

In situ settlement rates and early survivorship of hard corals: a good year for a Caribbean reef

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ABSTRACT: Coral settlement and early survivorship play an important role in reef resilience. In this study, we investigated the temporal and spatial variation of coral settlement and post-settlement survivorship in different reefs with high and low coral cover in Los Roques Archipelago, Venezuela. *In situ* estimations of settlement and post-settlement survivorship were compared between months of expected gamete release for broadcasters, and months when larval supply was expected mainly from brooders. Terracotta tiles were deployed at reefs with high (>50%) or low (<15%) hard coral cover, and recruit survivorship was evaluated during their first 4 mo of age by monthly examination of the tiles. Overall, mean (\pm SD) settlement rates varied between 30 ± 46 and 236 ± 143 ind. $m^{-2} mo^{-1}$. At particular reefs and times, settlement rates were up to 7 times higher than previously reported for the Caribbean region. Settlement rates varied between reefs, but were similar between seasons, suggesting that settlement does not increase significantly after a spawning event. Survivorship of settled corals up to 4 mo old varied from 22 to 49% between reefs and was higher at reefs with more coral cover. Our results support the theory that preserving reefs with high coral cover (and maintaining the biological and environmental factors that promote this condition) will result in enhanced settlement and survivorship of coral in its early life-stages, and therefore is a key factor in the conservation of coral reefs.

KEY WORDS: Coral reproduction · Settlement rates · Survivorship rates · Spatio-temporal patterns · Coral cover

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INTRODUCTION

Coral cover in Caribbean reefs has declined by an average of 80% since the mid-1970s (Jackson et al. 2014). This radical decline has been attributed to reductions in settlement rates, coral diseases, storms, and phase shifts from coral to algal dominance due to the loss of major groups of herbivores (Côté et al. 2005). Similar declines in coral cover during the last 50 yr have also been reported in other regions (Bruno & Selig 2007, De'ath et al. 2012). This enormous loss in coral cover worldwide emphasizes the urgent need to understand the processes responsible for coral population recovery. Larvae availability, settle-

ment and post-settlement survivorship have long been recognized as key factors driving the recovery of coral reefs after disturbances (Hughes et al. 2000). However, the study of these factors *in situ* has been particularly scarce for early life stages of corals, delaying the assessment of their spatial and temporal variability. This approach, which has proven useful for a better understanding of the dynamics of many other marine invertebrates, is an essential step for advancing coral population management plans aimed at enhancing coral reef resilience.

Coral settlement patterns have been widely studied in order to characterize and elucidate their dynamics. Settlement rates have shown large inter-

annual and seasonal variability (e.g. Fisk & Harriott 1990), with spatial variation in coral settlement also reported. Sites separated by 10s to 100s of km (Hughes et al. 2000) and even larger spatial scales (100s to 1000s of km; Hughes et al. 2002) have shown significantly different settlement rates. However, less information is available about early survivorship patterns (Arnold et al. 2010, Arnold & Steneck 2011), since the cryptic nature and microscopic size of recruits makes them difficult to relocate under natural conditions. Assertions or speculations about the causes of post-settlement mortality rely on infrequent sampling (Wilson & Harrison 2005) or indirect observations (Box & Mumby 2007). Nonetheless, biotic factors such as predation and competition (Chadwick & Morrow 2011, Doropoulos et al. 2012) and abiotic factors such as temperature, acidification, sedimentation and salinity (Gilmour 1999, Vermeij et al. 2006, Nozawa & Harrison 2007, Albright & Langdon 2011) have been reported as determinants of post-settlement survivorship and recruitment patterns.

Recruitment failure and low post-settlement survivorship rates have been highlighted as the principal factors determining the low resilience of Caribbean reefs in comparison to Indo-Pacific reefs (Roff & Mumby 2012). Recoveries after disturbances are common in Indo-Pacific reefs, but comparable levels of recovery are uncommon in the Caribbean region (Roff & Mumby 2012). Furthermore, lower settlement rates on artificial substrates are more frequently reported in Caribbean reefs compared to the Indo-Pacific (see further review of these studies in the Discussion). These lower settlement rates could be a consequence of small adult population sizes, spawning asynchrony, low fertilization rates, absence of settlement substrate or low post-settlement survivorship rates (Ritson-Williams et al. 2009). However, several sites in the Caribbean have adequate adult population sizes that perform seasonal, synchronous and prolific spawning events (i.e. Bastidas et al. 2005, Vize 2006), with high fertilization rates also observed under natural conditions (i.e. Levitan et al. 2004). Early survivorship (i.e. first months of life) estimates of hard corals *in situ* are lacking worldwide (Connolly & Baird 2010), even though it is considered a key factor in the recovery of coral cover (Kuo & Soong 2010). Without early survivorship estimates, the importance of initial variation in settlement rates (i.e. when a larva first attaches to the substrate) to local population structure is almost impossible to determine (Caley et al. 1996). Hence, survivorship of coral settlers during the first months of life could be a determining factor in the recovery capacity of Caribbean reefs, an aspect that is worth ex-

amining in more detail given the increasing threats to coral reefs in this region and worldwide.

The goals of this study were to determine the spatial and temporal variation of settlement rates and post-settlement survivorship of hard corals in Los Roques Archipelago, Venezuela. As broadcasting reproduction is known to be highly seasonal (Richmond & Hunter 1990), and species with this mode of reproduction dominate the coral cover at Los Roques (Cróquer et al. 2010), a seasonality effect in settlement rates was expected. Southern Caribbean broadcast species are known to release their gametes between 2 and 15 d after the full moon in summer (July, August, September and October; Richmond & Hunter 1990, Bastidas et al. 2005), while brooders release larvae throughout the year (Harrison & Wallace 1990). To examine this temporal variability, settlement was evaluated during 2 seasons within 1 yr; one that included the months of expected gamete release for broadcasters, and another when most brooders were expected to contribute to larval availability. Assuming that settlers are derived from the larvae in the water column, higher rates were expected during the months when larvae of both types of reproduction overlapped.

To evaluate spatial variation in coral settlement, 2 reefs of relatively high hard coral cover (>50%) and 2 other reefs with relatively low hard coral cover (<15%) were selected. Because self-seeding occurs to some extent in both brooders and broadcasters (van Oppen et al. 2008, Gilmour et al. 2009) and since reef sites in Los Roques Archipelago differ in coral cover, higher settlement rates were expected in the reefs with higher coral cover. The survivorship of recruits was expected to vary between 10 and 50%, 3 mo after settlement (Wilson & Harrison 2005). Furthermore, higher survivorship rates were expected in the reefs with higher coral cover, which presumably provided better environmental and biological conditions. Although differences in coral cover may result from many biological and environmental factors, it was expected that to some extent, settlement, early survivorship or both would explain this difference in coral cover between reef sites in Los Roques Archipelago, fostering their relevance and the need to incorporate these variables in conservation and management efforts.

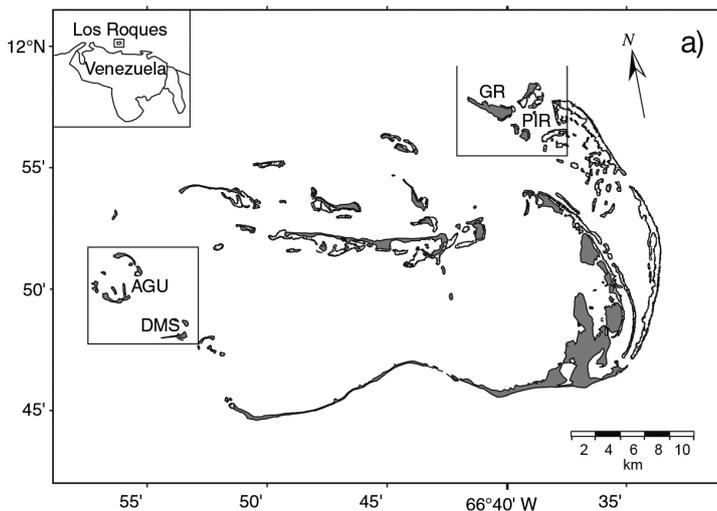
MATERIALS AND METHODS

Surveys were conducted at the fore-reef zone of 4 fringing reefs in Los Roques Archipelago, Venezuela:

Cayo Pirata (PIR), Gran Roque (GR), Cayo de Agua (AGU) and Dos Mosquises Sur (DMS). The maximum distance between reefs was 28 km; the minimum distance was 4.5 km between PIR and GR, and 6 km between AGU and DMS (Fig. 1a). To evaluate the effect of coral cover on settlement rates and early survivorship of corals, 2 reefs with considerably high coral cover (AGU and DMS; coral cover >50%) and 2 reefs with low coral cover (GR and PIR; coral cover <15%) were selected to conduct the study. Settlement rates over time were examined in two 6 mo experiments during specified 'seasons'. The first season (S1) was from August 2007 to January 2008, when broadcasters release their gametes and most of the brooders in the study sites release larvae (i.e. Richmond & Hunter 1990, Bastidas et al. 2005). During 2007, the release of gametes from broadcasters in the southern Caribbean was predicted to take place from 31 July to 13 August, and from 31 August to

13 September. The second season (S2) was between February and July 2008, when only brooders release larvae (Richmond & Hunter 1990).

During each season, terracotta tiles were deployed twice at each reef: periods P1 and P2 during S1, and P3 and P4 during S2. This was done in order to account for the variability in settlement rates within each season. Before deployment, tiles were pre-conditioned for 4 wk at the reef and depth where their installation occurred, to increase the chances of colonization of natural cues and habitat preferences. For this, tiles were suspended vertically, 20 cm above the substratum using a steel structure that allowed for colonization by biofilm. In S1, the P1 tiles were installed in August and the P2 tiles in September of 2007; while in S2, the deployment months were February (P3) and March (P4) of 2008 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m539p139_supp.pdf for exact dates). During each deployment period, 15 unglazed 25 × 25 cm terracotta tiles were secured horizontally above the substratum. A steel bar was passed through the tile and hammered to a carbonate rock with a piece of PVC separating the 2 surfaces by about 2 cm. At each reef, the tiles were arranged haphazardly over an area of 30 × 10 m, from 3 to 5 m deep, with a distance of approximately 5 m between tiles. A total of 120 tiles were deployed each season (2 periods × 4 reefs × 15 tiles).



b)

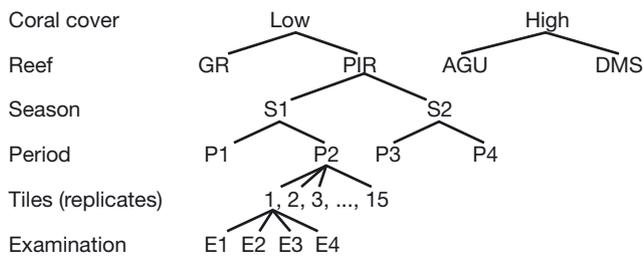


Fig. 1. (a) Los Roques National Park, Venezuela, showing the 4 reefs sampled (DMS: Dos Mosquises Sur, AGU: Cayo de Agua, GR: Gran Roque, PIR: Pirata) in the (1) northeast and (2) southwest sectors of the archipelago (squares). Image: Institute of Marine Remote Sensing. (b) Experimental design used to estimate monthly settlement rates and survivorship of hard coral settlers. S1: season 1 (broadcaster spawning season); S2: season 2 (larvae production mainly by brooders)

Estimation of settlement and survivorship using artificial substrates

To estimate settlement rates, tiles were removed monthly and transported to the laboratory in tanks containing seawater; after they were examined they were reinstalled on the reefs. Tiles were kept in 5000 l tanks in Fundación Científica Los Roques (DMS) for 2 to 4 d during their examination before they were returned to their respective reefs. Each tile was examined 4 times during each season (Fig. 1b), with the first examination occurring 1 mo after its deployment. Each settler observed in the first examination was followed to estimate its survivorship by re-deploying the tiles in the field. The total number of tiles decreased with time as some were broken by waves or swell (see Table S1). However, we were able to examine a minimum of 6 tiles at any particular time and reef (the mode and

the median both being equal to 13 tiles). The upper surface and undersurface of the tiles were examined with a stereomicroscope while submerged in seawater. No settlers were found on the upper surface of tiles during the study, where sediment accumulation and algae growth was considerably high; thus this area was excluded from rate estimations (see below). Settlers were mapped using a grid that allowed individuals to be re-identified in subsequent examinations, and the position and status (alive or dead) of each settler was recorded. Photos of settlers were taken for later identification with the help of an expert. Only those settlers that reached 4 mo of age showed diagnostic characters that allowed for identification to family level. Scanning electron micrographs were taken from representative settlers of each identified family after the last examination of the tiles.

Estimation of coral reef community cover

Since coral cover and species composition may vary at small spatial scales within a reef (100s of m), these variables were estimated in the area of tile deployment to corroborate the selection of sites based on their coral cover. For this, 25 quadrats of 1 m² each with a 10 × 10 cm grid were placed haphazardly between 3 and 5 m depth on the fore-reef zone at each site. In every quadrat, the benthic cover was estimated as percentage cover of the following types of substrate: live hard coral, soft coral, algae (macroalgae, crustose coralline algae and turf algae), rubble (dead old massive colonies, dead branching colonies and rocks) or sand. Live hard corals were identified to species level *in situ* by direct observation.

Data analysis

Spatial and temporal variations of settlement rates.

A settlement rate was calculated for each tile with the settlers that were observed during the first examination (Examination 1). The settlement rate was calculated by dividing the number of settlers by the area of the tile (only the undersurface area was considered: 0.0625 m²) multiplied by the time of tile deployment (number of days that the tiles were deployed in the reef). Rates were standardized by m² mo⁻¹ (30 d) to allow their comparison. To investigate the spatial and temporal variation of settlement, rates were analyzed using a multifactor ANOVA based on permutations with the PERMANOVA module of the PRIMER v.6

program (Anderson et al. 2008). PERMANOVA is an analysis of variance that uses permutation procedures to obtain p-values, allowing for unbalanced designs. The dependent variable was the number of recruits observed during the first examination of each tile. The analysis was run with 9999 permutations with untransformed data and Euclidean distance as the distance measure. The factors included in the analysis were reef (fixed, with 4 levels), season (2 for each reef, fixed and orthogonal to reef) and period (2 in each season, random and nested within seasons). All possible interactions between terms were included in the initial model. In order to simplify the model, interaction terms were removed in a hierarchical manner and pooled with the model's residual error if their p-values were >0.15 (Anderson et al. 2008).

Comparison of settlement rates with other studies.

In order to compare settlement rates estimated in this study with those from other studies that examined tiles over longer periods of deployment (see Table 2), a long-term settlement rate was calculated. For this, the number of settlers observed during the last examination of the tiles (Examination 4) was used. This rate considered all the recruits that were alive on the last examination independently of their settlement time, thus taking into account the effect of early post-settlement survivorship. Settlement rates were calculated and standardized the same way as previously described for Examination 1.

Spatial and temporal variation of post-settlement survivorship.

The number of corals that had settled in the first examination and survived to the fourth examination (4 mo old) was calculated for each tile. Survival curves of coral recruits at each reef and during the 2 seasons were estimated using the Kaplan-Meier method, a non-parametric statistic that estimates conditional survivorship probabilities at each time point. This method assumes that survivorship probabilities of individuals are independent, and has the advantage of considering the individuals that died during the course of the experiment as well as those still alive at the end of the experiment (censored and uncensored data). Based on our hypothesis, we expected higher survivorship rates in the reefs with higher coral cover, while no variation was expected in relation to the temporal factor season. To further investigate survivorship differences between reefs, multiple comparisons of mean survivorship after 4 mo were done with Tukey's contrasts. All calculations were conducted using the 'survival' and 'multcomp' packages in R (R Development Core Team 2011).

Coral cover. Total live coral cover was compared among reefs using a generalized linear model with

untransformed data and a quasi-binomial error distribution. Multiple comparisons of means were done with Tukey's tests using the package 'multcomp' in R (R Development Core Team 2011).

RESULTS

Spatial and temporal variation in settlement rates

A total of 1624 hard coral recruits were observed in 13.5 m², the cumulative area of 216 tiles examined in the first examination. The highest mean (\pm SD) settlement rate of 236 \pm 143 ind. m⁻² mo⁻¹ was obtained at a high coral cover site (DMS during S2-P4; Fig. 2), while the lowest rate of 30 \pm 46 ind. m⁻² mo⁻¹ was obtained at a low cover site (GR during S2-P4; Fig. 2). Differences between reefs accounted for 21 % of settlement rate variability (Table 1), and rates were dissimilar between reefs that had similar coral cover (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m539p139_supp.pdf). Settlement rates were highly variable among reefs, and similar estimations were found only between AGU and PIR (Table S2). Settlement rates differed weakly between reefs through time, and were inconsistent among reefs (Fig. 2, significant interaction of reef \times season in Table 1). The only reef that showed significant sub-yearly differences in settlement rates was GR, having a 2-fold increase during the broadcast spawning season (S1, $p > 0.001$; Fig. 2, Table S3 in

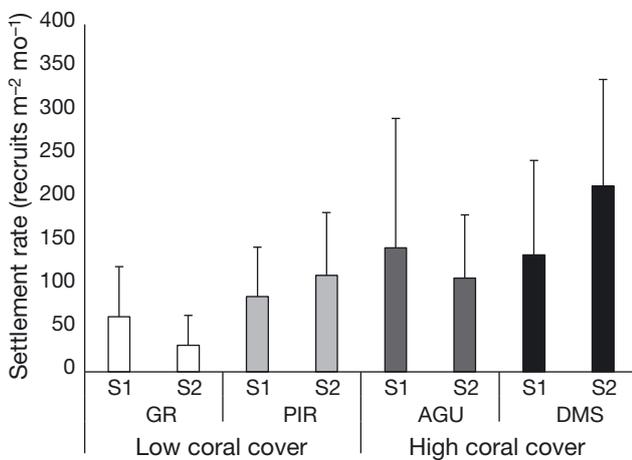


Fig. 2. Average settlement rates after the first examination of the tiles in the reefs with low coral cover (GR: Gran Roque, PIR: Pirata) and high coral cover (DMS: Dos Mosquises Sur and AGU: Cayo de Agua) during the broadcast spawning season (S1) and the brooding season (S2). Error bars: SD

Table 1. ANOVA based on permutations investigating the difference in settlement rates of hard corals estimated during the first examination of terracotta tiles (after 1 mo of deployment on the field) in reefs with different coral cover (low and high) during 2 seasons (spawning and broadcasting) and 2 periods per season (month of deployment) based on Euclidean distance. Each test was done using 9999 permutations of appropriate units, as shown. *p*-values in *italics* were obtained using 9999 Monte Carlo samples from the asymptotic permutation distribution; significant *p*-values in **bold**. Pooled terms: residuals + reef \times period (season); unique perms: no. permutations performed; VC: variance component; *p*-value was based on PERMANOVA or Monte Carlo methods depending upon the number of unique permutations

Source	df	Pseudo- <i>F</i>	<i>p</i> -value	Unique perms	VC
Reef	3	17.579	<0.001	9951	21.27
Season	1	1.076	<i>0.406</i>	6	0.02
Period (Season)	2	0.589	0.564	9953	0.00
Reef \times Season	3	0.589	0.004	9944	8.92
Pooled	209	4.478			69.76
Total	218				

the Supplement). No significant differences in settlement rates were found between seasons ($p > 0.05$; Fig. 2, Table 1).

Identification of settlers

Settlers that reached 4 mo old ($n = 1185$) that were identified to family level accounted for 69% of the total number of settlers recorded in Examination 4. Of these, 89% were Agariciidae, 5% Poritidae, 1% Faviidae and the rest remained unidentified (Fig. 3). The 367 settlers that could not be identified therefore could have been either brooders or broadcasters.

Spatial and temporal variations in survivorship

Survivorship rates differed significantly between reefs in each season (K-M, $p = 0.005$), being higher in the reefs with high coral cover (Fig. 4, Table S4). After 4 mo, mean (\pm SE) survivorship rates were higher in the reefs with high coral cover during both seasons (S1: 37.5 \pm 3.1%, S2: 36.4 \pm 2.4% for DMS, S1: 49.2 \pm 3.4%, S2: 31 \pm 3.5% for AGU; Fig. 4) than in the reefs with lower coral cover (S1: 22.3 \pm 4.4%, S2: 26 \pm 10.3% for GR, S1: 23.3 \pm 3.4%, S2: 22.3 \pm 3.1% for PIR; Fig. 4). During S1, rates were significantly different between reefs except for GR and PIR, while during S2 differences were only found

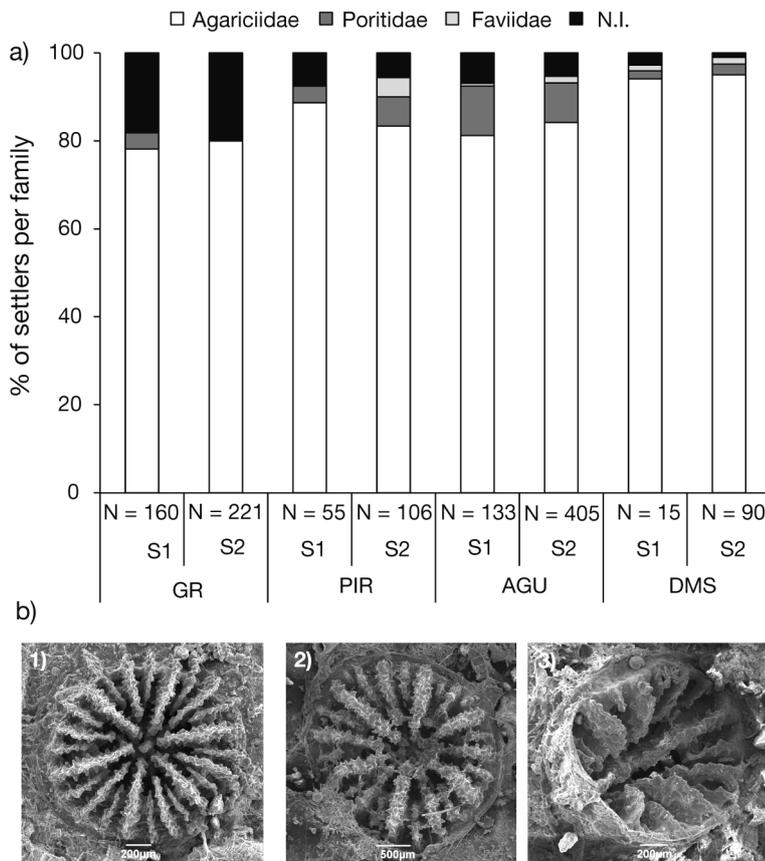


Fig. 3. (a) Identification of settlers up to 4 mo old during season 1 (S1) when both broadcasters and brooders reproduce, and season 2 (S2) when only brooders reproduce. N: total number of settlers; NI: not identified. For site abbreviations see Fig. 2. (b) Scanning electron micrographs of settlers from the 3 families identified: (1) Agariciidae: septa seldom fuse and are continuous between adjacent corallite centres with smooth margins; some species present well developed columnella. (2) Poritidae: paliform lobes present, porous skeleton, and inconspicuous coenosteum. (3) Faviidae: corallites with variable shapes ranging from conical to tubular (whatever the corallite shape, the walls are neatly rounded, columnella and wall structures developed). Septal structures are simple, columnellae are tangle of elongate septal teeth. Walls composed of thickened septa

between PIR and all the other reefs (Table S4 in the Supplement). Average survivorship rates, independent of reef and season, were $57.31 \pm 19.36\%$, $42.08 \pm 14.62\%$ and $28.89 \pm 10.30\%$ after 8, 12 and 16 wk respectively.

Coral cover

Massive hard coral species were more abundant at all sites (Table S5 in the Supplement), and were mainly represented by *Orbicella annularis* complex, which are gamete broadcast spawners (mean \pm SD cover at DMS: 54.93 ± 29.63 , AGU: 31.48 ± 26.68 , PIR:

6.08 ± 7.92 , GR: $6.08 \pm 7.92\%$). Other broadcasters were also present, but at lower abundances (DMS: 1.89 ± 3.4 , AGU: 12.35 ± 21.2 , PIR: 5.95 ± 8.18 , GR: $5.95 \pm 8.18\%$), while brooders showed relatively low coral cover in these reefs (DMS: 3.2 ± 4.55 , AGU: 4.26 ± 3.9 , PIR: 1.75 ± 2.4 , GR: $1.75 \pm 2.4\%$). The greatest richness of hard coral species was found in AGU (Table S5). This reef, together with DMS, had significantly higher coral cover (Table S6) compared with the reefs in PIR and GR ($p < 0.001$). The non-living substratum was represented by sand (DMS: 13.97 ± 25.33 , AGU: 7.26 ± 22.43 , PIR: 39.70 ± 41.63 , GR: $0.69 \pm 2.70\%$), and rubble (DMS: 2.08 ± 5.42 , AGU: 7.93 ± 17.36 , PIR: 45.14 ± 41.60 , GR: $59.45 \pm 26.38\%$).

DISCUSSION

Coral settlement rates varied significantly among reefs with no relation to coral cover, and variations corresponding to the reproductive seasonality of corals were negligible. Conversely, survivorship rates were higher in reefs with more coral cover during the season when broadcaster-spawning events were expected, while during the rest of the year this pattern was less obvious. Understanding recruitment dynamics and identifying factors influencing their spatial and temporal variation are essential for assessing their relative contribution to coral population structure. This information is crucial for advancing our knowledge of coral

recovery and incorporating it into the effective design and implementation of management plans for coral reefs.

The differences obtained in settlement rates between reefs suggest that low coral cover does not necessarily limit larval supply, as previously reported in other reefs (Penin et al. 2010, Salinas-de-León et al. 2013). Other factors, such as larval survivorship in the water column, currents, hydrodynamics and the characteristics of the available substrate for settlement are known to determine early settlement success (Harrington et al. 2004, Graham et al. 2008). The experimental design used in this study did not allow us to assess to what extent those other factors might

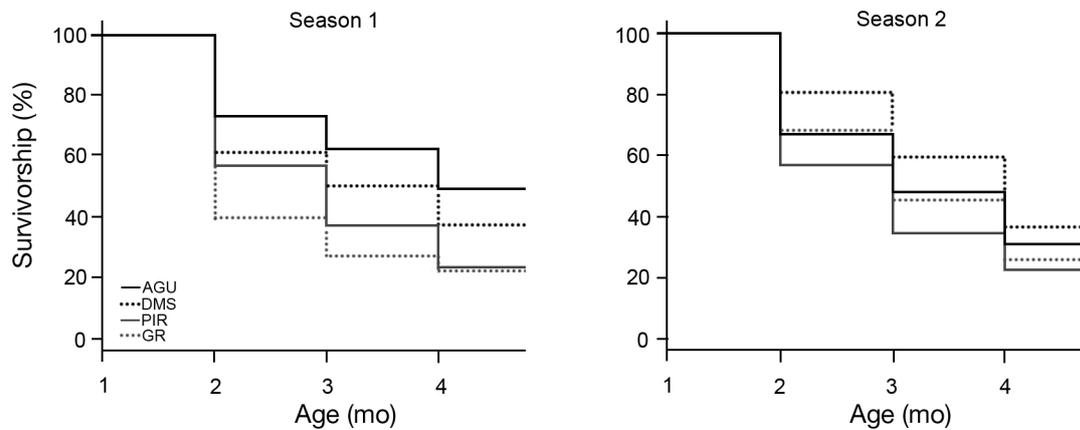


Fig. 4. Total survivorship rate of 4 mo old settlers in each reef (AGU: Cayo de Agua, DMS: Dos Mosquises Sur, PIR: Pirata, GR: Gran Roque) during the 2 seasons. Estimations were done following the fate of 4 wk old individuals

have affected settlement rates among reefs. However, the high variability observed among tiles suggests that factors related to the settlement process at the smallest spatial scale strongly influenced the rates obtained in each reef. Habitat differences at small spatial scales (e.g. variations in the biofilm between tiles), larval substrate selection, predation on early settlers (e.g. by fish, sea urchins) or competition (for space with other organisms such as bryozoans, sponges, crustose coralline algae) might result in high variability of settlement between tiles. Consequently, even if larval supply is high and similar between sites with high coral cover, large variation in settlement rates within a site can occur. These results suggest that small-scale variability processes during and a few days after settlement (until the primary polyp is established) are key in determining settlement rates.

The absence of a seasonal pattern in settlement rates agrees with the dominance of settlers from brooders in the Caribbean, which is consistent with their monthly reproduction throughout most of the year and their relatively short larval period (Harrison & Wallace 1990). This result was further supported by a predominance of Agariciidae (89%) in the subset of 4 mo old settlers that were identified (69% of the total settlers). Similarly, other coral studies using artificial substrates in the Caribbean reported that the settlers of brooders dominated in number over those with longer planktonic phases (e.g. Arnold & Steneck 2011, Green & Edmunds 2011). The predominance of brooders in the subset of recruits that was identified can have several implications for the recovery potential of the studied reef sites.

The absence of the recruits of main reef-building species could be of concern if the recruits found on

the artificial substrates are the result of larval availability in the water column. Many studies of coral reefs in the Caribbean have reported a shift in community dominance away from the major framework builders *Orbicella* and *Acropora* to the slow genera *Agaricia* and *Porites*, and even to a dominance of sponges (i.e. Ruzicka et al. 2013, van Woesik et al. 2014). The predominance of brooder settlers in artificial substrates can be considered an early indication of a potential shift in community structure at Los Roques Archipelago. This, together with recent mass mortalities of major reef building species like the one observed in 2010 (Bastidas et al. 2012), can be an undesired combination for a shift in community structure. Nevertheless, high abundance of *Agaricia* and *Porites* settlers compared to other families and to that of their adults have been observed since the early 1980s in the Caribbean (Tomascik 1991, Hunte & Wittenberg 1992), and this result can be biased by examining the undersurface of the tiles and/or with the use of artificial substrates. However, the predominance of Agariciidae and Poritidae has also been observed when recruits were simultaneously surveyed in artificial and natural reef substrates for juveniles up to 40 mm in size (Arnold et al. 2010). As these studies included a variety of natural and artificial substrates, conditioning periods, time of year and duration of deployment, the constant signature of settler assemblages that do not reflect the adult coral community seems to be a characteristic of Caribbean reefs. What remains unclear is whether this is already a shifted baseline or a poorly known ecological process that deserves further study.

A noteworthy result of this study was the high settlement rates that were recorded—up to 7 times greater than the highest rate previously reported for

the region using terracotta tiles (Carlson 2001). This result holds true when considering both early (1 mo of tile deployment) and long-term (4 mo after tile deployment) settlement rates (Table 2). Although encouraging, it must be noted that these high rates were found at a particular reef (DMS), and lower val-

ues similar to the ones reported in other studies in the Caribbean region were also found (Fig. 2, Table 2). Similarly high rates have been reported in the Pacific Ocean and the Australian Great Barrier Reef, but not previously for the Caribbean region (Table 2). Several biological (e.g. coral cover, bioregions), ocean-

Table 2. Comparative summary of coral recruitment in 31 studies using terracotta tiles since 1985. IM: deployment mode (I: individual, P: pairs, S: several); TA: total area of tiles evaluated per study site; CT: conditioning time before broadcast spawning expected dates; IT: immersion time after conditioning time; settlement rate: mean settlement rate expressed as recruits $m^{-2} mo^{-1}$ (rate transformations were done in those cases where the reported rates were not in the selected units for establishing comparisons); -: information not available

Locality	IM	Depth (m)	TA (m^2)	CT (wk)	IT (mo)	Settlement rate (recruits $m^{-2} mo^{-1}$)	Reference
CARIBBEAN							
West coast of Barbados	P	5	1.03	24	17	0–1.3	Hunte & Wittenberg (1992)
	I	2, 4	0.56	44	12	6–27	Tomascik (1991)
Northern coast of Bermuda	I	7–9	0.60	6, 11	1, 8	3–23	Smith (1985)
Western coast of Bonaire	I	10	2.4	17	27	8	Arnold et al. (2010)
Tobago	I	10	0.14	9	6, 12	0–9	Mallela & Crabbe (2009)
Guana Island, British Virgin Islands	P	6	1.79	4	12, 24	11–28	Carlson (2001)
Florida, USA	P/I	10	1.04	38	12	5–8	Smith (1997)
	I	2–5	0.1	9	4	1.5–7.8	van Woelk et al. (2014)
St. John, US Virgin Islands	I	5–6	0.33	2	6	13	Green & Edmunds (2011)
Cubagua, Venezuela	I	1.5–4	2.17	–	3.5	0.25–7	Rodriguez et al. (2009)
Los Roques, Venezuela	I	3–5	0.93	4–5	1	30–236	This study
	I	3–5	0.93	4–5	5	18–206	
RED SEA							
Gulf of Aqaba, Israel	I	6	0.12	0–12	3	16	Glassom et al. (2004)
	S	10	–	–	5–12	0–27	Abelson et al. (2005)
	I	5	0.18	0–16	4	25–100	Field et al. (2007)
PACIFIC							
Bahía de Banderas, México	I	3, 15	0.65	–	6	0.16–0.75	Medina-Rosas et al. (2005)
Great Barrier Reef, Australia	S	4–5	0.33	4	4, 9	95	Maida et al. (2001)
	I	1	0.12	1.4	2	1–413	Hughes et al. (2000)
	P	7–10	0.46	12	1.5	42–94	Babcock (1988)
	P	4	–	2	4.5	170	Harriott & Fisk (1987)
	P	5	0.72	6	6	58–601	Fisk & Harriott (1990)
	P	5	0.22	2	5	969	Fisk & Harriott (1992)
	I	9	0.33	9	5	3–6	Mundy (2000)
	P	2	2.74	2	8	0–655	Baird & Hughes (2000)
Solitary Islands, Australia	P	6–9	0.72	4, 17	5	14–64	Harriott & Banks (1995)
	P	9–19	0.40	4, 17	0.5–1	14	
Seychelles Islands	I	4	0.12	4	3	118–277	Chong-Seng et al. (2014)
Spermonde Archipelago, Indonesia	P	3–4	0.72	4	4	23–59	Sawall et al. (2013)
Taiwan	I	5	–	1–2	1.5–2.5	0–37	Soong et al. (2003)
Malakal Bay, Palau	P	10	3	8	0.2	17–133	Victor (2008)
Moorea, French Polynesia	I	2, 10	1.31	12	4	5–82	Gleason (1996)
Moorea, Raiatea and Tahiti, French Polynesia	I	6, 12, 18	0.51	0–12	3	17–92	Penin & Adjeroud (2013)
INDIAN OCEAN							
Sodwana Bay, South Africa	I	15–25	0.51	4–64	1, 16	0–83	Glassom et al. (2006)
Mombasa, Kenya	I	1.5	0.45	–	3	8–76	Mangubhai & Harrison (2008)

graphic (e.g. eddies) and methodological factors (e.g. immersion time of tiles, separation of the tiles and the substrate, depth; Table 2) have been proposed as potentially being responsible for the differences among sites (e.g. Richmond & Hunter 1990, Field et al. 2007). A standard methodology for comparing coral settlement rates between sites in the Caribbean that addresses inter-annual variation, or between the Caribbean and the Indo-Pacific is currently lacking. However, it is clear that independent estimates of settlement rates are at least one order of magnitude greater for Indo-Pacific than for Caribbean reefs (Table 2).

Several factors could explain the general trend of higher settlement rates of hard corals in Los Roques Archipelago compared to other Caribbean reefs: (1) the archipelago is located 160 km from the Venezuelan mainland and has a permanent population of only 2000 inhabitants. Therefore, it is only minimally influenced by detrimental urban and industrial activities that might diminish settlement (Tomascik 1991); (2) the archipelago is outside the regular routes of hurricanes that are known to cause extensive damage to reefs and to settlement (e.g. Mallela & Crabbe 2009); (3) before 2010 (when this study was done), the archipelago had been only slightly affected by massive bleaching events (Bastidas et al. 2012); (4) the National Park encompasses a relatively large marine area of 2211 km² while the area delimited by islands and keys is ca. 1100 km² where many reefs sites have relatively high coral cover (i.e. >30%, Cróquer et al. 2010); (5) the archipelago is in close proximity to reefs that are in relatively good condition with high coral cover (Curacao, Bonaire, the Lesser Antilles; Wilkinson 2004); and (6) inter-annual variations in settlement rates are known to occur (i.e. Fisk & Harriott 1990) and might be responsible for these higher numbers when compared to other localities in the Caribbean. The unprecedented high settlement rates for the Caribbean documented in this study were obtained for particular reefs during specific times, which highlights the importance of examining these factors simultaneously. In addition, artificial substrates can overestimate settlement rates since the proportion of available space might be higher and the colonizer community could be different than that on natural substrates.

Spatial differences found in early post-settlement survivorship in this study suggest that particular conditions of the reefs with low coral cover (GR, PIR) were detrimental to coral settlers during their first 4 mo of life compared to the reefs with high coral cover (AGU, DMS). The extent to which density-dependent or independent factors contributed to this

result is beyond the scope of this study. However, the reefs with low coral cover in this study are located within the inhabited area of the archipelago and thus are comparatively more influenced by tourism and marine transportation. Therefore, these reefs could be more negatively affected by the abiotic factors known to influence post-settlement survivorship of early recruits in a density-independent manner, such as sedimentation and nutrient enrichment (Gilmour 1999), increased noise (Vermeij et al. 2010) and altered salinity (Vermeij et al. 2006). However, the mechanisms that are driving the differences in settler survivorship between reefs and seasons, and how much these factors contribute to the dynamics of coral populations remains unknown.

A comparison of the survivorship rates estimated in this study with those of previous studies is limited due to differences in methodologies and the age of the recruits (Table 3). To our knowledge, there are only 2 studies (Arnold et al. 2010, Arnold & Steneck 2011) that have estimated early survivorship of recruits (up to 22 wk) using the same methodology as the one we used here (following 1 mo old recruits settled naturally on artificial substrates), and those estimates are similar to the ones we obtained for Los Roques (Table 3). Disregarding differences in methods, when comparing survivorship rates based on the age of individuals, average estimates in Los Roques are the third highest reported for 8 wk old and the highest for 12 and 16 wk old individuals. Although these survivorship results can be promising for reef resilience in Los Roques, the lack of information at a species level limits further interpretation. Furthermore, several factors could be responsible for these higher survivorship rates in comparison to previous reports, such as the fact that settlement occurred under natural conditions in the reefs and not under laboratory-controlled conditions. None of the studies that raised recruits settled under laboratory conditions and subsequently transplanted them to a natural reef estimated the effect of handling on survivorship, which could be an important factor in determining these rates. In addition, under controlled laboratory conditions settlement of larvae with lower fitness might initially be favored, but their mortality might be higher when transplanted to the reef, resulting in lower survivorship rates than those observed in this study. In that sense, this study provides the first estimates of survivorship rates for 8 and 12 wk old coral settlers when both settlement and growth occur under natural conditions on artificial substrates. Our results suggest positive outcomes for reef recovery efforts using this approach.

Table 3. Comparative summary of 21 studies since 1981 that estimated survivorship rates of hard coral settlers using different methodologies. Condition—1: Settlement on terracotta tiles deployed in the reef; 2: settlement in the reef under controlled conditions; 3: larvae reared in the laboratory left to settle and then transplanted to the reef; 4: larvae and settlers reared under laboratory conditions; -: data not available; NA: not applicable

Condition	Locality	Depth (m)	Taxon	No. individuals	Settlers' age in weeks [% survivorship]	Reference
1	Venezuela	3–5	–	1598	8 [39–80]; 12 [27–62]; 16 [22–49]	This study
	Belize	10	<i>Porites</i> spp. <i>Agaricia</i> spp.	26 41	22 [12]; 76 [0] 22 [37]; 76 [27], 127 [5]	Arnold & Steneck (2011)
	Bonaire	10		31	14 [59]; 29 [37]; 47 [22]; 93 [7]	Arnold et al. (2010)
	Australia	2	Pocilloporidae	213 8069	17 [9.8–25.3] 36 [28–34]	Baird & Hughes(2000) Maida et al. (1994), Maida et al. (2001)
	Taiwan	4–5	Pocilloporidae <i>Porites</i> spp.	277 168	24 [58]; 32 [41]; 40 [28]; 48 [24] 24 [90]; 32 [86]; 40 [78]; 48 [70]	Kuo & Soong (2010)
2	Australia	0–4.5	<i>Platygyra sinensis</i> <i>Oxypora lacera</i>	– –	16 [0.5] 16 [3.9]	Babcock & Mundy (1996)
3	Bonaire	3–5	<i>Agaricia humilis</i>	–	1.4 [10]	Raimondi & Morse (2000)
	Israel	–	<i>Favia fавus</i> <i>Platygyra lamellina</i>	45 / 304 191 / 388	2 [1.97]; 4 [0.21] 2 [1.79]; 4 [0.25]	Shlesinger & Loya (1991)
	Florida	–	<i>Orbicella faveolata</i> <i>Acropora</i> <i>Agaricia</i> <i>Siderastrea</i> <i>Porites</i>	– 128 11 1 5	4 [3–15]; 9 [3–11]; 40 [0] 8 [11] 8 [92] 8 [0] 8 [60]	Szmant & Miller (2006)
		–	<i>Orbicella faveolata</i> <i>Acropora palmata</i>	– –	6 [18–46.7] 8 [12–49.8]	Miller (2014)
	Australia	14	<i>Acanthastrea lordhowensis</i> <i>Goniastrea australensis</i> <i>Montastrea curta</i>	410 346 900	4 [15]; 16 [4]; 32 [1] 16 [14], 32 [2.8] 4 [8], 16 [2], 32 [0.2]	Wilson & Harrison (2005)
	Belize	3	<i>Acropora cervicornis</i> <i>Acropora palmata</i>	15 14	6 [13] 6 [15]	Ritson-Williams et al. (2010)
	Japan	5	<i>Acropora solitaryensis</i> , <i>Cyphastrea serailia</i> , <i>Alveopora japonica</i> <i>Favia fавus</i> <i>Hydnophora excesa</i> <i>Acropora solitaryensis</i>	– – – – 86 125	8 [40], 12 [18], 16 [16] 8 [5], 12 [0], 16 [0] 8 [38], 12 [0], 16 [0] 8 [10], 12 [5], 16 [2] 40 [0] 48 [17–33]	Nozawa et al. (2006) Nozawa (2010)
	Australia	2–4	<i>Acropora cytherea</i>	2540	4 [37–64]	Trapon et al. (2013)
4	NA	NA	<i>Porites porites</i> <i>Acropora tenuis</i> <i>Orbicella faveolata</i> <i>Acropora solitaryensis</i> <i>Favites chinensis</i>	– – 596 – –	11 [18] 2 [80], 4 [64], 34 [24] 24 [3–15] 0.7 [20] 0.7 [83]	Goreau et al. (1981) Harrington et al. (2004) Szmant & Miller (2006) Nozawa & Harrison (2007)

The mechanisms involved in the replacement of a population through recruitment as a function of population size are still largely unknown for hard corals (Edmunds et al. 2015). Low densities of young colonies has been suggested as one of the important causes of declining coral cover (Arnold et al. 2010, Arnold & Steneck 2011), since the replenishment of adult colonies is compromised. However, it is unclear

to what extent settlement rates and early survivorship influence juvenile colony abundance and the adult colonies that subsequently determine coral cover. Our results suggest that both mechanisms could play important roles in population dynamics, and that their individual impact on the stock–recruitment relationship can vary greatly among reefs and seasons.

The maintenance of high settlement rates could be essential to the replenishment of coral populations since early survivorship rates are low during the first month of life. This supports the notion that the first months of life could be a population bottleneck for coral, as it has been previously reported for other Caribbean reefs (van Woessik et al. 2014, Edmunds et al. 2015). Nonetheless, reefs with different coral cover had similar settlement rates while higher coral cover enhanced settler survivorship rates. This suggests that conservation efforts are better allocated to managing reefs with relatively high coral cover, preserving the environmental and human pressures that keep them in those conditions. However, the scope of our study is limited by unknown inter-annual variations of settlement and survivorship rates, an essential aspect to test the long-term relevance of early life history stages and further fine-tune this hypothesis. Also, our experimental design and analysis cannot demonstrate cause-and-effect relationships or be interpreted in a population regulation context, since that would require species-level resolution. Nevertheless, it suggests a positive association between coral early survivorship and total coral cover that deserves further investigation.

This is the first study in the Caribbean to assess coral settlement on artificial substrates at different spatial and temporal scales within a year. In addition, early survivorship of corals was estimated in the field during their first 4 mo of life, providing for the first time survivorship rates for spats younger than 14 wk of age. While settlement rates varied between reefs, early survivorship rates were higher in reefs with high coral cover compared to reefs of low coral cover. In addition to settlement and early survivorship, other ecological variables must contribute to the structure of coral communities based on the mismatch observed between the predominant families of adult coral colonies and the recently settled recruits found on artificial substrates. Alternatively, this could be a sign of vulnerability of the studied reefs to shift their species composition after further disturbances. The unprecedentedly high coral settlement rates found at Los Roques compared with other Caribbean reefs highlights the potential importance of this archipelago at a regional level as it could act as a source of larvae for other reefs. This trend deserves further examination through time, as management plans urgently need to incorporate positive feedbacks that enhance reef resilience. Common conservation efforts across the Caribbean, targeting reefs such as Los Roques, may play a key role in the recovery of coral populations in the region.

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