

The effect of artificial reef design on the attraction of herbivorous fish and on coral recruitment, survival and growth

Alwin Hylkema^{a,b,*}, Adolphe O. Debro^{b,c}, Raven A.R. Cammenga^d, Paolo M. van der Laan^{a,e}, Marit Pistor^{a,f}, Albertinka J. Murk^b, Ronald Osinga^b

^a Van Hall Larenstein University of Applied Sciences, P.O. Box 1528, 8901 BV Leeuwarden, the Netherlands

^b Marine Animal Ecology group, Wageningen University, Wageningen University & Research, P.O. Box 338, 6700 AH Wageningen, the Netherlands

^c Wageningen Marine Research, Wageningen University & Research, P.O. Box 57, 1780 AB Den Helder, the Netherlands

^d Rijkswaterstaat Noord Nederland, P.O. Box 2232, 3500 GE Utrecht, the Netherlands

^e Saba Conservation Foundation, The Bottom, P.O. Box 18, Saba, Dutch Caribbean, the Netherlands

^f St. Eustatius National Parks Foundation (STENAPA), Oranjebaiweg 59, St. Eustatius, Dutch Caribbean, the Netherlands

ARTICLE INFO

Keywords:

Caribbean
Saba
St. Eustatius
Reef ball
Layered cake
Territorial behavior

ABSTRACT

Fish assemblages of different types of artificial reefs can differ greatly in abundance, biomass and composition, with some reef types harboring over five times more herbivores than others. It is assumed that higher herbivorous fish abundance results in a higher grazing intensity, affecting the benthic community by means of enhanced coral recruitment, survival and growth. Territorial fish species might affect this process by chasing away other fish, especially herbivores. In this study we compared the fish assemblage, territorial behavior and grazing intensity by fish on two artificial reef types: reef balls and layered cakes, differing greatly in their fish assemblage during early colonization. In addition, the effect of artificial reef type on benthic development and coral recruitment, survival and growth, was investigated. Although layered cakes initially harbored higher herbivorous fish biomass, this effect was lost during consecutive monitoring events. This seems to be the result of the higher territorial fish abundance around the layered cakes where almost four times more chasing behavior was recorded compared to the reef balls. This resulted in a more than five times lower fish grazing intensity compared to the reef-ball plots. Although macroalgae were effectively controlled at both reefs, the grazing intensity did not differ enough to cause large enough structural changes in benthic cover for higher coral recruitment, survival or growth. The high turf algae cover, combined with increasing crustose coralline algae and sponge cover likely explained reduced coral development. We recommend further research on how to achieve higher grazing rates for improved coral development on artificial reefs, for example by facilitating invertebrate herbivores.

1. Introduction

Caribbean coral reefs are among the most degraded reefs worldwide (Pandolfi et al., 2003; Hughes et al., 2010). Since the 1970s, coral cover in many areas decreased with >80% (Gardner et al., 2003; Jackson et al., 2014). Without the three dimensional structure of the corals, shelter availability (Alvarez-Filip et al., 2009), biodiversity (Newman et al., 2015) and productivity (Rogers et al., 2018) of Caribbean reefs has decreased significantly. Artificial reefs, structures mimicking one or more functions of a natural reef (Baine, 2001), are often deployed as alternative fish habitat for the purpose of creating a dive site, to restore

ecosystems or to (temporarily) sustain fish catches (Lima et al., 2019; Hylkema et al., 2021). In addition, artificial reefs could provide hard substrate for cultivated coral transplants and for natural coral recruitment, both of which could potentially increase the artificial reefs' habitat value for other marine organisms (Cabaitan et al., 2008; Yap, 2009).

After the decline of coral cover, macroalgae and turf algae became the most dominant benthic groups on Caribbean coral reefs (Gardner et al., 2003; Jackson et al., 2014). Algae are important competitors of corals for space, can overgrow them, cause coral mortality (Jompa and McCook, 2002; Box and Mumby, 2007) and hinder their recruitment

* Corresponding author at: Van Hall Larenstein University of Applied Sciences, P.O. Box 1528, 8901 BV Leeuwarden, the Netherlands.

E-mail address: alwin.hylkema@hvhl.nl (A. Hylkema).

<https://doi.org/10.1016/j.ecoleng.2022.106882>

Received 30 June 2022; Received in revised form 23 December 2022; Accepted 24 December 2022

Available online 13 January 2023

0925-8574/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

(McCook et al., 2001; Box and Mumby, 2007; Arnold et al., 2010). To prevent algae from overgrowing artificial reefs, smothering transplanted corals (van Woessik et al., 2018) and hindering coral recruitment (Box and Mumby, 2007), it is essential to facilitate herbivores that can effectively reduce algae cover (reviewed by Seraphim et al., 2020). In the Caribbean, the most important grazers are parrotfish (Mumby, 2009; Adam et al., 2018), surgeonfish (Burkepile and Hay, 2010; Adam et al., 2015) and the long-spined sea urchin *Diadema antillarum* (Carpenter, 1986). The density of grazers is positively correlated with coral recruitment on natural reefs (Edmunds and Carpenter, 2001; Mumby, 2009; Adam et al., 2015, 2018), suggesting their presence can positively influence coral recruitment and growth on artificial reefs.

Most artificial reef studies focused on their habitat function for fish (reviewed by Lima et al., 2019) and clearly higher shelter availability results in a higher fish abundance (Hixon and Beets, 1989; Sherman et al., 2002; Gratwicke and Speight, 2005; Brotto et al., 2006; Hylkema et al., 2020) including potentially more herbivorous fish. Few studies reported on colonization of artificial reefs by corals (Perkol-Finkel and Benayahu, 2005, 2007) or the relationship between the benthic community of the artificial reef and the presence of corals (Miller et al., 2009). Studies integrating the herbivorous fish assemblage, corals and their interaction require multiple years of colonization time and are, possibly because of this, not yet available.

This study investigates how the herbivorous fish assemblage on artificial reefs may mediate coral recruitment, survival and growth. Hylkema et al. (2020) showed how two different artificial reef designs (“Reef Balls” and “Layered Cakes”) supported very different fish assemblages after early colonization (one year post-deployment), both in terms of abundance and biomass. The reef balls were domes with a single void space with multiple holes, while the layered cakes used had different layers of concrete with multiple contiguous shelters in between. After one year of colonization, 3.6 times more fish were observed on the layered cakes compared to the reef balls (Hylkema et al., 2020). More specifically, the layered cakes harbored over 10 times more parrotfish and over three times more surgeonfish, suggesting that grazing intensity at the layered cakes must have been significantly higher than at the reef balls. A higher herbivorous fish abundance is expected to differentially affect the benthic community and more specific, to enhance coral recruitment, survival and growth (Mumby et al., 2007). Interestingly, the abundance of territorial damselfish on the layered cakes was also over five times higher than on the reef balls (Hylkema et al., 2020). Damselfish are territorial, farm turf algae (Ceccarelli et al., 2011; Arnold et al., 2010) and chase away other herbivores (Ceccarelli et al., 2001) thereby reducing grazing intensity which could negatively impact coral recruitment (Arnold et al., 2010). Potentially, coral recruits on artificial reefs can also be affected by corallivorous fish (reviewed by Seraphim et al., 2020). However, the reef balls and layered cakes in the study of Hylkema et al. (2020) supported very low densities of fish corallivores.

In this study we assessed 1) to what extent differences in herbivorous and territorial fish abundances between artificial reef designs as found during early colonization persisted over time, 2) how herbivorous fish biomass related to overall grazing pressure on the artificial reefs, 3) the relationship between grazing pressure and the composition of the benthic community and 4) how these parameters influenced coral recruitment, survival and growth. We hypothesized that the higher abundance of herbivorous fish on layered cakes would persist, result in a higher grazing pressure on the layered cakes and that this would measurably affect the benthic community and the coral recruitment parameters.

2. Methods

2.1. Construction of artificial reefs

Artificial reefs deployment for this study was described by Hylkema

et al. (2020), in which reef balls, layered cakes and rock piles were constructed to compare fish assemblages on three locations around Saba and St. Eustatius, Dutch Caribbean. These locations were Twin Sisters (TS) and Crooks Castle (CC) on St. Eustatius and Big Rock Market (BRM) on Saba. Sand scouring at Twin Sisters resulted in the artificial reefs at this location slowly sinking into the sand over the course of the study. The layered cakes and reef balls could be cleared of sediment relatively easily, but this was not possible for the rock piles. As the rock piles at other locations also remained instable, it was decided to exclude rock piles from this study and to focus on the reef ball and layered-cake plots. All locations were damaged by hurricanes Irma and Maria in September 2017 but cleared of sediment and repaired where necessary in December 2017.

At each location, three reef ball and three layered cake units were deployed in May 2017. Reef balls and layered cakes were constructed from concrete, made from Portland I cement and locally-available volcanic sand and gravel, which was casted in a mold designed for this purpose (Reef Ball Foundation, Athens, USA, www.reefball.org). Each reef unit had a bottom diameter of 90 cm, a height of 60 cm and a weight between 300 and 450 kg. Three units of the same type, each covering an area of 0.64 m², were placed close together on previously-selected reef plots (Fig. 1). Each plot was selected based on the following criteria: 5 m from the natural reef, 25 m from the neighboring artificial reef plot, between 12 and 18 m depth and with limited reef slope. This resulted in a single layered-cake plot and a single reef-ball plot per location, both covering approximately 2 m² of the seabed. Although the reef balls and layered cakes had the same outer dimensions, the different designs resulted in a difference in total hard substrate surface area (inside and outside, including all shelters). While a reef-ball plot had slightly >12 m² of total hard surface area, layered-cake plots had around 8 m² (Hylkema et al., 2020). As not all of this surface area was equally used by fish or coral recruits (e.g. the underside of the layered-lake layers had very few coral recruits), it was not possible to fairly correct for surface area. These differences were therefore considered part of the specific designs and were not corrected for.

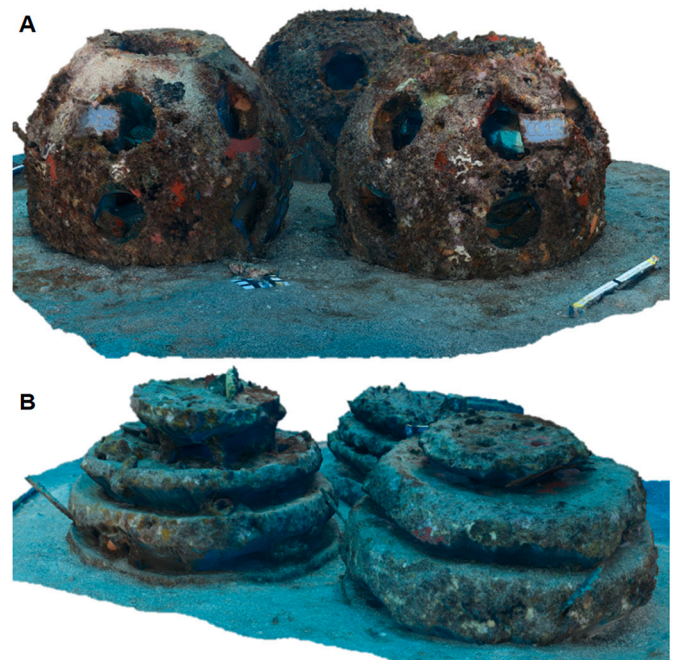


Fig. 1. The reef-ball (A) and layered-cake plot (B) at one of the three research locations.

2.2. Fish assemblages

The fish assemblage at each plot was surveyed 10 times during April and May 2018, 10 times during November and December 2018, 10 times in April and May 2019 and 3 times in December 2019. This resulted in 33 surveys per artificial reef plot, starting 1 year after deployment (4 months after restoration from hurricanes) and continuing till 2.5 years after deployment. Surveys were performed by six researchers that were all trained in species identification and size estimation prior to data collection. Surveys were conducted using SCUBA and were performed between 10 am and 2 pm, to minimize time related effects on fish counts. For each survey, an underwater visual census (UVC) was conducted consisting of a 3 min stationary point-count followed by a thorough search of the internal spaces of the artificial reefs to record all hiding fish (Hylkema et al., 2020). All fish within a virtual cylindrical column, extending 1 m sideways of the reef and extending 2 m upward from the bottom were included in the survey. 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. Grazing intensity is considered to depend on the biomass of the herbivores (Korzen et al., 2011). To determine herbivorous fish biomass, fish were categorized in major trophic groups, following Alvarez-Filip et al. (2011). The weight of all herbivorous fish was calculated using the length-weight relationship $W = a * TL^b$, where W is the weight in grams, TL is the average length of the size class in cm and a and b are species-specific constants obtained from 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 obtained from Froese and Pauly (2019) was used. Herbivorous fish biomass per species and in total were averaged per treatment, using the 33 surveys as replicates. Contrary to grazing intensity, territorial behavior is often determined by numerical abundance instead of biomass. Territorial fish species were identified using remote video surveys (see below) and territorial fish abundance per species and in total was averaged per treatment.

2.3. Grazing intensity and territorial behavior

To determine herbivorous grazing impact and territorial behavior, remote video surveys were conducted in November and December 2018. For this purpose, a buoy with camera (GoPro HERO+) was mounted, using ropes and anchors, 2 m above every artificial reef plot. The GoPro was facing downwards, capturing the entire artificial reef plot in the video. After mounting and activating the GoPro, the researchers left the dive site to minimize disturbance, and picked up the camera later that day using SCUBA. Per artificial reef plot, 6–11 videos with a total length of 6:17–7:32 h were recorded during daylight (between 10:00 and 14:00). The number of videos per plot and length of each video differed due to logistic reasons and due to the GoPro sometimes prematurely stopping the recording.

Videos were checked for visible “bites”, defined as contact between fish mouth and algae, to determine grazing intensity. Rapid bites in quick succession that could not be separated were counted as a single bite (Mantyka and Bellwood, 2007; Korzen et al., 2011). For each bite, the conducting fish was identified up to species level and categorized using visual estimation of total length (TL) in size classes of 5 cm (0–5, 5–10, etc). The top of the artificial reef modules was used as a size reference. The weight of all species and size-class combinations was calculated using known species-specific length-weight relationships (Froese and Pauly, 2019). A standardized “bite impact” was calculated per species and size class combination by: total bites within that species and size class combination \times body mass in grams following Korzen et al. (2011) and was expressed as number per hour depending on the duration of the video. Standardized bite impacts were summed and averaged per species and per survey. For some surveys, a change in current during

the survey resulted in a part of the reef being out of view. This was taken into account by dividing the bite impact by the part of the reef that was visible, which was never $<90\%$.

Territorial behavior was defined as one fish swimming rapidly towards another fish and chasing it away from a certain area of the artificial reef plot (Canterle et al., 2020). For every chase, the fish chasing and being chased were identified up to species level. It was also recorded if the chased fish successfully left the artificial reef plot after the chase. Chases were expressed as number per hour by correcting for the duration of the video while territorial behavior per survey was calculated by summing all chases of that survey. The fishes being chased were grouped per family and the chasing fish per species.

2.4. Benthic community composition

To examine succession of main benthic groups on both treatment groups, photo quadrats were made in April 2018, November 2018, May 2019 and December 2019 (Fig. 2). Two reef ball modules, one at CC and one at BRM had been broken in two parts during the hurricanes and had been covered by sediment for two months, after which they were repaired and colonization had to start again. These two modules were therefore excluded for all benthic community and coral analysis. On all other artificial reef units, a quadrat of 40×40 cm was randomly placed on the upper part (aligned with the top of the module) of the side. After it was photographed, the quadrat was flipped around the module horizontally and photographed two more times, resulting in 3 quadrates per artificial reef unit that never overlapped with other quadrats taken at the same time. If the quadrat ended up so close to a neighboring reef unit that it could not be photographed, it was moved horizontally till it was possible to make the photograph. In total, the three quadrates covered most of the side of the reef unit. Photographs were made with an Olympus PEN E-PL2 camera and two external strobes (INON S-2000).

Photo quadrats were analyzed with the software CPCe (Coral Point Count with Excel extensions) version 4.1 (Kohler and Gill, 2006). For each picture, 45 points were randomly placed and categorized in 16 main benthic groups: bryozoans, crustose coralline algae (CCA), Cyanobacteria, hydrozoans, milleporids, macroalgae, octocorals, sponges, scleractinians, tunicates, turf algae, zoantharians, sediment, bare concrete, unknown and shelter. The category shelter was used for points that fell in cavities, in the shade or otherwise on substrate not identifiable and this category was excluded for further analysis. The categories milleporids, bryozoans, hydrozoans and scleractinians never had $>2\%$ cover each on an artificial reef module and were summed as “other” for further analysis.

2.5. Coral recruitment abundance, survival and growth

In April 2018, one year after deployment, all artificial reef modules were thoroughly searched for hard coral recruits using UV lights (Nightsea BW-1). Since most hard corals exhibit fluorescence, the UV lights made it possible to detect even the smallest recruits. To reduce the amount of ambient light and make detection of corals easier, these dives were conducted around sunset with the use of a filter visor that removed the blue light and transmitted the fluorescence (Nightsea BlueBlock Filter Visor). All coral recruits were mapped and revisited the next day during daylight to make a picture (Olympus PEN E-PL2) with ID number and size reference of each coral. Using the pictures, the recruits were taxonomically identified. As classification of very small colonies is sometimes difficult, *Porites astreoides* and *P. porites* were pooled as *Porites* recruits and *Agaricia agaricites* and *A. humilis* were pooled as *Agaricia* recruits (Vermeij, 2006). All *Porites* recruits, by far the most abundant recruit category on the artificial reef modules, were mapped (Fig. S1) during the initial monitoring in April 2018 and were searched for again and photographed with a size reference in November 2018 (1.5 year after deployment), May 2019 (2 years after deployment) and December 2019 (2.5 years after deployment) to determine their survival and size.

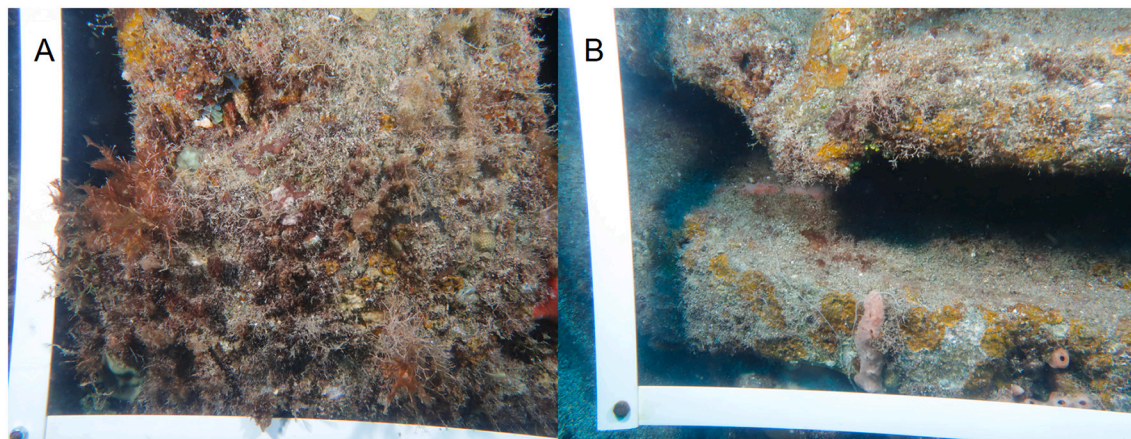


Fig. 2. Zoom-ins of the lower left corner of photo quadrats on a reef ball (A) and layered cake (B) made in May 2019, 2 years after deployment. Note the abundant turf algae cover, but also initial colonization by crustose coralline algae and sponges.

Porites recruits that were not found back after 5 min of searching with UV lights were considered to have died. *Porites* recruit surface area was determined using ImageJ version 1.52a (Abramoff et al., 2004) and growth was determined by dividing the increase in surface in between monitoring events by the growth period in years.

Additional coral recruit counts were conducted around sunset using UV lights in November 2018, May 2019 and December 2019 (1.5, 2 and 2.5 years after deployment). These counts included the earlier-mapped *Porites* recruits and were used to determine the total coral recruit abundance per artificial reef module.

2.6. Statistical analysis

For all response variables (Table 1), there was some form of dependence in the data collection, by measuring the same reef plot, artificial reef module or coral repeatedly in time. To account for this dependency, mixed modelling approaches (Zuur et al., 2009) were used, in which reef

ID, artificial reef module ID or coral ID were included as random factor. In all models, treatment and time after deployment (if applicable) were considered as fixed factors, while location was considered as random factor. All response variables, with the exception of cover of main benthic groups, were initially modelled using linear mixed models (LMMs, lmer function in the R package “lme4” (Bates et al., 2014)). The strong mean to variance relationship of count data (Warton et al., 2012) often resulted in a triangular-shaped graph when residuals were plotted against fitted values, which is an indication for heterogeneity of the variance. If this was the case, the model was refitted with a cube-root-transformed response variable. If this did not resolve the issue, generalized linear mixed models (GLMMs) with a Poisson distribution were fit and checked for overdispersion. This was the case for all the Poisson GLMMs and was solved by using GLMMs with a negative binomial-error distribution (glmer.nb function in the R package “lme4”). Interactions for all models were only included if data visualization clearly indicated such an effect (Zuur et al., 2009), which was

Table 1
Modelling approach, fixed and random factors of best fitting model and replication per response variable.

Response variable:	Modelling approach:	Data transformation:	Fixed factors best fitting model:	Random factor best fitting model:	Replication:
Total fish biomass (g plot ⁻¹)	LMM	Cube-root	Treatment + Time after deployment + Treatment * Time after deployment	Reef ID + Location	10 surveys at 3 locations during 3 monitoring periods and 3 surveys at 3 locations during 1 monitoring period = 99 surveys per treatment.
Herbivorous fish biomass (g plot ⁻¹)	LMM	Cube-root	Treatment + Time after deployment + Treatment * Time after deployment	Reef ID + Location	
Total fish abundance (n plot ⁻¹)	GLMM	–	Treatment + Time after deployment + Treatment * Time after deployment	Reef ID	
Territorial fish abundance (n plot ⁻¹)	GLMM	–	Treatment + Time after deployment + Treatment * Time after deployment	Reef ID	
Territorial behavior (chases hour ⁻¹)	GLMM	–	Treatment	Reef ID + Location	6–11 videos at 3 locations = 26 reef ball videos and 25 layered cake videos.
Grazing intensity (g hour ⁻¹)	LMM	–	Treatment	Reef ID + Location	
Benthic cover (% per major group)	multivariate GLMs	–	Treatment + Time after deployment	–	2–3 modules at 3 locations during 4 monitoring periods = 28 reef ball surveys and 36 layered cake surveys.
Coral recruit abundance (n module ⁻¹)	GLMM	–	Treatment + Time after deployment	Artificial reef module ID + Location	
Coral recruit survival (n module ⁻¹)	LMM	–	Time after deployment	Artificial reef module ID	
Coral recruit size (mm ²)	LMM	Cube-root	Treatment + Time after deployment	Coral ID + Location	16–48 corals on layered cakes and 19–38 corals on reef balls during 4 monitoring events.*
Coral recruit growth (mm ² year ⁻¹)	LMM	Cube-root	Monitoring interval	Coral ID + Location	16–50 corals on layered cakes and 19–38 corals on reef balls during 3 monitoring intervals.*

* Exact n-values per monitoring event or interval are indicated in results section.

only the case for the interaction between treatment and time after deployment for the fish biomass and abundance models. Best fitting models were selected based on Akaike's Information Criterion (AIC) (Zuur et al., 2009; Bolker et al., 2009). For statistical inference, an F-test with Kenward-Roger's approximation to degrees of freedom was performed for the LMMs, while for the GLMMs likelihood ratio tests (LRT) were performed using the drop1 function. If the final model showed an effect of time after deployment, Tukey's post-hoc tests were conducted using estimated marginal means (EMM) from the package "emmeans" (Lenth and Herve, 2019). For the models including interactions, treatment was contrasted within every monitoring event using the package "emmeans" to find out when treatments differed significantly.

Part of the *Porites* recruits disappeared during the course of a monitoring interval and growth rates could only be calculated for the recruits that were alive at the beginning and the end of a certain monitoring interval. This results in a slightly different dataset than the *Porites* recruit size dataset, where every recruit alive at a certain monitoring event contributed to the dataset.

Relative cover of main benthic groups showed a strong mean to variance relationship, which is one of the properties of count data (Warton et al., 2012). In order to account for this, the package "mvabund" (Wang et al., 2012) was used to test whether treatment and time after deployment affected the composition of the benthic community. The "manyglm" function of this package fitted multivariate GLMs with a negative binomial distribution. The best-fitting models were selected based on AIC; these were the models including treatment and monitoring period. Residuals were plotted to examine if the model assumptions were met, which was the case when negative binomial distributions were used. Univariate GLMs, adjusted for multiple testing, were then used to assess which benthic groups drove the main effects (Wang et al., 2012).

All statistical analyses were performed with R (R Core Team, 2021) using R studio version 1.2.5001. P -values < 0.05 were considered statistically significant and reported values are means \pm standard deviation, with the exception of the fish biomass and fish abundance graphs, where mean \pm standard error was used.

3. Results

3.1. Total and herbivorous fish biomass

Total fish biomass (Fig. 3) at the artificial reef plots was significantly affected by time after deployment ($P < 0.001$, Table S1) and the interaction between treatment and time after deployment ($P = 0.001$), while treatment did not affect the total fish biomass. Pairwise comparisons of reef type per monitoring event (time after deployment) revealed that total fish biomass was significantly higher on layered-cake plots compared to reef-ball plots after one year ($P = 0.006$) and 1.5 year (0.044), but not after two and 2.5 years.

Herbivorous fish biomass (Fig. 3) was significantly affected by the interaction between treatment and time after deployment ($P < 0.001$, Table S1). Pairwise comparisons of reef type per monitoring event revealed that layered cakes had significant higher herbivorous fish biomass than the reef balls after one year ($P < 0.001$). This difference became smaller in consecutive monitoring periods and was not significant anymore after 1.5 year. The relative contribution of herbivorous fish to the total fish biomass decreased over the course of the study. One year after deployment, average herbivorous biomass was 33% of the total fish biomass at the layered-cake plots and 22% at the reef-ball plots (Table S2). After 2.5 years, the relative contribution had declined to 12% at the layered-cake plots and 10% at the reef-ball plots. *Sparisoma aurofrenatum* (redband parrotfish), *Acanthurus coeruleus* (blue tang), *Scarus taeniopterus* (princess parrotfish) and *Acanthurus tractus* (ocean surgeonfish) contributed most to herbivorous fish biomass.

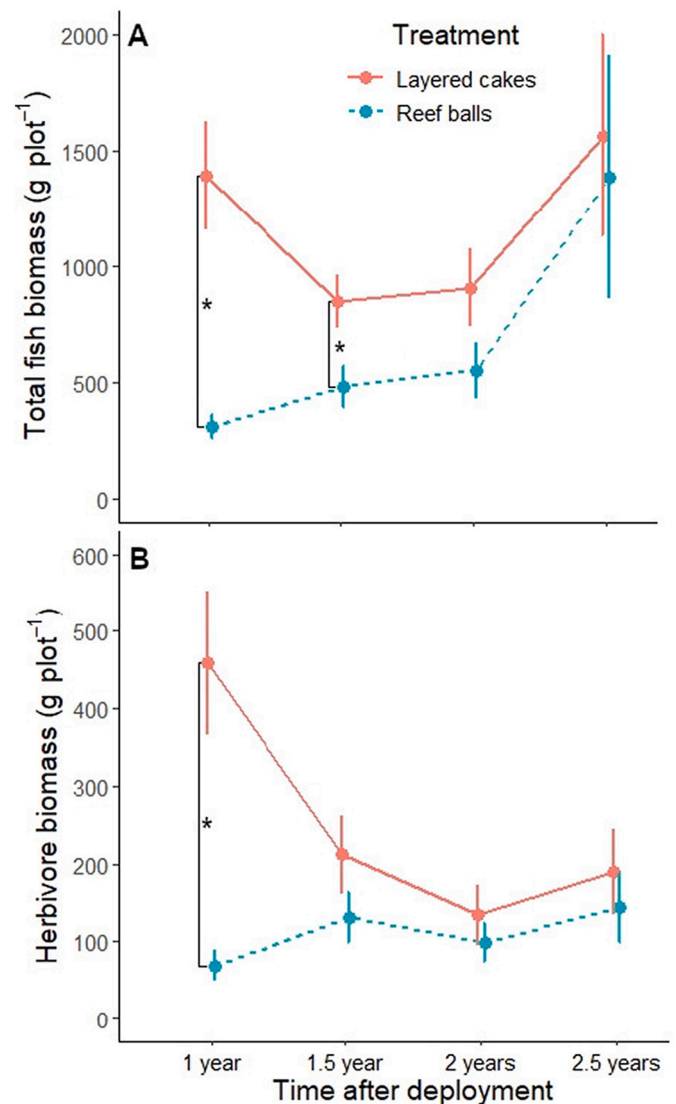


Fig. 3. Average total fish biomass (A) and herbivore fish biomass (B) (\pm SE) per treatment in time after deployment. * indicates a significant difference between treatments for that specific time after deployment.

3.2. Total and territorial fish abundance

Total fish abundance (Fig. 4, Table S3) was significantly affected by treatment ($P < 0.001$, Table S1), time after deployment ($P < 0.001$) and the interaction between treatment and time after deployment ($P < 0.001$). One year after deployment, the total fish abundance at the layered-cake plots was 5 times higher than on the reef balls ($P < 0.001$). Total fish abundance at the layered cakes decreased between one and two years after deployment, but remained significantly higher compared to the total fish abundance at the reef-ball plots ($P < 0.001$ after 1.5 year, $P = 0.019$ after two years), which increased in this time period. At the end of the study, the fish abundance at the layered cakes was 1.5 time higher than at the reef-ball plots ($P = 0.045$).

Total territorial fish abundance (Fig. 4), which is the sum of *Holocentrus adscensionis* (long-spined squirrelfish), *Abudefduf saxatilis* (sergeant major), *Myripristis jacobus* (blackbar soldierfish) and *Stegastes partitus* (bicolor damselfish) (species identified using video surveys in Section 3.3), was significantly affected by time after deployment ($P < 0.001$, Table S1) and the interaction between treatment and time after deployment ($P < 0.001$). Treatment had no significant effect on the territorial fish abundance. Average territorial fish abundance at the

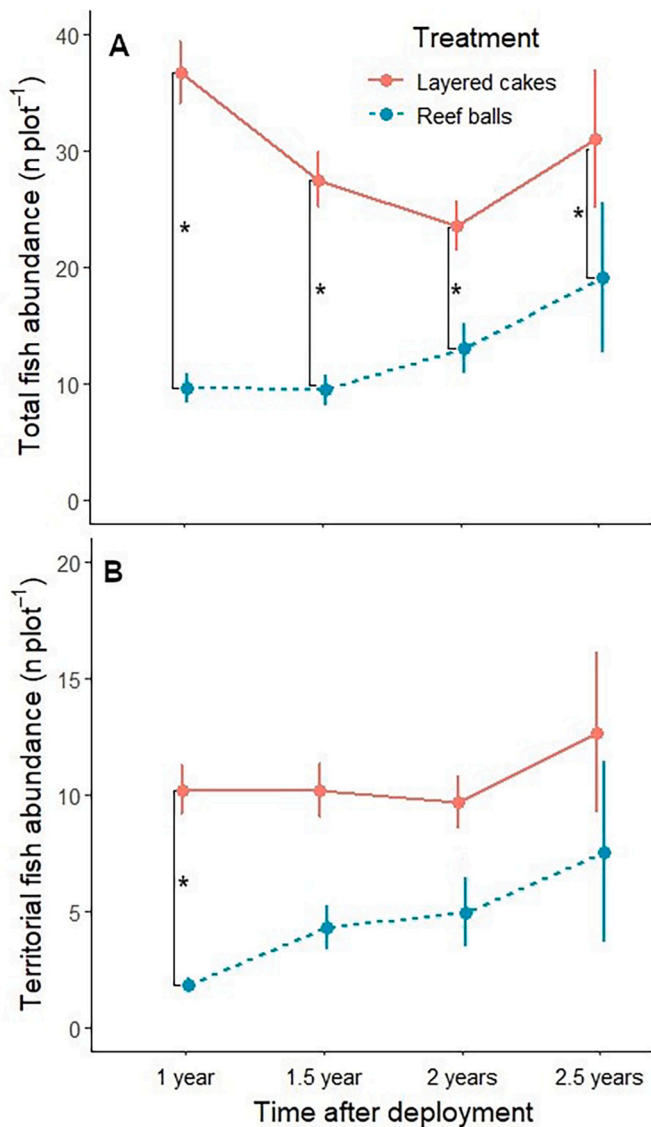


Fig. 4. Average total (A) and territorial fish abundance (B) (\pm SE) per treatment in time after deployment. * indicates a significant difference between treatments for that specific time after deployment.

layered-cake plots was 5.5 times and significantly higher compared to the reef-ball plots after one year ($P < 0.040$). Average territorial fish abundance was relatively stable over the course of the study at the layered cakes plots, while average territorial fish abundance steadily increased at the reef-ball plots, reducing the difference between treatments, which was not significant for the remainder of the study. The relative contribution of territorial fish to the total fish abundance increased over the course of the experiment from 19% at the reef-ball plots and 28% at the layered-cake plots to around 40% at both treatments.

3.3. Territorial behavior

Territorial behavior (Table 2) was significantly affected by treatment ($P = 0.017$, Table S1). Layered-cake plots experienced an average of 31.8 ± 31.9 chases hour^{-1} , which was significantly higher than the 7.9 ± 12.4 chases on the reef-ball plots. Exactly 90% of all territorial behavior was conducted by four species: *H. adscensionis* (33%); *A. saxatilis* (22%); *M. jacobus* (23%); and *S. partitus* (12%). The remainder of territorial behavior was conducted by 16 other species

Table 2

Territorial behavior (chases) (\pm SD) by 4 most common chasing fish species, the sum of 16 other species, chases by unidentified fish and the total average per treatment. Species are sorted based on the overall number of chases.

Name	Common name	Family	Average territorial behavior (chases hour^{-1} plot^{-2})	
			Reef ball	Layered cake
<i>Holocentrus adscensionis</i>	Long-spined squirrelfish	<i>Holocentridae</i>	0.4 ± 0.7	13.2 ± 16.1
<i>Abudefduf saxatilis</i>	Sergeant major	<i>Pomacentridae</i>	2.0 ± 3.5	6.9 ± 11.9
<i>Myripristis jacobus</i>	Blackbar soldierfish	<i>Holocentridae</i>	4.6 ± 8.0	4.4 ± 6.5
<i>Stegastes partitus</i>	Bicolor damselfish	<i>Pomacentridae</i>	0.2 ± 0.3	4.2 ± 4.6
16 other species			0.3 ± 0.2	2.7 ± 1.5
Unidentified fish			0.1 ± 0.1	0.4 ± 0.1
Total			7.9 ± 12.4	31.8 ± 31.9

(9%) or unidentified fish (1%). Territorial behavior of all but one species (*M. jacobus*) was much more common on the layered-cake plots as compared to the reef-ball plots. Territorial behavior at the layered-cake plots was 33 times more frequent for *H. adscensionis*, three times more frequent for *A. saxatilis* and 21 times more frequent for *S. partitus* compared to the reef-ball plots. *H. adscensionis*, *A. saxatilis* and *S. partitus* appeared more aggressive at the layered cake plots, as the number of chases per fish (chases per species divided by the fish abundance of that species) were respectively 2.1, 1.4 and 11.0 times higher at the layered cake plots compared to the reef ball plots.

Almost 80% of all chases were directed to five fish families: *Holocentridae* (43%), *Pomacentridae* (24%), *Acanthuridae* (6%), *Labridae* (4%) and *Scaridae* (4%) (Table 3). The remainder of chases were directed towards 13 other fish families (15%) or unidentified fish (4%). All families were chased more often at the layered-cake plots as opposed to the reef-ball plots. In 17% of all cases, territorial behavior resulted in the chased fish leaving the artificial reef plot, but this percentage differed greatly per family. *Holocentridae* almost never left the artificial reef plot after being chased in contrast to especially *Scaridae* and *Acanthuridae* that left the artificial reef plot much more often after they were chased.

3.4. Grazing intensity

Treatment was a significant predictor ($P < 0.001$, Table S1) for the

Table 3

Territorial behavior (chased) (\pm SD) against 5 most commonly chased families, the sum of 13 other families, unidentified chased fish and the total average per treatment. In addition, the percentage of chased fish which were chased off the artificial reef plot (%). Species are sorted based on the overall number of chases received. The assessment was done 1.5 years after deployment.

Family	Experienced territorial behavior (chased hour^{-1} plot^{-1})		% of chased fish leaving the artificial reef plot (%)	
	Reefball	Layered cake	Reef ball	Layered cake
<i>Holocentridae</i>	4.0 ± 7.0	14.2 ± 22.0	1%	3%
<i>Pomacentridae</i>	1.8 ± 3.0	7.6 ± 8.9	10%	22%
<i>Acanthuridae</i>	0.1 ± 0.1	2.1 ± 0.8	48%	32%
<i>Labridae</i>	0.2 ± 0.2	1.4 ± 0.6	0%	21%
<i>Scaridae</i>	0.4 ± 0.4	1.0 ± 0.7	39%	68%
13 other families	1.2 ± 2.1	4.1 ± 2.1	59%	12%
Unidentified	0.1 ± 0.1	1.4 ± 2.1	0%	51%
Total	7.8 ± 12.3	31.8 ± 31.8	14%	16%

standardized bite impact (assessed 1.5 years after deployment). The average standardized bite impact at the reef-ball plots was 86 ± 24 kg hour⁻¹, which was 5.4 times higher than the 16 ± 10 kg hour⁻¹ of the layered-cake plots (Table 4).

The most important grazers at both the reef ball and the layered-cake plots were medium sized Acanthurids: *Acanthurus tractus* (ocean surgeon fish) of 15–20 cm and *Acanthurus coeruleus* (blue tang) of 15–20 cm conducted 60% of all grazing on the reef ball and 50% of all grazing on the layered-cake plots. Other important grazers were *Scarus taeniopterus* (princess parrot fish) of 15–20 and 20–25 cm. All species and size classes conducted more grazing at reef-ball plots compared with layered-cake plots, with the exception of *Sparisoma aurofrenatum* (redband parrot-fish) of 15–20 cm.

Grazing sea urchins were never observed on the videos but were observed sporadically during the sunset surveys. Single *Diadema antiillarum* were observed at the CC location reef-ball plot and the CC layered-cake plot in November 2018 and at BRM layered-cake plot in December 2019. *Echinometra viridis* was recorded once at the BRM location layered-cake plot in November 2018 and once at the BRM reef-ball plot in May 2019.

3.5. Benthic succession

One year after deployment, turf algae were the dominant benthic group and had a relative abundance of ~80% cover on all artificial reef modules (Fig. 5, Table S4). Cyanobacteria, tunicates and CCA were other first colonizers and formed the majority of the remaining cover. Treatment ($P = 0.001$, Table S1) and monitoring period ($P = 0.001$) all had significant effects on benthic community composition. Post-hoc univariate tests revealed that reef ball modules had significant higher tunicate ($P = 0.003$) and sponge ($P = 0.065$) cover and significantly lower sediment cover ($P = 0.007$) compared to layered cake modules during all monitoring events. Over the course of study, the cover of turf algae ($P = 0.001$) declined significantly to around 50–60%, although turf algae remained the dominant benthic group. Cyanobacteria ($P = 0.038$) and bare concrete ($P = 0.001$) also declined significantly during the study, while cover of sponges ($P = 0.001$), CCA ($P = 0.001$) and other benthic groups ($P = 0.001$) increased significantly over time.

Table 4

Standardized bite impact (g hour⁻¹) (\pm SD) per species, size class and in total per treatment. The assessment was done 1.5 years after deployment. n.o. = not observed.

Name	Common name	Family	Size class	Bite impact (g hour ⁻¹)	
				Reef ball	Layered cake
<i>Acanthurus tractus</i>	Ocean surgeonfish	<i>Acanthuridae</i>	5–10	11 \pm 19	23 \pm 21
<i>Acanthurus tractus</i>	Ocean surgeonfish	<i>Acanthuridae</i>	10–15	2000 \pm 2133	1120 \pm 1008
<i>Acanthurus tractus</i>	Ocean surgeonfish	<i>Acanthuridae</i>	15–20	26,302 \pm 45,095	6014 \pm 5911
<i>Acanthurus tractus</i>	Ocean surgeonfish	<i>Acanthuridae</i>	20–25	n.o.	849 \pm 754
<i>Acanthurus chirurgus</i>	Doctofish	<i>Acanthuridae</i>	5–10	n.o.	142 \pm 245
<i>Acanthurus chirurgus</i>	Doctofish	<i>Acanthuridae</i>	10–15	n.o.	81 \pm 141
<i>Acanthurus chirurgus</i>	Doctofish	<i>Acanthuridae</i>	15–20	814 \pm 1410	n.o.
<i>Acanthurus coeruleus</i>	Blue tang	<i>Acanthuridae</i>	5–10	5.0 \pm 8.7	n.o.
<i>Acanthurus coeruleus</i>	Blue tang	<i>Acanthuridae</i>	10–15	281 \pm 469	505 \pm 72
<i>Acanthurus coeruleus</i>	Blue tang	<i>Acanthuridae</i>	15–20	26,239 \pm 18,614	1933 \pm 3295
<i>Acanthurus coeruleus</i>	Blue tang	<i>Acanthuridae</i>	20–25	6356 \pm 11,009	275 \pm 255
<i>Scarus taeniopterus</i>	Princess parrotfish	<i>Scaridae</i>	5–10	n.o.	0.1 \pm 0.2
<i>Scarus taeniopterus</i>	Princess parrotfish	<i>Scaridae</i>	10–15	n.o.	195 \pm 302
<i>Scarus taeniopterus</i>	Princess parrotfish	<i>Scaridae</i>	15–20	8372 \pm 12,288	2019 \pm 3078
<i>Scarus taeniopterus</i>	Princess parrotfish	<i>Scaridae</i>	20–25	11,623 \pm 19,707	485 \pm 530
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	<i>Scaridae</i>	5–10	1.2 \pm 2.1	0.3 \pm 0.6
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	<i>Scaridae</i>	10–15	618 \pm 1062	120 \pm 88
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	<i>Scaridae</i>	15–20	1046 \pm 1114	1924 \pm 2820
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	<i>Scaridae</i>	20–25	930 \pm 1543	90 \pm 156
<i>Sparisoma chrysopterus</i>	Redtail parrotfish	<i>Scaridae</i>	10–15	8.7 \pm 15	n.o.
<i>Sparisoma rubripinne</i>	Yellowtail parrotfish	<i>Scaridae</i>	15–20	998 \pm 1728	n.o.
Total				85,605 \pm 23,872	15,775 \pm 10,413

3.6. Coral recruit abundance

Coral recruit abundance (Table S5) was significantly affected by time after deployment ($P < 0.001$, Table S1), while treatment showed no significant effect. The lowest average abundance of coral recruits was 7.4 ± 3.6 coral per reef module, one year after deployment. This was significantly less than at all other monitoring moments ($P < 0.001$ for all comparisons). After 1.5 years, average coral recruit abundance was highest at both the reef balls (28.6 ± 19.1 recruits) and the layered cakes (30.3 ± 23.5). This was significantly higher compared to 2 years after deployment ($P = 0.033$), but not compared to 2.5 years.

3.7. Porites recruit survival

One year after deployment, during the first monitoring, a total of 103 coral recruits were found on the 16 artificial reef structures. These recruits belonged to three genera: *Porites* recruits ($n = 88$), *Agaricia* recruits ($n = 13$), and *Siderastrea* recruits ($n = 2$). While *Porites* recruits were found on all artificial reef modules at all locations, *Agaricia* recruits were found on 6 of the 16 modules and *Siderastrea* recruits were only found on a single layered cake at the BRM location.

Of the 88 *Porites* recruits found one year after deployment, 35 recruits (40%) were still alive 2.5 years after deployment. The number of these initial *Porites* recruits surviving (Table S5) significantly decreased with time after deployment ($P < 0.001$, Table S1), but did not differ by treatment. The average *Porites* recruit abundance, 1 year after deployment, was 5.4 ± 3.3 per reef ball module and 5.6 ± 3.2 per layered cake module. After 1.5 year this abundance was significantly lower ($P = 0.014$). *Porites* recruit abundance further declined between 1.5 and 2 years ($P = 0.014$, Table S1), but not between 2 and 2.5 years after deployment. At the end of the study 2.7 ± 2.6 recruit per reef ball module and 1.8 ± 1.9 per layered cake module were remaining of the initial *Porites* recruits, which was 40% of the initial settlement.

Of the 88 *Porites* recruits, 53 (60%) had disappeared by the end of the study. Going back to the last live picture of each recruit revealed that, at their last picture, 13 recruits were overgrown by CCA, four by turf algae, two by a sponge and two by a tunicate. Of 32 disappeared recruits, there was no clear indication of overgrowth by a competing organism, although all recruits were surrounded by other benthic organisms.

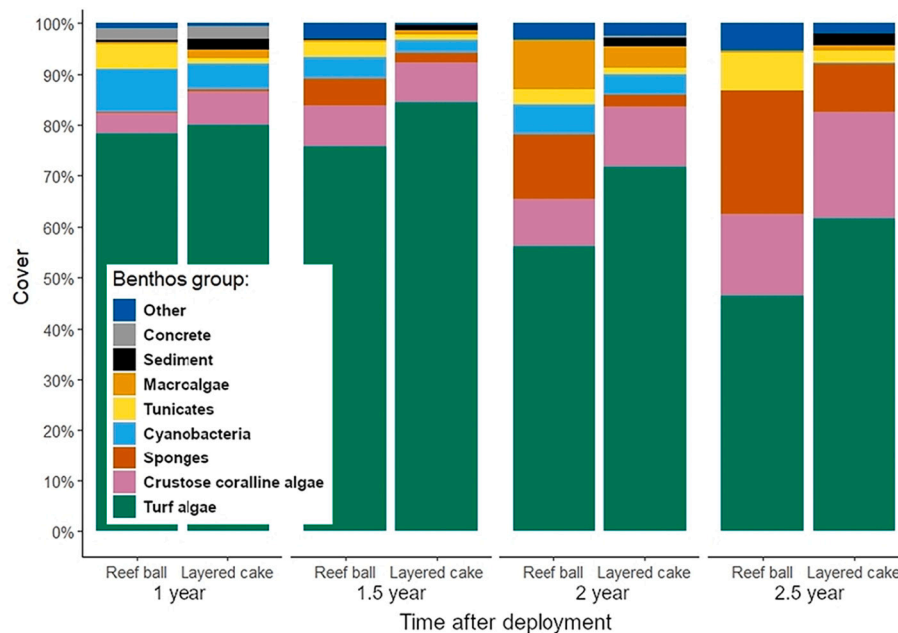


Fig. 5. Percentage cover of major benthic groups per treatment per time period after deployment.

3.8. *Porites* recruit size and growth

Porites recruit size (Table S5) significantly increased over the course of the study ($P < 0.001$, Table S1), but was not affected by reef type. As a consequence, growth of *Porites* recruits (Table S5) significantly differed between monitoring intervals ($P = 0.003$), but not between reef types. Monitoring interval 1.5–2 years had significantly higher growth rates compared to 1–1.5 year ($P = 0.019$) and 2–2.5 years ($P = 0.002$), which did not differ among each other.

4. Discussion

As described by Hylkema et al. (2020) layered-cake plots were more attractive to fish than reef balls, one year after deployment. This resulted in a significantly higher fish abundance and herbivorous and total fish biomass compared to the reef-ball plots. Based on this, we hypothesized that differences in fish abundance and biomass between layered cakes and reef balls would persist over time. This would result in a higher grazing pressure at the layered cakes, which would positively affect the benthic community and the coral recruitment parameters. However, this predicted cascade of effects never took place. The herbivorous fish biomass at the layered-cake plots was no longer significantly different from that at the reef-ball plots after 1.5 year of colonization. Herbivorous biomass at both artificial reef types remained relatively stable during the rest of the study. Initially, total fish biomass followed the same trend and decreased at the layered-cake plots, while increasing at the reef-ball plots and did not differ between treatments from 2 years after deployment on. From 1.5 year after deployment on, total fish biomass at both treatments increased until the end of the study. Therefore, the relative contribution of herbivorous fish biomass to the total fish biomass decreased for both treatments.

One year after deployment, layered-cake plots had significantly more fish compared to the reef-ball plots. This difference became smaller over the course of the study, but total fish abundance was still significantly higher at the layered cakes compared to the reef-ball plots at the end of the study. Since total fish biomass became similar at both treatments, reef balls had on average larger fish, which might be related to their bigger shelter size (Hixon and Beets, 1989; Beets and Hixon, 1994). Average territorial fish abundance was significantly higher at the layered-cake plots compared to the reef-ball plots at every monitoring

period and increased on both treatments over the course of the study. The territorial fish abundance increased relatively more than the total fish abundance. The large differences in fish abundance and biomass between one and 2.5 years after deployment indicate that the fish assemblages at the artificial reefs were still developing one year after deployment. The disruption by hurricanes in September 2017 required restoration of the artificial reefs in December 2017, which might have reset fish colonization. Although fish assemblages on artificial reefs have been suggested to stabilize within a year (Yeager et al., 2011), we have the impression that the initial colonization still was in progress, and the fish assemblages appeared more stabilized during consecutive monitoring.

The herbivorous fish abundance on the layered-cake plots might have been reduced by the territorial behavior from especially *H. adscensionis*, *A. saxatilis*, *S. partitus* and *M. jacobus*. *A. saxatilis* become very territorial when guarding a nest (Cummings, 1968). Although nests could often not be identified on the remote videos, the behavior of territorial *A. saxatilis* indicated they were guarding eggs, which was confirmed during the visual underwater surveys. *S. partitus* maintain permanent territories and defend them against much larger fish, especially during reproductive periods (Myrberg Jr, 1972; Luckhurst and Luckhurst, 1978). *M. jacobus* are known to chase other fish away from their shelter, likely because of refuge protection (Canterle et al., 2020). No observations in the literature were found about territorial behavior of *H. adscensionis*, but given the relatedness and a lifestyle similar to *M. jacobus*, it is likely that this species was also guarding its hiding place. In addition to conducting more chases in total, *H. adscensionis*, *A. saxatilis* and *S. partitus* appeared more aggressive at the layered-cake plots, as the number of chases per fish (chases per species divided by the fish abundance of that species) were substantially higher at the layered-cake plots compared to the reef-ball plots. This might be the combined result of 1) more suitable habitat in the layered cakes worth defending, 2) a higher abundance of other fish that had to be chased away (Canterle et al., 2020) and 3) more breeding activity at the layered cakes (Cummings, 1968).

The higher number of chases at the layered-cake plots is probably due to greater hiding opportunities facilitating more territorial fish. The positive effects of shelter availability on the fish abundance is well documented (e.g. Hixon and Beets, 1989; Gratwicke and Speight, 2005) and one of the reasons to initiate this study. However, this is the first

time that the attractiveness of a reef with a high shelter availability to territorial fishes in particular was shown. Through this mechanism, the layered shelters of the layered-cake design, initially facilitating a high fish abundance and biomass (Hylkema et al., 2020), were ultimately responsible for the reduction in overall fish abundance and biomass, as well as in grazing pressure. Possibly, the design of the shelter affects its attractiveness for certain territorial fish species. Especially *M. jacobus* is known for its preference for cave-like habitat (Canterle et al., 2020) and this is probably also true for *H. adscensionis*. Holes might be less attractive to these fish species than layers and an artificial reef design which is intermediate between layered cakes (high shelter availability) and reef balls (holes instead of layers) might combine advantages of both treatments compared in this study.

In contrast to our initial hypothesis that grazing would be more intense at the layered cakes, reef-ball plots experienced a much higher grazing intensity, which could have been the result of the lower chasing intensity at these reefs. Grazing intensity was determined 1.5 year after deployment, when layered-cake plots had a similar herbivorous fish biomass and a much higher territorial fish abundance compared to reef-ball plots. The similar herbivorous fish biomass and higher grazing intensity at the reef balls indicates that the majority of the grazing at the reef-ball plots was conducted by herbivores that only visited the artificial reef plots during foraging trips. The visual underwater surveys might have refrained roving herbivores from entering the artificial reef plots, excluding them from the fish surveys. These fishes were probably included in the longer video surveys, where they were not disturbed by divers. Since less territorial fishes were residing at the reef-ball plots, the visiting herbivores were less prone to be chased away, resulting in higher grazing intensity compared to the layered-cake plots. The most influential groups of herbivores, *Acanthuridae* and *Scaridae* were indeed the groups most affected by territorial behavior. Chases targeting these groups most often effectively induced the grazers to leave the plots, thereby effectively terminating their foraging activity.

On natural Caribbean coral reefs macroalgae (Gardner et al., 2003; Jackson et al., 2014), turf algae and cyanobacterial mats (De Bakker et al., 2017) often dominate the benthic community. All three groups are recognized as important competitors of corals and known to hinder coral recruitment (McCook et al., 2001, Kuffner et al., 2006, Box and Mumby, 2007, Arnold et al., 2010). Macroalgae cover on both artificial reef types was very low (< 2%) for the majority of the study. On the natural reefs around St. Eustatius macroalgae cover was around 15% in 2020 (Kitson-Walters, 2020). This suggests that grazing intensity at both artificial reef types was high enough to keep macroalgae under control. Although the artificial reefs in this study covered only 2 m² of seabed, fish swimming one meter around the artificial reef were considered part of the artificial reef fish assemblage and included in the surveys. This makes it hard to compare the herbivorous biomass per m² with that of areas which are an integral part of natural reefs. Depending if the biomass per plot is divided by the ground surface of the reef (2 m²) or the area included in the survey (9 m²) the herbivorous biomass per m² is estimated to be in the range of 12–75 g m⁻¹ for both reef types during most of the study. Even the lower end of this range is considered high for the Caribbean (Roff and Mumby, 2012; Edwards et al., 2014) and could explain why macroalgae cover on both reefs was relatively low over the course of the study.

On all artificial reef modules, benthic cover was dominated by turf algae, which had an average cover of ~80% one year after deployment. During the study, turf algae cover declined significantly, ultimately being replaced by mostly sponges and CCA. The higher grazing intensity documented at the reef-ball plots did not result in significantly lower turf algae or macroalgae cover compared to the layered cakes. Reef balls did have a significantly higher tunicate or sponge cover, which could be an indication that grazing created more space for other benthic groups than turf algae. Initial cyanobacterial cover at the artificial reefs was lower (5–8%) than the 10% recorded for the natural reef in 2020 (Kitson-Walters, 2020) and significantly declined further over the course of

the study.

Higher grazing intensities can facilitate coral recruitment (Arnold et al., 2010), but the higher grazing pressure at the reef-ball plots did not coincide with differences in coral recruit abundances although benthic community succession was different. Overall coral recruit abundance increased over time and significantly differed among the locations. This could be related to less competition or more suitable growing conditions at some locations. Also, other studies reported that location was more determining for coral recruitment than other factors, such as substrate material (Burt et al., 2009). Despite the low cover of Cyanobacteria and macroalgae, coral recruits were still often overgrown by other benthic groups, especially turf algae, sponges and CCA. As the high herbivorous fish biomass (by Caribbean standards) was not able to reduce turf algae cover, we recommend further research on how to achieve higher turf algae grazing efficiency by including trials with invertebrate herbivores, during early colonization of artificial reefs. Promising candidates could be the sea urchin *Diadema antillarum* or the Caribbean king crab, *Maguimithrax spinosissimus*, both known to effectively reduce turf algae cover and facilitate coral recruitment on natural reefs (Edmunds and Carpenter, 2001; Davies et al., 2013; Spadaro and Butler IV, 2021).

The most frequently observed coral recruits were *Porites astreoides* or *P. porites*, two brooding species (Fadlallah, 1983) of which the juveniles are very common on Caribbean coral reefs (Bak and Engel, 1979; Green et al., 2008; Davies et al., 2013). The higher grazing intensity at the reef-ball plots did not result in significantly higher coral recruit survival or growth, which had been suggested before (Arnold et al., 2010). *Porites* ssp. survival measured over 1.5 year was around 40% on both reef ball and layered cake modules. Coral recruit survival is highly variable and dependent on numerous factors such as recruit size, benthic competition, the species concerned (Vermeij, 2006) and unpredictable events such as cover by sand from big storm surges. Although difficult to compare, the six month survival rates in the present study seems to be similar to the 70% survival of *P. astreoides* over four months as reported by Davies et al. (2013). Survival rates in the present study were higher than the 18% survival of mostly *Agaricia* and *Porites* recruits over a year as reported by Arnold et al. (2010). Growth of some *Porites* recruits was hampered between 1.5 years after deployment till the end of the study. This could have been the result of many factors, but we noted that quite some coral recruits at especially the Twin Sisters location were buried by sediment when we monitored them after 2 and 2.5 years and sedimentation has been associated with partial coral mortality (Nugues and Roberts, 2003). Careful site selection based on sediment grain size distribution and sedimentation rates could potentially avoid mortality on newly recruited corals.

On average, growth and survival of *Porites* recruits on the concrete reef ball and artificial reef modules was similar to those for *Porites* recruited on materials that are comparable to the natural reef (Vermeij, 2006; Arnold et al., 2010; Davies et al., 2013). This suggests that concrete as substrate yields comparable coral growth and survival rates as natural reef materials. This is in accordance with Hsiung et al. (2020), who found no difference between concrete and natural rock material in the associated benthic communities. Studies comparing coral recruitment and survival on concrete and natural substrates are scarce (Burt et al., 2009), while studies including the effect of different types of concrete on coral development as far as we know, not yet been done. Marine infrastructure construction is increasing for decades and is expected to increase even further in the near future (Firth et al., 2016; Bishop et al., 2017). As concrete has been the most-often used material in marine infrastructure (McManus et al., 2018) we recommend a more systematic study into effects of concrete types on coral recruitment, survival and growth. The acquired knowledge on this topic would be beneficial to marine managers or conservationists for making better choices for artificial reef materials.

5. Conclusions

We conclude that the higher attraction potential of layered cakes to territorial fishes and the subsequent relative increase in territorial behavior of these fishes reduced the grazing intensity of roving herbivores on these structures over time. The herbivorous fish biomass on both artificial reef types appeared high enough to effectively control macroalgae and the higher grazing intensity documented on the reef balls did result in small but significant differences in benthic community development. This difference, however, did not influence coral recruitment, survival or growth. Especially the high turf algae cover might have impaired coral recruitment, while other benthic groups may have reduced coral recruit survival by competing for space. Sedimentation was a likely factor explaining negative growth rates and underlines the importance of proper site selection when the deployment of artificial reefs is considered. Despite their small size, the experimental reefs used in this study provided additional habitat for fish, coral recruits and other marine organisms. We therefore expect that larger artificial reefs, when designed and managed appropriately, can potentially provide added-value in terms of habitat, biodiversity and ecosystem services. We therefore recommend comparative research including larger artificial reefs, natural reefs and sand patches, to determine the net benefit of artificial reefs to the wider Caribbean coral reef ecosystem. In addition, we recommend research into new artificial reef designs, in which advantageous aspects of the reef balls (holes) and layered cakes (high and diverse shelter availability) could be combined to better facilitate herbivorous fishes and invertebrate grazers, which can reduce turf algae cover and increase coral recruit survival and growth.

CRedit authorship contribution statement

Alwin Hylkema: Writing – original draft, Methodology, Investigation, Formal analysis, Funding acquisition. **Adolphe O. Debrot:** Methodology, Writing – review & editing, Funding acquisition, Supervision. **Raven A.R. Cammenga:** Investigation. **Paolo M. van der Laan:** Investigation. **Marit Pistor:** Investigation. **Albertinka J. Murk:** Writing – review & editing, Supervision. **Ronald Osinga:** Writing – review & editing, Supervision.

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.

Data availability

Data will be made available on request.

Acknowledgements

This research was conducted in the context of the AROSSTA (Artificial reefs on Saba and Statia) project (project# RAAK.PUB03.048), which was partly funded by SIA, part of the Dutch Organization for Scientific Research. The authors want to thank Ayumi Izioka, Callum Reid, Daniel Heesink, Kevin de Jong and Esmee van de Griend, for their help with building the artificial reefs and restoring them after the hurricanes. We want to thank David Zaat, Lars ter Horst, Martijn Peters, Marnik van Cauter and Tom van Ee for their help with the fish surveys and Alex van der Last, Esther van de Pas, Fedor den Elzen, Jasper Bleijenberg and Michelle Mulken for their help with analyzing the videos. We are grateful to Jelle van der Velde, Kai Wulf, Walter Hynds and Jens Odinga from the Saba Conservation Foundation, to Jessica Berkel and Francois Mille from STENAPA, to Johan Stapel, Masru Spanner and Kimani Kitson-Walters from CNSI and to David and Sarah Hellevang from Golden Rock Dive Centre for their assistance. We thank Matan

Yuval and Aviad Adni from Marine Imaging Lab, University of Haifa, who made the three-dimensional models of the artificial reef types. Finally, we want to thank three anonymous reviewers who provided valuable feedback on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2022.106882>.

References

- Abramoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophoton. Int.* 11 (7), 36–42.
- Adam, T.C., Burkepile, D.E., Ruttenberg, B.I., Paddock, M.J., 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* 520, 1–20.
- Adam, T.C., Duran, A., Fuchs, C.E., Roycroft, M.V., Rojas, M.C., Ruttenberg, B.I., Burkepile, D.E., 2018. Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Mar. Ecol. Prog. Ser.* 597, 207–220.
- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B Biol. Sci.* 276 (1669), 3019–3025.
- Alvarez-Filip, L., Gill, J.A., Dulvy, N.K., 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere* 2 (10), 1–17.
- Arnold, S.N., Steneck, R.S., Mumby, P.J., 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Mar. Ecol. Prog. Ser.* 414, 91–105.
- Baine, M., 2001. Artificial reefs: a review of their design, application, management and performance. *Ocean Coast. Manag.* 44 (3–4), 241–259.
- Bak, R.P.M., Engel, M.S., 1979. Distribution, abundance and survival of juvenile hermatypic corals (*Scleractinia*) and the importance of life history strategies in the parent coral community. *Mar. Biol.* 54 (4), 341–352.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4 arXiv preprint arXiv:1406.5823.
- Beets, J., Hixon, M.A., 1994. Distribution, persistence, and growth of groupers (*Pisces: Serranidae*) on artificial and natural patch reefs in the Virgin Islands. *Bull. Mar. Sci.* 55 (2–3), 470–483.
- Bishop, M.J., Mayer-Pinto, M., Airoidi, L., Firth, L.B., Morris, R.L., Loke, L.H., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. *J. Exp. Mar. Biol. Ecol.* 492, 7–30.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24 (3), 127–135.
- Box, S.J., Mumby, P.J., 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar. Ecol. Prog. Ser.* 342, 139–149.
- Brotto, D.S., Krohling, W., Zalmon, I.R., 2006. Fish community modeling agents on an artificial reef on the northern coast of Rio de Janeiro-Brazil. *Brazilian Journal of Oceanography* 54, 205–212.
- Burkepile, D.E., Hay, M.E., 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS One* 5 (1), e8963.
- Burt, J., Bartholomew, A., Bauman, A., Saif, A., Sale, P.F., 2009. Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *J. Exp. Mar. Biol. Ecol.* 373 (1), 72–78.
- Cabaitan, P.C., Gomez, E.D., Aliño, P.M., 2008. Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *J. Exp. Mar. Biol. Ecol.* 357 (1), 85–98.
- Canterle, A.M., Nunes, L.T., Fontoura, L., Maia, H.A., Floeter, S.R., 2020. Reef microhabitats mediate fish feeding intensity and agonistic interactions at Príncipe Island Biosphere Reserve, Tropical Eastern Atlantic. *Mar. Ecol.* 41 (5), e12609.
- Carpenter, R.C., 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecol. Monogr.* 56 (4), 345–364.
- Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* 39, 355–389.
- Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *J. Exp. Mar. Biol. Ecol.* 399 (1), 60–67.
- Cummings, W.C., 1968. Reproductive Habits of the Sergeant Major, *Abudefduf saxatilis*, (*Pisces, Pomacentridae*) with Comparative Notes on Four Other Damselfishes in the Bahama Islands. University of Miami.
- Davies, S.W., Matz, M.V., Vize, P.D., 2013. Ecological complexity of coral recruitment processes: effects of invertebrate herbivores on coral recruitment and growth depends upon substratum properties and coral species. *PLoS One* 8 (9), e72830.
- De Bakker, D.M., Van Duyl, F.C., Bak, R.P., Nugues, M.M., Nieuwland, G., Meesters, E.H., 2017. 40 years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. *Coral Reefs* 36 (2), 355–367.
- Edmunds, P.J., Carpenter, R.C., 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc. Natl. Acad. Sci.* 98 (9), 5067–5071.

- Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P., Smith, J.E., 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B Biol. Sci.* 281 (1774), 20131835.
- Fadlallah, Y.H., 1983. Sexual reproduction, development and larval biology in scleractinian corals. *Coral Reefs* 2 (3), 129–150.
- Firth, L.B., Knights, A.M., Bridger, D., Evans, A.J., Mieszkowska, N., Moore, P.J., Hawkins, S.J., 2016. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Annu. Rev.* 54, 189–262.
- Froese, R., Pauly, D., 2019. *FishBase*. <http://www.fishbase.org>.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. *Science* 301 (5635), 958–960.
- Gratwicke, B., Speight, M.R., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Mar. Ecol. Prog. Ser.* 292, 301–310.
- Green, D.H., Edmunds, P.J., Carpenter, R.C., 2008. Increasing relative abundance of *Porites* astreoides on Caribbean reefs mediated by an overall decline in coral cover. *Mar. Ecol. Prog. Ser.* 359, 1–10.
- Hixon, M.A., Beets, J.P., 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44 (2), 666–680.
- Hsiung, A.R., Tan, W.T., Loke, L.H., Firth, L.B., Heery, E.C., Ducker, J., Todd, P.A., 2020. Little evidence that lowering the pH of concrete supports greater biodiversity on tropical and temperate seawalls. *Mar. Ecol. Prog. Ser.* 656, 193–205.
- Hughes, T.P., Graham, N.A., Jackson, J.B., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25 (11), 633–642.
- Hylkema, A., Debrot, A.O., Osinga, R., Bron, P.S., Heesink, D.B., Izioka, A.K., Murk, A.J., 2020. Fish assemblages of three common artificial reef designs during early colonization. *Ecol. Eng.* 157, 105994.
- Hylkema, A., Hakkaart, Q.C., Reid, C.B., Osinga, R., Murk, A.J., Debrot, A.O., 2021. Artificial reefs in the Caribbean: a need for comprehensive monitoring and integration into marine management plans. *Ocean Coast. Manag.* 209, 105672.
- Jackson, J.B.C., Donovan, M.K., Cramer, K.L., Lam, V.V., 2014. Status and trends of Caribbean coral reefs. In: *Global Coral Reef Monitoring Network*. IUCN, Gland, Switzerland, pp. 1970–2012.
- Jompa, J., McCook, L.J., 2002. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnol. Oceanogr.* 47 (2), 527–534.
- Kitson-Walters, K., 2020. St. Eustatius GCRMN Caribbean Report. CNSI.
- Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* 32 (9), 1259–1269.
- Korzen, L., Israel, A., Abelson, A., 2011. Grazing effects of fish versus sea urchins on turf algae and coral recruits: possible implications for coral reef resilience and restoration. *J. Mar. Biol.* 2011.
- Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R., Beach, K.S., 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar. Ecol. Prog. Ser.* 323, 107–117.
- Lenth, R., Herve, M., 2019. *Emmeans: Estimated Marginal Means, Aka Least-Square*.
- Lima, J.S., Zalmon, I.R., Love, M., 2019. Overview and trends of ecological and socioeconomic research on artificial reefs. *Mar. Environ. Res.* 145, 81–96.
- Luckhurst, B.E., Luckhurst, K., 1978. Diurnal space utilization in coral reef fish communities. *Mar. Biol.* 49 (4), 325–332.
- Mantyka, C.S., Bellwood, D.R., 2007. Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs* 26 (2), 435–442.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19 (4), 400–417.
- McManus, R.S., Archibald, N., Comber, S., Knights, A.M., Thompson, R.C., Firth, L.B., 2018. Partial replacement of cement for waste aggregates in concrete coastal and marine infrastructure: a foundation for ecological enhancement? *Ecol. Eng.* 120, 655–667.
- Miller, M.W., Valdivia, A., Kramer, K.L., Mason, B., Williams, D.E., Johnston, L., 2009. Alternate benthic assemblages on reef restoration structures and cascading effects on coral settlement. *Mar. Ecol. Prog. Ser.* 387, 147–156.
- Mumby, P.J., 2009. Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? *Coral Reefs* 28 (3), 683–690.
- Mumby, P.J., Harborne, A.R., Williams, J., Kappel, C.V., Brumbaugh, D.R., Micheli, F., Blackwell, P.G., 2007. Trophic cascade facilitates coral recruitment in a marine reserve. *Proc. Natl. Acad. Sci.* 104 (20), 8362–8367.
- Myrberg Jr., A.A., 1972. Ethology of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae): a comparative analysis of laboratory and field behaviour. *Anim. Behav. Monogr.* 5, 197–IN2.
- Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J., Polunin, N.V., 2015. Reef flattening effects on total richness and species responses in the C aribbean. *J. Anim. Ecol.* 84 (6), 1678–1689.
- Nugues, M.M., Roberts, C.M., 2003. Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. *Mar. Pollut. Bull.* 46 (3), 314–323.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., Jackson, J.B., 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301 (5635), 955–958.
- Perkol-Finkel, S., Benayahu, Y., 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. *Mar. Environ. Res.* 59 (2), 79–99.
- Perkol-Finkel, S., Benayahu, Y., 2007. Differential recruitment of benthic communities on neighboring artificial and natural reefs. *J. Exp. Mar. Biol. Ecol.* 340 (1), 25–39.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.** <https://www.R-project.org/>.
- Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* 27 (7), 404–413.
- Rogers, A., Blanchard, J.L., Mumby, P.J., 2018. Fisheries productivity under progressive coral reef degradation. *J. Appl. Ecol.* 55 (3), 1041–1049.
- Seraphim, M.J., Sloman, K.A., Alexander, M.E., Janetski, N., Jompa, J., Ambo-Rappe, R., Harborne, A.R., 2020. Interactions between coral restoration and fish assemblages: implications for reef management. *J. Fish Biol.* 97 (3), 633–655.
- Sherman, R.L., Gilliam, D.S., Spieler, R.E., 2002. Artificial reef design: void space, complexity, and attractants. *ICES J. Mar. Sci.* 59 (suppl), S196–S200.
- Spadaro, A.J., Butler IV, M.J., 2021. Herbivorous crabs reverse the seaweed dilemma on coral reefs. *Curr. Biol.* 31 (4), 853–859.
- van Woesik, R., Ripple, K., Miller, S.L., 2018. Macroalgae reduces survival of nursery-reared *Acropora* corals in the Florida reef tract. *Restor. Ecol.* 26 (3), 563–569.
- Vermeij, M.J.A., 2006. Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. *Coral Reefs* 25 (1), 59–71.
- Wang, Y.I., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund—an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* 3 (3), 471–474.
- Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol.* 3 (1), 89–101.
- Yap, H.T., 2009. Local changes in community diversity after coral transplantation. *Mar. Ecol. Prog. Ser.* 374, 33–41.
- Yeager, L.A., Layman, C.A., Allgeier, J.E., 2011. Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* 167 (1), 157.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer, New York.