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PRIMARY RESEARCH PAPER

Low natural repopulation of marginal coral communities under the influence of upwelling

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Abstract The study of coral repopulation in marginal communities may provide a useful analog for understanding the dynamics of coral reefs subjected to deleterious environmental changes. Repopulation of scleractinian reef corals may strongly impact the community structure on tropical reefs; however, the extent of this process on coral communities influenced by upwelling is unknown, especially in the Caribbean. In this study, the potential for natural repopulation of coral communities subjected to wind-driven upwelling was evaluated at three sites on the island of Cubagua, Venezuela. Coral spawning behavior was recorded and both larval settlement and juvenile abundance were estimated. Upwelling did not appear to affect coral spawning behavior, since at this locality spawning occurred at dates and times similar to those reported for well-developed reefs in the Caribbean. Also, juveniles produced by brooding corals were six times more abundant than those of broadcasting species, similar to patterns on other Caribbean reefs that are not under the influence of upwelling. By contrast, mean larval settlement (4 settlers m^{-2}) and juvenile abundance (0.1 juveniles m^{-2}) in Cubagua were both lower than those elsewhere in the Caribbean and on Pacific reefs. Thus, the potential for repopulation of these marginal communities seems lower than for well-developed coral reefs in other regions. These results suggest that more fully developed coral reefs also may have reduced repopulation potential, as they become influenced by suboptimal environmental conditions.

Keywords Marginal reefs · Scleractinians · Reproduction · Settlement · Recruitment · High sedimentation

Introduction

Marginal coral communities generally occur outside the tropical belt or at its edge, where conditions are close to the environmental thresholds for coral survival (Harriott & Banks, 2002). Consequently, these communities usually have limited accretion, extension, depth distribution, and biological diversity. Marginal communities also occur within the tropical belt where environmental conditions are suboptimal for reef development, such as in areas influenced by upwelling, heavy runoff, or river deltas (Perry & Larcombe, 2003). In contrast to this definition of marginal coral communities, in the present study “well-developed reefs” refer to communities where

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corals grow under favorable environmental conditions and mild human impacts, usually producing a reef framework (Perry & Larcombe, 2003).

While marginal reefs may contribute very little to reef accretion globally, they increase the diversity of reef ecosystems and represent localized sites of carbonate sediment production and accumulation (Benzoni et al., 2003). In addition to their ecological and geological relevance, the study of marginal coral communities may provide useful analogs for understanding the dynamics of coral reefs subjected to deteriorating environmental changes (Perry & Larcombe, 2003). Firstly, reefs stressed by upwelling and sediments have been common at many times in the past, for instance, during the Holocene, when increases in sea level caused low water quality (Adey, 1978). Secondly, many well-developed reefs may become “marginal” in response to climate changes (Hoegh-Guldberg, 1999; Guinotte & Buddemeier, 2003) and/or anthropogenic influences (Grigg & Dollar, 1990).

In view of impending global and local environmental changes, it is important to understand the natural repopulation of coral reefs following disturbances and to contrast these processes between marginal and well-developed coral communities. To estimate natural repopulation, parameters such as rates of gamete production, larval settlement, and juvenile abundance (recruitment) are suitable proxies (Harrison & Wallace, 1990; Gittings et al., 1992; Connell et al., 2004) that have been used extensively to study well-developed reefs (Hughes et al., 1999, 2000; Hughes & Tanner, 2000). By contrast, studies on marginal communities have been limited to reports on the occurrence of spawning and juvenile densities (Harriott & Banks, 2002; Wilson & Harrison, 2003; Medina-Rosas et al., 2005). In the Caribbean in particular, the potential for repopulation of marginal coral communities has been estimated only from juvenile abundance in the field, and to date, no study has integrated this variable together with larval settlement and coral spawning behavior.

It has been suggested that coral spawning is synchronized by the annual sea temperature cycle acting as a seasonal cue (reviewed in Harrison & Wallace, 1990), and that settlement and recruitment can be affected by environmental stressors, like sedimentation, turbidity, and nutrient enrichment (Harrison & Ward, 2001; Harriott & Banks, 2002; Hodgson, 2004; Nozawa & Harrison, 2007). Therefore, we expected that corals in upwelling communities could have a different spawning behavior compared to their conspecifics at the same or at different latitudes in non-upwelling communities. Furthermore, during the upwelling season, the surficial waters also show an increased turbulence, sedimentation, nutrient enrichment, and turbidity (Astor et al., 2003). Therefore, less settlement and recruitment could also be expected in upwelling communities compared with well-developed reefs. Despite the potential effect of upwelling on coral repopulation (at least on reproductive behavior, settlement, and recruitment), and therefore on community structure, the extent of this effect is unknown, especially for Caribbean reefs.

The eastern coast of Venezuela is subject to annual events of upwelling (Astor et al., 2003), resulting in marginal coral communities developing on shallow hard substrata (Olivares, 1971; Ramírez-Villarroel, 2001; Weil, 2003). Limited coral reef development near these upwelling areas has been ascribed to the low temperatures caused by the annual upwelling event (Ramírez-Villarroel, 2001; Weil, 2003). Because this upwelling is driven by trade winds, the area also has increased sedimentation rates and turbidity (e.g., up to 2,331 g m^{-1} d^{-1} in Rodríguez, 2004). Despite their marginal designation, these coral communities represent a large proportion of the coral areas in Venezuela (Fig. 1). The island of Cubagua is situated well within this upwelling zone of the northeast coast of Venezuela. Thus, to estimate the potential for natural repopulation of coral communities subjected to this upwelling, the following variables were quantified in three marginal communities on the island of Cubagua: (a) the spawning behavior of five corals species during 2003; (b) the abundance of larval settlers in artificial tiles in 2003 and 2004; and (c) juvenile abundance in the field in 2003.

Materials and methods

Study area

The island of Cubagua is located within the upwelling zone on the eastern coast of Venezuela (10 47′–10 51′ N, 64 08′–64 14′ W; Fig. 1). Mean monthly

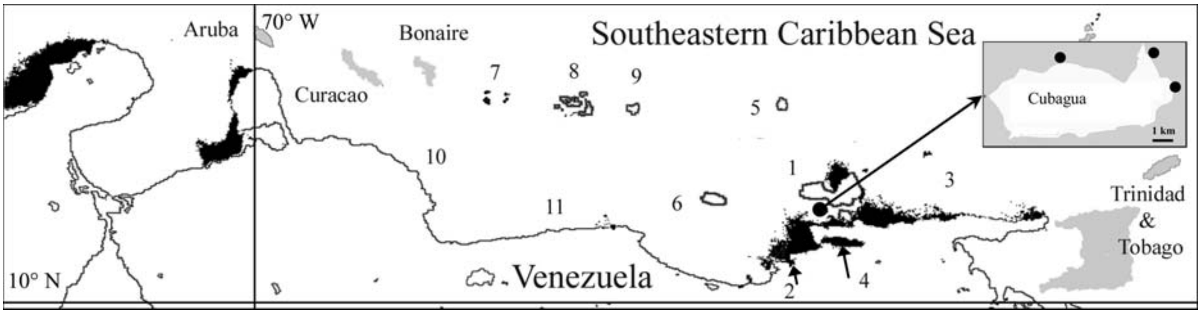

Fig. 1 Main areas of coral growth (*numbers*) and upwelling (marked in *black*) along the coast of Venezuela. Average surface temperature at the upwelling eastern area was <24.7°C during the first trimester of 2006. Coral areas within the upwelling zone include Islas de Margarita, Coche, Cubagua (*inset* in the figure, *black points* are the study localities) and Los Frailes (1), Parque Nacional Mochima (2), Los Testigos (3), and Golfo de Cariaco (4). Coral areas partially affected by upwelling include La Blanquilla (5) and La Tortuga (6). Coral areas out of the upwelling influence include Archipiélago de Aves (7), Archipiélago Los Roques (8), isla La Orchila (9), Parque Nacional Morrocoy and Cuare (10), and various sites of the Central coast (11). The figure frame shows 8–16 and 58–77 W. Sea surface temperatures were obtained from MODIS sensor, data available at CARIACO web page (http://cariaco.ws/)

sea surface temperature (SST) ranges between 23°C in January to 29°C by September. On the northeast of Cubagua, there are approximately seven widely dispersed coral communities with areas ranging from 0.01 to 0.3 km^2, and with scleractinian coral cover of 5–15% (Rodríguez, 2004). These coral communities are limited to 0–4 m depth, and their species richness is low at 7–11 species of scleractinian corals in each community (Rodríguez, 2004). We examined three community sites: Las Cabeceras, El Mercado, and Los Acantilados, which are a minimum of 2 km apart and are located from east to west (Fig. 1), following the direction of the surface currents (Walsh et al., 1999; Astor et al., 2003).

Spawning behavior

Broadcast spawning of gametes was assessed in five coral species at El Mercado during 2003. Colonies of *Diploria strigosa* (Dana, 1846; $n = 11$), *Diploria clivosa* (Ellis & Solanders, 1786; $n = 10$), *Colpophyllia natans* (Houttuyn, 1772; $n = 10$), *Montastraea annularis* (Ellis & Solanders, 1786; $n = 10$), and *Siderastrea siderea* (Ellis & Solanders, 1786; $n = 5$) were tagged. These colonies were observed during 21:00–23:30 h, on the second to the ninth nights after the full moon (NAFM) in August, the second to eighth NAFM in September, and the fifth to ninth NAFM in October 2003. The potential spawning times and dates to survey these colonies were established according to those observed for the main spawning events in the southern Caribbean (Van-Veghel, 1993; de-Graaf et al., 1999; Bastidas et al., 2005). The time and the number of colonies that spawned on each night were registered. Although the time of spawning and proportion of colonies that spawned are not a comprehensive predictor of reproductive effort; we considered this information relevant for evaluating repopulation at the local scale due to the potential effect of larval retention on this reef.

Larval settlement

Larval settlers were counted on 20 terracotta tiles of 33 × 33 cm at each of the three sites above. The tiles were rough underneath and smooth on top, and they were placed horizontally, attached to the substratum with screws and ramplugs previously inserted in the bottom of the reef (e.g., Harriott & Fisk, 1988; Fisk & Harriott, 1990; Hughes et al., 1999). Tiles were fixed ~3 cm above substratum, at 1.5–4 m depth and were separated from each other by 1.5–5 m. The tiles were deployed 2 weeks before the predicted start of the main spawning events in the southern Caribbean (Van-Veghel, 1993; de-Graaf et al., 1999; Bastidas et al., 2005), and they were left in the field for 90 days. Tiles were placed at all three sites in 2003 and in 2004, but in 2004 we were unable to recover them from Los Acantilados; probably due to storm damage. Therefore, for the 2003 data a two-way permutation analysis of variance (PERMANOVA; Anderson, 2001) was applied to test the variation in

Table 1 Observations of coral spawning at El Mercado, Cubagua

Coral species	Month	NAFM	Time of spawning	Number of colonies that spawned (out of total observed)	Percent of colony surface that spawned
Montastraea annularis	August	7	22:23–22:35	1 (10)	<25
	September	8	21:53–22:01	2 (10)	<25
	October	7	21:20–21:35	1 (10)	NA
Diploria strigosa	August	6 and 7	21:40–23:25	6 (11)	6 NAFM: <25 7 NAFM: >75

NAFM nights after the full moon of August, September, or October of 2003; *NA* data not available

coral settler densities (settlers m^{-1}) between sides of the tile (the upper and lower sides) and among the three sites. Also, a three-way PERMANOVA was applied to test the variability of larval settlement densities between sides of the tile (the upper and lower side), between sites (El Mercado and Las Cabeceras), and between years (2003 and 2004).

In the sampling of 2003, the percent cover of benthic organisms and predation marks on the tiles was also estimated, using the point intersect technique with 100 points. Three months after deployment, the encrusting community that colonized the tiles was compared among the three sites and tile sides (upper versus lower) with a PERMANOVA test. For this test, the percent cover estimates of 15 taxa were considered as variables and “site” and “tile side” as the two factors of interest. The percent dissimilarity of the encrusting community for each of these factors, which have a significant effect ($\alpha = 0.05$), was calculated with a SIMPER analysis. For the encrusting community that colonized the tiles, a principal component analysis (PCA) was done and the abundance of those benthic categories that explained most of the variability was superimposed onto that PCA (Clarke & Gorley, 2006). This was also done for the abundance of settlers to relate the encrusting community with this variable.

Juvenile abundance

To estimate the abundance of juvenile corals at each site, juvenile colonies were counted in three plots of 20 m × 4 m (=80 m^2) at each of the following depth intervals: 0–1, 1.1–2, 2.1–3, and 3.1–4 m. Thus, at each site, 240 m^2 was examined per depth and 960 m^2 total. Colonies were considered to be juveniles if their sizes ranged from the minimum size visible in the field (Harrison & Wallace, 1990), which was ≈5 mm in diameter to the minimum size at sexual maturity: 5 cm for relatively large species such as *Montastraea* spp. and *Diploria* spp., which broadcast their gametes, and 2 cm for smaller species such as *Siderastrea radians* (Pallas, 1766), *Porites* spp., and *Favia fragum* (Eper, 1788), which are brooders (Miller et al., 2000). Colonies within this size range that were clearly the product of partial mortality or fragmentation were not considered to be juveniles. A PERMANOVA was used to compare juvenile abundance of species that brood their larvae versus those that broadcast their gametes (two variables), among depths (four levels) and sites (three levels).

Results

Spawning behavior

Two out of the five coral species examined spawned: 40% of tagged colonies of *M. annularis* (4 out of 10) and 55% of colonies of *D. strigosa* (6 out of 11) (Table 1). Colonies of *M. annularis* spawned during all 3 months of observation, whereas those of *D. strigosa* spawned only during August.

In August, 27% and 36% of *D. strigosa* colonies spawned for 70 min on the sixth and for 85 min on the seventh NAFM, respectively. One colony of *D. strigosa* spawned gametes during two consecutive nights: from <25% of the colony surface area on the first night and >75% of the surface area on the second. By contrast, colonies of *M. annularis* did not spawn gametes consecutively over more than one night or month, and the colony surface areas that simultaneously liberated gametes always were <25%

(Table 1). In August, only 10% of *M. annularis* colonies spawned on the seventh NAFM for 12 min, while in September, an additional 20% of colonies spawned for 8 min during the eighth NAFM. However, rough sea conditions precluded observations during the sixth and seventh NAFM of that month. In October, 10% of marked colonies of *M. annularis* spawned on the seventh NAFM, for 10 min after 21:20 h. In addition to the tagged colonies, we also observed that 11 colonies of *D. strigosa* spawned in August and two colonies of *M. annularis* in August and October, within the vicinity and synchronously with those that were tagged.

Larval settlement

During August to November in both 2003 and 2004, 43 coral larvae settled on tiles at our study sites, both years combined (3.8 larval settlers m^{-2}). Newly settled corals of at least five different morphologies were observed, and four of them are shown in Fig. 2. During 2003, larval settlement was nine times higher at Los Acantilados, the western-most site, than at the other two sites (7.2 vs. 0.8 larval settlers m^{-2}). Also, only at Los Acantilados this settlement was larger underneath the tiles, where the abundance of settlers was 30× that of the top side (23 vs. 0.62 larval settlers m^{-2}; Table 2, Fig. 3). The abundance of larval settlers was similar at Las Cabeceras and El Mercado (Fig. 3), where this variable was not significantly different between tile sides or between 2003 and 2004 ($P > 0.05$ for each factor and their interactions).

Table 2 Permutation analysis of variance for larval settlement (settlers m^{-2})

Source	df	SS	MS	*F*	*P*-value
Side: Sd	1	2266.89	2266.889	10.00	0.519
Site: St	2	4744.78	2372.39	23.09	0.073
Sd × St	2	4533.78	2266.89	22.06	*0.045*
Residual	66	67807.17	1027.38		
Total	71	79352.61			

Side was a fixed factor (upper versus under sides), and site was a random factor with three levels. Italic number denotes significant value ($\alpha = 0.05$)

After 3 months, the encrusting community that colonized the tiles differed between the top and bottom sides of the tiles (Table 3; ~84% dissimilarity, Fig. 4A, B). The encrusting communities of the top versus the bottom sides of the tiles separated better along the first axis of the PCA (PC1 = 65.8%

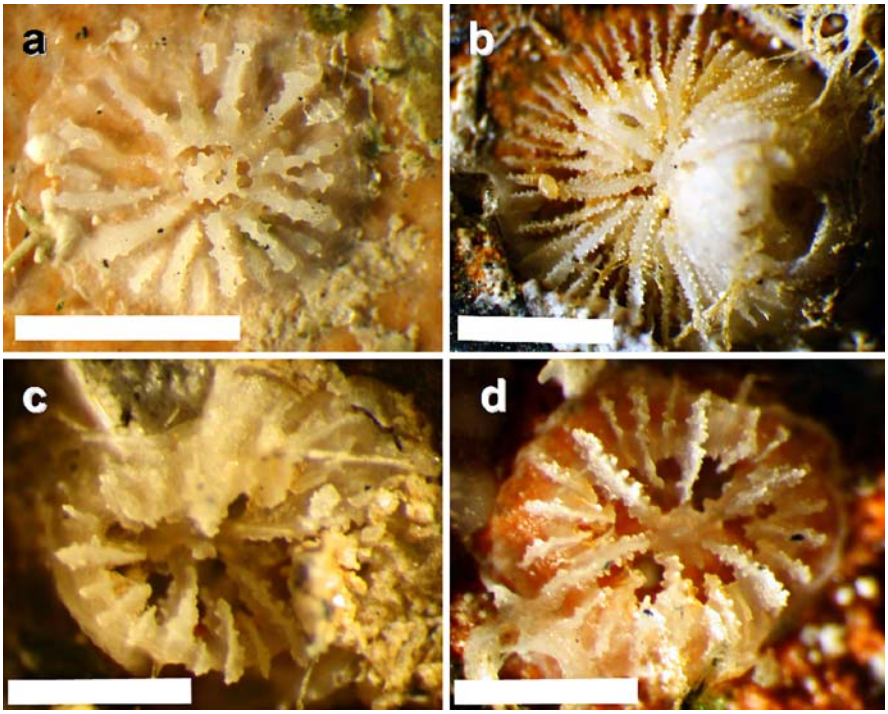

Fig. 2 Four out of the five morphologies of larval settlers of scleractinian corals found on our settlement tiles. b shows the most common morphology observed (32 of 40 settlers), probably belonging to the genus *Agaricia*. Scale bars are 1 mm long each

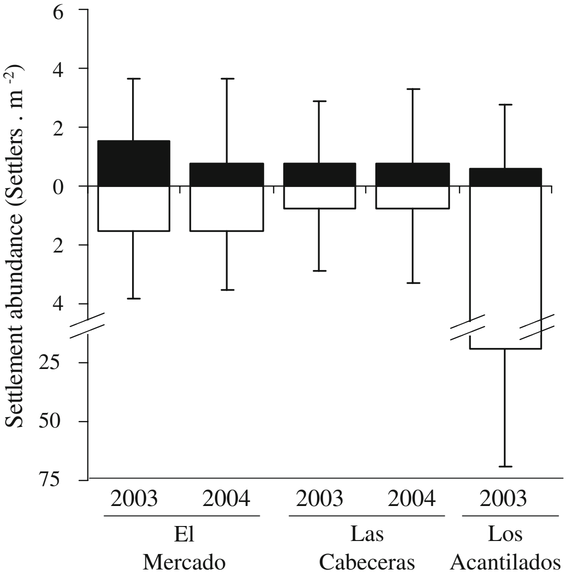

Fig. 3 Abundance of larval settlers (mean + SE) on the upper side (*black bars*) versus the under side (*white bars*) of tiles at the three study sites during 2003, and at two of them during 2004. Between 14 and 19 tiles were examined at each site and year combination

Table 3 Permutation analysis of variance for the cover of benthic organisms on the tiles (encrusting community) after 3 months in the field

Source	df	SS	MS	*F*	*P*-value
Site: St	2	10543.85	5271.93	19.656	0.072
Side: Sd	1	3768.56	376.856	23.374	*0.039*
St × Sd	2	3224.64	1612.32	0.6011	0.727
Residual	66	177018.19	2682.09		
Total	71	194555.24			

Side was a fixed factor (upper versus under sides), and site was a random factor with three levels. Italic number denotes significant value ($\alpha = 0.05$)

of the total variability), which was explained by a high cover of fleshy algae (Falg: +0.87; Fig. 4C) and a low cover of bare substrate (Bare: −0.45; Fig. 4D), encrusting coralline algae (Ealg: −0.13; Fig. 4E), and colonial ascidians (Casc: −0.12; Fig. 4F). The difference between the top and bottom encrusting communities is not as clear over the second axis of ordination. However, this axis explained an additional 15.2% of the variability, and it was mainly characterized by high cover of bare substrate (Bare: +0.82) and filamentous algae (Fila: +0.34), and low cover of colonial ascidians (Casc: −0.37) and predation marks (Predation: −0.35). Also, abundance of larval settlers (Set. m^{-2}) seemed to have a positive relationship with cover of bare substrate (Fig. 4H vs. C) and a negative relationship with the cover of filamentous algae (Fig. 4H vs. D), and with that of predation marks (Fig. 4H vs. G).

Juvenile abundance

The abundance of juvenile corals in the field varied significantly among depths and sites (significant depth × site interaction: Table 4). At Las Cabeceras, it was highest between 1 and 2 m (0.3 juveniles m^{-2}), whereas at Los Acantilados and El Mercado juvenile abundance increased with depth to a maximum of 0.04 and 0.03 juveniles m^{-2}, respectively, at a depth of 3–4 m (Fig. 5). The type of recruits also differed among sites, as at Las Cabeceras, the juveniles were almost exclusively brooding species, and it was ×10 larger than that of brooders at El Mercado and Los Acantilados. By contrast, the juvenile abundance of broadcasting species was lowest at Las Cabeceras, intermediate at El Mercado, and highest at Los Acantilados. The coral species with the highest abundances of juveniles, in decreasing order, were: *Porites* spp and *S. radians* at Las Cabeceras; *S. radians*, *Porites astreoides* Lamarck, 1816, *D. strigosa*, and *M. annularis* at El Mercado; and *Acropora palmata* (Lamarck, 1816), *D. strigosa,* and *Agaricia agaricites* (Linnaeus, 1758) at Los Acantilados.

Discussion

Spawning behavior

In this marginal coral community affected by upwelling on the northeast coast of Venezuela, the reef corals *D. strigosa* and *M. annularis* spawned synchronously with conspecifics at other well-developed reefs in other areas of the Caribbean. Spawning dates, time of day, and spawning duration observed in this study for *D. strigosa* were similar to those reported for Puerto Rico, Bermuda, Gulf of Mexico, Panama, and other sites in Venezuela (Szmant, 1986; Richmond & Hunter, 1990; Soong, 1991; Gittings et al., 1992; Bastidas et al., 2005). However, the proportion of colonies of *D. strigosa* that spawned in

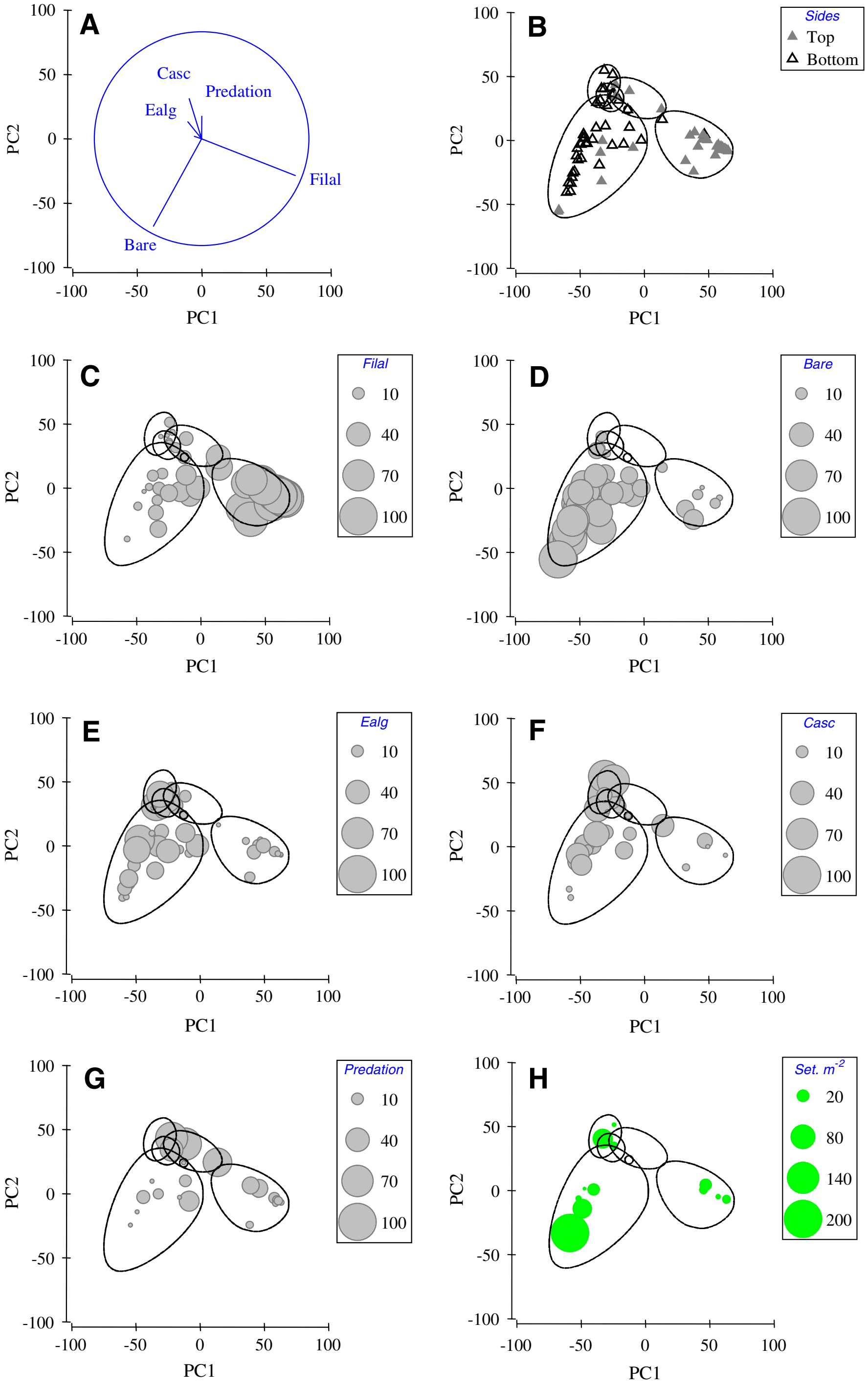

Fig. 4 Principal component analysis for the encrusting community that colonized the tiles after 3 months in the field (A), with the side of tiles superimposed (B). The continuous *lines* group the community on the sides of the tiles (upper or lower) with at least 40% of similarity (Bray–Curtis similarity index). The two first axis explained >81% of the total variability (PC1 = 65.8% and PC2 = 15.2%). C–G show the cover (%) of those components that explained most of the total variability of the PCA: filamentous algae (Filal), bare substrate (Bare), encrusting coralline algae (Ealg), colonial ascidians (Casc), predation marks (Predation). H shows the abundance of larval settlers (Set. m^{-2})

Cubagua (6 out of 11) was two to five times higher than that observed on well-developed reefs in Venezuela (in Los Roques only 1 out of 8; and in Morrocoy 4 out of 14 colonies; sites 8 and 10 in Fig. 1; Bastidas et al., 2005). Despite our small sample size and limited number of observations, we suggest that this species spawned predictably and the proportion of its population that spawned is equivalent to or even larger than on well-developed reefs in the Caribbean. This may partly explain the

Table 4 Permutation analysis of variance for juvenile abundance (recruits m^{-2})

Source	df	SS	MS	*F*	*P*-value
Site: S	2	1753.72	876.86	1.5424	0.089
Depth: D	3	3291.64	1097.21	0.9141	0.653
S × D	6	7201.61	1200.27	2.1113	*0.001*
Residual	24	13644.00	568.50		
Total	35	25890.97			

Site was a random factor with three levels, and depth was a fixed factor with four levels. Italic number denotes significant value ($\alpha = 0.05$)

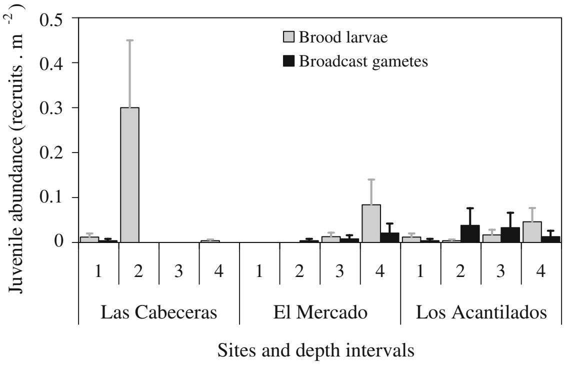

Fig. 5 Abundance of juvenile corals (mean + SE) of species that broadcast their gametes and of species that brood their larvae at each site and depth interval (1: 0–1 m; 2: 1–2 m; 3: 2–3 m; 4: 3–4 m). Data from three plots of 4 × 20 m evaluated at each site and depth combination

dominance of *D. strigosa* in the coral communities of the eastern coast of Venezuela (Olivares, 1971; Weil, 2003).

The spawning dates of *M. annularis* at Cubagua also coincided with those recorded from other field and histological studies, i.e., the sixth, seventh, and/or eighth NAFM, between July and October (Szmant, 1986, 1991; Soong, 1991; Knowlton et al., 1997). The proportion of colonies of *M. annularis* that spawned in Cubagua (4 out of 10) was similar to that observed in 2002 on well-developed reefs in Venezuela (at Los Roques 7 out of 10, Morrocoy 4 out of 10; Bastidas et al., 2005). Despite differences in coral abundance and environmental conditions between marginal coral communities in upwelling areas versus more developed reefs, the spawning behavior of *D. strigosa* and *M. annularis* at Cubagua indicates that spawning synchrony is maintained across different reef types.

Our lack of observations of spawning in *S. siderea, D. clivosa*, and *C. natans* is similar to the paucity of spawning observations in these species elsewhere in the Caribbean. Histological studies of *S. siderea* have shown that this species is gonochoric with external fertilization and spawns between July and October (Szmant, 1986; Harrison & Wallace, 1990; Richmond & Hunter, 1990; Soong, 1991), but only recently it has been observed spawning in the field (A. Ross, personal communication). Observations on *D. clivosa* spawning are limited to a single colony in one study in Curaçao (Van-Veghel, 1993). In the Gulf of Mexico, from 1997 to 2003, *C. natans* was observed to spawn between the ninth and eleventh NAFM in August and September (Vize et al., 2005). If spawning behavior is similar between the corals in the Gulf of Mexico and those in Cubagua, it is possible that the spawning of *C. natans* occurred later than the last date of observations in this study, the ninth NAFM. Bastidas et al. (2005) recorded the spawning of only 1 out of 33 colonies of this species on the seventh NAFM of September at Morrocoy, Venezuela, but their last date of observation was also the ninth NAFM.

Larval settlement

Coral larval settlement increased at our study sites from east to west, following the direction of the dominant current pattern. The high abundance of settlers at the western-most site, Los Acantilados, may have resulted in part from a cumulative effect of larval transport by currents. Alternatively, the higher larval settlement at Los Acantilados could have been affected by the proximity of brooding adults, as in this site, brooders and more specifically *A. agaricites* were more abundant than in the other two sites. It is known that brooders are more efficient in localized recruitment; thus, the proximity of brooding adults to tiles affects settlement abundance on artificial substratum (Harrison & Wallace, 1990). Coral settlement is affected by many factors; thus, understanding its spatial and temporal variability is difficult. However, the interactions between local oceanography and biological factors are well-recognized drivers of recruitment in marine communities, particularly affecting the abundance of coral settlers (e.g., Harriott & Fisk, 1988; Vermeij, 2006).

The much larger abundance (×20) of settlers on the bottom versus the top of the tiles observed at Los Acantilados was likely in part due to the large amounts of filamentous algae, sedimentation, and predation pressure on the top sides of the tiles, together with less crustose coralline algae and empty space available (Harrison & Wallace, 1990). Larvae of *Pocillopora domicornis* preferred to settle on bare glass versus substrata covered with fine sediments (Hodgson, 2004) and on relatively dark places (Raimondi & Morse, 2000). Larvae also prefer rough surfaces to settle, and in this study the rough side of the tile was always orientated down. The pattern of higher abundance of settlers on the bottom than on the tops of tiles observed here is similar to that in other studies on well-developed coral reefs (e.g., Harriott & Fisk, 1988; Fisk & Harriott, 1990; Hughes et al., 1999).

However, the abundance of larval settlers (0.5–9 settlers m^{-2}) observed at Cubagua was 2–60× lower than that at well-developed reefs in the Caribbean, where 17–29 settlers m^{-2} were found in 2002 at two non-upwelling Venezuelan coral reefs (Bastidas, unpublished data) and 10–37 settlers m^{-2} at reefs in Bermuda (Smith, 1992). By contrast, the abundance of larval settlers in Cubagua was similar to, or even higher than, that observed in other marginal coral communities of the Caribbean (0.6 and 1.9 settlers m^{-2}; Miller et al., 2000). One possible explanation for the relatively low abundance of settlers observed in marginal communities is their low cover of adult corals compared with well-developed reefs, although studies on well-developed reefs have failed to find this type of relationship (Hughes et al., 1999, 2000).

Juvenile abundance

Following the pattern of larval settlers, the abundance of juveniles at Cubagua (0.01–0.19 juveniles m^{-2}) was 5–10× lower than that reported at well-developed Caribbean reefs (e.g., Guzmán & Guevara, 1999), and approximately three orders of magnitude lower than that observed on Indo-Pacific reefs (e.g., Tamelander, 2002; Glassom & Chadwick, 2006). The low coral abundance of the eastern Venezuelan upwelling zone and the high turbidity, high sedimentation, and low temperature reported for Cubagua (Rodríguez, 2004) may reduce the larval supply of corals as well as the survivorship of settlers. For instance, the site with the lowest juvenile abundance in this study had the highest sedimentation rate, which in turn was up to 25× higher than the maximum reported for well-developed reefs in the Caribbean (Rogers, 1990). In view of the low abundance of larval settlers and juvenile corals, the marginal coral communities of Cubagua might have a lower potential for repopulation than other well-developed reefs of the Caribbean and the Pacific.

Eighty-six percent of coral recruitment in Cubagua came from species that brood their larvae, a value that coincides with findings on other Atlantic reefs (e.g., Smith, 1992; Edmunds, 2000; Hughes & Tanner, 2000; Miller et al., 2000). Brooded larvae have a shorter pre-competency period than do planktonic ones, among other characteristics that allow brooders to be more efficient in localized recruitment (Harrison & Wallace, 1990). Therefore, the dominance of recruits from brooding species at Las Cabeceras was probably related to the dominance of adult colonies of poritids and *S. radians* in this community (Rodríguez, 2004). However, at Los Acantilados, the abundance of juveniles and adults was higher for broadcasting species than for brooders, in contrast to the other two sites. It is possible that localized recruitment also occurred for broadcasting coral species at Los Acantilados, given that (1) local oceanographic conditions can favor local recruitment of species with planktonic larvae of relatively long duration (Jones et al., 1999; Swearer et al., 1999); (2) larvae of some broadcasting coral species prefer to recruit nearby conspecifics (Baird et al., 2003) or may have rapid development and attach only a few days after spawning (Harrison, 2006).

The similarity in species composition and abundance between adult and juvenile corals at each site in Cubagua (Rodríguez, 2004) suggests an important role for localized recruitment in these coral communities. Alternatively, differences in post-recruitment mortality among sites for some of these species may explain this result.

Conclusion

In summary, we predicted a low potential for natural repopulation in this Caribbean marginal coral community, relative to that on well-developed reefs, based on our data on coral spawning, larval settlement, and juvenile abundance. The spawning of the coral species *M. annularis* and *D. strigosa* in

Cubagua occurred on dates and times similar to those reported for well-developed reefs. Also, the proportion of coral colonies of *M. annularis* and *D. strigosa* that spawned in Cubagua was similar to or higher than values reported for well-developed reefs. However, the abundances of settlers and juvenile corals were lower in Cubagua than on well-developed reefs of both the Caribbean and the Pacific. As well as for these marginal coral communities, well-developed reefs may also face reduced potentials for repopulation in view of impending global and local changes that decrease the quality of environmental conditions for their development.

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