Benthic structure drives butterflyfish species composition and trophic group abundance

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Corals provide structure and food sources vital for the maintenance of coral reef fish diversity. However, coral reefs are currently under threat from climate change, which has led to the largest recorded loss of live coral. The loss of live coral, and corresponding shift in reef benthic composition, are predicted to impact the abundance and composition of coral reef fish species and communities. In this study, we investigate the effect of changes in reef benthic composition (eg. live coral, dead coral, algae), on the diversity and composition in an assemblage of butterflyfish species, in Faafu Atoll in the Maldives after the 2016 bleaching event. We show that differences in community composition of butterflyfish are associated to benthic structure, reflecting species feeding preferences. Interestingly, however, we also show that lower coral cover is not associated to lower abundance and species richness of butterflyfish. Our results suggest that maintenance of coral reef structure after a disturbance provides key microhabitats to accommodate non-corallivorous butterflyfish, thus maintaining abundance and species richness. Overall our study provides support for regulation of richness and abundance of coral reef fish assemblages to short term changes in coral reef benthic composition after disturbance via turnover in composition.

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BENTHIC STRUCTURE DRIVES BUTTERFLYFISH SPECIES COMPOSITION AND TROPHIC GROUP ABUNDANCE

Running title: Butterflyfish Species Trophic Abundance

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ABSTRACT

Corals provide structure and food sources vital for the maintenance of coral reef fish diversity. However, coral reefs are currently under threat from climate change, which has led to the largest recorded loss of live coral. The loss of live coral, and corresponding shift in reef benthic composition, are predicted to impact the abundance and composition of coral reef fish species and communities. In this study, we investigate the effect of changes in reef benthic composition (eg. live coral, dead coral, algae), on the diversity and composition in an assemblage of butterflyfish species, in Faafu Atoll in the Maldives after the 2016 bleaching event. We show that differences in the community composition of butterflyfish are driven by benthic structure, which was concordant with species feeding preferences. Interestingly, however, we also show that loss of benthic composition produced no change in the abundance and in species richness of butterflyfish. Our results suggest that maintenance of coral reef structure after a disturbance provides key microhabitats to accommodate other non-corallivorous butterfly fish, thus maintaining species richness. Overall our study highlights the potential resilience of coral reef fish assemblages to changes in coral reef benthic composition after disturbance via turnover in composition.

INTRODUCTION

Corals are important niche constructors. The shape, form and size of corals physically modify the characteristics of the habitat, which determine the assemblage of species that associate with coral reefs. High spatial heterogeneity in coral's shapes and forms are key to sustaining one of the most diverse ecosystems on Earth, with over one million species associated with coral reefs (Vernon 1995, Moberg & Folke 1999, Halford et al. 2004). Worryingly, coral reefs throughout the world are under threat from human-induced climate change (Hughes et al. 2017). The loss of reef corals and the respective impact on the associated fauna they support can lead to dramatic ecological shifts in the ecosystem, likely to have serious economic effects in locations that rely heavily on fisheries and tourism. Understanding how changes in reef benthic composition shape the community they support is therefore of crucial ecological as well as economic importance.

Reefs are heterogeneous in their benthic composition, which directly impacts the diversity of the associated fish fauna. For example, the percentage of live coral is an accurate predictor of the abundance of corallivorous reef fishes (Bell & Galzin 1984). Shifts in the dominance and heterogeneity of reef benthic composition are related to disturbance history (De'ath et al. 2012). For instance, bleaching events are often accompanied by a shift in the benthic composition away from a scleractinian reef-builders dominated reef towards an algae dominated reef system (McManus & Polsenberg 2004). While live coral loss has an immediate effect on the abundance of corallivorous fish species, other fish species may also be affected in the long term by loss of structural complexity essential for shelter, habitat and settlement of many fish larvae (Feary et al. 2007).

The joint effect of shifts in reef benthic composition and the potential loss of coral structure is an important driver of patterns of diversity and community structure among reef fish species (Morgan et al. 2008, Graham et al. 2014). The direction and magnitude of such impact in terms of community and diversity change, is, however, not linear. The loss of live coral does not always leads to loss of fish diversity because coral reef fish species differ in the degree to which they are impacted by changes in reef benthic composition (Syms & Jones 2000). Some species rely exclusively on live coral, but others depend on other components of the benthos such as turf algae or cyanobacteria. Differences in dependence upon live coral is likely to shape how fish respond to change in benthic cover. A stronger understanding of the impacts and implications of disturbance in shaping fish communities must, therefore, include understanding of changes in fish abundance in relation to live coral cover, as well as in relation to other benthic organisms.

Here we examine the effect of spatial differences in benthic composition and relate this to patterns in community composition and diversity of coral reef species. Specifically, we ask how butterflyfish (Chaetodontidae) communities reflect reef benthic composition. Butterflyfish are one of the most conspicuous, common, and well-studied coral reef fish groups. Their wide geographic range, relative abundance, and ease of identification make them a popular model organism when studying the links between reef fish ecology and coral reef condition (Bell & Galzin 1984, Pratchett & Berumen 2008). Butterflyfish rely on coral for providing habitat and shelter against predators and wave action (Graham et al. 2009). Corals are also a key component of the dietary requirements of butterflyfish (Pratchett 2005, Pratchett & Berumen 2008). However, the degree of dietary dependence on corals varies within the group, ranging from obligate corallivore species, to facultative corallivore species, to invertebrate feeding species (Cole et al. 2008). The existence of such heterogeneity in feeding preferences within the single genus provides an opportunity to investigate the extent to which changes in reef benthic composition and structure shape community of butterflyfishes. Species with specific dietary requirements are more vulnerable to changes in food availability than generalist ones (Pratchett et al. 2006). We predict that sites with lower live coral cover are inhabited by communities of generalist butterflyfish. Conversely, sites with higher live coral cover should be dominated by obligate corallivore butterflyfish species.

The sea surface temperature anomalies caused by the 2015-2016 El Niño led to the largest bleaching event recorded in the Maldives, with more than 70% of corals completely or partially bleached (Ibrahim et al. 2017). Understanding the impact of this disturbance in changing benthic composition and coral reef fish community structure is especially important for countries, such as the Maldives, where the economy relies heavily on services provided by coral reef ecosystem. Fishing and tourism are the two main sources of revenue of the Maldivian economy (World Bank Report 2017). Investigating the impacts of spatial heterogeneity in benthic cover caused by bleaching in shaping butterflyfish community will give us invaluable information about ecosystem resilience, which can be used for predicting the knock-on effects of climate change on corals (Berumen & Pratchett 2006, Swain et al. 2017).

The aim of this study is to quantify trophic community composition of butterflyfish assemblage in response to variation in reef benthic composition caused by recent environmental disturbance. Namely, we ask how differences in benthic composition and reef structure contribute to promoting differences in butterflyfish assemblages. We first compare two sites in terms of abundance and species richness in both corals and butterflyfish species. Second, we investigate how differences in benthic reef composition are reflected in patterns in butterflyfish species and trophic composition.

MATERIALS & METHODS

STUDY SITE

This study was conducted at Magoodhoo Island, Faafu Atoll, Maldives across two reef sites within the atoll: Blue Cove and Maaga (Figure 1). These two sites were selected for having different levels of benthic reef cover (Figure 1). We randomly identified two points on the crest of each reef and conducted transect surveys parallel to the reef crest, 4-7 m deep, in opposite directions from the starting point. We used GPS to ensure the start of the second set of transects was more than 300 m from the first, and thus the survey areas did not overlap. We conducted four 60-minute SCUBA dives at each reef site between 0845 and 1145 hours.

BUTTERFLYFISH SURVEYS

There are 37 species of butterflyfish found in the Maldives (Froese & Pauly 2016). We categorized the butterflyfish species based on their trophic group, as obligate corallivores (oc), non-coral feeders (nc), and generalist (ge) (Table 1). On each dive, two divers conducted a census of butterflyfish species using an adaptation of established “coral reef visual fish census” methods (English et al. 1997). We conducted 4 transects per site. The divers descended to the survey site and swam slowly while deploying 100 m of tape measure. They tallied and identified to species level all butterflyfish within 1.25 m on either side of the tape measure and recorded the time each species was first seen on the dive and at the reef site. Divers were careful to not double count fish that followed them, and only tallied fish while swimming away from the starting point.

BENTHIC COMPOSITION SURVEYS

We surveyed each site four times. At each dive we conducted three 20 m line intersect transects to evaluate benthic composition following the established line intersect transect procedure (English et al. 1994). Each buddy pair laid a 20 m tape measure parallel to the fish transect, starting at 0, 25, and 50 m and following the contour of the reef. Each diver recorded the category of benthos directly below the tape measure to 5cm resolution. Benthos composition was categorized as live coral, dead coral, algae, and other. Morphology of any living or deceased coral was recorded as branching, foliose, tabular, massive, plate, encrusting or mushroom. Any live coral was identified to genus level using the Indo Pacific Coral Finder 2.0 (Kelley 2011). When divers were not confident in the identification of a coral underwater, it was photographed for later review.

STATISTICAL ANALYSIS

We used a Principal Component Analysis (PCA) to determine site-level differences in benthic composition and in butterflyfish community trophic composition between sites (based on trophic groups, see Table 1). To infer about benthic composition differences between sites, and to identify the main drivers of these differences, we used a PCA with total cover for each benthic type as variables for each transect. We also ran a PCA on the fish data, using each trophic level as variables. In both analyses, variables were not standardised as each variable was measured on the same scale (i.e. benthic cover and abundance of butterflyfish species). We added 95% confidence ellipses for the mean position of each site to the PCA in order to infer whether the sites were distinct. We selected the number of principal components (PC) to retain using the cumulative explained variation in the data from the first PC onwards. We also examined the loadings of each variable on the retained PCs to determine which variables were most important for each PC.

Finally, we calculate the total number of individuals, total number of species (species richness) and evenness for each site. We used the Pielou's metric to estimate evenness using the Vegan package (Oksanen et al. 2018). Differences in community metrics between sites were assessed using a one-way ANOVA (*p*-values were considered significant after Bonferroni correction). All analyses were performed using R (Team 2018).

RESULTS

<u>Linking trophic community structure with benthic composition.</u>

Live coral cover was significantly higher at Blue Cove compared to Maaga ($F = 69.43$, $df = 22$, $p < 0.001$, Figure 2, Table 1). The abundance of obligate corallivore individuals was also higher at Blue Cove ($F = 23.58$, $df = 6$, $p = 0.002$, Figure 3, Table 1). Contrastingly there was greater abundance of non-corallivore species at Maaga ($F = 29.68$, $df = 6$, $p = 0.001$, Figure 3, Table 1), which was characterized by greater cover of dead coral (cm) ($df = 28.42$, $p = 0.001$, Figure 2, Table 1).

Despite the differences in trophic composition of butterflyfish community between sites, we did not detect a correspondent difference in both total abundance ($F = 0.54$, $df = 6$, *p*

= 0.496), butterflyfish richness (F = 4.42, df = 6, p = 0.138), between the two sites (Figure 4). We did, however, found that the relative abundance of butterflyfish species at Blue Cove was more even than the one found at Maaga (evenness between sites, F = 7.91, df = 6, p = 0.03).

Benthic composition

Eighty-three percent of the variation in benthic composition was captured by the first principal component (PC) (Figure 5). The variables that most contributed to this were live coral (63%) and dead coral (60%). The second principal component captured 10% of the variation with tabular morphology (74%) and branching morphology (40%) contributing the most. The two sites are well delineated in the PCA, with Maaga located in the right quadrant suggesting it had low live coral cover and with both tabular and branching coral morphologies. Blue Cove seats in the left corner and it best described by the presence of live coral and by encrusting and massive coral morphologies (Figure 5).

Butterflyfish Community Structure

Eighty-one percent of the variation in fish community structure was captured by the first principal component (PC) (Figure 6). The variable that contributed to this was “obligate corallivore” (80%). The second principal component captured 9.5% of the variation with “non-coral feeders” (72%) contributing the most. The two sites had distinctive butterflyfish trophic community structures, with Maaga located towards the right suggesting it is comprised of non-corallivore species, such as the Black Pyramid butterflyfish (*Hemitaurichthys zoster*) and the Blue Cove site was characterised by obligate corallivore species (Figure 6).

DISCUSSION

Our study reveals that butterflyfish species assemblages in the Maldives reflect differences in the composition of the benthic substrate. Sites with lower percentage of live coral cover have significantly greater abundance of non-corallivorous butterflyfish species, such as *H. zoster*, while obligate corallivorous species such as the Pinstriped butterflyfish (*Chaetodon trifasciatus*) are more abundant in sites with greater live coral cover. Our results are consistent with the links between benthic composition and butterflyfish feeding preferences reported for the Great Barrier Reef and for the Indo-Pacific region (Halford et al. 2004). Despite the significant difference in benthic composition between our sites, we did not detect an effect in total abundance and species richness of butterflyfish. This result contrasts with evidence that spatial heterogeneity in coral cover is linked to a reduction in the abundance of butterflyfish (Öhman et al. 1998, Berumen & Pratchett 2006, Pratchett et al. 2006). We did find, that changes in benthic composition are accompanied by changes in the trophic composition of butterflyfish. Overall, our results strengthen the view that benthic composition and the maintenance of coral structure are the main driving factors controlling the distribution of butterflyfish species.

Decline in coral populations and associated degradation of reef communities are being reported worldwide (Hughes et al. 2017, Hughes et al. 2018). Namely, increasing sea surface temperature caused by global warming creates physiological stress to corals, which in extreme cases leads to the end of the endosymbiotic relationship between the corals and the zooxanthella (Dove & Hoegh-Guldberg 2006). Spatial heterogeneity in coral mortality caused by bleaching leads to changes in coral community composition (Glynn 1996, Lenihan et al. 2008). Our two sites were remarkably different in terms of benthic composition on this occasion, despite both sites having high coral cover before the 2016 bleaching event (Davide Seveso personal observation). It was not possible to investigate the causes of benthic differences in this study because of the timing of our observations. However, the greater percentage in recently dead coral found at the Maaga site suggests that the difference in benthic composition between sites is likely to be caused by the 2016 bleaching event, which is known to have impacted this region severely (Ibrahim et al. 2017).

Loss of live coral cover after a disturbance is often linked to a reduction in the abundance and composition of coral reef fish species (Jones et al. 2004, Pratchett et al. 2006, Komyakova et al. 2018). Our results show mixed results in terms of community effects of changes in benthic struct. Firstly, we found that the relative abundance of butterflyfish species is different between sites. The greater percentage of live coral cover found at Blue Cove is likely to have an impact in reducing the pressure associated with feeding, which is expected lower the level of inter-specific competition. Reduction in local competitiveness for resource acquisition can lead to greater evenness among the community (Wilsey & Stirling 2007).

Secondly, while, there were differences in the percentage of live coral cover between the two sites in our study, we also failed to detect and effect of benthic composition in total abundance and richness of butterflyfish. This result is in agreement with a recent study that reported a spatial mismatch between abundance of coral reef fish species and bleaching (Wismer et al. 2018). This later study reports that coral reefs that experienced bleaching did not have significantly fewer fish than coral reefs un-affected by bleaching. In fact, in some cases fish number increased after bleaching, suggesting the replacement of some fish species by others. Structural complexity is predicted to have more of an effect in regulating the abundance of reef fish than live coral cover (Garpe et al. 2006). Despite having a greater proportion of dead coral, the Maaga site also had a greater abundance of coral shapes of greater structural complexity such as tabular and branching shapes. Greater heterogeneity in coral structural complexity creates microhabitats that reduce inter-specific competition while providing refuge from predation, thus likely to support greater abundance of fish (Graham & Kirsty 2013). Our results strongly suggest reefs changes caused by environmental disturbance are likely to have consequences in leading to shifts in trophic composition of butterflyfish assemblage.

More broadly, our results are consistent with prevalent patterns across ecosystems that show species replacements in the form of turnover are a much more prevalent response to disturbance than richness declines (Supp & Ernest 2014). Indeed, elevated turnover is the strongest and most prevalent pattern of biodiversity change in our times (Dornelas et al. 2014). Our results are also consistent with evidence that both abundance and species richness are regulated in most assemblages (Gotelli et al. 2017). Our results suggest that indirect effects of drastic differences on one assemblage are likely to be reflected as turnover in composition in other assemblages of the same ecosystem.

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AUTHORS CONTRIBUTION

MB, MD, CP contributed with funding; MD, CP, NC, CD, EH, KMJ, MJ, CJM, DP, GER conceived the idea and designed the experimental protocol; CP, NC, CD, EH, KMJ, MJ, CJM, DP, GER collected the data; MB, MD, KZ analysed the data and prepared the figures and tables; MB wrote the paper. All authors approved the publication.

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CAPTIONS

Table 1 – Mean and standard deviation values for benthic and trophic composition for Maaga and Blue Cove.

Figure 1 – Sampling site location. Magoodhoo Island, Faafu Atoll, Maldives. (Blue) Blue Cove characterized by higher live coral cover, and (Pink) Maaga characterized by having greater proportion of dead coral.

Figure 2 – Percentage of benthic composition found at Maaga and Blue Cove. Error bars denote standard deviations.

Figure 3 – Percentage of trophic composition in butterflyfish assemblage found at Maaga and Blue Cove. Error bars denote standard deviations.

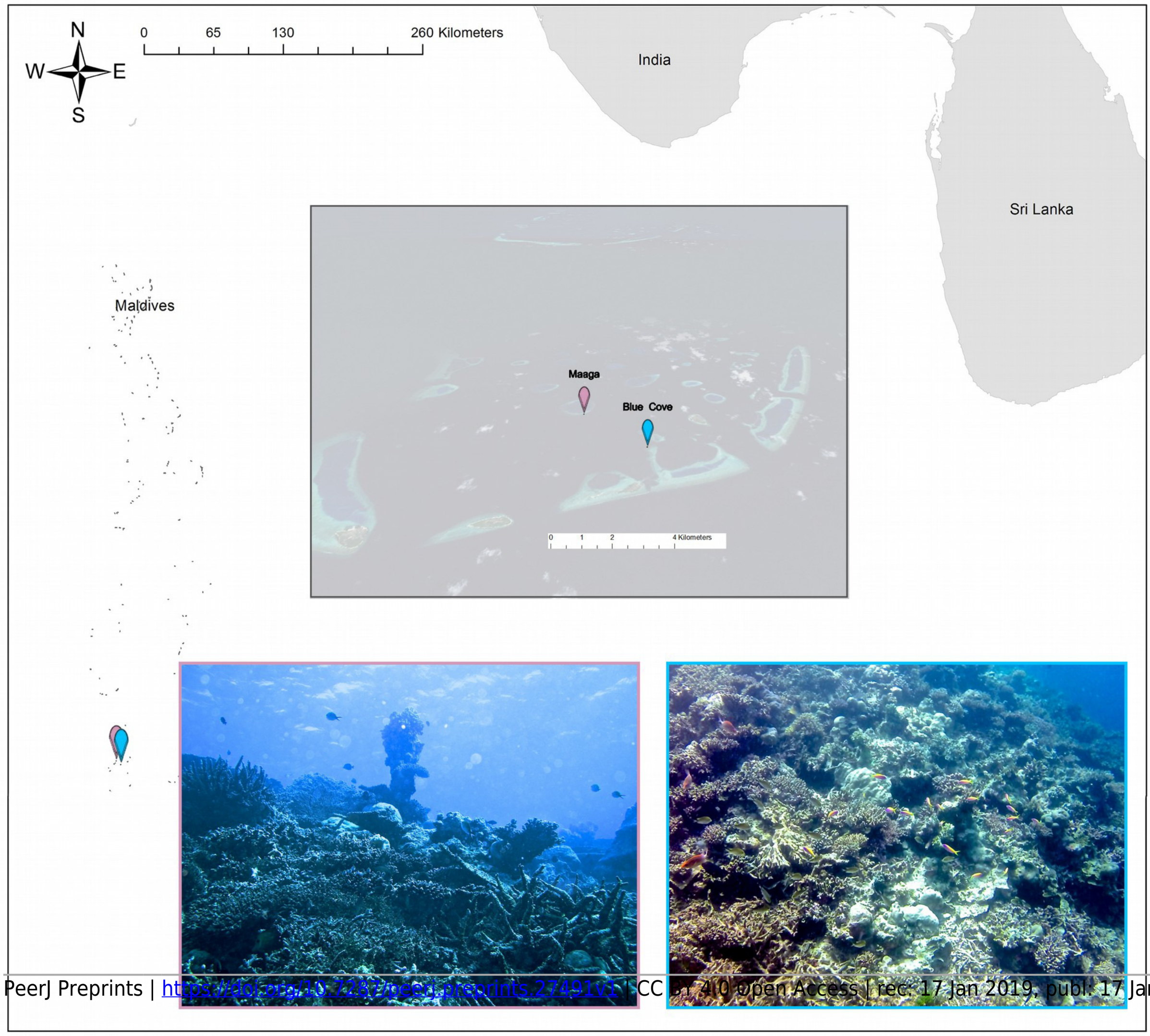
Figure 4 – Total abundance (A), Species Evenness (B) and richness (C) at Maaga and Blue Cove. Error bars denote standard deviations.

Figure 5 - PCA plots of; (A) reef benthic cover and (B) abundance and trophic groups composition, at Maaga and Blue Cove. Benthic variables were grouped into benthic type and coral morphology. Fish trophic composition was categorized using species feeding preferences. Points represent transects and are coloured by site (Maaga – blue, Blue Cove - pink). Ellipses are 95% confidence ellipses for the average position of each site.

Table 1

	Sites	
	Maaga	Blue Cove
Benthic Composition		
Algae	90.8 ± 100.5	4.58 ± 11.5
Dead Coral	1613 ± 224.6	1066.6 ± 275.1
Live Coral	43.3 ± 35.9	562.1 ± 212.6
Other	196.6 ± 105.7	346.6 ± 283.3
Trophic composition		
Generalist	19.25 ± 5.61	21.5 ± 3.11
No coral feeders	23.25 ± 4.34	7.25 ± 3.94
Obligate corallivores	5.75 ± 1.5	25.25 ± 7.88

Figure 1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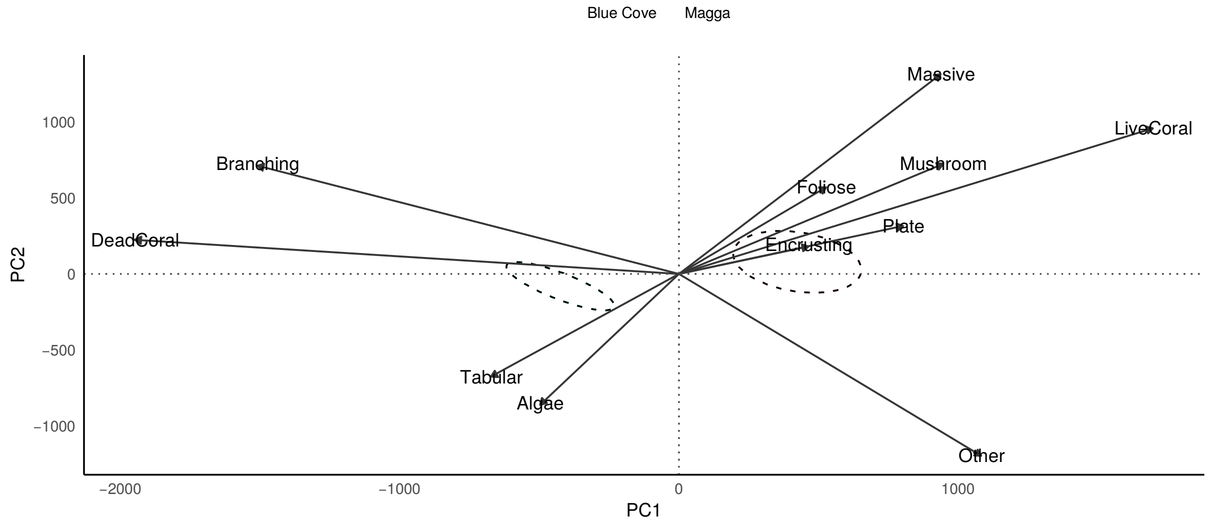
Sri Lanka
Maldives
Maaga
Blue Cove

Figure 5

(A)



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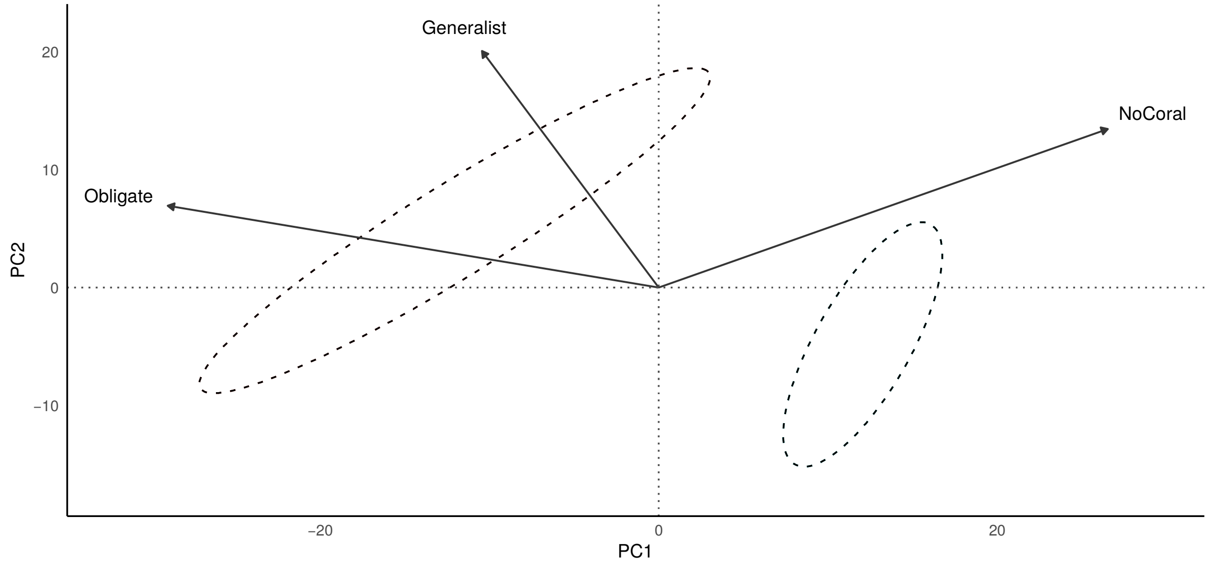

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Figure 1(on next page)

Sampling site location. Magoodhoo Island, Faafu Atoll, Maldives. (Blue) Blue Cove characterized by higher live coral cover, and (Pink) Maaga characterized by having greater proportion of dead coral.

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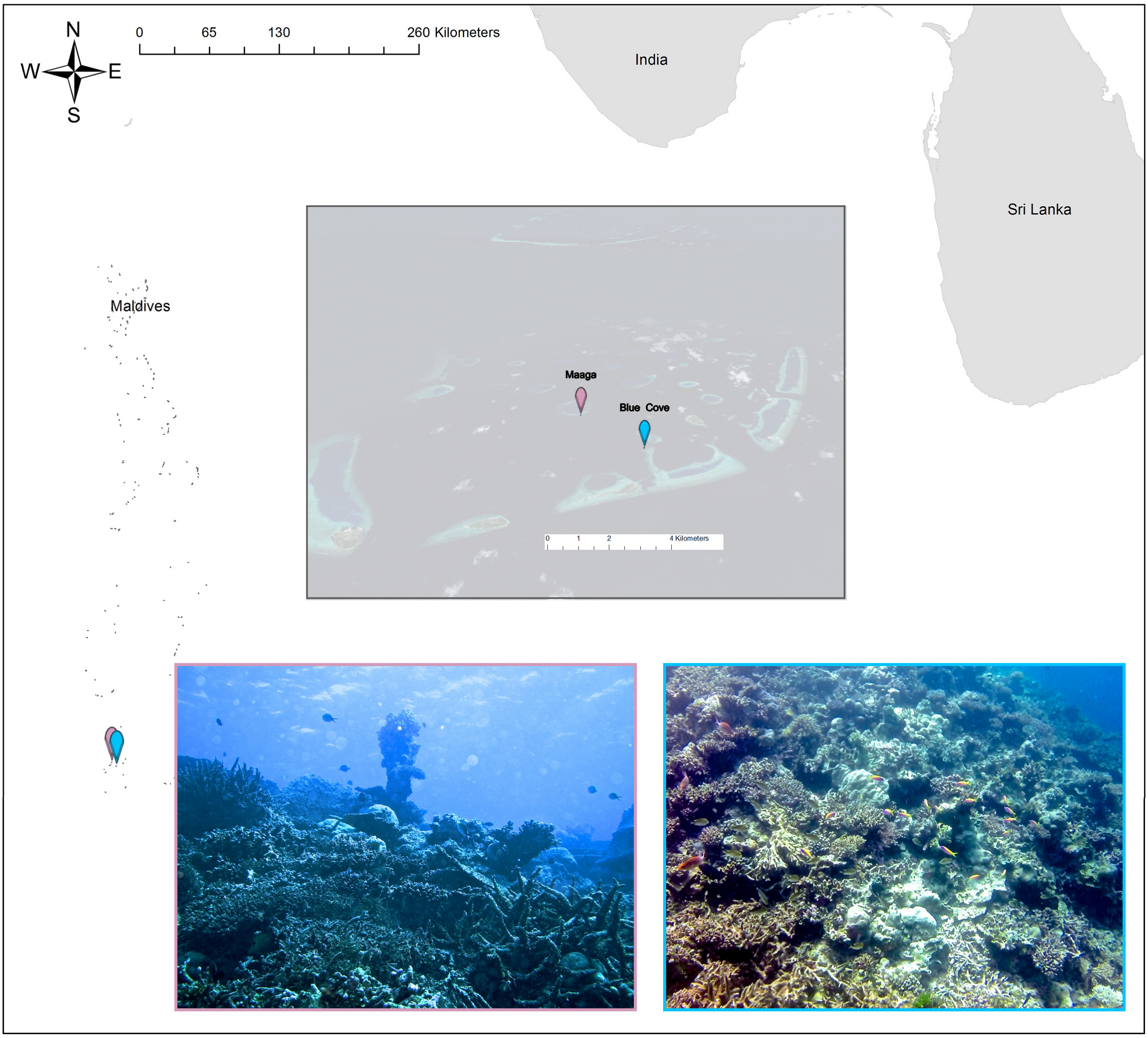
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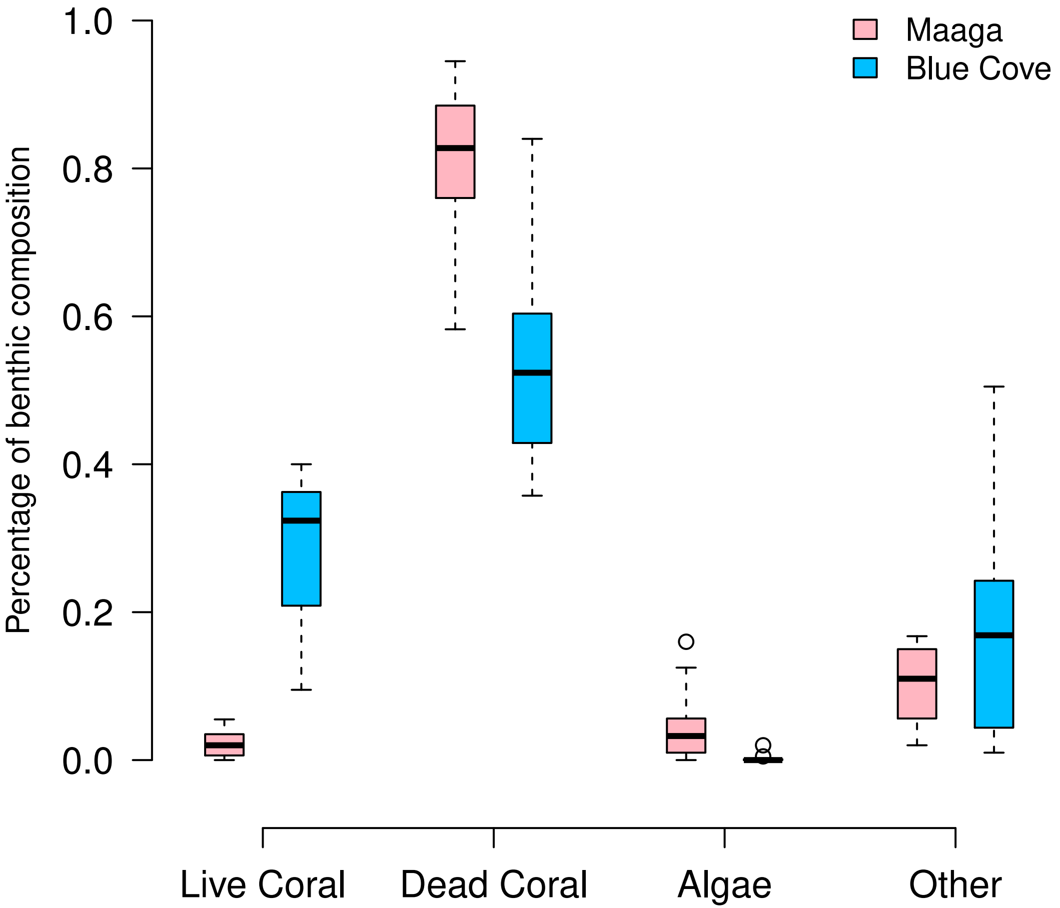
Figure 2(on next page)

Percentage of benthic composition found at Maaga and Blue Cove. Error bars denote standard deviations.

Percentage of benthic composition found at Maaga and Blue Cove. Error bars denote standard deviations.

Figure 2



1.0
0.8
0.6
0.4
0.2
0.0
Percentage of benthic composition
Maaga
Blue Cove
Live Coral
Dead Coral
Algae
Other

Figure 3(on next page)

Percentage of trophic composition in butterflyfish assemblage found at Maaga and Blue Cove. Error bars denote standard deviations.

Percentage of trophic composition in butterflyfish assemblage found at Maaga and Blue Cove. Error bars denote standard deviations

Figure 3

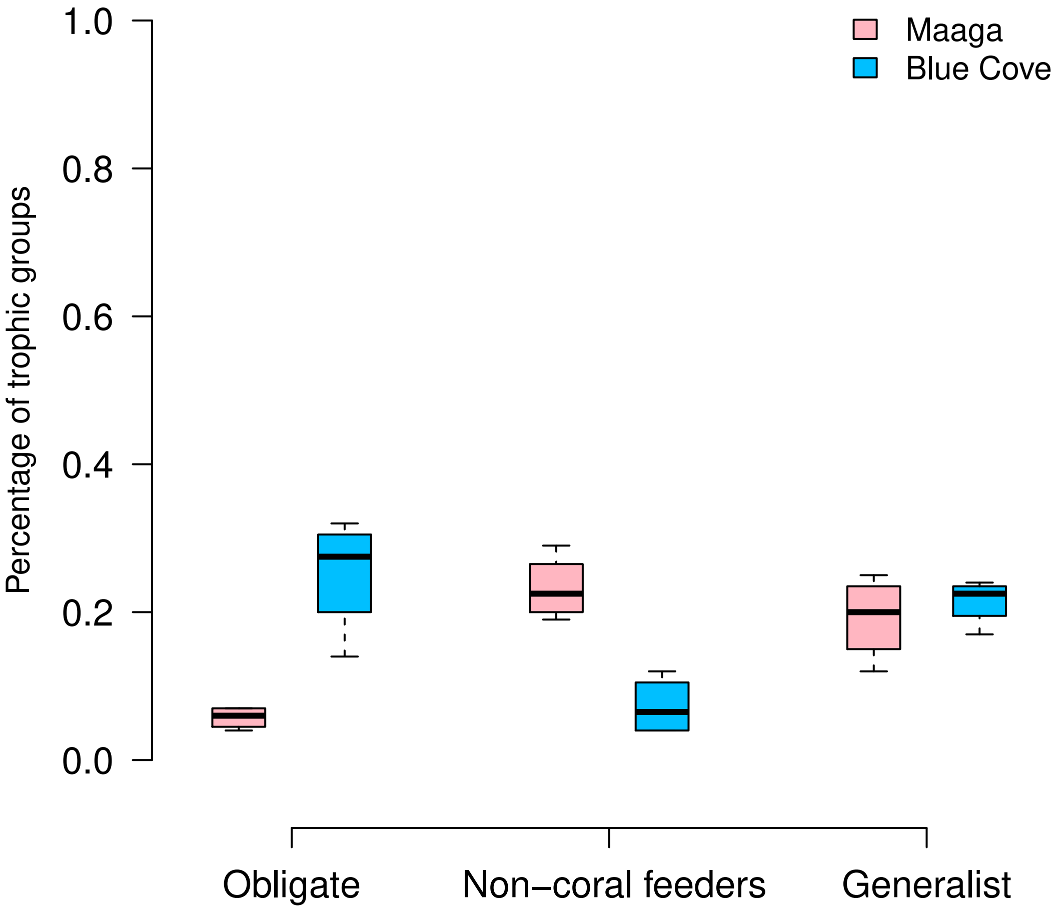


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Figure 4(on next page)

Total abundance (A), Species Evenness (B) and richness (C) at Maaga and Blue Cove. Error bars denote standard deviations.

Total abundance (A), Species Evenness (B) and richness (C) at Maaga and Blue Cove. Error bars denote standard deviations.

Figure 4

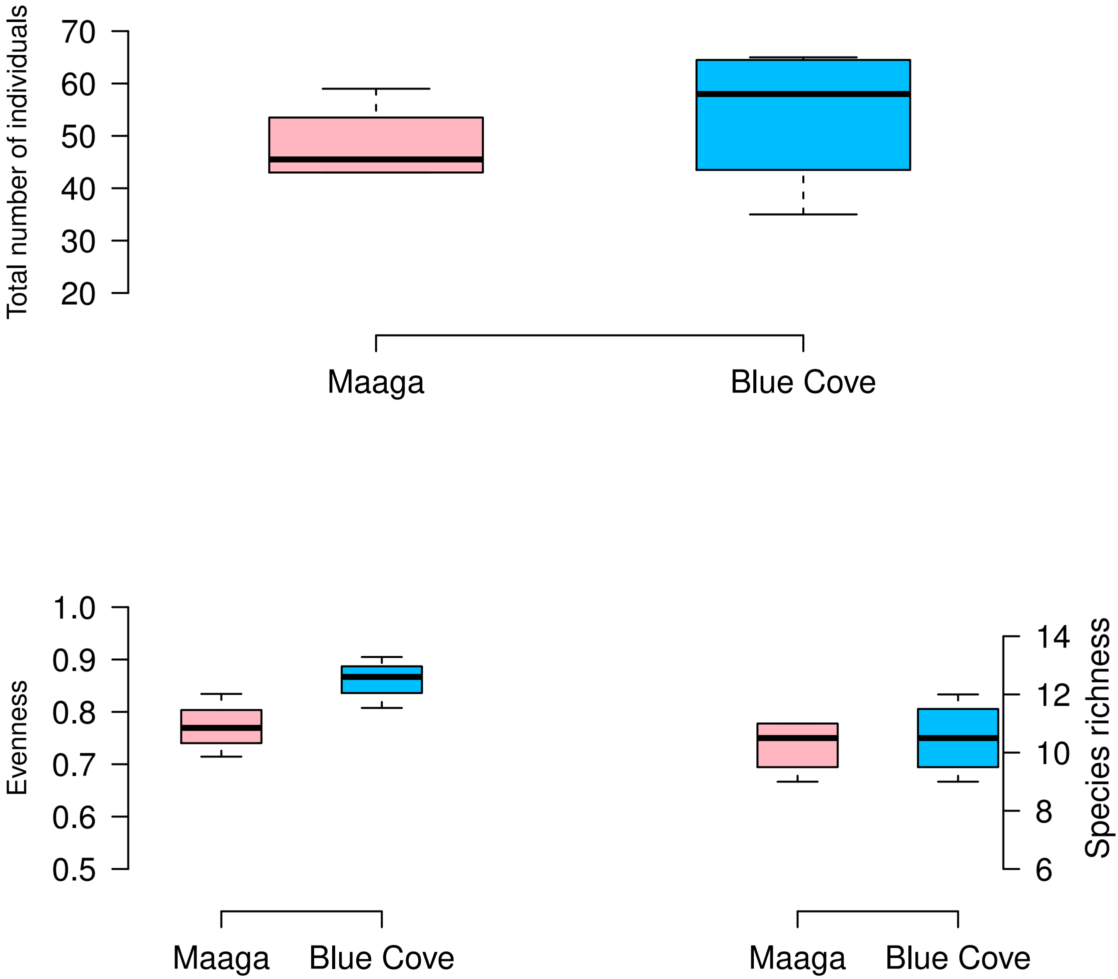

Total number of individuals
70
60
50
40
30
20
Maaga
Blue Cove
Evenness
1.0
0.9
0.8
0.7
0.6
0.5
Maaga
Blue Cove
Species richness
14
12
10
8
6
Maaga
Blue Cove

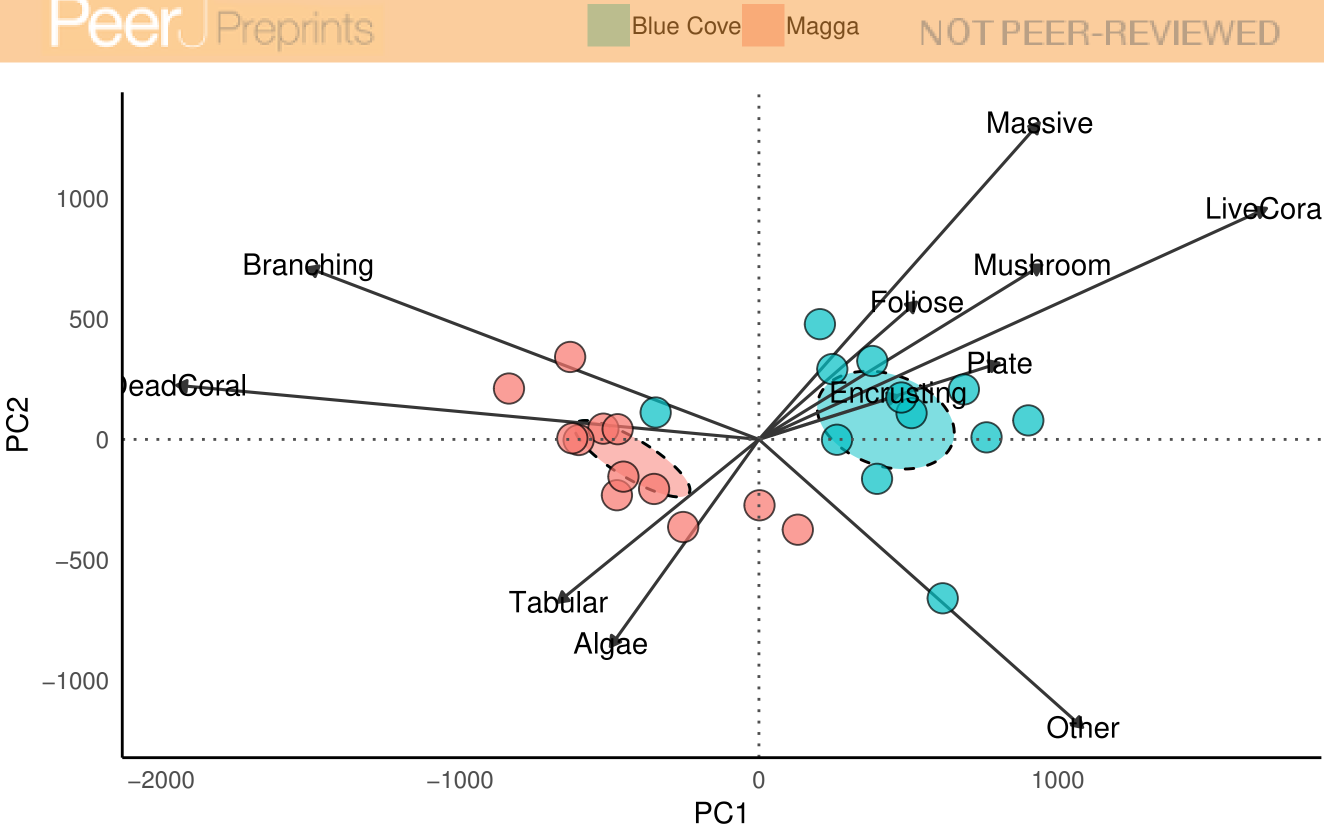
Figure 5(on next page)

PCA plots of (A) reef benthic cover and (B) abundance and trophic groups, at Maaga and Blue Cove.

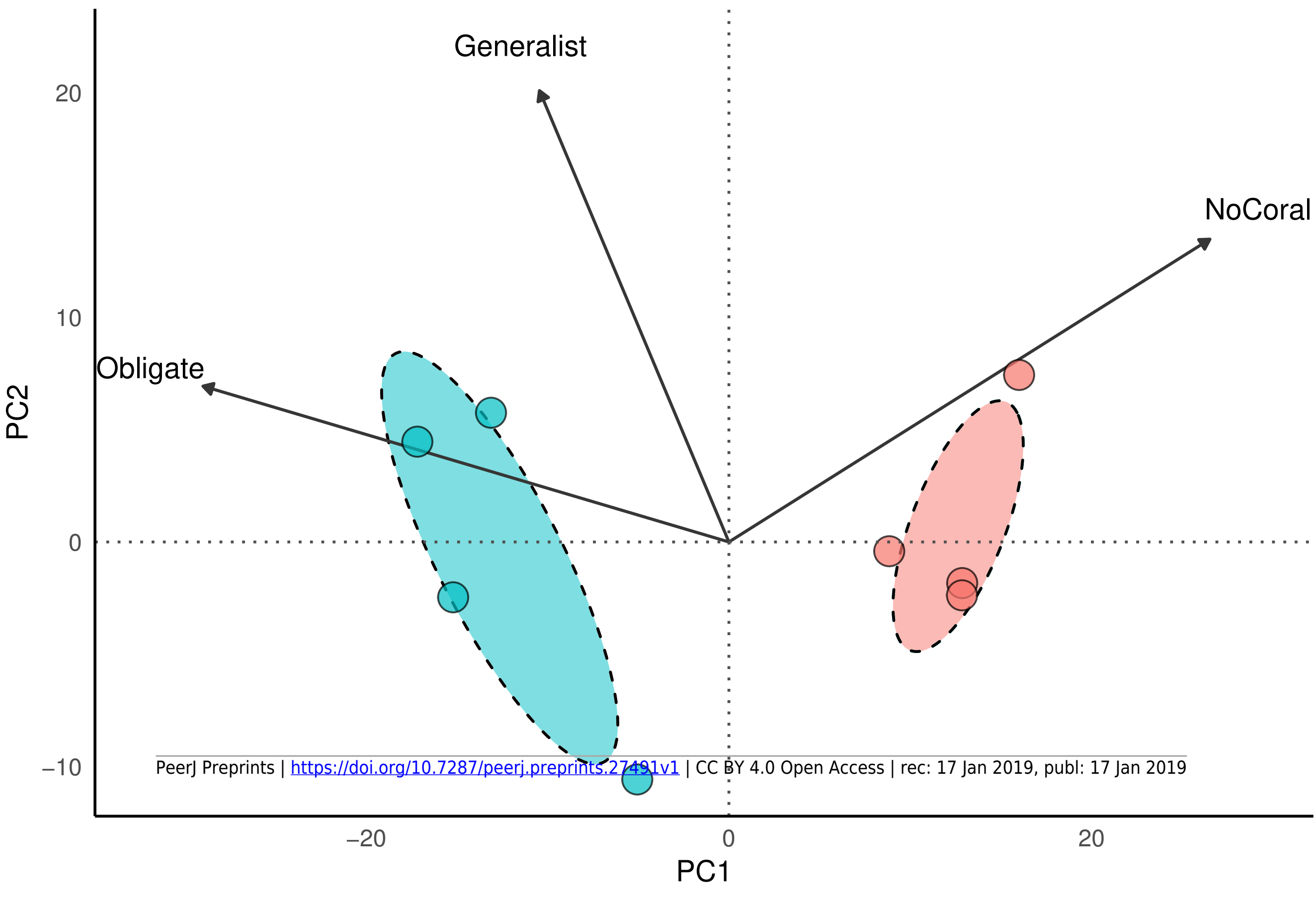
Benthic variables were grouped into benthic type and coral morphology. Fish trophic composition was categorized using species feeding preferences. Points represent transects and are coloured by site (Maaga – blue, Blue Cove - pink). Ellipses are 95% confidence ellipses for the average position of each site.

Figure 5

(A)


Blue Cove
Magga
Massive
LiveCora
Branching
Mushroom
Foliose
DeadCoral
Plate
Encrusting
Tabular
Algae
Other
1000
500
0
−500
−1000
PC2
−2000
−1000
0
1000
PC1

(B)


Generalist
NoCoral
Obligate
20
10
0
−10
PC2
−20
0
20
PC1