

The relationship between physical and biological habitat conditions and hermatypic coral recruits abundance within insular reefs (Colombian Caribbean)

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Received 11-VII-2011. Corrected 20-II-2012. Accepted 19-III-2012.

Abstract: Little evidence exists on the dependence between the presence and abundance of juvenile hermatypic corals and the conditions of their habitats, despite that juveniles contribute with the understanding of the community structure and its reproductive success. To assess this, the abundance of nine species of juvenile corals was correlated with eight macro-habitat (location of the reef on shelf, depth) and micro-habitat (type and inclination of the substrate, exposure to light, texture and amount of sediment accumulated on bottom, potential growth area for juveniles) conditions. Sampling was conducted in four insular coral reefs in the Colombian Caribbean: two oceanic and two continental reefs (influenced by large rivers), covering a total of 600m² and the distribution of corals on a vertical gradient. Contingency tables and coefficients (magnitude) and multiple correspondence analyses were used to evaluate the dependency ratios for each species. The results showed that *Agaricia tenuifolia* displayed the most robust pattern of dependence (two high and two moderate), significant for juveniles present at a high frequency in continental reefs, devoid of potential area for juvenile growth (surrounded by macroalgae), and covering horizontal substrates exposed to light. The juveniles were associated with a habitat of moderate to high bottom accumulation of extremely fine sediment. *Porites astreoides* presented four moderate dependencies; ocean reefs between 2-16m depths, a high frequency of juveniles on horizontal substrates, exposed to light, non-sedimented and occupied by competitors. *Siderastrea siderea* displayed three moderate dependences for juveniles in cryptic zones, inclined substrate and devoid of competitors. *A. lamarcki*, *Leptoseris cucullata* and *A. agaricites* presented two moderate dependences; these species share high abundance of juveniles in habitats with no sediment, exposed to light and occupied by competitors (except *A. agaricites*). The *P. porites*, *Favia fragum* and *Montastraea cavernosa* species had a moderate dependence with high incidence of juveniles in ocean reefs and microhabitats exposed to light. For the nine species, results indicate that the presence (colonization), abundance and survival of juveniles, depend on certain species-specific particularities of the habitat. However, the juveniles show high tolerance and plasticity to a range of habitat variables, given their independence and low dependence observed in over 50% of the variables assessed. Rev. Biol. Trop. 60 (3): 995-1014. Epub 2012 September 01.

Key words: recruitment, coral recruits, habitat, insular reefs, Caribbean, Colombia, *Agaricia*, *Porites*, *Siderastrea*, *Leptoseris*, *Favia*, *Montastraea*.

Hermatypic coral recruitment, defined as the introduction of new individuals to a population, occurs when a larva settles, undergoes metamorphosis (formation of the calcium carbonate skeleton) and endures a length of time (Sale *et al.* 2010). The ecological and evolutionary significance is that recruitment is a key process within the reef's successional cycle, since it determines the structure of the

coral community, the renewal and continuity of local populations, favoring an increase of genetic variability, which in turn implies an adaptive advantage to climate change (Porter & Tougas 2001).

Recruitment measurable *in situ* by the presence of juveniles between 4mm and 2-4cm (depending on species) is considered the result of the synergy of several processes: partial

and total mortality, that results in the quantity or coverage of reproductive adults, the total number of gametes and larvae released through sexual reproduction (reproductive output), the dispersal and survival of larvae in the water column, larval macro and micro habitat selection behavior for attachment before loss of competitiveness, larval attachment according to the extent, quality and availability of the most advantageous substrate (Baird *et al.* 2003, Sale *et al.* 2010). The process of metamorphosis to form polyps, asexual reproduction for juvenile growth, resistance to the physical environment conditions (Baird *et al.* 2003), and competition for resources such as substrate and light (McCook *et al.* 2001, Fabricius 2005) also partake in this synergy. When these processes are favorable it is reflected in the presence, abundance and distribution of juveniles in a particular habitat; this success is mediated by species life history, and the pressure of local natural selection caused by abiotic and biotic factors (Hughes & Jackson 1985).

There are several possible explanations for the spatial distribution of juveniles of a particular coral species (Mundy & Babcock 1998, 2000, Dornelas *et al.* 2006): 1- settlement and thus recruitment is an entirely random spatial process (not larval selection), in which the physical and biological habitat do not determine the pattern of recruitment (independent); 2- larvae of each species settle on preferential reef habitats according to their resource requirements, and habitat factors do not affect the distribution of recruits; 3- larvae select suitable settlement habitat, and habitat factors cause post-settlement mortality to produce the recruitment pattern; 4- distribution and abundance are independent of larval behavior but dependent on selective factors in the environment.

Vermeij *et al.* (2006) have reported that in the case of environments providing conditions of high stress (drastic changes in salinity, sedimentation, light and competition) larvae do not present specific habitat selection; therefore, settlement becomes opportunistic and random. Contrastingly, coral larvae when

under favorable macro-habitat conditions (no pollution), and having different micro-habitat options, is more active in its selection, creating a pattern of settlement and recruitment that varies by species (Harrington *et al.* 2004). There is no consensus on which of these hypotheses correctly explain the distribution and abundance of juvenile corals in a reef; it is a complex process, where multiple habitat variables interact, at different temporal and spatial scales, with larval settlement behavior. What is evident is that the fitness of any adult coral depends on the conditions of the habitat where the juvenile lived and developed.

Globally, we know that there are key factors of macro and micro-habitat that affect the survival of juvenile coral. At a macro-scale, for example, are the type and geographic location of the reef, depth and the degree of environmental degradation (Richmond 1997). At micro-scale are the availability and complexity of the substrate (Ruiz-Zárte *et al.* 2000), the type and amount of accumulated sediment and the competition for resources with other sessile organisms (McCook *et al.* 2001).

At micro-scale, the characteristics of the settlement substrate, is one of the factors that determine habitat preference and the pattern of juvenile survival (Ruiz-Zárte *et al.* 2000, Sale *et al.* 2010). The differential location of larvae on the substrate, is related to site selection, the irregularity and substrate availability, resistance to sedimentation, depth and variation of light intensity (Ruiz-Zárte *et al.* 2000, Baird *et al.* 2003). There is evidence that suggests that most larvae prefer roughened substrates, such as rocks and dead coral, as they offer countless micro-spaces with binding potential (Smith 1997); however, larvae species such as the *Manicina aerolata* prefer attachment onto encrusting red algae because they facilitate settlement, metamorphosis and survival in conditions of high sedimentation (Ruiz-Zárte *et al.* 2000).

Factors such as vulnerability to foraging (sea urchins, fish) and the ability to compete with macroalgae and other sessile organisms for space are involved in juvenile survival,

after settlement takes place (Ruiz-Zárate *et al.* 2000, McCook *et al.* 2001). It has been shown that some algae not only compete for space and light with adult corals, but also with juveniles (overgrowth and suffocating), especially under conditions of nutrient enrichment, high sedimentation and low herbivores density (Birrell *et al.* 2008, Elmhirst *et al.* 2009).

The type and amount of sediment accumulated in the microhabitat is considered as the most significant factor determining larval and juvenile survival worldwide (Edmunds *et al.* 2004, Fabricius 2005). The proximity to river mouths causes an increase in the amount of particulate organic and inorganic matter entering the reef, causing nutrification, turbidity and sedimentation. This favors the proliferation of macroalgae (Fabricius 2005), the reduction of available surfaces for coral settlement (Edmunds *et al.* 2004, Hughes *et al.* 2007); a decrease of the larvae's sensory ability to select microhabitat, and a decline in the rate of juvenile survival and diversity (Gardner *et al.* 2003). The negative effects of sediment runoff entering the reef have been reported by Fabricius (2005) in even the early reproductive stages (gametogenesis, fertilization and embryogenesis) as well as the late stages (larval survival, settlement, metamorphosis, juvenile growth and survival).

An increase in reef regime alterations since the early seventies has caused a modification in the settlement habitats and the survival of juveniles in the Caribbean (Gardner *et al.* 2003). Juvenile coral communities are enduring a "community shift" (Aronso *et al.* 2004, Hughes *et al.* 2007), caused by the dominance of brooding species such as the *Agaricia* spp. and *Porites* spp., which replaced spawning species, such as *Montastraea annularis* and *Siderastrea siderea* (Porter & Tougas 2001, Green *et al.* 2008).

Although it is clear that the habitat factors mentioned above are important for both adult and juvenile corals, the differential effects of each factor in the post-settlement survival by species that determine the frequency, density, juvenile survival and fitness of the species

have not been thoroughly examined (Mundy & Babcock 2000, Victor 2008, Birrell *et al.* 2008). Consequently, it is unknown whether the recruitment and survival of coral species in the Caribbean, in fact, depends on certain physical and biological habitat factors or if it is entirely random (Mundy & Babcock 2000). Investigating the consequences (juveniles of the same species present in the same macro or micro-habitat=frequency) could help to infer the causal agents that are affecting the larval settlement (selective or not) and/or the selective factors of the environment (present or not).

The contribution of this study is to demonstrate whether the frequency of juvenile hermatypic corals depends on certain physical factors of the habitat on a macro-scale (location of the reef on the shelf and depth) and on a micro-scale (type and angle of the substrate, exposure to light, texture and amount of sediment accumulated around the juveniles) and micro-biological factors of the micro-habitat (competition for potential juvenile development space). The results will be a key tool to define habitat variables that favor or limit the survival of nine dominant coral species in the Colombian Caribbean. This information is vital for the conservation, rehabilitation (translocation and transplantation of juveniles, larval supply) and protection of reef habitats.

MATERIALS AND METHODS

Study area: The study was conducted in four insular reefs in the Colombian Caribbean (Fig. 1), two on the continental shelf (Isla Fuerte and Isla Grande) subject to different levels of disturbance caused by freshwater input from large rivers, and two on the ocean platform (San Andres and Providencia).

Continental shelf reefs: Isla Grande is part of the Islas del Rosario archipelago, located Southwest of Cartagena in the Parque Nacional Natural Corales del Rosario and San Bernardo. It is influenced by the Magdalena River (average flow=7 149.53m³/s, Garay 2001), which flows into the Canal del Dique with an average

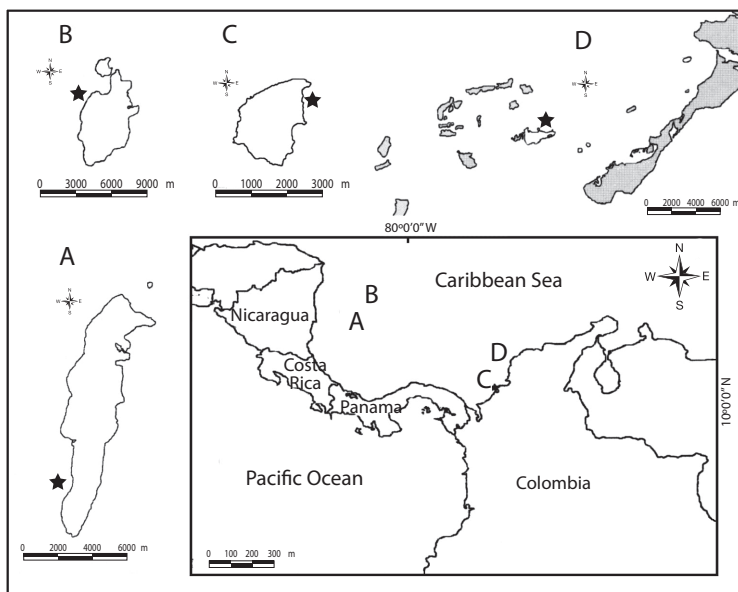


Fig. 1. Location of the islands studied (letter) and detail of the sampled reefs (star): A. Isla de San Andres, leeward reef; B. Isla de Providencia, leeward reef; C. Isla Fuerte, windward reef; D. Isla Grande, windward reef - Islas del Rosario Archipelago.

flow of $455.32\text{m}^3/\text{s}$ (Garay 2001) and is the main affluent of the archipelago. The profile of the windward terraces ($10^{\circ}10'21''$ N - $75^{\circ}42'36''$ W) is characterized by a reef crest less than 10m wide and a slope with coral cover up to 25m. The reefs feature a predominance of *M. annularis*, *Agaricia tenuifolia* and *Porites astreoides*, along with deteriorated coral patches of *Acropora palmata* and extensive coverage of macroalgae such as *Dictyota* spp. and *Halimeda* spp. (Alvarado *et al.* 1989).

Isla Fuerte is part of the Bajo Bushnell and Bajo Burbujas reef complex (Díaz *et al.* 1996); it is influenced by the following rivers: the Sinú (average flow= $290.8\text{m}^3/\text{s}$, Garay 2001), the Atrato (average flow= $2\ 366.13\text{m}^3/\text{s}$, Garay 2001) and the Magdalena ($7\ 149.53\text{m}^3/\text{s}$, Garay 2001). The windward zone ($9^{\circ}23'15.6''$ N - $76^{\circ}10'10.1''$ W) has a terrace formed by a fringing reef up to a depth of 20m, followed by a sandy bottom, with a coral zonation typical of the Caribbean (Díaz *et al.* 2000), with high algal growth (*Dictyota* spp.) and the

accumulation of extremely fine sediment (silt-clay). The annual loss rate by species or genus in continental reefs, caused by sedimentation and pollution has been estimated at 0.4-2.2% (Acosta & Martínez 2006).

Ocean platform reefs: Sampling was conducted west of San Andres and Providencia, at coordinates $12^{\circ}30'01''$ N - $81^{\circ}45'56''$ W and $13^{\circ}23'54.6''$ N - $81^{\circ}23'57''$ W, respectively. The best coral formations in San Andres are found on the leeward terraces (fringing reef). The shallow terrace features a calcareous pavement with areas exposed or covered with algae, corals, octocorals and scattered sponges. The submerged terrace is a sandy plain where at a depth of 12m we find a coral carpet of *Dendrogyra cylindrus*, *Diploria labyrinthiformis*, *D. strigosa*, *Colpophyllia natans* and *Montastraea* (Díaz *et al.* 1995). The latter terrace ends abruptly at 20-22m with an inclined coral-covered slope and sediment to 30-35m (Díaz *et al.* 1995, Acosta & Martínez 2006).

Leeward in Providence has a broad lagoon terrace covered with sediment and sea grass areas. The shallow zone is strewn with skeletons of *Acropora palmata*, *Millepora complanata*, zoanthids, and fleshy and coralline algae. The fore-reef terrace (12-15m) has an assortment of corals, predominantly of the *Diploria* spp., *M. annularis*, *Dichocoenia stokesi*, *P. astreoides* species, as well as octocorals, while in deeper waters, the coverage of *Montastraea cavernosa*, *M. annularis*, *D. labyrinthiformis* and *C. natans* increases, as well as the presence of sponges and octocorals (Díaz *et al.* 2000). Coral coverage on the slope decreases rapidly (Acosta & Martínez 2006).

Sampling: A line was traced from the deepest point (maximum 30m), where the reef ends or the sandy bottom begins, to the coast, in areas of the most thriving coral reefs (richness, coral coverage). Perpendicular to this line and at increasing depths of 2m, 12 quadrants of 1m² were measured, six on each side of the line and 1m from each other (following Vidal *et al.* 2005); this procedure was repeated along the entire length of the reef depth gradient. The transects were grouped by depth in four categories (Acosta *et al.* 2011): 1- Shallow (2, 4, 6 and 8m), 2- Medium (10, 12, 14 and 16m), 3- Deep (18, 20, 22 and 24m) and 4- Very deep (≥ 26 m), the latter only found in oceanic reefs, totaling 600m² sampled. Juveniles were defined as colonies of less than 4cm in diameter for large species (diameter ≥ 15 cm) such as *Montastraea* spp., *Diploria* spp. and *S. siderea* (Bak & Engel 1979, Richmond & Hunter 1990, Dueñas *et al.* 2010); and 2cm in diameter for small species (diameter < 15 cm), such as *P. astreoides* and *Favia fragum*. Taxonomic identification was done according to the Dueñas *et al.* (2010) guide.

As the number of species and juveniles per quadrant was recorded, the physical and biological characteristics of the habitat in which each one of the juveniles was found were described as follows: 1- Location of the reef on the platform; 2- Range of depth; 3- Type of substrate colonized by the juvenile; 4- Substrate

inclination on which the juvenile was found; 5- Juvenile's exposure to light; 6- Texture of the sediment accumulated on the substrate around the juvenile; 7- Amount of accumulated sediment on the bottom, around the juvenile; 8- Potential space around the juvenile for growth. See table 1 for further details on classification and measurement criteria for each variable.

The 3000 juveniles and 45 species presenting recruitment were used to conduct an exploratory analysis of the absolute frequencies of all juveniles in the four coral reefs; the aim was to identify the most common species that had a sampling error less than or equal to 10%, and 95% confidence, using the formula of Pita (1996): $E = (Z\alpha^2)(pq)/n$, where $Z\alpha = 1.96$ at 95% confidence, p = percentage of the community expected to be sampled (75%), $q = 1 - p$, n = sample size (total number of individuals per species). These species were *Agaricia agaricites*, *Leptoseris cucullata*, *P. astreoides*, *S. siderea*, *F. fragum*, *Scolymia* spp., *A. lamarcki*, *M. cavernosa*, *A. fragilis*, *P. porites*, *S. radians* and *A. tenuifolia*. These 12 species were used to analyze the pattern of dependencies between juveniles and the characteristics of their habitat, by employing the chi-square (X^2) test for contingency tables (CT). The Yates continuity correction was used on 2x2 CT. When at maximum 20% of the table cells had an expected frequency under five, we applied Fisher's exact test. However, the proper application of the X^2 test to *Scolymia* spp., *A. fragilis* and *S. radians* was impossible, as more than 20% of the cells in the contingency tables continuously resulted in frequencies equal to zero; consequently, they were excluded from the analysis. For the nine remaining species, in cases where H_0 was rejected (independence of variables), we calculated the contingency coefficient (C) to determine the extent of dependence. This coefficient ranged between zero and a maximum value of association (C_{maximum}) which corresponds to the number of categories of the variables that were evaluated. Values closer to zero were considered of low association between the variables and those that came closest to its C_{maximum} as a high association

TABLE 1
Classification of habitat variables assessed for hermatypic coral recruits

Scale	Factor	Variable	Categories	Criteria	
Macro-scale	Reef	Location of the reef regarding the platform	1. Oceanic 2. Continental	Islands on an oceanic platform, San Andres and/or Providencia. Islands on a continental platform, Isla Grande and/or Isla Fuerte.	
	Depth	Range of depth*	1. Shallow 2. Medium 3. Deep 4. Very Deep	2-8m 10-16m 18-24m 26-30m	
Micro-scale	Substrate	Substrate type (Garzón-Ferreira <i>et al.</i> 2002)	1. Dead Coral 2. Rock 3. Rubble 4. Encrusted red algae	Consolidated matrix of dead coral. Metamorphic stone. Unstable substrate of organic and inorganic origin <30cm diameter. Encrusted algae creating a reddish cover.	
		Substrate inclination (Smith 1997)	1. Horizontal 2. Inclined 3. Vertical	<10° >30° y <70° >80°	
	Light	Exposure to light	1. Exposed 2. Cryptic	Juvenile located in a visible area, exposed to direct or indirect light. Juvenile hidden in crevices, devoid of light or direct light.	
	Sediment	Sediment texture	1. Coarse 2. Fine 3. Very fine - Clay-silt 4. No sediment	Algal or coral origin, particles with diameters of >4mm. Organic and inorganic origin, particles with diameters of >1mm and <4mm. Muddy texture, particles with diameters of <1mm. Absence of sediment surrounding juvenile.	
			Amount of accumulated sediment (measured with a gauge, perpendicular to the substrate)*	1. Disperse 2. Moderate 3. High	<1mm thickness >1mm and <1cm thickness >1cm and <5cm thickness
			Competitors	Potential growth space (modified from McCook <i>et al.</i> 2001)	1. Available 2. Occupied

* Variables measured quantitatively.

Competitors: variable that corresponds to a biological factor. The remaining are physical factors.

TABLE 2
Maximum coefficient of association between variables (C_{max})

Rows x Columns	C_{max}	Level of association		
		Low	Moderate	High
2 x 2	0.71	0 to 0.24	0.25 to 0.47	0.48 to 0.71
3 x 3	0.82	0 to 0.27	0.28 to 0.55	0.56 to 0.82
3 x 2	0.82	0 to 0.27	0.28 to 0.55	0.56 to 0.82
4 x 2	0.87	0 to 0.29	0.3 to 0.58	0.59 to 0.87
4 x 3	0.87	0 to 0.29	0.3 to 0.58	0.59 to 0.87

Criteria used to define magnitude of association according to the number of rows and columns of contingency tables.

(Table 2). Not all combinations of variables were tested; when crossing certain categories of independent variables in the CT some had frequencies of zero and expected frequencies under five, this precluded the application of the test. Subsequently, a multiple correspondence analysis (MCA) was used to reduce variable information to two dimensions on a Cartesian

plane (Díaz 2002), graphically representing the association of the variables with the species.

RESULTS

The χ^2 test ($p < 0.05$) and the MCA (Fig. 2) evidenced the most robust pattern of dependency in juveniles of *A. tenuifolia*. Only this

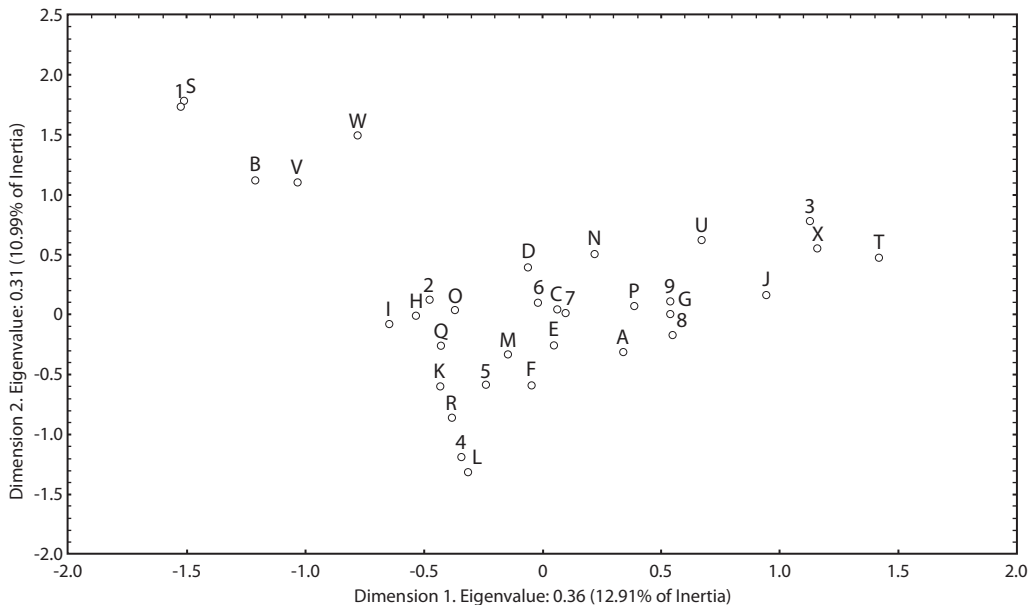


Fig. 2. Multiple correspondence analysis (MCA), representing the habitat of nine species of dominating corals. 1: *A. tenuifolia*, 2: *P. astreoides*, 3: *S. siderea*, 4: *A. lamarcki*, 5: *L. cucullata*, 6: *A. agaricites*, 7: *P. porites*, 8: *F. fragum*, 9: *M. cavernosa*. A: Oceanic reef, B: Continental reef, C: Shallow (2-8m), D: Medium (10-16m), E: Deep (18-24m), F: Very deep (26-30m), G: Available space around juvenile, H: Space around the recruit occupied by competitors, I: Coral skeleton substrate, J: Rubble, K: Rock, L: Encrusted red algae, M: Exposed to light, N: Cryptic, O: Horizontal substrate, P: Inclined substrate, Q: Vertical substrate, R: No sediment, S: Very fine, silt-clay sediment, T: Fine sediment, U: Coarse sediment, V: Dispersed sediment accumulated on the bottom, W: Moderate sediment accumulated, X: High sediment accumulated (See Table 1).

species showed a significantly high dependence (CT 2x2, C=0.59; Fig. 3A), between the frequency of juveniles and habitats located in continental reefs and juveniles surrounded by competitors (78.7% continental reefs and 82.5% with macroalgae and corals). High dependence was also found among juveniles on substrates exposed to light and those on horizontal substrates (CT 3x2, C=0.55; Fig. 3A). Additionally, moderate dependence was found, between juveniles in continental reefs, and juveniles found on substrates exposed to light, and in turn, of those located on substrates exposed to light with those sharing space with other competitors (CT 2x2, C=0.25-0.3; Fig. 3A). Graphically, the MCA illustrates how *A. tenuifolia* settled apart from other species, beside the habitat with moderate to high

silt-clay sediment in continental reefs (10-16m). It is the only species to have 75.2% of its juveniles under these conditions (Table 3).

The frequency of juvenile *P. astreoides*, moderately depended (CT 2x2, 3x2 y 4x2, C=0.3-0.5; Fig. 3B), on oceanic reefs (61.7%) with substrates exposed to light (72.6%), the latter with horizontal substrates (48.4 %) and non accumulated sediment (56%); in the same way, habitats with non accumulated sediment, but with competitors around the juveniles. The dependence on substrates exposed to light and substrates without accumulated sediment presented the highest value for the species (C=0.5).

It was also established that the frequency of juvenile *S. siderea* on cryptic substratum (60.2%) depended on its location at a depth

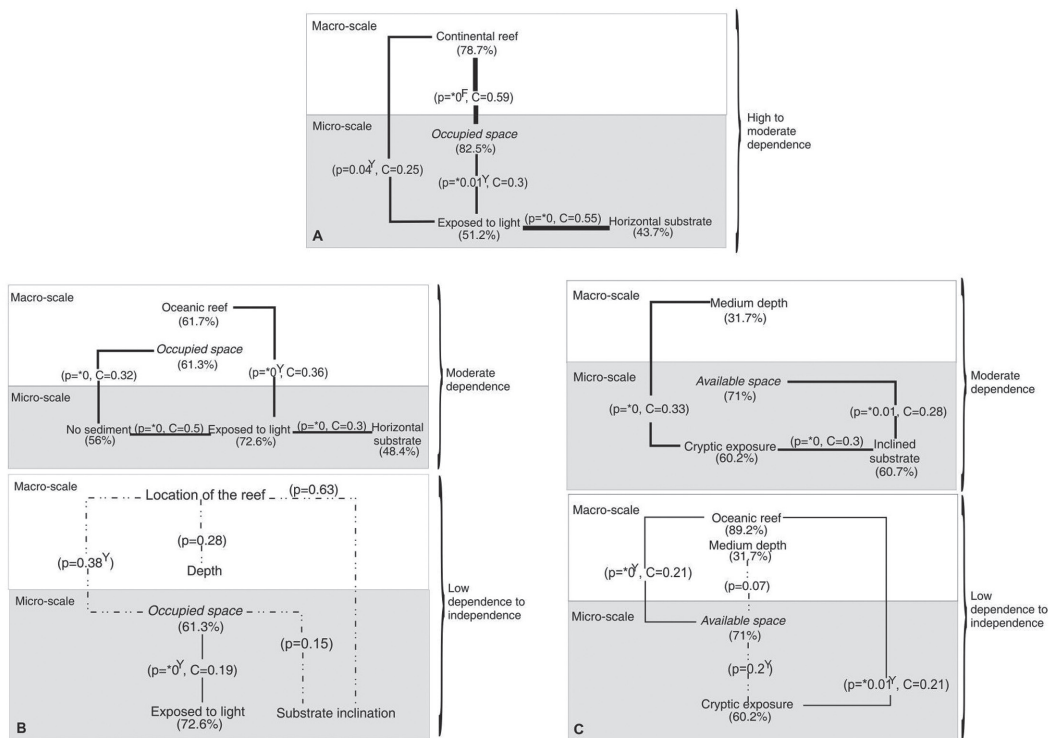


Fig. 3. Dependency relationship between habitat variables and the frequency of juveniles by species for the first group of species with the most dependences in respect to the macro and micro-habitat variables. **(A)** *A. tenuifolia*, n=80. **(B)** *P. astreoides*, n=248. **(C)** *S. siderea*, n=186. $p=\chi^2$. C= contingency coefficient when $p<0.05$. *=statistical dependence. Y= Yates's correction. F=Fisher's exact test. — =high dependence. — =moderate dependence. — =low dependence. Dotted line indicates independence. Italics indicate a biological variable.

TABLE 3
Summary of dependences (between the frequency of juveniles of nine coral species and physical and biological habitat conditions) tested

Species	Reef	Depth	Space	Substrate type	Exposure	Inclination	Sediment type	Amount of sediment
<i>A. tenuifolia</i>	Continental ⁺	N/A	Occupied	N/A	Exposed	Horizontal	Very fine-Clay-silt*	Disperse-Moderate*
<i>P. astreoides</i>	Oceanic	N/A	Occupied ⁺	N/A	Exposed	Horizontal	No sediment	No sediment
<i>S. siderea</i>	Oceanic	Medium	Available	Rubble*	Cryptic	Inclined	Fine and Coarse*	High*
<i>A. lamarcki</i>	N/A	N/A	Occupied	N/A	Exposed	N/A	No sediment ⁺	No sediment ⁺
<i>L. cucullata</i>	Oceanic	Deep	Occupied	N/A	Exposed	Inclined	No sediment	No sediment
<i>A. agaricites</i>	Oceanic	Medium	Available	N/A	Exposed	Inclined	No sediment	No sediment
<i>P. porites</i>	Oceanic	N/A	Available	N/A	N/A	N/A	N/A	N/A
<i>F. fragum</i>	Oceanic	N/A	Available ⁺	N/A	Exposed	Inclined	N/A	N/A
<i>M. cavernosa</i>	Oceanic	Medium	Available ⁺	N/A	Exposed	Inclined	N/A	N/A

*= Variables determined by the MCA. += Variables determined by the χ^2 and MCA. Variables without an accompanying symbol were determined by χ^2 . N/A: insufficient data for some categories.

of 10-16m (31.7%), on an inclined substrate (60.7%), as well as juveniles on an inclined substrate devoid of competitors (71%); all of these moderate dependences (CT 3x2 and 4x2, C=0.28-0.33; Fig. 3C). Graphically (by the MCA) it was established that the higher frequency of juveniles of the species was on rubble-type substrates (78.5%), cryptic (60.2%), of coarse and fine sediment (47.3% and 39.8% respectively), accumulated in amounts greater than 1cm (69.9%). See Appendix 1 for further details on species frequencies for all measured variables.

The highest frequency of *A. lamarcki* juveniles depended on substrates occupied by competitors (63.5%), with no sediment accumulated (91.5%) on substrate exposed to light (62.8%). The magnitude of the dependence between variables ranged from low to moderate (CT 2x2 and 4x2; C=0.24-0.34; Fig. 4A). Graphically it was confirmed that the factor closest to *A. lamarcki* and which determined the frequency of its juveniles, was the absence of sediment on the substrate since, through the MCA, the species was located apart from the other species. However, statistical independence (χ^2 , p>0.05) was proved between light exposure and inclination of the substrate, and between the inclination of the substrate and space for growth around the juveniles (Fig. 4A). Abundance was lowest in continental reefs (0.8%) and at depths under 10m (2.3%).

Like *P. astreoides*, juveniles of *L. cucullata* and *A. agaricites* showed that despite being in a variety of habitat conditions, as shown in the figures representing dependencies between variables (Fig. 4B and 4C) and the MCA's two-dimensional plane, the strongest dependence (moderate) was presented by juveniles in substrate devoid of accumulated sediment and substrate exposed to light; with 71.8% and 59.6% of *L. cucullata* juveniles under these conditions (CT 4x2, C=0.43; Fig. 4B). Additionally, moderate dependence was proven (CT 4x2, C=0.33; Fig. 4B) for *L. cucullata* between the frequency of juveniles on non-sedimented substrates (71.8%) and substrates occupied by competitors (55.4%).

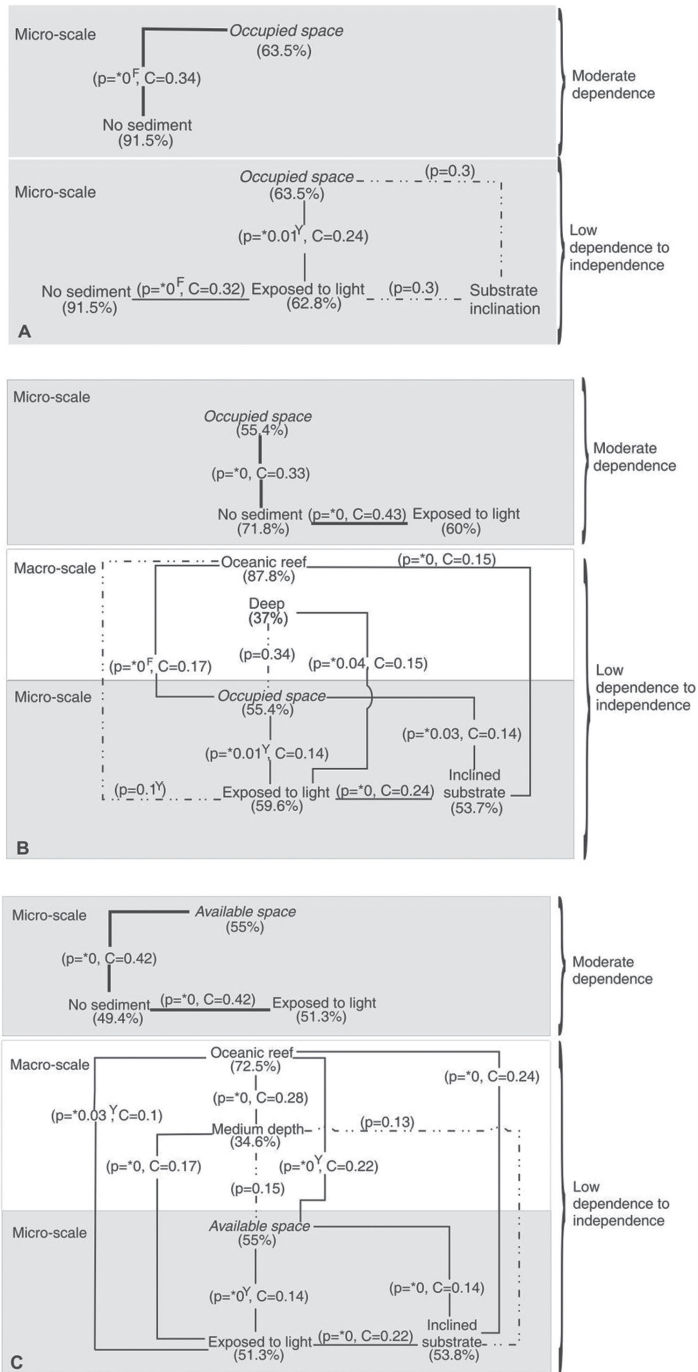


Fig. 4. Dependency relationship between habitat variables and the frequency of juveniles by species that displayed the least number of dependences and recruit in a wide range of habitat conditions. **(A)** *A. lamarcki*, $n=129$. **(B)** *L. cucullata*, $n=354$. **(C)** *A. agaricites*, $n=593$. $p=X^2$. C = contingency coefficient when $p<0.05$. * =statistical dependence. Y =Yates's correction. F =Fisher's exact test. — =moderate dependence. — =low dependence. **Dotted line indicates independence.** **Italics** indicate a biological variable.

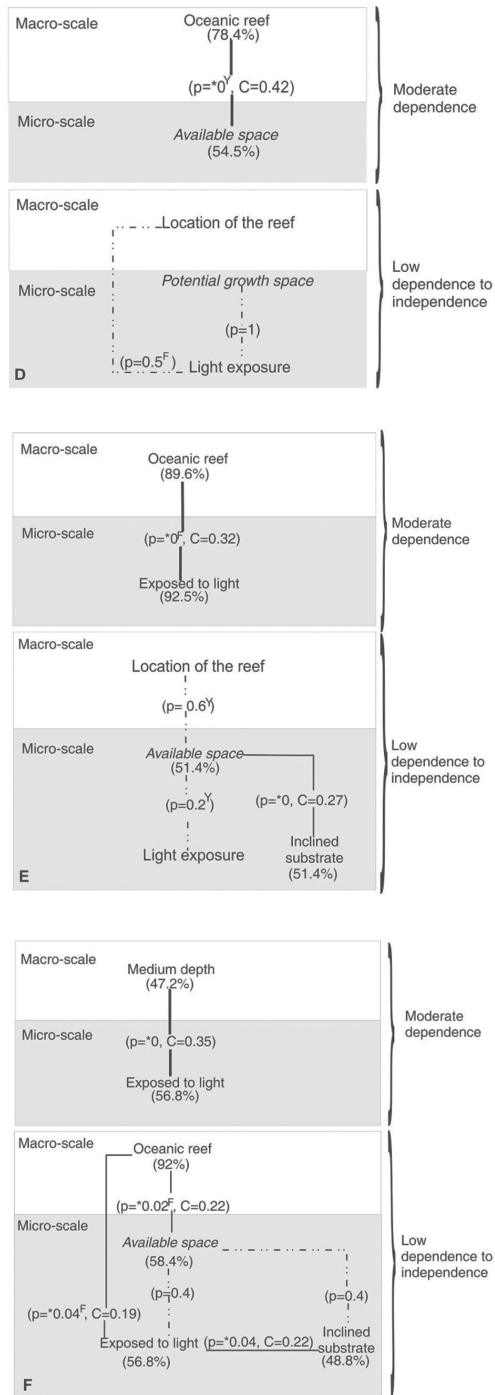


Fig. 4. Dependency relationship between habitat variables and the frequency of juveniles by species that displayed the least number of dependences and recruit in a wide range of habitat conditions. **(D)** *P. porites*, n=88. **(E)** *F. fragum*, n=173. **(F)** *M. cavernosa*, n=125. $p=X^2$. C= contingency coefficient when $p<0.05^*$ =statistical dependence. Y =Yates's correction. F =Fisher's exact test. — =moderate dependence. — =low dependence. **Dotted line indicates independence.** **Italics** indicate a biological variable.

A. agaricites also showed moderate dependence (CT 4x2, C=0.42; Fig. 4C) between non-sedimented substrates (49.4%) and light availability (51.3%), and those without sediment and no competitors (55%).

The juveniles of *P. porites* showed dependence on oceanic environments (78.4%) and microhabitats without interaction or the presence of other sessile organisms (54.5%), of moderate dependence (CT 2x2; C=0.42; Fig. 4D). Independence between its location in the reef and light exposure (X^2 , $p>0.05$) was proven for this species.

As for *F. fragum*, we found that the abundance of juveniles depended on ocean reefs (89.6%) and substrates exposed to light (92.5%) of moderate intensity (CT 2x2; C=0.32; Fig. 4E). The species was abundant at depths under 16m and on rubble, but lower in habitats with coarse sediment (Appendix 1). However, statistical independence was confirmed between the location of the reef and the potential space available for juvenile growth, and the latter with light exposure (X^2 , $p>0.05$).

The juveniles of *M. cavernosa* showed moderate dependence (CT 4x2; C=0.35; Fig. 4F) on substrates exposed to light (56.8%), at depths of 10-16m (47.2%). In addition, the independence between light exposure and the potential space to grow was established, and the latter with substrate inclination (X^2 , $p>0.05$).

While juveniles of species such as *A. tenuifolia* and *S. siderea*, were most abundant in environments with accumulated sediment, the strongest relationships (higher frequency of juveniles) for *A. lamarcki*, *P. astreoides*, *L. cucullata* and *A. agaricites* juveniles, were present in micro-habitats exposed to light and without sediment accumulation around juveniles; this evidenced that the frequency of juveniles of some species increased in environments of low accumulated sediment.

L. cucullata, *A. agaricites*, *P. porites*, *F. fragum* and *M. cavernosa* were grouped within the MCA plane, amid many categories of the different physical and biological variables of the habitat and the dependences tested were

mostly of low magnitude (none of these species showed high dependence). Homogeneous frequencies between the different categories of each factor confirm that juveniles of these species can be effectively found under diverse habitat conditions (tolerant).

DISCUSSION

These results suggest that the frequency, abundance and survival of juvenile hermatypic corals in insular reefs of the Colombian Caribbean are affected by physical and biological features of their environment and that they depend on certain peculiarities of the habitat, which are species-specific. According to the characteristics of relationships and the number of dependences of moderate to high magnitude, the following two groups of species were recognized: 1- species with the highest number of dependences (3-4) with regard to the macro and micro-habitat variables (*A. tenuifolia*, *P. astreoides* and *S. siderea*) and species that displayed the least number of dependences (1-2) and recruit in a wide range of habitat conditions (*A. lamarcki*, *L. cucullata*, *A. agaricites*, *P. porites*, *F. fragum* and *M. cavernosa*).

The mechanism that describes the dependence of juveniles on certain habitat categories and variables could be simply explained as the balance between larval input where the larvae perform or not a selection within the spectrum of habitat conditions and provide a new individual to the population, and the output to the system generated by the differential mortality of juveniles (natural selection), where ultimately, one of the habitat categories evaluated is favored (disproportionate number of juveniles). Following are two scenarios where this would happen: 1. The combination of high habitat selection by the larva, that is, it requires a specific resource or habitat condition (population's habitat preference), and low post-settlement differential mortality in that specific habitat where juveniles frequently occur (Mundy & Babcock 1998, Ruiz-Zárata *et al.* 2000, Harrington *et al.* 2004), 2. No larval selection, random or similar colonization in all habitat categories evaluated

(Mundy & Babcock 2000, Vermeij *et al.* 2006) and strong selection pressure in all but one of the habitat categories, which would explain the dependence identified. In turn, larval substrate selection depends on habitat characteristics (quality, quantity and resource availability) and conditions of the environment, which have not been quantified for any species, in the reefs assessed. Meanwhile, the number of larvae reaching a system depends on population size, number of reproductive individuals, reproductive effort (Alvarado & Acosta 2009); strategy and mode of sexual reproduction of each species (Miller & Barimo 2001), and type of larva and dispersion rate vs. self-seeding (Sale *et al.* 2010). Also, the natural selection that occurs in larval stages, affects the settlement and metamorphosis (Mundy & Babcock 2000, Baird *et al.* 2003) and later post-settlement (Vermeij *et al.* 2006, Victor 2008). The complexity of the variables involved and the lack of understanding regarding the early life stages of the species make discussion on the findings difficult.

The independence between habitat variables and the abundance of juveniles could be explained by the combination of the following: 1. Absence of larval selection or opportunistic behavior at the time of settlement (Vermeij *et al.* 2006), concurrently with low natural selection of juveniles within the categories of the variable; 2. High preference for one habitat category (Mundy & Babcock 1998, 2000) and natural selection directed on that category presenting most frequency of juveniles, which would generate an equilibrium in frequency among the categories of the variable compared, and therefore, independence. The results reflect the adaptation and high tolerance of juvenile coral to numerous habitat factors, which allows for their survival (Baird *et al.* 2003) in a system with high spatial heterogeneity and where resources and conditions are distributed in patches or follow a gradient.

Some of the traits most relevant to the higher survival rate of coral species are: high phenotypic plasticity, which confers them tolerance to various conditions of the environment (Miller & Barimo 2001, Green *et al.* 2008)

and resistance to changes in habitat conditions (Lirman & Manzello 2009), efficiency in the removal of accumulated sediment (mostly by massive or foliar growth, Huitric & McField 2001), a high energy investment to protect and reduce possible inter-specific competition for potential growth space (Green *et al.* 2008); rapid colonization of empty substrates as a result of a high investment in sexual reproduction and periodic release of planulae resistant to limiting resources (Smith 1997, Kramer 2003). These strategies are likely to provide them predominance as an adult and even as a youth in many regions of the world (Smith 1997). The graphic association (on the MCA) of species of the second group with various habitat factors confirms the almost homogeneous distribution and frequency of juveniles under different conditions of the environment and its evidence of tolerance.

The robust pattern of high and moderate dependences displayed by *A. tenuifolia* could be accounted by their life history traits and their ability to withstand extreme conditions. Its vertical growth could provide an advantage by minimizing the effects of continental sediment and capturing sufficient light in areas presenting algal growth (Aronso *et al.* 2004).

The combination of turbidity, high sedimentation rate and increased nutrient concentrations, typical of continental reefs in this region (Aronso *et al.* 2004, Gardner *et al.* 2003, Acosta & Martínez 2006) especially of Isla Fuerte, favors the proliferation of macroalgae and decreases substrate availability for coral recruitment. Because it is a brooder and has a high level of reproductive effort and tolerance to adverse mediums, *A. tenuifolia* has been able to rapidly colonize empty substrates and increase their recruitment (Hughes & Jackson 1985). As a result, the presence of *A. tenuifolia* juveniles and adults has been favored by conditions that predominate in Caribbean reefs, where it is the most abundant and has replaced *Porites* sp. in recent decades (Aronso *et al.* 2004). The low number of *A. tenuifolia* juveniles in ocean reefs, where there is adequate numbers of adult reproductive individuals and

where sedimentation is lower, may suggest that the species is a better competitor in stressful conditions, such as in areas with high silt-clay sediment (Miller & Barimo 2001), or that this ocean reef habitat type was not available at the time of larval selection and settlement (Edmunds 2004).

P. astreoides' light requirements are consistent with the high frequency of juveniles in horizontal locations, exposed to light, in clear water ocean reefs and recruitment at shallow depths (Vidal *et al.* 2005). Cofforth (1985) and Miller *et al.* (2000) assert that *P. astreoides* invest high levels of energy in protection and competition, producing mucus and presenting a gregarious behavior, which reduces possible cases of inter-specific competition and aggression by algae, giving them a higher rate of survival (Green *et al.* 2008). This strategy and the colonization of substrates devoid of sediment accumulation or with strong hydrodynamics, produces a lower energy expenditure for cleaning, energy that it can invest in competition with macroalgae such as *Lobophora* sp. and *Halimeda* sp., which occupy 12-15% of the substrate (Alvarado & Acosta 2009). Although Miller & Barimo (2001) and Green *et al.* (2008) state that *P. astreoides* is tolerant to different physical and biological habitats, juveniles appear to show specificity to habitat factors.

The favorable relationship of *S. siderea* juveniles and cryptic locations, inclined substrates and the lack of competitors could reveal the strategy employed by the larvae to colonize crevices, clefts and holes. This occurs when the larvae are faced with limitations of settlement substrate (e.g. due to high algal cover). This type of environment is abundant in ocean reefs at depths between 10-16m, where the reef has higher rugosity and presents a 3D structure. The amount of coarse and fine sediment accumulated in holes (greater than 1cm) presents a disadvantage for juveniles in this type of habitat as it may causes larvae to settle and recruit on inclined sections, precisely where the highest frequency of juveniles was observed. Smith (1997) proposes that *S. siderea* boasts a resistance to sedimentation, which probably gives

it an advantage to settle in holes or rubble, as shown in the MCA in this study. Another disadvantage caused by the crevices is the reduction of direct light necessary for juvenile growth, which in turn is advantageous since it repels macroalgae and prevents the expenditure of energy on competition. Barrios (2000) stresses the high sensitivity of *S. siderea* juvenile to the aggression of other sessile organisms. However, although it has been proposed that *S. siderea* is an indicator species for pollution and sedimentation (Guzmán & Jiménez 1992), juveniles were scarce in continental environments where these factors are present, this may be due to low roughness and 3D structure of the system to recruit, a small number of adults and hence low reproductive effort of this spawner species, as Alvarado & Acosta (2009) found with lower number of gametes for *M. annularis* in Isla Grande, Colombian Caribbean, or due to lower larval survival in the water column by factors such as low salinity.

For its part, the dependence of juvenile *A. lamarcki*, *L. cucullata* and *A. agaricites* on a non-sedimented bottom, exposed to light and ocean reef habitats, reveals that recruitment and survival is lower in degraded areas (Hughes 1985), influenced by rivers. These species may secure the energy investment made by the larva during settlement, by locating itself specifically in areas sheltered from sediment (Hughes & Tanner 2000). Despite the slow colonization of new areas by *A. lamarcki* larvae, this species has high survival rate (Hughes 1988), higher than even *A. agaricites* and *L. cucullata*, the dominant species of juveniles in this study (593 and 354 juveniles, respectively) and in most Caribbean reefs (Hughes 1988, Kramer 2003). This potentially allows the species to maintain stable populations in areas with low sedimentation rate in the Colombian Caribbean, in areas like reef terraces presenting high hydrodynamic or a high gradient slope. The horizontal form in which these species grow explains their dependence on habitats exposed to light and for *A. lamarcki*, the monopolization of substrate in deep oceanic reefs the interaction with corals of the same species. Among all the species,

A. agaricites is the most proficient at recruitment; it colonizes different microhabitats at depths ranging from 2-30m and can endure a broad spectrum of conditions in the environment (Vidal *et al.* 2005), in agreement with Chiappone & Sullivan (1996) and the study by Edmunds (2000) in Florida and St. John - Virgin Islands, respectively.

Juvenile *P. porites*, *F. fragum* and *M. cavernosa* had a dependence on ocean reefs, a microhabitat exposed to light and unoccupied by competitors. The susceptibility of *P. porites* to competition with macroalgae may explain its requirement to colonize spaces without competitors and with direct light. River & Edmunds (2001) assert that the growth rate of *P. porites* decreases up to 80% when surrounded by macroalgae. Contrary to Lewis (1974), who found that most larvae colonize cryptic sites, displaying a gregarious behavior by juveniles and adults, the presence of *F. fragum* juveniles was detected on coral rubble, in shallow terraces exposed to light and unoccupied by competitors. In turn, juveniles of *M. cavernosa* were associated with environments presenting high sediment load (60.8%). Their massive shape makes it more resistant to wave action and more efficient in the removal of sediments (Huitric & McField 2001, Martínez & Acosta 2005). Its relatively low recruitment rate (Smith 1997) is offset by an increase in its inter and intra-specific aggression (Hughes & Jackson 1985); this allows it to compete for potential growth-space. These survival strategies provide it dominance in many regions, as an adult (Martinez & Acosta 2005) and even as a juvenile.

Although the variables assessed here are those considered as critical to the recruitment of hermatypic corals in Caribbean reefs, exploring and evaluating other biotic (foraging) and abiotic factors of the habitat is essential, given the dependence of the species on specific factors. Moreover, the diverse causes of the observed patterns of dependency and the synergy between larval selection behavior and natural selection factors should also be investigated. This study presents an examination of

the entire juvenile coral community; however, more detailed studies by species are necessary, particularly those that are rare, vulnerable and spawners with low fertility/fecundity rates and growth. In order to find possible dependences and associations not detected in this study and apply statistical independence analyses to other species, it is recommended a minimum sampling size of 100-150 juveniles/species.

The density of juveniles found is not considered sufficient to replace the dying adults in the reefs studied; this makes juvenile richness and density very low when compared to that of adult corals (Acosta *et al.* 2011). As the fitness of coral species decreases because of recruitment failure, so does the resilience of the reef, its recovery and populations' viability (Sale *et al.* 2010). Seven of the most active species in recruitment were brooders, with the exception of *M. cavernosa* and *S. siderea*, which as Carlon (2002) proposes, may be an indication of a potential change in dominance of the coral assemblage from building species for short-lived brooding species (juvenile *A. agaricites*, *L. cucullata* and *P. astreoides*). The low recruitment and the poor recovery of populations in the system also facilitate a community shift in continental reefs (algae for corals), as is the case in shallow areas of Isla Grande (Alvarado & Acosta 2009, Acosta *et al.* 2011).

The reality of Caribbean reefs is the great decline caused by anthropic disturbance and inland waters that increase the direct input of sediment and nutrients. This according to Alvarado & Acosta (2009) creates stress, population mortality, reduction in colony size, low number of breeding individuals, low reproductive output, lower quality and limited availability of habitat for larval selection (Montenegro & Acosta 2008, 2010), random settlement (Mundy & Babcock 2000, Vermeij *et al.* 2006), recruitment in sub-optimal locations and post-settlement mortality (Fabricius 2005, Vermeij *et al.* 2006, Victor 2008) and consequently, low recruitment (Acosta *et al.* 2011). To achieve successful coral recruitment, the favorable or ideal environment would occur in oceanic islands or areas not exposed to the effect of

rivers, with good visibility, availability of dead coral for settlement, in a wide range of depths to set up the assembly of coral, inclined microhabitats that receive plenty of direct light, with not accumulated sediment and with low numbers of macroalgae or competitors. These habitat requirements should be considered by the decision makers in conservation efforts.

In conclusion, the presence, abundance and survival of juveniles depend on certain features of the habitat, which are species-specific. However, the juveniles of six species, mostly brooders, display specificity to one or two factors and high tolerance to a wide range of variables of the habitat evaluated. Most juveniles recruit on dead coral (except *S. siderea* and *F. fragum* on rubble), on inclined areas, exposed to direct light (except *S. siderea* and species of the *Agaricia* genus, cryptic), where *F. fragum* and the *Porites* genus are highly dependent on light (abundant in shallow and medium zones). This indicates the importance of clear water with low turbidity (low concentration of dissolved and particulate organic matter). Few species used rocky or encrusted red algae substrates; this reflects their low number and availability. Similarly, juveniles seem to prefer substrates where sediment does not accumulate, particularly *A. lamarcki* and *L. cucullata*, in contrast to what was observed for *S. siderea*, *A. tenuifolia* and *M. cavernosa* that tolerate high sediment loads. Juveniles recruit and survive on substrates occupied, primarily by macroalgae; this is evident for *A. tenuifolia* and in a lesser degree for *A. lamarcki* and *P. astreoides*, while *S. siderea* displays the lowest number of interactions. Most species use a wide range of depths (two or three categories), or specific ranges depending on their requirements and life history; juveniles of *A. tenuifolia* are favored, specifically between 10-16m and *F. fragum* between 2-8m. All species recruit disproportionately, in higher numbers in oceanic reefs except for *A. tenuifolia*, which prefers

continental reefs, indicating that oceanic islands offer the best conditions for recruitment.

ACKNOWLEDGMENTS

To the Academic Vice-rectory of the Pontificia Universidad Javeriana that financed this project (0417; 4803), to Flavia Cárdenas, Mónica Sepúlveda, Claudia Villamil and Andrés Vidal for the field work that yielded the data used in this study, as well as to Margarita Ordoñez and Miguel Pinzón for their statistical advice. To Gypsy Espanol for the translation into the English version. (Traducciones Técnicas T y T; www.traduccionesty.com).

RESUMEN

Existe poca evidencia sobre la dependencia entre la abundancia de juveniles de corales hermatípicos y las condiciones del hábitat. La abundancia de corales juveniles se relacionó con condiciones del hábitat a macro (ubicación del arrecife, profundidad) y microescala (tipo e inclinación del sustrato, exposición a luz, textura y cantidad de sedimento, área de crecimiento potencial de juveniles). El muestreo se realizó en cuatro arrecifes insulares del Caribe colombiano. La dependencia se evaluó usando tablas y coeficientes de contingencia y análisis de correspondencias múltiples. *Agaricia tenuifolia* mostró las dependencias más robustas, siendo significativas para juveniles presentes frecuentemente en arrecifes continentales, sustrato horizontal expuesto a luz, con competidores. Los juveniles se asociaron con moderado a alto sedimento muy fino acumulado en el fondo. *Porites astreoides* presentó cuatro dependencias; alta frecuencia en sustrato expuesto a luz, horizontal, sin sedimento, con competidores y en arrecifes oceánicos entre 2-16m. *Siderastrea siderea* exhibió tres dependencias, para juveniles en lugares crípticos, sustrato inclinado y sin competidores. *A. lamarcki*, *Leptoseris cucullata*, *A. agaricites*, *P. porites*, *Favia fragum* y *Montastraea cavernosa* mostraron el menor número de dependencias, compartiendo alta frecuencia en hábitats sin sedimento, expuestos a luz, con competidores y en arrecifes oceánicos. Los resultados sugieren que la abundancia y sobrevivencia de juveniles dependen de ciertas particularidades especie-específicas del hábitat; sin embargo, los juveniles presentan tolerancia a una amplia gama de variables del hábitat.

Palabras clave: reclutamiento, corales juveniles, hábitat, arrecifes insulares, Caribe, Colombia, *Agaricia*, *Porites*, *Siderastrea*, *Leptoseris*, *Favia*, *Montastraea*.

REFERENCES

- Acosta, A. & S. Martínez. 2006. Continental and oceanic coral reefs in the Colombian Caribbean after a decade of degradation. Proc. 10th Int. Coral Reef Symp. 2: 1926-1930.
- Acosta, A., L.F. Dueñas & V Pizarro. 2011. Review on hard coral recruitment (Cnidaria: Scleractinia) in Colombia. Univ. Sci. 16: 200-218. (también disponible en línea: www.javeriana.edu.co/universitas_scientiarum/articulos/online.html).
- Alvarado, E., G. Pinilla, T. León & A. Cortes. 1989. Plan de Manejo - Parque Nacional Corales del Rosario. Inderena, Universidad Jorge Tadeo Lozano, Bogotá, Colombia.
- Alvarado, E. & A. Acosta. 2009. Fertilidad y fecundidad de *Montastraea annularis* en un arrecife degradado. Bol. Invest. Mar. Cost. 38: 91-108.
- Aronso, R.B., I.G. Macintyre, C.M. Wapnick & M.W. O'Neill. 2004. Phase shifts alternative states and the unprecedented convergence of two reef systems. Ecology 85: 1876-1891.
- Baird, A.H., R.C. Babcock & C.P. Mundy. 2003. Habitat selection by larvae influences the depth distribution of six common coral species. Mar. Ecol. Progr. 252: 289-293.
- Bak, R.P. & M.S. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. 54: 341-352.
- Barrios, L.M. 2000. Evaluación de las principales condiciones de deterioro de los corales pétreos en el Caribe colombiano. Tesis de Posgrado en Biología - Línea Biología Marina, INVEMAR, Universidad Nacional de Colombia, Santa Marta, Colombia.
- Birrell, C.L., L.J. McCook, B.L. Willis & G.A. Díaz-Pulido. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr. Mar. Biol. 46: 25-63.
- Carlson, D.B. 2002. Production and supply of larvae as determinants of zonation in a brooding tropical coral. J. Exp. Mar. Biol. Ecol. 268: 33-46.
- Chiappone, M. & K.M. Sullivan. 1996. Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. Bull. Mar. Sci. 58: 555-569.
- Cofforth, M.A. 1985. Mucous sheet formation on poritid corals: effects of altered salinity and sedimentation. Proc. 5th Int. Coral Reef Symp. 4: 165-170.
- Díaz, J.M., J. Garzón-Ferreira & S. Zea. 1995. Los arrecifes coralinos de la Isla de San Andrés, Colombia: estado actual y perspectivas para su conservación. Acad. Col. Cienc. Exact. Fis. Nat., Colección Jorge Álvarez Lleras 7, Bogotá, Colombia.
- Díaz, J.M., J.A. Sánchez & G. Díaz-Pulido. 1996. Geomorfología y formaciones arrecifales recientes de Isla Fuerte y Bajo Bushnell, Plataforma continental del Caribe colombiano. Bol. Invest. Mar. Cost. 25: 87-105.
- Díaz, J.M., L.M. Barrios, M.H. Cendales, J. Garzón-Ferreira, J. Geister, M. López-Victoria, G.H. Ospina, F. Parra-Velandia, J. Pinzón, B. Vargas-Ángel, F.A. Zapata & S. Zea. 2000. Áreas Coralinas de Colombia. INVEMAR, Ser. Pub. Esp. 5, Santa Marta, Colombia.
- Díaz, L.G. 2002. Estadística multivariada: inferencias y métodos. Universidad Nacional de Colombia, Panamericana, Bogotá, Colombia.
- Dornelas, M., S.R. Connolly & T.P. Hughes. 2006. Coral reef diversity refutes the neutral theory of biodiversity. Nature 440: 80-82.
- Dueñas, L.F., J. Montenegro, A. Acosta, F. Cárdenas, M. Sepúlveda, A. Vidal & C. Villamil. 2010. Guide to Scleractinian coral recruits from the Caribbean. Pontificia Universidad Javeriana, INVEMAR Serie de Documentos Generales No. 42, XPRESS, Bogotá, Colombia.
- Edmunds, P.J. 2000. Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. Mar. Ecol. Progr. Ser. 202: 113-124.
- Edmunds, P.J. 2004. Juvenile coral population dynamics track rising seawater temperature on a Caribbean reef. Mar. Ecol. Progr. Ser. 269: 111-119.
- Edmunds, P.J., J.F. Bruno & D.B. Carlton. 2004. Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. Mar. Ecol. Progr. 278: 115-124.
- Elmhirst, T., S.R. Connolly & T.P. Hughes. 2009. Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs 28: 949-957.

- Fabricius, K.E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50: 125-146.
- Garay, J. 2001. Calidad ambiental marina en Colombia año 2000, p. 97-114. *In* INVEMAR (eds.). Informe del estado de los ambientes marinos y costeros en Colombia: 2000. Ser. Doc. Gral. 7, Santa Marta, Colombia.
- Gardner, T.A., I.M. Cote, F.A. Gill, A. Grant & A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301: 958-960.
- Garzón-Ferreira, J., M.C. Reyes-Nivia & A. Rodríguez-Ramírez. 2002. Manual de métodos del SIMAC - Sistema Nacional de monitoreo de Arrecifes Coralinos en Colombia. INVEMAR, Ministerio del Medio Ambiente, Santa Marta, Colombia.
- Green, D.H., P.J. Edmunds & R.C. Carpenter. 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Mar. Ecol. Progr.* 359: 1-10.
- Guzmán, H.M. & C.E. Jiménez. 1992. Contamination of coral reefs by heavy metals along the Caribbean coast of Central America (Costa Rica and Panamá). *Mar. Pollut. Bull.* 24: 554-561.
- Harrington, L., K. Fabricius, G. De'ath & A. Negri. 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85: 3428-3437.
- Hughes, T.P. 1985. Life histories and population dynamics of early successional corals. *Proc. 5th Int. Coral Reef Symp.* 4: 101-106.
- Hughes, T.P. 1988. Long-term dynamics of coral populations: contrasting reproductive modes. *Proc. 6th Int. Coral Reef Symp.* 2: 721-725.
- Hughes, T.P. & J.B.C. Jackson. 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55: 141-166.
- Hughes, T.P. & J.E. Tanner. 2000. Recruitment failure, life histories and long term decline of Caribbean corals. *Ecology* 81: 2250-2263.
- Hughes, T.P., M.J. Rodriguez, D.R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanivskyj, M.S. Pratchett, R.S. Steneck & B. Willis. 2007. Phase shifts, herbivory and the resilience of coral reefs to climate change. *Curr. Biol.* 17: 360-365.
- Huitric, M. & M. McField. 2001. Effects of multiple disturbances on hard coral recruits in Glovers Reef Atolls lagoon, Belize. *Beijer Discussion Paper* 138: 1-20.
- Kramer, P.A. 2003. Synthesis of coral reef health indicators for the Western Atlantic: results of the AGRRA program (1997-2000). *Atoll. Res. Bull.* 496: 1-57.
- Lewis, J.B. 1974. The settlement behavior of planulae larvae of the hermatypic coral *Favia fragum* (Esper). *J. Exp. Mar. Biol. Ecol.* 15: 165-172.
- Lirman, D. & D. Manzello. 2009. Patterns of resistance and resilience of the stress-tolerant coral *Siderastrea radians* (Pallas) to sub-optimal salinity and sediment burial. *J. Exp. Mar. Biol. Ecol.* 369: 72-77.
- Martínez, S. & A. Acosta. 2005. Cambio temporal en la estructura de la comunidad coralina del área de Santa Marta - Parque nacional Natural Tayrona (Caribe Colombiano). *Bol. Invest. Mar. Cost.* 34: 161-191.
- McCook, L.J., J. Jompa & G. Díaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417.
- Miller, M.W. & J. Barimo. 2001. Assessment of juvenile coral populations at two reef restoration sites in the Florida Keys National Marine Sanctuary: indicators of success? *Bull. Mar. Sci.* 69: 395-405.
- Miller, M.W., E. Weil & A.M. Szmant. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19: 115-123.
- Montenegro, J. & A. Acosta. 2008. Havistat 2008 V.1.0. ©Programa para inferir uso y preferencia de hábitat. Unesis, Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Bogotá, Colombia.
- Montenegro, J. & A. Acosta. 2010. Habitat preference of *Zoantharia* genera depends on host sponge morphology. *Universitas Scientiarum* 15: 110-121.
- Mundy, C.N & R.C. Babcock. 1998. Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? *J. Exp. Mar. Biol. Ecol.* 223: 235-255.
- Mundy, C.N & R.C. Babcock. 2000. Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? a case study of three contrasting species. *Mar. Ecol. Progr.* 198: 109-119.

- Pita, S. 1996. Determinación del tamaño muestral. *Cad. Aten. Primaria* 3: 138-141.
- Porter, J.W. & J.I. Tougas. 2001. Reef ecosystem: threats to their biodiversity, p. 73-95. In S.A. Levin (ed.). *Encyclopedia of Biodiversity*. Academic, San Diego, USA.
- Richmond, R.H. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs, p. 175-197. In C. Birkeland (ed.). *Life and death of Coral Reefs*. Chapman & Hall, New York, USA.
- Richmond, R.H. & C.L. Hunter. 1990. Reproduction and recruitment of corals: comparison among the Caribbean, the Tropical Pacific, and the Red sea. *Mar. Ecol. Progr.* 60: 185-203.
- River, G.F. & P.J. Edmunds. 2001. Mechanisms of interactions between macroalgae and scleractinian on a coral reef in Jamaica. *J. Exp. Mar. Biol. Ecol.* 261: 159-172.
- Ruiz-Zárate, M.A., J. Espinoza-Avalos, J.P. Carricart-Ganivet & D. Fragososo. 2000. Relationships between *Manicina areolata* (Cnidaria: Scleractinia), *Thalassia testudinum* (Anthophyta) and *Neogoniolithon* sp. (Rhodophyta). *Mar. Ecol. Progr.* 206: 135-146.
- Sale, P.F., H. Van Lavieren, M.C.A. Lagman, J. Atema, M. Butler, C. Fauvelot, J.D. Hogan, G.P. Jones, K.C. Lindeman, C.B. Paris, R. Steneck & H.L. Stewart. 2010. *Preserving Reef Connectivity: A Handbook for Marine Protected Area Managers*. Connectivity Working Group, Coral Reef Targeted Research & Capacity Building for Management Program, UNU-INWEH, Melbourne, Australia.
- Smith, S.R. 1997. Patterns of coral settlement, recruitment and juvenile mortality with depth at Conch Ref., Florida. *Proc. 8th Int. Coral Reef Symp.* 2: 1197-1202.
- Vermeij, M.J.A., N.D. Fogarty & M.W. Miller. 2006. Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*. *Mar. Ecol. Progr.* 310: 119-128.
- Victor, S. 2008. Stability of reef framework and post settlement mortality as the structuring factor for recovery of Malakal Bay Reef, Palau, Micronesia: 25 years after a severe COTS outbreak. *Estuar. Coast. Shelf Sci.* 77: 175-180.
- Vidal, A., A. Acosta & C. Villamil. 2005. Composición y densidad de corales juveniles en dos arrecifes profundos de San Andrés Isla, Caribe colombiano. *Bol. Invest. Mar. Cost.* 34: 211-225.

APPENDIX 1
Juvenile frequencies for all measured variables

Variable	Categories	<i>A. tenuifolia</i>		<i>P. astreoides</i>		<i>S. sidera</i>		<i>A. lamarki</i>		<i>L. cucullata</i>		<i>A. agaricoides</i>		<i>P. porites</i>		<i>F. fragum</i>		<i>M. cavernosa</i>	
		Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr	Fi	Fr
Location of the reef regarding the platform	Oceanic	17	21.2	153	61.7	166	89.2	128	99.2	311	87.8	430	72.5	69	78.4	155	89.6	115	92
	Continental	63	78.7	95	38.3	20	10.7	1	0.8	43	12.2	163	27.5	19	21.6	18	10.4	10	8
	Shallow	14	17.5	125	50.4	47	25.3	3	2.3	13	3.7	145	24.4	33	37.5	136	78.61	12	9.6
Range of depth	Medium	60	75	100	40.3	59	31.7	28	21.7	99	28	205	34.6	40	45.5	33	19.08	59	47.2
	Deep	6	7.5	22	8.9	53	28.5	45	34.9	131	37	160	27	13	14.8	4	2.31	31	24.8
	Very deep	0	0	1	0.4	27	14.5	53	41.1	111	31.4	83	14	2	2.3	0	0	23	18.4
Substrate type	Dead coral	70	87.5	150	60.5	36	19.3	99	76.7	249	70.3	354	59.7	47	53.4	51	29.48	61	48.8
	Rock	2	2.5	12	4.8	4	2.1	2	1.6	7	2	12	2	6	6.8	6	3.47	4	3.2
	Rubble	8	10	84	33.9	146	78.5	28	21.7	98	27.7	225	37.9	35	39.8	111	64.16	60	48
Substrate inclination	Encrusted red algae	0	0	2	0.81	0	0	0	0	0	0	0	0.3	0	0	5	2.89	0	0
	Horizontal	35	43.7	120	48.4	54	29	23	17.8	91	25.7	163	27.5	39	44.3	68	39.3	33	26.4
	Vertical	18	22.5	36	14.5	19	10.2	41	31.8	73	20.6	111	18.7	10	11.4	16	9.2	31	24.8
Exposure to light	Inclined	27	33.7	92	37.1	113	60.7	65	50.4	190	53.7	319	53.8	39	44.3	89	51.4	61	48.8
	Exposed	41	51.2	180	72.6	74	39.8	81	62.8	211	59.6	304	51.3	66	75	160	92.5	71	56.8
	Cryptic	39	48.7	68	27.4	112	60.2	48	37.2	143	40.4	289	48.7	22	25	13	7.5	54	43.2
Sediment texture	Very fine - Clay-silt	61	76.2	50	20.2	13	7	0	0	30	8.5	69	11.6	11	12.5	14	8.1	2	1.6
	Fine	1	1.2	29	11.7	74	39.8	0	0	21	5.9	84	14.2	31	35.2	82	47.4	32	25.6
	Coarse	0	0	30	12.1	88	47.3	11	8.5	49	13.8	147	24.8	4	4.5	1	0.6	50	40
Amount of accumulated sediment	No sediment	18	22.5	139	56	11	5.9	118	91.5	254	71.8	293	49.4	42	47.7	76	43.9	41	32.8
	Disperse	4	5	23	9.3	5	2.7	1	0.8	13	3.7	50	8.4	6	6.8	8	4.6	8	6.4
	Moderate	43	53.7	36	14.5	40	21.51	4	3.1	34	9.6	75	12.6	8	9.1	6	3.5	13	10.4
Potential growth space	High	15	18.7	50	20.2	130	69.9	6	4.6	53	15	175	29.5	32	36.4	83	48	63	50.4
	No sediment	18	22.5	139	56	11	5.9	118	91.5	254	71.8	293	49.4	42	47.7	76	43.9	41	32.8
	Available	14	17.5	96	38.7	132	71	47	36.4	158	44.6	326	55	48	54.5	89	51.4	73	58.4
Occupied by	Occupied	66	82.5	152	61.3	54	29	82	63.5	196	55.4	267	45	40	45.5	84	48.6	52	41.6
	Macroalgae	42	63.6	64	42.1	38	20.37	0	0	36	18.4	99	37.1	21	52.5	23	27.38	29	55.8
	Macroalgae/corals	15	22.7	8	5.3	1	1.85	0	0	2	1.02	23	8.6	0	0	1	1.19	0	0
No identified	Macroalgae/sponges	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	0	0
	Octocorals	0	0	2	1.3	3	5.56	0	0	2	1.02	4	1.5	0	0	1	1.19	1	1.9
	Sponges	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	0	0
No identified	Corals	5	7.6	4	2.6	7	12.96	81	98.8	10	5.1	6	2.2	0	0	2	2.38	2	3.8
	No identified	4	6.1	74	48.7	5	9.26	1	1.2	146	74.5	159	59.5	19	47.5	57	67.86	20	38.5

Fi= Absolute frequency. Fr= Relative frequency with respect to the independent-variable categories.