



Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Human activities influence benthic community structure and the composition of the coral-algal interactions in the central Maldives



Kristen T. Brown^{a,b,c,*}, Dorothea Bender-Champ^{a,c}, Dominic E.P. Bryant^{a,b,c}, Sophie Dove^{a,b,c}, Ove Hoegh-Guldberg^{a,b,c}

^a School of Biological Sciences, University of Queensland, 4072 St. Lucia, QLD, Australia

^b Global Change Institute, University of Queensland, 4072 St. Lucia, QLD, Australia

^c ARC Centre for Excellence for Coral Reef Studies, University of Queensland, 4072 St. Lucia, QLD, Australia

ARTICLE INFO

Keywords:

Coral-algal interactions
Competition
Human population
Maldives
Crustose coralline algae
Coral reef

ABSTRACT

Competitive processes and their outcomes, such as interactions between scleractinian corals and macroalgae, are important drivers of the structure and function of coral reef ecosystems. Human communities can alter the dynamics of coral-algal interactions by changing species abundance and by affecting competitive ability. Here, we investigated how a natural human population gradient in the Maldives influences the relative abundance of benthic organisms, and if changes in benthic cover can influence the diversity, frequency and outcomes of coral-algal interactions. We observed a decline in some coral assemblages and an increase in coral mortality and filamentous algae on reefs with the highest human population pressures. At the highest level of human population, the diversity of coral-algal interactions was significantly reduced, with some genera of plating corals locally sparse. Human population pressures did not increase the frequency of coral-algal interactions or the competitive ability of macroalgal types. Regardless of human population, interactions between filamentous algae and cyanobacteria were the most damaging to competing corals. Interactions between crustose coralline algae and *Halimeda* were not only the most common and least harmful to coral, but were also positively correlated with coral cover, emphasizing the role that positive species interactions can play in regulating community structure and function.

1. Introduction

Competition in benthic coral reef ecosystems is driven by the most important limiting resource, space (Jackson and Buss, 1975), which regulates species diversity (Connell, 1973; Lang, 1973; Menge and Sutherland, 1976). The struggle for space between coral and macroalgae is critical to the structure and function of coral reef ecosystems and often, the interplay between coral and macroalgae is used to define ecosystem health (Bruno et al., 2009; Mumby et al., 2007). Anthropogenic stressors have been shown to disrupt coral-algal dynamics, shifting competitive advantage in the favor of macroalgae (Diaz-Pulido et al., 2011; Done, 1992; Hughes et al., 2007). Coral-algal interactions play a fundamental role in the degradation of coral reefs (McCook, 1999). Yet, coral-algal interactions, their outcomes, and implications for ecosystem dynamics are not well understood (Jorissen et al., 2016).

Interference competition between coral and macroalgae is often defined by whether or not physical contact is involved (Barott et al., 2009, 2011, 2012b; Dixson and Hay, 2012; Jorissen et al., 2016;

Nugues et al., 2004b; Titlyanov et al., 2007). Although the coral-algal border is important in determining competitive outcomes (Barott et al., 2009, 2011, 2012b), the fact that coral and macroalgae are in contact does not necessarily suggest a competitive relationship (Clements and Hay, 2015; Hay et al., 2004; Jompa and McCook, 1998; Seveso et al., 2012). However, coral growth (Ferrari et al., 2012; Thurber et al., 2012), survival (Tanner, 1995) and reproduction (Box and Mumby, 2007; Foster et al., 2008), for example, can be inhibited by contact with macroalgae. Outcomes of coral-algal interactions are dependent on a range of factors including the species involved (Barott et al., 2009; Barott et al., 2012b; Bender et al., 2012; Vermeij et al., 2010), the size of the coral colony (Barott et al., 2012b; Ferrari et al., 2012; Paul et al., 2011; Swierts and Vermeij, 2016), and the proportion of macroalgae in contact with the coral (Ferrari et al., 2012; Foster et al., 2008).

Human activities can influence the frequency, outcomes, and processes, which govern coral-algal interactions, particularly by removing key herbivores through overfishing, or the increased input of nutrients and sediments from coastal agriculture and land use (Hughes, 1994;

Abbreviations: CCA, crustose coralline algae

* Corresponding author at: School of Biological Sciences, University of Queensland, 4072 St. Lucia, QLD, Australia.

E-mail address: kristen.brown@uq.edu.au (K.T. Brown).

<http://dx.doi.org/10.1016/j.jembe.2017.09.006>

Received 15 March 2017; Received in revised form 11 September 2017; Accepted 11 September 2017

0022-0981/ © 2017 Published by Elsevier B.V.

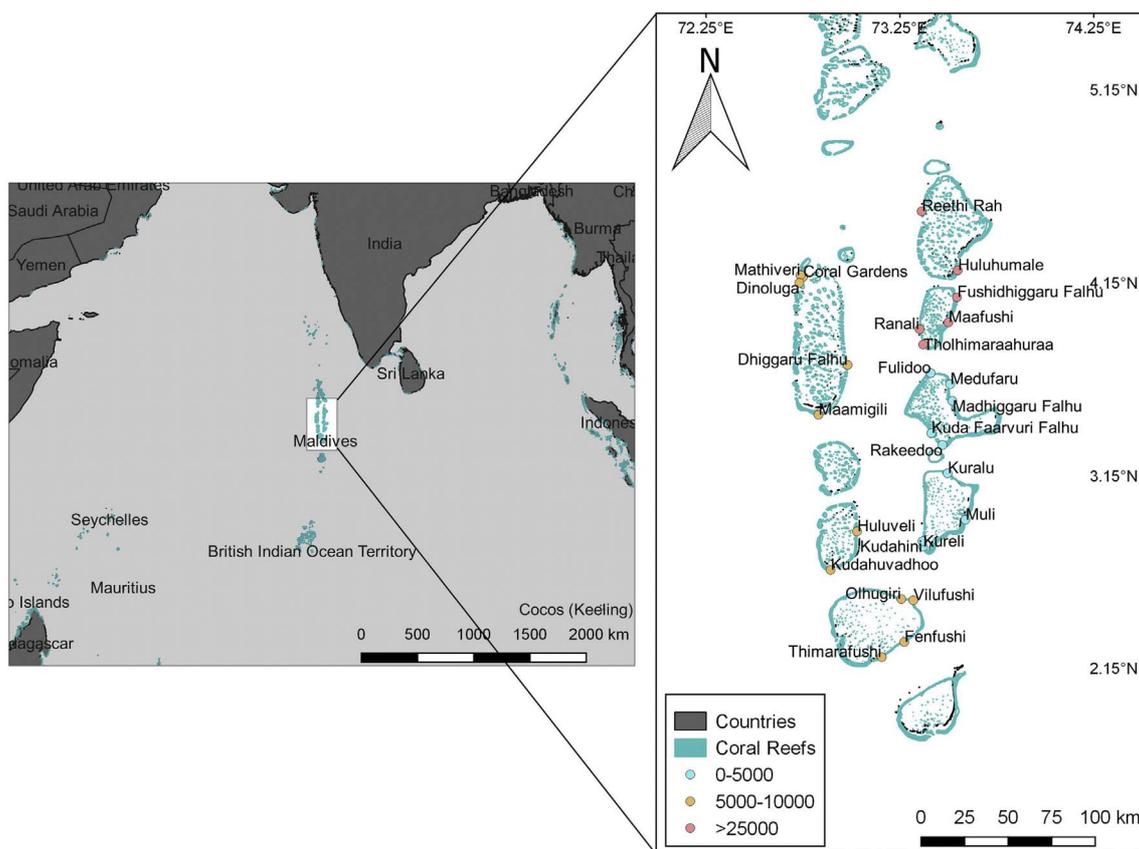


Fig. 1. Map of the study locations in the central Maldives. Dots represent sites, with population levels delineated by color: (blue) = 0–5000, (orange) = 5000–10,000, and (pink) \geq 25,000. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hughes et al., 2003; Hughes et al., 1987; Lirman, 2001; McCook, 1999). The removal of herbivorous fishes is responsible for increases in the abundance of fleshy macroalgae and cyanobacteria as well as decreases in CCA (Burkpile and Hay, 2008; Hughes et al., 2007; Rasher et al., 2012). Similarly, eutrophication and sedimentation can promote the growth of fleshy macroalgae (Fabricius, 2005; McCook, 1999), while suppressing CCA at the same time (Fabricius and De'Ath, 2001). Corals observed on unpopulated reefs have been shown to win a greater proportion of competitive interactions against typically detrimental filamentous algae (Barott et al., 2012b), whereas filamentous algae can become unrivaled on populated reefs subject to sedimentation and eutrophication (Barott et al., 2011; Vermeij et al., 2010). Additionally, communities dominated by CCA are positively correlated with coral cover, and negatively correlated with reefs dominated by filamentous algae (Barott et al., 2011; Smith et al., 2016). Like macroalgae, distinct coral forms respond differently to the effects of eutrophication and sedimentation (Fabricius et al., 2005). *Acropora* and *Montipora* are generally the most sensitive to increases in sediments and nutrients, while *Porites* tend to be among the most tolerant genera (Fabricius et al., 2005; Ganase et al., 2016; Stafford-Smith and Ormond, 1992). Furthermore, eutrophication from human activities can lead to increases in coral disease, particularly in corals of the genus *Acropora* (Montano et al., 2016).

Human communities in the Maldives ($3^{\circ} 15' N$, $73^{\circ} 00' E$) are predominantly concentrated within several atolls in the central region of the country. The clumped nature of human populations in the Maldives presents a unique opportunity to study a natural gradient in human influences on interactive dynamics between coral and macroalgae. High numbers of people in some regions of the Maldives may influence the composition of coral reefs, indicating the possible role of certain anthropogenic drivers (McClanahan and Muthiga, 2014; Morri et al., 2015). The predominant fishing industry in the Maldives is pole-and-

line tuna fishery and associated bait fish (McClanahan, 2011; McClanahan et al., 2000). Because of this, there is little evidence to suggest the overfishing of herbivorous reef fish is a major contributor to macroalgal overgrowth on coral reefs of the Maldives (McClanahan, 2011). Sedimentation and pollution, primarily due to harbor construction, dredging and waste disposal, are the main local anthropogenic stressors contributing to the degradation of Maldivian reefs (Jaleel, 2013). Marine pollution due to agricultural contaminants is negligible in this region due to a lack of land, arable soil and associated agriculture (Jaleel, 2013). Therefore, human-derived eutrophication can only be attributed to localized point-source influences of human waste and sewage, as effluent is discarded at unregulated, yet specified sites along the shoreline because of insufficient waste management facilities (Jaleel, 2013).

In the present study, we sought to gain a more complete understanding of the influence of local human activities on coral reefs by focusing on a centrally important ecological process, competition. Specifically, we investigated if and to what extent a natural gradient of human population influences the benthic cover, as well as the diversity, frequency, and outcomes of coral-algal interactions. Our hypothesis was that human populations will influence benthic cover and coral-algal composition, particularly on reefs adjacent to the highest levels of human population. Furthermore, we expected that filamentous algae would be more damaging to competing corals than calcifying macroalgae, regardless of human population pressures and activities.

2. Materials and methods

2.1. Survey site and human influences

The investigation was conducted during a XL Catlin Seaview Survey (<http://catlinseaviewsurvey.com/>) expedition to the Maldivian

archipelago from late March to mid-April 2015. The focus of this study was on the central atoll region between 2°21'N degrees to 4°31'N degrees. Surveys were completed at 26 sites, across the atolls: North Male, South Male, North Ari, South Ari, Dhallu, Thaa, Meemu, and Vaavu (Fig. 1). Atolls were distinguished by different levels of human population, from 0 to > 150,000 per atoll (National Bureau of Statistics, 2014) (Fig. 1). Three population levels were defined: 1. 'Low' with a population range of 0–5000 (9 sites) 2. 'Intermediate' with a population range of 5000–10,000 (11 sites) and 3. 'High' with a population of > 25,000 inhabitants (6 sites). It is understood that the degradation of ecosystems is not necessarily due to the number of people, but instead due to intensified human activities. However, increased human densities lead to increased levels of influence on their environment (Sanderson et al., 2002) and in most instances, the number of people correlate with their activities (Sanderson et al., 2002; Mora, 2008).

Another significant factor influencing benthic composition is the alternating seasonal monsoons, northeast (NE) and southwest (SW), which drive variations in key winds and currents. The NE monsoon is characterized by dominant NE winds and west flowing currents from approximately December to March (Anderson et al., 2011). The SW monsoon stretches from May to October, with predominate west and SW winds and currents flowing to the east (Anderson et al., 2011). Both wave exposure (Roff et al., 2015) and nutrient enhancement (Fabricius, 2005; McCook, 1999) can lead to changes in macroalgal abundance and composition. Our sampling occurred during the transition period from late March to mid-April to mitigate the effects of hydrodynamic forcing and natural nutrient input due to upwelling across sites on both the east and west of the atoll chain. During this time period, chlorophyll *a* concentrations are most similar on the east and west side of the central Maldives (Anderson et al., 2011).

2.2. Benthic community composition

Benthic community composition was measured by estimating the percent cover from 60 0.5 m × 0.5 m photo quadrats per site shot *in situ* with strobe lighting. Quadrats were placed alternately left and right along 2 × 15 m transect tapes every 0.5 m at a constant depth of 10 m at each site. At a depth of 10 m, influence due to wave exposure is limited (Lowe et al., 2005). Percentage of benthic community composition was estimated from 22 categories. The four central categories consisted of Hard Coral, Other Invertebrates, Macroalgae, and Abiotic Substrate. Commonly encountered coral families were chosen, representing a range of growth forms (Acroporidae - tabular/corymbose; Acroporidae - branching/columnar (including *Isopora*); Acroporidae - plating/encrusting (including *Montipora*); Pocilloporidae; Poritidae - massive; Poritidae - encrusting/plating varieties; Poritidae - branching; Favidae-Lobophyllidae; and other hard corals (including non-scleractinian corals)). Macroalgae were differentiated as: fleshy macroalgae (e.g., *Tydemania expeditionis*, *Caulerpa*), *Halimeda*, filamentous algae/cyanobacteria, and crustose algae. Contact with *Halimeda* has been shown to be less damaging to corals than non-calcareous fleshy macroalgae, and therefore was separated (Ferrari et al., 2012). Other Invertebrates included organisms such as soft corals, giant clams, sea cucumbers, and all other invertebrates (e.g., sponges, ascidians). Abiotic Substrate was defined as other non-living substrate. The category was divided into sand/sediment, coral rubble, recently dead hard coral, and 'bare' rock (Fig. 2A–D).

2.3. Composition of coral-algal interactions

Frequencies of coral-algal contact were recorded by use of a modified method used in previously described studies (Barott et al., 2009). Two replicate 15 m transects were used per site at a constant depth of 10 m, where a 1 m belt of the transect line was examined and any corals physically touching algae were documented (area totaling 30 m²). Coral-algal interactions were normalized to the area surveyed at each

site. Corals were identified to genus, where *Porites* spp. were distinguished by four growth forms (plating, branching, encrusting and massive). *Porites* was split into multiple growth forms as massive growth forms (i.e., *Porites lobata*) tend to be more stress-tolerant, compared to branching growth forms (i.e., *Porites rus*), which are described as weedy (Darling et al., 2012). All macroalgae that were encountered interacting with a coral colony were recorded to genus, with the exception of cyanobacteria, filamentous algae, and CCA, which generally cannot be identified to genus *in situ* (Steneck and Dethier, 1994). The coral colony diameter and length of the coral edge in contact with macroalgae were also recorded for each coral interacting with algae, as both can influence coral-algal interaction outcomes. The outcome of each interaction was recorded; the three outcomes being coral overgrowing algae (coral 'winning'), algae overgrowing coral (coral 'losing') and apparently neutral (Barott et al., 2009) (Fig. 3). The total number of coral and macroalgal genera/functional groups present were determined from coral-algal interaction surveys. This study only provides a snapshot into the interactive dynamics of coral and algae, and seasonal and long-term investigations should be implemented in the future.

2.4. Statistical analysis

All statistical analyses were conducted using Statistica v13.1 software. A multivariate analysis of variance (MANOVA) was used to analyze the effects of human population on the benthic community composition. The factor 'Human Population' was defined at three different levels (0–5000, 5000–10,000 and > 25,000), with 18, 22, and 12 transects, respectively. Tukey HSD test *post hoc* analyses were performed to determine significant differences within categories.

To compare how the frequency of coral-algal interactions varied with human population, analyses of covariance (ANCOVAs) were performed within each continuous, mutually exclusive benthic cover group (covariates: Hard Coral, Macroalgae, and Abiotic Substrate). An additional test of the homogeneity of regression slopes was performed to satisfy the assumption that for each independent variable, the relationship between the covariates and dependent variable was linear. Linear regressions were calculated to predict the relationship between overall frequency of coral-algal interactions and Hard Coral, Macroalgae, and Abiotic Substrate. Linear regressions were also calculated to determine if there was a relationship between Hard Coral and the number of coral-CCA interactions, number of coral-*Halimeda*, and number of coral-filamentous interactions. The goodness of fit (R^2) was determined.

To determine the effect of human population on the number of unique coral-algal interactions, as well as to determine whether human population was influencing the presence of interacting hard coral or macroalgae genera/functional groups, coral-algal interactions were given unique identifiers. The first three to four letters of each coral-algal pair were merged to create one identifier per interacting pair. The interactions were summed to determine how many unique coral-algal interaction pairs were occurring (total observed interactions). To determine which interacting organism was driving the trend, we created a presence/absence matrix of the interacting corals and macroalgae at each population level (Supp. Table 1). One-way analyses of variance (ANOVAs) were performed to determine the effect of human population on the number of unique coral-algal interactions as well as if human population was influencing the presence of interacting hard coral or macroalgal genera/functional groups. Two-way ANOVAs were conducted to investigate whether the outcome of coral-algal interactions was influenced by Human Population and 1. macroalgal type (CCA, filamentous, *Halimeda*, cyanobacteria and all other macroalgae); 2. coral colony size (≤ 5 cm, > 5 – ≤ 10 cm, > 10 – ≤ 20 cm, > 20 cm); or 3. percentage of the coral edge in contact with macroalgae (0–25, 25–50, 50–75, 75–100). Because a low number of coral colonies were encountered measuring > 20 cm in diameter, all coral colonies > 20

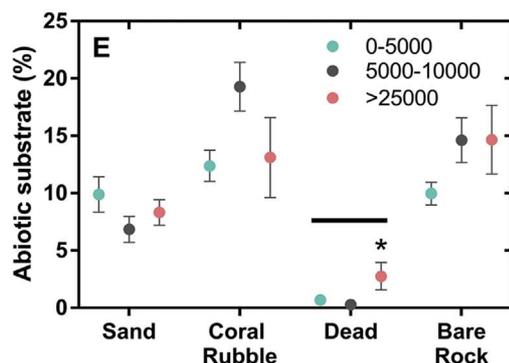
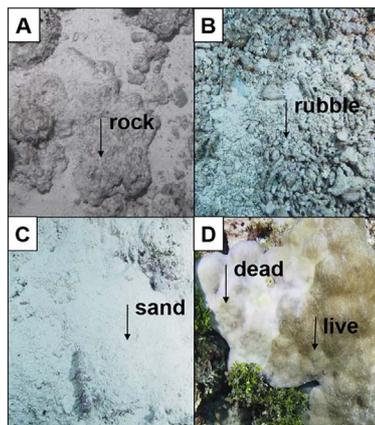


Fig. 2. Definition of abiotic substrate categories and corresponding composition across human population. (A) Rock. (B) Coral rubble. (C) Sand. (D) Recently dead hard coral and live hard coral. (E) The average composition of explicit abiotic categories (% \pm SE) across all transects of each human population level. Bar indicates significance between categories, with asterisk indicating significance within categories ($p < 0.03$).

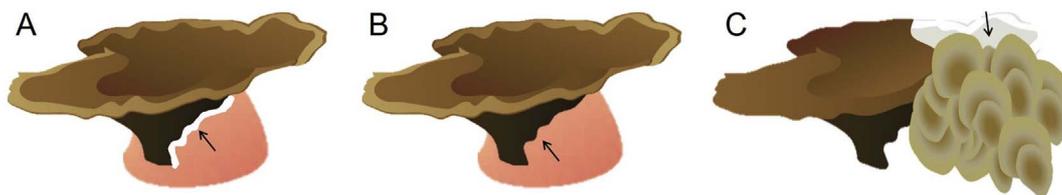


Fig. 3. Definition of coral-algal interaction outcomes. (A) A tabular *Acropora* sp. overgrowing crustose coralline algae (CCA), resulting in discoloration to the alga. (B) A neutral interaction between a tabular *Acropora* sp. and CCA, with no discoloration to either the coral or the alga. (C) Macroalgae overgrowing *Acropora* sp. resulting in discoloration to the coral. The arrows draw attention to the interaction zone, where pigmentation loss in coral and macroalgae can be seen.

cm were combined. Data were tested for homogeneity of variances (Levene's test), outliers, and normality. Tukey HSD *post hoc* analyses were performed to determine significant differences between levels of factors.

3. Results

3.1. Benthic community composition

Human Population had a significant effect on benthic community composition (MANOVA, $F_{(44,56)} = 2.21$, $p = 0.0026$) (Supp. Fig. 1). For the 'Abiotic Substrate' category, there was significantly more dead hard coral at the highest population of humans when compared to that recorded at low (*post hoc*: $p < 0.03$) and intermediate levels (*post hoc*: $p < 0.008$) (Fig. 2E). In the 'Hard Coral' category, there were significantly less *Acroporidae* (plating/encrusting) at the highest population level than both low (*post hoc*: $p < 0.01$) and intermediate (*post hoc*: $p < 0.003$). For the 'Macroalgae' category, there were significantly more filamentous/turf algae at the highest population level than at the intermediate level (*post hoc*: $p < 0.02$).

3.2. Effect of human population density and benthic composition on frequency and diversity of coral-algal interactions

An average of $2.86 (\pm 0.22 \text{ SE})$ coral-algal interactions per m^2 were observed across all transects. 'Human Population', as a driver, did not significantly influence the frequency of coral-algal interactions (ANOVA, $F_{(2,49)} = 0.70$, $p = 0.5$). There were no significant effects of Human Population on the frequency of coral-algal interactions after controlling for the abundance of Hard Coral (ANCOVA, $F_{(2,48)} = 1.29$, $p = 0.28$) and Macroalgae (ANCOVA, $F_{(2,48)} = 1.26$, $p = 0.29$). There was, however, a significant effect of Human Population on the frequency of coral-algal interactions when controlling for the effect of Abiotic Substrate (ANCOVA, $F_{(2,48)} = 3.23$, $p = 0.04$). A positive relationship between benthic coral cover and the number of coral-CCA interactions was found (Linear regression, $F_{(1,50)} = 6.906$, $p = 0.01$; $R^2 = 0.1214$) (Fig. 4A). The number of coral-*Halimeda* spp. interactions

were also positively correlated to coral cover (Linear regression, $F_{(1,50)} = 8.193$, $p = 0.006$; $R^2 = 0.1408$) (Fig. 4B).

A total of 37 coral genera/functional groups were reported across all transects. Human Population had a significant effect on the presence of interacting coral genera/functional groups (ANOVA, $F_{(2,108)} = 5.76$, $p = 0.004$). The highest percent of total coral types were reported at the lowest population level (33 = 89%), which declined significantly as population increased to the highest level (21 = 58%) (Supp. Table 1). Human Population did not significantly affect macroalgae genera/functional groups (ANOVA, $F_{(2,27)} = 2.1$, $p = 0.142$) (Supp. Table 1).

A total of 152 unique coral-algal interactions were observed across all transects (Supp. Table 2). Human Population had a significant effect on the number of unique coral-algal interactions (ANOVA, $F_{(2,411)} = 7.846$, $p = 0.0005$). A total 96 (63%) coral-algal interactions were observed at the lowest level of Human Population, 103 (68%) at the intermediate level, and declining significantly to 72 (47%) at the highest level. The 10 most abundant coral-algal interactions were determined at each Human Population level, and combined totaling 14 of the most abundant interactions across all transects (Fig. 5A). The 14 most abundant coral-algal interactions accounted for over half of the observed interactions (Fig. 5B).

3.3. Outcomes of coral-algal interactions

There was a significant effect of the type of macroalgae in contact with the coral in determining the interaction outcome (two-way ANOVA, $F_{(4,168)} = 82.62$, $p = 0.0001$) (Fig. 6A). Coral colonies lost significantly more against filamentous/turf algae (94.2%) and cyanobacteria (91.5%) than all other macroalgae (81.3%). Furthermore, coral colonies were winning more than half of the time against *Halimeda* (58.4%) and CCA (77.1%).

The diameter of the majority (94%) of coral colonies interacting with algae was < 20 cm. Out of the 2009 coral colonies that were evaluated, only 114 had a diameter > 40 cm. There was a significant effect of coral colony size in determining the interaction outcome (two-way ANOVA, $F_{(3,183)} = 10.631$, $p = 0.00001$) (Fig. 6B). The smallest size class (≤ 5 cm) was winning against macroalgae significantly more

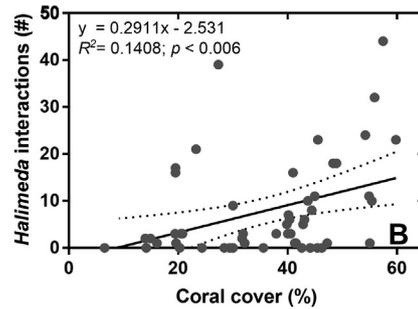
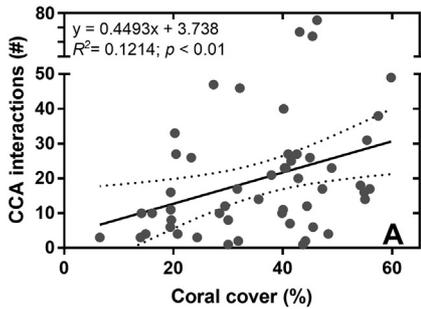


Fig. 4. Linear regression predicting the number of coral-algal interactions from coral cover. (A) A significant linear regression line (solid black line) with 95% confidence interval (dotted lines) was estimated for the number of coral-crustose coralline algae (CCA) interactions and (B) the number of coral-*Halimeda* interactions. Dots represent each transect.

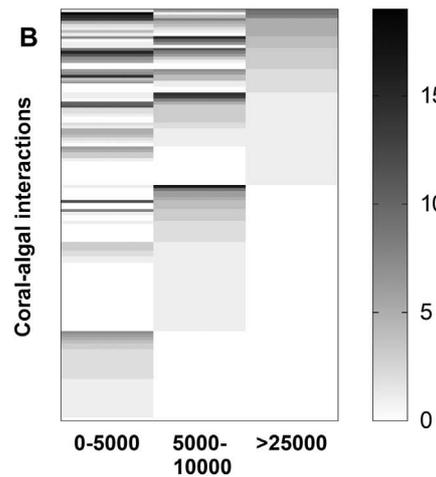
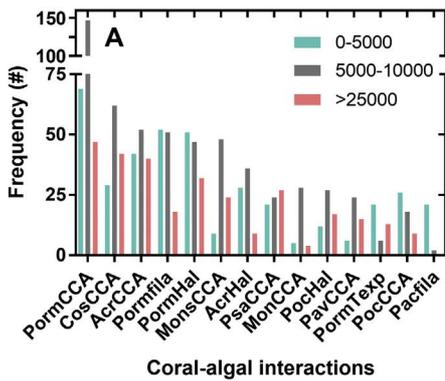


Fig. 5. Frequency of coral-algal interactions. (A) The top 14 most abundant coral-algal interactions at the three different human population levels. Coral-algal interactions are abbreviated listing the interacting coral first and algae second. (B) The remaining 138 coral-algal interactions, with each cell representing a unique coral-algal interaction. Lighter shading represents the lowest frequency, with darker shading representing the highest frequency. Coral: Porm = *Porites* (massive); Cos = *Coscinarinaea*; Acr = *Acropora*; Mons = *Montastrea*; Psa = *Psammacora*; Mon = *Montipora*; Poc = *Pocillopora*; Pav = *Pavona*; Pac = *Pachyseris*. Macroalgae: CCA = crustose coralline algae; fila = filamentous; Hal = *Halimeda*; Texp = *Tydemania expeditionis*.

than all other size classes. The largest size class observed (> 20 cm) lost against macroalgae significantly more than the two smaller size classes (≤ 5 cm and > 5–≤ 10 cm).

4. Discussion

As human population and associated activities exert influence coral reef ecosystems, it is important to understand how the community composition as well as the frequency, diversity, and outcomes of coral-algal interactions are affected (Barott et al., 2012b; Vermeij et al., 2010). Here, we demonstrate that human populations have a strong influence on benthic composition, specifically through a decline in certain categories of reef-building corals and through an increase in dead hard coral and filamentous algae on reefs adjacent to the greatest number of human inhabitants. The composition of coral-algal interactions was altered exclusively at the highest level of human populations, with the reduction in interaction diversity potentially due to a decline in plating coral genera via local human impacts. The frequency of coral-

algal interactions was not correlated to hard coral or macroalgal cover but was negatively correlated to abiotic substrate, suggesting that interactions increase when there is greater competition for space. Filamentous macroalgae were more damaging to competing coral than either CCA or algae of the genus *Halimeda*. Furthermore, while coral-algal interaction frequency was not generally correlated to hard coral cover, coral-CCA and coral-*Halimeda* interactions were positively correlated to hard coral cover. Together these observations support other findings in the literature that suggest that CCA and *Halimeda* facilitate, rather than impede, hard coral cover and hence promote functions and services that are unique to coral reef ecosystems (Smith et al., 2016).

4.1. Benthic community composition

Corals of the genera *Acropora* and *Montipora* are reported to be quite sensitive to sedimentation and nutrient enrichment, displaying low sediment rejection efficiency compared to corals with larger polyps (Fabricius et al., 2005; Ganase et al., 2016; Stafford-Smith and Ormond,

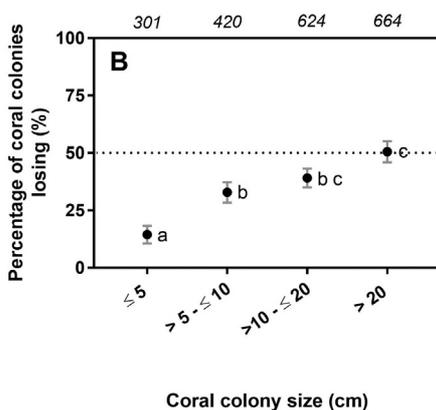
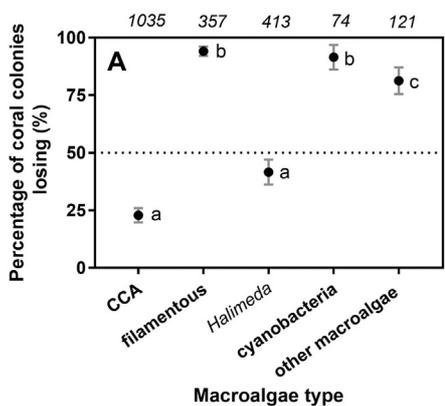


Fig. 6. Coral-algal interaction outcomes. (A) Percentage of coral colonies (± SE) where corals are losing against different types of macroalgae. (B) Percentage of coral colonies (± SE) where corals are losing across coral colony size classes. Italicized numbers indicate the number of coral colonies evaluated with at least one macroalgal interaction.

1992). At the highest level of human population, the abundance of plating/encrusting Acroporids decreased, while the abundance of dead hard coral and filamentous algae increased. The decline in the hard coral group Acroporidae (plating/encrusting) may be due to increased sedimentation and nutrient enrichment near the largest human population pressures (Jaleel, 2013). The loss of structurally important corals such as *Acropora* has ecosystem-wide consequences, such as changes to fish communities due to declines in architectural complexity (Wilson et al., 2008, 2010). *Acropora* adjacent to large human populations are also at increased risk of developing coral diseases, which can lead to mortality (Montano et al., 2016). Cyanobacteria and filamentous algae are often the first to colonize open substrate following coral mortality (Diaz-Pulido and McCook, 2002), and are positively influenced by nutrient enhancement and sedimentation (McClanahan et al., 2003; Nugues and Roberts, 2003).

4.2. Effect of human population density and benthic composition on frequency and diversity of coral-algal interactions

Generally, the frequency of coral-algal interactions increased with fleshy macroalgal cover in environments that experience coral-algal phase shifts (Bonaldo and Hay, 2014; Hughes, 1989; Hughes, 1994; Montano et al., 2012). Herbivores are central to the prevention of such macroalgal proliferation (Bellwood et al., 2004; Hughes et al., 2007; Mumby et al., 2007). The frequency of coral-algal interactions in the Maldives was found not to be correlated to coral or macroalgal cover. Based on overall low levels of fleshy macroalgae and no relationship between the number of coral-algal interactions and macroalgal cover, there is no evidence the reefs investigated had experienced a coral-algal phase shift. Furthermore, herbivorous reef fish (e.g., Scaridae, Acanthuridae) are plentiful (McClanahan, 2011) and presumably sufficient in terms of suppressing macroalgal overgrowth.

The negative correlation between the frequency of coral-algal interactions and abiotic substrate suggests that interactions increase when there is greater competition for space. At the highest level of human population, the frequency of coral-algal interactions was reduced, which is partially attributable to observed increases in dead hard coral and decreases in certain coral genera. A reduction in coral-algal interactions, in combination with low macroalgal populations, may be beneficial in the short-term with less competition for space potentially allowing for coral populations to recover from local anthropogenic impacts.

Macroalgal diversity, to the level examined here, remained equivalent across human populations, indicating the decline in diversity of coral-algal interactions was likely driven by interacting coral genera/functional groups. Interacting coral genera present at all population gradients included 'stress-tolerant' taxa: *Asterozopora*, *Coscinaraea*, *Favia*, *Favites*, *Galaexa*, *Hydnophora*, *Montastrea*, *Pavona*, *Porites* (massive), and *Psammocora* (Darling et al., 2013). These observations are consistent with other studies from the Maldives, with these coral genera recorded as abundant coral recruits in both 2000 (McClanahan, 2000) and 2005 (McClanahan and Muthiga, 2014). Interactions between the comparatively rare (McClanahan and Muthiga, 2014) plating coral genera *Echinopora*, *Echinophyllia*, *Merulina*, *Mycedium*, and *Pachyseris* were only observed on reefs adjacent to low and intermediate human populations. Plating corals lack sediment rejection capabilities and are more likely to retain sediments due to their growth form (Erftemeijer et al., 2012; Stafford-Smith and Ormond, 1992). Because the loss of these corals is noted at the highest level of human influence, sedimentation due to harbor construction, land-fill, and/or dredging may be contributing to their absence (Jaleel, 2013). Even small decreases in species diversity have implications for ecosystem stability and function (Micheli et al., 2014). Furthermore, coral reefs that have reduced coral diversity, where entire functional groups are missing, are the most vulnerable to human impacts (Bellwood and Hughes, 2001; Ferrigno et al., 2016).

4.3. Outcomes of coral-algal interactions

Coral colony size is an important factor in coral physiology, influencing resource allocation priorities (Barott et al., 2012b; Swierts and Vermeij, 2016). We found that the outcomes of coral-algal interactions were dependent on coral colony size. Overall, large coral colonies (i.e., > 40 cm) were uncommon, which is consistent with previous studies from the Maldives (Lasagna et al., 2010; McClanahan and Muthiga, 2014; Tkachenko, 2012). The dominance of small coral colonies is likely due to repetitive thermal stress disturbances leading to recurring declines in coral (Tkachenko, 2015). At least 26 different coral genera were encountered in each size class, representing a diversity of coral morphologies and life histories, suggesting significance was driven by coral colony size. This result is in contrast with a recent study from the Caribbean, which found that coral morphology was the most important determinant in the outcome of interactions between coral and filamentous algae (Swierts and Vermeij, 2016). Generally, we found smaller (< 5 cm) coral colonies were better competitors. This observation is consistent with a previous study, which argues smaller coral colonies invest more resources into growth and competition (Barott et al., 2012b), and in contrast to other studies which suggest that coral colonies > 30 cm may be large enough to escape from competition altogether (Ferrari et al., 2012; Swierts and Vermeij, 2016).

Algal functional groups differ greatly in their ability to compete with corals (McCook et al., 2001), with allelopathic algae considered the most damaging to competing coral (Bonaldo and Hay, 2014; Jompa and McCook, 2003a). In the present study, corals lost more interactions against filamentous algae, cyanobacteria, and all other fleshy macroalgal types (i.e., *Tydemania expeditionis*, *Dictyota*, and *Caulerpa*) across human population levels. Nutrient enhancement (Vermeij et al., 2010) and sedimentation (Nugues and Roberts, 2003) have been shown to increase the competitive ability of filamentous algae. Although we observed an increase the abundance of filamentous algae on reefs adjacent to the greatest number of inhabitants, there was no increase in the frequency of interactions or the competitive ability of the most detrimental types of macroalgae across sites, which is similar to a previous study (Jompa and McCook, 2003a). Species-specific effects have been uncovered within the filamentous algae functional group, and it is possible that with finer identification, differences between species and sites may have been uncovered (Jompa and McCook, 2003a, 2003b). Nearly all (> 90%) of the interactions with filamentous algae or cyanobacteria resulted in damage to coral, suggesting that contact resulted in hypoxia on the adjacent coral tissue (Barott et al., 2012a), enhanced or altered microbial communities (Barott et al., 2012a; Thurber et al., 2012), and/or algal filaments were efficiently trapping sediment (Jompa and McCook, 2003a).

Corals interacting with CCA have been shown to be more successful on reefs (Barott et al., 2011; Barott et al., 2012b), with CCA acting secondarily to facilitate coral settlement (Harrington et al., 2004; Littler and Littler, 2013), and prevent recruitment of more detrimental algal species (Vermeij et al., 2011). We found corals were superior competitors when interacting with CCA. This is consistent with previous studies, which have shown interactions with CCA are not physiologically detrimental to coral (Barott et al., 2009; Barott et al., 2011; Bender et al., 2012). Our results revealed a positive correlation between the amount of coral-CCA interactions and benthic coral cover, which is consistent with Barott et al. (2011, 2012a). Reef communities with an abundance of CCA have been linked to enhanced herbivore biomass (Steneck, 1986), and recently, have been hypothesized to have a greater recovery potential following large-scale disturbance (Smith et al., 2016). Interactions between coral and CCA were just as common on reefs with the highest human population as reefs with low and intermediate population pressures. Therefore, the high presence of coral-CCA interactions observed throughout the Maldives may indicate the facilitation of a positive feedback in coral colonization and recovery of

coral communities.

Similar to the interaction with CCA, corals were also the superior competitors when interacting with *Halimeda*. In more than half of observed interactions, corals showed no visible signs of damage from *Halimeda* while causing pigmentation loss in *Halimeda* segments. Contact with *Halimeda* has been shown to be less damaging to coral than non-calcareous fleshy macroalgae (Atapattu, 2009; Barott et al., 2011). Coral can increase in growth when in contact with *Halimeda*, but not when competing with fleshy macroalgae (Ferrari et al., 2012). By extruding mesenterial filaments, coral are able to deflect contact by macroalgae, exhibiting the greatest competitive advantage against *Halimeda* (Nugues et al., 2004a). *Halimeda* are often grouped into fleshy macroalgae categories (Bruno et al., 2009; Bruno and Valdivia, 2016). However, *Halimeda* were less damaging to coral, suggesting that these calcifying algae may be unique from other erect, non-calcifying macroalgae. Our results also revealed a positive correlation between the amount of coral-*Halimeda* interactions and hard coral cover. Corals may tolerate *Halimeda* as a neighbour because it is less harmful than nearly all other types of macroalgae. As a low preference macroalgae for herbivores (Hay et al., 1988; Paul and Van Alstyne, 1988), *Halimeda* may be more persistent and may act to preempt the recruitment of more damaging types of macroalgae. Considered in combination with coral-CCA interactions, an increase in interactions with calcifying macroalgae promoted hard coral cover, suggesting these interactions generate positive benefits to coral reef ecosystems.

The results presented here demonstrate a strong influence of human population pressure on ecological interactions among coral and macroalgae in the Maldives. However, this study only provides a snapshot into the interactive dynamics of coral and algae, and seasonal and long-term investigations should be implemented. Nonetheless, the results of our study have implications for the effects of human populations on coral-algal interactions, drawing attention to how these drivers influence reef processes such as coral-algal competition. These changes are becoming more important to understand in the face of growing anthropogenic global change that has the potential to jeopardize even the most isolated and pristine ecosystems globally (Bruno and Valdivia, 2016). Nevertheless, local management that reduces impacts like sedimentation and eutrophication will help to maintain ecosystem functions (Kennedy et al., 2013) and ecological resilience in the face of a changing climate (Hoegh-Guldberg and Bruno, 2010).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2017.09.006>.

Acknowledgements

This study was undertaken as part of the XL Catlin Seaview Survey, designed and undertaken by the Global Change Institute, and funded by XL Catlin in partnership with The Ocean Agency and the University of Queensland. OHG was supported by an ARC Laureate Fellowship (FL120100066). We would like to thank David Harris, Sara Naylor, Abbie Taylor, Shari Stepanoff, and Susie Green for logistical support and Peter Dalton for technical field support. We would like to thank the M/V Emperor Voyager from the Emperor Divers Maldives fleet, the Ministry of Fisheries and Agriculture (MoFA), and the Marine Research Centre (MRC) in the Maldives. We would like to thank Richard Vevers, Christophe Bailhache, and Lorna Parry of The Ocean Agency. We would also like to thank Peter Mumby and Catherine Lovelock for improvements during the development of this manuscript.

References

Anderson, R.C., Adam, M.S., Goes, J.I., 2011. From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fish. Oceanogr.* 20, 104–113.
 Atapattu, S.S., 2009. The effect of two common reef organisms on the growth of the common reef coral *Acropora formosa*. *Mar. Biodivers. Rec.* 2, e61.
 Barott, K., Smith, J., Dinsdale, E., Hatay, M., Sandin, S., Rohwer, F., 2009. Hyperspectral and physiological analyses of coral-algal interactions. *PLoS One* 4, e8043.

Barott, K.L., Rodriguez-Brito, B., Janoušek, J., Marhaver, K.L., Smith, J.E., Keeling, P., Rohwer, F.L., 2011. Microbial diversity associated with four functional groups of benthic reef algae and the reef-building coral *Montastraea annularis*. *Environ. Microbiol.* 13, 1192–1204.
 Barott, K.L., Rodriguez-Mueller, B., Youle, M., Marhaver, K.L., Vermeij, M.J., Smith, J.E., Rohwer, F.L., 2012a. Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proc. R. Soc. Lond. B Biol. Sci.* 279, 1655–1664.
 Barott, K.L., Williams, G.J., Vermeij, M.J., Harris, J., Smith, J.E., Rohwer, F.L., Sandin, S.A., 2012b. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Mar. Ecol. Prog. Ser.* 460, 1–12.
 Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292, 1532–1535.
 Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827–833.
 Bender, D., Diaz-Pulido, G., Dove, S., 2012. Effects of macroalgae on corals recovering from disturbance. *J. Exp. Mar. Biol. Ecol.* 429, 15–19.
 Bonaldo, R.M., Hay, M.E., 2014. Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLoS One* 9, e85786.
 Box, S.J., Mumby, P.J., 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar. Ecol. Prog. Ser.* 342, 139–149.
 Bruno, J.F., Valdivia, A., 2016. Coral reef degradation is not correlated with local human population density. *Sci Rep* 6, 29778.
 Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R., Schutte, V.G.W., 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90, 1478–1484.
 Burkepille, D.E., Hay, M.E., 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc. Natl. Acad. Sci.* 105, 16201–16206.
 Clements, C.S., Hay, M.E., 2015. Competitors as accomplices: seaweed competitors hide corals from predatory sea stars. *Proc. R. Soc. B Biol. Sci.* 20150714.
 Connell, J.H., 1973. Population ecology of reef-building corals. In: *Biology and Geology of Coral Reefs*. vol. 2. Academic Press, pp. 205–245.
 Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., Côté, I.M., 2012. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* 15, 1378–1386.
 Darling, E.S., McClanahan, T.R., Côté, I.M., 2013. Life histories predict coral community disassembly under multiple stressors. *Glob. Chang. Biol.* 19, 1930–1940.
 Diaz-Pulido, G., McCook, L.J., 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar. Ecol. Prog. Ser.* 232, 115–128.
 Diaz-Pulido, G., Gouezo, M., Tilbrook, B., Dove, S., Anthony, K., 2011. High CO₂ enhances the competitive strength of seaweeds over corals. *Ecol. Lett.* 14, 156–162.
 Dixon, D.L., Hay, M.E., 2012. Corals chemically cue mutualistic fishes to remove competing seaweeds. *Science* 338, 804–807.
 Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. In: *The Ecology of Mangrove and Related Ecosystems*. Springer, pp. 121–132.
 Ertfemeijer, P.L., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Mar. Pollut. Bull.* 64, 1737–1765.
 Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50, 125–146.
 Fabricius, K., De'Ath, G., 2001. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19, 303–309.
 Fabricius, K., De'ath, G., McCook, L., Turak, E., Williams, D.M., 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar. Pollut. Bull.* 51, 384–398.
 Ferrari, R., Gonzalez-Rivero, M., Mumby, P.J., 2012. Size matters in competition between corals and macroalgae. *Mar. Ecol. Prog. Ser.* 467, 77.
 Ferrigno, F., Bianchi, C., Lasagna, R., Morri, C., Russo, G., Sandulli, R., 2016. Corals in high diversity reefs resist human impact. *Ecol. Indic.* 70, 106–113.
 Foster, N.L., Box, S.J., Mumby, P.J., 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. *Mar. Ecol. Prog. Ser.* 367, 143–152.
 Ganase, A., Bongaerts, P., Visser, P., Dove, S., 2016. The effect of seasonal temperature extremes on sediment rejection in three scleractinian coral species. *Coral Reefs* 35, 187–191.
 Harrington, L., Fabricius, K., De'Ath, G., Negri, A., 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85, 3428–3437.
 Hay, M.E., Paul, V.J., Lewis, S.M., Gustafson, K., Tucker, J., Trindell, R.N., 1988. Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory, and chemical versus morphological defenses. *Oecologia* 75, 233–245.
 Hay, M.E., Parker, J.D., Burkepille, D.E., Caudill, C.C., Wilson, A.E., Hallinan, Z.P., Chequer, A.D., 2004. Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Annu. Rev. Ecol. Syst.* 35, 175–197.
 Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. *Science* 328, 1523–1528.
 Hughes, T.P., 1989. Community structure and diversity of coral reefs: the role of history. *Ecology* 70, 275–279.
 Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551 AAAS-Weekly Paper Edition.
 Hughes, T.P., Reed, D.C., Boyle, M.-J., 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J. Exp. Mar. Biol. Ecol.* 113,

- 39–59.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J., Kleypas, J., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929–933.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365.
- Jackson, J.B.C., Buss, L., 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proc. Natl. Acad. Sci.* 72, 5160–5163.
- Jaleel, A., 2013. The status of the coral reefs and the management approaches: the case of the Maldives. *Ocean Coast. Manag.* 82, 104–118.
- Jompa, J., McCook, L., 1998. Seaweeds save the reef? *Sargassum* canopy decreases coral bleaching on inshore reefs. *Reef Res.* 8.
- Jompa, J., McCook, L.J., 2003a. Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Mar. Ecol. Prog. Ser.* 258, 79–86.
- Jompa, J., McCook, L.J., 2003b. Coral-algal competition: macroalgae with different properties have different effects on corals. *Mar. Ecol. Prog. Ser.* 258, 87–95.
- Jorissen, H., Skinner, C., Osinga, R., De Beer, D., Nugues, M.M., 2016. Evidence for water-mediated mechanisms in coral–algal interactions. *Proc. R. Soc. B Biol. Sci.* 20161137.
- Kennedy, E.V., Perry, C.T., Halloran, P.R., Iglesias-Prieto, R., Schönberg, C.H., Wisshak, M., Form, A.U., Carricart-Ganivet, J.P., Fine, M., Eakin, C.M., 2013. Avoiding coral reef functional collapse requires local and global action. *Curr. Biol.* 23, 912–918.
- Lang, J., 1973. Coral reef project—papers in memory of Dr. Thomas F. Goreau. 11. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bull. Mar. Sci.* 23, 260–279.
- Lasagna, R., Albertelli, G., Morri, C., Bianchi, C.N., 2010. *Acropora* abundance and size in the Maldives six years after the 1998 mass mortality: patterns across reef typologies and depths. *J. Mar. Biol. Assoc. U. K.* 90, 919–922.
- Lirman, D., 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19, 392–399.
- Littler, M.M., Littler, D.S., 2013. The nature of crustose coralline algae and their interactions on reefs. *Smithson. Contrib. Mar. Sci.* 39, 199–212.
- Lowe, R.J., Falter, J.L., Bandet, M.D., Pawlak, G., Atkinson, M.J., Monismith, S.G., Koseff, J.R., 2005. Spectral wave dissipation over a barrier reef. *J. Geophys. Res. Oceans* 110.
- McClanahan, T., 2000. Bleaching damage and recovery potential of Maldivian coral reefs. *Mar. Pollut. Bull.* 40, 587–597.
- McClanahan, T., 2011. Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs—Maldives vs. Kenya. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 21, 186–198.
- McClanahan, T., Muthiga, N., 2014. Community change and evidence for variable warm-water temperature adaptation of corals in Northern Male Atoll, Maldives. *Mar. Pollut. Bull.* 80, 107–113.
- McClanahan, T.R., Sheppard, C.R., Obura, D.O., 2000. *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*. Oxford University Press on Demand.
- McClanahan, T., Sala, E., Stickels, P., Cokos, B., Baker, A.C., Starger, C., Jones IV, S., 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glovers Reef, Belize. *Mar. Ecol. Prog. Ser.* 261, 135–147.
- McCook, L., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417.
- Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 351–369.
- Micheli, F., Mumby, P.J., Brumbaugh, D.R., Broad, K., Dahlgren, C.P., Harborne, A.R., Holmes, K.E., Kappel, C.V., Litvin, S.Y., Sancheziro, J.N., 2014. High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biol. Conserv.* 171, 186–194.
- Montano, S., Seveso, D., Strona, G., Arrigoni, R., Galli, P., 2012. *Acropora muricata* mortality associated with extensive growth of *Caulerpa racemosa* in Magoodhoo Island, Republic of Maldives. *Coral Reefs* 31, 793.
- Montano, S., Strona, G., Seveso, D., Maggioni, D., Galli, P., 2016. Widespread occurrence of coral diseases in the central Maldives. *Mar. Freshw. Res.* 67, 1253–1262.
- Mora, C., 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society of London B Biol. Sci.* 275, 767–773.
- Morri, C., Montefalcone, M., Lasagna, R., Gatti, G., Rovere, A., Parravicini, V., Baldelli, G., Colantoni, P., Bianchi, C.N., 2015. Through bleaching and tsunami: coral reef recovery in the Maldives. *Mar. Pollut. Bull.* 98, 188–200.
- Mumby, P.J., Hastings, A., Edwards, H.J., 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450, 98–101.
- National Bureau of Statistics, Ministry of Finance and Treasury, 2014. *Maldives Population and Housing Census*. <http://statisticsmaldives.gov.mv/nbs/wp-content/uploads/2015/10/Census-Summary-Tables1.pdf>.
- Nugues, M., Roberts, C., 2003. Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* 22, 507–516.
- Nugues, M.M., Delvoe, L., Bak, R.P., 2004a. Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. *Mar. Ecol. Prog. Ser.* 278, 103–114.
- Nugues, M.M., Smith, G.W., Hoodonk, R.J., Seabra, M.I., Bak, R.P., 2004b. Algal contact as a trigger for coral disease. *Ecol. Lett.* 7, 919–923.
- Paul, V.J., Van Alstyne, K.L., 1988. Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). *Coral Reefs* 6, 263–269.
- Paul, V.J., Kuffner, I.B., Walters, L.J., Ritson-Williams, R., Beach, K.S., Becerro, M.A., 2011. Chemically mediated interactions between macroalgae *Dictyota* spp. and multiple life-history stages of the coral *Porites astreoides*. *Mar. Ecol. Prog. Ser.* 426, 161–170.
- Rasher, D.B., Engel, S., Bonito, V., Fraser, G.J., Montoya, J.P., Hay, M.E., 2012. Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. *Oecologia* 169, 187–198.
- Roff, G., Chollett, I., Doropoulos, C., Golbuu, Y., Steneck, R.S., Isechal, A.L., van Woelk, R., Mumby, P.J., 2015. Exposure-driven macroalgal phase shift following catastrophic disturbance on coral reefs. *Coral Reefs* 34, 715–725.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. *BioScience* 52, 891–904.
- Seveso, D., Montano, S., Strona, G., Orlandi, I., Vai, M., Galli, P., 2012. Up-regulation of Hsp60 in response to skeleton eroding band disease but not by algal overgrowth in the scleractinian coral *Acropora muricata*. *Mar. Environ. Res.* 78, 34–39.
- Smith, J.E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura, D., Rohwer, F., Sala, E., 2016. Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central Pacific. *Proc. R. Soc. B Biol. Sci.* 20151985.
- Stafford-Smith, M., Ormond, R., 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Mar. Freshw. Res.* 43, 683–705.
- Steneck, R.S., 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu. Rev. Ecol. Syst.* 273–303.
- Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 476–498.
- Swierst, T., Vermeij, M.J., 2016. Competitive interactions between corals and turf algae depend on coral colony form. *PeerJ* 4, e1984.
- Tanner, J.E., 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J. Exp. Mar. Biol. Ecol.* 190, 151–168.
- Thurber, R.V., Burkepille, D.E., Correa, A.M., Thurber, A.R., Shantz, A.A., Welsh, R., Pritchard, C., Rosales, S., 2012. Macroalgae decrease growth and alter microbial community structure of the reef-building coral, *Porites astreoides*. *PLoS One* 7, e44246.
- Titlyanov, E., Yakovleva, I., Titlyanova, T., 2007. Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *J. Exp. Mar. Biol. Ecol.* 342, 282–291.
- Tkachenko, K.S., 2012. The northernmost coral frontier of the Maldives: the coral reefs of Ihavandippolu Atoll under long-term environmental change. *Mar. Environ. Res.* 82, 40–48.
- Tkachenko, K.S., 2015. Impact of repetitive thermal anomalies on survival and development of mass reef-building corals in the Maldives. *Mar. Ecol.* 36, 292–304.
- Vermeij, M.J., Van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S.M., Visser, P.M., 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS One* 5, e14312.
- Vermeij, M., Dailer, M., Smith, C., 2011. Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Mar. Ecol. Prog. Ser.* 422, 1–7.
- Wilson, S., Fisher, R., Pratchett, M., Graham, N., Dulvy, N., Turner, R., Cakacaka, A., Polunin, N., Rushton, S., 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. *Glob. Chang. Biol.* 14, 2796–2809.
- Wilson, S., Fisher, R., Pratchett, M., Graham, N., Dulvy, N., Turner, R., Cakacaka, A., Polunin, N., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* 20, 442–451.