



Fish assemblages associated with natural, transplanted, artificial, and accidental reefs in Puerto Rico

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ABSTRACT

When accompanied with well-informed management actions, active restoration strategies such as coral gardening and deployment of artificial reef structures can help mitigate negative effects of human impact on fish assemblages associated to natural reefs. However, ecological patterns of variation of fish assemblages associated with artificial reefs are poorly understood. From mid-April 2018 to mid-June 2019, we compared fish assemblages associated to one of four types of reef structures: natural reefs (NR), transplanted reefs (TR; i.e., *Acropora palmata* colonies), concrete modules or restoration reefs (RR), and accidental reefs (AC; submerged docks and shipwrecks) across twelve sites around Puerto Rico. Response variables were abundance, biomass, and number of species per sample and these were correlated with environmental factors that could influence the observed patterns of spatial and temporal variation in fish assemblages. Despite natural seasonal fluctuations, differences in fish assemblages between reef types were generally greater than differences among sites, although less obvious between TR and NR. Based on these results, and on the assumption that the general aim of artificial reef deployment is to mimic natural reef function, we highlight the need for management strategies that are tailored to site-specific or reef-specific goals and needs. Our study reinforces the importance of multivariate statistics to recognize patterns of spatial and temporal variation at the smallest spatial scales, understand ecosystem function, and to improve the effectiveness of management actions concerning active restoration strategies like coral gardening and creation of artificial reef habitats.

1. Introduction

The socioeconomic importance of the goods and services provided by healthy coral reefs (e.g., high biodiversity, coastal protection, enhanced fishing and tourism, etc.) (Cesar et al., 2003; Moberg and Folke, 1999) is amplified in the many small developing island states, especially those which are commonly subjected to high coastal population densities, weak economies, geographic isolation, scarce resources, and to natural disturbances like hurricanes and sea level rise (Nurse et al., 2017; Burke et al., 2011). Despite their importance and estimated asset value of 1 trillion USD (Hoegh-Guldberg et al., 2017) anthropogenic disturbances exacerbated by global warming continue to degrade coral reefs and the ecosystem services they provide (Bruno and Valdivia, 2016; Sweet and Brown, 2016; Precht and Robbart, 2006) especially in the Caribbean

(Burke et al., 2011; Weil et al., 2009; Weil et al., 2003). As coral reefs degrade, coastal fisheries productivity could be reduced, decreasing food security, increasing unemployment, and decreasing tourist appeal for coral reef sites, which in turn affects tourism revenue (Hoegh-Guldberg et al., 2017; Cesar et al., 2003).

With adequate management, and if habitat degradation is not severe and stressors are reduced, passive restoration strategies such as Marine Protected Areas (MPAs) and No Take Zones (NTZs) have been shown to be an effective method for conserving biological diversity (Bustamante et al., 2014). However, these types of closures can also have adverse economic effects on the stakeholders that benefit from activities at these sites (Fabinyi, 2008; Valdés-Pizzini and Schärer-Umpierre, 2011; Daw et al., 2011). Active restoration and habitat enhancement strategies like deployment of artificial reef structures and coral gardening and

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transplanting are alternatives that can help reduce human impact on natural reefs without compromising the resources that stakeholders target (Galvan, 2016; Shani et al., 2012; Stolk and Markwell, 2007).

Artificial reefs (ARs) are human-made structures that, when deployed on the seabed, influence physical, biological, and/or socio-economic processes related to marine resources (Stolk and Markwell, 2007; Seaman, 2000). They can provide resources like shelter, spawning and nursery grounds and surface for settlement, and have been shown to enhance different types of fisheries (Banqueiro-Cárdenas, 2011; Fabi and Spagnolo, 2011; Whitmarsh et al., 2008). Artificial reefs have also

been used to improve tourism and the diving experience (Stolk and Markwell, 2007), surfing and sand retention (Innes et al., 2005), and have helped to divert attention of humans away from NR (Kirkbride-Smith et al., 2013; Shani et al., 2012) including the prevention of trawling (Norman-Barea, 2010) highlighting their use for conservation and management.

The benefits that ARs provide are tightly linked to physical characteristics of the reef itself (Sheng, 2000; Precht and Robbart, 2006; Bohnsack, 1991) which can significantly affect biological assemblages at reef sites (Bohnsack et al., 1991; Clynick et al., 2008; Becker et al.,

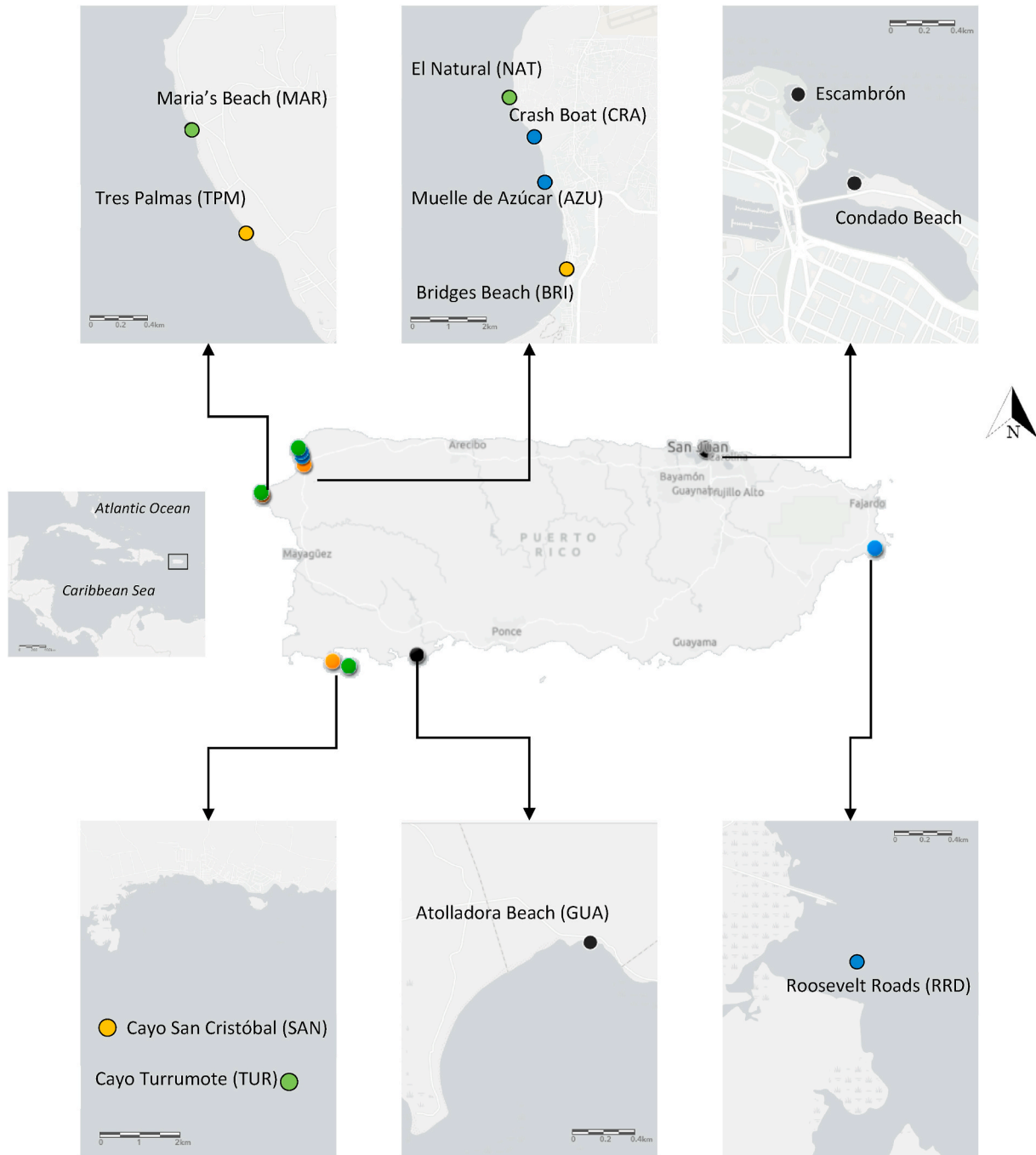


Fig. 1. Study site map labeled with site names and their respective abbreviations. Colors represent reef type: black = restoration (RR), blue = accidental (AC), orange = transplanted (TR), and green = natural reef (NR). Scale bars represent 400 km in the centered-left figure showing the location of Puerto Rico with respect to the North Atlantic Ocean and the Caribbean Sea, 0.4 km in the figures located at the top-left, top-right, center-bottom, and bottom-right, and 2.0 km for the center-top and lower left. Maps were built using Arc GIS Online (Sources: Esri, DeLorme, HERE, Mapmy India). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2016). Therefore, different ARs can serve different and multiple purposes and are not a “one size fits all” tool for habitat enhancement (Paxton et al., 2020).

There are three main ARs types in Puerto Rico: 1) artificially transplanted (*Acropora* spp.) reefs (TR), 2) restoration reefs (RR) made of concrete modules (Reef Balls™ or Taíno Reefs™), and 3) accidental reefs (AC) (i.e., docks/piers and shipwrecks) (Supplementary Table 1, Supplementary Fig. 4). Coral gardening and TR were developed following the worldwide decline of corals over the past decades (Young et al., 2012), especially of the Caribbean *Acropora* spp. (Weil et al., 2009; Weil et al., 2003) and consists of two steps: 1) mariculture of coral fragments within a nursery and 2) transplanting the nursery-grown corals onto a degraded reef (Rinkevich, 1995). Reef Balls are concrete domes with a solid base and various sized holes throughout their surface (The Reef Ball Foundation, 2020; Ortiz-Prosper et al., 2001). Comparatively, Taíno Reefs are like Reef Balls in terms of building materials. However, instead of dome shaped, Taíno Reefs closely resemble the trapezoidal prism shape of a *cemí*, which were religious sculptures that represented different spiritual beings in the native Taíno culture (Oliver, 2009). Lastly, AC are structures that were not built to purposely create a reef yet “accidentally” function as one. These include shipwrecks, plane-wrecks, automobiles, docks and piers (submerged columns and platforms), and defense-structures like breakwaters, groins, and jetties (Clynick et al., 2008; Bohnsack et al., 1991; Shani et al., 2012). Oil platforms are also considered AC but these are not present in Puerto Rico.

Due to reasons yet uncertain, ARs (TR, RR, AC) sometimes exceed many of the benefits (e.g., higher fish densities, biomass, and number of species) that NR provide (e.g., Shani, et al., 2012; Bohnsack et al., 1991) though results might be biased towards publishing success stories more than failures (Bayraktarov et al., 2019). Here lies the general assumption that ARs “perform” better than NR. Because of the high aggregation of marine life around these structures, support for deployment of ARs has come from different stakeholders like fishermen (recreational and commercial), tourism industries, diving community and environmental managers (Kirkbride-Smith et al., 2013; Shani et al., 2012; Bortone et al., 2011). However, if they are not adequately managed, ARs could have negative effects over biological communities like facilitating overfishing (Grossman et al., 1997; Polovina, 1991a,b) and invasion by lionfish (*Pterois* spp.) (Smith and Shurin, 2010).

Motivations for TR creation in Latin American countries, including Puerto Rico, include restoring and enhancing habitat for reef fishes (Bayraktarov et al., 2019). Restoration reefs (RR) were also purposely built for restoring and enhancing sport reef fish habitat (at Atolladora Beach) (Zegarra, 2003) and to create habitat for reef fish and invertebrate species (at Condado and Escambrón) (Fig. 1) with the added benefit of enhancing tourism (Ruiz, 2015; HJR Reefscaping, 2010). However, to our knowledge, no one has compared different ARs (RR, TR, and AC) in Puerto Rico with respect to their fish assemblages and, therefore, there are knowledge gaps about their current function and potential uses for management and conservation.

It is therefore necessary to understand the spatial and temporal patterns of fish assemblages and the environmental processes within the boundaries of ARs within the larger context of reef function (Precht, 2006; Sheng, 2000; Bohnsack et al., 1991). By comparing the structure and composition of the fish assemblages at different reef types, while considering key environmental variables within each reef’s boundaries, it is possible to develop an initial understanding of why a reef functions (or not) as intended (Becker et al., 2016; Precht, 2006; Carr and Hixon, 1997). Comparing ARs to control sites is also essential (Baine, 2001; Carr and Hixon, 1997) since it is useful for separating temporal changes at the ARs, from regional changes also affecting nearby NR (Becker et al., 2016). Considering that enhancing fish habitat is one of the main goals for construction of ARs (Paxton et al., 2020; Opel et al., 2017), and that assessments of fish assemblage structure can function as indicators of ecosystem integrity and health (Pittman et al., 2010) comparing fish

assemblages between ARs and NR is a useful method for evaluating reef performance.

Consequently, the overall goal of this study was to produce useful ecological information to inform management decisions regarding artificial and natural reefs in Puerto Rico. Specifically, the objectives of this study were: 1) to describe patterns of spatial and temporal variation of fish assemblages and other species of commercial, recreational, cultural, or SCUBA diving interest (e.g., sea turtles; Supplementary Table 2) associated with transplanted (TR), restoration (RR), accidental (AC), and natural reefs (NR) in Puerto Rico, 2) to compare trends of temporal variation of fish assemblages among the four types of reefs, and 3) to provide management recommendations that could benefit resilience of the reef communities and conservation strategies. Considering that the physical characteristics of the reef (Precht and Robbart, 2006; Sheng, 2000; Bohnsack, 1991) and of their surrounding environment can significantly affect biological assemblages at reef sites (Precht, 2006; Bohnsack et al., 1991), we also recorded environmental variables and reef features that could potentially explain the observed patterns in fish assemblages (Table 1).

It was predicted that if reef type is an important influencing factor on spatial patterns of fish assemblages, we expected to find consistent and significant differences in the abundance, biomass, and number of species at different reef types, regardless of the time of year (e.g., season) or intrinsic variation among sites at different localities.

Although we evaluate reefs under the assumption that “success” lies in the ability of an ARs mimicking biological assemblages in NR, we are aware that some of the reefs studied were built with additional (or no) purposes in mind (e.g., RR serving as underwater trails; Ruiz, 2015; HJR Reefscaping, 2010) and therefore cannot be expected to function in the same way. However, the data collected in this study can be used to improve decisions regarding reef design and location selection (Becker et al., 2016), and highlights the usefulness of using multivariate analyses on fish assemblage data for assessing ecological function, reef restoration success and enhancing management strategies (Paxton et al., 2020; Pittman et al., 2010; Frid et al., 2008).

2. Materials and methods

2.1. Study site selection

An inventory of all types of reef of Puerto Rico was conducted using existing scientific literature, coral reef restoration agencies’ websites, and through personal communication with diving instructors, coral reef researchers, NGOs, and volunteers involved in coral reef restoration projects. Data mining resulted in a list of 45 potential sites that fulfilled the selection criteria (explained in *Sampling Design*) of being, transplanted (TR; n = 15), restoration (RR; n = 5), or accidental reefs (AC; n = 22) (Supplementary Table 1). Three sites were a combination of TR and RR (i.e., concrete domes with corals transplanted on them), but these were ignored in this study.

After visiting and evaluating some of the sites through pilot visual surveys using SCUBA, 12 sites (Fig. 1) were assigned to one of the four reef type categories. Restoration reefs had either Reef Balls™ (Atolladora Beach) or Taíno Reefs™ (Escambrón and Condado Beach). Accidental reefs were a shipwreck (Roosevelt Roads), an abandoned sugar cane pier (Muelle de Azúcar) and the submerged ruins of another pier (Crash Boat Beach). Transplanted reefs (Bridges, Tres Palmas, and Cayo San Cristobal) were sites who had *Acropora palmata* artificially transferred to a coral reef area within the past 10 years (pers. comm. H. J. Ruiz, E. Hernández-Delgado, and C. Tuhooy, 2018). Natural reefs (El Natural, María’s Beach, and Cayo Turrumote) are those whose benthos had qualitatively more Scleractinia coral cover than gorgonians. On average, all sites were <10 m deep, at least 500 m away from each other, and on the inner-shelf, except for Cayo San Cristobal (TR) and Turrumote (NR) which were at mid-shelf environments and were accessed by boat.

Table 1

Intrinsic (i.e., constant variables, **bold**) and *in situ* (i.e., dependent on sampling time, underlined) environmental variables used for BIOENV analyses in Primer v7.

Site	Condado	Escambrón	Atolladora	Crash Boat	Muelle Azúcar
Site Abbrev.	CON	ESC	GUA	CRA	AZU
¹ Latitude (N)	18°27'40.24"	18°27'55.07"	17°57'22.76"	18°27'25.66"	18°26'41.79"
¹ Longitude (W)	-66°4'56.28"	-66°5'13.38"	-66°51'15.62"	-67°9'45.62"	-67°9'38.70"
Coast	North	North	South	Northwest	Northwest
² Mineral Type (aragonite = AR, Metal = MT, concrete = CO)	CO	CO	CO	CO	MT
² Reef Shape ** (coral reef = CR, Reef Ball/Taino Reef = RB, shipwreck = SH, dock = DK)	RB	RB	RB	DK	DK
² Habitat Type ** (PA = pavement; AR = aggregate reef; SC = scattered coral and rocks; SF = sand flat; SG = seagrass)	SG	SF	SG	SF	SF
² Relative rugosity **	Low	Med	Low	Med	High
¹ Distance to Shore (m) *	40	120	25	110	155
¹ Dist. Mangrove (m) *	4000	5000	1750	6000	6000
¹ Dist. to Slope (m) ***	3120	2740	2000	1200	1300
³ Reef Height (h) *	0.5	0.5	1.5	2.7	16
³ Max Diameter (MD; m)	1	1	1	10.7	12
³ Perpendicular to MD (m)	0.5	0.5	1	7.13	12
⁴ Surface Area (m³) ***	16	101	240	638	2963
⁵ Year *	2009	2010	2002	1940	1955
⁴ Age (2020-Year) *	11	10	18	80	65
² Patch Type	2	1	1	1	1
³ SFC Start (hr: min) *					
³ SFC End (hr: min) *					
³ SFC Duration (min) *					
³ Visibility (m) **					
³ Depth (m) **					
³ Adjacent Substrate					
³ Dist. Adjacent Substrate (m)					
³ SFC Cylinder Area (m ²) *					

Site	Roosevelt Roads	Bridges	San Cristobal	Tres Palmas	El Natural	Marías	Turumote
Site Abbrev.	RRD	BRI	SAN	TPM	NAT	MAR	TUR
¹ Latitude (N)	18°13'25.04"	18°25'35.03"	17°56'28.32"	18°21'2.33"	18°27'46.11"	18°21'26.73"	17°56'5.92"
¹ Longitude (W)	-65°36'4.61"	-67°9'21.10"	-67°4'40.43"	-67°15'56.63"	-67°10'5.58"	-67°16'9.04"	-67°1'6.99"
Coast	East	Northwest	South	West	Northwest	West	South
² Mineral Type (aragonite = AR, Metal = MT, concrete = CO)	MT	AR	AR	AR	AR	AR	AR
² Reef Shape (coral reef = CR, Reef Ball/Taino Reef = RB, shipwreck = SH, dock = DK) **	SH	CR	CR	CR	CR	CR	CR
² Habitat Type (PA = pavement; AR = aggregate reef; SC = scattered coral and rocks; SF = sand flat; SG = seagrass) **	SC	PA	AR	PA	PA	PA	AR
² Relative rugosity	High	Med	High	Med	Low	Med	High
¹ Distance to Shore (m) *	360	30	1600	25	70	80	3300
¹ Dist. Mangrove (m) ***	1500	6000	1600	6000	6000	6000	3300
¹ Dist. to Slope (m) ***	15350	2320	7390	1730	1190	1910	5490
³ Reef Height (h) *	4.5	1.5	6	2	6	3	10
³ Max Diameter (MD; m)	13	120	40	100	250	500	300
³ Perpendicular to MD (m)	48	50	45	50	50	80	47
⁴ Surface Area (m³) ***	1797	6000	1800	5000	12500	40000	14100
⁵ Year *	1992	2015	2011	2017	4000	4000	4000
⁴ Age (2020-Year) *	45	5	9	3	1980	1980	1980
² Patch Type	1	2	2	2	2	2	2
³ SFC Start (hr: min) *							
³ SFC End (hr: min) *							
³ SFC Duration (min) *							
³ Visibility (m) *							
³ Depth (m) *							
³ Adjacent Substrate							
³ Dist. Adjacent Substrate (m)							
³ SFC Cylinder Area (m ²) *							

* Non-categorical data used for environmental data * sample analyses in Table 4 and Fig. 4. ** BIOENV results used for LINKTREE analyses. Surface area was only used for biomass analyses.

¹ Google Earth™

² Qualitative record: *Relative rugosity* was defined depending on relative amount of vertical relief (i.e., up-and-down profile) and habitat complexity (i.e., availability and diversity of crevices and refuge). *Patch Type 1* = discreet reef over low relief and uniform bottom; *Patch Type 2* = hard reef contiguous to a natural reef structure.

³ Quantitative *in situ* record; *reef height* = average height of the three highest hard structures; *MD* = longest width of hard reef structure, *PMD* = longest perpendicular distance with respect to *MD*; *visibility* = estimated horizontal; *adjacent substrate type & distance to adjacent substrate* were recorded after each SPC.

⁴ Calculated from recorded data; the following equations were used to estimate surface area at each reef type: dome = GUA; trapezoid prism = CON, ESC, RRD; and triangular prism at TR and NR using MD, PMD and reef height.

⁵ Personal communication: sites CON + ESC + GUA through HJR Reefscaping™, CRA + MAZ from Fletes-Monroy (2011), Edwin Hernández-Delgado for site BRI, HJR Reefscaping for SAN, and Chelsea Tuhoy and Michelle Schärer for TPM. RRD from Naval Sea Systems Command (1992). MAR + NAT + TUR were given an “extreme” value of 4000 years.

Data on physical characteristics (e.g., reef material type, reef shape, and habitat type) and environmental variables (e.g., depth, visibility, adjacent substrate; Table 1) at each site were not included in site selection criteria, as it was impossible to standardize all these across sites, but were incorporated as factors in the analyses (explained below).

2.2. Sampling design

The sampling design considered the following factors: season (5 fixed levels; *Spring 18'*, *Summer*, *Fall*, *Winter*, and *Spring 19'*), visit number per season (3–4 random levels; nested in season), reef type (4 fixed levels; *restoration* [RR], *accidental* [AC], *transplanted* [TR], and *natural* [NR]), and sites (3 random levels and nested in reef type; 12 total). Due to their nature and purpose of their deployment (i.e., docks built in deep water sandy bottoms [AC] vs. reefs built in shallow water for tourists [RR] or coral restoration [TR]), the different reef types are not fully interspersed in space and time. This limitation is considered in the discussion.

Fish assemblages were sampled using Stationary Point Counts (SPCs) (Ayotte et al., 2011; Bohnsack and Bannerot, 1986), which consisted of censuses taken at different points through the reef, where either one or two trained divers (at least 15 m apart in case of the latter) rotate around themselves and visually identified (to the lowest taxonomic level possible), counted, and measured fish and other species of importance for commercial, recreational, cultural or SCUBA diving activities (Supplementary Table 2) within a visual cylinder of 7.5 m radius and throughout all depths during 10 min. Once the 10 min passed, the transect line was redeployed to conduct the next SPC.

A single site visit consisted of 3–4 SPCs, depending on the number of trained divers and on bottom time. On average, sampling start time was 9:30 a.m. and end time 10:20 a.m. local time, with the earliest sampling start time recorded at 7:45 a.m. and the latest at 12:30pm. The transect line was deployed so that each diver was found at least within 1 m of a reef structure, between 1 and 13 m depths, and on the forereef (in the case of SAN (TR) and TUR (NR)). SPC cylinder radius was adjusted from 7.5 m (at visibilities >7.5 m) to 5 m when visibility was between 3 and 5 m. If visibility was between 3 and 5 m, after the first 7 min of the SPC, the diver slowly roved away from the center of the SPC to explore for additional species within the 5 m cylinder radius for the remainder of the visual census. We set the visibility threshold for aborting SPCs at 3 m due to consistently low visibilities at site GUA, mostly due high winds and massive arrivals of *Sargassum* spp. during summer and winter that increased suspended particles in the water column (pers. obs.). Differences in cylinder area resulting from visibility thresholds were accounted for by standardizing samples by total of the sample or by *SPC Cylinder Area* (m²) prior to multivariate and univariate analyses, respectively (detailed below).

Through fish identification we calculated number of species and used individual fish counts to calculate abundance. Size estimates were used for post-census calculation of biomass using weight-length (W-L) relationships in FishBase (Froese and Pauly, 2019). If W-L relationships of a specific species were not available, the estimate of a congeneric was used. If W-L relationships were not available for a species or its congeners, they were excluded from all biomass calculations and analyses (Supplementary Table 2). Analyses on number of species and abundances included all taxa in Supplementary Table 2.

These data were used to create two matrices (*species* (rows) x *samples* (columns)): with each cell representing individual fish counts (abundance) or weight (biomass). Through visual analysis of shade plots, we decided to fourth root transform raw abundance and biomass data for multivariate analyses, thereby down-weighting the contribution of dominant species relative to less-common species (Clarke and Gorley, 2015). Data were then standardized by the total of the sample to account for differences in the total volume surveyed resulting from visibility thresholds, depth differences and diver bias. Since data for multivariate analyses was standardized by the total of the sample, abundance and biomass data in these matrices used transformed data not normalized for

SPC Cylinder Area.

Conversely, data for univariate analyses was not transformed, but was standardized by dividing total abundance or biomass in a sample by *SPC Cylinder Area* to calculate densities (i.e., no. individuals/m² and kg/m² respectively). Using DIVERSE (which calculates univariate diversity-related indices based on the relatedness of species in a single sample) (Clarke and Gorley, 2015), on both abundance and biomass *species* * *sample* matrices separately, we created three matrices of samples (rows) by univariate diversity indices (columns) that were used for analyses: 1) abundance density (no. individuals/m²), 2) number of species per sample, and 3) biomass density (g/m²).

In addition to estimations of biological parameters (i.e., biomass and abundance), several environmental/structural/habitat variables were recorded (Table 1) to consider the heterogeneity of sites where different reef types were located. Environmental variables were classified into *intrinsic* (characteristics that did not change through time and were therefore recorded only once) and *in situ* (characteristics that did change and were recorded during each SPC).

Intrinsic environmental variables were: *coast*, *mineral type* (i.e., reefs' construction material), *reef shape*, *habitat type*, *relative rugosity*, *distance to shore*, *distance to mangrove*, *distance to slope or drop-off*, *height of structure* (max reef height), *max diameter*, *perpendicular to max diameter*, *hard surface area* (m²), *year of settlement/age*, and *patch type* (Table 1).

Since geographical location among sites has been shown to influence fish assemblages (Ambrose and Swarbrick, 1989; Bohnsack et al., 1991) classifying sites by *coast* was a way to account for differences between locations.

The physical characteristics of the reef (i.e., construction material, shape, arrangement, etc.) can also significantly affect biological assemblages at reef sites (Sheng, 2000; Precht, 2006; Bohnsack et al., 1991) highlighting the importance of recording the *mineral type* (i.e., concrete, metal, aragonite) (Burt et al., 2009). Other physical reef characteristics that can influence fish assemblages include reef size (Bohnsack et al., 1994), reef height (Clynick et al., 2008; Becker et al., 2016), and different aspects of habitat complexity including reef shape, surface rugosity, available hard substrate, and shelter size (Gratwicke and Speight, 2005; Sherman et al., 2002; Bohnsack et al., 1991). Therefore, to account for possible effects of these physical reef characteristics on fish assemblages we recorded *reef shape*, which refers the general three-dimensional reef structure (i.e., shipwreck, Reef Ball ©, dock or pier, etc.), *relative rugosity* (qualitative value of low, med, or high relative amount of vertical relief [i.e., up-and-down profile] and habitat complexity [i.e., availability and diversity of crevices and refuge sizes]), *reef height* (maximum height of hard structure), *max diameter* (MD; longest length of hard structure), *perpendicular to max diameter* (PMD; longest line perpendicular to MD), and *hard surface area* (estimated from MH, MD, and PMD). We used the formulas of area of a cylinder to estimate surface area of columns in docks and piers, cubetangle for platforms and bridges, dome for Reef Balls©, trapezoid prism for shipwreck and Taíno Reefs©, and rectangle-triangle area for low rugosity sites in NRs and TRs using half of the depth as height, except on TUR which had relatively high rugosity structures that could be measured from the bottom.

Since fishes respond to benthic habitat structure at multiple spatial scales, with various groups of fishes each correlated to a unique suite of variables (Grober-Dunsmore et al., 2008) including proximity to mangroves (de la Morinière et al., 2002), seagrass (Dorenbosch et al., 2007), and horizontal distribution from shore (Leis, 1991; Aguilar-Perera and Appeldoorn, 2008), we visually recorded *habitat type* (where the reef itself is located; e.g., sand flat, seagrass, aggregate reef, etc.), and measured distance from our sites to mangroves, the shoreline, and to the nearest slope or drop-off using Google Earth™. We also classified sites according to *patch types*, referring to whether the ARs represent a unique habitat structure in a relatively uniform benthos, like a sand flat (e.g. *patch type 1*) or whether it is an additional habitat patch between various other habitat patches (e.g. *patch type 2*). *Patch type* was used as a proxy

for the relative “isolation” of the reef from other habitats, which has been shown to influence fish assemblages at some ARs (Becker et al., 2016; Bohnsack et al., 1991).

Reef age has also shown to influence fish assemblages in different types of artificial reefs (Seaman and Jensen, 2000; Relini et al., 2002) including shipwrecks (Arena et al., 2007), and transplanted *Acropora cervicornis* reefs (Opel et al., 2017). From a literature review and personal communication with Hernández-Delgado (2019), Chelsea Tuhoy (2019), Weil (2019), and Ruiz (2019) and online records (Naval Sea Systems Command, 1992) we recorded the year each reef was settled or transplanted and calculated the age of the reef (i.e., reef age = 2020 - year settled) to account for potential differences in fish assemblages driven by variation in age or year that the reef settled.

In contrast to *intrinsic* factors, *in situ* environmental variables changed between sampling times and were recorded after each SPC (except SPC start time). *In situ* variables include: SPC start time, SPC end time, SPC duration, visibility, depth, current speed, adjacent substrate, distance to adjacent substrate, and SPC cylinder area. SPC start, end and duration times were recorded to account for diel patterns in reef fish behavior and reduce systematic bias in our sampling (Willis et al., 2006; Sancho et al., 2000; Hitt et al., 2011). Horizontal visibility was also recorded as it has been shown to affect visual censuses (Sale, 1997). The effects of depth and currents over fish assemblages have also been well documented (Bohnsack et al., 1991; MacDonald et al., 2016; Jankowski et al., 2015).

Both *intrinsic* and *in situ* were recorded in the form of an *environmental variable x sample* matrix with each cell containing the numerical value of each observation at a specific sample. Categorical data in the environmental matrix was coded as binomial (presence/absence of a given category) to conduct canonical analyses. Environmental variables were used as potential predictors for biological variables using BIOENV and LINKTREE (explained below).

2.3. Statistical analyses

Abundance and biomass matrices were used to construct resemblance matrices (among samples) using the Bray-Curtis similarity index for multivariate data (Bray and Curtis, 1957) and Euclidian distances for univariate data (Anderson et al., 2008). Permutational Multivariate Analyses of Variance (PERMANOVA) were used on these five resemblance matrices (2 multivariate [abundance and biomass] and 3 univariate [abundance density, biomass density, and species per sample]) using a random subset of 9999 permutations of residuals under a reduced model to test hypotheses about patterns of temporal and spatial variation of fish assemblages.

Differences in the observed spatial patterns of abundance and biomass of fish assemblages among reef types were statistically compared using the dispersion among centroids for each combination of *season x site(reef type)* [hereafter Se x Si(Re)] and illustrated in a principal coordinate ordination (PCO) to show the magnitude of those differences (Guerra-Castro et al., 2016). Species responsible for multivariate patterns were identified by correlating the raw estimation of abundance or biomass of each species with each one of the PCO axis.

For the recorded environmental variables (Table 1), *distance from shore*, *distance to drop-off*, *reef height*, *hard surface area*, *year*, and *age* were Log(V+1) transformed and *visibility* and *depth* were square root transformed following visual interpretation of Draftmann's plots. All environmental data was then normalized to account for differences among sampling units and ranges. Resemblance matrices (*sample * sample*) were created from multivariate data using Euclidean distances and then analyzed with a PERMANOVA (9999 permutations) as above. As per fish assemblages, multivariate patterns of variation were illustrated in two principal coordinate ordination (PCO) after calculating distances among centroids for Se x Si(Re). One PCO used a combination of both *intrinsic* and *in situ* variables and another used only *in situ* variables. This helped visualize which type of variable(s) (*intrinsic vs in situ*) better explained

environmental differences among samples.

To infer about potential environmental drivers of patterns of spatial and temporal variation of fish assemblages, BIOENV (99 permutations) and LINKTREE (999 permutations) analyses were done to determine the group of environmental factors and variables that best correlated with biological patterns (Clarke and Gorley, 2015). BIOENV searches for high matrix correlations, of all possible variable combinations, between similarity matrices of species assemblages (abundance and biomass separately) and a resemblance matrix of combined *environmental factors* and *variables* averaged by Se x Si(Re). LINKTREE, alternatively, creates a dendrogram in which terminal nodes represent Se x Si(Re) groups, with each branch node identifying the environmental variable(s) (determined from BIOENV) that best describe the split. By doing this, BIOENV generates a list of combinations of environmental variables that best correlate with the observed biological patterns, while LINKTREE helps visualize groupings of fish assemblages in terms of the particular environmental variables that could be responsible for those patterns (Clarke and Gorley, 2015).

3. Results

3.1. Fish assemblage description

We successfully conducted 95% (n = 512) of maximum total SPCs and 91% (n = 163) of planned site visits (Supplementary Table 3), which allowed for a robust quantitative analysis of the data. A total of 74,972 individuals were counted and classified into 158 taxa (93% identified to species, 4% to genera and 3% to family) (Supplementary Table 2). Overall, the most abundant species were the blue head wrasse (*Thalassoma bifasciatum*; 20% of total), bicolor damselfish (*Stegastes partitus*; 11%), sergeant major (*Abudefduf saxatilis*; 8%), tomtate (*Haemulon aurolineatum*; 6%), and ocean surgeon (*Acanthurus tractus*; 5%). The most frequent species (present in $\geq 70\%$ of site visits) were the blue tang (*Acanthurus coeruleus*; 99%), *A. tractus*; 96%, *T. bifasciatum* (80%), slippery dick (*Halichoeres bivittatus*; 74%), *A. saxatilis* (72%), and dusky damselfish (*Stegastes adustus*; 71%).

In terms of families, the most abundant were Pomacentridae (29% of total), Labridae (23%), Haemulidae (16%), Acanthuridae (9%), Scaridae (4%), and Carangidae (3%). Most frequently seen families were Acanthuridae (96% of total SPCs), Labridae (93%), Pomacentridae (92%), Haemulidae (78%), Scaridae (77%), Holocentridae (57%), and Lutjanidae (52%). The most speciose families were Serranidae (n = 14), Haemulidae (n = 13), Labridae, Pomacentridae, and Scaridae (n = 11), Lutjanidae (n = 8) and Carangidae (n = 7).

For individuals whose W-L relationships of biomass could be calculated (n = 61,489 belonging to 117 species), a total 3,343,853 g was estimated. The species showing highest contributions to total of biomass were *A. saxatilis* (8.4%), *A. coeruleus* (5.8%), stoplight parrotfish (*Sparisoma viride*; 5.7%), *A. tractus* (5.3%), yellowtail snapper (*Ocyurus chrysurus*; 4.6%), atlantic tarpon (*Megalops atlanticus*; 4.3%), *H. aurolineatum* (4.1%), spotted-eagle ray (*Aetobatus narinari*; 3.5%), horse-eye jack (*Caranx latus*; 3.4%), yellow goatfish (*Mulloidichthys martinicus*; 3.3%), smallmouth grunt (*Haemulon chrysargyreum*; 3.3%), and barjack (*Caranx ruber* 2.6%); which together, comprised >50% of total recorded biomass.

3.2. Patterns of temporal and spatial variation of fish assemblages – abundance and biomass

For both abundance and biomass, PERMANOVA analyses showed that despite significant variation at the smallest random source of spatiotemporal variation considered in this study (i.e., *visit no.* and *site*) there was a significant difference among reef types (Table 2). Multivariate ordinations (PCO) show the structure and composition of fish assemblages associated with the various reef types are clearly different, especially those assemblages associated with AC and RR (Fig. 2). The

Table 2

Multivariate Permutational Multivariate Analyses of Variance (PERMANOVA) based on B–C similarities of fourth root transformed and standardized by total of the sample for abundance (n = 158) and biomass (n = 117) data. Numbers in **bold** indicate interpretable significant sources of variation. Factors are season (Se), reef type (Re), visit number (Vi) and site (Si).

Source	Abundance				Biomass			
	df	MS	Pseudo-F	P(perm)	df	MS	Pseudo-F	P(perm)
Se	4	3762.9	1.479	0.0006	4	4097.2	1.4853	0.0008
Re	3	84409	3.1588	0.0001	3	77682	2.9815	0.0001
Vi(Se)	11	1667	0.93756	0.6944	11	1882.7	0.92326	0.7319
Si(Re)	8	27605	15.585	0.0001	8	26864	13.225	0.0001
SexRe	12	2770.4	1.0418	0.2609	12	2911.9	1.0538	0.213
SexSi(Re)	32	2622.4	1.4764	0.0001	32	2807.5	1.3782	0.0001
Vi(Se)xRe**	30	1824.5	1.0244	0.3633	30	1961.2	0.96009	0.7055
Vi(Se)xSi(Re)**	62	1784.4	1.4642	0.0001	62	2046.8	1.4841	0.0001
Res	349	1218.7			349	1379.1		
Total	511				511			

shipwreck at site RRD was a notable exception since centroids for this site separated conspicuously from other reef type. Differences between NR and TR, however, were not as clear, especially for biomass data (Fig. 2).

There was a significant interaction between seasons and sites for both abundance and biomass (Table 2), yet differences in seasonal variability of sites within the same reef type were much smaller than spatial differences among reef types (Fig. 2).

Although patterns were consistent for the two types of data (abundance or biomass), species correlated to those patterns were not the same in each case. Only three species that correlated >75% with the first axis of the ordination were common to both abundance and biomass (Fig. 2) and also explained differences between RR and other reef types: *H. bivittatus*, *S. rubripinne*, and *A. tractus*. Both *H. bivittatus* and *S. rubripinne* were overall consistently more abundant and had higher biomass on RR than on other reef types, and greater overlap between AC, TR, and NR (Supplementary Fig. 1). *Acanthurus tractus* showed overall higher and similar values for both abundance and biomass between RR, TR, and NR, with a pronounced peak during Winter in TR, and lower values in AC (Supplementary Fig. 1).

The porkfish (*Anisotremus virginicus*) showed no clear differences in abundances between reef types (Supplementary Fig. 2). *Thalassoma bifasciatum* was more abundant on NR, followed by similar values in AC and TR, and lower in RR. *Stegastes adustus* had higher abundances on TR, followed by NR and lower in RR and AC (Supplementary Fig. 2).

The blackbar soldier fish (*Myripristis jacobus*) and glass eye snapper (*Heteropriacanthus cruentatus*) drove biomass differences between the sites CRA and AZU (AC) and were practically absent at other reef types (Supplementary Fig. 3). The striped parrotfish (*Scarus iseri*) showed higher and similar biomass values between AC and TR and lower in NR and RR (Supplementary Fig. 3) with peaks during summer and winter, respectively. *Sparisoma viride* showed similar biomass values between reef types throughout the study, except for a pronounced peak in Winter due to large schools of large (>35 cm) individuals (pers. obs.).

3.3. Total abundances, species, and biomass

Overall, abundance, number of species and biomass were significantly influenced by reef type showing higher values in AC, similar values between TR and NR, and lowest in RR (Table 3, Fig. 3). Univariate analyses on total fish abundances showed significant differences between sites and seasons (Table 3). Despite this spatial and natural variation, significant differences were observed among reef types (Table 3).

Abundances were overall higher in AC (min = 0.8 ± 0.1 ind/m²; max = 1.6 ± 0.2 ind/m²), followed by NR (min = 0.8 ± 0.1 ind/m²; max = 1.7 ± 0.5 ind/m²), TR (min = 0.6 ± 0.1 ind/m²; max = 1.6 ± 0.1 ind/m²) and show greater variation, whereas RR showed consistently lower and less variable values (min = 0.21 ± 0.02 ind/m²; max = 0.34 ± 0.2

ind/m²) (Fig. 3). When averaged across reef types, abundances were higher in AC (1.3 ± 0.1 ind/m²) followed by NR (1.1 ± 0.1 ind/m²), TR (0.8 ± 0.04 ind/m²), and RR (0.2 ± 0.01 ind/m²) (data not shown).

With respect to number of species per sample, despite significant natural variation between site, visit number, and season, there were consistent differences among reef types throughout the sampling period (Table 3; Fig. 3). Similar to the observed patterns in abundance, number of species per sample were consistently highest in AC (20 ± 0.5 species/sample), similar between NR (16 ± 0.2 species/sample) and TR (16 ± 0.4 species/sample) and lowest in RR (11 ± 0.3 species/sample) (data not shown).

When considering biomass, there was a significant interaction between season and site (Table 3) indicating that patterns of seasonal variation were different between sites. Despite this interaction, there were significant and consistent differences among reef types throughout the study (Table 3; Fig. 3). Overall, AC showed the highest values (78 ± 5.6 g/m²), while TR (41 ± 9.0 g/m²), RR (22 ± 1.9 g/m²), and NR (20 ± 1.7 g/m²) showed lower and similar values except for a peak in TR during winter (103 ± 38.0 g/m²) (Fig. 3).

3.4. Environmental characteristics

When analyzing both *intrinsic* and *in situ* environmental variables, both together and apart, there was a significant interaction between the two random factors visits and site, and a significant interaction between season and reef type (Table 4) suggesting that patterns of seasonal variation of environmental variables was different among reef types. Since only *in situ* variables changed through time, the observed *season x reef type* interaction could only have been caused them, though their contribution was overshadowed by *intrinsic* characteristics as those shown by correlation vectors in Fig. 4.

Overall, RR had the most clearly clustered centroids, suggesting high similarity in the environmental characteristics at those sites, including having the smallest size (i.e., smallest *surface area*, *reef height*, *max diameter*, and *perpendicular to max diameter*) (Fig. 4). The shipwreck site RRD (AC) and site SAN (TR) were characterized by being farthest away from a drop-off and from the shore. Sites belonging to NR were overall older and larger than all other sites.

Spatial variation between *in situ* variables alone were not as clear (Fig. 4) though they suggest that RR and TR were in shallower areas, prone to stronger currents, and had a smaller volume area sampled (due to being shallower and therefore having a smaller *SPC cylinder volume*). Sites belonging to AC and NR tended to be deeper than RR and TR and had weaker currents.

3.5. Environmental-biological relationships

BIOENV analyses revealed that a combination of six environmental variables: *reef shape*, *relative rugosity*, *distance to slope*, *surface area*,

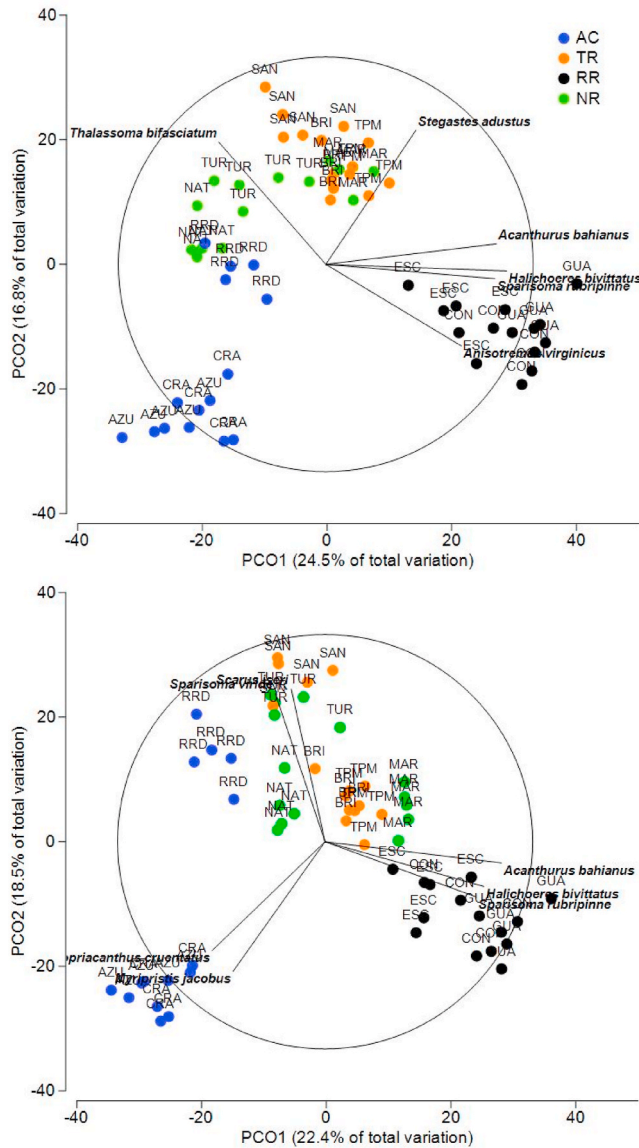


Fig. 2. Principal coordinates analysis (PCO) of Bray-Curtis similarity among centroids per season (April 12, 2018 (Spring 18') to June 12, 2019 (Spring 19')) and site (n = 12) for abundance (top) and biomass (bottom) of fourth root transformed data standardized by total of the sample. Vectors represent species (*italic*) best correlated (>75%) with the axes of the PCO. Black = restoration reef (RR), blue = accidental reef (AC), orange = transplanted reef (TR), and green = natural reef (NR). Labels represent site abbreviations (Fig. 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

visibility and depth, were best correlated for both abundances (Rho = 0.81; p = 0.01) and biomass (Rho = 0.81; p = 0.01) centroids. Using these six variables, LINKTREE analyses revealed that at the most significant levels (B% > 50) neither of the two *in situ* variables (i.e., depth or visibility) explained spatial patterns in fish assemblages (Fig. 5). For both abundance and biomass, *intrinsic* variables mostly explained biological patterns of fish assemblages at our sites, especially for RR and AC.

Nodes C and A for abundance and biomass, respectively (Fig. 5), were partitioned solely by differences in distance to slope, suggesting that fish assemblages at these three sites were strongly influenced by their proximity to a drop-off and, possibly, to each other. In all other nodes, however, several factors simultaneously explain the split at the same branches. Therefore, unequivocal identification of the specific factor(s) responsible for the split is not possible due to lack of replicates at the

Table 3

Univariate Permutational Multivariate Analyses of Variance (PERMANOVA) based on Euclidean distances of abundance (top) and biomass (bottom) densities standardized by area of the sample (i.e., *SPC Cylinder Area*), and number of species per sample (middle) based on a mixed multifactorial model. The probabilities associated with each pseudo-F value were obtained with 9999 permutations of residuals under a reduced model. Numbers in **bold** indicate interpretable significant sources of variation. Factors are season (Se), reef type (Re), visit number (Vi) and site (Si).

Source	Abundance (no. individuals/m ²)			
	df	MS	Pseudo-F	P(perm)
Se	4	2.1837	2.333	0.0314
Re	3	21.845	3.0374	0.0126
Vi(Se)	11	0.52248	0.74831	0.6605
Si(Re)	8	7.1585	10.274	0.0001
SexRe	12	1.191	1.0541	0.4126
SexSi(Re)	32	0.9674	1.3863	0.153
Vi(Se)xRe**	30	0.8652	1.238	0.2291
Vi(Se)xSi(Re)**	62	0.69963	1.2157	0.1972
Res	349	0.57549		
Total	511			
Source	Species/sample			
	df	MS	Pseudo-F	P(perm)
Se	4	94.145	2.6658	0.0178
Re	3	1120.8	6.1736	0.0002
Vi(Se)	11	29.514	2.0054	0.0435
Si(Re)	8	180.38	12.291	0.0001
SexRe	12	10.487	0.60183	0.9573
SexSi(Re)	32	22.213	1.5105	0.0801
Vi(Se)xRe**	30	19.075	1.2945	0.198
Vi(Se)xSi(Re)**	62	14.756	1.303	0.0751
Res	349	11.324		
Total	511			
Source	Biomass (kg/m ²)			
	df	MS	Pseudo-F	P(perm)
Se	4	17397	3.1985	0.0049
Re	3	75904	8.9763	0.0001
Vi(Se)	11	3052.9	1.1352	0.3449
Si(Re)	8	7544	2.7978	0.0167
SexRe	12	5355.3	1.1742	0.2748
SexSi(Re)	32	5011.6	1.8622	0.0485
Vi(Se)xRe**	30	2016.4	0.75063	0.7871
Vi(Se)xSi(Re)**	62	2682.7	0.82013	0.7959
Res	349	3271.1		
Total	511			

scale of sites. For example, in the abundance LINKTREE (Fig. 5, top), the branching node A suggests either “reef shape = shipwreck” or “distance to slope” are responsible for the separation of RRD from the other sites. Since both these factors (shipwreck and specific distance to slope) are unique to RRD, lack of replication renders it impossible to distinguish which factor (or combination) has the strongest effect. A similar case happened in node B in the biomass LINKTREE (Fig. 5, bottom) between “reef shape” and “surface area”; all RR had the same exact shape and the lowest surface areas overall. However, it is evident that sites within the same reef type mostly grouped together, with TR and NR showing the greatest overlap.

4. Discussion

Since different artificial reef (AR) types are deployed under different environmental conditions and are built with different materials and shapes depending on the purpose for which they were built, some of the recorded environmental variables (e.g. reef age, reef shape, reef size) are nested within the reef type. Therefore, our study sites should not be considered to be fully interspersed (Hurlbert, 1984) and our experimental design does not allow for unequivocal determination of what specific *intrinsic* or *in situ* environmental variable (or combination of them) drove the observed spatial patterns in fish assemblages

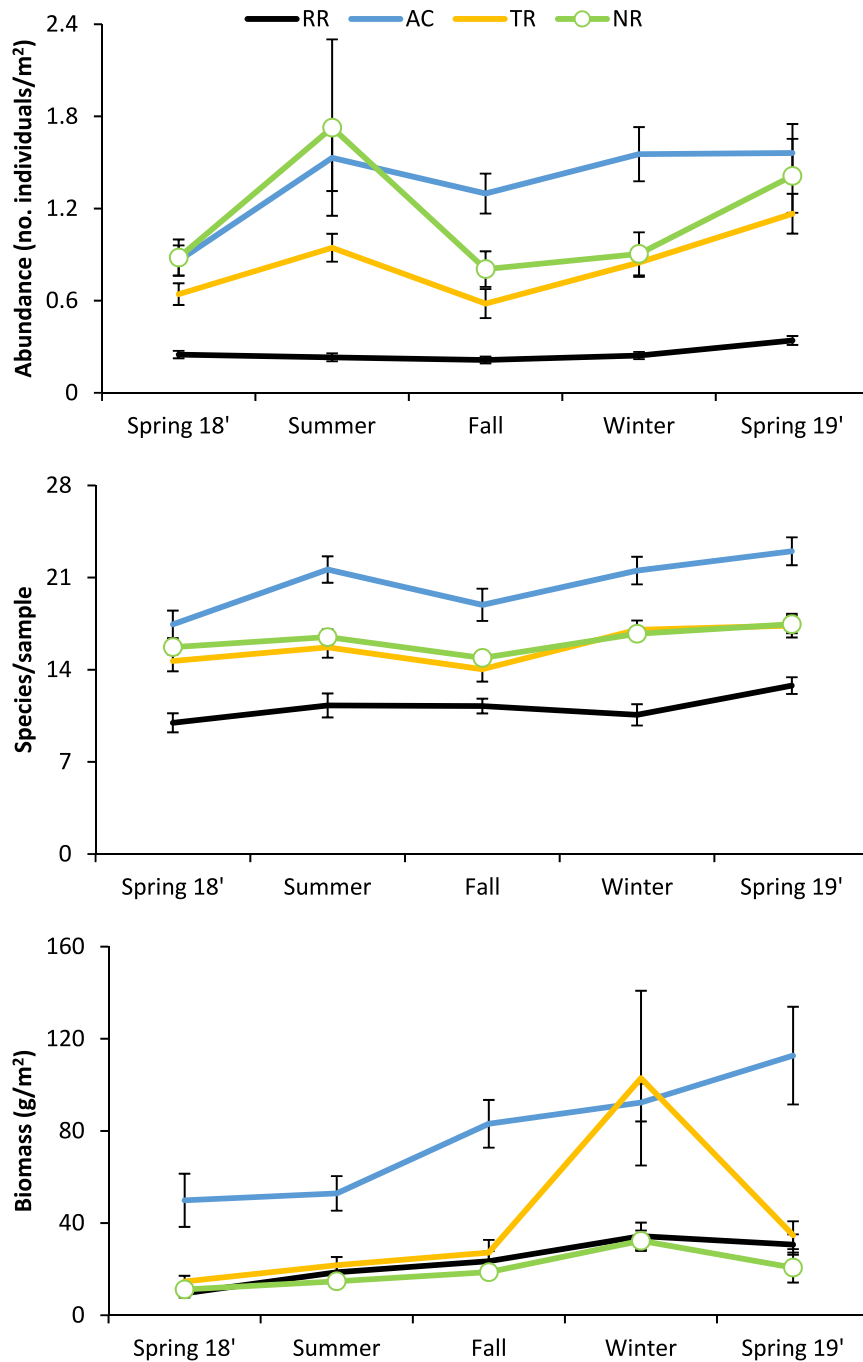


Fig. 3. Abundance (top), number of species per sample (middle), and biomass (bottom) from April 12, 2018 (Spring 18') to June 12, 2019 (Spring 19') at four different reef types. Black = restoration reef (RR), blue = accidental reef (AC), orange = transplanted reef (TR), and green = natural reef (NR) (Table 1). Error bars denote standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Underwood, 1990).

For example, when interpreting our results, one must consider the differences between the age of deployment of the different AR types, and therefore the influence of time in successional processes, mainly those affecting changes in abundance, diversity and biomass values over time (Santos et al., 2011; Arena et al., 2007). It's been generalized that artificial reefs achieve a relatively stable assemblage structure within one to five years (Bohnsack et al., 1991). In this study, accidental reefs (AC) have been submerged for longer (≥ 45 years) than restoration reefs (RR; 10–18 years), and these in turn were older than transplanted reefs (TR; 3–9 years). The observed differences in fish assemblage structure across

reef types might be strongly influenced by reef age and other variables that affect ecological succession at specific sites (e.g., identities and life history traits of the first colonizing fish species, rate of colonization, degree of isolation from other habitats, etc.; see Bohnsack et al., 1991). However, to address this, full interspersed for this mensurative study would require that additional sites belonging to all four reef types be randomly distributed in time and space, across a fixed range of environmental gradients (e.g., similar and different-aged reefs of the same shape and size replicated across different depths). Two ways to achieve this are: 1) large scale manipulative experiments that target specific *intrinsic* and/or *in situ* variables, or 2) long term-monitoring of a much

Table 4

Univariate PERMANOVA based on Euclidean distances of environmental data (Table 1) using non-categorical data that includes both *intrinsic* and *in-situ* variables (left) and using only *in situ* variables (right). Analyses used 9999 permutations of residual under a reduced model to construct null hypotheses. All variables were normalized, and the following variables were transformed using Log (V+1): *Dist. Shore*, *Dist. Slope*, *Height*, *Surface Area*, *Year*, and *Age*. Depth and visibility were square root transformed. Numbers in **bold** indicate interpretable significant sources of variation. Factors are season (Se), reef type (Re), visit number (Vi) and site (Si).

Source	<i>Intrinsic + in situ</i> variables				<i>In situ</i> variables			
	df	MS	Pseudo-F	P (perm)	df	MS	Pseudo-F	P(perm)
Se	4	62.644	1.9219	0.0003	4	57.812	1.8461	0.0003
Re	3	2582.5	3.1595	0.0001	3	343.93	3.2181	0.0001
Vi(Se)	11	20.881	0.81787	0.8576	11	20.62	0.81998	0.8471
Si(Re)	8	865.75	34.281	0.0001	8	100.68	4.0476	0.0001
SexRe	12	58.879	1.5454	0.0001	12	53.953	1.4898	0.0003
SexSi(Re)	32	32.862	1.2908	0.0215	32	31.538	1.2578	0.035
Vi(Se)xRe**	30	23.653	0.92193	0.7386	30	23.265	0.92066	0.7418
Vi(Se)xSi(Re)**	62	25.797	10.287	0.0001	62	25.408	10.432	0.0001
Res	349	2.5078			349	2.4356		
Total	511				511			

larger cohort of existing artificial and natural reef sites across replicated environmental gradients. This would allow a stronger interpretation of whether reef type and their respective *intrinsic* variables, are indeed the main factors influencing fish assemblages at these sites. However, these are far-beyond the scope of this study which aims solely to: 1) describe the actual state of fish assemblages associated to the four reef types, 2) compare fish assemblage structure among those reef types, and 3) provide recommendations to improve conservation strategies.

The factor reef type consistently explained the observed spatial differences in fish assemblages regardless of the region (i.e., *coast*), location of our study sites, or expected natural variation. The high concentration of marine life and uniqueness of some ARs is highlighted, with AC having the highest recorded abundances, number of species, and biomass among all reef types. Additionally, all three ARs (RR, TR, and AC) were relatively easy to access, and offered a unique setting for underwater activities like SCUBA. These features have been shown to attract divers and divert attention from overutilized natural coral reef areas (Kirkbride-Smith et al., 2013; Shani et al., 2012; Stolk and Markwell, 2007) highlighting their potential to be promoted to enhance tourism activities at these sites and encourage conservation.

The physical characteristics of the reef (i.e., construction material, shape, arrangement, etc.) can significantly affect biological assemblages at reef sites (Bohnsack, 1991; Sheng, 2000; Precht, 2006; Bohnsack et al., 1991). For example, the amount and height of vertical surfaces and potential refuges due to increased rugosity and complexity are known to influence species composition (Opel et al., 2017; Gratwicke and Speight, 2005; Sheng, 2000) and could explain the overall higher values in AC, including the higher biomass of zooplanktivores like *H. cruentatus* and *M. jacobus* (Champion et al., 2015). Therefore, disparities in fish assemblages between AC and other reef types are likely to persist, and should be expected, as long as their habitat structure and composition remain different (Fowler and Booth, 2012; Arena et al., 2007).

Differences in *reef shape* and other *intrinsic* environmental variables (Fig. 5) also better explain why fish assemblages in AC sites at Crash Boat Beach (CRA) and Muelle de Azúcar (AZU) were so different from RRD and from nearby NR (El Natural) and TR (Bridges) (Fig. 1). Although differences in geographic location can have a strong influence over fish assemblages (Ambrose and Swarbrick, 1989), LINKTREE analyses showed that, not differences in *coast* (west vs east), but environmental differences in *reef shape* (dock + metal scraps vs shipwreck), *distance to drop-off* (close vs far), *distance to mangrove* (close vs far), or a combination of these factors, that were *intrinsic* to either CRA + AZU or RRD, respectively, better explained differences in fish assemblages observed between these AC sites.

Fish assemblages in RR remained different from all other reef types in terms of abundance and biomass (Fig. 2). Interestingly, a similar pattern was observed for RR centroids in the environmental PCO

(Fig. 4), suggesting that RR are exposed to a consistently different set of environmental variables than other reef types. The unique combination of *intrinsic* and *in situ* environmental variables to which they are exposed could account for RR consistently showing the lowest abundances and average number of species per sample than the other reef types (Bohnsack, 1991; Bohnsack et al., 1991) and could suggest that RR are purposely deployed on sites with similar environments due to their intended purpose. Conversely, the combination of environmental variables at these sites could also account for RR having a unique reef fish assemblage, especially sustaining the highest abundances and biomass of two (*H. bivittatus* and *S. rubripinne*) out of the three species (and *A. tractus*) that were relatively common at all sites and were largely responsible for the spatial patterns observed in both PCOs (Fig. 2; Supplementary Fig. 1). Both *H. bivittatus* and *S. rubripinne* inhabit a wide range of habitats from reefs, rocks, and soft muddy and feed on either benthic macroalgae and seagrasses (*S. rubripinne*) or on benthic invertebrates common to seagrass beds (*H. bivittatus*) (Smithsonian Tropical Research Institute, 2015), all of which were found in greater proportion in RR than in other sites (Fig. 4). Aggressive interactions with territorial damselfish can also affect spatial distribution of *H. bivittatus* populations (Jones, 2005), which could explain higher *H. bivittatus* abundances in places with low numbers of damselfish, such as the case of RR which had the 2nd lowest abundances of the dusky damselfish (*Stegastes adustus*) (Supplementary Fig. 2).

The exclusive fish assemblages at RR and AC suggest these ARs are providing unique habitat characteristics that may not be found on surrounding NR (Arena et al., 2007; Clynick et al., 2008; Becker et al., 2016). Therefore, like RR, AC also behave as their own unique reef type, highlighting their potential to offer a unique environment to enhance the diving experience at areas of easier access than to “pristine” natural sites, and to redistribute tourists away from natural reef locations and generate higher revenues (Stolk and Markwell, 2007). However, it is important to consider that AZU is a heavily degraded sugar pier located on private property, and therefore warrants further research and physical restoration of the structure if adequate management and safe use of the structure is desired (Caballero, 2013). Considering that ARs are prone to overfishing if not adequately managed (Polovina, 1991a,b) promoting fishing and other extractive activities at these sites would require additional research and careful examination that is beyond the scope of this study, though people that specifically target lionfish (*Pterois* spp.) could benefit from these sites (Smith and Shurin, 2010).

Despite evident environmental differences between TR and RR (Fig. 4), similarities in fish assemblages between these reef types (Fig. 2) can be expected since *Acropora* sp restoration projects tend to happen in areas where naturally occurring reef populations have been degraded in some way (Lirman et al., 2010; Young et al., 2012). An event of abnormally high abundances of large *S. viride* individuals at TR site SAN was detected during winter and could therefore be largely responsible of

Table 5

Sets of explanatory environmental variables for LINKTREE analyses (Fig. 5) of abundance (left) and biomass (right) data of fish assemblages among centroids per season (Spring 18' – Spring 19'; n = 5) and site (n = 12). Units of measurement for each environmental variable are given in Table 1.

Abundance	Biomass
A: R = 0.56; B% = 80; Reef Shape (ship = SH) < -0.299 (> 3.29) or Distance to slope < -1.32 (> 2.28)	A: R = 0.53; B% = 80; Reef Shape (dock = DK) < -0.443 (> 2.22)
B: R = 0.61; B% = 69; Reef Shape (Reef Ball/Taino Reef = RB) > 1.72 (< -0.573) or Surface area (m ²) < -1.12 (> -0.518)	B: R = 0.61; B% = 81; Reef Shape (ship = SH) < -0.299 (> 3.29) or Distance to slope < -1.32 (> 2.28)
C: R = 0.78; B% = 58; Distance to slope > -0.585 (< -0.96)	C: R = 0.68; B% = 64; Reef Shape (Reef Ball/Taino Reef = RB) > 1.72 (< -0.573) or Reef Shape (coral reef = CR) < -0.992 (> 0.992)
D: R = 1.00; B% = 52; Reef Shape (dock = DK) < -0.443 (> 2.22) or Relative Rugosity (Low) > 1.72 (< -0.573) or Reef Shape (coral reef = CR) > 0.992 (< -0.992) or Surface area (m ²) > 0.964 (< -0.0947) or Distance to slope < -1.08 (> -1.07)	D: R = 0.53; B% = 28; Distance to slope < -0.395 (> 0.0181)
E: R = 0.94; B% = 10; Relative Rugosity (High) > 1.4 (< -0.701) or Relative Rugosity (Med) < -0.838 (> 1.17) or Depth (m) > 1.51 (< -0.885) or Surface area (m ²) > 0.0947 (< -0.518) or Distance to slope > -0.96 (< -1.07)	E: R = 0.58; B% = 9; Visibility (m) < -1.46 (> -0.916)
F: R = 0.67; B% = 5; Depth (m) > 1.58 (< 1.51)	F: R = 1.00; B% = 3; Depth (m) < -0.713 (> -0.668)
G: R = 1.00; B% = 3; Visibility (m) < 1.01 (> 1.54)	G: R = 0.69; B% = 25; Depth (m) > -1.04 (< -1.11)
H: R = 1.00; B% = 2; Visibility (m) > -0.0505 (< -0.699)	H: R = 0.56; B% = 44; Visibility (m) > -0.456 (< -0.678)
I: R = 0.92; B% = 4; Visibility (m) > 2.3 (< 1.47) or Depth (m) < 0.647 (> -0.787)	I: R = 1.00; B% = 13; Visibility (m) < -1.09 (> -0.855)
J: R = 0.75; B% = 3; Depth (m) < 0.79 (> -0.816)	J: R = 0.92; B% = 13; Relative Rugosity (Low) < -0.573 (> 1.72) or Relative Rugosity (Med) > 1.17 (< -0.838) or Depth (m) > 0.095 (< -1.04) or Distance to slope < 0.0181 (> 0.189)
K: R = 1.00; B% = 3; Depth (m) > 0.763 (< 0.322)	K: R = 0.67; B% = 8; Depth (m) > 0.107 (< 0.095)
L: R = 0.56; B% = 1; Depth (m) < 1.06 (> -1.28)	L: R = 0.56; B% = 5; Visibility (m) < -0.834 (> -0.456) or Depth (m) < 0.333 (> 0.607)
M: R = 1.00; B% = 1; Visibility (m) < 1.04 (> 2.76) or Depth (m) < 0.871 (> 1.06)	M: R = 1.00; B% = 4; Depth (m) < 0.153 (> 0.333)
N: R = 0.84; B% = 31; Relative Rugosity (High) > 1.4 (< -0.701) or Relative Rugosity (Med) < -0.838 (> 1.17) or Distance to slope > 0.93 (< -0.2)	N: R = 0.66; B% = 42; Relative Rugosity (High) > 1.4 (< -0.701) or Distance to slope > 0.93 (< -0.2)
O: R = 1.00; B% = 14; Depth (m) > 0.883 (< -0.885) or Surface area (m ²) > 1.03 (< -0.194) or Distance to slope < 0.93 (> -1.32)	O: R = 0.89; B% = 42; Relative Rugosity (Low) < -0.573 (> 1.72) or Relative Rugosity (Med) > 1.17 (< -0.838) or Depth (m) < -0.276 (> 0.322) or Distance to slope > -0.585 (< -1.08)
P: R = 1.00; B% = 6; Visibility (m) > -0.0122 (< -0.0505) or Depth (m) > 0.912 (< 0.883)	P: R = 0.56; B% = 15; Depth (m) > -0.854 (< -0.864)
Q: R = 1.00; B% = 3; Depth (m) > 1.27 (< 0.912)	Q: R = 0.75; B% = 12; Distance to slope < -0.585 (> -0.2)
R: R = 1.00; B% = 2; Depth (m) > 1.46 (< -1.27) or Visibility (m) < 0.316 (> -0.348)	R: R = 0.33; B% = 2; Visibility (m) < -0.324 (> 0.198)
S: R = 0.83; B% = 6; Depth (m) > -0.885 (< -0.893)	S: R = 1.00; B% = 3; Depth (m) > -1.08 (< -1.09)
T: R = 0.78; B% = 3; Visibility (m) > 0.812 (< 0.707)	T: R = 0.42; B% = 9; Depth (m) > -0.903 (< -0.903)
U: R = 1.00; B% = 1; Depth (m) > -0.893 (< -1.01)	U: R = 0.00; B% = 8; Visibility (m) < -0.602 (> 0.488) or Depth (m) > -0.903 (< -0.953)
V: R = 0.72; B% = 14; Surface area (m ²) > 1.42 (< 0.663) or Depth (m) > -0.854 (< -0.864)	V: R = 0.42; B% = 3; Depth (m) > -0.479 (< -0.821)

Table 5 (continued)

Abundance	Biomass
W: R = 0.82; B% = 9; Distance to slope < -0.585 (> -0.2) or Surface area (m ²) < 0.588 (> 0.663)	W: R = 1.00; B% = 3; Depth (m) > -0.342 (< -0.479)
X: R = 0.33; B% = 2; Visibility (m) > -0.385 (< -0.916)	X: R = 1.00; B% = 3; Depth (m) > 1.06 (< 0.871)
Y: R = 1.00; B% = 2; Depth (m) < -1.04 (> -1.01)	Y: R = 1.00; B% = 0; Visibility (m) < 1.04 (> 2.48) or Depth (m) > 0.763 (< 0.322)
Z: R = 1.00; B% = 1; Depth (m) > -1.09 (< -1.22) or Visibility (m) < 0.198 (> 0.257)	Z: R = 1.00; B% = 14; Depth (m) > 0.883 (< -0.885) or Distance to slope < 0.93 (> 1.32)
AA: R = 0.42; B% = 6; Depth (m) < -1.09 (> -0.953)	AA: R = 1.00; B% = 6; Visibility (m) > -0.0122 (< -0.0505) or Depth (m) > 0.912 (< 0.883)
AB: R = 0.25; B% = 6; Visibility (m) < -0.602 (> 0.488)	AB: R = 1.00; B% = 3; Depth (m) > 1.27 (< 0.912)
AC: R = 0.92; B% = 3; Depth (m) > -0.479 (< -0.821)	AC: R = 0.00; B% = 1; Depth (m) > 1.46 (< 1.27) or Visibility (m) < 0.316 (> 0.348)
AD: R = 1.00; B% = 1; Depth (m) > -0.342 (< -0.479)	AD: R = 0.50; B% = 6; Depth (m) > -0.885 (< -0.893)
AE: R = 0.59; B% = 23; Distance to slope < -0.395 (> 0.0181) or Surface area (m ²) > -1.12 (< -1.25)	AE: R = 0.56; B% = 4; Visibility (m) > 0.812 (< 0.707)
AF: R = 0.67; B% = 9; Visibility (m) < -1.46 (> -0.916)	AF: R = 1.00; B% = 3; Depth (m) > -0.893 (< -1.01)
AG: R = 0.00; B% = 4; Visibility (m) > -1.46 (< -1.67) or Depth (m) > -0.713 (< -0.759)	AG: R = 0.75; B% = 15; Depth (m) < 0.322 (> 0.354)
AH: R = 0.66; B% = 20; Relative Rugosity (Low) < -0.573 (> 1.72) or Relative Rugosity (Med) > 1.17 (< -0.838) or Depth (m) > 0.095 (< -1.04) or Surface area (m ²) > -1.25 (< -1.97) or Distance to slope < 0.0181 (> 0.189)	AH: R = 1.00; B% = 8; Visibility (m) < -1.21 (> -1.18)
AI: R = 1.00; B% = 9; Depth (m) > 0.107 (< 0.095)	AI: R = 0.94; B% = 9; Relative Rugosity (High) > 1.4 (< -0.701) or Relative Rugosity (Med) < -0.838 (> 1.17) or Depth (m) > 1.51 (< -0.885) or Distance to slope > -0.96 (< -1.07)
AJ: R = 0.78; B% = 5; Visibility (m) < -0.834 (> -0.456) or Depth (m) < 0.333 (> 0.607)	AJ: R = 0.33; B% = 4; Visibility (m) < 1.01 (> 1.54)
AK: R = 1.00; B% = 3; Depth (m) < 0.153 (> 0.333)	AK: R = 0.78; B% = 5; Depth (m) > 1.58 (< 1.51)
AL: R = 0.42; B% = 24; Visibility (m) > -0.456 (< -0.678)	AL: R = 1.00; B% = 3; Depth (m) > 1.7 (< 1.58)
AM: R = 1.00; B% = 12; Visibility (m) < -0.916 (> -0.855)	AM: R = 0.50; B% = 3; Visibility (m) > 2.3 (< 1.47) or Depth (m) < 0.647 (> 0.787)
AN: R = 1.00; B% = 16; Depth (m) < 0.322 (> 0.354)	AN: R = 0.50; B% = 2; Depth (m) < 0.79 (> 0.816)
AO: R = 1.00; B% = 6; Visibility (m) < -1.21 (> -1.18)	

the high variability observed at TR and have been strong enough to cause the observed interaction between season and reef type in biomass analysis. The greater presence and size of parrotfish at TR sites is expected, however, considering they are known herbivores that feed on plants, algae and corals (Smithsonian Tropical Research Institute, 2015; Froese and Pauly, 2019), a combination that was overall more abundant in TR than in other reef types (Fig. 4).

By showing similar fish assemblages to NR, our results support the thesis that TR can provide benefits for conservation (Lirman and Schopmeyer 2016) by helping to mimic natural fish assemblages. Coral gardening and TR projects in the Caribbean and western Atlantic have contributed to the rapid creation of fish and invertebrate habitat on depleted reefs, a process that would take decades through natural processes alone (Bostrom-Einarsson et al., 2020). Additionally, in the Dominican Republic, the Punta Cana Ecological Foundation (<http://www.puntacana.org/>) initiated a coral gardening program that has increased employment and tourism opportunities (Lirman and Schopmeyer, 2016; Galvan, 2016). Furthermore, there is a general consensus that coral gardening projects using *Acropora* spp. can be successfully

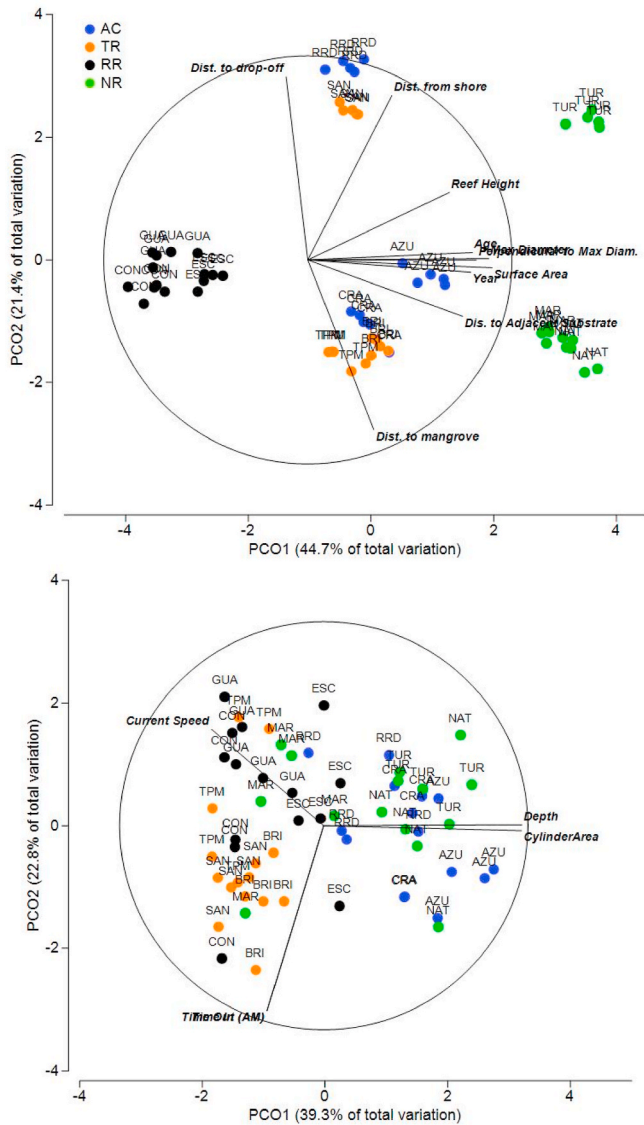


Fig. 4. Principal coordinates analysis (PCO) from Euclidean distances among centroids per season (April 12, 2018 = Spring 18' to June 12, 2019 = Spring 19'; n = 5) and site (n = 12) of transformed and normalized non-categorical (both *intrinsic* and *in situ*) environmental data (top; Pearson correlation (>0.75) vectors) and using only *in situ* environmental variables (bottom; Pearson correlation (>0.65) vectors). Distance from shore, distance to slope, reef height, hard surface area, year, and age were Log(V+1) transformed, depth and visibility were square root transformed. All data was normalized. Black = restoration reef (RR), blue = accidental reef (AC), orange = transplanted reef (TR), and green = natural reef (NR). Labels represent site abbreviations (Fig. 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

implemented at relatively low costs with readily available materials, making it one of the most effective management tools for reef restoration (Young et al., 2012; Bostrom-Einarsson et al., 2020). Our results support the continuous use of TR to restore specific functions of NR, especially those targeted towards conservation of reef fish assemblages to restore NR function. However, in order to determine whether TR effectively restore NR function, there need to be manipulative experiments that show changes in fish assemblage structure in NR after a disturbance event, which are reduced or mitigated after TR deployment, especially when compared to control sites where no restoration occurred. However, achieving substantial recovery of marine habitats, especially coral reefs, in the next coming decades will require that major pressures,

especially accelerated climate change, are mitigated (Duarte et al., 2020). Therefore, neither TR deployment, nor any other active restoration strategy, should be seen as a “silver bullet” to restore coral reef habitats, but as a tool to be combined with other restoration and mitigation strategies to achieve or exceed the desired outcomes (Bostrom-Einarsson et al., 2020; Duarte et al., 2020; Abelson, 2006).

Overall, the factor reef type consistently explained the observed spatial differences in fish assemblages regardless of the region (i. e. coast), study site, or expected natural variation. Although site-specific dynamics played a significant role in driving patterns of fish assemblages (Olds et al., 2012; Opel et al., 2017), our experimental design did not allow for unequivocal determination of what site-specific environmental processes (or combination of them) drove the observed spatial patterns in fish assemblages (Underwood, 1990). The variety of materials used for artificial habitats and the range of environmental conditions in which they are deployed make generalizations on ecological processes difficult (Bohnsack et al., 1991; Paxton et al., 2020). Other factors that were not considered in our study (e.g., temperature, fish extraction or movement, nutrient levels, trophic diversity) could have also influenced the observed differences in fish assemblages (Lefcheck et al., 2019; Opel et al., 2017; Seaman, 2000). What is noteworthy, however, is that differences among reef types were larger than natural variation at the scale of sites and sampling units in our study. These results were consistent with those reported in very different ecosystem and regions (Clynick et al., 2008; Becker et al., 2016; Opel et al., 2017) and contrast others (Walker et al., 2002; Carr and Hixon, 1997).

4.1. Implications for management

If managers aim to restore or increase the goods and services provided by different reefs (NR or ARs), it is important to understand how the different reef types function, in terms of the biological assemblages associated to them, and the purpose(s) for which they were originally built (in the case of ARs). Descriptions of biological patterns are a necessary first step to understand reef function, but cause-consequence relationships can only be identified by large scale manipulative experiments (Underwood, 1990; Hurlbert, 1984). Considering that at the scale of restoration manipulative experiments can be logistically challenging (Bayraktarov et al., 2019), including artificial reef sites into long-term monitoring programs, such as the Puerto Rico Coral Reef Monitoring Program (PRCRMP) (DRNA, 2020) or the National Coral Reef Monitoring Program (NCRMP) (NOAA, 2020), could help address this issue and improve our understanding about the success or failure of past and present reef restoration efforts (Becker et al., 2016; Bostrom-Einarsson et al., 2020). Adequate management, informed by long term monitoring, could then be used to enhance the resilience of reef communities while promoting sustainable use over reef areas, either NR or ARs (Seaman, 2000; Garcia-Sais et al., 2015; Bayraktarov et al., 2019).

Active restoration strategies alone are unlikely to serve as a “one size fits all” tool for biological restoration despite their well-known benefits (Paxton et al., 2020). If the aim of reef restoration is to return a degraded reef to its original ecosystem function and provision of ecosystem services (Wiens and Hobbs, 2015; Young et al., 2012), management plans should also consider both the spatial and temporal environmental patterns at the smallest scales (Cruz-Motta et al., 2020), and a combination of restoration strategies tailored to reef type- and site-specific needs (Abelson, 2006; Bostrom-Einarsson et al., 2020). Management strategies that account for small scale processes have been shown to be more effective than region-wide management plans (McLeod et al., 2019; Cruz-Motta et al., 2020). However, mitigating the drivers of ecosystem degradation, especially accelerated climate change, are also imperative for rebuilding marine life (Duarte et al., 2020; Bostrom-Einarsson et al., 2020; Hoegh-Guldberg et al., 2017). Nevertheless, the uniqueness and current function of artificial reefs in Puerto Rico is highlighted, as well as their potential to enhance conservation and economic activity in those areas, especially tourism and SCUBA diving and other non-extractive

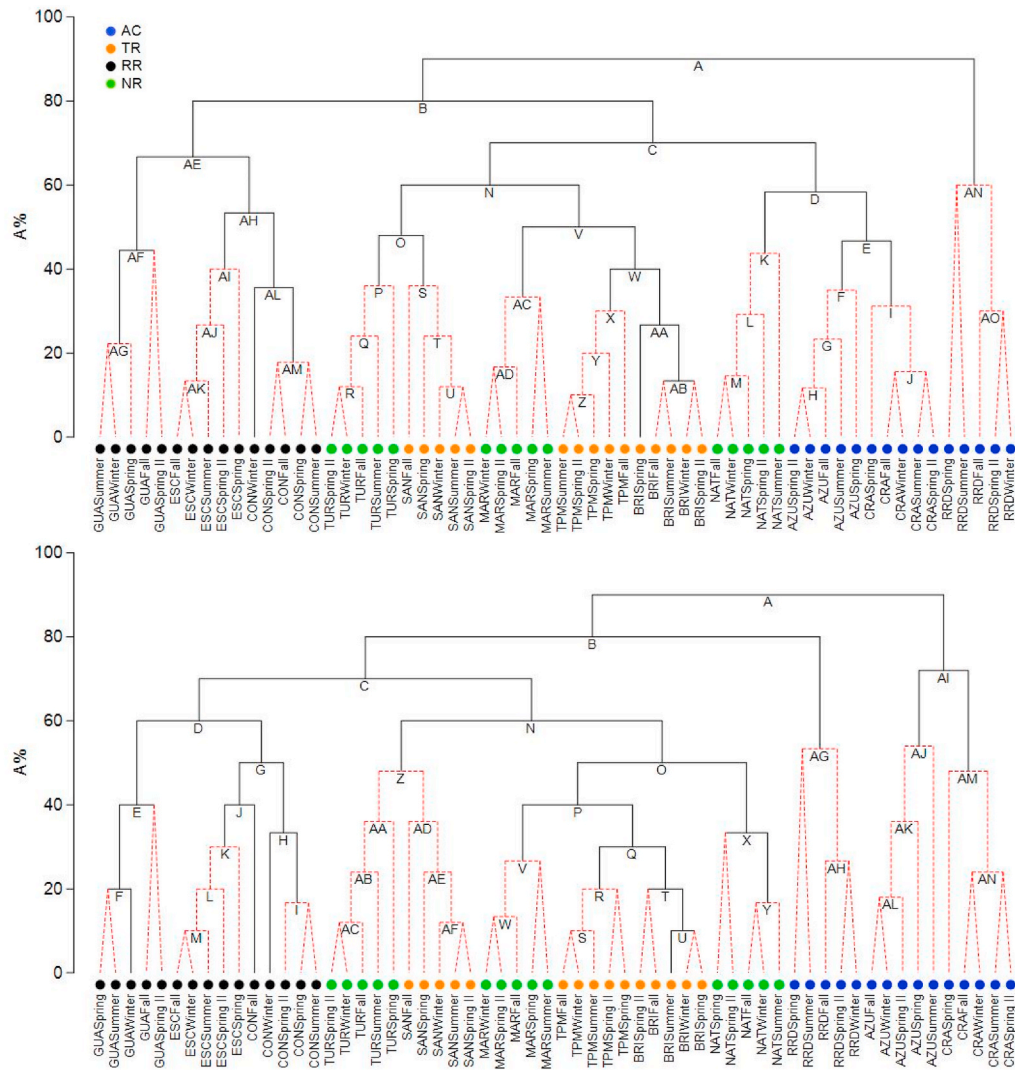


Fig. 5. Linkage tree constructed using fish species abundances (top; n = 158 species) and biomass (bottom; n = 117 species) among centroids per season (Spring 18' – Spring 19'; n = 5) and site (n = 12). Capital letters in branching nodes show environmental variables that explain the split between centroids (Table 5). Units of measurement for each environmental variable are given in Table 1. Black = restoration reef (RR), blue = accidental reef (AC), orange = transplanted reef (TR), and green = natural reef (NR). Labels represent season x site (reef type) centroid abbreviations (Fig. 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

uses.

Contributors

Nieves-Ortiz had the conception of the study and was the main data collector and drafter of the manuscript. Experimental design and analyses were optimized by Cruz-Motta. Weil and Ruiz contributed to the acquisition of data for NR and TR. Appeldoorn, and Cruz-Motta critically revised the article, and aided in interpretation of the data. All authors provided comments and approved the final version.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Manuel A. Nieves-Ortiz reports financial support was provided by National Science Foundation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ocecoaman.2021.105901>.

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