



## Survival, growth, and recruitment of octocoral species (Coelenterata: Octocorallia) in Coiba National Park, Pacific Panama

<sup>1</sup> Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama. Email: <guzmanh@si.edu>.

<sup>2</sup> Department of Biology, McGill University, 1205 Docteur Penfield, Montréal, Québec, Canada, H3A 1B1. Email: <andrew.gonzalez@mcgill.ca>, Phone: (1) 514-398-6444.

<sup>3</sup> Centro de Investigación en Ciencias del Mar y Limnología, Centro de Investigación en Estructuras Microscópicas, Universidad de Costa Rica, 11501-2060 San José, Costa Rica. Email: <odaliscab@gmail.com>, Phone: (506) 2511-4468.

\* Corresponding author email: <gomezcc@si.edu>, Phone: (507) 212-8736.

**Catalina G Gomez** <sup>1\*</sup>  
**Hector M Guzman** <sup>1</sup>  
**Andrew Gonzalez** <sup>2</sup>  
**Odalisca Breedy** <sup>1, 3</sup>

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**ABSTRACT.**—Octocorals (order Alcyonacea) from the tropical eastern Pacific have been largely ignored in coral reef studies, with the exception of recent taxonomic reviews. This study is the first to examine the population dynamics of 10 shallow water species in six genera (*Leptogorgia*, *Pacificogorgia*, *Muricea*, *Psammogorgia*, *Heterogorgia*, and *Carijoa*) found in rocky coral communities in Coiba National Park, Pacific Panama. For a 17-mo period, we monitored, every 4 mo, 1445 colonies of 15 species in fixed plots at 20 m depth in four coral communities. Size distribution, survivorship, and recruitment rates were calculated. Growth rate was calculated for *Leptogorgia alba* Duchassaing and Michelotti, 1864, *Pacificogorgia irene* Bayer, 1951, *Psammogorgia arbuscula* Verrill, 1868, and *Muricea austera* Lamouroux, 1821. Average octocoral density was 38.7 (SD 27.55) colonies m<sup>-2</sup> ( $n = 1394$ ) with a range of 1–103 colonies m<sup>-2</sup> and 1–11 species within a study plot. An overall population decline of 25.2% was observed in 1 yr. *Leptogorgia alba* was the most common species; it was abundant at all sites and exhibited characteristics of an *r*-selected species. In contrast, *M. austera* showed traits of a *K*-selected species, with low mortality and recruitment rates. Studied species were grouped into two distinct clusters based on their distribution, average density, mortality, and recruitment rates. Five species were grouped with *L. alba* and six species were grouped with *M. austera*.

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Octocorals (order Alcyonacea) are sessile colonial marine invertebrates found in many environments, ranging from cold deep oceans to shallow tropical seas (Bayer 1981, Alderslade 1984). The life histories of octocorals vary greatly due to species-specific symbionts (Mosher and Watling 2009), different growth forms (Breedy 2009), depth ranges, and reproductive strategies (e.g., Lasker 1990, Jordán-Dahlgren 2002), and the presence or absence of zooxanthellae (Van Open et al. 2005). Shallow water octocorals have lower dispersal capacities than scleractinian corals (Concepcion et al. 2010) and can occur in patchy distributions (e.g., Guzman et al. 2004, Linares et al. 2007).

For centuries, humans have exploited gorgonian octocoral species for ornamental purposes (Tsounis et al. 2010). Recently, more species, including those in the eastern Pacific, have been recognized as a source of novel natural products and active compounds that can be used in medicine (e.g., Blunt et al. 2004, Gutierrez et al. 2005, 2006) by those seeking to exploit the coral's chemical defenses against predators (Epifanio et al. 2000). In addition, human activities have damaged soft coral communities directly, through trawling, and indirectly through sedimentation and other forms of habitat degradation (Shester and Ayers 2005).

The biology and ecology of octocoral species have been well studied in the Indo-Pacific, Caribbean, Mediterranean, off Hawaii, and in the deep ocean. These studies examined symbiotic relationships with zooxanthellae algae (e.g., Lewis and Coffroth 2004, Koike et al. 2004, Van Oppen et al. 2005) and brittle stars (Mosher and Watling 2009); growth (e.g., Mistri and Ceccherelli 1992, 1994, Castanaro and Lasker 2003, Lasker et al. 2003, Cadena and Sanchez 2010, Munari et al. 2013); sexual reproduction (e.g., Kahng et al. 2008, Linares et al. 2008b, Hellström et al. 2010, Kahng et al. 2011); asexual reproduction (Lasker 1990); recruitment (Jamison and Lasker 2008); predation (Lasker and Coffroth 1988); feeding (Lasker et al. 1983); life history patterns (Linares et al. 2007, Linares et al. 2008a); and bleaching (Prada et al. 2010). Grigg (1972, 1974, 1975, 1977) studied life history trends in *Muricea* species in the eastern Pacific; however, knowledge about the species in the tropical eastern Pacific (TEP) is restricted mainly to taxonomy, biogeography, and phylogeny (Breedy and Guzman 2002, 2007, 2011, Vargas et al. 2008, 2010, Guzman and Breedy 2011).

Octocoral species present in the TEP are found in high-energy environments such as seamounts and rocky walls exposed to strong currents, waves, and swells (Breedy and Guzman 2002). These conditions may explain the lack of studies in these areas. Unlike octocorals in other locations, none of the 27 species studied by Van Oppen et al. (2005) in the TEP are associated with zooxanthellae, meaning that they are obligate heterotrophs and obtain nutrients via suspension feeding.

The TEP ranges from the Sea of Cortez to northern Peru (Robertson and Cramer 2009) and includes different octocoral communities that encompass 11 genera in four families with high levels of diversity, abundance, and endemism (Bayer 1953, Guzman et al. 2008). The Gulf of Chiriquí in Panama is a biodiversity hot spot in the TEP, with 52 octocoral species in seven genera (Guzman and Breedy 2008a). Coiba National Park (CNP), which is located along the Gulf of Chiriquí, is the largest marine protected area on the Pacific coast of Panama; it is part of the Marine Conservation Corridor of the TEP that includes Cocos Island (Costa Rica), Malpelo and Gorgona (Colombia), and Galápagos Islands (Ecuador) (see Fig. 1).

The most common octocoral genera in CNP are *Pacificorgia*, *Leptogorgia*, *Muricea*, *Psammogorgia*, *Eugorgia*, *Heterogorgia*, and *Carijoa*. The park contains 35 reported species, many of which are endemic to Coiba Island and the Gulf of Chiriquí (Guzman et al. 2004, Breedy and Guzman 2011). These species are distributed in highly diverse patches, along a depth gradient, and on occasions are found in monospecies patches. At CNP, octocorals share the substratum with encrusting coralline algae, scleractinian corals, algal turf, sponges, and tunicates (CGG, HMG, OB pers obs).

Of the 35 species present at CNP only one, *Carijoa riisei* (Duchassaing and Michelotti, 1860), has been studied. Until 2010, *C. riisei*, which inhabits reefs in the Indo-Pacific, and off Hawaii (Kahng and Grigg 2005, Kahng et al. 2008), Indonesia,

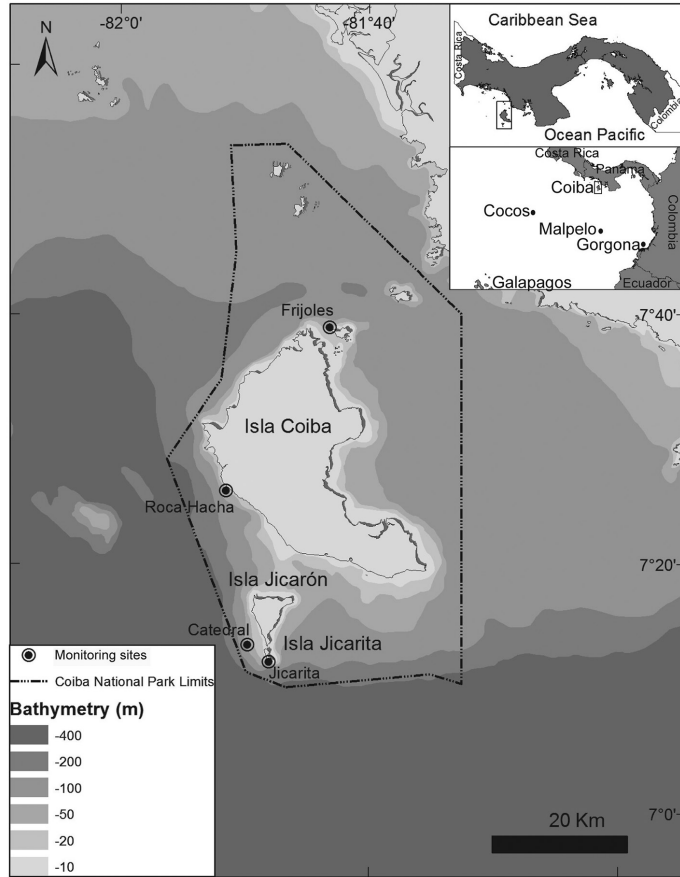


Figure 1. Study sites Jicarita, Catedrales, Roca Hacha, and Frijoles, in Coiba National Park, located in Panama and part of the Marine Conservation Corridor of the tropical eastern Pacific, which also includes Cocos (Costa Rica), Gorgona, Malpelo (Colombia) and Galápagos Islands (Ecuador).

and Vietnam (Calcinai et al. 2004), was recognized as an alien invasive species; however, Concepcion et al. (2010) confirmed that this species is native to the Pacific. It is a fast-growing azooxanthellate octocoral that prefers shaded places (Kahng and Grigg 2005) and exhibits density-dependent sexual reproduction (Kahng et al. 2008). *Carijoa riisei* is considered a fouling species (Bayer 1961) that often overgrows other sessile organisms (Grigg 2003).

The present study describes the octocoral community composition in four highly-diverse areas and the population dynamics of 10 common species in six genera in permanent monitoring plots located in CNP. It quantifies species mortality, recruitment, and growth rates in order to classify species into an  $r$  to  $K$  selection gradient. The present study is the first contribution on the biology of octocoral species and the ecology of octocoral communities in the tropical eastern Pacific.

## METHODS

## STUDY SITE

CNP is the largest marine protected area in Pacific Panama. It encompasses an archipelago with nine main islands and about 30 islets with an area of 270,125 ha, of which 80.2% are marine. The Park, including its Special Zone of Marine Protection, was declared a UNESCO World Heritage Site in 2005 because of its high levels of endemism and key ecological interactions, both in terrestrial and marine communities (Guzman et al. 2004, Maté et al. 2009). A management plan designed to protect its highly diverse marine and terrestrial ecosystems took effect in 2009. This plan established a non-take zone of 1.61 km around all islands and rocks and regulated artisanal fishery and tourism activities inside the park (Maté et al. 2009). Marine communities at the CNP are considered special because they are located in the Gulf of Chiriquí, which is unaffected by upwelling and trade north winds (D’Croz and O’Dea 2007), but experiences the influence of El Niño–Southern Oscillation (ENSO) every 2–7 yrs (Enfield 2001).

Study sites were chosen based on previous descriptions of the abundance and richness of the octocoral communities in the protected area (Guzman et al. 2004) and the tropical eastern Pacific (Guzman and Breedy 2008a), with one site on the leeward side and three on the seaward sides of the archipelago. These sites in CNP have basaltic rocky substrata inhabited by coral communities; they are exposed to different levels of wave action, currents, and swell. Site descriptions follow.

*Frijoles* (7°38′59.6″N, 81°43′09.4″W).—This small islet is located approximately 2.5 km offshore of the northern part of Coiba Island, about 17 km from the mainland, on the leeward side of the archipelago, protected from strong currents and swell. It is surrounded by shallow water (20 m depth) and located approximately 30 km away from the 400 m drop-off. The islet forms a vertical basaltic rocky wall from the surface down to 20 m depth. Encrusting coralline algae, small scleractinian colonies, macroalgae, and sponges cover the substrate. This site is located in a medium-high diversity area for corals and octocorals (Guzman et al. 2004). However, the octocoral community on the protected southeastern side of this islet is not diverse, and the most common species is *Leptogorgia alba* (Duchassaing and Michelotti, 1864). The coral predator *Acanthaster planci* (Linnaeus, 1758) is frequently seen in the area.

*Roca Hacha* (7°25′55.0″N, 81°51′29.0″W).—This basaltic rocky outcrop is located approximately 0.7 km offshore from the western seaward side of Coiba Island and is exposed to a strong swell. It is located in an area where natural mudslides are common, which create occasional sedimentation events. It is surrounded by shallow water (20 m depth) and located approximately 5 km away from the 400 m deep drop-off. This area was described as having medium-high diversity of corals and octocorals (Guzman et al. 2004). Roca Hacha forms a vertical rocky wall with a decrease in slope at 20 m depth. A highly diverse octocoral community covers the substrate (Guzman and Breedy 2008b) as well as encrusting coralline algae, macroalgae, algal turf, sponges, tunicates, and small scleractinian corals.

*Catedrales* (7°13′33.7″N, 81°49′45.4″W).—This underwater basaltic rocky outcrop, which forms two peaks 10 m below the sea surface, is located in the southwest region of CNP, approximately 2.6 km off of Jicarita Island. It is surrounded by shallow water

(20 m depth) and located approximately 3 km away from the 400 m deep drop-off. It is located in one of the four highly diverse areas of corals and octocorals within CNP (Guzman et al. 2004). Catedrales is exposed to strong currents from different directions and has a rich octocoral community. Encrusting coralline algae, sponges, tunicates, and small scleractinian corals also inhabit the substrate.

*Jicarita* (7°12'12.5"N, 81°48'02.3"W).—This island is located in the southernmost region of CNP. It has a 30 m high cliff that continues vertically down into the water and decreases in slope at 20 m depth; it is 3 km away from the 400 m deep drop-off. It is exposed to surf and a strong swell, which brings sediment up from the bottom during the rising tide. A very diverse octocoral community, as well as encrusting coralline algae, algal turf, sponges, and small scleractinian corals cover Jicarita's basaltic rocky substrate. This site has the highest coral diversity in Pacific Panama (Guzman and Breedy 2008b), and like Catedrales, it is located in one of the four most highly diverse areas of corals and octocorals within CNP (Guzman et al. 2004).

#### POPULATION DYNAMICS AND COLONY MONITORING

Nine 1-m<sup>2</sup> fixed plots were haphazardly established at a depth of 20 m at each site described above during the first week of June 2009. Fixed plots were marked within the octocoral community by installing 2 × 2 cm stainless steel square bars in the substrate with underwater cement; these markers were arranged parallel to shore and placed 5 m apart. An aluminum 1-m<sup>2</sup> (0.84 × 1.20 m) quadrat was designed to fit on the fixed stainless steel bars. The quadrat was divided into eight 0.42 × 0.30-m sections summing to a square meter. Each section was photographed using a digital high-resolution Nikon D-80 camera with a wide-angle lens inside an Ikelite underwater case and two external digital strobe flashes. The camera was attached to a stainless steel tripod to maintain a fixed distance (0.80 m) from the quadrat. To monitor changes in water temperature, a logger (HOBO Pro v.2) was attached to the first fixed bar on each site and programmed to record the water temperature every 30 min. Loggers were attached to the bars with plastic cable ties and replaced every monitoring period. Data were downloaded using manufacturer software HOBOWare® Pro Onset Computers and analyzed using SigmaPlot v.11 software.

Each octocoral colony within the fixed plots was identified to the species level and assigned a unique ID number. The colonies were then manually marked in the pictures using Nikon NX2 and Corel PHOTO-PAINT X3 software. *Carijoa riisei* colonies were identified as individual colonies when they were spatially separated from one another. Unlike the other studied species, *C. riisei* is stolonal and colonies are difficult to distinguish due to their vegetative growth. All colonies within the fixed plots were monitored about every 4 mo for a 17-mo period from June 2009 to November 2010, for a total of five monitoring periods: (t1) 20 June, 2009, (t2) 20 October, 2009, (t3) 28 March, 2010, (t4) 21 July, 2010, (t5) 30 November, 2010. Species abundance, local diversity, recruitment rates, colony survivorship, damage, and mortality for each monitoring period were quantified.

Colonies present at the beginning of the study (t1) were classified into species-specific relative size classes from 1 to 4, with 1 representing recruits, and 4 representing the largest colony in the study plots. Colony size in each size class is detailed in (Table 1). Data obtained were analyzed to measure differences in community composition among sites, species-specific survivorship, and recruitment rates.

Table 1. Colony size at each size class per species.

Species	Measurement	Size class (cm)			
		1	2	3	4
<i>Leptogorgia alba</i>	height	<2	2–5	5–10	10–15
<i>Pacifigorgia rubicunda</i>	width	<2	2–7	7–14	14–21
<i>Pacifigorgia irene</i>	width	<5	5–15	15–25	25–35
<i>Carrijoa riisei</i>	area (cm <sup>3</sup> )	<2	2–50	50–100	100–150
<i>Heterogorgia verrucosa</i>	width	<2	2–4	4–8	8–12
<i>Leptogorgia cofrini</i>	width	<1	1–3	3–6	6–9
<i>Pacifigorgia cairnsi</i>	width	<2	2–5	5–10	10–15
<i>Muricea austera</i>	width	<5	5–15	15–25	25–35
<i>Psammogorgia arbuscula</i>	width	<5	5–15	15–25	25–35

### COLONY GROWTH

Colony growth was studied for four species encompassing four genera within the study sites: *L. alba* at Frijoles, *Pacifigorgia irene* (Bayer, 1951) at Jicarita, and *Muricea austera* (Verrill, 1868), and *Psammogorgia arbuscula* (Verrill, 1866) at Roca Hacha. *Pacifigorgia rubicunda* (Breedy and Guzman, 2003) colonies were initially studied at Catedrales; however, it was not possible to identify the studied colonies in the field, and no growth analysis was performed for this site or this species. Ten colonies of each species were tagged within the monitoring plots and repeatedly photographed in June and October of 2009, and March, July, and November of 2010. Digital photographs were taken using a 1 × 1-cm reference grid board. Colonies were later measured to the closest millimeter with the aid of ImageJ 64 software (Lasker et al. 2003). Due to the variability of growth forms (e.g., seafan, branching), two kinds of measurements were taken: for the branched species (*L. alba* and *M. austera*), four measurements were taken: (1) colony width was measured between the farthest two points perpendicular to an imaginary *y*-axis intercepting the holdfast; (2) colony height was measured from the holdfast to the farthest point on the *y*-axis; (3) number of branch tips were counted, which included small ( $\geq 0.5$  cm) growing tips; and (4) branch growth involved measuring 10 individual branches at the beginning and end of the study period in five of the studied colonies. For the fan-like species (*P. irene* and *P. arbuscula*), the fan surface-area was measured as well as the maximum width and length.

### DATA ANALYSES

*Community Composition and Species Densities.*—Rank abundance distribution plots (RADs; MacArthur 1957) were used to describe octocoral communities within each site. RADs are common community composition descriptors that provide a graphic means for comparing the proportion of rare species among communities (McGill et al. 2007). The relative abundance of each species was calculated and plotted on a logarithmic scale against the species rank in abundance, from most to least common (from 1 to *n*). Overall species densities were calculated by dividing the number of colonies present on each plot by the total number of study plots. This calculation included the plots on sites where the focal species was not found.

*Survival Analysis.*—The difference in survivorship between species and within species among sites for all size classes (1–4) was analyzed using survival curves.



Kaplan-Meier log-rank survival analysis for multiple groups was used to examine for a significant difference among survival curves using the “s” statistic (Kaplan and Meier 1958). Analyses were performed using SigmaPlot 11.2 Software (Systat Software 2009). The non-parametric log-rank test uses chi-square statistics to test for differences between survival curves. It assumes equal accuracy among all data at a given time. For the purposes of the analysis, colonies that survived for the entire study period (17 mo) were marked as “censored.” Colonies that died were marked as “failure” and the survival time was the number of months that the colony remained alive or present in the study plots. For example, a colony that was recorded at t1 and t2, but not at t3, t4, and t5 had a survival time of 4 mo. Mortality rates between monitoring periods were calculated by dividing the number of dead colonies at  $t_{n+1}$  by the total number of colonies at  $t_n$ . Yearly mortality indices were calculated by dividing the total number of dead colonies by the total number of monitored colonies on each study plot over the course of a year. A significant difference in survivorship among species, sites, and across colony sizes was calculated with repeated measurements analysis of variance. Mortality peaks among sampling periods and the distribution of size classes within species were identified with a chi-square analysis ( $\chi^2$ ). When necessary, data were transformed to achieve normality ( $\log_{10}x$  for density and  $\sqrt{x + 1}$  for mortality and recruitment data).

*Recruitment Rate.*—The number of new colonies present in the study plots during each monitoring time was quantified. Analysis of variance (ANOVA) on ranks was performed to test for significant differences among monitoring sites. Friedman repeated measures of variance on ranks (Friedman 1937) were performed to test for significant differences among monitoring periods; the statistic for this test is represented as “q.” An overall yearly recruitment rate per m<sup>2</sup> was also calculated as well as significant differences between sites among species (ANOVA). This recruitment rate was calculated by dividing the total number of new colonies by the initial number of colonies on each study plot over a 12-mo period. Analyses were performed using SigmaPlot 11.2 Software.

*Colony Growth.*—The difference in size (height, width, area) between monitoring periods and the total difference from the beginning to the end of the study period were calculated for each monitored colony ( $n = 10$  per species). When a colony died before the study was over, size differences were calculated only if the colony remained alive for more than two monitoring periods ( $\geq 8$  mo). The difference in size was divided by the number of months over which the colony was studied, and the average monthly growth was calculated for each species. To calculate branch length growth, 10 individual branches from a single colony in five *M. austera* and three *L. alba* individuals were measured to the closest millimeter at the beginning and end of the study, and the differences were divided by the total study period (17 mo).

*Life History Strategies.*—To identify groups of species with similar life history patterns we performed a hierarchical cluster analysis using the function `pvclust` in the R package “`pvclust`” (Suzuki and Shimodaira 2011) performed in R Software 2.13 (R Development Core Team 2012). The analysis was executed using Euclidean distance with the “Ward” hierarchical method. This multivariate analysis calculates *P* values via multiscale bootstrap resampling that indicates how strong each cluster is supported by the data. The analysis compared studied species using four biological variables: distribution, density, and mortality and recruitment rates.

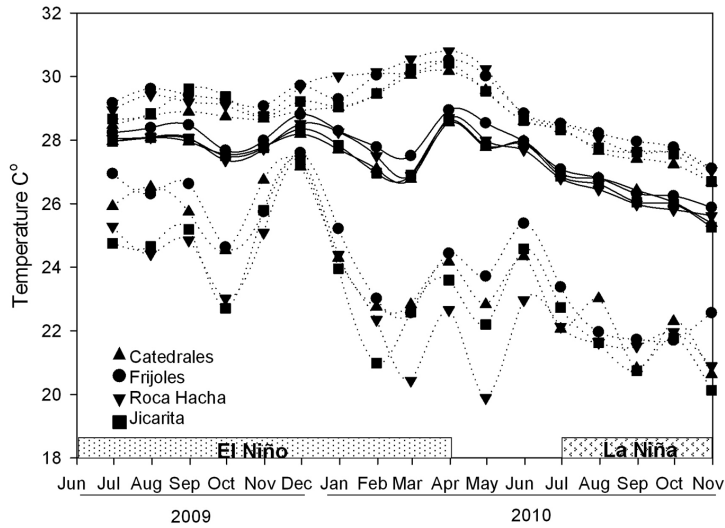


Figure 2. Monthly seawater temperature profiles for study sites in Coiba National Park, Panama. Average temperature (straight lines) and maximum and minimum values (dotted lines), with El Niño (ENSO) and La Niña (LNSO) events overlapping the study period.

## RESULTS

### SITE COMPARISONS

Mean monthly water temperatures ranged from 25.3 to 28.9 °C. Monthly standard deviations were relatively high (up to 1.65 °C) from February to May 2010. According to the National Oceanic and Atmospheric Administration's (2011) sea surface height records, the study period overlapped with an ENSO warming event from June 2009 to April 2010 and a La Niña–Southern Oscillation (LNSO) cooling event from July 2010 until the end of the study (Fig. 2). The average monthly water temperature did not differ significantly among sites (ANOVA:  $F = 1.62$ ,  $P = 0.19$ ). Temperature for monitoring period 4 (July–November 2010), however, which overlapped with the LNSO event, differed significantly from the rest of the monitoring periods after allowing for the differences in temperature between sites (two-way ANOVA:  $F = 40.78$ ,  $P < 0.001$ ). The interaction between sites and monitoring periods was not significant ( $F = 0.12$ ,  $P = 0.99$ ; Fig. 2). The highest recorded temperatures were 30–30.8 °C during March and April 2010 at all four sites. The coldest temperatures were 20–20.6 °C at Catedrales and Jicarita in November 2010 and at Roca Hacha in March 2009. The lowest temperature, at Frijoles, was 21.7 °C in October 2010.

In total, 1445 colonies of 15 species were monitored. There was an overall average density of 38.7 (SD 27.5) colonies  $m^{-2}$  ( $n = 1394$ ) with a range of 1–103 colonies  $m^{-2}$  and 1–11 species within a study plot. An overall annual population decline of 25.2% was observed. There was a significant difference in colony density between study sites (ANOVA:  $P < 0.001$ ). This difference was significant between all sites except Jicarita and Catedrales (Holm-Sidak:  $P > 0.1$ ). Roca Hacha contained 14 species, with a mean density of 77.6 (SD 19) colonies  $m^{-2}$  ( $n = 678$ ) and a 1-yr population decline of 17%. Catedrales had 12 species, a mean density of 44.3 (SD 18) colonies  $m^{-2}$  ( $n = 350$ ), and a 1-yr population decline of 14%. Jicarita contained 12 species, with a mean



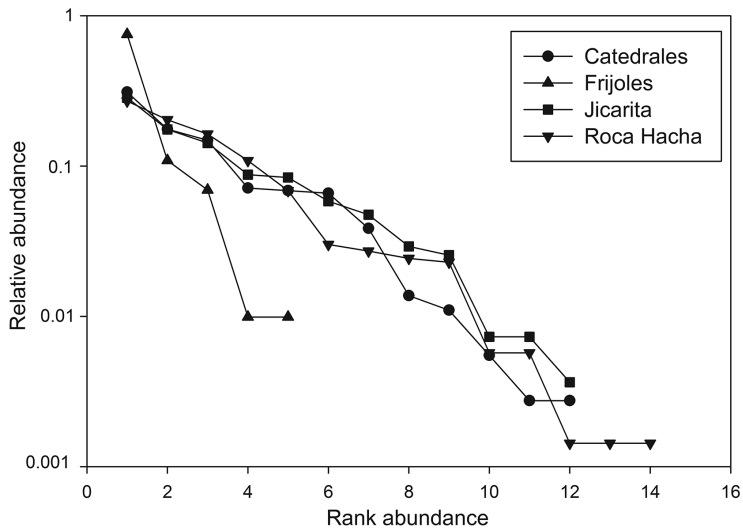


Figure 3. Rank abundance distribution (RAD) for each study site in Coiba National Park, Panama during t1 (June 20, 2009).

density of 30.3 (SD 14) colonies  $m^{-2}$  ( $n = 268$ ) and a 1-yr population decline of 24%, and Frijoles had five species, a mean density of 11.2 (SD 5) colonies  $m^{-2}$  ( $n = 98$ ), and a 1-yr population decline of 30%. There was higher species dominance at Frijoles, where *L. alba* was the dominant species, and there was a high occurrence of rare species in Catedrales, Jicarita, and Roca Hacha (Fig. 3).

A site comparison analysis that included all species present at each site revealed a significant and strong positive relationship between density and yearly mean recruitment (Pearson's correlation:  $n = 4$ ,  $r^2 = 0.99$ ,  $P < 0.01$ ). At the species level, a positive relationship was found between species density and recruitment (Pearson's correlation:  $n = 13$ ,  $r^2 = 0.70$ ,  $P < 0.01$ ), but not a significant relationship between density and mortality. A positive relationship was also found between species recruitment and mortality rates (Pearson's correlation:  $n = 13$ ,  $r^2 = 0.56$ ,  $P < 0.05$ ).

#### SURVIVAL CURVES

The global Kaplan-Meier log rank survival analysis, which included all species at all sites, resulted in survival curves that differed significantly among colony size groups ( $s = 144.55$ ,  $P < 0.001$ ). Larger sized colonies had higher survivorship than smaller colonies (Fig. 4A). Similarly, survival curves differed significantly among sites ( $s = 17.23$ ,  $P < 0.001$ ) due to low survivorship at Frijoles (Fig. 4B). A significant difference in survivorship curves among species also was detected ( $s = 225.32$ ,  $P < 0.001$ ). *L. alba* and *C. riisei* had the lowest survivorship and *M. austera* and *P. rubicunda* had the highest (Fig. 4C, Table 2). Overall colony mortality did not differ among monitoring periods after allowing for the differences in mortality among sites ( $F = 0.43$ ,  $P = 0.72$ ).

#### RECRUITMENT

An overall comparison, in which all species were pooled, showed that recruitment peaks differed among sites. Frijoles and Jicarita had a peak during the first

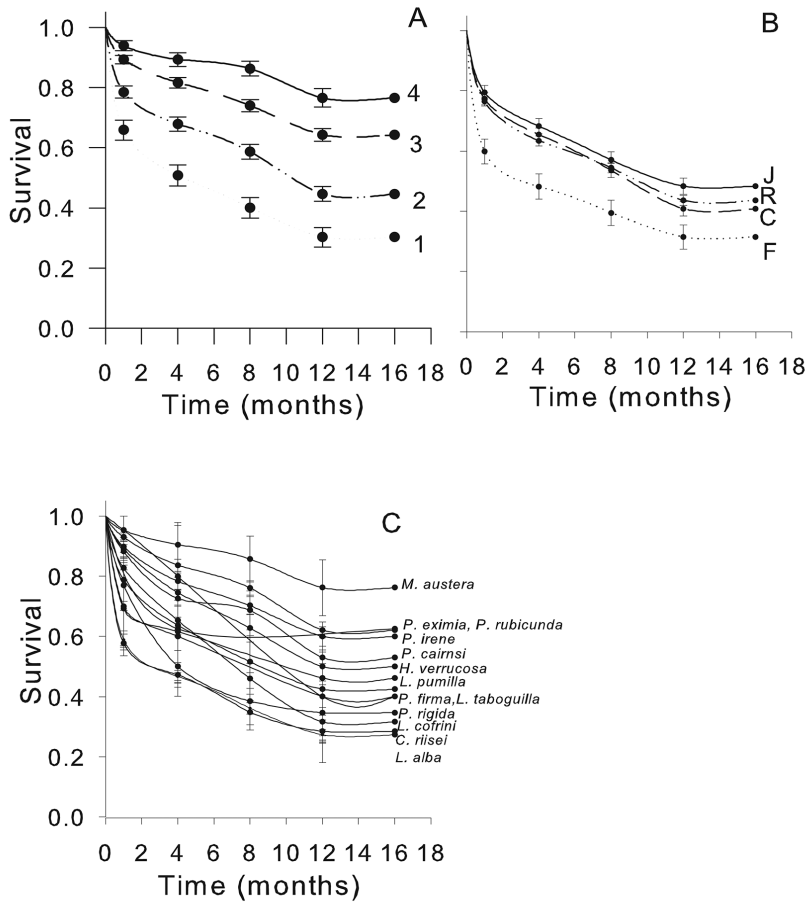


Figure 4. Global survivorship plots for octocorals in Coiba National Park, Panama. (A) Among size classes, with all species and sites together, larger colonies (4) had an overall higher survivorship than smaller colonies (1). (B) Among sites, with all species and size classes together, colonies at Frijoles had an overall lower survivorship. (C) Among species, wide survivorship variation among species.

monitoring period (June–October 2009), with a total of 77 and 81 recruits, respectively. Catedrales exhibited a peak during t2 (October 2009–March 2010) with a total of 106 recruits, and Roca Hacha showed a peak during t5 (July 2010–November 2010) with a total of 184 recruits (Fig. 5). Yearly recruitment rates for *L. alba*, *H. verrucosa*, and *P. rubicunda* were calculated using information from all monitored plots (36 m<sup>2</sup> plots). Study plots from Frijoles (9 m<sup>2</sup>) were not used to calculate recruitment rates for the rest of the species, which were absent or very rare at this site.

*Leptogorgia alba* recruits were the most abundant (3.55 colonies m<sup>-2</sup>), followed by *P. rubicunda* and *P. irene* (1.07 and 1.05 colonies m<sup>-2</sup>, respectively). Recruits of *M. austera*, *Pacifigorgia stenobrochis* (Valenciennes, 1846) (an azooxathellate species), and *Leptogorgia taboguilla* (Hickson, 1928) were not observed during the study period (Table 2).

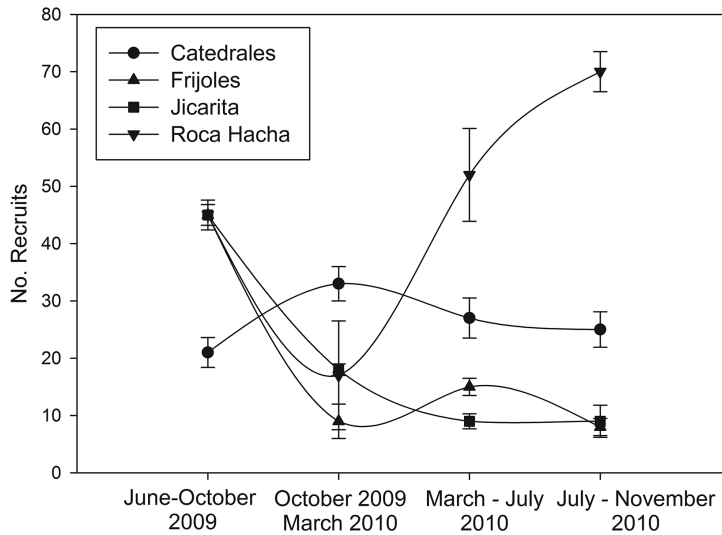


Figure 5. Recruitment rates for each study site in Coiba National Park, Panama. Peaks occurred during different monitoring periods.

#### SPECIES-SPECIFIC ANALYSES

*Leptogorgia alba* colonies were found at all of the study sites, and a total of 607 colonies were monitored. The species' overall mean density was 11.8 (SD 9.0) colonies  $m^{-2}$  ( $n = 426$ ) and ranged between 0 to 40 colonies  $m^{-2}$ . It had an average mortality rate of 0.4 (SD 0.1) and an annual recruitment rate of 0.3 (SD 0.3) (Table 2). Mortality rates were not significantly different among monitoring periods. However, recruitment was not constant over the study period; there was recruitment peak during t3 and t4 ( $\chi^2 = 13.5$ ,  $P < 0.01$ ). Size classes were not randomly distributed ( $\chi^2 = 33.8$ ,  $P < 0.001$ ); sizes 2 and 3 were the most common at every site (Table 3). Survival curves were significantly different for all size classes ( $s = 44.98$ ,  $P < 0.001$ ); larger colonies had higher survivorship than smaller colonies, and the order of survivorship by size class was  $4 > 3 > 2 > 1$ . In terms of growth measurements, only 3 of the 10 colonies that were initially measured and marked for monitoring survived to the end of the study period. The average monthly growth of these three colonies was 0.34 (SD 0.14) cm in height and 0.37 (SD 0.32) cm in width, with a monthly increase of 1 (SD 1.2) for branch tips and an increase in branch length of 0.19 (SD 0.02) cm. An increase in branch length was followed by an increase in branch tips (at t4 and t5). The maximum-recorded monthly growth was an increase in branch length of 0.41 cm (between t3 and t4) and an increase of 3.2 new branches between t4 and t5 (Table 4).

*Leptogorgia alba* was a dominant species at Frijoles and very common at the other three sites, with a mean density of 12.6 (SD 6.4) colonies  $m^{-2}$  ( $n = 113$ ) at Catedrales; 8.4 (SD 3.5) colonies  $m^{-2}$  ( $n = 76$ ) at Frijoles; 5.3 (SD 3.8) colonies  $m^{-2}$  ( $n = 48$ ) at Jicarita; and 21 (SD 11.4) colonies  $m^{-2}$  ( $n = 189$ ) at Roca Hacha (Table 2). When analyzing the population at each site, a significant difference in survivorship among size classes was detected only at Roca Hacha, where all size classes differed ( $s = 26.29$ ,  $P < 0.001$ ), and at Frijoles between size class 1 and 4 ( $p = 0.040$ ,  $s = 8.31$ ). Overall

Table 2. Mean and standard deviation ( $\text{m}^2 \text{yr}^{-1}$ ) of density, mortality, and recruitment for species found at study sites in Coiba National Park, Panama. A diamond indicates a significant difference between sites, an asterisk a significant difference between monitoring periods, and a triangle is a significant difference in survivorship between size classes, "n1" is the number of colonies at monitoring period 1, and "n2" the number of colonies during all monitored period. Not seen during the study period = n/s, not applicable = na.

Species/site	n1/n2	Density (n1)	SD	Range	Mortality (n2)	SD	Recruitment (n1)	SD
<i>Carrigjoa riisei</i>								
Overall	117/144	3.3	7.5	0–41	0.5	0.3	0.20	0.50
Catedrales	25/35	2.8	4.3	0–12	0.6	0.1	0.30	0.90
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	16/18	1.8	2.6	0–20	0.9	0.4	0.10	0.20
Roca Hacha	76/90	8.4	13.3	0–41	0.5*	0.2	0.06	0.10
<i>Heterogorgia verrucosa</i> <sup>▲</sup>								
Overall	93/111	2.6*	2.9	0–9	0.2	0.2	0.10	0.20
Catedrales	26/36	2.9	2.5	0–6	0.1	0.9	0.90	0.20
Frijoles	11/12	1.2	2.9	0–9	0.4	0.4	0.00	0.00
Jicarita	8/9	0.9	1.5	0–4	0.04	0.1	0.03	0.10
Roca Hacha	48/54	5.3	2.3	1–9	0.2*	0.2	0.07	0.10
<i>Leptogorgia alba</i> <sup>▲</sup>								
Overall	426/607	11.8*	9.0	0–40	0.4	0.1	0.30	0.30
Catedrales	113/150	12.6	6.4	3–22	0.4	0.1	0.30	0.20
Frijoles	76/107	8.4	3.5	5–15	0.5*	0.3	0.40	0.30
Jicarita	48/68	5.3	3.8	0–12	0.5	0.4	0.20	0.20
Roca Hacha	189/282	21.0	11.4	5–40	0.6	0.3	0.40*	0.30
<i>Leptogorgia cofrini</i> <sup>▲</sup>								
Overall	82/92	2.3	3.7	0–16	0.4	0.2	0.10	0.20
Catedrales	24/27	2.7	2.5	0–7	0.5	0.2	0.10	0.10
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	39/44	4.3	6.4	0–16	0.2*	0.3	0.02	0.10
Roca Hacha <sup>▲</sup>	19/26	2.1	1.8	0–5	0.3	0.2	0.20	0.30
<i>Leptogorgia rigida</i>								
Overall	25/26	0.7	2.3	0–11	0.3	0.3	0.01	0.04
Catedrales	0/0	0.0	na	na	na	na	na	na
Frijoles	1/1	0.1	0.3	0–1	n/s	na	n/s	na
Jicarita	24/25	2.7	4.2	0–11	0.4	0.1	0.01	0.04
Roca Hacha	0/0	0.0	na	na	na	na	na	na
<i>Leptogorgia pumilla</i>								
Overall	9/11	0.3	0.6	0–2	0.2	0.3	0.10	0.20
Catedrales	1/1	0.1	0.3	0–1	n/s	na	n/s	na
Frijoles	2/1	0.0	na	na	0.4	0.5	0.20	0.30
Jicarita	7/5	0.8	0.8	0–2	0.1	0.3	n/s	na
RH	1/3	0.1	0.3	0–1	n/s	na	0.10	0.20
<i>Leptogorgia taboguilla</i>								
Overall	5/6	0.1	0.5	0–3	na	na	na	na
Catedrales	4/5	0.4	0.5	0–3	na	na	na	na
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	0/0	0.0	na	na	na	na	na	na
Roca Hacha	1/1	0.1	0.3	0–1	n/s	na	n/s	na

Table 2. Continued.

Species/site	n1/n2	Density (n1)	SD	Range	Mortality (n2)	SD	Recruitment (n1)	SD
<i>Muricea austera</i>								
Overall	22/22	0.6*	1.3	0–6	0.20	0.30	ns	na
Catedrales	1/1	0.1	na	0–1	n/s	na	n/s	na
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	0/0	0.0	na	na	na	na	na	na
Roca Hacha	21/21	2.3	1.7	1–6	0.20	0.30	n/s	n/s
<i>Pacifigorgia cairnsi</i> ▲								
Overall	43/50	1.2	1.4	0–6	0.20	0.20	0.20	0.40
Catedrales	14/17	1.6	1.5	0–4	0.40	0.30	0.20	0.30
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	13/15	1.4	1.0	0–3	0.20	0.30	0.20	0.50
Roca Hacha	19/18	1.8	1.7	0–6	0.20	0.30	0.20	0.30
<i>Pacifigorgia eximia</i>								
Overall	6/8	0.2	0.4	0–1	0.10	0.30	0.10	0.30
Catedrales	2/1	0.2	0.4	0–1	0.40	0.50	ns	na
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	0/0	0.0	na	na	na	na	na	na
Roca Hacha	4/6	0.4	0.5	0–1	n/s	na	0.20	0.50
<i>Pacifigorgia firma</i>								
Overall	7/10	0.2	0.4	0–1	0.10	0.30	0.10	0.10
Catedrales	1/1	0.1	0.3	0–1	n/s	na	n/s	na
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	2/4	0.2	0.4	0–1	0.10	0.10	0.20	0.10
Roca Hacha	4/5	0.4	0.5	0–1	0.20	0.40	0.10	0.20
<i>Pacifigorgia irene</i>								
Overall	193/232	5.4*	5.8	0–24	0.10	0.10	0.20	0.20
Catedrales	54/70	6.0	2.8	2–11	0.20	0.20	0.20	0.20
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	23/30	2.6	2.3	0–7	0.04	0.10	0.20	0.30
Roca Hacha	116/132	12.9	5.2	6–24	0.20	0.09	0.10	0.10
<i>Pacifigorgia rubicunda</i> ▲								
Overall	291/332	8.1*	7.0	0–26	0.20*	0.20	0.10	0.20
Catedrales	64/83	7.1	2.4	3–11	0.20	0.20	0.10*	0.20
Frijoles	7/9	0.8	0.8	0–2	0.30	0.40	0.20	0.30
Jicarita	78/84	8.7	5.7	2–20	0.05	0.06	0.04	0.06
Roca Hacha	142/156	15.8	6.7	7–26	0.20*	0.05	0.07	0.05
<i>Psammogorgia arbuscula</i> ▲								
Overall	25/32	0.7	1.5	0–7	0.20	0.30	0.10	0.30
Catedrales	5/6	0.6	0.8	0–2	n/s	na	0.10	0.20
Frijoles	1/1	0.1	0.3	0–1	n/s	na	n/s	na
Jicarita	2/3	0.2	0.4	0–1	0.50	0.40	0.10	0.20
Roca Hacha	17/22	1.9	2.5	0–7	0.20	0.20	0.20	0.50
<i>Pacifigorgia stenobrochis</i>								
Overall	2/2	0.1	0.3	0–1	n/s	na	n/s	na
Catedrales	0/0	0.0	na	na	na	na	na	na
Frijoles	0/0	0.0	na	na	na	na	na	na
Jicarita	1/1	0.1	0.3	0–1	n/s	na	n/s	na
Roca Hacha	1/1	0.1	0.3	0–1	n/s	na	n/s	na

Table 3. Size class distributions of octocoral species at study sites in Coiba National Park, Panama. Relative class sizes: 1 represents small recruits, 2 small colonies, 3 medium size colonies, and 4 large colonies. Asterisks indicate species for which the survivorship curves significantly differed between class sizes. Not applicable = na.

Species/site	n	Size class (%)			
		1	2	3	4
<i>Carrijoa riisei</i>					
Overall	115	39.1	23.5	25.2	12.2
Catedrales	25	52.0	12.0	28.0	8.0
Frijoles	0	na	na	na	na
Jicarita	16	25.0	56.3	18.8	0.0
Roca Hacha	74	37.8	20.3	25.7	16.2
<i>Heterogorgia verrucosa</i> *					
Overall	91	27.5	36.3	25.3	11.0
Catedrales	26	30.8	15.4	30.8	23.1
Frijoles	11	54.5	27.3	18.2	0.0
Jicarita	7	0.0	57.1	28.6	14.3
Roca Hacha	47	23.4	46.8	23.4	6.4
<i>Leptogorgia alba</i> *					
Overall	406	19.2	37.9	34.5	8.4
Catedrales	104	11.5	33.7	34.6	20.2
Frijoles	72	25.0	29.2	38.9	6.9
Jicarita	46	26.1	39.1	32.6	2.2
Roca Hacha	184	19.6	43.5	33.2	3.8
<i>Leptogorgia cofrini</i> *					
Overall	78	9.0	38.5	46.1	6.4
Catedrales	22	4.5	27.3	59.1	9.1
Frijoles	0	na	na	na	na
Jicarita	38	13.2	44.7	34.2	7.9
Roca Hacha	18	5.6	38.9	55.6	0.0
<i>Muricea austera</i>					
Overall	20	0.0	15.0	30.0	55.0
Catedrales	0	na	na	na	na
Frijoles	0	na	na	na	na
Jicarita	0	na	na	na	na
Roca Hacha	20	0.0	15.0	30.0	55.0
<i>Pacifigorgia cairnsi</i> *					
Overall	38	13.2	26.3	39.5	21.1
Catedrales	11	0.0	36.4	36.4	27.3
Frijoles	0	na	na	na	na
Jicarita	11	0.0	18.2	45.5	36.4
Roca Hacha	15	33.3	26.7	33.3	6.7
<i>Pacifigorgia irene</i>					
Overall	178	8.4	24.7	36.5	30.3
Catedrales	51	11.8	19.6	27.5	41.2
Frijoles	0	na	na	na	na
Jicarita	23	13.0	8.7	30.4	47.8
Roca Hacha	104	5.8	30.8	42.3	21.2



Table 3. Continued.

Species/site	n	Size class (%)			
		1	2	3	4
<i>Pacifigorgia rubicunda</i> *					
Overall	276	5.1	26.4	53.6	14.9
Catedrales	57	1.8	19.3	54.4	24.6
Frijoles	7	28.6	71.4	0.0	0.0
Jicarita	75	2.7	20.0	58.7	18.7
Roca Hacha	137	6.6	30.7	53.3	9.5
<i>Psammogorgia arbuscula</i> *					
Overall	25	8.0	24.0	28.0	40.0
Catedrales	5	0.0	20.0	80.0	0.0
Frijoles	0	na	na	na	na
Jicarita	0	na	na	na	na
Roca Hacha	17	5.9	23.5	11.8	58.8

survivorship did not differ among sites. Recruitment was only significantly higher at Roca Hacha during t3 ( $q = 4.39$ ,  $P = 0.001$ ) and t5 ( $q = 3.92$ ,  $P = 0.021$ ).

*Pacifigorgia rubicunda* was common at all sites except Frijoles. A total of 332 colonies were monitored. Overall mean density was 8.1 (SD 7.0) colonies  $m^{-2}$  ( $n = 291$ ), with a range of 0 to 26 colonies within a square meter, a mean annual mortality rate of 0.2 (SD 0.2) and an annual recruitment rate of 0.1 (SD 0.2) (Table 2). There was a significantly higher mortality during t5 ( $\chi^2 = 39.37$ ,  $P < 0.001$ ). However, there was not a significant difference in recruitment rates between sampling periods. Colony size was distributed unevenly with 53.6% of the colonies in size class 3 ( $\chi^2 = 145.8$ ,  $P < 0.01$ ). There was a significant difference in survivorship between size classes ( $P < 0.01$ ). Size 1 had lower survivorship than sizes 2, 3, and 4.

*Pacifigorgia rubicunda* colony density was significantly different among sites ( $F = 6.88$ ,  $P < 0.001$ ): there was an average of 15.8 (SD 6.7) colonies  $m^{-2}$  ( $n = 142$ ) at Roca Hacha; 8.7 (SD 5.7) colonies  $m^{-2}$  ( $n = 78$ ) at Jicarita; 7.1 (SD 2.4) colonies  $m^{-2}$  ( $n = 64$ ) at Catedrales; and 0.8 (SD 0.8) colonies  $m^{-2}$  ( $n = 7$ ) at Frijoles (Table 2). Mortality rates were significantly different among sites ( $P < 0.01$ ) and ranged from 0.05 (SD 0.06) in Jicarita to 0.3 (SD 0.4) in Frijoles. There was not a significant difference in recruitment rate among sites for this species. Size class 3 was more frequent at Catedrales, Jicarita, and Roca Hacha, and size class 2 was more frequent at Frijoles (Table 3). The survivorship curve was higher at Jicarita ( $s = 13.01$ ,  $P < 0.001$ ), and there was an overall (all sites together) difference in survivorship among size classes ( $s = 18.12$ ,  $P < 0.001$ ), with size 1 having a lower survivorship than sizes 3 and 4 and size 2 having a lower survivorship than size 4. A difference in survivorship among monitoring periods occurred only at Roca Hacha, where it was higher at t2 than t5 ( $q = 4.77$ ,  $P = 0.001$ ). Recruitment differed among monitoring periods only at Catedrales, where it was higher at t4 than t5 ( $q = 4.75$ ,  $P = 0.01$ ). Recruitment did not differ among sites (Table 2).

*Pacifigorgia irene* colonies were frequently found in monospecific patches, in which most of the colonies shared the same orientation. A total of 233 colonies were monitored, with a mean density of 5.4 (SD 5.8) colonies  $m^{-2}$  ( $n = 193$ ), ranging from 0 to 24 colonies  $m^{-2}$ . This species had an annual mortality rate of 0.1 (SD 0.1) and an annual recruitment rate of 0.2 (SD 0.2) (Table 2). Size class was not randomly distributed ( $\chi^2$

= 31.03,  $P = 0.01$ ); only 0.8% of the population was in size class 1 (Table 3). Survival curves did not differ among size classes or monitoring periods. Recruitment was not significantly different between monitoring periods. Colonies used for growth measurements were in size classes 3 and 4. There was an average monthly increase in colony area of 0.84 (SD 5.64)  $\text{cm}^2$  ( $n = 10$ ). Area measurements provided a better growth estimator than height and width because of colony breakage and uneven growth (Table 4). Colonies had frequent fan breakages, but these did not cause colony death. Density differed significantly among sites ( $F = 18.62$ ,  $P < 0.001$ ), with a mean density of 12.9 (SD 5.2) colonies  $\text{m}^{-2}$  ( $n = 116$ ) at Roca Hacha; 6 (SD 2.8) colonies  $\text{m}^{-2}$  ( $n = 54$ ) at Catedrales; and 2.6 (SD 2.3) colonies  $\text{m}^{-2}$  ( $n = 23$ ) at Jicarita. There were no *P. irene* colonies in the study plots at Frijoles at the beginning of the study, but there was one recruit during t3. Size class 4 was more common at Jicarita and Catedrales, and size class 3 was more common at Roca Hacha (Table 3). There was no significant difference in survival curves or recruitment rates among sites.

*Carijoa riisei* colonies exhibited rapid growth, during which small recruits merged into larger adjacent colonies, making it difficult to distinguish individual colonies. A total of 144 colonies was monitored with an average density of 3.3 (SD 7.5) colonies  $\text{m}^{-2}$  ( $n = 117$ ), ranging from 0 to 41 colonies  $\text{m}^{-2}$ . Colonies had a mortality rate of 0.5 (SD 0.3) and a recruitment rate of 0.2 (SD 0.5) (Table 2). Size classes were not evenly distributed ( $\chi^2 = 16.6$ ,  $P < 0.01$ ); almost 40% of the monitored colonies were in size class 1 (Table 3). Survivorship did not differ significantly among size classes, even when the colonies were grouped in two size categories. Mortality and recruitment rates did not differ between monitoring periods.

Densities of *C. riisei* colonies varied between study sites: there was a mean density of 8.4 (SD 13.3) colonies  $\text{m}^{-2}$  ( $n = 76$ ) at Roca Hacha; 2.8 (SD 4.3) colonies  $\text{m}^{-2}$  ( $n = 25$ ) at Catedrales; and 1.8 (SD 2.6) colonies  $\text{m}^{-2}$  ( $n = 16$ ) at Jicarita (Table 2). Survivorship curves differed among sites; colonies at Roca Hacha had higher survivorship than colonies at Catedrales and Frijoles ( $s = 31.69$ ,  $P = 0.001$ ). Survivorship differed among monitoring periods only at Roca Hacha, with higher values during t2. There was no significant difference in recruitment rates among sites.

*Heterogorgia verrucosa* (Verrill, 1868): One hundred eleven colonies were monitored, with a mean density of 2.6 (SD 2.9) colonies  $\text{m}^{-2}$  ( $n = 93$ ) which ranged from 0 to 9 colonies per  $\text{m}^2$ . This species had an overall mortality rate of 0.2 (SD 0.2) and a recruitment rate of 0.1 (SD 0.2) (Table 2). Size classes were not randomly distributed ( $\chi^2 = 11.98$ ,  $P < 0.01$ ), only 11% of the colonies were in the larger size class (Table 3). Survivorship was different among size classes ( $s = 15.82$ ,  $P = 0.001$ ); size class 1 had lower survivorship than size classes 3 or 4. Neither recruitment nor mortality rates differed significantly among sampling periods.

*Heterogorgia verrucosa* colony density was significantly different between sites ( $F = 9.75$ ,  $P < 0.001$ ); there was an average of 5.3 (SD 2.3) colonies  $\text{m}^{-2}$  ( $n = 48$ ) at Roca Hacha; 2.9 (SD 2.5) colonies  $\text{m}^{-2}$  ( $n = 26$ ) at Catedrales; 1.2 (SD 2.9) colonies  $\text{m}^{-2}$  ( $n = 11$ ) at Frijoles; and 0.9 (SD 1.5) colonies  $\text{m}^{-2}$  ( $n = 8$ ) at Jicarita (Table 2). Size classes 1 and 3 were equally abundant at Catedrales, whereas size 1 was most abundant at Frijoles and size 2 was most abundant at Jicarita and Roca Hacha (Table 3). Survivorship curves did not differ significantly among sites. A size class difference in survivorship was not found when analyzing sites separately. Survivorship differed between monitoring periods only at Roca Hacha, where it was higher at t2 than t4 ( $q = 3.87$ ,  $P < 0.05$ ). There was not a significant difference in recruitment among sites.

*Leptogorgia cofrini* (Breedy and Guzman, 2005): Ninety-two *L. cofrini* colonies were monitored. The species occurred at a mean density of 2.3 (SD 3.7) colonies  $m^{-2}$  ( $n = 82$ ) with a range of 0 to 16 colonies  $m^{-2}$ . Its mean mortality rate was 0.2 (SD 0.1) and its mean recruitment rate was 0.2 (SD 0.2) (Table 2). Mortality and recruitment rates did not differ among monitoring periods. Size classes were not randomly distributed ( $\chi^2 = 38.41$ ,  $P < 0.01$ ): most of the colonies (84.7%) were in size classes 2 and 3 (Table 3). There was a significant difference in survivorship between size classes ( $s = 8.95$ ,  $P = 0.03$ ); size class 4 had higher survivorship than size class 2.

*Leptogorgia cofrini* density was not significantly different among sites: it had an average density of 4.3 (SD 6.4) colonies  $m^{-2}$  ( $n = 39$ ) at Jicarita; 2.7 (SD 2.5) colonies  $m^{-2}$  ( $n = 24$ ) at Catedrales; 2.1 (SD 1.8) colonies  $m^{-2}$  ( $n = 19$ ) at Roca Hacha; and was not present in the monitored plots at Frijoles (Table 2). Survivorship curves did not differ among sites, and when analyzed separately, a difference in survivorship between size classes was only observed at Roca Hacha ( $s = 7.99$ ,  $P = 0.02$ ). Survivorship curves differed among monitoring periods only at Jicarita ( $q = 3.83$ ,  $P = 0.02$ ), where they were higher at t2 than t5. Recruitment did not differ significantly among sites.

*Pacifigorgia cairnsi* (Breedy and Guzman, 2003): Fifty colonies were monitored, with an average density of 1.2 (SD 1.4) colonies  $m^{-2}$  ( $n=43$ ), an average mortality rate of 0.2 (SD 0.2), and a recruitment rate of 0.2 (SD 0.4) (Table 2). There was not a significant difference in the distribution of size classes. However, survivorship curves differed among size classes ( $s = 9.16$ ,  $P = 0.03$ ); size class 4 had higher survivorship than size class 2. There was not a significant difference between mortality and recruitment rates among sampling periods.

*Pacifigorgia cairnsi* densities did not differ between sites: the mean density at Jicarita was 1.4 (SD 1) colonies  $m^{-2}$  ( $n = 13$ ); 1.6 (SD 1.5) colonies  $m^{-2}$  ( $n = 14$ ) at Catedrales; and 1.8 (SD 1.7) colonies  $m^{-2}$  ( $n = 19$ ) at Roca Hacha. There were no *P. cairnsi* colonies at study plots in Frijoles (Table 2). The difference in survivorship between size classes was not observed when the sites were analyzed separately. There was no difference in recruitment or survivorship among sites.

*Leptogorgia rigida* (Verrill, 1864) was only found at Jicarita, with the exception of one small colony at Frijoles. Twenty-six colonies were monitored, with a mean abundance of 2.7 (SD 4.2) colonies  $m^{-2}$  ( $n = 24$ ) at Jicarita (Table 2). The estimated mortality rate for this specie is 0.3 (SD 0.3). There was only one recruit during t3 at Jicarita, which was used to estimate a recruitment rate of 0.01(SD 0.04) (Table 2).

Twenty-two colonies of *Muricea austera* were monitored with a mean density of 0.6 (SD 1.3) colonies  $m^{-2}$  ( $n = 22$ ) with a range of 0 to 6 colonies  $m^{-2}$ . It had a mortality rate of 0.2 (SD 0.3), which did not differ between monitoring periods or size classes. No recruits were seen over the duration of the study (Table 2). Size class was not distributed randomly among colonies ( $\chi^2 = 13.2$ ,  $P < 0.01$ ), with 55% of the colonies in size class 4 (Table 3). *M. austera* colonies had slow growth with a monthly net increment of 0.03 (SD 0.1) cm in height, 0.04 (SD 0.2) cm in width, and an increase in the number of branch tips of 0.33 (SD 0.4) cm. The net branch length growth was negative due to bites from possible predators in individual branches [ $-0.01$  (SD 0.06) cm]. The maximum-recorded monthly growth was an increase of 0.95 cm in height, 1.55 cm in width, 3 new branches, and an increase in branch length of 0.14 cm (Table 4). This species was only common at Roca Hacha, where it had a mean abundance of 2.3 (SD 1.7) colonies  $m^{-2}$  ( $n = 21$ ) (Table 2). This species was rare at Catedrales, with a mean density of 0.1 ( $n = 1$ ), and was absent in the study plots at Frijoles and Jicarita.

Table 4. Monthly mean growth and maximum growth recorded for four species at Coiba National Park. Colony superficial area was only measured for fan-like species. Height, width, and branch length values given in centimeters, area given in centimeters squared. Value with asterisk is  $n = 5$ .

Species	$n$	Height (SD)	Width (SD)	Area (SD)	Number of branches (SD)	Branch length (SD)
Average monthly net growth						
<i>Leptogorgia alba</i>	3	0.34 (0.14)	0.37 (0.32)	–	1.00 (1.02)	0.19 (0.02)
<i>Pacifigorgia irene</i>	10	–0.05 (0.18)	–0.01 (0.21)	0.84 (5.64)	–	–
<i>Psammogorgia arbuscula</i>	9	0.08 (0.17)	0.08 (0.32)	–	–	–
<i>Muricea austera</i>	10	0.03 (0.12)	0.04 (0.17)	–	0.33 (0.42)	–0.01 (0.06)*
Maximum recorded monthly growth						
<i>Leptogorgia alba</i>		0.86	0.79	–	3.50	0.41
<i>Pacifigorgia irene</i>		1.12	1.17	20.6	–	–
<i>Psammogorgia arbuscula</i>		0.84	0.93	–	–	–
<i>Muricea austera</i>		0.95	1.55	–	3.2	0.14

*Psammogorgia arbuscula* had a mean density of 0.7 (SD 1.2) ( $n = 25$ ). A total of 32 colonies were monitored, presenting a mortality rate of 0.2 (SD 0.3) and a recruitment rate of 0.1 (SD 0.3) (Table 2). These rates were not significantly different between sampling periods. Colonies were randomly distributed in size classes. A significant difference among size class survivorship curves was detected ( $s = 18.77$ ,  $P < 0.001$ ), with size class 1 having lower survivorship than size classes 3 and 4 ( $P = 0.01$  and  $P = 0.01$ , respectively) and size class 2 having a lower value than size class 4 ( $P = 0.01$ ) (Table 3). Measured colonies had a net monthly growth of 0.08 (SD 0.17) cm in height and 0.08 (SD 0.32) cm in width. The maximum growth was an increase of 0.84 cm in height and 0.93 cm in width. Nine of the ten monitored colonies remained alive at the end of the study (Table 4).

*Psammogorgia arbuscula* was common at Roca Hacha and very rare at Jicarita, Frijoles, and Catedrales, with a mean abundance of 1.9 (SD 2.5) colonies  $m^{-2}$  at Roca Hacha ( $n = 17$ ); 0.6 (SD 0.8) colonies  $m^{-2}$  at Catedrales ( $n = 5$ ); 0.1 (SD 0.3) colonies  $m^{-2}$  at Frijoles ( $n = 1$ ); and 0.2 (SD 0.4) colonies  $m^{-2}$  at Jicarita ( $n = 2$ ) (Table 2). Recruits ( $n = 5$ ) were only observed at Roca Hacha during t4 and t5 (Table 2).

#### LIFE HISTORY STRATEGIES

Based on four biological variables (species distribution, average density, recruitment, and mortality rates), the cluster analysis divided species in two significantly distinct groups ( $P < 0.05$ ) (Fig. 6). Group 1 clustered six species: *C. riisei*, *H. verrucosa*, *L. alba*, *L. cofrini*, *P. irene* and *P. rubicunda*. The average density of these species was 5.6 colonies  $m^{-2}$  (SD 3.7), average mortality rate of 0.3 (SD 0.2), average recruitment of 0.2 (SD 0.1) and an average distribution among study sites of 3.7 (SD 0.5). Group 2 clustered seven species: *L. rigida*, *Leptogorgia pumilla* (Verrill, 1868), *M. austera*, *P. cairnsi*, *Pacifigorgia eximia* (Verrill, 1868), *Pacifigorgia firma* (Breedy and Guzman, 2003), and *P. arbuscula*. These species had an average density of 0.6 colonies  $m^{-2}$  (SD 0.4), average mortality of 0.2 (SD 0.1), average recruitment of 0.1 (SD 0.1), and an average distribution among study sites of 2.7 (SD 0.1).

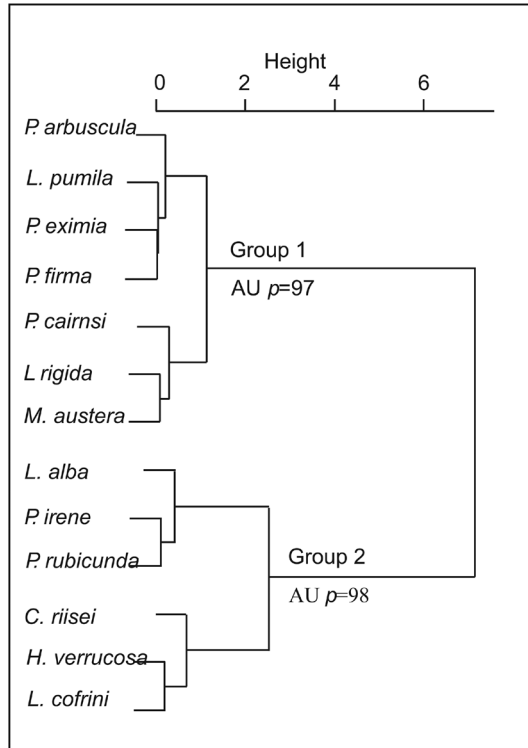


Figure 6. Hierarchical cluster analysis of similarities between species explained by four variables (species distribution, average density, and mortality and recruitment rates) Group 1 clusters *r*-selected species and Group 2 clusters *K*-selected species.

## DISCUSSION

### INTER-REGIONAL DIFFERENCES

The octocoral densities (up to 106 colonies  $\text{m}^{-2}$  with a mean of 38.7 colonies  $\text{m}^{-2}$ ) found at CNP were higher than those reported in the Caribbean: 25.1 colonies  $\text{m}^{-2}$  in south Florida (Goldberg 1973); 17.6 colonies  $\text{m}^{-2}$  in Carre Bow Cay, Belize (Lasker and Coffroth 1983); 9.98 colonies  $\text{m}^{-2}$  in Providencia Island, Colombia (Sanchez et al. 1998); 3.6–5.9 colonies  $\text{m}^{-2}$  in the Florida Keys (Chiappone and Suvillan 1994); and 62.3 colonies  $\text{m}^{-2}$  in southwest Puerto Rico (Yoshioka 1996). Octocorals were certainly dominant species in these communities, especially at Roca Hacha, Jicarita, and Catedrales. These findings support statements of Bayer (1953) in the tropical eastern Pacific, who described these species as the most characteristic components of rocky communities. At CNP, octocorals shared the rocky substrata with sponges, tunicates, and encrusting coralline algae; however, the corals were the only organisms creating complex three-dimensional structures, hosting a variety of invertebrates, and serving as aggregation areas for fish.

Octocoral species richness at CNP was found to be high compared to other islands along the Marine Conservation Corridor of the tropical eastern Pacific. There are a total of 34 reported species in CNP (Guzman et al. 2004); 15 of those species were present in the study plots, compared to 12 reported in Cocos (Breedy and Cortes

2008), 10 in Colombia's Pacific (Prahl et al. 1986), and 7 in Galápagos (Hickson 1928, Williams and Breedy 2004, Breedy and Guzman 2007, Breedy et al. 2009). This level of species richness was similar to that reported in Bocas del Toro (29 species) in Caribbean Panama (Guzman and Guevara 1999) and Costa Rica, with 26 species found in the Caribbean Sea and 30 in the Pacific Ocean (Breedy 2009). It was also similar to the levels found in Japan, where there were 27 species above 40 meters (Matsumoto et al. 2007). Octocoral species richness at CNP was low, however, compared to the Indo-Pacific region, which reports 90 genera in 23 families in shallow waters (Fabricius and Alderslade 2001); the Mediterranean region, with 43 reported species (Koukouras et al. 2001); the Jaragua National Park, Dominican Republic, with 47 species in 15 genera (Weil 2006); and Hong Kong, which has 42 species in 23 genera (Fabricius and McCorry 2006).

Octocoral colonies were distributed with patches of very high densities (106 colonies  $m^{-2}$ ) and low densities (5 colonies  $m^{-2}$ ). This patchy distribution is reflected in the high standard deviation in colony density in the overall analysis (average density  $38.7 \pm 27.5$  colonies  $m^{-2}$ ) and for each site and species separately (see Table 2). There are two potential reasons for this type of uneven distribution: asexual reproduction due to branch breakage, which is thought to be common in octocorals (e.g., Lasker 1990), and a possible reproductive strategy in which the new recruit settles near the parental colony.

Mortality rates ranged between 1% and 6%  $yr^{-1}$ , which is similar to the rates found in protected areas in the Mediterranean with low (2.7%) and high (7.4%) diving activities (Coma et al. 2004), and relatively low compared to the 8% mortality rate reported for the Caribbean (e.g. Yoshioka and Yoshioka 1991, Yoshioka 1994). Smaller colonies (sizes 1 and 2) had higher mortality rates than larger colonies; the relationship between size and survivorship has been reported in a variety of environments, including the genus *Muricea* in the Gulf of Mexico (Grigg 1977), and shallow water *Pseudopterogorgia* spp. from Puerto Rico, where larger colonies had 96% survivorship compared to 62% in smaller colonies (Yoshioka 1994). Mortality in larger colonies was mainly due to detachment, which was seen in the temperate octocoral *Paramuricea clavata* in areas frequented by tourist divers (Coma et al. 2004) and Caribbean octocorals in shallow and exposed areas (Wahle 1985, Yoshioka and Yoshioka 1991). Mortality in smaller colonies and among recruits was mainly due to overgrowth by macroalgae, sponges, or other octocorals, especially *C. riisei*. Detachment and abrasion, rather than predation, were the main causes of mortality for two *Muricea* species in Baja California (Grigg 1977). Grigg (1977) explained that high mortality rates in *M. californica* were due to bioerosion by bivalves and other invertebrates, which weakened the basal attachment of older colonies.

The distribution of octocorals is limited by the availability of substrata (Grigg 1977, Preston and Preston 1975, Birkeland 1974, Opresko 1974) and functional larvae (Jordan-Dahlgren 2002). Free rocky space available in our sites suggests that the distribution in the study site is controlled by recruitment of new larvae.

At the species level recruitment rates were lower than mortality rates, reflected in the decline in natural population observed during the study (25.2%). This decline was relatively low, however, compared to the 1999 mass mortality event in the Mediterranean Sea, which caused a decrease of >50% of the *Corallium rubrum* population (Cerrano et al. 2000) and 48% of the *Paramuricea clavata* population (Linares et al. 2005). This mass mortality event was probably related to a positive anomaly in



sea surface temperatures of 4 °C followed by extensive colony attacks by opportunistic pathogens like protozoans and fungi (Cerrano et al. 2000), and subsequent colony death (Linares et al. 2005). Conversely, although there were ENSO and LNSO events, no abrupt changes in temperature were recorded during the present study and the presence of opportunistic pathogens was not observed.

Net growth measurements reported in the present study include negative growth caused by predation or colony breakage. During the monitoring periods we observed sea turtles and *Scaridae* and *Acanthurus* fish biting at colonies on several occasions. We attempted to study the effect of predation on mortality and growth, but unfortunately, the exclusion cages were lost twice from the study site, and it was not possible to collect this type of data. Due to negative growth and further tissue regeneration, measurements of the fan area were a better measure of growth than fan height and width alone, especially for *P. irene*. Another barrier to studying growth was the high colony mortality rate in *L. alba* colonies, with only three out of ten monitored colonies surviving to the end of the study. Growth rates (measured by colony height) in species in Puerto Rico averaged about 2.0 cm yr<sup>-1</sup> (0.8 to 4.5 cm yr<sup>-1</sup>) (Yoshioka and Yoshioka 1991), which is relatively low compared to our calculations for *L. alba* (4.0 cm yr<sup>-1</sup>) and high compared to our calculations for *P. arbuscula* (0.1 cm yr<sup>-1</sup>) and *M. austera* (0.3 cm yr<sup>-1</sup>). The Puerto Rican study only measured colony height, however, and in an effort to avoid negative growth, did not include broken or predated colonies. Grigg (1974) found that colony growth decreased consistently with colony height, but this relationship was not significant in Puerto Rico's octocorals (Yoshioka and Yoshioka 1991). In the 5-yr study in Puerto Rico, there was high intraspecific variability, which supported the idea that variability was not just an "artifact" of short-term observations (Yoshioka and Yoshioka 1991).

#### INTER-SITE DIFFERENCES

Differences among the study sites in species richness, abundance, mortality, and recruitment could be the result of a combination of factors. The low diversity and abundance of octocorals in Frijoles, relative to the other three study places, could be explained by its geographic position. Frijoles is located on the leeward side of the archipelago and closer to the mainland (about 17 km) than the other three sites. These sites are located on the seaward side of the archipelago, farther away from the mainland (>50 km) with no land protection, leaving them exposed to a variety of currents, breaking waves, and surges (see Fig. 1). Frijoles is surrounded by shallow water (20 m deep); it is approximately 30 km away from deep water (>400 m), which is not the case for the other three sites: Roca Hacha is approximately 5 km, and Jicarita and Catedrales are only approximately 3 km from the >400 m drop-off (see Fig. 1).

The Frijoles location is closer to the mainland, protected from strong currents, and surrounded by shallow water, which could be why this site had the warmest mean monthly temperature profile. Although its temperature was not significantly different from the other sites, its higher temperature may indicate that this site is less influenced by the cold deep water near Coiba. Fabricius and De'ath (2008) reported higher octocoral richness in locations with high water column productivity, greater depth, and more water flow, which may also be the case in Roca Hacha, Jicarita, and Catedrales, but not in Frijoles. This idea would support Jordan-Dahlgren's (2002) proposal that octocoral distribution is controlled by the availability of functional larvae,

which could be reduced at Frijoles if the larvae come from cold and productive deep water or off shore currents bringing larvae from more populated communities.

In addition, the invasive coral predator, *A. planci*, was seen at Frijoles during every monitoring period but never seen at the other three locations. *Acanthaster planci* is known to feed on soft corals and gorgonians when there is low hard coral cover (Moran 1990), which is the case in the studied rocky coral communities. Predation by this sea star could decrease the possibility of octocoral recruits surviving to adulthood. Interestingly, this coral predator seems to affect species other than *L. alba*, which was a dominant species at Frijoles, and recruitment and mortality rates of this species did not differ among sites.

#### INTER-SPECIES DIFFERENCES

Life history traits varied widely among studied species; however, the cluster analysis suggested two main life history strategies among studied species, one group of species resembling *K* selection and another group resembling *r* selection. The interaction between species density, distribution among study sites, and recruitment and mortality rates in species found in group no. 1 (Fig. 6) resembled *r*-selected species. These species were commonly found in most of the sites where highly dense patches were common (with up to 41 colonies m<sup>-2</sup>). These species also had higher recruitment and mortality rates than species in group 2.

Two of these species were widely distributed and had the highest densities and growth rates (*L. alba* and *P. irene*) of the studied species. Out of these species, *L. alba*, which is widely distributed at CNP, and present in Cocos Island, Costa Rica's mainland shores (Breedy and Cortés 2008), El Salvador (Bielschowsky 1929), Colombia (Prahl et al 1986), Galápagos (Breedy and Guzman 2007), and continental Ecuador (Bielschowsky 1929), had the most active life history as shown through high recruitment and mortality rates. *Pacifigorgia irene* and *P. rubicunda* had relatively high recruitment values but lower mortality indices relative to *L. alba*. These species are widely distributed at CNP and also reported in Costa Rica (Breedy and Guzman 2003). Although *C. riisei* was not as common as these other three species, it showed high distribution and high mortality and recruitment values. Species in this group also exhibited a patchy distribution pattern, with some plots being very densely populated (24–41 colonies m<sup>-2</sup>) and others having only one or two colonies, as reflected in the large density ranges and SD values in Table 2. Additionally, most *P. irene* colonies in a patch shared the same fan orientation, which has been described for *Muricea californica* (Aurivillius, 1931) and *Muricea fruticosa* (Verrill, 1869) as a response to water flow direction (Grigg 1972).

Group 2 resembles *K*-selected species (Fig. 6). These species had a lower density, very low or no recruitment during the study period, low mortality and were absent in some of the study sites. Additionally growth studies for *M. austera* and *P. arbuscula* showed low growth rates compared to species in Group 1. These species were rare compared to species in Group 1 and were not found in highly dense patches, with a maximum of 11 colonies m<sup>-2</sup> (*L. rigida*).

In general, the genus *Pacifigorgia* had a greater survivorship than the genus *Leptogorgia*, at least among the studied species in the studied sites (average mortality rates of 0.17 (SD 0.11) for five *Pacifigorgia* species and 0.29 (SD 0.11) for four *Leptogorgia* species). These genera are among the most diverse and abundant of shallow water octocoral fauna in the eastern Pacific (Breedy and Guzman 2002, Breedy

and Guzman 2007). These differences could be due to colony morphology. In general, *Pacificorgia* species have thicker branches, which create a relatively strong compound or single network that is securely attached to the substratum by a holdfast of different dimensions and forms, and in some cases the colonies are strengthened by midribs (Breedy and Guzman 2002). Conversely, *Leptogorgia* species have slender branches and are attached to the substrate by a single mother branch (Breedy and Guzman 2007), possibly making them more vulnerable to colony damage and detachment. Branch thickness has been described as an adaptation to strong water movement on at least three occasions (Grigg 1972, Velimirov 1976, Kin et al. 2004). Although these studies have compared intra-species adaptations, we hypothesize this is also the case when comparing different species.

As reported for four species in the tropical eastern Pacific (Patton 1972, Cantera et al. 1987, Neira et al. 1992, Ramos 1995), octocorals at CNP were highly associated with symbiotic invertebrates. These kinds of associations have been described as obligated to the point that the two individuals are “partners for life” (Mosher and Watling 2009). Therefore, the range of different life histories among octocoral species found in this study could also be associated with the life history of associated taxa; as Grigg (1975) stated, the stability of these foundation species reflects the suitability and stability of their associated taxa.

The present study is the first contribution on the biology of these species, which are the main components of rocky coral communities at CNP and in similar environments in the tropical eastern Pacific. The information presented here serves as baseline knowledge in the event of future exploitation of any of these species, which are known to be a source of active compounds (Maia et al. 2000, Gutierrez et al. 2005, Gutierrez et al. 2006, Reimão et al. 2008). This baseline knowledge will also inform management of octocoral communities inside and outside marine protected areas.

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