

REPORT

# Experimental analysis of the effects of consumer exclusion on recruitment and succession of a coral reef system along a water quality gradient in the Spermonde Archipelago, Indonesia

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**Abstract** The composition of coral reef benthic communities is strongly affected by variation in water quality and consumer abundance and composition. This is particularly evident in highly populated coastal regions where humans depend on coral reef resources and where terrestrial run-off can change the chemical composition of the water. We tested the effects of grazing pressure and ambient water conditions along an established eutrophication gradient on the recruitment and successional development of benthic communities of the Spermonde Archipelago, Indonesia, through caging experiments with settlement tiles. Within 1 month, benthic community composition of the closest reef to land, near the city of Makassar, was significantly different from other sites further offshore, driven primarily by differences in recruitment of invertebrates or turf algae. In contrast to other caging experiments, consumer exclusion had no effect after 3 months, suggesting that larger, mobile consumers had

little effect on the benthic communities of these reefs at all sites. Despite conditions that usually favour macroalgal development, this group was rarely observed on recruitment tiles even after 4 months of consumer exclusion. Furthermore, tiles from both the caged and open treatments retained high proportions of open space indicating the possible role of small-sized or non-fish consumers that were not excluded from the experiment. These results indicate that, unlike many other studies, benthic consumers in the Spermonde Archipelago had little effect on the recruitment and early succession of the reef habitat and that unexamined biota such as mesograzers may be significant in degraded systems.

**Keywords** Turf algae · Macroalgae · Eutrophication · Caging experiment · Herbivory · Succession

## Introduction

The increased introduction of terrestrial effluents and high fishing pressure from increasing human populations along the coastal zone have strong impacts on coral reef benthic communities (Hughes et al. 2007). Generally, coral reef communities evolve under oligotrophic water conditions; however, coastal development and/or alteration increases stress on coral reef systems due to increased inputs of dissolved inorganic nutrients and suspended particulate matter which reduce light attenuation and increase sedimentation (Fabricius 2005). Understanding of the effects of changing water conditions is often confounded because these same reef communities also experience high fishing pressure. On coral reefs, the combined effects of increased inorganic nutrient input and particulate matter and the removal of fish species can be far-reaching because they

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impact competition among benthic biota and thus potentially severely affect community composition (Bellwood et al. 2004).

In most experiments that have tested top-down and bottom-up controls on coral reefs, results have shown that increased nutrients and decreased grazing pressure facilitate growth of macroalgae, leading to overgrowth, reduction in light, and resultant competitive success over scleractinian (hard) corals (McCook et al. 2001). However, evidence of in situ phase shifts to macroalgal dominance has been ambiguous (Bruno et al. 2009), with examples more predominant on Caribbean and Western Indian Ocean reefs than on Indo-Pacific coral reefs. In fact Bruno et al. (2009) paralleled hard coral loss in the Indo-Pacific with higher levels of other non-algal taxa such as sponges and gorgonians.

The response of non-scleractinian reef species to changing water conditions can severely affect the health and abundance of hard corals, the primary reef-building organisms, thus affecting the greater community. Generally, non-scleractinian organisms affect the reef by competing for space, inhibiting hard coral recruitment, and therefore altering structural strength of the reef substratum by not contributing to reef accretion (Fabricius 2005). For instance, crustose coralline algae (CCA) are essential for hard coral settlement, yet their survival is compromised under conditions of fine sediment accumulation or organic enrichment (Harrington et al. 2004). Filter feeders can thrive in degraded marine systems (Cooper et al. 2008); however, many of these species are also macrobioeroders which can physically bore into or chemically erode (Lazar and Loya 1991) the carbonate reef substratum. Responses by algae to changing water conditions can be species- or groups-specific, although increases in any type of algae create competition for space through chemical means or by the trapping of sediment and/or shading (Szmant 2002).

Generally, it is accepted that the presence of a healthy herbivore population can mitigate algal populations when nutrient conditions are no longer limiting (Hughes et al. 2007). Behavioural and biological studies on parrotfish have found that, although algae are often the primary constituent of their diet, incidental consumption of other reef benthic biota does occur (Choat et al. 2002; Plass-Johnson et al. 2013). Likewise, other groups of fishes such as the wrasses (Labridae) and breams (Nemipteridae) are important consumers of non-algal benthic biota. These fishes can compose a significant proportion of fisheries in countries that rely on coral reefs for resources (Lokrantz et al. 2010), indicating that fishing can have indirect effects on benthic communities. However, the effects of the removal of these fishes may vary among sites experiencing different levels of habitat degradation because of variation in resource availability and competition (Shears et al. 2008).

Unfortunately, the deterioration of coral reef systems is becoming commonplace (Burke et al. 2011). Thus, it is essential to understand how these degraded systems will develop under increasing disturbance. To understand coral reef development, its examination should be conducted under representative conditions. Of particular concern is the Coral Triangle of Southeast Asia. This area is one of the most biodiverse areas on the planet with 75 % of known hard coral species and >3000 fish species (Veron et al. 2009). These marine resources are used directly by more than 130 million people, and more are indirectly used overseas (Burke et al. 2011). Many of the reefs in the area are exposed to altered environments because of intense agriculture, aquaculture, and destructive coral reef resource use. One of the largest reef fisheries in the region occurs in the Spermonde Archipelago of south-west Sulawesi (Ferse et al. 2014). The reefs of the region are examples of heavily developed coastal regions where land run-off and destructive fishing practices have existed for decades (Edinger et al. 1998; Pet-Soede and Erdmann 1998; Pet-Soede et al. 2001). In the region, hard coral biodiversity (Edinger et al. 1998, 2000), ecological dynamics (Sawall et al. 2011, 2013), and fish community composition (Pet-Soede et al. 2001) are subject to intense nutrient input and fishing pressure. Many studies have found strong links with localised eutrophication and fishing impacts (Cleary et al. 2005; Becking et al. 2006; Cleary and Renema 2007), the former associated with patterns of hard coral distribution related to distance to Makassar (Edinger et al. 1998; Renema and Troelstra 2001). Unselective, destructive fishing practices are common and intense in the area (Pet-Soede and Erdmann 1998), and near-shore water particulate matter and dissolved organic nutrient levels are high (Edinger et al. 1998; Sawall et al. 2011, 2012) for coral reefs. Despite a situation which would be expected to facilitate a change to macroalgal dominance, macroalgal populations on the reefs are relatively low, and hard corals are still present even at the most impacted, near-shore sites (Sawall et al. 2013; Jompa unpub. data).

In this study, we expand the knowledge about coral reef community development under pre-existing conditions of eutrophication and high levels of reef resource extraction. We observed the recruitment and successional development of three reefs varying in distance from the main city Makassar (1–19 km) over a 4-month period, under conditions of natural consumer exposure and with large consumers excluded, to test the effects of further increased fishing pressure. Additionally, we observed temporal and spatial variation in benthic community recruitment to identify bottom-up insufficiencies in community maintenance. The main goals of our study were to (1) describe early succession of coral reef communities with varying water quality, (2) describe variation in monthly

recruitment, (3) identify the impacts of consumers on the succession and recruitment of benthic communities, and (4) discuss the implications of our results for future development of reefs among the Spermonde Archipelago.

## Methods and materials

### Study site

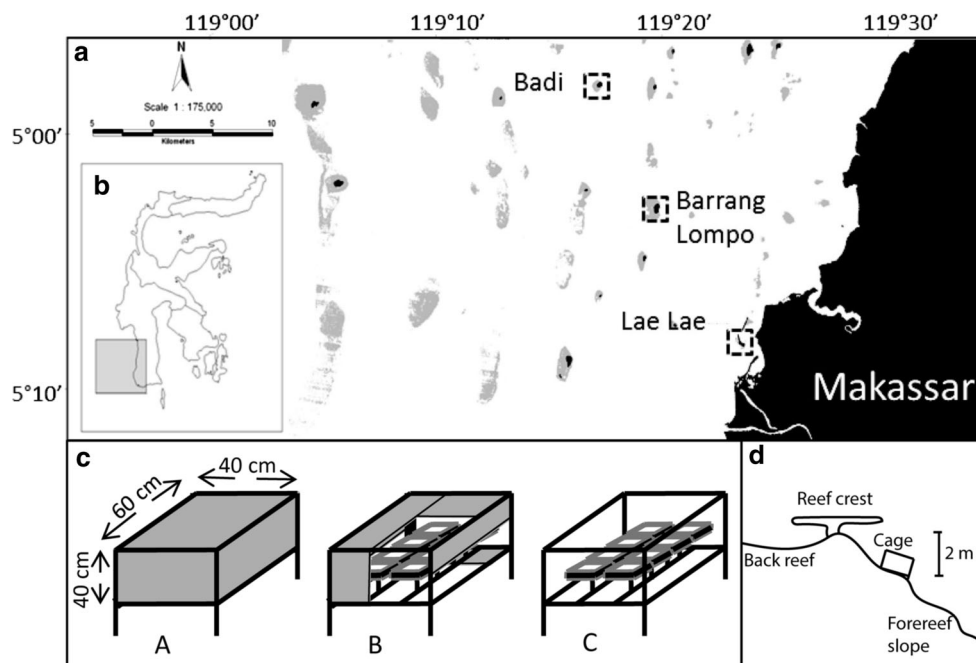
This study was conducted for 4 months between 16 November 2012 and 20 February 2013, on three islands of the Spermonde Archipelago, Indonesia, along a transect of increasing distance from the city of Makassar (Fig. 1). The near-shore island, Lae Lae (LL; 05°08S, 119°23E) at 1 km from land, is highly affected by effluents from the city's harbour, sediments, aquaculture outflow, and the fluvial discharge of the nearby rivers (Renema and Troelstra 2001). Barrang Lompo (BL; 05°02S, 119°19E) is 11 km from the mainland and regularly receives effluents from the city during the wet season. The farthest island, Badi (BA; 04°57S, 119°16E), is 19 km from the city and receives effluents only during the heaviest rains of the wet season (Renema and Troelstra 2001; Fig. 1).

To standardise sampling among sites, we chose the north-west corner of the three islands which have similar

bathymetric profiles. The western coast of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest is shallow ( $\sim 3$  m), and the slope extends down to 10–20 m.

### Water parameters

All water quality parameters [suspended particulate matter (SPM), ammonium ( $\text{NH}_4$ ), nitrate + nitrite ( $\text{NO}_x$ ), phosphorus ( $\text{PO}_4$ ), chlorophyll-*a* (Chl-*a*), dissolved organic carbon (DOC), dissolved oxygen (HDO), temperature ( $^{\circ}\text{C}$ ), salinity, and light attenuation ( $K_d$ )] were collected at the beginning and the end of the experiment, during the first week of November (2012) and the first week of February (2013). Water samples were collected in six replicates from the same depth as the experimental cages. Subsamples were taken for the measurement of SPM, DOC, and nutrients. DOC samples were filtered through 0.45  $\mu\text{m}$  pore GF/F filters and acidified with HCl. To determine SPM mass, pre-combusted GF/F filters were weighed before and after filtration of a known volume of sample water. Difference was determined after the filters were again dried at 40  $^{\circ}\text{C}$  for 24 h. Nutrient concentrations were determined using a continuous flow analyser (FlowSys Alliance Instruments). Temperature, salinity, HDO, and Chl-*a* data were logged with a Eureka Manta logger (GEO Scientific



**Fig. 1** **a** Map of the Spermonde Archipelago indicating sampling sites Lae Lae (LL), Barrang Lompo (BL), and Badi (BA). **b** The location of the Spermonde Archipelago on the island of Sulawesi. **c** Treatments used for the experimental exclusion of benthic consumers. (A) Full cage for complete consumer exclusion. (B) Procedural control to test caging artefacts. (C) Control treatment. Tiles

had a 10-mm-diameter hole drilled through the middle for mounting on to the cage. The legs of the cages were hammered into the benthos, and the grey area indicates area that was covered with netting. Caged area was 60 × 40 × 40 cm (L × W × H), and legs extended an extra 20 cm. **d** The placement of the cages 5 m deep on the fore-reef

Ltd.) recording at 2-min intervals across 6 h (0800–1400 hrs) each day.  $K_d$  was calculated from underwater light profiles taken with a light metre (LiCor Li-192SA, Lincoln, USA):

$$K_d = \ln \left[ \frac{Ed(z_2)}{Ed(z_1)} \right] \times (z_1 - z_2)^{-1}$$

where  $Ed(z_2)$  and  $Ed(z_1)$  are measurements at 0.05 m ( $z_1$ ) and 4.5 m ( $z_2$ ) below the surface (Kirk 1994). Due to bad weather conditions, light data were not collected during the second sampling at all stations.

### Habitat assessment

Benthic communities were quantified at each island in the first week of February 2013, with 20 benthic photographic quadrats per 50 m transect (see *Fish surveys*). Photographs were taken at 1 m above the substratum every 2 m along the transect. Coral Point Count with Excel extensions (CPCe; Kohler and Gill 2006) was used to analyse 20 randomised points (based on results from power analysis; Electronic Supplementary Material, ESM, Fig. S1) per photograph for the following functional groups: ascidians, sponges, soft corals, other invertebrates, cyanobacteria, macroalgae, turf algae, CCA, live hard coral, sand, open space (non-overgrown hard substrate), and other (shadow, garbage, etc.).

### Fish surveys

Visual surveys of herbivore and invertivore fish species were conducted along three replicate 50 m transects within the area of the caging experiment. Surveys were completed twice in November and twice in January. The two days sampling per month were grouped, meaning that there were six replicates for each season. The surveys were conducted between 0900 and 1000 hrs, 2.5 m to the left and right of the 50-m transect line. All fish species >3 cm were counted, and their size estimated to the nearest cm. Cryptic fishes were not recorded because accurate counts and identification could not be guaranteed. Species identification and diets followed Allen and Erdmann (2012) and FishBase.org. Biomass of fishes was calculated from individual size observations, and length–weight relationships were obtained from Kulbicki et al. (2005).

### Experimental design and treatments

To separate the effects of grazing, recruitment, and succession within each site, tiles were exposed to a fully caged treatment, control (open) treatment, and procedural controls (Fig. 1). All were replicated three times at each site. To fully exclude large grazers, the caged treatments were

60 × 40 × 40 cm (L × W × H) and were fully covered with nylon netting of 1.5 cm mesh. Procedural controls were used to account for any artefacts of the caged treatment (water movement and shading) while allowing access to the tiles for larger benthic and pelagic consumers. Procedural controls consisted of cages of the same size but only enclosed by 1/3 of the mesh on the top, sides, and bottom (Fig. 1). The side for the mesh was randomly chosen for procedural controls. The open treatment consisted of a cage frame with no mesh. All cages were constructed from 12 mm steel rods. To make sure that cages did not move, all cages had 20 cm legs, which were hammered into the sediment, guaranteeing a secure attachment to the reef. Cages were cleaned of all epiphytic growth once per week. Within the cages, tiles were fastened to the steel rods via a welded stainless steel screw of 10 mm diameter. These rods placed the tiles 10 cm from the substratum, allowing room for recruitment to the bottom of the tiles. Tiles were placed in two rows of four tiles with ~3 cm between tiles, and ~5 cm from the sides of the cage (Fig. 1).

Tiles were cut in 10 × 10 cm (100 cm<sup>2</sup>) segments from flat, unglazed 1.5 cm granite rock slates. These had a naturally rough surface similar to that of terracotta tiles commonly used in recruitment experiments (Burt et al. 2009). A hole ~1 cm diameter was drilled in the middle of the tiles for attachment to frames. Tiles were installed in double, one facing up (top) and one facing down (bottom), providing the same surface on both sides to allow discrimination between the differing settlement communities on light-exposed (top) versus shaded (bottom) surfaces.

At each site, cages were haphazardly installed within a 100-m<sup>2</sup> area, at 2 m below the reef crest (~5 m deep) on the fore-reef (Fig. 1). Generally, open areas of the reef with soft sediment were chosen for the location of each cage to allow for the legs to be hammered into the sediments. Thus, tiles were positioned 10 cm above the sand substratum possibly introducing bias towards the recruitment of organisms that prefer such habitats. However, this location was standardised among sites allowing for our comparisons to be relative to each other. Within the cages, the angle of the tiles was horizontal, but the angle of the cages in situ was not constant and depended on the natural bathymetry of the attaching surface.

Two temporal designs of allocation and sampling of tiles were chosen for recruitment or for community succession. These time periods were applicable to both the top and bottom tiles. For recruitment, tiles were collected and replaced every month after 1 month of exposure to investigate differences in recruitment over the course of the experiment. Succession tiles were collected after accumulated times of 1, 2, 3, and 4 months of exposure to follow success of communities over the course of the experiment.

A total of eight tiles were collected from any individual cage at each sampling time. This included four recruitment tiles (two top and two bottom) and four succession tiles (two top and two bottom). Tiles were randomly collected, but they were always represented by a corner set and a side set of tiles, standardising edge effects. Tiles were put in pre-labelled, ziplock bags in situ. After collection, all tiles were cleaned of sediments, dried, and photographed.

### Data analysis

Tile photographs were analysed with the programme CPCe by overlaying 50 randomised points on each tile. This allowed us to estimate per cent cover of the benthic biota. Grouping of organisms was based on observed presence after collection. Organisms were categorised by functional group: tube worms (polychaete worms), cyanobacteria, moss animals (bryozoan), barnacles, hard coral, turf algae, macroalgae, CCA, sponges, mussels, or open space.

At each sampling, data from the two sampled tiles (either the top or bottom) for each time period (recruitment or succession) per cage were collated to represent one replicate. Thus, an individual cage was one replicate represented by a surface area of 200 cm<sup>2</sup>. Percent cover was square-root-transformed to reduce the influence of the highly abundant organisms. The effect of site (3 levels) and treatment (3 levels) were tested among months for both recruitment and succession with a fully factorial permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) preceded by a Bray–Curtis similarity matrix. PERMANOVA was chosen because it is robust to heteroscedasticity, an issue with our low replication ( $n = 3$ ). A time-dependent sampling design can lend itself to a repeated-measures analysis; however, this was not applicable because new tiles were assessed at each time period. Pair-wise PERMANOVA comparisons were used to identify which treatment caused statistical differences. When the number of unique permutations was low (<3 comparisons), the Monte Carlo test was employed. The effects of the procedural controls were tested against the open cages using a factorial PERMANOVA to check for artefacts of the cages. After pair-wise post hoc PERMANOVAs were applied on data for month four, similarity percentages (SIMPER) was used to identify groups of organisms that contributed most to intersite differences in communities. It should be noted that PERMANOVA and SIMPER analyses were conducted independently for both recruitment and succession, but also independently for the side (top or bottom) of the tiles. The percentage of open space was removed from community analyses (therefore cover no longer equalled 100 %) to identify changes specific to the benthic community. However, a separate

PERMANOVA was conducted on the open space alone because it can reflect the process of grazing and it also represents area for new recruitment. Open space was only analysed on the successional tiles, and the statistical design was the same as for the community analysis. Weather conditions restricted the collection of recruitment tiles at LL in months two and three. These analyses did not include LL as a level within factor site. All analyses were completed in Primer + (v.7) with the PERMANOVA add-on. Plots were created in the same programme but also with SigmaPlot (v.12.5). Differences among sites in water quality parameters and fish biomass were assessed with one-way ANOVAs. Differences among sites were established with Fisher's LSD test.

## Results

### Water parameters

Water quality conditions at LL were very different from the other two sites at the beginning and end of the experiment. Although water NH<sub>4</sub>, NO<sub>x</sub>, and PO<sub>4</sub> were quite low at all sites, NH<sub>4</sub> and NO<sub>x</sub> were significantly higher at LL in November (Table 1). SPM and Chl-*a* were significantly higher at LL than at BL and BA in both sampling times, while DOC was more variable between sites and sampling dates. The HDO was significantly lower at LL than the other sites (Table 1). Differences between BL and BA were minimal although DOC varied between samplings (Table 1). At all three sites, there was a noticeable decrease in salinity from November to February, influenced by increases in precipitation. Similarly, water temperatures were 1.5–2.0 °C higher in November than in February. In November, there was a 1 °C decrease in water temperature from LL to BA (Table 1). The light attenuation coefficient, *K<sub>d</sub>*, was also higher at LL compared to BL and BD (Table 1), indicating a lower water transparency at that site.

### Habitat assessment

Live hard coral cover was lowest at LL, the site closest to shore, and increased with distance from shore (Fig. 2). The benthic cover at LL was distinct from the rest of the sites, with the highest proportion of sand and relatively equal proportions of macroalgae, turf algae, soft coral, and cyanobacteria. Surprisingly, macroalgae were not a dominant feature of the other sites and showed no clear relationship with distance from shore. Rather, cover of turf algae was high at all sites, but the proportional contribution of turf algae decreased away from shore as hard coral cover and open space increased (Fig. 2).



**Table 1** Water quality parameters and biomass of herbivore and invertivore fishes measured in November (Month: N) 2012 and February (Month: F) 2013 at each sampling site

	Month	Lae Lae	Barrang Lompo	Badi	Post hoc result
SPM ( $\text{mg L}^{-1}$ )	N	12.19 (0.97)	5.19 (0.25)	4.37 (0.33)	LL > BL = BA
	F	3.64 (0.70)	2.19 (0.63)	2.59 (0.30)	LL > BL = BA
NH <sub>4</sub> ( $\mu\text{M}$ )	N	0.22 (0.01)	0.05 (0.01)	ND	LL > BL
	F	0.07 (0.01)	0.07 (0.01)	0.06 (0.01)	
NO <sub>x</sub> ( $\mu\text{M}$ )	N	0.60 (0.05)	0.18 (0.01)	ND	LL > BL
	F	0.46 (0.05)	0.48 (0.04)	0.25 (0.03)	LL = BL > BA
PO <sub>4</sub> ( $\mu\text{M}$ )	N	ND	ND	ND	
	F	0.11 (0.01)	0.09 (0.01)	0.08 (0.01)	
Chl- <i>a</i> ( $\mu\text{M L}^{-1}$ )	N	2.84 (0.05)	1.13 (0.04)	1.02 (0.01)	LL > BL = BA
	F	1.53 (0.02)	0.97 (0.02)	0.58 (0.02)	LL > BL = BA
DOC ( $\mu\text{M}$ )	N	122.09 (2.56)	104.67 (7.96)	109.37 (3.70)	LL = BL > BA
	F	78.46 (8.88)	84.90 (1.38)	87.36 (1.76)	LL < BL < BA
HDO ( $\text{mg L}^{-1}$ )	N	5.71 (0.12)	6.543 (0.10)	6.478 (0.08)	LL < BL = BA
	F	5.69 (0.03)	6.31 (0.09)	6.19 (0.10)	LL < BL = BA
Temperature ( $^{\circ}\text{C}$ )	N	31.5	31.1	30.5	
	F	29.7	29.8	29.7	
Salinity (ppt)	N	34.1	34.1	33.8	
	F	30.2	31.8	31.9	
K <sub>d</sub>	N	0.36 (0.07)	0.46 (0.07)	0.19 (0.05)	LL = BL > BA
	F	NA	NA	NA	
Total fish biomass ( $\text{g m}^{-2}$ )	N	3.9 (0.7)	9.0 (2.5)	19.1 (5.5)	LL < BL < BA
	F	4.4 (1.3)	9.6 (1.8)	40.4 (9.3)	LL < BL < BA

Statistical differences were tested with one-way ANOVA; the inclusion of Fisher's post hoc results indicates significant differences among sites

SPM suspended particulate matter, NH<sub>4</sub> ammonium, NO<sub>x</sub> nitrate + nitrite, PO<sub>4</sub> phosphorus, Chl-*a* chlorophyll-*a*, DOC dissolved organic carbon, HDO dissolved oxygen, K<sub>d</sub> light attenuation, ND not detectable, NA not available

### Fish biomass and composition

Fish biomass varied greatly among the sites. BA had the highest biomass, five times higher than LL and twice that of BL (Table 1). Differences in biomass between samplings were minimal at LL and BL, but fish biomass at BA nearly doubled at the February sampling due to an increase in pomacentrids. At all sites, Labridae (wrasses and parrotfish), and Pomacentridae, had the highest biomass, while Acanthuridae, Chaetodontidae, and Siganidae had much lower biomass (Fig. 3). Pomacentrids and Labrids (parrotfish) made up most of the herbivore group. Pomacentrids were the only herbivores at LL. Labrids (wrasses) and pomacentrids made up most of the invertivore group (Fig. 3).

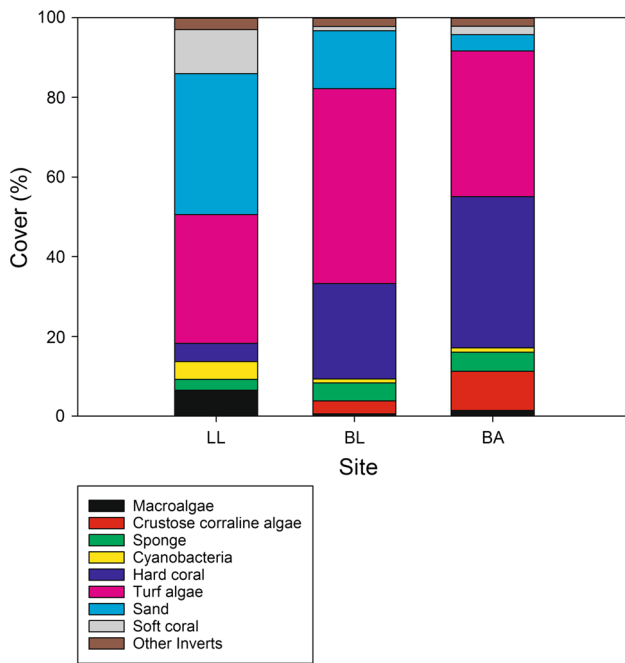
### Caging artefacts

The main focus of the experiment was to test recruitment and succession in the absence of consumers in relation to the open treatment. Communities (ESM Figs. S3, S4; Table S1) and open space (Table S2) in the procedural controls did not differ from open treatments at any time or

side of exposure. This indicates that there were no caging artefacts found throughout the experiment, and therefore, differences in community structure were due to the environment and to the exclusion of consumers.

### Succession experiment

Individual groups of organisms developed differently depending on the site, treatment, or the side of the tile (Fig. 4). Bryozoans grew only on the bottom tiles at BA, specifically in the open cages. Mussels grew on the bottom, caged tiles at BL. Tube worms mostly grew at LL, but they were non-existent on the top tiles open to consumers. Barnacles only grew at LL, but not on the shaded, caged tiles (Fig. 4). CCA had low cover at all sites although it grew in small proportions at BL on both top and bottom tiles. Macroalgae were always absent except for one top, caged replicate at BL in month four. Sponges grew on the bottom sides of the tiles only, and there was little effect of site. Turf algae grew at BA and BL on the top of the tile in both treatments and also in the bottom open treatment (Fig. 4). Turf algae had lower cover at LL than either BL or BA (Fig. 4). Furthermore, differences in mussels,



**Fig. 2** Benthic community composition on reefs at sampling sites (LL: Lae Lae, BL: Barrang Lompo, BA: Badi). Data represent a mean across three replicate transects. *Error bars* are omitted from the benthic data for better visualisation. Standard error was never greater than  $\pm 5\%$  (LL sand)

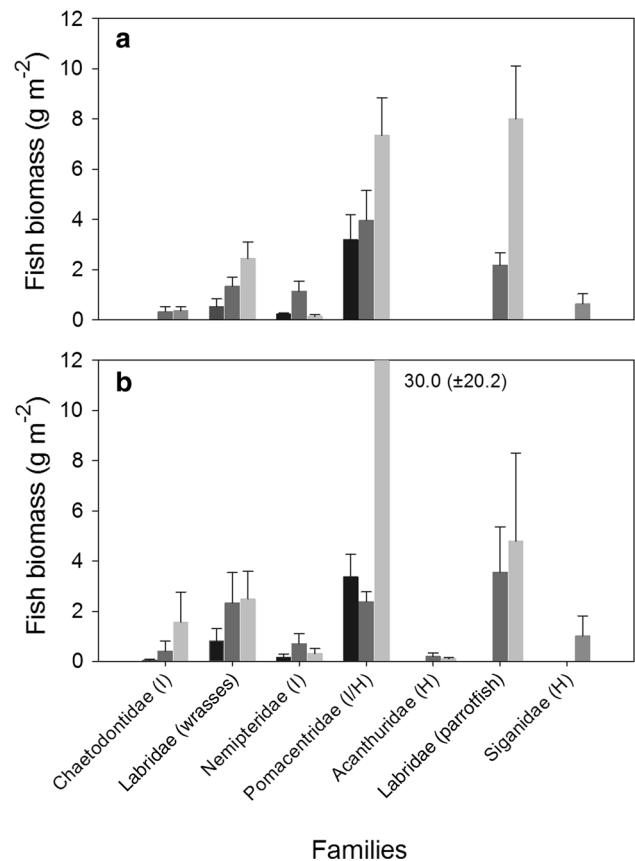
bryozoans, barnacles, CCA, and sponges suggest that caging had an effect on the bottom tiles; however, this was not consistent among islands (Fig. 4).

Differences between LL and the other two sites were persistent throughout the experiment. Consumption (differences between caged and open treatments) affected both the top and bottom tiles, starting in month two and month one, respectively, but these effects were lost by month four (Fig. 5; Table 2). The main differences in community composition between LL and the other sites were due to high cover of tube worms and barnacles, while BL and BA were largely dominated by turf algae (ESM Fig. S2; Table 3).

On the top tiles at month four, all sites and treatments had  $\sim 45\%$  open space with the exception of the open tiles at BA which had  $\sim 20\%$  open space (Figs. 4, 5). There was no statistical difference in the amount of open space among sites or between treatments with the exception of months one and two (Table 4). At month one, there was a difference among sites on both the exposed and shaded tiles, while at month two there was a small effect of treatment on the exposed tiles (Table 4).

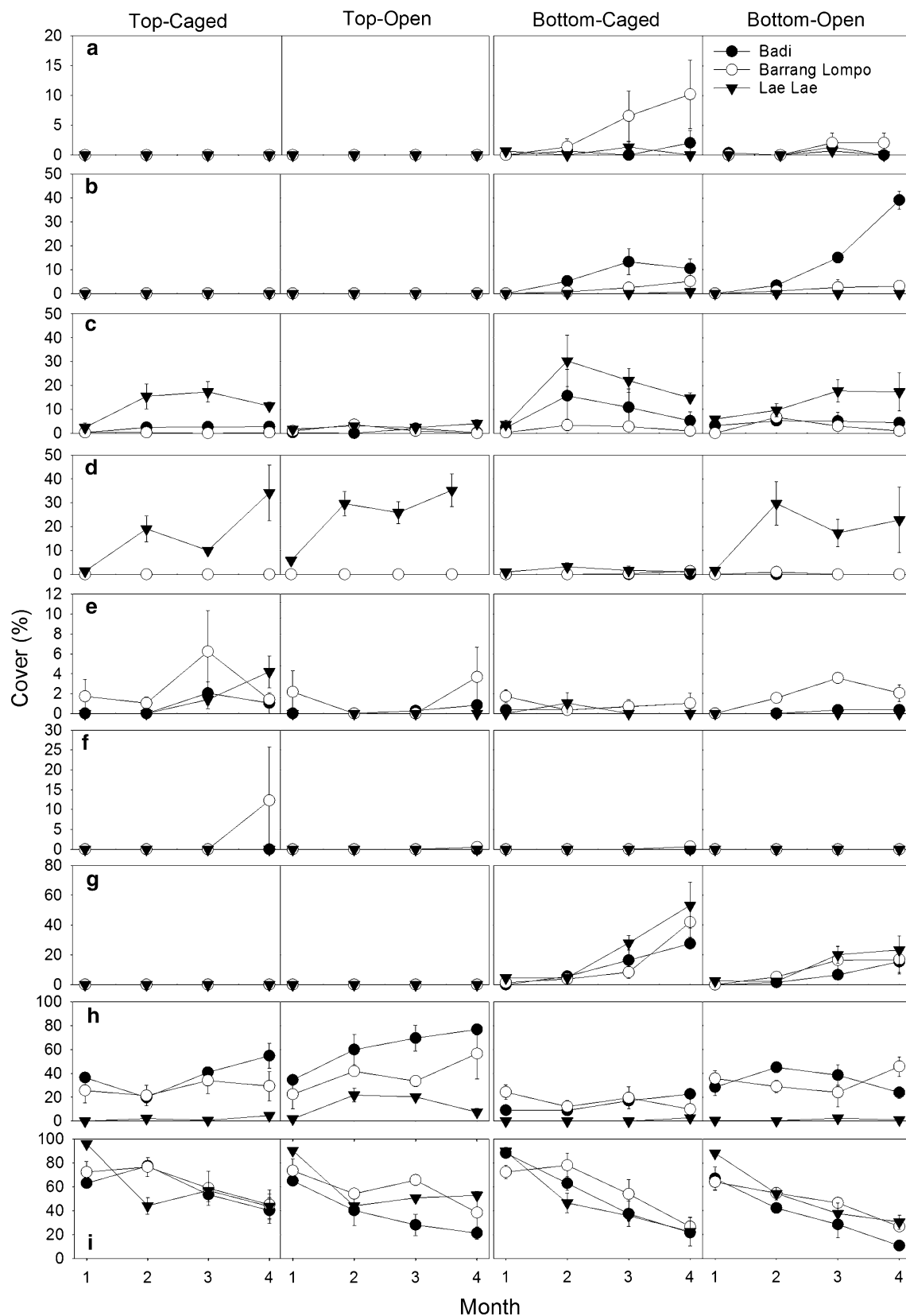
### Recruitment

There was much higher recruitment at both BL and BA than at LL, based on months one and four (Fig. 6). In



**Fig. 3** Mean ( $\pm$  SE) biomass ( $\text{g m}^{-2}$ ) of each fish family at each site in **a** November and **b** February. Sites increase in distance from shore from left to right with *black* representing Lae Lae (LL), *dark grey* being Barrang Lompo (BL), and *light grey* representing Badi (BA). Invertivore (I) and herbivore (H) trophic groups are indicated in *parentheses*. Text within **b** represents the mean ( $\pm$  SE) of Pomacentridae at BA

general, there was much more recruitment on the bottom control tiles, and they also showed a higher diversity of recruits particularly in months one and two at BA (Fig. 6). When LL was included in the analysis (months one and four), the effect of site was pronounced, but this was not apparent in months when LL was not included (Table 2). At BL and BA, recruitment on the top tiles was dominated by turf algae with small amounts of CCA (Fig. 6). The bottom tiles were much more diverse, particularly at BA where the controls had higher proportions of barnacles and tube worms (Fig. 6). On the top tiles, LL was characterised by much less turf algae than the other sites. Overall, LL had little recruitment, but the main differences from the other sites were due to the occurrence of tube worms and CCA (Fig. 6). Caging had an effect on bottom tiles at BL and BA (Monte Carlo:  $p < 0.05$ ) and at BA (Monte Carlo:  $p < 0.05$ ) for months one and four, respectively, resulting in a significant interaction term (site  $\times$  treatment; Table 2). There was no effect of caging during months two

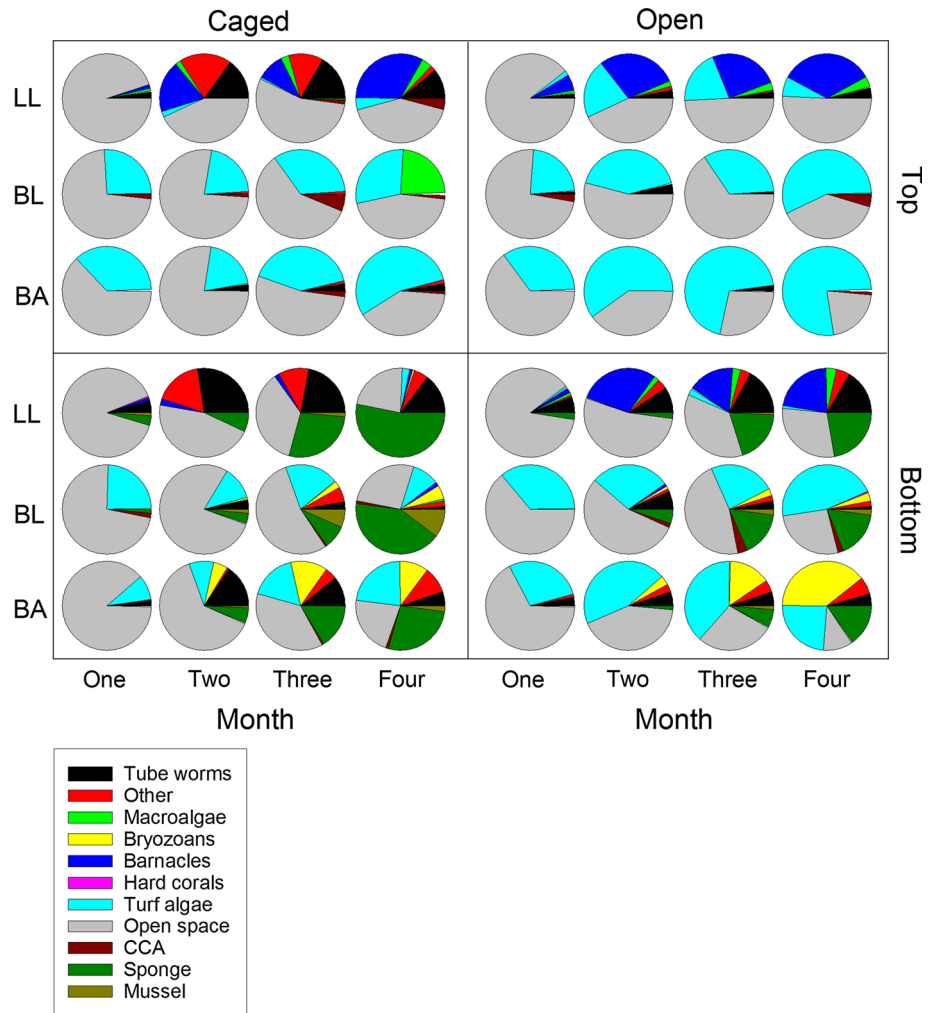


**Fig. 4** Per cent cover (mean  $\pm$  SE) of functional groups over their successional development on top and bottom tiles under caged and open treatments over time at Lae Lae (closed inverted triangles),

Barrang Lompo (open circles), and Badi (closed circles). **a** mussels, **b** bryozoans, **c** tube worms, **d** barnacles, **e** crustose coralline algae, **f** macroalgae, **g** sponge, **h** turf algae, and **i** open space



**Fig. 5** Patterns in community structure (based on mean percentages per group from Fig. 3) over successional development on top and bottom tiles under caged and open treatments at Lae Lae (LL), Barrang Lompo (BL), and Badi (BA)



and three for the top tiles (BL and BA only), but there was an effect for the bottom tiles. Interestingly, in the first two months, BA had a large proportion of sponge recruits in the controls but not the caged treatments (Fig. 6).

## Discussion

While several other studies have examined the effects of increased nutrients and the removal of consumers via caging experiments on coral reef benthic communities, most have done so through artificial nutrient enrichment (e.g., Thacker et al. 2001; McClanahan et al. 2005; Burkepille and Hay 2009; Smith et al. 2010; Rasher et al. 2011; Jessen et al. 2013). Many of these studies show a stronger effect of herbivores and little effect of nutrients (summarised in Burkepille and Hay 2006). In our study, we did not manipulate nutrients experimentally, but instead observed changes in caged and uncaged communities over time in their natural environment at sites varying in

distance from shore. Although nutrients in the water column were generally low among our sites, all other water quality parameters, such as SPM, Chl-*a*, and DOC, were higher nearer to shore. These results agree with Fabricius (2005) who suggested that the quick uptake of dissolved inorganic nutrients by phytoplankton may result in low dissolved inorganic nitrogen concentrations. Therefore, elevated Chl-*a* can act as an adequate proxy for the determination of relative nutrient levels and eutrophication. This is reflected at our near-shore site where there is a greater influence of nutrients and organic matter. Unlike nutrient enrichment experiments, our results represent a comparative approach that takes into account spatial variation in environmental conditions among sites. Although we were not able to isolate impacts on the communities driven by individual water parameters, we capture the combined effects of degraded water quality due to nutrient pollution in structuring benthic communities. The influence of water quality at the sites can be seen by the difference in the communities after 4 months of exposure between the

**Table 2** PERMANOVA results for succession and recruitment for each month of sampling

	<i>df</i>	Month one			Month two			Month three			Month four		
		ms	<i>F</i>	<i>p</i>	ms	<i>F</i>	<i>p</i>	ms	<i>F</i>	<i>p</i>	ms	<i>F</i>	<i>p</i>
<i>Succession</i>													
Top tiles													
St	2	1998.3	11.2	<b>&lt;0.01</b>	2896.7	27.7	<b>&lt;0.01</b>	2955.3	21.1	<b>&lt;0.01</b>	4231.8	13.2	<b>&lt;0.01</b>
Tr	1	16.0	0.1	0.84	1427.6	13.7	<b>&lt;0.01</b>	1557.3	11.1	<b>&lt;0.01</b>	551.2	1.7	0.18
St × Tr	2	155.5	0.9	0.54	493.1	4.7	<b>&lt;0.01</b>	457.7	3.3	0.04	405.7	1.3	0.31
Res	12	179.9			104.6			140.0			321.5		
Total	17												
Bottom tiles													
St	2	2394.6	24.5	<b>&lt;0.01</b>	2684.4	10.9	<b>&lt;0.01</b>	2798.7	10.1	<b>&lt;0.01</b>	2758.5	8.6	<b>&lt;0.01</b>
Tr	1	613.3	6.3	<b>&lt;0.01</b>	908.4	3.7	<b>0.02</b>	359.3	1.3	0.29	879.5	2.7	0.07
St × Tr	2	142.6	1.5	0.28	608.0	3.5	<b>0.03</b>	274.1	1.0	0.47	617.2	1.9	0.09
Res	12	97.9			246.0			277.1			320.2		
Total	17												
<i>Recruitment</i>													
Top tiles													
St	2(1)	7037.2	8.6	<b>&lt;0.01</b>	379.8	0.9	0.50	209.0	0.5	0.60	1288.8	5.6	<b>&lt;0.01</b>
Tr	1	105.3	0.1	0.84	721.4	1.6	0.20	448.0	1.1	0.38	537.6	2.3	0.12
St × Tr	2(1)	1080.6	1.3	0.29	250.7	0.6	0.68	1640.8	4.2	0.06	463.5	2.0	0.10
Res	12	821.5			443.4			393.7			231.5		
Total	17												
<i>Bottom tiles</i>													
St	2(1)	7413.5	16.0	<b>&lt;0.01</b>	1817.1	2.8	0.08	1735.4	1.7	0.20	2336.4	3.2	<b>&lt;0.01</b>
Tr	1	2327.5	5.0	<b>0.01</b>	6547.8	9.9	<b>&lt;0.01</b>	5529.2	5.3	<b>&lt;0.01</b>	3726.8	5.1	<b>&lt;0.01</b>
St × Tr	2(1)	3061.6	6.6	<b>&lt;0.01</b>	961.7	1.5	0.28	898.8	0.9	0.50	2768.1	3.8	<b>&lt;0.01</b>
Res	12	463.4			659.5			1051.6			731.1		
Total	17												

Recruitment tiles were not collected for Lae Lae at months two and three, so results represent a comparison of Badi and Barrang Lompo only. Degrees of freedom (*df*) in brackets represent adjustments for the exclusion of Lae Lae in those months. All significant results are indicated in bold

St is site (Lae Lae, Barrang Lompo, and Badi), and Tr is treatment (caged or open)

site closest to the coast and the other two sites further from the coast. After 4 months, successional tiles showed that the exclusion of consumers had little effect on communities at any of the sites.

The differences in the LL communities compared to the other two sites were considerable, with the former composed mostly of invertebrates on both the top and bottom tiles, and the latter composed mostly of turf algae. Differences in communities reflected in water quality differences among sites suggest that community composition at the near-shore site may be a product of decreased water quality. Unfortunately, our limited replication of water quality sampling (two time points) restricts the elucidation of community differences due to water quality among sites. However, differences among sites become substantiated when combined with previous literature (Edinger et al. 1998; Sawall et al. 2011, 2012) revealing significant spatial

variation across decades. The non-significant effect of consumer exclusion on community composition across the gradient after 4 months is particularly interesting because these results suggest that the effect of consumers on the benthic community composition is minimal. Based on results from months one and four, spatial differences in recruitment were present and probably facilitated differences seen in the successional development of tiles. Interestingly, exposure to consumers increased recruitment and diversity on the bottom tiles at months one and four.

The differences in communities among sites, presumably driven in part by differences in ambient water quality, were immediate and long-lasting. Throughout the year, regardless of the season, LL is exposed to continuous industrial wastes, untreated sewage outflow, sedimentation, and commercial port activity (Edinger et al. 1998; Renema and Troelstra 2001). Similar to our study, previous studies

**Table 3** Results of the SIMPER conducted on data from month four of the successional tiles after PERMANOVA pair-wise post hoc comparisons indicated differences between Lae Lae (LL) and the other two sites (Barrang Lompo, BL, and Badi, BA), but not between BL and BA

Group	LL versus BL	LL versus BD
<i>Top tiles</i>		
Barnacles	33.18	35.47
Turfing algae	19.83	33.91
Tube worms	12.86	11.4
Macroalgae	12.59	
Crustose coralline algae	9.78	5.83
<i>Bottom tiles</i>		
Turfing algae	23.78	22.37
Barnacles	20.94	19
Tube worms	16.43	11.23
Sponge	11.69	9.82
Bryozoans	6.78	22.85
Crustose coralline algae	6.07	

Numbers indicate how much a specific group contributed to the difference between sites (%). Only the groups which contributed to greater than 5 % difference between sites were included. Percentage cover and the change over time can be seen in Figs. 3 and 4

have shown that other sites close to Makassar differ in community composition compared to sites further from shore (Sawall et al. 2013; Plass-Johnson et al. 2015) and our data suggest that this exposure to effluents also affects benthic recruitment and early successional stages of reef development. Nutrients would increase phytoplankton biomass and SPM, thus affecting light attenuation and increasing oxygen demand, possibly to the point where hard corals are impacted (Guzmán et al. 1990). Increases in phytoplankton, SPM, and nutrients provide a competitive

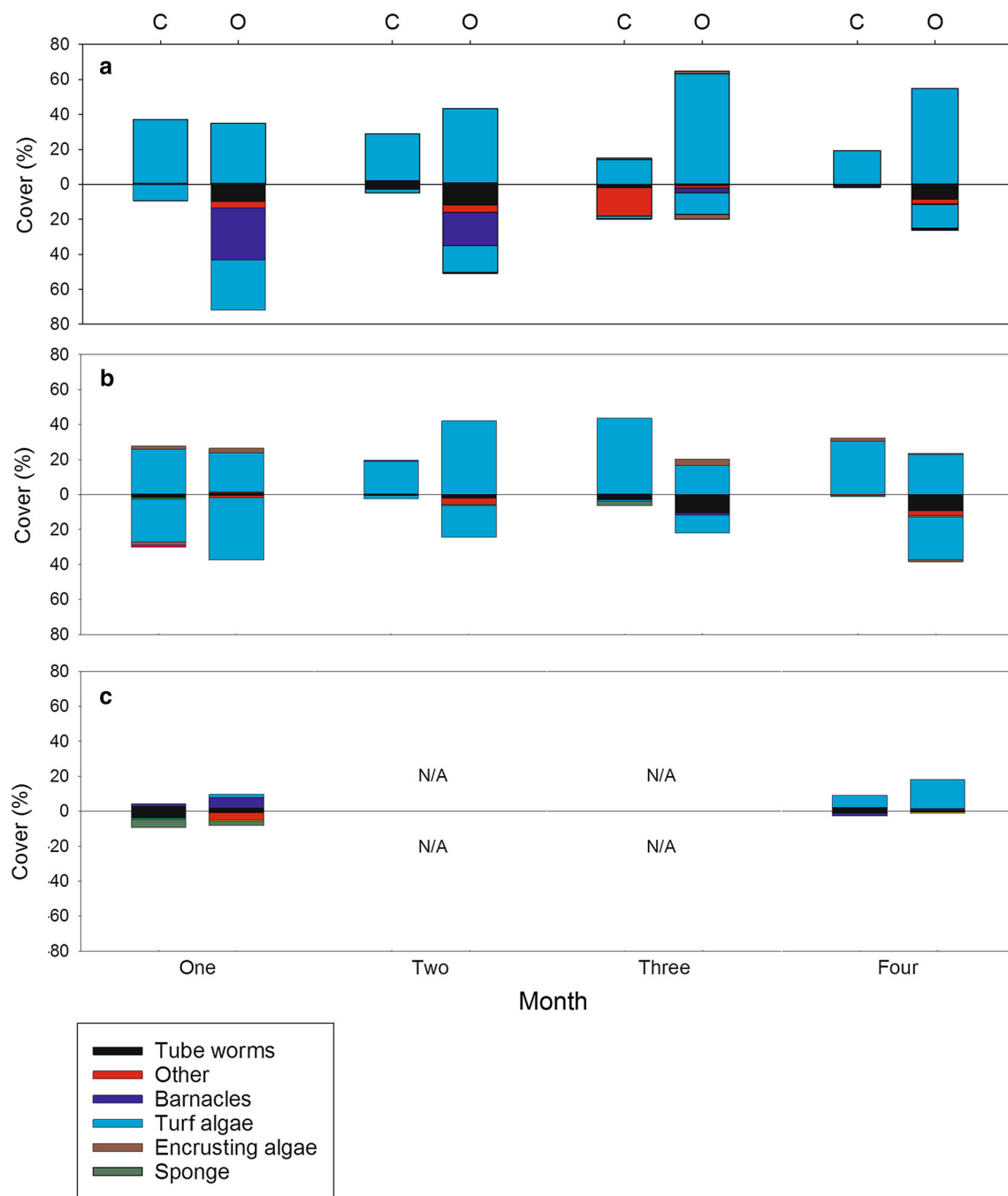
advantage for non-scleractinian organisms through sedimentation smothering existing colonies and also providing conditions for faster growth of algae. LL retains much lower live hard coral cover compared to the other sites. Cover of soft coral cover, a group that has been shown to proliferate once hard corals have declined (Fox et al. 2003), is higher. After four months of succession, LL showed high abundance of barnacles, but this is not reflected in the benthic community. This discrepancy could be a product of the benthic community sampling where identification of barnacles from photographs at 1-m distance would not allow for identification of these small individuals. Similarly, these results may show that barnacles prefer the tile substrate (granite) compared to carbonate reef or that recruits are sourced from the nearby harbour but they do not grow to adults (Jones 1990). Nonetheless, it is not uncommon for filter feeders such as barnacles and soft corals to proliferate in areas only marginally suitable for hard corals. In such instances, the high abundance of filter feeders is not a product of direct competition between hard corals and filter feeders, rather high productivity in the water column leads to the smothering of hard corals and reduced light attenuation, while filter feeders use water column production for nutrition (Smith et al. 1981; Fabricius 2005).

The results of Smith et al. (2010) in Hawai'i found that herbivore effects were immediately apparent, but the effects of nutrient enrichment were not realised until the third or fourth month. There were, however, particularly strong differences between Hawai'i and Spermonde; in Hawai'i, there were relatively high herbivore biomass and high artificial nutrient levels (Hawai'i: herbivore biomass  $\sim 40 \text{ g m}^{-2}$  and dissolved inorganic N  $\sim 4.0 \mu\text{M}$ ) compared with Spermonde [herbivore biomass

**Table 4** Differences in the amount of open space on successional tiles at four sampling times. St is site (Lae Lae, Barrang Lompo, and Badi), and Tr is treatment (caged or open)

	df	Month one			Month two			Month three			Month four		
		ms	F	p	ms	F	p	ms	F	p	ms	F	p
Open space													
Top tiles													
St	2	139.3	10.7	<0.01	127.3	2.8	0.11	211.5	3.1	0.07	243.0	1.6	0.27
Tr	1	0.1	0.1	0.95	311.0	6.8	0.02	113.4	1.7	0.24	124.4	0.8	0.40
St × Tr	2	2.1	0.2	0.85	134.6	2.9	0.88	178.1	2.6	0.11	157.1	1.0	0.38
Res	12	13.1			46.0			67.9			152.2		
Total	17												
Bottom tiles													
St	2	71.0	5.8	0.02	67.5	2.6	0.12	222.2	1.7	0.22	258.5	1.5	0.27
Tr	1	59.8	4.9	<0.05	87.9	3.4	0.11	41.6	0.3	0.63	1.5	0.1	0.98
St × Tr	2	18.4	1.5	0.28	89.3	3.4	0.07	24.2	0.2	0.85	413.1	2.4	0.15
Res	12	12.2			26.0			128.8			172.5		
Total	17												

All significant results are indicated in bold



**Fig. 6** Recruitment each month by taxonomic groups in caged (C) and open (O) treatments at **a** Badi, **b** Barrang Lompo, **c** Lae Lae. Bars above the x axis represent recruitment on top tiles, and bars

below the x axis indicate recruitment on the bottom tiles. The difference between total percentage displayed and 100 % is open space

(Acanthuridae + Labridae (parrotfish) + Siganidae; Fig. 3)  $\sim 6 \text{ g m}^{-2}$ ,  $\text{NO}_x \sim 0.6 \mu\text{M}$ ]. These differences were reflected in the algal communities where capacity for growth was limited by nutrients and herbivore communities were not adequate to control any growth. Our results from Spermonde are more similar to those from the Solomon Islands where differences between caged and control treatments

were minimal at the most degraded sites showing comparable nutrient and herbivore conditions (Solomon Islands: herbivore biomass  $\sim 2.17 \text{ g m}^{-2}$  and  $\text{NO}_x \sim 1.1 \mu\text{M}$ ; Albert et al. 2008).

The most commonly cited phase change in coral reefs is that from hard coral to macroalgal dominance. Despite this, the commonality of this has recently been questioned by

Bruno et al. (2009), particularly in the Indo-Pacific. In the Spermonde Archipelago, macroalgae are not a common component of benthic communities of the reef crest and slope (Sawall et al. 2013) and these observations seem uncharacteristic as diverse macroalgal communities exist on the reef flat (JPJ and MT, unpublished data). Alternatively, turf algae increased cover at BL and BA to roughly 50 % after four months; however, turf algae had relatively low cover at LL. In Belize, McClanahan et al. (2005) found that experimental increase in POM inhibited turf and macroalgal growth, even when inorganic nutrients were increased. This would help explain the low abundances of macroalgae and turf algae at LL, as POM may smother new recruits. However, in treatments exposed to increased POM and inorganic nutrients, McClanahan et al. (2005) found an increase in the brown macroalgae, *Padina*. Our study indicates that macroalgal recruitment to the reef slope is low, pointing to inefficient self-maintenance of macroalgal populations. However, the proliferation of turf algae should not be overlooked as this group can also have strong impacts on the benthic community. Turf algae can cause damage to other organisms through allelochemical mechanisms (Jompa and McCook 2003). Furthermore, filamentous algae can trap sediments (Stewart 1989) and shade other organisms (Nugues and Roberts 2003) while also altering water flow (Eckman and Duggins 1991). Likewise, recent studies have found that turf algae had a significant effect on the hard coral composition of Belizean coral reefs (Wild et al. 2014) and also impeded hard coral recruitment and development (Birrell et al. 2005, 2008). In our study, hard coral did not develop, possibly influenced by the presence of turf algae.

Open space is generally rare on a coral reef, often only occurring after feeding by benthic consumers. Thus, we expected open space to be more common in the treatments open to herbivores, an effect that has repeatedly been shown in studies with similar methodology (Albert et al. 2008; Smith et al. 2010; Jessen et al. 2013). These studies also showed that increasing nutrients and caging can result in significantly less open space, between 0 and 10 % total open space, over time periods comparable to our study. The presence of ~45 % open space in our caged treatments could indicate an artefact of the experiment, but also lends possible insight into other processes affecting the benthic community. Mesograzers such as gastropods and amphipods were not quantified, yet their small size suggests they could have moved in and out of the caged treatments. This group can have a strong effect on algae, especially filamentous turf algae (Carpenter 1986). Overfishing of large-bodied fishes could reduce predation on mesograzers increasing their effect on the coral reef. Furthermore, some species of mesograzers show little change under eutrophic conditions (Fox et al. 2009), while low HDO concentrations can reduce mesograzers abundances (Fox et al. 2008). It is possible that

at LL, a subset of mesograzers limited by HDO combine with sedimentation to impact recruitment and succession. This indirect evidence of mesograzers may suggest a functional group that significantly affects the benthic community at the Spermonde Archipelago warranting further investigations into their ecology on disturbed reefs.

Caging experiments that utilise an artificial increase in nutrients to display potential changes in benthic coral reef communities due to eutrophication and overfishing overlook other abiotic processes occurring within the greater environment such as the production of SPM and DOC and decrease in dissolved oxygen. Thus, our results show that decreased water quality and the exclusion of consumers along with changes in abiotic environmental conditions may not lead to the proliferation of macroalgae on all coral reefs; in Spermonde, macroalgae was absent in early successional communities despite consumer absence. At the most impacted site, non-scleractinian invertebrates were seen throughout the experiment. This was associated with a continuation of open space, perhaps facilitated by unaccounted consumers and SPM.

The Spermonde Archipelago most likely represents reefs of the Southeast Asian region because of the similar resource use, land usage, and seasonal environmental patterns (Burke et al. 2011). Increased urbanisation resulting in deteriorating water quality at other Southeast Asian areas may result in an increase in turf algae rather than macroalgae. Furthermore, deteriorating water quality, resulting in higher productivity, may change coral reef benthic communities to become characterised by non-scleractinian invertebrates. In the face of ever-increasing local stressors on coral reefs, we need to gain a better understanding of the dynamic relationships between water quality, consumers and the greater community. Our study demonstrates the changes that can occur to benthic reef communities exposed to long-term degradation of water quality and fishing pressure and also highlights how the response of a benthic coral reef community to stressors can differ compared to other tropical regions.

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