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Status of the coral formations of Bajo Nuevo Reef Complex, Western Caribbean, Colombia

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ABSTRACT

Introduction: Although many reefs have been disturbed by the combined effects of climatic and non-climatic stressors, there still are regions largely free from direct human pressures such as runoff, pollution, and maritime traffic due to their geographic remoteness. This suggests that they are replicas of "pristine reefs", that allow the investigation of relationships between reef communities and their environment.

Objective: To evaluate the status of the coral formations of Bajo Nuevo, Seaflower Biosphere Reserve.

Methods: The coral health and the relative cover of reef-building organisms and of their main competitors were evaluated. In every station (11), ten photo quadrants of 0.25 m^2 were evaluated along a 10 m tape measure combined, along with ~3 min videos.

Results: 32 coral species were recorded, 30 of them Scleractinia and two of hydrocorals, with the highest richness in the reef lagoon. In 2021, the reefs in Bajo Nuevo were dominated by non-reef-building organisms (61.7 ± 0.10 %), the building species represented only 23.9 ± 0.10 %; 3.2 ± 0.03 % was coral skeleton with recent and transitional death less than 15 days old. Signs of diseases affected three genera, 13 species and 23.5 % of the colonies evaluated, of which 84.9 % showed one of the four signs related to the stony coral tissue loss disease.

Conclusions: With previous expeditions (2010-2011) as a reference, this reef complex registered in 2021 a drop in the cover of hard corals and calcareous algae, and coral richness; an increase in the cover of non-reef-building organisms, with a high prevalence of signs of unhealthiness associated with different coral diseases. This confirms that these reefs are in danger (EN), as suggested by the red list of marine and coastal ecosystems of Colombia.

Keywords: stony corals; diversity; epizooties; atoll; coral mortality.

RESUMEN

Estado de las formaciones coralinas del complejo arrecifal de Bajo Nuevo, Caribe Occidental, Colombia

Introducción: Aunque muchos arrecifes han sido alterados por los efectos combinados de estresores climáticos y no climáticos, aún existen regiones en gran medida libres de presiones humanas directas, como escorrentía, contaminación y tráfico marítimo, debido a su lejanía geográfica. Esto permite suponer que son réplicas de "arrecifes prístinos", lo que facilita investigar las relaciones entre las comunidades de arrecifes y su entorno.

Objetivo: Evaluar el estado actual de las formaciones de coral de Bajo Nuevo, Reserva de la Biosfera Seaflower.

Métodos: Se evaluaron la salud del coral y la cobertura relativa de organismos constructores de arrecifes y de sus principales competidores. En cada estación (11), se evaluaron diez cuadrantes fotográficos de 0.25 m^2 a lo largo de una cinta métrica de 10 m, junto con videos de aproximadamente 3 minutos.
Resultados: Se registraron 32 especies de coral, 30 de corales pétreos y dos de hidrocorales, presentándose la mayor riqueza en la laguna arrecifal. En 2021, los arrecifes de Bajo Nuevo estaban dominados por organismos no constructores de arrecifes (61.7 ± 0.10 %), mientras que las especies constructoras representaban sólo el 23.9 ± 0.10 %; y un 3.2 ± 0.03 % era esqueleto coralino con muerte reciente y transicional menor a 15 días. Los signos de enfermedad afectaron a tres géneros, 13 especies y al 23.5 % de las colonias evaluadas, de la cuales el 84.9 % presentaron alguno de los cuatro signos relacionados con la enfermedad de pérdida de tejido de coral duro.
Conclusiones: Con expediciones anteriores (2010-2011) como referencia, este complejo arrecifal registró en 2021 una caída en la cobertura de corales duros y algas calcáreas, y en la riqueza coralina; un aumento en la cobertura de organismos no constructores de arrecifes y, una alta prevalencia de signos de enfermedades coralinas. Esto confirma que los arrecifes de Bajo Nuevo están en peligro (EN), como lo sugiere la lista roja de ecosistemas marinos y costeros de Colombia.

Palabras claves: corales pétreos; diversidad; epizootias; atolón; mortalidad coralina.

INTRODUCTION

Although many reefs have been disturbed by the combined effects of climatic and non-climatic stressors, there are still regions largely free from direct human pressures due to their geographic remoteness and difficulties for human settlement. Distance in remote ocean environments has kept reefs out of the direct effect of runoff, pollution and maritime transport, and even until the early twentieth century, they were thought of as pristine zones (Brainard et al., 2005). This allows them to be replicas of "pristine reefs", allowing to investigate the relationships between reef communities and their environment, mainly the effect of large-scale disturbances (Bindoff et al., 2019; Perry et al., 2015; Williams et al., 2015).

Knowledge gaps remain on the synergistic and cumulative effects of global (i.e. ocean warming) and regional (i.e. epizooties) scale disturbances in these remote environments; and few studies have compared the effect of disturbances between remote reefs and those close to areas of human populations (Bruckner, 2002; Díaz-Pulido et al., 2004; Woodley et al., 2003). Hence the importance of studies in reef formations and in general in remote ecosystems as reference points to advance in the understanding of the isolated effect of pressures operating on a large scale in a climate change scenario.

In the Caribbean, after the large decline of coral cover between 1970 and 1983, Souter et al. (2021) estimated, with meta-analyses, an additional decline of 2.1 % between 1999 and 2019. From Colombia to Mexico, the decline was between 21.6 and 22.6 %; and only in the Greater Antilles, coral cover increased (from 5.4 to 16.1 %) (Souter et al., 2021). Bajo Nuevo reef complex is situated in the NW Caribbean, at the northern end of the Seaflower Biosphere Reserve (Seaflower BR), and the joint regime area Colombia-Jamaica. Due to its remote location, the area has little historical data, all obtained in expeditions organized by the Colombian Navy, first in 2010 (Abril-Howard et al., 2012) and 2011 (Vega-Sequeda et al., 2015), through Rapid Reef Assessments (RRA) in 400 m^2 plots, and during the Seaflower 2021 Scientific Expedition, through 10 m transects. Because of its distance from the continent, Bajo Nuevo is a model to assess the effect of large-scale pressures on the status of remote coral formations.

The objective of this study was to evaluate the current status of the coral formations of Bajo Nuevo, Seaflower Biosphere Reserve. To test the hypothesis that coral formations in remote environments remain in good condition due to distance to direct human pressures, comparisons of diversity, cover and coral health were performed between Expeditions (2010, 2011 and 2021) (Abril-Howard et al., 2012; Vega-Sequeda et al., 2015) and their relationship with the variation in the sea surface temperature (SST).

MATERIALS AND METHODS

Study area: Bajo Nuevo reef complex, also known as Petrel islands, is located in the NW Caribbean and is part of what is called the Archipelago of San Andrés, Providencia and Santa Catalina, belonging to Colombia. Bajo Nuevo is located 475 km northeast of the island of San Andrés, at coordinates 15°53' N & 78°38' W. It is part of the Seaflower Biosphere Reserve declared by UNESCO in 2000. In 2005, the Colombian Ministry of Environment, Housing and Territorial Development recognizing that the archipelago shows high species diversity and endemism (Acero & Garzón-Ferreira, 1994), created the Seaflower Marine Protected Area, with an area of 65 000 km^2 (Abril-Howard et al. , 2011). This Reserve homes to approximately 76.5 % of the coralline areas of the Colombian Caribbean (Díaz et al., 2000).

At Seaflower, reef complexes are a series of isolated structures, aligned in NE direction along the southern flank of the Nicaragua Elevation (Díaz et al., 2000). These formations are the result of volcanic activity during the early Cenozoic, basement subsidence between the Cenozoic-Quaternary and the accumulation of reef limestone on shallow peaks (Díaz, 2005). The seasonal nature of the climate in the region governed by the migration of the intertropical convergence zone (Guzmán et al., 2014). The body of water that surrounds this zone has an average surface temperature of 29.3 °C and, up to 200 m, salinity is on average lower (36.4) than in deep waters (37.11) (Monroy-Silvera & Zambrano, 2017). In the Seaflower reef complexes, the direction and strength of the NE trade winds and the energy they move along the Caribbean translate into similar geomorphological and ecological structure between atolls (Díaz et al., 2000).

Bajo Nuevo is the northernmost reef complex of Seaflower and is part of the Colombia-Jamaica joint regime area (~225 km), an area of high fishery resource exploitation due to its proximity to Pedro Bank (~136 km) (Abril-Howard et al., 2012). This complex of 100 km^2, is made up of two elongated atolls, each with a barrier which is continuous to windward and truncated to leeward and separated from each other by a deep channel of ~90 m to (Díaz, 2005). From the Expeditions it was demonstrated that the ecological units present the traditional scheme of the Caribbean atolls, with a fore-reef terrace and a barrier to windward, followed by a lagoon terrace and a lagoon basin with anastomosed patch reefs. After the reef slope, depths up to 1 500 meters are reached (Díaz et al., 1996). Most of the seabed between 5 m and 20 m is calcareous pavement covered by an extensive layer of gravel and coarse sand, the result of erosion of dead coral. In the emerged area (< 20 m^2) there is a lighthouse and nearby are the ruins of a cargo ship.

Field work: Between November 24 and 30, 2021, during the "Seaflower Scientific Expedition: Bajo Nuevo Island Cay 2021", aboard the ARC Providencia, relative cover of reef-building organisms (stony corals and coralline algae) and their main competitors (macroalgae, sponges and soft corals), and the coral health were evaluated. Methods followed the recommendations of the Global Coral Reef Monitoring Network (GCRMN) since a combined view of these components allows the description of the current condition of the reef and understand the possible trajectories over time (International Coral Reef Initiative, 2016).

Sampling stations were selected using the work grids from the 2010 expeditions (Abril-Howard et al., 2012) and 2011 (Vega-Sequeda et al., 2015) (Table 1, Fig. 1). At each station, a band transect (10 x 2 m) was marked with a measuring tape, and photographs were done using the alternate photo-quadrat technique, using a Canon Powershot G7 digital camera, and a 50 x 50 cm, 1" PVC pipe reference frame. Ten (10) 0.25 m^2 quadrats of were evaluated, for a total of 2.5 m^2 per transect. (Gómez-Cubillos et al., 2019). Additionally, three videos were

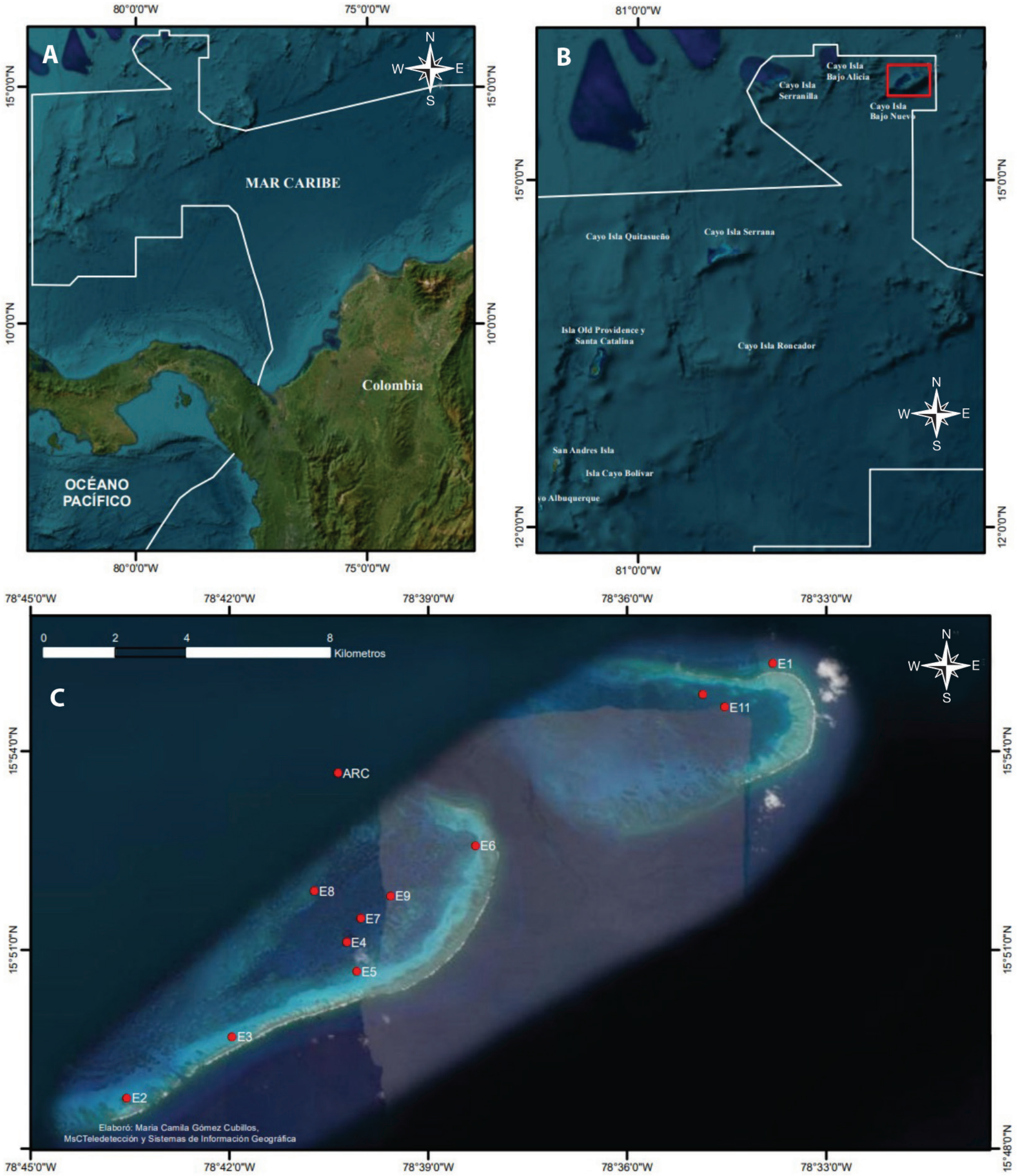


Fig. 1. Map of the study area: **A.** Location of the Seaflower Reserve, **B.** location of the Bajo Nuevo reef complex and **C.** location of the stations evaluated in Expedition 2021.

recorded along the transects (~3 min) at no more than 1 m above the bottom, with GoPro Hero 9 digital camera.

Twelve stations were evaluated in total (two on the windward fore-reef terrace, three on the lagoon terrace and seven on the lagoon). In 11 stations, transects were made with the photo quadrant technique (27.5 m^2), and for 12 stations were reviewed 2 hours of video (Table 1, Fig. 1).

Image processing: Photo quadrants were processed using ImageJ 1.52v (Schneider et al., 2012). Per quadrant, using at 100-point

Table 1
Location and general characteristics of the stations evaluated in Bajo Nuevo during Expedition 2021.

Station ID	Coordinates		Depth Level	Exposure Level	Geomorphological Unit
	Latitude	Longitude			
E1	15.922056	-78.563389	Medium	2	FT
E2	15.812750	-78.725889	Medium	1	LT
E3	15.828222	-78.699361	Shallow	1	LT
E4	15.851917	-78.670611	Medium	0	L
E5	15.844583	-78.668083	Shallow	1	LT
E6	15.876222	-78.638194	Medium	1	L
E7	15.857917	-78.667111	Deep	0	L
ARC	15.894500	-78.672750	Deep	2	FT
E8	15.864861	-78.678722	Medium	0	L
E9	15.863583	-78.659611	Medium	0	L
E10	15.914250	-78.581111	Medium	0	L
E11	15.911111	-78.575583	Medium	0	L

Abbreviations: Depth Level: Shallow > 7 m; Medium between 7 and 12 m; Deep > 12 m (Garzón-Ferreira et al., 2002). Exposure Level: 0 (none); 1 (low); 2 (moderate); 3 (high), with respect to swell and depth of the water column (Zea, 2001). Geomorphological Unit: FT (Windward fore-reef terrace); LT (Lagoon terrace); L (Lagoon with coral patches) (Díaz et al., 1996). Metadata can be downloaded at the Marine Biodiversity Information System site (SiBM for its initials in Spanish) (Gómez-Cubillos et al., 2023).

grid, the coverage (%) of the benthic categories described by Caribbean Coastal Marine Productivity (2001) and Garzón-Ferreira et al. (2002) was calculated. Then, with polygons and layers of the ROI Manager tool, by coral species, the cover (cm^2) of living tissue and skeleton with recent (1-3 days), transitional (4-14 days) and old (weeks to months) death, was estimated (Bruckner, 2020).

From photos and videos, coral richness (number of species) and abundance (number of colonies) and the presence of signs associated with diseases were estimated. Per video, ~10 frames were selected. By image (photograph and video frame), easily distinguishable colonies were counted by species. As a colony, any area of coral tissue growing independently and separately from other neighboring colonies was considered (Jackson et al., 1985). By colony, the presence of signs related to coral diseases was evaluated (Bruckner, 2020; Raymundo et al., 2008; Weil et al., 2019). The signs were selected taking as reference: a) changes in coral tissue coloration (darkening, paleness, bleaching), b) shape of the lesion (regular and irregular), and c) exclusivity with the host. The signs were tentatively assigned to one or more coral diseases reported in the Caribbean (Gil-Agudelo et al., 2009).

Data analysis: Data were processed using Microsoft Excel spreadsheets. Per station, richness was estimated as the number of species; abundance was estimated from the number of colonies; total and relative cover (%) was estimated from random points and polygons, and the prevalence of signs (%) by coral species and colonial type (# cases with sign$_i$ / # total colonies sp$_j$) (Weil & Rogers, 2011). Geomorphological unit, depth and level of exposure to swell were used as analysis factors (Díaz et al., 1996; Garzón-Ferreira et al., 2002; Zea, 2001). The results were classified, according to the life history types of coral species proposed by Darling et al. (2012) and Randazzo-Eisemann & Garza-Pérez (2022), as competitive, generalist, stress tolerant and weedy.

The representativeness of the sampling was calculated using the estimator proposed by Chao & Jost (2012), which is a measure of the completeness of the sample with respect to the size of the community. Diversity was calculated by Chao interpolation and extrapolation analysis, using Hill numbers in units of the effective number of species (Chao et al., 2014; Hill, 1973; Jost, 2006). The values of true diversity, ${}^{0}D$ (species richness), ${}^{1}D$ (common species) and ${}^{2}D$ (very abundant species), with their respective confidence intervals at 95 %, were calculated using the iNEXT package (Hsieh et al., 2022). Using data of presence-absence of species with the help of the BAT package (Cardoso et al., 2022), beta diversity (β) was calculated based on Jaccard dissimilarity. In this, total dissimilarity (β_{cc}) = replacement of species (β_{-3}) + differences in richness (B_{rich}), as proposed by Carvalho et al. (2013). These analyses were performed using the R software version 4.3.1 (R Development Core Team, 2017). The changes in composition and structure of the assembly between geomorphological units were analyzed with the technique of non-metric multidimensional scaling (nMDS) using as distance measure the binary Bray-Curtis similarity index (Primer-E V.6), with the cover data in % previously processed with the angular transformation (arc sine $\sqrt{(x / 100)}$).

To catalog the species according to their abundance (colonies), the proportion of individuals with respect to the total was calculated in each species, ordered from highest to lowest by the base 10 logarithm. Confidence limits at 95 % were obtained by resampling, using a Bootstrap with the boot package (Canty & Ripley, 2022); this analysis was carried out using the R program version 4.3.1 (R Development Core Team, 2017). In this way, the species that were found above the upper limit of that interval were cataloged as abundant, those found within the interval were cataloged as common, and those below the lower limit were cataloged as scarce (Cruz et al., 2017).

Expedition 2021 results were compared with those obtained in previous expeditions from 2010 (Abril-Howard et al., 2012) and 2011 (Vega-Sequeda et al., 2015). To explain trends observed in 2021 about the health status of the coral formations in Bajo Nuevo, the sea surface temperature (SST) was estimated from NOAA interactive maps (series: 2009-2021) (National Oceanic and Atmospheric Administration [NOAA], 2023).

RESULTS

In the windward fore-reef terrace (depth: 7 m), an environment very exposed to swell, the structural complexity was low, fleshy macroalgae (*Turbinaria* spp.) dominated, and the corals were small, scabby and scattered. In the lagoon terrace (depth: 5.6-7.2 m), where the swell has already dissipated at the barrier, patches of reefs with variable structural complexity were observed, consisting of *Orbicella* spp. and very old skeletons of *Acropora palmata*. Finally, in the reef lagoon (depth: 7.3-14 m), a relatively calm water habitat increased the structural complexity in the form of anastomosed patches of *Orbicella* spp. and giant standing skeletons of brain corals (*Colpophyllia natans, Diploria labyrinthiformis* and *Pseudodiploria strigosa*) and of *Siderastrea siderea*.

Richness of coral species: In November 2021, 32 species of hard corals were recorded, 30 of which were scleractinian and two hydrocorals (Fig. 2). The greatest richness was present in the reef lagoon with 32 species, seven of them exclusive to the lagoon. In contrast, on the windward fore-reef terrace, 20 species were observed (Fig. 2). In general, the lowest richness (17 spp.) was recorded at the stations most exposed to swell and increased as the degree of exposure decreased. All species were found at medium depth (7-12 m; 32 spp.), while in deeper (> 12 m; 25 spp.) and shallow (< 7 m; 20 spp.) waters the diversity decreased (Table 2).

The richness observed in Expedition 2021 (32 spp.) was lower than the records of 2010 (36 spp.) and 2011 (37 spp.) (Abril-Howard et al., 2012; Vega-Sequeda et al., 2015) (Fig. 2; Table 1). When comparing beta (β) diversity between Expeditions, a dissimilarity (β_{cc}) of 48.9 % was estimated with what was recorded for April 2010 by Abril-Howard et al. (2012). This value was mainly attributed to species

Table 2

Species of hard corals recorded in Bajo Nuevo during the 2010 (Abril-Howard et al., 2012), 2011 (Vega-Sequeda et al., 2015) and 2021 expeditions.

Species	Type	Total 2010	Total 2011	2021			
				Total	FT	LT	L
Acropora cervicornis	C	x	x^{+}	x^{+}			x^{*}
Acropora palmata	C	x	x^{+}	x^{++}	x	x	x
Agaricia agaricites	W	x	x^{++}	x^{+++}	x	x	x
Agaricia fragilis	W	x	x^{+}	x^{+++}	x	x	x
Agaricia grahamae	W			x^{+++}		x	x
Agaricia humilis	W			x^{++}	x	x	x
Agaricia lamarcki	W	x	x^{+}				
Agaricia tenuifolia	W		x^{+}	x^{++}		x	x
Cladocora arbuscula	NC			x^{+}			x
Colpophyllia natans	ST	x	x^{+}	x^{++}		x	x
Colpophyllia breviserialis	NC			x^{+}			x^{*}
Dendrogyra cylindrus	C	x	x^{+}				
Dichocoenia stokesii	ST	x	x^{+}				
Diploria labyrinthiformis	ST	x	x^{+}	x^{++}	x	x	x
Eusmilia fastigiata	NC	x	x^{+}				
Favia fragum	W	x	x^{+}	x^{++}	x	x	x
Helioseris cucullata	W	x	x^{+}	x^{++}	x	x	x
Isophyllia rigida	W	x	x^{+}	x^{+}		x	x
Isophyllia sinuosa	W	x	x^{+}				
Madracis decactis	W	x	x^{+}	x^{+++}	x	x	x
Madracis cf. *myriaster*	NC	x					
Manicina areolata	W	x	x^{+}	x^{+}			x^{*}
Meandrina meandrites	ST	x	x^{+}				
Millepora alcicornis	NC	x	x^{++}	x^{+++}	x	x	x
Millepora complanata	NC	x	x^{+}	x^{+}	x		x^{*}
Montastraea cavernosa	ST	x	x^{+}	x^{+}			x^{*}
Mycetophyllia aliciae	W		x^{+}	x^{+}			x^{*}
Mycetophyllia danaana	NC			x^{+}			x^{*}
Mussa angulosa	W	x					
Mycetophyllia ferox	W	x					
Mycetophyllia lamarckiana	W	x	x^{+}				
Orbicella annularis	ST	x	x^{++}	x^{+++}	x	x	x
Orbicella faveolata	G	x	x^{++}	x^{+++}	x	x	x
*Orbicella franks*i	G	x	x^{+}	x^{+++}		x	x
Porites astreoides	W	x	x^{++}	x^{+++}	x	x	x
Porites divaricata	W		x^{+}	x^{+++}	x	x	x
Porites porites	W		x^{++}	x^{+++}	x	x	x
Porites furcata	W	x					
Pseudodiploria clivosa	ST	x	x^{+}	x^{+}	x		x
Pseudodiploria strigosa	ST	x	x^{++}	x^{++}	x	x	x
Scolymia sp.	W		x^{+}				
Scolymia cubensis	W	x					
Siderastrea radians	W	x	x^{+}	x^{++}	x	x	x
Siderastrea siderea	ST	x	x^{++}	x^{+++}	x	x	x
Stephanocoenia intersepta	ST	x	x^{+}	x^{+}	x		x
Stylaster roseus	NC	x	x^{+}				
Tubastraea coccinea	NC		x^{+}				

Abbreviations: Type (according to life story): C = competitive, W = weed, ST = stress tolerant, G = generalist and NC = Not classified. FT = Windward fore-reef terrace; LT = Lagoon terrace and L = Lagoon with coral patches. x (presence); x^{*} (exclusive species); abundance: + (scarce), ++ (common), +++ (abundant) (Cruz et al., 2017).

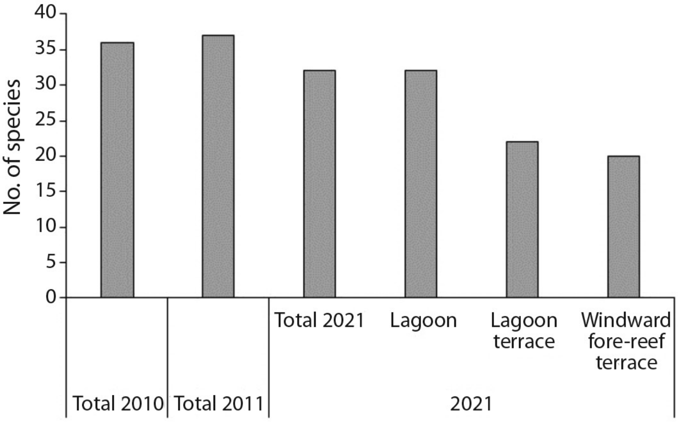


Fig. 2. Richness of hard corals recorded for the Bajo Nuevo reef complex during expeditions 2010 (Abril-Howard et al., 2012), 2011 (Vega-Sequeda et al., 2015) and 2021.

replacement (β_{-3}) (40 %) and to a lesser extent to the difference in richness (β_{rich}) between expeditions (8.9 %). When comparing with the records of Vega-Sequeda et al. (2015) of August 2011, the dissimilarity (β_{cc}) was lower (35.7 %) and was due to species replacement (β_{-3}) (23.8 %) (Table 1). This species replacement (β_{-3}) between the 2021 expedition and the previous ones, is evidenced in new records for Bajo Nuevo with species such as *Agaricia humilis*, *A. grahamae*, *Cladocora arbuscula, Mycetophyllia danaana* and *Colpophyllia breviserialis*, the latter being a new record for the San Andrés Archipelago. On the contrary, species recorded in 2010 and 2011 expeditions, such as *Agaricia lamarcki*, *Dendrogyra cylindrus*, *Dichocoenia stokesii*, *Eusmilia fastigiata*, *Isophyllia sinuosa*, *Meandrina meandrites*, *Mycetophyllia lamarckiana* and *Stylaster roseus* were not observed in 2021 (Table 2).

For Bajo Nuevo, the representativeness of the sampling reached 100 % in 2021, according to the Chao & Jost (2012) estimator. Using diversity analysis (iNEXT), a species richness of ${}^{0}D$ = 32 ± 3.44 (effective species ± I.C) was estimated. When considering all species with a weight proportional to their abundance, a diversity of ${}^{1}D$ = 9.8 ± 0.31 effective species was estimated, evidencing a low uniformity with species with a high number of colonies and other scarce species. Finally, by giving greater weight to dominant species, a diversity of ${}^{2}D$ = 5.6 ± 0.23 was estimated. Of 7 123 colonies counted, the most abundant species were *Orbicella annularis* (2 415 colonies), *Agaricia agaricites* (1 191), *Porites astreoides* (481), *Orbicella faveolata* (438) and *Porites porites* (356).

Benthic cover: In November 2021, the reefs in Bajo Nuevo were dominated by non-reef-building organisms (61.7 ± 0.10 %) ($\overline{X}$ ± 1 standard deviation - S.D.). The building species (corals, hydrocorals and calcareous algae) only accounted for 23.9 ± 0.10 %. The abiotic substrate (14.4 ± 0.09 %) was made up of soft bottoms of sand and debris (11.2 ± 0.10 %) and coral skeleton with recent and transitional death less than 15 days old (3.2 ± 0.03 %) (Fig. 3). The highest cover of reef-building organisms was found in the lagoon (29.1 %), habitat with medium depth and low exposure to swell. In general, non-reef-building communities dominated in all environments (Lagoon-L = 57.1 %; Lagoonal Terrace-LT = 65.8 %; Windward fore-reef terrace-FT = 82.3 %) as well as in the different depths and levels of exposure.

When excluding the abiotic substratum to recalculate the living cover, it was confirmed that fleshy macroalgae have been increasing in the last decade, becoming dominant in the

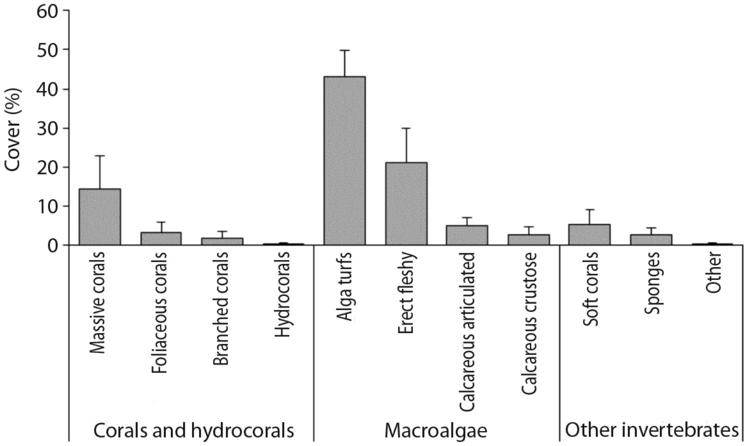


Fig. 3. Cover % (relative to total alive) of reef-building organisms and their main competitors (macroalgae and other sessile invertebrates) in the Bajo Nuevo reef complex, in November 2021. (Average $\overline{X}$ ± 1 S.D.).

community, as they increased from 27.3 ± 10.47 % in 2010 (Abril-Howard et al., 2012), to 37.8 % in 2011 (Vega-Sequeda et al., 2015) and to 72 ± 0.10 % in 2021. The high macroalgal cover recorded in 2021 is mainly attributed to turf algal growth (43.2 ± 0.07 %) (Fig. 3). Corals and hydrocorals contributed 19.8 ± 0.08 %, especially massive corals (14.5 ± 0.08 %) (Fig. 3). Hard coral cover in 2021 was higher than what was recorded in 2011 by Vega-Sequeda et al. (2015) (12.1 %), but lower than what was recorded in 2010 by Abril-Howard et al. (2012) (30.2 ± 19.1 %). The contribution of other invertebrates was 8.2 ± 0.04 %, mostly soft corals (5.3 ± 0.04 %) (Fig. 3, Table 3).

Macroalgae dominated in all stations; the highest covers were recorded in the windward terrace (88.4 %) and the lowest ones were recorded in the lagoon (65.5 %). Among geomorphological units, turf algal cover varied between 40.2 and 49.7 %. Erect fleshy algae (*Dictyota* spp. and *Turbinaria* spp.) dominated on the windward terrace (42.1 %) and crustose and articulated calcareous algae (*Halimeda* spp. and *Amphiroa* spp.) were more abundant in protected environments (Lagoon-L = between 3.4 and 5.6%) than in exposed environments (Windward fore-reef terrace-FT = between 0.7 and 0.9 %).

The highest covers of corals and hydrocorals were recorded in the lagoon (24.8 %) and the lowest ones were recorded in the windward terrace (6.9 %), differences attributed mainly to the contributions of massive corals (Lagoon-L = 19.9 %, Lagoonal Terrace-LT = 5.6 %, Windward fore-reef terrace-FT = 5.7 %). The foliaceous and branched corals presented the highest covers in the lagoon terrace (2.7-5.4%) and the lowest ones in the windward terrace (0-0.2 %). The highest hard coral cover recorded in the lagoon in 2021 coincides with what was reported by Abril-Howard et al. (2012); however, the records in 2010 are approximately three times higher (70 %) than what was evidenced in 2021 (Table 3). In addition, in 2021, in no transect hydrocorals exceed a 1 % cover.

The highest cover of other sessile invertebrates was recorded in the lagoon (9.7 %), followed by the lagoon terrace (5.7 %) and the windward terrace (4.7 %). This pattern is attributed to the contribution of soft corals in the lagoon (6.5 %) and in the lagoon terrace (4.3 %) and their absence in the windward terrace; habitat where sponges presented the highest cover (4.7 %).

In terms of coral cover, *O. annularis* was the most abundant species (7.1 ± 0.08 %), followed by *Agaricia* spp. complex (3.2 ± 0.03 %)

Table 3

Total and mean cover ± 1 S.D. (%) of coral species and other benthic categories recorded during the 2010 (Abril-Howard et al., 2012), 2011 (Vega-Sequeda et al., 2015) and 2021 expeditions.

Species / Category	2010	2011*	2021**
Total corals and hydrocorals	30.19 ± 19.11. Up to 70 in the lagoon	12.1	19.83 ± 0.08
Orbicella annularis		4.72 ± 2.97	7.08 ± 0.08
Agaricia spp.		1.67 ± 0.87	3.24 ± 0.03
Orbicella faveolata		3.45 ± 2.83	2.90 ± 0.03
Porites porites			1.00 ± 0.01
Orbicella franksi		1.16 ± 0.76	0.93 ± 0.02
Siderastrea siderea		2.04 ± 1.09	0.70 ± 0.01
Porites astreoides			0.58 ± 0.01
Madracis decactis			0.55 ± 0.01
Acropora palmata			0.43 ± 0.01
Pseudodiploria clivosa			0.42 ± 0.01
Diploria labyrinthiformis		0.65 ± 0.50	0.41 ± 0.01
Millepora spp.			0.32 ± 0.00
Porites divaricata			0.32 ± 0.01
Colpophyllia natans			0.30 ± 0.01
Siderastrea radians			0.28 ± 0.00
Pseudodiploria strigosa		1.02 ± 1.19	0.21 ± 0.01
Favia fragum			0.11 ± 0.00
Cladocora arbuscula			0.04 ± 0.00
Mycetophyllia aliciae			0.02 ± 0.00
Helioseris cucullata			0.01 ± 0.00
Meandrina meandrites		0.33	-
Eusmilia fastigiata		0.50	-
Macroalgae	27.35 ± 10.47	37.8	71.98 ± 0.10
Turfs			43.18 ± 0.07
Erect fleshy			21.02 ± 0.09
Calcareous articulated			5.10 ± 0.02
Crustose algae			2.67 ± 0.02
Other sessile invertebrates			8.19 ± 0.04
Gorgonaceans		13.5	5.26 ± 0.04
Sponges		6.7	2.70 ± 0.02
Other			0.22 ± 0.00
Soft bottoms		27.6	11.18 ± 0.10

* Average cover of coral species susceptible to SCTLD (Kramer et al., 2020), based on the results of the 2011 Expedition (Vega-Sequeda et al., 2015). / ** Cover relative to total alive in 2021, except for the Soft Bottoms category.

and *O. faveolata* (2.9 ± 0.03 %). The individual contributions of the other coral species (29 spp.) were less than 1 % (Table 3).

When comparing the coral cover between stations, stations E1 (FT) and E5 (LT) were the most extreme along axis 1 of the nMDS (Fig. 4), due to the presence of species that were recorded only in these stations, such as *Pseudodiploria clivosa* (4.7 %) in station E1 (total coral 6.9 %), and *A. palmata* (4.7 %) and *C. arbuscula* (0.4 %) in station E5 (total coral 15.7 %). In addition, in E5 *Favia fragum* had its highest cover (0.7 %). In the group comprising stations E2-E3 (Fig. 4), located on the lagoonal terrace, cover varied between 12.2 % and 13.6 %, with *Agaricia* spp. (E2 = 6.6 % and E3 = 8.6 %) being the largest

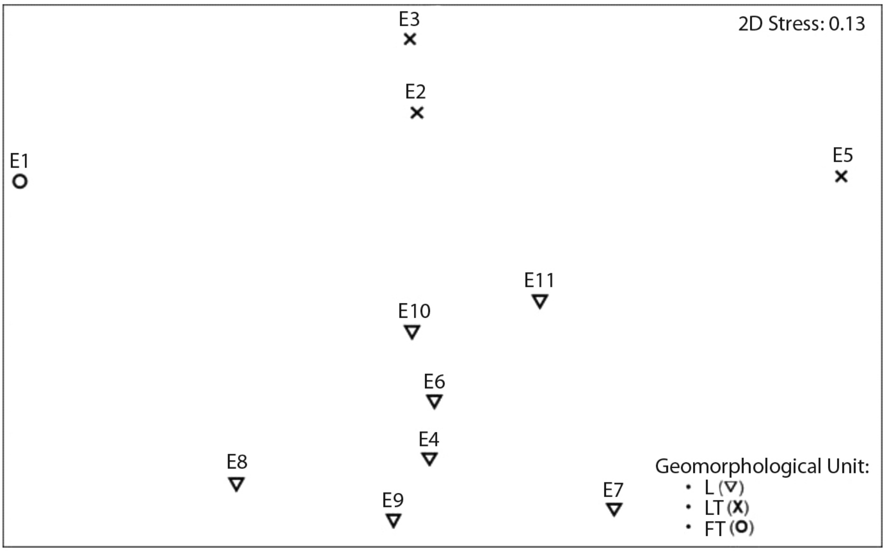


Fig. 4. Non-metric multidimensional scaling analysis (nMDS), based on a Bray-Curtis similarity matrix of hard coral cover, comparing among geomorphological units. Abbreviations: FT = Windward fore-reef terrace; LT = Lagoonal terrace and L = Lagoon with coral patches.

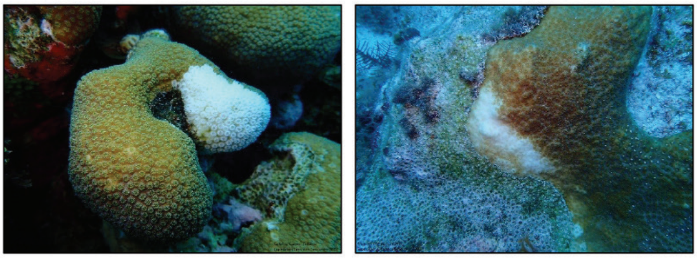
contributor. The highest cover occurred in the lagoon groups of stations, varying between 19 and 33.2 %, excepting in station E11 (11.6 %). In this habitat, *Agaricia* spp. had a lower cover (1.3 and 6.1 %) and *O. annularis* had a greater cover (0.7 and 25.4 %). The differences within the lagoon group were given by the species specific to each station [E7 = *Colpophyllia natans* (3.3 %) and *Mycetophyllia aliciae* (0.2 %), E10 = *Helioseris cucullata* (0.1 %), E11 = *Diploria labyrinthiformis* (4.5 %)] (Fig. 4).

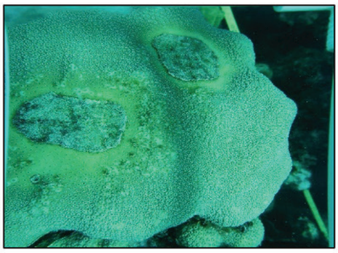
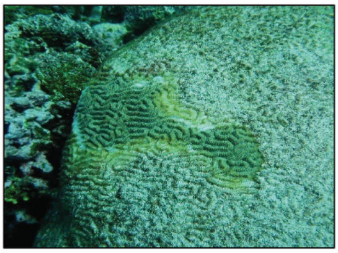
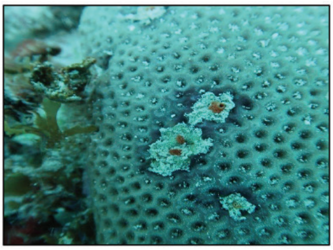
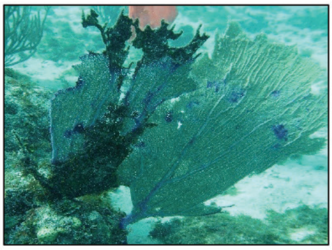
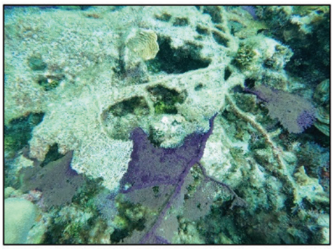
It is noteworthy that in November 2021, 45.4 ± 0.1 % of the benthic cover was ancient coral skeleton (Bruckner, 2020), covered by organisms with encrusting growth such as algal turf, gorgonaceans (*Erythropodium caribaeorum*), sponges (*Chondrilla caribensis*) and tunicates (*Trididemnum solidum*). The contribution of these organisms together in the different geomorphological units was very homogeneous, varying between 42.9 and 49.1 %. The greatest cover was found in shallow (49.1 %) stations, compared to mid-depth (45.3 %) and deep (39.9 %) stations. These results, together with the proportion of coral skeleton with recent and transitional death (3.2 ± 0.03 %), suggest that recent pulses of coral tissue loss have occurred in Bajo Nuevo, being more intense in shallow waters.

Coral health: In 2021, seven signs associated with six coral diseases and health conditions [White Band Disease (WBD); White Plague Disease (WPD); Yellow Band Disease (YBD); Dark Spots Disease (DSD); Aspergillosis (ASP) and bleaching] were identified (Gil-Agudelo et al., 2009). In addition, four of these signs can be associated with Stony Coral Tissue Loss Disease (SCTLD) (Table 4). The highest number of colonies with signs of disease was found in the lagoon (76.7 %), followed by the lagoon terrace (20.9 %) and the windward terrace (2.4 %).

The reported signs affected three genera, 13 species and 23.5 % (1 674) of the colonies evaluated (Table 4; Fig. 5). The massive meandroid forms (*Colpophyllia natans, Diploria labyrinthiformis* and *Pseudodiploria strigosa*) showed a 53.4 % sign prevalence of, followed by the plocoid forms (*Orbicella* spp. complex)

Table 4
Evaluated health signs, associated diseases and host coral species.

Sign	Description	Associated diseases	Host species
1	Polyps with loss of color. Dispersed or regular pattern.	SCTLD Bleaching	*O. annularis* *O. faveolata*
			
2	Bands and/or spots of exposed skeleton (white) in contact or not with necrotic tissue.	White Band Disease (WBD)	*A. cervicornis* *A. palmata*
			
3	Irregular patches of exposed skeleton. In contact or not with necrotic tissue and high production of mucus.	SCTLD Bleaching White Plague Disease (WPD)	*Agaricia spp.* *C. natans* *D. labyrinthiformis* *M. decactis* *Millepora spp.* *O. annularis* *O. faveolata* *P astreoides* *Porites spp.* *P. strigosa* *S. siderea*
			

Sign	Description	Associated diseases	Host species
4	Patches and rings of yellow color, in contact or not with necrotic tissue or exposed skeleton (white).	SCTLD Bleaching Yellow Band (Blotch) Disease (YBD) White Plague Disease (WPD)	*Agaricia spp.* *O. annularis* *O. faveolata* *O. franksi* *P astreoides* *P. strigosa*
	 		
5	Dark spots from black to violet, with irregular shape and size, can be depressed, low-lying with respect to healthy tissue. Inside it can have necrotic zones. High production of mucus.	SCTLD Bleaching Dark Spots Disease (DSD)	*Agaricia spp.* *C. natans* *D. labyrinthiformis* *O. faveolata* *S. siderea*
	 		
6	Dark spots from black to violet. Small with irregular shape.	Dark Spots Disease (DSD)	*S. siderea*
	 		
7	Violet spots of irregular size and shape. In contact or not with necrotic tissue.	Aspergillosis (ASP) Predation	*G. ventolina1* *G. flabellum*
	 		

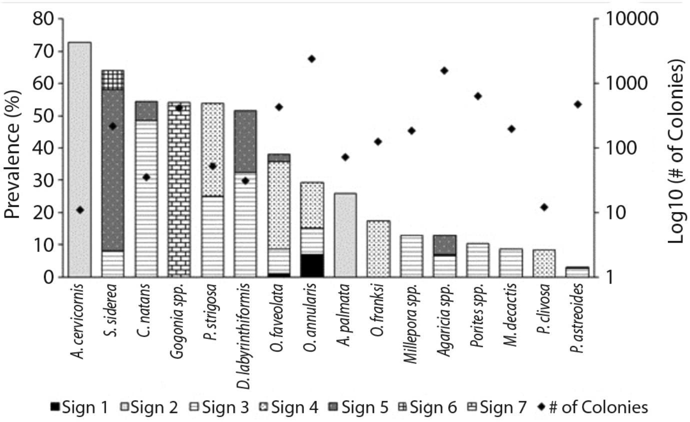


Fig. 5. Prevalence (%) total and by signs of deterioration and coral species for the Bajo Nuevo reef complex, in November 2021. For more details, see Table 2. The diamonds indicate the total number of colonies.

with 30 %. Of the total affected colonies, 84.9 % showed one of the four signs related to SCTLD. Among massive corals, *S. siderea* (63.9 %) showed the highest prevalence of unhealthy signs (Fig. 5).

Of the total cases, signs three and four, described for four diseases (Table 4), presented the highest occurrence (30.6 and 30 %, respectively). Then, sign seven, exclusive to the genus *Gorgonia*, represented 13.5 % of the cases, with a prevalence of 54.1 %. Sign five was present in 13 % of all the affected colonies, with a higher prevalence in *S. siderea* (49.8 %) and *D. labyrinthiformis* (19.4 %). Sign one represented 10.5 %, while sign two, exclusive to the genus *Acropora*, was present in 1.6 % of the affected colonies; but its prevalence in *Acropora cervicornis* was of 72.7 % and in *A. palmata* was of 26 %. Finally, sign six was present exclusively in *S. siderea* with a prevalence of 5.9 % (Fig. 5).

Sea surface temperature (SST): According to the NOAA interactive portal, in the South Atlantic region, where Bajo Nuevo is located, the annual cycle of the SST begins with the progressive warming of the waters at the end of June (28-29 °C), reaching the maximum values (31 °C) during the height of the rainy season (September-October) and decreasing to 27 °C between January and February. In the analyzed series (2009-2021), during the rainy seasons of 2010, 2015 and 2017, the maximum sustained SST was ~32 °C and in 2019 it recorded ~33 °C, values above the physiological optimum upper limit estimated for corals and zooxanthellae (> 31.5 °C) (Baumann et al., 2016; Fitt et al., 2000; Kleypas et al., 1999) (Fig. 6).

DISCUSSION

In 2021, coral richness was lower than that recorded in previous expeditions (Abril-Howard et al., 2012; Vega-Sequeda et al., 2015). Between expeditions, species replacement presented greater importance in terms of beta diversity (β); process that generates a homogenization in the types of life history and a tendency to favor species considered weeds, which opportunistically colonize recently disturbed habitats (Randazzo-Eisemann & Garza-Pérez, 2022). Darling et al. (2013) suggest that thermal bleaching and other anthropogenic stressors overfishing may drive changes in the composition of reef communities. Moreover, during these transitions, surviving corals have stress-tolerant, and these changes in community structure affect reef ecosystem functions and services essential to human well-being (Randazzo-Eisemann & Garza-Pérez, 2022).

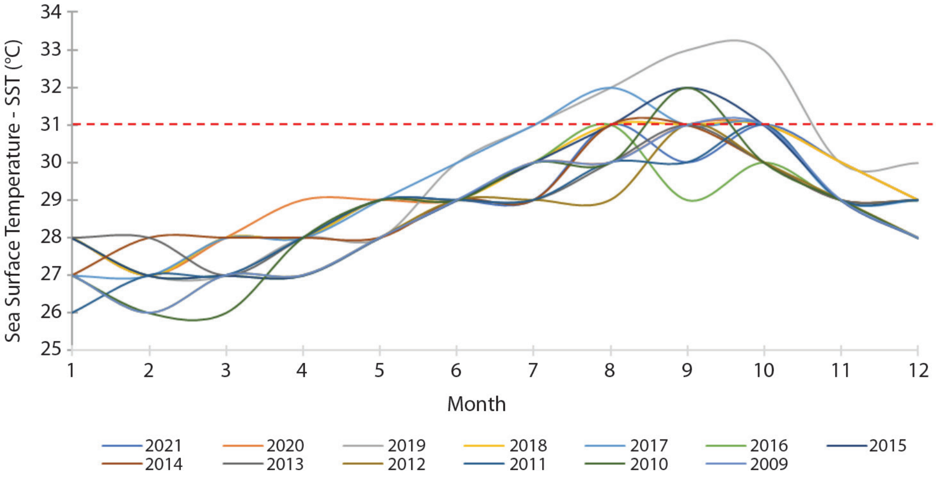


Fig. 6. Average values of Sea Surface Temperature – SST (°C) in the South Atlantic region, between 2009-2021 (NOAA, 2023). Red line marks limits of physiological stress for corals and zooxanthellae.

In the last decade, in Bajo Nuevo, the low cover and abundance of competitive species such as Acropora spp. and the absence of *D. cylindrus* during 2021, in part, may be related to large-scale disturbances that caused a significant reduction of Acroporidae populations in the Caribbean since the late 1980s, and the documented low recovery rates for the Caribbean (García-Ureña et al., 2020; Gardner et al., 2003; Souter et al., 2021). Furthermore, several authors agree that competitive species only dominate in "ideal" environments, so that a decrease in their cover and in the structural complexity of the reef is to be expected with the increase of these disturbances, due to its high sensitivity to breakage and dislodgment during storms, low tolerance of stress and high mortality after bleaching from thermal anomalies and epizooties (WBD and serratiosis) (Baumann et al., 2016; Darling et al., 2012; Madin, 2005; McClanahan et al., 2007).

Conversely, in the last decade, the areas with the greatest coral development in Bajo Nuevo have been dominated by the Orbicella spp. complex, both in cover and abundance. This is because O. annularis is more tolerant to stress, has higher fecundity, episodic spawning events and large corallites. These characteristics allow it to store energy and resist sustained recruitment failure for decades, increasing its long-term survival in stressful environments (Hughes & Tanner, 2000; van Woesik et al., 2012). In addition, O. faveolata and O. franksi are generalist and more competitive species (Baumann et al., 2016; Darling et al., 2012). However, a high prevalence of unhealthy signs (30 %) in 2021 suggests that these species have been affected by bleaching and other diseases, causing pulses of massive loss of tissue, as has been recorded in other Caribbean reefs (Álvarez-Filip et al., 2011); events that may recur as temperature stress increases (Buglass et al., 2016; Gardner et al., 2003; Greenstein et al., 1998).

Despite differences in coral richness and cover between expeditions, probably influenced by the methodologies used in each of them, the results indicate that the reefs of Bajo Nuevo are experiencing a change from the dominance of corals to the dominance of macroalgae, mainly of algal turfs, a trajectory already described for other Caribbean reefs (Souter et al., 2021).

Coral diseases are one of the main causes of degradation in reefs and the estimation of their prevalence is an approximation to recognize the potential degradation of a reef area (Gil-Agudelo et al., 2009). Although diseases are a natural process, they are problematic when outbreaks negatively affect populations, leading them to vulnerable or near-extinction states (Raymundo et al., 2008). In this regard, the Caribbean is considered a hot spot of epizooties, due to the high number of pathologies, high virulence rates and number of species affected (~75 %) (Raymundo et al., 2005). Likewise, the islands of San Andrés and Providencia, in Seaflower, are classified as a center of high prevalence of diseases, especially WBD and DSD (Navas-Camacho et al., 2010), although there is no clarity of the factors that contribute to it (Weil et al., 2002). However, in 2021 there were no signs associated with Black Band Disease, considered one of the infectious diseases that has most influenced the deterioration of many reefs worldwide (Ainsworth et al., 2007).

In 2021, 3.2 % of the Bajo Nuevo hard benthos was coral skeleton with recent and transitional death less than 15 days old. In addition, 23.5 % of the colonies showed signs associated with bleaching and epizooties. According to Lirman et al. (2014), values > 2 % of recent mortality reflect significantly stressful conditions. So, the high prevalence of signs un unhealthy, the number of affected species and the proportion of recently dead coral skeleton, show that this reef complex was going through a pulse of mortality caused by outbreak of mixed epizooties, with similar signs but different etiologies. Besides, the evaluated signs suggest the presence of at least six different epizooties, including SCTLD. This disease represents an important threat to the Caribbean reefs due to its wide geographic range, extended duration, high mortality rates (weeks to months) and the large number of coral species affected (Reefresilience, 2023).

Mixed epizooties outbreaks have already been previously documented in coral reef, as well as their significant relationship with thermal anomalies (Bruno et al., 2007). It is recognized that host density (coral cover) acts as a threshold in the incidence of these outbreaks (Bruno et al., 2007) and that horizontal transfer due to the proximity between healthy and unhealthy colonies, together with the presence of vectors (fish and invertebrates) determines the severity of each outbreak (Jones et al., 2004; Kuta & Richardson, 2002). different studies have shown that anomalies in SST linked to the climate change increases the occurrence of coral diseases (Jaap, 2000; Patterson et al., 2002), because induce bleaching episodes and outbreaks of YBD, DSD and ASP (Gil-Agudelo et al., 2009), which can be more aggressive in reefs with high coral cover (e.g. Bajo Nuevo in 2010). These findings indicate that, in Bajo Nuevo, a probable cause of this mixed outbreak in 2021 is the thermal stress generated by anomalies in SST, which increase stress in corals and favor the proliferation of certain groups of pathogens associated with these diseases (Bruno et al., 2007; Francini-Filho et al., 2010; Kuta & Richardson, 2002).

Another important finding was the proportion of standing ancient skeletons of giant colonies of *S. siderea* and meandroid corals (*C. natans*, *D. labyrinthiformis* and *P. strigosa*), without evidence of physical or mechanical damage. Although storms have drastic effects on the composition, stability, and structure of communities, and Seaflower is located within the Caribbean hurricane belt (Díaz et al., 2000), in 2021 there was no evidence of recent coral damage caused by storms. These skeletons, with varying degrees of erosion, were occupied by communities with irregular shapes and encrusting growth such as algal turf, gorgonaceans, sponges and tunicates. In 2021 this portion of the benthos accounted for approximately half of the monitored benthic cover. These indicate that Bajo Nuevo has experienced different pulses of coral death in the last decade. In addition, the historical decrease in the cover of meandroid corals and the absence of other species such as *Eusmilia fastigiata* and *Meandrina meandrites*, which were previously abundant (2010-2011), are evidence of the occurrence of different mortality pulses and that some of them could be related to SCTLD, because this disease is lethal for these species (advance rate of 3-4 cm/day; Weil et al., 2019).

Climatic and oceanographic conditions modify a wide variety of ecological processes and thermal anomalies influence the severity and dynamics of epizooties (Bruno et al., 2007). Experimental studies have shown that thermal stress significantly affects the photosynthetic efficiency, growth and survival of corals, although the specific responses depend on the species and age of the coral (Kuanui et al., 2015), thus positioning itself as a critical factor in the structuring of reef communities (Baumann et al., 2016). Therefore, the anomalies in the SST between 2009 and 2021 partly explain the causes of coral deterioration (mixed epizooties) and the consequences of these changes on the structure of reef communities in Bajo Nuevo (replacement of coral species and changes towards the dominance of fleshy macroalgae, particularly alga turf).

With this study, it is concluded that the hypothesis that remote ocean reefs experience less deterioration due to their remoteness from direct human disturbances, is ruled out for Bajo Nuevo. Taking as reference the results of previous expeditions (2010-2011), this reef complex registered in 2021 an evident drop in the cover of hard corals and calcareous algae; a decrease in coral richness and increase in the cover of non-reef-building organisms (macroalgae) and high prevalence of signs unhealth associated with different coral diseases. This condition may be a response of the communities to large-scale pressures, such as anomalies in sea surface temperature (SST). The results on the current status of Bajo Nuevo confirm that these reefs are endangered (EN), as suggested in the red list of marine and coastal ecosystems of Colombia (Uribe et al., 2020).

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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