

Temporal dynamics of coral and algal cover and their drivers on a coral reef of Gorgona Island, Colombia (Eastern Tropical Pacific)

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Abstract

Coral reefs are highly dynamic ecosystems often affected by diverse natural disturbances. However, dramatic declines in coral cover during recent decades raise the question of whether such declines are due to increasing anthropogenic impacts. To this end, the dynamics of coral and algal cover were studied based on data collected between 1998-2014 from 20 fixed 10-m transects at two depths in two sites of La Azufrada, a coral reef free of local human impacts, located at Gorgona Island, Colombia. Coral cover declined from 66.9 % in 1998 to 39.4 % in 2008, but then increased to 50.7 % in 2014. Fleshy and turf algae were low between 1998-2004, increased to 49.5 % in 2007, and then declined to < 33.0 %. Crustose coralline algae were lowest until 2009 when they increased as fleshy and turf algae decreased. Temporal variation was different between depths with shallow areas exhibiting major declines in coral cover until 2008 but a significant recovery since then. In contrast, coral cover in deep areas declined only slightly. Prolonged subaerial exposure of corals during extreme low tides appears to drive a cycle of coral disturbance and recovery. Coral growth makes the reef flat prone to subaerial exposure, after which corals bleach, die and are colonized by filamentous turf and fleshy algae. Sea urchins and herbivorous fishes increase their abundance in response to increased algal cover and control algal growth, leaving the substrate covered by crustose coralline algae and making it suitable for settlement by sexually-produced coral larvae. Fragmentation by both physical and biological agents (such as corallivores) enhances coral recruitment and the reef enters a coral recovery phase. Although this reef is resilient to subaerial exposure because it is protected from anthropogenic perturbations, increasing threats from global climate change may compromise its future resilience. © 2017. Acad. Colomb. Cienc. Ex. Fis. Nat.

Key words: Coral reefs; Disturbance; Recovery; Spatial variation; Subaerial exposure; Temporal dynamics.

Dinámica temporal de la cobertura de corales y algas y sus impulsores en un arrecife coralino de Isla Gorgona, Colombia (Pacífico Tropical Oriental)

Resumen

Los arrecifes coralinos son ecosistemas altamente dinámicos, a menudo afectados por diversas perturbaciones naturales. Sin embargo, descensos dramáticos en la cobertura coralina durante décadas recientes llevan a preguntar si tales descensos han sido causados por crecientes impactos antropogénicos. Con este fin, la dinámica de la cobertura de coral y algas se estudió a partir de datos recolectados entre 1998-2014 de 20 transectos fijos de 10 m a dos profundidades en dos sitios de La Azufrada, un arrecife coralino libre de impactos humanos locales, situado en Isla Gorgona, Colombia. La cobertura coralina disminuyó de 66,9 % en 1998 a 39,4 % en 2008, pero luego aumentó a 50,7 % en 2014. La cobertura de algas carnosas y de césped fue baja entre 1998-2004, aumentó a 49,5 % en 2007 y luego disminuyó a < 33,0 %. Las algas coralinas incrustantes fueron las más escasas hasta 2009, cuando aumentaron al disminuir las algas carnosas y de césped. La variación temporal fue diferente entre profundidades con las áreas someras exhibiendo los mayores descensos en la cobertura coralina hasta 2008, pero una recuperación significativa desde entonces. En contraste, la cobertura coralina en áreas profundas disminuyó sólo ligeramente. La exposición subaérea prolongada de los corales durante mareas bajas extremas parece impulsar un ciclo de perturbación y recuperación de los corales. El crecimiento de los corales hace que el arrecife sea más propenso a la exposición subaérea, después de lo cual los corales se blanquean, mueren y son colonizados por algas filamentosas y carnosas. Los erizos de mar y los peces herbívoros aumentan su abundancia en respuesta al aumento de la cobertura de algas y controlan el crecimiento de algas, dejando el sustrato cubierto por algas coralinas incrustantes que lo adecúan para el asentamiento de larvas de coral producidas sexualmente. La fragmentación por agentes físicos y biológicos (como los coralívoros) incrementa el reclutamiento de coral y el arrecife entra en una fase de recuperación coralina. Aunque este arrecife es resiliente a la exposición subaérea porque está protegido de perturbaciones antropogénicas, las crecientes amenazas del cambio climático global pueden comprometer su futura resiliencia. © 2017. Acad. Colomb. Cienc. Ex. Fis. Nat.

Palabras clave: Arrecifes coralinos; Dinámica temporal; Exposición subaérea; Perturbación; Recuperación; Variación espacial.

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Introduction

Coral reefs were once believed to be highly organized, stable, biologically accommodated assemblages of coevolved species coexisting at an equilibrium under benign and predictable environmental conditions (Grassle, 1973; Connell, 1978; Smith, 1978). Nearly two decades later this view had changed drastically and coral reefs were perceived as highly dynamic, non-equilibrium assemblages with dramatic changes often occurring as part of natural cycles of disturbance and recovery over varied spatial and temporal scales (Connell, 1978, 1997; Aronson and Precht, 1997; Brown, 1997a; Connell, *et al.*, 1997, 2004; Pandolfi, 1999). While change was recognized as a normal feature of coral reefs, signs of degradation began to be observed in the late 1970s and early 1980s (Gladfelter, 1982; Glynn, *et al.*, 1988; Porter and Meier, 1992) and have continued to increase at alarming rates ever since (Bryant, *et al.*, 1998; Wilkinson, 2008; Jackson, *et al.*, 2014). Evidence of such degradation includes a continuing decline of live coral cover and a concomitant increase of benthic algae (Hughes, 1994; Gardner, *et al.*, 2003; Bruno and Selig, 2007; De'ath, *et al.*, 2012), massive mortalities of functionally important organisms (Gladfelter, 1982; Lessios, *et al.*, 1984; Carpenter, 1990; Liddell and Ohlhorst, 1992; Hughes, 1994), increased incidence of coral diseases (Santavy and Peters, 1997; Sutherland, *et al.*, 2004), depletion of fisheries resources (Rogers, 1985; Hughes, 1994) and an increase in the frequency, intensity and geographic distribution of coral bleaching events (Williams and Bunkley-Williams, 1990; Glynn, 1993; Brown, 1997b; Glynn, *et al.*, 2001; McWilliams, *et al.*, 2005).

In general, the causes of coral reef degradation are strongly associated with increases in anthropogenic stressors such as increased human population densities near coral reefs (Birkeland, 1997; Jackson, *et al.*, 2014), coastal pollution, continental runoff and sewage discharge that increase turbidity, sedimentation and nutrient loads in coastal zones (Szmant, 2002; Fabricius, 2005), overfishing of commercially valuable organisms (Munro, 1983; Jennings and Polunin, 1996; Jackson, *et al.*, 2001; Pandolfi, *et al.*, 2003), recreational activities that damage or disturb coral reef organisms (Díaz, *et al.*, 2000; Roupheal and Inglis, 2002), the introduction of invasive species (Jackson, *et al.*, 2014) and ocean warming (Baker, *et al.*, 2008) and acidification (Hoegh-Guldberg, *et al.*, 2007; Veron, 2011). Even though natural perturbations such as tropical storms, hurricanes, extreme-low-tide subaerial exposures, earthquakes and tsunamis have undoubtedly played a role in such degradation (Hughes, 1994; Jackson, *et al.*, 2014; Miller, 2015), it is now thought that the impacts of natural disturbances are being exacerbated by their interaction with anthropogenic pressures (Nyström, *et al.*, 2000; Hughes, *et al.*, 2003; Pandolfi, *et al.*, 2003). For instance, human-induced global warming appears to be increasing the intensity and frequency of El Niño warming events and the frequency of hurricanes and crown-

of-thorns (*Acanthaster planci*) outbreaks (Enfield, 2001; Aronson, *et al.*, 2002; Harvell, *et al.*, 2002; Hughes, *et al.*, 2003; Buddemeier, *et al.*, 2004).

Most Colombian coral reefs have also shown signs of degradation (Díaz, *et al.*, 2000; Jackson, *et al.*, 2014). In the Colombian Caribbean, for instance, live coral cover decreased by an average of ~ 38 % during the last three decades of the 20th century reaching an average of 20-30 % in most areas (Garzón-Ferreira and Kielman, 1994; Garzón-Ferreira, 1997; Díaz, *et al.*, 2000; Garzón-Ferreira, *et al.*, 2002a); these values have remained relatively constant between 1998 and 2013 (Bastidas-Salamanca, *et al.*, 2014). While the decline of Colombian Pacific coral reefs was much more severe due to the massive coral mortality that occurred throughout the Eastern Tropical Pacific (ETP) during the 1982-83 El Niño event (Glynn, 1990; Vargas-Ángel, *et al.*, 2001), recovery to pre-disturbance levels was achieved within a decade (Zapata, *et al.*, 2001; Zapata and Vargas-Ángel, 2003) and levels of live coral cover are relatively high (\geq 50-74 % average; Rodríguez-Ramírez, *et al.*, 2006; Zapata, *et al.*, 2010). Although several studies have described many of Colombian coral reefs and documented their most significant changes (Garzón-Ferreira and Kielman, 1994; Díaz, *et al.*, 1995, 1996, 2000; Zea, *et al.*, 1998; Zapata, *et al.*, 2001, 2010; Zapata and Vargas-Ángel, 2003), the lack of detailed quantitative assessments through time has hampered the identification of drivers of change. In this paper, I use data collected by the National Monitoring System for the Coral Reefs of Colombia (SIMAC for its Spanish acronym; Garzón-Ferreira and Rodríguez-Ramírez, 2010) to describe the dynamics of coral and algal cover during a 17 yr-long (1998-2014) time series at La Azufrada reef, one of the largest and best developed coral reefs of Gorgona Island, in the Colombian Pacific Ocean (Zapata and Vargas-Ángel, 2003). I address the following questions: What are the dynamics of coral and algal cover at La Azufrada coral reef? What are the major drivers of these dynamics? What do these dynamics tell us about the resilience of this coral reef?

Materials and methods

Study area. The largest and most developed coral reefs of the Colombian Pacific occur at Gorgona Island (2°58' N, 78°10' W), a continental island located 30 km off the Colombian mainland, in one of the rainiest regions of the world, near the southern end of Panama Bight (Glynn, *et al.*, 1982; Díaz, *et al.*, 2000; Zapata and Vargas-Ángel, 2003; Figure 1). The latitudinal displacement of the Intertropical Convergence Zone (ITCZ) strongly influences climatic and oceanographic conditions at Gorgona Island, which are notably seasonal. Mean annual precipitation at Gorgona Island exceeds 6600 mm (Blanco, 2009). Mean monthly precipitation is lower between January and April, when the ITCZ is at its southernmost position, coinciding with a shallow (7.5 m) thermocline, and cold and high salinity

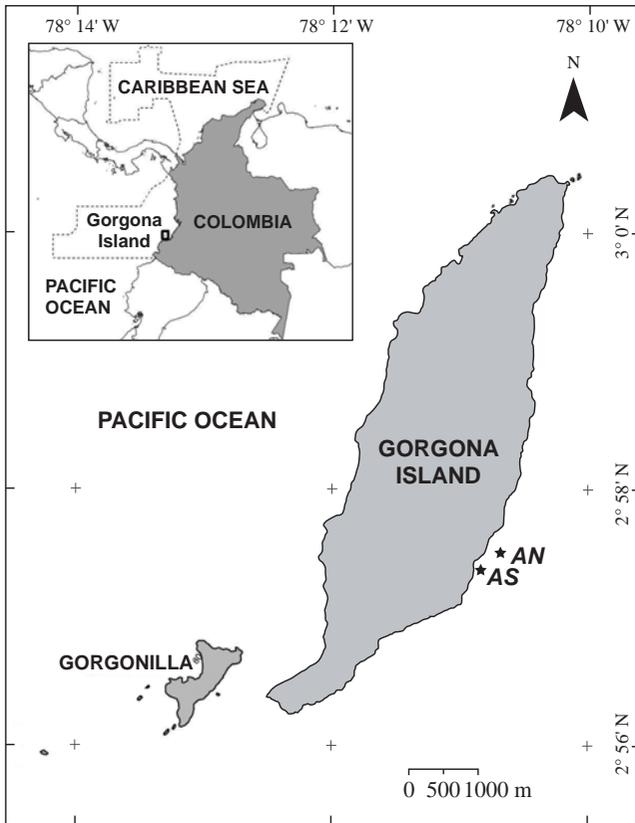


Figure 1. Location of Gorgona Island and monitoring sites (AN and AS) at La Azufrada coral reef, Gorgona Island, Colombia.

sea surface waters. The rest of the year, when the ITCZ is in the north, precipitation is higher, the thermocline is deeper (47 m) and sea surface waters are warm and have low salinity (Giraldo, *et al.*, 2008; Blanco, 2009). Sea surface temperatures around Gorgona vary between 26 and 29 °C, occasionally decreasing to < 19 °C during upwelling events that occur during the dry season (Díaz, *et al.*, 2001; Zapata, 2001; Giraldo, *et al.*, 2008), or increase to 30-32 °C during anomalous conditions associated with El Niño events (Vargas-Ángel, *et al.*, 2001). Seawater salinity at Gorgona is relatively low and variable (29-33) compared to that of the open ocean, but it is nonetheless higher and more stable than that of the mainland coast, which is usually < 20 (Devis-Morales, *et al.*, 2002). In fact, Gorgona Island is one of the localities with coral reefs and lowest salinities in the world (Kleypas, *et al.*, 1999). The tidal regime at Gorgona is semidiurnal with a maximum vertical range of ~ 5.7 m (IDEAM, 2000). Besides strong El Niño warming events that periodically cause severe coral bleaching and mortality (Glynn, 1990; Vargas-Ángel, *et al.*, 2001), the most significant physical perturbation on Gorgona Island coral reefs are repeated subaerial exposures during extreme low tides, which most often occur between January and April and occasionally cause coral bleaching and mortality on the shallowest portions of reefs (Zapata, *et al.*, 2001;

Zapata and Vargas-Ángel, 2003; Castrillón-Cifuentes, *et al.*, 2017). Gorgona Island is a National Natural Park and it is well-protected from local human impacts.

Study sites. La Azufrada reef, located on the leeward side of the island, is the largest (11.2 ha) continuous coral reef of Gorgona Island. This fringing reef extends approximately for 1 km along the eastern coast. Following an inshore-offshore transect, the reef has an ~80-130 m reef flat with high pocilloporid coral cover, a sloping reef front also dominated by pocilloporids and an outer reef base where massive species of the genus *Pavona* and *Gardineroseris* occur in patches (Glynn, *et al.*, 1982; Zapata, 2001; Zapata and Vargas-Ángel, 2003). Two study sites were selected on this reef in November 1998 based on their good state of conservation and similarity in reef development. The first site (La Azufrada North; Figure 1) is located in the northern portion of the reef near a circular depression (known locally as El Hueco), which is a notable, persistent feature of this reef (Glynn, *et al.*, 1982; Zapata, 2001). The second site (La Azufrada South) is located in the southern section of the reef about 400 m from the north site (Figure 1). At each site, a shallow and a deep plot were established, each consisting of five 10-m long transects haphazardly laid out and permanently marked with stainless steel rods driven into the substrate, one at each end of each transect. The shallow plot was located on the reef flat at ~0.5 m below the Mean Lower Low Water 0-m tidal datum (IDEAM, 2000), while the deep plot was located further offshore at the interface between the reef front and the outer reef base at ~4 m below the 0-m tidal datum. The complete setup consisted of a total of two sites, four plots and 20 permanent transects. More detailed information on the two sites may be found in Zapata, *et al.* (2010).

Data collection. Data on the benthic cover and abundance of herbivorous fishes were collected once a year between 1998 and 2014. Data on sea urchin abundance were collected between 2002 and 2014. All data was obtained each year during a single week of August - November (depending on the year) by a team of 5-8 divers. The cover of different benthic organisms (mostly live coral and algae) was estimated using the continuous line intercept, chain-transect method (Loya, 1978). Live coral cover represents mostly the abundance of pocilloporids because these are the dominant corals at La Azufrada reef, except at the deep plot of the north site, where agariciids (mostly species of *Pavona*) are common. While fleshy and turf algae were considered as separate categories during data collection, for analysis they were combined in a single category because fleshy algae were relatively scarce. Calcareous algae were overwhelmingly crustose coralline algae (CCA) and were considered separately because of their important role facilitating coral recruitment (Birrell, *et al.*, 2008). Sea urchins were counted since 2002 along a 1 m-wide band along each of the two sides of each 10-m permanent transect (20 m² area per transect). Herbivorous fishes were visually censused since 1998 along 30 x 2 m

belt transects haphazardly placed within each plot each year. Two to ten transects were censused at each plot each year for a total of 535 fish visual censuses over the study period. Methods followed protocols modified from **CARICOMP** (2001; see also **Garzón-Ferreira and Rodríguez-Ramírez, 2010, Zapata, et al., 2010**).

Statistical analyses. The benthic cover (coral, fleshy and turf algae, and crustose coralline algae) data were analyzed with a linear mixed model with two fixed factors, each with two levels: site (North and South) and depth (shallow and deep plots). Because the same transects were repeatedly sampled every year, this design additionally included one within-subject, repeated measures factor (years) with 17 levels representing the number of consecutive years. The model also included a variance heterogeneity term as a function of year to account for the heteroscedasticity structure within years. This analysis was performed with package nlme (**Pinheiro, et al., 2017**) in the R software Ver. 3.3.1 (**R Core Team, 2016**). Analysis of residuals indicated that assumptions of normality and homoscedasticity were satisfied only by the live coral cover data, but not by the fleshy and turf algae or CCA data. The heteroscedasticity structure within years included in the models improved homoscedasticity of residuals in the live coral and CCA data but not in the fleshy and turf algae data. Since the arcsine square root transformation is no longer recommended for statistical analyses of percentages (**Warton and Hui, 2011**) and the logit transformation did not improve normality and heteroscedasticity of residuals for both types of algae, the analyses reported are based on the original percentage data for all variables. The total abundance of sea urchins or herbivorous fishes was analyzed with a three-way factorial (13 or 17 years, respectively, x 2 sites x 2 depths) generalized linear mixed model with a negative binomial error distribution and a Log-link function using the R software package lme4 (**Bates, et al., 2015; R Core Team, 2016**). For the sea urchin data, transect was used as a random effects factor because the same transects were sampled repeatedly through the years. In contrast, the model fitted to the herbivorous fish data did not include a repeated measures structure because fish were not censused on the same transects every year.

Results

Live coral was the dominant component of the benthic cover on La Azufrada coral reef throughout the 17 years of study except in 2007, when fleshy and turf algae, the second most important component, was more abundant than coral (Figure 2). Calcareous algae represented the third major component of benthic cover, particularly since 2009. Both coral and algal cover varied significantly through the years (Table 1). Overall (all sites and depths combined), mean percent live coral cover declined from $66.9 \pm 4.4\%$ (\pm SE) in 1998 to a minimum of $39.4 \pm 7.8\%$ in 2008, but showed an increasing trend since then reaching $50.7 (\pm 5.7\%)$ in 2014. Thus, during the 17 years there was a net absolute loss of live coral

cover of 16.2 %, representing a relative loss of 24.2 % of the coral existing in 1998. At the same time, fleshy and turf algae tended to show temporal patterns of variation opposite those of coral because these two components of benthic cover were negatively correlated every year ($r = -0.592 - -0.955, p \leq 0.006, N = 20$ within any given year). Overall, fleshy and turf algal cover was below 29.0 % between 1998-2004, and above 33.0 % between 2005-2008, reaching a peak of $49.5 \pm 8.8\%$ in 2007 and then declining to levels below 33.0 % (Figure 2). The net absolute change in fleshy and turf algal cover between 1998 and 2014 was of only 0.6 %, which represents a 2.3 % increase relative to 1998. Crustose coralline algae also varied through the study period between a minimum yearly mean of $3.4 \pm 0.5\%$ in 1998 and a maximum yearly mean of $26.0 \pm 6.7\%$ in 2009. By 2014 the mean cover by calcareous algae was $18.8 \pm 3.8\%$ indicating an absolute net increase of 15.4 % or a 452.9 % increase relative to 1998 levels.

Temporal and spatial variation in coral and algal cover.

Coral cover was higher on the south than on the north site throughout the study period (Table 1; Figure 3). Overall (all years and depths combined) mean coral cover was $61.0 \pm 6.1\%$ on the south site and $42.2 \pm 6.1\%$ on the north site. This difference was maintained throughout the study period as indicated by the lack of a significant year x site interaction (Table 1). Both sites exhibited trends of coral cover loss through the entire study period like that observed for the whole reef, with a net absolute decrease of 18.1 % in the north and 14.2 % in the south, which represent net decreases of 30.9 % and 18.9 % relative to 1998 levels, respectively. Both sites also showed a similar pattern of coral decrease from 1998 to 2008 and a recovering trend afterwards.

Based on all sites and years combined, there were pronounced differences in mean coral cover between depths ($34.8 \pm 6.1\%$ in shallow vs $68.5 \pm 6.1\%$ in deep plots; Table 1). While coral cover in shallow areas declined dramatically

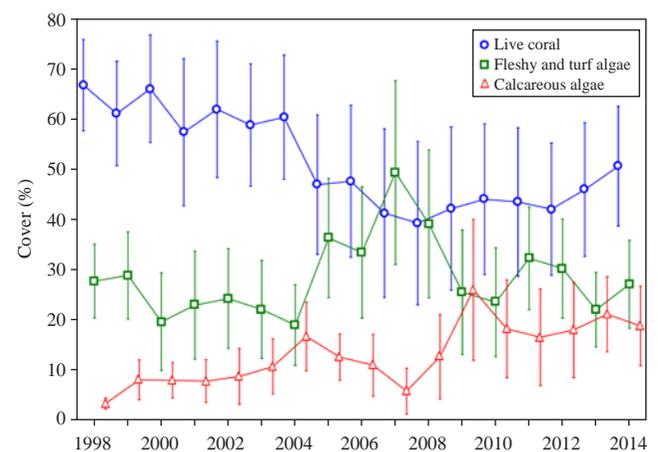


Figure 2. Temporal variation in mean (\pm 95 % C.I.) cover by live coral, fleshy and turf algae, and crustose coralline algae at La Azufrada coral reef, Gorgona Island, from 1998 to 2014.

Table 1. Results of a linear mixed model analysis of percent cover by coral, fleshy and turf algae, and crustose coralline algae (CCA). The model included two fixed factors, Site (North and South) and Depth (shallow and deep) and a random factor (Transect) repeatedly sampled over 17 years. The model also included a variance heterogeneity term as a function of year to account for the heteroscedasticity structure within years. F tests and associated degrees of freedom (DF) and probabilities are shown for each response variable.

Source	DF	Coral		Fleshy & turf algae		CCA	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1, 316	138.27	<0.0001	114.18	<0.0001	190.55	<0.0001
Site	1, 160	4.78	0.0440	0.35	0.5640	30.32	<0.0001
Depth	1, 160	15.99	0.0010	25.34	0.0001	19.27	0.0005
Site x Depth	1, 160	0.97	0.3400	0.52	0.4827	9.80	0.0064
Year	1, 316	149.17	<0.0001	3.42	0.0653	186.46	<0.0001
Site x Year	1, 316	1.57	0.2113	12.52	0.0005	48.93	<0.0001
Depth x Year	1, 316	3.19	0.0752	2.76	0.0974	91.35	<0.0001
Site x Depth x Year	1, 316	0.00	0.9577	7.38	0.0070	41.90	<0.0001

from $61.0 \pm 5.7\%$ in 1998 to $14.1 \pm 7.6\%$ in 2008 and then increased to $40.1 \pm 7.1\%$ in 2014, in deep areas it tended to increase from $72.7 \pm 5.7\%$ in 1998 to $81.5 \pm 5.7\%$ in 2002 and then decline to $55.3 \pm 7.6\%$ in 2012. Despite these apparently different patterns of temporal variation between depths, the year x depth interaction was not significant ($p = 0.075$; Table 1).

In contrast to coral cover, extent of cover by fleshy and turf algae was very heterogeneous and depended on the combination of site, depth and year (Table 1). Nonetheless, fleshy and turf algal cover combined over all depths and years did not differ significantly between sites ($27.8 \pm 3.9\%$ vs $29.2 \pm 3.9\%$ in the south and north, respectively). However, differences in algal cover between sites were not constant through the years and exhibited a significant site by year interaction (Table 1). In particular, algal cover was more often lower on the south than on the north site during the first half of the study, while the reverse was true for the second half of the study period. Nonetheless, both sites showed similar patterns of temporal variation with relatively lower values between 1998 – 2004, higher values between 2005 – 2008 and a peak in 2007, and relatively lower values again for the remaining of the study period. Fleshy and turf algal cover varied oppositely coral cover with higher values ($42.3 \pm 3.9\%$) in shallow than in deep areas ($14.7 \pm 3.9\%$). Similar to coral cover, patterns of temporal variation in algal cover tended to differ between depths, although not sufficiently for a significant year x depth interaction ($p = 0.097$; Table 1). In shallow areas, algal cover declined from $34.9 \pm 4.2\%$ in 1998 to $24.2 \pm 5.3\%$ in 2004, increased to $80.9 \pm 7.0\%$ in 2007 and then declined to $31.8 \pm 6.2\%$ in 2014. In contrast, in deep areas, algal cover was much more stable fluctuating between values as low as 4.0 to 4.5 % in 2000, 2001 and 2010, and values as high as 23.6 % in 2012.

CCA cover was also very variable spatially and temporally exhibiting a significant site x depth x year interaction (Figure 3; Table 1). Clearly, the shallow area of the north site

exhibited a much more pronounced temporal variation in CCA cover than any of the other site by depth combinations. CCA cover was low in the deep plots of the two sites during all the study period, but it increased notably in shallow areas at both sites since 2008, after a decrease in fleshy and turf algae, particularly so in the north site, where CCA became the dominant component of the substrate cover.

Abundance of sea urchins and herbivorous fishes.

Diadema mexicanum was the most abundant sea urchin at La Azufrada (78.1 % of all sea urchins observed during the study), followed by *Centrostephanus coronatus* (~20.7 %). Other sea urchin species observed were, in decreasing order of abundance, *Hesperocidaris asteriscus*, *Astropyga pulvinata*, *Toxopneustes roseus*, *Eucidaris thouarsii* and *Tripneustes depressus*.

Abundance of sea urchins depended significantly on the interactions among all factors (i.e., there was a significant site x depth x year interaction; Table 2). Mean total sea urchin abundance (all sites and depths combined) varied significantly among years (Figure 4). The highest yearly mean (134.2 ± 26.3 per 20 m²; \pm S.E.) was observed in 2002 and the lowest (35.4 ± 7.8) in 2005. Yearly means showed signs of oscillations with alternating peaks (2002, 2006, 2009, 2012, 2013) and troughs (2005, 2008, 2011). Overall (all years and depths combined) total sea urchin abundance was similar between sites. However, abundance peaks observed in 2006, 2009 and 2012 were much more pronounced at the north than at the south site, particularly in the shallow area (Figure 3). Therefore, considering all years and sites combined, shallow areas had higher total sea urchin abundance than deep areas.

Only six species accounted for 96.7 % of all herbivorous fishes observed during the study. These were, in decreasing order of abundance, *Acanthurus xanthopterus* (30.6 %), *Stegastes acapulcoensis* (29.1 %), *Scarus ghobban* (26.8 %), *Acanthurus triostegus* (7.4 %) and *Scarus rubroviolaceus* (2.8 %). Also observed were other four species with abundances < 1.2 %.

Table 2. Results of three-way factorial (years x 2 sites x 2 depths) generalized linear mixed model analyses of sea urchin and herbivorous fish abundance. For the sea urchin data, transect was used as a random effects factor because the same transects were sampled repeatedly through 13 years. In contrast, the model fitted to the herbivorous fish data did not include a repeated measures structure over the 17 years of sampling. Values of the Chi-square tests and associated degrees of freedom and probabilities are shown for each response variable.

Source	Sea urchins			Herbivorous fish		
	Chi-square	DF	P	Chi-square	DF	P
Site	0.80	1	0.3696	3.85	1	0.0497
Depth	16.19	1	<0.0001	121.15	1	<<0.0001
Year	121.07	12	<<0.0001	156.43	16	<<0.0001
Site x Depth	0.13	1	0.7228	3.82	1	0.0507
Site x Year	71.15	12	<0.0001	113.64	16	<<0.0001
Depth x Year	145.58	12	<<0.0001	98.38	16	<<0.0001
Site x Depth x Year	50.07	12	<0.0001	31.58	16	0.0113

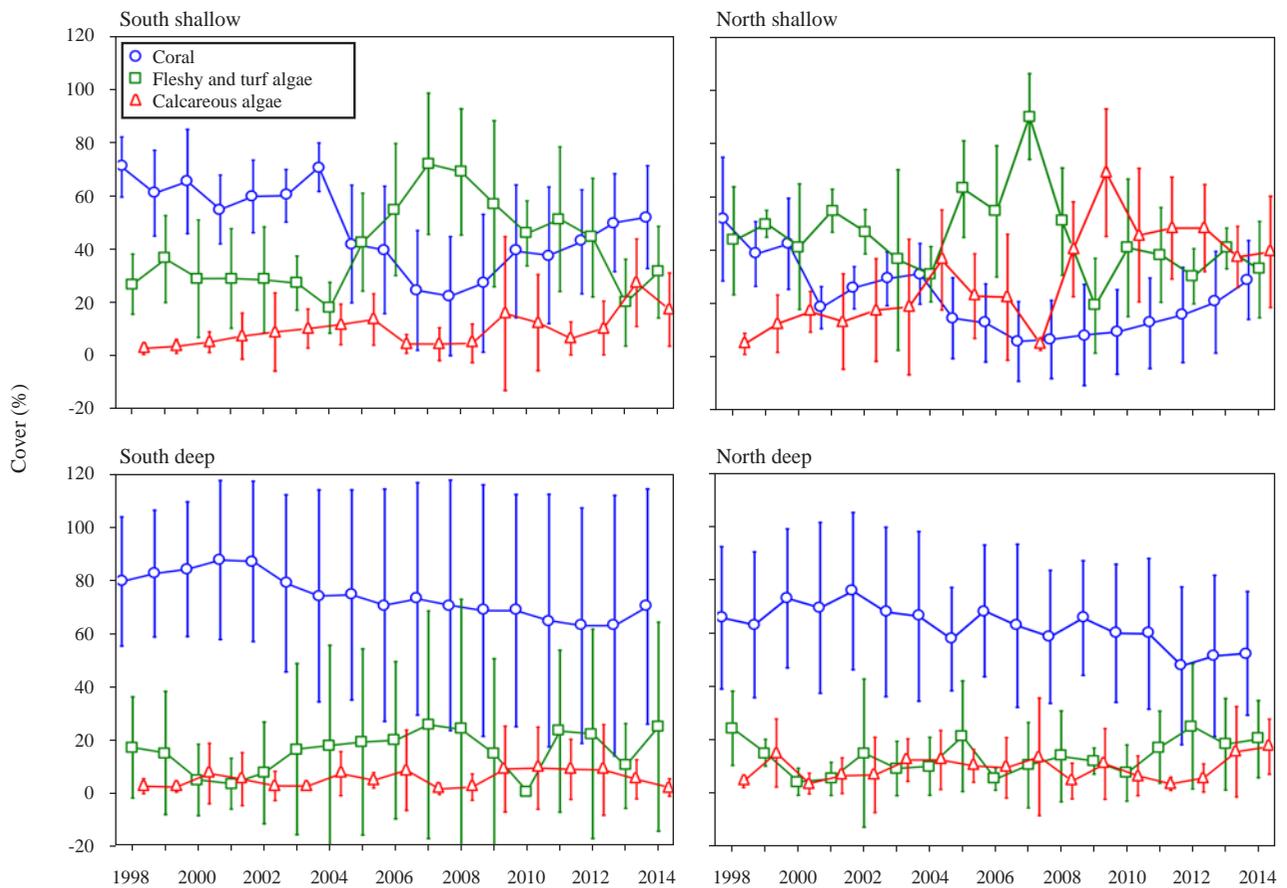


Figure 3. Temporal patterns of variation in mean (\pm 95 % C.I.) cover by live coral, fleshy and turf algae, and crustose coralline algae at two depths (shallow and deep) within two sites (North and South) of La Azufrada coral reef during the study period.

Total abundance of herbivorous fishes varied with site, depth and year (i.e., there was a significant three-way interaction; Table 2). Considering all sites and depths combined herbivorous fish abundance varied sharply among years (Figure 5). Yearly means varied between 8.5 ± 2.1 fish per 60 m^2 (\pm S.E.) in 2012 and 38.8 ± 11.3 in 2001 followed by 36.1

± 18.6 in 2000. The latter two years showed clearly unusually high mean abundances and large within-year variation, particularly at the south site. Herbivorous fish abundance varied irregularly through the years although peaks and troughs did not coincide with those exhibited by sea urchins. Overall (all years and depths combined), there were only

marginally significant differences between sites ($p = 0.049$), due to the much higher values observed in 2000 and 2001 in the south site. On average (all sites and years combined), herbivorous fish abundance was greater on shallow areas than in deep areas and this occurred particularly in 2003, 2004 and 2009 at the south site, and 2003-2004, 2008-2010 and 2013 at the north site. Clearly, herbivorous fish were more consistently abundant in the north site than in the south site (Figure 5).

Discussion

This study extends the results of a previous study (Zapata, *et al.*, 2010) on the benthic dynamics of La Azufrada coral reef that spanned the first seven years (1998-2004) of the period considered here. The larger duration of the current study allows a more detailed evaluation of the observed dynamics and its potential drivers in the light of hypotheses previously proposed (Zapata, *et al.*, 2010). A major (~27.5%) decline in coral cover was observed over the first decade (1998-2008) of the study, causing concern that coral reefs of Gorgona Island were exhibiting a decline like that observed in many coral reefs worldwide (Gardner, *et al.*, 2003, Bruno and Selig, 2007, De'ath, *et al.*, 2012, Jackson, *et al.*, 2014). However, the recovering trend observed since 2009 and the lack of major changes in environmental conditions around La Azufrada coral reef during the time of the study suggest that changes in coral cover are not simply the result of deteriorating conditions caused by local anthropogenic impacts.

Although coral reefs have long been known to be affected by acute natural perturbations that cause significant coral mortality (Miller, 2015), they have usually been able to recover from such perturbations within a few years (Connell, 1997; Connell, *et al.*, 1997, 2004). However, coral reefs have also been increasingly exposed to anthropogenic, usually chronic, perturbations. Even though both natural and anthropogenic perturbations can be significant drivers of change in coral communities, the latter are increasingly becoming the dominant drivers of coral reef dynamics and appear to be responsible for the widespread decline of coral reefs (Gardner, *et al.*, 2005; McClanahan, *et al.*, 2008; Miller, 2015). However, because Gorgona Island is within a well-managed marine protected area, it is unlikely that the initial decline in coral cover observed in this study was caused by local, anthropogenic disturbances.

One important natural perturbation potentially responsible for the decline in coral cover observed at La Azufrada during the first decade of the study is the occurrence of El Niño warming (Glynn, *et al.*, 2017a). While the 1982-1983 El Niño event was responsible for declines in coral cover of up to 85 % in Eastern Tropical Pacific coral reefs (Glynn, 1990), the 1997-1998 El Niño event, which was of similar intensity and duration as the 1982-1983 event, did not cause such dramatic decline even though it negatively affected reefs in the region, including Gorgona Island's reefs (Vargas-Angel, *et al.*, 2001). Levels of coral mortality during the 1997-1998 El Niño were 5 % at Caño Island,

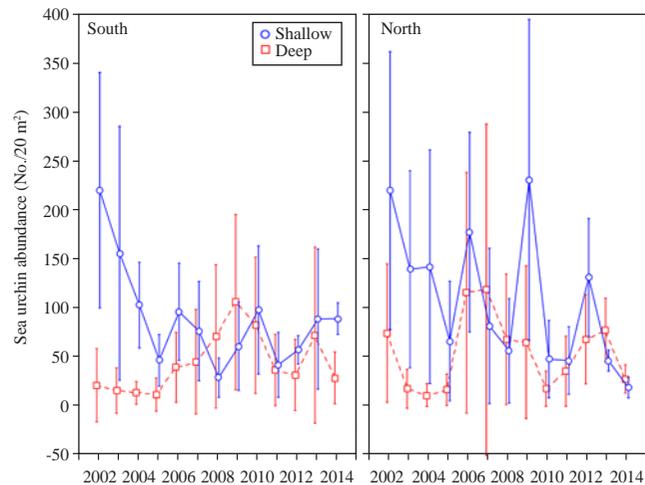


Figure 4. Temporal patterns of variation in mean ($\pm 95\%$ C.I.) sea urchin abundance at two depths (shallow and deep) within two sites (North and South) of La Azufrada coral reef between 2002 and 2014.

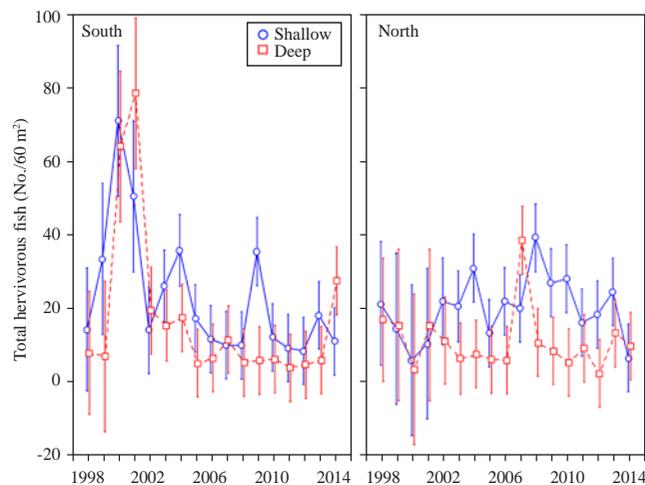


Figure 5. Temporal patterns of variation in mean ($\pm 95\%$ C.I.) abundance of herbivorous fishes at two depths (shallow and deep) within two sites (North and South) of La Azufrada coral reef between 1998 and 2014.

Costa Rica (Guzmán and Cortés, 2001), 7 % on mainland Ecuador and 13 % in the Gulf of Chiriquí, Panama (Glynn, *et al.*, 2001). Levels of bleaching reported for La Azufrada were at most 32 % of live coral cover on the reef slope at the peak of this event but coral mortality was low ($< 1\%$; Vargas-Angel, *et al.*, 2001). Even though the 1997-1998 El Niño event might explain the 6 % decline in coral cover observed from 1998 to 1999, no other major El Niño events occurred during the study period that could help explain the decline in coral cover observed until 2008. I conclude, therefore, that El Niño warming events are not a significant driving force explaining the dynamics of coral and algal cover at La Azufrada reef during the study period.

Major differences in the benthic dynamics of shallow and deep areas observed in this as well as in the previous study by **Zapata, et al.** (2010) help reveal a major driver of benthic dynamics at La Azufrada reef. Clearly, the magnitude of fluctuations in coral and algal cover were much greater in shallow than in deep areas of the reef. Furthermore, patterns of temporal variation in benthic cover were similar between the two study sites, indicating the occurrence of a phenomenon at a sufficiently large spatial scale to encompass the two sites separated by ~400 m. One major, recurrent natural perturbation affecting coral reefs at Gorgona Island and capable of differentially affecting shallow and deep areas of reefs is the subaerial exposure of corals during extreme low tides (**Zapata, et al.**, 2001; **Zapata and Vargas-Ángel**, 2003). This phenomenon occurs every few years at Gorgona Island as it does elsewhere in the ETP (**Glynn**, 1976; **Eakin and Glynn**, 1996; **Cortés and Jiménez**, 2003; **Maté**, 2003; **Glynn, et al.**, 2017a) and explains much of the differences observed in the dynamics of coral and algal cover between depths. Estimates made at La Azufrada reef indicate that subaerial exposure of corals occurs at tide levels below ~ -0.4 m relative to the 0.0 m tide table datum (**IDEAM**, 2000). Because the lowest astronomical tides can reach down to -0.7 m relative to the tidal datum, large areas of the shallowest portions of the reef crest and reef flat can be exposed to air, whereas deeper areas are not affected by this phenomenon (Figure 6A,B). While short-time (15 – 40 min) subaerial exposure of corals can reduce zooxanthellae density and fecundity in *Pocillopora damicornis* (**Castrillón-Cifuentes, et al.**, 2017), prolonged (> 1 h) subaerial exposure occurring at mid-day or coinciding with unfavorable weather conditions (e.g., intense solar radiation or heavy rain, **Maté**, 2003) and occurring repeatedly during several consecutive days can cause severe coral bleaching (Figure 6C) and mortality (**Glynn**, 1976; **Zapata and Vargas-Ángel**, 2003; **Glynn, et al.**, 2017a). Once dead, the colonies are quickly colonized by filamentous algae. Often, only the most distal tips of branches are subaerially exposed in some colonies, and subsequently only those affected portions bleach and die, while the remaining unexposed, lower portions of colonies maintain healthy tissues (Figure 6D). Nonetheless, the dead tips of branches are also colonized by algae, which, after growing for a few weeks, form a thick algal mat that overgrows and kills the remaining tissue, most likely by preventing light penetration. This process creates algal patches of varying sizes on the most elevated portions of the reef (Figure 6D-F). Thus, generally the effect of aerial tidal emersion is a decrease in coral cover and a concomitant increase in algal cover on shallow areas. In contrast, deep areas of the reef are never subaerially exposed during extreme low tides and therefore exhibit much less among-year variation in coral and algal cover.

While extreme low-tide subaerial exposure of corals explains most of the decreases in live coral and increases in algal cover observed in shallow areas of the reef until

2008, what explains the recovery of live coral and decline in algal cover observed after 2008? For any recovery to occur, a process of succession must ensue after perturbation (**Connell and Slatyer**, 1977; **Doropoulos, et al.**, 2016). I suggest that once algae become abundant after coral death following subaerial exposures, herbivores play a crucial, facilitating role in the recovery process by exerting two important effects: first, they remove the algae from dead coral substrates, and second, they erode the reef substrate and therefore increase its depth making it less likely to be subaerially exposed during a subsequent extreme low tide. Evidence for this idea is provided by the fact that on average, sea urchins and herbivorous fish are more abundant in shallow than in deep areas. Although clearly highly dynamic and variable, at both sites the abundance of sea urchins and herbivorous fish was greater in shallow than in deep areas of the reef most of the years. Once herbivores remove the fleshy and turf algae, crustose coralline algae growing on coral rubble become dominant, and later a hard-calcareous pavement is formed as result of cementation by the encrusting calcareous algae. These crustose coralline algae are known to induce coral larval settlement and affect post-settlement survival generally facilitating coral recruitment (**Heyward and Negri**, 1999, **Harrington, et al.**, 2004).

Three mechanisms of recovery of live coral cover can occur: 1) Sublethal effects of subaerial exposure on corals are frequently observed even after major mortality has occurred throughout the reef flat and crest. Small surviving portions of colonies act as effective juvenile coral colonies that can grow back (**Glynn and Fong**, 2006). 2) Settlement of sexually produced larvae and their subsequent juvenile recruitment also contribute to repopulate affected areas of the reef. While it has been difficult to observe coral larval settlement on artificial substrates in the eastern tropical Pacific (**Medina-Rosas, et al.**, 2005; **López-Pérez, et al.**, 2007), including Gorgona Island (**Lozano-Cortés and Zapata**, 2014), histological evidence clearly indicates that gonad maturation and sexual reproduction indeed occur in ETP coral populations (**Glynn, et al.**, 2017b), including those at La Azufrada reef (**Castrillón-Cifuentes, et al.**, 2015). In fact, juvenile colonies are often seen on the bare carbonate pavement on the reef flat of La Azufrada reef suggesting that recruitment of sexually-produced colonies is occurring (**Jaramillo-González**, 2012). However, it is not known whether coral populations at Gorgona Island are self-replenishing or are open. Given its negative effects on coral fecundity and zooxanthellae density at Gorgona Island (**Castrillón-Cifuentes, et al.**, 2017), subaerial exposure could affect coral reproduction and subsequent settlement and recruitment success. 3) Recruitment of new colonies produced by the fragmentation of adult colonies. It has been long-known that fragmentation is an important and common mechanism of asexual reproduction in eastern tropical Pacific coral reefs (**Highsmith**, 1982; **Glynn, et al.**, 2017b). In fact, several mechanisms causing coral fragmentation of

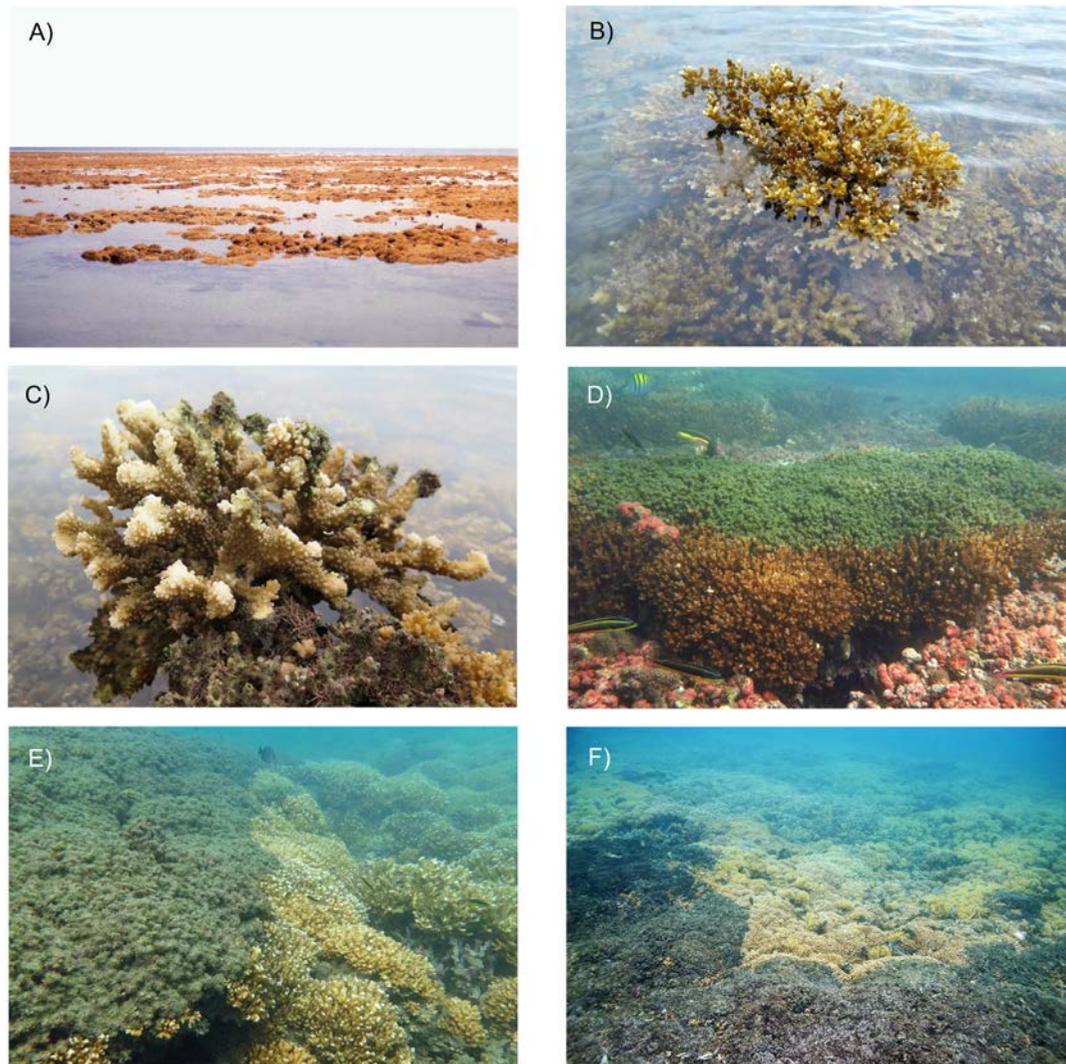


Figure 6. Effects of extreme low tidal subaerial exposure of coral reefs at Gorgona Island, Colombian Pacific Ocean. A) Extensive subaerial exposure of La Azufrada coral reef. B) Recently exposed coral colony showing healthy tissue. C) Partially bleached coral colony during a subaerial exposure event. D) Cluster of coral colonies with upper portion covered by filamentous algae a few weeks after subaerial exposure. E) and F) Contrast between shallow areas of the reef extensively covered by filamentous algae as consequence of a subaerial exposure event (dark areas on left or lower portions of photographs) and healthy coral (pale yellow-khaki color on the right) in adjacent deeper areas not subaerially exposed.

pocilloporid colonies have been documented on Gorgona Island coral reefs, including fish predation (Guzmán and López, 1991; Palacios, *et al.*, 2014; Enochs and Glynn, 2017) and breakage of colonies by drifting logs (Muñoz, *et al.*, 2015). Fragments produced often survive and grow successfully and significantly contribute to the recovery of areas affected by subaerial exposures. Because shallow areas of the reef are overwhelmingly dominated by branching (pocilloporid) corals, fragmentation is a major, perhaps the most important, coral recovery mechanism at La Azufrada reef. Paradoxically, once the coral cover is recovered, the reef starts to build up until it reaches a point in which it again becomes vulnerable to subaerial exposure starting a new cycle of disturbance and recovery.

Conclusions

This study suggests that La Azufrada coral reef exhibits cyclic dynamics that are the result of the interplay between a physical disturbance (subaerial exposure during extreme low tides) and biological processes. The latter include two interspecific interactions: herbivory, which plays a vital role at the beginning of the process of succession after disturbance, and corallivory, which is responsible for much coral asexual reproduction by fragmentation and enhances the recovery of coral cover. Other biological processes are coral sexual reproduction, recruitment, and subsequent coral growth. Although the evidence presented here is strongly suggestive, the 17-year-long time series considered in this paper is still too short to demonstrate a complete cycle of

disturbance and recovery at la Azufrada reef; however, it indicates that the period of such cycle, if it indeed occurs, is in the order of decades. The view that coral reef benthic dynamics are driven by disturbance-recovery cycles dates to the work of **Connell** (1978) and there is good evidence that in the absence of anthropogenic disturbances coral reefs recover from acute natural disturbances (**Connell**, 1997; **Connell, et al.**, 1997, 2004; **Miller**, 2015). This study strongly suggests that such is the case at La Azufrada reef and other coral reefs of Gorgona Island because they are exempt from the local environmental insults that many other reefs worldwide are exposed to. Currently, there is much debate regarding whether coral reef decline worldwide is due to global climate change or to local anthropogenic impacts (**Knowlton and Jackson**, 2008; **Kennedy, et al.**, 2013), and the case of La Azufrada reef suggests that if local human impacts are low, ecosystem resilience to natural perturbations will not be compromised. However, there is increasing concern that anthropogenic global change will increase the frequency and intensity of natural perturbations such as El Niño warming and bleaching events, and ocean acidification (**Eakin, et al.**, 2009; **Hoey, et al.**, 2016), both of which will reduce coral reef resilience in the eastern tropical Pacific.

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Conflict of interest

The author declares no conflict of interests.

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