

Fish assemblages of three common artificial reef designs during early colonization



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ABSTRACT

In this study, we compared the early fish colonization of three types of artificial reefs deployed in the coastal waters of Saba and St Eustatius in the Caribbean: reef balls®, layered cakes and piles of locally obtained basaltic rock. As an indicator of performance, three fish assemblage parameters (abundance, biomass, species richness) were measured using underwater visual censuses at 11 months post-deployment and 4 months after restoration from hurricane damage. All artificial reef plots showed higher values for fish abundance, biomass and species richness than control plots covered by bare sand, which shows that artificial reefs can locally enhance the fish assemblage. However, the effect differed among artificial reef plots. Fish abundance was 3.8 times higher on the layered cake plots compared to the reef ball plots, while fish biomass was 4.6 times higher. Rock pile plots had intermediate values. Species richness did not differ significantly among different artificial reef plots. Three-dimensional modelling revealed that layered cakes had a smaller gross volume, shelter volume and total surface area than reef balls. The availability of multiple small shelters in the layered cake design appeared to be more relevant than other physical parameters, as the layered cake plots had higher fish abundance than the reef balls plots. We concluded that on Saba and St. Eustatius, layered cake plots performed better than reef ball plots after one year of colonization. Rock pile plots, made of local volcanic rock, showed an intermediate performance, and were 4–10 times cheaper to construct. If observed differences are consistent with other locations and persist during further colonization, current efforts to deploy reef balls could better be allocated to deploy artificial reef structures with a higher shelter density.

1. Introduction

Coral reefs are among the most productive ecosystems on earth (e.g. Odum and Odum, 1955) and millions of people depend on their ecosystem services (Moberg and Folke, 1999). These services are partly the result of the reef's complex framework, which provides a three-dimensional habitat with many niches and refuges from predation. Stony corals, the main architects of the reef framework, are adversely affected by local stressors and climate change and their abundance is declining worldwide (Bellwood et al., 2004). In the Caribbean, the degradation of coral reefs began in earnest in the 1980s (Hughes, 1994), when diseases

decimated the most important herbivore *Diadema antillarum* (Lessios et al., 1984) and dominant reef building corals of the genus *Acropora* (Gladfelter, 1982; Aronson and Precht, 2001). The ecological extinction of *Diadema* and *Acropora* led to an increase in macroalgae (Hughes, 1994; Jackson et al., 2014) and cyanobacterial mats (De Bakker et al., 2017), both groups inhibiting coral recruitment and preventing natural recovery of the reefs (McCook et al., 2001). Other threats, such as hurricanes and periods of higher than average seawater temperatures, further reduced Caribbean coral cover, until by 2014 less than 20% remained (Gardner et al., 2003; Jackson et al., 2014). The large-scale disappearance of corals as the main ecosystem engineers of reefs

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resulted in a substantial loss of three-dimensional structure (so-called “flattening” of the reef) (Alvarez-Filip et al., 2009). Without its three-dimensional framework, refuge opportunities are reduced and this resulted in a measurable reduction of fish abundance (Paddack et al., 2009), biomass (Rogers et al., 2014), biodiversity (Newman et al., 2015) and fisheries productivity (Rogers et al., 2014, 2018) of Caribbean coral reefs.

The reduced productivity of reef fish and fisheries is not exclusively a Caribbean issue, but a worldwide concern (Graham et al., 2007; Newton et al., 2007). However, the relatively low species richness of Caribbean coral reefs makes them even more vulnerable to ecological and economical degradation than their Indo-pacific counterparts, as most functional groups are only represented by one or two species (Bellwood et al., 2004). The degradation of Caribbean coral reefs is severe and threats are prominent, with as a consequence that reefs are practically unable to recover naturally (Goreau and Hilbertz, 2005; Mumby and Steneck, 2008). Without active intervention and management, coral reefs might not be able to sustain the ecosystem services that millions of people are dependent on (Bellwood et al., 2004). One of the possible intervention methods is the deployment of artificial reefs, structures that are placed on the seabed to mimic certain characteristics of the natural reef ecosystem and help restore the habitat function (Baine, 2001). Artificial reefs can instantly increase three dimensional structure and are often used to restore or enhance fish populations or fisheries productivity (Baine, 2001; Seaman, 2007; Becker et al., 2018). Part of the fish colonizing artificial reefs are the result of enhanced productivity, while others are attracted from neighbouring areas (Grossman et al., 1997; Pickering and Whitmarsh, 1997).

Artificial reefs can be constructed from different materials and in multiple designs (Baine, 2001; Becker et al., 2018; Lima et al., 2019), which result in a broad variety of artificial reefs currently being deployed. Reef balls® are one of the most applied artificial reef types (Lima et al., 2019) and over 600,000 reef balls have been deployed worldwide (reefballfoundation.org). The fish assemblages around reef balls are relatively well studied (Sherman et al., 2002; Brotto et al., 2006; Dos Santos et al., 2010; Folpp et al., 2013; Mills et al., 2017). Adding more refuges to the reef ball design, by placing concrete blocks in the central void space (Sherman et al., 2002) or adding extra holes (Brotto et al., 2006) resulted in a higher fish abundance and species richness, indicating that increased shelter availability will support a greater fish diversity on the artificial reefs. Studies in which small experimental reefs were used, confirmed that more shelter availability resulted in a higher fish abundance and species richness (Hixon and Beets, 1989; Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006). These studies used piles of concrete building blocks or oyster shells, which are easy to deploy and modify, but are unstable over time (Ogden and Ebersole, 1981) and therefore not suitable for large scale application. Comparative studies including multiple artificial reef designs that are also used for other purposes than research are scarce (Sherman et al., 2002; Brotto et al., 2006; Hackradt et al., 2011) and totally lacking for the Caribbean. Such comparisons are essential, as they give conservationists, marine park managers, fisheries departments and researchers the opportunity to make science-based choices in the deployment of artificial reefs.

Despite strong indications that the reef ball design may need improvement (Sherman et al., 2002; Brotto et al., 2006), no follow-up studies have been performed and reef balls remain more often used than alternative designs that provide more shelter opportunities (Lima et al., 2019). One of these alternatives is the layered cake design, which is made with the same outer mold as the reef ball, but has a higher shelter availability. To our knowledge, the layered cake design was never included in any comparative study. The most simple and cheap to construct alternative is to use a pile of rocks. Studies investigating rock pile reefs show high fish (Abelson and Shlesinger, 2002) and coral (Abelson and Shlesinger, 2002; Fox et al., 2002) densities and conclude that applying rock pile reefs, if available, may be an inexpensive and

effective way to restore coral reefs. However, none of these studies compared the fish assemblage of rock pile reefs with alternative artificial reef designs.

The current study aims to compare the fish assemblages of the three different artificial reef designs introduced above: reef balls, layered cakes and rock piles. The reef ball and layered cake designs have a similar gross volume, but are very different in shelter availability. Rock piles have an intermediate shelter availability and are relatively easy and cheap to construct from natural material (rock instead of concrete). As fish colonization of artificial reefs starts immediately after deployment and fish assemblages on small artificial reefs can be stabilized within 150 days (Yeager et al., 2011), fish assemblage descriptors such as abundance, biomass and species richness are useful indicators for the performance of an artificial reef. We hypothesize that based on their higher shelter availability, layered cakes and rock piles will have higher fish abundance, biomass and species richness than reef balls.

2. Methods

2.1. Construction of artificial reefs

In May 2017, artificial reefs were deployed at 4 locations in the waters surrounding Saba and St. Eustatius, Dutch Caribbean (Fig. 1). The locations, Ladder bay (LB) and Big rock market (BRM) on Saba and Twin sisters (TS) and Crooks castle (CC) on St. Eustatius, were selected according to the following criteria: a sandy bottom along the edge of a natural reef, between 12 and 18 m depth and with limited slope. On all locations, 4 plots were set out with a 25 m interval, at 5 m distance from the natural reef. Four different treatments (reef balls, layered cakes, a rock pile and a control plot on bare sand) were randomly assigned to the plots on each location. Two extra rock piles were deployed on the Saba locations.

Each reef ball or layered cake plot was composed of respectively 3 reef ball or layered cake units. Reef balls and layered cakes were constructed from concrete using a mold designed for this purpose (Reef Ball Foundation, Athens, USA, www.reefball.org). Reef balls have one central void with multiple openings, while layered cakes have different layers of concrete with multiple low, yet contiguous shelters in between (Fig. 2). Each reef unit had a bottom diameter of 90 cm, a height of 60 cm high and a weight between 300 and 450 kg. Three units, each covering an area of 0,64 m², were placed close together forming one reef plot of approximately 2 m². The rock piles were made from natural, previously unweathered basaltic rocks from Saba and St. Eustatius and each rock weighted between 30 and 50 kg. Rock piles were constructed atop an iron concrete wire mesh to evenly distribute the weight of individual rocks (Fig. 2C). Rock piles were designed to cover the same seafloor surface area (160 × 125 cm) and to have the same height (highest point 60 cm) as the other reefs. Habitat architecture differed between rock pile plots and other reef plots, as rock piles formed a single reef while reef ball and layered cake plots consisted of multiple units. Also, the chemical constituency of the used material was different for the rock piles compared to the other two reef plots. These differences were considered part of the specific designs and were therefore not corrected for.

In September 2017, hurricanes Irma and Maria hit the islands of Saba and St. Eustatius, resulting in high waves and considerable sediment movement. All artificial reefs became at least partially buried in the sand and became ecologically ineffective. In December 2017, all artificial reefs were cleared of sand and repaired if necessary, after which fish colonization started again. In February 2018, unusual big swells relocated so much sediment that all plots at the LB location were entirely buried under sand. As restoration was not possible, this location was not surveyed and excluded for the remainder of this study. All other locations were unaffected by the swells.

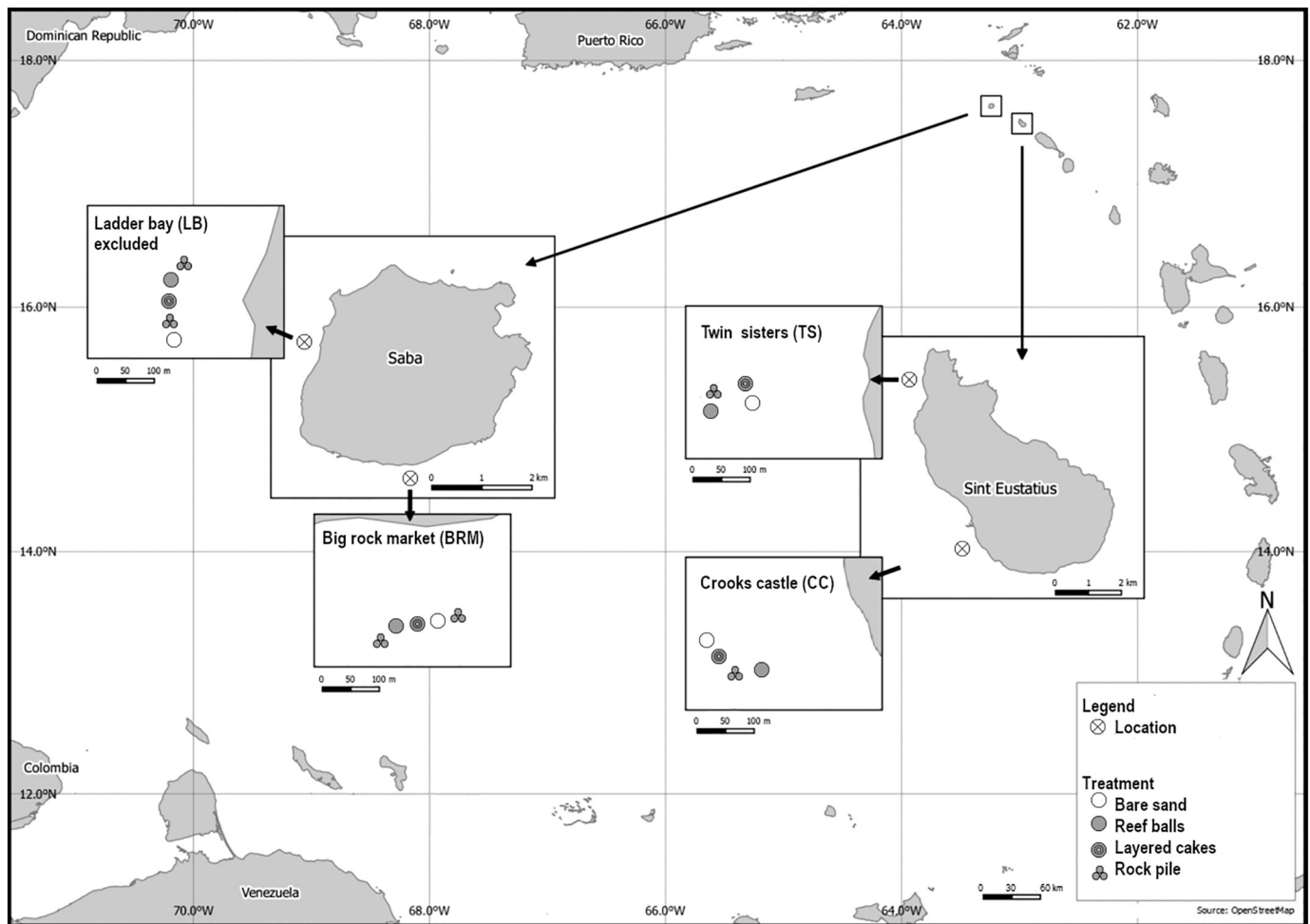


Fig. 1. Locations of the experimental plots around Saba and St. Eustatius. All plots at the LB location were covered with sediment during swells and were not included in this study.

2.2. Fish assemblage monitoring

During the months April and May 2018 (11 months post-deployment and 4 months after restoration from hurricane damage), each plot was surveyed 10 times using underwater visual censuses (UVC). Surveys were spread over the two months and the interval between successive surveys was minimally 48 h. UVC were performed using a modification of the stationary point count (Bohnsack and Bannerot, 1986; Lowry et al., 2012), followed by a systematic search of the structures. All surveys were conducted by two researchers using SCUBA. One researcher recorded the fish on underwater paper, while the other filmed the survey for future reference. During each survey, the researchers approached the plot horizontally and started recording fish fleeing from the plot as soon as the structure was within 5 m. All fish within a virtual cylindrical column, extending 1 m sideways of the plot and extending 2 m upward from the bottom were included in the survey. At two meters from the artificial reef, the observers stopped swimming and started the stationary count, first recording all schools and then recording all other fish (Bohnsack and Bannerot, 1986). All fish were identified up to species level, counted and categorized using visual estimation of total length (TL) in size classes 0–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50 and 50+ cm. After three minutes, the stationary point count ended and new fish entering the column were not included in the survey. Subsequently, the plot was thoroughly searched to record all fish residing within the internal spaces of the artificial reef. The survey ended after all fish, with the exception of small (< 5 cm TL) cryptic species such as blennies and gobies, had been

recorded.

2.3. Reef plot modelling to determine physical parameters

For reproducibility, a thorough and quantitative description of the reefs to be compared is essential, but typically absent in most studies. To address this issue, all reef plots on the CC location were three-dimensionally modelled using a diver-held imaging system composed of a DSLR camera (Nikon D850 with a Nikkor 35 mm lens) and four strobes (INON Z-240). Images were acquired at 1 Hz using the camera's "intervalometer" while circling around the structure to obtain as many angles of view from a constant distance of 1–2 m. For each reef plot, 70–140 images were used to generate a 3D mesh and texture in Agisoft Metashape (Professional Version 1.5). The models were scaled using a scale-bar placed in the scene prior to image acquisition. To measure the gross volume, the total outer volume including shelters, we used a convex hull function in Meshlab (Cignoni et al., 2008). To measure the total surface area, the combined surfaces of the reef structures (outside and inside) and the sand in between structures within the plot, and net volume, the gross volume excluding shelters, we used the "Measure area and volume" function in Metashape. The shelter volume of each reef plot was obtained by subtracting the net volume from the gross volume.

2.4. Cost estimation

The costs to construct a single plot were estimated based on the used

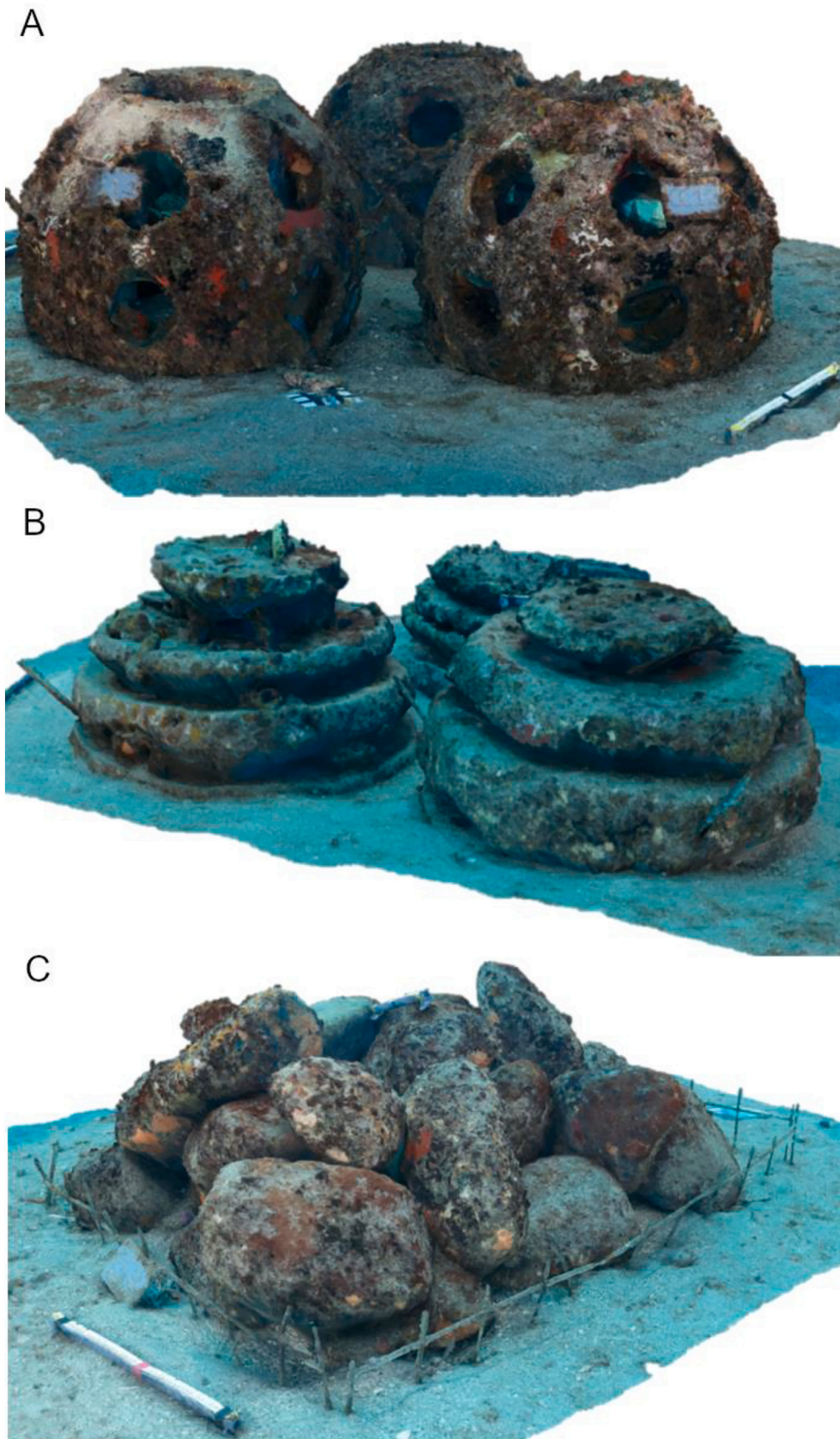


Fig. 2. Three different artificial reef design plots which were compared in this study: reef ball (A), layered cake (B) and rock pile (C) plot. Each plot covers approximately 2 m² seafloor area.

materials and the time spend to construct the plots. An hourly wage of \$ 20.00 was used to calculate labor costs. As certain materials can be reused and upscaling would reduce the price per unit, we also estimated the costs per 10 plots. We did not include boat use or monitoring costs, as these did not differ between treatments and are highly variable throughout the world, and because monitoring is not always part of an artificial reef program.

2.5. Data analysis

Fish abundance (per species, family, trophic group, size class and total) was summed per survey and averages per treatment were calculated using all 30 or 40 surveys (considering 10 surveys per plot on 3 locations and an extra rock pile plot on 1 location). Six major trophic categories (planktivores, herbivores, invertivores, omnivores, carnivores and piscivores) were distinguished, following the classification used by Paddack et al. (2009) and Alvarez-Filip et al. (2011). As only 4 fish greater than 40 cm were observed (1 *Gymnothorax moringa* of 40–50 cm on the layered cakes, 1 *Sphyrna barracuda* of 60–70 cm above the layered cakes and 2 *Gymnothorax moringa* of 60–70 in the rock piles) these recordings were combined into the size class 40+. Fish biomass per treatment was calculated by summing the weight of all species present and averaging total biomass over the 10 surveys. The weight of all species and all size classes was calculated using the length-weight relationship $W = a * TL^b$, where W is the weight in grams, TL is the average total length of the size class in cm, while a and b are species-specific constants obtained from literature (Froese and Pauly, 2019). If a and b values were not available, parameters of closely-related species with a similar shape and maximum length were used. If fork length (FL) was needed for the length-weight relationship, a species-specific TL - FL ratio was used (Froese and Pauly, 2019). A total of 31 *Heteroconger longissimus* were excluded from the biomass analysis, because they were always observed in their sand burrows and their length could not be estimated. Fish species richness (S) was obtained by summing the total number of species observed during 10 surveys. An average S per treatment was calculated using the 3 or 4 replicates per treatment.

Statistical analyses were performed with R (R Core Team, 2019) using R studio version 1.1.463. Generalized Linear Mixed Models (GLMM) with a negative binomial error distribution (`lmer.nb` function in the R package “lme4”) (Bates et al., 2015) were used to test whether fish abundance was affected by treatment or location (fixed factors). To control for the 10 repeated surveys per plot, surveys were included as a random factor. Model selection and validation was performed according to Bolker et al. (2009). The Akaike Information Criterion (AIC) was used to select the best fitting model, which was the model including both treatment and location. Pearson's residuals were summed to test for over-dispersion. This was the case when a Poisson distribution was used, but was solved by using a negative binomial distribution. Likelihood ratio tests (LRT) were performed for statistical inference of the fixed factors using the `drop1` function. Linear mixed models (LMM, `lmer` function in the R package “lme4”) (Bates et al., 2015) were used to test whether fish biomass was affected by treatment or location (fixed factors). Model selection and validation was performed according to Zuur et al. (2009); the model including both treatment and location had the lowest AIC and was used for further analysis. To control for the 10 repeated surveys, individual reefs were included as a random factor. Residuals of the initial model indicated heteroscedasticity, which was solved after the data were cube-root transformed. For statistical inference, an F-test with Kenward-Roger's approximation to degrees of freedom was performed using the R packages “lmerTest” (Kuznetsova et al., 2017) and “pbkrtest” (Halekoh and Højsgaard, 2014). As species richness only has one value per reef (the total number of species found during 10 surveys), Generalized Linear Models (GLM) with a Poisson distribution were used, including treatment and location as fixed factors. Model selection and validation for GLM was performed according

to Zuur et al. (2009); the model including both treatment and location had the lowest AIC. Wald χ^2 tests were performed for statistical inference of the fixed factors (Bolker et al., 2009), using the Anova function of the “car” package (Fox and Weisberg, 2019). For all final models Tukey's post-hoc tests were conducted to examine significance of treatment and location using estimated marginal means (EMM) from the package “emmeans” (Lenth and Herve, 2019).

The package “mvabund” (Wang et al., 2020) was used to test whether treatment and location affected the composition of fish species, family, trophic group or size class. The “manyglm” function of this package was used to fit a multivariate GLM, taking the strong mean-variance relationship of abundance data into account (Warton et al., 2012). As it is not possible to include a random factor in this function, data of all surveys per reef were aggregated. Species or families that occurred on fewer than 3 plots were excluded from this analysis, as these contained little information. We first fitted main models and selected the best fitting model based on AIC; this was the model including both treatment and location for all composition descriptors. Residuals were plotted to examine if the model assumptions were met, which was the case when negative binomial distributions were used. Univariate GLMs were then used to assess which taxa or groups drove the main effects. Pairwise comparisons, adjusted for multiple testing (Wang et al., 2012), were conducted to assess which treatment or location had a significant different composition. P values < 0.05 were considered statistically significant and reported values are means \pm sd.

3. Results

In total, 2102 fish representing 48 species were observed during 130 surveys. Treatment (LRT = 18.67, $df = 3$, $P < 0.001$) and location (LRT = 6.164, $df = 2$, $P = 0.046$) were significant predictors of fish abundance (Fig. 3). Layered cake plots had an average abundance of 36.7 ± 14.3 fish, which was significantly higher than the 9.6 ± 7.0 fish on the reef ball plots ($P = 0.0044$). Rock pile plots had an average abundance of 15.5 ± 8.3 fish and neither differed significantly from layered cake ($P = 0.3018$) nor from reef ball ($P = 0.2672$) plots. Fish abundance on all artificial reef plots was significantly higher than the fish abundance on control plots with bare sand ($P < 0.0001$ for layered cake and rock pile plots and $P = 0.0175$ for reef ball plots), which had an average abundance of 3.1 ± 3.7 fish. The only significant difference in fish abundance for combined reef plots at a location was that CC had a significantly higher fish abundance than location BRM ($P = 0.0353$).

Treatment ($F = 22.05$, $df = 3$, $P = 0.006$) and location ($F = 9.23$, $df = 2$, $P = 0.011$) were significant predictors for fish biomass (Fig. 3). Layered cake plots had an average fish biomass of 1434 ± 1287 g, which was significantly higher than the average biomass on the reef ball plots (309 ± 273 g fish; $P < 0.0142$) and the control plots with bare sand (35 ± 78 g fish, $P = 0.0005$), but not significantly different from the rock pile plots (459 ± 273 g fish, $P = 0.1169$). The average fish biomass on the rock pile and reef ball plots did not significantly differ from each other ($P = 0.2980$), but differed significantly from the average fish biomass on bare sand ($P = 0.0381$ for reef ball plots and $P = 0.0033$ for rock pile plots). Location BRM had a significantly lower fish biomass for all plots there than location TS ($P = 0.0105$), but did not differ from location CC. Locations CC and TS did not differ in fish biomass.

Treatment ($\chi^2 = 40.15$, $df = 3$, $P < 0.001$) and location ($\chi^2 = 15.20$, $df = 2$, $P < 0.001$) were significant predictors for species richness (S , Fig. 3). Average S did not differ among the three artificial reef plots, but all artificial reef plots had a significantly higher S than the control plots with bare sand ($P < 0.0001$, $P = 0.0001$, $P = 0.0018$ for layered cake, rock pile and reef ball plots, respectively). Location BRM had a significantly lower S than locations TS ($P = 0.0009$) and CC ($P = 0.0080$). Locations CC and TS did not differ in S .

Average abundance per fish species followed the general trend in

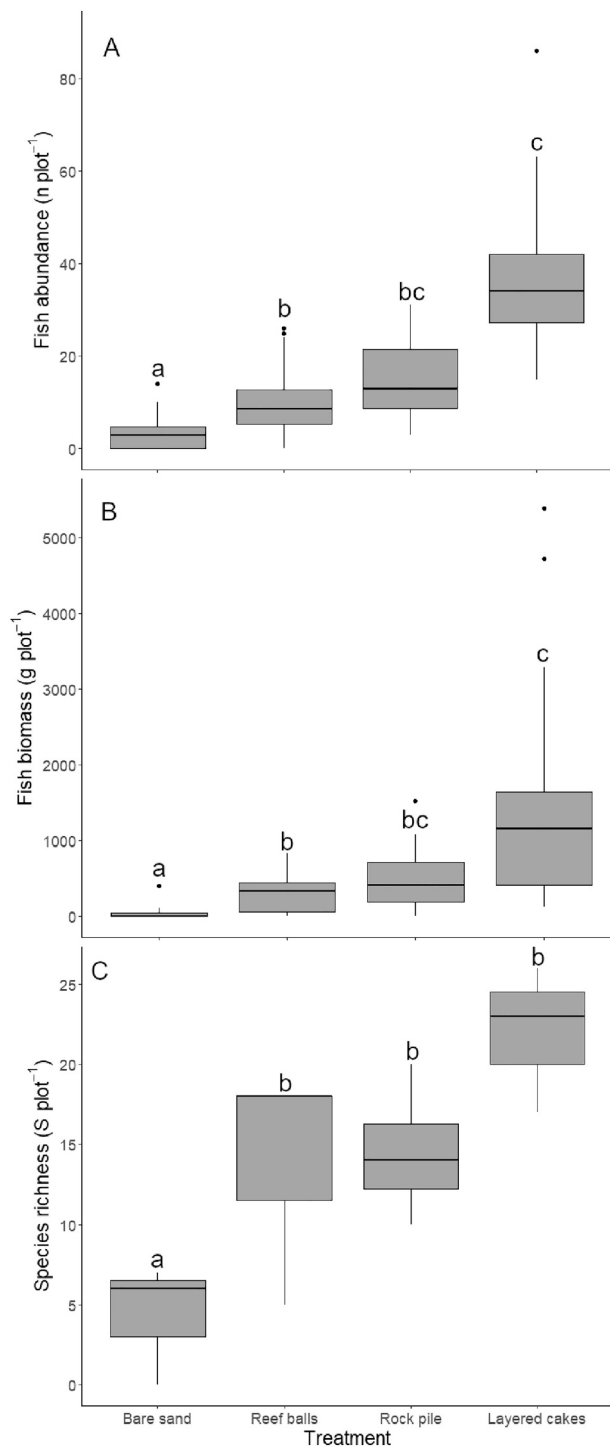


Fig. 3. Fish abundance (A), biomass (B) and species richness (C) per treatment. The boxplots show the median (black line), the first and third quartiles (grey shaded box), and the lower and upper extremes, black dots represent outlying values (> 1.5 inter-quartile range from third quartile). Treatments sharing the same letter are not significantly different ($P > 0.05$).

fish abundance and most fish species had the highest abundance on the layered cake plots, followed by the rock pile plots, reef ball plots and control plots with bare sand (Table 1). Bluehead wrasses *Thalassoma bifasciatum*, were the most abundant species on all treatments and accounted for 32% of all observations. Fish species composition was affected by location (sum-of-LR = 274, $df = 2$, $P = 0.0001$), but not by treatment (sum-of-LR = 162, $df = 3$, $P = 0.063$). The key species that drove the location effect were Princess parrotfish, *Scarus taeniopterus*,

Redband parrotfish, *Sparisoma aurofrenatum*, Slippery dick, *Halichoeres bivittatus*, Spotted goatfish, *Pseudupeneus maculatus*, and Sergeant major, *Abudefduf saxatilis*. The only species that differed significantly in abundance between treatments was the Coney, *Cephalopholis fulva*. When pairwise comparisons were conducted between locations, none of the comparisons were significant, indicating that the location effects were not very large.

The species observed in the present study belonged to 27 families (Table 2). Overall, Labridae were the most frequently observed family on all treatments, accounting for 43% of all fish observations. Fish family composition was affected by treatment (sum-of-LR = 103, $df = 2$, $P = 0.020$) and location (sum-of-LR = 119, $df = 3$, $P = 0.005$). The key family driving the effect of treatment were Serranidae, while Scaridae and Mullidae drove the effect of location. Pairwise comparisons revealed that these effects were not significant when adjusted for multiple testing, indicating that the effect was not very large.

Average abundance of the six major trophic groups (planktivores, herbivores, omnivores, invertivores, carnivores and piscivores) was highest at the layered cake plots (Table 3), lowest on the bare sand plots and significantly influenced by treatment (sum-of-LR = 57 $P = 0.009$), but not by location (sum-of-LR = 25 $P = 0.194$). This effect was mainly driven by the abundance of carnivores, although pairwise comparisons revealed no significant differences between treatments.

On all artificial reef plots, the 0–5 fish size class was most recorded, while the size class of 5–10 cm was most dominant on the bare sand control plots (Table 4). Fish in the size classes of 25–30 cm and bigger were scarce on all reef plots. Size class composition was significantly affected by treatment (sum-of-LR = 80 $P = 0.010$) and location (sum-of-LR = 81 $P = 0.009$). These effects were driven by the size classes 0–5 cm and 15–20 cm, respectively. Pairwise comparisons showed no significant differences between treatments or locations.

The gross and net volume of the reef ball plots was higher than of the other plots (Table 5). Layered cake plots had the lowest gross volume, while the rock pile plot had the lowest net volume. Layered cakes were made using the same mold (i.e. with the same outer volume) as the reef balls. However, four rocks, functioning as legs, were placed at the bottom of the mold during the construction of every layered cakes. These legs made it easier to deploy the layered cakes, but the legs sunk in the sand after deployment, reducing the gross volume of this design. Shelter volume of the reef ball plots and the rock pile plots was the same, while the shelter volume of the layered cake plots was less than half the size of the other designs. The total surface area covered by the reef ball plots was highest, followed by the layered cake plots and the rock pile plots.

The total costs per plot were highest for the layered cake and reef ball plots, while rock pile plots were 10 times cheaper to construct (Table 6). The small difference between layered cake and reef ball plots was due to more material used and more labour needed for construction of layered cake units. Scaling up efforts resulted in a large reduction in costs for a single layered cake or reef ball unit, as molds and lift bags can be reused, but rock piles were still 4 times cheaper.

4. Discussion

Our analysis shows that all artificial reef plots had a higher fish abundance, biomass and species richness than controls plots of only bare sand. This is no surprise, as any addition of hard substrate on bare sand habitat generally results in an increase in habitat volume and shelter availability, crucial for fish abundance and species richness (Gratwicke and Speight, 2005). However, the magnitude of this increase differed greatly depending on the type of artificial reef. Plots with layered cake structures had a higher fish abundance and biomass compared to reef ball plots, while rock pile plots had intermediate fish assemblage parameters. This confirmed our hypothesis that structures that provide more shelter spaces will result in higher fish abundance and biomass. This is in line with previous research, indicating that the

Table 1

Average fish abundance (n) (± SD) of 20 most common fish species, the sum of all 28 other species and the total average per treatment. Species are sorted based on their overall abundance. *As according to Paddack et al. (2009) and Alvarez-Filip et al. (2011).

| Name | Common name | Family | Trophic | Average fish abundance (n plot ⁻¹) | | | |
|---------------------------------|----------------------|---------------|-------------|--|-----------|------------|-------------|
| | | | | Group* | Bare sand | Reefball | Rock pile |
| <i>Thalassoma bifasciatum</i> | Bluehead wrasse | Labridae | Planktivore | 0.4 ± 1.1 | 3.9 ± 4.4 | 5.4 ± 6.4 | 10.7 ± 7.8 |
| <i>Holocentrus adscensionis</i> | Squirrelfish | Holocentridae | Invertivore | 0.0 ± 0.0 | 0.3 ± 0.5 | 0.5 ± 0.5 | 4.9 ± 3.7 |
| <i>Halichoeres garnoti</i> | Yellowhead wrasse | Labridae | Invertivore | 0.0 ± 0.0 | 0.5 ± 0.8 | 2.1 ± 4.1 | 0.8 ± 1.2 |
| <i>Stegastes partitus</i> | Bicolor damselfish | Pomacentridae | Herbivore | 0.1 ± 0.3 | 0.9 ± 1.0 | 0.9 ± 1.1 | 1.5 ± 1.0 |
| <i>Myripristis jacobus</i> | Blackbar soldierfish | Holocentridae | Omnivore | 0.0 ± 0.0 | 0.3 ± 0.5 | 0.1 ± 0.2 | 3.1 ± 2.4 |
| <i>Halichoeres bivittatus</i> | Slippery dick | Labridae | Invertivore | 0.6 ± 1.4 | 1.2 ± 2.2 | 0.7 ± 1.9 | 0.1 ± 0.3 |
| <i>Sparisoma aurofrenatum</i> | Redband parrotfish | Scaridae | Herbivore | 0.1 ± 0.3 | 0.2 ± 0.5 | 0.5 ± 0.8 | 1.6 ± 1.7 |
| <i>Acanthurus tractus</i> | Ocean surgeonfish | Acanthuridae | Herbivore | 0.0 ± 0.2 | 0.2 ± 0.5 | 1.0 ± 1.4 | 0.7 ± 0.8 |
| <i>Chromis multilineata</i> | Brown chromis | Pomacentridae | Planktivore | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 | 2.1 ± 3.5 |
| <i>Cephalopholis fulva</i> | Coney | Serranidae | Carnivore | 0.0 ± 0.0 | 0.2 ± 0.5 | 0.6 ± 1.3 | 1.0 ± 1.0 |
| <i>Scarus taeniopterus</i> | Princess Parrotfish | Scaridae | Herbivore | 0.0 ± 0.0 | 0.1 ± 0.5 | 0.3 ± 0.8 | 1.4 ± 3.8 |
| <i>Chromis cyanea</i> | Blue chromis | Pomacentridae | Planktivore | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 | 1.8 ± 3.5 |
| <i>Haemulon flavolineatum</i> | French Grunt | Haemulidae | Invertivore | 0.0 ± 0.0 | 0.0 ± 0.0 | 1.3 ± 2.1 | 0.0 ± 0.0 |
| <i>Haemulon aurolineatum</i> | Tomtate | Haemulidae | Invertivore | 0.1 ± 0.3 | 0.1 ± 0.4 | 0.5 ± 1.4 | 0.7 ± 1.9 |
| <i>Apogon maculatus</i> | Flamefish | Apogonidae | Invertivore | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.1 ± 0.5 | 1.3 ± 2.8 |
| <i>Acanthurus coeruleus</i> | Blue tang | Acanthuridae | Herbivore | 0.0 ± 0.0 | 0.2 ± 0.4 | 0.4 ± 0.7 | 0.6 ± 1.5 |
| <i>Abudefduf saxatilis</i> | Sergeant major | Pomacentridae | Omnivore | 0.0 ± 0.0 | 0.3 ± 0.6 | 0.1 ± 0.2 | 0.7 ± 1.4 |
| <i>Heteroconger longissimus</i> | Brown garden eel | Congridae | Planktivore | 1.0 ± 1.5 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 |
| <i>Pseudupeneus maculatus</i> | Spotted goatfish | Mullidae | Invertivore | 0.1 ± 0.4 | 0.2 ± 0.5 | 0.2 ± 0.4 | 0.3 ± 0.5 |
| <i>Bodianus rufus</i> | Spanish hogfish | Labridae | Invertivore | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.2 ± 0.6 | 0.4 ± 1.3 |
| 28 other species | | | | 0.7 ± 1.3 | 1.0 ± 0.9 | 0.9 ± 1.1 | 3.2 ± 2.3 |
| Total | | | | 3.1 ± 3.7 | 9.6 ± 7.0 | 15.5 ± 8.3 | 36.7 ± 14.3 |

Table 2

Average (n ± SD) fish abundance of 10 most common fish families, the sum of all 17 other families and the total average per treatment. Families are sorted based on their overall abundance.

| Family | Average fish abundance (n plot ⁻¹) | | | |
|---------------|--|-----------|------------|--------------|
| | Bare sand | Reef ball | Rock pile | Layered cake |
| Labridae | 1.6 ± 3.4 | 5.5 ± 6.2 | 8.4 ± 9.9 | 12 ± 8.2 |
| Holocentridae | 0 ± 0 | 0.7 ± 1 | 0.6 ± 0.6 | 8 ± 4.9 |
| Pomacentridae | 0.1 ± 0.3 | 1.2 ± 1.1 | 1 ± 1.2 | 6.1 ± 5.9 |
| Scaridae | 0.1 ± 0.4 | 0.3 ± 0.8 | 0.9 ± 1.4 | 3.2 ± 5.2 |
| Acanthuridae | 0 ± 0.2 | 0.5 ± 0.8 | 1.5 ± 1.8 | 1.6 ± 1.9 |
| Haemulidae | 0.1 ± 0.3 | 0.1 ± 0.4 | 1.7 ± 2.3 | 0.7 ± 1.9 |
| Serranidae | 0 ± 0 | 0.3 ± 0.5 | 0.7 ± 1.4 | 1.5 ± 1.7 |
| Apogonidae | 0 ± 0 | 0 ± 0 | 0.1 ± 0.5 | 1.3 ± 2.8 |
| Congridae | 1 ± 1.5 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Mullidae | 0.1 ± 0.4 | 0.2 ± 0.5 | 0.2 ± 0.4 | 0.3 ± 0.5 |
| Other | 0 ± 0.2 | 0.8 ± 0.6 | 0.5 ± 0.9 | 2.1 ± 2 |
| Total | 3.1 ± 3.7 | 9.6 ± 7 | 15.5 ± 8.3 | 36.7 ± 14.3 |

Table 3

Average fish abundance (n) (± SD) per trophic group and in total per treatment. Trophic groups, according to Paddack et al. (2009) and Alvarez-Filip et al. (2011), were sorted based on their overall abundance.

| Trophic group | Average fish abundance (n plot ⁻¹) | | | |
|---------------|--|-----------|------------|--------------|
| | Bare sand | Reef ball | Rock pile | Layered cake |
| Planktivore | 1.4 ± 1.6 | 3.9 ± 4.4 | 5.4 ± 6.4 | 14.9 ± 8.4 |
| Invertivore | 1.4 ± 2.7 | 3 ± 2.4 | 5.7 ± 3.7 | 9.5 ± 7.8 |
| Herbivore | 0.2 ± 0.6 | 1.7 ± 1.6 | 3.3 ± 2.6 | 6.6 ± 6.1 |
| Omnivore | 0 ± 0 | 0.7 ± 1 | 0.1 ± 0.4 | 3.9 ± 3.3 |
| Carnivore | 0 ± 0 | 0.3 ± 0.5 | 0.8 ± 1.6 | 1.5 ± 1.7 |
| Piscivore | 0 ± 0.2 | 0.1 ± 0.3 | 0.1 ± 0.3 | 0.2 ± 0.5 |
| Total | 3.1 ± 3.7 | 9.6 ± 7 | 15.5 ± 8.3 | 36.7 ± 14.3 |

fish assemblage is positively affected by shelter availability (Hixon and Beets, 1989; Sherman et al., 2002; Gratwicke and Speight, 2005; Brotto et al., 2006; Lingo and Szedlmayer, 2006; Hackradt et al., 2011). Compared to the layered cake plot, the reef ball and rock pile plots had

Table 4

Average fish abundance (n) (± SD) per size class and in total per treatment. *The size class unknown consisted entirely of Brown garden eel *Heteroconger longissimus*, which were always observed in their burrows.

| Size class | Average fish abundance (n plot ⁻¹) | | | |
|------------|--|-----------|------------|--------------|
| | Bare sand | Reef ball | Rock pile | Layered cake |
| 0–5 | 0.1 ± 0.3 | 3.8 ± 3.1 | 8.1 ± 8.5 | 17.7 ± 8.9 |
| 5–10 | 1.6 ± 3.3 | 2.7 ± 4.9 | 1.3 ± 2.4 | 2.4 ± 2.4 |
| 10–15 | 0.2 ± 0.4 | 0.9 ± 1.4 | 2.5 ± 2.5 | 5 ± 3.7 |
| 15–20 | 0.1 ± 0.4 | 1.1 ± 1.4 | 2.8 ± 3 | 8.9 ± 8.6 |
| 20–25 | 0.1 ± 0.4 | 0.7 ± 1 | 0.7 ± 0.9 | 2.5 ± 3.9 |
| 25–30 | 0 ± 0 | 0.3 ± 0.4 | 0.1 ± 0.4 | 0.1 ± 0.3 |
| 30–35 | 0 ± 0 | 0 ± 0.2 | 0 ± 0.2 | 0.1 ± 0.3 |
| 35–40 | 0 ± 0 | 0.1 ± 0.3 | 0 ± 0 | 0 ± 0 |
| 40+ | 0 ± 0 | 0 ± 0 | 0.1 ± 0.2 | 0.1 ± 0.3 |
| Unknown* | 1 ± 1.5 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Total | 3.1 ± 3.7 | 9.6 ± 7 | 15.5 ± 8.3 | 36.7 ± 14.3 |

twice as much total shelter volume than the layered cake plots. Clearly, the central void space of a reef balls provides a single large shelter opportunity, but this is not ideal for attracting big fish assemblages of especially smaller fish. Filling the void space of reef balls with concrete building blocks has been shown to increase the number of fish (Sherman et al., 2002). The rock pile plots had the same total shelter volume as the reef ball plots, but provided many more shelter spaces. Because of the complex nature and connectedness of the rock pile shelters, it was not possible to determine the number of shelters. The high shelter volume combined with a similar total surface area indicates that the shelters of the rock piles were bigger than those in the layered cakes.

Three-dimensional modelling revealed that the reef ball plot had the highest gross volume, followed by the rock pile plot. Despite that artificial reef size is usually positively correlated with fish abundance (Tupper and Hunte, 1998; Abelson and Shlesinger, 2002) the plots with layered cakes (smaller gross volume) performed better in terms of fish abundance and biomass than the reef ball plots and comparable to the rock pile plot.

Total surface area per bottom area is often used to describe rugosity

Table 5
Physical parameters of reef ball, layered cake and rock pile plots.

| Physical parameter | Reef ball plot | Rock pile plot | Layered cake plot |
|---|----------------|----------------|-------------------|
| Gross volume, including shelter (m ³) | 1.14 | 0.98 | 0.78 |
| Net volume, excluding shelter (m ³) | 0.63 | 0.47 | 0.55 |
| Shelter volume (m ³) | 0.51 | 0.51 | 0.23 |
| Total surface area (m ²) | 12.23 | 7.39 | 8.14 |
| images (n) | 131 | 77 | 143 |

Table 6
Estimated costs, excluding boat and monitoring costs, in USD for a single and 10 reef ball, layered cake and rock pile plots. *One-time expenses.

| | Reef ball plot | Rock pile plot | Layered cake plot |
|--------------------------|----------------|----------------|-------------------|
| Costs | 3 units | 27 rocks | 3 units |
| Mold * | \$ 1.350.00 | – | \$1.350.00 |
| Lift bag for deployment* | \$ 700.00 | – | \$ 700.00 |
| Material | \$ 77.78 | \$ 22.50 | \$ 100.00 |
| Construction | \$ 360.00 | – | \$ 420.00 |
| Deployment | \$ 360.00 | \$ 240.00 | \$ 360.00 |
| Total per plot | \$ 2.847.78 | \$ 262.50 | \$ 2.930.00 |
| | 30 units | 270 rocks | 30 units |
| Total per 10 plots | \$ 9.927.78 | \$ 2.625.00 | \$ 10.850.00 |

(Luckhurst and Luckhurst, 1978) and is known to positively affect fish abundance on artificial reefs (Gratwicke and Speight, 2005). Gratwicke and Speight (2005) kept the shelter availability constant while modifying the rugosity, clearly showing that rugosity alone affects fish abundance. In this study the reef ball plot had 1.5 times more surface area per bottom area than the layered cake or rock pile plot, but harbored a respectively lower or comparable fish abundance. This indicates that rugosity, at least in this study, is subordinate to shelter availability in determining fish abundance.

No large differences were detected between treatments in species, family, trophic group or size class composition. Although the fish assemblage composition on layered cake plots appeared to be more homogenous than on reef ball and rock pile plots, this difference was not significant. It could be that we were not able to detect any differences due to low statistical power, which was the result of the low number of replicates per treatment. Other studies showed that artificial reef design can affect fish assemblage composition (Hixon and Beets, 1989; Beets and Hixon, 1994; Gratwicke and Speight, 2005) and that larger shelter sizes can result in a higher abundance of larger fish (Hixon and Beets, 1989; Beets and Hixon, 1994). Our results did not show this effect. As we observed few fish in this size class on all treatments, possible explanations could be that (1) there was no lack of large shelters on the natural reef, so larger fish were not attracted to the artificial reef plots or (2) the fish assemblage of the surrounding natural reef lacked larger fish, resulting in few fish in this size class on the artificial reefs.

In the current study, one location (BRM) had a significantly lower fish abundance, biomass and species richness than one or both other locations. This confirms the statement of (Baine, 2001) that comparing results of different artificial reef studies performed at different locations with distinct environmental parameters cannot be done or are tenuous at best. Also, this underlines the importance of comparative studies in which all studied artificial reef designs are deployed at the same locations. In our study all intra-location comparisons of the plots yielded the same results but distributed over different locations the outcomes would be compromised.

The effects of hurricanes Irma and Maria on the artificial reefs used in this study show the necessity of making deployed reefs surge and weather-proof. Artificial reefs in dynamic, sandy environments where former reefs have been damaged by natural forces may be quite vulnerable to sinking in, or being smothered by, hurricane or swell-driven

sand movement. Careful site selection based on criteria such as sand abundance, depth and local knowledge of weather impact helps prevent later failures. Also the need for anchoring should be considered and the opportunities to do so. In areas with expected (increasing) hurricane impact, hurricane resistant structures are needed that also could help protect the coast or rehabilitation should occur only at depths relatively sheltered from impact of hurricanes or surface waves.

Our study shows that artificial reef design can greatly enhance fish abundance and biomass. On Saba and St. Eustatius, layered cake plots performed better than reef ball plots and had higher average fish abundance and biomass, while rock pile plots had intermediate fish assemblage outcomes. Analysis revealed that the availability of multiple small shelters in the layered cake design was responsible for these results and that gross volume (reef size), shelter volume and total surface area (rugosity) were subordinate in determining fish assemblage parameters. Our results also suggest that the cost-benefit ratio of artificial reef implementation for the purpose of reef restoration, could be greatly improved by deploying either layered cake (better performance, similar price) or rock pile plots (similar performance, 4–10 times lower price) instead of the commonly used reef balls. In the coming years we will be monitoring further developments in the reef fish faunas at our experimental plots to study whether the main differences in fish assemblages between the reefs observed during early colonization will persist over time.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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