El Colegio de la Frontera Sur

Complejidad estructural a escalas espaciales finas de un parche arrecifal impactado por encallamiento en Punta Cancún, Quintana Roo, México

TESIS
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A mis padres y mi hermano.

Porque su amor y apoyo incondicional son el motor que me mueve siempre hacia adelante.

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ÍNDICE

INTRODUCCIÓN

Actualmente, la mayoría de los ecosistemas marinos se encuentran amenazados a causa de una variedad de estresores. Los arrecifes coralinos son ecosistemas particularmente sensibles a distintos disturbios y aquellos de origen antropogénico se están convirtiendo en los principales conductores de la estructura comunitaria (Graham et al., 2011). Un disturbio de tipo agudo puede orientar al ecosistema a un cambio de estado dominado por macroalgas, al reforzar mecanismos de retroalimentación tales como la reducción de espacios para reclutamiento larval, evitando la recuperación coralina (Hughes, 1994), disminuyendo tanto su cobertura como la estructura tridimensional del hábitat; es decir, qué tan complejos son estructuralmente (Chabanet et al., 1997). Esta complejidad estructural, se define como la heterogeneidad en el arreglo de la estructura física del hábitat (Lassau y Hochuli, 2004), o la estructura física tridimensional de un ecosistema (Graham y Nash, 2013).

Un hábitat estructuralmente complejo, por su mayor área de superficie, provee refugios temporales y permanentes, además de brindar sitios de forrajeo y reclutamiento (Luckhurst y Luckhurst, 1978; Bejarano et al., 2011). Por lo tanto, la complejidad estructural determina el asentamiento de diversos grupos de invertebrados marinos como balanos, esponjas y corales escleractinios (Lewis, 1974; Russ 1980; Carleton y Sammarco, 1987). La complejidad del hábitat se ha encontrado relacionada positivamente con variables biológicas como la diversidad, abundancia, talla o conducta en peces de agua dulce (Shumway et al., 2007), así como en sistemas arrecifales coralinos (Luckhurst y Luckhurst, 1978; Chabanet et al., 1997). Las relaciones de la

complejidad estructural con las comunidades de peces son las que han sido mejor documentadas (Graham y Nash, 2013), por lo cual es necesario aumentar estudios del efecto de la complejidad estructural arrecifal sobre otros organismos. Es claro que la complejidad estructural juega un papel fundamental al mantener procesos ecológicos que repercuten en la obtención de servicios ecosistémicos en arrecifes coralinos (Graham y Nash, 2013). No obstante, estos procesos pueden verse afectados por un gran número de estresores naturales y antropogénicos (Graham et al., 2011), como los encallamientos, tormentas, depredadores (De'ath et al., 2012), y respuestas al cambio climático; tales como acidificación del océano y blanqueamiento coralino, entre otras (McClanahan et al., 2007; Hughes et al., 2010; Graham et al., 2011; Guest et al., 2012). El resultado de estos disturbios conduce a un decremento en la cobertura coralina y alteraciones en la complejidad estructural. Sin embargo, la información detallada sobre la dinámica de la comunidad arrecifal posterior al disturbio es aún escasa.

En general, se supone que los arrecifes que mantienen su estructura y función pueden recuperarse de disturbios a gran escala (Alvarez-Filip et al., 2011). Por ejemplo, en un evento de blanqueamiento, la respuesta de los corales es variable (Guest et al., 2012); pero en caso de mortalidad coralina, el esqueleto permanece intacto manteniéndose la configuración tridimensional, con lo que se esperaría que se facilitara la recuperación coralina (Alvarez-Filip et al., 2011). En contraparte, disturbios físicos como huracanes y encallamientos, provocan pérdida inmediata de la configuración tridimensional, y retardan o impiden en gran medida, la recuperación del sistema (Alvarez-Filip et al., 2011; Graham et al., 2011). En México, el estado con la mayor incidencia de encallamientos en arrecifes de coral es Quintana Roo, con 24 de los 41

registrados y una superficie afectada de más de 12,000 m^2 (CONANP, 2009). La pérdida de complejidad estructural tiene profundos impactos ecológicos, sociales y económicos, pues podría conducir a una pérdida de diversidad y de los servicios ambientales que prestan los arrecifes coralinos (Alvarez-Filip et al., 2009; Graham et al., 2011). Por esta razón, es importante analizar la respuesta del ecosistema ante un disturbio a distintas escalas, tanto temporales como espaciales. Éstas escalas determinarán la forma en la que se puede estudiar el sistema (Rogers, 1993) dado que los procesos ecológicos se diferencian o actúan en función de la escala (Schoch et al., 2006; Knudby y Ledrew 2007).

Los estudios de disturbio, estabilidad y cambio en arrecifes coralinos se han realizado principalmente a una escala de paisaje (>10^4 m^2) (Edmunds y Bruno, 1996), lo que ha impedido tener información detallada de la dinámica comunitaria y dificultado las predicciones a una escala menor (Jackson, 1991; Knudby y LeDrew, 2007; Sandin y McNamara 2012). Los arrecifes coralinos parecen ser más susceptibles a los disturbios e impredecibles a una escala de tiempo amplia, por lo que las escalas de observación han sido argumentos centrales para analizar los cambios recientes en la estructura comunitaria (Edmunds y Bruno, 1996). La clasificación multi-escala de los arrecifes coralinos propuesta por Chabanet et al., (2005), mostró que las escalas espaciales presentan patrones particulares, susceptibles a distintos tipos de disturbio. De esta forma, la necesidad de estudios a resolución fina aumenta al hacerse más evidente el incremento del impacto antropogénico sobre los ecosistemas a nivel mundial (Schoch et al., 2006).

Para evaluar la complejidad de un arrecife, tradicionalmente se mide la proporción entre dos puntos; la distancia del contorno del sustrato arrecifal en relación a la distancia lineal, conocida como rugosidad (Luckhurst y Luckhurst, 1978). La rugosidad calcula la topografía de la superficie arrecifal y se ha utilizado para cuantificar la variación espacial y temporal de la complejidad estructural de arrecifes a lo largo del Caribe (Alvarez-Filip et al., 2011). Para medir la complejidad estructural se han desarrollado una variedad de métodos que difieren de acuerdo a los atributos evaluados, la escala de medición y la resolución de observación (McCormick, 1994; Shumway et al., 2007; Alvarez-Filip et al., 2009). El método más utilizado es la determinación de un índice para lo cual se utilizan diversas técnicas, entre las que destaca, por su sencillez y precisión, el método de la cadena (Risk, 1972). Este método brinda una aproximación a escala fina del relieve, y permite correlacionar la rugosidad con la influencia de grupos funcionales en la estructura arrecifal (Alvarez-Filip et al., 2011; Bejarano et al., 2011).

En el presente estudio, se evaluó la complejidad estructural de un parche arrecifal impactado por encallamiento en el norte del estado de Quintana Roo, a una escala espacial fina y a nivel de comunidad, de acuerdo a la clasificación de Chabanet et al., (2005). Se evaluaron tres resoluciones espaciales, entendiéndose la resolución como el nivel de detalle de una dimensión espacial o temporal. Las resoluciones fueron elegidas a partir de la más utilizadas en estudios de cobertura en arrecifes coralinos; cuadrantes de 100x100 cm, y se utilizaron dos resoluciones más finas: 50x50 y 10x10 cm. La medición de la rugosidad se llevó a cabo dentro de 40 cuadrantes permanentes de 1m^2; 20 en el área impactada y 20 en un área adyacente dentro del mismo parche,

sin impacto por encallamiento, la cual fue tomada como referencia. Como medida de complejidad, se estimó la rugosidad del sustrato por el método de Risk (1972) y Hill y Wilkinson (2004), con una cadena fina de eslabones de 0.5 cm de largo. Los datos se obtuvieron bimensualmente, durante un año; para discernir si los cambios estructurales observados son efímeros o permanentes a dicha escala.

En un contexto de disturbio, la respuesta de adaptación de un sistema arrecifal, su alta variabilidad ambiental y la tasa de crecimiento diferencial de los distintos elementos estructurales hacen suponer que la complejidad estructural es un atributo variable y dinámico, por lo que se plantearon las siguientes hipótesis: 1) la rugosidad, como un subrogado de la complejidad estructural, es menor a escalas espaciales pequeñas y aumenta su valor a escalas mayores. 2) la composición y abundancia de los elementos estructurales arrecifales variará entre escalas. 3) el crecimiento diferencial de estos elementos estructurales influenciará la contribución particular de cada elemento a la complejidad estructural, y 4) existen valores bajos de rugosidad con mayor frecuencia en zonas con encallamiento, que en zonas sin impacto de este tipo. Por lo que el objetivo de esta investigación fue evaluar la complejidad estructural a escalas espaciales finas en un parche arrecifal impactado por encallamiento y evaluar los cambios en la rugosidad, en función de la estructura comunitaria.

ARTÍCULO

Structural complexity at fine spatial scales in a ship-grounded patch reef in Quintana Roo, Mexico

sometido a *Coral Reefs*

Structural complexity at fine spatial scales in a ship grounded patch reef in Quintana Roo, Mexico

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Abstract

The loss of live corals of Caribbean reefs in the last decades has been accompanied by a reduction in structural complexity. This physical attribute is important in view of global reef degradation. However, most studies about disturbance and structural complexity have focused on larger scales, leaving out structural patterns that may help to understand the responses of coral reefs at smaller scales under actual changing conditions. We evaluated structural complexity on a patch reef with a ship grounding impacted zone at the Mexican Caribbean. The control was a reference zone without ship grounding. We measured substrate rugosity at three fine spatial resolutions bimonthly for one year in both zones, to test the hypothesis that community dynamic, composition and permanence of functional benthic groups determined the structural complexity at those scales. Since 15 years elapsed after the disturbance occurred, we expected that structural patterns would indicate a habitat recovery of the impacted zone. Our results showed differences on rugosity between zones and among resolutions, suggesting a scale-dependant threshold of rugosity. Community structure also showed differences between zones; sponges in the impacted zone determined those differences whilst the reference zone was associated to crustose coralline algae and massive corals, mainly *Porites astreoides*. An effect of time over community structure was also detected. The functional group associated to the differences between October and the other periods on community was fleshy macroalgae, which may be related to the seasonal precipitation regime of the area. The low general diversity recorded, the prevalence of opportunistic species at both zones and the contribution of non-coral groups to rugosity, might be a sign that the reference zone is no longer in a healthy condition, despite the protection efforts applied by park authorities on the study site.

Introduction

Structural complexity can be defined as the heterogeneity in the arrangement of physical structure in the habitat surveyed (Lassau and Hochuli, 2004). A structurally complex habitat provides shelter, feeding grounds and recruitment sites to different organisms (Luckhurst and Luckhurst 1978; Bejarano et al. 2011); and is positively related to processes that define reef community structure (McCormick 1994; Alvarez-Filip et al. 2009). In coral reef ecosystems, the importance of structural complexity has been recognised for decades (Risk 1972; Luckhurst and Luckhurst 1978; Alvarez-Filip et al. 2009; Graham and Nash 2013). However, the ecological processes influenced by the structural complexity can also be affected by several stressors (Graham et al. 2011), that decrease coral cover and modify the structural complexity itself (Alvarez-Filip et al. 2009). Disturbances such as coral bleaching, usually leave coral skeletons intact; this may maintain ecological processes and facilitate recovery, in contrast to those that remove corals and reduce three dimensional structure, such as ship groundings (Chabanet et al. 2005; Graham et al. 2011). The widespread loss of live coral reported for the Caribbean (Gardner et al. 2003) is usually accompanied by a reduction of structural complexity (Alvarez-Filip et al. 2009).

Currently, studies of disturbance and stability in coral reefs are mainly approached at a landscape scale (> 10^4 m^2) (Edmunds and Bruno 1996), and community dynamic patterns occurring at smaller scales may be overlooked (Knudby and LeDrew 2007; Sandin and McNamara 2012). Although benthic communities can be sampled at almost any scale, recent studies have focused within a scale of tens of meters to tens of kilometres (Hughes 1994). Quantifying the contribution of different benthic elements to structural complexity at smaller

scales is also important to understand the trajectory of coral reefs under recent changing environmental conditions (Alvarez-Filip et al. 2011b).

The occurrence of disturbances at different scales, the resilience of community structure, the differences in life histories and growth rates of the biotic groups in a reef system lead to assume that structural complexity is a dynamic attribute that changes consequently to every temporal and spatial scale. We evaluated the structural complexity of a patch reef with ship grounding in northern Quintana Roo, the State in Mexico with the highest incidence of ship groundings in Mexican coral reefs. We measured substrate rugosity as a surrogate of structural complexity at fine spatial (1 m^2 and less) and short temporal (within a year) scales at a ship grounded and unaffected areas. We tested the hypothesis that structural complexity at these scales is a dynamic attribute, determined by community dynamic, composition and permanence of functional reef groups.

Materials and methods

Study area

This study was carried out at Cuevones, a patch reef within the National Park "Costa Occidental de Isla Mujeres, Punta Cancún y Punta Nizuc" in the Mexican Caribbean (Fig. 1). The patch is located ca. 2.5 km north of Punta Cancún (21º04'N, 86º44'W); it is approximately 180 m long, 25 m wide, and 4-7 m in depth. In 1997 a cruise ship impacted Cuevones at its southeastern tip, resulting in ca. 475 m^2 of damaged area (10% of patch reef total area). Additionally, the impact caused a 15 m long and 2.3 m wide fracture on the reef framework. According to an evaluation done by the park staff (unpublished data), reef-building species *Acropora palmata*, *A. cervicornis*, *Porites astreoides*, *Orbicella annularis* (=*Montastraea annularis*, sensu Budd et al.

2012), *Montastraea cavernosa* and *Agaricia* spp. were affected. However, no measurements of structural complexity were made before or after the wreck. Since the ship grounding, the area has been closed to recreational and commercial activity (CONANP 2009). Additionally, the site has been hit by two tropical storms and two hurricanes during 2003, 2005 and 2007 (NOAA, 2012).

Sampling design

We used a three factor crossed design in order to determine if differences were noticeable in terms of structural complexity, 15 years after the impact occurred, between the impacted and a reference areas; among three spatial scales of resolution (quadrats of $0.01m^2$, $0.25m^2$ and $1m^2$); and among five bimonthly observations, from October 2012 to June 2013. Observations were made on 40 permanent $1m^2$ quadrats, 20 quadrats per area (impacted and reference), marked in its north and south corners with No. 316 stainless steel pins following the method proposed by Jokiel et al. (2001). Each quadrat was labelled using an aluminium plate. Sample size was 6 independent randomly selected quadrats per resolution, at each condition (impacted and reference area) and time of measurement. Total sample size was 180 random and independent quadrats where rugosity and community structure coverage of functional groups were evaluated.

The rugosity was estimated by the chain method (Risk 1972), measuring the contour of reef bottom. The rugosity index (RI) was obtained by dividing the contour distance and the linear distance between the two bottom points being evaluated. Thus, a flat surface has a RI of 1 (Alvarez-Filip et al. 2011b). To mimic the bottom contour as close as possible, we used a chain with 0.5 cm links. The evaluated linear distance was the length of the diagonal of the quadrats used for each resolution: 14, 70 and 141 cm for $0.01m^2$, $0.25m^2$ and $1m^2$ resolution, respectively. Coverage measurements were estimated according to Jordán-Dahlgren (1989), by counting the number of links on each benthic biotic element lying under the chain. Number of links was

transformed into percentage cover per benthic group. We defined five functional groups: hard corals, soft corals, macroalgae, sponges and other invertebrates. Each coral colony was identified to species and classified into a growing form: branching, plate and massive coral. Algae were classified according to the AGRRA protocol (2010): fleshy macroalgae, branching algae, crustose coralline algae, crustose non coralline algae, and turf algae. We measured other sessile organisms that contribute to the three-dimensional configuration like zoanthids and tunicates. Non-live elements were measured but not considered for the analyses.

Statistical analyses

Univariate analyses were accomplished using a three-way crossed analysis of variance using STATISTICA software to test the hypothesis of differences in rugosity between time, condition and resolution based on log transformed data. Community structure was analysed according to the three factor experimental design with a covariate using permutational multivariate analysis of variance, PERMANOVA (Anderson 2001; McArdle and Anderson 2001). This approach partitions the variability in the original dissimilarity matrix according to the full multifactorial design plus the covariate, with tests of individual terms obtained using permutations, and calculates a distance based pseudo-F statistic of the mean squares. PERMANOVA allows pair-wise comparisons for the main factor and interaction terms of interest separately. An angular (arcsine) transformation was used for cover data because it is especially appropriate for percentages (Sokal and Rohlf 1997). We included RI as a covariate to analyse the response of the data cloud to this variable, assuming that a relationship existed between rugosity and community structure of benthic elements.

We tested for one temporal and two spatial factors to identify differences in patterns of community structure associated with rugosity: (i) among times (fixed, 5 levels; October,

December, February, April and June), (ii) between conditions (fixed, two levels; impacted and reference), and (iii) among scales (fixed, 3 levels; ($0.01m^2$, $0.25m^2$ and $1m^2$). For all analyses, RI was included as a covariate. The statistical significance of each pseudo multivariate variance component was tested using a random subset of 9999 permutations of residuals. To characterise the significant differences obtained with PERMANOVA, visualize the differences among samples, and assess how distinct these groups were from one another in the multivariate space, we performed discriminant canonical analysis of principal components (CAP).

Constrained multivariate methods such as CAP use an a priori hypothesis, using cross validation to produce ordination plots, so they allow detecting patterns that could be masked by overall dispersion in unconstrained methods such as multidimensional scaling (Anderson 2001). Spearman's rank correlations were calculated for RI against each functional group of the reef community and vectors of association were overlaid on the CAP ordination to find the axes in the multivariate space that separate groups. As a complementary analysis, bubble plots were used to graphically represent the association of relevant functional groups on the CAP correlation of community structure and RI. Statistica 9 software was used to analyse univariate data, while multivariate analyses were performed using Primer 6.0 and PERMANOVA + for PRIMER (Clarke and Gorley 2001). Hard coral frequency was estimated through the effective number of species at each condition.

Results

The three-way crossed analysis of variance revealed significant differences for condition and resolution (Table 1). The reference area presented higher RI average values than the

impacted area, while for resolution, RI values increased from resolution 1 to 3 (Fig. 2a,b). Both factors behaved as predicted in our hypothesis. Although time showed no significant differences on RI, the impacted area showed the lowest average value in October (Fig. 2,c).

The multivariate analyses of community structure showed spatial and temporal significant differences for main factor effects and interaction terms (Table 2). The results indicated that there is a strong and significant relationship of rugosity with community structure. A significant interaction between RI and resolution indicated that the nature of the relationship between rugosity and community structure differs within levels of resolution. The canonical correlation analysis of RI against community structure for the resolution factor indicated that the relationship of RI was negative for resolution 1, but positive for levels 2 and 3. High percentage cover of fleshy macroalgae appears to be associated with low values of RI for resolution 1 and 3 (Fig 3). Also, a significant interaction was detected for condition x resolution, i.e. community structure differences between impact and reference areas varied within levels of resolution, and vice versa.

The pair-wise test for the interaction term condition x resolution showed differences at the three levels of resolution (Table 3). The interaction was present as differences between levels of condition for resolution 1 and large variability in community structure within levels of condition (Fig 4a). Differences between levels of condition and variability in community structure within levels of condition decreased for levels 2 and 3 of resolution (Fig 4b,c) and a correlation started to appear at resolution 2 and became clearer at resolution 3 (Fig. 4). The interaction for pairs of levels of resolution within levels of condition was present as larger average differences between levels of resolution at the impacted area than the reference one for resolution levels 1 against 2 and 3 (Fig. 5). Also, a correlation was discernible at the reference level but absent at the impacted area. The functional groups that characterise the differences between pairs of levels for the interaction term were explored by overlaying vectors of Spearman rank correlations (rank value >

0.3) of individual groups with the CAP axes (Table 4). For the community structure of benthic functional groups, sponges increased in cover at the impacted area, and crustose coralline algae at the reference area only within resolution level 1 (Fig 4a). Branching algae, branching corals and soft corals increased in cover at resolution levels 2 and 3, but other invertebrates increased in cover at resolution level 1 (Fig. 5). The most frequent hard coral was *Porites astreoides* on both impact and reference areas, followed by *Millepora complanata* on the impacted area (Table 5).

Main effect of time was significant and pairwise comparison indicated that October was different from all of the remaining levels (Table 6). The functional groups that characterised the differences between October and the other four levels of time were fleshy macroalgae, with a Spearman rank correlation value of 0.95 (Fig. 5). Fleshy macroalgae cover increased from October throughout April and starting a decrease in June.

In summary, the proposed hypotheses were validated using univariate and multivariate approaches. Significant differences were detected in RI between conditions with lower values for the impacted area and RI increased as the resolution increased. Regarding spatial differences in the community structure, we found a similar pattern of dominant groups on resolution 2 and 3 in contrast to resolution 1. Between levels of condition, we observed that sponges, soft corals and branching algae, determined community structure of the impact area. *Porites astreoides*, however, determined the structure on the reference area. Community structure over time had similar patterns among months except for October. Differences between October and the other periods were determined by fleshy macroalgae. The contribution of benthic elements to rugosity showed a negative relationship with resolution 1, but positive for resolutions 2 and 3, where lower rugosity values were associated to high percentage cover of fleshy macroalgae.

Discussion

In comparison to the reference area, our results showed that the impacted area presented lower rugosity values as a result of the shipwreck even after 15 years of the disturbance, as hypothesized. Although there is no available information related to the time it takes for an impacted site by a shipwreck to recover to its previous structural complexity, our data suggest that 15 years is not sufficient time to reach similar rugosity values between the impacted and nearby reference areas. Differences in RI values between resolutions were notorious, as a pattern of increasing rugosity as spatial scale increases. This pattern might be the result from the probability to include complex species such as scleractinian corals as the scale of observation increases, and the smaller the area the fewer complex elements would be present. Most RI measurements from the Caribbean are reported on a reef scale (tens of meters), which makes it more likely to include large, complex reef building species. At reef scale, complexity increases with increasing coral cover and reef area (Arias-González et al. 2011), but the rate of this increase in complexity depends on coral community composition and the identity of dominant species (Alvarez-Filip et al. 2011). Chabanet et al. (1997) mentioned that branching coral cover may be particularly likely to contribute to fine-scale structural complexity to reefs. At the fine scales used in our study, there are no previous reports on this pattern of increasing rugosity with increasing scale. Our findings may suggest that there is a scale-dependant threshold of rugosity at fine scales of 0.25-1m^2.

Rugosity as a surrogate of structural complexity may be seen as a dynamic attribute, where physical structure itself provides positive feedbacks for the establishment of species that add complexity, such as reef building corals. Several studies have mentioned that structural

complexity depends on coral community composition and the identity of dominant species (McCormick 1994; Alvarez-Filip et al. 2009, 2011b). Our results showed spatial differences in community structure as spatial resolution changes. The elements associated to the ordination of our data were sponges for the impacted area, and crustose coralline algae, massive corals and other invertebrates for the reference area at resolution 1. It is important to mention that the massive coral associated to the ordination was *Porites astreoides*, a small, opportunistic brooding species that has become dominant under the present condition of overall Caribbean reef degradation (Huntington et al. 2011). Alvarez-Filip et al. (2011a) mentioned that this species is typical of flat reefs, since does not provide structural complexity. The fact that sponges were associated to the impacted rather than the reference area at resolution 1 may be supported by previous literature. Arnold and Steneck (2001) mentioned that when a disturbance creates primary substrate, opportunistic organisms such as sponges overgrow microhabitats becoming dominant at the new stable state. In contrast, the reference area did not present this primary substrate, and the associated species were massive corals, other invertebrates and encrusting algae, being the latter a favourable substrate for promoting coral settlement (Vermeij et al. 2011). This differential composition may suggest different stages of succession, which may depend on the severity, and time elapsed since the last disturbance (Bythell et al. 2000; Mumby and Steneck 2011). The variation in community structure among conditions at resolution 1 could be driven by several related factors including local history and stochastic events such as larval recruitment (Edmunds and Bruno 1996). The elements associated to the ordination for resolutions 2 and 3 were soft corals, branching algae and branching corals, and there was no difference between impact and reference areas.

An effect of time over community structure, independent of condition and resolution, was detected. The functional group associated to the difference between October and the other periods

was fleshy macroalgae. This difference is consistent with the temporal tendency observed on average RI at the impacted area, despite that there were no significant differences. In October we observed the lowest values of fleshy macroalgae cover on both sites increasing during the following months. This pattern of increasing macroalgae cover may be related to a delayed response to the seasonal precipitation regime for the area. The rainy season in the area ranges from June to November increasing the fresh water discharge off the coastal zone into the reef area. This drainage could increase the organic load and nutrients availability for macroalgae. Fleshy macroalgae is a fast-growing, ephemeral group whose response in our study occurred within a 6 months period. Its influence over rugosity may vary as they grow filling out the crevices at small scale with a flattening effect and a concomitant reduction of rugosity. The independent effect of time might be a sign that the reference site is no longer in optimal conditions as fleshy macroalgae might be causing a bottom flattening similar to the impact area. Average rugosity value obtained for the reference site (1.55) is below that reported for the Caribbean (1.73) (Alvarez-Filip et al. 2009). However, it is higher than the value reported for other nearby reefs (Arias-González et al. 2011).

Despite the management efforts since the shipwreck occurred, our study site has been hit by hurricanes (*Claudette*, 2003 and *Wilma*, 2005), and it is located in the main touristic area of Mexico, which implies heavy load of water sewage and vessel traffic. According to Connell (1997), coral cover loss by acute, short-term disturbances, such a shipwreck, might recover faster than those affected by chronic, long-term disturbances. The present condition of our study site may indicate that combined influences of different natural and anthropogenic stressors have a synergistic effect that delays its recovery to the previous state (Bythell et al. 2000). This is supported by the low diversity recorded, the prevalence of *P. astreoides* at both areas and the contribution of non-coral groups to rugosity.

According to Hatcher (1984), a 12 year period might be enough for a reef system to recover after a maritime accident. The recovery processes require that the cascading of positive effects occur under a relatively absence of additional stressors. However, chronically disturbed habitats undermine the resilience capacity for returning to the previous stable state, therefore the time needed for cascading positive effects may exceed the 15 years as is the case for our study site. Despite the protection measures implemented since the patch reef was disturbed. Several studies have showed that reserves are unlikely to be successful if they are located in stressed, degraded or frequently disturbed habitats (Jameson et al. 2002).

The results of this study draw attention to the high variation prevalent in coral community structure. While no single scale can be considered correct for system analysis (Levin 1992), care should be taken in selecting the appropriate sampling scale according to the purpose of a study. A better understanding of small scale processes might help to formulate hypothesis to determine the causes and consequences of the decline in coral cover and richness of many reefs, and design effective management strategies. The efficacy of management tools to build coral resilience remains uncertain in the face of regional stressors, but to reverse degraded coral reef states, research and management must focus on weakening the resilience of already degraded reefs to re-establish coral dominance, instead of the actual tendency to focus on maintaining coral dominance, or to avoid phase shifts from coral-dominated to degraded states (Graham et al. 2013).

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Fig. 1 Study site location map

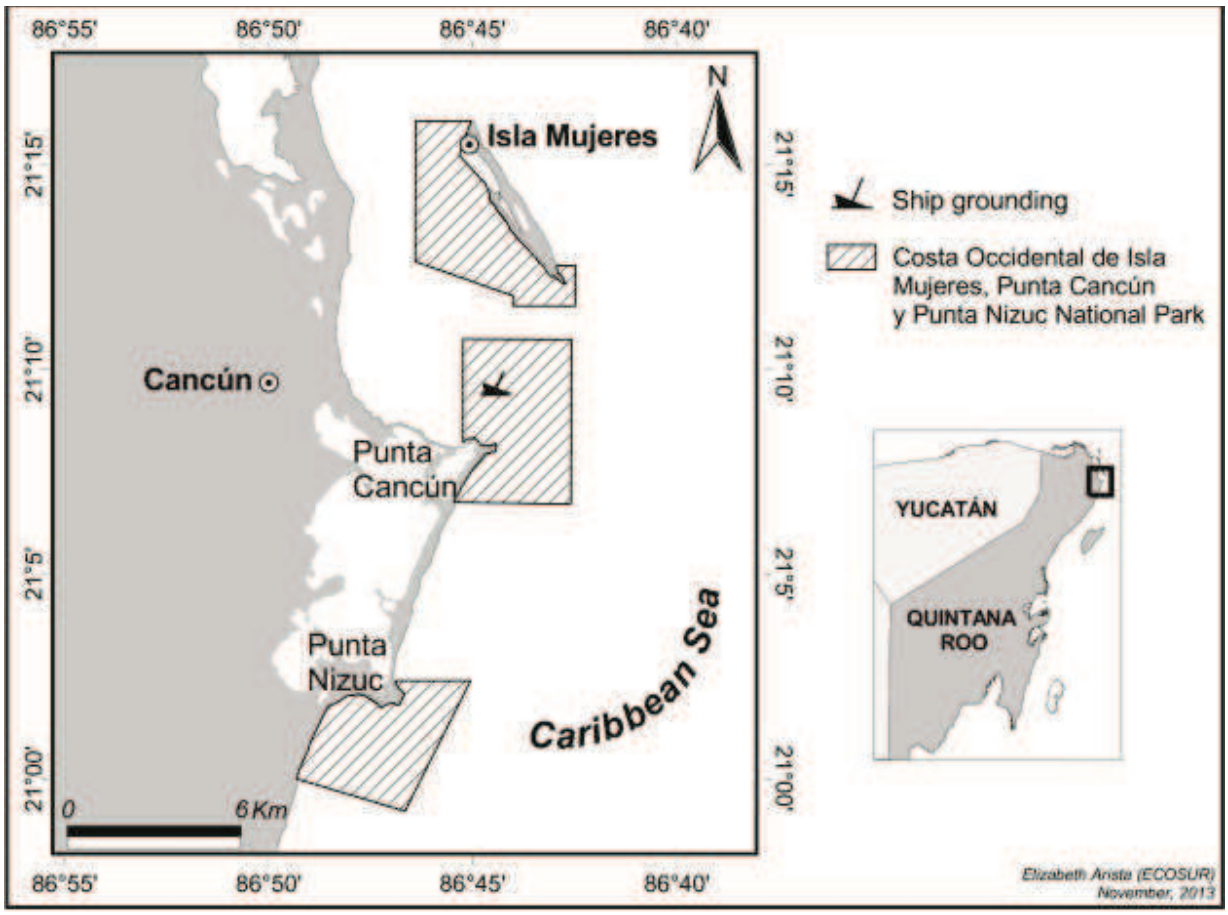


Fig. 2 Rugosity index average differences on levels of condition (a); resolution (b), and non-significant Time (c) (p=0.2780). Vertical bars denote 0.95 confidence intervals

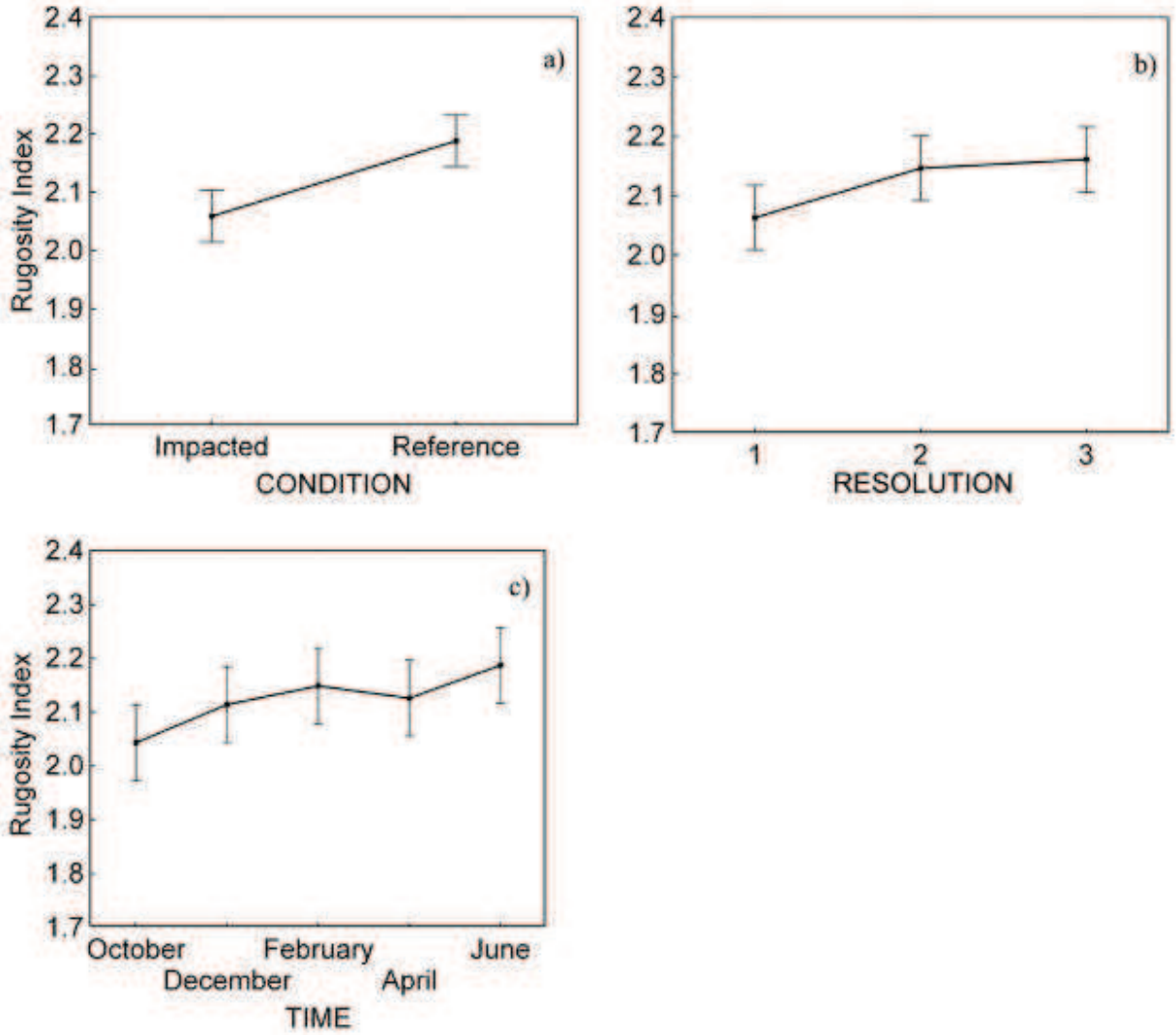


Fig. 3 CAP ordination plot, based on canonical correlation of the percentage cover associated with rugosity index (RI) at 1 (a), 2 (b) and 3 (c) levels of resolution. Bubble size indicates percentage cover of fleshy macroalgae (FMA)

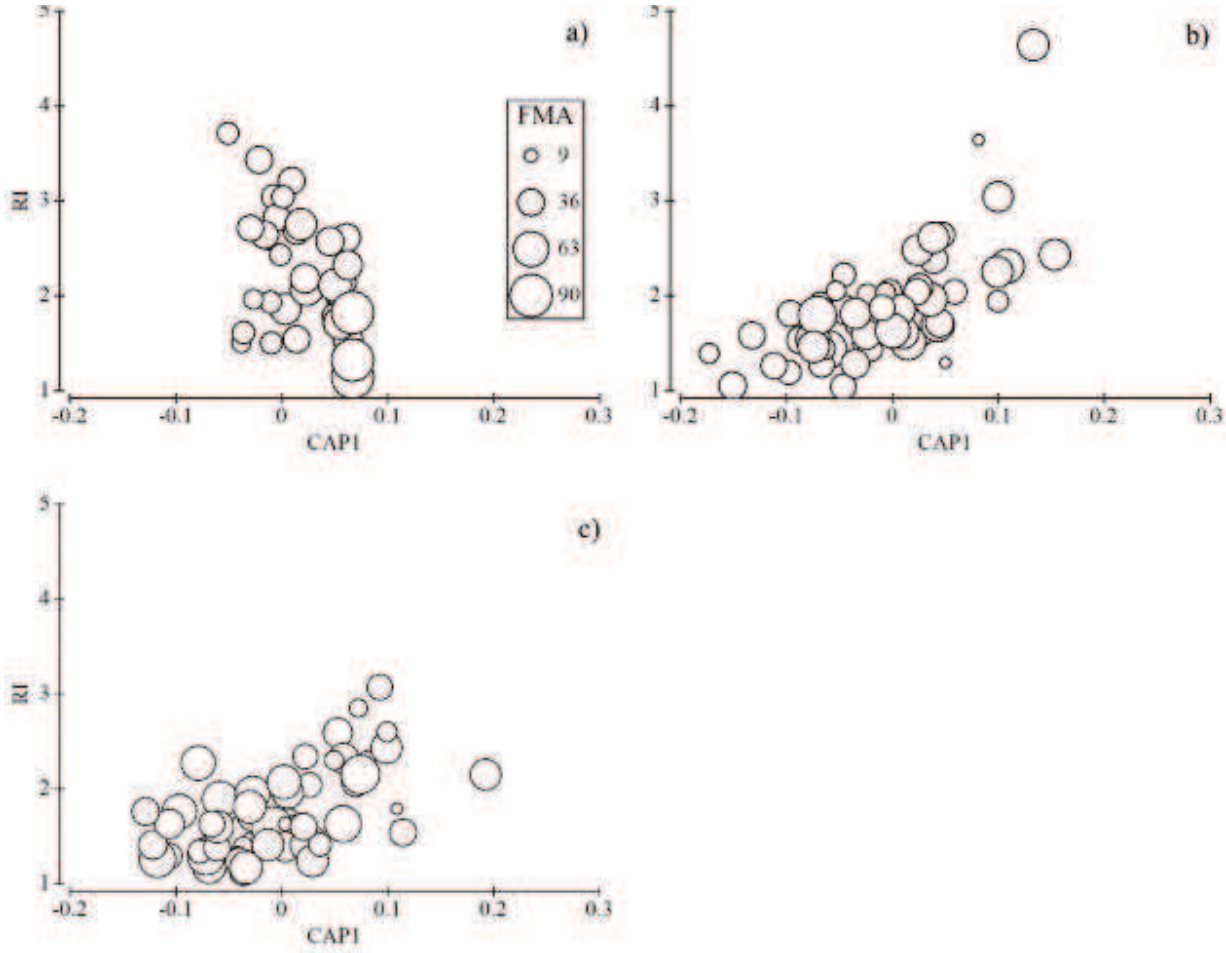
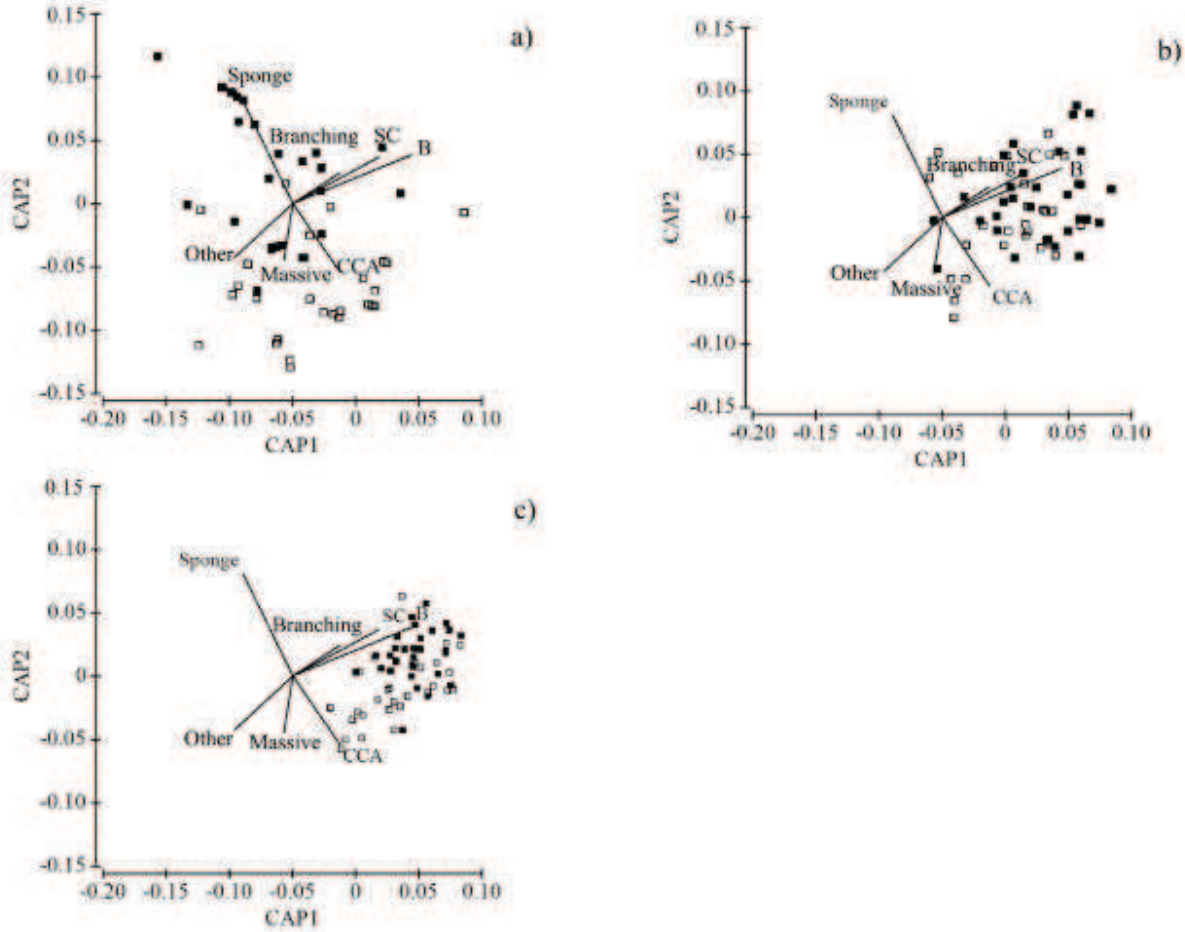


Fig. 4 CAP ordination plot of levels of condition are showed as blank symbols (reference area) and filled symbols (impacted area). The most important benthic groups within the community structure for the interaction are presented in axes with correlation rank >0.3. Groups are: Sponge, branching coral (Branching), soft coral (SC), branching algae (B), other invertebrates (Other), massive corals (Massive) and crustose coralline algae (CCA)



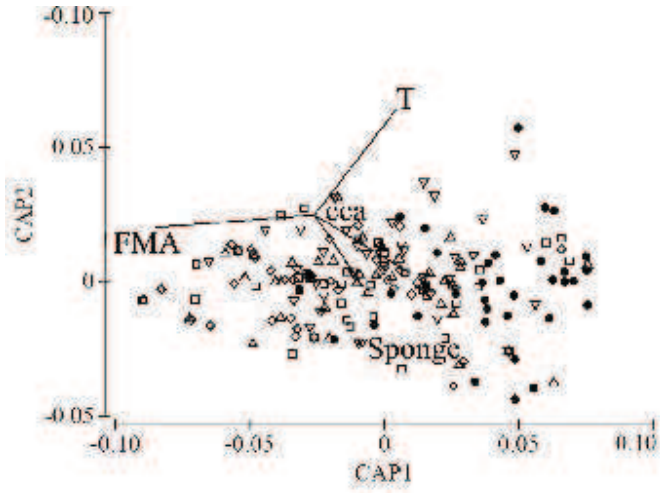


Fig. 5 CAP ordination plot of main effect Time over community structure. Represented vectors are fleshy macroalgae (FMA), turf algae (T), crustose coralline algae (CCA) and Sponges (Sponge). (●= October; △= December; □=February; ◊=April; ▽= June)

Table 1 Results of the three-way crossed ANOVA for condition, resolution and time, with rugosity index as a response variable. Bold values indicate significant differences (P<0.05)

	ss	d.f	MS	F	P
Intercept	811.34	1.00	811.34	17763.61	0.00
Time	0.40	4.00	0.10	2.21	0.07
Condition	0.76	1.00	0.76	16.53	**0.00**
Resolution	0.33	2.00	0.17	3.66	**0.03**
TimexCondition	0.24	4.00	0.06	1.29	0.28
TimexResolution	0.39	8.00	0.05	1.06	0.39
ConditionxResolution	0.10	2.00	0.05	1.10	0.34
TimexConditionxResolution	0.19	8.00	0.02	0.52	0.84
Error	6.85	150.00	0.05		

Table 2 Results of the three-factor permutational multivariate analysis of variance (PERMANOVA) on abundance data: Rugosity index (RI, covariate); condition (Co), resolution (Re) and time (Ti). Bold values indicate significant differences (P<0.05).

Source	Df	SS	MS	Pseudo-F	P(perm)
RI	1	6615.8	6615.8	4.86	**0.0007**
Ti	4	28539	7134.7	5.24	**0.0001**
Co	1	16163	16163	11.86	**0.0001**
Re	2	30079	15040	11.04	**0.0001**
RIxTi	4	7993.4	1998.3	1.47	0.1096
RIxCo	1	2470.3	2470.3	1.81	0.1274
RIxRe	2	8998.6	4499.3	3.30	**0.0014**
TixCo	4	5137.6	1284.4	0.94	0.5268
TixRe	8	5652	706.51	0.52	0.9842
CoxRe	2	16284	8142.2	5.97	**0.0001**
RIxTixCo	4	4390.3	1097.6	0.80	0.6791
RIxTixRe	8	5834.7	729.34	0.54	0.9789
RIxCoxRe	2	2227.7	1113.8	0.82	0.6117
TixCoxRe	8	5457.7	682.22	0.50	0.99
RIxTixCoxRe	8	4472	559	0.41	0.9977
Res	120	1.63E+05	1362.2		
Total	179	3.14E+05			

Table 3 Pair-wise test for the interaction term Condition x Resolution, showing results for pairs of levels of factor resolution within levels of condition, and pairs of condition within levels of resolution. Bold values indicate statistical differences (P<0.05).

Factor	Level	Groups	t	P(perm)
Condition	Impacted	1, 2	3.29	**0.0001**
		1, 3	3.88	**0.0001**
		2, 3	1.74	**0.0114**
	Reference	1, 2	2.54	**0.0004**
		1, 3	2.85	**0.0002**
		2, 3	1.71	**0.0234**
Resolution	1	Impacted, Reference	3.29	**0.0001**
	2	Impacted, Reference	2.07	**0.0014**
	3	Impacted, Reference	1.92	**0.0046**

Table 4 Spearman's rank correlation of individual benthic groups (rank value >0.3) on CAP axes

Functional group	CAP1	CAP2
Crustose coralline algae	0.30	-0.44
Crustose non coralline algae	0.28	0.02
Branching algae	0.76	0.31
Fleshy macroalgae	0.17	0.06
Turf algae	0.25	-0.13
Soft coral	0.55	0.30
Branching coral	0.30	0.20
Plate coral	0.22	0.04
Massive coral	-0.06	-0.36
Sponge	-0.32	0.65
Non live	0.17	0.06
Other	-0.37	-0.35

Table 5 Hard coral frequency based on number of species on impacted and reference areas

Growing Form	Species	Frequency	
		Impacted	Reference
Branching	*Acropora cervicornis*	2	1
	A. palmata	2	2
	Millepora alcicornis	0	0
	M. complanata	0	8
	Porites furcata	0	1
	P. porites	1	2
Massive	*Orbicella faveolata*	0	1
	Siderastraea radians	1	0
	Porites astreoides	10	14
Plate	*Agaricia sp.*	0	0

Table 6 Pair-wise test results for levels of factor time. Bold values indicate statistical differences (P<0.05).

Groups	t	P(perm)
October, December	30.47	**0.0001**
October, February	25.17	**0.0001**
October, April	38.30	**0.0001**
October, June	31.26	**0.0001**
December, February	0.78	0.6768
December, April	11.81	0.23
December, June	11.87	0.2324
February, April	13.85	0.1066
February, June	0.93	0.4986
April, June	1.22	0.212

CONCLUSIONES

La complejidad estructural en el área de impacto es menor que en el área sin encallamiento; sin embargo, el valor del índice de rugosidad obtenido para este último se encuentra por debajo del promedio reportado para el Caribe. Esto indica que, más que una recuperación del sitio impactado, puede existir una degradación del sitio de referencia. Posterior al disturbio, el parche arrecifal ha estado sujeto a presiones constantes tanto de origen natural (huracanes, tormentas tropicales), como antrópicas (contaminación indirecta de origen costero y tránsito de embarcaciones), además de los cambios climáticos a nivel global. Los valores de rugosidad registrados en ambos sitios sugieren que 15 años no ha sido tiempo suficiente para que el sitio de impacto recupere su complejidad estructural y alcance valores similares al sitio de referencia.

El patrón de aumento de rugosidad en función de la escala espacial, es el resultado de una mayor frecuencia de especies constructoras de arrecife principalmente a escalas mayores de $0.25m^2$. Es necesario un mejor entendimiento de los procesos a pequeña escala para determinar las causas de la condición actual de los arrecifes. A pesar de que no existe una única escala “adecuada” para estudios de complejidad, es necesario tomar en cuenta la importancia que tiene la resolución de observación para la evaluación de parámetros físicos.

A pesar de que el tiempo no mostró un efecto significativo sobre la rugosidad entre condiciones, el patrón de incremento de valores de rugosidad de octubre a

febrero, disminuyendo en abril y aumentando nuevamente en junio, coincide con el patrón de decremento de macroalgas carnosas. Este grupo funcional otorga poca rugosidad y tiene un crecimiento efímero, posiblemente relacionado al régimen de lluvias en la zona.

Las diferencias en la estructura comunitaria respecto a la rugosidad en las distintas resoluciones se asocian al crecimiento de macroalgas. La relación negativa de la rugosidad con la resolución más fina está asociada a un alto porcentaje de cobertura de macroalgas carnosas, grupo funcional efímero que da un efecto de “aplanamiento” ya que crece en oquedades, reduciendo la complejidad del sustrato. No obstante, dado su carácter efímero, la influencia de este grupo es temporal y presentó un patrón de incremento en cobertura durante seis meses.

A pesar de que existen diferencias en la estructura comunitaria entre el sitio de impacto y de referencia, ambas zonas tienen una frecuencia baja de corales constructores de arrecife. Las diferencias entre zonas están determinadas por la presencia de especies oportunistas, de rápido crecimiento y asociadas a etapas tempranas de sucesión. Mientras que en el sitio de impacto las diferencias en estructura comunitaria están determinadas por esponjas, en el sitio de referencia los corales masivos de la especie *Porites astreoides* son el grupo con mayor importancia. Esta especie, cuya contribución a la complejidad estructural es mínima, es el coral duro más frecuente tanto en el sitio de impacto como en el de referencia, lo que ayuda a entender por qué este último presenta valores bajos de rugosidad.

A pesar de los esfuerzos de manejo en el parche desde el encallamiento, hace 15 años, el cierre a toda actividad no ha sido suficiente para que el sitio de impacto logre una recuperación frente a una serie de estresores y presiones crónicas de tipo regional que van más allá de las soluciones locales. Es necesario evaluar la efectividad de distintas estrategias de manejo cuya tendencia actual está orientada a mantener un estado dominado por corales. Esta condición, sin embargo, es cada vez más difícil de encontrar en el Caribe, cuya tendencia generalizada es una dominancia por macroalgas, como en nuestro sitio de estudio. Ante este escenario, se debe valorar una estrategia que busque disminuir la resiliencia de los elementos estructurales del nuevo estado estable, específicamente las macroalgas.

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