Spatial and temporal variability in juvenile coral densities, survivorship and recruitment in La Parguera, southwestern Puerto Rico

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Abstract.—Juvenile coral survivorship (the proportion of juvenile colonies surviving from t_1 to t_2) was assessed by counting, photographing and mapping all juveniles found in 2003 within random permanent 0.25m² quadrats at four depth intervals at each of four inshore and mid-shelf reefs and at deeper habitats (>18m) in two shelf-edge reefs (N=96/reef) in La Parguera, southwest coast of Puerto Rico. Quadrats were re-surveyed and photographed in 2005 to evaluate surviving juveniles, mortality and new recruits. Total number of juveniles dropped from 718 in 31 scleractinian species in 2003 to 396 in 28 species in 2005, an average juvenile survivorship of 54.8%. Mean juvenile density decreased from 1.2 (± 0.06) colonies/0.25 m² in 2003 to 0.7 (± 0.05) colonies/0.25 m² in 2005. Juvenile coral composition, relative abundances, survivorship and recruitment varied significantly across depth intervals within reefs and among reefs. Some species with high relative abundances in 2003 showed high survivorship in 2005 [*Siderastrea siderea* (28.3% and 65% respectively), *Porites astreoides* (15.1% and 55.6%), and *Diploria strigosa* (7.5% and 45.2%)]. Other taxa had relative low abundances but high survivorship [*Montastraea cavernosa* (4.6% and 66.7%) and *Stephanocoenia intersepta* (4.6% and 48.3%)]. Survivorship was significantly higher in deeper habitats at three of the four fringing reefs. Furthermore, the semi-exposed inshore, highly sedimented reefs, showed higher juvenile survivorship than the mid-shelf and shelf-edge reefs. There was no clear relationship between survivorship and reproductive mode (brooding vs. broadcast spawning) of sexual reproduction. Overall, only 78 new recruits were found in 2005.

Keywords.—Juvenile coral survivorship, recruitment, Puerto Rico, spatial/temporal variability

Introduction

Caribbean coral reefs are experiencing deterioration due to the synergistic action of natural and anthropogenic factors (Gardner et al. 2003; Aronson et al. 2003; Weil 2004). Coral reef resilience may become challenged if keystone and structural scleractinian species are significantly reduced in their live cover, abundance and reproductive output (Hughes et al. 2003; Bellwood et al. 2004; Pandolfi and Jackson 2006; Weil et al. 2009). The sudden decline of the sea urchin *Diadema antillarum*, an important grazer in shallow habitats, and the population demise of *Acropora spp*, an important reef building genus in shallow water habitats in the early 1980's (Gladfelter 1982; Lessios *et al*. 1984) brought about significant changes in the structure and dynamics of reefs Caribbean-wide (Hughes 1994; Macintyre *et al.* 2005 Aronson and Precht 2001). In the last decades,

bleaching and disease have produced further major losses of important components of the reef fauna in Caribbean reefs resulting in further changes to reef communities (Aronson and Precht 2001; Miller et.al. 2000; Smith and Weil 2004; Bruckner and Bruckner 2006; McClanahan et al. 2009; Weil and Croquer 2009; Weil et al. 2009). This pattern is predicted to continue in the near future if climate trends do not change (Bellwood et al. 2004; Weil 2004; Hoegh-Guldberg et al. 2007; Weil et al. 2009).

Sexual reproduction and survivorship of offspring are key elements to the maintenance of populations and species through time as well as being critical to recovery of depleted populations. Two modes of sexual reproduction are known for Caribbean corals: (1) broadcast spawners (hermaphrodites or gonochoric) that release gametes into the water, and (2) brooders (hermaphrodite

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or gonochoric) that breed and release live, developed larvae into the water column for a short planktonic phase (Szmant 1986; Harrison and Wallace 1990; Richmond 1997; Weil and Vargas 2009). The arrival and survivorship of these new sexually produced individuals to the populations is known as recruitment (Caley et al. 1996; Sale 1999).

Sexual reproduction in corals is sensitive to biotic and abiotic factors (Harrison and Wallace 1990; Richmond 1997; Szmant 1986). Bleaching and disease directly affect the reproductive output (fitness) of mature colonies (Szmant and Gassman 1992; Weil et al. 2009), and juveniles are susceptible to many anthropogenic and natural stressors such as sediment discharges which can produce mortality rates much greater in juvenile than adult corals (Wolanski et al. 2003), grazing (Birkeland 1977) and algae overgrowth (Vermeij 2006, Vermeij et al. 2008). A direct consequence of coral tissue loss is a significant reduction in reproductive output or, a cessation of sexual reproduction altogether if the effective reproductive size falls below the threshold for viable sexual reproduction (Szmant 1986). Larval settlement is also affected by the quality and orientation of the substratum (Harrison and Wallace 1990; Szmant 1986). Benthic microbial bio-films and crustose coralline algae (CCA) may be necessary to induce settlement in particular habitats (Morse et al. 1988; Vermeij et al. 2008).

Once the larva settles and metamorphoses into a polyp, fast asexual production of new polyps is important for its survivorship. Juvenile survivorship is highly variable across species and in space and time (Bak and Engel 1978; Rogers et.al 1984; Connell et al. 1997, Wallace 1985; Soong et al. 2003). Survivorship may be affected by habitat quality (Baird et.al. 2003; Edmunds et.al. 2004), interactions with other organisms (predation and competition) and other natural hazards (Yoshioka 2005; Vermeij et al. 2008). Population structure of gorgonians in shallow water habitats for example, was principally driven by the survivorship of recruits in Puerto Rico (Yoshioka 1996). Edmunds (2000a) also argues that the community structure of coral reefs in St. Johns (U.S.V.I) is loosely related to the distribution and survivorship of juvenile corals and events which influence the early life stages. More quantitative data on coral spat survivorship under natural conditions may elucidate processes and their interactions (e.g. competition, predation, sensitivity to physical processes, etc.) that operate under different spatial and temporal scales (Birkeland 1977).

Most of the abundant juvenile corals observed across depth habitats are usually from brooding species which have been reported to be superior competitors for space under unfavorable conditions than broadcasting species (Birkeland 1977; Bak and Engel 1979). In the Caribbean, broadcasting species are reported to have low recruitment and few surviving juveniles compared to brooding species (Rogers et al. 1984; Szmant 1986; Miller et al. 2000).

Juvenile survivorship in benthic alcyonarian species has been studied by Yoshioka and Yoshioka (1991) and Yoshioka (1996) in southwest Puerto Rico. However, no research has focused on the distribution, composition, abundance, recruitment and survivorship of juvenile scleractinian corals. The main goals of this study were: (1) to assess the variability in composition of juvenile corals across reefs and along depth gradients within reefs, (2), to assess juvenile survivorship and recruitment rates and compare them at different spatial scales, and (3) to compare species life-history strategies of successful survivors across depth gradients within reefs and between reefs along an inshore-offshore gradient.

Material and Methods

Study area

The study was conducted in the La Parguera Natural Reserve, an extensive coral reef ecosystem located on the southwest coast of Puerto Rico. La Parguera is one of the driest areas along the southwestern coast of Puerto Rico, with an insular shelf that extends 8-10 km offshore (Morelock et al. 1977, Garcia et al. 1998). Two distinct lines of emergent reefs run parallel to the coastline dividing the insular shelf into inner, middle, and outer shelf areas (Morelock *et al*. 1977). Reefs located in the inner

and middle shelf are typical fringing reef structures bordering mangrove keys with shallow areas of *Acropora* rubble and small crustose and massive coral colonies on the exposed reefs, with alcyonarian dominated platforms, and *Montastraea*-dominated fore-reefs and slopes that extends to 15-20 m depth. Reefs in the outer shelf occur below 18 m, with conspicuous spur and groove formations that extend over the platform edge. Reef localities included two inner fringing reefs close to shore [Pelotas (17° 57.442′ N; 67° 04.176′ W) and Enrique (17° 56.658′ N; 67° 02.213′ W)], two fringing reefs at the mid-shelf [Media Luna (17° 56.093′ N; 67° 02.931′ W) and Turrumote (17° 56.097′ N; 67° 01.130′ W)] at the mid-

shelf, and one shelf-edge spur and groove reef [Weinberg (17° 53.429′ N; 66° 59.320′ W)] and a coral community area over consolidated pavement [El Hoyo (17° 52.630 N; 67° 02.579 W)] (Fig. 1).

Juvenile and recruit surveys

Juvenile abundance and survivorship was assessed along an inshore-offshore gradient utilizing a stratified sampling with a two-way factorial design with depth intervals (habitat) and reef localities. Juvenile scleractinians were identified to genus/species level to the degree possible based on criteria established by Szmant (1986) and Bak and Engel (1977). Sexually produced juvenile
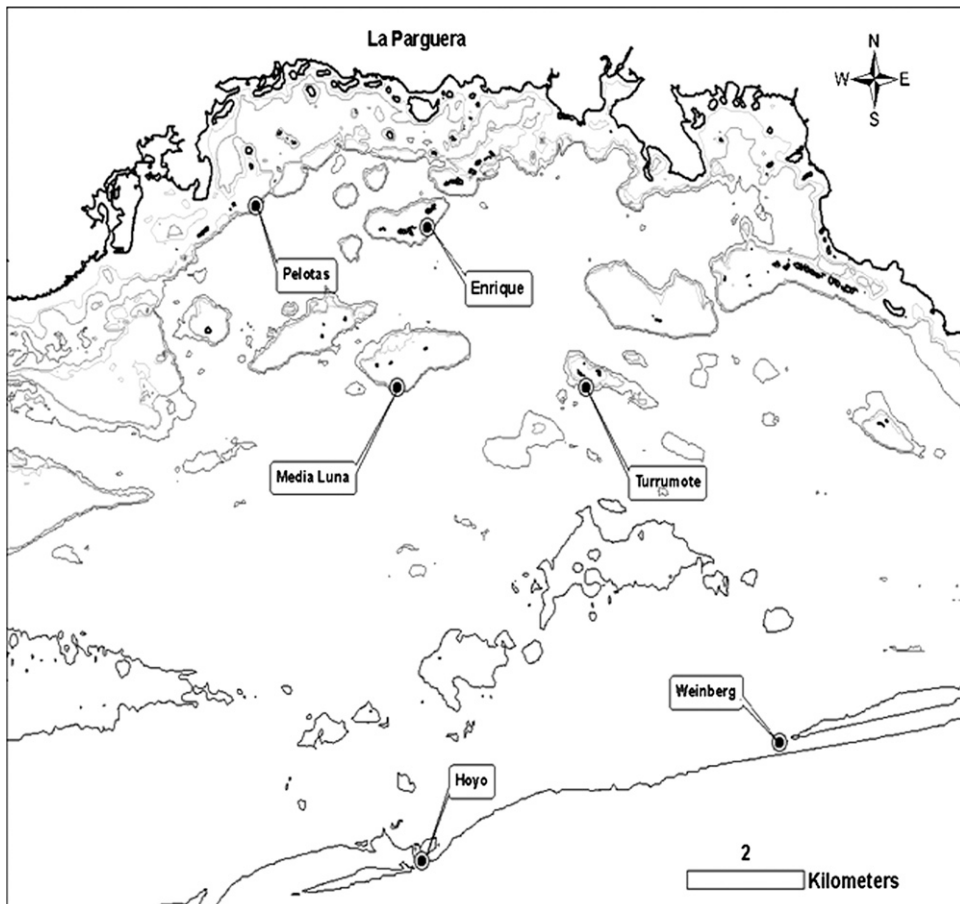

Fig. 1. Map of La Parguera Natural Reserve showing the location of study sites along an inshore-offshore gradient. Pelotas and Enrique are located in the inshore zone, Media Luna and Turrumote are located in the mid-shelf zone, and Weinberg and El Hoyo in the shelf-edge zone.

colonies can be distinguished from isolated live, fragments because they are smaller than most post-fission ramets resulting from partial mortality and they belong to a different species from that of the substratum on which they are growing (Hughes and Jackson 1985). Depending on the species and its average size/area, a criterion of minimum size was used. For example, colonies < 5 cm in diameter for large-sized species (*Montastraea* spp. *Colpophyllia natans*, *Diploria* spp., etc.), and < 2 cm for medium-small-sized colonies (*Siderastrea siderea*, *Porites* spp., *Mycetophyllia* spp. etc.), were considered as sexually produced juveniles if there were no signs of being a surviving ramet of partial mortality. New recruits were those new juveniles found in the second survey (t_2) that were not found in the first surveys (t_1) and that were usually under 3 cm in diameter. For every occasion that a potential juvenile was found, careful observations of the underlying substratum and surroundings were made, and they were photographed and mapped. Juveniles in taxonomically difficult genera were pooled together at the genus level, for example, all deeper water agaricids (*Agaricia lamarcki*, *A. grahamae*, etc) were grouped as *Agaricia* spp, and all shallow water agaricids (*Undaria agaricites*, *U. humilis*, *U. danae*, etc.), were pooled as *Undaria* spp. (Stemann 2002).

After fanning away loose sediment within each quadrat, all juveniles were identified (genus/species) and counted in each of six randomly placed quadrats (0.5 x 0.5m = 0.25 m²) along the sides of each of four 20m long transects at each of four depth intervals (0-3m, 3-5m, 5-10m, >15m) (N = 24 quadrats per depth and 96 per reef) at each of the two inshore and two mid-shelf fringing reefs. At the shelf-edge reefs (Weinberg and El Hoyo), all 96 quadrats were located below 15m depth. Each 0.25 cm² quadrat was photographed with an Olympus C-4000 digital camera in UW Housing and juvenile locations were mapped on plastic underwater paper. The underwater map with the position of the different juveniles for each quadrat was transferred to the digital photo of the quadrat using Adobe Photoshop (Adobe Inc.), and each set of maps was laminated so it could be taken underwater as a reference to relocate juveniles. The same quadrats were surveyed using the same methods as utilized in the summer-fall of 2003. New juvenile colonies (i.e. recruits) were also recorded.

Data analysis

Differences in juvenile coral densities between August 2003 and August 2005 among depth intervals within reef sites were tested with a repeated measurement ANOVA (RM ANOVA) after log (x+1) transformation of the data. (However, it should be noted that the RM ANOVA results must be interpreted with caution since the number of surviving colonies cannot exceed the initial number of colonies.) Differences in survivorship of juvenile corals were compared among sites with a G-test of independence contingency table (site x [dead vs. alive]) pooled by genera and then for the most common species (Edmunds 2000). Differences in survivorship based on reproductive mode (e.g. spawners vs. brooders) among reef sites and depth intervals were tested with correspondence analysis and contingency table using the G-test.

Results and Discussion

A total of 718 juvenile colonies belonging to 31 scleractinian species were counted in the 576 quadrats surveyed in 2003 with an overall mean juvenile density of 1.2 ± 0.06 col/0.25m². This represents a high juvenile density compared to reports from other Caribbean localities (Chiappone and Sullivan 1996; Edmunds 2000a,b; Edmunds et al. 2004). One possible explanation is a natural preference of settlers to natural limestone, substrata (conditioned crustose coralline algae, microbial biofilm, etc.) compared to the artificial substrata (terracotta, fiberglass, cement) often used in recruitment studies. However, it is also likely that these results represent successful reproductive events and/or high juvenile survivorship in the recent past. More experimental data is needed to support either of these hypotheses.

A total of 394 surviving juvenile colonies were found in the quadrats in 2005, which represents an overall juvenile survivorship

of 54.9% for the six reefs surveyed. The overall mean density of live juvenile corals decreased significantly from 1.2 (± 0.06) in 2003 to 0.7 (± 0.05) col/0.25m² in 2005 (RM ANOVA, p<0.05) due to juvenile mortality by different factors over the two years.

Relative abundances of the different species varied across habitats within reefs, across reefs and temporarily. Most species with a higher mean relative abundance (%) in 2003, at the start of the study, showed a higher relative abundance of surviving juveniles
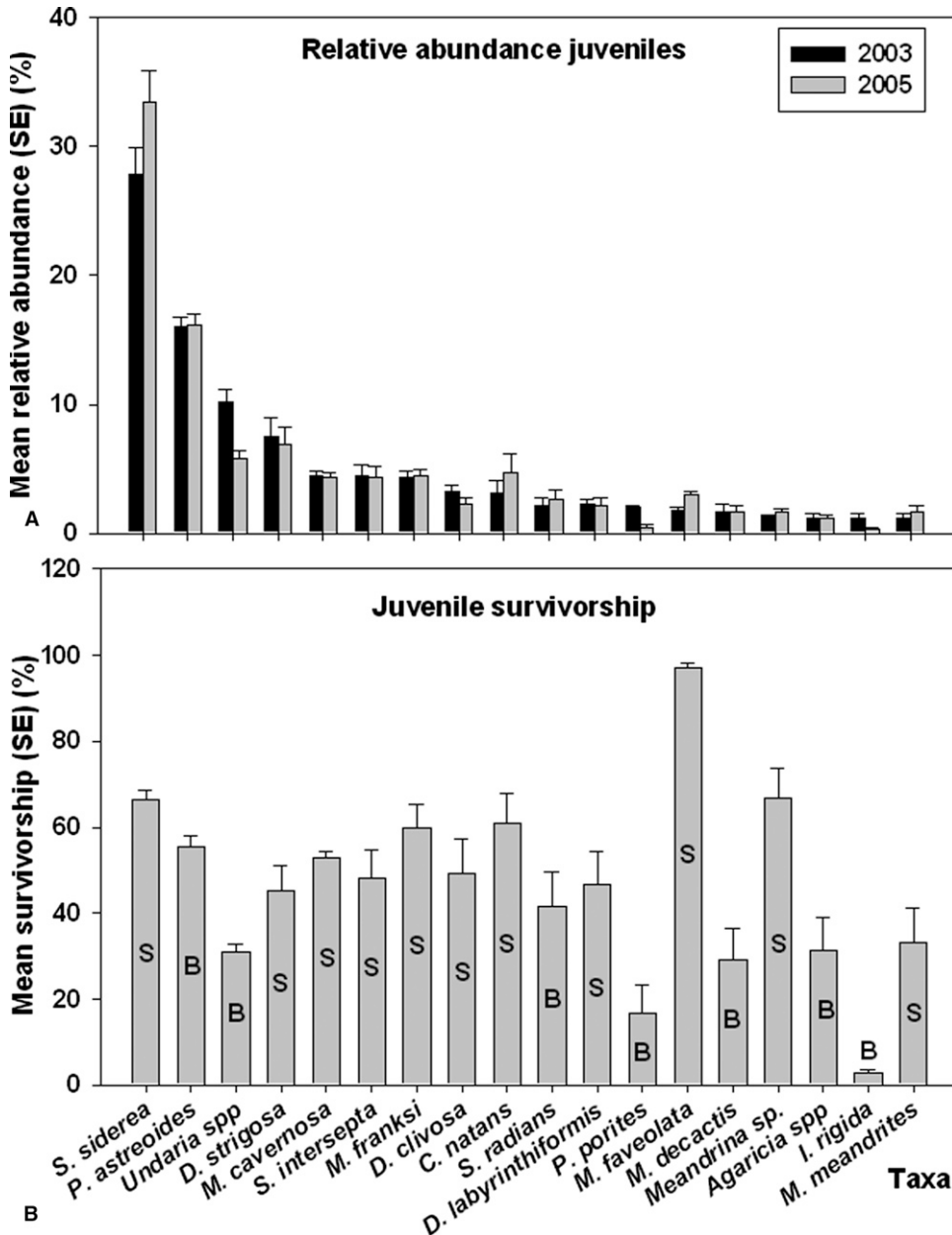

Fig. 2. Relative mean (SE) abundances of scleractinian juvenile colonies (%) for the six reefs surveyed in 2003 and 2005 for the most abundant species (A), and their survivorship (%) and their reproductive mode (letters inside the bars: S = spawners and B = brooders) in 2005.

in 2005 (Fig. 2A). Those with higher abundances in the two sampling years include *Siderastrea siderea* (27.9% and 33.5 % respectively), *Porites astreoides* (16.1% and 16.2%), *Undaria* spp (10.2% and 5.8%), *Diploria strigosa* (7.5% and 6.9%), *Montastraea cavernosa* (4.4% and 4.3%), *Stephanocoenia intersepta* (4.5% and 4.4%), and *M. franksi* (4.4% and 4.4%) (Fig. 2A). Most species overall, showed a moderate to high survivorship, with *Montastraea faveolata*, the main reef-building species in reefs of La Parguera, showing the highest mean juvenile survivorship, followed by *Meandrina* sp., *Siderastrea siderea*, *Colpophyllia natans* and *M. franksi* (Fig. 2B).

Nine of the 14 species with relative abundances higher than 1.5% were (reproductively) broadcasters (i.e. release their gametes into the water column for external fertilization and larval development), three of these were gonochoric species (*M. cavernosa*, *S. siderea* and *S. intersepta*) and the remainder were hermaphrodites. The remaining five species were brooders (i.e. internal fertilization and partial or total larval development) and hermaphrodites (Table 1, Fig. 2B).

Six of the species with higher survivorship were spawners, and in general, brooders showed lower survivorship compared to spawners during this period (Fig. 2B). Thus, under the conditions of this study, there was no clear pattern between overall juvenile abundances and mode of reproduction, contrary to long-held ideas that brooders in general have higher recruitment and survivorship than spawners (Harrison and Wallace 1990; Szmant 1986).

At Enrique Reef, 74 of the 94 juvenile corals surveyed in the first census were alive in 2005, a high survivorship (78.73%). No significant differences in mean juvenile densities were found for the reef between 2003 and 2005 (1.0 ± 0.3 to 0.8 ± 0.2 col/0.25m^2) (RM ANOVA, F = 9.93, df = 1, p<0.01) or for each depth-intervals (Figs. 3A, 4A). Survivorship was high at all depths with 11 of the 16 juvenile species showing 100% survivorship in 2005, four between 40 and 82% survivorship and one species, *Scolymia cubensis* with no survivorship (Table 1, Fig. 3A).

At Pelotas, the other inner-shelf reef, the number of juveniles decreased from 89 in 2003 to 43 in 2005, a moderate survivorship

TABLE 1. Summary table for juvenile relative abundances (%) (AB) in 2003, survivorship (%) (SU) and new recruits (RE) in 2005 for the most common species in the six reefs surveyed.

| Juvenile Species	Enrique AB %	Enrique SU %	Enrique RE	Pelotas AB %	Pelotas SU %	Pelotas RE	Turrumote AB %	Turrumote SU %	Turrumote RE	M. Luna AB %	M. Luna SU %	M. Luna RE	Weinberg AB %	Weinberg SU %	Weinberg RE	El Hoyo AB %	El Hoyo SU %	El Hoyo RE
S. siderea	40	82	4	9	50	-	36	78	3	18	58	16.	30	76	5	35	55	4
P. astreoides	23	64	2	16	50	-	13	39	1	12	47	9	18	78	2	15	56	1
D. strigosa	7	100	-	13	42	-	1	50	-	22	34	1	-	-	-	1	0	-
D. clivosa	5	100	-	7	0	-	4	80	-	4	17	-	-	-	-	-	-	-
Undaria spp	5	40	-	13	25	5	16	36	-	5	13	1	17	38	-	5	33	1
M. cavernosa	3	67	-	2	50	1	1	50	-	7	40	1	8	60	1	5	50	-
D. labyrinthiformis	2	100	-	2	67	1	4	0	-	1	0	-	2	20	1	-	-	-
P. porites	2	100	-	2	0	-	4	0	-	1	50	3	2	0	-	1	0	-
M. faveolata	2	100	-	1	100	-	4	83	-	1	100	-	1	100	-	2	100	-
S. intersepta	2	100	-	-	-	-	-	-	4	3	25	-	9	73	-	13	44	3
C. natans	1	100	-	15	77	-	-	-	-	2	67	1	-	-	-	1	0	-
M. franksi	1	100	-	4	75	-	5	0	-	2	67	1	7	56	-	7	63	-
S. radians	1	100	-	-	-	-	9	83	-	3	25	-	-	-	-	1	0	-
Meandrina. nsp	1	100	-	-	-	-	2	67	-	1	100	1	1	100	-	2	33	1
M. ferox	1	100	-	-	-	-	1	0	-	1	0	-	-	-	-	1	0	-
S. cubensis	1	0	-	1	0	-	-	-	-	1	0	-	-	-	-	-	-	-
M. meandrites	-	-	-	4	0	-	1	100	-	2	33		-	-	1	-	-	1
Agaricia spp	-	-	-	1	0	-	-	-	-	5	25		1	100	-	-	-	-
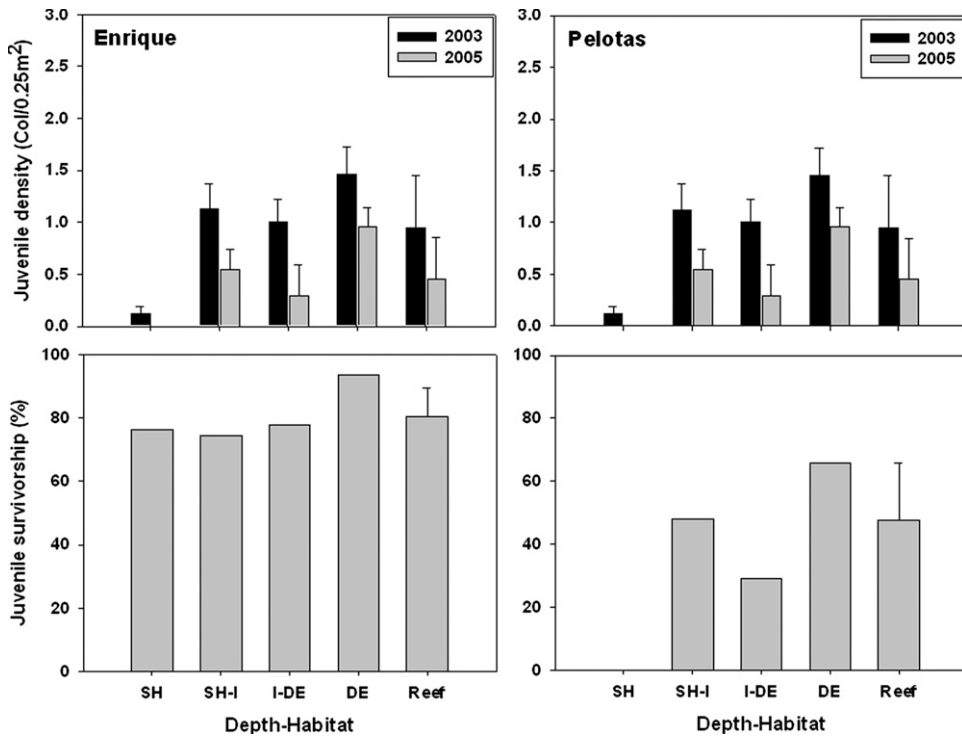
Fig. 3. Spatial (across depths) and temporal (between 2003 and 2005) variability in juvenile mean densities (col/0.25m^2) and survivorship (%) for each of the four depths (SH = shallow (0-3m); SH-I = shallow-intermediate depth (4-8m); I-DE = intermediate depth (9-13m); and DE=deep (>15m) for the two inshore reefs, Enrique and Pelotas (A) and the two mid-shelf reefs Turrumote and Media Luna (B).

(48.3%). Average juvenile coral density decreased significantly from 0.9 ± 0.5 to 0.5 ± 0.3 col/0.25m^2 (RM ANOVA, F = 32.90, p>0.05) (Figs 3A, 4A) but no significant differences in densities between 2003 and 2005 were found for any of the depths (RM Anova, F = 2.14, p=0.09) (Fig. 2A). Survivorship was higher in deeper compared to shallower habitats (4 x 2 contingency table, G = 11.90, df = 3, p<0.05) (Fig. 5). Species with the highest juvenile survivorship included *Montastreaea faveolata* (100%), *Colpophyllia natans* (77%), *M. franksi* (75%), *Diploria labyrinthiformis* (67%), *Porites astreoides*, *Siderastrea siderea* and *M. cavernosa* (50%) (Table 1, Fig. 3A).

At Turrumote, a total of 82 of the 142 juvenile colonies observed in August 2003 were found alive in 2005, a relatively high survivorship of 58%. There was a significant decrease in the mean density of juveniles from 1.5 ± 0.4 to 0.9 ± 0.1 col/0.25m^2

(RM ANOVA, F = 7.38, p<0.05) (Figs 3B, 4A). Significant lower juvenile densities were found for the shallow-intermediate depth (5m) (Fig. 3B) (RM ANOVA, F = 0.52, p = 0.66). Juvenile coral survivorship was high at the shallow (79.5%) and deep habitats (79.6%) (4 x 2 G = 47.31, df = 3, p<0.05) compared to the intermediate depths. *Meandrina meandrites* showed that highest survivorship (100%), followed by *M. faveolata* and *Siderastrea radians* (83%), *Diploria clivosa* (80%) and *Siderastrea siderea* (78%).

Only 58 of the 147 juvenile corals observed in Media Luna in 2003 were found alive in 2005, the lowest survivorship (39%) among the fringing reefs. Mean juvenile densities also significantly decreased from 1.5 ± 0.4 in 2003 to 0.6 ± 0.3 col/0.25m^2 in 2005 (RM ANOVA, F = 66.44, df = 1; p<0.05) during the period (Figs 3B, 4A). Significant lower densities were found in 2005 compared to 2003 for the two shallower habitats
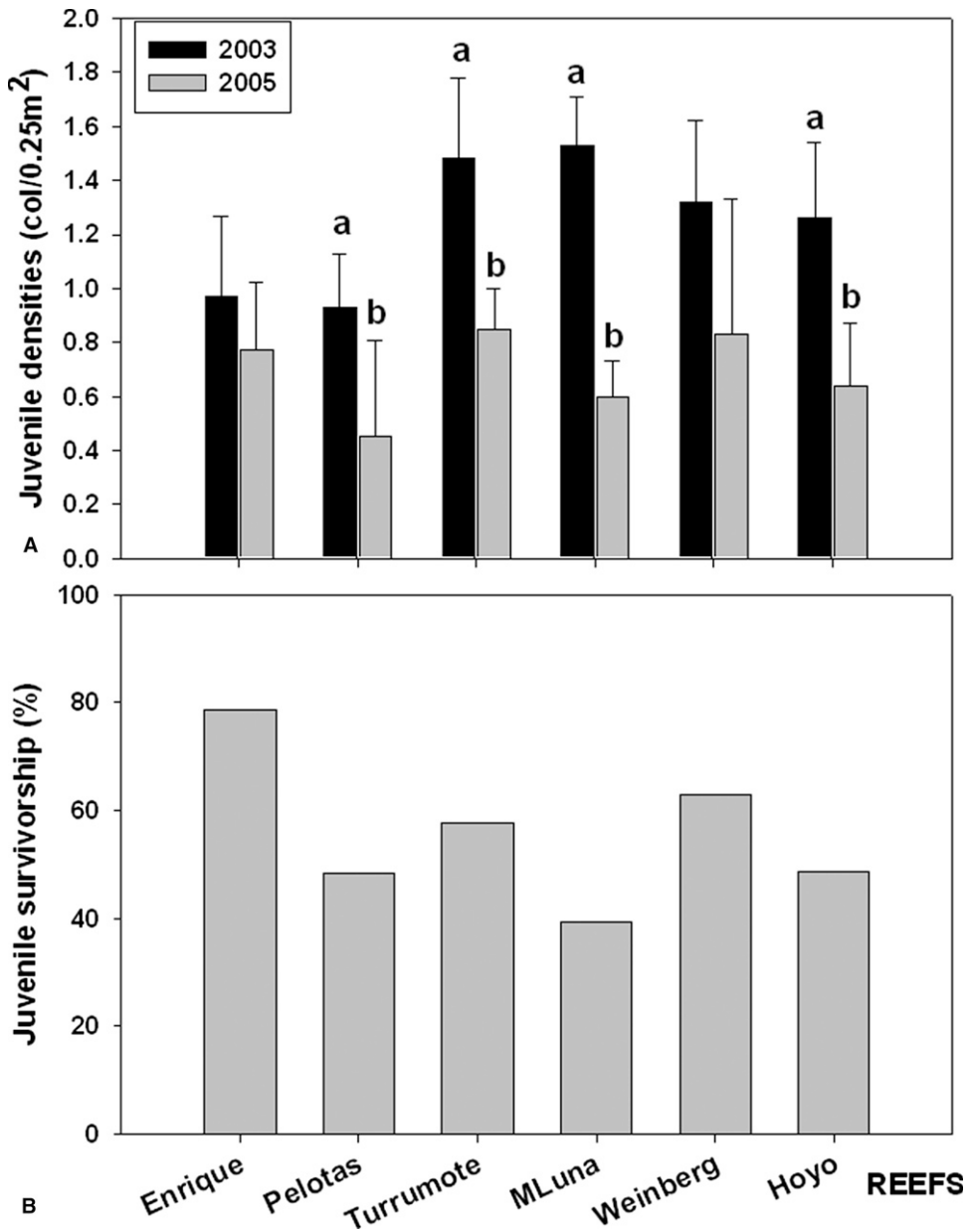
FIG. 4. Spatial and temporal variability in overall mean juvenile densities (col/0.25m^2) in the six reefs surveyed in La Parguera in 2003 and 2005 (A) (letters above columns indicate significant difference between years for that reef), and overall survivorship of juveniles at each reef along the inshore-offshore gradient in 2005 (B).

(1.5 to 0.5 col/0.25m^2 for the shallow depth (3m) and 1.95 to 0.37 col/0.25m^2 for the shallow-intermediate depth (5m)] (RM ANOVA, F = 4.35, df = 3; p<0.05). No significant temporal differences were found for the intermediate deep habitat (10m) (1.0 to 0.5 col/0.25m^2) and the deep habitats (15m) (1.7 to 1.0 col/0.25m^2). Survivorship was higher at the two deeper habitats compared to the shallower (Fig. 2B). *Montastraea faveolata* and *Meandrina* sp. showed the highest survivorship (100%), followed by *M. franksi*,
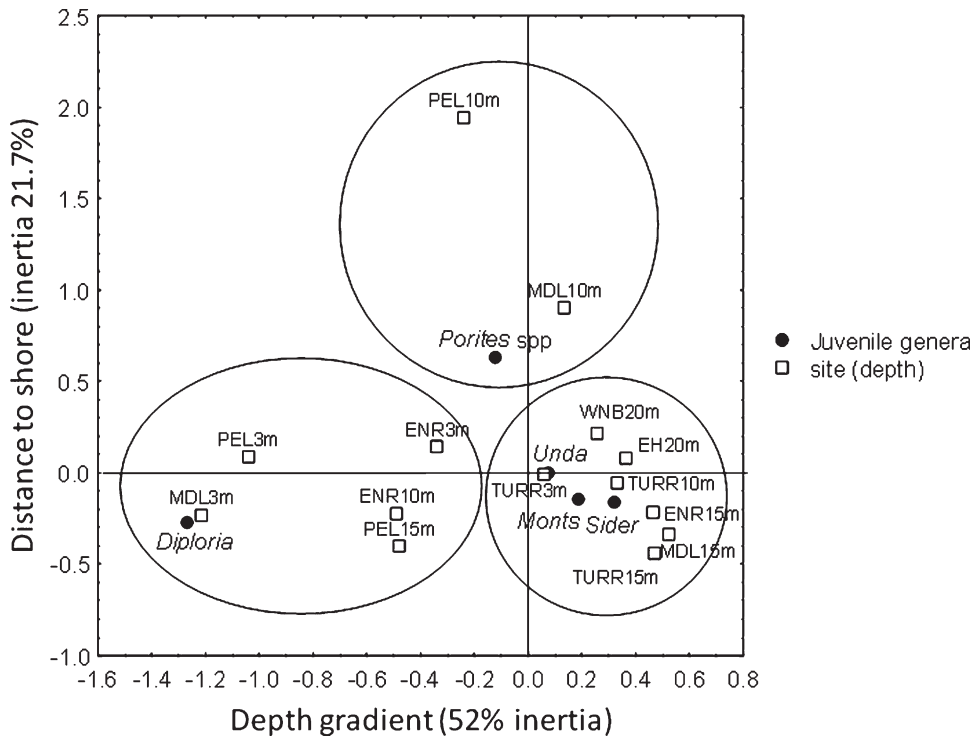
Fig. 5. Correspondence analysis (CA) biplot showing the ordination of juvenile genera in 2005 along the first dimension which corresponds to a depth gradient and a second axis which represents distance to shore (inshore-mid-shelf reefs). (EH = Enrique; PEL = Pelotas, TURR = Turrumote, MDL = Media Luna, Unda = *Undaria*, Monts = *Montastraea*, Sider = *Siderastrea*).

C. natans and *Porites porites* (67%, 67% and 50% respectively). Overall, survivorship was low at shallow depths (36%) and relatively high at intermediate deep and deeper areas habitats (54.2% and 57.5 % respectively) (4 x 2 contingency table, G = 10.74, df = 3, p<0.05).

At the shelf-edge reefs, 62% of juvenile corals were alive in 2005 at Weinberg and only 48% juvenile corals survived at El Hoyo (Fig. 4A). Juvenile coral densities decreased significantly from 1.3 col/0.25m² in 2003 to 0.7 col/0.25m² in 2005 at the outer shelf zone (RM Anova, F = 76.48, p<0.05). Proportions of live juvenile corals were significantly higher at Weinberg compared to El Hoyo (2 x 2 contingency table, G = 5.11, df = 1, p<0.05). At Weinberg, overall survivorship was higher than at El Hoyo and was similar to the mid-shelf reefs (Fig. 4B). *Montastraea faveolata*, *Meandrina* sp. and *Agaricia* spp. had the highest survivorship (100 %) followed by *Porites astreoides* (78%), *Siderastrea siderea* (76%) and *Stephanocoenia intersepta* (73%) (Table 1) at Weinberg. *Montastraea faveolata* (100%) and *M. franksi* (67%) had the highest survivorship, followed by *P.astreoides* (56%), *S.siderea* (55%) and *M. cavernosa* (50%) at El Hoyo (Table 1, Fig. 4B).

Overall, juvenile densities decreased significantly from 2003 to 2005 (RM ANOVA, F = 120.78, p<0.05). There was no pattern in the level of survivorship/mortality across reefs and zones along the inshore-offshore gradient. The lowest overall juvenile mortality was found at Pelotas, an inshore reef usually affected by high sedimentation and turbidity. The other less protected inshore reef, Enrique, showed high survivorship. Media Luna and El Hoyo also had higher mortalities compared to the other reefs surveyed in the mid-shelf and shelf-edge zones (Turrumote and Weinberg respectively) (Fig. 3B).

TABLE 2. Correspondence Analysis (CA) scores of reef site with respect to reef zones and depth intervals based on the juvenile colonies genera (*Diploria*, *Montastraea*, *Porites*, *Siderastrea* and *Undaria*) alive in August 2005.

CA scores	Reef site (depth)	Reef zone	depth
−1.21762	MDL3m	Mid	shallow
−1.04092	PEL3m	Inner	shallow
−0.48980	ENR10m	Inner	intermediate
−0.48234	PEL15m	Inner	deep
−0.34102	ENR3m	Inner	shallow
−0.24167	PEL10m	Inner	intermediate
0.05819	TURR3m	Mid	shallow
0.13438	MDL10m	Mid	deep
0.25412	WNB20m	Outer	deep
0.32960	TURR10m	Mid	intermediate
0.36141	EH20m	Outer	deep
0.46459	ENR15m	Inner	deep
0.46789	TURR15m	Mid	deep
0.52296	MDL10m	Mid	intermediate

TABLE 3. Contingency table showing the total number of juvenile colonies alive of brooders and spawners across depth intervals. Significant differences were found among the survivorship of brooders and spawners compared across depth intervals (G = 25.54, df = 4, p<0.05).

Depth(m)	Brooders	expected	Spawners	expected	Total
3m	33	115	66	276	99
5m	54	215	85	377	139
10m	42	156	52	205	94
15m	24	76	116	551	140
20m	77	334	171	879	248
Total	230	896	490	2288	720

Generic survivorship (e.g. *Diploria*, *Montastraea*, *Porites*, *Undaria, Siderastrea*) showed significant differences among sites (6 X 5 contingency table, G = 111.93, df = 20, p<0.05) and among depth intervals (G = 149.91, df=16, p<0.05). The Correspondence Analysis (CA) was able to account for 74% of the total variability in the first two axes. Based on the (CA) scores (Table 2), the first axis showed an ordering of juvenile coral genera with respect to depth gradients and the other axis to an inshore-offshore gradient. It can be inferred that *Montastraea* spp, *Undaria* spp and *Siderastrea* spp, survived to a greater degree in deeper habitats (15m>), while *Porites* spp., and *Diploria* spp., showed higher survivorship at the inshore shallow reef habitats. Overall survivorship of juvenile corals based on their reproductive strategies (i.e. spawners and brooders) showed significant differences related to depth (2 X 5 contingency table, G = 25.54, df = 4, p<0.05) (Table 3) but not among reef sites (2 x 6 contingency table G = 5.52, df = 5, p> 0.05). It was 4 times more probable for spawners to survive in deep habitats (15m), while survivorship for brooders was one time more likely at the shallower (3m) habitat and two times at the deepest and far away (shelf-edge) habitat (20m).

The overall higher survivorship in deeper habitats and higher juvenile mortality at the shallower and intermediate depths contrast with results from the Florida Keys where no correspondence between survivorship and depth was found (Edmunds et al. 2004). There are many biological and environmental factors regulating juvenile survivorship and their impact and interactions vary across spatial and temporal scales (Bak and Engel 1978; Rogers et al. 1984; Connell et al. 1997, Wallace 1985; Soong et al. 2003). Juveniles in shallower habitats are more exposed to greater variability in environmental conditions such as water temperature, UV radiation, storm surge and wave action, substratum stability, salinity fluctuation, sediment bed load, sedimentation, etc. that could increase mortality rates (Edmunds 2000a,b, 2005; Edmunds et al. 2004; Carpenter and Edmunds 2006). The shallow habitats at the inner and mid-shelf reefs were subjected to all of these factors as a result of Hurricanes Ivan and Jeanne which could have led to some of the juvenile mortality observed during this study. Habitats with high frequency and/or intensity of disturbances tend to have lower biological diversities than those with intermediate disturbance regimes (Connell, 1978; Connell et al. 1997).

Recruitment

There were only 78 new recruits within the quadrats in 2005 (Table 1), an overall density of 0.14 col/0.25m². This represents a low successful recruitment for two years of reproductive activity, possibly an indication of high settler mortality, fitness loss (lower

reproductive output) in the major reef-building species, or a combination of these. During the last decades, major reef-building and other coral species in this area have been affected by colony and tissue mortalities due to disease and bleaching (Weil et. al. 2006, Weil and Croquer 2009; Croquer and Weil 2009a,b; Weil et al. this issue), and there is evidence of reduced fecundity in colonies affected by bleaching and/or diseases (Szmant and Gassman 1990; Weil et al. 2009).

The mid-shelf reef Media Luna showed the highest recruitment as compared with the other reefs even though juvenile mortality from 2003-05 was the highest (lowest survivorship) over this period (Fig. 4B and Fig. 6A). Weinberg reef showed the second highest recruitment. All other reefs had similar recruitment (Fig. 6A, Table 1). Overall, the mid-shelf reefs had a significantly higher mean abundance of
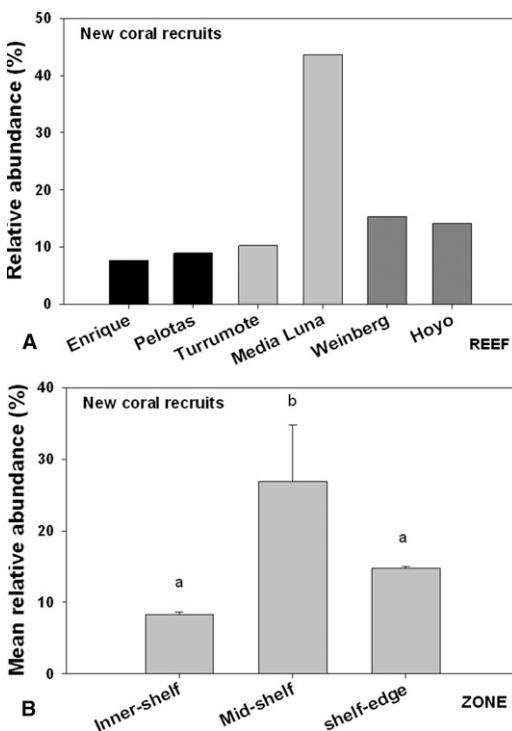

FIG. 6. Relative abundance (%) of new coral recruits in each of the six reefs surveyed in La Parguera (A) (reefs oriented from east to west and inshore to offshore), and the average recruit abundance for the three zones (average between the two reefs in each zone) along the inshore-offshore gradient (B).

new recruits compared to the shelf-edge and inner reefs (Fig. 6B) (ANOVA, $p<0.05$). A more complex reef structure with higher coral diversity and live cover (Weil unpubl.) might favor the recruitment and survivorship of coral spats in these intermediate reefs. Densities and composition of coral recruits have been shown to differ among seasons and between years, often by several orders of magnitude (e.g., Wallace 1985).

Species showing the highest number of recruits were those less susceptible to bleaching (McClanahan et al. 2009) and disease (Weil 2004; Weil et al. this issue) and, with the exception of *Porites astreoides*, they had the lowest abundance at different reef localities (Table 1). Similarly to survivorship results, there was no clear pattern between successful recruitment and mode/pattern of sexual reproduction as two gonochoric-spawners, *Siderastrea siderea* (n=32 new recruits), and *S. intersepta* (n=7) as well as two hermaphroditic-brooders, *Porites astreoides* (n=15) and *Undaria* spp (n=7) showed the highest number of recruits (Table 1). The species with the highest number of recruits were also among the most abundant in these reefs (Weil unpubl.). Successful recruitment could be better expressed as the number of recruits relative to the number of adult colonies; i.e. recruits/adult. A rare species may have high numbers of recruits/adult but these numbers may be low compared to an abundant species (Yoshioka personal communication).

Brooders may be efficient in colonizing the substratum but they may suffer more severely from post settlement mortality, and spawners may not be as efficient during settlement but following settlement, they have higher survival. Although some of the common, large, reef-building spawning species (*Montastraea faveolata, M. franksi, Diploria strigosa* and *Colpophyllia natans*) had moderately high survivorship (Table 1), the number of new recruits of these species was low in 2005. *Montastraea faveolata* colonies have lost significant areas of live tissue due to Caribbean yellow band and white plague disease in the last 10 years and were highly susceptible to the bleaching events of 1998, 2003 and 2005 (McClanahan et al. 2009; Weil et al. 2009) which probably affected their fitness (reproductive output) and reduced

the probability of successful recruitment in recent years (Weil et al. 2009). These corals are long-lived organisms which reproduce annually and many of these reproductive events could fail due to unfavorable conditions for larval survivorship, successful settlement and/or post-settlement survival. One or two successful reproduction years over their life duration might be sufficient to maintain populations, and therefore, their reproductive and/or recruitment success should probably be measured over years or decades.

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