Spatio-temporal variability in coral (Anthozoa: Scleractinia) larval recruitment in the southern Gulf of California

By Rafael A. Cabral-Tena, David A. Paz-García, Héctor Reyes-Bonilla, Sergio S. González-Peláez and Eduardo F. Balart*

Abstract
Sexual recruitment allows corals to maintain their populations through time, reach new habitats, and repopulate areas after an environmental or anthropogenic disturbance. This study aimed to estimate the spatio-temporal variation of sexual recruitment along two areas of the southwestern coast of the Gulf of California (Bahía de La Paz and Bahía de Loreto) considered to be sub-optimal for coral development (strong seasonality and variability of sea surface temperature, incidence of hurricanes, turbidity and nutrient concentration, and low $\Omega_{ar}$). Recruitment data were compared to sea surface temperatures and with recruitment data from other sites in the Eastern Pacific that have less stressful environments. Terracotta tiles were used as collectors of larval coral propagules; tiles were immersed for three-month periods between August 2004 and September 2005. Higher recruitment was found during the warm season and coral recruits were found at almost all sites, including a vessel grounding area. Recruitment was higher in Bahía de La Paz (12.80± 29.57 ind m$^{-2}$ yr$^{-1}$) than in Bahía de Loreto (0.99± 1.49 ind m$^{-2}$ yr$^{-1}$). Coral recruits belonged to five coral genera in Bahía de la Paz, with Porites as the dominant genus (102 recruits), followed by Pocillopora (six), Psammocora (three), Pavona and Tubastrea (one each). At Bahía de Loreto, recruits of two coral genera were recorded: Porites (four) and Psammocora (one). Despite being conducted in a highly stressful environment, this study reports the second highest rate of Porites recruits in the Eastern Pacific, and the first instance of Psammocora recruits (4 ind) in the area.

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Introduction

Hertmatypic coral populations are maintained by colony fragmentation and sexual larval recruitment (Smith and Hughes 1999, López-Pérez et al. 2007, Glynn et al. 2017a). During sexual recruitment, coral release propagules (i.e. gametes or larvae), which are scattered by water flow and settle near their origin area or reach new regions, promote genetic exchange and re-colonize sites after natural or anthropogenic disturbances (Fox 2004, Miller and Ayre 2004, López-Pérez et al. 2007). Generally, the timing of coral sexual reproduction and recruitment depends on the environment, especially sea surface temperature (SST), light and nutrients, but other environmental conditions such as, sedimentation, daily light/dark periods and lunar cycles have also been related to coral reproduction in the Eastern Pacific (Glynn et al. 2017a).

In recent years, sexual recruitment has been measured to understand how coral communities survive after natural or anthropogenic disturbances. However, most of these studies have been conducted in the Indo-Pacific and Caribbean regions (Babcock et al. 2003, Heyward and Negri 2010, Ritson-Williams et al. 2010). Sporadic studies have addressed coral sexual recruitment in the Eastern Pacific. The first studies were carried out in Central America where low recruitment rates were found (0 to 0.21 ind m$^{-2}$ yr$^{-1}$, Birkeland 1977, Wellington 1982, Richmond 1985).

Studies done along the Pacific coast of Mexico showed higher recruitment rates (between 0.21 and 20.4 ind m$^{-2}$ yr$^{-1}$, Reyes-Bonilla and Calderon-Aguilera 1994, Glynn and Leyte-Morales 1997, Medina-Rosas et al. 2005, López-Pérez et al. 2007). Differences in recruitment rates between areas have been attributed to spatial and temporal variation in coral reproduction cycles and to different oceanographic conditions of each site and region (López-Pérez et al. 2007, Carpizo-Ituarte et al. 2011, Rodriguez-Troncoso et al. 2011, Chávez-Romo et al 2013, Glynn et al. 2017a), especially to SST. Sexual reproduction studies conducted along the Pacific coast of Mexico on Pocillopora damicornis, Porites panamensis and Pavona gigantea showed that egg
development activity increases during periods of high SST (Chávez-Romo and Reyes-Bonilla 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011), thus, larval recruit pulses are expected during warm seasons.

The Gulf of California is considered a stressful area for coral development, due to the large seasonal SST range which is often associated to coral bleaching and mass mortality, high incidence of hurricanes, high turbidity and nutrient concentration due to upwelling events, naturally low pH and $\Omega_{ar}$ and high pCO$_2$ (Manzello et al. 2008, Reyes-Bonilla et al. 2002, Paz-García et al. 2012a, Glynn et al. 2017b). Thus, sexual recruitment of corals in the area is expected to be low, since Glynn et al. (1991, 1994, 1996, 2000, 2011) found that sexual reproduction in Central America is more common in environments that have optimal conditions through the year, and corals living harsh environments often maintain their populations through asexual reproduction (fragmentation). Nevertheless, despite of the stressful environmental conditions of the Gulf of California, histological (Chávez-Romo and Reyes-Bonilla 2007) and genetic studies (Paz-García et al. 2012b, Aranceta-Garza et al. 2012, Pinzón et al. 2012, Chávez-Romo et al. 2013) indicate that sexual reproduction is frequent in the coral communities of the Gulf of California. However, no study has quantified coral larval recruitment in the area. To address this, our study describes the spatial-temporal variation of coral larval recruitment at 12 sites along the south-western coast of the Gulf of California, including a restored reef affected by vessel grounding. Larval recruitment data was contrasted with SST of each studied area and with recruitment data from other sites in the Caribbean, Indo-Pacific and Eastern Pacific with more favorable environments for hermatypic coral development. Due to harsh environmental conditions, coral larval recruitment is expected to be low in our study areas (especially in Bahía de Loreto) in comparison with more environmentally favorable reef sites; recruitment pulses
during the warm season are also expected because of dependency of coral reproduction cycles on SST.

**Materials and Method**

**Study sites**

Coral recruitment was measured in two areas of the southern peninsular coast of the Gulf of California, Bahía de La Paz and Bahía de Loreto, where six sites were selected in each area. In Bahía de La Paz (Figure 1a), three sites were at San Lorenzo reef. The first is a restored reef, consisting of 30 modules of concrete and rock on which fragments of *Pocillopora* spp. were cemented. This area (847 m²) was severely disturbed by the grounding of a tanker ship on September 22, 2001 (we refer to this area as Modules). An adjacent area to Modules, of 7625 m² (referred form here as Secondary) was affected by coral fragments dispersed by Hurricane "Juliette" (Balart, 2001). A third sampling site at San Lorenzo reef was a control area which was not affected by the tanker ship (referred to as Control). In addition, two sites were selected along the mainland coast (Punta Diablo and Portugués) and one at Isla Espíritu Santo (San Gabriel). In Bahía de Loreto (Figure 1b), three sites were selected at Isla Danzante (Submarino, La Biznaga and Candeleros), two at Isla Carmen (Choya and Las Palmas) and one at Isla Coronados (El Cardón).

<<Fig 1 near here.>>

**Recruitment and sea surface temperature**

To quantify the number of recruits, terracotta tiles (24 x 9.4 x 2.5 cm) were tied to the modules, rocks and/or coral colonies using a synthetic rope, at depths of 1 to 5 meters. Tiles were tied with some separation to the modules, rocks or corals in such a way that the entire tile surface was accessible for recruitment. The total available settlement area of each tile was 0.062 m². To assess spatial variation in recruitment, 30 tiles were placed in the restored area and six tiles were
placed in the other study sites. The difference in the numbers of tiles was due to the priority of
detecting recruits in the restored reef area. To estimate the temporal variation of recruitment at
each site, all tiles were removed and replaced approximately every three months. The average
exposure time of each tile was 95 days and the total exposure time was 478 days in Bahía de La
Paz and 354 days in Bahía de Loreto. In total, 150 tiles were placed in the restored reef while 24
tiles were placed in the remaining sites. Some tiles were lost in the field between sampling
campaigns due to environmental action and therefore were not considered in the analysis (Table
1).
Terracotta tiles were extracted from the sites and fixed in 4% formalin. Later, tiles were rinsed in
a solution of 20% sodium hypochlorite for 24 hours to remove all organic matter (López-Pérez et
al. 2007). A stereoscopic microscope (Olympus SZ40) was used to count and measure coral
recruits in all tiles. Identification of recruits was made using available literature (Babcock et al.
2003; Minton and Lundgren 2006). Photographs of samples of *Psammocora, Porites, Pocillopora, and Tubastrea* recruits were taken with a Scanning Electronic Microscope
(Hitachi S-3000N) to corroborate microscope identification.
Recruitment was calculated as density (ind m⁻²), dividing the number of recruits by the analyzed
surface of each site, considering each terracotta tile as an individual sampling unit. Annual
recruitment rate (ind m⁻² yr⁻¹) was calculated multiplying the calculated density for each site for
365 days and dividing it by the total exposure time of each site (478 days in Bahía de La Paz and
354 days in Bahía de Loreto). To evaluate spatial (sites) and temporal (months) differences on
recruitment, we applied a one-way ANOVA; data were normalized previously by transformation
(log x+1) to approach normality. Post hoc comparison of means was performed using Tukey’s
HSD for unequal number of samples.
During the study period, *in situ* SST was recorded every hour in all locations using underwater thermograph data loggers (HOBO Pendant Temperature; Onset Computer Corporation Bourne, MA, USA) at 3 m depth. Linear regressions were used to assess relationships between coral recruitment and average temperature of each sampled period.

**Results**

**Spatial analysis and recruit size**

A total of 115 coral recruits were recorded, 110 were recruited at Bahía de La Paz and five at Bahía de Loreto. Five coral genera were identified among recruits at Bahía de la Paz (Figure 2, Figure 3); *Porites* was the dominant genus (99 recruits, 6.54 ind m$^{-2}$), followed by *Pocillopora* (six, 0.39 ind m$^{-2}$), *Psammocora* (three, 0.19 ind m$^{-2}$), and *Pavona* and *Tubastrea* (one each, 0.06 ind m$^{-2}$). At Bahía de Loreto, two coral genera were recorded, *Porites* (four, 0.77 ind m$^{-2}$) and *Psammocora* (one, 0.19 ind m$^{-2}$).

Average recruit density at Bahía de La Paz was $16.76 \pm 38.74$ ind m$^{-2}$. The recruitment maximum was found in Punta Diablo (95 recruits, 95.77 ind m$^{-2}$) while the minimum was found in Portugués (0.90 ind m$^{-2}$). Modules, San Gabriel and Portugués had 11, three and one recruits, respectively; no recruits were found at Secondary and Control sites. All the *Pocillopora* recruits (n= 6) were found at Modules (Table 1). All sites were statistically similar except for Punta Diablo ($F_{(5,29)}= 2.57, p< 0.05$).

On the other hand, in Bahía de Loreto, three *Porites* recruits were found at Submarino (3.84 ind m$^{-2}$), one *Porites* (1.19 ind m$^{-2}$) in El Candelero, and one *Psammocora* (0.92 ind m$^{-2}$) was found in Las Palmas. No recruits were found at La Choya, El Cardon or La Biznaga (Table 2). No differences were found among sites ($F_{(5,23)}= 1.19, p > 0.05$).
Temporal analysis

Higher coral recruitment \( (F_{(4,29)}= 2.08, p< 0.05, \text{Table 2}) \) was recorded during warm seasons of 2004 \((38.04\pm 86.75 \text{ ind m}^{-2})\) and 2005 \((7.53\pm 18.44 \text{ ind m}^{-2})\) at Bahía de La Paz; recruitment pulses corresponded to maximum SST records (~28 °C; Figure 3). Minimum recruit density \((0.09\pm 0.22 \text{ ind m}^{-2})\) was found from November 2004 to February 2005, coinciding with the lowest SST record (~21°C).

The average annual recruitment rate at Bahía de la Paz was \(12.80\pm 29.57 \text{ ind m}^{-2} \text{ yr}^{-1}\). Most recruits were found at Punta Diablo, with two periods of high recruitment: the first during the period of August to November 2004 \((77 \text{ Porites recruits and three Psammocora recruits})\) and another from June to September 2005 \((14 \text{ Porites recruits}, \text{Figure 4})\). Eleven coral recruits \((\text{six Pocillopora, three Porites, one Tubastrea, one Pavona})\) were observed at Modules from June of 2004 to February of 2005 \(\text{Figure 4, Table 2}\).

The average annual recruitment in Bahía de Loreto was \(0.99 \pm 1.49 \text{ ind m}^{-2} \text{ yr}^{-1}\), the highest density of recruits settled during the warm season of 2004 \((\text{August-October 0.2 }\pm 0.6 \text{ ind m}^{-2})\) and during winter \((\text{October 2004-January 2005, 0.35 }\pm 0.59 \text{ ind m}^{-2}, \text{Figure 4})\). No recruits were settled during the warm season of 2005 \(\text{Figure 4}\). The warm season of 2004 corresponded to the maximum SST at Bahía de Loreto (~27°C). However, there were no significant differences in the number or recruits settled between the analyzed time periods \((F_{(3,23)}= 0.69, p> 0.05)\). Linear regressions between the density of recruits and SST showed no significant association \((r^2= 0.43, N= 9, p> 0.05)\).

<<Figure 4 and Table 2 near here.>>

Discussion

This is the first quantitative report of coral larval recruitment in the Gulf of California, and the second highest record of coral recruits in the Eastern Pacific (López-Pérez et al. (2007))
registered 20.4 ind m⁻² in Huatulco, Mexico). While most of coral communities in the Eastern Pacific are dominated by *Pocillopora* corals (Glynn and Ault 2000, Reyes-Bonilla 2003), most of the coral recruits recorded in this study are *Porites*. This is in accordance with previous recruitment studies in the Pacific coast of Mexico, which showed *Porites* as a common coral recruit compared to other genera (Medina-Rosas et al. 2005, López-Pérez et al. 2007). This may be associated with the reproductive strategy of each species. Some authors (Stimson 1978, Harrison and Wallace 1990) mention larvae produced by brooding species are larger and have more settlement success and a higher post-fixation survival but have a shorter swimming phase compared to larvae derived from broadcast spawner corals. In the Eastern Pacific, *Porites* corals are known to be gonochoric brooders, while *Pocillopora* and *Pavona* are sequential hermaphrodites spawners (Glynn et al. 1991, 1994, 1996, Chávez-Romo and Reyes-Bonilla 2007, Rodríguez-Troncoso 2011). This study is the first record of a *Psammocora* sexual recruit in the Eastern Pacific (Figure 3), a coral without reproductive studies along the Pacific coast of Mexico or the eastern Pacific; studies in the Indo-Pacific show that they are gonochoric spawners (Baird et al. 2009). Successful recruitment of *Porites* found in our study could be associated to their brooding type larvae. *Porites panamensis* is a known gonochoric coral that broods larvae thought the year (Glynn et al. 1996, Rodríguez-Troncoso 2011). On the other hand, pocillogorid corals can show sexual or asexual reproduction depending on local environmental conditions (Aranceta-Garza et al. 2012, Pinzón et al. 2012, Chávez-Romo et al. 2013). In our study, *Pocillopora* recruits were found in the restored area, confirming successful sexual recruitment derived from broadcast gametes in the area, as suggested by Chávez-Romo and Reyes-Bonilla (2007).

The recruitment rate found in this study is lower than reported in the Caribbean (8.0 to 79 ind m⁻² yr⁻¹) and the Red sea and Indo-Pacific regions (over 100 ind m⁻² yr⁻¹; Table 4). These contrasting
values may result from differences in species richness, coral cover, colony abundance and oceanographic conditions in each region (Spalding et al. 2001). Sexual reproduction of corals is driven by environmental factors such as temperature, light and nutrients (Glynn et al. 1991, Harrison and Wallace 1990). The highest recruitment season recorded in this study occurred during the warm months (summer) in both areas (Figure 2). This coincides with histological reports in the study area which show that during periods of high SST, reproductive activity of coral increases (Chávez-Romo and Reyes-Bonilla 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011, Glynn et al. 2017a).

In the Eastern Pacific two regions, the Gulf of California (this study) and Oaxaca (López-Pérez et al. 2007) have showed higher recruitment rate (12.8 and 20.4 ind m$^{-2}$ yr$^{-1}$ respectively) in comparison with other Eastern Pacific sites (less than 1.0 ind m$^{-2}$ yr$^{-1}$; Birkeland 1977, Guzman 1986, Glynn and Leyte-Morales 1997, Glynn et al. 2000, Medina-Rosas et al. 2005, Table 3). Results of previous coral reproduction studies done along the Pacific coast of Mexico (Medina-Rosas et al. 2005, Chávez-Romo and Reyes-Bonilla 2007, López-Pérez et al. 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011, Paz-García et al. 2012b), indicate that sexual reproduction has an important role in maintaining populations of coral in areas with high environmental seasonal variability. Studies conducted in Hawaii and the Caribbean (Stimson 1978, Szmant 1986) showed that coral under stressful environmental conditions and with high mortality rates tend to sexually reproduce several times through the year. On the other hand, Glynn et al. (1991, 1994, 1996, 2000, 2011) found the opposite for many species of corals in Central America. These authors stated that sexual reproduction is more common in optimal environments, and corals living in harsh environments often maintain their populations through asexual reproduction. The Pacific coast of Mexico has high environmental seasonal variability
(temperature, tides, dissolved oxygen, nutrients and organic matter) compared with southernmost regions of the Eastern Pacific (Glynn and Ault 2000; Fiedler et al. 2017, Glynn et al. 2017).

Thus, our results agree with Stimson (1978) and Szmant (1986) and are opposed to what has been reported by Glynn et al. (1991, 1994, 1996, 2000, 2011), nevertheless, it may be a matter of spatial scale of each study, since the works of Glynn et al. (1991, 1994, 1996, 2000, 2011) were carried out in regions very close to each other with similar oceanographic conditions between sites, compared to the Pacific coast of Mexico, where documented sites are more distant from each other and the oceanographic conditions are more contrasting.

This study complements and confirms a coral recruitment trend reported by other authors in the eastern Pacific (Reyes-Bonilla and Calderon-Aguilera 1994, Medina-Rosas et al. 2005, López-Pérez et al. 2007). This trend indicates higher recruitment rates in the northern region (Gulf of California) in comparison to lower latitude localities (e.g. Jalisco, Oaxaca, and Central America); the only outlier site is Punta Diablo (Bahía de la Paz) where a very high recruitment rate was recorded. This may be attributed to particular oceanographic or structural conditions of this site. One possible hypothesis is that oceanic currents of Bahia de La Paz converge on Punta Diablo during some part of the year (Sánchez-Velasco et al. 2006, Obeso-Nieblas et al. 2007); also, high productivity in the area has been reported (Reyes-Salinas et al. 2003, Verdugo-Díaz et al. 2014), these environmental conditions may, somehow, promote coral larval recruitment in the area, but this hypothesis deserves further scrutiny.

Acknowledgements

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whose recommendations substantially improved the manuscript.

**Literature Cited**


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Figure 1. Study sites: a) Bahía de La Paz and b) Bahía de Loreto. X are ship grounding sites.
Figure 2. Photographs of recruits. A) *Porites* Scanning Electronic Microscope 55x; B) *Pocillopora* Scanning Electronic Microscope 65x; C) *Tubastrea* Scanning Electronic Microscope 230x; D) *Pavona* Stereoscopic microscope 4x.
Figure 3. Photographs of Psammocora sp. recruit settled in this study. A) Stereoscopic microscope 2x; B) Scanning Electronic Microscope 25x; C) Scanning Electronic Microscope 90x; D) Scanning Electronic Microscope 110x.
Figure 4. Density of coral recruits and sea surface temperature (SST) per site and study period a) Bahía de La Paz and b) Bahía de Loreto.
<table>
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<tr>
<th>Location</th>
<th>Recovered settlement plates</th>
<th>Analyzed area (m²)</th>
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<th>Annual recruitment rate (ind m⁻² yr⁻¹)</th>
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TABLE 2
Density of recruits (ind m$^{-2}$) at each site in Bahía de La Paz and Bahía de Loreto by time period, no recruits were found in: Secondary, Control, Choya, El Cardon and La Biznaga, so these sites are not shown in Table. *significant differences between time periods at p< 0.05.

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<td>0.99</td>
<td>92 Porites, 3 Psammocora</td>
<td>This study</td>
<td></td>
</tr>
<tr>
<td>Eastern Pacific (Portugués)</td>
<td>0.68</td>
<td>1.12</td>
<td>1 Porites</td>
<td>This study</td>
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<td>Eastern Pacific (San Gabriel)</td>
<td>2.05</td>
<td>1.12</td>
<td>3 Porites</td>
<td>This study</td>
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<tr>
<td>Eastern Pacific (La Paz)</td>
<td>12.80 ± 29.57</td>
<td>2.52 ± 3.20</td>
<td>99 Porites, 6 Pocillopora, 3 Psammocora, 1 Pavona, 1 Tubastraea</td>
<td>This study</td>
<td></td>
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<tr>
<td>Eastern Pacific (Submarino)</td>
<td>3.84</td>
<td>0.81</td>
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<td>Eastern Pacific (El Candelero)</td>
<td>1.19</td>
<td>0.87</td>
<td>1 Porites</td>
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<tr>
<td>Region</td>
<td>Recruitment Duration</td>
<td>Recruitment Rate</td>
<td>Genus</td>
<td>Comment</td>
<td></td>
</tr>
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<td>--------------------------------</td>
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<tr>
<td>Eastern Pacific (Las Palmas)</td>
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<td>1.12</td>
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<td>Psammocora</td>
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<td>Eastern Pacific (Loreto)</td>
<td>0.99 ± 1.49</td>
<td>0.86 ± 0.21</td>
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<td>This study</td>
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<tr>
<td>Indo-Pacific (Grate barrier reef)</td>
<td>2092</td>
<td>40</td>
<td>NA</td>
<td></td>
<td>Sammarco et al. (1991)</td>
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<td>Red Sea (Eliat)</td>
<td>190</td>
<td>10</td>
<td>680</td>
<td>Pocilloporidae, 150 Acroporidae</td>
<td>Glassom et al. (2004)</td>
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<tr>
<td>Caribbean (Colombia)</td>
<td>8.04</td>
<td>47</td>
<td>34</td>
<td>Agaricia, 34 Porites, 27 Montastrea, 24 Syderastrea 21 Scolymia.</td>
<td>Vidal et al. (2005)</td>
</tr>
<tr>
<td>Caribbean (Bermuda)</td>
<td>37</td>
<td>-</td>
<td>668</td>
<td>Porites, 13 Syderastrea 1 Isophyllia</td>
<td>Smith (1992)</td>
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<tr>
<td>Caribbean (Barbados)</td>
<td>79</td>
<td>22.5</td>
<td>Agaricia, Porites, Pseudodiploria, Favia (90 recruits in total, not specified by genus)</td>
<td>Hunte y Wittenberg (1992)</td>
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