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ORIGINAL ARTICLE

Abundance and composition of juvenile scleractinian corals on a fringing reef (Little Reef) off San Andres Island, Colombian Caribbean

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Abstract
Colombian Caribbean reefs have deteriorated significantly over the last three decades. Coral recruitment is an important demographic process that determines the replenishment of populations and the natural potential for recovery of reef ecosystems after perturbations. We studied the composition and abundance of juvenile corals on a fringing reef (Little Reef) off San Andres Island, Colombia, using 1 m^2 quadrats ($N = 33$) spread randomly on the reef. We surveyed a total of 190 juvenile corals belonging to seven families and 15 species, with a total density of 5.75 ± 3.47 (mean ± SD) juveniles m^{-2}. The population of juvenile corals was dominated by species of the genera *Favia*, *Agaricia* and *Porites* (85.8%), while the adult population was dominated by *Diploria*, *Acropora* and *Orbicella* (78.4%). Most (71.6%) juveniles were between 1.1 and 2.0 cm. The most abundant species was *Favia fragum* (67 individuals), while *Agaricia agaricites* was the most frequently occurring (26.9%), covering the highest percentage (76.9%) of the substrate and having the largest Importance Value Index (44.6%). The community of juvenile corals on Little Reef was dominated by species that brood planulae while the adult community was dominated by species that spawn gametes. Furthermore, the two most abundant juvenile coral species had negatively skewed size–frequency distributions, indicating low recent recruitment. This study provides a demographic baseline for monitoring future changes in recruitment patterns.

Key words: *Caribbean Sea, juveniles, recruitment, San Andres Island, scleractinian corals*

Introduction

Healthy coral reefs harbour high biodiversity and are important sources of economic and cultural resources (Birkeland 1997). It is estimated that in recent decades 20% of the world's coral reefs have been degraded and more than 60% are at risk of collapse, mainly as a result of human activity (Wilkinson 2008; Burke et al. 2011). Loss of coral cover has been particularly noticeable in the Caribbean with approximately 80% since 1977 (Gardner et al. 2003), including the Colombian Caribbean (Garzón-Ferreira & Kielman 1994). As a result, Caribbean coral communities have become dominated by algae (Diaz-Pulido et al. 2004), reducing potential settlement space for coral planulae and delaying the recovery of reefs (Mumby et al. 2007).

In benthic marine organisms with open populations, recruitment is the addition of new individuals to local populations after settlement and subsequent survival of the larvae in the benthic environment (Rogers et al. 1994; Caley et al. 1996). Recruitment is a fundamental process that determines the turnover, persistence and the future structure of the populations that make up the coral communities (Bak & Engel 1979; Vidal et al. 2005). Therefore, the recovery of declining populations and disturbed reefs largely depends on successful recruitment of unoccupied available space (Pearson 1981; Smith 1992; Connell 1997; Lozano-Cortés & Zapata 2014).

Sexually produced juvenile corals generally provide new genotypes and maintain genetic variability in the ecosystem (Caley et al. 1996; Vidal et al. 2005). The establishment of new juvenile colonies generally indicates good conditions for the development and growth of a coral reef (Rogers et al. 1994), and consequently efforts to preserve these environments require an understanding of this important

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demographic process (Dunstan & Johnson 1998; Babcock et al. 2003). The evaluation of the composition and abundance of juvenile corals on a reef is a first step in providing basic information on coral recruitment success and also indicates the health of the reef and the viability of its coral populations.

Knowledge of coral settlement and recruitment in reef areas of Colombia is limited (Acosta et al. 2011). For San Andres Island in the southwestern Caribbean, live coral cover has declined by over 50%, leading to algal dominance on reefs (Diaz-Pulido et al. 2004; Rodríguez-Ramírez et al. 2010). These ecosystems are subject to the sporadic occurrence of storms, bleaching events, algal blooms and diseases, some of which are associated with anthropogenic activities that increase sedimentation, eutrophication and pollution in these areas (Garzón-Ferreira & Díaz 2003). The aim of this study was to determine the composition and abundance of juvenile corals on a shallow reef off San Andres Island, Seaflower Biosphere Reserve, Colombian Caribbean.

Materials and methods

Study area

This study was conducted on Little Reef (12° 32′N, 81° 42′W; Figure 1), a fringing reef located off the northeastern (windward) coast of San Andres Island, Seaflower Biosphere Reserve. Little Reef is approximately 1800 m long × 50 m wide and is interrupted by three passages. It is located inside the lagoon behind the main barrier reef (Big Reef). Moving seawards from the shoreline the zonation of Little Reef begins with a seagrass bed, where *Manicina areolata* Linnaeus, 1758 colonies are scattered. This is followed by the backreef, where coral becomes dominant, and then by the reef flat, which is dominated by *Porites astreoides* Lamarck, 1816, *Diploria clivosa* (Ellis & Solander, 1786), *Diploria strigosa* (Dana, 1846), *Favia fragum* (Esper, 1795) and *Millepora* sp. Finally, the outer margin of the reef is formed by large colonies of partially alive *Acropora palmata* (Lamarck, 1816) and other corals such as *Porites porites* (Pallas, 1766) and *Agaricia agaricites* (Linnaeus, 1758). Here, the depth increases abruptly from < 1 m to a 4–6 m sandy bottom, where patches of *Montastraea*/*Orbicella* spp. are common (Geister 1973; Prada et al. 2006; Pizarro et al. 2007). Geister & Díaz (1997) give detailed information about sea surface currents and reef structure.

The oceanic island of San Andres is permanently exposed to the impact of waves generated by trade winds on an effective wave fetch of about 2000 km. The prevailing surface current is the Caribbean Current, the average sea surface temperature is 27.5°C and salinity fluctuates between 34.0 and 36.3 PSU (Geister & Díaz 1997).

Methods

We quantified juvenile scleractinian corals in 33 quadrats of 1 m^2 (in November 2007), placed randomly on the reef, starting on the back reef (< 1 m deep) and ending at the reef's outer edge where the outer sandy bottom begins (4–6 m deep). Each quadrat was separated by 10 m to avoid parallax error (Rogers et al. 1994). In each

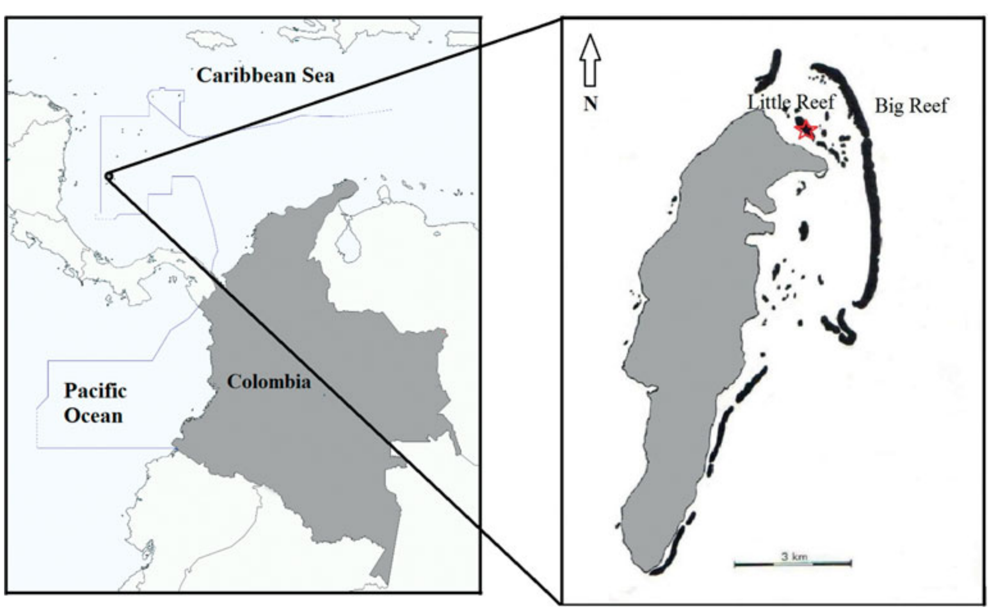

Figure 1. Position of study site (red star), San Andres Island, Colombian Caribbean.

quadrat, juvenile corals were identified to species level, except for species of *Diploria*, where the absence of distinctive morphological characters made it difficult to identify juveniles to species level (Babcock et al. 2003).

Juvenile corals were defined as colonies under 4 cm in diameter for large species such as those belonging to the genera *Montastraea*/*Orbicella*, *Diploria* and *Siderastrea*, among others (Bak & Engel 1979; Richmond & Hunter 1990; Miller et al. 2000). For small species such as *Porites astreoides* and *Favia fragum*, juvenile corals were defined as those whose colonies had a diameter of < 2 cm (Chiappone & Sullivan 1996; Dueñas et al. 2010).

In each quadrat, the diameter of each juvenile was measured to the nearest millimeter with calipers. Following the study by Vidal et al. (2005), using diameter data, we calculated the total cover of juvenile corals and from this, the relative cover by species. Similarly, we calculated the density (absolute and relative) and frequency (absolute and relative) of each species and the Importance Value Index (IVI):

$$\frac{\text{relative density} + \text{relative frequency} + \text{relative coverage}}{3} \times 100\%$$

Finally, we examined the size–frequency distribution (on a logarithmic size scale) for each of the two most abundant juvenile species and determined its skewness (lack of symmetry in the proportion of large and small coral colonies). These two statistical variables can be used as a proxy for quality of the environment (Bak & Meesters 1988; Vermeij & Bak 2002; Bauman et al. 2013).

To establish whether there was a relationship between the abundance of adult and juvenile corals of the same species on the reef, the adult coral cover was estimated in three 10 × 1 m transects. One transect was located in each reef zone (backreef, flat and slope). In each transect all adult corals were identified, counted and measured. As with juveniles, density, frequency and IVI were calculated for adults. Finally, we used the reported growth rate for each species (Table II) and the size of juvenile colonies recorded to back-calculate juvenile recruitment dates (Crabbe et al. 2004).

Results

A total of 190 juvenile corals belonging to 15 species from seven families (Faviidae, Agariciidae, Poritidae, Siderastreidae, Astrocoenidae, Acroporidae and Meandrinidae) were found (Table I). In contrast, the population of adult corals was dominated by Acroporidae and Faviidae, which were scarce in the juvenile population. The average total density was 5.75 ± 3.47 juveniles/m^2 (mean ± SD). The abundance of juvenile corals was highly variable between species. The species most abundant as juveniles were *Favia fragum* (2.03 juveniles/m^2) and *Agaricia agaricites* (1.73 juveniles/m^2), while four species (*Siderastrea siderea* (Ellis & Solander, 1768), *Acropora palmata*, *Dichocoenia stokesi* Milne Edwards & Haime, 1848 and *Leptoseris cucullata* (Ellis & Solander, 1786)) were rare with a density of only 0.03 juveniles/m^2 (Table I).

The abundance of adult corals was dominated by spawning species while juveniles were dominated by hermaphrodite and brooding species. Therefore, there was no positive relationship between the abundance of juvenile and adult corals as would have been expected (Figure 2). Juvenile corals ranged in size between 0.4 and 3.8 cm in diameter (Table II), with an average of 1.6 cm. Most juveniles (71.6%) had a diameter of between 1.1 and 2.0 cm, with few juveniles (6.2%) with a diameter greater than 3.0 cm (Figure 3). Size–frequency distributions of juveniles were negatively skewed on a logarithmic scale in both *A. agaricites* (skewness = −0.42) and *F. fragum* (skewness = −0.69). This means that there was a greater proportion of large and old than small and young colonies in the population (Table II, Figure 3).

The mean live coral cover of juveniles was 33.3 ± 19.1 cm^2 (median ± quartile range), while the total cover was 500 cm^2. The species that contributed most to live coral cover was *A. agaricites* (76.9% of cover), which was the most common species and had the highest IVI. *Favia fragum* was the most abundant species and the second species according to the IVI, while *S. siderea*, *L. cucullata*, *A. palmata* and *D. stokesi* had the lowest IVI values (Table I). Finally, in the adult population *Diploria* sp. was the most abundant species and presented the highest IVI, followed by *A. palmata* and *Orbicella annularis* (Ellis & Solander, 1786), while individuals of *Porites astreoides*, *P. porites* and *A. agaricites* were rare (Table I).

Discussion

The total density of juvenile corals observed on Little Reef was higher than the value reported for most of the Colombian Caribbean reefs (mean = 3.94 juveniles m^{-2}; Villamil 2005; Acosta et al. 2006; Dueñas 2005; López-Londoño 2011; López-Londoño et al. 2007) and the Caribbean in general (mode = 3, median = 4.9 juveniles m^{-2}; Figure 4). The dominance of the community of juvenile corals by species of the genera *Favia*, *Porites* and *Agaricia*, and of the adult community by *Diploria*, *Acropora* and *Montastrea* on Little Reef is consistent with several studies of coral recruitment in the Caribbean

Table I. Mode of reproduction, abundance, density, frequency, cover and importance value index (IVI%) for juvenile and adult coral species present on Little Reef, San Andres Island, Colombia.

Species	Family	Mode of reproduction	Abundance	Absolute density (juv/m^2)	Relative density (%)	Relative frequency (%)	Relative cover (%)	IVI (%)
Juveniles								
Favia fragum	Faviidae	Brooder	67	2.03	35.3	21.3	34.8	30.4
Agaricia agaricites	Agariciidae	Brooder	57	1.73	30.0	26.9	76.9	44.6
Porites astreoides	Poritidae	Brooder	22	0.67	11.6	14.5	11.9	12.7
Porites porites	Poritidae	Brooder	17	0.51	8.9	12.3	5.39	8.90
Eusmilia fastigiata (Pallas, 1766)	Meandrinidae	Brooder	5	0.15	2.6	3.37	2.49	2.83
Manicina areolata	Faviidae	Brooder	4	0.12	2.1	3.37	4.64	3.37
Siderastrea radians (Pallas, 1766)	Siderastreidae	Brooder	3	0.09	1.6	3.37	0.69	1.88
Orbicella annularis	Faviidae	Spawner	3	0.09	1.6	3.37	5.85	3.60
Montastraea cavernosa	Faviidae	Spawner	3	0.09	1.6	2.24	1.52	1.78
Diploria sp.	Faviidae	Spawner	3	0.09	1.6	2.24	6.23	3.35
Stephanocoenia intersepta (Lamarck, 1816)	Astrocoeniidae	Spawner	2	0.06	1.0	2.24	0.93	1.41
Siderastrea siderea	Siderastreidae	Spawner	1	0.03	0.5	1.12	0.72	0.79
Acropora palmata	Acroporidae	Spawner	1	0.03	0.5	1.12	2.87	1.51
Dichocoenia stokesi	Meandrinidae	Spawner	1	0.03	0.5	1.12	2.09	1.25
Leptoseris cucullata	Agariciidae	Brooder	1	0.03	0.5	1.12	0.72	0.79
Total	7		190	5.76				
Adults								
Diploria sp.	Faviidae	Spawner	18	0.60	48.65	16.67	47.98	37.76
Acropora palmata	Acroporidae	Spawner	7	0.23	18.92	16.67	24.69	20.09
Orbicella annularis	Faviidae	Spawner	4	0.13	10.81	8.33	15.20	11.45
Porites astreoides	Poritidae	Brooder	3	0.10	8.11	25.00	3.79	12.30
Porites porites	Poritidae	Brooder	3	0.10	8.11	16.67	2.72	9.17
Agaricia agaricites	Agariciidae	Brooder	1	0.03	2.70	8.33	3.49	4.84
Millepora sp.	–	–	1	0.03	2.70	8.33	2.13	4.39
Total	4		37	1.23				

(Bak & Engel 1979; Sammarco 1985; Smith 1992; Huitric & McField 2000; Carlon 2001).

Interspecific differences in the mechanisms of recruitment, dispersal and mortality of juveniles may be the most important elements in determining the composition of coral populations in different habitats (Bak & Engel 1979). These differences are a reflection of the life-history strategies of species and are observed in their abundance patterns. Thus, the community of juvenile corals on Little Reef was dominated by species that brood planulae while the adult community was dominated by species that spawn gametes.

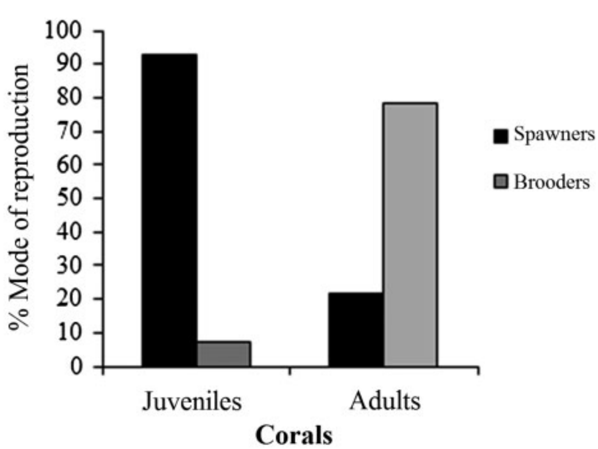

Figure 2. Ratio of the number of individuals by reproductive mode (brooder or spawner) between juvenile (N = 190) and adult (N = 37) coral populations recorded on Little Reef, San Andres Island.

The dominance of *Favia fragum* observed in this study is associated with its reproductive strategy, fertility of colonies, and mortality rate. Because this species has a low capability for larval dispersal, as the larvae only swim for approximately 4 min after being released, its settlement on the substrate immediately increases its local abundance (Knowlton 2001; Carlon 2002). Moreover, its high recruitment has been associated with low post-settlement mortality, e.g. differences between sites in comparison with other species (Edmunds 2000). Larvae of *F. fragum* also have a tendency to settle on either well-lit or dark inert substrates such as rubble and dead coral

Table II. Growth rates and time required to reach the registered size for juvenile coral species recorded on Little Reef, San Andres Island, Colombia.

Species	Growth rate (cm year^{-1})	Mean size (cm), range	Time (months)	Reference
Favia fragum	0.38*	1.8 (0.5–2.0)	57	Schelten (2002)
Agaricia agaricites	1.92*	2.2 (0.8–3.8)	14	Van Moorsel (1985)
Porites astreoides	0.92*	1.4 (0.4–2.0)	18	Schelten (2002)
Porites porites	1.47*	1.03 (0.4–1.9)	8	Schelten (2002)
Eusmilia fastigiata	1.02*	1.3 (0.8–2.1)	15	Schelten (2002)
Manicina areolata	1.44*	2.1 (1.3–3.0)	18	Van Moorsel (1988)
Siderastrea radians	1.7*	0.9 (0.6–1.1)	6	Edmunds (2007)
Orbicella annularis	0.76	2.7 (1.7–3.8)	43	Gladfelter et al. (1978), Hubbard & Scaturo (1985), Torres & Morelock (2002)
Montastraea cavernosa	0.27*	1.4 (0.9–1.9)	62	Schelten (2002)
Diploria sp.	0.37	2.8 (1.9–3.7)	91	Hubbard & Scaturo (1985)
Stephanocoenia intersepta	0.18	1.2 (0.4–1.9)	80	Hubbard & Scaturo (1985)
Siderastrea siderea	0.25*	1.7	82	Schelten (2002)
Acropora palmata	0.73	3.4	56	Gladfelter et al. (1978)
Dichocoenia stokesi	0.78*	2.9	45	Schelten (2002)
Leptoseris cucullata	2.16*	1.7	9	Schelten (2002)
Mean	0.96	1.90	40	

*Data for juvenile corals.
Note: Mean size and range is shown for species with more than one individual recorded in the quadrats.

(Baggett & Bright 1985; Bernal-Sotelo & Acosta 2012), which are widespread and common in the study site, where only 15% of the substrate is represented by live coral and the rest is mainly dead coral (Prada et al. 2006).

Because larvae of brooding species have short planktonic phases, recruitment density is likely to be determined by the local adult coral density (Black et al. 1991; Mumby et al. 2007), and the existence of a positive relationship between the abundance of adult and juvenile corals would be expected. For some Caribbean reefs, a strong positive relationship between these variables has been found (Chiappone & Sullivan 1996), while in others this relationship has

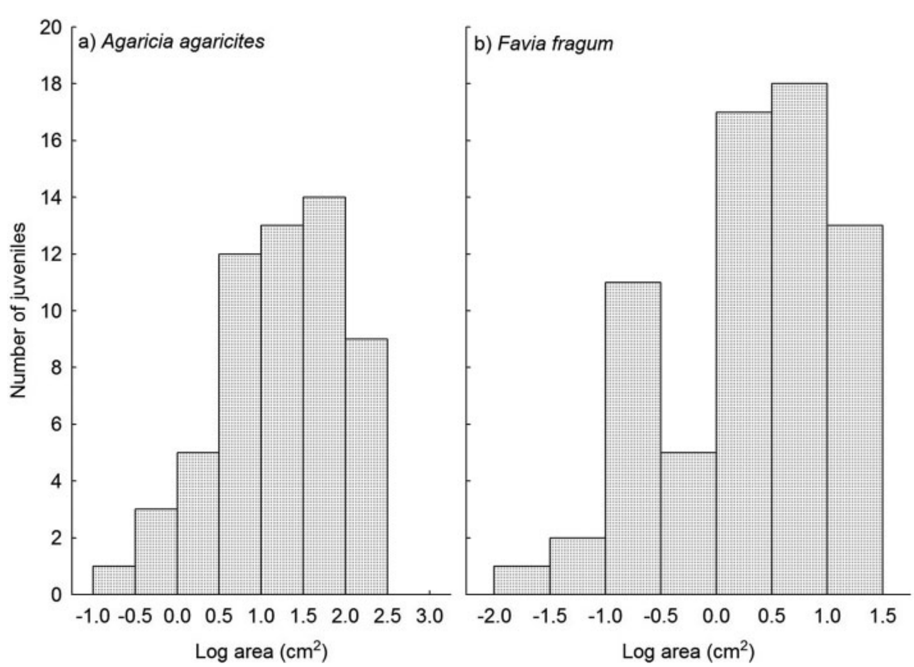

Figure 3. Size–frequency distribution (logarithmic scales) of the two most abundant juvenile coral species recorded on Little Reef (San Andres Island). (a) *Agaricia agaricites*. (b) *Favia fragum*. Descriptive statistics (a/b): mean 1.21/0.26, SD 0.73/0.75, skewness −0.42/−0.69.

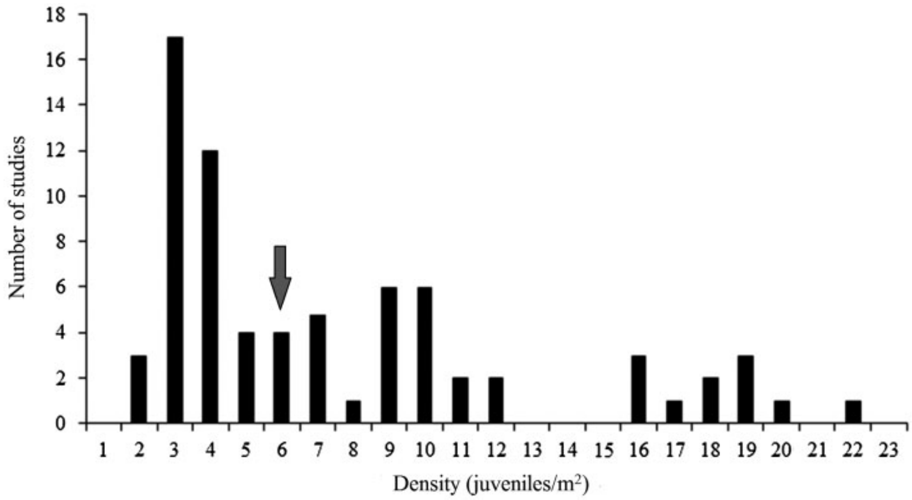

Figure 4. Distribution of the values of juvenile coral density reported in this study (arrow) and the Caribbean. The data used (N = 79) to construct this graph were obtained from the following studies: Dustan (1977), Bak & Engel (1979), Rogers et al. (1984), Smith (1992), Wittenberg & Hunte (1992), Edmunds et al. (1998), Mumby (1999), Edmunds (2000), Huitric & McField (2000), Miller et al. (2000), Carlon (2001) Edmunds & Carpenter (2001), Miller & Barimo (2001), Schelten (2002), Ruiz-Zárate & Arias-González (2004), Edmunds et al. (2004), Piniak et al. (2005), Quinn & Kojis (2005), Moulding (2005), Vidal et al. (2005), Acosta et al. (2006), López-Londoño et al. (2007), Mumby et al. (2007), González-Rivero et al. (2008), Huebner et al. (2008), Irizarry (2006), Dueñas (2005), López-Londoño et al. (2011), Irizarry & Weil (2008), Rodrıíguez et al. (2009), Green et al. (2010).

not been detected (Bak & Engel 1979; Edmunds 2000; Vidal et al. 2005). The existence of this relationship has been associated with disturbed environments. Few species can adapt to disturbed conditions while being able to persist and reproduce without showing changes in species composition between cohorts (Bak & Engel 1979; Edmunds 2000).

Because a positive relationship between adult and juvenile coral abundance was not found in this study (Figure 2), it is possible that local adult corals are not the source of the existing juveniles on the reef. However, it is also likely that this is a result of (1) a consequence of the spatiotemporal scale of the study, or (2) the lack of uniformity in the processes controlling the abundance of corals (Hughes et al. 1999). For example, in the first case, the distribution of the species can affect this result because some species have a clumped spatial distribution while others are widely dispersed and it may contribute to the under-/over-sampling of certain species. In the second case, differences in post-recruitment mortality rates generate differences in the composition and abundance of juvenile corals at different locations even if the initial population of recruits from the same cohort was homogenous in terms of abundance of species.

Bak & Meesters (1988) and Meesters et al. (2001) used the size–frequency distributions of juvenile corals in Curaçao to differentiate between coral populations on reefs with different levels of degradation. They found that negatively skewed populations, like those in this study, are associated with more degraded reefs, whereas low rates of recruitment result in fewer numbers of small colonies. Similarly, Bauman et al. (2013) found negatively skewed populations associated with higher and more variable sea surface temperature and salinity values. Colombian Caribbean reefs have recently been affected by various stressors that reduce live coral cover such as disease outbreaks (Navas-Camacho et al. 2010) and bleaching events (Bayraktarov et al. 2013). As a result, algae now dominate many reefs, especially off San Andres (53%; Rodríguez-Ramírez et al. 2010). The dominance of algae may be affecting coral recruitment because algae hinder the settlement of coral planulae (Mumby et al. 2007). These community changes along with the increasing anthropogenic impact on the island, primarily through tourism, increase the risk of reef collapse.

The decrease in Colombian Caribbean coral populations has been attributed in part to anthropogenic impacts, which now constitute the greatest threat to the reefs of San Andres Island (Pizarro et al. 2007). The cumulative effects of anthropogenic impacts reduce the abundance, diversity and recruitment of corals (Nemeth et al. 2003). In this study, there is evidence of a potential loss in diversity on the reef as 85.8% of juveniles were restricted to three genera (Table I), resulting in a pattern of coral abundance on the reef dominated by few species. Furthermore, the negative skewness of the size–frequency distribution for the two most abundant juvenile coral species, indicating the presence of fewer smaller colonies (i.e. low recent recruitment;

Table II), is demographically important as a baseline for decision-makers and scientists monitoring future changes in recruitment patterns. A low rate of recruitment is likely to result in slower rates of recovery of reefs following perturbations (Hughes et al. 1999). Nonetheless, as juveniles are defined by size and only those colonies below a certain size are counted, the latter pattern may be just a methodological artifact. Finally, because the main mechanism of recovery of coral communities after a severe disturbance is through larval settlement and recruitment and due to the very slow growth of juvenile corals, it is necessary to perform long-term studies to evaluate the natural recovery process on Little Reef.

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