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RESEARCH ARTICLE

Status of the coral community in three reef complexes of the Seaflower Biosphere Reserve, Colombian Caribbean

Estado de la comunidad coralina en tres complejos arrecifales de la Reserva de la Biosfera Seaflower, Caribe colombiano

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ABSTRACT

Despite the contemporary trends of generalized coral loss, it is presumed, in part from lack of information, that remote oceanic coral reefs must be in a better condition than continental ones, assuming that from their geographic remoteness, direct human pressures have a lower effect. This work was aimed at determining if the coral community of three oceanic atolls of the Seaflower Biosphere Reserve (Alburquerque, Bolívar and Bajo Nuevo) in the southwestern Caribbean, Colombia, have also experienced changes towards new benthic configurations. To estimate benthic cover, coral richness and prevalence of signs associated with diseases, photo quadrat transects were evaluated. To study algal turfs in interaction with live coral tissue, cores were extracted. Only in Bolívar, herbivores were quantified through stationary censuses. Forty-eight coral species were found in these reef complexes, but the benthic cover was dominated by non-reef-building organisms (59.1 - 61.7 %), especially algal turfs. Nine signs associated with seven coral diseases were identified. In the algal turf - coral interactions, 15 groups of turf morpho functional groups were identified. Twenty herbivore species of 5 functional groups were recorded, showing a low functional redundancy in comparison to continental Colombian Caribbean reefs, and thus a high vulnerability to species loss. These results show that the current state of the studied reefs, despite being remote, show changes in dominance from corals to macroalgae, especially turf algae.

KEYWORDS: Coral community, functional groups, algal turfs, herbivores, coral decline, Seaflower

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RESUMEN

A pesar de las tendencias contemporáneas de pérdida coralina generalizada, se presume, en parte por falta de información, que los arrecifes oceánicos remotos deben estar en mejor estado que los arrecifes continentales, asumiendo que por su lejanía geográfica hay un menor efecto de presiones humanas directas. Este trabajo tuvo como objetivo determinar si la comunidad coralina de tres atolones oceánicos de la Reserva de Biósfera Seaflower (Alburquerque, Bolívar y Bajo Nuevo) en el Caribe Suroccidental, Colombia, están experimentando cambios hacia nuevas configuraciones bentónicas. Para estimar la cobertura bentónica, riqueza coralina y prevalencia de signos asociados con enfermedades se evaluaron transectos con fotocuadrantes. Para estudiar los céspedes algales en interacción con tejido coralino vivo se extrajeron núcleos. Solo en Bolívar se incluyó el estudio de herbívoros mediante censos estacionarios. Se encontraron 48 especies de corales duros en estos complejos arrecifales, pero la cobertura bentónica estuvo dominada por organismos no constructores de arrecifes (59.1-61.7 %), especialmente céspedes algales. Se identificaron nueve signos asociados con siete enfermedades coralinas. En los bordes de interacción coral-césped se identificaron 15 grupos morfofuncionales de céspedes. Se registraron 20 especies herbívoras afines a 5 grupos funcionales, mostrando baja redundancia funcional respecto a arrecifes continentales del Caribe colombiano, y por lo tanto una alta vulnerabilidad ante la pérdida de especies. Estos resultados muestran que el estado actual de los arrecifes estudiados, a pesar de ser lugares remotos, exhiben cambios del dominio de corales hacia macroalgas, especialmente de céspedes.

PALABRAS CLAVES: *comunidad coralina, grupos funcionales, céspedes, herbívoros, deterioro coralino, Seaflower.*

INTRODUCTION

Coral reefs are strategic ecosystems for the well-being of human societies. However, the current climate change scenario, the high rates of degradation documented in recent decades, and their uncertain resilience capacity to respond to disturbances derived from natural and anthropogenic hazards, make them highly sensitive and high-risk ecosystems (Jackson, Donovan, Cramer, & Lam, 2014; Bindoff *et al.*, 2019).

The Sixth Report on the State of the World's Corals demonstrated through meta-analyses that ~14% of global coral cover was lost between 2009 and 2018 (Souter, Serge, Wicquart, Logan, Obura, & Staub, 2021). Specifically in the Caribbean, the average coral cover loss between 1983 and 2019 was close to 2.1% (a calculation after the large coral loss that occurred in the early 80s), thus favoring the proliferation of macroalgae (> 50%) (Souter, Planes, Wicquart, Logan, Obura, & Staub, 2022), especially turf-like algae, which are currently the dominant cover on several reefs (Harris, 2015). This report points out that these changes are the product of the synergy between disturbances that operate at different scales, such as outbreaks of white-banded epizootics (1970-1980) and the loss of hard coral tissue (SCTLD, documented from 2014 to date); the mass mortality of key species such as the herbivorous sea urchin *Diadema antillarum* (1983-1984 and 2022); overfishing; extreme events such as hurricanes and mass bleaching (1998, 2003, 2005, 2006, 2023), and all those human activities linked to unplanned coastal development (Souter *et al.,* 2021).

Despite these trends of coral loss and deterioration, there are still gaps in up-to-date information on the state of ocean reefs, assuming that their geographical remoteness and difficulty for human settlement keep them exempt from the effect of direct human pressures (Brainard *et al.,* 2005). Therefore, these remote reefs are natural laboratories for investigating the effects of global and regional disturbances on the relationships between coral communities and their environment (Perry *et al.,* 2015; Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015).

The Seaflower Biosphere Reserve (RB) (12°-16°N and 78°-82°W) is home to 76.5% of the coral areas of the Colombian Caribbean (Díaz *et al.,* 2000). However, due to their large area (180,000 km^2), most research efforts have focused on the islands of San Andres and Old Providence (Taylor, Howard, & Baine, 2011). For this reason, since 2014, the Colombian Ocean Commission (CCO) has carried out ten scientific expeditions to generate knowledge about the RB Seaflower and demonstrate its relevance to humanity (https:// pnec.cco.gov.co/seaflower/) on a scientific basis.

Within this research platform, the Colombian Marine Fauna: Biodiversity and Uses research group, of the Institute of Studies in Marine Sciences (CECIMAR) of the Universidad Nacional de Colombia – Sede Caribe, participated in three expeditions (Alburquerque: 2018; Bajo Nuevo: 2021, and Bolívar: 2022) with the project 'Coral-algal turf interaction and its effect on reef communities in the Seaflower Biosphere Reserve'. This was made in order to collect information that allows us to advance in the understanding of the mechanisms that drive changes in reefs and their consequences, to take a glimpse into how current reef communities experience changes towards new benthic configurations that drive the proliferation of non-reef-building organisms, as well as to identify the role of coral-turf interactions in these trajectories.

STUDY AREA

The Seaflower Biosphere Reserve, declared by the United Nations Educational, Scientific and Cultural Organization (UNESCO) in 2000, has high rates of diversity and endemism of species (Acero and Garzón-Ferreira, 1994), and in 2005 the Ministry of Environment, Housing and Territorial Development of Colombia recognized it as a marine protected area (MPA) (Coralina, 2011). Seaflower is the largest MPA in the Caribbean and the second largest in Latin America (Guarderas, Hacker, & Lubchenco*,* 2008). It is made up of seven atolls (Alburquerque or Southwest, Bolívar or Courtown, Quitasueño, Serrana, Roncador, Serranilla and Bajo Nuevo), two inhabited islands (San Andres and Old Providence and Ketlina) and one shallow reef (Alice Shoal) (Córdoba and López, 1997).

At Seaflower, reef complexes are a series of isolated structures, aligned in a NE direction along the southern flank of Nicaragua's elevation (Díaz *et al.,* 2000). They are the result of volcanic activity during the early Cenozoic geological period, basement subsidence between the Cenozoic-Quaternary periods, and the accumulation of reef limestone on shallow tops (Díaz, 2005).

Throughout the year, the migration from the intertropical convergence zone (ICZ) determines the seasonal nature of the region's climate, which is relatively dry and follows the typical seasonality of the Western Caribbean; with a dry season with winds from the NE between December and March; a transitional season between April and August, and a rainy season from September to November (Guzmán, Ruiz & Cadena*,* 2014; Lonin, Andrade, & Monroy*,* 2022). Tides are mixed with a strong diurnal component, with intervals between 0.3 m and 0.6 m (Geister and Díaz, 2007), and storms occur mainly during the second half of the year due to Seaflower being within the Caribbean hurricane belt (Díaz, Díaz-Pulido, Garzón-Ferreira, Geister, Sánchez, & Zea, 1996).

Alburquerque or Southwest Cays (12°10'N, 81°51'W) is the only atoll with a circular contour (8 km E-W, 6 km N-S and area of 63.8 km^2), is located ~37 km SE of San Andres Island and has two densely vegetated cays (North Cay and South Cay), separated from each other by a shallow channel (IGAC, 1986; Díaz 2005) (Figure 1). The Bolívar Atoll or Courtown Cays (12°24'N and 81° 28'W) are located ~30 km SE of San Andres Island, is kidney-shaped and has four cays (La Virgen, Bolívar, Pescadores and Norte) with variable shape and size over time (Díaz, 2005) (Figure 1). On the other hand, Bajo Nuevo Bank or Petrel Islands (15°53′N and 78°38'W) is located ~475 km northeast of San Andres Island, is the northernmost reef complex of Seaflower and is part of the Colombia-Jamaica common regime zone (~225 km) (CCO, 2015). It is made up of two elongated atolls, with a continuous barrier to windward and truncated to leeward, and separated from each other by a deep channel of ~90 m (Figure 1).

In general, in these atolls, the direction and strength of the NE trade winds, and the energy of the waves that move along the Caribbean translate into geomorphological similarity and ecological structure, following a gradient from windward to leeward (Díaz *et al.,* 2000; Geister & Díaz, 2007). In Alburquerque, Bolívar and Bajo Nuevo, the ecological units present the traditional scheme of the Caribbean atolls (Díaz *et al.,* 1996), made up of a fore reef terrace and peripheral reef continuous to windward, followed by a lagoonal terrace and a lagoon basin with patches of anastomosed or reticulated reefs, surrounded to leeward by a terrace with patches of poorly developed reefs, which end in a reef slope that can reach depths of up to 1,500 m (Dainco, 1980). In the inner part of the leeward fore reef terrace of some atolls there are reef lines that reach the surface in sections, forming an incomplete leeward peripheral reef (Díaz *et al*., 1996).

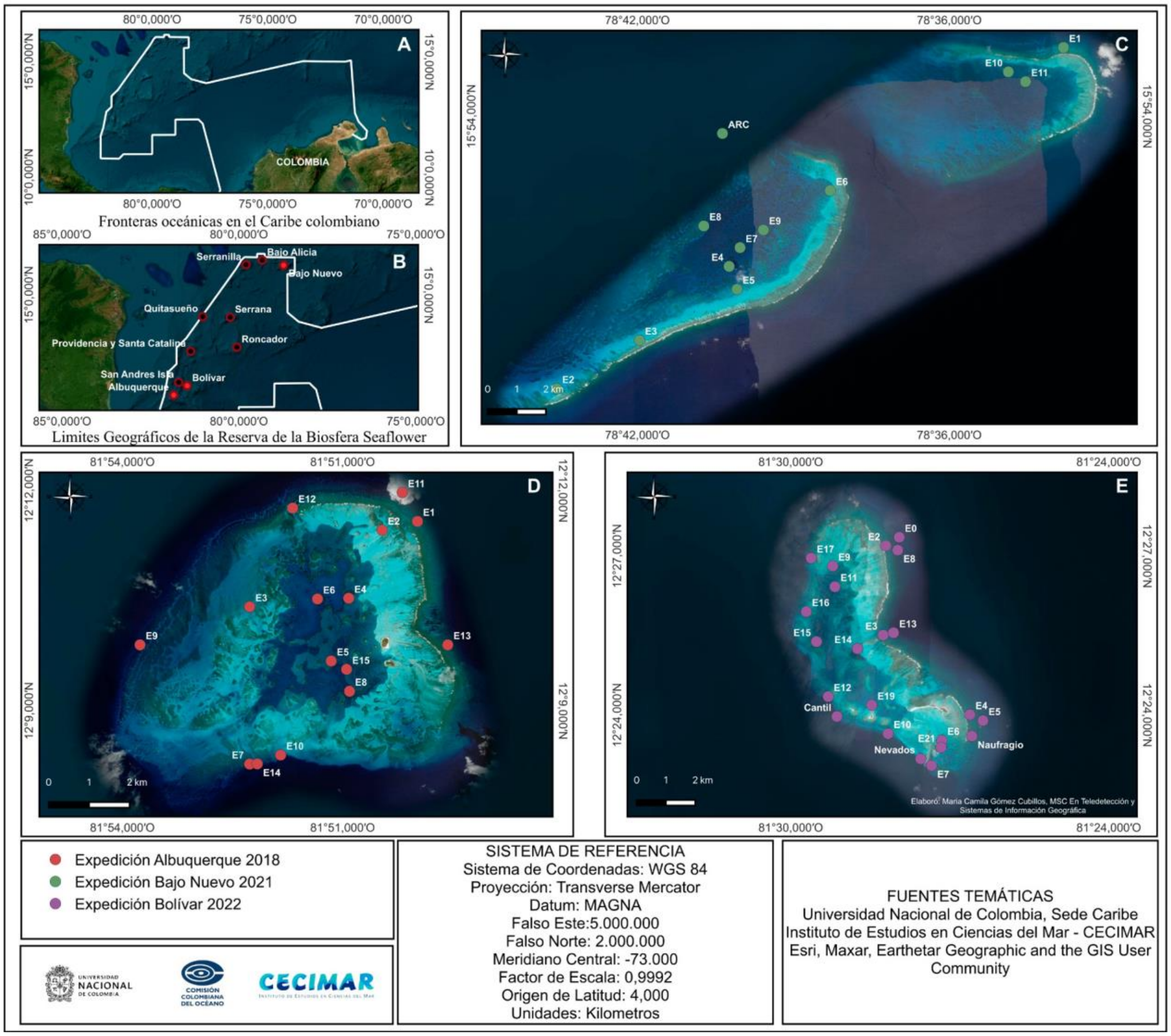

Figure 1. Study Area (A and B) and sampling stations in the atolls of Alburquerque (D), Bolívar (E) and Bajo Nuevo (C), RB Seaflower.

METHODOLOGY

To describe the current condition of a reef and infer its possible trajectories over time, the Global Coral Reef Monitoring Network (GCRMN) proposes for the Caribbean to assess the relative coverage of reef-building organisms (stony corals and coralline algae) and their main competitors (macroalgae, sponges and soft corals), coral health and abundance of key taxa of reef fish and other macroinvertebrates (with emphasis on herbivores) (ICRI, 2016).

With the Seaflower scientific expeditions, progress was made in the standardization of methodologies in the field, in accordance with the GCRMN initiative, which are easy to implement in remote reefs. Between expeditions, methods were adjusted according to logistical and environmental capacities, thus allowing the improvement of initial techniques (2018) and the integration of new methodological components (2021 and 2022) (Gómez-Cubillos, Daza-Guerra, Márquez, & Zea, 2023).

Field information was collected by scuba diving *in* the reef complexes of Alburquerque (September 25 to October 2, 2018), Bajo Nuevo (November 24 to 30, 2021) and Bolívar (September 22 to 30, 2022). The selection of the sampling stations in Alburquerque and Bolívar was based on the stations of the project 'Bioecological and environmental evaluation of reef areas of the Colombian Caribbean 1994-1996' (Díaz *et al.,* 1996), and in Bajo Nuevo the work meshes of the 2010 expeditions (Abril-Howard, Orozco-Toro, Bolaños-Cubillos and Bent-Hooker, 2012) and 2011 (Vega-Sequeda, Díaz-Sánchez, Gómez-Campo, López-Londoño, Díaz-Ruiz, & Gómez-López*,* 2015).

Benthic cover, coral richness and coral health

In each station, guided by a tape measure lying on the bottom, a belt transect (10 x 2 m) was evaluated, using the photoquadrat technique each meter, alternating them on either side of the tape measure. With a Canon Powershot G7 digital camera with an adapted waterproof box, mounted on a frame of PVC pipes, photographs of the substrate were taken in 10 quadrats (0.25 cm2) for a total of 2.5 m2 per transect (Gómez-Cubillos, Gómez-Cubillos, Sanjuan-Muñoz, & Zea, 2019) (Figure 2a).

The photographs were processed with ImageJ 1.52v. By quadrat, from a mesh of 100 random points, the coverage (%) of the benthic categories described by Caricomp (2001) and Garzón-Ferreira, Reyes-Nivia, and Rodríguez-Ramírez (2002) was calculated. By photograph, coral richness and the presence of signs associated with coral diseases were estimated (Raymundo, Couch, & Harvell, 2008; Weil & Rogers, 2011; Weil *et al.,* 2019; Bruckner, 2020). These signs were selected taking as a reference: a) changes in the coloration of the coral tissue (darkening, paleness, bleaching), b) shape of the lesion (regular and irregular) and c) exclusivity with the host (Gómez-Cubillos *et al.,* in press). Signs were assigned to one or more coral diseases reported in the Caribbean (Gil-Agudelo *et al.,* 2009).

The data were processed in Microsoft Excel. By reef complex, the following were estimated: *i)* coral richness as the number of species per sampling site, *ii)* by transect (combining the 10 photoquadrats), total and relative coverage (%) from random points, *iii)* prevalence of signs (%) by coral species (# cases with sign_i / # total sp_j colonies) (Weil & Rogers*,* 2011).

Algal turf assemblages in interaction with living coral tissue

Following the methodological recommendations of Gómez-Cubillos, Gavio and Zea *(*2020); Gómez-Cubillos, Daza-Guerra, Márquez and Zea, 2023), between 1 and 2 morphologically contrasting massive coral colonies were selected per station, according to their type of colonial organization (meandroid, plocoid, cerioid), which had active interaction edges with algal turfs. Photographs of the colony and macros of the interaction edges of interest were taken. On the selected interaction, containing live coral and turf, a coral skeleton core was extracted using a hammer and impact corer of 27 mm in diameter (5.7 cm^2). The samples were fixed separately in 96% alcohol. (Figure 2b).

In the laboratory, each core was wet checked, using a Zeiss-Discovery-V8 stereoscope (1.0 - 4.0 X) and an Epson Perfection-V850Pro scanner. The structure of the algal assemblages in interaction with coral tissue was evaluated in terms of composition, relative coverage per taxa (%), canopy height (mm), and filament density (Gómez-Cubillos *et al.,* 2020). With a Zeiss-AX10 optical microscope, with a DCM510-CMOS digital camera, scale photographs of the algae taxa were taken, using the ScopePhoto 3.1 program. Taxonomic identification was carried out at the genus level, using specialized keys and expert consultation.

Based on the structure of the assemblages and the identified genera, groupings were made into empirical categories or "morphofunctional" groups, defined based on taxonomic affinities (phylum) and on the morphological bases of thallus structure, growth form, and branching pattern (Balata, Piazzi, & Rindi, 2011).

Diversity and functional redundancy of herbivores

This component was only developed during the Bolívar 2022 expedition. Using the stationary census method (Bohnsack and Bannerot, 1986) at three points per station fish and herbivorous macroinvertebrates were recorded. This method consists of observing organisms within a cylinder of 7 m radius

($79\ m^2$) for 5 minutes. With a GoPro Hero 9 camera, the species/genus richness and abundance of herbivorous fish belonging to the families Acanthuridae (surgeons), Labridae-Scarinae (parrots), Ephippidae (catalinas) and Kyphosidae (poplars) were recorded. For mobile macroinvertebrates, specimens of urchins (Echinoidea) and crustaceans *Maguimithrax* spp. were searched, with a total length greater than 1 cm (Francis, Filbee-Dexter, Yan, & Côté*,* 2019; Bortone, Samoilys, & Francour*,* 2000; Spadaro & Butler, 2021; Williams, 2021) (Figure 2c).

The organisms surveyed were categorized into functional groups according to their way of interacting with the substrate when consuming algae in: a) macroalgae browsers; b) cutters; (c) bioeroding grazers, (d) scraper grazers, and (e) sediment suckers (Bellwood and Choat, 1990; Bellwood, Hoey, & Choat, 2003; Bellwood, Hughes, Folke, & Nyström*,* 2004; Johansson, Van de Leemput, Depczynski, Hoey, & Bellwood, 2013; Tebbett, Siqueira, & Bellwood, 2022). It is clarified that the same family can have more than one functional group, as is the case of Labridae and Acanthuridae. The degree of functional redundancy was determined from the richness of genera and species, and the reserve capacity was carried out following the recommendations of Johansson *et al.* (2013).

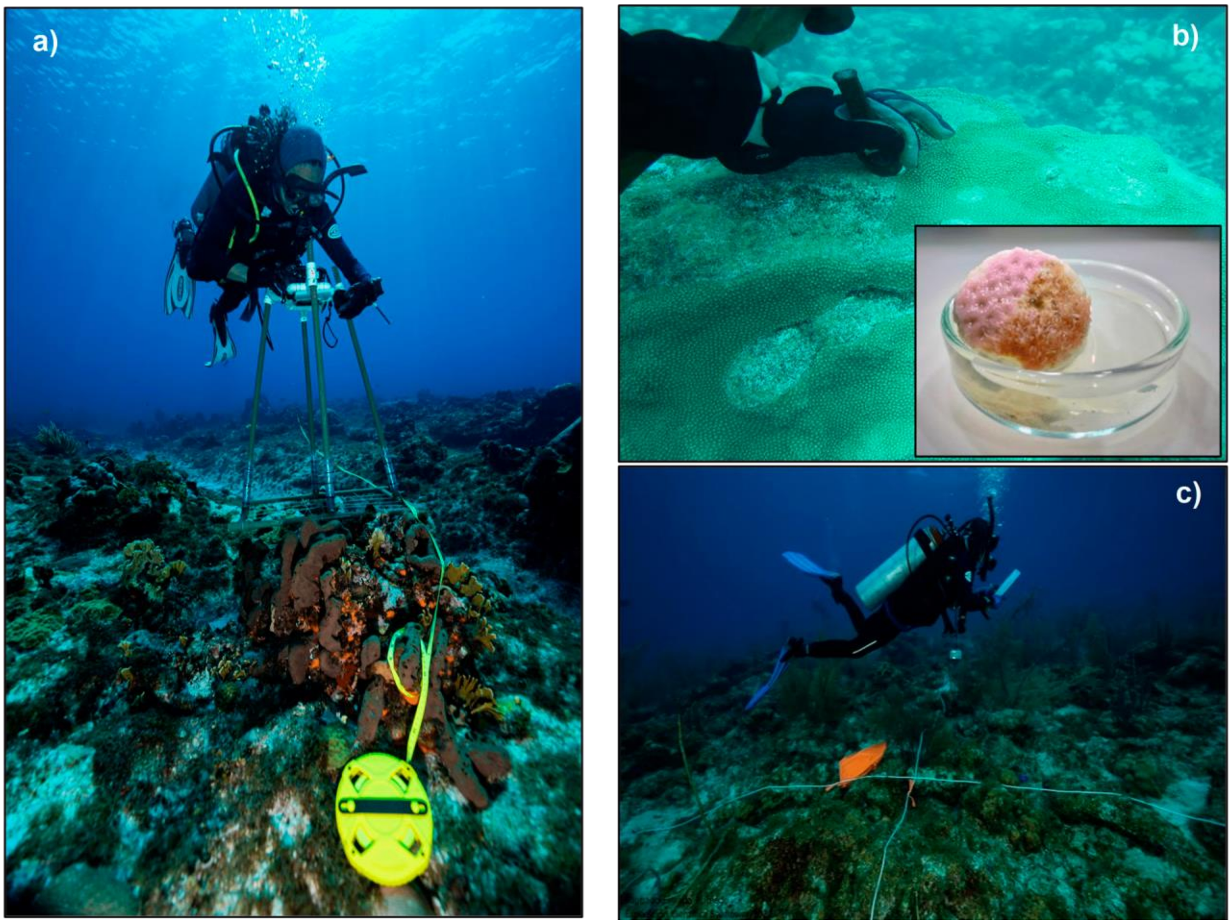

Figure 2. a) Transect with alternating photoquadrats, **b)** core extraction with coral-turf and macro interactions from the excreted core; **c)** census of fish and herbivorous macroinvertebrates. (Photos a and c: Santiago Estrada; b: Catalina Gómez-Cubillos and Helena Benavides-Marchena).

RESULTS AND DISCUSSION

In the three expeditions, 49 stations were evaluated: 15 in Alburquerque, 22 in Bolívar and 12 in Bajo Nuevo (). Of the total number of stations, 17 were located in the lagoon basin, 12 on the leeward terrace and outer slope, 8 on the windward fore reef terrace, 7 on the lagoonal terrace and 5 on the windward peripheral reef. With 53% of the stations, medium-depth reefs (between 7 m and 12 m) were evaluated, with 24% for deepest reefs (between 12 m and 19 m) and with the remaining 22% for shallow reefs (between 2 m and 7 m). Of the total number of stations evaluated, 32 were environments with little or no exposure to the prevailing waves (excluding storms) and the other 17 were environments with a moderate to high level of exposure, according to the classification proposed by Zea (2001) (Table 1).

Table 1. Location and general characteristics of the stations evaluated in Alburquerque (2018), Bajo Nuevo (2021) and Bolívar (2022).

Station ID	Coordinates		Level of Depth	Exposure Level	Geomorphological unit
	Latitude	Longitude			
Alburquerque Expedition 2018					
E1	12,193000	-81,83300	Middle	3	TP
E2	12,191000	-81,84100	Shallow	2	TL
E3	12,173608	-81,87111	Shallow	1	TS
E4	12,175550	-81,84861	Middle	0	Lg
E5	12,161299	-81,85259	Middle	0	Lg
E6	12,175377	-81,85570	Deep	0	Lg
E7	12,137910	-81,87111	Deep	2	TS
E8	12,154440	-81,84844	Middle	0	Lg
E9	12,164968	-81,89600	Deep	1	TS
E10	12,139963	-81,86407	Deep	0	TS
E11	12,199530	-81,83643	Deep	3	TP
E12	12,196010	-81,86132	Middle	3	B
E13	12,164968	-81,82613	Middle	3	B
E14	12,137949	-81,86936	Deep	1	TS
E15	12,15941	81,84909	Shallow	3	Lg
Bajo Nuevo Expedition 2021					
E1	15,922056	-78,563389	Middle	2	TP
E2	15,812750	-78,725889	Middle	1	TL
E3	15,828222	-78,699361	Shallow	1	TL
E4	15,851917	-78,670611	Middle	0	Lg
E5	15,844583	-78,668083	Shallow	1	TL
E6	15,876222	-78,638194	Middle	1	Lg
E7	15,857917	-78,667111	Deep	0	Lg
ARC	15,894500	-78,672750	Deep	2	TP
E8	15,864861	-78,678722	Middle	0	Lg

Station ID	Coordinates		Level of Depth	Exposure Level	Geomorphological unit
	Latitude	Longitude			
E9	15,863583	-78,659611	Middle	0	Lg
E10	15,914250	-78,581111	Middle	0	Lg
E11	15,911111	-78,575583	Middle	0	Lg
Bolivar Expedition 2022					
E0	12,431806	-81,4855	Middle	0	Lg
E2	12,45325	-81,470111	Shallow	3	TP
E3	12,425139	-81,470972	Middle	3	B
E4	12,400139	-81,443667	Shallow	3	B
E5	12,39825	-81,439556	Deep	2	TP
E6	12,392028	-81,4525	Shallow	1	TL
E7	12,384139	-81,455694	Shallow	2	TS
E8	12,451861	-81,466361	Middle	2	TP
E9	12,446861	-81,486806	Middle	0	Lg
E10	12,394139	-81,469389	Middle	0	TS
E11	12,440361	-81,486111	Middle	0	Lg
E12	12,405806	-81,488222	Middle	1	TS
E13	12,425861	-81,467694	Deep	2	TP
E14	12,420889	-81,479028	Shallow	1	TL
E15	12,423083	-81,491917	Deep	0	Lg
E16	12,432528	-81,495111	Middle	1	TS
E17	12,449361	-81,493583	Middle	1	TS
E19	12,403111	-81,474528	Middle	0	Lg
E21	12,389806	-81,452694	Shallow	1	TL
Nevados	12,38625	-81,459139	Middle	0	TS
Naufragio	12,393389	-81,442972	Middle	3	B
Cantil	12,399556	-81,485472	Deep	0	TS

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 (scarce); 2 (moderate); 3 (strong), with respect to the waves and the depth of the water column (Zea, 2001). Geomorphological unit: TP (fore reef or windward terrace); B (windward peripheral reef); TL (lagoonal terrace); Lg (lagoon with coral patches) and TS (leeward terrace and outer slope) (Díaz *et al.*, 1996). Metadata can be downloaded at: Alburquerque (https://doi.org/10.15472/b3hg97); Bajo Nuevo (https://doi.org/10.15472/2ke98s); Bolívar (https://doi.org/10.15472/0skaoj)

Benthic cover

In Alburquerque, Bajo Nuevo and Bolívar, the benthos was dominated by non-reef-building organisms (fleshy macroalgae, soft corals and poriferans) (between 59.1 ± 11.3 and 61.7 ± 10.2 % - mean ± D.E., values calculated from the sampling units, this is, one transect per station, separately for each atoll); while the reef-building species (scleractinian corals, hydrocorals and coralline algae) ranged from 23.9 ± 10.4 to 26.7 ± 15.2 %. On the other hand, the abiotic substrate represented between 11.7 ± 11.6 and 15 ± 11.1 % of the substrate (Figure 3).

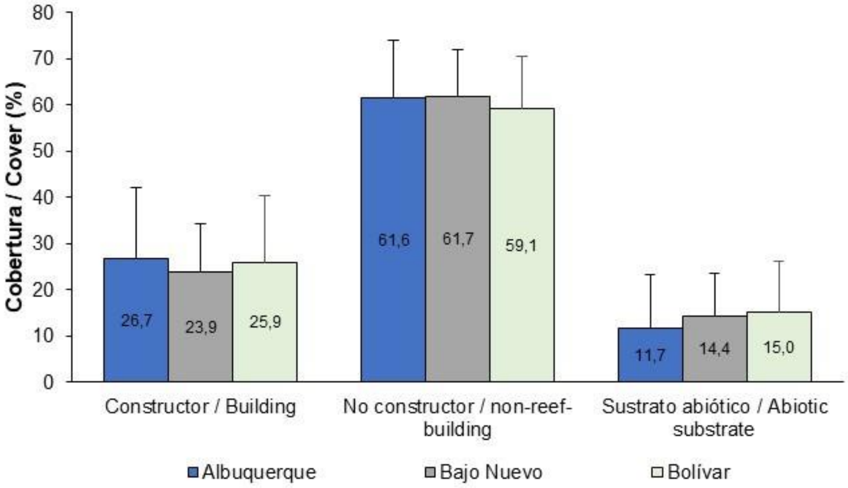

Figure 3. Overall cover (%) of the main benthic components in the Alburquerque, Bolívar and Bajo Nuevo reef complexes (Mean ± D.E.).

By excluding the abiotic substrate to recalculate the living cover, it was confirmed that macroalgae dominated in the three reef complexes (between 69.3 ± 15.8 and 72 ± 10.7 %), particularly algal turfs, with percent covers between 43.2 ± 7.1 and 44.7 ± 12.7 %. Scleractinous and hydrocoral corals (between 19.8 ± 12.4 and 21.2 ± 12.5 %) were mainly represented by massive colonies (between 14.2 ± 10.9 and 14.7 ± 9.3 %); while hydrocorals contributed less than 2%. The other benthic organisms (soft corals, sponges and others) registered the lowest coverage (between 8.2 ± 4.2 and 9.5 ± 7 %); but, in Alburquerque and Bajo Nuevo, gorgonaceans were the most representative communities (between 7.7 ± 6.4 % and 5.3 ± 4.2 %, respectively), while in Bolívar the greatest contribution was sponges (5.4 ± 6.9 %) (Figure 4).

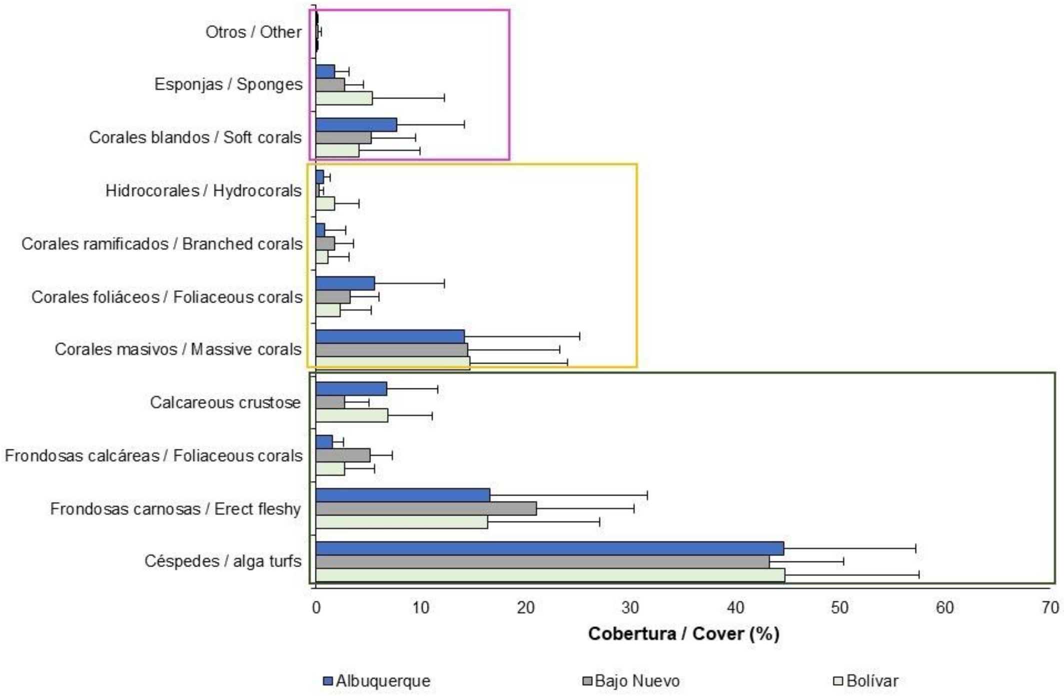

Figure 4. Cover % (relative to total living) of reef-building organisms (yellow box) and their main competitors macroalgae and other sessile organisms (green box and fuchsia, respectively) in the reef complexes of Alburquerque, Bolívar and Bajo Nuevo (Mean ± 1 D.E., of the stations of each complex).

The dominance of algal turfs suggests that these reefs are experiencing a shift from coral dominance to macroalgae, a trajectory already described for other Caribbean reefs (Souter *et al.*, 2021). These changes towards the dominance of macroalgae are preceded by a loss of resilience, as a result of the increase in the frequency and intensity of anthropogenic disturbances, including the overfishing of herbivores, leaving the ecosystem vulnerable to new disturbances (Mumby *et al.,* 2006; Nyström, Folke, & Moberg, 2000). The dominance of macroalgae is maintained due to feedback mechanisms; for example, an initial disturbance (*e.g.* outbreaks of epizootics) generates coral mortality, leaving substrate available for the colonization of macroalgae (turf algae in this case); but these algae will increase their cover if the abundance of herbivores is low or if they proliferate at a sufficient speed to exceed the grazing capacity of herbivores (Williams, Polunin & Hendrick, 2001). In sum, these loops affect coral recruitment, reduce coral growth rate, and can lead to additional mortality in colonies (Tanner, 1995; Kuffner, Walters, Becerro, Paul, Ritson-Williams, & Beach, 2006; Smith *et al*., 2006; Box & Mumby, 2007; Norström, Nyström, Lokrantz, & Folke, 2009).

Diversity of coral species

In the three atolls, the presence of 48 species of hard corals, 45 species of scleractinean corals and 3 species of hydrocorals (Table 2). The greatest richness was found in Bolívar (43 spp.), followed by Alburquerque (34 spp.) and Bajo Nuevo (32 spp.).

The variation in coral species richness between reef complexes reflects a complex interaction between biotic and abiotic factors (Guzmán and Cortés, 1993). Greater diversity may be a response to more favorable environmental conditions, such as high availability of suitable substrates for coral settlement and better water quality (López-Londoño *et al.,* 2023). In addition, the particular geomorphological characteristics of each complex can lead to a wide variety of microhabitats that promote species diversification (Díaz *et al.,* 1996). Conversely, overfishing, especially of herbivores, can limit the system's ability to maintain coral richness (Roberts, 1995), which together with outbreaks of epizootics can alter community structure (Márquez and Díaz, 2005). The effect of tropical storms and hurricanes must also be recognized, which model diversity differentially between atolls, depending on the intensity and proximity of the event. For example, in 1988 Hurricane Joan's path was about ~50 km from the southern cays (Vega-Sequeda *et al.,* 2015), and in 2020 hurricanes Iota and Eta hit hardest the northern area of the RB Seaflower.

Of the 48 coral species observed, two are new records for the RB Seaflower (*Colpophyllia breviserialis* and *Porites colonensis*) and for 13 species their range is extended to the northern and southern cays (*Agaricia fragilis*, *A. grahamae*, *A. humilis*, *A. tenuifolia*, *Cladocora arbuscula*, *Dendrogyra cylindrus*, *Isophyllia sinuosa*, *Madracis formosa*, *Meandrina jacksoni*, *Mycetophyllia danaana*, *Porites divaricata, Siderastrea radians* and *Solenastrea bournoni*) (Table 2). These findings suggest that the position of these reef complexes, in terms of ocean circulation, promotes connectivity between populations, expanding the ranges of distribution and diversity of species (Lopera-García, 2020). However, it is important to recognize that the sampling methods and technologies used during the Seaflower expeditions allowed the data to be collected systematically and, therefore, to estimate coral richness more accurately.

Table 2. Species of hard corals recorded in scientific expeditions Alburquerque (2018), Bajo Nuevo (2021) and Bolívar (2022).

Species	Category and criteria IUCN	Reef complex		
		Alburquerque	Bajo Nuevo	Bolívar
Acropora cervicornis	CR ↓ (A2bce)	X	X	X
Acropora palmata	CR ↓ (A2bce)	X	X	X
Agaricia agaricites	VU ↓ (A3c)	X	X	X
Agaricia fragilis	LC ¿?	X†	X	X†
Agaricia grahamae	NT ↓ (A2bce)	X†	X†	
Agaricia humilis	CR ↓ (A3c)	X†	X†	X†

Species	Category and criteria IUCN	Reef complex		
		Alburquerque	Bajo Nuevo	Bolívar
Agaricia lamarcki	CR ↓ (A3c)			X
Agaricia tenuifolia	CR ↓ (A3c)		X	X†
Agaricia undata	LC ¿?			X
Cladocora arbuscula	LC ¿?		X†	
Colpophyllia natans	VU ↓ (A3c)	X	X	X
Colpophyllia breviserialis	CR ↓ (A3c)		X†	
Dendrogyra cylindrus	CR ↓ (A2bce)	X		X†
Dichocoenia stokesii	VU ↓ (A3c)	X		X
Diploria labyrinthiformis	CR ↓ (A3c)	X	X	X
Eusmilia fastigiata	CR ↓ (A3c)	X		X
Favia fragum	LC ¿?	X	X	X
Helioseris cucullata	CR ↓ (A3c)	X	X	X
Isophyllia sinuosa	LC ¿?			X†
Isophyllia rigida	LC ¿?	X	X	X
Madracis decactis	CR ↓ (A3c)	X	X	X
Madracis formosa	NT ↓ (A2bce)	X†		X†
Manicina areolata	LC ¿?	X	X	
Meandrina jacksoni	CR ↓ (A3c)			X†
Meandrina meandrites	CR ↓ (A3c)	X		X
Millepora alcicornis	VU ↓ (A3c)	X	X	X
Millepora complanata	CR ↓ (A3c)	X	X	X
Montastraea cavernosa	LC ¿?	X	X	X
Mussa angulosa	NT ↓ (A2bce)			X
Mycetophyllia aliciae	LC ¿?		X	
Mycetophyllia danaana	CR ↓ (A3c)		X†	X†
Mycetophyllia ferox	CR ↓ (A3c)			X
Mycetophyllia lamarckiana	LC ¿?	X		X
Orbicella annularis	EN ↓ (A2bce)	X	X	X
Orbicella faveolata	EN ↓ (A2bce)	X	X	X
Orbicella franksi	NT ↓ (A2bce)	X	X	X
Porites astreoides	LC ¿?	X	X	X
Porites colonensis	VU ↓ (B2ab iii)	X†		X†
Porites divaricata	LC ¿?	X	X	X†
Porites porites	LC ¿?	X	X	X
Pseudodiploria clivosa	NT ↓ (A2bce)	X	X	X
Pseudodiploria strigosa	CR ↓ (A3c)	X	X	X
Scolymia spp.	CR ↓ (A3c)			X
Siderastrea radians	LC ¿?	X	X	X†
Siderastrea siderea	CR ↓ (A3c)	X	X	X
Solenastrea bournoni	LC →			X†
Stephanocoenia intersepta	NT ↓ (A2bce)	X	X	X
Stylaster roseus	Not evaluated			X

Abbreviations: X (presence); X† (new record for the reef complex). IUCN categories: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT); least concern (LC), decreasing population trend (↓), unknown (?), stable (→).

Coral health

In the three reef complexes, nine signs associated with seven coral diseases were identified [White Band Disease (WBD); White Plague Disease (WPD); Yellow Band Disease (YBD); Dark Spots Disease (DSD); Black Band Disease (BBD); Aspergillosis (ASP) and bleaching] (Gil-Agudelo *et al.,* 2009). In addition, four of these signs are associated with Stony Coral Tissue Loss Disease (SCTLD). Of the total number of colonies evaluated (17 379), the signs found affected 4 genera, 14 species and 11.4 % of the colonies. The highest prevalence of signs was recorded in Bajo Nuevo (23.5 %), followed by Alburquerque (3.3 %) and Bolívar (1.8 %). The sign associated with BBD was only recorded in the southern cays, while neighborhoods affected by signs associated with SCTLD accounted for 63 % in Bolívar and 84.9 % in Bajo Nuevo.

Diseases have been an important source of coral mortality in recent decades on Colombian reefs (Garzón-Ferreira, Gil-Agudelo, Barrios, & Zea*,* 2001). The results of the expeditions confirm that coral deterioration linked to mixed epizootics is differential between reef complexes, and that the reefs of Bajo Nuevo are the most deteriorated, despite the fact that in the 1990s they were classified as the best preserved in the Colombian Caribbean (Bruckner, 2012).

Algal turf assemblages in interaction with living coral tissue

At the edges of interaction between living coral tissue and turf algae, 15 morphofunctional groups were identified, 14 of them present in the samples collected in Alburquerque, 10 in Bajo Nuevo and 9 in Bolívar (Table 3). These assemblages were made up of 50 morphotypes, belonging to 33 genera, 12 orders and 23 families. Assemblages with morphologies based on thin non-calcareous filaments, with erect and/or prostrate thalluses were the most recurrent in the interaction edges evaluated. By contrast, turfs with vesicular shapes and calcareous thalli were unique to Alburquerque.

In Bolívar and Bajo Nuevo, the assemblages were dominated by groups of prostrate uniseriate and multiserial algae, corticated, of smaller size and laminar with forked thalli, which together form short, dense mats with tangled thalli. In contrast, in Alburquerque the assemblages were, for the most part, of smaller and larger corticated algae, and complex non-filamentous functional groups, such as non-calcareous crusty algae, foliar and vesicular. These differences may be a response to the combination of local environmental factors such as the availability of nutrients, light, grazing, among others (López, Rodríguez, & Silva*,* 2004). However, the presence of less morphologically complex algae also suggests primary processes of colonization of the new available substrate, assuming that the disturbance linked to the loss of tissue and exposure of the coral skeleton, possibly epizootics, was operating recently, as observed in the reefs of Bajo Nuevo (Gómez-Cubillos *et al.,* in press). These findings suggest that the structural complexity of turf algae interacting with living coral tissue provides clues about the chronology of disturbance.

Table 3. Proposal of morphofunctional groups of algal grasses that interact with remaining living coral tissue in reefs of the Seaflower BR.

Growth form	Morphofunctional group	Description	Genus	Edge	Reef complex		
					Alburquerque	Bajo Nuevo	Bolívar
Filamentous	Cianobacteria	Filaments generally epiphytic, with a thallus less than 1 mm, intertwined or attached to the host. Organized in clusters like bouquets.	*Lyngbya* spp. Oscillatoriaceae *Spirocoleus* spp	Cyanobacteriota	X	X	X
Filamentous	Uniseriate prostrate	Filaments in corticated, uniserial, branched or no. With or without rhizoids. Without stolons.	*Cladophora* spp. *Chaetomorpha* spp. *Ectocarpus* spp. *Hincksia* spp.	Chlorophyta	X	X	X
		Filaments in corticated, uniserial, branched. Prostrate thallus, without rhizoids, with or without thick stolons.		Ochrophyta	X	X	
Filamentous	Uniserials and multiserials erect _	Non-cortical filaments, thin (up to 2 µm wide), with one or more series of cells. Thallus erect with or without stolons, with or without rhizoids.	*Aglaothamnion spp.* *Bostrychia spp.* *Ceramium spp.* *Centroceras spp* *Heterosiphonia spp.*	Rhodophyta	X	X	X
Filamentous	Smaller multi-series	Multi-seriate uncorticated filaments, less than 2 µm wide. Unbranched and rhizoid-containing stolons.	*Sphacelaria* spp.	Ochrophyta	X		
Filamentous	Pluriseriate Prostrate	Fine filaments (up to 2 mm wide) not cortified, with an extensive prostrate system from which erect shafts emerge, branched or not. With or without rhizoids or stolons.	*Herposiphonia* spp.	Rhodophyta	X	X	X
			Polisiphonia spp		X	X	X
Filamentous	Cortical Hollow Stalk	Erect thalluses, formed by hollow tubes of few layers, branched or not, with or without rhizoids or stolons.	*Champia* spp. *Griffithsia* spp.	Rhodophyta	X	X	
Filamentous	Cortical smaller size	Filaments erect, cortical, branched, with thin axes (up to 2 µm wide). No stolons, no rhizoids.	*Chondria* spp. *Dasya* spp.	Rhodophyta	X	X	X

Growth form	Morphofunctional group	Description	Genus	Edge	Reef complex		
					Alburquerque	Bajo Nuevo	Bolívar
Filamentous	Cortical larger size	Filaments erect, corticate, branched, with thick (more than 2 μm wide) and polysiphonic axes. With one or more apical cells. With rhizoids, without stolons.	*Gellidiela* spp. *Gellidium* spp. *Gelidiopsis* spp. *Hypnea* spp. *Pterocladiella* spp.	Rhodophyta	X	X	X
Vesicular	Siphonic with vesicular thallus	Single-celled vesicles with a rounded or elongated shape.	*Valonia* spp.	Chlorophyta	X		
Vesicular	Siphonic with hollow vesicular thallus	Stem hollow, erect, Uniseriate, without branches or stolons. Rounded vesicles.	*Enteromorpha* spp.	Chlorophyta	X		
Crustose	Crustose Non-chalky	Flattened cortical thalluses adhered to the substrate, but not strictly adherent. With or without branches. No stolons or rhizoids.	*Peyssonnelia* spp.	Rhodophyta	X		
Foliate	Foliaceous with cenocytic filaments	Cortical thalluses, with variable growth, forming sheets of one to a few layers of thick polychotomous cells of interlaced cenocytic filaments. With rhizoids.	*Anadyomene* spp.	Chlorophyta	X		
Foliate	Laminar with forked thallus	Laminar thallus, flattened, with dichotomous bifurcations, branched with rounded and bilobed apices. With rhizoids.	*Dictyota* spp.	Ochrophyta	X	X	X
Foliate	Laminar corticated	Flat, erect laminar thallus, with cortical area with 2 to 3 rows of cells.	*Cryptonemia* spp.	Rhodophyta		X	
Articulate	Coral articulated smaller size	CaCO3-impregnated cell walls, dichotomous ramifications with articulated regions, and connections between adjacent filaments.	*Amphiroa* spp.	Rhodophyta	X	X	X

Richness and abundance of herbivores

In Bolívar, 20 herbivorous species were recorded with a total abundance of 3,171 individuals. This diversity was represented by 14 species of fish belonging to 3 families (Acanthuridae = 3 spp.; Labridae = 9 spp. and Kyphosidae = 2 spp.), 4 species of sea urchins (*Diadema antillarum*, *Echinometra lucunter*, *Echinometra viridis*, *Eucidaris tribuloides*) and 2 species of crustaceans (*Percnon gibbesi* and *Maguimithrax spinosissimus*) (Table 4).

The average richness was 15.8 ± 2.8 species, with the lagoon terrace (19 spp.) and the pre-reef terrace (18 spp.) being the most diverse environments. The highest total average abundance was recorded in the lagoon and in the lagoonal terrace (85.05 ± 78.3 and 40.3 ± 88.6 individuals, respectively). The most representative family in number of species was Labridae (parrots and wrasses) with 9 species and with the greatest abundance in the lagoon and the leeward terrace. In the other environments, the most abundant family was Acanthuridae (surgeonfishes), with 1 367 individuals. The abundances for this family in descending order were the blue surgeon *Acanthurus coeruleus* (832 individuals), the brown surgeon *Acanthurus tractus* (471) and the striped parrot *Scarus iseri* (380) (Figure 5).

In general, several studies from the Caribbean confirm that the Acanthuridae and Labridae are the most abundant families in reef fish assemblages. This is because surgeons are very abundant given their high biomass, herbivorous diet, food availability, and ability to form aggregations of massive schools for feeding (Bellwood *et al.,* 2003). Parrotfish, on the other hand, have been described as generalist habitat species, capable of persisting in a wide range of environmental conditions and conspicuous in reef environments (Cheal, Emslie, Miller, y Sweatman*,* 2012).

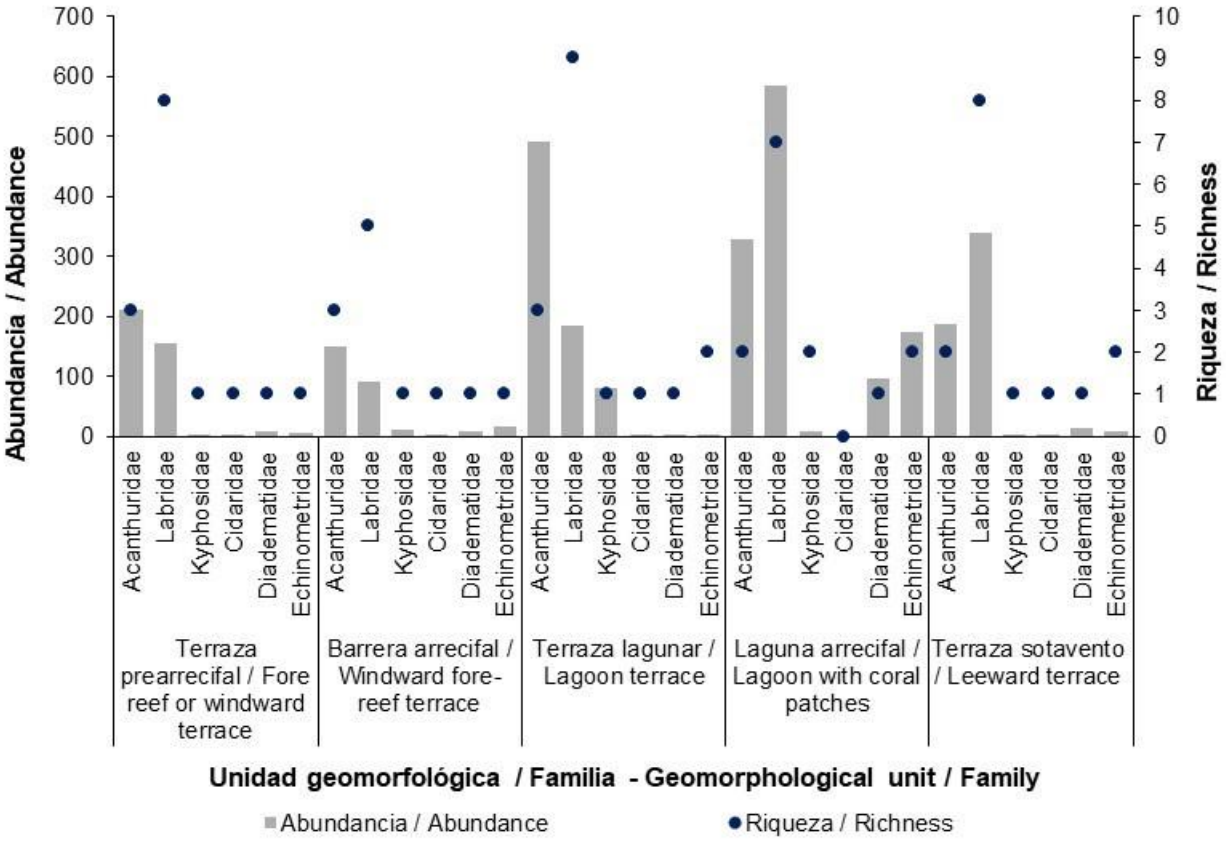

Figure 5. Abundance and richness of herbivorous species families in Bolívar Atoll.

These results are similar to other studies at Seaflower. The 14 species richness of herbivorous fish reported in 2022 was slightly lower than those in the southern cays (17 spp.), San Andres Island (19 spp.), and Old Providence (18 spp.), where the presence of *Scarus guacamaia*, *Scarus coeruleus*, *Sparisoma radians, Kyphosus sectatrix*, *Kyphosus cinerascens* and *Cryptotomus roseus* was recorded (Bolaños-Cubillos, Abril-Howard, Hooker, Caldas and Acero*,* 2015); but it was greater than that found in the northern cays (Alice Shoal: 6 spp., Serranilla: 11 spp., Bajo Nuevo: 13 spp.) (Vega-Sequeda *et al.*, 2015). When comparing between expeditions in which other researchers conducted fish censuses on the other atolls, 15 species of herbivorous fish were recorded in Alburquerque, including *S. coeruleus* and *S. radians* (Rivas, Acero, Tavera, Abril-Howard, d Bolaños-Cubillos*,* 2020), while in Bajo Nuevo, in 100 m^2, of the 20 most abundant fish taxa, 6 were herbivorous (Santos-Martinez, Gavio, Prato, Dorado, d Macaris*,* 2023)(Table 4).

Table 4. Species of fish and herbivorous invertebrates recorded in expeditions scientists from Alburquerque 2018; Bajo Nuevo 2021 and Bolívar 2022.

Species	Reef complex		
	Alburquerque	Bajo Nuevo	Bolívar Cay
Acanthurus chirurgus	X	X	64
Acanthurus coeruleus	X	38	832
Acanthurus tractus	X	8	471
Diadema antillarum			128
Echinometra lucunter		51*	88
Echinometra viridis		4*	117
Eucidaris tribuloides			9
Kyphosus spp.			97
Kyphosus vaigiensis	X		5
Maguimithrax spinossisimus			2
Percnon gibbesi			4
Scarus coelestinus	X		3
Scarus coeruleus	X		
Scarus iseri	X	11	380
Scarus taeniopterus	X	4	247
Scarus vetula	X		91
Sparisoma atomarium	X	X	25
Sparisoma aurofrenatum	X	7	226
Sparisoma chrysopterum	X		27
Sparisoma radians	X		
Sparisoma rubripinne	X	X	130
Sparisoma viride	X	4	225

Note: Alburquerque: presence (X) reported by Rivas *et al*. (2020). Bajo Nuevo: Presence and density of individuals in 100 m^2 reported by Santos-Martínez *et al*. (2023). Bolívar: total abundance (# individuals censused). * Total abundance data taken by the authors in 2021.

In relation to sea urchins, despite the fact that 31 species of echinoids have been recorded in the RB Seaflower, the 4 species found in 2022 are the same as those reported most commonly in shallow waters, which are abundant and are officially recorded for San Andres Island, Bolívar, Old Providence, Bajo Nuevo and Serranilla (Borrero-Pérez *et al.,* 2019). Only in Alice Shoal there was a low abundance of *D. antillarum* (Vega-Sequeda *et al.,* 2015), and in the common regime area with Jamaica only *E. tribuloides* and *D. antillarum* were reported (Borrero-Pérez *et al.,* 2019).

Considering the habitat preference by species, it was confirmed that certain families and species registered higher abundances in some geomorphological units compared to others (Table 5). In general, the factors that seem to have the greatest influence on the abundance of herbivores are the degree of exposure to waves, the water-column depth, and the characteristics of the substrate (Alevizon, Richardson, Pitts and Serviss*,* 1985; McGehee, 1994 — Brazil). When comparing the results of 2022 with the study of Mejía and Garzón-Ferreira (2000) it is possible to affirm that *S. iseri*, *S. taeniopterus*, *S. aurofrenatum, A. coeruleus*, *A. tractus* and the youth of *Sparisoma* spp. and *Scarus* spp. are characteristic species of the lagoon basin and the windward and leeward terraces, environments where the depth of the water column reduces exposure to waves; whereas *Kyphosus* spp. *Acanthurus* spp. and *Scarus* spp., prefer shallow environments where high light irradiance favors macroalgae blooms.

Functional redundancy of herbivores

Functional redundancy is the potential ability of a species to replace the ecological function of another in the event of its disappearance, and is measured from the richness of genera and species within the same functional group (Johansson *et al.,* 2013). According to this definition, in Bolívar, the functional groups macroalgae-browser (4 genera and 5 species) and bioeroding grazers (5 genera and 6 species) had the highest capacity for functional redundancy. On the contrary, the groups of cutters, grazers, scrapers and sediment suckers each registered a genus and 1 to 3 species (Table 5). In general, all groups recorded the highest abundances in the reef lagoon, except for the sediment suckers that were more abundant in the windward lagoon and fore reef terrace.

In the context of surgeonfish taking into account all genera and species globally, six functional groups are categorized (macroalgae browsers, cutters, sediment suckers, brushers, hidden cutters, and water column feeders) (Tebbet *et al.,* 2022). According to this, the 2022 records correspond to only 33.3 % of the total functional groups for this family. The small number of genera, species and therefore functional groups in the Caribbean is a consequence of several factors, including the biogeographic origin of fish diversity, which represents one of the reasons why these environments have been less resilient to changes from coral to macroalgae dominance (Roff and Mumby, 2012; Burkepile, Rasher, Adam, Hoey, & Hay, 2018).

The macroalgae browsers were the most diverse group with the greatest functional redundancy in Bolívar (fish: 2 genera and 6 species; invertebrates: 2 genera and 2 species). In the Indo-Pacific this group is composed of 21 species from 5 genera, of which only the genus *Calotomus* (5 species) and *Leptoscarus vaigiensis* are parrots. In the Atlantic, this functional group corresponds almost exclusively to the genus *Sparisoma* and contains the most dominant consumers of macroalgae on reefs and seagrasses (Burkepile and Hay, 2010; Adam, Burkepile, Ruttenberg, & Paddack*,* 2015).

For bioeroding-grazers, 2 genera of parrotfish and 3 of echinoderms are included. In terms of fish, these species are a low record compared to what was reported for the Indo- Pacific (5 species) (Cheal *et al.,* 2012). This is because large parrotfish have declined in the Caribbean due to pronounced herbivore fishing, depleting populations that fulfill this function (Burkepile *et al.,* 2018; Rivas *et al.,* 2020). A limited functional redundancy in this group indicates that these environments are highly vulnerable to the loss of any of these species and that, consequently, bioerosion rates are likely to decrease. For scrapers, 3 species of the genus *Scarus* were recorded. This richness is low compared to the Indo-Pacific (17 species and 2 genera).

In addition, other large scraper species such as *S. coeruleus* were not observed in Bolívar, despite being reported for Seaflower (Bolaños-Cubillos *et al.,* 2015). Apparently, these species are more resilient to the negative effect of fishing, possibly due to their size and greater reproductive capacity, so they may be safeguarding this function and providing greater functional redundancy.

Burkepile and Hay (2010) showed that complementarity among parrotfish improves reef resilience. The joint presence of *S. taeniopterus* and *S. aurofrenatum* causes unique and complementary changes in the algal community. *S. taeniopterus* prevents the establishment of macroalgae and promotes the settlement of crustose coralline algae in the new available substrate; but its impact is low on already established macroalgae occupying an old substrate. On the other hand, *S. aurofrenatum* reduces the abundance of already established leafy macroalgae, but feeds to a lesser extent on filamentous algae. Therefore, this effect taken together is critical for coral recovery after a disturbance.

Considering that there are differences in the spatial distribution of species and, therefore, of functional groups, in response to factors such as food availability, habitat preference, among others (Burkepile *et al.,* 2018), it was shown that the sediment sucking group was more abundant in the fore reef terrace and in the lagoonal terrace, since their habitat preference is around and in the sandy areas of the reefs, where there is a greater presence of sediments and mats of turf algae (Tebbet *et al.,* 2022). On the other hand, cutter species and browsers which feed on the body and stem of filamentous and leafy macroalgae, were more abundant in the lagoonal basin and in the windward peripheral reef. Finally, bioeroders and scrapers that feed on endolithic and epilithic algae were more frequent in exposed environments, such as the windward peripheral reef and the leeward terrace, although they were also recorded in the lagoonal basin (Burkepile *et al.,* 2018).

Generally speaking, Bolívar reefs are defined by low functional redundancy, regardless of diversity (Micheli and Halpern, 2005). The differences between the complementarity between the Caribbean and the Indo-Pacific are a consequence of evolutionary history, over and above differences in the herbivory process. Through this perspective, it is corroborated that the Caribbean has a high degree of vulnerability to the loss of any herbivorous species or worse, of an entire functional group. The richness of herbivorous species is critical to maintaining the structure and function of coral reefs, which is why it is vitally important to maintain and safeguard the richness of genera and species. The foregoing, understanding that the complementarity provided by the different modes of feeding produces an indirect but positive effect on the settlement, maintenance and recovery of corals and therefore of the entire reef ecosystem (Burkepile and Hay, 2010).

Table 5. Habitat preference, functional groups and ecosystem function performed by herbivore species in the coral reefs of the Bolívar Atoll.

Family	Species	Preference of habitat	Functional group	Ecosystem function
Acanthuridae	*Acanthurus chirurgus*	Lagoonal terrace	Sediment sucker	They consume microalgae films and particulate matter from the surface of the soft substrate (sand around corals or mixed substrate with gravel and sand).
	Acanthurus tractus	Fore reef terrace		
	Acanthurus coeruleus	Lagoonal terrace and lagoonal basin	Cutter	They consume usually filamentous algae by cutting them above the substrate.
Diadematidae Echinometridae Cidaridae	*Diadema antillarum* *Echinometra lucunter* *Echinometra viridis* *Eucidaris tribuloides*	Lagoonal basin Fore reef terrace and leeward terrace	Bioeroding grazerer	They feed on the algal epilithic matrix and endolithic turfs of algae, by disturbing or deeper excavation of the substrate.
Kyphosidae	*Kyphosus spp.* *Kyphosus vaigiensis*	Lagoonal terrace	Macroalgae browser	They select individual components of the algae and remove only the algae and the epilithic material.
Mithracidae	*Maguimithrax spinosissimus*	Lagoonal terrace and fore reef terrace		
Percnidae	*Percnon gibbesi*	Lagoonal terrace		
Labridae	*Scarus coelestinus* *Sparisoma viride* *Scarus iseri* *Scarus taeniopterus* *Sparisoma aurofrenatum* *Sparisoma atomarium* *Sparisoma chrysopterum* *Sparisoma rubripinne*	Lagoonal basin and fore reef terrace Lagoonal terrace Lagoonal basin and leeward terrace Lagoonal basin Fore reef terrace and lagoonal terrace Outlying Reef windward	Bioeroding grazer Scrapers Macroalgae browser	They feed on the algal epilithic matrix and endolithic turfs of algae by disturbing or digging deeper into the substrate. They feed on the algal epilithic matrix and endolithic turfs of algae, but only disturb the surface. They select individual components of the algae and remove only the algae and the epilithic material.

CONCLUSIONS

In the reef complexes of Alburquerque, Bolívar and Bajo Nuevo, the benthic cover was dominated by non-reef-building organisms, with algal turfs being the dominant community; while reef-building organisms accounted for less than 26%. This trend is partly due to low richness, abundance, and functional redundancy of herbivores, which reduces natural control over macroalgae. Additionally, disease outbreaks induce significant losses of coral cover, favoring the proliferation of turf algae on the exposed skeleton. These results show that in these reefs the coral domain is changing to the macroalgae domain, a trajectory already described in other Caribbean reefs.

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AUTHORS' CONTRIBUTION

Conceptualization: C.G. and C.D.; methodology: C.G., C.D., and S.Z.; analysis: C.G., C.D., L.F., M.B., and R.D.; research: C.G., C.D., L.F., M.B., R.D., and S.Z.; drafting - preparation of original draft: C.G., C.D., L.F., M.B., R.D., and S.Z.; drafting - revision and editing: C.G., C.D. and S.Z.; supervision: S. Z.; project management: S. Z. All authors have read and accepted the published version of the manuscript.

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