The role of geomorphic zonation in long-term changes in coral-community structure on a Caribbean fringing reef

Alexis Enrique Medina-Valmaseda Corresp., 1 , **Rosa E. Rodríguez-Martínez** 2 , **Lorenzo Alvarez-Filip** 2 , **Eric Jordan-Dahlgren** 2 , **Paul Blanchon** 2

1 Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, Mexico

2 Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico

Corresponding Author: Alexis Enrique Medina-Valmaseda
Email address: alexismedina67@gmail.com

Ecological processes on coral reefs commonly have limited spatial and temporal scales and may not be recorded in their long-term geological history. The widespread degradation of Caribbean coral reefs over the last 40 years therefore provides an opportunity to assess the impact of more significant ecological changes on the geological and geomorphic structure of reefs. Here, we document the changing ecology of communities in a coral reef seascape within the context of its geomorphic structure. By comparing basic ecological indices between historical and modern data we show that in 35 years the reef-front zone was transformed from a complex coral assemblage with a three-dimensional structure, to a size-homogenized and flattened one that is quasi indistinguishable from the adjacent non-accretional rock-terrace zone. Today coral assemblages at Punta Maroma are characterized by the dominance of opportunistic species which are either tolerant to adverse environmental conditions, including sedimentation, or are known to be the first scleractinian species to recruit on disturbed reefs, implying they reflect a post-hurricane stage of adjustment. Despite an increase in similarity in ecological indices, the reef-front and hard-ground geomorphic zones still retain significant differences in coral assemblages and benthic habitat and are not homogeneous. The partial convergence of coral assemblages certainly has important consequences for the ecology and geological viability of the reef and its role in coastal protection, but environmental physical drivers continue to exert a fundamental role in the character and zonation of benthic communities of this reef seascape.

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Medina-Valmaseda, A.E[1]**, Rodríguez-Martínez R.E.**[2]**, Álvarez-Filip L.**[2]**, Jordán-Dahlgren E.**[2]**, and Blanchon, P.**[2]

[1]**Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México; Av. Ciudad Universitaria 3000, C.P. 04510, Coyoacán, Ciudad de México, México.**
[2,3,4,5]**Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Unidad Académica de Sistemas Arrecifales Puerto Morelos, Quintana Roo, México.**

Corresponding author:

Medina-Valmaseda, A.E.[1]

Email address: alexismedina67@gmail.com

ABSTRACT

Ecological processes on coral reefs commonly have limited spatial and temporal scales and may not be recorded in their long-term geological history. The widespread degradation of Caribbean coral reefs over the last 40 years therefore provides an opportunity to assess the impact of more significant ecological changes on the geological and geomorphic structure of reefs. Here, we document the changing ecology of communities in a coral reef seascape within the context of its geomorphic structure. By comparing basic ecological indices between historical and modern data we show that in 35 years the reef-front zone was transformed from a complex coral assemblage with a three-dimensional structure, to a size-homogenized and flattened one that is quasi indistinguishable from the adjacent non-accretional rock-terrace zone. Today coral assemblages at Punta Maroma are characterized by the dominance of opportunistic species which are either tolerant to adverse environmental conditions, including sedimentation, or are known to be the first scleractinian species to recruit on disturbed reefs, implying they reflect a post-hurricane stage of adjustment. Despite an increase in similarity in ecological indices, the reef-front and hard-ground geomorphic zones still retain significant differences in coral assemblages and benthic habitat and are not homogeneous. The partial convergence of coral assemblages certainly has important consequences for the ecology and geological viability of the reef and its role in coastal protection, but environmental physical drivers continue to exert a fundamental role in the character and zonation of benthic communities of this reef seascape.

INTRODUCTION

Coral reefs develop over geologic timescales through a complex process termed accretion (Perry and Hepburn, 2008; Pandolfi et al., 2011). Most consider this to involve a dynamic interplay between three ecological and sedimentological processes: framework growth, physical and biological erosion and internal sedimentation and cementation (Rasser and Riegl, 2002; Perry and Hepburn, 2008). Framework

38 growth is accomplished primarily by scleractinian corals but with important contributions from calcifying
39 encrusters, such as crustose coralline algae. This growth is balanced by biological, chemical and physical
40 erosion and mediated by environmental gradients in wave-energy, light penetration, and sediment flux
41 (Geister, 1977; Huston, 1985), and produces a layer of geomorphically zoned framework (Geister, 1977;
42 Graus and Macintyre, 1989; Kennedy and Woodroffe, 2002). Left undisturbed, this framework has the
43 potential to accrete vertically, as one coralgal cohort develops over another through time producing a
44 geological reef deposit (Geister, 1980; Done et al., 2011).

45 Vertical reef accretion is clearly dependent upon short-term ecological processes persisting over
46 thousands of years and generating a positive balance of growth and accumulation over erosion and
47 removal. And even in zones with a positive balance, that accretion should vary significantly depending
48 on the size and growth rate of corals in assemblages dominating each zone. For example, drilling on
49 Caribbean reefs protected from hurricanes has shown that frameworks dominated by branching Acroporid
50 corals have undergone significant vertical accretion and produced large geological reef structures during
51 the Holocene (Macintyre and Glynn, 1976). However, in more hurricane-prone areas, drilling in the
52 same zones have instead shown that Holocene reef structures are biodetrital consisting mostly of the
53 fragmented remains of corals that once covered their surfaces (Blanchon et al., 1997, 2017). Furthermore,
54 'non-accretionary' coralgal frameworks, or coral grounds, have been reported from the extensive shelf
55 zones both adjacent to and between the accretionary reef structures (Rodríguez-Martínez et al., 2011).
56 Clearly the natural ecological seascape of reefs is complex and transient and surface coral assemblages
57 may not always indicate how accretion occurs or even if it occurs at all.
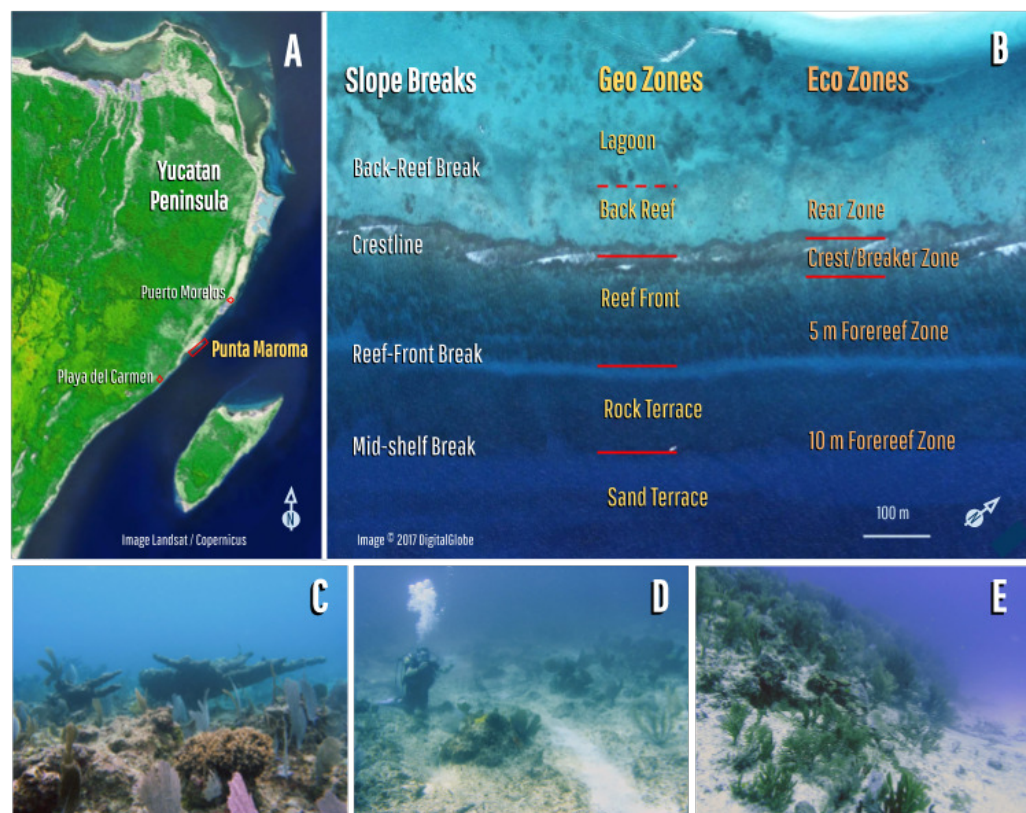
58 With the demise and deterioration of Caribbean reefs during the last 40 years, and the decimation of
59 keystone Acroporids in particular (Gardner et al., 2005; Jackson et al., 2014), this complex ecological
60 seascape is radically changing (Perry and Alvarez-Filip, 2019). Biodiversity loss and biotic homogeniza-
61 tion are not only compromising the ecological functioning of reefs (Olden and Poff, 2003; Burman et al.,
62 2012; Alvarez-Filip et al., 2013; Elliff and Silva, 2017) and their ability to provide local and regional
63 services (Alvarez-Filip et al., 2009, 2011), but are predicted to reduce their potential for long-term
64 accretion (Perry et al., 2013; Estrada-Saldívar et al., 2019). Assessing the accuracy and validity of these
65 accretion predictions, however, is problematic for several reasons (Lange et al., 2020). First, biotic
66 homogenization stemming from the loss of large reef-builders, like Acroporids, makes it difficult to
67 locate geomorphic boundaries between framework zones and adjacent non-accretionary communities that
68 veneer the surrounding shelf. Combining such geomorphic zones would give less representative accretion
69 potentials for reef systems. Second, use of ecological 'snapshots' to estimate the accretion potential of
70 entire reefs makes two questionable assumptions: that drivers which exist outside of ecological timescales
71 are unimportant in the accretion process, and that accretion is uniform in space and time (Perry, 2011;
72 Courtney et al., 2016; Manzello et al., 2018). In terms of drivers, we know that hurricanes have played an
73 important role in Caribbean reef accretion during the Holocene (Blanchon et al., 2017). However, little is
74 known about changes in accretion rates, although it seems unlikely that they would remain constant given
75 that sea level and climate has varied during the Holocene (Blanchon and Shaw, 1995; Gischler, 2006;
76 Toscano and Macintyre, 2006; Khan et al., 2017).

77 In this study, we evaluate the homogenization process between the two most conspicuous geomorphic
78 zones along a windward reef at Punta Maroma, Mexico, where the long-term history of accretion is known
79 from drilling (Blanchon et al., 2017). Although surveys indicate there has been some homogenization
80 in the abundance, species composition, and size structure of coral assemblages in adjacent geomorphic
81 zones, we find that coral communities covering these zones continue to be statistically different. In
82 addition, ecological indices provide assessments of accretion potential that are inconsistent with the actual
83 accretion determined from geological data.

METHODS

Study site

The study site is a 4.5 km-long fringing reef at Punta Maroma, in the northeastern Yucatan Peninsula, close to Playa del Carmen, Quintana Roo, Mexico (Fig. 1A). It has a typical tripartite geomorphic zonation, with a reef-front, crest, and back-reef, and is flanked by a shallow (< 6m) lagoon, on its landward side, and a deeper (> 8 m) coral-veneered rock terrace, on its seaward side (Fig.1B). The geological structure of the reef front was reported by Blanchon et al. (2017) who showed that it consists of clast-dominated hurricane deposits, with a maximum age of 5.5 ka. Cores from this study also showed that the seaward coral-veneered rock terrace is a late Pleistocene extension of the coastal bedrock with no evidence of reef accretion during the Holocene.

Figure 1. Ecological seascape and zonation of the fringing reef at Punta Maroma. (A) Location of Punta Maroma; (B) Reef zonation and geomorphology showing: slope breaks and geomorphological zones (following Blanchon et al., 2017) and ecological seascape zones (following Jordán-Dahlgren et al., 1981 and Estrada-Saldívar et al., 2019); (C) View of the Reef-Front zone (or Fore reef) at 5 m; (D) View of the Rock-Terrace zone (or Fore reef) at 10 m; (E) View of the Mid-shelf break (or Fore reef) between 10 to 15 m.

The combination of these geomorphic zones produces an extensive ecological seascape (> 2000 m^2), which consists of a shallow accretionary reef-front (RF), from the crest down to 6 meters depth (Fig. 1C), and a non-accretionary deeper coral hard-ground (HG) community (Fig. 1D), extending from the limit of the RF out across the rock-terrace to a mid-shelf slope break (Fig. 1E) at 10 m depth (Rodríguez-Martínez et al., 2011; Blanchon et al., 2017). These zones have been collectively referred to as the 'fore-reef' in other studies (Fig. 1B).

Survey methodology and Historical analysis

In order to compare recent coral assemblages from the RF and HG zones at Punta Maroma reef, we surveyed coral species abundance and size between March and June, 2019. The sampling effort consisted of ten 30 m-long belt transects, randomly placed in an orientation roughly parallel to the crestline. Sample size was determined based on historical cumulative species diversity curves, empirically determined in previous studies (Jordan et al., 1981; Jordán-Dahlgren, 1989). All scleractinian colonies within one-metre-wide belt transects were sampled, including those intercepted by the belt line, following Zvuloni et al. (2008). Other environmental data, including depth, spatial position and distance to the mid-shelf edge, were also recorded. Scleractinian coral species were classified based on their morphology and life history following Estrada-Saldívar et al. (2019).

To determine if coral assemblages from the RF and HG zones at Punta Maroma reef experienced changes in the last few decades, we used ecological surveys taken in 1979 (Jordan et al., 1981) and in 1985 (Jordán-Dahlgren, 1989). These data were obtained from 20-m long line-intercept transects, separated from each other by distances of 5-25 m. In these studies, the transects were delimited by plastic chains (with 2.73 cm chain links) that followed the bottom topography. Transects were taken from three zones, described as 'rear-reef', 'breaker zone' and 'fore-reef'. In both surveys the 'fore-reef' transects were placed perpendicular to the coast at two depths: 5 and 10 m. These three zones correspond to four geomorphological zones described by Blanchon et al. (2017): the Back Reef ('rear reef'), Reef Crest ('breaker zone'), Reef Front ('forereef' at 5 m) and Rock Terrace and Mid-shelf break ('forereef' at 10 m). All scleractinian corals below the chain were counted using the chain link as the measurement unit. In 1979, the number of transects per depth was five and in 1985 four. Additionally, in 1985 colonies were measured by their maximum diameter.

Given the differences in the methodological approach (e.g., geomorphic zone classification and LIT vs. belt transects), we included a contrast-based statistical analysis (below) of datasets considering that all surveys fulfilled the minimal sampling effort necessary to accurately describe the coral communities according to cumulative species diversity curves (Gleason, 1922). Also, because in the 1979 and 1985 *M. annularis, M. faveolata* and *M. franksi* were considered as part of the same species complex (*M. annularis*), for our 2019 surveys we combined these three species in one (*Orbicella* [formerly *Montastrea*]"*annularis*" complex).

Approach to accretion processes

Coral colonies were categorized using a two-level classification of their role in the accretion process. Levels were: a) Key species (key spp.), consisting of branching Acroporids and massive *Orbicella* [formerly *Montastrea*]"*annularis*" complex,Budd et al. (2012)) which are considered to be the main reef builders in the Caribbean (Goreau, 1959; Lewis, 1984; Toth et al., 2019) and b) Less influential species like small massive, sub-massive or encrusting, digitate and foliose morphologies with lower growth rates, including *Agaricia agaricites* and *Porites astreoides* (Aronson, 2006; Toth et al., 2019).

In addition to classifying their role in accretion, we also use a species Importance Value Index (IVI) (Curtis and McIntosh, 1951; Finol Urdaneta, 1971) as a proxy to estimate the relative importance of each species in the accretion processes within each geomorphic zone. The IVI of each species is calculated as $IVI = (RA + RSD + RF)/3$, where RA is relative abundance, calculated from the number of individuals per species with respect to the number of individuals of all species found in the community; where RSD is relative spatial dominance defined as the area covered by each species (using the colonies maximum and minimum diameters and assuming a planar area for the 2019 data) with respect to the cover of all species; and where RF is relative frequency, estimated as the proportion of transects where a species is present, normalised to the frequency of all species in the community. This is done because different geomorphic zones within a reef have a heterogeneous accretion capacity due not only to the composition of the coral community but also to external environmental gradients (Geister, 1977; Perry, 1999).

Statistical analyses

To compare ecological and morpho-functional data of coral assemblages in the RF and HG zones through time we conducted a multivariate statistical analysis using Plymouth Routines in Multivariate Ecological Research (Primer-e version 7.0.13, serial number 4901, (Clarke and Gorley, 2015) and free software platform of RStudio Team (2020).

To determine the contribution of species to coral assemblages in each zone through time, we conducted a two-way similarity percentage analysis (SIMPER), for zone by time periods, based on Bray-Curtis similarity measures of transformed square-root matrix abundance data, making a 70% cut-off for low contributions (Clarke and Warwick, 1994; Clarke et al., 2014). To evaluate changes in beta-diversity we conducted a PERMDISP test on the basis of a Jaccard transformed data matrix using previously transformed to Presence/Absence data. Shade plots were created to visualize the relative contribution of all surveyed coral species to the assemblages of each geomorphic zone before the 1990s and in 2019. Data were square-root transformed to reduce the differential between the largest and smallest non-zero value in the transformed matrix.

To evaluate changes in coral communities of the two zones through time, we performed a two-way crossed permutational analysis (PERMANOVA) of the same Bray-Curtis matrix under an orthogonal design of two fixed factors: time, with three levels (1979, 1985 and 2019), and zone, with two levels (RF and HG). Additionally, for the factor year we designated two linear contrasts: C1 (1979 vs 1985) and C2 (1979 and 1985 vs 2019). The test was done using permutation of residuals under a reduced model and Type III (partial Square Sums) in 9999 permutations (Anderson, 2001; Anderson and Braak, 2003; Anderson, 2017). To measure and test the homogeneity of multivariate dispersions of data, we performed a non-parametric permutational analysis of multivariate dispersions (PERMDISP), along with pairwise comparisons of Bray-Curtis matrix of similarities. PERMDISP was performed on the basis of distances to centroids, with P-values obtained using permutations (P(perm)) and 9999 permutations, giving the best overall results expected in terms of type I error and power (Anderson, 2006). Results are presented in a Principal coordinates analysis (PCO; (Torgerson, 1958; Gower, 1966) constructed by calculating the distances between samples in a transformed Bray-Curtis similarities merged matrix, of previously standardized and square root transformed relative abundances matrices, for both periods in time. Pearson correlation coefficients of selected taxa were superimposed over the PCO as vectors, to indicate the taxa that most strongly contributed to reef community variation. The taxa selected were derived from a similarity percentage breakdown (SIMPER) analysis of the characteristic and distinguishing reef taxa.

RESULTS

Contemporary Assemblages

In 2019, we identified and measured 724 coral colonies in the RF zone and 732 colonies in the HG zone, resulting in coral densities of 2.41 and 2.44 col. m^{-2} respectively (Table 1, Fig.4A). In the RF zone, coral colonies belong to 23 species of 13 genres, and five species account for 89.4% of the colonies in the sample: *Porites astreoides* (55.7%), *Agaricia agaricites* (11.9%), *Siderastrea siderea* (9.4%), *A. tenuifolia* (6.9%), and *P. porites* (5.5%); the other 18 species represent the remaining 10.6% of the sample, with none representing over 5% (Table 2, Figure 4A). In the HG zone, coral colonies belong to 23 species of 16 genres, and five species account for 81.5% of the sample: *A. agaricites* (32.5%), *P. astreoides* (15.8%), *Montastraea cavernosa* (10.2%), *S. siderea* (16.4%), and *P. porites* (6.4%). The coral species that are considered to contribute most to reef accretion (Acroporids and some massive forms) represent 35% of colonies in the non-accretionary HG zone, whereas they represent only 12.8% in the RF zone with the cornestone species *A. palmata* represented by a minimal number of individuals. In both zones combined, these key species represent 23.9% of all colonies (Table 2, Figure 2A).

Coral colony sizes in both, the RF and HG zones are predominantly small, independent of their morphology (mean = 17.9 ±14.7 cm in the RF and 19.3 ±15.4 cm in the HG (*Data S1.A,S1.B*), with

Coral zone	No. transects	Av. Depth (m)	N	S	Density (ind m^{-2})	SD
RF	10	3.7	724	23	2.41	0.89
HG	10	9.8	732	23	2.44	0.95

Table 1. Table 1. Selected ecological parameters of coral assemblages at two coral zones in the Punta Maroma reef seascape in 2019. HG: Hard-ground community, RF: shallow accretionary reef front, N: Number of coral colonies, S: Species richness, SD: Standard Deviation of the colony density.

only 2.5% of them having diameters larger than 50 cm in both zones. Additionally, coral colonies of all morphologies have low heights in both zones (mean = 6.5 ±8.0 cm in the RF and 10.8 ±11.1 cm in the HG). Corals with massive and sub-massive encrusting morphologies dominate both zones, contributing 83.8% of the colonies in the RF and 87.8% in the HG (Fig.2A), but the identity of dominant species differ, with the small massive *P. astreoides* dominating in the RF zone and the sub-massive encruster *A. agaricites* in the HG zone. The SIMPER test shows the groups of species that co-occur between transects (*Data S2*), and indicates that four species have a high degree of overlap within the HG zone: *A. agaricites, S. siderea, P. astreoides,* and *M. cavernosa* (Average similarity: 70.7), whereas in the RF zone three species overlap: *P. astreoides, A. agaricites* and *S. siderea* (Average similarity: 58.4).

Historical Assemblages

Historically, all coral morphologies had higher coral coverage in the RF zone than in HG zone; the RF zone showed a dominance of branching morphologies and the HG zone a dominance of massive ones (Table 2; Fig. 2B).The SIMPER test for historical data shows three species overlapped in the RF zone: *A. palmata, A. cervicornis,* and *A. tenuifolia* (Average similarity: 52.8) and five in the HG zone: *M. cavernosa, D. stokesi, S. siderea, A. agaricites,* and *M. annularis* complex, now *Orbicella* spp. (Average similarity: 42.6) (*Data S1*). In the RF zone, *A. tenuifolia* and *A. palmata* accounted for the largest live coral coverage (30.0% and 23.3% respectively), and in the HG zone the dominant species were *M.annularis* species complex and *M.cavernosa* (12.6% and 9.2% respectively, Table 2, Figure 4B). In 1985 the average diameter maximum of coral colonies (mean = 42.1 ±24.4 cm) was more than double of those in 2019 (mean = 18.6 ±3.2 cm, *Data S1.A*).

According to the Importance Value Index, the main species in the RF zone in 1985 were *Porites astreoides, Agaricia tenuifolia* and *Acropora palmata* and in 2019 they were *P. astreoides, A. prolifera* and *A. palmata*. The main species in the HG zone in 1985 were *M. annularis* complex, now *Orbicella* spp., *Montastraea cavernosa, P. astreoides* and *Pseudodiploria clivosa*, and in 2019 they were *A. agaricites, Colphophilia natans* and *Siderastrea siderea*. So in RF zone, the relative importance of *A. palmata* and *P. astreoides* increased in time whereas that of *A. tenuifolia* decreased, and in HG zone the dominant species were replaced (Fig. 3, *Data S3*).

Comparative analysis of Coral Communities.

Coral assemblage of the HG zone underwent significant changes in beta diversity (PERMDISP, Jaccard matrix, Fc: 4.47, P(perm) < 0.01; *Data S4.A*), as shown in Fig. 4 shade plot (Fig. 4). Changes in the coral community composition of two zones and heterogeneity in species distribution were analyzed using a two-way crossed (orthogonal) PERMANOVA. This shows strong effect of zone- and time-factors over coral assemblages (P < 0.001 for each test), with the zone-factor being slightly more important (Pseudo-F = 18.66 and 15.38 respectively). The test indicates a statistically significant interaction in the effects of zone and time (P < 0.001), although the combined effect was lower (Pseudo-F = 3.34). Linear contrasts indicate that the effect of time was relevant when comparing 2019 vs before 1990s although there was an effect of zonation. *A posteriori* PERMANOVA pairwise test for both zone- and time-factors versus the zone factor, shows that the average similarity between FR and HG groups is 52.6 (*Data S4.B*).
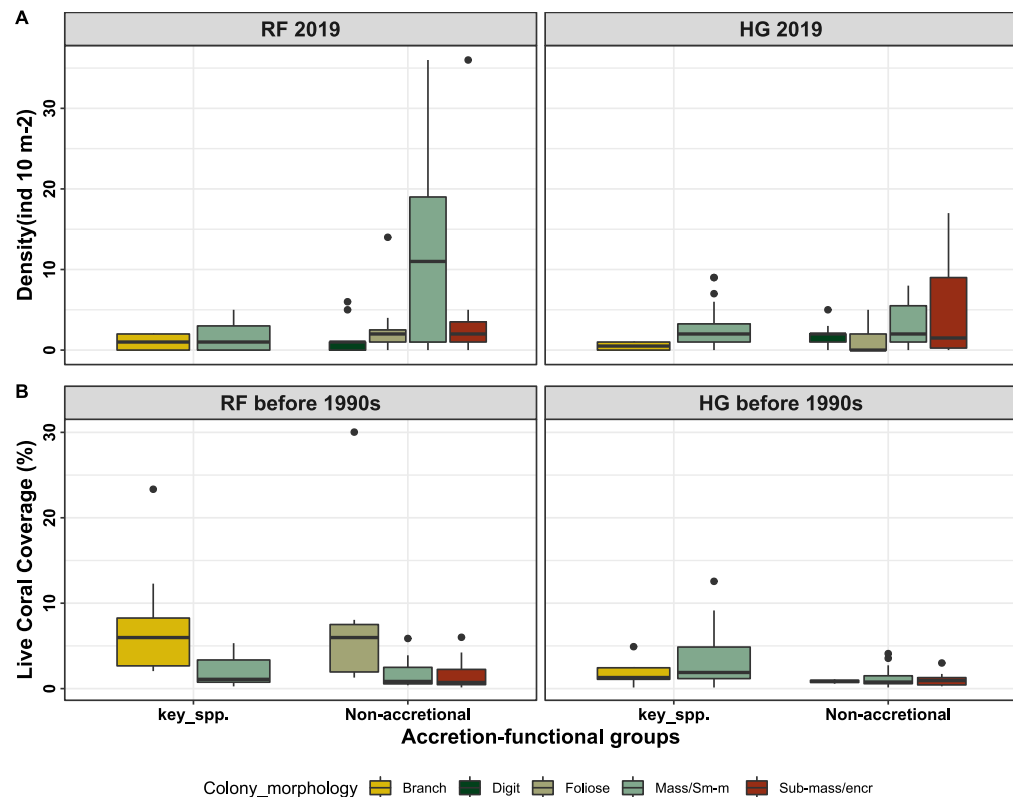
These differences in abundance and composition of coral assemblages for the two zones through time

Accretion potential of species and Colony morphology	Species richness	Before 1990s		Species richness	2019	
		RF	HG		RF	HG
Key_Spp.						
Massive: *Colpophyllia natans, Diploria labyrinthiformis, Montastraea cavernosa, M. annularis spp. Complex (Orbicella faveolata, O. annularis), Pseudodiploria. strigosa, Siderastrea siderea.*	**4**	11	26	**7**	78	253
Branching: *Acropora palmata, A. cervicornis, A. prolifera*	**2**	16	5	**3**	15	5
Non- accretional Spp.						
Small massive: *Solenastrea bournoni, Isophyllia rigida, Favia fragum, Dichocoenia stokesii, Meandrina meandrites, Porites astreoides*	**9**	10	26	**6**	408	136
Sub-massive or encrusting: *Agaricia agaricites, S. radians, Stephanocoenia intersepta*	**3**	11	14	**3**	121	254
Digitates: *Porites porites, P. furcata, P. divaricata*	**2**	3	0	**3**	49	50
Foliaceous: *Agaricia fragilis, A. humilis, A. tenuifolia, A. lamarcki, Leptoseris cucullata, Mycetophyllia lamarckiana*	**1**	7	0	**5**	53	34
	21	**55**	**74**	**28**	**724**	**732**

Table 2. Coral species and number of colonies recorded in two geomorphic zones at Punta Maroma reef seascape before 1990s and in 2019. Coral species are classified according to their growth morphology (Darling et al., 2012). HG: Hard Ground zone, RF: Reef front zone of the fringing reef. Key spp.: 'reef-building' species, Non-accretional Spp.: less influential species for accretion processes

233 are mirrored in a Principal Coordinates Analysis (PCO) ordination procedure (Fig. 5), which shows that *A.*
234 *agaricites, S. siderea, M. cavernosa*, and *P. astreoides* have a strong negative relationship with the PCO1
235 axis (indicative of 2019 sites), while *A. agaricites, S. siderea* and *A. cervicornis* are neutrally related to
236 the PCO2 axis. However, the main reef builders (acroporids and orbicellids) are strongly and positively
237 related to the PCO1 axis (indicative of the period before 1990s), with *A. palmata* being positively related
238 to RF zone before 1990s, whereas species of *M. annularis* spp. complex are related to HG zone (Fig. 5).
239 Other species, such as *M. cavernosa, D. stokesii*, and *P. strigosa*, have strong negative relationships with
240 negative sections of both axes (indicative of the HG zone).

241   *A posteriori* pairwise PERMDISP test highlights that the RF zone conserve a homogeneous dispersion
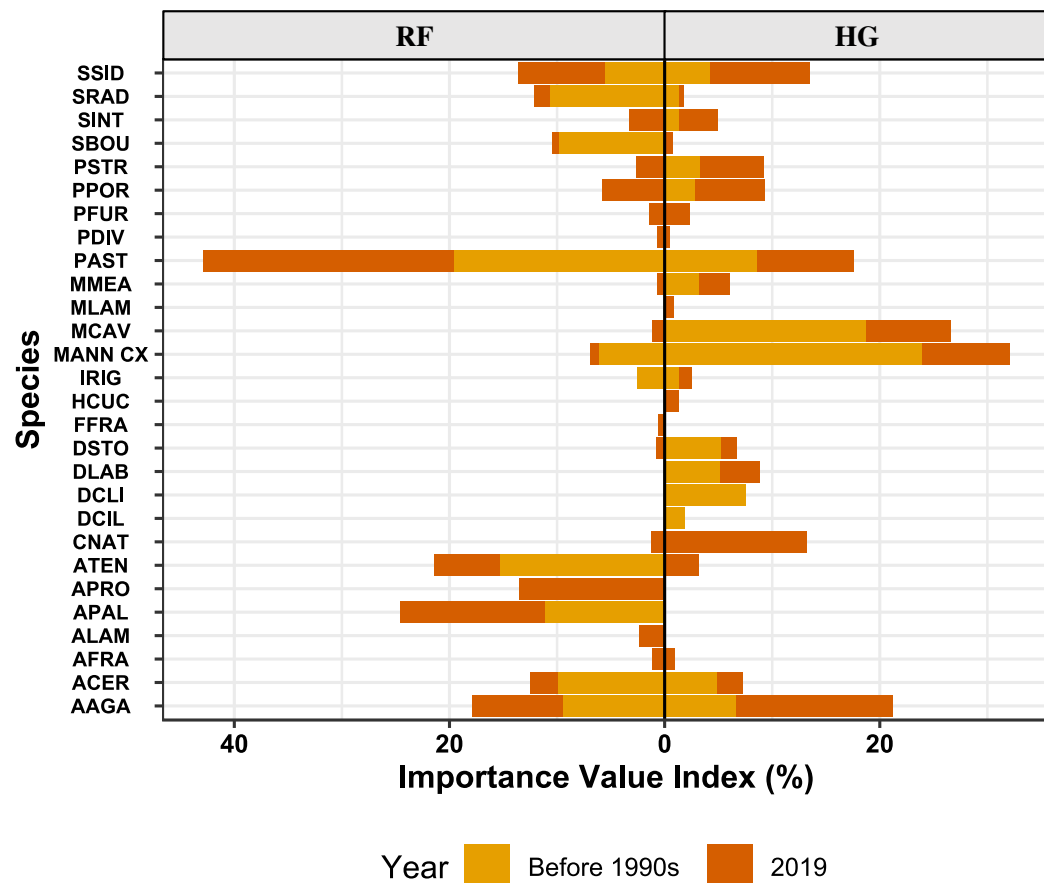
Figure 2. Box Plots of A. Coral colony densities in 2019 and B. Live coral coverage before the 1990s, by accretion-functional groups, coral morphology and geomorphic zone in two reef zones at Punta Maroma reef. The bottom and top of the box are the first and third quartiles, respectively, the black line inside the box is the median. Whiskers are the lowest datum still within 1.5 times that of the lower quartile and the highest datum still within 1.5 times that of the upper quartile. The open circles at the end of the box-plot represent outliers (values 1.5 times less or greater than the interquartile range). RF: Reef front, or accretionary zone, HG: Coral hard ground or non-accretionary zone; key_spp.: key reef building species; Non-accretional: non-accretional species.

242 in variances before 1990s and 2019 data, whereas the HG zone shows heterogeneity in variance of data
243 (P(tables): 0.59 and < 0.01 respectively; *Data S4.C*). Therefore, the analyses indicate changes between
244 period before 1990s and 2019 in the composition of both zones (PERMANOVA) and in the variance of
245 sample distribution (PERMDISP) in the HG zone.
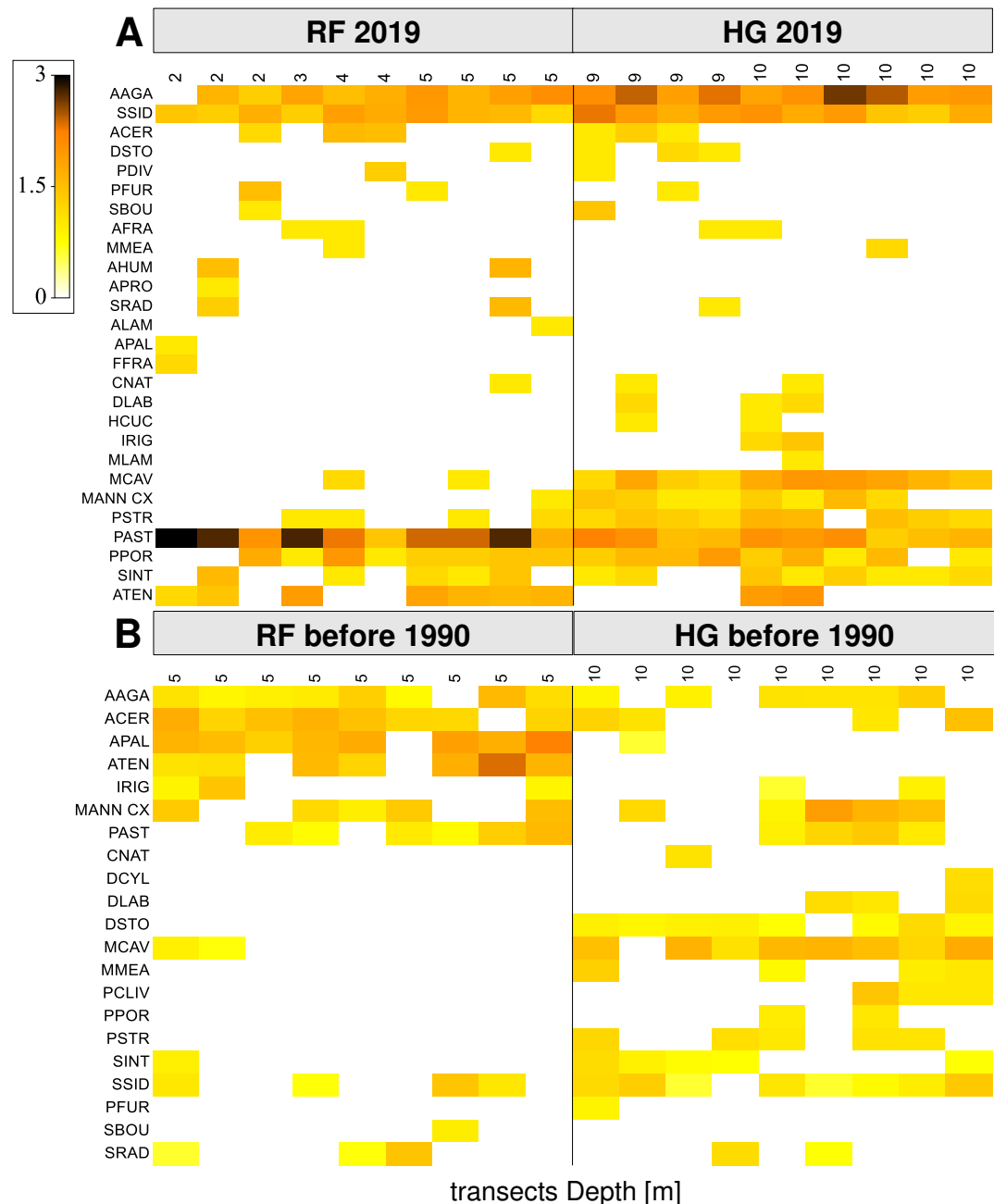
246 **Discussion**

247 Regrettably, like in other Caribbean reefs, coral assemblages covering the reefal seascape at Punta
248 Maroma have declined in the past 35 years. Prior to the 1990's, there was a clear differentiation of coral
249 assemblages between the shallow reef front (RF) and the deeper coral hardground (HG), with the former
250 having higher presence of *Acropora* spp. and *Agaricia tenuifolia*, and the latter with higher presence
251 of small massive species such as *M. cavernosa, S. siderea, D. stokesii* and *A. agaricites*. These coral
252 assemblages had become more homogeneous in abundance and species composition, with similarity
253 among zones rising from 21.5%, before the 1990's, to 52.6%, by 2019. Furthermore, by 2019, both the
254 accretionary RF and the non accretionary HG community had the same coral species richness (S = 23),
255 roughly the same colony density (2.4 per m^2) and were dominated by small colonies (< 20 cm) of *S.*
256 *siderea, P. astreoides, A. agaricites*, and *P. porites*. However, according to the Index Value of Importance

Figure 3. Ecological Importance Value Index of coral species by geomorphic zones in Punta Maroma reef before 1990s (based on 1985 data) and in 2019. The index is based on the relative abundance, frequency and spatial contribution of each species with respect to the coral assemblage. RF: Reef front, HG: coral hard ground. Species are represented by codex as follow: APAL: *Acropora palmata*, ACER: *A. cervicornis*, APRO: *A. prolifera*, AAGA: *Agaricia agaricites*, AFRA: *A. fragilis*, AHUM: *A. humilis*, ALAM: *A. lamarcki*, ATEN: *A. tenuifolia*, CNAT: *Colpophyllia natans*, DSTO: *Dichocoenia stokesii*, DLAB: *Diploria labyrinthiformis*, FFRA: *Favia fragum*, IRIG: *Isophyllia rigida*, LCUC: *Leptoseris cucullata*, MMEA: *Meandrina meandrites*, MCAV: *Montastraea cavernosa*, MANN CX: *M. annularis* spp. Complex (*Orbicella faveolata*, *O. annularis*), MLAM: *Mycetophyllia lamarckiana*, PAST: *Porites astreoides*, PFUR: *P. furcata*, PDIV: *P. divaricata*, PPOR: *P. porites*, PSTR: *Pseudodiploria. strigosa*, SSID: *Siderastrea siderea*, SRAD: *S. radians*, SBOU: *Solenastrea bournoni*, SINT: *Stephanocoenia intercepta*
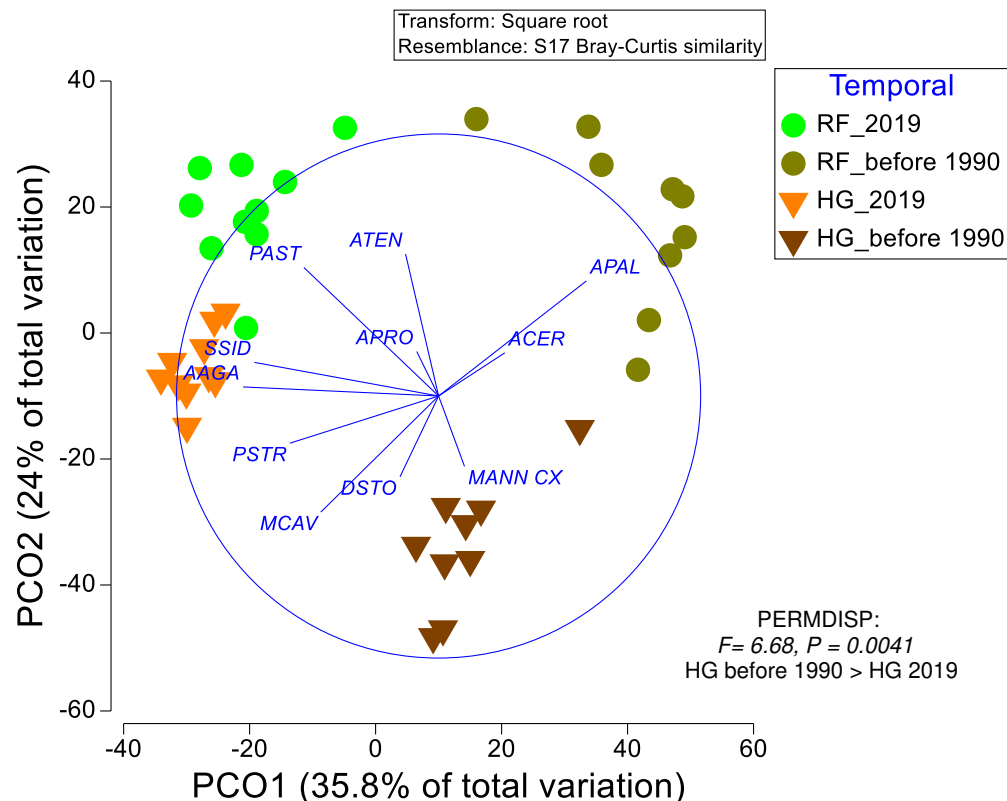
257 (IVI), reef builders like *Acropora palmata* conserved its high ecological value in the RF zone, despite its
258 reduction in abundance through time and the *Orbicella* (formerly *Montastrea*) reef-building group has a
259 high value in the HG zone through time, despite the fact that this is a non-accretionary zone.

260 Reductions of live coral cover and decline in the abundance of large framework-building species
261 have been reported from other Caribbean reefs, together with the increase in the similarity of the coral
262 assemblages among shallow coral reef zones (Gardner et al., 2003; Jackson et al., 2014). Recently,
263 Estrada-Saldívar et al. (2019) reported that similar ecological changes led to functional convergence and
264 homogenization between back-reef and fore-reef sites along the north-east Yucatan, including the one at
265 Punta Maroma. However they considered the RF and HG zones as a single 'fore-reef' zone (ecozones

Figure 4. Comparison of the contemporary and historical abundance for each species at transect level. Color shaded plots of four root transformed species abundance (rows) by transect (columns) and zone (reef front vs hard coral ground) for (A) contemporary (2019) and (B) historical (before 1990s) data .(A) The (linear) colored scale is shown in the key with back-transformed counts where white squares indicate zero counts or species accounting for 5% or less of the total abundance. x.axis represents the transect depth of n- samples. y.axis represent species as in codex detailed in captions of Figure 3.

266 in Fig.1b). Our findings therefore show that on a more detailed scale this ecological homogenization
267 is incomplete and that each geomorphic zone still retains differences. It may be that this 'partial'

Figure 5. Principal Component Analysis (PCO) derived from the Bray–Curtis similarity matrix constructed using a fourth root transformed matrix of standardized abundances of scleractinian coral species in two sampling zones at Punta Maroma reef seascape before 1990s and in 2019: a frontal zone of a fringing reef (RF) and a hard coral ground (HG) zone. Vectors visualize, through Pearson correlation coefficient, the potential monotonic relationship between the species accounting for 70% of total abundances and ordination axes a PCO. *AAGA: Agaricia agaricites, ATEN: A. tenuifolia, ACER: Acropora cervicornis, APAL: A. palmata, DSTO: Dichocoenia stokesii, MCAV: Montastraea cavernosa, MANN CX: M. annularis spp. complex, PAST: Porites astreoides, PSTR: Pseudodiploria strigosa, SSID: Siderastrea siderea*

268 homogenization results from a convergence in species succession within each geomorphic zone, as
269 reported on other Caribbean reefs (e.g. (Curran et al., 1995; Aronson and Precht, 1997).

270   The ecological differences in species distribution and their relative importance between adjacent
271 geomorphic zones may be related to the interaction between environmental processes and geomorphic
272 substrate over long time-scales. Despite changes in community structure, the RF zone still has an irregular
273 substrate, with stumps of dead *A. palmata* and several acroporid spur-and-groove sets that slope up to
274 the crest, and the HG zone is still a flat undulating rocky terrace crossed by shallow furrows and coral
275 veneered ridges. These conditions favour the persistence of sediment-tolerant species, like *M. cavernosa,*
276 *A. agaricites* and *S. siderea* in the HG zone, whereas in the RF zone the higher dominance of *P. astreoides*,
277 which colonized space vacated by *A. palmata* may be a successional stage following disturbance. If this
278 interpretation is correct then it highlights the importance of long-term adaptive responses of coral species
279 to geomorphic substrates.

280   Although retaining some of their geomorphic character, these once easy to differentiate geomorphic
281 zones are now more difficult to separate based on coral cover or other ecological indices. This difficulty
282 stems from the functional loss of major reef builders such as Acroporids (e.g., *A. palmata, A. cervicornis*)

which are largely responsible for long-term accretion in shallow Caribbean reefs (Macintyre and Glynn, 1976; Blanchon et al., 2017; Toth et al., 2019). These losses were likely driven by multiple strikes from major Hurricanes that crossed the study area (Allen in 1980, Gilbert in 1988, Emily in 2005 and Wilma in 2005), and their coincident timing with white band/pox epidemics that were decimating acroporids elsewhere (e.g.,(Gladfelter, 1982; Lewis, 1984; Aronson and Precht, 2001; Bruckner, 2002). Although there is debate over the proximate cause (hurricanes vs disease outbreaks) the result was the same: a convergence of shallow coral communities with a concomitant structural deterioration ((Jackson et al., 2014; Elliff and Silva, 2017). At Punta Maroma the largest decline in Acropids had taken place by the mid-1980s, and no additional evidence of large-scale species succession has been reported since, although disturbances have not decreased ((Nyström et al., 2000; Schutte et al., 2010; Graham et al., 2011; Rioja-Nieto and Álvarez-Filip, 2019). This rapid decline at Punta Maroma is likely related to a regional species succession reported by Aronson and Precht (2001).

The rapid transition to a partially homogenized coral community at Punta Maroma today is inconsistent with the reef's Holocene record, implying the importance of these changes for the future accretion potential of the reef. But assessing the contribution of key reef-building species, such as *A. palmata*, in this accretion process based on their current ecological condition is a challenging exercise which depends on the type of ecological indicator used. Analysis of changes in species abundance and composition on a relatively short time-scale indicates a reduction in its contribution and an inferred loss in accretion potential. However, more complex measures than relative abundance, like the IVI analysis, indicates that some acroporids have retained their relative importance, highlighting the important contribution of this species to reef accretion. This is because the IVI includes other data such as colony size in addition to species abundances, and so gives a more complete picture. Nevertheless, such indices may still not provide an accurate picture of which species is important for accretion. For example, relative abundance data indicate that the HG zone now has more reef-building species, implying a higher accretion potential, despite the fact that geological data indicate no accretion during the Holocene. As a consequence, even the best-suited ecological indices of reef-accretion potential may not give accurate estimates unless the geomorphic context of coral communities is considered in more detail. Furthermore although ecological studies may provide a detailed snapshot on historical timescales, they may not be fully representative of the long-term development in complex geomorphologically zoned reef structures (Aronson and Precht, 1997; Bellwood et al., 2004; Bruckner, 2012).

Finally, the ecological dynamics of reef-building communities raises an interesting question about how they create geological structures over thousands of years. Ecological assessments assume that reef accretion is constant in time and space. Yet the assumption that reefs were always covered by dense coral thickets is questionable and ignores processes which exist outside of ecological timescales. Indeed, little is known about the patterns of long-term accretion because geological reconstructions are largely two dimensional, deriving data from single drill holes or drill transects. It may be, for example, that accretion is heterogeneous in space and time and that some sections of reef develop at different intervals, in different areas through time. In this case, some ecological conditions may not be representative of geological trends (Jackson, 1992)

CONCLUSIONS

Over the last 40 years coral assemblage data show that the two main windward geomorphic zones at Punta Maroma have maintained ecologic and benthic differences, implying that physical environmental drivers continue to exert a fundamental control on this reefal seascape. These data also indicate there has been a partial homogenization of coral assemblages over that interval involving the loss of important reef building species, which has raised concern about future accretion potential and the long-term role of reef structures and services they provide. However, by considering the more detailed changes between geomorphic zones, our data do not rule out the possibility that this may be a successional stage prolonged by recruitment failure and that accretion may in-fact be heterogeneous in space and time. As a consequence we suggest that a consideration of geomorphic zonation is a fundamental prerequisite for determining the accretion potential of entire reef systems.

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