulation curves for each reef on the Gulf of Panama and the Gulf of Chiriqui. Black lines indicate the first monitoring year, red lines the last monitoring year (2012) and grey lines the years in between. Confidence intervals of each year are represented with dashed lines. In open circles Chao estimate (Chao, 1987) and its confidence interval for the total number of estimated species, including unseen ones (black for first year and red for last year of monitoring).

Supplemental 1.2. Timeline of scleractinian species percent cover on each studied reef within the Gulf of Panama (GP) and the Gulf of Chiriqui (GC).

Supplemental 1.3. Temporal variation in Rényi diversity profiles for each reef; species richness had a higher temporal variation than species evenness, except for Jicarita. Most reefs had a steep decline from species richness to evenness, reflecting the high degree of domination by a single species, to a lesser extent in Jicarita and Canales reefs.

Supplemental 3.1. Example of mosaic images used for the analysis. a) Experimental plot cleared from sessile organisms competing for space, see small recruits in white circles, and b) Control plot. Circles and numbers were used to quantify octocoral colonies within study sites.

Supplemental 3.2. Recruitment timeline (mean and standard error) for common octocoral species on the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan).

Supplemental 3.3. Water temperature timeline in coral reefs (10 m) and octocoral communities (15-20 m) in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Note water temperature decreases at the beginning of each year at both gulfs in octocoral communities and not in coral reefs. Water temperature data for coral reefs (Chapter 1) and octocoral communities obtained by *insitu* HOBO logger stations recoded every 30 minutes.

Supplemental 4.1. The dynamic properties of each octocoral species, as well as the dynamic properties of the entire community were quantified using the following Hill et al. (2004) formulations where: "P" is the transition matrix of the stationary community (Supplemental 4. 2), "*j"* is the column of species *j*, "*i"* is the row of species *i, "s"* is a non-octocoral state, called "bare rock" in Hill et al. (2004), "p" is an entry in any given point of P, "w" is the matrix dominant eigenvector normalized to sum to 1, "λ_1" and "λ_2" are the largest and second largest eigenvalues of P.

Supplemental 4. 2. Transition matrices of the stationary community for each gulf and each reef. Warmer colors indicate higher transition values. Temporal mean ± standard error. Crustose coralline algae (CCA), algae turf (Turf).

General introduction

Diversity trends in the anthropocene

The term “anthropocene” refers to the last two centuries (Crutzen, 2006), during which planet Earth left its natural geological epoch as a result of the high-impact of human activities, which are now shaping the earth’s climate and resources (Steffen et al., 2007). The industrialization of the global economy during this epoch has triggered the sixth mass extinction, which is driving major worldwide ecological changes (Dirzo et al., 2014). Globally, one-third of reef building corals are at risk of extinction (Carpenter et al., 2008), with many coral reefs undergoing major changes in their community composition (Hughes et al., 2003).

Biological diversity has decreased globally due to habitat destruction, pollution, overharvesting, climate change, and invasive species (Alcamo et al., 2005). Coral species are threatened by anthropogenic factors acting at different spatial scales; at a global scale corals are affected by global warming and ocean acidification, which causes coral bleaching and reduced calcium carbonate accretion (Hoegh-Guldberg et al., 2007); at the regional scale they are affected by overfishing and water pollution; and at the local scale they are affected by destructive practices, such as anchoring, trawling, and explosives, which destroy the entire habitat (Pandolfi et al., 2003). Destruction of natural ecosystems is happening so fast that a species can be threatened or extinct even before it is described and studied, especially in remote areas such as marine environments.

It is difficult to quantify the effect of such losses (Worm et al., 2006). A reduction or change in species richness can be followed by species turnover in natural communities, which can lead to changes in ecosystem services (Cardinale et al., 2012). This becomes particularly important in foundation species, whose life histories are linked to many other taxa (Dayton, 1972). Therefore, studies of temporal trends in diversity are crucial for forecasting future changes in community structure and ecosystem functioning (Dornelas et al., 2013).

The world's oceans cover 70.8% of the planet (Snelgrove, 1999) and serve a variety of purposes. FAO estimates that the oceans assure the livelihood of 10-12% of the world's population and provide the food supply for billions of people; marine life accounts for 16% of the animal protein ingested globally (FAO, 2014). Marine ecosystems afford coastal protection, prevent erosion, and provide water purification (Adger et al.,2005; Danielsen et al., 2005) and carbon storage (Jiao et al., 2010). They also deliver cultural benefits through recreation, sustaining a multibillion-tourism industry (Moberg & Folke, 1999). Most of the ocean's diversity and services are associated with shallow productive areas, such as coral ecosystems (Moberg & Folke, 1999). However, marine biodiversity loss is increasing and this is compromising the ocean's capacity to provide food, maintain water quality, and recover from disturbances (Worm et al., 2006).

Although it seems like the damage is done, decreasing trends in diversity are still reversible (Worm et al., 2006). Therefore, it is worth increasing efforts to study diversity changes and increase knowledge about lesser-known fauna before it is too late. This is especially important in tropical marine ecosystems, which are underrepresented in meta-analyses (Gonzalez et al., 2016).

The detection and attribution of biodiversity change is relatively complex; the conclusions depend on scale and location (Gonzalez et al., 2016). Therefore, it is important to assess changes in diversity at different spatial scales using standardized protocols (Gonzalez et al., 2016). Diversity can be quantified using different metrics. Alpha diversity, which describes a natural community by its species richness and their abundance, can be quantified using a variety of metrics ranging from the number of species per unit area to evenness of species abundance in the community (Rényi, 1961). Beta diversity describes the variation in community composition in space or in time (Legendre & Salvat, 2015). The diversity of a community is expected to increase its stability, which can be measured by the dynamics of the community and its ability to recover after disturbance (Gonzalez & Loreau, 2009).

Stability and its different meanings

The relative stability and resilience of a community depends on how these terms are defined. Ives and Carpenter (2007) define stability in the following ways: how many alternative stable states are possible in a community and how prone the community is to change between these states, for example, the likelihood of a coral reef turning into an algae-dominated reef (Fung et al., 2011); the fluctuations in population dynamics, either periodical or chaotic, that are the results of predator-prey interactions; how susceptible a community is to invasive species; how susceptible a community is to species extinctions, which can cause secondary extinctions; and a community's relative resistance to disturbance and its ability to recover (resilience). A disturbance can be a one-time only event (pulse), such as a hurricane, which allows the community to recover a previous state, or it can be an ongoing state (press), such as global warming, to which the community may need to adapt (Rowan, 2004).

Stability of coral systems

In Coral reef, as well as in other tropical subtidal communities, the presence of alternative stable states is associated with a lack of strong annual changes in the physical environment (Knowlton 1992). These alternative states are associated to different ecosystem process, functions and feedback mechanisms (Scheffer et al. 2001, Mumby et al. 2007). Corals inhabit relatively stable environments, however, when a strong environmental changes happens, such as a water warming by a strong El Niño event, coral cover declines due to bleaching associated coral mortality (Brown, 1997). When this occurs the entire community may switch to an algae dominated state (Nyström et al. 2000, Hughes et al. 2003, Mumby et al. 2007). This algae dominated state will be stable if the herbivore fish population cannot control the rapid growth of algae (Hoegh-Guldberg, 2007), or if conditions do not favor coral regrowth (Díaz-Pulido et al. 2009). Strong pressure from human-related activities, such as global warming, overfishing, pollution and over-harvesting, may affect the resilience of coral reef ecosystems impairing their ability to resist phase shifts and regenerate after disturbances have diminished over time (Bellwood et al. 2004). These changes may also lead to decreases in the ecosystem goods and services, such as fisheries, tourism and aesthetic cultural values (Moberg & Floke, 1999).

Some softcorals populations (octocorals), such as the red coral (*Corallium rubrum*) in the Mediterranean Sea, tend to be relatively stable and resilient, even in the presence of global warming and strong harvesting (Santangelo et al. 2007). However, in the presence of drastic mortality events, some species (*Paramuricea clavata*) may reach a new equilibrium at lower densities than at pristine values (Santangelo et al. 2015). Wainbauer et al. (1996) relate the stability of a softcoral species (*Eunicella cavolini*) off the coast of France to habitat type, with differences in light intensity, substratum occupation and intensity of water movement.

Corals as foundation species

Dayton (1972) introduced the term "foundation species" to describe *species that define much of the structure of a community by creating locally stable conditions for other species and modulating and stabilizing fundamental ecosystem processes*. As habitat builders, these species have an important role in structuring a community and can be used to study the stability and resilience of an ecosystem in a simplified approach (Dayton, 1972). Losses of foundation species alter trajectories of succession, which can lead to novel ecosystems (Ellison et al., 2005) and alternative stable states (Norström, 2009). Marine foundation species include sea grass (Franssen, et al. 2011), mangroves (Ellison, et al. 2005), and corals (Hinz, 2016; Sanchez, 2016).

There are two distinct main types of corals: hard and soft (Table i1). Hard corals (Class Anthozoa, subclass Hexacorallia) accumulate calcium carbonate and become the basic building blocks of tropical coral reefs. Most hard corals depend on a symbiotic relationship with zooxanthellae algae (dinoglagellates), which provides most of the energy that the coral needs (Dubinsky & Jokiel, 1994). This association obligates hard corals to inhabit shallow clear water with enough light penetration for photosynthesis. These corals are generally found within a small water temperature range. Warmer and colder temperatures result in coral bleaching, which happens when the coral loses its zooxanthellae and dies (Brown, 1997). Drastic temperature changes are usually linked to El Niño and La Niña ENSO events (Hidaka, 2016).

Soft corals (Class Anthozoa, Subclass Octocorallia), on the contrary, do not accumulate calcium carbonate and do not form reef structures. They attach to the substrate using a relatively small holdfast with most of their biomass on the water column, resembling a tree in a forest (Sanchez, 2016). Soft corals have flexible colonies that allow them to cope with strong water movement without breaking. Most soft corals lack the zoozanthellate association; they filter feed and actively trap food resources with their tentacles (Van Oppen et al., 2005) and are therefore not limited to shallow clear water. They are found in shallow, deep, cold, and warm locations.

The Tropical Eastern Pacific:

A natural laboratory to study diversity changes in foundation species

The Tropical Eastern Pacific (TEP) is the biogeographic region that ranges from the Sea of Cortez to northern Peru (Robertson & Cramer, 2009). Its shallow areas are inhabited by coral systems that are relatively simple and can be used as models for studying biodiversity (Cortés et al., 2017). Although simple, this area hosts biodiversity hotspots (Guzman et al., 2004, 2008) and high levels of endemism (Guzman et al. 2008, Hickman 2009).

Within the TEP there are two types of foundation species that comprise the main sessile marine communities: coral reefs, with 27 scleractinian coral species, and octocoral communities, with 64 reported species (Cortés et al., 2017). There are important differences between these sessile marine ecosystems (Table *i*1), which do not spatially overlap in this area. The most outstanding difference, however, is the high number of studies on coral reefs (Cortés, 2003; Glynn et al., 2016) and the relative lack of studies on octocoral communities (Gómez, et al., 2014; 2016).

Coral reefs in the TEP are composed of a reef frame dominated by *Pocillopora damicornis* (Maté, 2003). These frames can extend several kilometers, so coral diversity tends to be low (Guzman et al., 2004). The reefs are located at about 10 m depth as most scleractinian corals are limited to calm, shallow, and clear water due to their association with zooxanthellae symbiodinium (Maté, 2003). In contrast, octocoral communities are very diverse, with at least 14 species coexisting in a square meter (Gómez et al., 2014). These communities are usually found at a depth gradient from the intertidal to the deep water, sometimes even occurring as mesophotic reefs (Breedy & Guzman, 2013). These communities are usually found in very active water where they are subject to breaking waves, surges, and strong currents (Gómez et al., 2014).

Both coral reefs and octocoral communities in the TEP provide a wide variety of ecosystem services including food production, coastal protection, and support for the growing tourism industry (Cortés & Reyes-Bonilla, 2017; Taylor et al., 2003). Additionally, some octocoral species from the area (including *Muricea austera* and *Leptogorgia alba* (Gutierrez et al., 2005, 2006) have been described as the source of active compounds to defeat cancer, malaria, Chagas disease, and leishmaniasis (Boya et al., 2012). The production of such compounds has been linked to an octocoral-associated bacteria (Boya et al., 2012) that is described as the coral's chemical defense against predators (Epifanio et al., 2000).

Despite all the services these two groups of foundation species provide (Cortés & Reyes-Bonilla, 2017; Sanchez, 2016) they are under a variety of direct and indirect stressors at different spatial scales, especially with non-efficient management of protected areas (Alvarado et al., 2017). At the very local scale, coral reefs and octocoral communities are subject to direct damage through anchoring and destructive fishing practices, such as trawling and the use of explosives (Alvarado et al., 2017; Cortés & Reyes-Bonilla, 2017); at a medium scale, they are damaged by overfishing (Guzmán et al., 1991), water pollution (Glynn et al., 1984), sedimentation (Guzman & Holst, 1994), algae blooms (Guzmán et al., 1990), and disease outbreaks (Sánchez et al., 2011, 2014; Ward et al., 2006); and at a more regional scale, reefs are damaged by increases in water temperature (Manzello et al., 2017), ocean acidification (Manzello, et al. 2017), and increases in storm frequency and strength (Done, 1999; Woodley et al., 1981; Yoshioka & Yoshioka, 1987). Some octocorals, however, have been found to be more resistant than scleractinian reef building corals to bleaching and ocean acidification (Enochs et al., 2016; C.E. Gómez et al., 2015; Sanchez, 2016).

Pacific Panama as a study area

The Pacific coast of Panama, located within the TEP, is a convenient location in which to study stability and diversity changes in marine sessile communities. It is divided in two distinct gulfs at the same latitude with extensive coral reefs and diverse octocoral communities: the Gulf of Panama (GP) and the Gulf of Chiriqui (GC). These gulfs are semi-open areas separated by a *ca.* 100 km wide peninsula. The GC presents a nearly constant sea surface temperature (SST) of 28 ^{o}C, low $NO^{-}_{3,}$ and chlorophyll *a* concentrations near the surface all year around (D'Croz L & O'Dea, 2007). In contrast, the GP has drastic seasonal temperature changes of 10 ^{o}C and high concentrations of NO^{-}_{3} and PO^{3-}_{4} in the upper layer during the dry season (December to March), which causes the chlorophyll *a* to rise from less than 0.34 to 1.5 mg m^{-3} (D'Croz L & O'Dea, 2007). These differences in seasonal productivity are due to the presence of a wind-driven seasonal upwelling that only occurs in the GP (Xie et al., 2005) (Table *i*2).

Coral reefs in Panama

Coral reefs in both the GP and the GC are composed of reef frames with low species evenness (Guzman et al., 2004, 2008). *Pocillopora* is the main reef constructor in shallow areas (Maté, 2003) and *Porites* and *Pavona* are the primary builders at greater depths (Glynn et al., 1972). There are 22 coral species reported for the GC and 20 for GP (Guzman et al., 2004, 2008); species in the genera *Pocillopora*, *Porites*, *Pavona*, *Psammocora*, and *Millepora* are the most common (Maté, 2003). These reefs are located at about 10 m depth and rest on basaltic foundations. In the GC, reefs have vertical buildups of 10-12 m and are as much as 5,600 years old (Glynn & Macintyre, 1977). In the GP, reefs have vertical buildups of 5.6-6.1 m and maximum ages of 4,500 years (Maté, 2003).

The extreme warming event that took place in 1982/83 affected corals in the GP and the GC. Water temperature rose above 29 °C, killing 75% of hermatypic corals in the GC and 85% in the GP (Glynn, 1990). Age estimates for the massive corals killed during this event suggested that a disturbance of this magnitude had not occurred in the past 200 years (Glynn, 1990). The similar ENSO event of 1997/98, during which the temperature rose to 29 °C in the GP and more than 30 °C in the GC for over three weeks, caused only 13.1% coral mortality in the GC and no mortality in the GP. The upwelling season in the GP delayed the effects of the 1982/83 warming, however Pocilloporid mortality in this gulf was 92%, compared to 75% in the CG (Maté, 2003). The second warming (1997/98) only affected corals in the GC (Glynn et al., 2001), with more impact in off-shore sites such as Montuosa, Jicaron, and Jicarita islands. In general, the most affected species were *Millepora boschma, Millepora platyphylla, Millepora intricata,* and *Porites panamensis* (Glynn, 1990; Glynn et al., 2001). The species *Pavona gigantea* and *Psammocora stellata* showed little or no damage (Glynn, 1983, 1984). Hydrocorals were the most affected, with two local extinctions: *M. boschma* and *M. platyphylla* (Maté, 2003). As noted, different ecological and biological aspects of scleractinian corals in Panama have been studied, however, community changes in the absence of strong El Niño events, but in the presence of small but constant warming, still needs to be addressed.

Octocoral communities in Panama

Little is known about the octocoral species and communities inhabiting the TEP (Gómez et al., 2014; Sanchez, 2016). At the beginning of the present century a regional initiative to study these species for the first time began with extensive taxonomic reviews (Breedy & Guzman, 2002, 2007, 2011, 2015, 2016; Breedy et al., 2009) and 28 new species were discovered and named. During the same decade several reports described community structure in Colombia (Sánchez & Ballesteros, 2014) near the islands of Gorgona (Sánchez et al., 2014) and Malpelo (Sánchez et al., 2011), and in Mexico (Abeytia et al., 2013). Following the reviews, I study, for the very first time the population dynamics of 14 common species in Pacific Panama (Gómez et al., 2014), reporting a 25% decline in species abundance in 17-month period (C. G. Gómez et al., 2015).

Octocorals from Panama can be divided into two groups based on their dynamics: an r-selected group with high recruitment and mortality rates and low survivorship, and a k-selected one, with high survivorship and low recruitment and mortality rates (Gómez et al., 2014). Recruitment of new individuals is an important factor that limits populations (Hixon et al., 2012; Kuffner et al., 2006; Yoshioka, 1996). In octocorals, recruitment can be related to the mode of reproduction (Kahng et al., 2011) and limited by demographic (Yoshioka, 1996) or environmental factors (Birkeland, 1974; Grigg, 1988; Opresko, 1974). As foundation species, octocoral communities are ecologically important, however, the stability and resilience of these communities is still unknown.

Thesis objectives and hypotheses

Through monitoring, observation, experiments, and modeling this thesis studies trends in the diversity and stability of coral and octocoral communities at different spatial scales. It also contributes much needed knowledge about the biology and ecology of octocorals, which are still largely unstudied (Figure *i*1).

The first chapter uses coral reef monitoring data from 17 reefs along the Pacific coast of Panama to detect temporal diversity changes in scleractinian corals (reef forming coral species). It attributes those changes to environmental factors and identifies the species with higher contributions to detected trends. During the monitoring period for which I have data (2000-2012) no major El Niño warming happened, therefore, I hypothesize that in the absence of strong El Niño warming events measures of the structure of the scleractinian coral community will not change significantly, with no apparent differences between the GP and the GC (Chapter 1).

The second chapter aims to increase our knowledge of basic biological aspects of octocoral species, such as the temporal variation of reproductive traits (fecundity and output), and estimates a potential spawning time in three common species of three different genera. I hypothesize that the reproductive output of these species relates to their life history strategies (r-k spectrum). I expect that species with high recruitment rates (*Leptogorgia alba*) will also have high reproductive output, and species with low recruitment rates (*Muricea austera*) will have low reproductive output.

The third chapter aims to detect demographic and environmental factors limiting octocoral recruitment. I hypothesize that recruitment is related to adult abundance, as seen in octocoral species at different locations (Yoshioka, 1996), and that is also related to the space available for colonization (Birkeland ,1974; Opresko, 1974), which can be also occupied by sponges, tunicates, crustose coralline algae, and algae turf (Gómez et al., 2014).

Finally, the fourth chapter quantifies stability and resilience properties of octocoral communities and uses information from Chapters 2 and 3 to explain the observed patterns. Octocoral species are present on both gulfs (Table *i*3), however, the gulfs have different environmental patterns (Table *i*2), therefore, I hypothesize that octocoral communities present in the gulf with stable temperature and nutrient levels through the year (Gulf of Chiriqui) will be more stable than communities inhabiting the Gulf of Panama, which has significant annual changes in temperature and nutrient levels.

These findings will provide knowledge needed to understand how octocoral communities function and will contribute to a general understanding of the stability, resilience, and diversity changes in marine sessile communities, which are currently severely threatened by the impact of human activities.

Table *i*1. Important differences between two main types of foundation species in marine systems off the Tropical Eastern Pacific: coral reefs and octocoral communities

Scleractinian corals	Octocorals
Found in <15 meters depth	From the intertidal to deep mesophotic areas.
Distribution limited to warm, shallow, clear water	Predominant in very active environments, strong currents, and swell
Hard/stiff morphology that breaks with intense water motion	Flexible morphology allows them to cope with water movement
Mutualistic zooxanthellae symbiosis, which makes them susceptible to bleaching	No zooxanthellae symbiosis reported so far (Van Open et al., 2005)
90% of nutrients acquired from zooxanthellae photosynthesis (Marshall & Schuttenberg, 2006)	Heterotrophs, filter feeding
Create calcium carbonate accumulations known as coral reef and reef frames	Do not create calcium carbonate accumulations; instead most of their biomass is in the water column (Sanchez, 2016)
More calcified, secrete aragonite, a less stable mineral form of calcium carbonate	Less calcified, secrete calcite, a more stable mineral form of calcium carbonate (Kahng et al., 2011)
Less resistant to environmental disturbances	More resistant to environmental disturbances (C.E. Gómez et al. 2015)
Well-studied species and system	Recent taxonomic reviews allowed an initiative to study, for the first time, the biology and ecology of these communities since 2009.

Table *i*2. Physical and chemical differences between the Gulf of Panama and the Gulf of Chiriqui. From Reijimer et al. (2012) and D'Croz & O'Dea (2007).

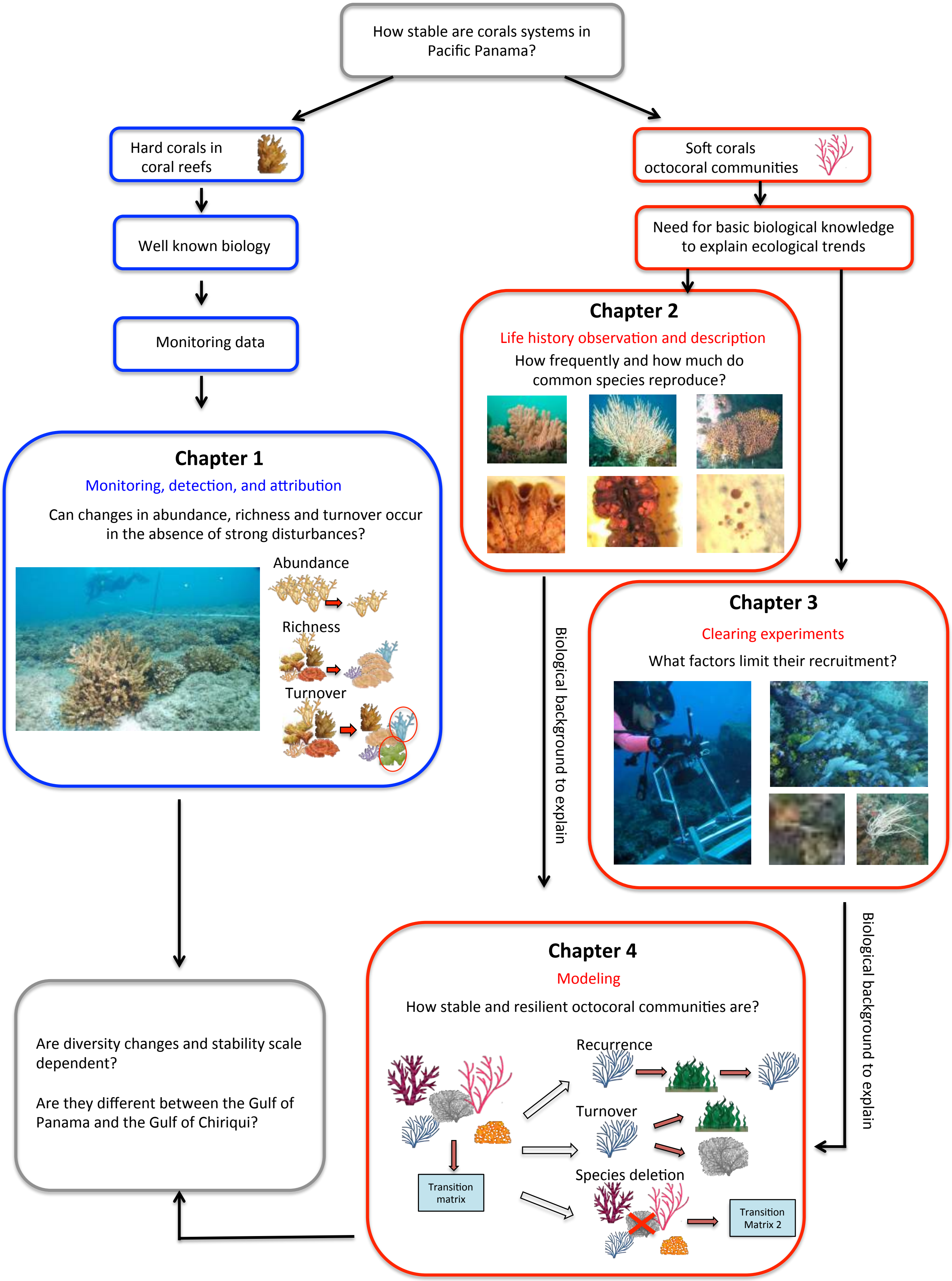
Gulf of Panama	**Gulf of Chiriqui**
Enclosed on the north, east, and west	Enclosed to the north and east but only semi-enclosed on the west
Gradually deepening shelf ramp	Narrower and deeper shelf
Water depths less than 75m	Max depth near Hannibal Bank of 459 m
Mean water depth 65m	Mean water depth of 110m
Las Perlas archipelago, with 250 islands and islets (38)	Coiba archipelago, with 9 main islands and about 30 islets (30)
Water temperature 18-27.7 ^{o}C	Water temperature 28 ^{o}C
Salinity (psu) 29.2 - 33.6	Salinity (psu) 30.5-32.0
NO^{-}_{3} (μM) 0.27 - 14.45	NO^{-}_{3} (μM) 0.34 – 0.75
PO^{3-}_{4} (μM) 0.14 – 1.20	PO^{3-}_{4} (μM) 0.16 – 0.24
Chl *a* (mg m^{-3}) 0.27- 1.44	Chl *a* (mg m^{-3}) 0.16 – 0.34
Euphotic zone (m) 13.8 – 37.1	Euphotic zone (m) 40.4 – 62.4

Table *i*3. Octocoral regional and local species pool based on Guzman et al. (2004) and Guzman et al. (2008)

Species	**Gulf of Chiriquí**	**Gulf of Panama**
Carijoa riseii	1	1
Eugorgia ampla		1
Eugorgia daniana	1	1
Eugorgia rubens		1
Eugorgia sp. 2	1	
Heterogorgia cf. papillosa		1
Heterogorgia sp.	1	
Heterogorgia verrucosa		1
Leptogorgia alba	1	1
Leptogorgia cf. ramulus	1	
Leptogorgia cofrini	1	1
Leptogorgia cuspidata	1	1
Leptogorgia diffusa		1
Leptogorgia pumila		1
Leptogorgia regis		1
Leptogorgia sp.		1
Leptogorgia sp. 1		1
Leptogorgia sp. 1	1	
Leptogorgia sp. 2	1	
Leptogorgia sp. 3	1	
Leptogorgia sp. 4	1	
Leptogorgia taboguilla		1
Muricea appressa		1
Muricea cf. appressa		1

Muricea austera	1	1
Muricea cf. crassa	1	
Muricea cf. hispida		1
Muricea crassa		1
Muricea diffusa		1
Muricea fruticosa	1	1
Muricea purpurea		1
Muricea sp.		1
Muricea sp. 2	1	
Muricea sp. 3	1	
Muricea squarrosa		1
Pacifigorgia adamsii	1	
Pacifigorgia bayeri	1	1
Pacifigorgia cairnsi	1	
Pacifigorgia catedralensis	1	
Pacifigorgia cf. firma	1	1
Pacifigorgia cf. smithsoniana		1
Pacifigorgia eximia	1	1
Pacifigorgia ferruginea	1	1
Pacifigorgia firma	1	1
Pacifigorgia irene	1	1
Pacifigorgia rubicunda	1	1
Pacifigorgia rubinofy	1	
Pacifigorgia sculpta		1
Pacifigorgia senta	1	
Pacifigorgia smithsoniana		1
Pacifigorgia sp. 1	1	
Pacifigorgia sp. 2	1	
Pacifigorgia stenobrochis	1	1

Psammogorgia arbuscula	1	
Psammogorgia sp.		1
Psammogorgia sp.	1	
Psammogorgia sp. 1		1
Psammogorgia sp. 1	1	
Psammogorgia sp. 2	1	
Total general	**36**	**38**



How stable are corals systems in Pacific Panama?

Hard corals in coral reefs

Well known biology

Monitoring data

Chapter 1

Monitoring, detection, and attribution

Can changes in abundance, richness and turnover occur in the absence of strong disturbances?

Soft corals octocoral communities

Need for basic biological knowledge to explain ecological trends

Chapter 2

Life history observation and description

How frequently and how much do common species reproduce?

Chapter 3

Clearing experiments

What factors limit their recruitment?

Chapter 4

Modeling

How stable and resilient octocoral communities are?

Are diversity changes and stability scale dependent?

Are they different between the Gulf of Panama and the Gulf of Chiriqui?

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CHAPTER ONE

Multiscale change in reef coral species diversity and composition in the Tropical Eastern Pacific

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Abstract

Both natural and anthropogenic factors are changing coral reef structure and function worldwide. This has been seen in long-term monitoring studies that revealed declines in the local composition and species diversity of reefs. Here we report changes in coral reef community structure over twelve years (2000-2012) at 17 reef sites and three spatial scales (reef, gulf, and country) in the Tropical Eastern Pacific (Panama). We found a significant 4% decline in annual population size at the country and gulf scales and significant declines ranging from 3% to 32% in all but one reef. No significant temporal change in expected richness was found at the country scale or in the Gulf of Chiriqui, but a 7% annual decline in expected species richness was found in the Gulf of Panama. There was a 2% increase in community evenness in the Gulf of Chiriqui, but no change in the Gulf of Panama. Significant temporal turnover was found at the country and gulf scales and in 29% of the reefs, a finding mostly explained by changes in species abundance and losses and gains of rare species. Temporal trends in alpha and beta diversity metrics were explained by water temperature maxima, anomalies, and variation that occurred even in the absence of a strong El Niño warming event.

Introduction

Globally, one-third of reef building corals are at risk of extinction (Carpenter et al., 2008) with many coral reefs experiencing large-scale degradation (Pandolfi et al., 2003) and major changes in community composition (Hughes et al., 2003); 2016 was exceptional in this regard (Normile, 2016). Long-term trends in coral species diversity may be complex, reflecting countervailing drivers, with trends in diversity differing at local and regional scales (Gonzalez et al., 2016). Global reef degradation is attributable to warming (Hoegh-Guldberg, 1999) and ocean acidification (Kleypas & Yates, 2009) while at the local level it is caused by overfishing (Hughes ,1994), sediment run-off (Bellwood et al., 2004; Alvarez-Filip et al., 2013), water pollution (Guzman & Holst, 1994), diseases (Francini-Filho et al., 2008), and direct damage to the reef structure through anchoring and trawling (Guzman et al., 1991; Graham et al., 2013). These disturbances are predicted to increase in frequency and severity over the coming century (Hoegh-Guldberg, 1999; Cai et al., 2014).

Knowledge of trends in local diversity stems from meta-analysis, in which data are combined from many different studies. Some meta-analyses, in which average trends in local diversity have been estimated for marine systems, report no net change (Dornelas et al., 2014) and even increases in coastal biodiversity (Elahi et al., 2015). The conclusions depend on whether data are collected from areas of low or high human impact (e.g. Elahi et al., 2015) and the spatial scale at which they are analyzed. It is important to note, however, that marine tropical areas are underrepresented in these meta-analyses (Gonzalez et al., 2016).

In contrast, studies that have quantified changes in coral cover over time and space have consistently reported significant declines in the Caribbean (Gardner et al., 2003), the Indo-Pacific (Bruno & Selig, 2007), and the Great Barrier Reef (Sweatman et al., 2011; De'ath, et al., 2012).

However, quantifying coral cover can mask changes in the community composition of coral species (Gardner et al., 2003). Trends in coral diversity can be measured at the population level, according to decreasing or increasing species abundance (Loh et al., 2005), or at the community level (Dornelas et al., 2014), where changes in species composition can be detected by evaluating alpha diversity and spatial and temporal beta diversity. Alpha diversity is measured as the number of species, or expected number of species, within a sample. This measure can be related to the abundance of individual species through various diversity indices (Jost, 2006). Spatial beta diversity quantifies the variation in species composition among communities, while temporal beta diversity, or turnover, quantifies the variation in species composition over time, which can provide a more sensitive method for identifying temporal biodiversity change (Magurran & Henderson, 2010; Dornelas et al., 2014).

In this study we use a multi-scale approach to test whether changes in coral diversity, measured as abundance, richness, evenness, and turnover, can be detected in coral reefs off Pacific Panama over a 12-year period, and whether these changes can be attributed to environmental and physical factors. We hypothesize that there have been significant changes in coral diversity in reefs in Pacific Panama, as in other regions, with an expected decline in abundance as well as changes in species richness, evenness, and turnover. We also hypothesize that these changes have occurred at the local and regional spatial scales. We further hypothesize that the attribution of the potential changes is different in reefs inside and outside Marine Protected Areas due to direct impact to the reef frames. Finally, we hypothesize that environmental factors, such as water temperature, could have affected all reefs, even in the absence of a strong ENSO event during the study period.

Methods

Study area

The Pacific coast of Panama is divided in two gulfs, the Gulf of Panama (GP) and the Gulf of Chiriqui (GC), which are semi-open areas separated by a *ca.* 100 km wide peninsula. Oceanographic differences between the gulfs have shaped the reefs that inhabit them (Toth et al., 2017). The GC presents a nearly constant sea surface temperature (SST) of 28^{o}C, low and constant $NO^{-}_{3,}$ and chlorophyll *a* concentrations near the surface. In contrast, the GP has seasonal temperature changes of 10^{o}C and high concentrations of $NO^{-}_{3,}$ and chlorophyll *a* in the upper layer during the dry season (December to March) (D'Croz & O'Dea, 2007). These conditions promote phytoplankton blooms that can restrict coral growth in the GP (Glynn et al., 2017b). These differences are due to a wind-driven seasonal upwelling that only occurs in the GP (Xie et al., 2005; Fielder & Lavín, 2017).

Extensive coral reefs are present in both the GP and the GC (Guzman et al., 2004, 2008; Glynn et al., 2017b). These reefs are composed of low evenness frameworks that extend several kilometers; coral diversity tends to be low in coral reefs when compared to coral communities from the same region (Guzman et al., 2004, 2008). There are 22 coral species reported for the GC (Guzman el al., 2004) and 19 for the GP (Guzman et al., 2008), with a total of 27 species reported for Pacific Panama (Cortés et al., 2017). Reef framework accumulation is lower in the GP than the GC (Toth et al., 2017). These reefs are located at about 10 m depth and are limited to shallow and clear water due to their association with zooxanthellae *Symbiodinium*. Reef frames rest on basaltic foundations; the GC reefs have vertical buildups of 10-12 m, with up to 5,600 years of age (Glynn & Macintyre, 1977), and in the GP 5.6-6.1 m and 4,500 years (Maté, 2003). The extreme warming event that took place in 1982/83 affected corals in both the GP and the GC. Water temperature rose >29°C, killing 75% of hermatypic corals in the GC and 85% in the GP

(Glynn, 1990). Age estimates for the massive corals killed during this event suggested that a disturbance of this magnitude had not occurred in the past 200 years (Glynn, 1990). A similar ENSO event in 1997/98, in which temperatures rose to 29°C in the GP and more than 30°C in the GC for over 3 weeks, was less severe and caused only 13.1% coral mortality in the GC and no mortality in the GP (Glynn et al., 2001a). The presence of extensive but simple coral reef systems and the history of reef bleaching at the country scale provide an important context for observing temporal changes in coral diversity (Cortés et al., 2017).

Community data

Community data (species percent cover yr^{-1}) was collected by the Smithsonian Tropical Research Institute's Panama Coral Reef Monitoring Network. This initiative monitored 17 coral reefs on the Pacific coast of Panama, seven reefs in the GP, and 10 in the GC (Figure 1,1a). The initiative, which began with 6 monitored reefs in 2000, concluded with 17 monitored reefs in 2012; not all reefs were monitored for the same amount of time (Table 1,1). Monitoring sites were selected based on the existence of a solid reef-building framework, regardless of reef health. The sites chosen include a range of levels of degradation and management. Six of the reefs in the GP were located inside the Marine Special Management Zone of Las Perlas Archipelago. Six of the reefs in the GC were located within Coiba National Park, the largest marine reserve in Pacific Panama, and one (Paridas) was located in the National Marine Park Golfo de Chiriquí (Table 1.1). Reefs were monitored annually on three permanent belt-transects located parallel to the coastline, 10 m long and 10 m apart at the reef-flat or upper slope (< 5m) and at the lower slope or reef base (>5 to 12m). Reefs in which the two transects were within a continuous reef frame were described as "continuous," while reefs in which at least one of the transects lay within a discontinuous reef frame, interrupted by sand channels and massive coral heads, were descried as "discontinuous" (Table 1.1). Each survey lasted 1.5 hr. on average. Each transect was marked at the beginning, middle, and end with a permanent metal rod driven into the reef. Ten quadrants (1 m^2 each) were measured along each transect with successive placements of the frame. A 1 m^2 PVC quadrant divided with strings into a 10 x 10 cm grid was used to census each transect (see Guzman et al., 2004, 2008). The percentage of each type of cover for all sessile organisms was estimated as a fraction of a grid square; therefore, a 2.5 cm^2 colony was ¼ of a square representing 0.25% cover.

Due to the long debate on morphological versus phylogenetic species identification, and the need for more studies to resolve the taxonomy of common coral species in the area Combosh & Vollmer, 2015), the species in the present study followed the Reyes-Bonilla (2002) species checklist, with the exception of *Psammocora superficialis*, which was synonymized with *Psammocora profundacella* by Benzoni (2010) and *Pavona chiriquensis* described in 2001 (Glynn et al., 2001b). Algae cover was divided into four functional groups: calcareous, crustose coralline algae (CCA), turf, and frondose macroalgae. Octocorals and sponges were recorded at the species level when possible. Water temperature (wt) loggers HOBO U22 Temp Pro V2 (Onset Computer Corporation) were installed in 10 of the monitored reefs (6 in GC and 4 in CP) (Table 1.1). HOBO stations were programmed to record *in situ* wt every 30 minutes. Data was downloaded and stations were redeployed every year.

Two approaches were used to analyze temporal trends in the biodiversity of scleractinians in coral reefs off Pacific Panama at three spatial scales (reef, gulf, and country). The first approach estimates temporal trends in alpha diversity by looking at changes in species richness and evenness and changes in species abundance (percent cover). The second approach estimates trends in temporal beta diversity, disentangling the contribution of species replacement and changes in species abundance (percent cover), and quantifying the contribution of each species to community changes. Independent analyses were done for each reef, grouped by gulf, and then pooled together. All analyses were performed using R-software version 3.2.2 (R Core Team 2015) unless otherwise indicated.

Temporal trend of alpha diversity

Expected species richness was estimated using species accumulation curves fitted to presence and absence data obtained from the sixty $1m^2$ plots at each reef for each year, using the function "specaccum," available in the *Vegan* R package (Oksanen et al., 2016). Analyses were done using the "random" method, which adds plots in a random order, with 500 permutations per run. The number of unobserved species per year per reef was calculated with the Chao estimator (Chao, 1987) using the function "specpool" in the same R package. Expected species richness in 60 plots was regressed against the year for each site. We did not rarify our estimates of species richness across time because equal sample effort (total number of plots) was applied at each census and on every reef. Analysis of temporal trends in estimated species richness for the entire study region (country scale) and for each gulf was conducted with a random intercept nested mixed model in which the intercept was allowed to change for each reef. We used function "lme" in the *nlme* package (Pinheiro et al., 2016) to fit the following model:

estimated richness ~ year + gulf + year x *gulf,* with reefs nested within gulfs as a random factor

The temporal variation in the community diversity was estimated at each site using a Rényi profile (Rényi, 1961). The Rényi profile, which summarizes the spectrum of diversity indices from richness to evenness, is an ordering technique designed to rank different communities from low to high diversity, in which a higher profile indicates higher overall diversity (Kindf et al., 2006). Rényi profiles were calculated for each year for each reef using the function “renyi” in the *Vegan* R package (Oksanen et al., 2016). A significant temporal difference in diversity indices was tested as follows:

ranked Rényi score ~ Rényi scale, with reefs nested within gulfs as a random factor

Hill numbers (Hill, 1973) 1 and 2, corresponding to Shannon index (H’), and species evenness were extracted from the diversity profiles and analysed individually for temporal trends.

A Minimum-Maximum Autocorrelation Factor Analysis (MAFA) was used to identify and explain common temporal trends in scleractinian species abundance for each reef. MAFA is a type of principal component analysis designed for time series data (Zuur et al., 2007); it estimates the maximum and minimum auto-correlation factor between time intervals to find a common trend (MAFA axis) in a multivariate time series dataset and then correlates it with an explanatory variable. We choose MAFA over simpler methods of analysis, such as quantifying total coral cover, because in these highly-uneven systems dominant species would mask changes in less common ones, leaving them under represented in the results. This approach also allowed us to analyzed the trends at different spatial scales (reefs, gulf and country) while taking into account the abundance of each species at the smallest scale. The first MAFA trend represents the main underlying pattern in the data (Zuur et al., 2007). This analysis does not create eigenvalues to quantify the importance of each trend, but it does calculate whether the auto-correlation of the axes is significantly different from zero (Zuur et al., 2007). This analysis also quantifies canonical correlations between the MAFA axes (e.g. reef trend) and each of the original variables (e.g. species abundances). The MAFA dependent variable was annual species percent cover (for common scleractinian corals only). Explanatory variables were annual number of days with average wt >29^{o}C; number of +0.5^{o}C and +1 C^{o} annual temperature anomalies; number of days with wt > local Maximum Monthly Mean; temperature coefficient of variation; and minimum and maximum wt. Analyses were performed using Brodgar Software version 2.7.4. Temperature was only used as an explanatory variable in reefs with *in situ* data loggers (Table 1.1).

A hierarchical mixed-effects model with a random intercept was used to estimate the temporal change in the MAFA trend (species abundance) at the gulf and country scales as follows:

MAFA trend ~ year + gulf + year x *gulf,* with reefs nested within gulfs as a random factor

Trends in temporal beta diversity

Temporal change in beta diversity was quantified as the variation in community composition, or species turnover, over survey events (*sensu* Legendre & Salvat, 2015). First, we calculated the Jaccard distance, which measures the dissimilarity among communities, between the last year of data (2012) and every monitored year for each reef (see also Dornelas et al., 2014).

The final year was used as the reference year because monitoring began in different years at different reefs, but the last year was common to all reefs. The Jaccard distance between each year and the final year was plotted against time and a best-fit line was used to calculate the slope of this long-term relationship. The same analysis was done to test for changes in beta diversity on an annual temporal scale by calculating the Jaccard distance between each consecutive year. This turnover metric includes shifts in species composition and is therefore a more sensitive indicator of community change than alpha diversity (Dornelas et al., 2014). Jaccard indices were calculated using the “vegdist” function, method “Jaccard” in the *Vegan* R package (Oksanen et al., 2016). An estimate of the temporal turnover at the country scale and for each gulf was calculated using a hierarchical mixed effects model with a random intercept using the Jaccard distance between each year and the last year of data, in the same way as the model for alpha diversity and species abundance.

The total temporal variance in community composition, as well as its components, was calculated following Legendre (2014). This method explains the dissimilarity between sampling times caused by species replacement and abundance differences. The calculation was done by setting Legendre's R Software function "beta.div.comp" (available at http://adn.biol.umontreal.ca/~numericalecology/Rcode/) to the quantitative form of the Jaccard-based b-diversity indices (Ruzicka indices in the Podani family), which takes into account species abundances and not only presence and absence (Legendre 2014). The contribution of species replacement and changes in species abundance to the total temporal beta diversity was calculated for each reef. Species contribution to beta diversity (SCBD) for each reef was calculated with Legendre and Caceres (2013) R-software function "beta.div" (http://adn.biol.umontreal.ca/~numericalecology/Rcode/). All analyses were performed using the Hellinger transformation, which is appropriate for measuring the variation of community composition data (Legendre & Caceres, 2013). SCBD of common species between gulfs were tested for correlation using the "rcorr" function of the *Hmisc* R package (Harrel et al., 2015).

Correlation to temperature parameters

Correlations with temperature parameters were only analyzed for reefs in which an *in situ* HOBO logger was installed (Table1.1). Temperature records were analyzed using different approaches to describe coral thermal stress: 1) Days with daily wt was above 30°C (Glynn et al. 2017a); 2) number and magnitude of wt positive anomalies (+0.5, +0.1, +0.15°C) per year, calculated by quantifying the difference between average daily temperature and daily regional long-term mean (December 1971- December 2000), with a 1-degree latitude grid resolution. Long term mean data was acquired from NOAA_OI_SST_V2, a product provided by the NOAA/ Earth System Research Laboratory, Physical Sciences Division website (NOAA); and 3) Maximum of the Monthly Mean (MMM) (Skirving et al. 2006), which is the mean temperature during the warmest month calculated for each site where HOBO devices were installed. The number of days with daily mean wt above MMM was quantified for each reef, as well as the number of days with wt 1^{o}C above the MMM (*sensu* Glynn & D'Croz, 1990). Additionally, degree-days and minimum, maximum, and coefficient of variation were calculated for each year for each reef. All analyses were done in R software version 3.2.2 (R Core Team 2015).

An asymmetric canonical ordination redundancy analysis (RDA), which quantifies the percentage of variation of the response variables explained by the predictor variables in a multivariate dataset (Peres-Neto et al., 2006), was performed to test the effect of temperature on community changes at the reef scale, with biodiversity indices (MAFA trend, expected number of species, and Jaccard dissimilarity) as response variables. A model selection tool (Vegan R function "ordistep") was used to select relevant temperature parameters as an explanatory variable. Only sites with more than one species and where temperature loggers were installed (Table 1.1) were used in the analysis. In the same way, a second RDA was performed to test the effect of degree of management, reef type (continuous or discontinuous frame), distance from human settlement, initial species richness, and initial coral cover (see Table 1.1) on the diversity trends descried above. All reefs where included in the second RDA.

Results

Temporal trends in coral alpha diversity

There was no overall temporal trend in expected species richness at the country scale (B = -0.03, SE = 0.02, $p > 0.05$), however, the trends were significantly different between the gulfs ($Chi^2 = 5.18$, $p < 0.05$). The slope of the decline in the GC was not statistically different from zero (B = 0.02, SE = 0.03, $p > 0.05$), but the slope in the GP indicated a significant decline in expected species richness of 7% yr^{-1} (B = -0.07, SE = 0.03, $p < 0.05$) (Table 1.2, Figure 1.2, Species accumulation curves for each reef and Chao estimate in Figure S1.1). Iguana and Saboga reefs, both with discontinuous reef frameworks in the GP, had significant decreasing trends ($Ad.r^2 = 0.30$ and 0.32 respectively). The reef at Saboga lost three of seven species: *Pavona gigantea, Pavona varians*, and *Pocillopora elegans*, and Iguana lost two of five species: *Gardineroseris planulata* and *Psammocora profundacella* (Figure S 1.2) during the survey period.

Rényi diversity profiles showed that most reefs had a steep decline in species richness to evenness, reflecting the strong dominance of a single species, *Pocillopora damicornis*, on most reefs. The temporal variations of these diversity profiles were significantly different among gulfs and sites ($p<0.001$) (Figure S 1.3). The hierarchical mixed-effect model for Shannon diversity did not reveal statistically significant temporal trends at the country or the gulf scales (all p values > 0.05) (Table 1.2). Evenness, however, significantly decreased in the GC (B = -0.02, SE = 0.01, $p < 0.05$), but no significant trends were found at the country scale and for the GP ($p > 0.05$ in both cases, Figure S 1.3, Table 1.2).

Temporal trends in coral abundance

The MAFA analysis revealed an overall decreasing trend in species abundance (percent cover), representing a 4% annual decline at the country scale (slope = 0.04, SE= 0.008, $p < 0.001$) and on each gulf (GC: B = 0.04, SE = 0.009, $p < 0.001$, GP: B = 0.04, SE = 0.01, $p<0.001$). In the GP, five reefs had significant changes. Four reefs had significant declining trends: San Pedro (slope = -0.11, Adj.r^2 = 0.44), Señorita (-0.08, 0.92), Iguana (-0.07, 0.92), and Saboga (-0.06, 0.65), while San Jose (0.15, 0.96) had a significant increasing trend (Table 1.2, Figure 1.3). In the GC, five reefs had significant declining trends in species abundance: Montuosa (slope = -0.32, Adj.r^2 = 0.788), Secas (-0.18, 0.95), Cebaco (-0.17, 0.79), Canales (-0.15, 0.90), and Coiba NE (-0.12, 0.55). None of the reefs in the GC had a significant increasing trend (Table 1.2, Figure 1.3). Trend slope was not correlated with the number of years (time points) of data (Pearson correlation, $p>0.05$).

Trends in temporal beta diversity

The hierarchical mixed model showed that as time progressed the original composition of the coral communities became more distinct from the community in the last monitoring year, which is represented by an overall declining temporal trend of 2% yr^{-1} (B = -0.02, SE = 0.004) (Pacific Panama). The Jaccard distance showed a negative trend of -0.02 in the GP (SE = 0.005), and -0.03 (SE = 0.005) in the GC (Figure 1.4). There was a significant interaction ($p > 0.05$), meaning that the trends were significantly different between gulfs. The temporal change in community similarity in the more thermally stable Gulf of Chiriqui was 1.6 times greater than in the more thermally variable Gulf of Panama.

Five reefs had significant declining trends in Jaccard distance over time, meaning they displayed a greater distance between communities during the first and last monitoring years: Canales (slope = -0.06, Adj.r^2 = 0.77), Mona (-0.05, 0.61), Cebaco (-0.04, 0.71), and Isla Coiba (-0.02, 0.28) in the GC and Iguana (-0.0005, -0.06) in the GP. Only one site, Saboga (GP), had a significant positive trend (0.03, 0.53) (Table 1.2, Figure 1.4). A change in community similarity was not observed on an annual scale when calculating Jaccard distances between consecutive years. The number of years of data was not related to the slope of the trend (Pearson correlation, $p > 0.05$).

Beta diversity decomposition using the Ruzicka index (quantitative form) showed that changes in temporal community similarity were better explained by changes in the abundance of species (78.7%) than by changes in species replacement (21.2%), with a similar pattern at the reef and gulf levels (Table 1.2, Figure 1.5a,b). However, temporal dissimilarity in community composition was best explained by species replacement in Jicarita (88%) and San Telmo (71%). Reefs San Pedro and Cebaco were excluded from this analysis because they only had one species, *P. damicornis*, during the study period.

Species contribution to beta diversity (SCBD) was correlated to species that were common in both gulfs ($n = 11$, correlation coefficient = 0.8, $p < 0.005$). However, in the GC most of the variation was due to changes in *P. elegans*, while in the GP, changes in temporal community similarity were best explained by six species *P. elegans*, *Psammocora stellata*, *Pavona frondifera*, *G. planulata*, *Pavona clavus*, and *P. produndacella* (Table 1.3, Figure 1.5c,d). Species SCBD index was not correlated with mean relative abundance at the reef level ($p > 0.05$), meaning that common and rare coral species contributed to community changes in the reefs.

Correlation with temperature parameters

A total of 4,918 days of *in situ* water temperature were recorded in the GP and 4,273 days in the GC from HOBO loggers installed in 10 reefs (Table 1.1, Figure 1.1b). The annual number of days above 29 °C ranged from 5 to 212 days in the GC and 0 to 63 in the GP. Years with a greater number of warm days were 2002, 2003, 2005, 2006, and 2012, all of which, except 2012, clearly coincided with moderate El Niño years. There were significantly more annual days with wt >29°C in GC reefs than GP reefs during the study period (Welch Two Sample t-test, $p < 0.001$). The mean annual number of temperature anomalies above 0.5°C degrees ranged from 0 to 65 in the GC and 0 to 30 in the GP; anomalies above 1°C ranged from 0-37 in the GC and 0-4 in the GP. The GC had significantly more daily temperature anomalies per year than the GP (Welch Two Sample t-test, $p < 0.001$). The year 2009 showed the greatest number of temperature anomalies; this was also an El Niño year.

Changes in diversity metrics were explained by increases in water temperature even in the absence of a strong El Niño event. At the country scale, changes in coral alpha diversity (expected species richness) and abundance (MAFA trend) were correlated with increases in water temperature (anomalies, mean, number of days with wt above 30^{o}C and degree days) and its variation (Adj. $r^2= 0.31$, $p<0.001$ (Table 1.4, Figure 1.6a). The maximum monthly mean (MMM), or maximum and minimum temperatures combined, explained 72% of the variation in diversity trends in reefs in the Gulf of Chiriquí (Adj $r^2=0.721$, $p<0.001$) (Table 1.4, Figure 1.6b). The coefficient of variation, number of anomalies, and maximum and mean temperature combined explained 43% of the variation in diversity metrics in reefs in the GP (Adj $r^2=0.43$, $p<0.001$) (Table 1.4, Figure 1.6c).

The second RDA, performed to test the possible effect of the initial number of species, initial coral cover, degree of reef protection, distance from human settlement on the response variables, and type of reef (continuous or discontinuous frame) did not reveal any significant effects on diversity trends.

Discussion

After 12 years of coral reef monitoring across 17 reefs in Pacific Panama, we detected significant changes in multiple diversity metrics at the reef, gulf, and country scales. These changes were partially explained by the different temperature parameters associated with warming and temperature fluctuations, even in the absence of strong El Niño or La Niña events. This study not only reports on coral cover decline, but it disentangles the diversity changes associated with the decline at different spatial scales.

The declining trend in species abundance was found at all spatial scales and equated to a 4% annual decline. This declines are smaller compared to the declines reported after massive bleaching events previously caused by strong El Niño, which reduced coral cover by 75% at the GC, 85% at the GP in 1982/1983 (Glynn, 1990), and 13.1% at GC in 1997/98 (Glynn et al, 2001a). However, the declines found in this study, in the absence of a strong warming, are greater than those reported for the Indo-Pacific, which had an annual decline of 2% between 1997 and 2003 (Bruno & Selig, 2007). In the absence of strong disturbances, however, reef at the Great Barrier Reef recovered 0.89% of cover per year (De´ath, et al., 2012) but this was not the case for Panamanian corals, which declined even in the absence of such disturbances.

A reduction in coral cover was significant in 59% of the monitored reefs. A significant increase occurred only at San Jose (GP), due to an increase in the already dominant *P. damicornis*, which was the main reason for the decrease in evenness described above. This general negative trend was mainly explained by the reduction in cover of common species (such as *P. damicornis*); it was present in reefs under all levels of protection, including reefs within the no take zone of Coiba National Park and at reefs with no protection, such as Cebaco and Islas Secas. Similar results were found in Caribbean coral reefs, which have had significant declines without major changes in species richness or local extinctions (Riegl et al., 2009).

Trends in species alpha diversity varied according to metric and spatial scale. When analyzed at the country scale, opposing positive and negative trends resulted in no net change in alpha diversity. At smaller scales, however, significant trends were found. There was a 7% annual decline in expected species richness in the Gulf of Panama and a 2% increase in species evenness in the Gulf of Chiriquí. The decrease in species richness was the result of the loss of common but not dominant species (*P. gigantea, P. varians, P. elegans, G. planulata*, and *P. profundacella*) and was more evident in Saboga and Iguana, reefs with discontinuous frames in their reef base. These two reefs are located in marine protected areas under a minimum level of management and protection, where direct human impact to the reef is expected to be low. However, the implementation of regulations is uncommon (Guzman et al., 1991) and anthropogenic stress comes indirectly through overfishing of surrounding areas. Iguana Island is a small uninhabited island with a 16 ha reef (Guzman et al., 1991) sheltered from river runoffs and sedimentation. Saboga's reef is found in front of a human settlement, and impacts to the reef via water pollution and sedimentation are known (Guzman et al., 2008). Most of the studied reefs were highly dominated by a single species (*P. damicornis*). With the loss of rare species and the decline in abundance of the dominant species, communities became more even, which was more evident at Coiba reef.

Changes in community composition were also seen at the three studied scales. The community change in the Gulf of Chiriquí was 1.6% greater than in the Gulf of Panama, where only two reefs, Saboga and Iguana, had significant declines. Temporal diversity changes in most reefs were explained by the overall decrease in abundance showed by the MAFA analysis and beta diversity decomposition. An important contribution to species replacement was seen at reefs in Jicarita, Iguana, San Jose, and San Telmo. Although San Jose, San Telmo, Jicarita, and Iguana are isolated, remotely located reefs that are not exposed to threats like human development, they are under considerable pressure from tourist activities. All of these reefs are also exposed to the indirect effects of nearby fishing and regional temperature fluctuations.

Even in the absence of strong El Niño warming events, which have caused major coral bleaching in the area (Hughes et al., 2003; Glynn et al., 2017a), sporadic and uneven bleaching was observed during this study. The sum of small but frequent positive anomalies, as well as a high maximum monthly mean and water temperature variation contributed to affect heat-vulnerable or less thermo-tolerant species, which our analyses revealed made greater contributions to community temporal changes.

Warming experiments and monitoring after mass mortality events have demonstrated that massive species, such as *P. gigantea, Porites lobata*, and *P. clavus* are more tolerant to warming (Hueerkamp et al., 2001) and have faster recovery (Guzman & Cortes, 2007) than the branching species *P. damicornis* and *P. elegans* (Hueerkamp et al., 2001). In previous experiments, *P. gigantea* exhibited the greatest resistance to bleaching and *P. lobata* showed the greatest recovery while *P. clavus* showed no recovery (Hueerkamp et al., 2001). In the present study, the ecological consequences of this tolerance are reflected in the contribution of each species to community changes, here quantified with the SCBD index. *P. gigantea* was one of the species with the smallest contribution to changes (0.03), compared to the contributions of *P. lobata* (0.1), *P. clavus* (0.2), and *P. elegans* (0.5).

Conclusions

We found that significant changes in coral diversity and community composition occurred over the course of a decade in reefs off the Pacific coast of Panama at the national, gulf, and reef scales even in the absence of a strong warming event. These changes imply alterations to the structural complexity and functioning of the coral communities (Alvarez-Filip et al., 2013). Our capacity to detect and attribute trends depended on the scale analyzed and the metric used, emphasizing the importance of multi-scaled biodiversity monitoring and quantitative attribution where possible.

This study shows that communities can diverge rapidly in composition even if a stress threshold is not reached (e.g., coral bleaching threshold). The sum of frequent smaller natural disturbances, in this case warm days, can lead to decreases in species abundance and species replacements (*sensu* Lamy et al., 2015). If these changes do not occur between similar species, a novel community will be created (Hobbs et al., 2006), which is highly likely to change the ecosystem services the previous community provided (Graham et al., 2014). These types of changes in community composition become especially important when they involve foundation species, such as pocilloporid corals, which based on these results and under the ocean-warming scenario for the region are especially threatened.

In the present analysis, the level of reef management and protection (no-take zone, protected area, or not protected) did not explain changes in coral species abundance or species turnover. This could be a result of ineffective management in protected areas (Alvarado et al., 2017) and a region-wide suite of anthropogenic impacts (Cortés & Reyes-Bonilla, 2017).

Lastly, we believe this study, as well as the previous reports on bleaching; can be used as a reference to understand the shifting baseline of diversity and coral abundance (Pauly, 1995), but also for the lasting effects of the warm temperatures of the 2015-2016 ENSO event (Jacox et al., 2016). Resampling this monitoring network would allow assessment of the effect of this latest temperature stress on communities living close to their environmental tolerance (GC) and communities living in variable but less stressful environments (GP). A detailed evaluation of the trends of heat-intolerant coral species is needed, because this study has identified them as responsible for the community changes we detected.

We recommend that future long-term studies use a monitoring network that is designed for both detection and attribution of biodiversity change. This should be done so that sites are distributed across a gradient of stress factors, both natural and human, and hierarchically structured to pick up local and regional trends in diversity (Gonzalez et al., 2016). Future biodiversity assessments will require adequate baselines and reference sites to ensure robust conclusions about past, present and future trends in biodiversity (Gonzalez et al., 2016).

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Table 1.1. Principal characteristics of studied coral reefs. Level of management: 0 = no protection, 1= located in a protected area, 2= located within the no-take zone of a protected area. *Pocillopora damicornis (Pd)*, *Pocillopora elegans (Pe), Porites lobata (Pl), Gardineroseris planulata (Gp).* Reefs with continuous (C) or discontinuous (D) frames. Discontinuous were interrupted by sand channels and massive coral heads. In situ temperature data collected by HOBO logger = Yes (Y), No (X).

Gulf	**Reef**	**Depth (m)**	**Years of data**	**Temperature**	**Initial richness**	**Initial dominance**	**Main reef builder**	**Reef type**	**Level of management**
Gulf of Chiriquí 10 reefs 5-13 years	Coiba	4.5	13	Y	6	Algae	*Pd*	D	2
	Paridas	2.5	12	Y	2	Algae	*Pd*	C	1
	Canales	2.5	11	Y	7	Algae	*Pd*	C	2
	Coiba NE	3	8	N	1	Coral	*Pd*	C	2
	Ranchería	2	8	Y	4	Coral	*Pd*	D	2
	Jicarita	3	8	Y	10	Algae	*Pd*	D	2
	Cebaco		7	Y	1	Algae	*Pd*	C	0
	Secas		7	N	6	Coral	*Pd*	C	0
	Montuosa		5	N	5	Algae	*Pl*	D	1
	Mona		7	N	8	Algae	*Pd*	C	0
Gulf of Panama 7 reefs 5-13 years	Saboga	6	13	Y	4	Algae	*Pd*	D	1
	Iguana		13	N	4	Coral	*Pd*	D	1
	Señorita	3.6	12	Y	2	Algae	*Pe*	D	1
	San Pedro	5.4	9	Y	1	Coral	*Pd*	C	1
	San Jose	4.5	9	Y	2	Coral	*Pd*	C	1
	Achotines		5	N	5	Coral	*Pd*	C	0
	San Telmo		5	N	6	Algae	*Gp*	D	1

Table 1.2. Temporal trends in diversity at different special scales and at the population and community levels. Significant levels 0.001 ‘***’, 0.01 ‘**’,0.05 ‘*’, 0.1‘ -’. For country and gulfs: estimate(SE), for reefs scales: slope (Adj R^2), Not included in the analysis (NI)

Scale / site		**Population abundance**	**Community Alpha diversity**				**Community Temporal beta diversity**	
		MAFA slope	**Expected richness Slope**	**Hill Value 0 Species richness**	**Hill Value 1 Shannon diversity**	**Hill Value 2 Species evenness**	**Jaccard**	**Beta diversity change (species replacement%, abundance difference%)**
Country / Pacific Panama Estimate (Std. error)		-0.04 (0.008)***	-0.03 (0.02)	-0.04 (0.02) -	0.01 (0.01)	-0.01 (0.008)	-0.02 (0.004) **	0.35 (21.2, 78.7)
Gulf / Gulf of Chiriqui Estimate (Std. error)		-0.04 (0.009)***	0.02 (0.03)	-0.03 (0.03)	0.02 (0.01) -	0.02 (0.01)*	-0.03 (0.005) **	0.32 (20.3, 79.6)
Gulf / Gulf of Panama Estimate (Std. error)		-0.04 (0.01) ***	-0.07 (0.03) *	-0.04 (0.03)	-0.0006 (0.01)	-0.0006 (0.01)	-0.02 (0.005) **	0.35 (23.4, 76.6)
Coral reef/ Gulf of Chiriqui slope (Adj.R^2)	Isla Coiba	-0.14 (0.85) *	0.09 (0.09)	0.09 (0.03)	0.006 (0.43) *	0.002 (0.48)**	-0.02 (0.28	0.14 (3, 97)
	Paridas	-0.03 (0.05) *	0.04 (-0.23)	-0.02 (-0.07)	0.0004 (-0.05)	0.0001 (-0.04)	-0.01 (-0.05)	0.1 (0.4, 99.6)
	Canales	0.15 (0.90)	0.02 (-0.1)	0.02 (-0.10)	0.05 (-0.01)	0.03 (-0.06)	-0.06 (0.77)	0.22 (20, 80)
	Coiba NE	-0.12 (0.55) **	NI	NI	NI	NI	-0.05 (0.3)	0.13 (9, 91)
	Ranchería	-0.15 (0.94)	-0.15 (0.08)	-0.32 (0.35)	-0.02 (-0.03)	-0.008 (-0.06)	-0.01 (-0.001)	0.06 (21, 79)
	Jicarita	-0.15 (0.87)	-0.2 (0.35) -	-0.20 (0.35)	0.18 (0.24)	0.24 (0.33)	-0.02 (0.13)	0.16 (88, 12)

Scale / site		Population abundance	Community Alpha diversity				Community Temporal beta diversity	
		MAFA slope	Expected richness Slope	Hill Value 0 Species richness	Hill Value 1 Shannon diversity	Hill Value 2 Species evenness	Jaccard	Beta diversity change (species replacement%, abundance difference%)
Coral reef/ Gulf of Chiriqui slope (Adj.R^2)	Cebaco Norte	-0.17 (0.79) *	NI	NI	NI	NI	-0.04 (0.71)	NI
	Secas	-0.18 (0.95) **	-0.32 (0.32) -	-0.32 (0.31)	-0.06 (0.40)	-0.03 (0.33)	-0.04 (0.49)	0.1 (20, 80)
	Montuosa	-0.32 (0.79) *	-0.09 (0.29)	-0.2 (-0.17)	-0.05 (0.54)	-0.02 (0.58)	-0.06 (0.49)	0.1 (21, 79)
	Mona	0.18 (0.98)	0.21 (0.12)	0.21 (0.12)	-0.07 (0.24)	-0.04 (0.15)	-0.05 (0.61)	0.12 (18, 82)
Coral reef/ Gulf of Panama slope (Adj.R^2)	Isla Saboga	-0.06 (0.65) **	-0.1 (0.3) *	-0.1 (0.30) *	0.002 (-0.08)	0.002 (-0.03)	0.03 (0.53)	0.13 (3, 97)
	Isla Iguana	-0.07 (0.92) ***	-0.12 (0.32)*	-0.13 (0.32) *	-0.008 (0.37) *	-0.003 (0.29) *	-0.0005 (-0.06)	0.02 (44, 56)
	Isla Señorita	-0.08 (0.92) **	0.0001 (-0.2)	-0.02 (-0.09)	0.03 (-0.001)	0.01 (-0.03)	-0.09 (0.72)	0.35 (10, 90)
	San Pedro	-0.11 (0.44) *	NI	NI	NI	NI	0.00007 (-0.16)	NI
	San Jose Oeste	0.15 (0.96) ***	0.03 (-0.1)	0.033 (-0.10)	-0.03 (0.68) **	-0.02 (0.77) *	-0.01 (0.23)	0.05 (42, 58)
	Achotines	0.30 (0.89)	-0.001 (-0.33)	0 (-0.33)	-0.003 (0.80) *	-0.0008 (0.77) *	0.01 (0.04)-	0.02 (6, 94)
	San Telmo	0.29 (0.78)	-0.09 (-0.29)	-0.1 (-0.28)	0.04 (-0.20)	0.03 (-0.01)	-0.01 (-0.35)-	0.07 (71, 29)

[t] Temporal Beta Diversity calculated with the Ruzicka index in a scale [0:1]. Value of "1" being complete dissimilarity between time intervals.

Table 1.3. List of scleractinian species found in studied reef, UICN status and mean and standard deviation of their contribution to species turnover (SCBD). Near threatened (NT), Least concern (LC), Vulnerable (V), Not assessed (NA). Ordered by degree of SCBD value.

Species	**ICN status**	**Mean SCBD (0-1)**	**Lost at**	**Gained at**	**Gained and lost at**
Pocillopora elegans	V	0.5 ± 0.3	Rancheria Secas Saboga		Coiba NE Coiba Senorita San Jose
Psammocora stellata	V	0.3 ± 0.3	Rancheria Jicarita Montuosa	Achotines	Achotines Canales Coiba Paridas Secas
Pavona clavus	LC	0.2 ± 0.2		Canales	Achotines
Pavona chiriquensis	LC	0.02 ± 0.01	Secas		Coiba
Millepora intricata	LC	0.1			
Pocillopora damicornis	LC	0.1 ±0.1			
Porites lobata	NT	0.1 ±0.1	Secas	Rancheria	Canales Coiba
Pavona frondifera	LC	0.1 ± 0.1	Saboga Jicarita		
Psammocora produndacella	LC	0.1 ± 0.1	Rancheria Iguana	Secas	Iguana Paridas San Jose
Gardineroseris planulata	LC	0.1 ±0.2	Iguana		
Porites panamensis	LC	0.04 ± 0.05		Senorita Mona	Canales Coiba

Povona varians	LC	0.04 ± 0.04	Saboga		Coiba
Pavona gigantea	LC	0.03 ± 0.03	Saboga San Jose	Rancheria Montuosa	Achotines Coiba
Pocillopora eydouxi	NT	0.005 ± 0.003	Senorita	Secas	

Table 1.4. Water temperature parameters partially explained temporal changes in alpha and beta diversity in coral reefs communities off Pacific Panama. F value and significant levels: '***' 0.001 '**' 0.01 '*' 0.05. Important temperature parameters where selected by forward and backward ordination at each scale.

	Study Area	Gulf of Panama	Gulf of Chiriqui
Variation explained			
RDA Adj. R^2	0.31***	0.42***	0.72***
Temperature parameters as explanatory variables			
Mean	23.1**	17.1**	
Minimum			5.3*
Maximum		16.5**	8.4*
Maximum monthly mean	3.0*		12.8**
Positive anomalies	6.0* (+1 ^{O}C) 5.5* (+1.5 ^{O}C)	8.15 **	
Days >30^{O}C	7.5*		
Degree days	14.0**		
Coefficient of variation	4.3*	4.3*	

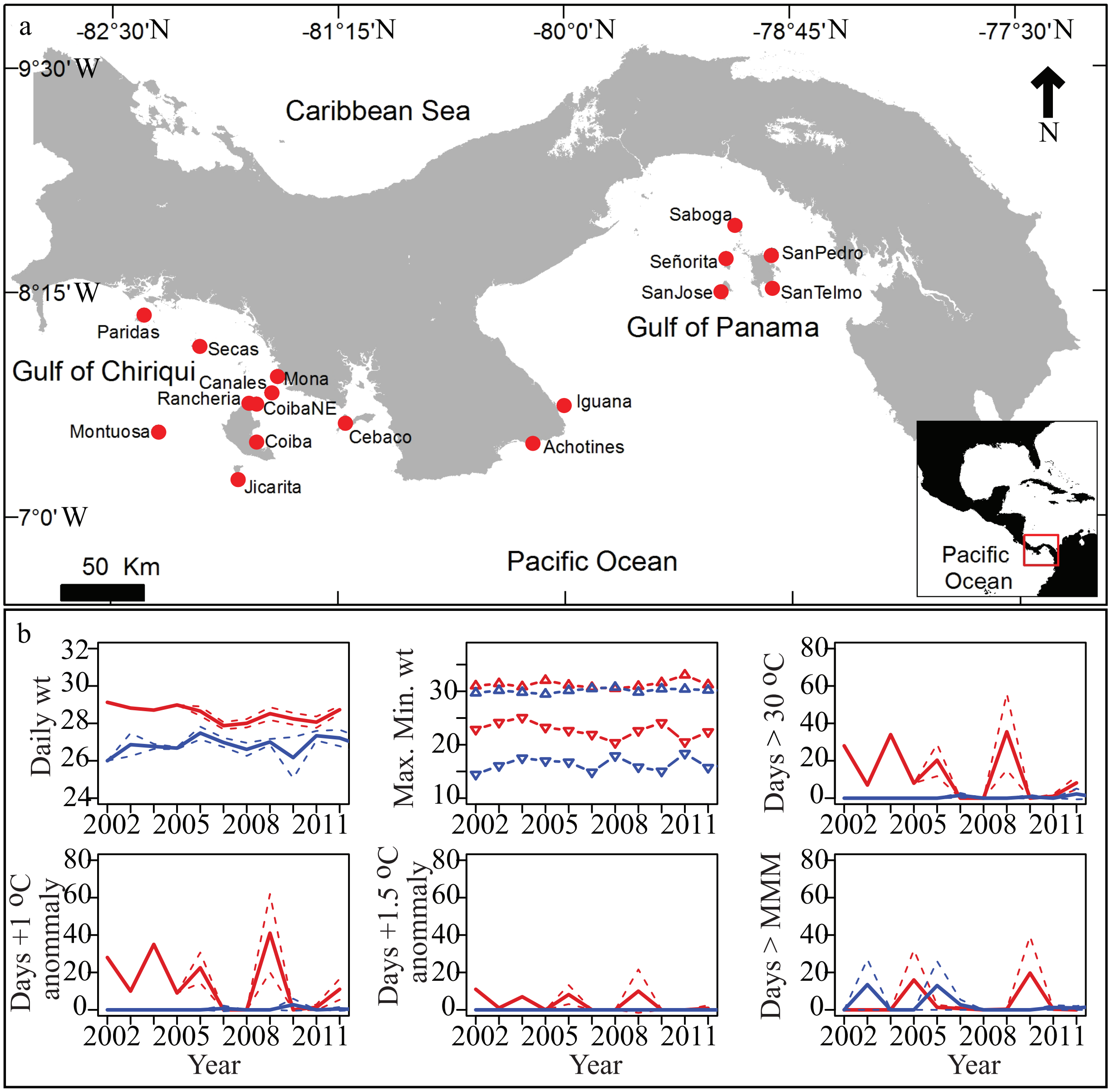


Figure 1.1. Location of the 17 monitored reefs in the Pacific Panama (a). (b) In situ water temperature ºC in the GP (blue) and in the GC (red): mean, maximum (up-pointing triangles) and minimum (down-pointing triangle), number of warm days (> 30 Co), + 1 Co and + 1.5 Co anomalies, and days away from maximum monthly mean (MMM). Mean as solid lines and standard deviation as dashed lines.

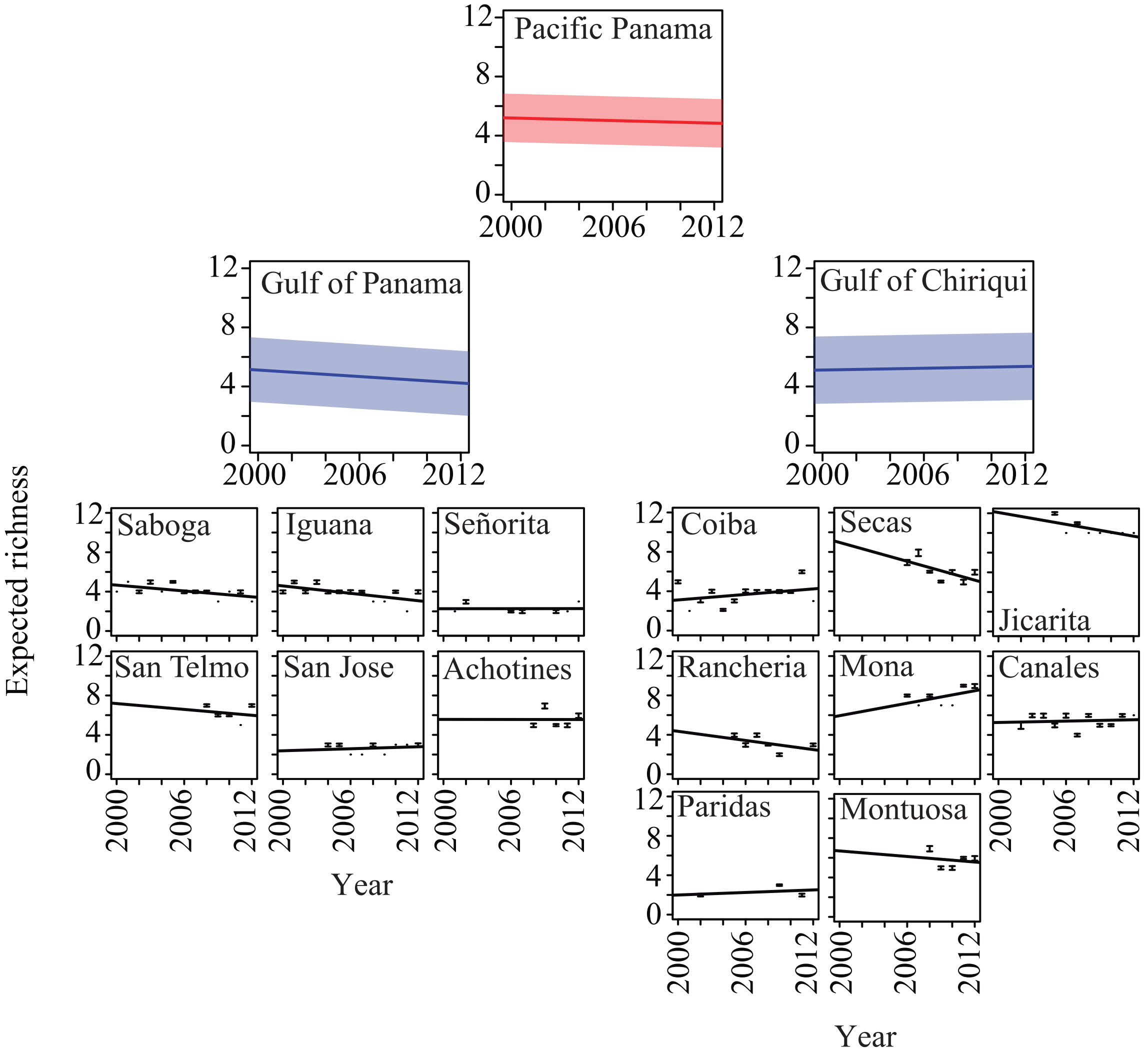


Figure 1.2. Expected species richness per year based on species accumulation curves. Individual reef trends in black lines, modeled trend for each gulf in blue lines and red for the entire study region, Pacific Panama. Shaded coloration for model standard error. There was a 2% annual decline in expected species richness in the Gulf of Panama.

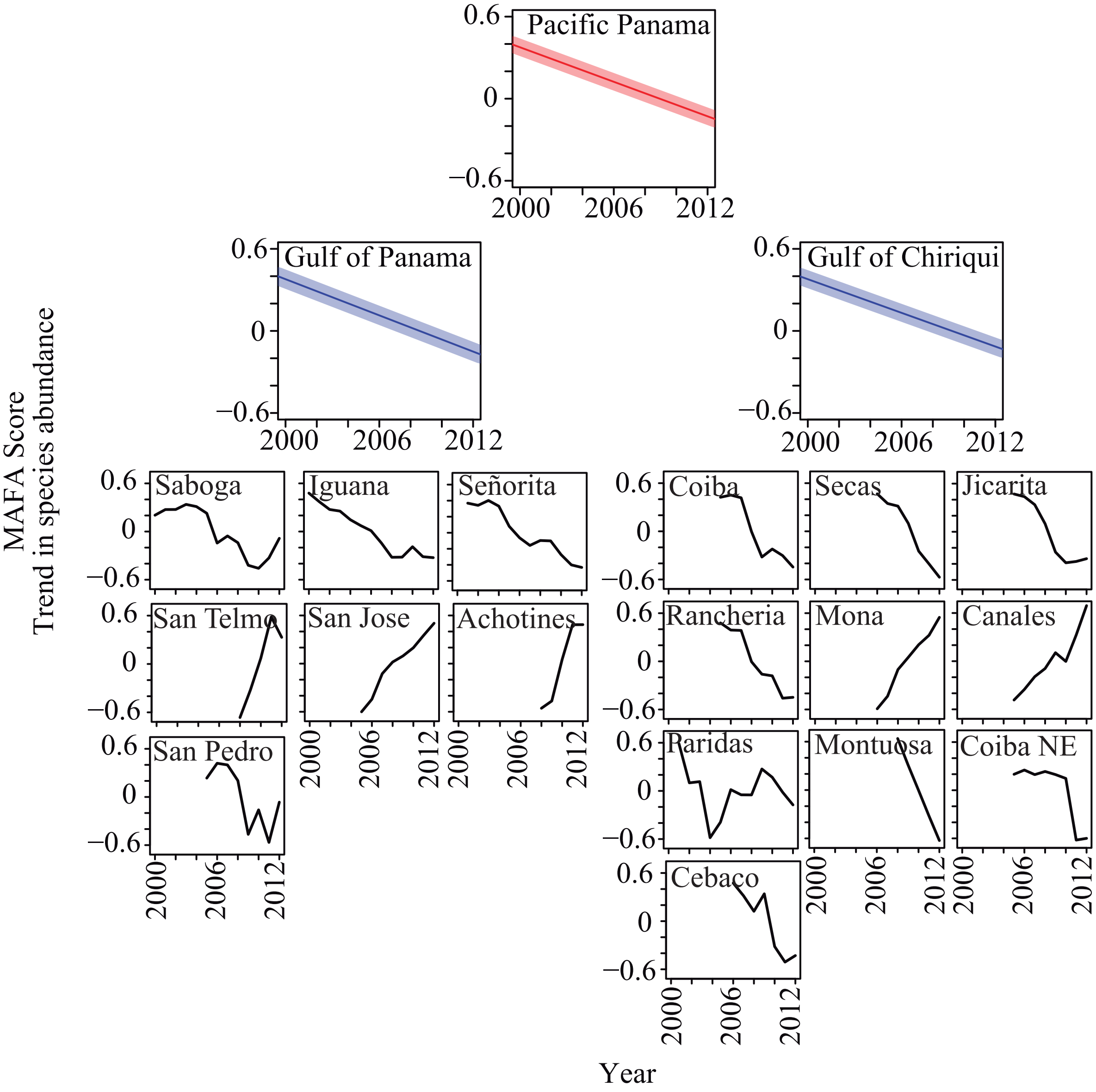


Figure 1.3. Temporal trends in species abundance (MAFA). Individual reef trends in black lines, model results for each gulf in thick black lines, modeled trend for each gulf in blue lines and red for the entire study region, Pacific Panama. Shaded coloration shows the model standard error. There was a 4% annual decline in species abundance at the country and at the gulf scales, with variation within individual reefs.

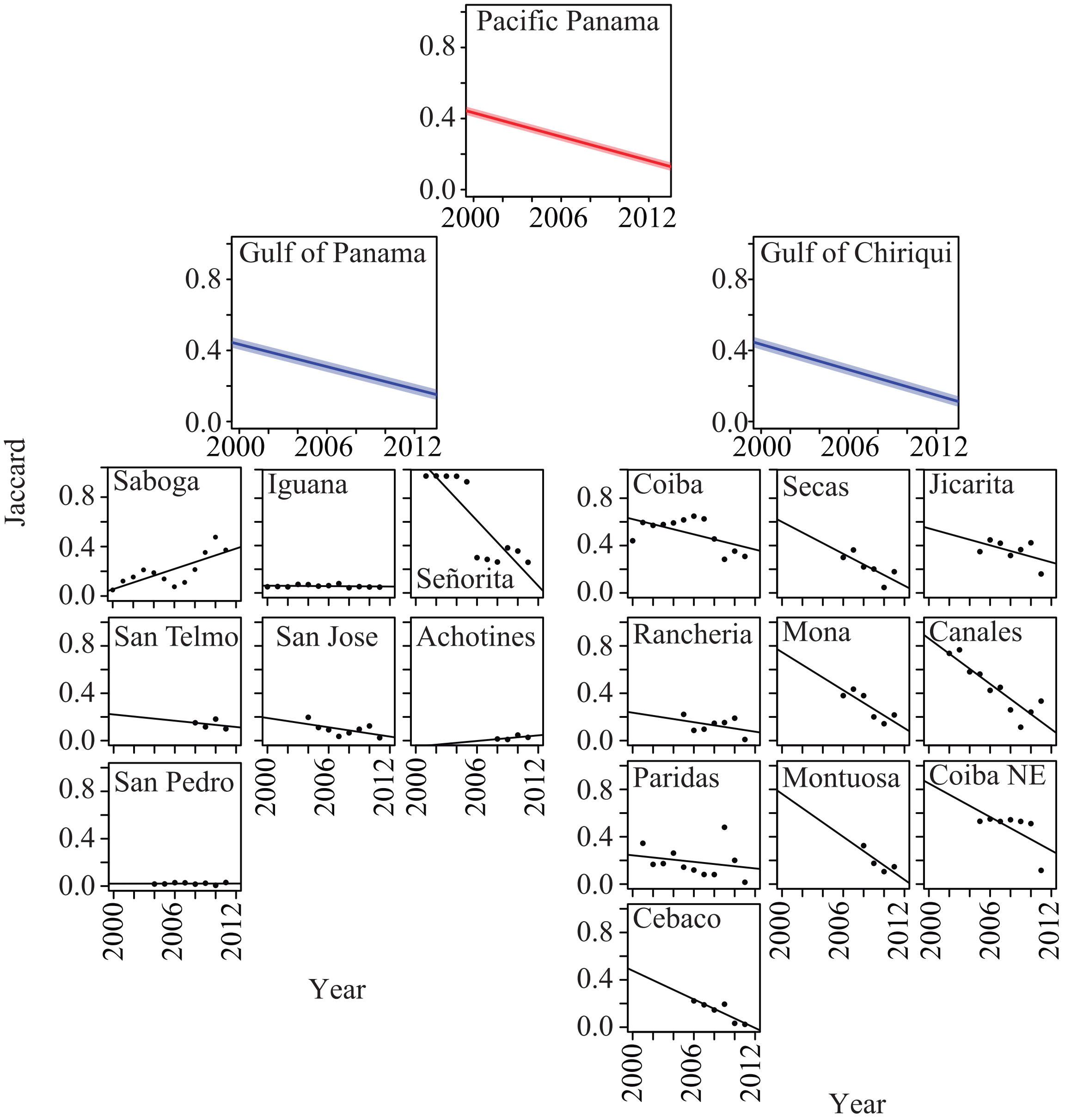


Figure 1.4. Temporal decline in beta diversity indicates significant changes in community structure at all studied scales. Individual reef trends in black lines, model results for each gulf in thick black lines, modeled trend for each gulf in blue lines and red for the entire study region. Shaded coloration shows model standard error.

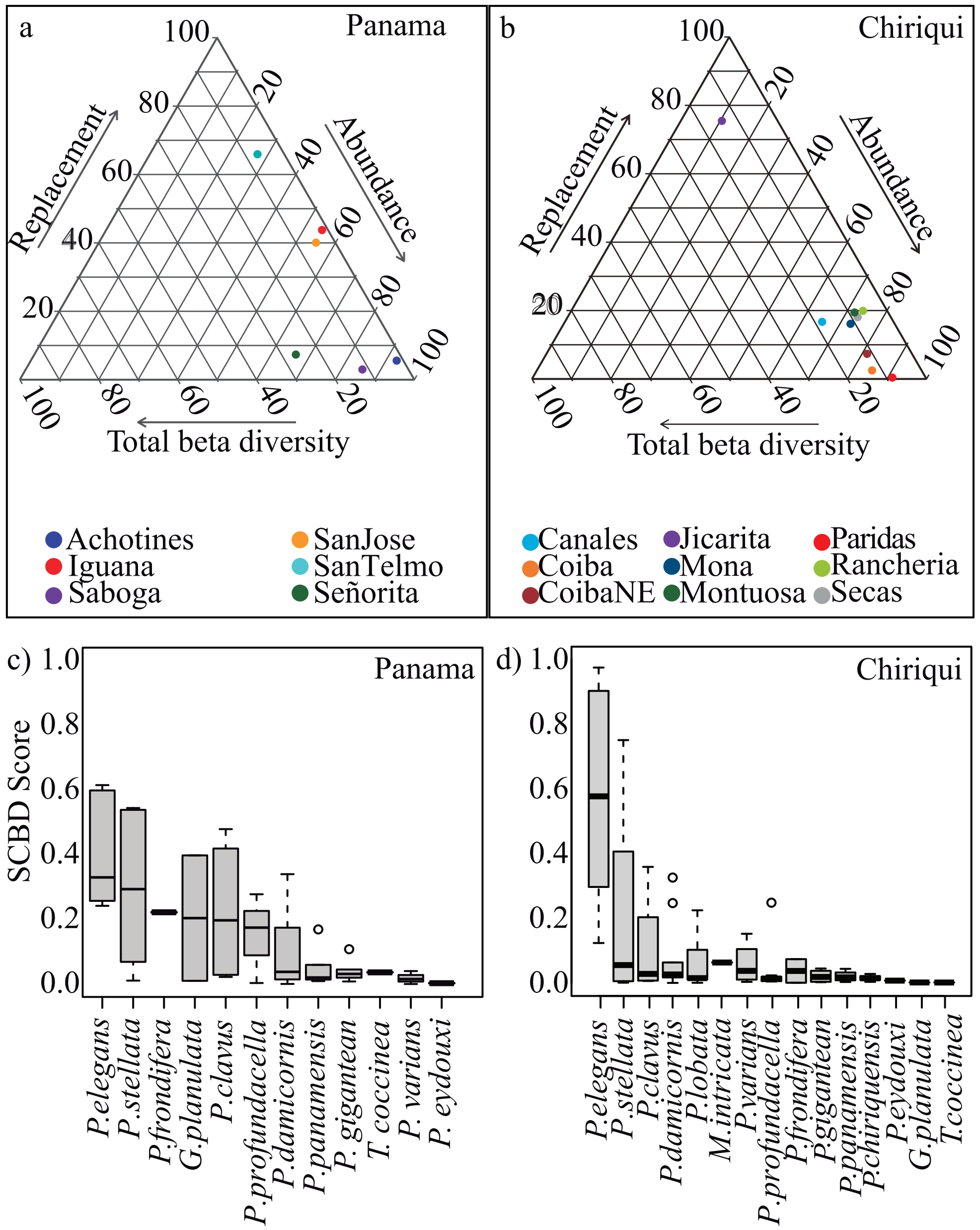


Figure 1.5. Components of temporal beta diversity. (a) Relative contribution of species replacement and changes in abundance (%) to the total temporal beta diversity for the GC and the GP (b), where most changes were due to a reduction in species abundance. Mean and temporal variation of the contribution of each species to temporal beta diversity changes in the GC (c) and the GP (d). These contributions were correlated between gulfs and not correlated with the species relative abundance. Species full names in Table 1.3.

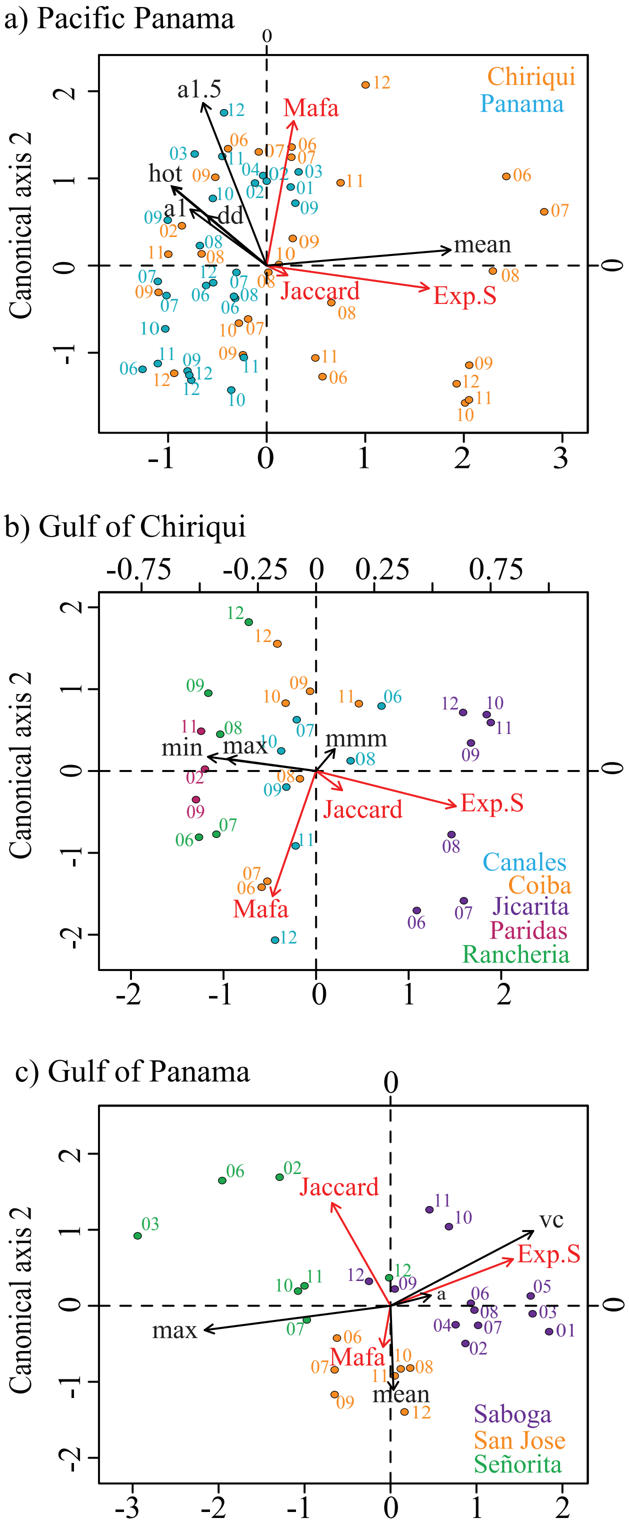
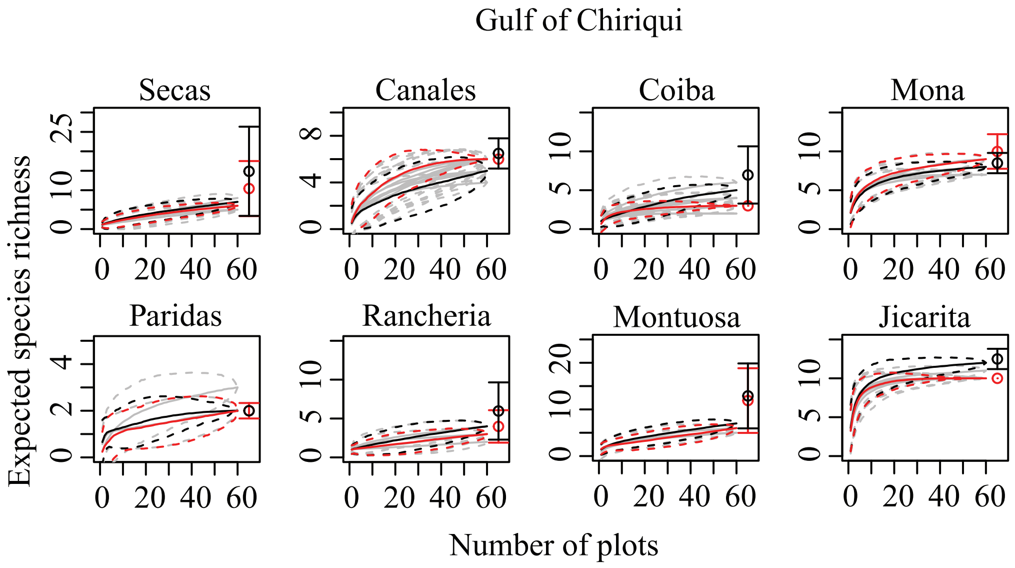
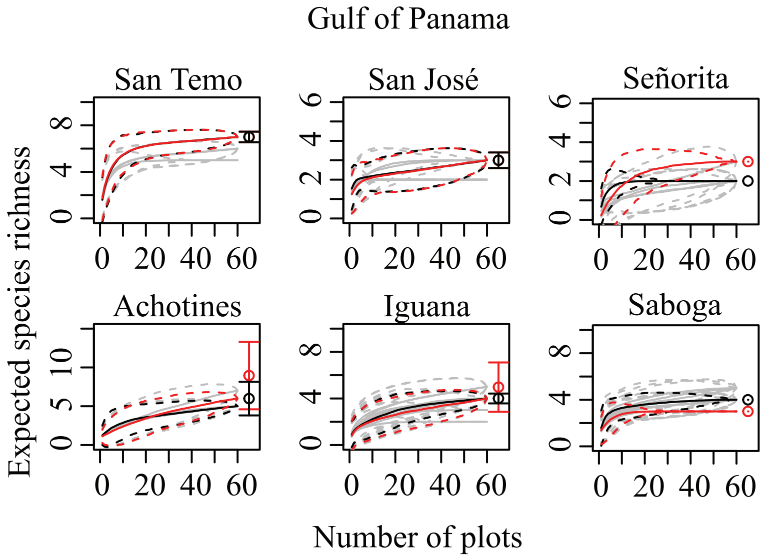
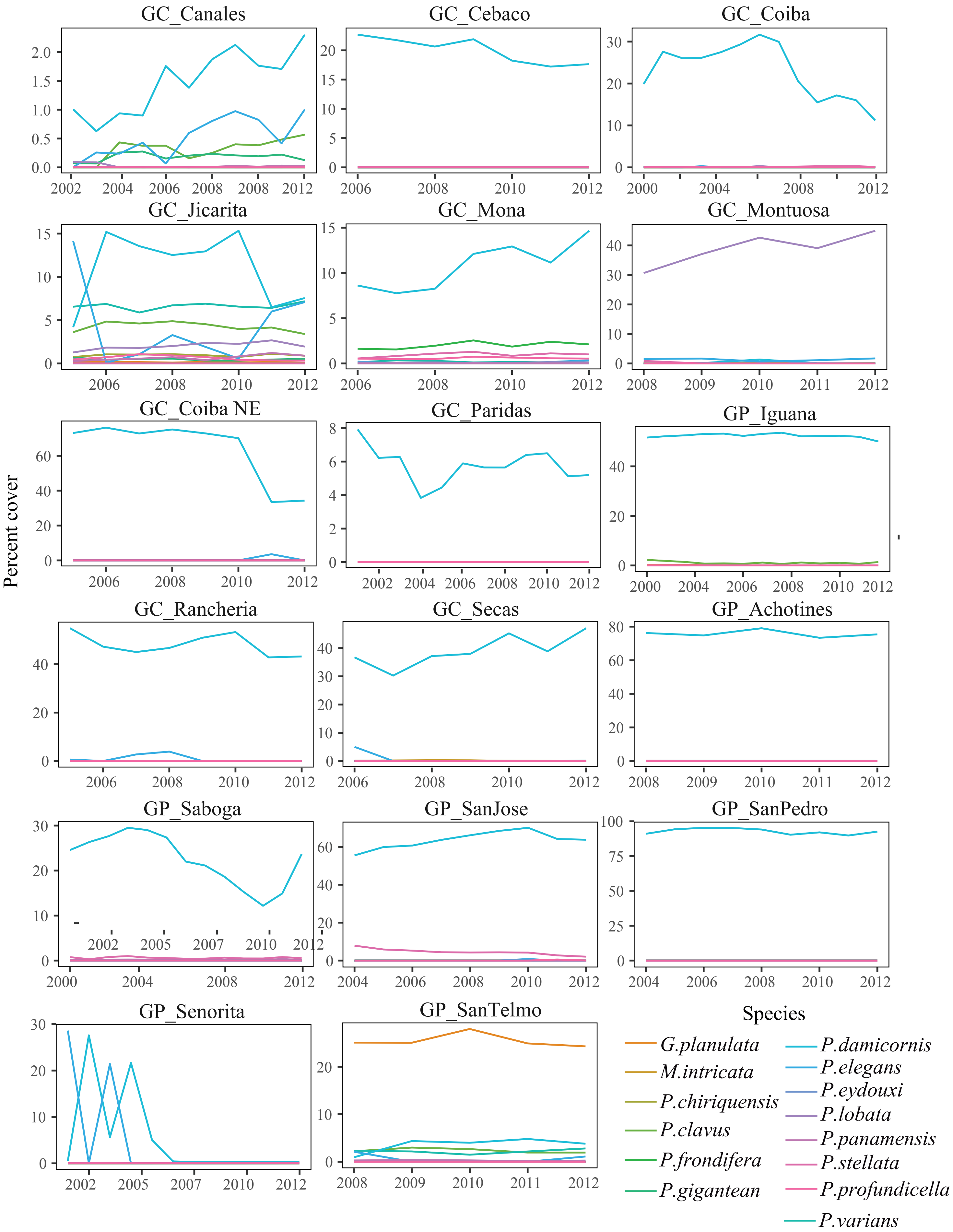


Figure 1.6. Redundancy analysis of the correlation between changes in diversity metrics (red arrows): MAFA (species abundance), Jaccard (temporal turnover) and Exp.S (Expected species richness) with temperature parameters as explanatory variables (black arrows): a1 (anomalies above 1 oC), a1.5 (anomalies above 1.5 oC), dd (degree days), hot (number of days above 30oC), MMM (Maximun Monthly Mean), vc (variation coefficient), mean, maximum and minimum water temperature recorded from insitu temperature loggers. Model for the entire study area (a), from five reefs in the Gulf of Chiriqui (b) and from three reefs in the Gulf of Panama (c).

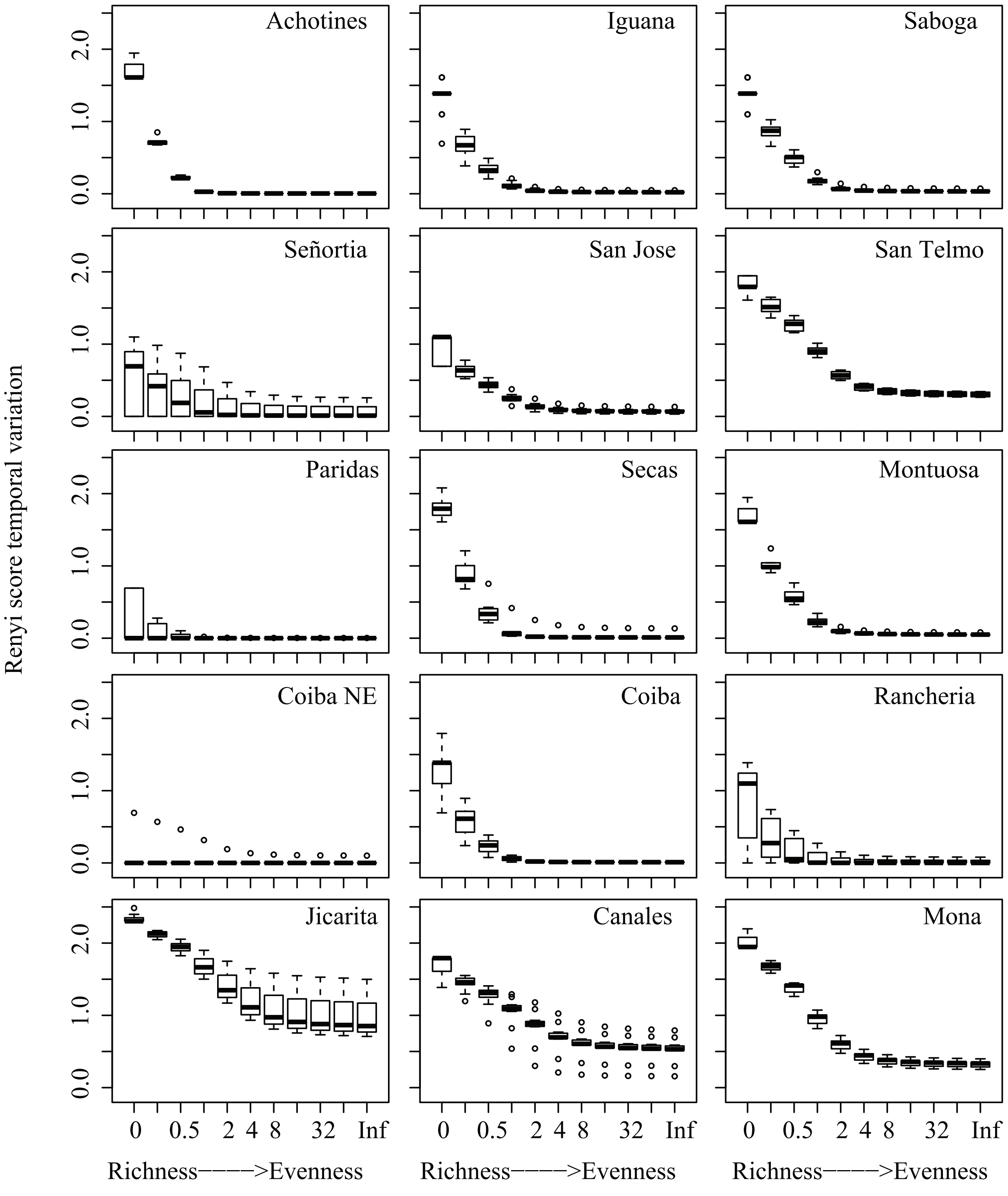




Supplemental 1.1. Species accumulation curves for each reef on the Gulf of Panama and the Gulf of Chiriqui. Black lines indicate the first monitoring year, red lines the last monitoring year (2012) and grey lines the years in between. Confidence intervals of each year are represented with dashed lines. In open circles Chao estimate and its confidence interval for the total number of estimated species, including unseen ones (black for first year and red for last year of monitoring).



Supplemental 1.2. Timeline of scleractinian species percent cover on each studied reef within the Gulf of Panama (GP) and the Gulf of Chiriqui (GC).



Supplemental 1.3. Temporal variation in Renyi diversity profiles for each reef; species richness had a higher temporal variation than species evenness, except for Jicarita. Most reefs had a steep decline from species richness to evenness, reflecting the high degree of domination by a single species, to a lesser extent in Jicarita and Canales reefs.

Linking statement 1

Sleractinian coral species (reef building corals) have been the subject of many studies in the Tropical Eastern Pacific. The knowledge of their biology and ecology provided by these studies facilitates the interpretation of long-term trends and a better understanding of the reef's functioning. In contrast, their counterparts, octocorals, were ignored by science for over a century. Hector Guzman, Odalisca Breedy, Catalina Gómez, and Andrew Gonzalez started an initiative to fill this gap in knowledge in 2008. The following chapter contributes to this initiative by studying the basic reproductive biology of octocoral species. The information presented in this chapter will allow us to interpret more complex ecological processes for octocorals, as is now possible for coral reefs.

CHAPTER TWO

Reproductive traits and their relationship with water temperature in three common octocoral (Anthozoa: Octocoralia) species from the Eastern Tropical Pacific

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Abstract

Octocoral species are the main foundation species in rocky wall coral communities off Pacific Panama, however, little is known about their biology and nothing is known about their reproductive biology. This study quantifies the annual variation of reproductive traits in three common octocoral species from the Tropical Eastern Pacific with different colony morphology: the sea whip *Leptogorgia alba* (Duchassaing & Michelotti 1864), the sea rod *Muricea austera* (Verrill 1869) and the sea fan *Pacifigorgia ferruginea* (Breedy & Guzman 2004). Samples were collected on a monthly basis from March 2015 to February 2016 at a site affected seasonally by upwelling in the Gulf of Panama. The reproductive peak of *L. alba* showed a two-month delay relative to the coldest period (February), while the reproductive period of *M. austera* and *P. ferruginea* occurred one month before the warmest period (July). *Muricea austera* oocytes were constantly produced, with relative large size and in significant quantities (~ 0.34 mm in diameter and ~33 oocytes per polyp). *Leptogorgia alba* and *P. ferruginea* had distinct reproductive seasons with fewer (~ 3 and 2) and smaller oocytes (~0.05 and 0.22 mm respectively). It is suggested that the three species are broadcast spawners and that spawning is related to water temperature.

Introduction

Octocorals are the main foundation species in rocky walls off the Tropical Eastern Pacific (TEP) (Bayer, 1953; Cantera et al., 1987; Guzman et al., 2004, Guzman et al., 2008; Breedy & Cortes, 2008), and are found from the rocky intertidal to deep coral communities (Bayer, 1981; Alderslade, 1984). Their arborescent and branching morphology provides physical relief and biotic cover, attracting epibenthic marine invertebrates and demersal fish (Beasley, et al. 2003; Sánchez 2016). The TEP is known to be one of the octocoral hot-spots for species richness and abundance with endemic species found at particular sites within the region (Breedy & Guzman, 2003; Guzman et al. 2004, 2008; Guzman & Breedy 2008).

Both sexual and asexual reproduction has been reported for octocorals (Lasker, 1984; Kahng et al., 2011). However, sexual reproduction is thought to be the most important mode for maintaining population structure (Kahng et al., 2011). Within studied species a gonochoric reproductive mode, where individual colonies are either females or males, predominates across clades and climates (Kahng et al., 2011). Most species are broadcast spawners (Kahng et al., 2011), meaning that gametes are released into the water column to be externally fertilized. Few species, most of them from deep or cold habitats, reproduce as internal and external brooders (Kahng et al., 2011), where fertilization and embryogenesis occurs inside the polyps (internal) or on the colony surface (external) (Benayahu & Loya, 1983) (for reviews, see Benayahu et al., 1990; Kahn et al. 2011). Brooding species usually have extended breeding seasons, and tend to recruit locally (Harrison & Wallace 1990). On the contrary, broadcast spawners have distinct reproductive seasons (Brazeau & Lasker, 1989; Harrison & Wallace, 1990) and gamete dispersal is facilitated by marine currents and water flow (Stimson, 1978).

Octocoral species can have continuous gametogenesis with overlapping generations, indicated by the presence of more than one oocyte size class inside the polyp (*sensu* Dahan & Benayahu, 1997; Eckelbarger et al., 1998; Kahng et al., 2008), or can have annual reproductive cycles, with only one oocyte size class at a time (Orejas et al., 2007). Environmental cues are known to trigger synchronized spawning among polyps and colonies (Gori et al., 2007). Seasonal fluctuations in seawater temperature are considered the most important environmental factor controlling the reproductive cycle of coral species that live with seasonal changes (Brazeau & Lasker, 1990), and where gamete maturation is related to an increase in temperature (*sensu* Grigg ,1977; Beasley et al., 2003). Additionally, lunar phase has been related to spawning date (*sensu* Benayahu & Loya, 1983), and the day-night cycle to timing of egg release (Gori et al., 2007).

Other factors have been proposed to determine the reproductive biology of octocorals. Orejas et al. (2007) related the reproductive strategy to colony morphology in Antartic octocorals. On the other hand, Ribes et al. (2007) proposed that investment in gonad development was related to resource availability in the abundant *Eunicella singularis* in the Mediterranean Sea. However, studies on the reproductive biology of octocorals are not evenly distributed (Kahng et al., 2011); most of them come from the Indo-Pacific, and to a lesser extent from the Mediterranean, the Red Sea, the Caribbean, and the Antarctic (Kahng et al., 2011). Today, the reproductive biology of octocorals from the TEP and how it relates to local ecological process is still unknown.

The Tropical Eastern Pacific (TEP) is considered a hotspot for octocoral diversity and abundance (Guzman et al., 2004, 2008; Guzman & Breedy, 2008; Gomez et al., 2014). Octocoral rich communities within the TEP include the Gulf of Panama (Guzman et al.,

2008) and Gulf of Chiriqui (Guzman et al., 2004) in the Republic of Panama, Costa Rica (Breedy & Guzman, 2003; Breedy & Cortés, 2008), Colombia (Sánchez & Ballesteros, 2014), including the islands of Gorgona (Sánchez et al., 2014), and Malpelo (Sánchez et al., 2011). In the TEP species with branching and fan morphologies inhabit rocky walls from intertidal to deep environments (Breedy & Guzman, 2002, 2007, 2011, 2015, 2016; Breedy & Cortés, 2008; Breedy et al., 2009).

Significant declines in the abundance of the main marine foundation species at TEP have been reported lately; In recent years a significant decline in octocoral populations was observed in Pacific Panama, accounting for a 25% reduction in the number of colonies without changes to the community structure (Gomez et al., 2015). Significant declines in percent cover were also reported for reef building coral species, but with significant changes to community structure (Chapter 1).

Since reproduction strategy is a key aspect in the population dynamic and biogeography of marine organisms (Grosberg & Levitan, 1992; Giangrande et al., 1995), knowledge about the reproductive biology of common octocoral species is necessary to understand their life history and their ability to recover from disturbances.

This study describes for the first time the reproductive biology of three common and morphologically distinct octocoral species within three genera from the TEP. We quantified colony fertility, reproductive output, spawning seasonality and its relationship to water temperature in the sea whip *Leptogorgia alba* (Duchassaing & Michelotti, 1864), the sea fan *Pacifigorgia ferruginea* (Breedy & Guzman, 2004), and the sea rod *Muricea austera* (Verrill, 1869) inhabiting rocky walls off eastern Panama.

Methods

Study area and organisms

Within the TEP the Gulf of Panama (GP), in eastern Panama, is a particularly interesting habitat. This gulf is subject to annual wind-driven upwelling. At the beginning of the year the northern-winds push away surface water, the thermocline reaches the surface reducing water temperature by up to 10 ^{o}C and bringing nutrient-rich water to shallow environments (D´Croz & O´Dea, 2007). This upwelling does not happen in western Panama where a high elevation mountain range prevents the northern winds resulting in no change in the thermocline depth, water temperature and nutrient contents in surface water throughout the year (D´Croz & O´Dea, 2007). The GP is also known to have the lowest salinity levels in the entire TEP (Pennington et al., 2006), and is considered one of the world hotspots for ocean acidification. This is mainly due to low pH in the surface water linked to sulfuric and nitric acids originating from heavy shipping traffic near the entrance of the Panama Canal (Hassellöv et al., 2013) and to the upwelled waters rich in CO_2 (Manzello et al., 2008; Manzello, 2010).

Las Perlas Archipelago Marine Special Management Zone, within the Gulf of Panama, is the second largest archipelago in the TEP and probably the second highest area of coral diversity in the Marine Conservation Corridor of the Tropical Eastern Pacific (Guzman et al., 2008). It is composed of 250 islands and islets, most of them uninhabited, and covered by relatively pristine tropical forest (Guzman et al., 2008). In this area octocoral species are more common in coral communities than in coral reefs (Guzman et al., 2008), and are found attached to basaltic rocks from 5-15 m of depth. There are 38 octocoral species reported (Guzman et al., 2008) and they share the substrata with sponges, crustose coralline algae, and algae turf. Semidiurnal marine tides change within a six meters-range. There are two distinct seasons, the dry season from mid-December to mid-April, and the wet season for the remainder of the year, with an annual precipitation of 2158 mm (D'Croz & O'Dea, 2007).

Gomez et al. (2014) described the population dynamics of 14 common octocoral species from Pacific Panama, which included species from the genera *Leptogorgia, Muricea* and *Pacifigorgia*. In general, *Leptogorgia* species had faster dynamics, with high recruitment and mortality rates, compared to *Pacifigorgias*, which had intermittent dynamics, and to *Muricea*, which had very slow dynamics, with low mortality rates and scarce recruitment (Gomez et al., 2014). In western Panama *L. alba* is one of the most common octocoral species, with up to 40 colonies per m^2 (Gomez et al., 2014). This abundant species is widely distributed along the TEP, where it is found from Baja California to Ecuador (Breedy & Guzman, 2007). After disturbance it shows a fast recovery (Gomez et al., 2015) implying efficient reproduction. *Leptogorgia alba* (Figure 2.1a) is associated with eleven symbiotic species that inhabit the external part of the colony, including echinoderms (Cantera et al., 1987; Neira et al., 1992; Alvarado & Fernandez, 2005), arthropods (Cantera et al., 1987, Ramos, 1995), molluscs and crustaceans (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).

Muricea austera (Figure 2.1b) is also widely distributed in the region, being found from Baja California to Peru (Breedy & Guzman, 2016). It is a common species but not as abundant as *L. alba*. In western Panama *M. austera* has a mean density of 0.6 colonies per m^2 and up to six colonies in a single m^2 (Gomez et al., 2014), and due to its slow dynamics it can easily be locally extirpated after disturbance (Gomez et al., 2015). *Pacifigorgia* *ferruginea* (Figure 2.1c) is known to live along the Pacific coasts of Costa Rica, Panama and northern Colombia (Vargas et al., 2008). The presence of zooxanthellate algae in these species has not been studied, however, we presumed they are azooxanthellate, as all studied species within the Tropical Eastern Pacific are (Van Oppen et al., 2015). This assumption is supported by the type of habitat they occupy, with high siltation levels (Gomez et al., 2014) and deeper environments (Breedy & Guzman 2002, 2007, 2006) that are not occupied by zooxanthellalte scleractinians (Gomez et al., 2014).

Sampling protocol

We studied the annual variation of reproductive traits in three common octocoral species from Pacific Panama (*L. alba*, *M. austera* and *P. ferruginea).* Ten haphazardly selected samples of each species were collected on a monthly basis from March 2015 to February 2016 at a depth of 15 m off Elefante Island (8.406835° N, 78.802712° W), which is located within the moderate diversity area in the southeastern area of Las Perlas MPA (Guzman et al., 2008). Samples were 10 cm fragments cut-off haphazardly from individual colonies located more than 5 m apart. After collection, samples were immediately stored in 70% alcohol until processed. Samples were collected from colonies of the largest size classes (>10cm heigth in *L. alba*, >10 cm width in *P. ferruginea* and *M. austera*) found at Elefante. Monthly collections were performed 2-3 days prior to each new moon to account for the potential correlation between moon phase and gonad development. In the laboratory, samples were directly stained with aniline blue and azocarmin (as in Guzman & Holst, 1993). Ten arbitrarily chosen polyps per sample were dissected under a stereoscope *Zeiss Stemi 2000-CS* with a 10x eyepiece. We measured the following parameters: colony fecundity (frequency of polyps with oocytes), reproductive output (number of visible oocytes within each polyp), and oocyte diameter (all oocytes within each polyp). Individual oocyte diameter was measured by photographing oocytes using a mounted High Definition camera (*AxioCamER C5S*) and measured by using the software ZEN (ZEIS Software). Oocytes with a diameter above the third quartile of the entire distribution were identified as "large" oocytes. Average number of large oocytes per polyp was also quantified for each sample. Gonadal output can be affected by annual growth (Coma et al., 1995); therefore dissection of polyps at the apical ends was avoided. Additionally, the average branch width of each sample was quantified after measuring its width at three different locations with an electronic caliper to 0.01 mm.

To test any potential correlation between *in situ* water temperature and oocyte development, a temperature logger *HOBO* water temperature Pro v2 (ONSET computers) was installed at 15 m depth by attaching it to a permanent rod at the study site. The logger was set to record water temperature every 30 minutes during the entire year of study.

Statistical analyses.

Sample means for each reproductive trait were tested for significant differences among months using a Tukey's Honest Significant Difference method with the R software function "TukeyHSD" within the "stats" package in R.3.1 version (R Core Team, 2015). To identify the reproductive season for each species, a general trend in reproductive trait variation and its correlation to water temperature (explanatory variable) was calculated with a MAFA analysis (Minimum-Maximum Autocorrelation Factor Analysis). MAFA is a type of principal component analysis designed for time series data. It calculates the main temporal trend that summarizes a multivariable dataset in the best possible way and correlates it to an explanatory variable (Zuur et al., 2007). MAFA summarized the temporal variation of reproductive variables (oocyte size, colony fecundity and reproductive output) in a single temporal trend, which was tested for correlation with monthly mean water temperature. MAFA analyses were performed in Brodgar software (Highland Statistics). *In situ* daily mean, maximum and minimum water temperature was calculated from data collected by the HOBO logger.

Results

Reproductive traits of *L. alba* reached their maximum values in February. From February to March colony fertility was significantly reduced ($p<0.001$, Tukey's HSD); in February 66 ± 0.05% (mean ± standard error) of the polyps within a colony contained oocytes, compared to only 2 ± 0.01% in March. Reproductive output followed the same pattern; in February there was an average of 2.5 ± 0.3 oocytes per polyp, which was significantly greater ($p<0.01$) than in March, when there were only 0.02 ± 0.01 oocytes per polyp. Oocyte size was also significantly greater in February with a mean diameter of 0.05mm ± 0.01 (Figure 2.2, Table 2.1). The significant decline in colony fertility and reproductive output between February and March indicated that oocytes were spawned to the water column during that period. Large oocytes were ≥ 0.08 mm in diameter.

Leptogorgia alba oocytes were round with a pale, almost transparent white coloration and turned pink after staining. The oocytes were located inside the gastrovascular cavity (Figure 2.1a). After dissected from colonies previously fixed on 70% ethanol, oocytes were negatively buoyant. *Leptogorgia alba* showed a distinct reproductive seasonality that started in September and ended in February (MAFA trend axis 1 autocorrelation axis1= 0.77, $p<0.04$). Oocyte development was negatively correlated to water temperature with a two-month time-lag (MAFA canonical correlation -0.86) (Figure 2.3a, Table 2.2). Gonads developed through the end of the rainy season reaching maximum numbers and diameter before spawning during the coldest months, between February's and March' new moons; during this period colony fertility was reduced to zero. There was no sign of internal fertilization and no larva was observed inside polyps during dissections. Sampled colonies had an average branch thickness of 1.13 ± 0.02 mm (mean ± standard error).

Reproductive traits of *P. ferruginea* reached their maximum mean value in June; during this month 73 ± 11% of the polyps contained oocytes, with a significant decline by July ($p<0.001$), when only 29 ± 13% of the polys were fertile. A significant decline in reproductive output was also seen after June ($p<0.05$): there were an average of 1.5 ± 0.3 oocytes per polyp in June, 0.4 ± 0.2 in July, and 0.03 ± 0.03 in August. Oocytes were significantly bigger in June ($p<0.05$) with a mean diameter of 0.22 ±0.03mm. The significant reductions in reproductive traits indicated that most oocytes were spawned to the water column after June's new moon (Figure 2.2, Table 2.1). Large oocytes were ≥ 0.28 mm in diameter.

Pacifigorgia ferruginea showed a distinct reproductive period starting in April and ending in July (MAFA trend axis 1 autocorrelation axis1= 0.79, $p<0.05$) and it was positively correlated to an increase in water temperature with a one-month time-lag (correlation coefficient= 0.45) (Figure 2.3b, Table 2.2). There was no evidence of internal fertilization, and no larva was observed within polyps during dissections. Eggs were located inside the polyp gastrovascular cavity, were round and white in color and turned pink after staining (Figure 2.1b). After dissected from colonies previously fixed on 70% ethanol, oocytes were negatively buoyant. Sampled colonies had an average branch thickness of 1.35 ± 0.04 mm.

Muricea austera had constant oocyte production. We found no evidence for a significant difference in colony fertility over the year ($p>0.05$) with 82 ± 0.1% of polyps containing oocytes all year round. However, mean reproductive output was significantly higher in June ($p<0.05$ for all pairwise compassion) with an average of 33 ± 4 oocytes per polyp. Oocytes were bigger in April ($p<0.05$) with a mean size of 0.36 ± 0.03 mm in diameter and 0.34 ±0.03mm in June ($p<0.05$) (Figure 2.2, Table 2.1). Large oocytes were defined as larger than 0.35 mm in diameter.

As with *P. ferruginea*, the reproductive peak of *M. austera* was observed in June (MAFA trend axis one autocorrelation axis1= 0.80, $p<0.05$), and was correlated to an increase in water temperature (cc 0.70) (Figure 2.3c, Table 2.2). Oocytes were attached to the gastro vascular filaments, were round and beige in coloration and turned pink after staining (Figure 2.1c). There was no sign of internal fertilization, no larva was observed inside polyps during dissections. After dissected from colonies previously fixed on 70% ethanol, oocytes were negatively buoyant. Oocyte size distribution within each polyp was highly variable with a mean variation coefficient of 26.5 ± 4.5. Small, medium and large oocytes co-occurred within a polyp all year around, which indicates continuous oogenesis and overlapping generations in the population. Sampled colonies had an average branch thickness of 7.01 ± 0.14 mm.

Discussion

This manuscript is the first contribution to the study of the reproductive biology of octocoral species in the Tropical Eastern Pacific. The three species had different patterns in the variation of their reproductive traits and these differences may be linked to intrinsic differences in their population dynamics and the structure of these marine benthic communities. Gomez et al. (2014) studied the population dynamics of two of these species in the Gulf of Chiriqui (GC). Although there are important environmental differences between the GC and the Gulf of Panama (GP) (where the present study took place) some generalities can be made.

In the GC *L. alba* is a very common species, widely distributed, and with fast population dynamics; having relatively high number of recruits, high mortality rates and faster growth rates compared to other 13 octocorals in the gulf (Gomez et al., 2014). It can be concluded that *L. alba* larvae have high survivorship, due to its low reproductive output (2.5 ± 0.3 oocytes per polyp) and high recruitment rates (Gomez et al., 2014). *L. alba* reproductive output compares to different populations of the commercially important Mediterranian red coral *Corallium rubrum*, which produces around 2 oocytes per polyp (Vighi, 1972; Santangelo et al., 2003; Tsounis et al., 2006). By contrast, *M. austera,* which is also a common species, was reproductively active all year around and produced an average 33 ± 4 oocytes per polyp during the reproductive peak. This reproductive output is considerably greater compared to most reported species (Chia & Crawford, 1973; Coma et al, 1995) except for the North Atlantic pennatulacean *Umbellula lindahli,* which produces about 200 oocytes per polyp (Tyler et al., 1995).

Gomez et al. (2014) showed that adult *M. austera* colonies had low mortality and unseen recruitment over a two-year period in the GC, even after experiments that cleared the substrate to reduce competition for space (Gomez et al., 2015). Therefore, it is likely that *M. austera* larvae stay in the water column relatively long periods of time or that they have high mortality rates, which are then compensated by the high survivor rate of adult colonies, which is the mechanism proposed by Einum et al., (2004). *Muricea austera* had constant development of oocytes and a high variability of egg sizes within each polyp, which could indicate overlapping generations. Other octocorals are known to have immature oocytes year-around with mature eggs developing only during the seasonal oogenic cycle (Kahng et al., 2011), which seems to be the case for this species, which had significantly larger eggs during its reproductive peak. Year-around breeding has been reported for species with different life histories, such as the invasive-like species *Carijoa riisei* (Kahng et al., 2008), the zoozanthelate sea whip *Leptogorgia virgulata* (Adams, 1980) the leather coral *Lobophytum crassum* (Fan et al., 2005) and in deep water species such as *Anthomastus ritteri* (Cordes et al., 2001) and *Pennatula aculeata* (Eckelbarger et al., 1998).

Oocyte diameter was noticeable different among studied species. *Leptogorgia alba* and *P. ferrginea* had relatively small eggs (with a maximum diameter of 0.23 mm and 0.44 mm respectively). *Leptogorgia alba´s* oocytes were smaller than Mediterranean red coral *Corallium rubrum´s* oocytes (0.33 mm) (Vighi, 1970), the smallest reported by Orejas et al. (2002). By contrast, *M. austera´s* oocytes were larger than those from the southwest Pacific *Heliophora coerulea* (0.92 mm), the largest are within the range reported by Orejas et al. (2002). Differences in colony morphology could explain differences in oocyte size. Average branch thickness in *L.alba* was 1.13 mm, 1.35 mm in *P. ferruginea* and 7.91 mm in *M. austera*, which could indicate that eggs size is limited by the available space in the gastrovascular cavity, as proposed by Brazeau & Lasker (1990). However, egg size can vary even among species with similar polyp size (Gutierrez-Rodrioguez & Lasker, 2004).

Additionally, oocyte size variation among species has been related to reproductive strategy and fertilization success (Kruger et al., 1998), with large oocytes (> 0.6 mm) generally occurring among brooding species with internal fertilization (Orejas et al., 2002) and among species with non-feeding and non-pelagic larvae (Hartnoll, 1975; Orejas et al., 2002; Cordes et al., 2001). Large oocytes are also associated to greater nutrient storage, which may be required for larvae with prolonged development, especially with azooxanthellae planula (Wallace, 1985; Coma & Lasker, 1997, Gutierrez-Rodruigez & Lasker, 2004), which may be the case for *M. austera*.

Water temperature also seems to be an important factor in controlling the reproductive cycle of octocoral species in Pacific Panama, as it does in other tropical regions like the Caribbean (*sensu* Brazeau & Lasker, 1990) and in temperate regions (*sensu* Tsounis et al., 2006; Ribes et al., 2007). Gamete maturation in the *P. ferruginea*, and an increase in oocyte production in *M. austera* were correlated to an increase in water temperature, as described for *Leptogorgia hebes* (Beasley et al., 2003) and the two Muriceas studied by Grigg (1977) in California. The expected spawning of these two species occurred during the warmest months, which are associated with fewer nutrients in the water column (D'Croz & O'Dea, 2007). The expected spawning time for *L. alba* was after February's new moon, which coincided with the onset of the upwelling season. During this period, south winds (towards the equator) drive surface waters offshore (Ekman transport) (Fiedler & Lavín, 2017), which induces upwelling of cooler, nutrient rich deep water (D'Croz & O'Dea, 2007).

Octocorals inhabiting temperate regions tend to have a single season for gamete maturation during the warm months, which suggest that gonad development is related to resource availability (Ribes et al., 2007). Although the present study took place in a tropical area, it also took place in a region with an annual upwelling cycle, which significantly increases nutrient concentration during the first fourth months of the year (D'Croz & O'Dea, 2007). *Leptogorgia alba* and *P. ferruginea* had a single spawning season, however, only *L. alba* spawned during the nutrient-rich period. Therefore, *L. alba* larvae could be benefiting from these nutrients, by having heterotrophic larvae for example, if spawning time is considered an adaptive function to maximize productivity and/or minimize mortality (Hughes & Cancino, 1985). *P. ferrufinea*, on the other hand, could be minimizing offspring mortality by avoiding predation while spawning during the nutrient-poor season, as reported for *Alcyonium digitatum* in the Irish Sea (Hartnoll, 1975).

It is important to note that data for the present study was collected during a single year. Future studies are needed to test inter annual variation in reproductive traits (oocyte size, number and release time). Additionally, the study took place in an upwelling area, where water temperature decreases and nutrient levels increase during the first four months of the year (D´Croz & O´Dea, 2007). The species we studied inhabit a broader region, populating areas without this localized upwelling (Guzman et al., 2004, 2008). Due to the strong differences in oceanographic conditions between upwelling and non upwelling areas (D´Croz & O´Dea, 2007), and to the relationship between spawning time and water temperature, the same species could have different spawning behavior in areas with different oceanographic conditions. Future studies are needed to test this observation. During the present study oocytes were dissected from inside the polyp cavity and no larvae were observed in any of the studied species, therefore, we assumed that they are broadcast spawners. However, future studies are needed to confirm this assumption, as well as the dioecious condition of the species.

This study contributes to the general understanding of three common octocoral species inhabiting ecologically important marine ecosystems off the Tropical Eastern Pacific. This basic biological knowledge is one piece of information needed to understand the ecological consequences of population declines reported for the area (Gomez et al., 2015) and the resilience of these species to disturbances.

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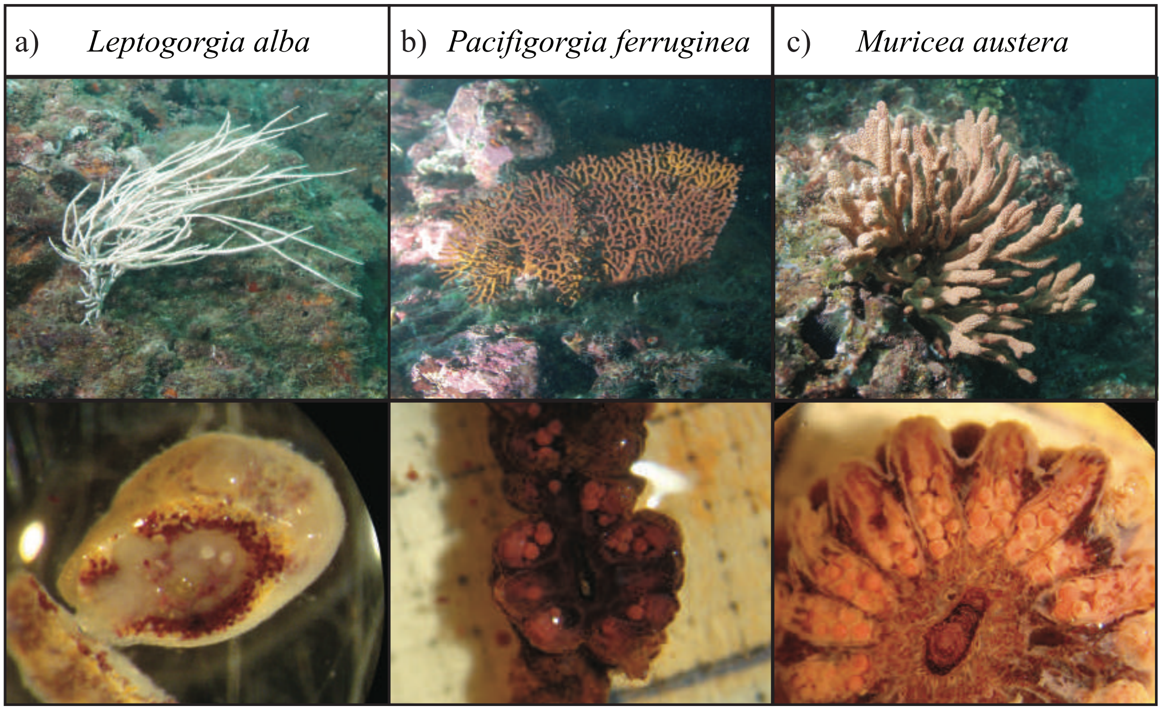
Table 2.1. Mean and standard error of reproductive traits of common octocoral species in the Gulf of Panama. Colony fecundity was measured as the proportion of polyps with eggs within a colony; reproductive output as the mean number of oocytes per polyp; and oocyte size was measured at the diameter (um).

Reproductive trait	*Leptogorgia alba*	*Pacifigorgia ferruginea*	*Muricea austera*
Sample size (number of colonies dissected)	112	112	112
Colony fecundity	66 ± 0.05%	73 ± 11%	82 ± 0.1%
Reproductive output	2.5 ± 0.3	1.5 ± 0.3	33 ± 4
Oocyte size (mm)	0.05 ± 1	0.22 ± 30	0.34 ± 30
Max. Oocyte size (mm)	0.23	0.44	0.99
Breeding Period	February	June	Continuous with peak in June

Table 2.2. Temporal trend summarized by a MAFA (Minimum-maximum Autocorrelation Factor Analysis) for three common octocoral species, its relationship to mean monthly water temperature and to individual reproductive traits.

		Leptogorgia alba	*Pacifigorgia ferruginea*	*Muricea austera*
MAFA Main temporal trend	Autocorrelation Axis 1	0.77	0.79	0.80
	Axis 1 p-value	0.04	0.04	0.03
	Correlation to temperature	-0.86	0.45	0.70
Canonical correlations of response variables to main MAFA trend	Colony fertility	0.87	0.88	0.42
	Reproductive output	0.98	0.83	0.50
	Oocyte size	0.88	0.95	0.60
	Number of "large" oocytes	0.47	0.88	0.75



a) *Leptogorgia alba*

b) *Pacifigorgia ferruginea*

c) *Muricea austera*

Figure 2.1. Colony and large oocytes inside gastro vascular cavity of a) *Leptogorgia alba,* b) *Pacifigorgia ferruginea* and c) *Muricea austera* at 15 m of depth in the Gulf of Panama, Tropical Eastern Pacific.

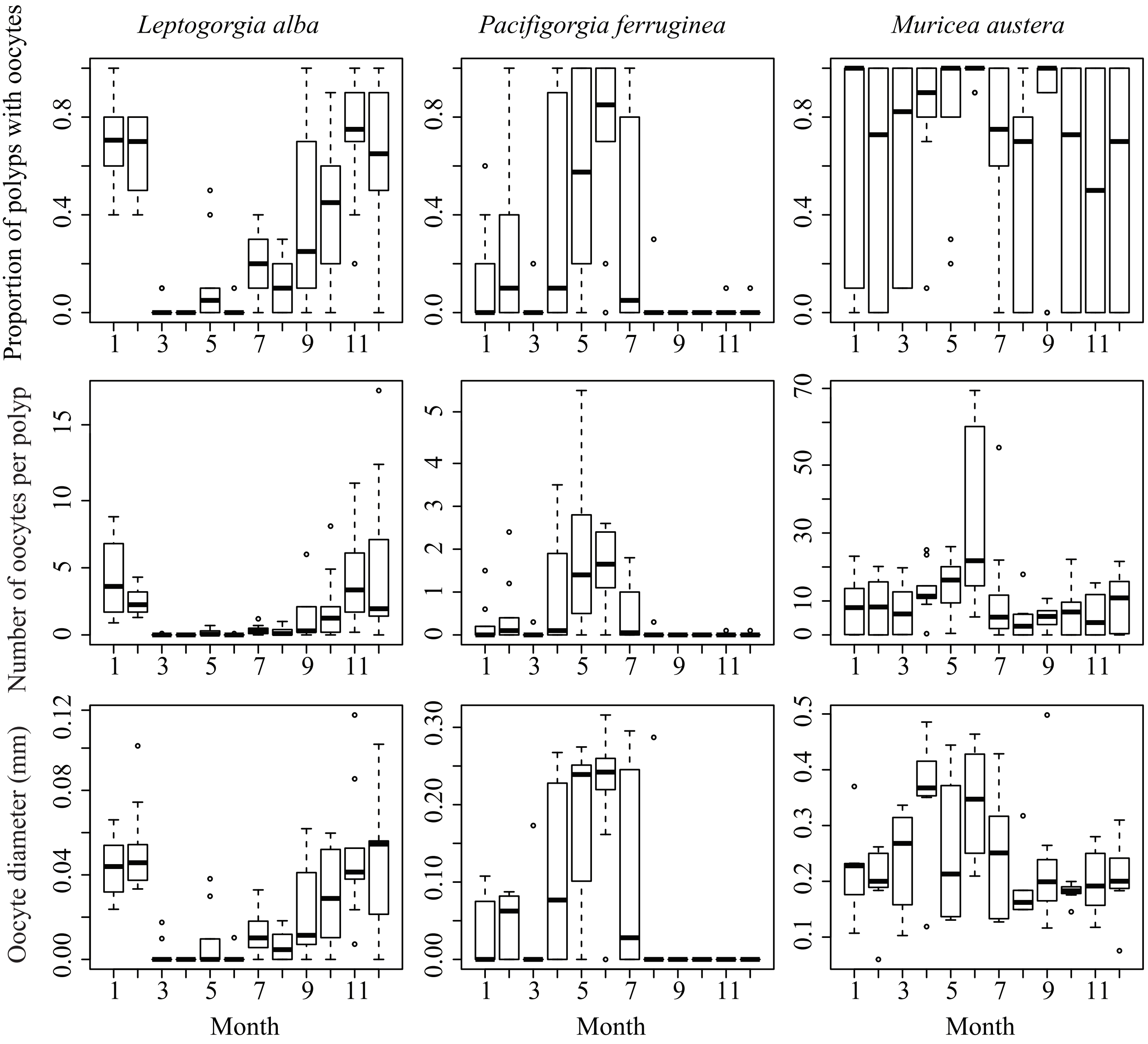


Figure 2.2. Temporal variation of reproductive traits; Colony fecundity (proportion of polyps with oocytes), reproductive output (number of oocytes per polyp), and oocyte size (diameter) for three common octocoral species off the Pacific coast of Panama: *Leptogorgia alba, Pacifigorgia ferruginea* and *Muricea austera*. Notice axis scales are different among species.

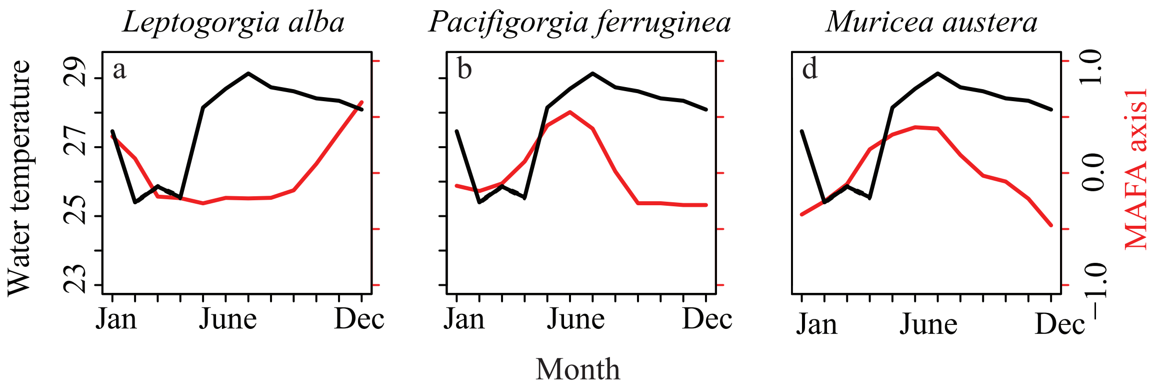


Figure 2.3. Reproductive season annual trend (red line) of three common octocoral species off the Pacific coast of Panama. Trend calculated from MAFA (Minimum-Maximum Autocorrelation Factor analysis) taking into account the temporal variation of colony fecundity (proportion of polyps with oocytes), reproductive output (number of oocytes per polyp), and oocyte size (diameter). HOBO water temperature monthly mean (black line) off Elefante Island at 15 m of depth, from March 2015 to February 2016.

Linking statement 2

From Chapter 1 and previous publications we know about the oceanographic differences between the Gulf of Chiriqui and the Gulf of Panama. In Chapter 2 we learned that octocoral reproduction is related to oceanographic conditions and recruitment rates reported for the studied species are not explained by their reproductive output. The third chapter of this thesis studies factors that could be limiting octocoral recruitment under different oceanographic settings, as well as recruitment timing, and whether recruitment follows the spawning season described in Chapter 2.

CHAPTER THREE

The effect of population density, space availability, community composition, and season on octocoral recruitment in Tropical Eastern Pacific communities

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Abstract

Octocorals are common and understudied habitat builders that inhabit rocky wall communities off the Tropical Eastern Pacific; the factors that limit their distribution and recruitment, however, are poorly understood. To evaluate the potential effects of space availability, population density, and community composition on colony recruitment in different oceanographic settings, unaltered permanent plots and experimentally cleared plots were monitored twice a year in eight octocoral communities living in shallow (≤ 20 m depth) rocky walls affected by different seasonal upwelling regimes off the Pacific coast of Panama. A total of 951 colonies that included 13 species were monitored over 18 months (June 2014 - January 2016) and 323 recruits from 11 species were observed. The most common species were the sea whips *Leptogorgia alba* and *Leptogorgia cofrini*. Overall, recruitment was positively correlated with adult density, but this seems to be true only when space is not a limiting factor. When species were analyzed independently, the effect of density was found in all common species; however, the effect of space was only observed in the sea fan *Pacifigorgia irene* and the sea whip *Leptogorgia alba. L alba* showed seasonal recruitment related to a decrese in water temperature and following a previously described spawning season, suggesting that local processes and population density promote population growth. It is concluded that octocoral adult colony density promotes recruitment with space as a limiting factor, especially in highly diverse environments.

Introduction

The Tropical Eastern Pacific is considered a hot spot for octocoral diversity (Bayer, 1953; Guzman et al., 2008). Rich and abundant communities are usually found from intertidal to deep waters (Breedy & Guzman, 2002), where they create a complex tri-dimensional habitat for many other taxa (e.g. Patton, 1972; Cantera et al., 1987; Neira et al., 1992; Ramos, 1995; Sanchez, 2016). However, little is known about what limits their distribution and abundance (Gómez et al., 2014). After extensive taxonomic reviews (e.g. Breedy & Guzman, 2002, 2007,2011, 2015, 2016; Breedy et al., 2009) a regional initiative was started to study the biology and ecology of these understudied but ecologically important species (e.g. Abeytia et al., 2013; Gómez et al. 2014, 2015; Sanchez & Ballesteros, 2014; Sanchez et al., 2014; Chapter 2). This initiative coincided with recent increases in octocoral abundance in decaying Caribbean coral reefs (e.g. Edmunds et al., 2016; Privitera-Johnson et al., 2015).

The factors and mechanisms that regulate population size, especially of marine sessile organisms in open populations remains poorly understood (Hixon et al., 2002, 2012; Sibly & Hone, 2002). One important factor that limits populations is the recruitment of new individuals into local communities (Yoshioka, 1996; Hixon et al., 2002; Kuffner et al., 2006). Historically, recruitment variation in sessile marine species has been related to adult reproductive output, larvael mortality before settlement, and larval dispersal (Gaines & Bertness 1992). However, more recent models predict that the distribution of marine sessile species in open populations, when recruits are supplied from the pelagic pool of larvae, depends on the rate of larval settlement, adult growth rate and the proportion of free space (Muko et al. 2001). Therefore, local diversity in these communities may be limited by dispersal and recruitment, rather than by species interactions (Lee & Bruno 2009, Palardy &Witman 2014).

Although recruitment processes are relatively well understood for scleractinian corals inhabiting the Tropical Eastern Pacific (e.g. Richmond, 1997; Glynn et al., 2000; Guzman & Cortes 2001, 2007), recruitment of octocorals is not as well understood (but see Gómez et al., 2014). In octocorals, the role of recruitment in controlling local octocoral abundance and community structure has been linked to habitat type. In isolated deep octocoral communities, recruitment is considered the major determinant of abundance and structure, while in rocky intertidal areas, competition for space, predation, and physical disturbances are more relevant (Grigg, 1988).

Factors that limit or control octocoral recruitment in other regions described so far include: competition for space (e.g. Birkeland, 1974; Opresko, 1974), especially when survival rates are very low (Grigg, 1970) or where the substratum is fully occupied (Grigg, 1977); strong predation of larvae (Grigg, 1977) and physical disturbances (Grigg, 1988), including strong grazing pressure from the sea urchin *Diadema antillarum* (Yoshioka, 1996); the availability of functional larvae due to limitations in ecological connectivity driven by the dynamics of oceanic currents at different scales (Jordan-Dahlgren, 2002); and priority effects (Edmunds et al., 2016). Species colonization in suitable habitats may depend on random local processes, when space availability coincides with larval arrival, creating the spatial variation (Edmunds et al., 2016) and mono-species patches (pers. obs.) that characterize these communities.

In coral reefs, where the coral biogenic framework mainly occupies the space, space availability becomes a limiting factor for octocoral recruitment (Kinzie, 1973). In other cases, however, recruitment may be limited by other factors. Kuffner et al. (2006) determined that the presence of filamentous cyanobacteria, rather than space availability, reduced survival and recruitment of the octocoral *Briareum asbestinum* in the Caribbean. Grigg (1988) also determined that recruitment was not space-limited in Hawaii's deep-water octocoral communities.

Recruitment may also be related to adult local densities. In the Caribbean, various studies have reported a positive correlation between adult density and recruitment (e.g. Yoshioka, 1996). However, the deep-water communities studied by Grigg (1988) showed the opposite, where recruitment was low and constant and independent of population density. The presence of this relationship can depend on the type of habitat; this study is focused on the shallow (≤ 20 m) rocky subtidal areas off the Tropical Eastern Pacific. The relationship between recruitment and adult density can also be species specific. In the Caribbean, recruitment was positively correlated with adult density when all octocoral species were pooled together, however, when species were analyzed independently, this relationship was true for some species but not for others (Privitera-Johnson et al., 2015). If this relationship is not consistently present for all species, we could expect to have recruits from species not present in the adult phase, especially if there is space available to be colonized.

The reproduction mode of each species can also influence larvae behavior and settlement. Two main modes of reproduction have been described for octocorals (Kahng et al., 2011): in spawning species female colonies release unfertilized eggs into the water column (e.g. Kahng et al., 2008; Grigg, 1977); in brooding species eggs are fertilized and brooded inside or on the female colony and released into the water column as planulae (e.g. Coma et al., 1995; Brazeau & Lasker, 1990). Spawned gametes that are released into the water column can travel to distant communities, independently of adult abundances, while brooded larvae may settle near the parental colony (Privitera-Johnson et al., 2015), which will increase this density-recruitment relationship.

The present study focuses on demography and space as limiting factors for octocoral recruitment, was well as recruitment seasonality and timing. If recruitment is local, a high local recruitment rate can be expected after spawning. In contrast, low and constant recruitment rates can be an indicator of more open populations and long-lived larvae with the capability to postpone settlement and long-distance dispersal, as seen in the deep-water communities studied by Grigg (1988).

It is beyond the scope of this study to determine how relatively open these communities are. We hypothesize that octocoral recruitment in Pacific Panama is limited by adult density and by space availability, and that these limitations are present under different oceanographic settings; the gulfs of Panama and Chiriqui. We also hypothesize that octocoral recruitment is seasonal and that it follows the reproductive season of each species (described in Chapter 2).

Methods

Study Area

The Tropical Eastern Pacific (TEP) extends from the Sea of Cortez to northern Peru (Robertson & Cramer, 2009). Octocoral communities that inhabit its rocky walls have high levels of diversity, abundance, and endemism (Bayer, 1953; Guzman et al., 2008), and are usually found in high-energy environments such as seamounts and rocky walls, where they are exposed to strong currents, waves, and swell (Breedy & Guzman, 2002). Within the TEP there are a variety of biodiversity hotspots, including Costa Rica (Breedy & Guzman, 2003; Breedy & Cortes, 2008), Panama (Guzman et al., 2004, 2008; Gómez et al., 2014), Colombia (Sanchez et al., 2011; Sanchez et al., 2014), and Ecuador (Breedy et al., 2009 b).

In Pacific Panama, octocoral communities are found in each of its two oceanographically distinct gulfs: the Gulf of Chiriqui (GC) (Guzman et al., 2004; Gómez et al., 2014) and the Gulf of Panama (CP) (Guzman et al., 2008). These gulfs, which lay at the same latitude, are divided by a ~100 km wide peninsula and experience significant seasonal environmental differences (Reijmer et al., 2012; D'Croz & O'Dea, 2007). About 2.8 million years ago, when the Isthmus of Panama closed completely (O'Dea et al., 2016), the American tropical ocean was divided into the Caribbean Sea and the Pacific Ocean, significantly shifting wind and oceanic currents, altering the worldwide climate (Haug & Tiedemann, 1998). High-elevation mountains formed exclusively in western Panama, serving as a windshield in the Gulf of Chiriqui, while leaving eastern Panama unprotected and affected by narrow wind-jets coming from the north. This wind displaces superficial water in the Gulf of Panama and creates an annual wind driven upwelling during the boreal winter (D'Croz & O'Dea, 2007). While water temperature is relatively constant in the shallow areas of the GC, the wind driven upwelling causes water temperatures to decline up to 18 ^{o}C during the first four months of the year in the GP (see Chapter 1). This decrease in temperature is associated with a peak in primary productivity that only occurs within this gulf (D'Croz & O'Dea, 2007). Therefore, octocoral recruitment can be limited seasonally by the upwelling. Despite the marked differences in water temperature variation between the gulfs, the entire Pacific coast of Panama has a distinct dry season (mid-December to mid-April) and a rainy season (mid-April to mid-December) (Guzman et al., 2004).

To determine if space, season, or adult density were related to octocoral recruitment at local (site) and gulf levels, four sites within each gulf were chosen as study sites. Site selection was based on previous surveys that identified these areas as medium to high diversity areas (Guzman et al. 2004, 2008): Roca Hacha, Jicarita, Prosper, and Catedrales in the GC (for detailed site information see Gómez et al., 2014), and Pedro Gonzalez, Elefante, San Telmo, and Galera in the GP (Table 3.1). Study sites where chosen based on previous descriptions (high diversity areas on Guzman et al., 2004, 2008), and based on their geographical distribution to have equitable and well-dispersed sampling on both gulfs.

Sites in the GC are located inside the largest marine protected area in Pacific Panama: Coiba National Park (CNP), which was created in 1992 and declared a UNESCO World Heritage site in 2005. CNP is an archipelago made up of nine large islands and about 30 islets (Guzman, et al. 2004). The CNP study sites are located inside the archipelago's no-take designated area, where fishing is prohibited. The GP sites are located at Las Perlas Archipelago, a Marine Special Management Zone created in 2007. This archipelago is composed of 250 small and large, mostly uninhabited, basaltic rock islands and islets that lay within the 50m isobaths (Guzman et al., 2008).

Experiment set-up

At each site, eight 1m^2 permanent plots were randomly selected and marked with stainless steel rods fixed into the substrate with underwater cement (see Gómez et al., 2014, 2015). Plots were spaced more than 5 m apart to increase the independence among them. At each site, four of the plots were experimentally cleared by brushing the rock surface with wire brushes, removing all space-competing sessile organisms to artificially increase space for octocoral settlement. The other four plots were left unaltered and used as controls. After the initial set-up, control and experimental plots were photo-monitored every six months from June 2014 to January 2016; eight high-resolution digital pictures were taken per plot. Each picture was taken at a distance of 80 cm from the substrate, which ensured enough picture quality to observe recruits on the computer screen. Pictures were taken with the aid of a PVC quadrat, divided into eight proportional grids (0.42 x 0.30 m) totalling 1 m^2 and specially designed to accommodate the permanently fixed rods. This method ensured that we could photograph the same location over time. The camera was mounted on a stainless-steel tripod to maintain a constant distance from the substrate (see Gómez et al., 2014).

Pictures were taken with a digital high-resolution camera (Nikon D-80, 10.2 megapixels) fitted with a wide-angle lens and two strobe flashes inside an Ikelite underwater case with a DSLR TTL system for light regulation. Pictures were processed and analyzed in the computer; the eight pictures corresponding to each plot were pasted as mosaic images using the *Picasa* software version 3.9 (Google Corporation). We used the mosaic images (Supplemental 3.1) to identify all octocoral colonies present at the study plots to the species level. A unique ID was assigned to follow each colony over time. Species identification was done both in the field and in the lab with the aid of sclerite analyses (Vargas et al., 2010) and expert advice. Species abundance and number of recruits for experimental and control plots were quantified during each monitoring. In this study, a recruit was defined as a small colony (< 4 cm) that was not present in survey *t* but was present in survey *t+1.* Water temperature was recorded *in situ* every 30 minutes with the HOBO Water Temperature Pro v2 Data Logger (Onset Computers), which was deployed at each site during the entire research period.

Analysis

A generalized linear mixed effect model was used to estimate the combined effect of adult density (D, centered data), gulf (G, Gulf of Panama and Gulf of Chiriqui), and space availability (T, experimental and control) on total recruitment with plot and site as random factors as follows: *Recruitment ~ density + gulf + treatment + density* x *gulf* x *treatment,* with plots nested within sites as random effects. We expect to find a positive relationship between recruitment and density, as well as recruitment and space availability, with no difference between gulfs.

The same model was also applied individually to each of the common species. The models were fitted using the function *lmer* within the lme4 package (Bates et al., 2015) in R software (R Core Team, 2015). Models were run using the Poisson distribution for count data. An additive model was compared to the interaction model using function *anova* to test the significance of each interaction, and the best fitted model was chosen based on the AIC criterion.

A mixed effect model was used to test recruitment differences between sampling seasons (June 2014 – January 2015, June 2015 – January 2016; and January 2015 – June 2015), gulf, treatment and temperature, with sites as a random factor. Since there are significant differences in the timing of reproduction of these species (see Chapter 2), individual models were created for each species. An additive model was compared to the interaction model using function *anova* to test the significance of each interaction, and the best fitted model was chosen based on the AIC criterion. Models where fit using the R function *lme* within the nlme package (Pinheiro et al., 2016) in R software version 3.2.2 (R Core Team, 2015).

Results

A total of 951 octocoral colonies were identified: 446 in the Gulf of Panama and 505 in the Gulf of Chiriqui, including 13 species. A total of 323 new recruits from 11 species were recorded during the study period. The sea whip *Leptogorgia alba* had the greatest number of recruits (n = 139), both in the GP (n = 88) and the GC (n = 51), followed by the sea whip *Leptogorgia coffrini* with 91 recruits, and the sea fan *Pacifigorgia cairnsi* with 17 recruits (Table 3.2). Study plots at San Telmo in the Gulf of Panama had the greatest number of recruits (n = 88), mostly within the genus *Leptogorgia* (88.6%), followed by Roca Hacha (GC, 55 recruits), and Elefante (GP, 51 recruits) (Table 3.2). All recruits observed during the study period were present as adult colonies within each study site and no new species were recorded. Recruits from *Pacifigorgia eximia* and *Leptogorgia* *cuspidata* were not recorded although adult colonies were observed inside and outside study plots (Table 3.2). During the study, four plots were lost at Galera (two controls and two experimental), therefore, mean species abundance and recruitment per m^2 for this site were calculated with the remaining four plots.

Recruitment as a factor of gulf, space availability, and adult density

In a general GLMM model in which species were pooled together, we found a significant three-way interaction between adult density, gulf (GP, GC), and treatment (control, experimental) on the number of recruits ($\beta = 0.184$, SE = 0.04, $p < 0.0001$) (Table 3.1, Figure 3.1). In general, there was a positive correlation between number of recruits and adult density at the site level ($\beta = 0.15$, SE = 0.03, $p < 0.0001$), as well as a general effect of treatment ($\beta = -0.39$, SE = 0.2, $p < 0.05$), with more recruits observed at both gulfs in experimentally disturbed plots, where space was artificially increased. However, the presence and strength of these correlations varied between gulfs and treatments. In the Gulf of Panama, both experimental and control plots showed a significant correlation between adult density and number of recruits. However, in the Gulf of Chiriqui this correlation was only true for experimental plots; adult density was not correlated with recruitment in control plots (Table 3.3, Figure 3.1).

The same type of model was applied to the most abundant species: *L. alba*, *L. coffrini* and *Pacifigorgia ferruginea* in both gulfs, *Carijoa riisei* only in GP, and *P. cairnsi*, *Pacifigorgia irene*, and *Pacifigorgia rubicunda* only in the GC (Table 3.4, Figure 3.2). Recruitment of *L. alba* showed a significant interaction between the three explanatory variables (adult density, treatment, and gulf) ($\beta = 0.71$, SE = 0.17, n = 48, $p < 0.0001$), following the same pattern as the overall GLMM (Figure 3.2). For *L. coffrini* the three-way interaction was not significant and only the interaction between local density and gulf was important, therefore, treatment was dropped from the model. In both gulfs the recruitment of *L. coffrini* was positively correlated with adult density and independent of available space (treatment), however the correlation was stronger in the GC ($\beta_{interaction} = -0.32$, SE = 0.12, n= 34, $p < 0.01$) (Figure 3.2). None of the explanatory variables were correlated with the recruitment of the less abundant sea fan *P. ferruginea.*

Recruitment of *C. riisei* ($\beta_{density} = 0.11$, SE = 0.04, n = 7, $p < 0.01$)*, P. cairnsi,* ($\beta_{density} = 0.08$, SE = 0.03, n = 17, $p < 0.01$) *and R. rubicunda* ($\beta_{density} = 0.20$, SE = 0.10, n = 18, $p < 0.1$) was positively correlated with adult density and independent of space (treatment) (Figure 3.2). The recruitment of *Pacifigorgia irene* was correlated to both colony density and treatment, but without an interaction between these variables ($\beta_{density} = 0.53$, $SE_{density} = 0.24$, $\beta_{treatment} = -3.08$, $SE_{treatmenty} = 1.28$ both with n = 17, $p < 0.01$) (Figure 3.2).

Recruitment timing and seasonality

The general mixed effect model for *L. alba*, indicated that recruitment was significantly different between seasons ($p < 0.05$). The effect of gulf, and treatment were not significant ($p > 0.05$ in interaction and additive models), therefore these two variables were dropped from the model, keeping sites as a random factor *recruits ~ season + temperature + season* x *temperature,* with sites as a random factor. To avoid collinearity, the effect of different temperature parameters (mean, maximum, minimum, and variation coefficient) was analyzed in independent models. *Leptogorgia alb*a recruitment was more common from January to June 2015 (β= 0.94, SE = 0.3, $p < 0.05$) with a significant decline during June 2015-January 2016, and it was explained by temperature minima (β = -0.19, SE = 0.04, $p < 0.001$), and temperature variation coefficient (β = 3.46, SE = 2.10, $p < 0.001$), which were lower and more variable during June 2015-January 2016 compared to the other two seasons (Table 3.5).

Leptogorgia coffrini also showed significant seasonal differences in recruitment after accounting for the differences among sites, recruitment was significantly higher from June 2014 to June 2015 (β = 1.03, SE = 0.3, $p < 0.05$) with a significant decline during June 2015 - January 2016. However, significant differences in recruitment among seasons were not explained by any temperature parameters (Maximum, minimum, or variation coefficient).

Seasonal recruitment difference for *C. riisei* was only calculated for the Gulf of Panama, since there were no recruits in the Gulf of Chiriqui. Although there were more recruits from January to June 2015, the difference was not significantly different (Figure 3.4). All other studied species had no seasonal differences in recruitment, probably due to the low number of observed recruits per m^2 per season.

Water temperature differences among gulfs and sampling seasons

Water temperature was significantly different among sampling seasons and gulfs (June 2014 – January 2015, June 2015 – January 2016; and January 2015 – June 2015) (water temperature ~ season + gulf + season x gulf, $p < 0.001$ in two-way interaction).

During the post-upwelling season (January 2015 - June 2015) wt in the GP was 26 ± 3 ^{o}C with a 11 ^{o}C difference between maximum and minimum temperature and in the GC wt was 27 ± 2 ^{o}C with a difference of 10 ^{o}C between maximum and minimum. During the pre-upwelling season 1 (June 2014 -January 2015) wt for the GP was 28.2 ± 0.7 ^{o}C and 28.2 ± 0.6 ^{o}C for the GC. The pre-upwelling season 2 (June 2015 - January 2016) coincided with the beginning of one of the strongest documented El Niño ENSO events (Jacox et al., 2016) and during this season wt was 28.5 ± 0.1^{o}C for the GP and 29.2 ± 0.4 ^{o}C for the GC (Table 3.5, Figure 3.3). Hobo stations at Galera and Pedro Gonzalez (GP) were lost before the end of the study. Therefore, daily mean calculations for this gulf were computed using only the remaining stations at Elefante and San Telmo.

Discussion

From this study it can be concluded that overall recruitment in octocoral communities located on shallow rocky walls (≤ 20 m) in Pacific Panama was limited by the combined effects of adult density, space (treatment), and environment (gulf). Previous studies have analyzed these relationships independently (e.g. Birkeland,1974; Opresko, 1974; Yoshioka, 1996; Privitera-Johnson et al., 2015), reaching different conclusions. This is the first study, however, that takes into account the interaction among these three important factors, all of which are known to contribute to octocoral recruitment in the Tropical Eastern Pacific.

The recruitment-density association was not present in colonies recruiting on control plots in the Gulf of Chiriqui. As can be seen in Table 3.1, the GC sites tend to have higher adult density and species richness than sites in the GP. Additionally, the benthic space in the GC is highly occupied by sponges, tunicates, crustose coralline algae, algae turf and by the azooxanthellate orange cup coral. Contrarily, the benthic space in the GP was only occupied by algae turf and sporadic and small scleractinian colonies. The presence of other sessile organisms could be liming the space for octocoral recruitment in the GC. Therefore, the correlation between recruitment and colony density could be present only when space is not a limiting factor.

However, when each species was analyzed separately, this 3-way interaction was only observed in *L. alba*, and abundant whip-shaped species, the effect of space and density was observed in the sea fan *P .irene*, and the effect of density alone was present in all common species.

The correlation between recruitment and local density does not establish a cause-and-effect relationship. This association could be caused by multiple mechanisms and doesn't necessarily indicate density dependent population regulation (Sale & Tolimieri, 2000). A stock-recruitment relationship is associated with a closed population (Caley et al., 1996). Due to the distance between our study sites, the frequent strong marine currents, and the mode of reproduction (spawners, Chapter 2) it is reasonable to assume they are open populations. This agree with Privitera-Johnson's (2015) hypothesis, that octocoral aggregations facilitate population growth as co-occurring adults positively influence recruitment of new colonies.

Colonization success could also be the result of the combined effect of chemical cues such as secondary metabolites known to inhibit overgrowth by other sessile organisms (Standing et al., 1984). High population density is also related to predation avoidance (O'Neal & Pawlik, 2002) and the triggering of larval settlement (Slattery et al., 1999), which may also explain higher recruitment in dense communities. Post-settlement success beneath the octocoral canopy can be improved by chemical and antimicrobial protection against predators and microbes from neighboring ocotocoral colonies, however, this effect can be reduced if space becomes limited, as seen in the control plots in the Gulf of Chiriqui.

No novel species colonized the experimental study plots, therefore, it can be hypothesized that a disturbance to the substrate need not lead to a change in local species composition. However, two factors need to be considered: 1) A longer study period would increase the chance of observing more recruits, but as time passes, the available space that was experimentally opened would be reduced by the recruitment and growth of other competitive sessile organisms, such as algae, sponges, and tunicates; 2) Priority effects and random processes at the site level need to be considered; the relationship between the timing of the experimental disturbance and larvae availability could alter the results, especially if the reproductive cycle is not synchronized among species (e.g. Chapter 2).

Although not significant, there was a tendency toward a higher number of recruits in the Gulf of Panama from January to June, which could be seen as a response to the upwelling, when oceanic currents at different scales may increase availability of functional larvae (*sensu* Jordan-Dahlgren, 2002). However, this did not affect the relationships between recruitment, space availability, and adult density.

Although recruitment of 11 species was observed within study plots, it was only possible to closely study *L. alba* and, to a lesser extent *C. riisei*, *L. coffrini*, *P. ferruginea, P. cairnsi*, *P. irene*, and *P. rubicunda*. This was mainly due to the low number of recruits for most species. *Pacifigorgia eximia*, how's reproductive traits were studied in Chapter two, was one of the species that did not colonize study plots, which could be explained by its relative rarity, low recruitment rates (Gómez et al., 2014), and low reproductive output (Chapter two).

It is reasonable to hypothesize that recruitment timing is related to the reproduction mode and cycle. In the Gulf of Panama, *L. alba* spawns in February (Chapter 2), and during the present study, this species had a recruitment peak from January to June on both gulfs, explained by low water temperature and large variations. Therefore, it can be concluded that *L. alba* larvae settles relatively fast, and that there is a degree of synchronization in sexual reproduction and settlement between the gulfs.

In contrast, there was not a significant seasonal difference in recruitment for *P. ferruginea*. The spawning timing observed in chapter 2 (June) was not followed by an increase in the number of recruits. Similarly, recruitment was not statistically seasonally different for *M. austera*, however, there was a slight increase in the number of recruits from January to June 2015 in the Gulf of Panama (Supplemental 3.2). This species has constant gamete production with a spawning peak in July, so the observed recruitment peak did not follow the spawning as predicted. Both *P. ferruginea* and *M. austera* could have reproductive strategies that involve spending longer periods of time in the water column as larvae than *L. alba*.

These differences between *L. alba* and *M. austera* are also reflected in their local dynamics. In the region, *L. alba* is considered a weedy species; it is broadly distributed along the TEP and has rapid dynamics in the Gulf of Chiriqui, with relatively high levels of recruitment, mortality, and growth (Gómez et al., 2014, 2015). Conversely, although *M. austera* is the most common *Muricea* species reported within the studies in Pacific Panama (Gómez et al., 2014), it has relatively slow dynamics, with low adult mortality, low recruitment, and slow growth (Gómez et al., 2014, 2015). The behavior of two other *Muricea* species (*M. californica* and *M. fruticosa*) studied by Grigg (1977) off the coast of California resembles the behavior of *M. austera*. These two species had enormous potential for increase as a result of the large number of eggs released into the water column; however, recruitment was close to zero likely due to large rates of larval mortality in the plankton (Grigg 1977).

C. riisei had a recruitment peak after the upwelling from January to June 2015 in the Gulf of Panama. This species exhibits both sexual and asexual reproduction (Barbosa et al., 2014). In Hawaii, it has continuous and asynchronous gametogenesis, and no seasonal or lunar periodicity (Kahng et al., 2008). If its reproductive behavior is similar in Pacific Panama, it can be suggested that a peak in recruitment could be caused by the seasonal arrival of benthic larvae, or an increase in fish predators, promoting asexual reproduction through fragmentation, which in this case coincides with the upwelling sites and season.

L. coffrini had constant recruitment within the first two seasons, however, it had a major decline during the last season, which coincided with a strong El Niño event. Temperature increases are known to negatively affect the reproduction and survival of other gorgonians; thermal stress during embryonic development could be the most critical factor for larval viability (Kipson et al., 2012). This warming event could explain the reduction in the number of recruits of this common and abundant species.

Although a quantification of how closed or open these populations are is outside the scope of this study, it can be concluded that local processes (e.g. space and adult density) and reproductive mode influence local abundance and population growth. However, these factors vary significantly between species and environments. As predicted by Hixon et al. (2002) even in open populations, persistence relies on direct demographic density dependence at some spatial and temporal scale. Competition for space is generally less important than local density, which can be controlled by other factors including species-specific predation.

During the present study, water temperature had significant changes among seasons on both, the gulf of Panama and the Gulf of Chiriqui at 15-20 m depth (Figure 3.3). This variation is related to *L.alba* reproductive cycle (Chapter 2) and recruitment timing along the Pacific Coast of Panama. However, water temperature variation in our study sites was different from what is seen at shallower locations, where temperature is relatively constant all year around in the GC but not in the GP (Chapter 1; D' Croz & O' Dea 2007; Supplemental 3.3). D' Croz and O' Dea (2007) found that the thermocline increased to nearly 30 m in the GC during the upwelling season, but was not notable in the surface waters, except for brief cooling events of up to 5 ^{o}C. The in-situ and continuous temperature recordings of the present study allow us to complement the findings of D' Croz and O' Dea (2007). Our sites were located at a depth of 20 m in the GC and showed a seasonal pattern similar to the one described for the GP. Although the temperature drops in the GC are not correlated with the wind-jets that drive the upwellings in the GP (D' Croz & O' Dea, 2007), some oceanographic processes, such as micro-upwelings or topographical features like coastal sea mountains (Cunningham et al., 2013) allow the thermocline to rise to at least 20m from the surface, decreasing water temperatures by 10 ^{o}C during the period of the GP upwelling.

The El Niño event that coincided with the last sampling season (June 2015 - January 2016) increased mean daily water temperature by one degree in the GC but not in the GP. On this occasion, the warming event occurred during the upwelling season and as a result, the upwelling reduced the effect of the ENSO event in the GP as proposed by Chollett et al. (2010). However, the oceanographic processes that raised the thermocline in the GC did not reduce the effect of El Niño at 20 m depth.

The present study concludes that octocoral recruitment in Pacific Panama is positively correlated to adult density when space is not a limiting factor, which is the case in the Gulf of Chiriqui. Additionally, recruitment of the abundant and widely distributed *Leptogorgia alba* is seasonal, it follows the species reproductive period and coincided with variable and cold water temperatures (June - July) on both, the Gulfs of Panama and Chiriqui.

We recommend future studies of water temperature variations with continuous recordings over a depth profile, noting any potential correlation between nutrient levels and ecological implications for coral communities.

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Table 3.1. Octocoral recruitment study sites off Pacific Panama, four sites located in the Gulf of Chiriqui (GC) and four in the Gulf of Panama (GP).

Site	**Gulf**	**Depth (m)**	**Description**	**Species richness**	**Adult density (m^2)**	**Shannon Diversity**	**Total number of recruits**
Prosper	GC	20	Small islet with vertical rocky wall	5	12.1	2.6	21
Roca Hacha	GC	20	Small islet with vertical rocky wall	9	16.5	7.1	55
Catedrales	GC	20	Underwater outcrop 10m below surface	7	11	4.0	31
Jicarita	GC	20	Island with vertical rocky wall	7	7	4.9	32
Pedro Gonzalez	GP	15	Island with vertical rocky wall	2	4.6	na	35
San Telmo	GP	17	Island with vertical rocky wall	6	22.5	2.3	88
Elefante	GP	18	Small islet surrounded by rocky formations	6	3.8	3.6	51
Galera*	GP	18	Small islet surrounded by rocky formations	3	3.5	2.8	10

* Four of the plots at Galera (two control, two experimental) were lost in the middle of the study, which explains the low number of total observed recruits compared to the other sites.

Table 3.2. Octocoral species adult sample size and total number of recruits within study plots at each site.

Species	Adult sample size/ total No. recruits	Gulf of Chiriqui				Gulf of Panama			
		Catedral	Roca Hacha	Jicarita	Prosper	San Telmo	Pedro Gonzalez	Elefante	Galera
Leptogorgia alba	173 / 139	37 / 14	20 / 29	7 / 6	21 / 2	46 / 36	36 / 35	6 / 17	
Leptogorgia coffrini	135 / 91	4 / 0	1 / 0	5 / 12	12 / 6	92 / 42	1 / 0	15 / 23	5 / 8
Pacifigorgia cairnsi	87 / 17	1 / 1	27 / 6	3 / 0	56 / 13				
Pacifigorgia irene	68 / 13	19 / 6	25 / 7	15 / 0		8 / 0		1 / 0	
Pacifigorgia rubicunda	51/ 15	21 / 7	21 / 5	9 / 3					
Carijoa riseii	25 / 16				7 / 0	16 / 7		2 / 9	
Pacifigorgia firma	22 / 4					14 / 3		3 / 1	5 / 0
Heterogorgia verrucosa	19 / 3	4 / 2	13 / 1	2 / 0					
Pacifigorgia ferruginea	18 / 12	2 / 0		8 / 11		4 / 0			3 / 2
Muricea austera	13 / 7		10 / 6					3 / 1	
Psammogorgia arbuscula	12 / 0		12 / 0						
Pacifigorgia eximia	3 / 1		3 / 1						
Leptogorgia cuspidata	1 / 0				1 / 0				

Table 3.3. Coefficients of the effect of colony density (D), treatment (T) and gulf (G) in the recruitment of octocoral species from the overall GLM model.

Significant values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Coefficients:					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.967	0.139	14.174	< 2e-16	***
Density (centered)	0.153	0.029	5.318	0.000	***
Gulf	-0.026	0.175	-0.148	0.882	
Treatment	-0.392	0.197	-1.988	0.047	*
Density x Gulf	-0.121	0.030	-4.085	0.000	***
Gulf x Treatment	0.207	0.250	0.828	0.408	
Density x Treatment	-0.163	0.033	-4.908	0.000	***
Density x Gulf x Treatment	0.184	0.036	5.065	0.000	***

Table 3.4. Coefficients of the effect of colony density (D), treatment (T) and gulf (G) in the recruitment of common octocoral species from individual GLM models.

Significant values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Species	Estimate	Std.E
Leptogorgia alba	$\beta_{interaction\ D,T,G}$ 0.71 ***	0.17
Leptogorgia cofrini	$\beta_{interaction\ D,G}$ -0.32 **	0.12
Carijoa riisei	β_D 0.11 **	0.04
Pacifigorgia cairnsi	β_D 0.08 **	0.03
Pacifigorgia rubicunda	β_D 0.2 .	0.10
Pacifigorgia irene	β_D 0.53 **	0.24
	β_T -3.1 **	1.28

Table 3.5. Seasonal water temperature; daily mean, standard deviation, maximum, minimum and variation coefficient for the Gulf of Panama and the Gulf of Chiriqui from June 2014 to January 2016. Temperature (^{o}C) was obtained from in-situ HOBO loggers.

Season	dates	Gulf	Mean	sd	Min-Max	Var. Coef
1) pre-upwelling	June 2014-January 2015	Chiriqui	28.20	±0.61	(25.6-29.4)	2.18
		Panama	28.24	±0.68	(23.9-29.7)	2.41
2) post-upwelling	January 2015-June 2015	Chiriqui	27.36	±1.89	(20.8-30.2)	6.96
		Panama	25.94	±2.96	(18.6-29.6)	11.40
3) pre-upwelling + Niño	June 2015-January 2016	Chiriqui	29.21	±0.40	(27.9-30.4)	1.38
		Panama	28.54	±1.09	(23.0-29.6)	3.82

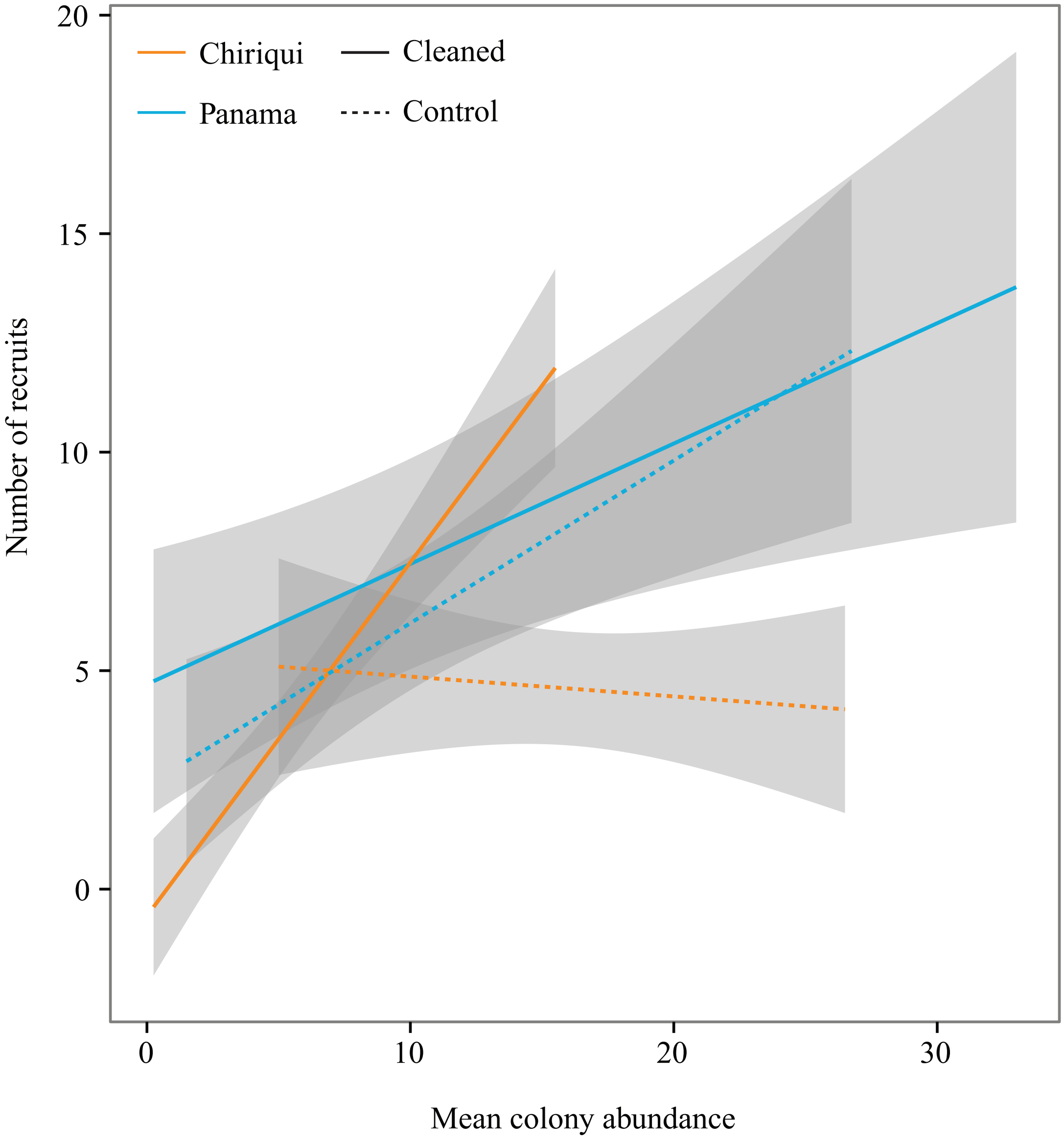


Figure 3.1. General GLM model (pooling all species together) with a significant interaction between number of recruits as a factor of adult density, geographic location (Gulf), and treatment (cleaned or control). The general correlation between recruitment and colony density was found for experimental and control plots in the Gulf of Panama, but was only observed for experimental plots in the gulf of Chiriqui. Space could be more limiting to recruitment in the GC due to higher densities in control plots.

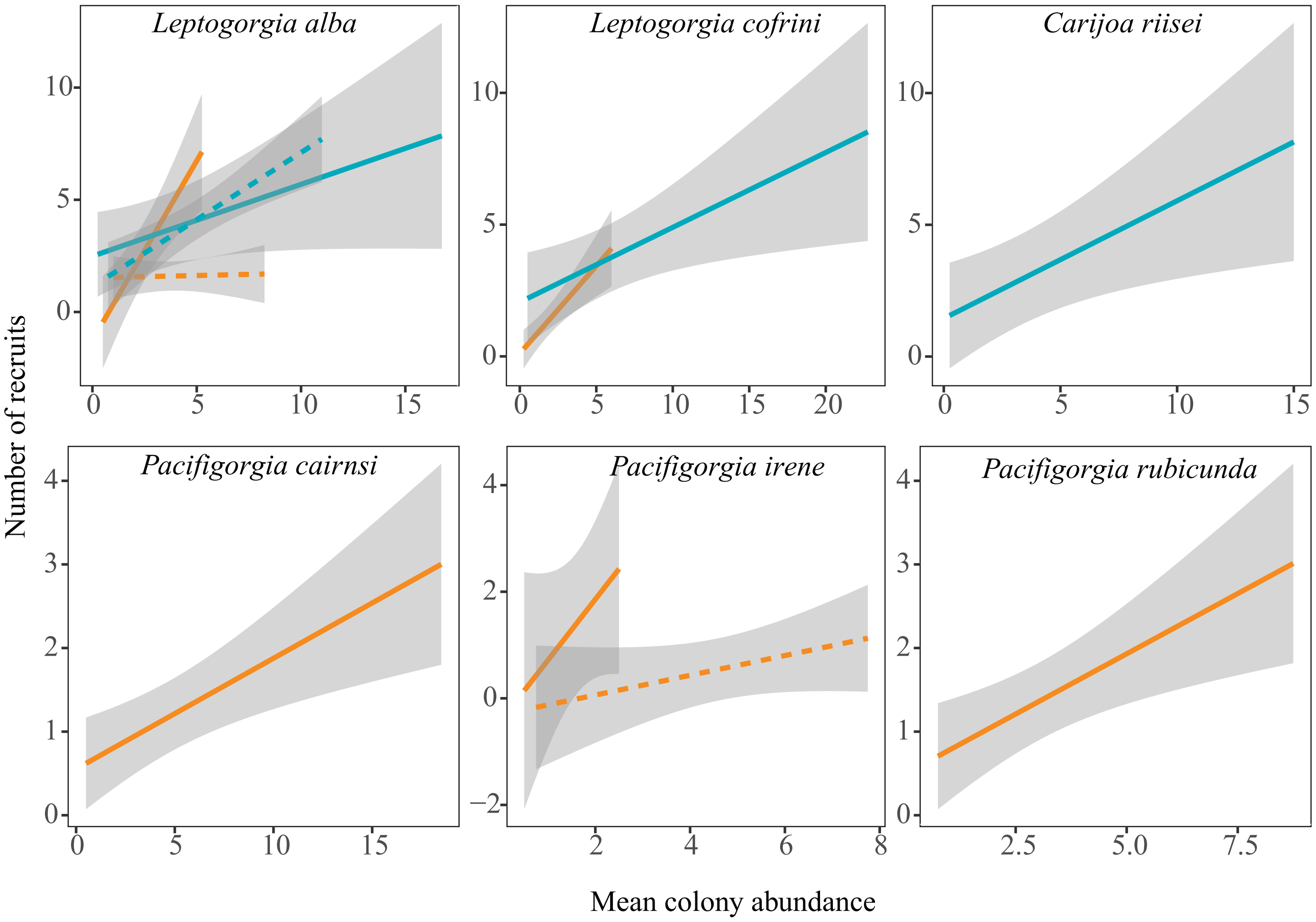


Figure 3.2. Species specific GLM models for the interaction between number of recruits as a factor of mean colony density, geographic location (GC = orange, GP = cyan), and treatment (cleared = solid, control = dashed). There was a significant three-way interaction for *L. alba* and *L. cofrini*. The interaction with treatment and abundance was found for P. irene. In *C. riisei*, *P. cairnsi*, and *P. rubicunda* only the correlation between recruitment and mean colony density was significant.

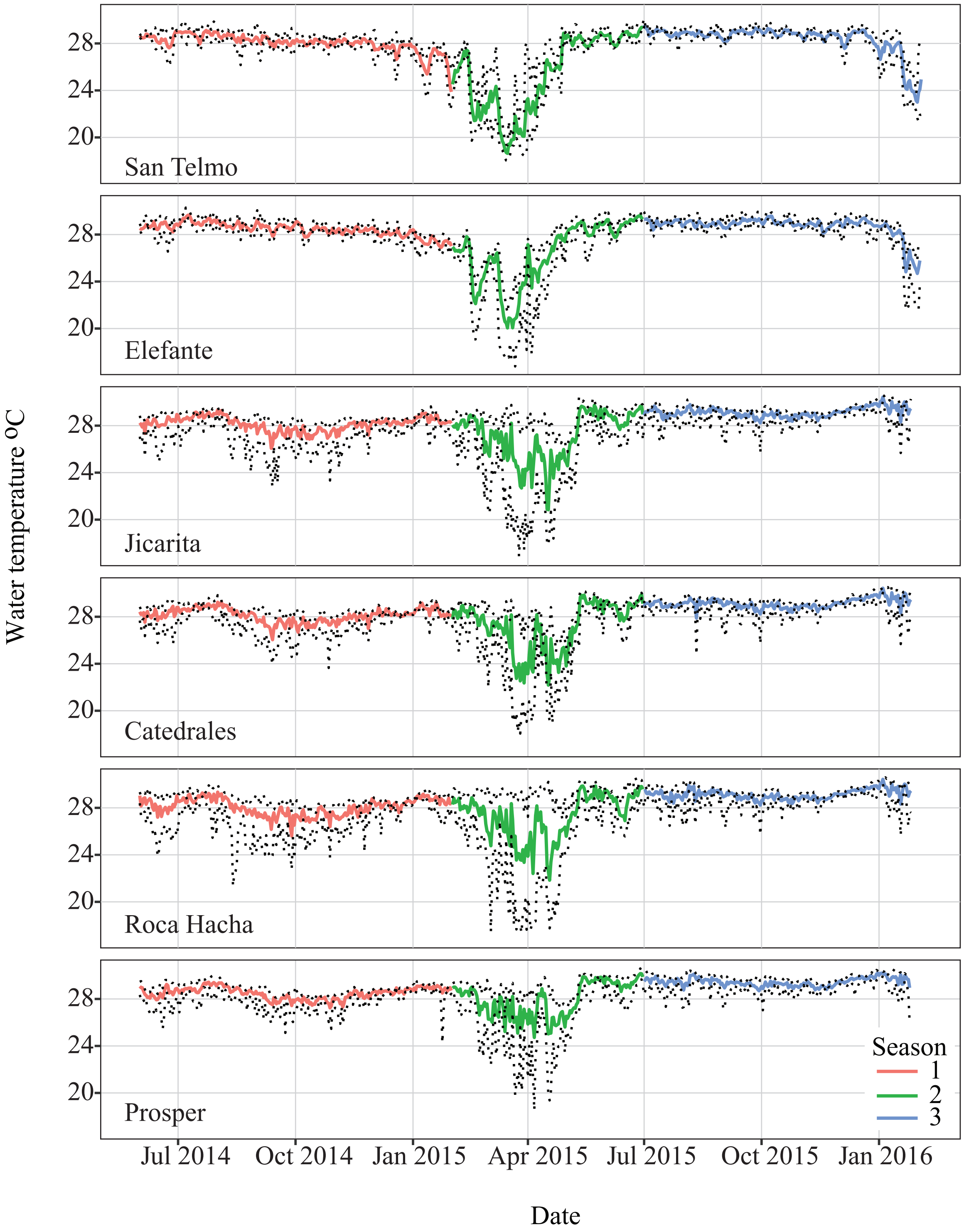


Figure 3.3. Mean daily temperature timeline during each sampling period. Notice the temperature fluctuations that take please in all the sites from January to June (season 2). Season 3 took place during a strong El Niño event. San Telmo and Elefante are sites in the Gulf of Panama, and Jicarita, Catedrales, Roca Hacha, and Prosper are in the Gulf of Chiriqui. Doted line represents maximum and minimum temperatures.

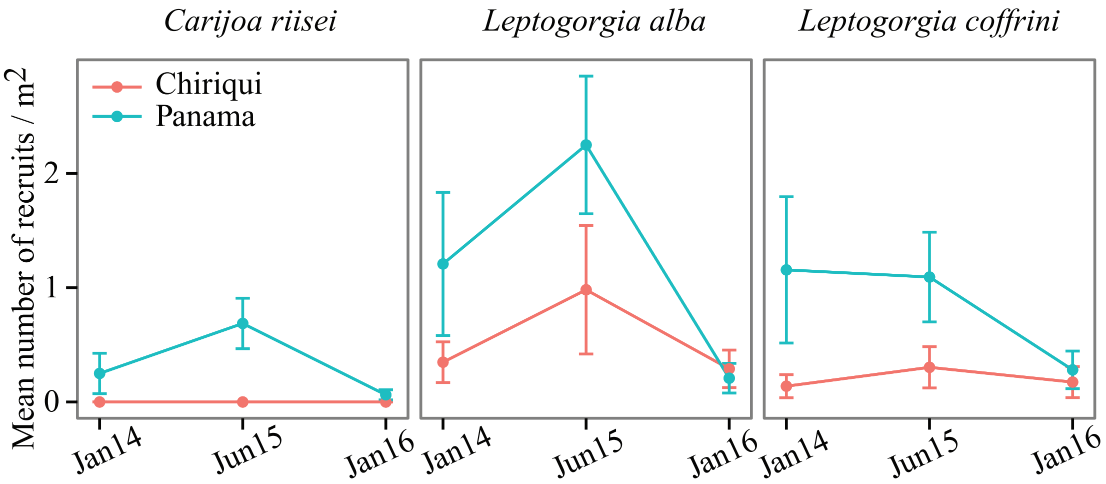
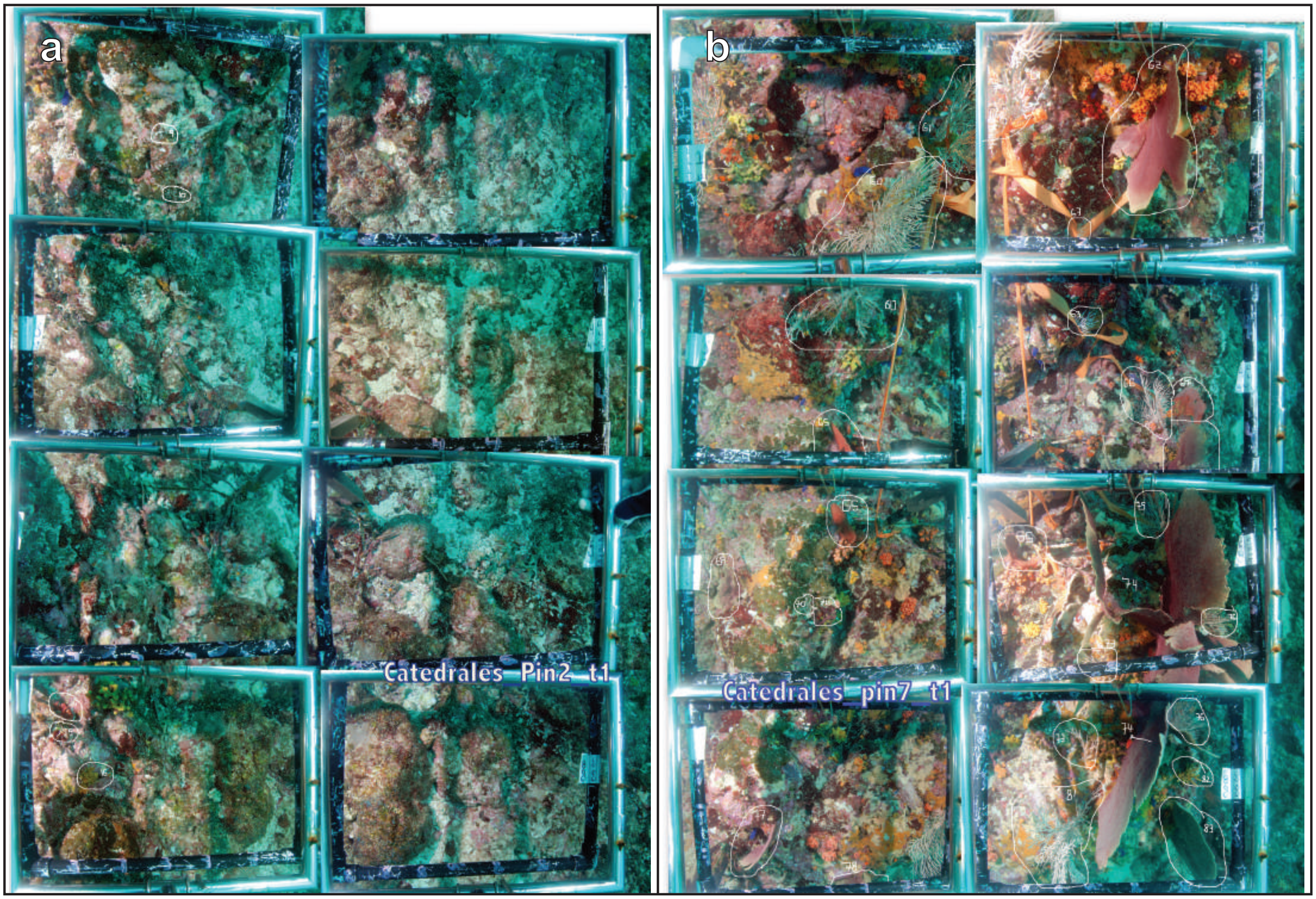
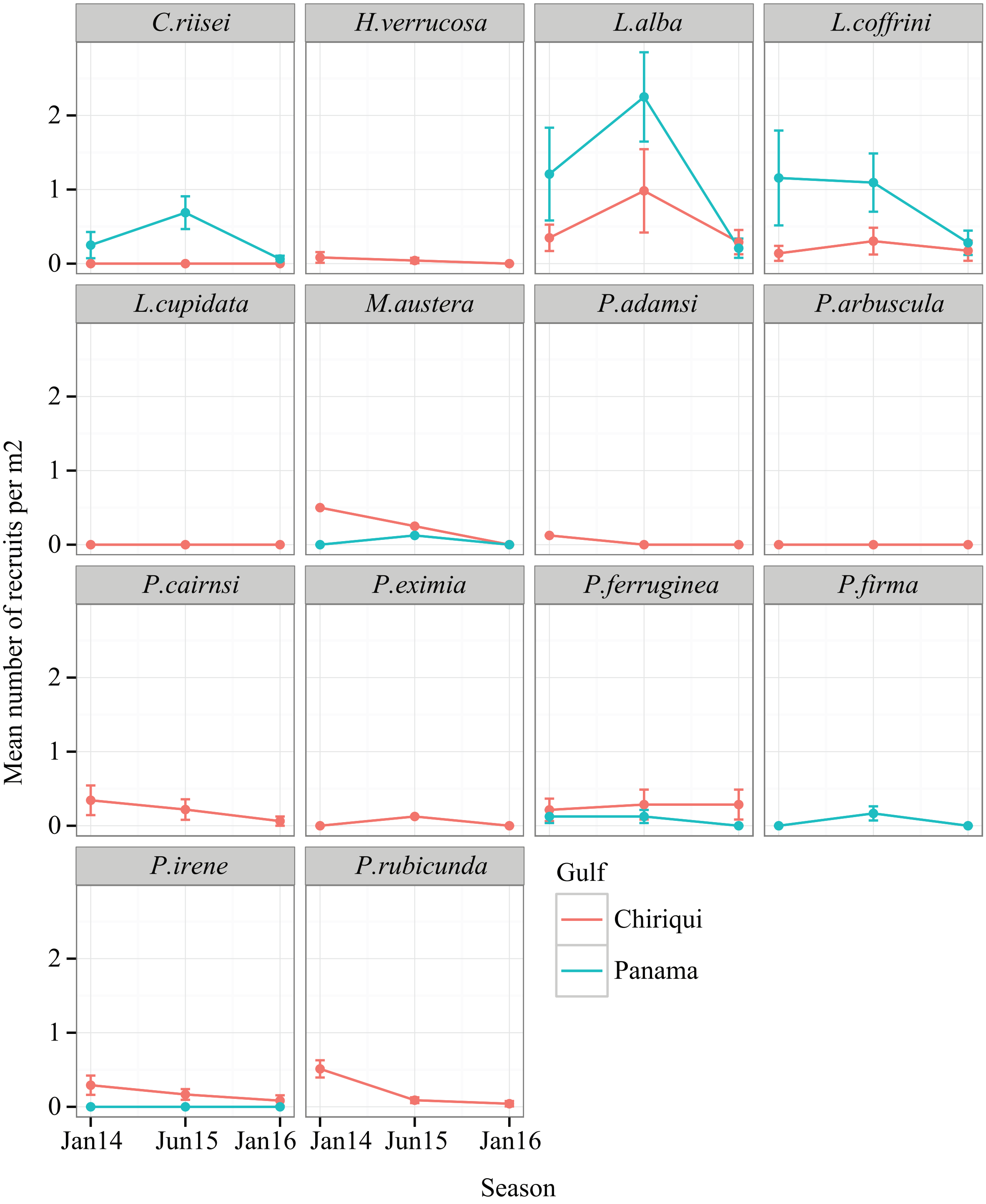


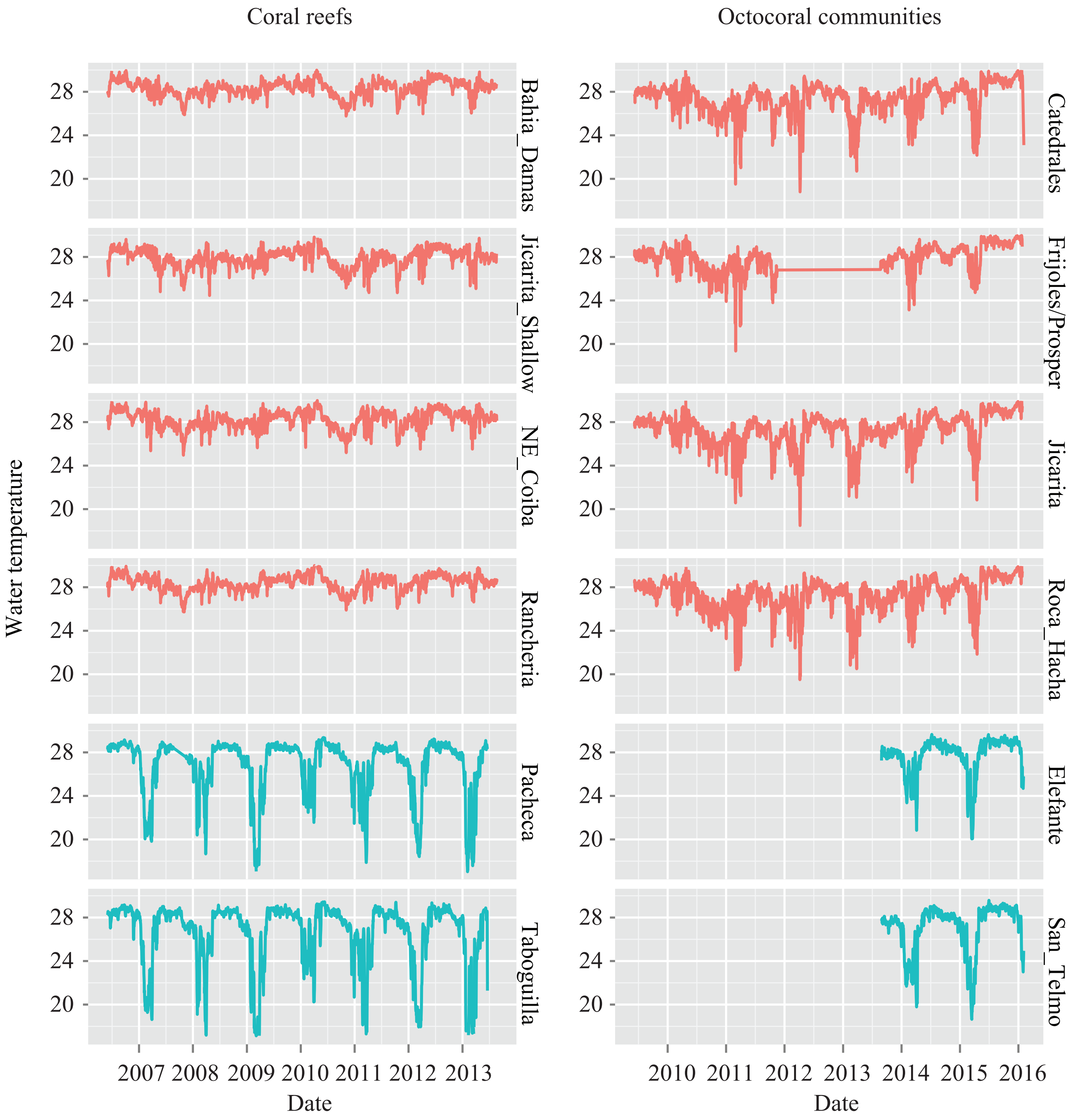
Figure 3.4. Mean number of recruits per m2 during each sampling season. *L. alba* had a significant peak from January to June 2015, as did *C.riisei*, but only in the Gulf of Panama. *L. coffrini* had a decline in recruitment during the last season, which coincided with an El niño ENSO event.



Supplemental 3.1. Example of mosaic images used for the analysis. a) Experimental plot cleared from sessile organisms competing for space, see small recruits in white circles, and b) Control plot. Circles and numbers were used to quantify octocoral colonies within study sites.



Supplemental 3.2. Recruitment timeline (mean and standard error) for common octocoral species on the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan).



Supplemental 3.3. Water temperature timeline in coral reefs (≤ 10 m) and octocoral communities (15-20 m) in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Note water temperature decreases at the beginning of each year at both gulfs in octocoral communities and not in coral reefs. Water temperature data for coral reefs (Chapter 1) and octocoral communities obtained by insitu HOBO logger stations recoded every 30 minutes.

Linking statement 3

Long-term monitoring data, such as that used in Chapter 1, are not available for octocoral communities. Therefore, if we aim to estimate how stable or resilient these communities are we can use models of community dynamics. The fourth chapter of this thesis uses a Markov Chain model to estimate the stability and resilience of octocoral communities at the Gulfs of Panama and Chiriqui. Results from Chapters 2 and 3 are then used to interpret the model outcomes with a biological and ecological framework. This model also allows us to understand octocoral communities through comparison to well-known systems, such as coral reefs.

CHAPTER FOUR

Stability and dynamic properties of octocoral communities in the Eastern Tropical Pacific

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Abstract

Octocorals are the main foundation species present in rocky-wall marine communities of the Eastern Tropical Pacific but the stability of these communities is not well understood. This study is the first attempt to quantify the transition probabilities and more complex stability properties, such as estimated turnover and recovery time of these communities using a Markov Chain model. We also compare octocoral communities inhabiting the Gulf of Panama (GP) and the Gulf of Chiriqui (GC), two distinct gulfs located at the same latitude in Pacific Panama. The model was parameterized by monitoring four fixed plots (1 m^2) at four sites per gulf from June 2014 to January 2016, recording the fate of spaces that were occupied by an octocoral colony at any time during the study period. Thirteen octocoral species were monitored over 989 locations in space. Octocoral dynamics in the GC, where communities were more species-rich, were three times more stable than communities in the GP, with an estimated turnover time of 9.6 years in GC in 3 years in GP. However, octocoral communities in the GC were 1.6 times less resilient to disturbance, with an estimated recovery time of 68 years in GC and 43 years in GP, possibly due to strong competition for space with other sessile organisms. In modeled communities from which one species was deleted at a time, the effect of diversity loss was low at the gulf and study area scales, but increased significantly at the reef scale, especially in species-poor sites. Further studies about environmental factors driving stability are needed to fully understand the mechanisms behind our results.

Introduction

Octocoral communities are ecologically important because they are the main foundation species that live on rocky walls (Bayer, 1953) and form “animal forests” (Sanchez, 2016), creating complex habitat and feeding substrate for many other taxa (Cantera et al., 1987; Sanchez, 2016). Octocoral species around the world are affected by a variety of stressors, including an increase in the frequency and strength of tropical storms (Woodley et al., 1981; Yoshioka & Yoshioka, 1987) and disease outbreaks that are the result of increases in seawater temperature (Sánchez et al., 2011, 2014; Ward et al., 2006). Still, some octocorals have been found to be more resistant than other marine foundation species to bleaching and ocean acidification (Enochs et al., 2016; C.E. Gómez et al., 2015; Sanchez, 2016).

The stability of octocoral communities in the Tropical Eastern Pacific (TEP) is not understood. An initiative to study the biology and ecology of these foundation species began early this century after extensive taxonomic reviews were published (Breedy & Guzman, 2002, 2007, 2011, 2015, 2016; Breedy et al., 2009). These studies have described the population dynamics of common species (Gómez et al., 2014), the effects of a 25% decline in population abundance on community structure (C.C. Gómez et al., 2015), their reproductive timing and output (Chapter 2), and the relationships between recruitment, adult densities, and space limitations (Chapters 3). To further our understanding of the dynamics of these understudied communities, we developed a Markov chain model to study the stability properties of octocoral communities along the Pacific Coast of Panama. This region has been described as a hotspot of octocoral diversity (Guzman et al., 2004, 2008) and a natural laboratory for the study of marine communities (Cortés et al., 2017).

The stability of a community can be defined and measured in different ways (Ives & Carpenter, 2007), many of which are relevant for octocoral communities. These include: how many alternative stable states a community can have, and how hard it is to change between them, such as coral reefs changing to an algae dominated state (Fung et al., 2011); the rate at which a community returns to equilibrium following perturbation; how resistant a community is to change in response to disturbance; the susceptibility of community to species invasions; the impacts of species extinction and the compensatory changes in species abundance that occur following an extinction event (Gonzalez & Loreau, 2009; Ives & Carpenter, 2007). Different definitions are relevant depending on the nature of the disturbance. Octocoral communities are exposed to pulse disturbances, such as hurricanes, or press disturbances, such as global warming and ocean acidification (Ives & Carpenter, 2007). So far, no alternative stable states have been reported for octocoral communities in the TEP, however, this may be due to the lack of studies in the area. Recent population declines (Gomez et al. 2015) suggest it is important to study community stability, rates of recovery after disturbance and the potential for compensatory changes after species extinctions.

The stability of a system has been linked to its diversity (Loreau et al., 2002); however, it has been a topic of debate, mainly because the strength and direction of this relationship depends on the definition of stability and the type of disturbance (Ives & Carpenter, 2007). To improve our understanding of this relationship Ives and Carpenter (2007) recommended models based on empirical data, which link the dynamics of the focal system to the relevant aspect of stability. Ultimately, the aim is to identify stabilizing mechanisms and understand how they are impacted by human caused environmental change.

Markov chain models have been used in ecology to understand succession and stability in a variety of natural systems, from forests (Waggoner & Stephens, 1970) and plants (Isagi & Nakagoshi, 1990) to marine communities such as subtropical, intertidal (Wootton, 2001a, b), and subtidal (Hill et al., 2004) sessile communities and Australian coral reefs (Tanner et al., 1994). Markov chains are simple multispecies models that use transition probabilities, which are relatively easy to quantify in the field, to estimate more complex measurements of stability (Wootton, 2001a) such as entropy, turnover, and recurrence times. It is a powerful tool for comparative analysis in community ecology (Hill et. al., 2004). In addition, the Markov chain model can also be used as a tool to predict the effect of species loss and identify the key species (Hill et al., 2004; Tanner et al., 1994) that, if removed, will cause disproportionate changes to the community (McArthur, 1972), without the need for experimental manipulation.

The parameters of this model are defined by field observations that quantify the transition probability—the frequency at which one species occupying a specific space is replaced by another species. Transition probabilities, such as the probabilities of colonization, persistence, replacement, and disturbance, can be quantified at the species level to describe the biology of each species in the context of a community (Hill et al., 2004). The probabilities can also be used to create a broader description of the entire community, which can be used to compare one community with others (Hill et al., 2004).

Our goal is to develop a first Markov chain model for octocoral communities to first quantify the transition probabilities within the system and then infer the stability properties for multiple communities across two gulfs off the coast Panama. In the present study stability is defined as the community resistance based on the turnover, which measures how often a space that was occupied by one species shifts to a different species (state); and by the recurrence time, which estimates how long would it take for a space to return to its original state after a disturbance (Hill et al., 2004). Additionally, this study evaluates the effect of local species extinction (removal of a species from a community) and interprets the stability of octocoral communities by the compensatory changes in species abundance after local extinction (*sensu* Hill et al., 2004; Wootton, 2004).

Methods

Study organisms

Octocorals are sessile marine invertebrates that inhabit rocky coral communities in very active environments (Gómez et al., 2014). They are considered foundation species (Sanchez, 2016) with high environmental tolerance (Enochs et al., 2016; C.E. Gómez et al., 2015) and can be found in shallow and deep environments in almost all latitudes on planet earth (Alderslade, 1984; Bayer, 1981). The Pacific coast of Panama has two recognized hot-spots of octocoral diversity and abundance located within the boundaries of the Tropical Eastern Pacific: Las Perlas Archipelago in the Gulf of Panama (GP) with 38 reported species, and Coiba Island in the Gulf of Chiriqui (GC) with 36 species (Breedy & Guzman 2011; Guzman et al., 2004, 2008). Fifteen of these species inhabit both gulfs and are found in high-density patches of ~38 colonies/m^2 (Gómez et al., 2014). The life histories of 13 of the 59 species inhabiting the Pacific coast of Panama have been studied. Gómez et al. (2014) found two distinct life history patterns in these species: 6 species had r-selected dynamics and 7 species had k-selected dynamics. However, the reproductive output of two common species within these two groups does not relate to their population dynamics (Chapter 2); *Leptogorgia alba* has high recruitment (Gómez et al., 2014) but low reproductive output (Chapter 2), and *Muricea austera* has very low recruitment (Gómez et al., 2014) and has high reproductive output (Chapter 2). Contrastingly, recruitment is limited by space and positively correlated with adult density (Chapter 3).

Study site

The Pacific coast of Panama is composed of two open gulfs: the Gulf of Panama and the Gulf of Chiriqui, both of which have diverse octocoral communities. Important environmental differences have been observed between the shallow environments (< 15 m depth) of the two gulfs. An annual wind-driven upwelling significantly reduces water temperature during the first four months of each year in the Gulf of Panama (D' Croz & O'Dea, 2007), but not in the Gulf of Chiriqui. This gulf-specific upwelling has ecological consequences for scleractinian coral reefs (Toth et al., 2017). However, in deeper environments where octocoral communities are found (> 15 m), the strong differences in water temperature regimes between the two gulfs are no longer evident (Chapter 3). Therefore, octocorals in both gulfs are subject to similar annual variation in water temperatures.

Four sites within each gulf were chosen as study sites based on previous descriptions of octocoral communities on the Pacific coast of Panama and the Tropical Eastern Pacific (Guzman et al., 2004, 2008). All study sites were located in exposed areas and subject to strong currents and swells. These sites were formed by basaltic rocky formations in which octocorals share the substratum with coralline algae, small and scarce scleractinian colonies, macro algae, tunicates, sponges, and algae turf.

Data acquisition

To parameterize the Markov chain model, four 1 m^2 fixed plots were installed between 15 and 20 m depth at each of the eight study sites using SCUBA equipment. Plots at the Gulf of Panama were located at shallower depths than plots in the Gulf of Chiriquí because this is where the octocoral colonies were found. In this Gulf sand bars surround rocky formations that generally do not extend deeper than 18 m. Plots were fixed by installing stainless steel square bars with underwater cement. Study plots were monitored in four ocations, every 6 months from June 2014 to January 2016. Plots were photo-monitored using a 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 custom-made stainless steel tripod in order to maintain a fixed object-to-lens distance (0.80 m) from the substrate. To survey each plot, an aluminum 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 quadrat was designed so it always attached to the square fixed bars in the same position, ensuring the monitoring of the exact same location over time. The quality of the pictures was improved by using Nikon NX2 software (*see* Gómez et al., 2014; Chapter 3).

Pictures taken from study plots were analyzed to obtain the data needed to set the parameters for the model. High-resolution mosaic images were created with the eight pictures taken from each $1m^2$ plot. On each image each octocoral colony was identified and located within the plot (Chapter 3), images from consecutive surveys were visually compared. Each point in space that was occupied by an octocoral colony, at any given time during the study period, was followed over time. For each survey, the state of each point was determined by the species that occupied it, either an octocoral species or the functional group of the organism that occupied the same space before or after the octocoral.

Data analysis

Transition probabilities and dynamic properties of stationary community

A Markov chain analysis was developed using the methods proposed by Hill et al. (2004). The model was defined by a transition probability matrix in which the state of a point in time t+1 was dependent upon the state of the point in time t. Transition matrices were estimated at three spatial scales – frequencies were averaged over time (among surveys) and space, among plots for reef scale, and among sites for gulf and study region scales. The dynamic properties (Table 4.1) of each octocoral species, as well as the dynamic properties of the entire community, were quantified for each site, at the gulf scale and for the entire study region following Hill et al. (2004) (Supplemental 4.1). However, in this case, the abiotic component was reinterpreted as the non-octocoral component, and included all functional groups other than octocoral species, e.g. sponge, algae turf, and crustose coralline algae. Eigenvector calculations and correlations were performed in R software version 3.2 (R Core Team, 2015), using the base R package and package “Hmisc” (Harrell & Dupont, 2015) respectively.

Community convergence

For each Markov chain (one per reef and one per gulf) the rate of convergence to the stationary distribution was measured with the damping ratio (p) (*sensu* Hill et al., 2004; Tanner et al., 1994; Wootton, 2001a), which measures the relationship between the largest and second largest eigenvalues. The closer these two eigenvalues are in magnitude, the slower the convergence rate, measured as the natural logarithm of p (Hill et al., 2004). The half-life of a perturbation was measured as the $\ln 2 / \ln p$ (*sensu* Hill et al., 2004). Damping ratios were calculated using function “Damping.ratio” in the R software package “Popbio” (Stubben & Milligan, 2007)

Species removal

The importance of each species to the diversity of its community was quantified by calculating the proportional change in evenness between the stationary community and a modeled community in the absence of a target species *ts* (*sensu* Hill et al., 2004). This analysis was performed for every octocoral species at the three spatial scales: reef, gulf, and study area. To model the community without the target species (*ts*), both the column and the row of *ts* were set to zero in the stationary community matrix, which was then column-wise renormalized to add up to 1, and subsequently, *ts* row and column were removed. Community evenness was calculated for the stationary community and after each species removal following Hill et al. (2004). To calculate evenness among octocorals alone, all non-octocoral states were added as a single state and treated as the "bare rock" state.

Results

A total of 438 and 551 points in space were followed in time in the Gulf of Panama and in the Gulf of Chiriqui, respectively. At some point in time during the study, each of these points in space was occupied by an octocoral colony, which persisted, recruited, or was disturbed into a different state. Three points from Jicarita (GC) were removed from the analysis because they were not visible in at least one of the time-steps. The stationary community matrix from the entire study region had 17 states (Table 4.1), 13 octocoral species, algae turf, crustose coralline algae, sponge, and pocilloporid scleractinian corals, 15 states in the GC (12 octocoral species), and 10 states in the GP (7 octocoral species). See individual transition matrices and their temporal standard error in Supplemental 4.2.

Community Transition Probabilities

At any given time, the maximum transition probability of the stationary matrix of the community at equilibrium was the persistence rate, which is when a point is occupied by the same species in *t* and in *t*+1. The persistence rate for Pacific Panama was 0.59, for the Gulf of Chiriqui was 0.66 and 0.61 for the Gulf of Panama (Figure 4.1 a, Table 4.2). At the species level, there was a variation that ranged from 1, species that persisted in the same point for the entire study period (*Leptogorgia cuspidata* in GC), to 0.4 (*Heterogorgia* *verrucosa* in GC) (Figure 4.2). Persistence rate was not correlated with the species mean abundance (GC: $r^2 = -0.23$, $p > 0.05$; GP: $r^2 = -0.03$, $p > 0.05$) (Table 4.3).

Next we studied the mean disturbance rate in both communities. This is the probability that a space occupied by an octocoral community in time *t* would change to a different functional group, such as a sponge, crustose coralline algae, or algae turf, in time *t*+1. The mean disturbance rate of the stationary community was 0.31 for Pacific Panama, 0.37 for the GP and 0.16 for the GC (Figure 4.1 a). The species with the highest disturbance rate in the GP was *Carijoa riseii*; as all the colonies changed to a different state. In the GC the species with the highest disturbance rate was *H. verrucosa*. *Muricea austera* had the lowest disturbance rate in the GC and *Pacifigorgia ferruginea* had the lowest disturbance rate in the GP (Figure 4.2). Disturbance rate was not correlated with the species mean abundance (GC: $r^2 = -0.16$, $p > 0.05$; GP: $r^2 = -0.07$, $p > 0.05$) (Table 4.3).

The mean colonization rate is the probability that a space that was occupied by a non-octocoral state in time *t* would change to an octocoral state in time *t*+1. Mean colonization rate was lower than the disturbance rate in both gulfs; it was 0.18 in Pacific Panama, 0.27 in the GP and 0.14 in the GC (Figure 4.1 a). In this case, it is the probability of an octocoral species recruiting in a space previously occupied by a sponge, crustose coralline algae, or algae turf. *Pacifigorgia cairnsi* and *Pacifigorgia eximia* had the highest probability of colonization in the GC and they were also the only species to colonize a space previously occupied by a sponge. *Leptogorgia alba* had the highest colonization rate in the GP and it was three times higher when colonizing a space previously occupied by algae turf. *Pacifigorgia firma* and *P. ferruginea* only colonized spaces previously occupied by crustose coralline algae (Figure 4.3). Probability of colonization was positively correlated with species mean abundance in the GP ($r^2 = 0.89$, $p < 0.05$) (Table 4.3).

Species replacements were rare among octocoral states (Figure 4.1 a, Table 4.2). They occurred when one octocoral colony overgrew another octocoral colony. Replacements were positively correlated with mean species abundance in the GP (Table 4.3). The species that had the highest rate of being overgrown by another octocoral (replacement of) was *C. riseii* (0.85 in GC). *Leptogorgia cofrini* (0.15) was most prone to replace another octocoral (Figure 4.2).

Community dynamics

The turnover time, which measures the frequency at which an octocoral state changes to a new state, was 3.7 for Pacific Panama, however, it was three times greater in the GC (9.58 years) than in the GP (3.04); a similar difference was not seen in the turnover rate (Table 4.2). The recurrence time, which measures the time required for a specific octocoral species to re-colonize a space that was previously lost, was 66.9 years for Pacific panama, however, it was 1.6 times greater in the GC (67.94 years) than in the GP (42.54 years) (Figure 4.1 a). Neither one of these measurements was correlated with species abundance (Table 4.3).

Within species, *M. austera* had the longest turnover time (GC, 27 years), followed by *P. ferruginea* (GP, 7 years). *C. riseii* had the fastest turnover time in both the GP and the GC (one year) (Figure 4.4). *Pacifigorgia ferruginea* showed the slowest recurrence time (928 years); it was over one hundred times slower than *L. alba* (8.35 years).

The normalized community entropy was 1.4 times greater in the GP than in the GC (Figure 4.1 c). The entropy, or predictability, of the species ranged from 1.3 (less predictable *L. alba*) to 0.15 (more predictable *M. austera*) in the GC, and 1.2 (less predictable *L. cofrini*) to 0.25 (more predictable *P. ferruginea*) in the GP. Maximum possible species entropy values were 2.3 in the GP and 2.7 in the GC.

Community convergence

The octocoral community in Pacific Panama had a damping ratio of 1.12, implying a convergence rate of 11.33% per year and a half-life of 6.12 years. Communities in the Gulf of Chiriqui had a damping ratio of 1.05, implying a convergence rate of 4.5% per year and a half-life of 15.6 years. The octocoral community in the Gulf of Panama had a damping ratio of 1.17, implying a convergence rate of 15.7% per year and a half-life of 4.4 years (Table 4.4). At the reef scale convergence rates were longer in Prosper (GC, 14 % per year), Elefante (GP 19 % per year), and Pedro Gonzalez (GP, 68 % per year), and shorter at Galera (GP, 0.75 % per year) (Table 4.1).

Species removal

Species evenness in the entire study region was 0.76: 0.82 in the GP and 0.77 in the GC. At the study region scale, the species that produced the most dramatic change in species evenness when removed was *P. cairnsi*, which decreased community evenness by 10%. In contrast, the removal of *L. cuspidata* produced no change at the same scale. The removal of *C. riseii* produced the greatest decrease in evenness (10%) in the GC and *L. alba* in the GP (15%). However, the individual effect of species removal changed drastically when analyzed at the reef scale (Figure 4.5). The removal of *P. firma* in Galera produced a decrease in evenness of 80% and the removal of *Pacifigorgia rubicunda* and *L. alba* in Catedrales produced decreases of 38% and 35% respectively; the removal of *L. cuspidata* and *L. cofrini* in Prosper produced decreases of 52% and 44%, respectively, rates similar to those seen after the removal of *L. cofrini* in San Telmo (51%) and Elefante (40%). The effect of species removal was correlated with species relative abundance only at Prosper and Catedrales (GC) (Table 4.5). No octocoral keystone species were evident at the country or gulf scales.

Discussion

The Markov chain model allowed us to quantify and compare measurements of community stability between octocoral communities inhabiting the Gulf of Panama and the Gulf of Chiriqui off the Pacific Coast of Panama, as well to compare how octocorals differ or resemble other marine sessile communities.

Stability of octocoral communities off Pacific Panama

We found that the disturbance and colonization rates varied between gulfs. Octocorals from the Gulf of Chiriqui had lower disturbance and colonization rates than octocorals from the Gulf of Panama. The difference in dynamics between these communities is evident when we compare their turnover time, which was three times greater in the GP. The other stability measurement we used was the recurrence time, which measured time the community required to return to a previous state after a disturbance. In this case, communities in the GP were more stable than those in the GC, since they took 1.6x less time to return to a previous state.

Although this type of model doesn't describe the mechanisms responsible for the transitions, it could be hypothesized that the stability in the dynamics of the GC is linked to its greater diversity. After a long debate on the stability-diversity relationship, Ives and Carpenter (2007) concluded that the strength and direction of this relationship depends on the definition of stability and the type of perturbation. In this study the diversity-stability relationship was positive when stability was measured as the resistance to change; the GC, which was more species rich (n = 12 octocoral species), took three times longer to change between states (turnover time). Nevertheless, if stability was measured as the rate of return (recurrence time) this relationship was negative; in this case the GP, which had less species (n = 7), returned 1.6x faster to its original state.

Our findings, based on a Markov model fitted to empirical data collected from a natural community, agree with theoretical formulations described by Ives and Carpenter (2007) of having both, negative and positive diversity-stability relationships. We propose that in this study the mechanism for the negative diversity-stability relationship is due to potential competition for space with other highly diverse sessile marine organisms (sponges, tunicates, crustose coralline algae, algae turf), which limit octocoral recruitment in the GC (Chapter 3), and reduces the ability for the community to recover after disturbance. On the other hand, we suggest that the positive diversity-stability relationship is due to a greater variation in species-specific dynamic properties in species-rich communities (as proposed by Yachi & Loreau 1990). A greater number of species guarantees that some will persist for longer periods of time even if others are frequently disturbed. We don't know, however, how tolerant each of these species is to environmental fluctuations, but we do know that there is a wide range of interspecific variation in persistence and disturbance rates.

Species transition properties

The transition probabilities of individual species found in this study are in accordance with previous studies of the Gulf of Chiriqui (C.G. Gómez et al., 2014, 2015), which grouped species based on their population dynamics. A persistence rate of 1 signified that all colonies of the species survived over the duration of the study, and a persistence rate of 0 signified that all colonies of the species died during the study period, as seen for *L. cuspidata* and *C. riisei* respectively.

The snowflake, *C. riseii*, a good competitor for space that exhibits invasive behavior (Concepcion et al., 2010), was the species most prone to being overgrown by octocorals and other sessile organisms, and had the fastest turnover time on both gulfs. This behavior contradicts the previous species descriptions made in other regions (Calcinai et al., 2004; Coles & Eldredge, 2002; Kahng & Grigg, 2005) and Panama (C.G. Gómez et al., 2014, 2015). The *C. riseii* population declined during the study period, which is worth exploring in future studies.

Although *M. austera* has abundant and constant reproductive output (Chapter 2), it was the species with the longest turnover time estimated by the model (27 years) and a relatively long recurrence time (115 years) explained by low disturbance (0.03) high persistence (0.9) and low colonization (0.07) rates. On the contrary, *L. alba*, which produces few oocytes during an annual reproductive season (Chapter 2) had short turnover (2.3 years) and recurrence times (8.3 years) explained by a high colonization rate (0.3). It is a reasonable hypothesis that the high colonization of *L. alba*, seen in this and other studies (C.G. Gómez et al. 2014, 2015; Chapter 3), could be due to recruits that are asexually produced by fragmentation or polyp detachment, behavior that is well known to happen in other octocoral species (Coffroth & Lasker, 1998; Lasker, 1988; Lasker & Coffroth, 1999).

During the present study octocoral colonization was frequently seen on spaces previously occupied by crustose coralline algae (CCA), additionally, the recruitment of *P. firma* and *P. ferruginea*, only occurred on CCA. Chemical cues from CAA are known to attract hard coral larvae facilitating recruitment (Heyward & Negri, 1999). It is possible that such interaction also occurs between CCA and octocorals.

None of the species transition properties were correlated with species abundance in Chiriqui, but colonization, replacement, and entropy were positively correlated with species abundance in Panama. The lack of correlation in the GC could be due to the high number of rare species and the low dominance present in this gulf (Gómez et al., 2014).

Species removal

As in many aspects of community ecology, our interpretation of an ecological process like biodiversity change is scale dependent (Levin, 1992). In this study the effect that species removal had on community evenness depended on the spatial scale at which it was analyzed. At the country and gulf scales, the effect of species deletions was minimal, and no key species were identifiable. However, when analyzed at the reef scale, the effect of the deletions increased considerably. The significant declines in species evenness after species deletions at the reef scale reflect the significance of the effect that species richness has on resilience.

The effect of species removal was measured as the compensatory changes in species abundance after one species was removed from the community (i.e. removed from the transition matrix). The effect of the species deletion on evenness was not as great in species rich communities (at the gulf or country scale), because the loss was compensated by the other species in the community. However, when analyzed at the reef scale, where species richness was lower, the effect of species deletion was considerably greater, the most dramatic change at the country scale was 10%, compared to 80% at the reef scale in Galera. This can be easily seen when comparing the effect of deletions in Roca Hacha, a species rich community, with deletions in Galera, a species poor one.

It is worth noting the high frequency of zeros within all the transition matrices (Attachment 4.1), which reveals a low degree of interaction among co-occurring octocoral species (Hill et al., 2004).

How octocoral communities differ from other marine sessile communtities

This analysis of our Markov Chain model allowed us to understand dynamical feature of our focal octocoral communities . The persistence rate of octocorals off Pacific Panama resembles the rate found in the subtropical subtidal rocky community studied by Hill et al. (2004) and the exposed pool of the Australian coral reef studied by Tanner et al. (1994). However, the estimated disturbance rate of octocorals was 6 orders of magnitude higher in the GC compared to the disturbance rate in the rocky subtidal (Hill et al. 2004) and 18 times higher than the rocky intertidal studied by Wootton (2001b). The estimated turnover time in the GP is relatively similar to that found in the rocky marine sessile communities studied by Hill et al. (2004) and Wootton (2001b). The estimated turnover time in the GC, however, is the highest reported, being almost 2 times greater than the next highest, which was the exposed pool of the Australian coral reef (Tanner et al. 1994; Hill et al. 2004). The estimated recurrence time for both the GC and the GP is higher than the other rocky communities, but within the range of coral reefs (Hill et al. 2004).

Model limitations

The presented model was based on transition probabilities measured in eight-1m^2 plots at eight sites, and assumed fix probabilities averaged in time and space. These probabilities, however, could vary due to the large spatial heterogeneity of these communities, and to the relatively short study period (19 months), which could mask long-term community dynamics.

This model is limited to three definitions of stability; resistance to change, return to previous state, and species compensations after extinction. However, because anthropogenic disturbances affect both, the stability and the diversity of natural systems simultaneously, it is necessary to identify the environmental factors that drive disturbances (Ives & Carpenter, 2007). These environmental factors are not well known for octocoral communities in the Tropical Eastern Pacific. It is especially important to study press perturbations such as warming and ocean acidification, which are major ecological drivers in other coral groups (Pandolfi et al., 2011). These perturbations are likely to change the number of species, their interaction and the nature and strength of the communities, which would change the fixed probabilities examined by this model.

Conclusions

The Markov chain model presented in this paper provided a first insight into the stability properties of octocoral communities off the Pacific coast of Panama. We found these communities have long persistence times. However, stability properties varied with location; communities at the Gulf of Chiriqui are three times more stable than those in the Gulf of Panama, but communities in the Gulf of Chiriqui were also less resilient. We hypothesized that this is due to strong competition for space with other sessile species, which limits octocoral recruitment and its ability to recover after disturbance. Modeled species extinctions had greater effect in species poor communities and at smaller spatial scales. Further studies are needed to identify environmental drivers affecting octocoral community stability.

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Table 4.1. Octocoral states at the studied locations in decreasing order of overall abundance: mean temporal abundance and standard error.

Species		Gulf of Chiriqui	Gulf of Panama
1	*Leptogorgia alba*	57.0 ± 2.7	60.3 ± 10.1
2	*Pacifigorgia cairnsi*	77.3 ± 4.0	0.0
3	*Leptogorgia coffrini*	6.0 ± 0.8	65.5 ± 13.7
4	*Pacifigorgia irene*	50.3 ± 1.6	3.8 ± 0.9
5	*Pacifigorgia rubicunda*	41.5 ± 2.6	0.0
6	*Pacifigorgia ferruginea*	11.0 ± 1.5	9.5 ± 3.6
7	*Pacifigorgia firma*	0.0	15.8 ± 0.5
8	*Muricea austera*	11.0 ± 0.7	2.5 ± 0.3
9	*Psammogorgia arbuscula*	8.0 ± 0.7	0.0
10	*Heterogorgia verrucosa*	6.3 ± 1.0	0.0
11	*Carijoa riisei*	1.8 ± 1.8	2.8 ± 1.2
12	*Pacifigorgia eximia*	3.0 ± 0.4	0.0
13	*Leptogorgia cuspidata*	1.0 ± 0.0	0.0

Table 4.2: Community dynamic properties and stability measurments calculated from transition matrices in octocoral communities off Pacific Panama, Gulf of Chiriqui (GC), and Gulf of Panama (GP),

Transition probabilities and dynamic properties	Pacific Panama	Gulf of Chiriqui	Gulf of Panama
Octocoral mean disturbance rate	0.31	0.16	0.37
Octocoral mean colonization rate	0.18	0.14	0.27
Octocoral mean persistence rate	0.59	0.66	0.61
Replacement by (Octocoral)	0.01	0.02	0.04
Replacement of (Octocoral)	0.09	0.18	0.02
Normalized entropy	0.39	0.34	0.48
Octocoral turnover rate	0.41	0.34	0.39
Octocoral turnover time (years)	3.70	9.58	3.04
Octocoral recurrence time (years)	66.88	67.94	42.54

Table 4.3. Correlation between species dynamic properties and their mean abundance

Property	Chiriqui		Panama	
	R^2	*P* value	R^2	*P* value
Disturbance	-0.16	0.6	-0.07	0.88
Persistence	-0.23	0.47	-0.03	0.9
Colonization	0.3	0.34	0.89	0.008*
Replacement of	0.33	0.29	0.95	0.01*
Replacement by	0.38	0.22	0.85	0.02*
Turnover rate	0.23	0.48	0.03	0.95
Turnover time	-0.21	0.52	-0.4	0.37
Recurrence time	-0.16	0.61	-0.43	0.34
Entropy	0.68	0.02*	0.84	0.02*

Table 4.4. Rate of convergence to stationary distribution

Location	Damping ratio	Convergence rate %/year	Half life
Pacific Panama	1.12	11.33	6.11
Gulf of Chiriqui	1.05	4.45	15.57
Gulf of Panama	1.17	15.71	4.41
Catedrales	1.07	6.70	10.35
Roca Hacha	1.06	5.50	12.61
Jicarita	1.04	3.81	18.18
Propser	1.15	13.99	4.95
Elefante	1.21	18.76	3.70
San Telmo	1.08	7.89	8.78
Galera	1.01	0.75	92.69
Pedro Gonzalez	1.98	68.36	1.01

Table 4.5. Relationship between the decline in species evenness after species removal and species relative abundance at different special scales.

Scale	Site	Species evenness of the stationary community	Relationship to species relative abundance	
			Slope	*P* value
Study Region	Pacific Coast of Panama	0.76	-0.14	0.20
Gulf	Gulf of Chiriqui	0.77	-0.03	0.80
Gulf	Gulf of Panama	0.82	-0.16	0.20
Reef	Catedrales	0.64	-1.06	0.02 *
Reef	Jicarita	0.75	-0.59	0.06
Reef	Roca Hacha	0.74	-0.29	0.29
Reef	Prosper	0.19	-1.06	0.02 *
Reef	Elefante	0.57	-0.59	0.34
Reef	Galera	0.30	-1.46	0.37
Reef	San Telmo	0.70	-0.75	0.11

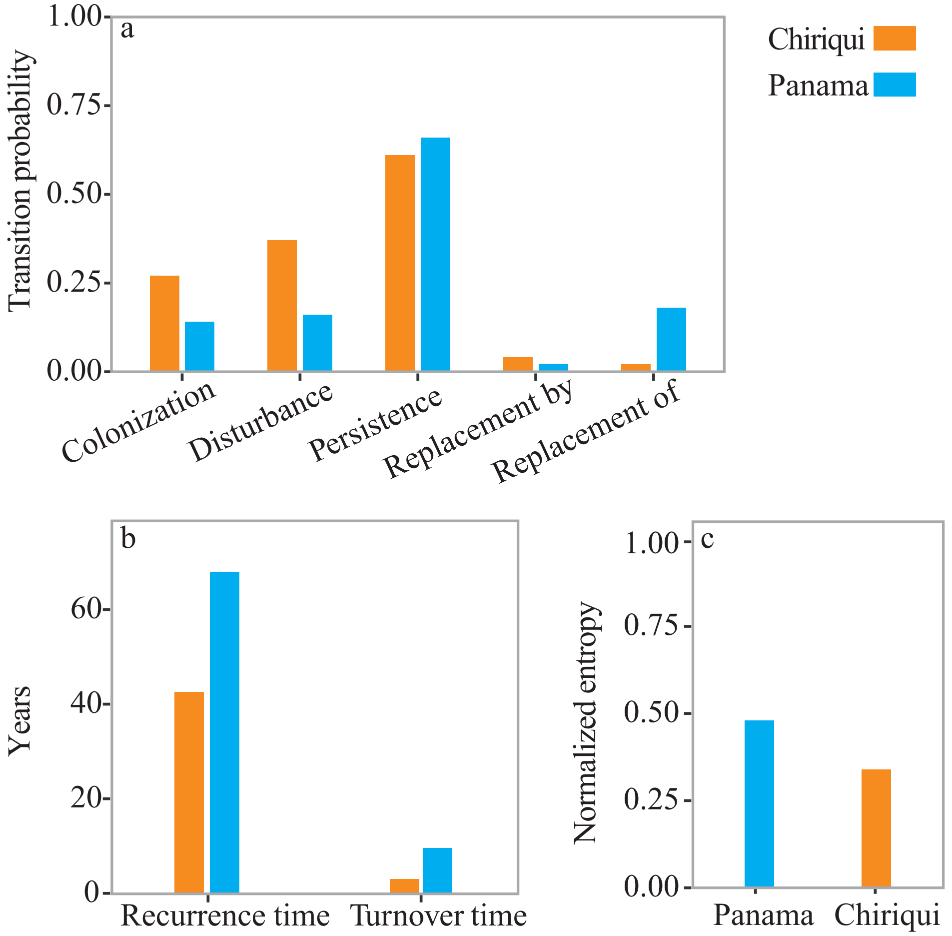


Figure 4.1. Transition probabilities (a), stability properties (b) and predictability (c) of octocoral communities in the Gulf of Panama (GP, cyan) and the Gulf of Chiriqui (GC, orange). In general octocorals in the communities had high persistence rate, with low probabilities of been replace (overgrown) by another octocoral. However, colonization and disturbance rates were higher in the GP (a). These differences made the GC be more stable (greater recurrence time) but less resilient (slower turnover time) (b). The faith of a point randomly taken from the stationary community was more predictable in the Gulf of Chiriqui (c).

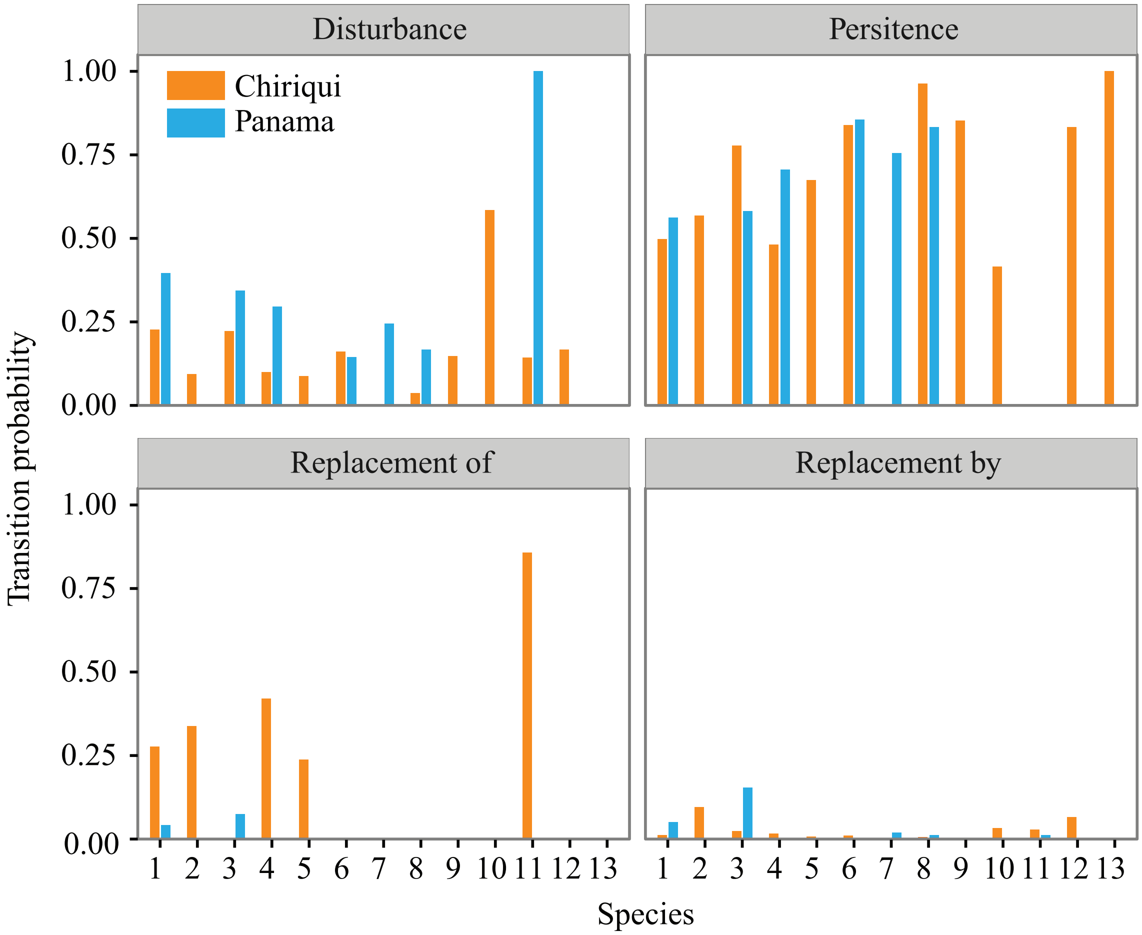


Figure 4.2. Species-specific transition probabilities from the community transition matrices of octocoral communities in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Species are displayed in decreasing order of abundance as in Table 4.1. Probability of disturbance, probability of persistence, probability that the species is replaced by another octocoral and probability that the species replaces another octocoral.

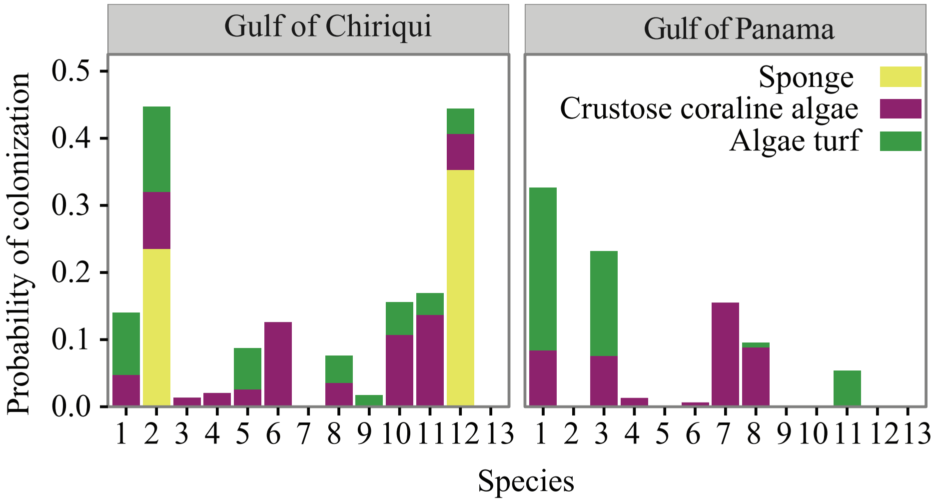


Figure 4.3. Species-specific transition probability of octocoral colonization in spaces previously occupied by sponges (green), crustose coralline algae (magenta) or algae turf (yellow) in communities located in the Gulf of Chiriqui and the Gulfof Panama. Species are displayed in decreasing order of abundance as in Table 4.1.

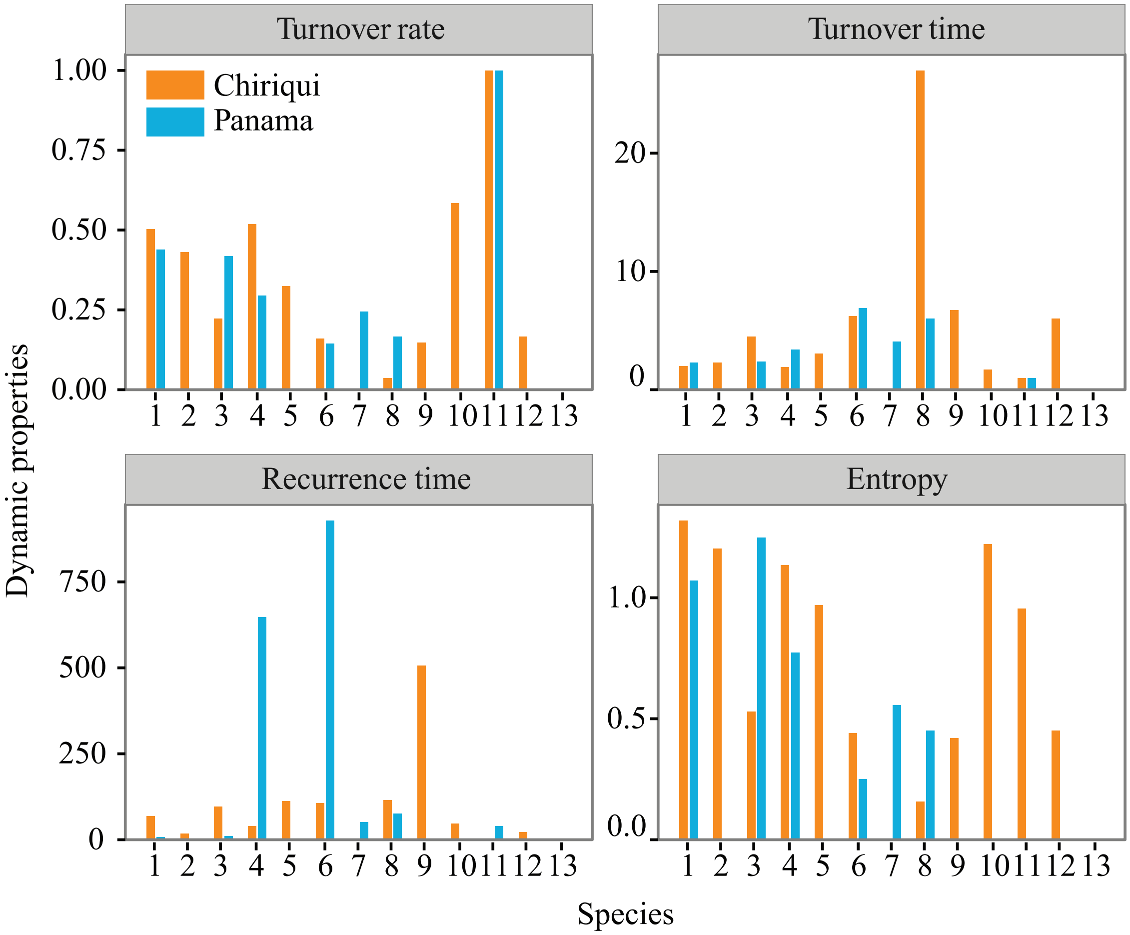


Figure 4.4. Species-specific dynamic properties of octocorals in the Gulf of Chiriqui (orange) and the Gulf of Panama (cyan). Turnover rate, turnover time, recurrence time and Predictability, quantified by the entropy of the species column in the transition matrix. Species are displayed in decreasing order of abundance as in Table 4.1.

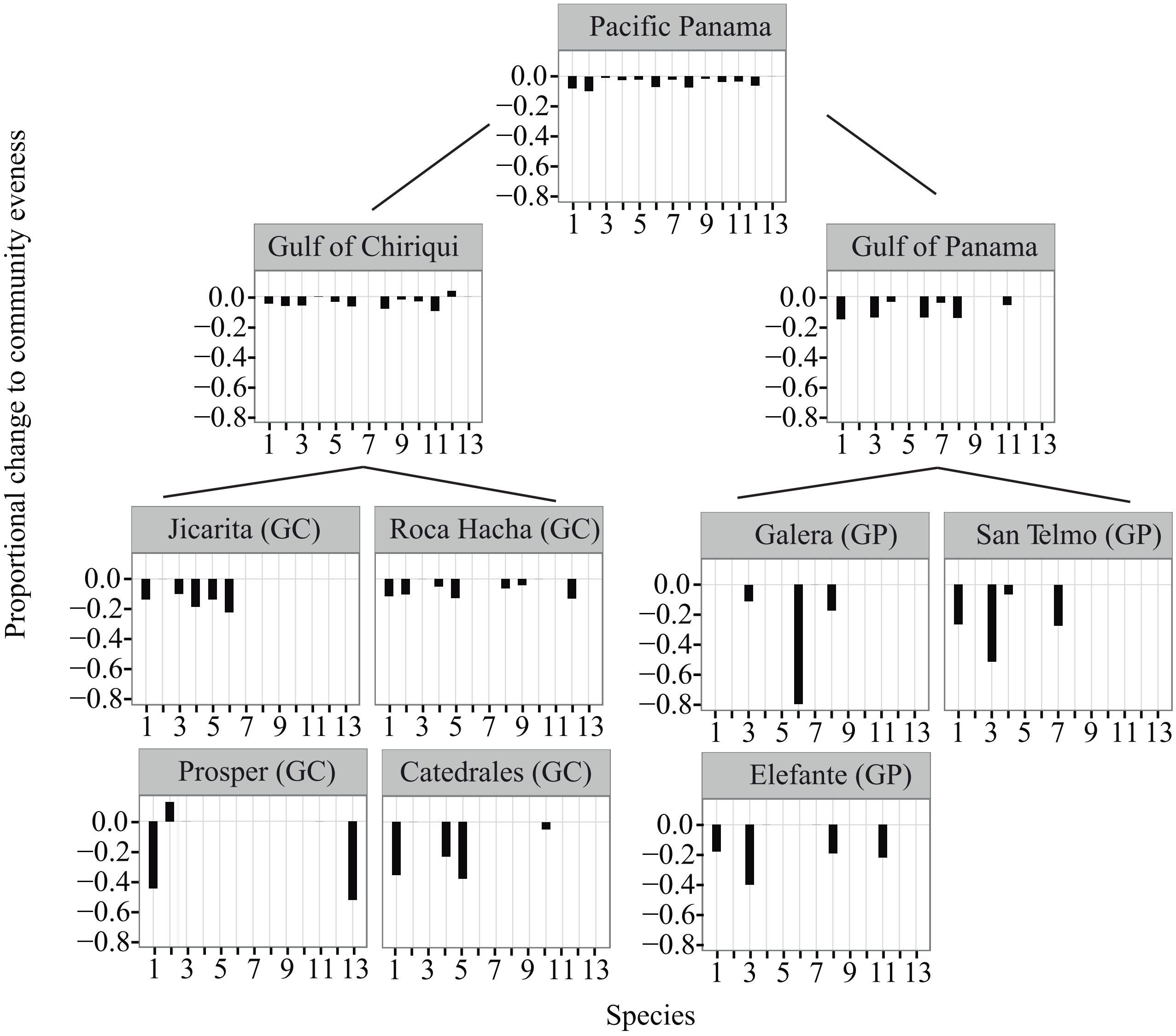


Figure 4.5. Proportional change of community evenness after species removal at three spatial scales: Pacific Panama, gulfs and individuals reefs. The effect of the removal of each species is displayed in decreasing order of abundance as in Table 4.1.

Supplemental 4.1.

The dynamic properties of each octocoral species, as well as the dynamic properties of the entire community were quantified using the following Hill et al. (2004) formulations where: “P” is the transition matrix of the stationary community (Supplemental 4. 2), “*j”* is the column of species *j*, “*i”* is the row of species *i,* “*s”* is a non-octocoral state, called “bare rock” in Hill et al. (2004), “p” is an entry in any given point of P, “w” is the matrix dominant eigenvector normalized to sum to 1, “λ_1” and “λ_2” are the largest and second largest eigenvalues of P.

Transition probabilities

	Species	Community
Colonization of *j*	$= p_{js}$	$= \sum_{i \neq s} p_{is} = 1 - p_{ss}$
Disturbance of *j*	$= p_{sj}$	$= \frac{\sum_{j \neq s} w_j p_{sj}}{\sum_{j \neq s} w_j}$
Replacement of *j*	$= 1 - p_{jj} - p_{sj}$	$= \frac{\sum_{i \neq s} w_i (1 - p_{ii} - p_{si})}{\sum_{i \neq s} w_i}$
Replacement by *j*	$= \frac{1}{s-2} \sum_{j \neq i, s} p_{ij}$	$= \frac{\frac{1}{s-2} \sum_{i \neq s} w_i \sum_{j \neq i, s} p_{ij}}{\sum_{i \neq s} w_i}$
Persistence of *j*	$= p_{jj}$	

Stability properties

	Species	Community
Turnover rate of *i*	T = (1-p_{ii})	
Turnover time of *i*	= 1/ T	$\bar{\tau}_{\text{bio}} = \dfrac{\sum_{i \neq s} \frac{w_i}{T_i}}{\sum_{i \neq s} w_i}.$
Recurrence time	$\theta_i = \dfrac{1 - w_i}{w_i(1 - p_{ii})}$	$\bar{\theta} = \sum_i w_i \theta_i,$
Entropy	$H(\mathbf{p}_{\cdot j}) = -\sum_i p_{ij} \log p_{ij}.$	$H(\mathbf{P}) = -\sum_{j=1}^{s} w_j \sum_{i=1}^{s} p_{ij} \log p_{ij}.$ Normalized entropy= $H_r(\mathbf{P}) = \dfrac{H(\mathbf{P})}{H_{\max}(\mathbf{P})}.$

Diversity measurements

Proportion of octocoral states	$w_i' = \dfrac{w_i}{1 - w_s} \quad i \neq s,$
Shannon-Wiener index	$H(\mathbf{w}') = -\sum_i w_i' \log w_i'.$
Community evenness	$J = \dfrac{H(\mathbf{w}')}{\log s}.$

Supplemental 4. 2. Transition matrices of the stationary community for each gulf and each reef. Warmer colors indicate higher transition values. Temporal mean ± standard error. Crustose coralline algae (CCA), algae turf (Turf).

Gulf of Chiriqui

	L.alba	*P.cairnsi*	*L.coffrini*	*P.irene*	*P.rubicunda*	*P.ferruginea*	*M.austera*	*P.arbuscula*	*H.verrucosa*	*C.riseii*	*P.eximia*	*L.cuspidata*	Sponge	CCA	Turf
L.alba	.50 ± .07	.0	.0	.01 ± .01	.0	.0	.0	.0	.0	.0	.0	.0	.0	.05 ± .03	.09 ± .01
P.cairnsi	.0	.57 ± .23	.0	.0	.22 ± .26	.0	.0	.0	.0	.57	.0	.0	.24 ± .28	.08 ± .08	.13 ± .04
L.coffrini	.0	.0	.78 ± .10	.0	.0	.0	.0	.0	.0	.29	.0	.0	.0	.01 ± .02	.0
P.irene	.0	.19 ± .19	.0	.48 ± .25	.0	.0	.0	.0	.0	.0	.0	.0	.0	.02 ± .02	.0
P.rubicunda	.0	.0	.0	.0	.67 ± .03	.0	.0	.0	.0	.0	.0	.0	.0	.03 ± .01	.06
P.ferruginea	.0	.0	.0	.0	.0	.84	.0	.0	.0	.0	.0	.0	.0	.13	.0
M.austera	.0	.0	.0	.0	.0	.0	.96	.0	.0	.0	.0	.0	.0	.04	.04
P.arbuscula	.0	.0	.0	.0	.0	.0	.0	.85	.0	.0	.0	.0	.0	.0	.02
H.verrucosa	.26 ± .27	.0	.0	.0	.0	.0	.0	.0	.42 ± .32	.0	.0	.0	.0	.11 ± .11	.05 ± .05
C.riseii	.01 ± .01	.14 ± .12	.0	.01 ± 0.1	.02 ± 0.1	.0	.0	.0	.0	.0	.0	.0	.0	.14 ± .14	.03 ± .03
P.eximia	.0	.0	.0	.40 ± .34	.0	.0	.0	.0	.0	.0	.83	.0	.35	.05 ± .06	.04 ± .04
L.cuspidata	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	1	.0	.0	.0
Sponge	.03 ± .05	.0	.0	.01 ± .01	.02 ± .02	.0	.0	.0	.09 ± .07	.0	.0	.0	.24 ± .29	.02 ± .02	.12 ± .13
CCA	.10 ± .10	.06 ± .05	.22 ± .10	.05 ± .03	.01 ± .01	.16	.0	.0	.36 ± .28	.0	.0	.0	.0	.30 ± .14	.05 ± .04
Turf	.10 ± .26	.04 ± .27	.0	.04 ± .33	.06 ± .32	.0	.04	.15	.13 ± .32	.14	.17	.0	.18 ± .18	.03 ± .28	.37 ± .14

Gulf of Panama

	L.alba	*L.coffrini*	*P.irene*	*P.ferruginea*	*P.firma*	*M.austera*	*C.riseii*	Pocillopora	CCA	Turf
L.alba	.56 ± .07	.07 ± .07	.0	.0	.0	.0	.0	.0	.08 ± .08	.24 ± .01
L.coffrini	.0	.58 ± .07	.0	.0	.0	.0	.0	1	.08 ± .05	.16 ± .11
P.irene	.0	.0	.70 ± .15	.0	.0	.0	.0	.0	.01	.0
P.ferruginea	.0	.0	.0	.76	.0	.0	.0	.0	.16	.0
P.firma	.0	.0	.0	.0	.86 ± .09	.0	.0	.0	.01 ± .01	.0
M.austera	.0	.0	.0	.0	.0	.83 ± .29	.0	.0	.09	.01 ± .01
C.riseii	.04	.0	.0	.0	.0	.0	.0	.0	.0	.05
Pocillopora	.0	.10	.0	.0	.0	.0	.0	.0	.0	.0
CCA	.11 ± .07	.11 ± .10	.22	.24	.03 ± .02	.0	.0	.0	.39 ± .02	.02 ± .02
Turf	.28 ± .12	.13 ± .08	.08 ± .06	.0	.11 ± .10	.17 ± .06	1	.0	.18 ± .12	.52 ± 0.4

Roca Hacha

	L.alba	*P.cairnsi*	*L.coffrini*	*P.irene*	*P.rubicunda*	*M.austera*	*P.arbuscula*	*H.verrucosa*	*P.eximia*	*Sponge*	CCA	Turf
L.alba	.75±.1	.0	.0	.02±.02	.0	.0	.0	.0	.0	.0	.09±.06	.14±.08
P.cairnsi	.0	.72±.08	.0	.0	.0	.0	.0	.0	.0	.0	.11±.08	.08±.04
L.coffrini	.0	.0	.67±.3	.0	.0	.0	.0	.0	.0	.0	.0	.0
P.irene	.0	.0	.0	.85±.03	.0	.0	.0	.0	.0	.0	.03±.03	.0
P.rubicunda	.0	.0	.0	.0	.89±.02	.0	.0	.0	.0	.0	.03±.03	.08±.08
M.austera	.0	.0	.0	.0	.0	.96±.04	.0	.0	.0	.0	.05±.03	.06±.06
P.arbuscula	.0	.0	.0	.0	.0	.0	.85±.1	.0	.0	.0	.0	.02±.02
H.verrucosa	.0	.0	.0	.0	.0	.0	.0	.92±.08	.0	.0	.0	.0
P.eximia	.0	.0	.0	.0	.0	.0	.0	.0	.83±.16	.5±.3	.0	.0
Sponge	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.03±.03
CCA	.06±.03	.21±.06	.66±.33	.07±.04	.02±.02	.0	.0	0	.0	.0	.67±.12	.07±.07
Turf	.19±.1	.08±.05	.0	.06±.04	.08±.01	.04±.04	.15±.1	.08±.08	.17±.16	.5±.3	.02±.02	.52±.1

Jicarita

	L.alba	*P.cairnsi*	*L.coffrini*	*P.irene*	*P.rubicunda*	*P.ferruginea*	CCA
L.alba	.57±.07	.0	.0	.0	.0	.0	.13±.04
P.cairnsi	.0	1	.0	.0	.0	.0	.0
L.coffrini	.0	.0	.67±.33	.0	.0	.0	.05±.04
P.irene	.0	.0	.0	.88±.08	.0	.0	.06±.06
P.rubicunda	.0	.0	.0	.0	.97±.03	.0	.05±.03
P.ferruginea	0	.0	.0	.0	.0	.84±.09	.2±.05
CCA	.43±.07	.0	.33±.33	.12±.08	.03±0.3	.16±.09	.52±.15

Prosper

	L.alba	*P.cairnsi*	*L.coffrini*	*C.reseii*	*L.cuspidata*	Tubastrea	Sponge	CCA	Turf
L.alba	.87±.02	.0	.0	.0	.0	.0	.0	.0	.11±.06
P.cairnsi	.0	.89±.04	.0	.57±.19	.0	1	1	.36±.14	.22±.11
L.coffrini	.0	.0	1	.29±.1	.0	.0	.0	.0	.0
C.reseii	.0	.0	.0	.0	.0	.0	.0	.0	.0
L.cuspidata	.0	.0	.0	.0	1	.0	.0	.0	.0
Tubastrea	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sponge	.0	.0	.0	.0	.0	.0	.0	.03±.03	.0
CCA	.08±.02	.05±.03	.0	.0	.0	.0	.0	.55±.05	.15±.08
Turf	.06±.00	.05±.02	..0	.14±.05	.0	.0	.0	.06±.06	.52±.14

Catedrales

	L.alba	*P.cairnsi*	*P.irene*	*P.rubicunda*	*H.verrucosa*	CCA	Turf
L.alba	.77±.03	.0	.0	.0	.0	.32±.19	.13±.02
P.cairnsi	.0	.67±.33	.0	.0	.0	.0	.0
P.irene	.0	.0	.95±.03	.0	.0	.16±.10	.10±.05
P.rubicunda	.0	.0	.0	.89±.11	.0	.02±.02	.22±.15
H.verrucosa	.0	.0	.0	.0	.79±.19	.02±.02	.0
CCA	.04±.02	.33±.33	.02±.02	.03±.03	.0	.40±.30	.09±.08
Turf	.19±.01	.0	.03±.03	.08±.08	.21±.17	.07±.07	.46±.22

Elefante	*L.alba*	*L.coffrini*	*P.irene*	*P.firma*	*M.austera*	*C.riseii*	Turf
L.alba	.67±.22	.0	.0	.0	.0	.0	.27±.09
L.coffrini	.0	.67±.18	.0	.0	.0	.0	.11±.11
P.irene	.0	.0	1	.0	.0	.0	.0
P.firma	.0	.0	.0	.67±.33	.0	.0	.0
M.austera	.0	.0	.0	.0	.83±.17	.0	.02±.02
C.riseii	.04±.04	.0	.0	.0	.0	.0	.06±.06
Turf	.29±.23	.33±0.18	.0	.33±.33	.17±.17	1±.33	.55±.17

San Telmo	*L.alba*	*L.coffrini*	*P.irene*	*P.firma*	CCA	Turf
L.alba	.70±0.18	.0	.0	.0	.21±.10	.24±.14
L.coffrini	.0	.61±.19	.0	.0	.20±.08	.10±.11
P.irene	.0	.0	.58±.21	.0	.02±.02	.0
P.firma	.0	.01±.01	.0	.93±.04	.02±.02	.0
CCA	.22±.14	.35±.19	.25±.12	.07±.04	.54±.17	.06±.07
Turf	.08±.05	.03±.00	.17±.10	.0	.02±.01	.60±.24

Galera	*L.coffrini*	*P.ferruginea*	*P.firma*	*M.austera*	Pocillopora	CCA	Turf
L.coffrini	.86±.10	.0	.0	.0	1	.08±.08	.5±.29
P.ferruginea	.0	.76±.12	.0	.0	.0	.19±.10	.0
P.firma	.0	.0	1	.0	.0	.0	.0
M.austera	.0	.0	.0	1	.0	.11±.11	.0
Pocillopora	.11±.11	.0	.0	.0	.0	.0	.0
CCA	.03±.03	.24±.12	.0	.0	.0	.44±.29	.0
Turf	.0	.0	.0	.0	.0	.17±.17	.5±.29

Pedro Gonzalez	*L.alba*	*L.coffrini*	CCA	Turf
L.alba	.44±.09	.25±.17	.0	.31±.15
L.coffrini	.01±.01	.50±.33	.0	.0
CCA	.02±.02	.0	.50±.33	.02±.02
Turf	.53±.07	.25±.17	.50±.33	.67±.18

General thesis conclusions

Temporal diversity trends

Context and contributions of Chapter 1

A variety of metrics and analyses at multiple spatial scales contributed to disentangling local community changes within the present context of human-driven mass extinction (Dirzo et al., 2014). Coral reefs from Pacific Panama declined in abundance and richness, which produced changes in community structure mainly explained by heat-intolerant species (Chapter 1). Although these changes occurred in both Gulfs (GP and GC), changes in community composition were 1.6 greater in the GC, the warmer gulf, and varied at different spatial scales (Figure d.1).

A reef's relative level of protection from human related activities (location inside or outside a Marine Protected Area (MPA) did not explain diversity changes. However, this doesn't mean that anthropogenic activities are not affecting these ecosystems. Instead, it exposes the lack of management and enforcement inside protected areas (Alvarado et al., 2017) and the negative regional effect of a small but constant water warming periods produced by a human-related global warming epoch.

Knowing our fauna before it is too late

Context and contributions of Chapter 2

Rapid declines in diversity are threatening species and entire ecosystems very quickly, so increasing knowledge about the biology and ecology of ecologically important species, such as foundation species, is essential if we want to be able to predict the ecological consequences of the population declines reported for the area (Gómez, et al. 2015) and the resilience to disturbance at the species and community levels and different spatial scales.

Although a great deal of information is known about the life cycle of scleractinian corals (reef building hard corals) in the Tropical Eastern Pacific, this thesis is the first contribution that describes the reproductive output, fertility, spawning time, recruitment limitations, and community stability of octocoral species (soft corals) from the Tropical Eastern Pacific.

In addition to being foundation species that create complex tri-dimensional "animal forests" (Sanchez, 2016), two of the octocoral species studied during this research, *Muricea austera* and *Leptogorgia alba*, are also the source of active compounds that can defeat life-threatening diseases (Gutierrez et al., 2005, 2006). Nevertheless, little was previously known about their life cycle.

L. alba is relatively common and fast growing, with frequent recruitment (Gómez et al., 2014) and fast recovery after disturbance (Gómez et al., 2015), however it has low reproductive output and a short reproductive period that coincides with the upwelling season (Chapter 2), when primary production is high and marine currents are strong

(D´Croz & O'Dea, 2007; Xie et al., 2005). In contrast, *M. austera* is less abundant and slower growing, with scarce recruitment (Gómez et al., 2014) and slow recovery (Gómez et al., 2015), but it has high reproductive output and continuous reproduction, with a spawning peak that coincides with the warmest month (Chapter 2), when primary production is low and marine currents are weak (D´Croz & O'Dea, 2007; Xie et al., 2005).

It can be concluded that the population dynamics, especially recruitment rates, of these two species is not related to their reproductive output. Asexual reproduction is common in octocoral species from the Caribbean (Kahng et al. 2011; Lasker, 1984); it happens through polyp detachments or colony breakage after disturbance (Lasker, 1984). The high recruitment rate of *L.alba* could be due to asexual reproduction, but it could also be the result of high survivorship of oocytes/larvae before settlement, which could be related to the oceanographic conditions at the time of spawning. *Muricea's* oocytes and/or larvae, on the other hand, may spend a significant amount of time in the water column with high mortality rates resulting in very low recruitment (Figure d.1).

Context and contributions of Chapter 3

Rich and abundant octocoral communities inhabit the GP (Guzman et al., 2008) and the GC (Gómez et al., 2014; Guzman et al., 2004), however, little was known about what limits their distribution and abundance. The third chapter of this thesis is the first approach to studying the environmental and demographic factors that limit octocoral recruitment under varying oceanographic conditions within the TEP. Studies from other regions have related octocoral recruitment to adult density, space, and environment, but have done so independently, reaching different conclusions. This study, however, evaluated the combined effect and interaction of these factors, which regulate octocoral recruitment in the TEP.

In general, octocoral recruitment was related to adult density. This relationship however, was not sustained if space became a limiting factor. In this study space was a limiting factor in the GC and not in the GP. Octocoral communities within study plots were more diverse in the GC, but the benthic space in this gulf was also highly occupied by sponges, tunicates, azoozanthellate corals (*Tubastrea coccinea*), coralline algae, and algae turf. The high degree and abundance of other sessile species in the GC, and not in the GP, could explain the space-limited recruitment only in the GC (Figure d.1).

The density dependent recruitment found on both gulfs and for all common species supports the hypothesis that octocoral aggregations facilitate population growth, as co-occurring adults positively influence recruitment of new colonies (Privitera-Johnson's 2015). Octocorals produce secondary metabolites, which are known to inhibit the growth of other sessile organisms (Standing et al., 1984), avoid predation (O'Neal & Pawlik, 2002) and trigger larvae settlement (Slattery et al., 1999). This facilitated recruitment, however, may only function when space in not limited.

Leptogorgia alba had a recruitment peak on both gulfs between January and June, which followed the potential spawning time described in Chapter 2. This indicates that oocyte development and larval settlement in this species occurs relatively quickly. On the contrary, no recruitment of *M. austera* was seen on either of the gulfs, meaning that the high number of oocytes produced by this species remained in the water column. These differences could indicate different dispersal abilities and therefore, a different degree of connectivity among populations.

Community Stability

Context and contributions of Chapter 4

With long term monitoring data we can estimate the stability and resilience of important ecosystems such as coral reefs. This data allows scientist to predict what would happen after a disturbance and how this would affect associated fauna. However, this type of long-term data is not available for octocoral communities, which also sustain a great suite of associated diversity (Cantera et al., 1987; Sanchez, 2016). With the aid of a Markov Chain model, the last chapter of this thesis used transition probabilities to estimate the stability and resilience of octocoral communities, as well as the effect of diversity loss on the GP and the GC.

In general, octocoral species had high persistence rates, however transition probabilities were different between the gulfs; octocoral communities in the GC had lower disturbance and colonization rates than those in the GP. These differences made the GC two to three times less dynamic (lower turnover time), and three times more stable. However, the low colonization rates at this gulf (GC) made it 1.6 times less resilient (lower recurrence time) than the GP (Figure d.1).

As proposed by Ives and Carpenter (2007) we found both, a positive and a negative relationship between species richness and stability. A greater diversity in the GC produced a greater variation in species-specific dynamic properties, in where species with low disturbance rates compensated for species with higher rates. This resulted in higher community stability when measured as resistance to change. However, because space is a limiting factor for octocoral recruitment in this gulf (Chapter 3) the ability to recover is reduced due to competition for space with other sessile organisms.

Spatial scale, challenges to interpret diversity changes and disturbance

The diversity changes in coral reefs studied in Chapter 1, as well as the stability properties in octocoral communities studied in Chapter 4, were scale specific, which is common in ecological processes (Levin, 1992). Alpha diversity trends in coral reefs averaged to zero when analyzed at a larger spatial scale (country), however, there were significant positive and negative temporal changes at the reef scale. In the same way, when an octocoral species was deleted from the modeled community in Chapter 4, the effect of the deletion in community evenness was significantly smaller at the gulf or the country scale than the effect at the site scale. Scale specific conclusions such as these make biodiversity studies challenging, and multi-scale approaches powerful (Gonzalez et al., 2016).

Different natural and anthropogenic stressors are expected to act at different spatial scales. For example, climate fluctuations and small but frequent regional warming events drove changes in abundance and composition of scleractinian species in coral reefs at the country scale. It was expected that reef protection, a reef's location inside or outside a Marine Protected Area (MPA), would explain diversity changes at the local scale, however, this was not the case in the trends detected in Chapter 1. Scale-depended drivers like this can be masked by the lack of management and regulation inside MPAs, where low budgets for patrolling and low governability for enforcement (Alvarado et al., 2017) make "managed" reefs as vulnerable as those that are not managed.

Diversity, ecosystem functioning, and environmental services

Decreases in coral abundance like that reported in Chapter 1, are related to extreme alterations in the structure, complexity, and functioning of the coral community (Alvarez-Filip et al., 2013). When coral abundance decreases significantly, reefs can change to a less desired algae dominated state, and the environmental services the reef used to provide are no longer possible (Bellwood et al., 2004).

Changes of such magnitude have been reported after extreme disturbances, such as reaching a given stress threshold (e.g. coral bleaching threshold) (Glynn, 1990). However, findings from Chapter 1 demonstrate that community composition can rapidly diverge in the presence of small and frequent warm periods that do not reach the given stress threshold.

Water temperature parameters in Pacific Panama

It is well accepted and reported that oceanographic conditions in the Gulf of Panama and the Gulf of Chiriqui are drastically different due to a wind driven annual upwelling that significantly reduces water temperature during the first four months of the year only in the GP (D´Croz & O'Dea, 2007; Xie et al., 2005). This difference in water temperature variation between the Gulfs has been used in numerous studies to explain patterns and responses of coral reefs, which are located <15m depth (e.g. D´Croz & Maté, 2004; Glynn, 1990; Glynn et al., 2001; Glynn et al., 2017; Glynn & Macintyre,1977; Maté, 2003).

However, temperature data collected for Chapter 3, with loggers located in octocoral communities on both Gulfs, showed that such significant differences in water temperature reported for coral reefs (>15 m depth) is not found in octocoral communities (15-20 m depth). Both, the GP and GC have significant declines in water temperature during the first four months of the year. Therefore, the oceanographic conditions that have shaped coral reefs in Pacific Panama cannot be extrapolated to octocorals.

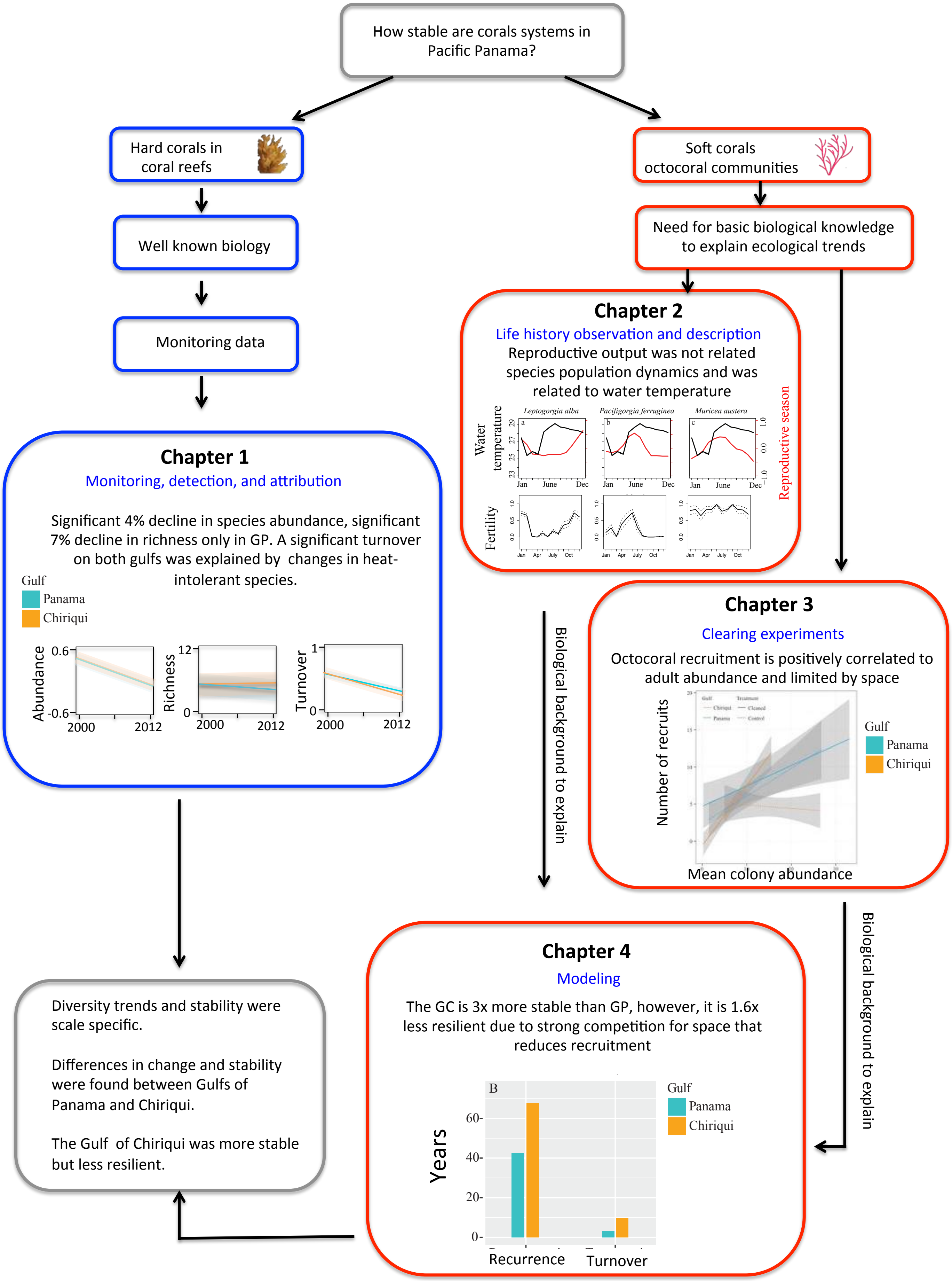
Answering simple questions leads to more open questions, ideas for future studies

The suite of new knowledge presented in this thesis can be used as a baseline for understanding the lasting effects of the 2015-2016 warming event (Jacox et al., 2016) in the two main groups of foundation marine species in Pacific Panama. This El Niño event was described as the strongest warming in fifty years (Whitney, 2015). It was called the "Godzilla El Niño" (Schiermeier, 2015) due to its potential devastation. Adequate baselines are the key to successful and robust biodiversity assessments.

Future coral reef monitoring should include anthropogenic and environmental descriptors around study sites in order to better detect biodiversity trends and also attribute those changes to specific events including, but not limited to, algae blooms, construction on shore, anchoring damage, and pouching reports inside MPAs.

Although this thesis has made significant contributions to knowledge about the biology and ecology of octocorals from the Tropical Eastern Pacific, there are many other topics to study before the historical gap of information about these species, which were ignored by science for more than a century (Bayer, 1981; Gómez et al., 2014), is filled.

These topics include; early development of oocyte and larvae settlement, dispersal abilities and connectivity among populations, chemical cues between octocorals and other taxa, interaction of small invertebrates that seem to complete their life cycle within an octocoral colony, and physiological effects of warming and ocean acidification.



How stable are corals systems in Pacific Panama?

Hard corals in coral reefs

Well known biology

Monitoring data

Chapter 1

Monitoring, detection, and attribution

Significant 4% decline in species abundance, significant 7% decline in richness only in GP. A significant turnover on both gulfs was explained by changes in heat-intolerant species.

Diversity trends and stability were scale specific.

Differences in change and stability were found between Gulfs of Panama and Chiriqui.

The Gulf of Chiriqui was more stable but less resilient.

Soft corals octocoral communities

Need for basic biological knowledge to explain ecological trends

Chapter 2

Life history observation and description

Reproductive output was not related species population dynamics and was related to water temperature

Biological background to explain

Chapter 3

Clearing experiments

Octocoral recruitment is positively correlated to adult abundance and limited by space

Biological background to explain

Chapter 4

Modeling

The GC is 3x more stable than GP, however, it is 1.6x less resilient due to strong competition for space that reduces recruitment

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