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

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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

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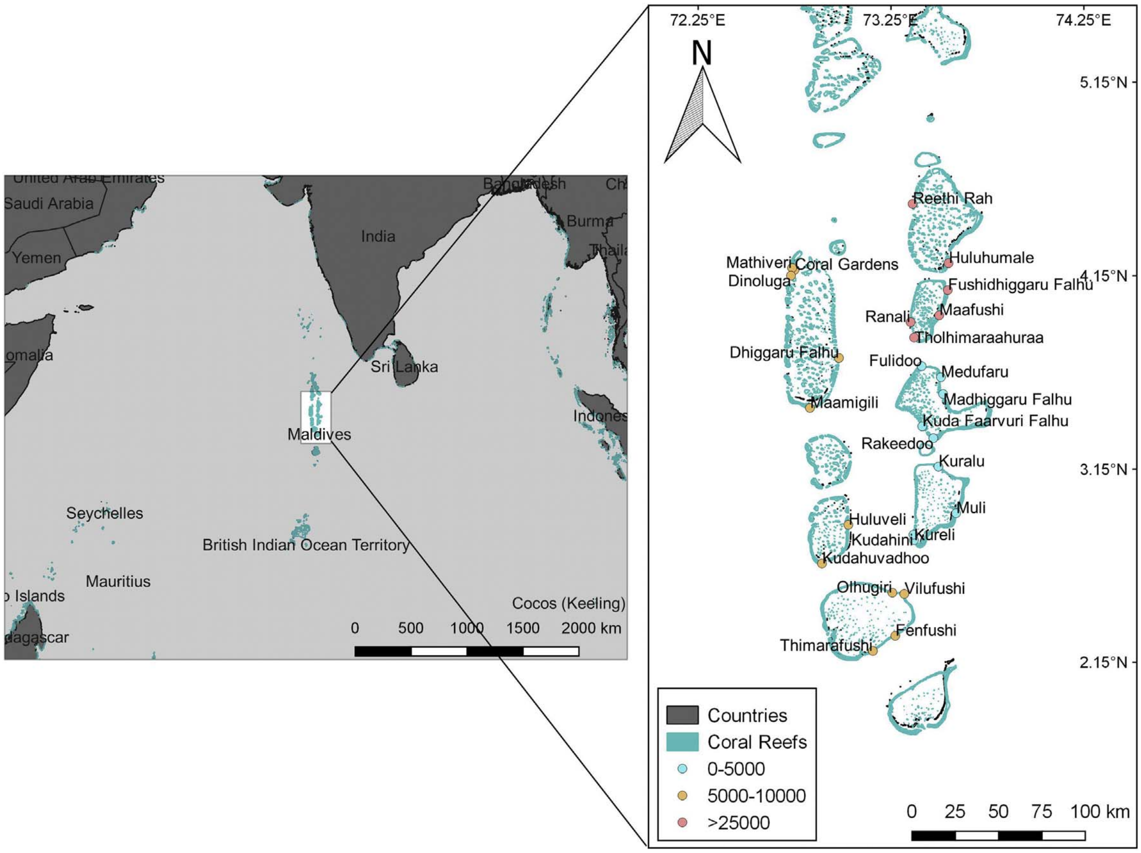

Fig. 1. Map of the study locations in the central Maldives. Dots represent sites, with population levels delineated by color: (blue) = 0–5000, (orange) = 5000–10,000, and (pink) ≥ 25,000. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of 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 (Burkepile 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° 15′ N, 73° 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

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