Abundance, Composition and Survivorship of Juvenile Corals in the Southwestern Puerto Rico, La Parguera

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A thesis submitted on partial fulfillment of the requirements for the degree of

MASTER OF MARINE SCIENCE
(Biological Oceanography)

UNIVERSITY OF PUERTO RICO
MAYAGÜEZ CAMPUS
2006

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Abstract

The distribution, abundance, species composition and survivorship of juvenile corals over natural substratum were quantified in 6 reefs along the insular shelf off La Parguera Puerto Rico from August 2003 to August 2005. Juvenile corals were measured in 6 1m^2 quadrats randomly placed along four 20 m long transects in four depth intervals (n = 96 quadrats /reef). Survivorship was estimated using six quadrats of 0.25 m^2 randomly placed along the same 20 m long transects in each reef. Spatial heterogeneity was estimated with the chain method along each transect line. Spatial variability of juvenile densities was determined with a nested ANOVA model I with quadrats nested within transects, transects within depths, depths within reefs and reefs within zones. A total of 882 juvenile colonies from 26 species were counted in an area of 576m^2 (1.5 ± 0.11 col/m^2). Juvenile densities increased from shallow habitats (lowest densities) to intermediate and deep habitats within reefs. The spatial scales that explained 85% of the total variability in juvenile distribution was found between the intermediate scales transects (meters) and depths (hundred of meters). Survivorship and recruitment were tested with a Repeated Measures ANOVA and G-test of independence. Survivorship was higher in the intermediate (50%) habitat compare to shallow and deeper habitats. The most abundant genera were *Diploria*, *Montastraea*, *Porites*, *Siderastrea* and *Agaricia* and were distributed across and inshore offshore gradient. Juvenile abundances and survivorship were higher at intermediate depths 2.45 (C.I: 2.06-2.92) compare to the shallow 1.31 (C.I: 1.18-1.46) col/m^2 and deep intervals 1.81 (C.I: 1.65-1.99) col/m^2. New recruits were observed for all the six reefs survey and Media Luna show a total of 30 new individuals among all reefs. Coral recruitment and juvenile survivorship in southwestern Puerto Rico was variable at spatial and temporal scales. This variation was explained by factors such as life history strategies, settlement orientation, the interaction with reef organisms and the possible effects of swells produced by passing hurricanes during the study period.

Resumen

En este estudio se cuantificó la abundancia, composición y supervivencia de juveniles de coral sobre el sustrato natural desde agosto de 2003 hasta agosto de 2005 a lo largo de la plataforma insular en La Parguera Puerto Rico. Se utilizaron seis cuadratas de 1 m^2 colocadas a lo largo de 4 transectas de 20 metros de largo, en cuatro intervalos de profundiad en seis arrefices. La supervivencia de juveniles de coral se midió en seis cuadratas de 0.25 m^2. Se utilizó un modelo anidado Anova para medir la variabilidad espacial en las densidades de juveniles de coral en 5 escalas espaciales (cuadratas anidadas en transectas, transectas en profundidades, profundidades en arrecifes y arrecifes en zonas). Un total de 882 juveniles de coral pertenecientes a 26 especies de corales escleractinios fueron contados en un area de 576m^2 indicando una densidad de 1.5 ± 0.11 col/m^2. El 85 % de la variabilidad espacial en la densidad de juveniles de coral fue explicado por transectas y profundidades. La escala temporal se midió con un modelo repetido de Anova utilizando la variable tiempo como la medida repetida. La densidad de reclutas tiende a disminuir desde la zona arrecifal interna hacia la zona arrecifal externa. Sin embargo, los reclutas de coral mostraron mayor sobrevivencia en los afrrecifes internos e intermedios. Los generos que mostaron mayor supervivencia, entre arrecifes y zonas fueron *Diploria* spp, *Montastraea* spp, *Porites* spp., *Siderastrea* spp., *Agaricia* spp. Por lo tanto, para este estudio la abundancia, composicion y supervivencia de juveniles de coral fue variable en la escala temporal y espacial a lo largo de un gradiente de profundidad. Dentro de las posibles causas que puedan estar aportando a es tas variaciones son el transporte de sedimento en el plano horizontal y la inclinación del sustrato. Asi como las marejadas causadas por el paso de los huracanes Jeanny e Ivan al Sur de la Isla de Puerto Rico.

Acknowledgements

I like to thanks Dr. Ernesto Weil, my chairman, for his patience, guidance, trust and support all these years. Dr. Paul Yoshioka for his advice and guidance at any time and Dra. Nilda Aponte for her support. Also, I would like to thanks, Dr. Alfonso Aguilar, Dr. Francisco Pagán and Dr. Aldo Cróquer for their helpful hints in the statistical analysis. Godoberto Lopez for his logistical support with the diving equipment, Luis Lugo "Vitamina" for his good will and positive vibration and to my friends and student fellows: Michael Nemeth, Michelle Sharer, Katie Flynn, Elizabeth Mclean, Hector Ruíz, Tony Marshack and Idelfonso Ruíz for all the great moments and field work. This study was funded by NOAA-CRES and logistic support by the Department of Marine Science.

I dedicate this work to the universal power of peace and love, to my lovely wife Yamille Pagán Rogriguez, for all her support, words of hope and unconditional love during all these years. To my lovely brother Juan Luis, as a gift to his will and dreams and to my lovely parents Geraldo and Nancy for your support, respect and all your unconditional love during all this years. Also to my uncle Harvey Rodriguez that went with me in my first immersions.

> "Hay hombres que luchan un dia y son buenos,
> hay otros que luchan un año y son mejores,
> hay quienes luchan muchos años y son muy buenos,
> pero hay quienes luchan toda la vida esos son los impresindibles"
>
> Bertold Bretch

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1. Introduction

Coral reefs provide a local environment in which thousands of species interact with each other and the reef environment, making coral reefs one of the most biodiverse ecosystems in the tropics (Burke *et al.* 2004). Coral reefs near coastal zones play an important role as natural barriers against tropical storms, income from tourism activities (e.g. sport diving, sport fishing) and scientific research (Wolanski *et al*. 2003). As part of the tropical seascape, the boundary between coral reefs, seagrass and mangrove forests provides habitat nurseries, foraging and spawning sites for a variety of fish and invertebrates of commercial and biomedical importance (Ogden, 1997). Over the past decades, increases in coastal activities, excessive fisheries and natural processes (e.g. climate change, hurricanes, diseases) have produced a decreased in coral cover, habitat area and biodiversity in coral reefs worldwide (Hughes *et al.* 2003; Bellwood *et al.* 2004).

Coral reefs in the Caribbean have been affected by an increase in sediment from land development, sewage pollution, fishing pressure and the proliferation of coral diseases and more frequent and intense bleaching (Burke *et al.* 2004; Wilkinson 2004). Some of the effects of these factors (e.g. diseases) have already produced significant losses of major components of the reef fauna. For example, the sudden decline in the population of the sea urchin *D.antillarum* in 1984, an effective grazer which promote substrate availability for coral settlement and the demise of *Acroporid* populations *A.palmata* and *A.cervicornis*, two important reef building species in shallower habitats, have produced a shift in coral dominated to algal dominated reefs with a decrease in substrate availability (Lessios *et al*. 1984; Hughes 1994; Macintyre *et al.* 2004).

Over the last decades, studies on reproduction and ecology of reef corals have elucidated the sensitivity of these processes to climatic and anthropogenic stresses (Wolanski *et al.* 2003; Edmunds 2005). These organisms are important as primary producers in the reef due to the symbiosis with the zooxanthellae algae and as builders of habitat structure (Cornell and Karlson 2000). However, it is still necessary to incorporate aspects of coral recruitment and survivorship as part of long term and monitoring efforts (Sammarco 1980; Connell *et al.* 1997; Ruiz 2003). The recruitment of sexual and asexual individuals plays major roles in the dynamics of reef ecosystems (Yoshioka 1996). Therefore, understanding this processes and determining spatial and temporal patterns of variability are important to keep track of short and long-term recovery (or decline) in coral populations and reef communities. In the Caribbean, several studies have shown that reef topography, depth gradient, oceanographic and environmental processes as well larval dispersion (i.e. life histories) contribute to the abundance, survivorship and distribution of coral recruits (Bak and Engel 1979; Chiappone and Sullivan 1996; Edmunds et al. 2004) (Table 1).

In Puerto Rico, coral reef research has largely focused on community characterization, monitoring programs, coral diseases and mitigation programs (Hernandez *et al.* 1988; Weil *et al.* 2002; Garcia *et al.* 2003). Nevertheless, no studies have focused on recruitment of scleractinian corals, while recruitment studies for other groups have been extensively conducted (Yoshioka 1996). Due to the critical role of this process in the structure and dynamics of populations and communities, and the possibility of natural recovery after disturbance (Yoshioka 1996; Connell *et al.* 1997), it was important to characterize the distribution, abundance, and survivorship of juvenile coral in La Pargüera, southwestern Puerto Rico.

Table 1.1 Reported densities of juvenile corals in studies in the wider Caribbean

Locality	Source	Mean density
Bonaire	Bak-Engel (1979)	18 colonies/m²
Curacao	Bak-Engel (1979)	15 colonies/m²
St. Croix	Rogers et al. (1984)	3-42 colonies/m²
Florida	Chiappone-Sullivan (1996)	2.03 colonies/m²
Bermuda	Smith (1997)	2-6 colonies/m²
St. John	Edmunds et al. (2000)	53 colonies/0.25m²
Florida	Miller et al. (2000)	1-4/m²
Florida	Edmunds et al. (2004)	1.9-2.1/ 0.25m²
Mesoamerican barrier	Ruiz-Arias (2004)	1-6.4/m²

Background information

Sexual reproduction in scleractinian corals involves the production of larvae either through internal or external fertilization (Richmond 1997). For Caribbean reef corals, two patterns and modes of sexual reproduction have been described: (1) Broadcast spawners (hermaphrodites or gonochoric) who spawn gametes into the water column where fertilization and larval development occurs; (2) brooders (hermaphrodite or gonochoric) who release breed live well-developed larvae into the water column (Szmant 1986). Both reproductive strategies reflect differences in larval development and settlement (Wilson and Harrison 1998; Miller and Mundy 2003). These strategies reflect a selection of traits in response to environmental changes in which larger colonies produced fewer offspring but with a higher probability of survival (i.e. K-strategy) and smaller colonies in size produced higher number of offspring but with a lower probability of survival (r-strategy) (Szmant and Gassman 1991; Hall and Hughes 1996). All of these reproductive traits have a direct effect on the patterns of recruitment and survivorship of juvenile corals; and therefore, for coral reef dynamics (Edmunds *et al*. 2004).

Coral recruitment

Recruitment has been defined as the arrival of new individuals into the community structure (Sale, 1999). However, Wallace (1985) and Connell (1985) defined recruitment as individuals that can be counted under field conditions. Recruitment depends on the ability of the larvae to identify a suitable substratum for settlement and metamorphose in new individuals (Richmond, 2001). Abundances and distribution of juvenile coral colonies have been shown to be associated with biological and physical factors, which affect the variability of settlement and survivorship (Soong *et al*. 2003; Glassom *et al*. 2004). Substrate complexity, competition, grazing, local, and regional oceanographic conditions have been shown to affect coral recruitment and survivorship (Sammarco 1985; Carlon 2001; Sprecher *et al*. 2003). Survivorship of juvenile corals was higher in the shade of vertical and overhanging substratum and where low light prevent the overgrowth of algae (Birkeland 1977). Sammarco (1985) observed that survivorship of juvenile coral was higher in cryptic areas protected from grazing activities by the sea urchin *D.antillarum*. Some of these substrates are composed of large coral skeletons; live coral species, proper texture and biochemical (i.e. biofilms) coating that combined provide refuge and contribute significantly to juvenile abundance and survivorship (Morse and Morse 1993; Edmunds *et .al*. 2004). Juvenile coral abundances and composition not only vary with reef complexity, but also across depth, distance from shore, reef site and community structure (Rogers 1984; Edmunds 2000; Hughes et al. 1999; Ruiz and Arias 2005). Most of the abundant species of juvenile coral observed along depth gradients and habitats are from brooders which seems to be superior competitors for space under unfavorable conditions (e.g. high nutrient input, acute disturbances) (Birkeland 1977; Bak and Engel 1979; Bellwood *et al*. 2004). Meanwhile, hermaphrodite broadcasters are reported to have low recruitment and few juveniles compared to brooders species in the Caribbean (Rogers et al. 1984; Szmant 1986; Miller *et al*. 2000). These broadcasting species, together with other reef organisms, contribute significantly to the topographic complexity and resilience of Caribbean coral reefs (Hughes *et al*. 2003). The early stages of development of these important species is poorly known because of the low abundance of juvenile observed on natural substratum (Rogers, 1984; Chiappone and Sullivan, 1996; Ruiz and Arias 2004).

Most of the knowledge that we have on recruitment comes from studies that have used artificial substrate (i.e. Plexiglas plates, terracotta tiles, PVC). These methods attempted to quantify the early stages of the pre-, and post-settlement processes of coral larvae which are important to understand factors that control the survivorship of these early stages. However, understanding coral recruitment over natural substratum is a further step into the knowledge of coral recruitment processes (Birkeland and Randall, 1981; Fairfull and Harriott, 1999; Maida et al., 1994). Successful recruitment of new, sexually produced larvae is an important step for resisting phase shifts to degraded alternate states, provides valuable information on the reproductive success of species and particularly in reefs that exhibit low rates of coral recruitment (Bellwood *et al.* 2004). Therefore, an understanding of coral recruitment patterns on natural substrata and juvenile abundance and composition over time are essential to understand ecological and physical processes that control population growth, distributions, and variability of community structures in time and space (Hughes 1986; Yoshioka 1996; Connell 1997). Thus, an “in situ” estimate of the number, species composition and distribution of juvenile corals on reef systems is a key issue for understanding of coral population dynamics. This sort of study might help to improve restoration programs and management strategies of damaged reef habitats and coral populations (*A.palmata, Montastraea* complex) which under natural conditions would take several years or decades to recover (Rinkevich 1995; Miller and Barimo 2001).

The insular shelf of La Parguera on the southwest coast of Puerto Rico is characterized by an extensive development of coral reefs, seagrass beds, and mangrove forests. Coral reefs extend throughout a wide range of depths and distances from the coast and consequently are exposed to gradients of physical, chemical and biological interacting forces (wave energy, light attenuation, suspended sediment), which affect the structure and biological community within and between reefs (Morelock et al. 1977; Garcia et al. 1998). Therefore, the goals of this study were to examine the spatial and temporal variability of coral recruitment in La Parguera.

1.4. Objectives:

a) To assess the spatial variability of juvenile coral abundance and species composition across depth intervals (habitats) within reef sites, across reefs within zones and across inshore to offshore zones.

b) To examine the relationship of juvenile abundance and adult colonies at different spatial scales between depth intervals within reef sites and across zones.

c) To explore relationships between coral recruitment, coral cover and reef rugosity.

d) To assess the survivorship of juvenile corals across depth intervals within reef sites, between reef sites within and across zones

e) To compare rate of recruitment and survivorship between reproductive strategies (spawners vs. brooders).

1.3. Questions and hypotheses addressed in the present study:

1. What is the spatial variability in the distribution, species composition and abundance of juvenile corals between depth intervals within reefs, reefs within zones and across zones?

- H_0: There is no significant difference in the abundance, distribution and composition of juvenile coral between depth intervals within reefs, across reefs and across zones.

- H_a: There is a significant difference in the abundance, distribution and composition of juvenile coral between depth intervals within reef site and across reef zones.

2. What is the relationship between juvenile corals, coral cover and reef rugosity?

- H_0: There is no significant relationship between coral recruitment, coral cover and reef rugosity.

- H_a: There is a significant relationship between coral recruitment, coral cover and reef rugosity.

3. Is there is a relationship between the proportions of adults and juveniles coral between depth intervals within reefs, reefs within zones and across zones

- H_0: There is no significant relationship in the proportions of adults and juvenile coral between depth intervals within reef site and across zones.

- H_a: There is a significant difference in the proportions of adults to juvenile coral between depth intervals within reef site and across reef zones.

4. Is there any spatial and temporal variability in the survivorship of juvenile coral between depth intervals within reefs, reefs within zones and across zones?

- H_0: There is no significant difference in the survivorship of juvenile of different species between depth intervals within reefs, reefs within zones and across zones.

- H_a: There is a significant difference in the survivorship of juveniles of different species between depth intervals within reefs, reefs within zones and across zones.

2. MATERIALS AND METHODS

2.1. Study site

Fieldwork was conducted in six coral reefs off La Pargüera southwestern Puerto Rico, from August 2003 to August 2005. La Pargüera is one of the driest and hottest areas along the southwestern coast of Puerto Rico. Most of the moisture carried by the easterly trade winds is lost by the time they reach Pargüera, due mainly to the interaction with the central mountain ridge located north of La Pargüera town (Garcia *et al.* 1998). The insular shelf of La Pargüera extends 8-10 KM offshore. The paucity of rainfall and the absence of large rivers, combined with the oligothrophic ocean waters contribute to high levels of water transparency and thus the formation of coral reefs and adjacent marine ecosystems (Morelock *et al*. 1977, Garcia *et al*. 1998).

Two distinct lines of emergent reef align east west, parallel to the coastline and divide the insular shelf of La Parguera into inner, middle, and outer shelf zone (Morelock *et al*. 1977, Garcia *et al*. 1998). This study includes two reefs in each of the three shelf zones (Fig.1).

2.1.1 Inner shelf

Pelotas (**17°57.442N and 67°04.176W)** is located 1 km from the shore. An extensive seagrass bed dominates the platform back reef. A well-mixed community of corals, sponges, hydrocorals and macroalgae with loose rubble characterized the reef top. The step slope is dominated by corals, octocorals and sponges reaching a maximum depth of 15m. Enrique (**17°56.658 N and 67°02.213 W)** is a semi-exposed fringing reef located 1.5 km from the shore. The reef fringes a long shallow platform with mangrove keys and sea grass beds in an east-west direction. The reef platform is short (30-50m) dropping to 15m and is dominated by coral-octocoral communities.

2.1.2 Mid shelf

Media Luna (**17°56.093N 67°02.931W)** is a well-developed fringing reef and extends from east to west located 2.0 km from shore. The lagoon habitat is formed by shallow accumulation of soft sediment with extensive seagrass beds. *A.palmata* skeletons and sand are characteristic of the reef crest. The reef platform extends 250 meters seaward to the south and is dominated by octocorals with low, mostly crustose and massive coral colonies. The reef slope drops to 20m ending in a sandy bottom and is dominated by large colonies of corals mostly *Montastraea* spp.

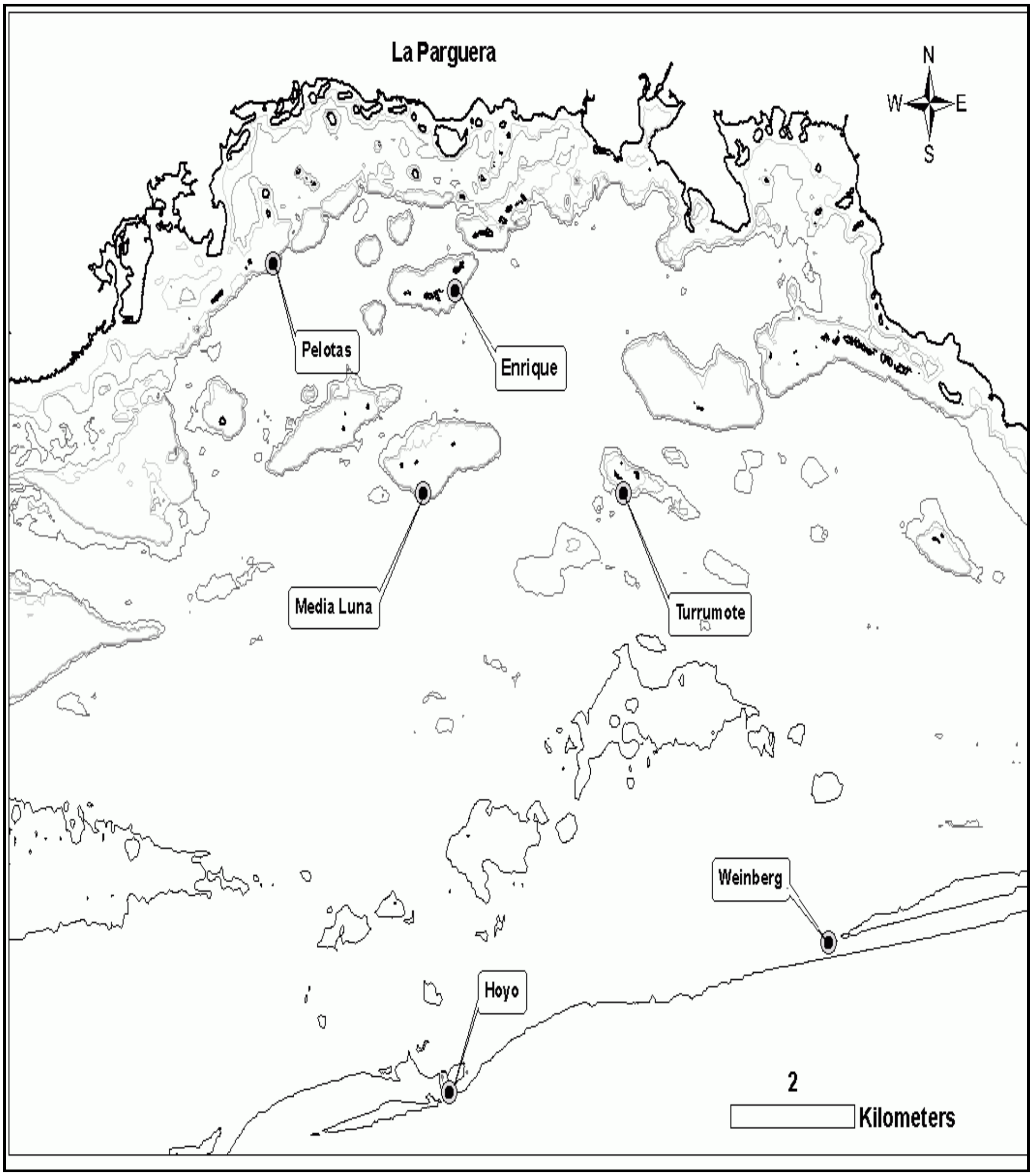


Figure 2.1 Map of La Pargüera area showing study sites: Pelotas and Enrique (inner shelf), Media Luna and Turrumote (mid shelf) Weinberg and El Hoyo (outer shelf).

Turrumote (**17°56.097N and 67°01.130W)** is an exposed mid-shelf fringing reefs located 2 km from shore. The reef borders the east and south regions of an exposed key formed by *A.palmata* storm rubble, sandy accumulation and mangrove growth. It has a short platform extending southward 50-70m with a depth range between 1 and 4 m dominated by octocorals at shallow and intermediate depths. The drop-off is highly complex and variable in morphology, mostly dominated by large colonies of *Montastraea spp*, *Colpophyllia spp* and *Diploria spp*. The platform is characterized by high relief topography.

2.1.3. Shelf edge

Weinberg (**17°53.429N and 66°59.320W)** is a well-developed bank reef system with spur and grove formations characterized by high diversity and cover of coral species, extending from 18 to 30m deep located 6 km from shore. El Hoyo (**17° 52.559 N and 67° 02.619 W)**, with a coral-octocoral-sponge community consolidated, low relief hard bottom. *Montastraea* spp. and large vase sponges dominated most of the hard bottom. The site has been known for spawning aggregation by groupers. Depths vary between 20-25m and is located 8 km from shore.

2.2 Experimental Design

2.2.1 Abundance and composition of juvenile and adults corals

Distribution and abundance of juvenile and adults corals were assessed using a six 1m^2 quadrants divided into 100 areas of 10 cm^2 placed randomly along four 20 m long permanent transects (N= 24 quadrats) at each of four depth intervals (3m, 5m, 10m, and > 15 m) in each reef (N=96 quadrats) . In each quadrat, the abundance of juvenile and adult corals and cover of the main coral species were measured.

To test if juvenile coral density was significantly different between depth intervals within reef sites and among reefs, a two way ANOVA was used after checking for normality and homogeneity of variance with Kolmogorov Smirnoff and Levene tests (Sokal and Rohlf 1997). Data involving counts were log transformed and expressed as mean ± (confidence intervals) (Sokal and Rohlf 1997). Since Weinberg and El Hoyo only have one depth (18 meters) significant differences in juvenile densities were tested with a t-test. Then, a nested design with five hierarchical levels quadrats within transect (6), transects within depths (4), depths within reef (4) and reef within zones (2) was used to test which of the five spatial scales measured accounts for most of the variability in juvenile coral density (Fig. 2). The satterthwaite approximation method was applied to calculate the degrees of freedom, F ratios and significances due to the unbalanced design at the deep sites (20 m) (Sokal and Rohlf 1997; Ruiz and Arias, 2004).

All juvenile and adult corals were identified to genus or species and counted in each quadrat. Several characteristics were observed to differentiate juveniles from remnants of tissue from extended partial mortality of a colony. Sexually produced juvenile colonies can be distinguished from isolated fragments because they are smaller than most post-fission ramets resulting from partial mortality and they may be different species from the substrate where they settled (Fig.3 and 4) (Hughes and Jackson 1985). Depending on the species and its average size/area, a criterion of minimum size was used. For example, larger colonies of *Montastraea,* isolated crusts of tissue less than 5 cm in diameter were considered sexual juveniles. For smaller species such as *P. astreoides* and *S. siderea,* isolated colonies less than 2 cm in diameter were considered sexual juveniles. In every occasion that a potential juvenile was found, careful observations of its surroundings were made to ensure that it was a new juvenile. Data was tabulated by species-quadrat-transect-reef-zones-date of survey, using an Excel spreadsheet program.

Juvenile abundances and proportions of adults: juvenile were tested for significant difference among reef sites and among depth intervals with a contingency tabled R x C using the G-test of independence (Sokal and Rohlf 1997). Species were pooled across genera, depth and site to eliminate low values from the analysis (Sokal and Rohlf 1997; Edmunds 2000). A correspondence analysis was used to explore what kinds of pattern arise from the ordination analysis. A Pearson correlation analysis was used to test if there was an association between coral cover and juvenile density, depth and distance from shore.

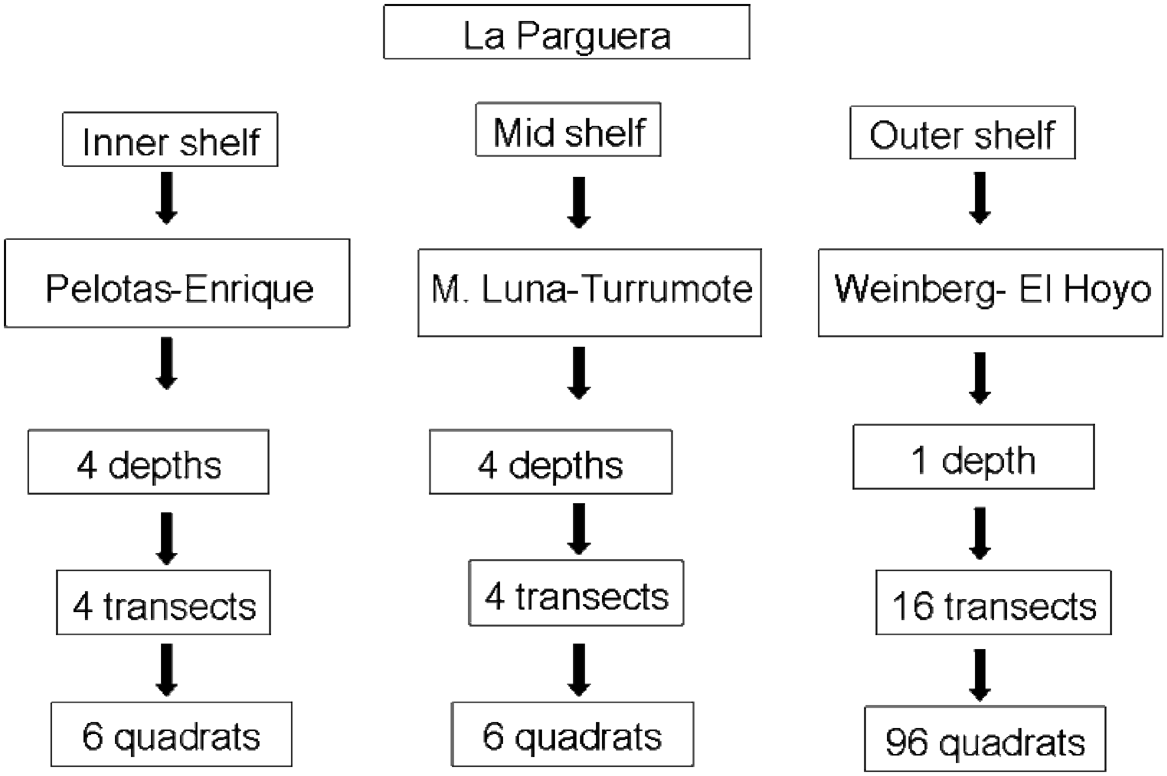


Figure 2.2 Diagram of the nested experimental design. Spatial scales include (1) 1 m^2 (6 quadrats, within each transect), (2) 20 meter (transect within each depths) (4) 100 m (4 depths within each reefs) (4) > 1 KM (2 reefs within each zones).

Figure 2.3 Newly established sexual juvenile colonies over different substrate (*Diploria strigosa*, *Diploria labyrinthiformis* and *Porites astreoides*). Notice the rounded-regular patters at the edge of the colony and lack of remnant tissue that result from partial mortality.

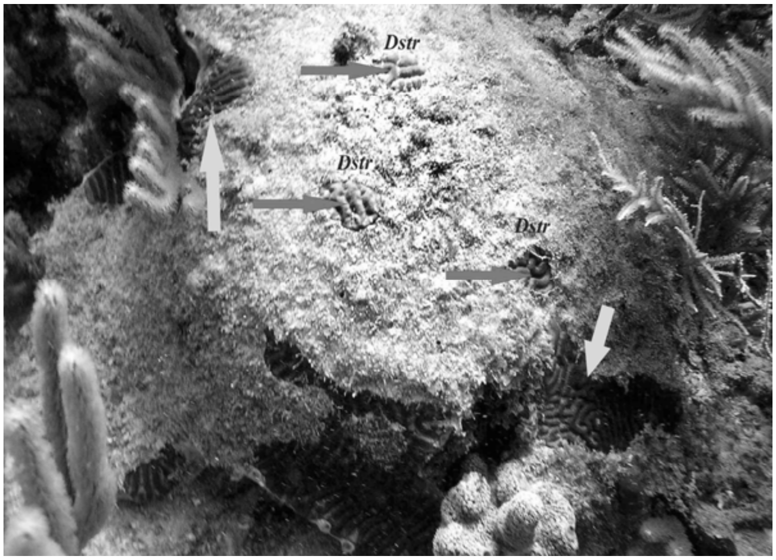


Figure 2.4 Ramets from of a partial mortality event in the species *Diploria strigosa*. Notice remnant tissue at the right bottom corner and upper left corner showed by arrows

2.2.2 Survivorship of coral recruits

Six permanent quadrats of 0.25 m^2 (0.61 m x 0.42 m) were haphazardly located, marked and tagged along each of the 20 m long transect in each of the four depth intervals (N= 24 replicate quadrats/depth; N=96 permanent quadrats/reef). Each quadrat was labeled with a number for identification and reference. After fanning away loose sediment, all juveniles were identified (genus/species) and their location was mapped on plastic underwater paper. Photographs of each 0.25 cm^2 quadrat were taken with an Olympus C-4000 digital camera in UW Housing. The position of the different juvenile mapped on underwater paper was transferred to the digital photo of the quadrat using a computer digital photo program (Adobe Photoshop) and each set of maps were laminated to use to follow juvenile through time. Surveys were done every six months from August 2003 to February 2005. Loss of juveniles and appearance of new ones were noted on the maps and changes were made on the digital images of the quadrat. Significant differences in juvenile coral density and survivorship between depth intervals within reef site at two time intervals (August 2003, August 2005) was tested with a repeated measurement ANOVA (RM ANOVA) after log (x+1) transformation of the data. Differences in survivorship of juvenile corals were compared among sites with a G-test of independence contingency table (site x [dead vs. alive]) pool by genera and then for the most common species (Edmunds 2000). Differences in survivorship based on life history strategy (e.g. spawners vs. brooders) among reef sites and depth intervals were tested with an R x C contingency table using the G-test.

In addition, reef rugosity was measured using the chain method described by Porter (1972) and Cintron *et al.* (1993). This data provided an estimate of topography complexity of the reef. A 10 m linked chain was laid on the reef contour trying to conform to the smallest and largest topographic features. The rugosity index was calculated using the ratio of the tape measurement to chain length referred as rugosity were RI= $D_{1/}D_2$ X 100. Were, D_1 = tape, D_2= Length of chain over the substrate. Departures of chain length from length of transect provide an estimation of topography complexity of the reef. To test if there was a relationship between reef rugosity and juvenile coral density a linear regression analysis was used.

3. Results

3.1. Overall juvenile densities for Parguera

Overall, mean juvenile coral density for La Parguera was 1.86 (C.I: 0.06-3.66) col/m^2, similar to densities (1.2 to 3.4 col/m^2) from other studies in the Caribbean (Chiappone and Sullivan 1996; Miller et.al. 2000, Ruiz and Arias 2004).

3.1.1 Pelotas.

Juvenile coral densities among depth ranged from 1.15 (C.I: 1.00-1.20) to 4.26 (C.I: 2.89-6.28) col/m^2 (ANOVA, F= 12.54, $p<0.05$). Densities were significantly higher in deep habitats 4.26 (C.I: 2.89-6.28) col/m^2 compared to the shallow 1.15 (C.I: 1.00-1.20) and intermediate habitats 1.94 (C.I: 1.48-2.56) col/m^2 (Tukey HSD test, $p<0.05$) (Fig. 3.1A).

3.1.2 Enrique.

Juvenile coral densities among depths ranged from 1.09 (C.I: 0.97-1.23) to 2.92 (C.I: 2.83-3.87) col/m^2. Densities were significantly higher (ANOVA, F= 8.26, $p<0.05$) at the intermediate habitats (10m) 2.92 (C.I: 2.83-3.87) (10m) compared to the shallow 1.09 (C.I: 0.97-1.23) and intermediate shallow habitat 1.51 (C.I: 1.17-1.95) col/m^2 (Tukey HSD, $p<0.05$) (Fig. 3.1B).

3.1.3 Media Luna

Juvenile coral densities between depth intervals ranged from 1.69 (C.I: 1.26-2.17) to 2.39 (C.I: 1.65-3.45) col/m^2. No significant differences where found in the mean densities of juvenile coral between depth intervals (ANOVA, F= 1.18, p=0.32) (Fig. 3.1C).

3.1.4 Turrumote.

The highest density of juvenile corals for Turrumote were observed at the deep habitat (15m) 2.29 (C.I: 1.64-3.19) col/m^2 and were significantly higher (ANOVA, F= 3.47, $p<0.05$), compare to the shallow and intermediate shallow habitat (3m-5m) 1.38 (C.I: 1.09-1.74) col/m^2 and (5m) 1.32 (C.I: 1.06-1.63) col/m^2 respectively (Tukey HSD, $p<0.05$) (Fig. 3.1D).

3.1.5 El Hoyo and Weinberg

No significant differences were found between mean juvenile densities in Weinberg 1.99 (C.I: 1.58-2.50) col/m^2 and El Hoyo and 1.69 (C.I: 1.24-2.31) col/m^2 (t= 0. 49, p=0.62) (Fig. 3.1E, F).

3.2 Juvenile densities across reef sites within zones

3.2.1 Inner shelf reefs. Overall, Juvenile coral densities were significantly higher (two way ANOVA, F= 4.79, $p<0.02$) in Pelotas 2.04 (C.I: 1.72-2.41) col/m^2 compared to Enrique 1.69 (C.I: 1.48-1.93) col/m^2 (Fig. 3.2A). Between depth intervals densities were significantly higher (two way ANOVA, F= 9.75, $p<0.05$) at the deep habitats 4.26 (C.I: 2.89-6.28) col/m^2 in Pelotas compared to the deep habitats 1.77 (C.I: 1.32-2.37) col/m^2 in Enrique (Fig 3.2E) (LSD test $p<0.05$).

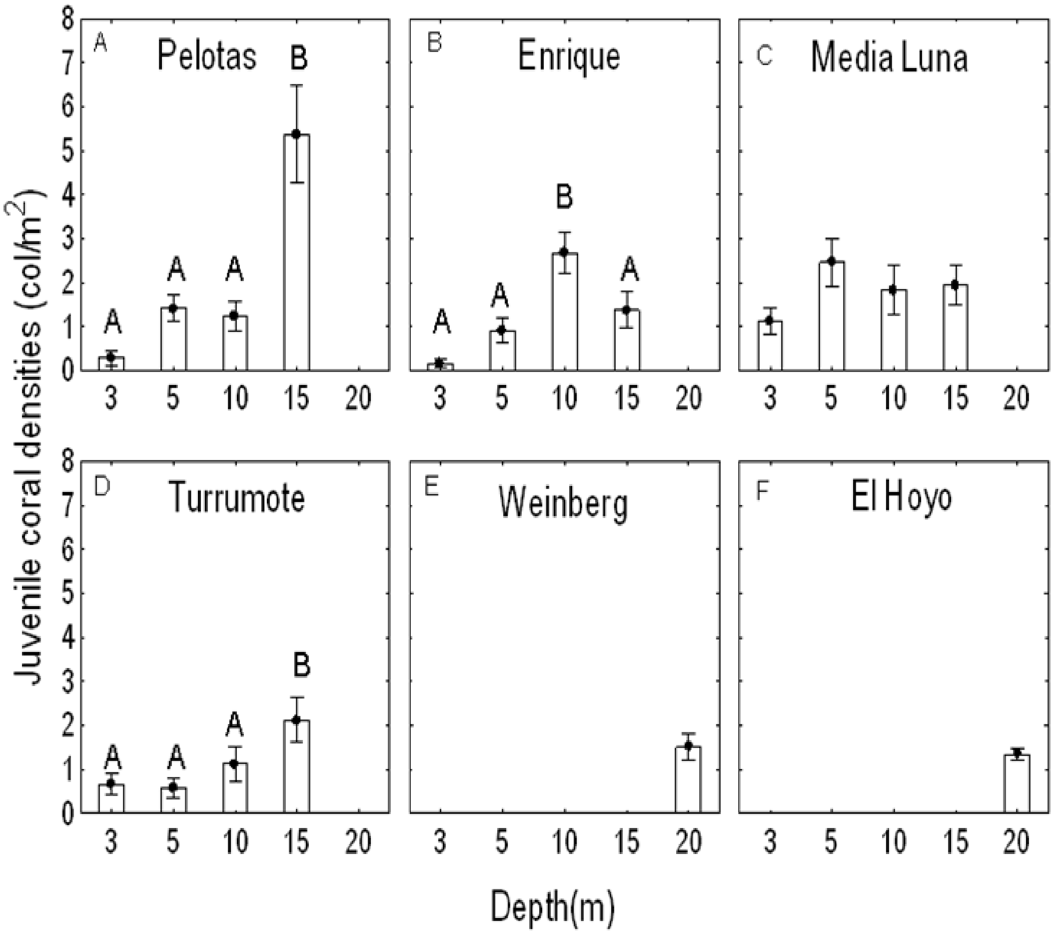


Figure 3.1 Mean (±SE) of Juvenile coral densities (col/m^2) between depth intervals for A) Pelotas B) Enrique C) Media Luna, D) Turrumote, E) Weinberg and F) El Hoyo. Equal upper case letter mean no significant difference (N= 24 quadrats/depth) (Tukey HSD test<0.05).

3.2.2 Mid shelf reefs. Juvenile coral densities were significantly higher at Media Luna 1.99 (C.I: 1.69-2.34) col/m^2 compared to Turrumote 1.58 (C.I: 1.38-1.80) col/m^2 (two way ANOVA, F= 5.16, $p<0.05$) (Fig. 3.3A). However, no significant differences were found between depths across reefs (two way ANOVA, F= 1.84, $p<0.05$) (Fig 3.3 B-E).

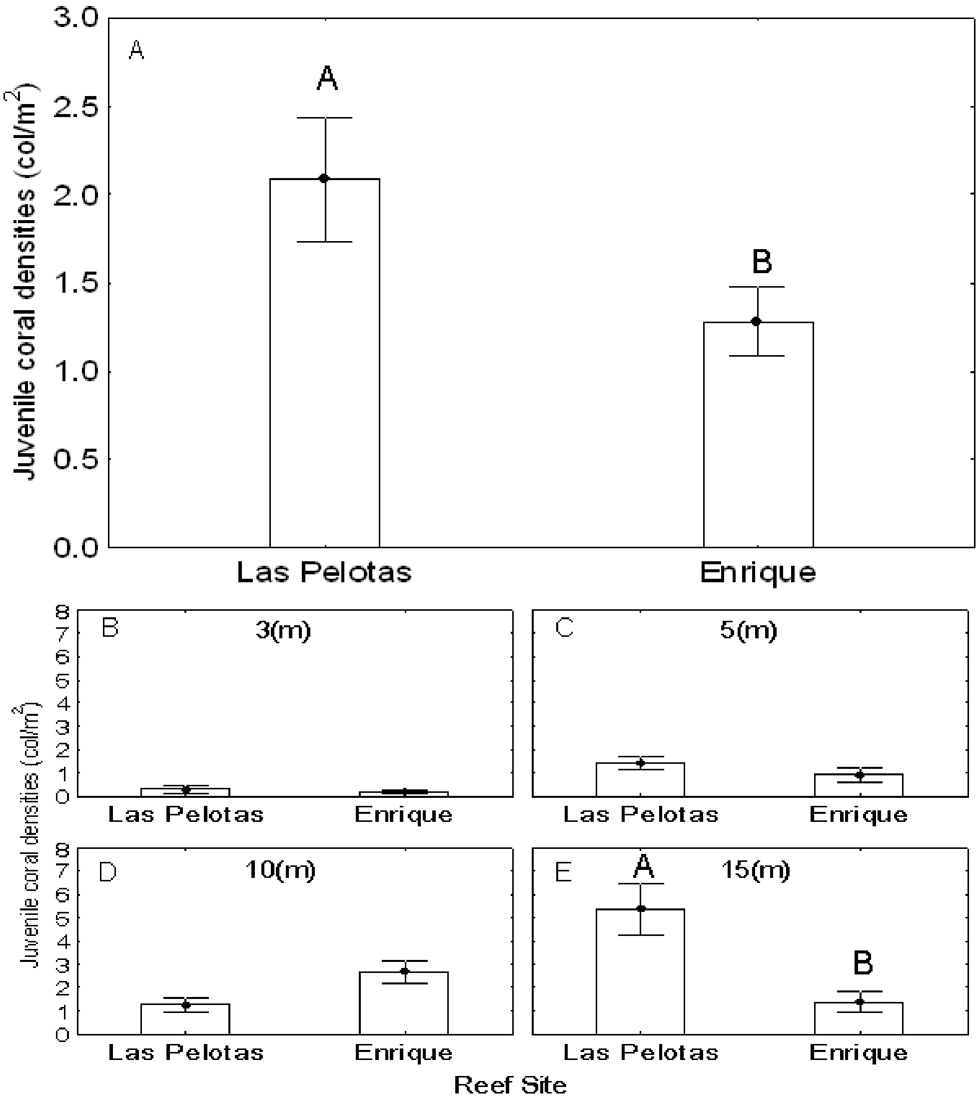


Figure 3.2 Mean (±SE) juvenile coral density (col/m^2) compared between reef sites and between the same depth intervals between reefs in the inner shelf zone (Pelotas and Enrique) (A-E). Pelotas showed the highest density in the deep zone compared to the depth interval of Enrique (N= 24 quadrats per depth) (Tukey HSD test, $p<0.05$). Equal letter denotes no significant difference.

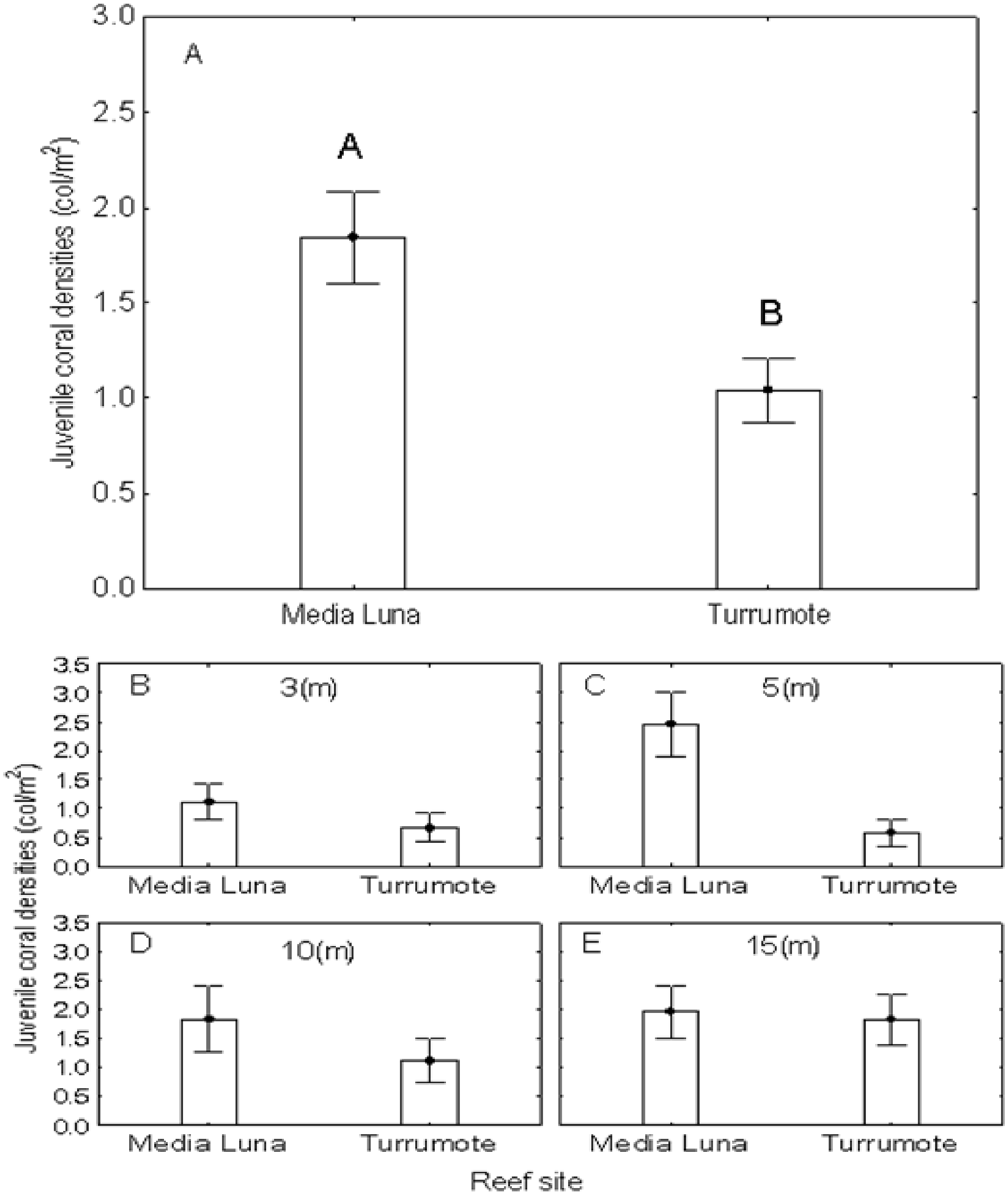


Figure 3.3 Mean (±SE) juvenile coral density (col/m^2) between (A) Reef site and (B-D) among depth intervals in the inner shelf reefs. (C) Juvenile densities were higher at the intermediate shallow zone (5m) in Media Luna compare to the intermediate shallow zone of Turrumote (LSD test, $p<0.05$).

3.2.3 Juvenile densities across zones (inshore-offshore). Juvenile densities tend to decreased slightly from inshore to offshore reefs however, no significant differences were found across the shelf zones (1.68 to 1.42 col/m^2) (Fig. 3.4B). Meanwhile, mean densities of juvenile corals pooled across depths (sum of total juvenile colonies regardless of sites) was higher in the intermediate habitats 2.45 (C.I: 2.06-2.92) col/m^2 compared to the shallow and deep habitats 1.31 (C.I: 1.18-1.46) col/m^2 and 1.81 (C.I: 1.65-1.99) col/m^2 respectively (Fig. 3.4A). The hierarchical nested ANOVA (F= 3.96, $p<0.05$) showed that among the five spatial scales measured 85% of the total variability in juvenile densities transect within depth and depth within sites (F= 12.89, $p<0.05$) accounted for 85 % of the total variability in juvenile densities.

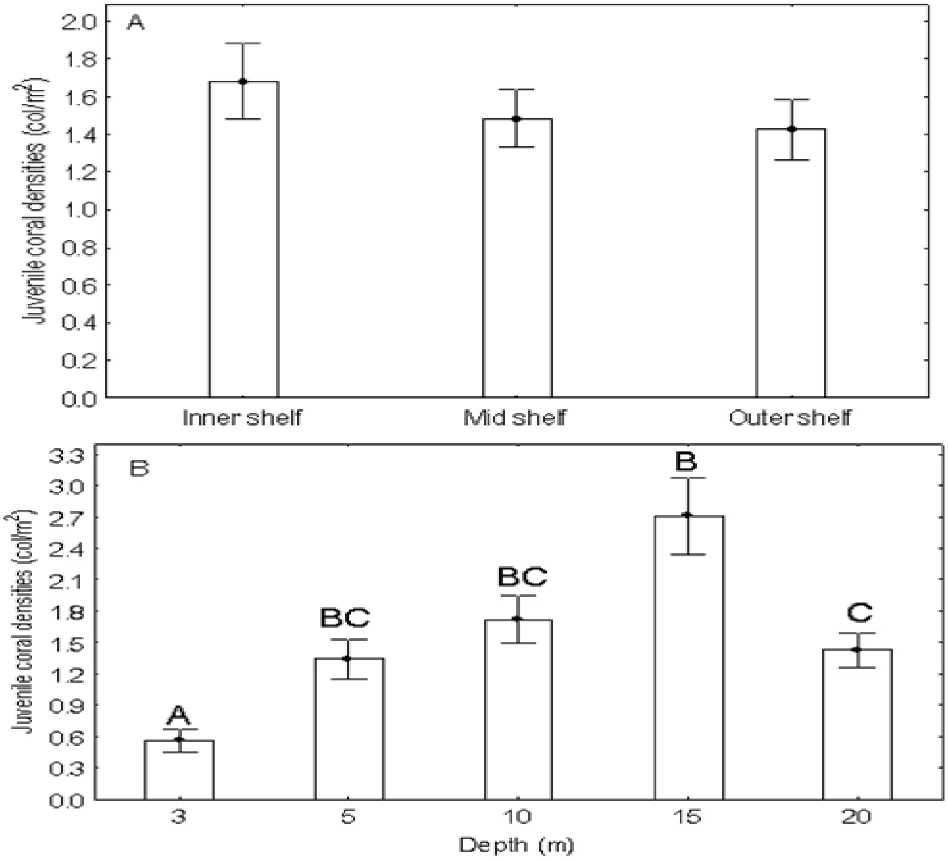


Figure 3.4 Mean juvenile coral densities (col/m^2) across reef zones. A) A trend in decreased density form inshore to out shore reef was observed however, no significant differences were found. B) Mean juvenile coral density (col/m^2) pooled across depth intervals (regardless of reef site). Juvenile densities tend to increase from the shallow habitat to the intermediate deep habitat and showed to be significantly different compared with the other depth intervals. (LSD test, $p<0.05$).

3.3 Relationship between juvenile coral densities and reef rugosity

Rugosity was significantly higher (one way ANOVA, F= 5.89, $p<0.05$) in the shallow habitat (3m) 1.51 (± 0.07) in Pelotas compared to the intermediate deep habitat (10m) 1.18 (± 0.01) (Tukey HSD, $p<0.05$) (Fig. 3.5A). In Enrique significantly higher rugosity index was found (one way ANOVA, F= 4.51, $p<0.05$) in the shallow habitat (3m) 1.70 (± 0.07) depth compared to the intermediate shallow and intermediate deep habitat (5-10m) (1.37-1.36) respectively (Tukey HSD, $p<0.05$) (Fig. 3.5B). Meanwhile, rugosity in Media Luna was significantly higher (one way ANOVA, F= 3.71, $p<0.05$) in the intermediate habitat (10m) 1.77 (± 0.18) compared to the shallow (3m), intermediate (5m) and deep habitat (15m) (Tukey HSD, $p<0.05$). In Turrumote a significantly higher rugosity was found at all depth intervals (one way ANOVA, F= 4.67, $p<0.05$). Rugosity was significantly higher at the intermediate habitat (10m) 1.79 (± 0.15) compare to the shallow habitat (3m) 1.27 (± 0.04) (Fig. 3.5C). No significant differences in reef rugosity were found at 20m between Weinberg and El Hoyo (Fig. 3.5 D-E). Despite the differences in reef rugosity across depth intervals within reefs, no significant correlation was found between juvenile density and reef rugosity (Fig. 3.6A-F).

3.4 Juvenile densities and live coral cover. Overall, coral cover was significantly different between reef sites (two way ANOVA, F= 51.32, $p<0.05$; arcsine transformed data). Coral cover was higher at Weinberg 38.59 (± 13.78 SE) % compare to the other sites (Tukey HSD, $p<0.05$). While El Hoyo was significantly lower compare to the other sites 7.89 (± 6.68 SE) % (Tukey HSD, $p<0.05$) (Fig. 3.7A).

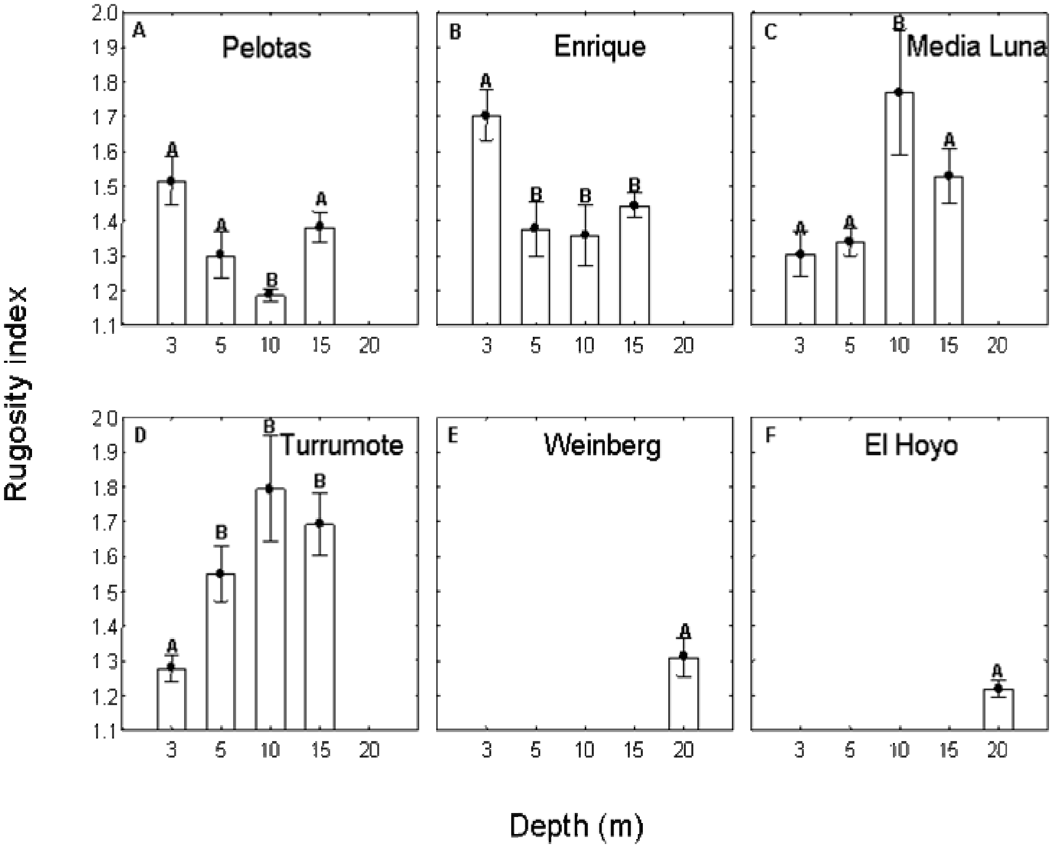


Figure 3.5 Mean rugosity index compare between depth intervals within reef site. Significant differences were (A) Pelotas, (B) Enrique, (C) Media Luna, (D) Turrunmote, (E) Weinberg and (F) El Hoyo.

Coral cover across depth intervals were significantly different (two way ANOVA, F= 10.31, $p<0.05$; arcsine transformed data). Coral cover was higher in the intermediate zone (10m) 25.37 (± 19.11) % and deep zone (20m) 23.24 ± (18.80) % compare to the other depth intervals (Tukey HSD, $p<0.05$) (Fig. 3.7B). However, no significant correlation was found between juvenile densities and coral cover (Fig. 3.8).

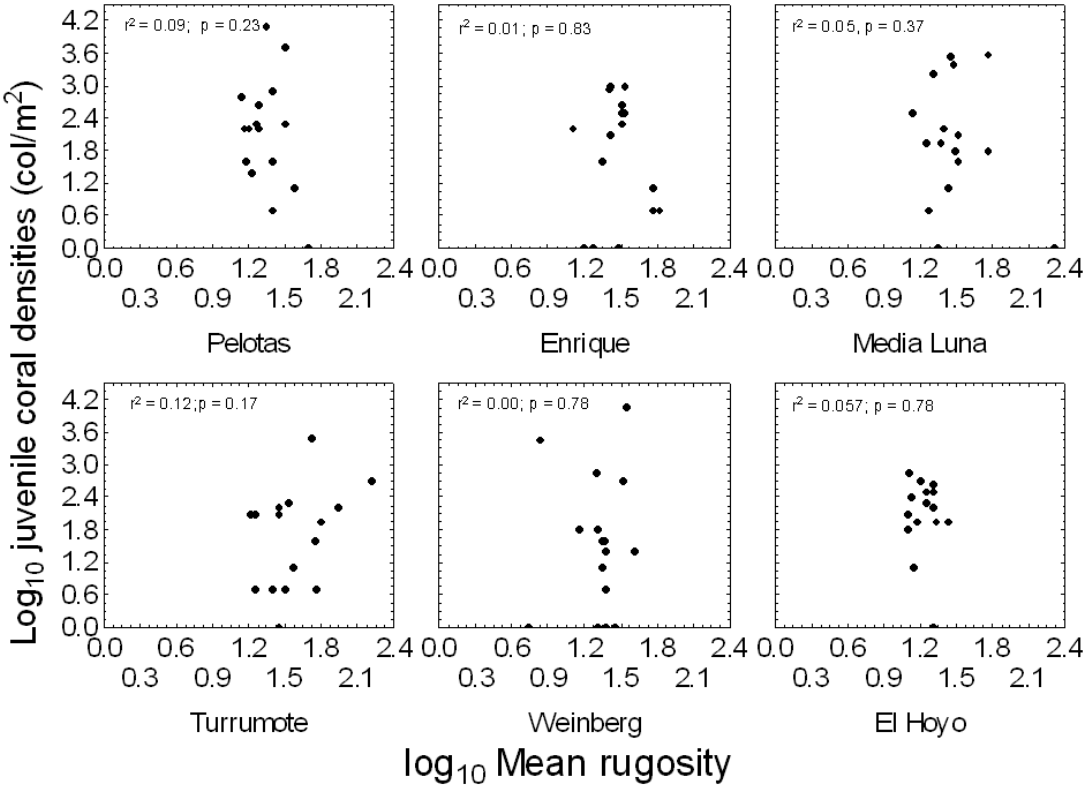


Figure 3.6 Mean log $_{10}$ (x+1) density of juvenile coral in function of reef rugosity. Points represent transect (16) per reef for (A) Enrique, (B) Pelotas, (C) Media Luna, (D) Turrumote, (E) Weinberg and (F) El Hoyo. No significant correlation was found between juvenile density and reef rugosity.

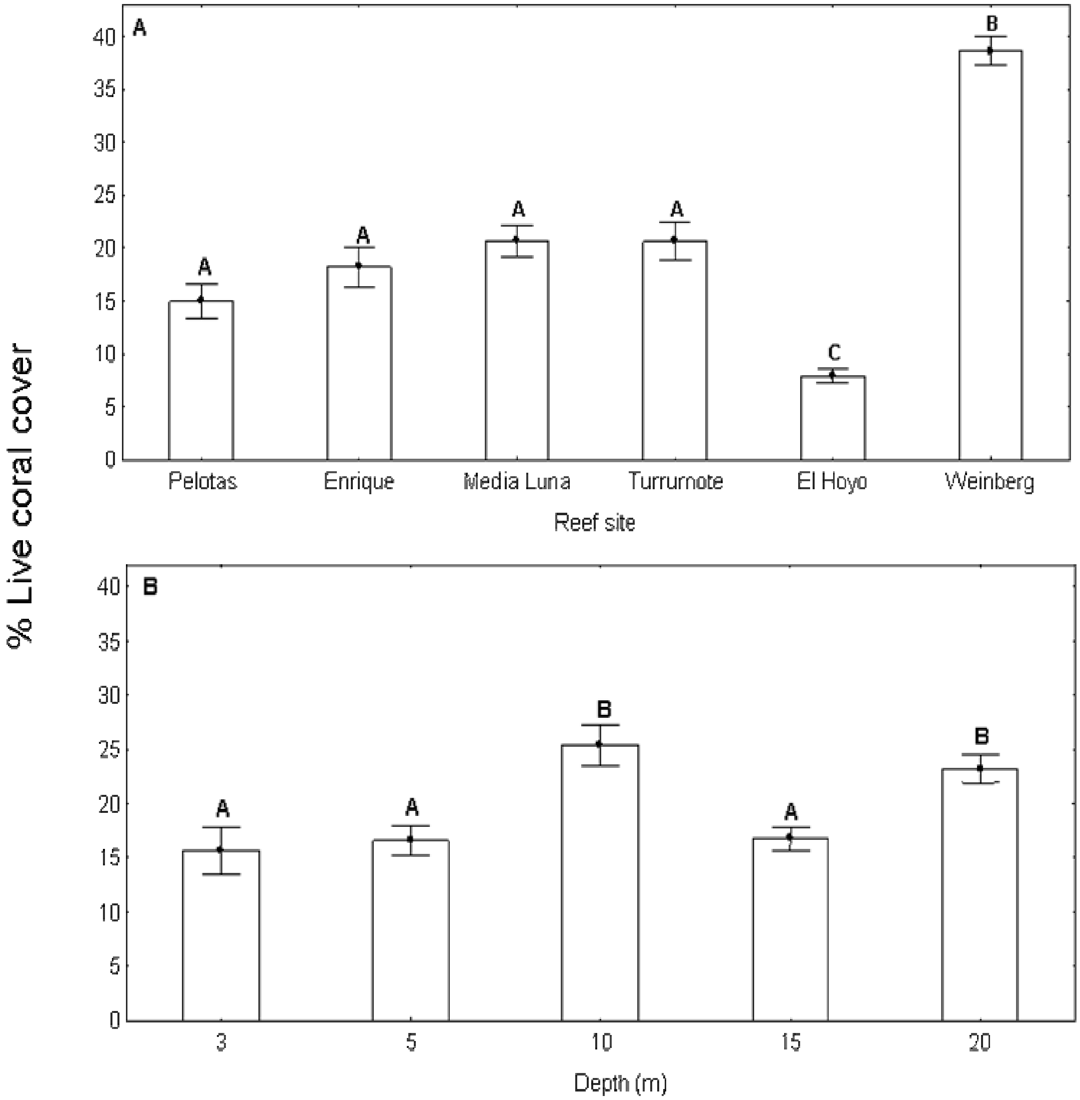


Figure 3.7 Mean coral cover (± SE) among reef sites (A) and between depth intervals (B). Coral cover was higher in Weinberg and at intermediate (10m) and deep habitat (20m) (LSD, $p<0.001$).

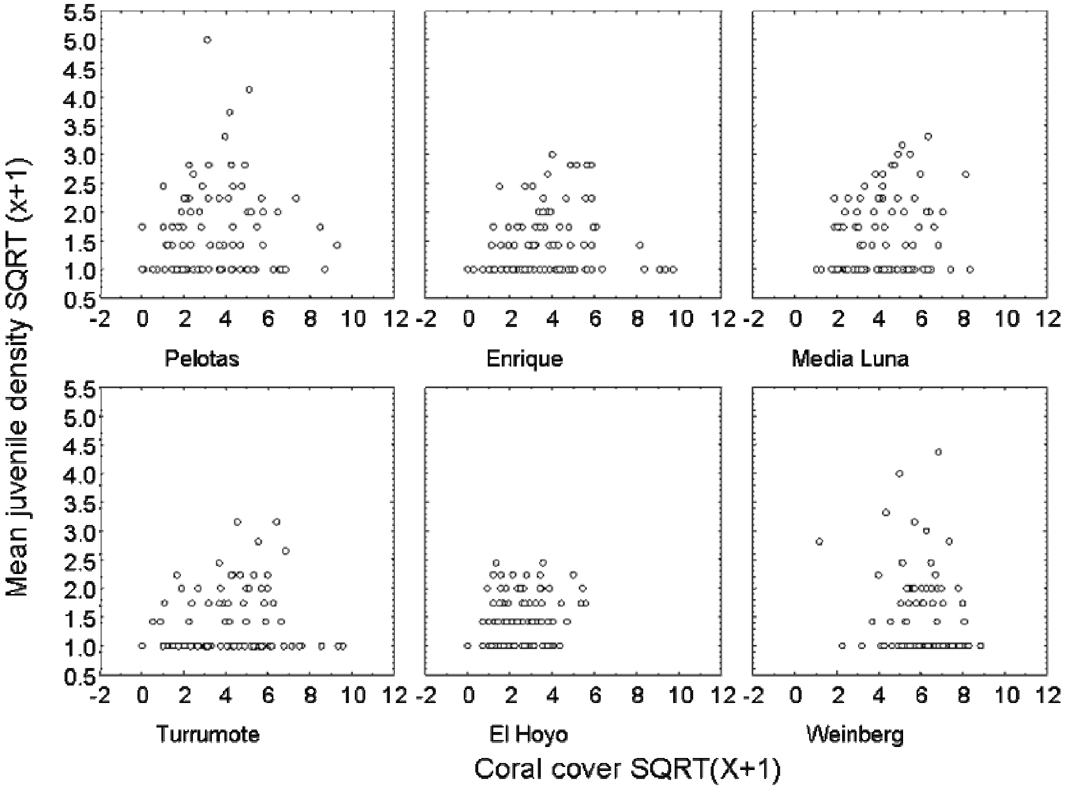
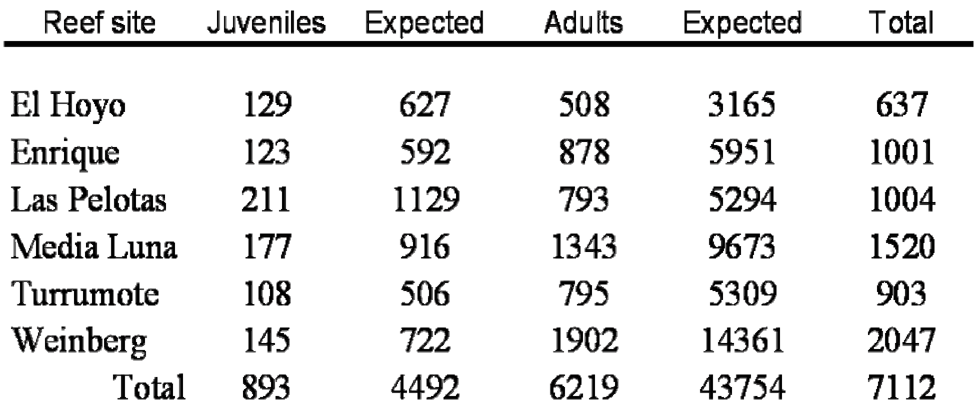


Figure 3.8 Pearson moment correlation analysis between juvenile densities and coral cover across reef sites. Points represent density of juvenile coral in each quadrat within each reef. No significant correlation was found between juvenile densities and coral cover among reef sites.

3.5. Relationship between juvenile and adults coral abundances

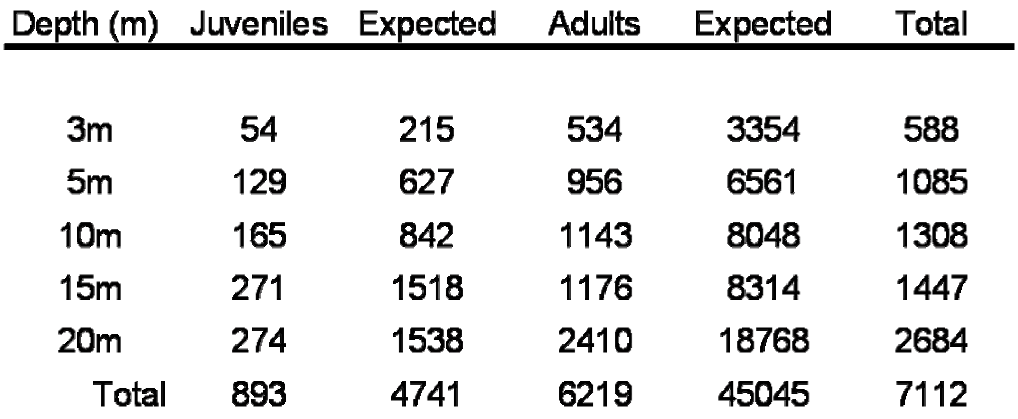
Both adult and juvenile abundances (total number of colonies) were depended on sites (G test= 152.16, df= 5, $p<0.05$) (Table 3.1). Overall, adults were 4 to 13 times more abundant than juvenile corals. In Pelotas and El Hoyo, it was four times more likely to find an adult colony than a juvenile coral. In Enrique, Media Luna and Turrumote adults were seven times more abundant than juveniles, whereas in Weinberg, it was 13 times more likely to find an adult than a juvenile coral. Comparisons between the abundances of adults and juvenile corals across depth intervals pooled across all reefs showed a significant difference in the abundances of adults and juvenile (G= 65.89, df= 4, p<0.05) (Table 3.2).

Table 3.1 Abundance (total colonies in each site) of juvenile and adult corals compared across sites. Juvenile and adult corals distribution were dependent across sites (G= 152.16, df=5, p<0.05).



Reef site	Juveniles	Expected	Adults	Expected	Total
El Hoyo	129	627	508	3165	637
Enrique	123	592	878	5951	1001
Las Pelotas	211	1129	793	5294	1004
Media Luna	177	916	1343	9673	1520
Turrumote	108	506	795	5309	903
Weinberg	145	722	1902	14361	2047
Total	893	4492	6219	43754	7112

Table 3.2 Abundance (total colonies in each site) of juvenile and adult corals compared across depth intervals. Juvenile and adult coral distribution were dependent on depth intervals (G= 65.89, df= 4, p<0.05).



Depth (m)	Juveniles	Expected	Adults	Expected	Total
3m	54	215	534	3354	588
5m	129	627	956	6561	1085
10m	165	842	1143	8048	1308
15m	271	1518	1176	8314	1447
20m	274	1538	2410	18768	2684
Total	893	4741	6219	45045	7112

Although, juvenile and adult distribution were dependent both across reef site and across depth intervals, a weakly correlation between juvenile and adult densities were found across reef sites and across depth intervals (Fig 3.8A-B).

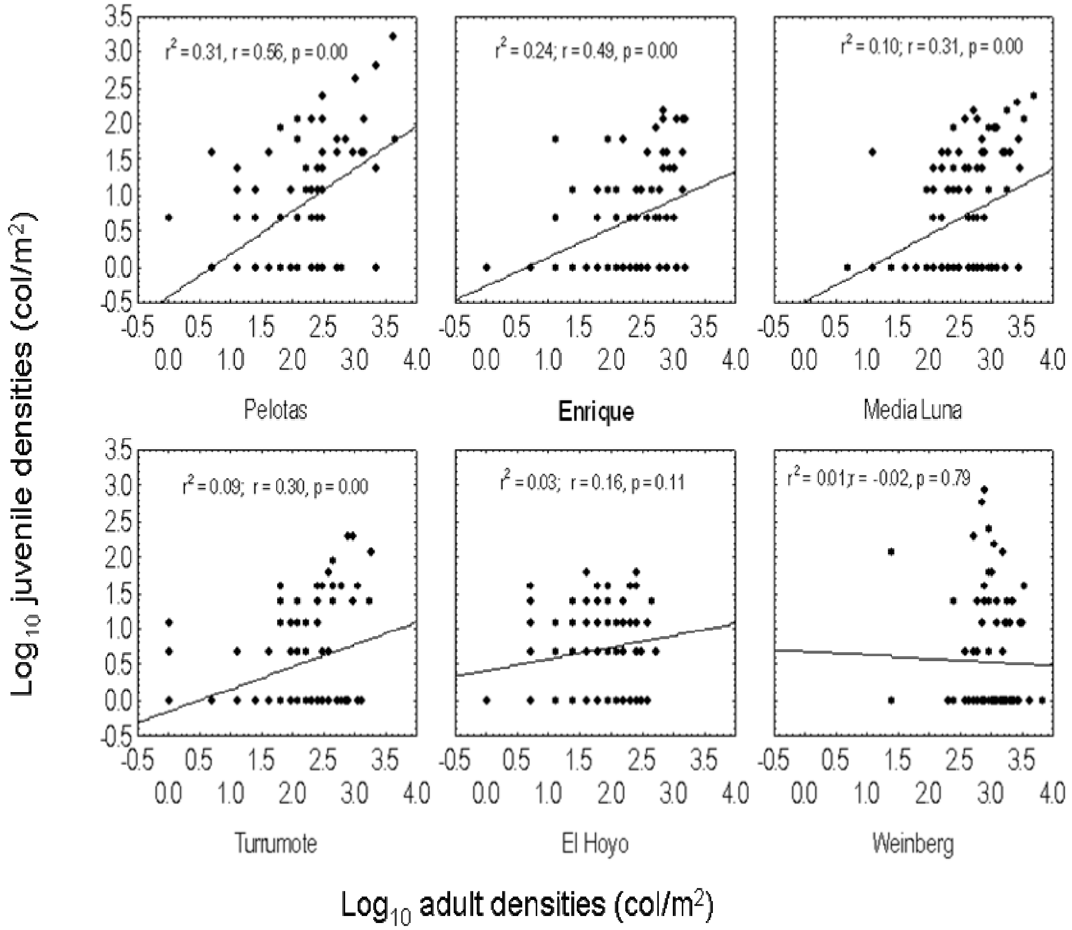


Figure 3.8 A. Correlation analysis between juvenile and adult corals across reef sites. A weakly correlation was found for Pelotas, Enrique and Media Luna.

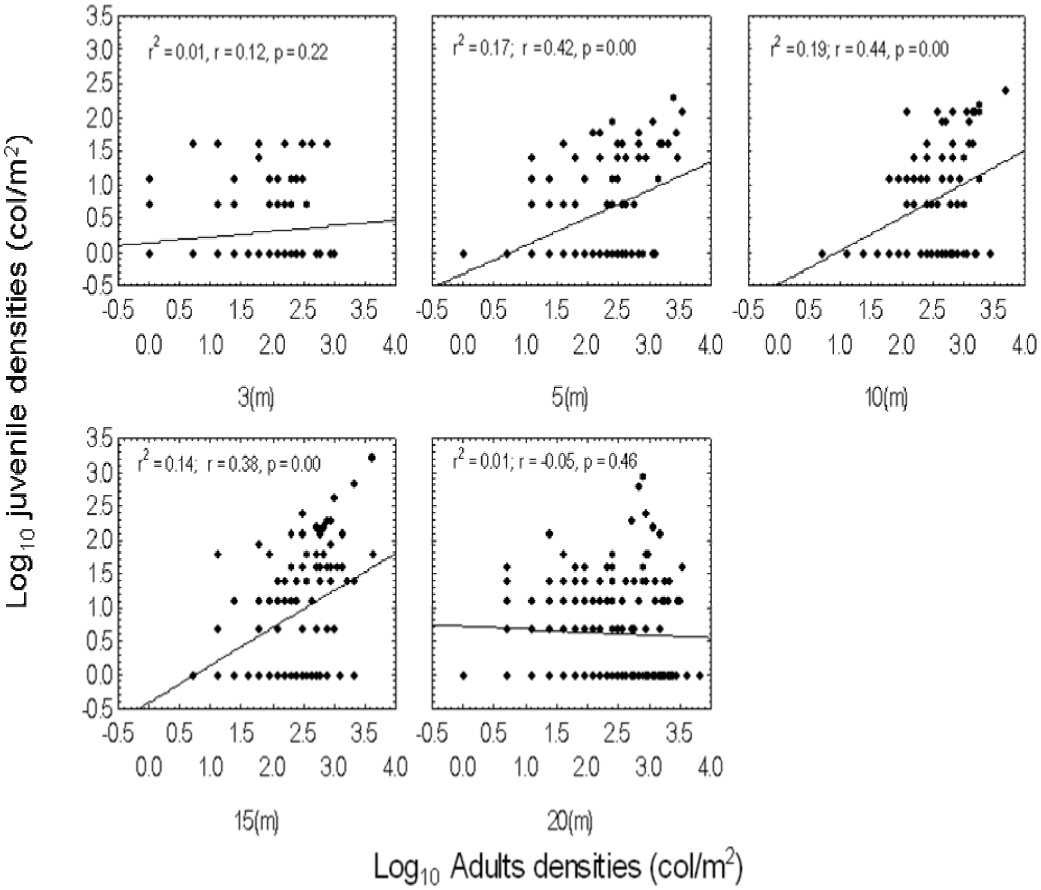


Fig 3.8 B. Correlation analysis between juvenile and adults corals densities across depth intervals. A weakly correlation was found for the 5m, 10m and 15m depth intervals.

3.6 Species composition and relative abundances of juvenile corals

Overall, 882 juvenile colonies and recruits belonging to 26 species were found in 576 m^2. The most abundance were *Siderastrea siderea* (18.03%), *Undaria sp* (15.08%), *Porites astreoides* (13.61%), *Montastraea cavernosa* (9.41%), *Stephanocoenia intercepta* (6.80%), *M.faveolata* (4.20%), *Diploria strigosa* (3.97%), *M.franksi* (3.70%) and *Madracis decactis* (3.06%) were the most abundant juveniles (Fig. 3.9).

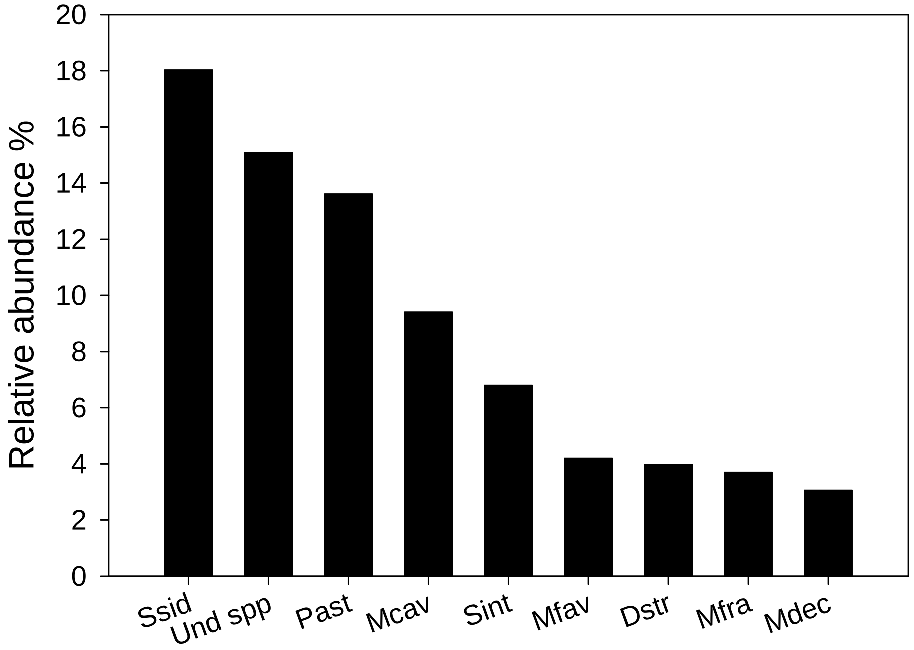


Figure 3.9 Relative abundances of the most common juvenile coral observed in La Parguera. (S.sid) = *Siderastrea siderea*, (Und sp*) = Undaria* spp, Past= *Porites astreoides*, Mcav= *Montastraea cavernosa*, Sint= *Stephanocoenia intercepta*, Mfav= *Montastraea faveolata*, Dstr= *Diploria strigosa*, Mfra= *Montastraea franksi*, Mdec= *Madracis decactis.*

3.6.1 Inner shelf zone. A total of 211 juvenile colonies and recruits of 22 coral species were observed in 96 quadrats (1m^2) surveyed in Pelotas (5.37 col/m^2). The most abundant species were *S. siderea* (16.50%), *P. astreoides* (15.50%), *S. intercepta* (13.50%), *M. cavernosa* (8.50%), *M.faveolata* (5.50%), D. *strigosa* and *M. franksi* (3.50%). All other species account for 33.5% (Fig 3.10A).

Enrique had a total of 123 juvenile colonies (1.28 col/m^2). The most abundant species observed were *S. siderea* (26.83 %), *P. astreoides* (18.70 %), *Undaria sp.* (12.2%), *M. cavernosa* (8.13 %), *M.franksi* and *D. clivosa* (4.88%). All the other species accounted for 24.38 % (Fig 3.10B).

3.6.2 Mid shelf zone. A total of 177 juvenile coral colonies from 21 coral species were observed in Media Luna (1.84 col/m^2). The most common one were *Undaria* (22.60 %), *S. siderea* (19.21 %), *D. strigosa* (12.43 %), *P. astreoides* (11.30%), *M. cavernosa* and *S. intercepta* (5.08 %) all other species accounted for (24.3 %) (Fig 3.10C). For Turrumote 108 juvenile colonies, form 18 species were observed the 96 quadrats (1.12 col/m^2). The most abundant species were *Undaria* spp. (27.78 %), *S. siderea* (19.44 %), *P.astreoides* (14.81 %), *M. faveolata* (12.04 %), *D. strigosa*, *S. intercepta* and *P. Porites* with (3.70 %) all of the other species accounted for 14.83 % (Fig 3.10D).

3.6.3 Outer shelf reef. In Weinberg, 145 juvenile colonies from 16 coral species were observed (1.51 col/m^2). *S.siderea* and *Undaria spp* had the highest abundance (19.31 % each), followed by *P.astreoides* (13.10 %), *M.franksi* (9.66 %), *M.cavernosa* (8.97 %), *M.decactis* (7.59 %) and *A.lamarcki* (2.07 %). All of the other species accounted for 19.99 % (Fig. 15E). For El Hoyo, 129 juvenile colonies from 13 coral species were observed (1.34 col/m^2). *S.siderea* (22.49 %), *P.astreoides* (20.16 %), *M.cavernosa* (16.28 %), *S.intercepta* (12.04 %), *M.faveolata* (7.75%), *M.franksi* and *M.decactis* (6.98 %), and *Undaria* spp (1.55%) were the most common species, all of the other species with (5.77 %) (Fig. 3.10F).

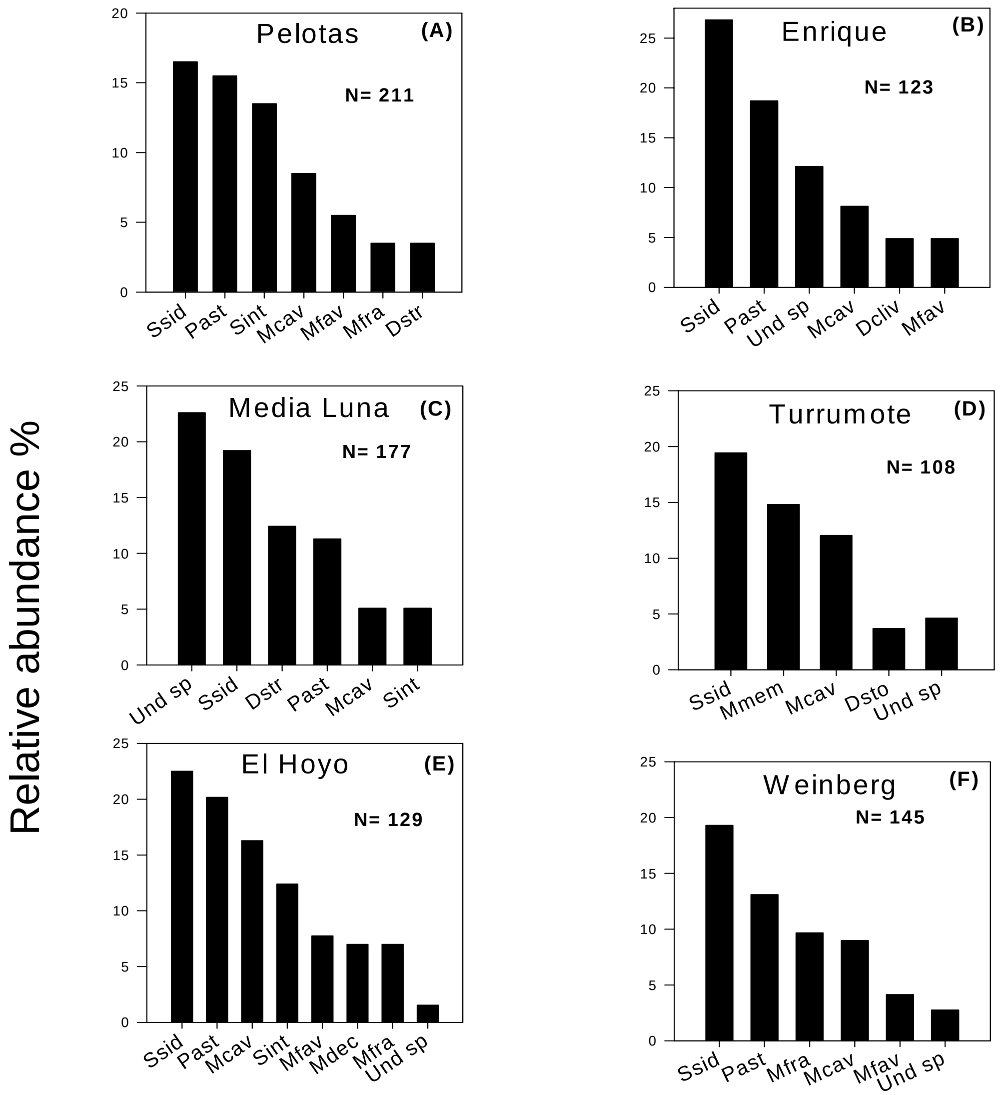
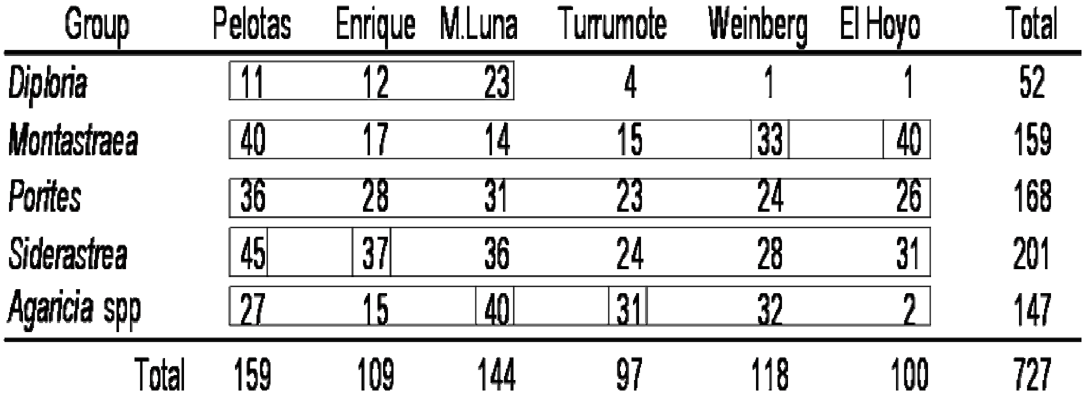


Figure 3.10 Relative abundance of the most common species observed in each reef site, N= total number of colonies for each reef site (Ssid)= *S. siderea*, (Past)= *P.astreoides*, (Mcav)= *M. cavernosa*, (Und spp)= *Undaria*, (Mfra)= *M. franksi*, (Mfav)= *M. faveolata*, (Mmem)= *M. memoriallis*, (Dsto)= *D. stockesi*, (Sint)= *S. intercepta*, (Mdec)= *M. decactis*.

3.6.4 Juvenile composition across reef sites and across depths intervals

The abundance of the five most common genera (*Diploria*, *Montastraea*, *Porites*, *Siderastrea* and *Agaricia*) were significantly different across reefs and amongst genera (G= 111.93, df= 20, p<0.05). Among reef sites, the genera *Diploria* was most abundant in the inner and mid-shelf reefs while *Montastraea, Porites, Siderastrea* and *Agaricia* were evenly distributed amongst reef sites. Likely, comparisons amongst genera within reefs shows that *Siderastrea* were more abundant in the inner reefs, *Agaricia* in the mid shelf reef and *Montastraea* were the most abundant genera in the outer reefs (Table 3.3).

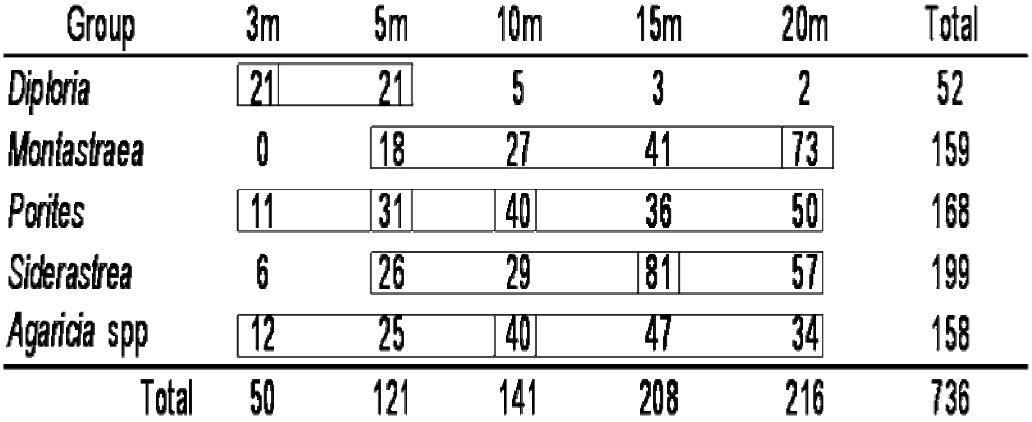
Table 3.3 Abundance (total colonies in each site) of juvenile corals genera compared among site and genera. Black and white bars shows the distribution of the genera across reef sites and small squares shows comparison among genera within reef (G= 111.93, df= 20, p<0.05).



Group	Pelotas	Enrique	M.Luna	Turrumote	Weinberg	El Hoyo	Total
Diploria	11	12	23	4	1	1	52
Montastraea	40	17	14	15	33	40	159
Porites	36	28	31	23	24	26	168
Siderastrea	45	37	36	24	28	31	201
Agaricia spp	27	15	40	31	32	2	147
Total	159	109	144	97	118	100	727

The abundances of the five most common juvenile genera pooled across genera (*Diploria, Montastraea, Porites, Siderastrea and Agaricia*) and across depth (regardless of site) were significantly different (G= 158.69, df= 16, p<0.05). *Diploria* showed to be the most abundant genera in the shallow habitat (3-5m), *Montastraea* and *Siderastrea* were the most abundant genera in the intermediate and intermediate deep habitat (10-20m) while, *Porites* and *Agaricia* were evenly abundant across all depth intervals (Table 3.4). From the Correspondence analysis (CA) an inshore-offshore gradient can be inferred, which explained the 54.70 % of the total chi-square. It can be seeing the genera *Diploria* were most abundant in the inner reef while *Siderastrea*, Porites, Agaricia and Montastraea were distributed along the mid and outer shelf. (Fig 3.11).

Table 3.4 Abundance (total colonies across depth) of juvenile coral genera compare among depth and genera. Juvenile genera were significantly depth dependent (G= 158.69, df= 16, $p<0.05$).



Group	3m	5m	10m	15m	20m	Total
Diploria	21	21	5	3	2	52
Montastraea	0	18	27	41	73	159
Porites	11	31	40	36	50	168
Siderastrea	6	26	29	81	57	199
Agaricia spp	12	25	40	47	34	158
Total	50	121	141	208	216	736

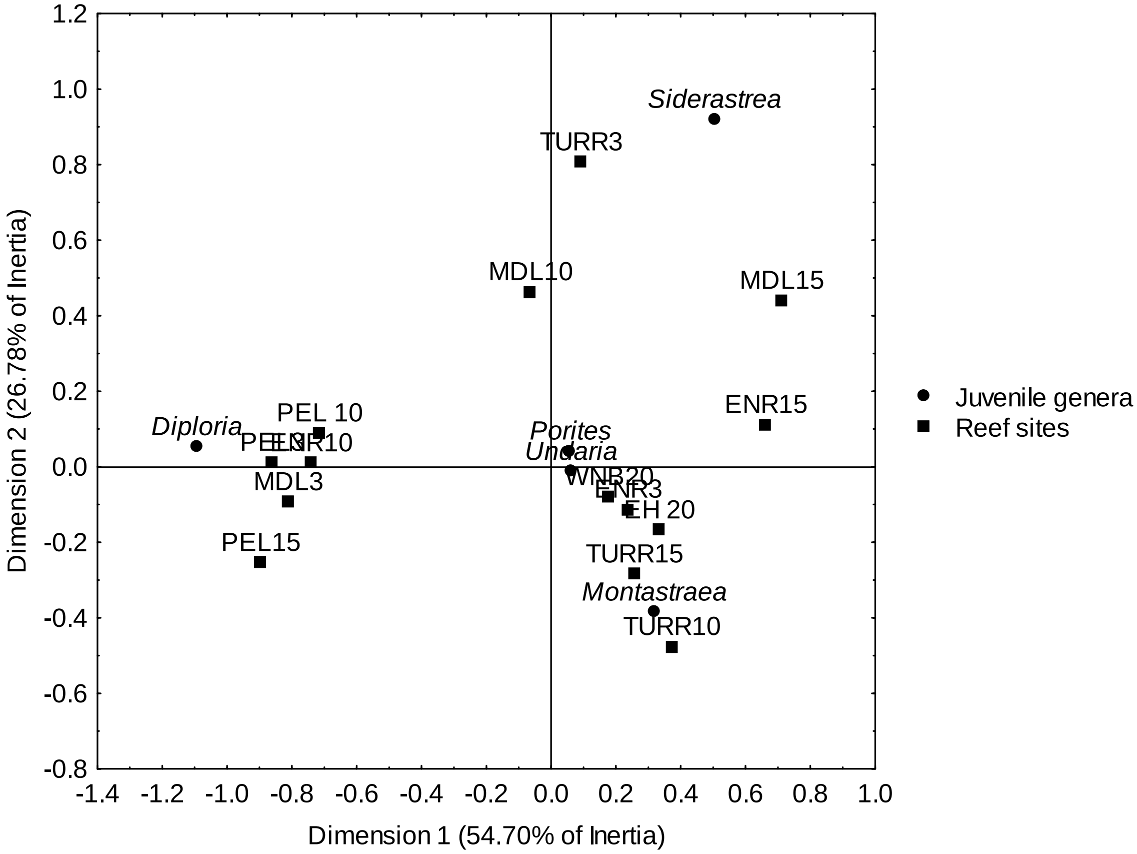


Figure 3.11 Correspondence analyses (CA) biplot showing the distribution of juvenile coral genera (dots) and reef site (depth) (squares). An inshore-offshore gradient can be inferred along the first dimension explained by 54.70% of the total chi-square.

3.7 Survivorship and new recruits of juvenile corals (Permanent quadrats 0.25m^2)

3.7.1 Pelotas.

89 juvenile coral were counted on August 2003 in 96 quadrats and only 43 juvenile colonies were found alive in August 2005 (50%) mortality. Juvenile coral density decreased significantly from 0.93 to 0.45 col/0.25m^2 (Repeated measurement Anova, F= 32.90, p>0.05) (Fig 3.14A). However, no significant differences in juvenile densities were found within depth intervals across time in Pelotas (RM Anova, F= 2.14, p=0.09) (Fig 3.14B). The proportions of live

juveniles differed significantly within depth intervals and survivorship was higher in deep habitat while lower in the shallow and intermediate habitat (4 x 2 contingency table, G= 11.90, df= 3, p<0.05) (Table 3.6). Species that showed high survivorship were *D.labyrinthiformis*, *P.astreoides* and *Undaria spp.* (11.11%) and *D.strigosa* (7.41%) at 5m, *C.natans* and *P.astreoides* (12.50%) at 10m and *C.natans* (20%), *S.siderea* (11.43%), *D.strigosa* and *M.franksi* (8.57%) at 20m. (Table 3.5).

Table 3.5 Juvenile survivorship (%) across depth intervals for Pelotas. Overall survivorship was high in the deep habitat (15m).

Juvenile coral species	3m	5m	10m	15m
F.fragum	-	3.70	-	-
L.cucullata	-	-	-	-
M.faveolata	-	3.70	-	-
Undaria	-	11.11	-	-
C.natans	-	-	12.50	20.00
S.siderea	-	-	-	11.43
D.strigosa	-	7.41	-	8.57
M.franksi	-	-	-	8.57
M.meandrina	-	-	4.17	5.71
P.astreoides	-	11.11	12.50	2.86
Agaricia sp.	-	-	-	2.86
D.labyrinthiformis	-	11.11	-	2.86
M.cavernosa	-	-	-	2.86

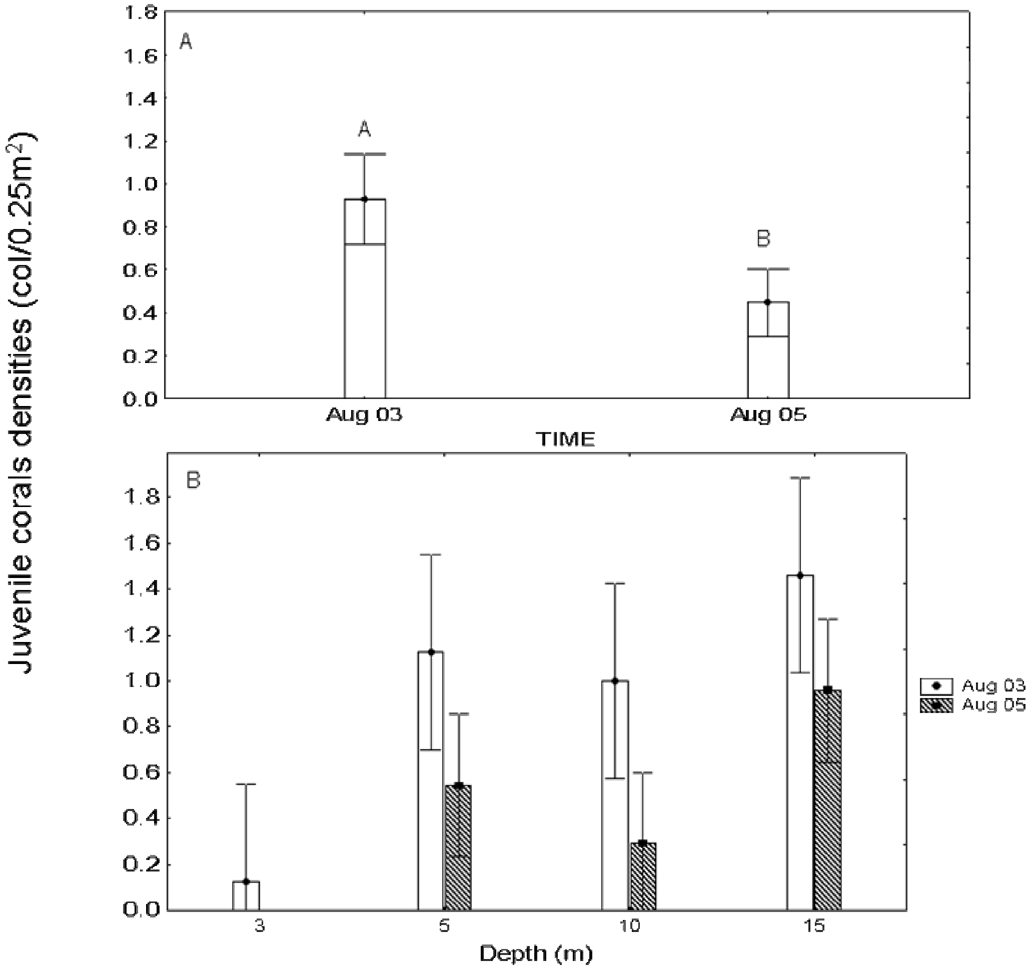
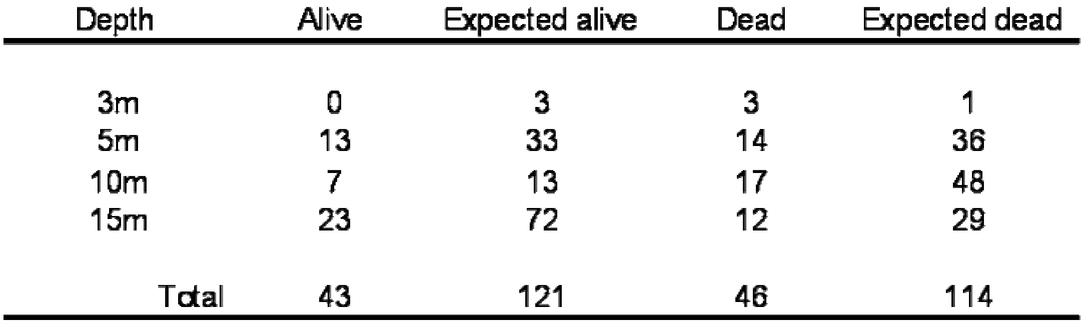


Figure 3.12 Mean juvenile density (± SE) for Pelotas between August 2003 and August 2005 (A) and between time within depth intervals (B). No significant differences were found in the mean density of juvenile coral between depth intervals within time.

Table 3.6 Total number of juvenile colonies alive (2) column and dead (4) column in each depth intervals for Pelotas. Survivorship of juvenile corals was dependent of depth intervals and higher in deep habitat (G= 11.90, df= 3, p<0.05).



Depth	Alive	Expected alive	Dead	Expected dead
3m	0	3	3	1
5m	13	33	14	36
10m	7	13	17	48
15m	23	72	12	29
Total	43	121	46	114

3.7.2 Enrique

In Enrique, 74 of the 94 juvenile corals surveyed in the first census were alive in August 2005 (78.73%) survivorship. No significant differences in juvenile densities were observed between August 2003 to August 2005 (0.97 to 0.77 col/0.25m^2) (RM Anova, F= 9.93, df= 1, p<0.01) (Fig 3.16A). No significant differences in juvenile densities within depth intervals across time (RM Anova F= 1.38, df= 3, p>0.05) (Fig 3.16B) were found. Survivorship was high at all depths (Fig 3.15B). Species that showed high survivorship were *P.astreoides* (28.57%), *S.siderea* (23.81%), *D.clivosa* and *P.porites* (9.52%) at 3m. *S.siderea* (35.90%), *P.astreoides* (12.82%) and *D.strigosa* (10.26%) at 5m. *S.siderea* (33.33%), *D.strigosa* and *P.astreoides* (11.11%) at 10m and *S.siderea* (37.50%) and *S.intercepta* (12.50%), lastly *M.faveolata*, *M.ferox*, *M.franksi*, *M.meandrites*, *P.astreoides* and *Undaria* with (6.25%) of survivorship (Table 3.7).

Table 3.7 Juvenile coral survivorship (%) across depth intervals for Enrique. Overall, high survivorship were observed across depth intervals.

juvenile coral species	3m	5m	10m	15m
C.natans	-	-	5.56	-
D.clivosa	9.52	5.13	5.56	-
D.labyrinthiformis	-	2.56	5.56	-
D.strigosa	4.76	10.26	11.11	-
M.cavernosa	-	2.56	5.56	-
M.faveolata	-	2.56	-	6.25
M.ferox	-	-	-	6.25
M.franksi	-	-	-	6.25
M.meandrites	-	-	-	6.25
P.astreoides	28.57	12.82	11.11	6.25
P.porites	9.52	-	-	-
S.intercepta	-	-	-	12.50
S.siderea	23.81	35.90	33.33	37.50
Undaria sp	-	2.56	-	6.25

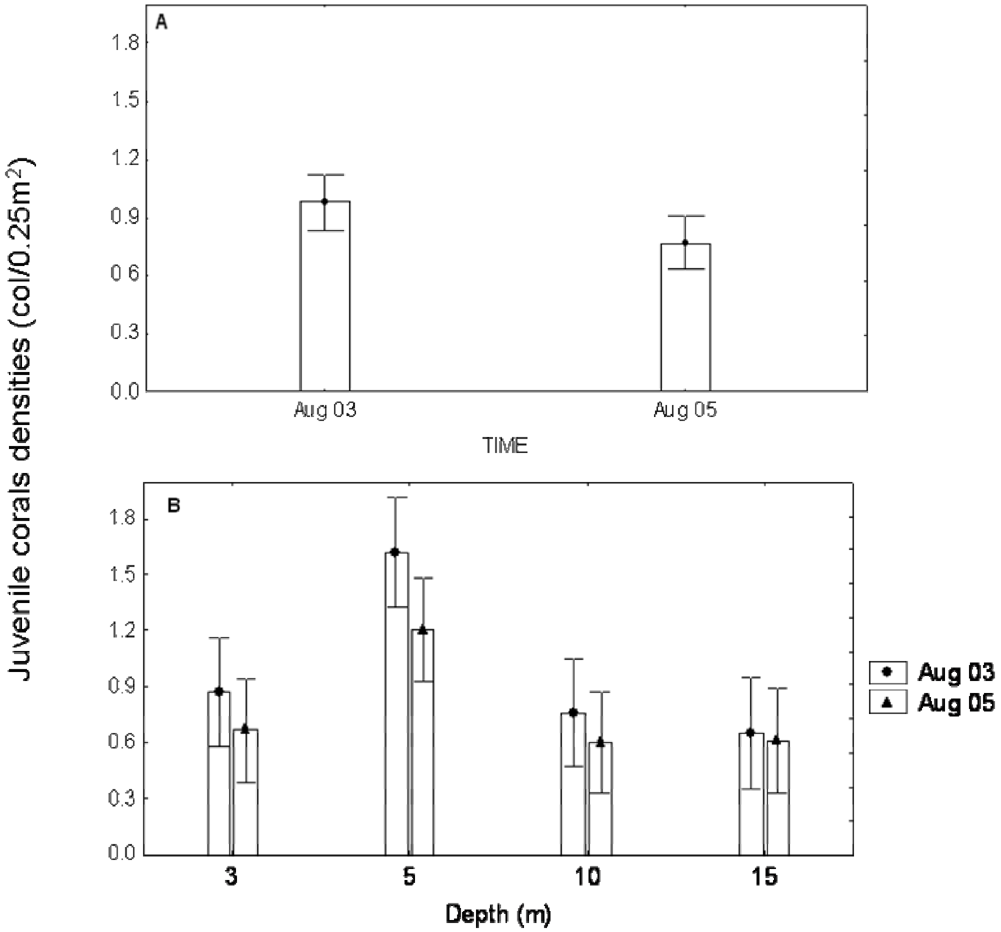


Figure 3.16 Mean juvenile densities (± 0.95 CI) for Enrique in August 2003-August 2005 (A). Mean of juvenile densities within each depth across time (B). No significant difference were found

3.7.3 Media Luna.

Only 58 of the 147 juvenile corals observed in August 2003 were found alive in 2005 (% 39) survivorship. Juvenile densities were significantly lower in August 2005, from 1.53 to 0.60 col/0.25m^2 (RM ANOVA, F= 66.44, df= 1; $p<0.05$) and within depth intervals across time (RM ANOVA, F= 4.35, df= 3; $p<0.05$). Lower juvenile densities were observed in the shallow habitat (3m) (1.50 to 0.54 col/0.25m^2) and intermediate shallow habitat (5m) (1.95 to 0.37 col/0.25m^2)

(Tukey HSD, $p<0.01$) (Fig 3.17A). No significant differences were found at the intermediate deep habitat (10m) (1.04 to 0.52 col/0.25m^2) and deep habitat (15m) (1.65 to 1.00 col/0.25m^2) across time (Tukey HSD, $p<0.01$) (Fig. 3.17B). Species that showed high survivorship among depth intervals were *A.lamarcki* and *C.natans* both with (8.33%), at (10m), *M.cavernosa* (5.56 to 2.13%) at 5m and 3m respectively, *P.astreoides* 16.67% to 2.13% and *S.siderea* 2.78-30.00% at 10m and 15m respectively (Table 3.8). Overall, survivorship was low in shallow habitats (36% of survivorship) and high at intermediate deep and deep habitats (54.17% and 57.50 %) respectively (4 x 2 contingency table, G= 10.74, df= 3, $p<0.05$) (Table 3.9)

3.7.4 Turrumote.

A total of 82 juvenile coral colonies of the 142 juveniles observed in August 2003 were found alive in August 2005 representing a significant reduction from 1.50 to 0.87 col/0.25m^2 (RM ANOVA, F= 7.38, $p<0.05$) (Fig 3.19A). However, no significant differences were found within depth intervals across time (RM ANOAV, F= 0.52, p= 0.66) (Fig. 3.19B). Juvenile coral survivorship live proportions was relatively high at the shallow habitat (79.49%) and deep habitat (79.59%) (4 x 2 G= 47.31, df= 3, $p<0.05$) (Table 3.10). The species with higher survivorship at this two zone were *D.clivosa* (10.26%), *P.astreoides* (12.82%), *S.siderea* (20.51%) in 3m and *M.faveolata* (4.08%), *M.meandrites* (4.08%), *S.siderea* (53.06%), *Undaria sp*. (8.16%) in 15m (Table 3.11).

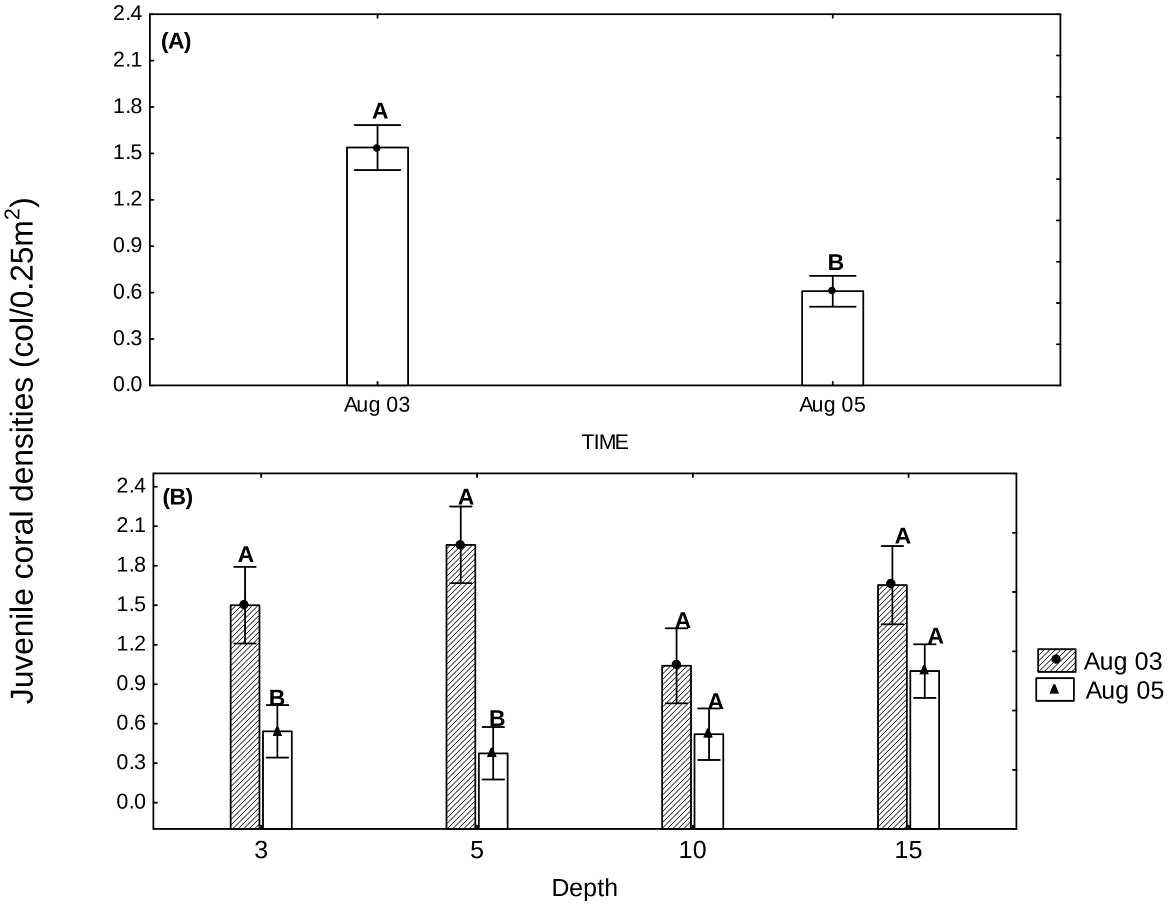
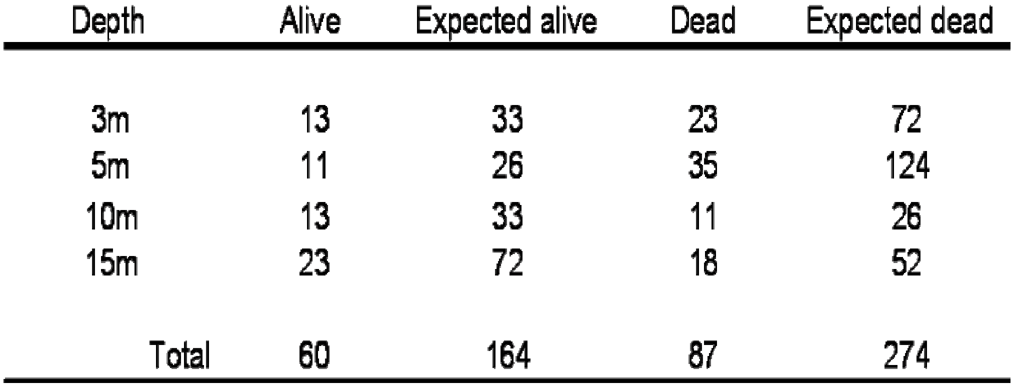


Figure 3.17 Mean juvenile densities (± 0.95 CI) for Media Luna between August 2003 and August 2005 (A), and within depth intervals across time (B). Survivorship was significantly lower in the shallow (3m) and intermediate (5m) habitat and relatively higher in the intermediate deep (10m) and deep habitat (15m) (Tukey HSD $p<0.05$).

Table 3.8 Percent survivorship of juvenile coral species between depth intervals for Media Luna. Overall survivorship was low in the shallow habitat and high in the intermediate and deep habitats (G= 10.74, df= 3, p<0.05).

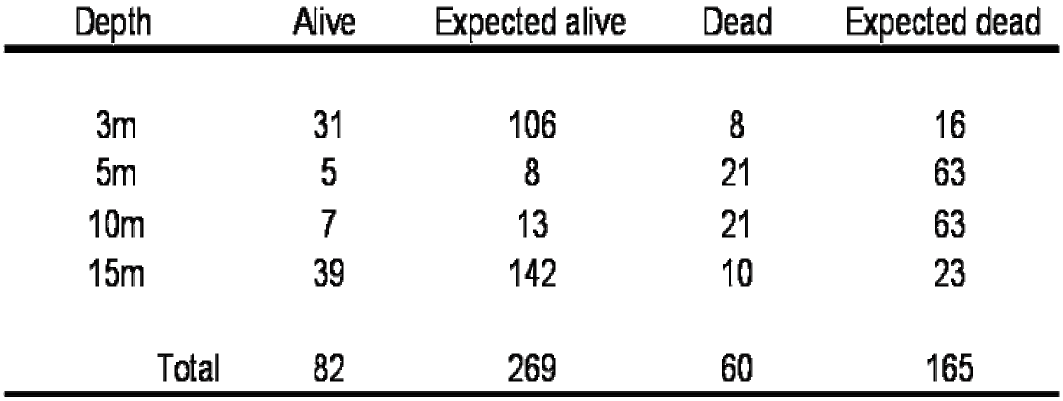
Juvenile coral	3m	5m	10m	15m
A.lamarki	-	-	8.33	-
C.natans	-	-	8.33	-
D.clivosa	-	2.13	-	-
D.labyrinthiformis	-	-	-	-
D.strigosa	19.44	8.51	-	-
E.fastigiata	-	-	-	2.50
I.rigida	-	2.13	-	-
L.cucullata	-	-	4.17	-
M.angulosa	-	-	4.17	-
M.cavernosa	5.56	2.13	-	2.50
M.faveolata	-	-	-	2.50
M.ferox	-	-	-	-
M.franksi	-	-	-	5.00
M.meandrites	-	-	-	2.50
M.memorialis	-	-	-	5.00
P.astreoides	8.33	2.13	16.67	-
P.divaricata	-	-	-	2.50
S.intercepta	-	-	-	2.50
S.lacera	-	-	-	2.50
S.radians	-	-	4.17	-
S.siderea	2.78	-	8.33	30.00
Undaria sp.	-	2.13	-	-

Table 3.9 Contingency table of the total number of colonies observed and expected alive and dead for Media Luna. Survivorship was significantly higher at intermediate deep and deep habitats (G= 10.74, df= 3, p<0.05).



Depth	Alive	Expected alive	Dead	Expected dead
3m	13	33	23	72
5m	11	26	35	124
10m	13	33	11	26
15m	23	72	18	52
Total	60	164	87	274

Table 3.10 Contingency table of the total number of colonies observed and expected alive and dead for Turrumote. Survivorship was significantly higher in shallow and deep habitats (G=47.31, df=3, p<0.05).



Depth	Alive	Expected alive	Dead	Expected dead
3m	31	106	8	16
5m	5	8	21	63
10m	7	13	21	63
15m	39	142	10	23
Total	82	269	60	165

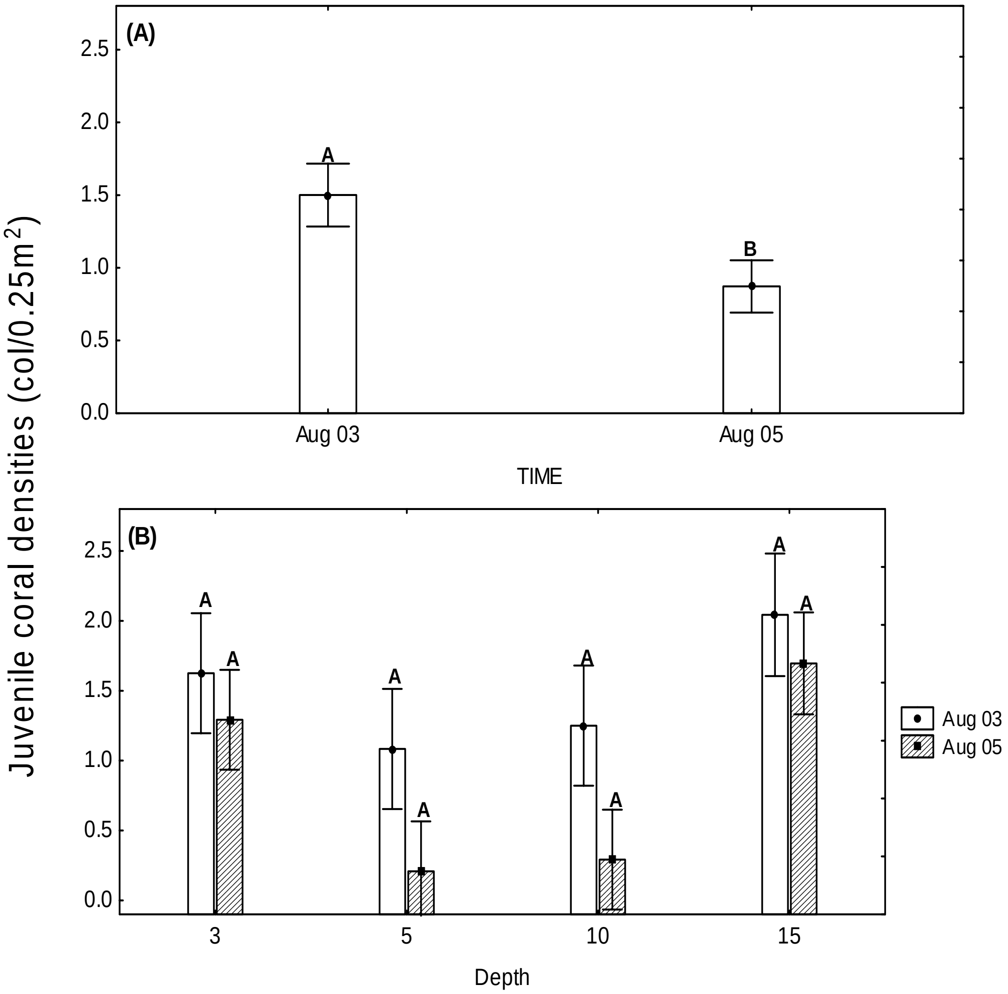


Figure 3.18 Mean juvenile density (col/0.25m^2) (± SE) for Turrumote between August 2003 and August 2005 (A) and within depth intervals between time (B). No significant differences were found between time intervals (RM Anova, $p>0.05$).

Table 3.11 Survivorship of juvenile coral species between depth intervals for Turrumote. Overall, survivorship was higher at shallow (3m) and deep habitats (15m).

Juvenile corals	3m	5m	10m	15m
A.palmata	2.56	-	-	-
D.clivosa	10.26	-	-	-
D.strigosa	-	-	-	2.04
I.rigida	-	-	-	-
L.cucullata	-	-	-	2.04
M.cavernosa	-	-	-	2.04
M.faveolata	-	-	10.71	4.08
M.meandrites	-	-	-	4.08
P.astreoides	12.82	7.69	3.57	-
S.radians	28.21	-	-	-
S.siderea	20.51	7.69	7.14	53.06
Undaria sp.	5.13	3.85	3.57	8.16

3.7.5 Weinberg and El Hoyo

A total of 80 colonies out of 127 juvenile corals survived in Weinberg (62% survivorship) and only 59 colonies out of 121 juvenile corals survived (48% survivorship) El Hoyo. Juvenile coral densities were significantly lower from August 2003 1.29 col/0.25m^2 to August 2005 0.72 col/0.25m^2 in the outer shelf zone (RM Anova, F= 76.48, $p<0.05$) (Fig 3.20A). However, No significant difference were found between juvenile densities in August 2003 and August 2005 within reef (RM Anova, F= 1.34, $p>0.05$) (Fig 3.20B). Proportions of live juvenile corals were significantly higher in Weinberg compared to El Hoyo (2 x 2 contingency table, G= 5.11, df= 1, $p<0.05$). Species with higher survivorship in Weinberg were *M.cavernosa* (4.72%), *P.astreoides* (14.17%) and *S.siderea* (20.47%). While in El Hoyo *S.siderea* (18.18%), *P.astreoides* (8.26%), *S.intercepta* (5.79%), *M.franksi* and *M.decactis* (4.13%) were the one with high survivorship.

Overall, survivorship was higher in Weinberg (62% of survivorship) that in El Hoyo (48% survivorship).

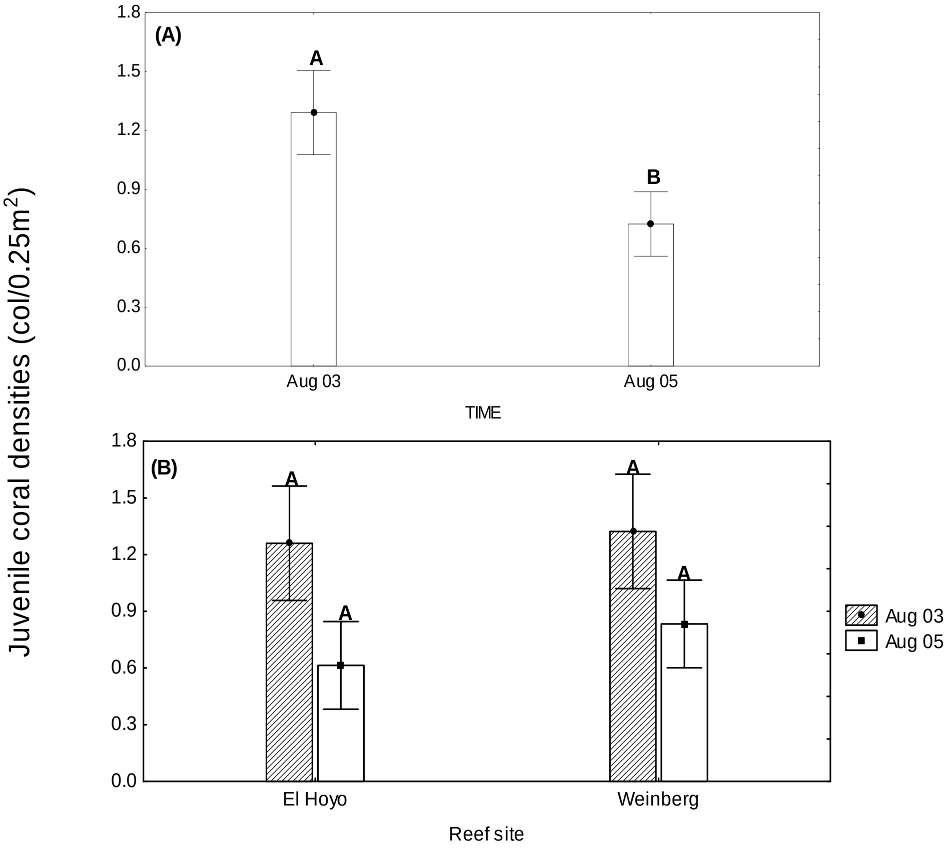
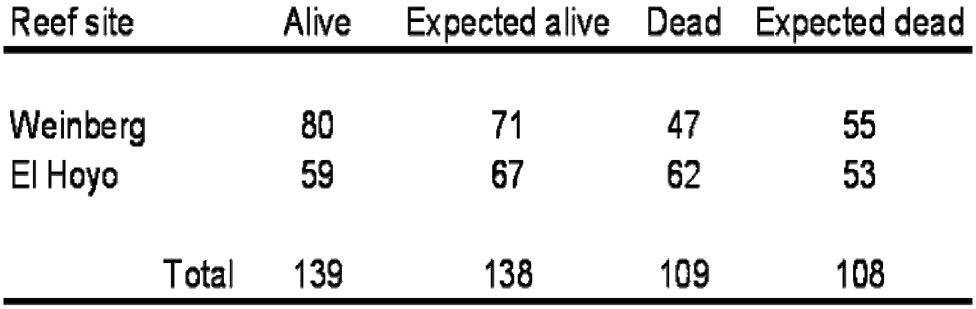


Figure 3.20 Differences in mean juvenile densities (± 0.95 CI) between August 2003 and 2005 for the outer shelf reef (Weinberg and El Hoyo combined) (A) and (B) Weinberg and El Hoyo between time intervals. No significant differences were found (RM- Anova, p>0.05).

Table 3.12 Contingency table of the total number of colonies observed and expected alive and dead for Weinberg and El Hoyo. Juvenile survivorship was higher for Weinberg compared to El Hoyo (G= 5.11, df= 1, p<0.05).



Reef site	Alive	Expected alive	Dead	Expected dead
Weinberg	80	71	47	55
El Hoyo	59	67	62	53
Total	139	138	109	108

3.7.6 Juvenile survivorship across reefs

Overall, juvenile densities decreased significantly from August 2003 to August 2005 (RM, Anova, F= 120.78, p<0.05). Lower survivorship was observed for Pelotas (48%), Media Luna (39%) and El Hoyo (49%), while a significantly higher survivorship was observed for Enrique (79%), Turrumote (58%) and Weinberg (63%) (RM Anova, F= 3.58, p<0.05) (Fig. 3.21). Survivorship of abundant genus (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 extract 74% of the total variability in the first two axis. Based on the (CA) scores the first axis showed and ordination of juvenile coral genera with respect to an inshore-depth gradient (Table 3.13). It can be inferred that *Montastraea* spp, *Undaria* spp and *Siderastrea* spp, survived better in deeper habitats (15m>), while *Porites* spp., and *Diploria* spp., may have a did better in the inshore shallow reef habitats (Fig. 3.22).

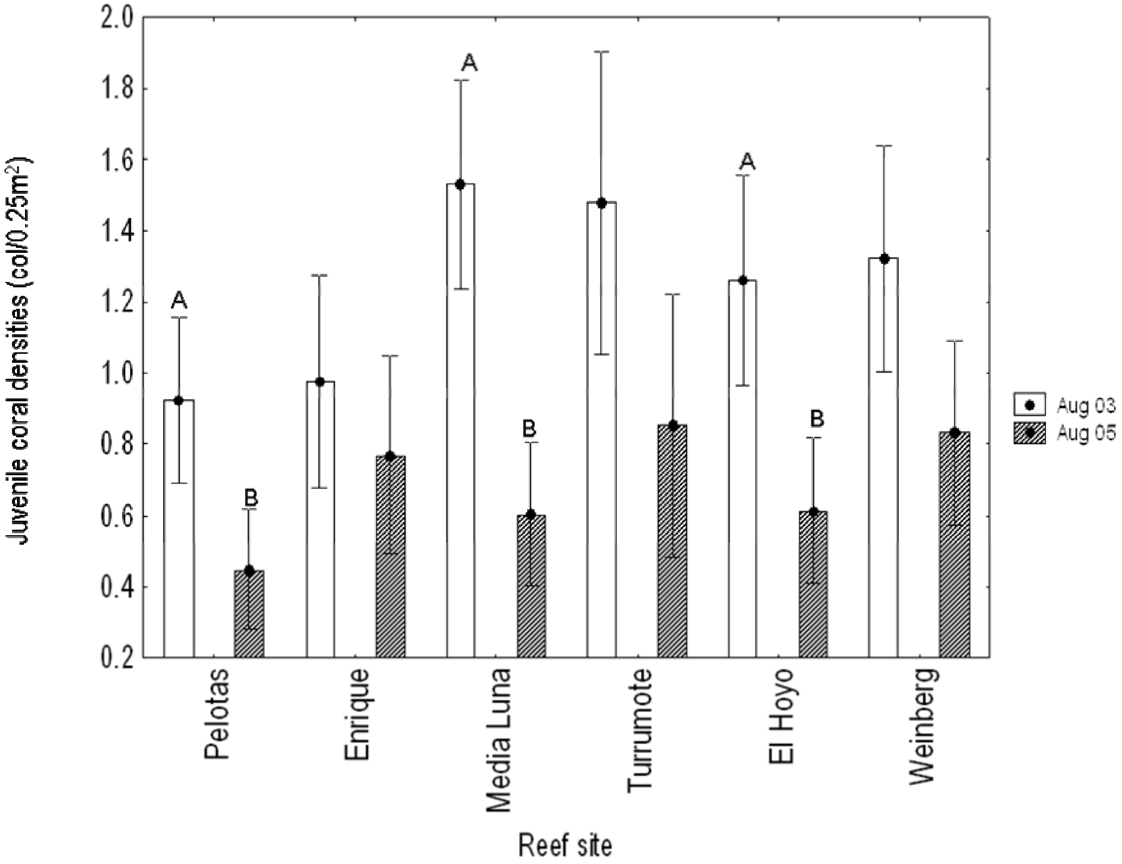


Figure 3.21 Mean (± 0.95 CI) juvenile densities compare within reef sites from August 2003 to August 2005. Juvenile densities decreased significantly in Pelotas, Media Luna and El Hoyo. While survivorship was relatively higher for Enrique, Turrumote and Weinberg. (Tukey HSD, $p<0.05$).

Overall abundances (i.e. survivorship) of juvenile coral based on reproductive strategies (i.e. spawners and brooders) showed a significant difference among depth intervals (2 X 5 contingency table, G= 25.54, df= 4, $p<0.05$) (Table 3.14) but not among reef site (2 x 6 contingency table G= 5.52, df= 5, $p> 0.05$). Proportions of spawners and brooders compare among depth intervals showed that it was 4 times more probable for spawners to survive at 15-meter, while survivorship for brooders was one and 2 times more likely between 3 and 20 meter (Fig. 3.23).

Table. 3.13 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	*deep*

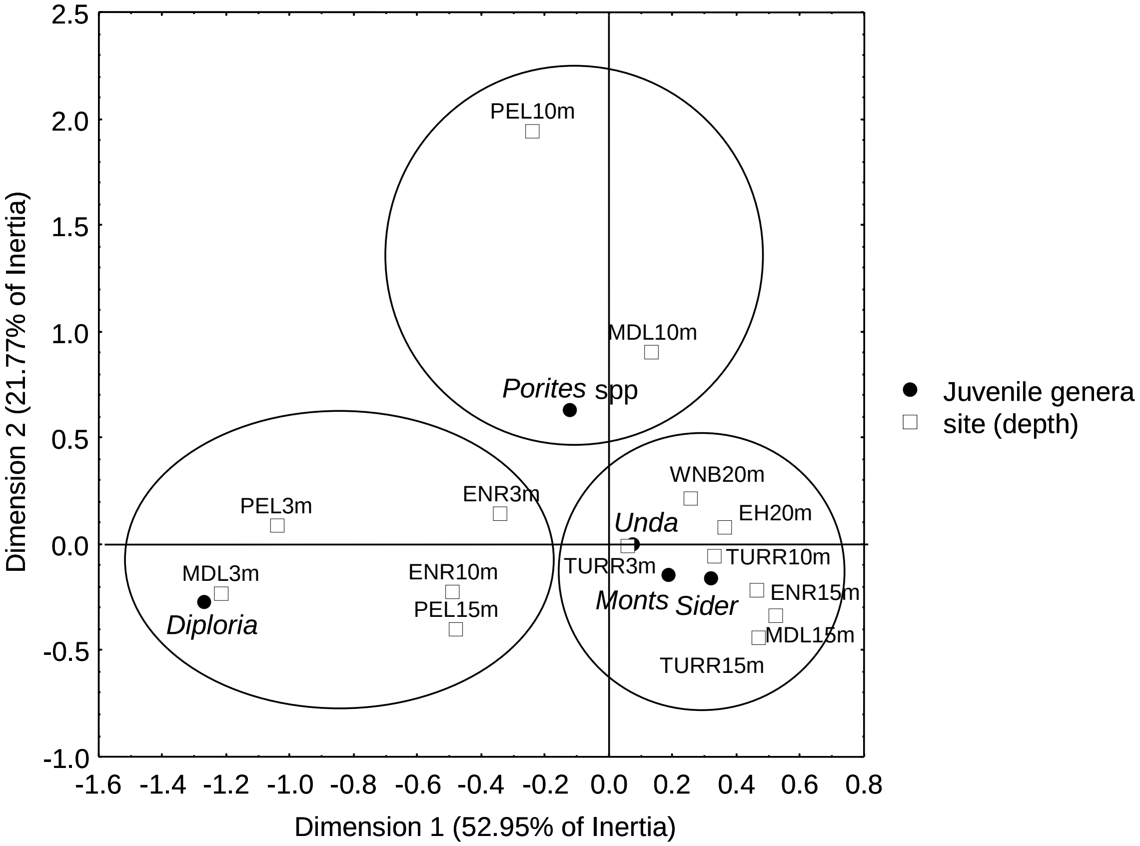
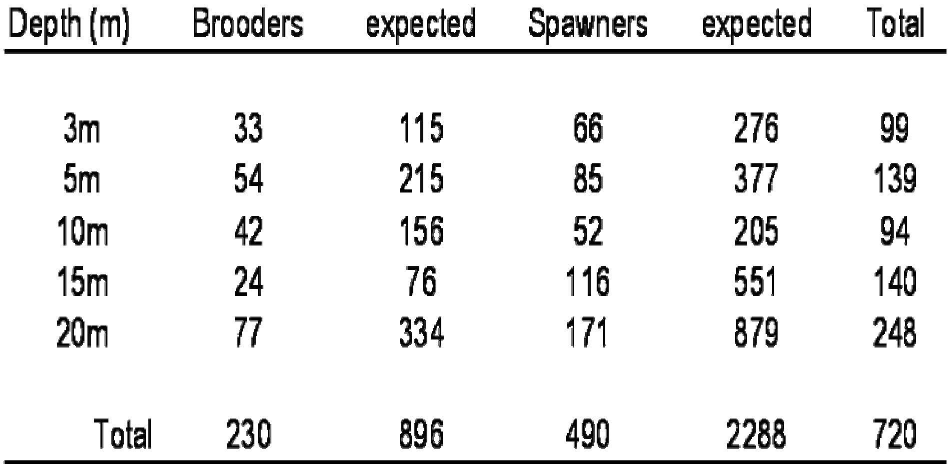


Figure 3.22 Correspondence analysis (CA) biplot showing the ordination of juvenile genera along the first dimension with respect to an inshore-depth gradient. Juvenile colonies are based on colonies alive in August 2005.

Table 3.14 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

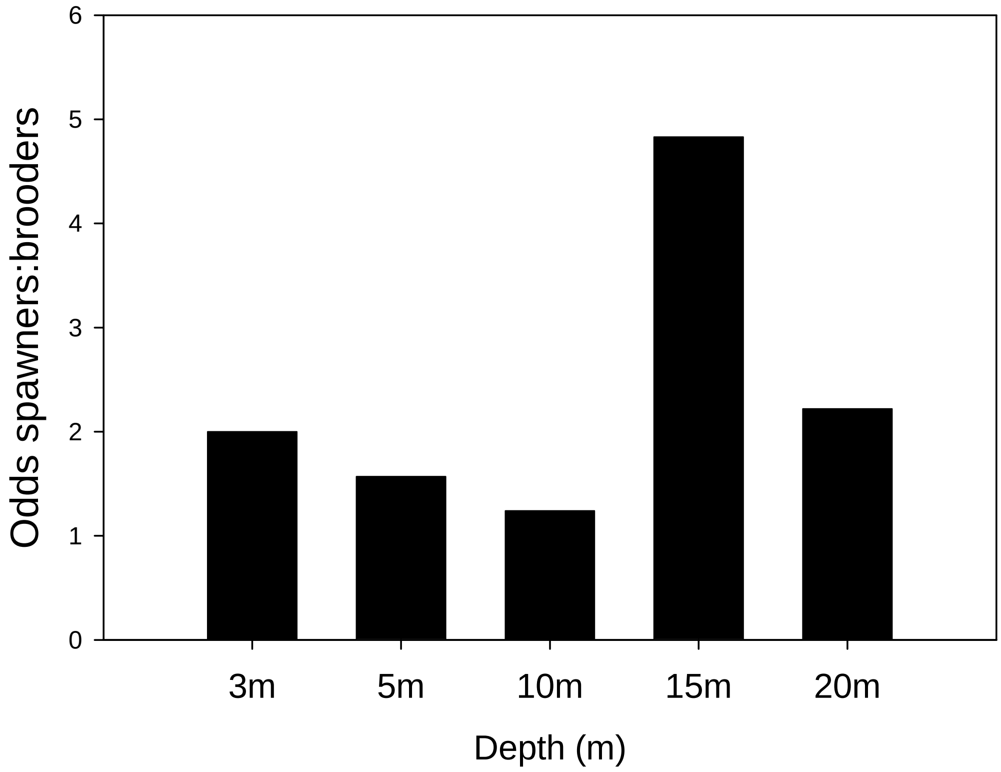


Figure 3.23 Analysis of proportions spawners/brooders pooled among depth intervals (regardless of reef sites). Spawners were almost 5 times more likely to survive than to die at 15m that a brooder.

4. Discussion

4.1 Abundance, composition and distribution of juvenile corals

Coral reefs in La Parguera have been studied for over 28 years with important contributions to the knowledge of these marine ecosystems in the southwestern Puerto Rico (Morelock 1977; Weinberg 1987; Garcia *et al.* 1998). Studies of recruitment conducted in octocoral communities showed juvenile densities ranging between 9.8 to 62.3 col/m^2 (Yoshioka 1996). However, coral recruitment studies have been lacking. In this study, a total of 882 juvenile corals belonging to 26 species were found in an reef area of 576 m^2. The average density of juvenile corals in La Parguera was 1.5 col/m^2, similar to densities (1.2 to 3.4 col/m^2) found in other recruitment studies for reefs in the Caribbean (Chiappone and Sullivan 1996, Miller et al. 2000; Ruiz and Arias 2004). Overall, juvenile densities increased from shallow habitats (lowest densities) to intermediate and deep habitats within reefs. Indeed, juvenile densities showed to be higher at intermediate deep (10-15m) habitats which accounted for 85 % of the total variability among the five spatial scales evaluated (quadrats within transects, transects within depths, depths within reefs and reefs within zones) across the insular shelf of La Parguera. Substrate monopolization (interaction with other benthic organisms), sediment transport (i.e. bedload) and reef topography all may affect recruitment and survival of juveniles. In this study, shallow habitats of the inner and mid shelf reefs (i.e. Pelotas, Enrique, Turrumote and Media Luna), were characterized by high wave movement and constant resuspension of coarse sediment. This type of stress have caused smothering and burial of octocoral recruits (Yoshioka 1996) and could also affect the distribution and orientation of coral recruits since juvenile colonies are sessile and subjected to sediment movement across the reef bottom (Rogers 1997). Similarly, at intermediate habitats the majority of surviving juvenile corals were found mostly on vertical substrates and sometimes at the edge of some hard substrata. While at deep habitats, juvenile corals were observed under bigger colonies showing variable orientation. Juvenile corals were not observed on flat areas in deeper habitats, even at the outer shelf. In Pelotas and Enrique, juveniles were more often observed growing onto vertical walls. The lack of correlations between rugosity and juvenile abundance suggest that substratum orientation could more important for coral recruitment than rugosity. This is consistent with previous studies in coral recruitment where correlation between rugosity and juvenile abundance has never been found (Huitric and Mcfield 2000; Edmunds 2004). Sediment will tend to roll down or not contact vertical surfaces therefore juvenile will have higher survivorship in this kind of habitats, consistent with observations made by Edmunds (2004) that showed most recruits between 14 and 26 meter were found in cryptic and exposed surfaces.

In deeper habitats, low light conditions and the interactions with other reef organisms (i.e. sponges, other corals, algae) for space might limit the settlement and or survivorship of some species and only few might overcome these conditions. Thus, intermediate habitats may provide settlers better environmental conditions favoring the settlement and survivorship of more species as predicted by the intermediate disturbance hypothesis (Connell 1978; Connell *et al.* 1997). However, the results of this study contrast a little with those of Chiappone and Sullivan (1996) which found a slightly increase in juvenile density with increasing depth and a shift in species composition based on reproductive strategies. It has been highlighted that coral recruitment is control by biological and physicochemical factors that affect recruitment to the benthos (Harriot and Fick 1987). These factors include substratum availability, fecundity, and mode of reproduction, disturbance, predation (e.g. gastropods) and grazing (e.g. sea urchins and parrotfish). While the physicochemical constrains include (1) temperature, (2) radiation (3) wave action, (4) sedimentation (5) rugosity and (6) substrate orientation (e.g. vertical or horizontal surfaces) (Smith 1997; Edmunds 2004). Likewise, Smith (1997) found the highest settlement rates at intermediate depth but with a shift towards vertical surfaces at deepest habitats. Furthermore, Rogers (1984) observed the majority of juvenile corals at intermediate depths with a similar orientation patterns. Even though substrate orientation was not assessed in this study, juvenile abundances tended to increase at intermediate habitats and in vertical substrates (Personal observation).

The results of this study are also consistent with the finding of Ruiz and Arias (2004), who found that the variability of juvenile corals in the Mesoamerican Barrier Reef System were explained by the smallest spatial scale (transect and sites). They explained this variability in view of the interaction of geological features, hydrological effluents and frequency and intensity of disturbances (i.e. storms). These gradients allow the colonization of different species able to exploit each of the different habitat conditions. Even though rugosity and coral cover where higher at intermediate depths, neither reef rugosity nor the coral cover was significantly correlated with juvenile coral density at intermediate habitats. Both factors might influence juvenile coral densities as living coral tissues can reduce the substrate availability for coral larvae recruitment and force them to settle into other habitats where substrate could not be adequate. While different topographic relief (i.e. rugosity) may enhance different degrees of exposure to environmental and biological gradients, factors such as coral-algae interactions, predation, sediment transport and substrate availability might change with reef heterogeneity. Cornell and Karlson (2000) argue that heterogeneity can increase local abundances by providing opportunities for specialist species to use the habitat in unique ways; so that, they avoid strong interactions with potential competitors. Based on the rugosity index for this study depth intervals may represent different habitats in which different types of disturbances work. Rugosity showed low values at shallow and deep habitats while higher at intermediate depth. Yet, this factor did not explain the patterns of juvenile abundance in for this study.

In this study, the most common genera found were *Diploria* , *Montastraea*, *Porites*, *Agaricia*, and *Siderastrea,* all common and widely distributed across depth intervals in most reefs. The genus *Diploria* was dominant in the shallow habitats (3m) where rugosity was lower. Although this genus is a spawner, their abundance in shallow habitat might reflect a high tolerance to extreme environmental conditions such as changes in temperature and UV exposition, especially during low tides (Edmunds 2000). Weil et al. (2000) found a novel asexual reproduction strategy in this genus in which asexual gemmae were continuously produced and detached from parental colonies throughout the year in several reef localities. These gemmae are well developed propagules that bypass all the risks of sexual reproduction and with high survivorship rates. Larval behavior is also an important factor that could explain the abundance of *Diploria* in shallow habitats as they tend develop and settle fast (few days) compared to other spawning species such as *Montastraea faveolata* (Szmant, per com). Similar patterns of larvae behavior have been observed for species such as *Acropora palmata* (Szmant and Miller, in press).

Juvenile corals of the genus *Montastraea* were found at deepest habitats, whereas *Porites* and *Agaricia* at intermediate habitats which suggest that juvenile *Porites* and *Agaricia* are more successful in these habitats even though live coral cover may represent a constraint for coral recruitment. The reproductive strategy (brooders) and the larvae behavior of these species might explain their success (Miller and Mundy 2003). Brooders reproduce on a monthly-basis and produce larger larvae that are ready to settle quickly after release. They receive zooxantellae from the parental colony so energy is available to complete metamorphosis after attachment compared to spawning corals (Harrison and Wallace 1990). Juveniles of *Montastraea* spp. could be better competitors at deeper habitats where they can expand laterally monopolizing more substrate. In terms of reproductive strategies for this study spawners were the ones that show higher survivorship among depth intervals. These findings agree with those of Chiappone and Sullivan (1996) who found that *Montastraea cavernosa* increased five-fold from high relief and groove sites to relict spur and groove. They argued that this pattern may be an adaptation to increasing sedimentation on the fore reef slope or more available substratum relative to shallower reef environment. Edmunds (2002) found that *M. annularis*, *M .cavernosa*, *Agaricia* spp., *D. strigosa*, *P. porites* and *P .astreoides*, were the most abundant species in St. Croix.

4.2. Juvenile survivorship

In this study juvenile coral survivorship was relatively higher at intermediate habitats compared with shallow and deeper habitats. Juvenile coral survivorship was 80% higher at Enrique and 60% higher at Weinberg but variable at all the other sites. This findings contrast with those found in other studies (e.g. Edmunds 2000 and Edmunds *et al.* 2004) where survivorship was not different among microhabitats, depths and life strategies (brooders vs. spawners). Among all juvenile species observed in this study the most common genera showing higher survivorship were *Diploria Montastraea*, *Porites*, *Siderastrea* and *Agaricia*. These results are in agreement and are consistent with the pattern of juvenile abundance described above as the same juvenile species belonging to these 5 genera dominated the coral community in la Parguera.

Therefore, these results agree with the hypothesis of intermediate disturbances which predicts that only few species that are better adapted to extreme environmental conditions and they tend to monopolize and exploit resources better in such habitats while intermediate zones will support a broader range of species. For *Diploria* and *Porites* this might be the case, while the other genera will be confined to other habitats as in the case of *Montastraea*. Survivorship was higher for *Siderastrea* and *Undaria* at the intermediate depth and deeper habitat respectively.. Most of the spawners observed as juvenile were from *Montastraea spp*, *Diploria spp* and *Siderastrea spp.* This further suggest that brooders might be efficient in colonizing the substrate but they might suffer more severely from post settlement mortality and spawners might not be as efficient during settlement but once they settle they might have better chances for survival. These differences might be explained by the contrasting life history traits of the contrasting reproductive strategies. Brooders show “K” strategies as they invest more energy in reproduction and less energy in growth, whereas spawners show “R” strategy which is the opposite (i.e. more energy put for grow and less in reproduction) so brooders are smaller than spawners and these differences might enhance the chances for survival after the larvae is settled as the faster the growth rate is, the better the chance to survive (Szmant and Gassman 1991).

In the Caribbean, studies on coral reproduction have shown that brooders have high rate of local recruitment in unstable habitats (Szmant 1986). However, species such as *Siderastrea* spp a gonochoric spawner and *Diploria* spp a hermaphrodite spawner, show high abundances of juvenile in unstable habitats such as shallow areas. These genera are well adapted to this environment where high temperatures, wave action and sediment transport might represent a constraint to other coral species. Although coral recruitment has been extensively study from more than a decade now, there has been a lack of effort to incorporate methodologies like this and others studies, into coral reef monitoring and management programs (Miller and Barrimo 2000). For example, data gathered from scleractinian recruitment studies in different reef habitats might be used to efficiently discuss how to enclosed a community that might provide new settles for a near by degraded reef habitat (i.e. reef connectivity) and at the same time follow the recovery of reef coral populations across time (Sale, 1997; Rinkevich 2000; Gardmark et.al. 2003). At last, during this study period, the surveyed areas were subjected to swells by hurricanes Ivan and Jeanne, which might have produced mortality in the community by low salinities, high sediment transport and sediment load.

5. Conclusions

1. Juvenile abundance was highly variable across depths within and across reefs sites in La Parguera. Juveniles were up to 3 times more abundant at intermediate depth habitats compared with shallow and deeper habitats. However, small to medium spatial scales explained 85% of the total spatial variability in recruit abundances.

2. Juvenile abundance tended to decrease from inner and more protected reefs to outer and deeper reefs, where juvenile corals were less abundant, therefore the null hypothesis of similar abundances of juvenile corals across the insular platform is rejected. Inshore reefs, even though more stressed from coastal development and influence, but with higher structure showed higher abundances of juveniles.

3. No significant correlation between live coral cover and rugosity and juvenile coral density were found. Juveniles were observed more on vertical structures than in flatter substrates. Orientation of substrate seems to be more important than rugosity and live coral cover in the recruitment and/or survivorship of juvenile corals.

4. Juveniles from spawner species were up to 5 times more abundant compared with those of brooders. This contradicts common statements that brooder's have higher juvenile recruitment and survivorship rates than spawners. This was consistent with the patterns of survivorship observed at all sites, where spawners had higher survivorship over 1 year of study.

5. Survivorship was higher at reef sites located in the inner shelf areas compared with the mid-shelf and outer reefs respectively. This was consistent and supports conclusion 2.

6. The genera with more abundant juveniles at all depths, sites and sectors were *Diploria, Montastraea, Porites, Agaricia, Siderastrea* and *Undaria.* This pattern of abundance was in concordance with the patterns of survivorship.

7. Studies of this kind might provide a step into the management and restoration of coral reefs and scleractinian populations because it provides a tool for assessing reef coral dynamics under natural conditions where biological and physical can be monitored.

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