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Nutrient dynamics, carbon storage and community composition on artificial and natural reefs in Bali, Indonesia

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Abstract

Artificial reefs are now commonly used as a tool to restore degraded coral reefs and have a proven potential to enhance biodiversity. Despite this, there is currently a limited understanding of ecosystem functioning on artificial reefs, and how this compares to natural reefs. We used water sampling (bottom water sampling and pore water sampling), as well as surface sediment sampling and sediment traps, to examine the storage of total organic matter (as a measure of total organic carbon) and dynamics of dissolved inorganic nitrate, nitrite, phosphate and ammonium. These biogeochemical parameters were used as measures of ecosystem functioning, which were compared between an artificial reef and natural coral reef, as well as a degraded sand flat (as a control habitat), in Bali, Indonesia. We also linked the differences in these parameters to observable changes in the community structure of mobile, cryptobenthic and benthic organisms between habitat types. Our key findings showed: (1) there were no significant differences in inorganic nutrients between habitat types for bottom water samples, (2) pore water phosphate concentrations were significantly higher on the artificial reef than on both other habitats, (3) total organic matter content in sediments was significantly higher on the coral reef than both other habitat types, and (4) total organic matter in sediment traps in sampling periods May and September were higher on coral reefs than other habitats, but no differences were found in November. Overall, in terms of ecosystem functioning (specifically nutrient storage and dynamics), the artificial reef showed differences from the nearby degraded sand flat, and appeared to have some similarities with the coral reef. However, it was shown to not yet be fully functioning as the coral reef, which we hypothesise is due its relatively less complex benthic community and different fish community. We highlight the need for longer term studies on artificial reef functioning, to assess if these habitats can replace the ecological function of coral reefs at a local level.

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Introduction

Artificial reef overview

Artificial reefs (ARs) are man-made structures deployed within the marine environment thought to have been utilised since the 1600 s as a tool used to attract fish for enhancing fish catch (Stone et al. 1979). Only since the rise of the environmental movement in the 1960s and 1970s, have artificial reefs gained attention for their potential in habitat restoration (Paxton et al. 2020). Research in the last decade has highlighted how ARs can quickly restore previously degraded and/or unproductive areas, through providing previously unavailable substrata and habitat complexity (Becker et al. 2017; Israel et al. 2017). The use of ARs as a habitat enhancement tool has been shown to be particularly

successful when deployed in previously degraded tropical coral reefs (Lemoine et al. 2019; Paxton et al. 2020, Boakes et al. 2022a), especially in cases where natural recovery would be unlikely or slow [e.g. if regime shifts to algal states have already occurred (Graham et al. 2015; Kenyon et al. 2020)]. Due to anthropogenic threats such as climate change induced bleaching, overfishing and pollution (Lesser 2011; Claar et al. 2018; Andrello et al. 2022), global coral reef health has substantially declined in recent decades (Heron et al. 2017; Hughes et al. 2018). ARs continue to be used as a tool to provide some degree of localised protection against this, and in certain cases, restore ecosystem services in tropical areas which have lost natural reefs entirely (Chen et al. 2013; Schulze et al. 2020; Boakes et al. 2022a).

ARs designed for habitat enhancement purposes may incorporate intentionally built structural complexity [e.g. in the form of multiple hiding spaces and exits, high surface areas and hollow interior spaces such as caves or tunnels (Marinaro 1995; Lemoine et al. 2019)]. This supports colonisation of mobile communities as spawning adults use the new substrata to lay their eggs, whilst juveniles are provided with shelter and protection, and utilise the AR as a nursery (Herbert et al. 2017). Artificial reefs may also be built with a rough and/or textured surface which allows the larvae of corals (and other benthos) to attach themselves, thus enhancing benthic recruitment (Bohnsack and Sutherland 1985; Harris 2009). When deployed in previously poor quality and/or degraded habitats, the new substrata and complexity provided by the ARs has been shown to consistently lead to increases in biomass and diversity of reef species (Godoy et al. 2002; Komyakova et al. 2019; Boakes et al. 2022a). Whilst a great deal of research has already associated ARs with the restoration of biodiversity, it remains debated whether their functioning is comparable to natural reefs (Carr and Hixon 1997; Paxton et al. 2020), with currently a very limited amount of research on the topic. Our previous study has highlighted that although well-designed AR structures can provide ecologically equivalent mobile faunal communities to a nearby natural coral reefs, exact species composition between ARs and their nearby natural reefs remain distinct 3 years after deployment (Boakes et al. 2022a).

Artificial reef fish communities

Literature has shown that ARs are especially effective at increasing fish biomass of a given area because they supply additional food, enhance feeding efficiency and offer protection from predators (Bohnsack 1989). The increased fish biomass associated with ARs can lead to higher biogenic deposits onto the reef system (Ambrose and Anderson 1990; Rizzo 1990; Fabi et al. 2002; dos Santos et al. 2005; Reeds et al. 2018). Rizzo (1990) and Leitão (2013) showed that

when these bio-deposits (e.g. excretion of ammonium, urea and faeces) enter the water column, they may be deposited and stored within sediments arounds ARs. This has been further demonstrated by Falcão et al. (2007), who highlighted that 2 years after deployment of ARs in Portugal, sediments displayed increased concentrations of organic and inorganic compounds by 30–60%, compared to pre-deployment levels. Other studies conducted on ARs in Portugal have demonstrated the link between higher levels of organic carbon (OC) and nitrogen on ARs with higher fish biomass (Vicente et al. 2008). It must be noted that literature investigating the links between fish and AR ecosystem functioning is still limited, with the majority of studies that do assess this being from temperate environments, and very few from tropical reefs. Despite this literature gap, research on the functioning of tropical natural reefs has shown that fish have key functional roles within coral reef systems [e.g. the role of surgeonfish in algal grazing; Bellwood et al. (2019)]. Furthermore, reef fish have been highlighted to make substantial contributions to exporting OC to surrounding sediments (Polunin 1996), and restored systems and healthy fish stocks have been linked with significantly higher carbon sequestration rates (Howard et al. 2017a, b; Stafford et al. 2021). More work is needed to specifically understand the roles fish play in the functioning of ARs, and if this is comparable to natural coral reefs.

Artificial reef benthic communities

Alongside providing habitats to fish, ARs are also colonised by corals, as well as fouling organisms such as sponges, tunicates and bryozoans (Perkol-Finkel and Benayahu 2007; Burt et al. 2009). Benthic invertebrates rapidly colonise ARs (Holmström and Kjelleberg 1994; Oren and Benayahu 1997; Mariani 2003) and have been shown to compete with each other for space on the substrata provided by artificial structures (Perkol-Finkel and Benayahu 2007). Despite the recruitment and growth of benthic invertebrates on ARs, studies have highlighted that their communities often remain distinct to those on nearby natural coral reefs (Perkol-Finkel et al. 2005, 2006), likely to some extent because coral reefs are formed over hundreds of years of complex, reef-forming processes (El-Naggar 2020). Currently, no research has assessed the role of tropical AR benthic communities on ecosystem functioning, and if they can contribute to similar levels of nutrient uptake and release to neighbouring natural coral reefs. Natural coral reef benthic communities (specifically corals and algae) have been shown to be important in terms of the uptake of dissolved inorganic nutrients (DINs) such as nitrate, phosphate and ammonium (Steven and Atkinson 2003, Den Haan et al. 2016). De Goeij et al. (2017) discussed the importance of sponges in terms of reef ecosystem functioning, where they are described as the "*ecosystem driver in the cycling of nutrients and energy on coral*

reef ecosystems". Current research is generally inconclusive with regard to the role of coral reefs in terms of net carbon sequestration, with Howard et al. (2017a, b) highlighting that coral reef ecosystems can be sources or sinks of atmospheric CO_2, depending on the balance between two sets of processes: photosynthesis/respiration and calcification/dissolution. Research by Gattuso et al. (1998), highlighted that on most reefs, the CO_2 taken in by the coral's photosynthetic algae is approximately equal to the CO_2 released as a result of coral, algal and microbial respiration. The same study concluded that many coral reef ecosystems may actually lead to little/no net carbon removal from the surrounding water column and atmosphere, especially when compared to other marine habitats such as mangroves and seagrasses.

Understanding the relationships between key nutrients and reef biota

Nutrient uptake and release is one of the core processes defining coral reef functioning (Brandl et al. 2019a) and is often used as a key measure for assessing ecosystem functioning (e.g. Lohrer et al. 2010; Trap et al. 2016; Griffiths et al. 2017). Research has shown that preserving these processes is fundamental in safeguarding the health and resilience of a given system (Isbell et al. 2017) as ecosystem functioning on reefs supports common conservation objectives such as high coral cover, structural complexity and fish abundance (Brandl et al. 2019a). It is important to understand the relationships between key nutrients and reef biota (Bellwood et al. 2019), especially with regards to OC (e.g. Atwood et al. 2018; Nelson et al. 2023); and dissolved inorganic nutrients (DINs; e.g. Hatcher and Frith 1985; Silbiger et al. 2018). Despite this, the current link between community structure and coral reef ecosystem functioning remains poorly researched (Brandl et al. 2019b). Given the rapid global decline in coral reef health, as well as their capacity to deliver ecosystem services, there is an ever-increasing need to better understand the functioning of coral reefs (Bellwood et al. 2019), including those which have been restored using ARs. Vivier et al. (2021) highlighted that there is a limited amount of research which has evaluated ecosystem function of ARs and suggested that more studies should investigate the complex relationships between their functioning and reef biota. Our study compared nutrient storage and dynamics on an AR to a neighbouring natural coral reef, as well as to a degraded sand flat in Bali, Indonesia. We aimed to examine, if, based on these biogeochemical parameters, functioning on ARs was comparable to natural coral reefs, or if they displayed more similarities with degraded sand flats. More specifically, we aimed to investigate the differences in storage of TOM, as well as dynamics of inorganic nitrites, nitrites, ammonium and phosphates between these habitat types, and whether these differences were linked to observable changes in the community structure of mobile, cryptobenthic and benthic organisms.

Methods

Location

All data were collected in Tianyar Bay, North Bali, Indonesia (Fig. 1) across three habitat types.

The three surveyed habitats, as shown by Fig. 2, included:

(A) *Artificial reefs*: which were constructed by the local community using a three part mix of cement, calcium and sand, producing what were known as 'roti buaya'; 1×0.5 m table shaped structures with a textured surface (e.g. with bumps, scratches, cracks and crevices) to allow natural recruitment of benthic species. The units were deployed between 5 and 10 m depth on top of sand flats (see below). The ARs were installed in clusters, each with 20–30 units, covering an area of approximately 10 m^2. In each group, structures were stacked haphazardly (in a similar configuration between groups, and also locations), with the aim of providing optimal protective space, such as holes, tunnels and caves which provide additional habitat for sheltering fish (see Fig. 2B). The ARs were deployed over a 3-year period and the data collected in this study were from ARs aged between 1 and 3 years.

(B) *Flat sand habitat (Herein 'sand flat')*: a sand-bottom area with little no/hard substrata and limited biological communities. Through conversations with the local community, it was understood that this sand flat was originally a healthy natural reef, but was destroyed several decades ago due to boat anchoring, coral harvesting and destructive fishing practices. After several decades of erosion and sedimentation, most of the remains of this degraded reef had disappeared and become covered with a layer of sand, hence the name 'sand flat'. It was decided that this habitat type would be included within our study, as it represented a control site (the AR habitat if no structures had been deployed there), therefore, directly highlighting the changes in ecological communities as a result of AR deployment.

(C) *Coral reef (CR)*: a relatively pristine coral reef with a high biodiversity of benthic and mobile species. Through conducting reef health index (RHI) surveys [following Díaz-Pérez et al. (2016)] on this area of reef, it was shown through our research that this area of reef had a RHI score of 4.5 ("good"–"very good"; Boakes et al., unpublished). Through personal communication with the local community, it was understood that this area of reef had not been previously targeted by the

Fig. 1 Location of the three sampling sites (Sand Flat, Artificial Reef (AR) and Coral reef (CR)) within Tianyar Bay, Bali, Indonesia. Created using ArcGIS OpenStreetMap powered by Esri
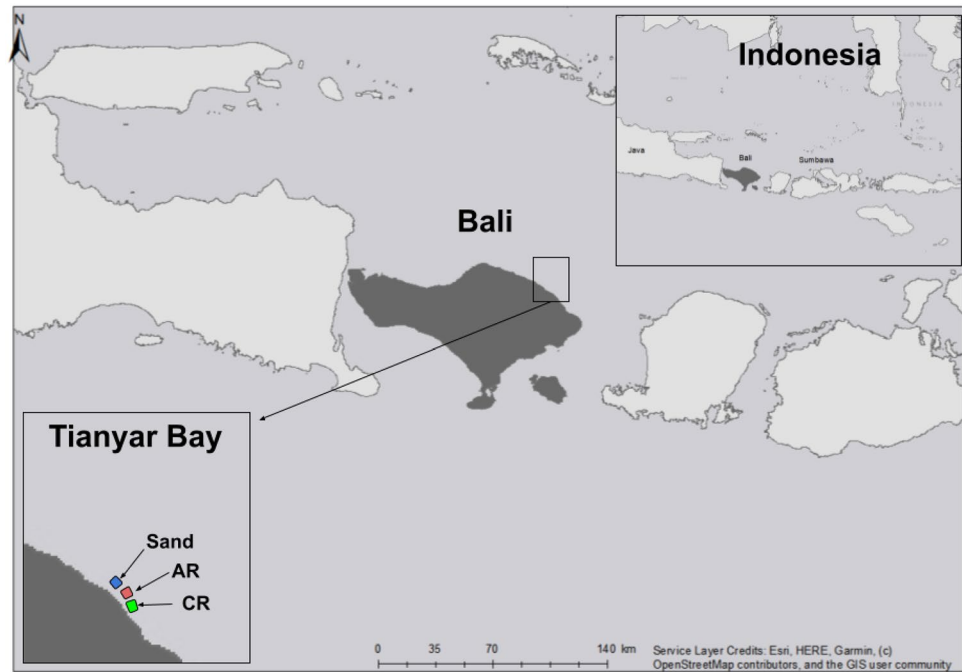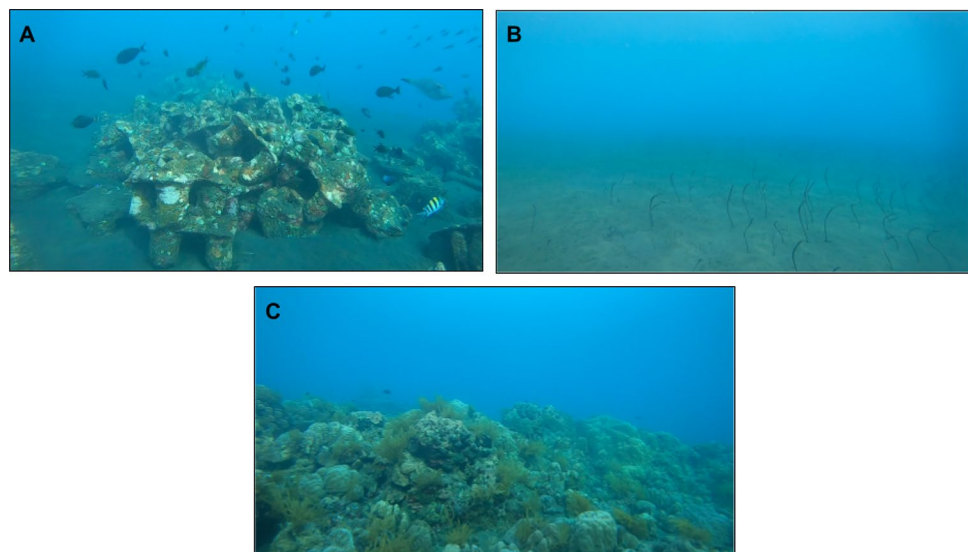

Fig. 2 Three habitat types were surveyed, including an artificial reef (**A**) and flat sand bed (**B**) and coral reef (**C**). These images were taken as screenshots from RUV recordings at each habitat type

same localised threats as the other degraded habitats in this study (notably the sand flat), likely explaining why it was still in good condition.

Each habitat was approximately 250 m apart and surveyed within the same depth range (5–10 m). Habitats were surveyed between the months of July 2021 to November 2022, with periodic nutrient sampling and ongoing ecological surveying (except the monsoon season due to poor fieldwork conditions) throughout the whole data collection period (see Fig. S1 data collection schedule). All three habitat types were located

within a marine protected area (MPA) managed by North Bali Reef Conservation, locally known as Yowana Bhakti Segara (www.northbalireefconservation.com; 8° 11′ 27.5″ S 115° 29′ 42.9″ E). The MPA (approximately 5 hectares (personal communication with local fishers) was established by the local community in 2017. At the time this study was conducted, the MPA continued to be well enforced, and the localised threats which were thought to previously degrade the reef appeared to have stopped, likely in large part due to establishment of this MPA.

Nutrient sample collection

Overview

As a measure of dynamics of DINs (nitrate, nitrite, phosphate and ammonium), bottom water and pore water samples were taken. As a measure of total organic matter (TOM) storage, surface sediment samples were taken over a 2-day period and sediment traps were deployed for 8 weeks (replicated three times) over an 8-month period.

Inorganic nutrients in bottom water samples

Bottom water samples were collected by SCUBA divers at the same frequency and sampling sites as the sediment samples (as described above). In total, across all three habitat types, 90 samples were taken. Bottom water samples were collected 0.5 m above the reef/sand surface, following Larned (1998) and Wild et al. (2009), which was measured using a 0.5 m measurement line. The samples were taken using 250 ml washed Nalgene polyethene bottles [following Lafferty et al. (2018)]. The bottle caps were opened at the desired sampling site, allowing the water to flow in, and were closed after 1 min once the bottle was free of air bubbles [following Limbong (2003)]. After the dive, the samples were filtered using 0.7 um Whatman glass microfiber filters, and then kept refrigerated in cool boxes (same as above) until they were tested in the lab [following Leichter et al. (2003)].

Inorganic nutrients in pore water samples

Fewer pore water samples were taken than bottom water samples because extraction of the pore water took substantially longer, meaning that SCUBA divers were limited in the amount of samples that could be taken per dive. In total, ten pore water samples were taken in each of the three habitat types ($n = 30$), across a transect where an even number of samples were taken at each depth between 5 and 9 m (two samples were taken at 5 m, two at 6 m, two at 7 m, two at 8 m and two at 9 m). Pore water was extracted using washed 300 ml syringes, attached to a tygon tube with a perforated steel pointed tip. The steel tip was injected 10 cm into the sediment [following Precht and Huettel (2004)], then, following the recommendations of Berg and McGlathery (2001), divers pulled back the syringe piston in a slow and steady movement so that pore water was drawn into the tygon tube. Once the syringe was filled to 300 ml, it was immediately taken to the surface to avoid contamination with other water, where it was filtered, cooled and analysed using the same methods as the bottom water samples,

as discussed above. Samples were kept refrigerated in cool boxes (as above) until they were tested in the lab [following Leichter et al. (2003)].

### Total organic matter in surface sediment samples

In each habitat type, 30 sediment samples were taken between a depth of 5–10 m, with five samples taken at 5 m depth, five at 6 m, five at 7 m, five at 8 m, five at 9 m and five at 10 m, similar to the methods of Pardo (2014). In total, across all three habitat types, 90 samples were taken. It was ensured that there was at least a 5 m distance between each sample. Following the methods of Jewett et al. (2008), surface samples were taken at a sediment depth of 5 cm at each sampling site, using washed 250 ml polyethylene bottles which were filled with surface sediment and then sealed [following Honjo et al. (1988)]. On the AR, samples were taken as close as possible to the transect points, whilst also ensuring samples were collected next to or directly below the artificial reef unit. On the CR, samples were taken on sediment areas closest to the transect points. After the samples were collected, they were sealed using screw bottle caps and then stored in dark cool boxes kept between 4 and 5 degrees °C [following Von Wachenfeldt (2008)] for 2 h, whilst they were taken to the lab for processing. Samples were processed immediately once they had arrived at the lab.

Total organic matter in sediment traps

Following Buesseler et al. (2007), sediment traps were collected and analysed as an measure of TOM sediment deposition. Sediment traps were made from PVC cones (with a height of 20 cm and a diameter of 13 cm at the mouth and 3 cm at the bottom [following Gust et al. (1994)]. The specific cone shape (highlighted in Fig. 3) was chosen over standard cylindrical tube sediment traps, to allow a greater collection of sediment over short time scales. Using steel wire, the cones were fitted and attached to purpose-built tripod stands which lifted the mouth of the traps 30 cm above the sand/sea floor (Fig. 3). The sediment traps and their tripod stands were deployed from a boat and then carried to their desired sampling sub-sites by SCUBA divers. Deployment sub-sampling sites were chosen haphazardly on the flat sand bed and the artificial reef; however, on the coral reef, they were placed only on small, empty sand patches (instead of directly on top of corals). On the AR, the sediment traps were deployed directly next to the AR units (as close as possible to them), which ranged in age between 1 and 3 years.

In total, 5 sediment traps were deployed in each of the three habitat types. The sediment traps were retrieved by removing the cones from their tripod frames and carefully brought to the surface. After being bought ashore, the samples were transferred to 250 ml PET bottles, sealed with

Fig. 3 Photographs of two of the sediment traps which were fitted to purpose-built tripods
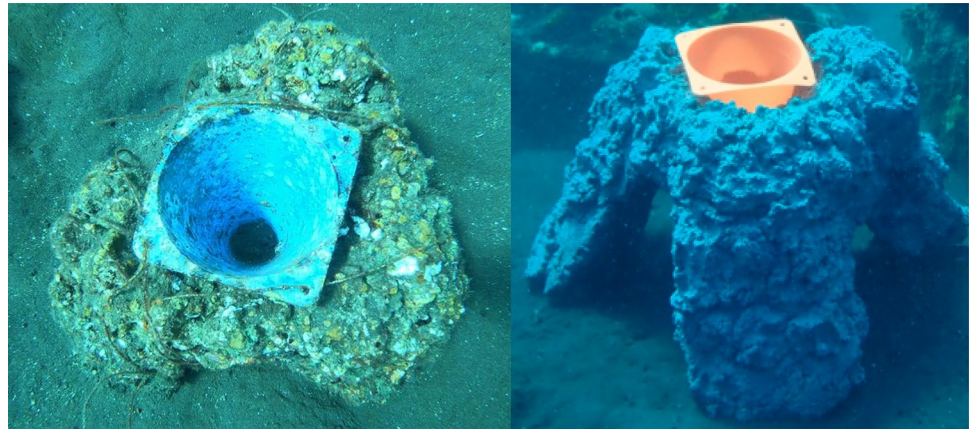
screw bottle caps and then stored in dark cool boxes [following Von Wachenfeldt (2008)] whilst they were taken to the lab for processing. Samples were deployed for 8 weeks [following Harrison and Hall (2021)] at a time, and then re-deployed two more times (three replicates) at the exact same locations. In total, the sampling period for the sediment traps was 8 months (Fig. S1), giving a total of 45 samples across all three habitat types over this time.

Lab analysis

Following the methods of Baum et al. (2015), water samples were analysed for nitrate, nitrite, ammonium and phosphate using a Hach DR900 using the cadmium reduction, diazotization, salicylate, and ascorbic acid method, respectively. Detection values followed those of Baalbaki et al. (2019) (e.g. the detection value for nitrate and nitrite was 0.01 mg/L and 0.001 mg/L, respectively). Sediment samples (both surface sediments and sediment trap) were tested for total organic matter (TOM) content using the 'loss-on-ignition' method, which compared the weight of the dry mass of the sample to the 'ashed' mass (after it had been combusted at 550 °C for 12 h, thus allowing percentage total organic matter (herein % TOM) to be calculated [following Wang et al. (2011)]. Given that the primary component of TOM in ocean sediments is total organic carbon (TOC; Sutherland 1998), these results were used as a measure of TOC within our sediment samples.

Biological community structure

For data collection on benthic, cryptic and mobile communities, three sample sites (herein sites) were established in each of the three habitat types, which were each approximately 50 m apart. Sampling sites were chosen haphazardly, and were marked using a coded sign, attached to a frame and a 30 cm^2 concrete base.

Mobile species

Following the methods of Boakes et al. (2022a), remote underwater video (RUV) was used as a measure of mobile community structure by comparing the abundance and diversity of mobile species between sites. Video samples were taken within 6 weeks of water and surface samples being taken and during the time of sediment trap data collection using a GoPro Hero 5 HD 1080p underwater camera between 8 and 10 am on sampling days (of varying tidal conditions), only on calm mornings when underwater visibility was at least 15 m (measured using a visibility measuring line). Again, following Boakes et al. (2022b), each habitat type had three sampling sites, which were each recorded twice over the research period, giving a total of 6 samples per habitat type, and 18 in total. RUV videos were recorded for a duration of 25 min, allowing for an initial 5 min settlement period and 20 min of analysis time [following Boakes et al. (2022b)], allowing appropriate estimates of community structure to be obtained, only missing low numbers of rarely occurring, often transient, species. From the videos, only clearly identifiable individuals were recorded. Mobile species were identified to species level and in circumstances of uncertainty, advice was sought from local expert, Yunald Yahya (LINI foundation). As a relative measure of abundance, the maximum number of individuals seen in any frame (herein MaxN; following Whitmarsh et al. (2017)) during the 20 min video (each sampling period) was calculated.

Cryptic species

It was noticed that there were several small, cryptobenthic (CB) fish species on the AR and CR which resided within the protective space provided by the substrata, and thus were not clearly identifiable from the RUV recordings. Due to the potentially important role of CBs in reef ecosystem functioning [as demonstrated by Brandl et al. (2019a)], it

was decided that a 'cryptical crawl' (underwater stationary point count) would be conducted to estimate CB community structure, following Mallet et al. (2014). In the same site as each of the RUV recordings (nine in total), two independent Underwater Visual Census surveys were performed by SCUBA divers in each of the three habitat types ($n = 6$), who recorded the cryptic fish species that were present within the refuge area provided by the substrata (thus making them mostly unrecorded from the RUV analyses). Following Watson (1997), all cryptic fish within a cylindrical column (of a 10 m radius) were recorded over a 12 min sampling period. One diver was responsible for recording fish species on a pre-prepared dive slate, whilst the other ensured all sampling was conducted within the 10 m cylindrical column. As with RUV analysis, the maximum number of individuals of each species (MaxN) was recorded.

Benthic species

Photo-quadrat sampling is a method commonly used to determine estimates on benthic community structure on coral reefs (Leujak and Ormond 2007). Following the methods of Clua et al. (2006) and Chaves et al. (2013), 40 cm^2 quadrats were placed randomly along fixed 20 m line transects running across each site (the same sites used for the RUV samples). Using SCUBA and an Olympus TG-6 camera, 10 photo-quadrats were taken at each of the three sites (90 in total across all three habitat types). Following Leujak and Ormond (2007), photos were taken approximately 2 m away from the substrate, thus fitting the whole quadrat into one photograph. Percentage cover was calculated by dividing each photograph into four 10 cm^2 sub-frames [following Mantelatto et al. (2013)], allowing benthos to be more accurately estimated. Within each sub-frame, benthos was identified to at least family level [following Schmidt-Roach et al. (2008)] and total percentage coral cover of each sub-frame was analysed using Coral Point Count with Excel extensions, following the guidance of Kohler and Gill (2006). Corals were identified with the help of multiple benthic ID guides and local experts were approached in times of uncertainty.

Statistical analysis

Two-way ANOVA was run to analyse inorganic nutrient concentrations in water samples, with water type (bottom, pore) and habitat type (CR, AR, S) as the two factors, separate analyses were conducted for each nutrient. Two-way ANOVA was also run to analyse % TOM in sediment traps, with sampling period (May, September, November) and habitat type as the two factors. A separate one-way ANOVA was run to analyse TOM between habitat types in surface sediments. In addition, to compare surface %TOM values with those collected from sediment traps, we included the surface samples as an additional sampling period in the sediment trap database, and ran a two-way ANOVA between habitat and sampling period again (with quasipoisson link functions). In all cases, assumptions of standard ANOVA (normality and homogeneity of variance) were not adequately met. Following Crawley (2007), GLMs with quasipoisson link functions were used with ANOVA p values calculated using F tests. Additional multiple comparison tests were conducted using the emmeans package in R (Russell et al. 2021). No p value adjustment was used as the number of comparisons of interest was much lower than the full set of interaction terms in the two-way models.

To explore community structures for mobile, CB and benthic assemblages, PERMANOVA was run (separately for each community) using the Vegan package in R (following Anderson (2001)) to assess the difference in communities (MaxN for mobile species and CBs, and percentage cover for benthos) between habitat types. Data were square-root + 1 transformed prior to use, to avoid the excessive weighting of common species over rare. A Bray–Curtis resemblance matrix was used with 9999 permutations and PERMANOVA run with unrestricted permutation of raw data. For mobile species, as RUV recordings were taken from the same sites within each habitat, site was nested within habitat. For other tests, there was independence between all samples. Principal Coordinate Analysis (PCoA) was used to visualise community variation between habitat types and to highlight key species which differentiated the different biological communities at the different habitat types (using criteria of $p < = 0.001$ and $r > 0.45$ to display discriminating species arrows).

Results

Inorganic nutrients in bottom and pore water samples

For nitrate, nitrite and ammonium, two-way ANOVA showed no significant interaction terms and no differences between habitat types ($p > 0.05$ in all cases); however, pore water had significantly higher concentration than bottom water for all three nutrients (Table 1).

Phosphate showed a significant interaction term between water type and habitat (Table 1), with significantly higher phosphate concentrations in pore AR samples compared to bottom water AR samples (AR bottom: AR pore $p < 0.001$;

Fig. 4). No other differences between water type within habitat type occurred. Pore water phosphate concentration was significantly higher on the AR than both other habitats (AR: CR $p < 0.001$, AR: Sand $p < 0.001$), but was not significantly different between the CR and sand flat (CR: Sand $p > 0.05$; Fig. 4). In terms of phosphate concentrations in bottom water samples, no significant difference were shown between habitat types, except between artificial reef and sand-bottom water ($p = 0.0434$).

Total organic matter in surface sediment samples and sediment traps

In terms of surface sediment sampling, one-way ANOVA showed significant differences between habitat types (Table 2). In surface sediments, the CR was found to have significantly higher % TOM than both other habitat types (multiple comparison $p < 0.001$). The AR was also found to have a significantly higher % TOM than the sand flat

Table 1 ANOVA results and mean ($\pm$ SD) concentrations of inorganic nutrients from water samples

Nutrient	Factors	d.f	f value	p value	Bottom water mean concentration (mg/L)	Pore water mean concentration (mg/L)
Nitrate	Water type	1, 114	51.6	< 0.001	0.0027 *(0.0058)*	0.0130 *(0.0091)*
Nitrite	Water type	1, 114	18.7	< 0.001	0.0030 *(0.0013)*	0.0042 *(0.001)*
Phosphate	Water type*habitat type	2, 114	12.02	< 0.001	0.9466 *(0.6446)*	1.8 *(1.3658)*
Ammonium	Water type	2, 114	3.95	0.0221	0.0052 *(0.0136)*	0.047 *(0.0449)*

Fig. 4 Interaction plot (means $\pm$ SE) of mean phosphate concentration from water samples in different habitats at the different sampling periods. 'S' indicated concentrations were significantly different ($p < 0.05$) between pore water and bottom water samples
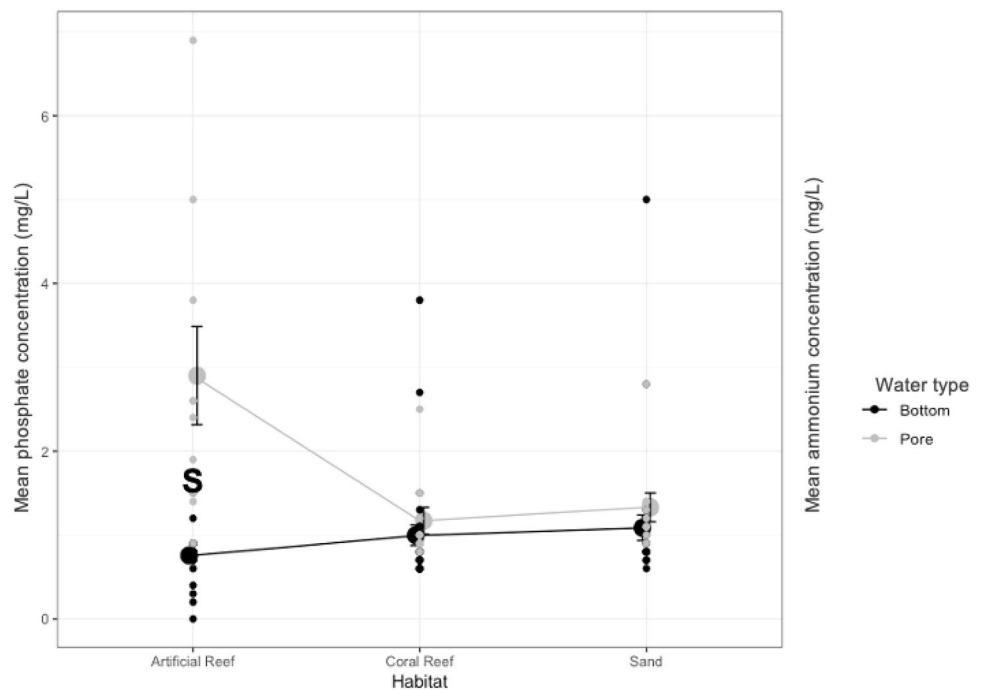

Table 2 ANOVA results and mean ($\pm$ SD) total organic matter content of sediment samples between habitat types

Sampling type	Factor (s)	d.f	F value	p value	Mean sand TOM content (%)	Mean AR TOM content (%)	Mean CR TOM content (%)
Surface sediment	Habitat types	2, 87	132.4	< 0.001	0.5489 *(0.165)*	0.6617 *(0.012)*	1.3158 *(0.029)*
Sediment traps	Habitat type * sampling period	4, 25	6.94	< 0.001	1.11 *(0.743)*	1.31 *(0.938)*	1.78 *(0.452)*
Comparing surface sediment and sediment traps	Habitat type * sampling period	6, 112	12.73	< 0.001	n/a	n/a	n/a

Fig. 5 Interaction plot (means ± SE) of % TOM content in sediment traps in different habitats at different sampling periods ($n = 5$ in most cases, although there were occasional missing/ broken samples). 'S' indicated coral reef % TOM was significantly higher than the other habitats at the sampling periods indicated ($p < 0.05$). No other differences between habitats within a time period occurred
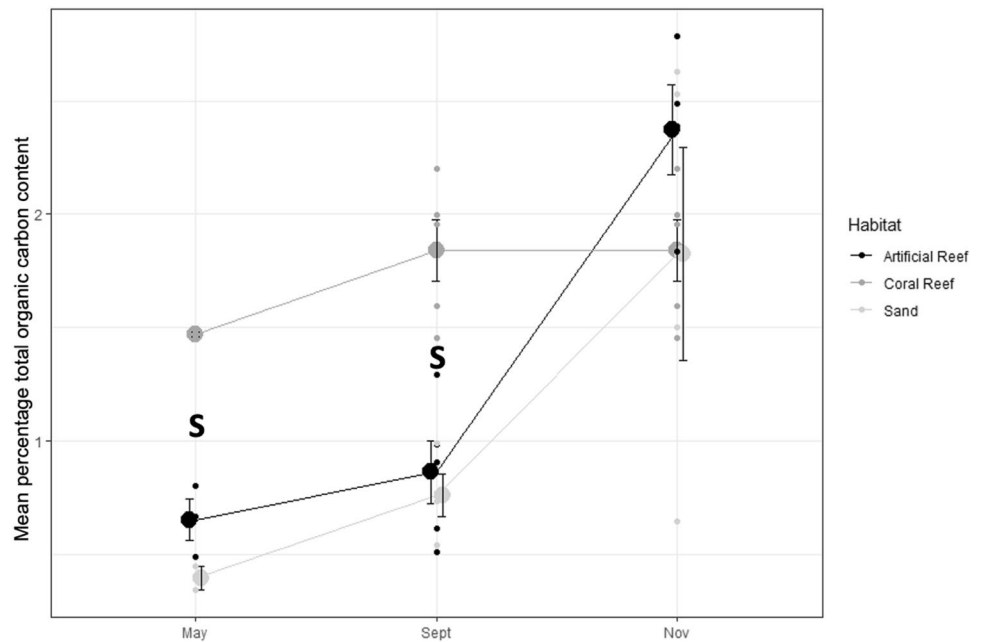

Table 3 PERMANOVA of community structure between habitat types

Community	d.f	F value	p value
Mobile	5, 15	8.89	< 0.001
Cryptobenthic	1, 4	2.22	0.10
Benthic	2, 87	65.62	< 0.001

($p = 0.0073$). In terms of sediment traps, % TOM showed a significant interaction between habitat type and sampling period (Table 2).

In May and September, the CR was shown to have significantly higher % TOM than the other habitats, but this difference was not present in the November samples, when both sand and AR samples were not significantly different that to the CR (Fig. 5). To compare surface %TOM values with those collected from sediment traps, we included the surface samples as an additional sampling period in the sediment trap database, and ran a two-way ANOVA between habitat and sampling period again (with quasipoisson link functions). Again, a significant two-way interaction term was found (Table 2), but no differences between the values
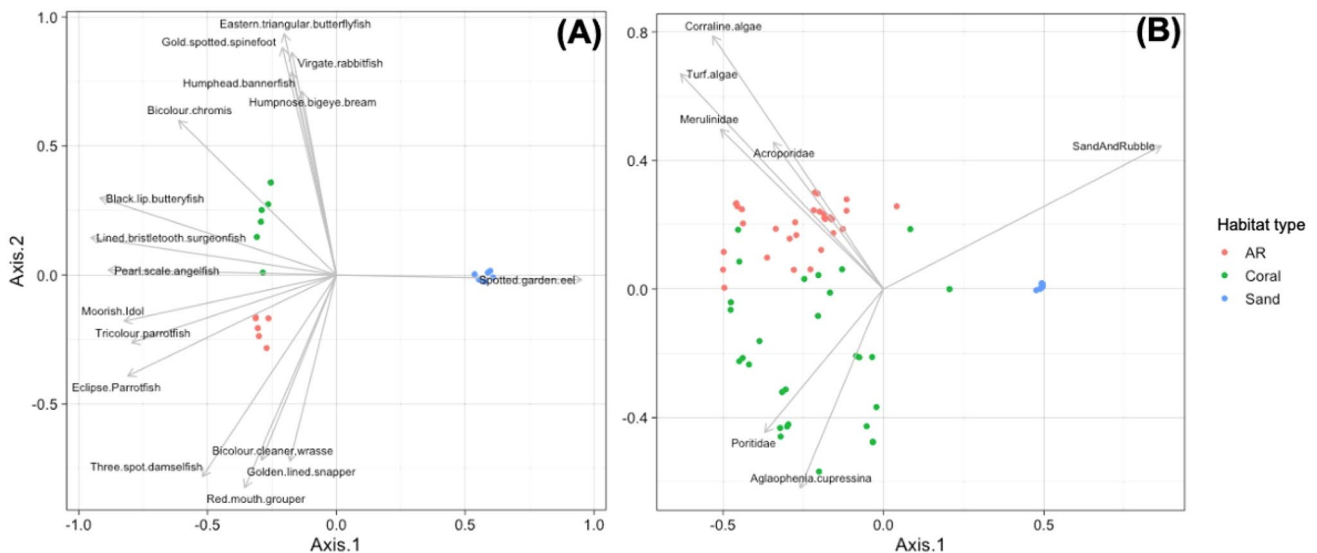

Fig. 6 Principal coordinate analysis (PCoA) plot for mobile community structure (**A**) and benthic community structure (**B**) within habitat type, with Pearson's correlation vectors (> 0.45) overlaid in black.

Note: unlike **A**, scientific names were used to describe benthos (**B**) as many of the genera have no known common name

Table 4 Mean (± SD) MaxN of mobile and cryptobenthic communities and percentage coral cover between habitat types

Habitat type	Average MaxN (mobile communities)	Average MaxN (cryptobenthic communities)	Coral cover (%)
CR	42.6 (5.7)	13.7 (1.5)	44.13 (35.2)
AR	42.8 (3.4)	9.6 (3.8)	13.09 (8.1)
Sand	4.8 (1.2)	0	0

of %TOM were found for the different habitats between the May values in the sediment traps and the surface values (multiple comparisons $p > 0.05$ in all cases), with May being the closest time period to when the surface samples were taken. Differences between habitats did occur between the surface sediments and the sediment traps at other times of year.

Biological community structure

In terms of community structure, PERMANOVA showed significant differences between habitat types for mobile and benthic communities, but no significant differences for cryptobenthic communities (Table 3). For mobile and benthic communities, pairwise comparisons showed significant differences between all habitat types ($p < 0.05$ in all cases).

Despite the AR and CR having distinct differences in terms of mobile and benthic communities, they were shown to be much more closely related to each other than the sand flat (which was substantially different to the AR and CR; Fig. 6a and b). Mobile and benthic communities on the sand flat were greatly different to both other habitat types. This was also highlighted by Table 4, which showed that the AR and CR had a similar MaxN of mobile and cryptobenthic communities, which were both very different to the sand flat.

Discussion

Summary of results

Our key findings showed: (1) there were no significant differences in inorganic nutrients between habitat types for bottom water samples, (2) pore water phosphate concentrations were significantly higher on the artificial reef than on both other habitats, (3) total organic matter content in sediments were significantly higher on the coral reef than both other habitat types, and (4) sediment trap sampling period three (September–November) displayed no significant differences between habitat types in terms of total organic matter. Below, we assess how the inputs and uptake of certain nutrients may provide possible explanations for our findings.

There were no significant differences in inorganic nutrients between habitat types for bottom water samples

Research has shown how nutrients in the nearshore water column (including bottom water) are strongly influenced by currents (Fonseca and Kenworthy 1987; Lourey et al. 2006), wind (Lee et al. 1992; Vicente et al. 2008) and tides (Anwar et al. 2014; Davies et al. 2014). These environmental factors may have had a stronger influence on bottom water nutrient concentration at each of the habitat types than localised ecosystem processes, and this may explain why there were no significant difference shown for inorganic nitrates, nitrites, phosphates and ammonium concentrations from bottom water samples. In contrast, pore waters are known for storage of inorganic nutrients as they are formed by sedimentation of particles from the overlying water column, thus 'trapping' and storing compounds that were previously in the water column (Bufflap and Allen 1995; Batley and Giles 2014; Huettel et al. 2014). This explains why pore waters may be less influenced by the environmental factors discussed above, and provides a likely reason for the significant difference in inorganic nutrients concentration between pore water and bottom waters.

Pore water phosphate concentrations were significantly higher on the AR than on both other habitats

In terms of uptake of phosphates, it is generally agreed that established coral reef communities have a very tight cycling of DINs (Steven and Atkinson 2003; Rädecker et al. 2015; Graham et al. 2018), and this may explain why the CR had significantly lower phosphate pore water concentration than the AR. Coral reefs are known to have a high phosphate uptake rates (Den Haan et al. 2016), as corals can efficiently utilise organic phosphate excreted by other organisms within their localised system (Shantz and Burkepile 2014). Furthermore, the AR had a less established benthic community (made up mostly of turf and coralline algae and pioneering acroporids, with a coral cover of ~13%) when compared to the CR [made up mostly of corals (notably massive poritids), sponges and hydroids, with a coral cover of ~44%]. Thanner et al. (2006) showed that assemblages of benthic organisms on tropical ARs may take up to 5 years before they begin to mimic natural communities. Given that the ARs in this study ranged between only 1 and 3 years, it was unsurprising that the AR had a substantially lower coral cover and less established benthic community than the CR. The lower coral cover on the AR likely explains why it absorbed less phosphate than the CR [based on Shantz and Burkepile (2014); Den Haan et al. (2016) as referenced above]. Furthermore, the dominance of massive poritids on the CR may provide

an additional reason why phosphate concentration was lower on the CR, especially because poritids have been shown to provide important contributions to phosphate uptake on reefs [e.g. D'Elia (1977); Atkinson et al. (1994)].

In terms of phosphate input, previous studies have highlighted that fish faecal pellets are high in micronutrients, especially phosphate (Geesey et al. 1984; Rempel et al. 2022). Groupers (specifically coral grouper and red mouth grouper) were one of the differentiating fish families for the AR, which are known to excrete large quantities of phosphate (Schiettekatte 2021), and this, along with the reduced potential for phosphate removal from the ARs, may help to further explain the trend that pore water phosphate concentrations were significantly higher on the AR than on both other habitats. Furthermore, cryptobenthic reef fish, despite often being overlooked, have been described as a cornerstone of ecosystem functioning on coral reefs (Brandl et al. 2019a; b) and are thought to play a key role in the cycling of reef nutrients, including phosphorus and nitrogen (Schiettekatte 2021). Given that this study found no significant difference between the AR and CR in terms of cryptobenthic fish, it was not possible to make further conclusions on how their communities affected ecosystem functioning between habitat types. Further research on the role of cryptobenthic fish in reef nutrient cycling would greatly increase understanding of the links between reef biota and ecosystem functioning.

Total organic matter levels in sediments were higher on the coral reef than both other habitat types

It must first be noted that the key component of TOM in ocean sediments is TOC (Sutherland 1998), and therefore, our % TOM findings were used as an approximate measure of TOC within our sediment samples. In terms of fish communities, one distinct mobile community characteristic of the CR was that it appeared to be made up of herbivorous fish, notably rabbitfish (gold spotted spinefoot and virgate rabbitfish) and surgeonfish (lined bristletooth). Communities on the other habitats did not appear to have such a strong representation of herbivorous fish, and instead were shown to have different communities, which were strongly driven by predatory fish (grouper and snapper) in the AR. Herbivorous reef fish play an important role in the carbon dynamics of marine sediments (Legendre and Le Fèvre 1995; Atwood et al. 2018) due to their specific gut bacteria, which is thought to cause increased sedimentation of OM (Montgomery and Pollak 1988; Mountfort et al. 2002; Smriga 2010). In fact, certain examples show that the faecal pellets surgeonfish are particularly high in OC (e.g. Ezzat et al. 2019), as well as research highlighting that rabbitfish faecal pellets may provide notable contributions to deposited organic matter within localised reef sediments (e.g. Peleg et al. 2020). It is possible that the higher levels of TOM recorded on the CR may be due to the differences in fish community structure, specifically the distinct communities of herbivorous fish on CR.

Despite storing less TOM than the CR, the AR was shown to store more TOM than the sand flat, with surface sediment samples having significantly higher TOM on the AR than the sand flat. Furthermore, sediment trap samples were shown to have notably higher (yet insignificant) TOM content on the AR than the sand flat. This was likely because the AR had a more complex and abundant fish community than the sand flat, which may have caused higher biogenic deposits onto the reef system and surrounding sediments [as shown by Dos Santos et al. (2005)]. These findings were supported by those of Vincente et al. (2008), which linked OC deposits on ARs on with fish biomass (Vicente et al. 2008). As the ARs mobile and benthic communities start to mimic those on CRs over time [e.g. Perkol-Finkel et al. (2006), Folpp et al. (2013)], the AR may begin to store similar levels of OC, given that biological communities are one of the key drivers of ecosystem functioning (Brandl et al. 2019b).

In terms of benthic communities, it is likely that a given proportion of the TOM observed in the CR (and the AR to a lesser extent) were exudate of the habitat's benthos, notably sponges and corals. Research has shown that sponges can release vast amounts OC species by rapidly expelling their filter cells (Pawlik et al. 2016; De Goeij et al. 2017). Furthermore, the literature has also shown that hard corals efficiently trap POM from the water column in their mucus, and release this carbon rich exudate to nearby sediments (Wild et al. 2004). This mucus is often considered as excess OC, because the corals have had to consume large amounts of 'low quality' food as a means of obtaining sufficient nutrients such as nitrogen and phosphorous (Bythell 1988; Pinnegar et al. 2007). Over half (56–80%) of the expelled coral mucus immediately dissolves (Moriarty et al. 1985), although much of the remaining mucus trap will increase in OC content as it traps more suspended particles, and is then thought to rapidly settle in nearby sediments (Wild et al. 2004). The transport of these materials via coral mucus sedimentation has been shown to contribute to 2–26% of the OC within sediments (Wild 2003). The results of this study showed that Poritidae and Agariciidae were two coral families which were proportionately more important on the CR. There are no known publications which directly compares mucus release rates between families; however, research has associated these two families as potentially important mucus producers. For example, Domart-Coulon et al. (2006) associated Poritidae with abundant mucus production, which has been shown to stimulate the growth of vast bacterioplankton communities within nearby sediments (Silveira et al. 2017). Furthermore, Glynn et al. (2011) highlighted that Agariciidae corals are often covered by mucus-laden strings that coat the colony surfaces. The dominance of these two coral

families (as well as CR's higher general coral coverage than other habitats) likely led to the CR having higher mucus release rates than the other habitats, providing another possible explanation as to why the CR samples had the highest observed TOM content.

Sediment trap sampling period three displayed no significant differences between habitat types in terms of total organic matter

Our results found that sampling period three showed no significant difference in % TOM content between any of the habitats, however, sampling periods one and two did. We also highlighted that surface sediments had significantly lower % TOM content than sediment trap in sampling period three, although they displayed no significant differences to the first two sampling periods. It must be noted that Indonesia's monsoon was between the months of October to March, and in this time, higher precipitation leads to increased runoff of nutrients. It is likely that sampling three's observed differences was because it was the only sampling period within the monsoon season, and therefore the only one which would be trapping the additional organic material as a result of it. These findings are in agreement with other studies, which have also shown that nutrient concentrations on coral reefs in Indonesia are higher during the monsoon season [e.g. Nugrahadi et al. (2010) and Damar et al. (2019)]. Furthermore, Wild (2003) showed that the release of OM by corals over a spawning period provides notable seasonal contributions to sedimentary OM deposition. The coral spawning season in north Bali is known to occur each November (*Yunaldi Yahya, pers. comms.*). If the coral spawning period had occurred whilst the sediment traps were still deployed, it may have provided additional contributions to OC deposition (collection within the traps), thus providing another potential reason why sampling period three had significantly higher % TOM content.

Conclusions

Overall, the AR in this study was shown to not yet be functioning at the same level as the CR, in terms of TOM storage and DIN dynamics. The difference between the AR and CR in terms of community structure, specifically less complex benthos (likely leading to less release of TOM to sediment and less uptake of phosphate), as well as different fish communities, which perhaps explained why the AR was not yet functioning as the CR. Despite this, in some cases, TOM storage and DIN dynamics, were shown to be different on the AR than the nearby sand flat (with levels on the AR being shown to be more similar to the CR), likely due to the ARs relatively more complex biological communities. Given that the ARs

in this study ranged between only 1 and 3 years old, and that tropical ARs may take up to 5 years to begin to mimic natural benthic communities and 6–7 years to begin to mimic natural fish communities, it is encouraging that an AR may start to show similarities to the functioning of a CR over a relatively short time scale. It is expected that the functioning of ARs will show more similarities to CRs over time, as communities increase in complexity and begin to mimic those on natural reefs. Our examination of nutrient cycling and storage compared to community structure on coral and artificial reefs has given rise to a number of key hypotheses which may determine the differences found. However, considerably more research is needed to confirm the links between biological community structure and ecosystem functioning on ARs and CRs, as well as directly identifying the important species of reef flora and fauna that is associated with depositing large amounts of TOM to nearby sediments.

Declarations

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